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

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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 and reconstructing 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 are discussed.

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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 and reconstructing 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 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 variation between shape and growth through its life-span. This allometry is called "ontogenetic allometry" by 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 acquired as a composite sample from many individuals), but few ones use longitudinal data (e.g. Klingenberg, 1996b; Maunz & German, 1997) (each individual is measured multiple times during their growths, and individual variability of allometric trajectories is obtained). Cases of cross-sectional data are frequent in paleontological studies, for example in trilobites (see Hughes, Minelli& Fusco, 2006 and references herein). Cases of longitudinal data are virtually impossible from fossil organism.

Bivalves have accretionary growth in their shells where the mantle adds constantly new layers of calcium carbonate to the edge (Panella & MacClintock, 1968). Therefore, they preserved in their shells a complete record of external traits of their post-larval life-spans (Crampton & Maxwell, 2000), and this makes them in a source of longitudinal data 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. 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, which consists in 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 has been 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 aim of this contribution is to study ontogenetic series in two examples of infaunal burrowing bivalves, *Claibornicardia paleopatagonica* (Ihering, 1903) (Archiheterodonta: Carditidae) and *Crassatella kokeni* Ihering, 1899 (Archiheterodonta: Crassatellidae). We discuss their changes in shape and evaluated the presence of allometric growth. Variability in shape of these two species led to 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 and changes present in other infaunal bivalves, and their paleoecological implications, are discussed. Also, this contribution is an attempt to expand the methodology developed by Crampton & Maxwell (2000). These authors indicated (p. 400) that their work was a contribution in the sense of Gould (1989, p. 537) that noted "Natural history is a science of relative frequencies; advance in many fields of palaeontology debate requires compilation of detailed observations across diverse fossil groups and time spans", and the present is a contribution in this sense.

Materials & Methods

Terminology and theoretical background

All terms about allometry follow to Klingenberg (1998). Geometric Morphometrics and Elliptic Fourier Analysis (EFA) terminology are explained in Kuhl & Giardina (1982), Lestrel (1997), and Crampton (1995).

According to Crampton & Maxwell (2000), two outlines that have identical shapes and differ only in size will plot at the same point in a morphospace being the degree of separation is a measure of shape difference, statements which we follow to perform our analysis.

Taxon sample

Allometric growth was studied in two species from Cenozoic of Argentina, *Claibornicardia paleopatagonica* (Ihering, 1903) (Archiheterodonta: Carditidae) (Fig. 1A) and *Crassatella kokeni* Ihering, 1899 (Archiheterodonta: Crassatellidae) (Fig. 1B). Archiheterodonts are non-siphonate bivalves, being it mainly shallow infaunal burrowing. All fossil shells used in this study are housed at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Pi and CIRGEO-PI) and Cátedra de Paleontología de la Universidad de Buenos Aires (CPBA). Details of sample are resumed in Supplemental Data S1.

The carditid species represents the most ancient record for the genus, and is represented in the early Danian of Patagonia (Argentina), in the Roca, Jagüel and Salamanca formations (Río Negro, Neuquén and Chubut provinces) and was recently studied by Pérez & del Río (2017), who placed it in the genus *Claibornicardia* (Stenzel & Krause, 1957). This genus is also recorded in the late Paleocene–early Oligocene of North America and Europe. In these analyses we used 15 shells of *C. paleopatagonica* from Puesto Ramírez (Salamanca Formation, Río Negro Province) (MACN-Pi 5197). The specimen assigned to *Venericardia camachoi* by Vigilante (1977) is included in MACN-Pi 5197.

Crassatella kokeni is the best known crassatellid from Cenozoic of Patagonia (Argentina) and is recorded 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). *Crassatellites patagonicus* Ihering, 1907 was considered as a junior synonymous of *Crassatella kokeni* by Santelli & del Río (2014). For our analyses, we used 32 shells of *C. kokeni* (including those previously assigned to *Crassatellites patagonicus* ~~for~~ other authors) 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; CPBA 9404).

Elliptic Fourier Analysis

The outline shape analyses allow to study the variation in this key character, that reflects autoecological features according to Stanley (1970; 1975). We choose the Elliptic Fourier Analysis (Kuhl & Giardina, 1982) methods to analyze the outlines of our examples. The methodology employed to obtain different outlines is derived from Crampton & Maxwell criteria (2000). Each valve was digitized in different angles for capture outlines limited by coarse growth lines across the entire shell (Fig. 2). Strict chronological ages of each individual have not been recognized, but previous analyses have well established 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 of chronological age of specimens, and size is an implicit estimation for time. In *Claibornicardia paleopatagonica* annual growth lines are noticeable but in *Crassatella kokeni* they are not easily evident. Growth lines are visible only in part of specimens of latter species but not in the entire shells. For this species, outlines were taken in intervals of 10 mm along the axial length, following attempt of Crampton & Maxwell (2000) for *Spissatella*. This methodology allows us perform an age-structured analysis for our data.

From digitized shells, we obtained 62 outlines from *C. paleopatagonica*, and 74 outlines from *C. kokeni*. Outlines were cleaned with image-edition software for noise given by external sculpture (following Crampton, 1995). Right valves were mirrored on the horizontal axis exploiting the equivalve character of shells, and the analysis was performed only with left valves. The outlines were grouped into three growth categories: “minor to two”, “from two to four”, and “plus to four”, each one indicating the number of precedent coarse growth lines. In the case of *C. kokeni*, due to difference geographic and stratigraphic occurrence of studied specimens, outlines were also grouped with this criterion. Four geological categories were established: ‘Monte León’, ‘Camarones’, ‘Puerto Madryn’, and ‘San Julián’, each one indicating the geological procedence of the material.

For each individual, chain codes were registered along the contour to calculate the Elliptic Fourier Descriptors (EFDs). Optimal number of harmonics was estimated according to Crampton (1995) (Fourier power), and stablished in ten harmonics for *C. paleopatagonica*, and seven harmonics for *C. kokeni*. Based on the first harmonic ellipse, the different outlines were normalized for discard effects of rotation, translation and size. Therefore, three of the four EFDs describing the first harmonic ellipse are constant for all the outlines (Crampton, 1995). The purposes of these analyses are normalize Fourier coefficients for each individual. The software Shape 1.3v (Iwata & Ukai, 2002) was used for all the analysis. Supplemental Tables S2 y S3 shows Fourier coefficients for each outline.

Morphospace construction and regression analysis

Once obtained the normalized coefficients, we performed a Principal Component Analysis (PCA) from the variance-covariance matrix, using PAST 2.15 (Hammer, Harper & Ryan, 2001). The average shape of the shell for extreme morphologies were reconstructed from the normalized coefficient mean values of the EFDs using the inverse Fourier transformations (Iwata & Ukai, 2002). Three categories previously defined were plotted in the PCA. Also, a Multivariate Regression Analysis (MRA) between sizes (obtained from two-dimensional area of each outlines) and shapes (using the first three principal components in both study-cases, all significant component according to broken stick model –Jackson, 1993–, see results), with a permutation test of 1000 randomization rounds.

Results

Claibornicardia paleopatagonica *allometric growth*

The first three components of PCA explain the 74.02% of total variance (Fig. 3A). First component (PC1) shows 46.55% of variance and exposed a transition between subcuadrate to subrectangular/subelliptic outlines, with a posterior-ventral expansion. Second component (PC2; 20.16%) reveals changes in the convexity and width of umbones. Third component (PC3; 7.3 %) is defined by the variation in concavity of lunular area. The result of MRA is significant (p-value<0.0001) (Fig. 4A). Results of PCA and MRA analyses included in Supplemental Data S4.

Growth categories plotted in the obtained morphospace show a transition across the PC1 from juvenile to adult outlines. The variation across life-span in *C. paleopatagonica* can be observed by the successive outlines of each individual. Juvenile outlines are strongly rounded and with subcentrally placed umbones. Towards more aged shells, an increase in the projection of posterior end is observable. Adult shells of this species have subrectangular to subelliptic outlines with anteriorly placed umbones. A reconstructed ontogenetic trajectory can be observed linking different stages of the same specimen in the morphospace (Fig. 3A). Different allometric variation can be detected when you overlap both outlines. Posterior end has positive allometry, while dorsal and anterior-ventral margin have negative allometry (Fig. 5A).

Crassatella kokeni *allometric growth*

In this case, the first three components of PCA explain the 90.72% of total variance (Fig. 3B). First component (PC1; 66.66%) shows the variation between more subtriangular to more subrectangular outlines. Second component (PC2; 19.27%) reflects the variation outlines with subcentrally placed umbones to outlines with anteriorly placed umbones. Third component (PC3;

4.79%) is associated to the variation between less to more truncated posterior end of valves. The result of MRA is significant (p-value<0.0042) (Fig. 4B). Results of PCA and MRA analyses included in Supplemental Data S5.

Geological categories show a non-structured arrangement when they are plotted in the morphospace. More numerous 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. Adult outlines of this species are markedly subrectangular with more rounded umbones. The reconstructed ontogenetic trajectory (Fig. 3B) and the overlapping of both extreme outlines show 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.

Discussion

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

The study of ontogeny in bivalves had evidenced that some species show allometric growth to certain characters (Stanley, 1975; Stanley, 1977; Tashiro & Matsuda, 1983; Savazzi & Yao, 1992). In our analyses we found allometric growth in both examples, and characteristics of them are the same in *C. paleopatagonica* and *C. kokeni*. Both species have positive allometry detected in the extension of posterior end, resulting in elongated shells. This morphological change is also recorded in other phylogenetically-related infaunal burrowing bivalves. Subquadrate juvenile and elongated adult specimens of the carditid *Claibornicardia alticostata*

(Conrad, 1833) show a similar 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 burrowing bivalves

In other infaunal bivalves, the ontogenetic trajectories were not described; but the same elongate adult morphology detailed here is known. Among archiheterodonts, the morphology described 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) finds a strong allometric growth developing in two phases in the trigoniid *Myophorella garatei* Leanza, 1981 with a strongly extension of the posterior margin.

Taxonomic implications of allometric growth

Differences between young and adult morphologies could 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 species fall into young variation of *Claibornicardia paleopatagonica* and *Crassatella kokeni*, respectively. Other examples are the carditids *Neovenericor paranensis* (Borchert, 1901) (late Miocene, Argentina) (adult morphology was called *Venericor crassicosta* Borchert, 1901) (Pérez, Alvarez & Santelli, 2017) and *Neovenericor ponderosa* (Suter, 1913) (late Oligocene, New Zealand) (young morphology was called *Venericardia caelebs* Marwick, 1929) (Beu & Maxwell, 1990). 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 most rapid 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 used a large angle of rotation, and there is a strong forward component in their burrowing movement because of their eccentric axis of rotation. Elongate bivalves generally had a life positon 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, and it can be achieved with a minimum of increase in shell developing, displacing to a deeper positon the centre of gravity and the visceral mass of organisms (Stanley, 1970; Crampton & Maxwell, 2000). Others possible related effects may be the 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 strategy to reach this morphology could be the positive allometry of posterior end.

Crampton & Maxwell (2000) suggests 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 be have played as selective pressures in the evolutionary history of these infaunal burrowing bivalves. Further stratigraphic structured analyses are needed in this way.

Evolutionary implications of allometric growth

Ontogenetic changes in the mentioned infaunal burrowing bivalves seem to be similar and may be conducted by similar conditions. Allometry plays a significant role in evolutionary trends of most lineages (Gould, 1966; Gould, 1977; Klingenberg, 1998), in particular for recognition of some cases of heterochronies. Learn more about the ontogenetic trajectories and allometric changes present in different taxa are the first step for heterochrony studies.

Conclusions

The allometry growth analyses allow us to describe the same ontogenetic changes in *Claibornicardia paleopatagonica* (Ihering, 1903) and *Crassatella kokeni* Ihering, 1899. In both species the ontogeny is characterized by the presence of positive allometry 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 juvenile portion of resulting morphospace. Our 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, and is the starting point for further allometric studies in bivalves. In the sense of Gould (1989) mentioned above, this study includes new observations and discussion about allometric growth in infaunal burrowing bivalves.

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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). B. MACN-Pi 3576, *Crassatella kokeni* Ihering, 1899 (mouth of Santa Cruz River, Monte León Formation, Early Miocene). Scale bar = 10 mm.

Figure 2. Example of successive outlines captured in one specimen (MACN-Pi 5197). First and last outline illustrated.

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 in the graph. Extreme morphologies of each principal component illustrated in the graph. Black lines in A and B shows ontogenetic trajectories of a selected specimen.

Figure 4. Results of Multivariate Regression Analyses. A. *Claibornicardia paleopatagonica*. B. *Crassatella kokeni*. Regression Score 1 composed by three first principal components.

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.

Figure 1

Case-studies of this work.

A. MACN-Pi 5197, *Claibornicardia paleopatagonica* (Ihering, 1903) (Puesto Ramírez, Salamanca Formation, Early Danian). B. MACN-Pi 3576, *Crassatella kokeni* Ihering, 1899 (mouth of Santa Cruz River, Monte León Formation, Early Miocene). Scale bar = 10 mm.

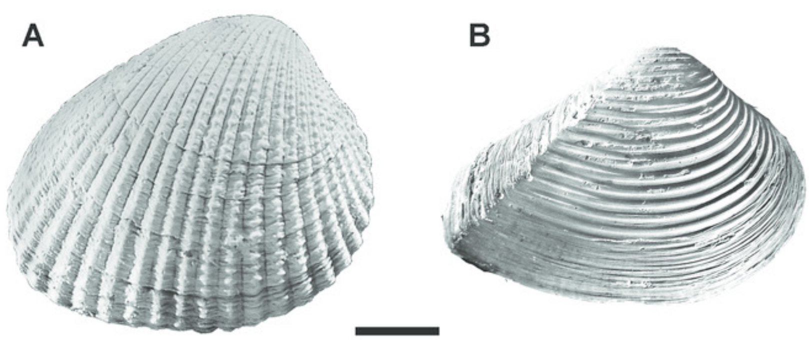

A
B

Figure 2

Example of successive outlines captured in one specimen (MACN-Pi 5197).

First and last outline illustrated.

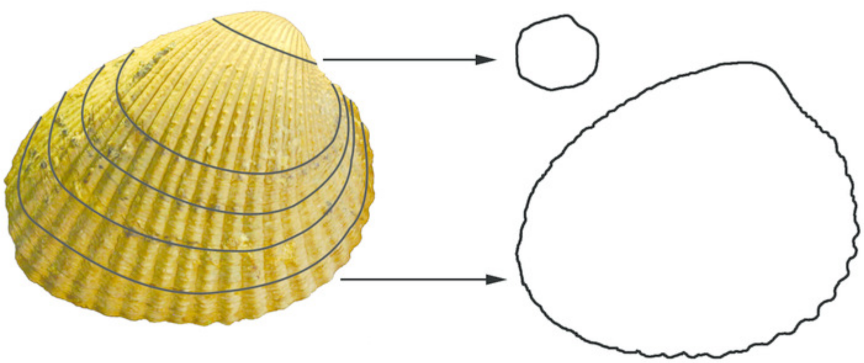


Figure 3

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 in the graph. Extreme morphologies of each principal component illustrated in the graph. Black lines in A and B shows ontogenetic trajectories of a selected specimen.

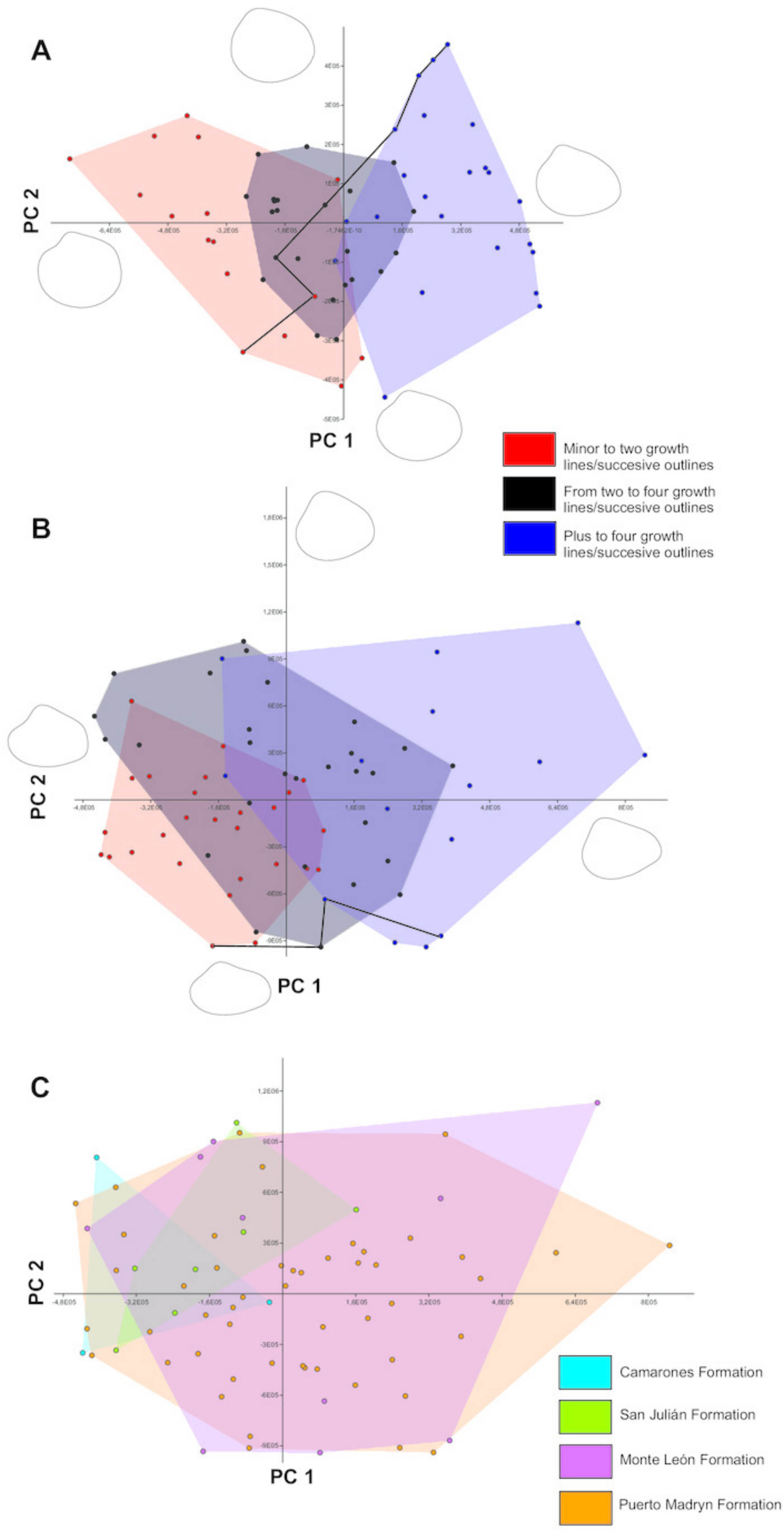

A
PC 2
PC 1
B
PC 2
PC 1
C
PC 2
PC 1
Minor to two growth lines/succesive outlines
From two to four growth lines/succesive outlines
Plus to four growth lines/succesive outlines
Camarones Formation
San Julián Formation
Monte León Formation
Puerto Madryn Formation

Figure 4

Results of Multivariate Regression Analyses.

A. *Claibornicardia paleopatagonica*. B. *Crassatella kokeni*. Regression Score 1 composed by three first principal components.

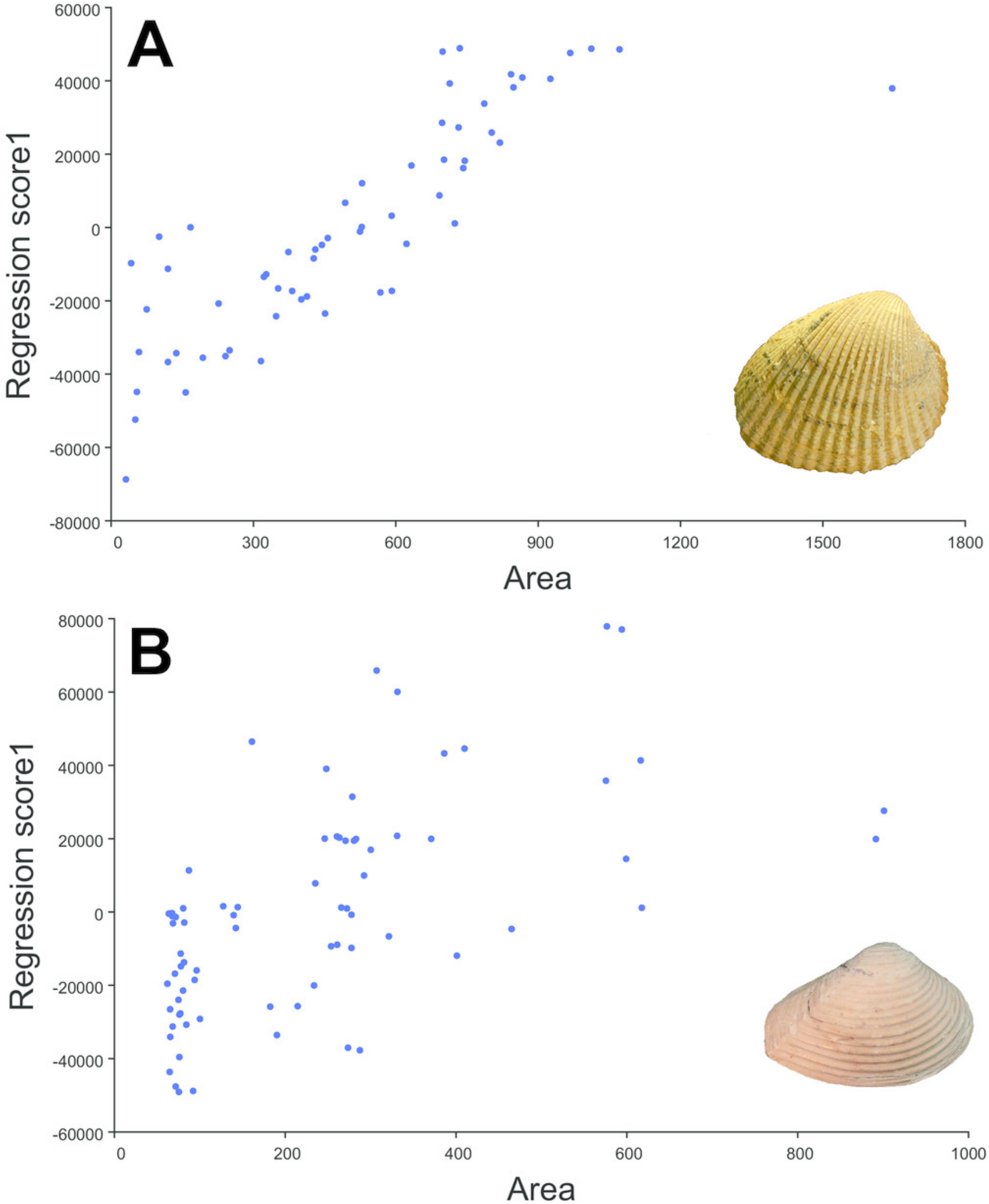
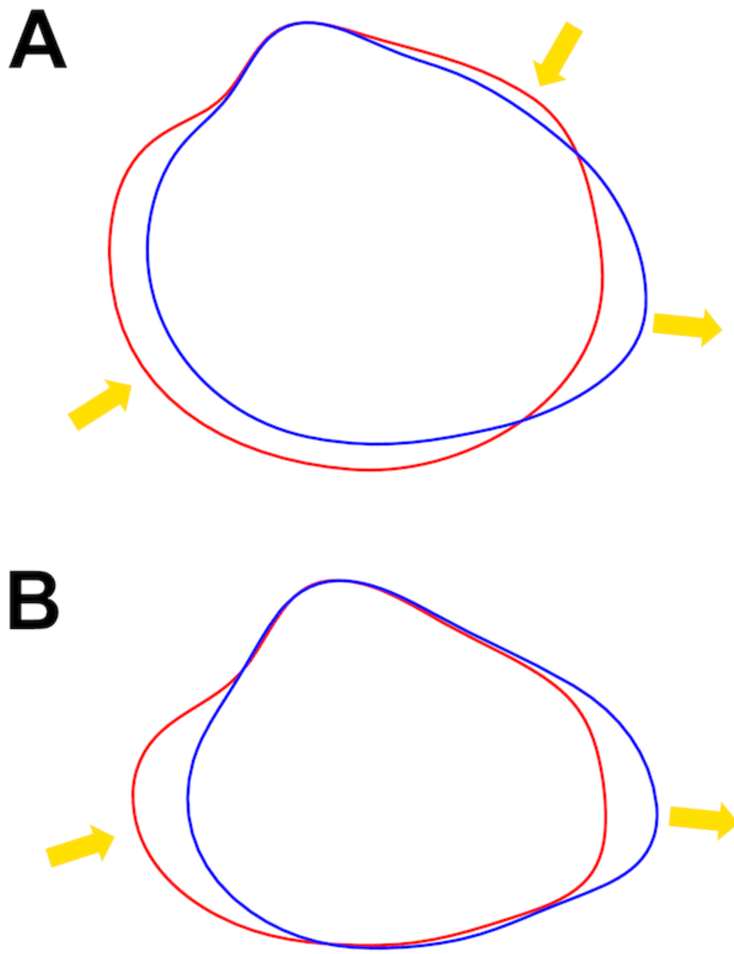

A
Regression score1
60000
40000
20000
0
-20000
-40000
-60000
-80000
0
300
600
900
1200
1500
1800
Area
B
Regression score1
80000
60000
40000
20000
0
-20000
-40000
-60000
0
200
400
600
800
1000
Area

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.


A
B