

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

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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.

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

4

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13 Abstract

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 25 Carditidae, Crassatellidae, Veneridae, Trigoniidae). Taxonomic, ecological and evolutionary
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27 Introduction

28 According to the Gould-Mosimann school (defined by Klingenberg, 1998), ‘allometry’ is
 29 the association between size and shape. The concept of allometry implies variation of a trait
 30 associated with variation of the overall size of an organism (Klingenberg, 1998). Size of an
 31 organism can be determined by its own biological growth (or ontogeny), and in these cases,
 32 allometry is the ~~variation~~ between shape and growth through its life-span.  his allometry is
 33 ~~called~~ “ontogenetic allometry” by Klingenberg (1996a; 1998). Studies on ontogenetic allometry
 34 mainly use cross-sectional data (each individual is measured at a single stage, and an average
 35 allometric trajectory is ~~acquired as~~ a composite sample from many individuals), but few ones use
 36 longitudinal data (e.g. Klingenberg, 1996b; Maunz & German, 1997) (each individual is
 37 measured multiple times during their growths, and individual variability of allometric trajectories
 38 is obtained). Cases of cross-sectional data are frequent in paleontological studies, for example in
 39 trilobites (see Hughes, Minelli & Fusco, 2006 and references herein). Cases of longitudinal data
 40 are virtually ~~impossible from~~ fossil organism.

41 Bivalves ~~have~~ accretionary growth in their shells where the mantle adds constantly new
 42 layers of calcium carbonate to the edge (Panella & MacClintock, 1968). Therefore, they
 43 preserved in their shells a complete record of external traits of their post-larval life-spans
 44 (Crampton & Maxwell, 2000), ~~and this makes~~ them in a source of longitudinal data for
 45 construction of ontogenetic trajectories. In a pioneer contribution, Crampton & Maxwell (2000)
 46 elaborate a methodology to explore this particular growth in bivalves. They re-constructed the
 47 ontogenetic trajectories of New Zealand species of *Spissatella* (Bivalvia: Crassatellidae) and
 48 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.



72 **Materials & Methods**

73 *Terminology and theoretical background*

74 All terms ~~about~~ allometry follow ~~to~~ Klingenberg (1998). Geometric Morphometrics and
75 Elliptic Fourier Analysis (EFA) terminology ~~are~~ explained in Kuhl & Giardina (1982), Lestrel
76 (1997), and Crampton (1995).

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

80

81 *Taxon sample*

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

89 The carditid species represents the most ancient record for ~~the~~ genus, ~~and is~~ represented
90 in the early Danian of Patagonia (Argentina), in the Roca, Jagüel and Salamanca formations (Río
91 Negro, Neuquén and Chubut provinces) and was recently ~~studied~~ by Pérez & del Río (2017),
92 ~~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 synonym 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 (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 precedence 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 established 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;

181 4.79%) is associated to the variation between less to more truncated posterior end of valves. The
 182 result of MRA is significant ($p\text{-value} < 0.0042$) (Fig. 4B). Results of PCA and MRA analyses
 183 included in Supplemental Data S5.

184 Geological categories show a non-structured arrangement when they are plotted in the
 185 morphospace. More numerous categories ('Monte León' and 'Puerto Madryn') occupy virtually
 186 the whole morphospace (Fig. 3C). Growth categories reflect a transition across the PC1 from
 187 juvenile to adult outlines. Juvenile outlines of *C. kokeni* are strongly subtriangular with pointed
 188 umbones. Adult outlines of this species are markedly subrectangular with more rounded
 189 umbones. The reconstructed ontogenetic trajectory (Fig. 3B) and the overlapping of both extreme
 190 outlines show an allometric variation similar to those observable in *C. paleopatagonica* (Fig.
 191 5B). Specimens originally assigned to *C. patagonicus* by previous authors fall into the juvenile
 192 sector of morphospace.



193

194 Discussion

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

196 The study of ontogeny in bivalves had evidenced that some species show allometric
 197 growth to certain characters (Stanley, 1975; Stanley, 1977; Tashiro & Matsuda, 1983; Savazzi &
 198 Yao, 1992). In our analyses we found allometric growth in both examples, and characteristics of
 199 them are the same in *C. paleopatagonica* and *C. kokeni*. Both species have positive allometry
 200 detected in the extension of posterior end, resulting in elongated shells. This morphological
 201 change is also recorded in other phylogenetically related infaunal burrowing bivalves.
 202 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.

225 Taxonomic implications of allometric growth

226 Differences between young and adult morphologies could be interpreted as taxonomic
 227 differences between species. In both studied cases, new species were proposed for specimens
 228 with young morphologies: *Venericardia camachoi* Vigilante, 1977 and *Crassatellites*
 229 *patagonicus* Ihering, 1907. These species fall into ~~young variation~~ of *Claibornicardia*
 230 *paleopatagonica* and *Crassatella kokeni*, respectively. Other examples are the carditids
 231 *Neovenericor paranensis* (Borchert, 1901) (late Miocene, Argentina) (adult morphology was
 232 called *Venericor crassicosta* Borchert, 1901) (Pérez, Alvarez & Santelli, 2017) and *Neovenericor*
 233 *ponderosa* (Suter, 1913) (late Oligocene, New Zealand) (young morphology was called
 234 *Venericardia caelebs* Marwick, 1929) (Beu & Maxwell, 1990). A different outline is frequently
 235 considered an important feature for taxonomic recognition but ontogenetic variation is not
 236 always taken into account (Alvarez & Pérez, 2016).

237

238 Ecological implications of this adult morphology

239 According to Stanley's experiments (1970), bivalve shells with streamlined outlines
 240 (cylindrical, blade-like, or disc-like) are the most rapid burrowers. Elongate outlines could be
 241 related to a fast burrowing in soft substrates but not in all cases. Also, Stanley (1970) established
 242 that moderately elongate burrowing species commonly used a large angle of rotation, and there is
 243 a strong forward component in their burrowing movement because of their eccentric axis of
 244 rotation. Elongate bivalves generally had a life position with the long axis in vertical position—for
 245 example, this is appreciated in living species of *Anomalocardia*—. Posterior portion of shell is
 246 directed to sediment surface, and it can be achieved with a minimum of increase in shell

developing, displacing ~~to a deeper position~~ 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 precedence. 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.

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

432 Figure 5. Overlapping of extreme outline configurations. A. *Claibornicardia paleopatagonica*.
433 B. *Crassatella kokeni*. Red outline = juvenile specimens. Blue outline = adult specimens.

434 Arrows indicate positive or negative allometry.

Figure 1

Case-studies of this work.

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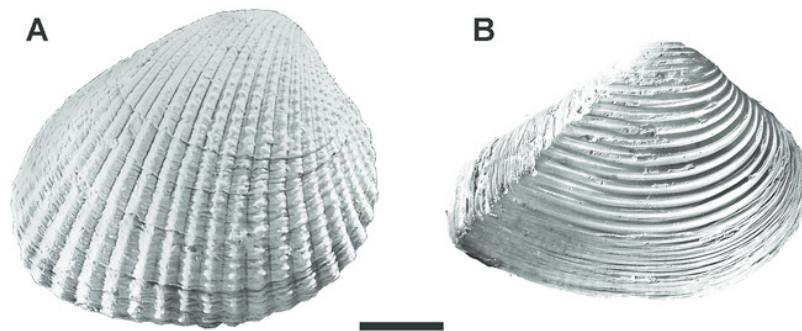


Figure 2

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

First and last outline illustrated.

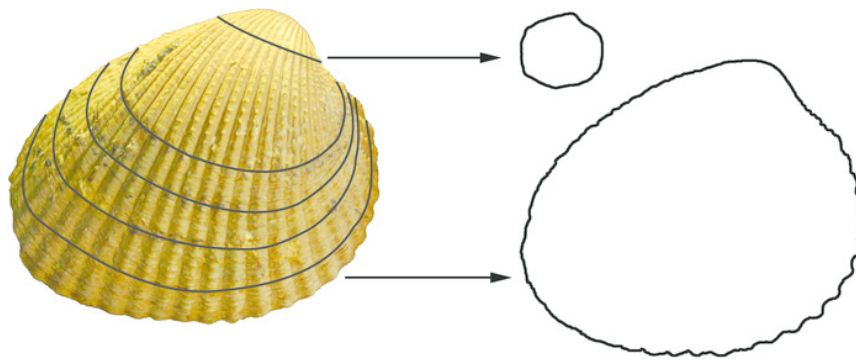


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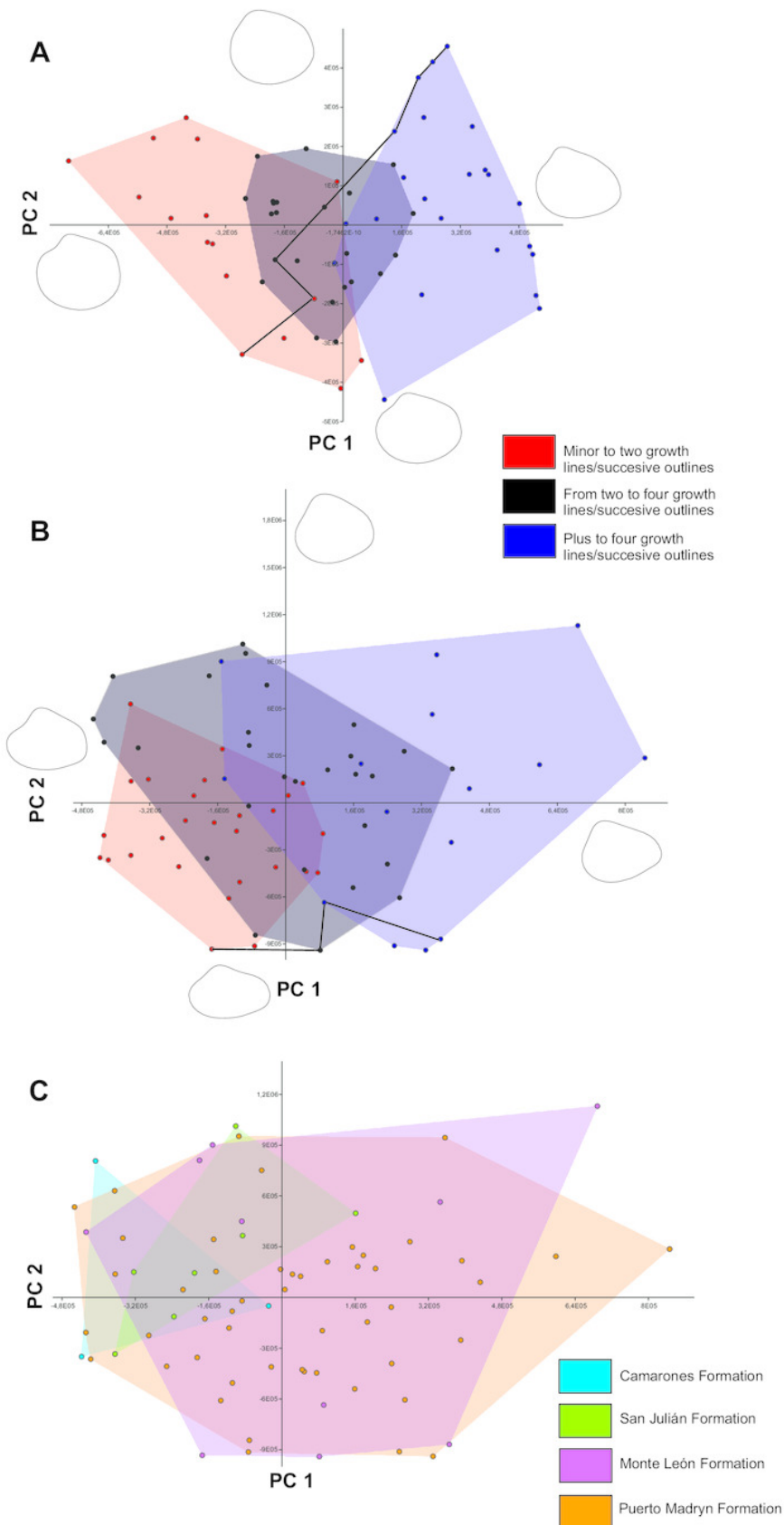


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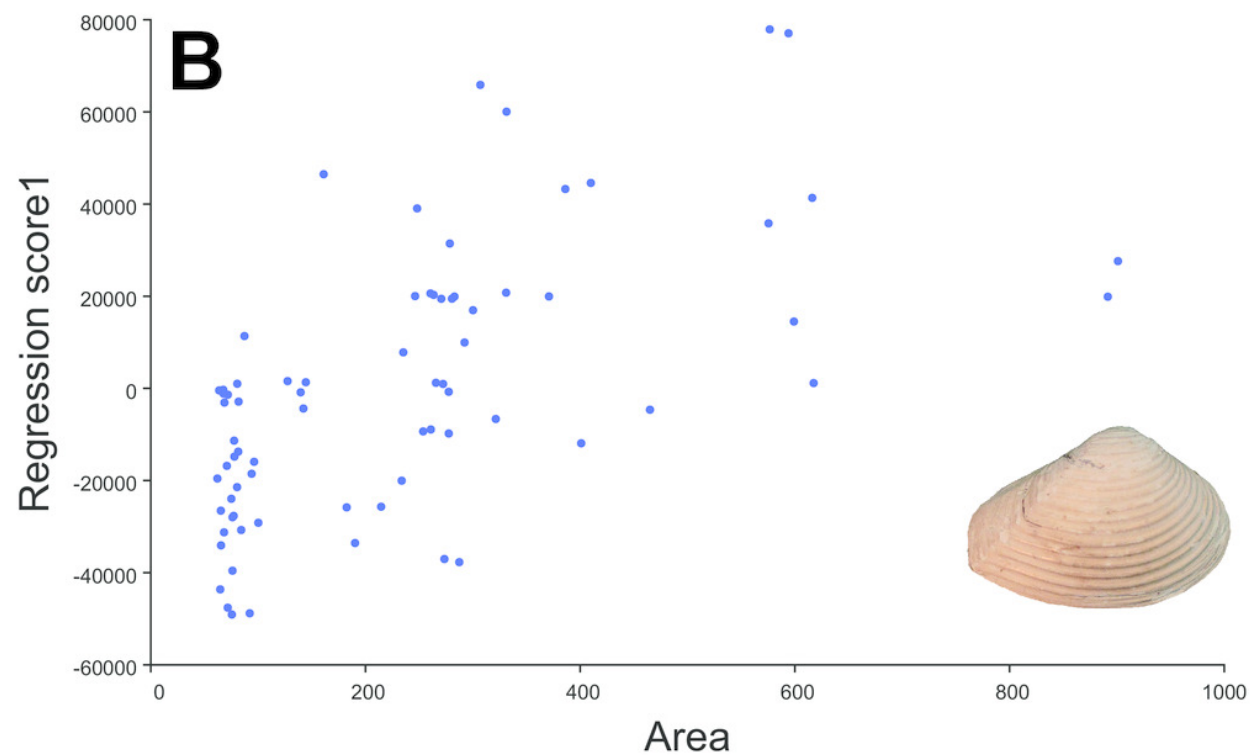
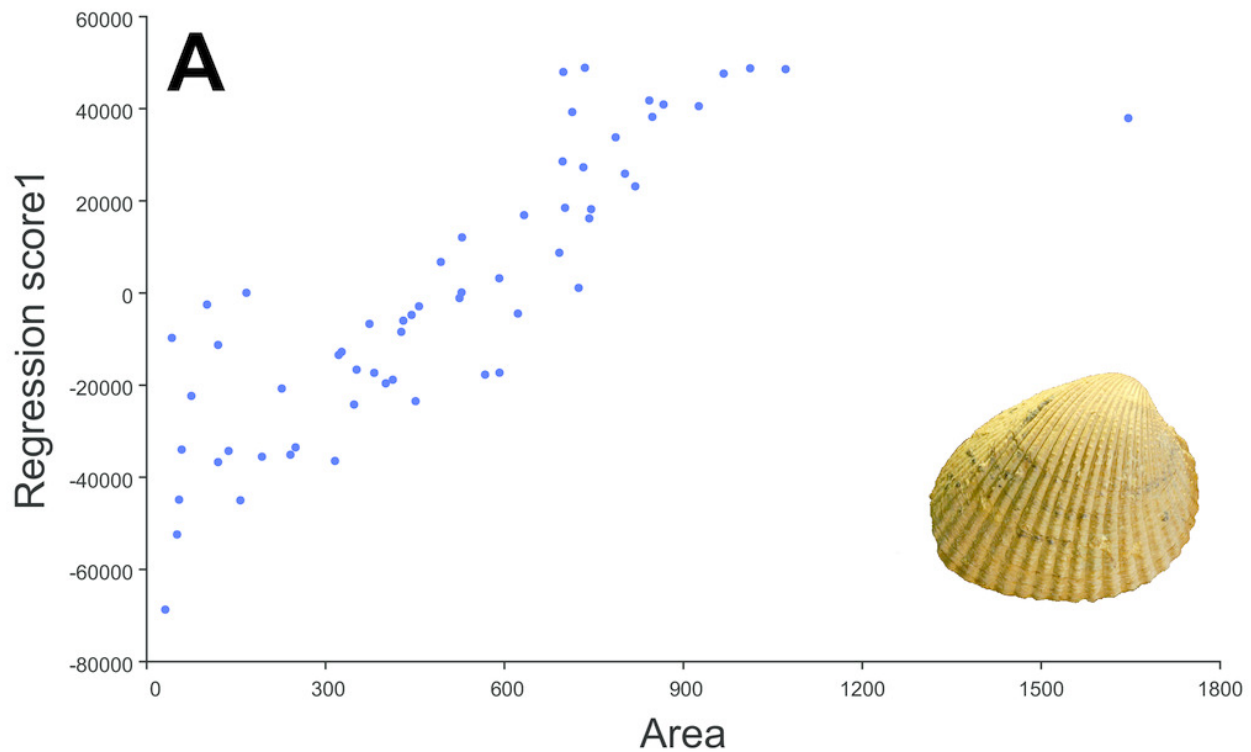


Figure 5

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.

