Allometric shell growth in infaunal burrowing bivalves: examples of the archiheterodonts *Claibornicardia paleopatagonica* (Ihering, 1903) and *Crassatella kokeni* Ihering, 1899 (#25256)

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Allometric shell growth in infaunal burrowing bivalves: examples of the archiheterodonts *Claibornicardia paleopatagonica* (Ihering, 1903) and *Crassatella kokeni* Ihering, 1899

Damián Eduardo Perez Corresp., [1] , **María Belén Santelli** [1]

[1] Paleoinvertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina

Corresponding Author: Damián Eduardo Perez
Email address: trophon@gmail.com

We present two cases of study of ontogenetic allometry in outlines of bivalves using longitudinal data, a rarity among fossils, based on the preserved post-larval record of shells. The examples are two infaunal burrowing bivalves of the southern South America, *Claibornicardia paleopatagonica* (Archiheterodonta: Carditidae) (early Paleocene) and *Crassatella kokeni* (Archiheterodonta: Crassatellidae) (late Oligocene–late Miocene). Outline analyses were conducted using a geometric morphometric approach (Elliptic Fourier Analysis), obtaining successive outlines from shells' growth lines, which were used to reconstruct ontogenetic trajectories. In both taxa, ontogenetic changes are characterized by the presence of positive allometry in the extension of posterior end, resulting in elongated adult shells. This particular allometric growth is known in others infaunal burrowing bivalves (*Claibornicardia alticostata* and some *Spissatella* species) and the resulting adult morphology is present in representatives of several groups (e.g. Carditidae, Crassatellidae, Veneridae, Trigoniidae). Taxonomic, ecological and evolutionary implications of this allometric growth pattern are discussed.

ALLOMETRIC SHELL GROWTH IN INFAUNAL BURROWING BIVALVES: EXAMPLES OF THE ARCHIHETERODONTS *CLAIBORNICARDIA PALEOPATAGONICA* (IHERING, 1903) AND *CRASSATELLA KOKENI* IHERING, 1899

Damián Eduardo Pérez [1], María Belén Santelli [1]

[1] División Paleoinvertebrados, Museo de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina

Corresponding Author:

Damián Eduardo Pérez

Email address: trophon@gmail.com

Abstract

We present two cases of study of ontogenetic allometry in outlines of bivalves using longitudinal data, a rarity among fossils, based on the preserved post-larval record of shells. The examples are two infaunal burrowing bivalves of the southern South America, *Claibornicardia paleopatagonica* (Archiheterodonta: Carditidae) (early Paleocene) and *Crassatella kokeni* (Archiheterodonta: Crassatellidae) (late Oligocene–late Miocene). Outline analyses were conducted using a geometric morphometric approach (Elliptic Fourier Analysis), obtaining successive outlines from shells' growth lines, which were used to reconstruct ontogenetic trajectories. In both taxa, ontogenetic changes are characterized by the presence of positive allometry in the extension of posterior end, resulting in elongated adult shells. This particular allometric growth is known in others infaunal burrowing bivalves (*Claibornicardia alticostata* and some *Spissatella* species) and the resulting adult morphology is present in representatives of several groups (e.g. Carditidae, Crassatellidae, Veneridae, Trigoniidae). Taxonomic, ecological and evolutionary implications of this allometric growth pattern are discussed.

Introduction

According to the Gould-Mosimann school (defined by Klingeberg, 1998), ‘allometry’ is the association between size and shape. The concept of allometry implies variation of a trait associated with variation of the overall size of an organism (Klingenberg, 1998). Size of an organism can be determined by its own biological growth (or ontogeny), and in these cases, allometry is the covariation between shape and growth through its life-span. This allometry is known as “ontogenetic allometry” (Klingenberg, 1996a; 1998). Studies on ontogenetic allometry mainly use “cross-sectional” data (each individual is measured at a single stage, and an average allometric trajectory is estimated from a composite sample from many individuals), but some ~~ones~~ use “longitudinal” data (e.g. Klingenberg, 1996b; Maunz & German, 1997) (each individual is measured multiple times during their growths, and individual variability in allometric trajectories is obtained). Cases of “cross-sectional” data (sensu Klingenberg, 1996b) are frequent in paleontological studies, for example in trilobites (see Hughes, Minelli & Fusco, 2006 and references herein), Cambrian arthropods (e.g. Haug *et al*., 2011), crinoids (e.g. Brower, 1988), gastropods (e.g. Gould, 1966a), diapsids (e.g. Ezcurra & Butler, 2015), dinosaurs (e.g. Horner & Goodwin, 2006, 2009), or mammals (e.g. Christiansen, 2012). “Longitudinal” studies (sensu Klingenberg, 1996b) are not possible for many fossil organisms, but are viable in organisms with accretionary growth. Some examples are shelled molluscs (Urdy *et al*., 2010), brachiopods (Rudwick 1968; Ackerly 1989; Tomašových, Carlson Sandra & Labarbera 2008), or ammonoids (Korn, 2012, 2017; De Baets, Klug & Monnet, 2013). Some researches often remain focused on adult stages, not taking into account the complete ontogeny (De Baets, Klug & Monnet, 2013).

Bivalves show accretionary growth in their shells where the mantle adds constantly new layers of calcium carbonate to the edge (Panella & MacClintock, 1968). Therefore, they preserve~~d~~ in their shells a complete record of external traits of their post-larval life-spans (Crampton & Maxwell, 2000), making them a source of “longitudinal” data (sensu Klingenberg, 1996b) for construction of ontogenetic trajectories. In a pioneer contribution, Crampton & Maxwell (2000) ~~elaborate~~ a methodology to explore this particular growth in bivalves. They re-constructed the ontogenetic trajectories of New Zealand species of *Spissatella* (Bivalvia: Crassatellidae) and related their allometric growth to macroevolutionary trends in the clade.

From the paleoecological point of view, fossil bivalves are one of the most valuable tools, as different morphologies of bivalve shell are strongly related to modes of life and environmental characteristics (Stanley, 1970). Infaunal burrowing habit of life is the most extended among ~~the~~ bivalves, consisting of the penetration of soft substrates ~~by mean~~ of a pedal locomotion while maintaining a life position of, at least, partial burial (Stanley, 1970).

Geometric morphometrics is a very useful tool for study of allometry and ontogeny (Zelditch, Bookstein & Lundrigan, 1992; Fink & Zelditch, 1995; Mitteroecker *et al.,* 2004; Mitteroecker, Gunz & Bookstein, 2005; Monteiro *et al.*, 2005; among others, see a revision on this topic in Adams, Rohlf & Slice, 2013). The use of morphometric methods is an objective, reliable and repeatable tool for quantify patterns of shape changes (Brown & Vavrek, 2015) and geometric morphometric allows ~~strong~~ graphical representations of allometry studies (Adams, Rohlf & Slice, 2013). In particular, ~~the~~ outline shape analyses allow to study the variation in this key character, the outline, which reflects autoecological features in bivalves according to Stanley (1970; 1975). The aim of this contribution is to study ontogenetic series in two examples of infaunal burrowing bivalves, *Clabornicardia paleopatagonica* (Ihering, 1903) (Archiheterodonta: Carditidae) and *Crassatella kokeni* Ihering, 1899 (Archiheterodonta: Crassatellidae). The changes in shape of these species are discussed and the presence of allometric growth is tested. Variability in shape of these two bivalves led previous authors to define new species based on possible juvenile specimens, *Venericardia camachoi* (Vigilante, 1977) and *Crassatellites patagonicus* Ihering, 1907 (nowadays considered as synonymies of *C. paleopatagonica* and *C. kokeni*, respectively). Changes in shape in these species and changes present in other infaunal bivalves, as well as their paleoecological implications, are discussed. Also, this contribution is an attempt to apply and to expand the methodology developed by Crampton & Maxwell (2000). As is already mentioned by Crampton & Maxwell (2000), Gould (1989, p. 537) noted "Natural history is a science of relative frequencies"; and these authors indicated "advance in many fields of palaeontological debate requires compilation of detailed observations across diverse fossil groups and time spans" (Crampton & Maxwell, 2000, p. 400).. The present is a contribution for thickening the literature of cases studying allometry patterns, and this is necessary since a debate addressing the relative frequencies of different phenomena (such as the paleontological debate) can only advance through the compilation of such cases.

Materials & Methods

Terminology and theoretical background

All terms regarding allometry follow the definitions provided by Klingenberg (1998). Positive allometry refers to a trait that increases respect to another one (a positive deviation to expected isometry), and negative allometry is the opposite. Geometric Morphometrics and Elliptic Fourier Analysis (EFA) terminologies are explained in Kuhl & Giardina (1982), Lestrel (1997), and Crampton (1995).

According to Crampton & Maxwell (2000), two outlines with identical shapes and differing only in size will occupy the same point in a morphospace as the distance in this space is a measure of shape difference, a statment that was followed to perform the analysis in this paper.

Bivalve species studied herein are considered as infaunal free burrowing bivalves because they live under the water/sediment interphase and they are not-attached by their byssus. This categorization was ~~descripted~~ by Stanley (1970) and its followed in this contribution. From this point, this mode of life will be called as “infaunal”.

Taxon sampling

Allometric growth was studied in two species from the Cenozoic of Argentina, *Clabornicardia paleopatagonica* (Ihering, 1903) (Archiheterodonta: Carditidae) (Fig. 1A) and *Crassatella kokeni* Ihering, 1899 (Archiheterodonta: Crassatellidae) (Fig. 1B). Archiheterodonts are non-siphonate bivalves, being mainly restricted to shallow infaunal free burrowing. All fossil shells used in this study are housed at Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-Pi and CIRGEO-PI) and Paleontological Collection of Universidad de Buenos Aires (CPBA). Sampling details are summarized in Supplemental Data S1.

The carditid species represents the most ancient record for its genus, being recorded in the early Danian of Patagonia (Argentina), in the Roca, Jagüel and Salamanca formations (Río Negro, Neuquén and Chubut provinces) and was recently included by Pérez & del Río (2017) in the genus *Claibornicardia* Stenzel & Krause, 1957. This taxon is also recognised in the late Paleocene–early Oligocene of North America and Europe. In these analyses 15 shells of *C. paleopatagonica* from Puesto Ramírez (Salamanca Formation, Río Negro Province) (MACN-Pi

5197) were used. The specimen assigned to *Venericardia camachoi* by Vigilante (1977) is also included in MACN-Pi 5197.

Crassatella kokeni is the most abundant crassatellid from the Cenozoic of Patagonia (Argentina), being represented in the San Julián, Monte León, Camarones and Puerto Madryn formations (late Oligocene–late Miocene, Chubut and Santa Cruz provinces). The systematics of this species was reviewed by Santelli & del Río (2014), who regarded *Crassatellites patagonicus* Ihering, 1907 as a junior synonymous of *Crassatella kokeni*. For our analyses, 32 shells of *C. kokeni* were used (including those previously assigned to *Crassatellites patagonicus*). These specimens come from Cañadón de los Artilleros, Punta Casamayor, Cabo Tres Puntas (late Oligocene–early Miocene, San Julián Formation, Santa Cruz Province); mouth of Santa Cruz River, Estancia Los Manantiales, Cañadón de los Misioneros, Monte Entrada (early Miocene, Monte León Formation, Santa Cruz Province); Camarones (early Miocene, Camarones Formation, Chubut Province), and Lote 39 (late Miocene, Puerto Madryn Formation, Chubut Province) (MACN-Pi 325–327, 331–332, 3576, 3600, 3907, 4775, 5374–5376; CIRGEO-PI 1501–1502; and CPBA 9404).

Elliptic Fourier Analysis

Elliptic Fourier Analysis (Kuhl & Giardina, 1982) method was chosen to analyse the outlines of our examples because it allows to work with the variation presents in valves shape. The methodology employed to obtain different outlines is derived from Crampton & Maxwell (2000) criteria. Each valve was digitally photographed in an inclined position with their growth lines placed parallel to the surface (Fig. 2A). The outlines obtained in different angles, regarding to the surface,were limited by coarse growth lines across the entire shell (Fig. 2B). Strict chronological ages of each individual have not been established, but previous analyses have ~~well~~ found a strong correlation between ages (based on the use of stable isotopes) and growth lines (Jones, 1988; Brey & Mackensen, 1997; Jones & Gould, 1999; Lomovasky *et al.*, 2002). As a result, growth lines are a good proxy for the chronological age of specimens, and size is an estimation for relative time. In *Claibornicardia paleopatagonica* annual growth lines are noticeable but in *Crassatella kokeni* they are not so evident, being perceptible only in part of ~~specimens of~~ specimens' shells. For this species, outlines were taken ~~in~~ intervals of 10 mm along the axial length, following the procedure undertaken by Crampton & Maxwell (2000) for *Spissatella*. This methodology allows to design an age-structured analysis for our data.

From ~~digitized~~ procedure using a digital camera, 62 outlines were obtained from *C. paleopatagonica*, and 74 outlines from *C. kokeni*. Noise generated by external sculpture was removed from outlines with an image-edition software (following Crampton, 1995). Right valves were mirrored on the horizontal axis taking advantage of the equivalve character of shells, and the analysis was performed only with left valves. The outlines were grouped into three growth categories: "less than two", "two to four", and "more than four", each one indicating the number of precedent coarse growth lines. In the case of *C. kokeni*, due to different geographic and stratigraphic provenance of the studied specimens, ~~outlines were into~~ four geological categories were established to group outlines: 'Monte León', 'Camarones', 'Puerto Madryn', and 'San Julián', each one representing the geological provenance of the material.

For each individual, chain codes were registered along the contour to calculate the Elliptic Fourier Descriptors (EFDs). Total Fourier power was calculated to estimate the optimal number of harmonics required for the analysis. The Fourier power of a harmonic is proportional to its amplitude and provides a measure of the amount of shape described by that harmonic (Crampton, 1995). A series of harmonics can be truncated when the value of average cumulative Fourier power reaches the 99% of the average total power (sum of the total harmonics used). The optimal number for this case was stablished in ten harmonics for *C. paleopatagonica*, and seven harmonics for *C. kokeni*. Outlines were normalized to discard effects of rotation, translation and size, using the parameters of the ellipse defined by the first harmonic (First Harmonic Ellipse method). Therefore, three of the four EFDs describing the first harmonic ellipse are constant for all the outlines (Crampton, 1995). The software Shape 1.3v (Iwata & Ukai, 2002) was used for all the analysis.

Morphospace construction and regression analysis

A Principal Component Analysis (PCA) was performed from the variance-covariance matrix of normalized coefficients (Supplemental Data S2 y S3 shows Fourier coefficients for each outline and for each taxon, respectively). The shapes of the shell for mean and extreme morphologies (the latter are representations of specimens with score values corresponding to -two and +two standard deviations from centre for each component) were reconstructed from the normalized coefficient mean values of the EFDs using the inverse Fourier transformations (Iwata & Ukai, 2002) and plotted alongside the morphospace reconstruction. The growth and geological categories previously defined were both plotted on the PCA. Also, a Multivariate Regression Analysis (MRA) between sizes (obtained from the two-dimensional area of each outlines) and shapes (using the first three principal components in both study-cases~~)~~. ~~These three~~ components ~~were~~ selected using a broken stick model (Jackson, 1993). The MRA includes an overall

MANOVA test of multivariate regression significance. These analyses were performed using PAST 3.19 (Hammer, Harper & Ryan, 2001).

Results

Claibornicardia paleopatagonica *allometric growth*

The first three components of PCA explain 74.02% of the total variance (Fig. 3A). The first component (PC1) explains 46.55% of variance and represents the transition between subcuadrate (negative extreme) to subrectangular/subelliptic (positive extreme) outlines, with a posterior-ventral expansion. The second component (PC2; 20.16% of variance) accounts for changes in convexity and width of umbones (more rounded umbos towards positive values and less rounded towards negative values). The third component (PC3; 7.3 % of variance) captures variation in concavity of the lunular area (more concave lunule towards negative values and more convex lunule towards positive values). The MANOVA test of MRA is significant (p-value<0.001) (Fig. 4A). Results of PCA and MRA analyses are included in Supplemental Data S4.

Growth categories plotted in the obtained morphospace show a transition across PC1 from juvenile to adult outlines. Variation across life-span in *C. paleopatagonica* can be distinguished in the successive outlines of each individual. Juvenile outlines are strongly rounded and shows subcentrally placed umbones. Towards more aged shells, an increase in the projection of posterior end is recognisable. Adult shells of this species have subrectangular to subelliptic outlines with anteriorly placed umbones. A reconstructed ontogenetic trajectory can be observed in Figure 3A linking different stages of the same specimen in the morphospace (this ontogenetic trajectory was obtained from a single actual specimen, from which the largest number of outlines were acquired). Different allometric variation can be detected when overlapping extreme outlines of PC1. Posterior end has positive allometry, while the dorsal and anterior-ventral margins have negative allometry (Fig. 5A).

Crassatella kokeni *allometric growth*

In this case, the first three components of PCA explain 90.72% of the total variance (Fig. 3B). The first component (PC1; 66.66% of variance) shows variation between more subtriangular and more subrectangular outlines. The second component (PC2; 19.27% of variance) reflects variation between outlines with subcentrally placed umbones and outlines with anteriorly placed umbones. The third component (PC3; 4.79% of variance) is associated to variation between less and more truncated posterior end of valves. The MRA shows more scattered points on the graphs than *C. paleopatagonica*, which could be related to the different geological procedence of shells. Nevertheless, the result of MANOVA test for the regression analysis is significant ($p\text{-value}<0.001$) (Fig. 4B). Results of PCA and MRA analyses are included in Supplemental Data S5.

Geological categories show a non-structured arrangement when they are plotted in the morphospace. The best sampled categories (‘Monte León’ and ‘Puerto Madryn’) occupy virtually the whole morphospace (Fig. 3C). Growth categories reflect a transition across the PC1 from juvenile to adult outlines. Juvenile outlines of *C. kokeni* are strongly subtriangular with pointed umbones, whereas adult outlines ~~of it~~ are markedly subrectangular having more rounded umbones. The reconstructed ontogenetic trajectory (Fig. 3B), obtained in the same way as the previous case, and the overlapping of both extreme outlines of PC1 shows an allometric variation similar to those observable in *C. paleopatagonica* (Fig. 5B). Specimens originally assigned to *C. patagonicus* by previous authors fall into the juvenile sector of morphospace (Fig. 3B).

Discussion

Morphological change across life-span in C. paleopatagonica *and* C. kokeni *and related species*

An allometric growth pattern shared by both species, *C. paleopatagonica* and *C. kokeni* was found in the analyses. Both taxa have positive allometry detected in the extension of posterior end, resulting in elongated adult shells. The study of ontogeny in bivalves had evidenced that some species show allometric growth in certain characters (Stanley, 1975; Stanley, 1977; Tashiro & Matsuda, 1983; Savazzi & Yao, 1992) and the morphological change recorded herein is also documented in other phylogenetically related infaunal bivalves. Subquadrate juvenile and elongated adult specimens of the carditid *Clabornicardia alticostata* (Conrad, 1833) have a similar allometric variation (Stenzel & Krause, 1957, and pers. obs. on syntypes ANSP 30562). Crampton & Maxwell (2000) described a similar variation in some representatives of the crassatellid genus *Spissatella*, especially in the species *S. subobesa* (Marshall & Murdoch, 1919) and *S. poroleda* Finlay, 1926.

Elongate adult morphology in other infaunal bivalves

Ontogenetic trajectories have not been described in other infaunal bivalves. However, the same elongate adult morphology described here is known. Among archiheterodonts, the morphology documented for adult shells of *C. paleopatagonica* and *C. kokeni* can be observed in species of the genera *Megacardita* Sacco, 1899 (La Perna, Mandic & Harzhauser, 2017); *Neovenericor* Rossi de García, Levy & Franchi, 1980 (Pérez, Alvarez & Santelli, 2017); *Venericor* Stewart, 1930 (Gardner & Bowles, 1939); and *Bathytormus* Stewart, 1930 (Wingard, 1993; Santelli & del Río, 2014). Among other bivalve groups, this adult morphology is also recorded in species of the Veneroidea and Palaeoheterodonta. Some species of Veneridae genera as *Anomalocardia* Schumacher, 1817, *Lirophora* Conrad, 1863, *Chionopsis* Olsson, 1932, *Lamelliconcha* Dall, 1902, *Macrocallista* Meek, 1876, and *Antigona* Schumacher, 1817, among others, have adult shells with a projected posterior end and elongate outlines. Some Trigoniidae taxa lead this morphology to extreme possibilities, with the development of wide and very projected posterior ends (e.g. Francis & Hallam, 2003). As an example, Echevarría (2014) found a strong allometric growth developing in two phases in the trigoniid *Myophorella garatei* Leanza, 1981 with a strong extension of the posterior margin.

Taxonomic implications of allometric growth

Differences between young and adult morphologies could have been be interpreted as taxonomic differences between species. In both studied cases, new species were proposed for specimens with young morphologies: *Venericardia camachoi* Vigilante, 1977 and *Crassatellites patagonicus* Ihering, 1907. These taxa fall into the variation representing young specimens of *Claibornicardia paleopatagonica* and *Crassatella kokeni*, respectively. The case of *C. kokeni* and *C. patagonicus* was already mentioned by Santelli & del Río (2014), being corroborated the synonymy in this study. Other examples are the carditids *Neovenericor paranensis* (Borchert, 1901) (late Miocene, Argentina), the adult morphology of which was described as *Venericor crassicosta* Borchert, 1901 (Pérez, Alvarez & Santelli, 2017) and *Neovenericor ponderosa* (Suter, 1913) (late Oligocene, New Zealand), the young morphology of which was named *Venericardia caelebs* Marwick, 1929 (Beu & Maxwell, 1990). These results reflect that this allometric change (~~including~~ into the instraspecific variation) must be considered in taxonomic revisions of similar infaunal bivalves. These examples show that a different outline is frequently considered an important feature for taxonomic recognition but ontogenetic variation is not always taken into account (Alvarez & Pérez, 2016).

Ecological implications of ~~this~~ adult morphology

According to Stanley's experiments (1970), bivalve shells with streamlined outlines (cylindrical, blade-like, or disc-like) are the fastest burrowers. Elongate outlines could be related to ~~a~~ fast burrowing in soft substrates but not in all cases. Also, Stanley (1970) established that moderately ~~elongate~~ burrowing species commonly use a large angle of rotation, having a strong forward component in their burrowing movement because of their eccentric axis of rotation. Elongate bivalves generally have a mode of life with the long axis in vertical position –for example, this is appreciated in living species of *Anomalocardia*–. Posterior portion of shell is directed to sediment surface, being achieved the elongate morphotype with a minimum of increase in shell growth, displacing the centre of gravity and the visceral mass of organisms to a deeper position (Stanley, 1970; Crampton & Maxwell, 2000). Other possibly related effects could be increasing in stability against scour (Stanley, 1977; Stanley & Yang, 1987; Francis & Hallam, 2003) or reduction of exposure and predation (Crampton & Maxwell, 2000; Francis & Hallam, 2003). One possible ~~approach~~ to reach this morphology could be the positive allometry of posterior end.

Crampton & Maxwell (2000) suggested that ontogenetic variation in *Spissatella* is an adaptation for life in more energetic environments with coarser substrates but these parameters were not explored in our data. Nevertheless, these conditions (along with others such as predation) may have played a part as selective pressures in the evolutionary history of these infaunal bivalves. Further stratigraphic structured analyses, including taphonomic and sedimentologic data, are needed to study these hypotheses.

Evolutionary implications of allometric growth

Ontogenetic changes in the mentioned infaunal bivalves seem to be similar and perhaps~~,~~ could be induced by similar conditions. Allometry plays a significant role in evolutionary trends of most lineages (Gould, 1966b; Gould, 1977; Klingenberg, 1998), in particular for recognition of some cases of heterochronies (e.g. Shea, 1983; McKinney, 1984; Mitteroecker, Gunz & Bookstein, 2005). Learning more about the ontogenetic trajectories and allometric changes present in different taxa is essential as the first step for heterochrony studies. These analyses require ontogenetic trajectories explored and phylogenetic relationships defined among species, being the cases ~~here demonstrated~~ fundamental and very important as a starting point.

Conclusions

Analyses of allometric growth allow to recognize similar ontogenetic changes in *Clabornicardia paleopatagonica* (Ihering, 1903) and *Crassatella kokeni* Ihering, 1899. In both species the ontogeny is characterized by the presence of positive allometry in the growth of posterior end, resulting in elongated adult shells. The species *Venericardia camachoi* Vigilante, 1977 and *Crassatellites patagonicus* Ihering, 1907, proposed as synonyms of both previously mentioned taxa, fall into portion of resulting morphospace that represents juvenile morphologies, so that the obtained results corroborate these synonymies.

This particular allometric growth, resulting in elongated adult shells, is presumed in other infaunal bivalve groups (e.g. Veneridae, Trigoniidae, Carditidae and Crassatellidae). The recognition of this character has taxonomic, ecologic and evolutionary implications, being important as the starting point for further ~~allometric~~ studies in bivalves. This study includes new observations and discussion about allometric growth in infaunal bivalves, and represented a contribution for thickening the literature of cases of allometric patterns.

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Explanations of figures

Figure 1. Case-studies of this work. A. MACN-Pi 5197, *Claibornicardia paleopatagonica* (Ihering, 1903) (Puesto Ramírez, Salamanca Formation, Early Danian) in lateral view. B. MACN-Pi 3576, *Crassatella kokeni* Ihering, 1899 (mouth of Santa Cruz River, Monte León Formation, Early Miocene) in lateral view. Scale bar = 10 mm. Photo credit: the authors.

Figure 2. Applied methodology to obtain successive outlines of a single valve. A. One valve oriented in different angles. Dotted lines indicate the parallel position of valves regarding to surface, arrows indicate position of digital camera. B. Example of successive outlines

captured in one specimen (MACN-Pi 5197). First and last outline illustrated. Photo credit: the authors.

Figure 3. Results of Principal Component Analyses. A. *Claibornicardia paleopatagonica* arranged by ontogenetic stage. B. *Crassatella kokeni* arranged by ontogenetic stage. C. *Crassatella kokeni* arranged by stratigraphic procedence. Color legends and the extreme morphologies of each principal component are illustrated in the graph. Black lines in A and B show ontogenetic trajectories of a selected specimen. Triangles indicate specimen previously assigned to *Venericardia camachoi* and squares indicate specimen previously assigned to *Crassatellites patagonicus*.

Figure 4. Results of Multivariate Regression Analyses, between area (size) and three first principal components (shapes). A–C includes principal components obtained from *Claibornicardia paleopatagonica*, and D–F those obtained from *Crassatella kokeni*. Red line indicates trend line. Photo credit: the authors.

Figure 5. Overlapping of extreme outline configurations. A. *Claibornicardia paleopatagonica*. B. *Crassatella kokeni*. Red outline = juvenile specimens. Blue outline = adult specimens. Arrows indicate positive or negative allometry.

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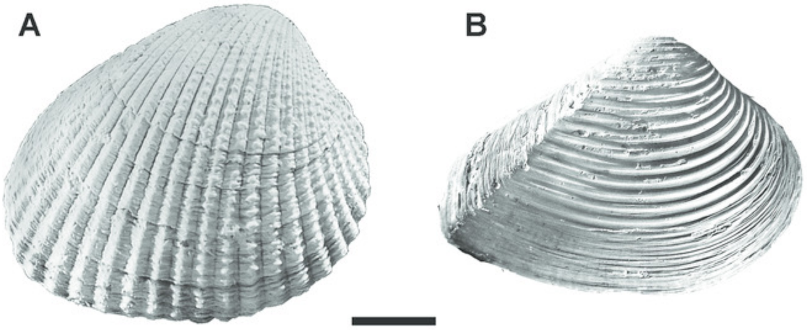
A
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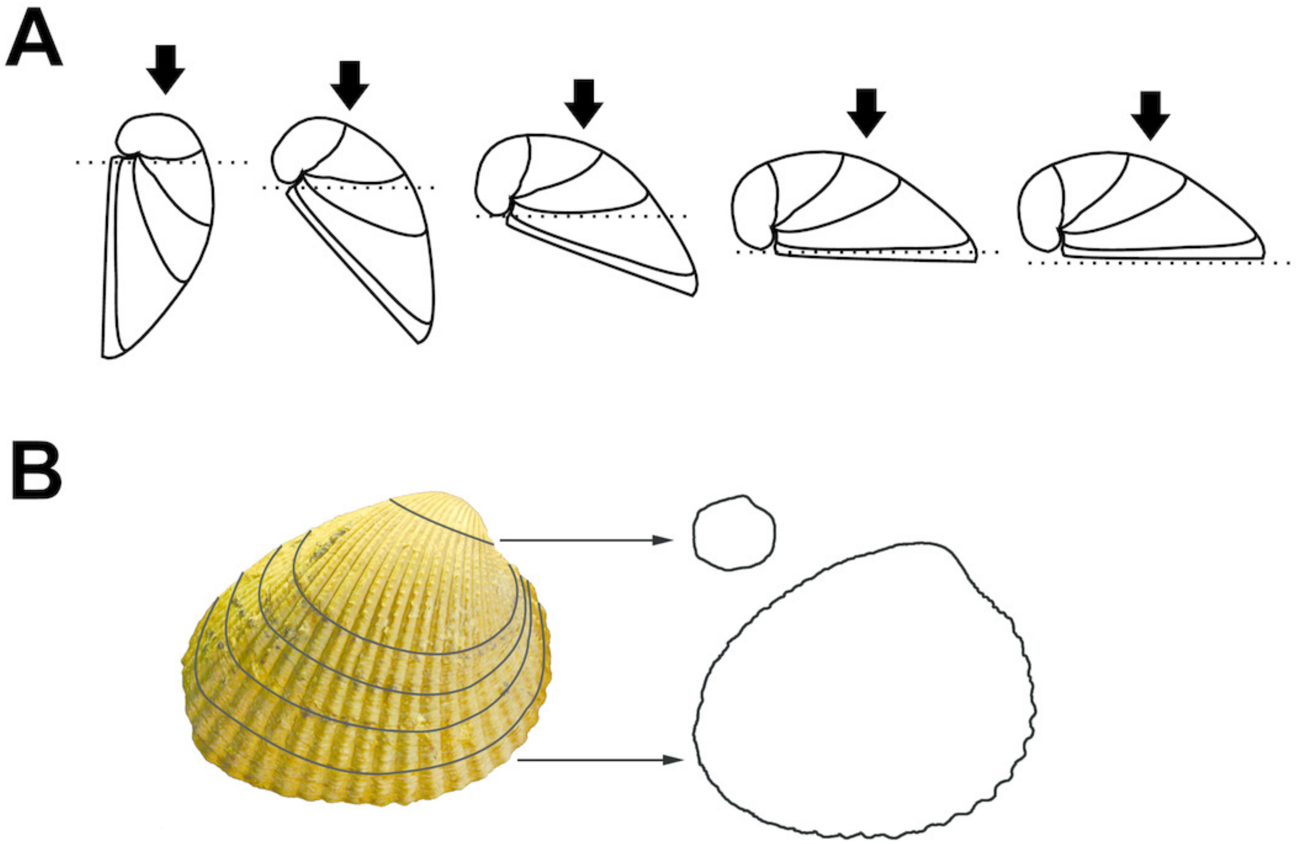
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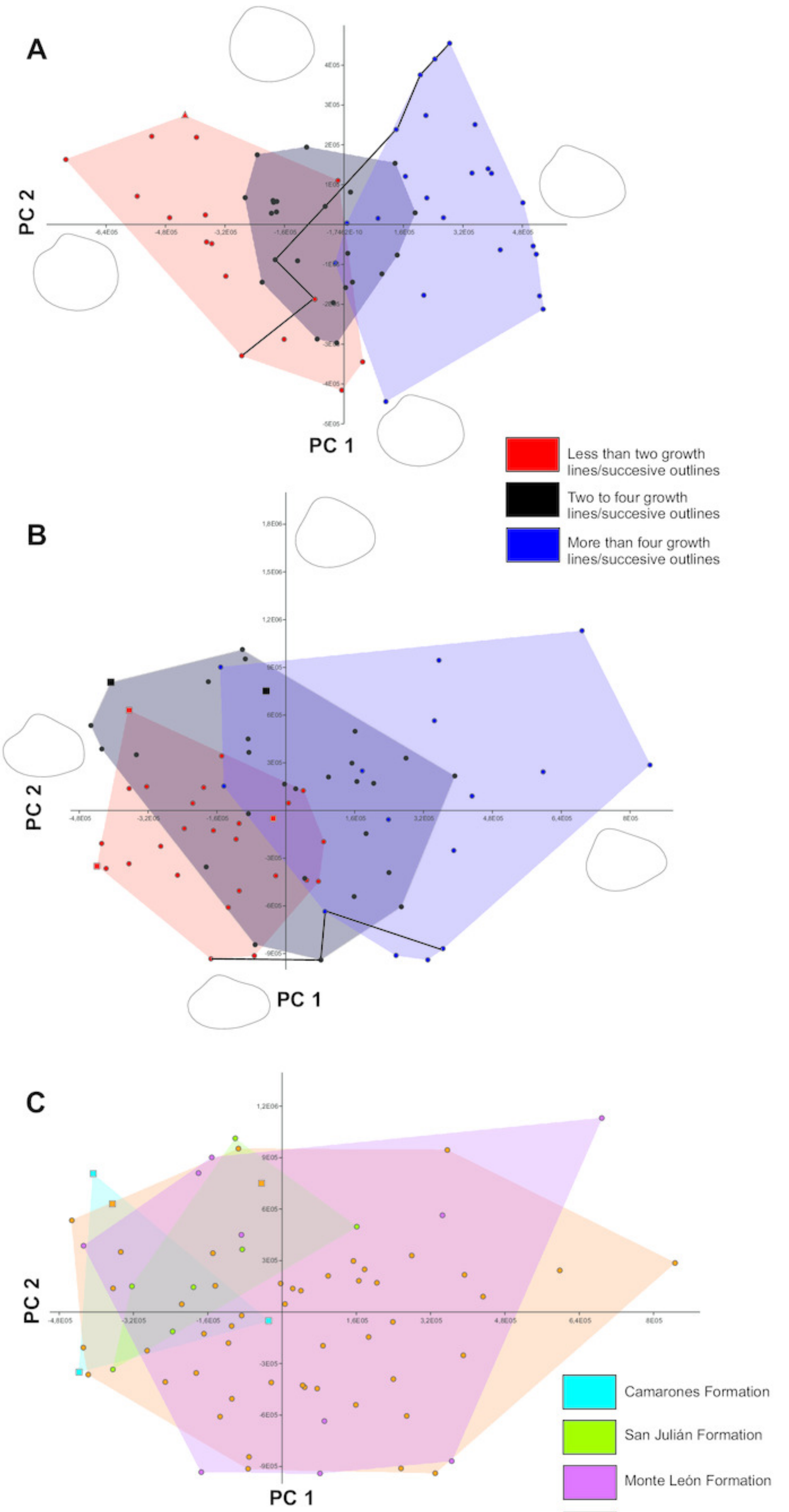
A
PC 2
PC 1
🟥 Less than two growth lines/succesive outlines
⬛ Two to four growth lines/succesive outlines
🟦 More than four growth lines/succesive outlines
B
PC 2
PC 1
C
PC 2
PC 1
Camarones Formation
San Julián Formation
Monte León Formation
Puerto Madryn Formation

Figure 4

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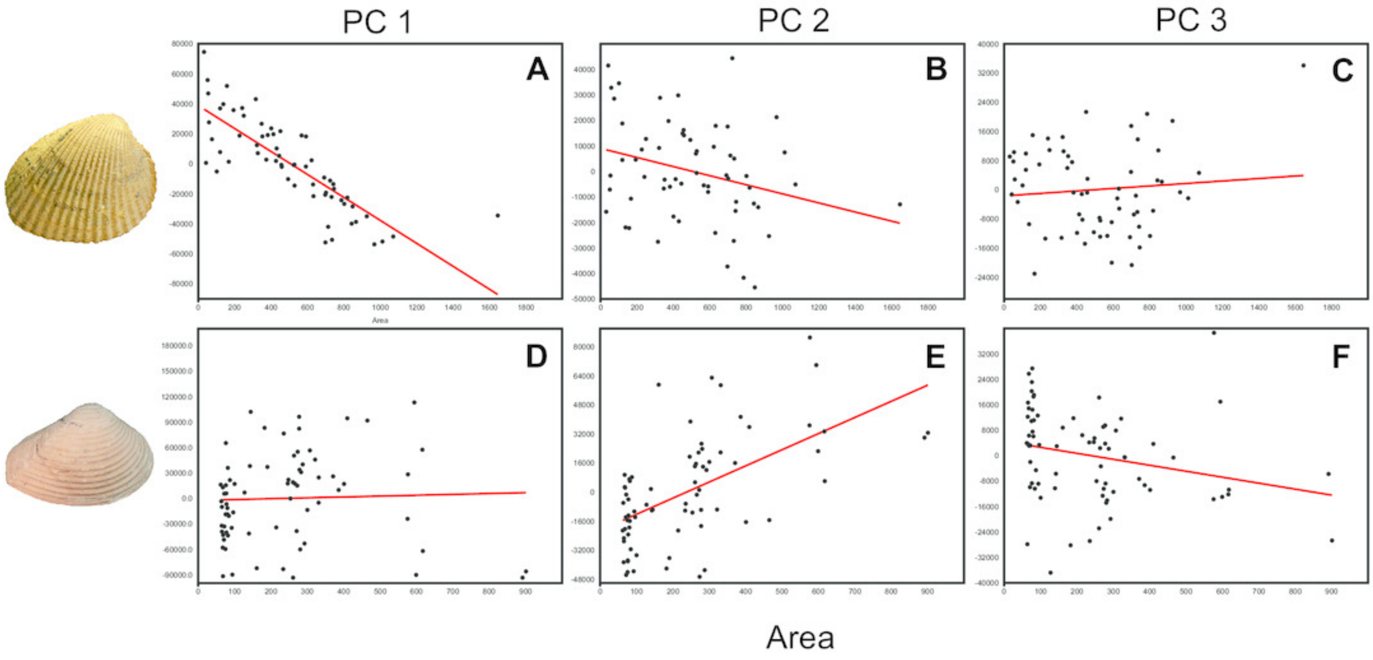

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Overlapping of extreme outline configurations.

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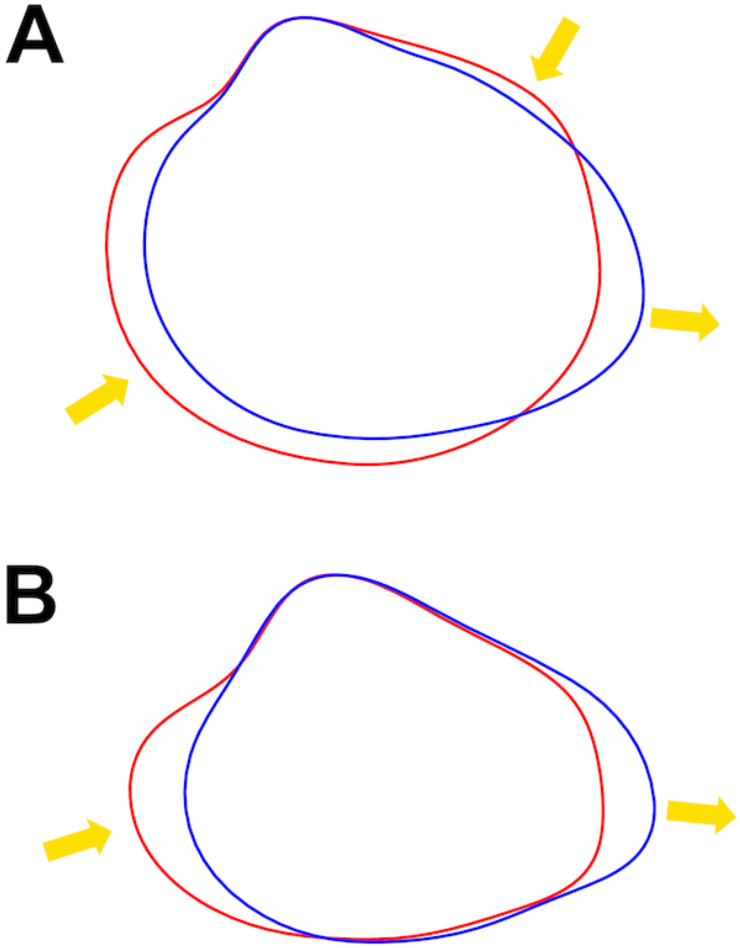
A
B