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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' 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.

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

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

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 covariation between shape and growth through its life-span. This allometry is
33 known as “ontogenetic allometry” (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 estimated from a composite sample from many individuals), but some
36 ones use “longitudinal” data (e.g. Klingenberg, 1996b; Maunz & German, 1997) (each individual
37 is measured multiple times during their growths, and individual variability in allometric
38 trajectories is obtained). Cases of “cross-sectional” data (sensu Klingenberg, 1996b) are frequent
39 in paleontological studies, for example in trilobites (see Hughes, Minelli & Fusco, 2006 and
40 references herein), Cambrian arthropods (e.g. Haug *et al.*, 2011), crinoids (e.g. Brower, 1988),
41 gastropods (e.g. Gould, 1966a), diapsids (e.g. Ezcurra & Butler, 2015), dinosaurs (e.g. Horner &
42 Goodwin, 2006, 2009), or mammals (e.g. Christiansen, 2012). “Longitudinal” studies (sensu
43 Klingenberg, 1996b) are not possible for many fossil organisms, but are viable in organisms with
44 accretionary growth. Some examples are shelled molluscs (Urduy *et al.*, 2010), brachiopods
45 (Rudwick 1968; Ackerly 1989; Tomašových, Carlson Sandra & Labarbera 2008), or ammonoids
46 (Korn, 2012, 2017; De Baets, Klug & Monnet, 2013). Some researches often remain focused on
47 adult stages, not taking into account the complete ontogeny (De Baets, Klug & Monnet, 2013).

48 Bivalves show accretionary growth in their shells where the mantle adds constantly new
49 layers of calcium carbonate to the edge (Panella & MacClintock, 1968). Therefore, they

50 preserved in their shells a complete record of external traits of their post-larval life-spans
51 (Crampton & Maxwell, 2000), making them a source of “longitudinal” data (sensu Klingenberg,
52 1996b) for construction of ontogenetic trajectories. In a pioneer contribution, Crampton &
53 Maxwell (2000) elaborate a methodology to explore this particular growth in bivalves. They re-
54 constructed the ontogenetic trajectories of New Zealand species of *Spissatella* (Bivalvia:
55 Crassatellidae) and related their allometric growth to macroevolutionary trends in the clade.

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

61 Geometric morphometrics is a very useful tool for study of allometry and ontogeny
62 (Zelditch, Bookstein & Lundrigan, 1992; Fink & Zelditch, 1995; Mitteroecker *et al.*, 2004;
63 Mitteroecker, Gunz & Bookstein, 2005; Monteiro *et al.*, 2005; among others, see a revision on
64 this topic in Adams, Rohlf & Slice, 2013). The use of morphometric methods is an objective,
65 reliable and repeatable tool for quantify patterns of shape changes (Brown & Vavrek, 2015) and
66 geometric morphometric allows strong graphical representations of allometry studies (Adams,
67 Rohlf & Slice, 2013). In particular, the outline shape analyses allow to study the variation in this
68 key character, the outline, which reflects autoecological features in bivalves according to Stanley
69 (1970; 1975). The aim of this contribution is to study ontogenetic series in two examples of
70 infaunal burrowing bivalves, *Claibornicardia paleopatagonica* (Ihering, 1903)
71 (Archiheterodonta: Carditidae) and *Crassatella kokeni* Ihering, 1899 (Archiheterodonta:
72 Crassatellidae). The changes in shape of these species are discussed and the presence of

73 allometric growth is tested. Variability in shape of these two bivalves led previous authors to
74 define new species based on possible juvenile specimens, *Venericardia camachoi* (Vigilante,
75 1977) and *Crassatellites patagonicus* Ihering, 1907 (nowadays considered as synonymies of *C.*
76 *paleopatagonica* and *C. kokeni*, respectively). Changes in shape in these species and changes
77 present in other infaunal bivalves, as well as their paleoecological implications, are discussed.
78 Also, this contribution is an attempt to apply and to expand the methodology developed by
79 Crampton & Maxwell (2000). As is already mentioned by Crampton & Maxwell (2000), Gould
80 (1989, p. 537) noted “Natural history is a science of relative frequencies”; and these authors
81 indicated “advance in many fields of palaeontological debate requires compilation of detailed
82 observations across diverse fossil groups and time spans” (Crampton & Maxwell, 2000, p. 400).
83 The present is a contribution for thickening the literature of cases studying allometry patterns,
84 and this is necessary since a debate addressing the relative frequencies of different phenomena
85 (such as the paleontological debate) can only advance through the compilation of such cases.

86

87 **Materials & Methods**

88 *Terminology and theoretical background*

89 All terms regarding allometry follow the definitions provided by Klingenberg (1998).
90 Positive allometry refers to a trait that increases respect to another one (a positive deviation to
91 expected isometry), and negative allometry is the opposite. Geometric Morphometrics and
92 Elliptic Fourier Analysis (EFA) terminologies are explained in Kuhl & Giardina (1982), Lestrel
93 (1997), and Crampton (1995).

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

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

101

102 *Taxon sampling*

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

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

116 5197) were used. The specimen assigned to *Venericardia camachoi* by Vigilante (1977) is also
117 included in MACN-Pi 5197.

118 *Crassatella kokeni* is the most abundant crassatellid from the Cenozoic of Patagonia
119 (Argentina), being represented in the San Julián, Monte León, Camarones and Puerto Madryn
120 formations (late Oligocene–late Miocene, Chubut and Santa Cruz provinces). The systematics of
121 this species was reviewed by Santelli & del Río (2014), who regarded *Crassatellites patagonicus*
122 Ihering, 1907 as a junior synonymous of *Crassatella kokeni*. For our analyses, 32 shells of *C.*
123 *kokeni* were used (including those previously assigned to *Crassatellites patagonicus*). These
124 specimens come from Cañadón de los Artilleros, Punta Casamayor, Cabo Tres Puntas (late
125 Oligocene–early Miocene, San Julián Formation, Santa Cruz Province); mouth of Santa Cruz
126 River, Estancia Los Manantiales, Cañadón de los Misioneros, Monte Entrada (early Miocene,
127 Monte León Formation, Santa Cruz Province); Camarones (early Miocene, Camarones
128 Formation, Chubut Province), and Lote 39 (late Miocene, Puerto Madryn Formation, Chubut
129 Province) (MACN-Pi 325–327, 331–332, 3576, 3600, 3907, 4775, 5374–5376; CIRGEO-PI
130 1501–1502; and CPBA 9404).

131

132 *Elliptic Fourier Analysis*

133 Elliptic Fourier Analysis (Kuhl & Giardina, 1982) method was chosen to analyse the
134 outlines of our examples because it allows to work with the variation presents in valves shape.
135 The methodology employed to obtain different outlines is derived from Crampton & Maxwell
136 (2000) criteria. Each valve was digitally photographed in an inclined position with their growth
137 lines placed parallel to the surface (Fig. 2A). The outlines obtained in different angles, regarding

138 to the surface, were limited by coarse growth lines across the entire shell (Fig. 2B). Strict
139 chronological ages of each individual have not been established, but previous analyses have well
140 found a strong correlation between ages (based on the use of stable isotopes) and growth lines
141 (Jones, 1988; Brey & Mackensen, 1997; Jones & Gould, 1999; Lomovasky *et al.*, 2002). As a
142 result, growth lines are a good proxy for the chronological age of specimens, and size is an
143 estimation for relative time. In *Claibornicardia paleopatagonica* annual growth lines are
144 noticeable but in *Crassatella kokeni* they are not so evident, being perceptible only in part of
145 specimens of specimens' shells. For this species, outlines were taken in intervals of 10 mm along
146 the axial length, following the procedure undertaken by Crampton & Maxwell (2000) for
147 *Spissatella*. This methodology allows to design an age-structured analysis for our data.

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

158 For each individual, chain codes were registered along the contour to calculate the
159 Elliptic Fourier Descriptors (EFDs). Total Fourier power was calculated to estimate the optimal
160 number of harmonics required for the analysis. The Fourier power of a harmonic is proportional

161 to its amplitude and provides a measure of the amount of shape described by that harmonic
162 (Crampton, 1995). A series of harmonics can be truncated when the value of average cumulative
163 Fourier power reaches the 99% of the average total power (sum of the total harmonics used). The
164 optimal number for this case was established in ten harmonics for *C. paleopatagonica*, and seven
165 harmonics for *C. kokeni*. Outlines were normalized to discard effects of rotation, translation and
166 size, using the parameters of the ellipse defined by the first harmonic (First Harmonic Ellipse
167 method). Therefore, three of the four EFDs describing the first harmonic ellipse are constant for
168 all the outlines (Crampton, 1995). The software Shape 1.3v (Iwata & Ukai, 2002) was used for
169 all the analysis.

170

171 *Morphospace construction and regression analysis*

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

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

185

186 **Results**

187 *Claibornicardia paleopatagonica allometric growth*

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

198 Growth categories plotted in the obtained morphospace show a transition across PC1
199 from juvenile to adult outlines. Variation across life-span in *C. paleopatagonica* can be
200 distinguished in the successive outlines of each individual. Juvenile outlines are strongly rounded
201 and shows subcentrally placed umbones. Towards more aged shells, an increase in the projection
202 of posterior end is recognisable. Adult shells of this species have subrectangular to subelliptic
203 outlines with anteriorly placed umbones. A reconstructed ontogenetic trajectory can be observed
204 in Figure 3A linking different stages of the same specimen in the morphospace (this ontogenetic

205 trajectory was obtained from a single actual specimen, from which the largest number of outlines
206 were acquired). Different allometric variation can be detected when overlapping extreme outlines
207 of PC1. Posterior end has positive allometry, while the dorsal and anterior-ventral margins have
208 negative allometry (Fig. 5A).

209

210 *Crassatella kokeni* allometric growth

211 In this case, the first three components of PCA explain 90.72% of the total variance (Fig.
212 3B). The first component (PC1; 66.66% of variance) shows variation between more
213 subtriangular and more subrectangular outlines. The second component (PC2; 19.27% of
214 variance) reflects variation between outlines with subcentrally placed umbones and outlines with
215 anteriorly placed umbones. The third component (PC3; 4.79% of variance) is associated to
216 variation between less and more truncated posterior end of valves. The MRA shows more
217 scattered points on the graphs than *C. paleopatagonica*, which could be related to the different
218 geological precedence of shells. Nevertheless, the result of MANOVA test for the regression
219 analysis is significant ($p\text{-value} < 0.001$) (Fig. 4B). Results of PCA and MRA analyses are
220 included in Supplemental Data S5.

221 Geological categories show a non-structured arrangement when they are plotted in the
222 morphospace. The best sampled categories ('Monte León' and 'Puerto Madryn') occupy
223 virtually the whole morphospace (Fig. 3C). Growth categories reflect a transition across the PC1
224 from juvenile to adult outlines. Juvenile outlines of *C. kokeni* are strongly subtriangular with
225 pointed umbones, whereas adult outlines of it are markedly subrectangular having more rounded
226 umbones. The reconstructed ontogenetic trajectory (Fig. 3B), obtained in the same way as the

227 previous case, and the overlapping of both extreme outlines of PC1 shows an allometric
228 variation similar to those observable in *C. paleopatagonica* (Fig. 5B). Specimens originally
229 assigned to *C. patagonicus* by previous authors fall into the juvenile sector of morphospace (Fig.
230 3B).

231

232 **Discussion**

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

234 An allometric growth pattern shared by both species, *C. paleopatagonica* and *C. kokeni*
235 was found in the analyses. Both taxa have positive allometry detected in the extension of
236 posterior end, resulting in elongated adult shells. The study of ontogeny in bivalves had
237 evidenced that some species show allometric growth in certain characters (Stanley, 1975;
238 Stanley, 1977; Tashiro & Matsuda, 1983; Savazzi & Yao, 1992) and the morphological change
239 recorded herein is also documented in other phylogenetically related infaunal bivalves.

240 Subquadrate juvenile and elongated adult specimens of the carditid *Claibornicardia alticostata*
241 (Conrad, 1833) have a similar allometric variation (Stenzel & Krause, 1957, and pers. obs. on
242 syntypes ANSP 30562). Crampton & Maxwell (2000) described a similar variation in some
243 representatives of the crassatellid genus *Spissatella*, especially in the species *S. subobesa*
244 (Marshall & Murdoch, 1919) and *S. poroleda* Finlay, 1926.

245

246 *Elongate adult morphology in other infaunal bivalves*

247 Ontogenetic trajectories have not been described in other infaunal bivalves. However, the
248 same elongate adult morphology described here is known. Among archiheterodonts, the
249 morphology documented for adult shells of *C. paleopatagonica* and *C. kokeni* can be observed in
250 species of the genera *Megacardita* Sacco, 1899 (La Perna, Mandic & Harzhauser, 2017);
251 *Neovenericor* Rossi de García, Levy & Franchi, 1980 (Pérez, Alvarez & Santelli, 2017);
252 *Venericor* Stewart, 1930 (Gardner & Bowles, 1939); and *Bathytormus* Stewart, 1930 (Wingard,
253 1993; Santelli & del Río, 2014). Among other bivalve groups, this adult morphology is also
254 recorded in species of the Veneroidea and Palaeoheterodonta. Some species of Veneridae genera
255 as *Anomalocardia* Schumacher, 1817, *Lirophora* Conrad, 1863, *Chionopsis* Olsson, 1932,
256 *Lamelliconcha* Dall, 1902, *Macrocallista* Meek, 1876, and *Antigona* Schumacher, 1817, among
257 others, have adult shells with a projected posterior end and elongate outlines. Some Trigoniidae
258 taxa lead this morphology to extreme possibilities, with the development of wide and very
259 projected posterior ends (e.g. Francis & Hallam, 2003). As an example, Echevarría (2014) found
260 a strong allometric growth developing in two phases in the trigoniid *Myophorella garatei*
261 Leanza, 1981 with a strong extension of the posterior margin.

262

263 *Taxonomic implications of allometric growth*

264 Differences between young and adult morphologies could have been be interpreted as
265 taxonomic differences between species. In both studied cases, new species were proposed for
266 specimens with young morphologies: *Venericardia camachoi* Vigilante, 1977 and *Crassatellites*
267 *patagonicus* Ihering, 1907. These taxa fall into the variation representing young specimens of
268 *Claibornicardia paleopatagonica* and *Crassatella kokeni*, respectively. The case of *C. kokeni*

269 and *C. patagonicus* was already mentioned by Santelli & del Río (2014), being corroborated the
270 synonymy in this study. Other examples are the carditids *Neovenericor paranensis* (Borchert,
271 1901) (late Miocene, Argentina), the adult morphology of which was described as *Venericor*
272 *crassicosta* Borchert, 1901 (Pérez, Alvarez & Santelli, 2017) and *Neovenericor ponderosa*
273 (Suter, 1913) (late Oligocene, New Zealand), the young morphology of which was named
274 *Venericardia caelebs* Marwick, 1929 (Beu & Maxwell, 1990). These results reflect that this
275 allometric change (including into the intraspecific variation) must be considered in taxonomic
276 revisions of similar infaunal bivalves. These examples show that a different outline is frequently
277 considered an important feature for taxonomic recognition but ontogenetic variation is not
278 always taken into account (Alvarez & Pérez, 2016).

279

280 *Ecological implications of this adult morphology*

281 According to Stanley's experiments (1970), bivalve shells with streamlined outlines
282 (cylindrical, blade-like, or disc-like) are the fastest burrowers. Elongate outlines could be related
283 to a fast burrowing in soft substrates but not in all cases. Also, Stanley (1970) established that
284 moderately elongate burrowing species commonly use a large angle of rotation, having a strong
285 forward component in their burrowing movement because of their eccentric axis of rotation.
286 Elongate bivalves generally have a mode of life with the long axis in vertical position –for
287 example, this is appreciated in living species of *Anomalocardia*–. Posterior portion of shell is
288 directed to sediment surface, being achieved the elongate morphotype with a minimum of
289 increase in shell growth, displacing the centre of gravity and the visceral mass of organisms to a
290 deeper position (Stanley, 1970; Crampton & Maxwell, 2000). Other possibly related effects

291 could be increasing in stability against scour (Stanley, 1977; Stanley & Yang, 1987; Francis &
292 Hallam, 2003) or reduction of exposure and predation (Crampton & Maxwell, 2000; Francis &
293 Hallam, 2003). One possible approach to reach this morphology could be the positive allometry
294 of posterior end.

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

301

302 *Evolutionary implications of allometric growth*

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

311

312 **Conclusions**

313 Analyses of allometric growth allow to recognize similar ontogenetic changes in
314 *Claibornicardia paleopatagonica* (Ihering, 1903) and *Crassatella kokeni* Ihering, 1899. In both
315 species the ontogeny is characterized by the presence of positive allometry in the growth of
316 posterior end, resulting in elongated adult shells. The species *Venericardia camachoi* Vigilante,
317 1977 and *Crassatellites patagonicus* Ihering, 1907, proposed as synonyms of both previously
318 mentioned taxa, fall into portion of resulting morphospace that represents juvenile morphologies,
319 so that the obtained results corroborate these synonymies.

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

326

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334

335 **List of references**

336 Ackerly, S. 1989. Kinematics of accretionary shell growth, with examples from brachiopods and
337 molluscs. *Paleobiology* 15, 147–164.

338 Adams, D., Rohlf, F.J. & Slice, D. 2013: A field comes of age: geometric morphometrics in the
339 21st century. *Hystrix, the Italian Journal of Mammalogy* 24, 7–14.

340 Alvarez, M. and Pérez, D. 2016: Gerontic intraspecific variation in the Antarctic bivalve
341 *Retrotapes antarcticus* (Sharman and Newton, 1894). *Ameghiniana* 53, 485–494.

342 Beu, A.G. & Maxwell, P.A., 1990: Cenozoic Mollusca from New Zealand. *Paleontological*
343 *Bulletin of the New Zealand Geological Survey* 58, 1–518.

344 Borchert, A., 1901: Die Molluskenfauna und das Alter der Parana-Stufe. Beiträge zur Geologie
345 und Paläontologie von Südamerika. *Neues Jahrbuch für Mineralogie, Geologie*
346 *Palaeontologie Beilagenband* 14, 171–245.

347 Brey, T. & Mackensen, A. 1997: Stable isotopes prove shell growth bands in the Antarctic
348 bivalve *Laternula elliptica* to be formed annually. *Polar Biology* 17, 465–468.

349 Brower, J. 1988: Ontogeny and phylogeny in primitive calceocrinid crinoids. *Journal of*
350 *Paleontology* 62, 917–934.

351 Brown, C. & Vavrek, M. 2015: Small sample sizes in the study of ontogenetic allometry;
352 implications for palaeobiology. *PeerJ* 3, e818.

- 353 Christiansen, P. 2012: The making of a monster: postnatal ontogenetic changes in
354 craniomandibular shape in the sabercat *Smilodon*. *PLoS One* 7, e29699.
- 355 Conrad, T.A., 1833: On some new fossils and recent shell of the United States. *American*
356 *Journal of Science and Arts* 23, 339–346.
- 357 Conrad, T.A. 1863: Descriptions of new Recent and Miocene shells. *Proceedings of the*
358 *Academy of Natural Sciences at Philadelphia* 14, 583–586.
- 359 Crampton, J.S. 1995: Elliptic Fourier shape analysis of fossil bivalves: some practical
360 considerations. *Lethaia* 28, 179-186.
- 361 Crampton, J. & Maxwell, P. 2000: Size: all it's shaped up to be? Evolution of shape through the
362 lifespan of the Cenozoic bivalve *Spissatella* (Crassatellidae). In Harper, E., Taylor, J. &
363 Crame, J. (eds): *The Evolutionary Biology of the Bivalvia*. *Geological Society London*,
364 *Special Publications* 177, 399–423.
- 365 Dall, W.H. 1902: Synopsis of the family Veneridae and of the North American recent species.
366 *Proceedings of the United States National Museum* 26, 335–412.
- 367 De Baets, K., Klug, C. & Monnet, C. 2013: Intraspecific variability through ontogeny in early
368 ammonoids. *Paleobiology* 39, 75–94.
- 369 Echevarría, J. 2014: Ontogeny and autecology of an Early Cretaceous trigoniide bivalve from
370 Neuquén Basin, Argentina. *Acta Palaeontologica Polonica* 59, 407–420.
- 371 Ezcurra, M. & Butler, R. 2015: Post-hatchling cranial ontogeny in the Early Triassic diapsid
372 reptile *Proterosuchus fergusi*. *Journal of Anatomy* 226, 387–402.

- 373 Fink, W. L., & M. L. Zelditch. 1995: Phylogenetic analysis of ontogenetic shape
374 transformations: a reassessment of the piranha genus *Pygocentrus* (Teleostei). *Systematic*
375 *Biology* 44, 343–360.
- 376 Finlay, H.J. 1926: New shells from New Zealand Tertiary beds: Part 2. *Transactions of the New*
377 *Zeland Institute* 56, 227–258.
- 378 Francis, A.O. & Hallam, A. 2003: Ecology and evolution of Jurassic trigoniid bi-valves in
379 Europe. *Lethaia* 36, 287–304.
- 380 Gardner, J.A. & Bowles, E., 1939: The *Venericardia planicosta* group in the Gulf Province.
381 *United States Geological Survey, Professional Paper 189-F*, 143–215.
- 382 Gould, S.J. 1966a: Allometry in Pleistocene land snails from Bermuda: the influence of size
383 upon shape. *Journal of Paleontology* 40, 1131 –1141.
- 384 Gould, S.J. 1966b: Allometry and size in ontogeny and phylogeny. *Biological Reviews* 41, 587-
385 640.
- 386 Gould, S.J. 1977: *Ontogeny and Phylogeny*, 501 pp. The Belknap Press of Harvard University
387 Press. Cambridge, Massachusetts.
- 388 Gould, S.J. 1989: A developmental constraint in *Cerion*, with comments on the definition and
389 interpretation of constraint in evolution. *Evolution* 43, 516-539.
- 390 Hammer, Ø., Harper, D.A.T. & Ryan, P.D., 2001: PAST. Paleontological Statistics Software
391 Package for Education and Data Analysis. *Palaeontologia Electronica* 4, 1–9.
392 <https://folk.uio.no/ohammer/past/>

- 393 Haug, J., Waloszek, D., Maas, A., Liu, Y. & Haug, C. 2011: Functional morphology, ontogeny
394 and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* 55, 369–399.
- 395 Horner, J. & Goodwin, M. 2006: Major cranial changes during *Triceratops* ontogeny.
396 *Proceedings of the Royal Society B* 273, 2757–2761.
- 397 Horner, J. & Goodwin, M. 2009: Extreme cranial ontogeny in the Upper Cretaceous dinosaur
398 *Pachycephalosaurus*. *PLoS One* 4, e7626.
- 399 Hughes, N., Minelli, A., & Fusco, G. 2006: The ontogeny of trilobite segmentation: A
400 comparative approach. *Paleobiology* 32, 602–627.
- 401 Ihering, H. von, 1899: Die Conchylien der Patagonischen Formation. *Neues Jahrbuch für*
402 *Mineralogie, Geologie und Palaeontologie* 2, 1-41.
- 403 Ihering, H. von. 1903: Les Mollusques des Terrains Crétaciques Supérieurs del'Argentine
404 Orientale. *Anales del Museo Nacional de Buenos Aires terc. serie* 2, 193–229.
- 405 Ihering, H. von. 1907: Les Mollusques fossiles du Tertiaire et du Cretacé Supérieur de l'
406 Argentine. *Anales del Museo Nacional de Buenos Aires, terc. serie* 14, 1–611.
- 407 Iwata, H. & Ukai, Y., 2002: SHAPE: a computer program package for quantitative evaluation of
408 biological shapes based on elliptical fourier descriptors. *Journal of Heredity* 93, 384–385.
- 409 Jackson, D.A. 1993: Stopping rules in principal components analysis: a comparison of heuristical
410 and statistical approaches. *Ecology* 74, 2204–2214.
- 411 Jones. D. S. 1988: Sclerochronology and the size versus age problem. In McKinney, M.L. (ed.):
412 *Heterochrony in Evolution: A Multidisciplinary Approach*, 93–108. Plenum Press. New York.

- 413 Jones, D. & Gould, S.J. 1999: Direct measurement of age in fossil *Gryphaea*: the solution to a
414 classic problem in heterochrony. *Paleobiology* 25, 58–187.
- 415 Klingenberg, C. P. 1996a: Multivariate allometry. In Marcus, L.F., Corti, M., Loy, A., Naylor,
416 G.J.P. & Slice, D.E. (eds.): *Advances in Morphometrics*, 23–49. Plenum Press, New York.
- 417 Klingenberg, C. P. 1996b: Individual variation of ontogenies: a longitudinal study of growth and
418 timing. *Evolution* 50, 2412–2428.
- 419 Klingenberg, C. 1998: Heterochrony and allometry: the analysis of evolutionary change in
420 ontogeny. *Biological Reviews* 73, 79–123.
- 421 Klug, D. 2012: Quantification of ontogenetic allometry in ammonoids. *Evolution & Development*
422 14, 501–514.
- 423 Klug, D. 2017: *Goniatites sphaericus* (Sowerby, 1814), the archetype of Palaeozoic ammonoids:
424 a case of decreasing phenotypic variation through ontogeny. *Paläontologische Zeitschrift* 91,
425 337–352.
- 426 Kuhl, F.P. & Giardina, C.R. 1982: Elliptic Fourier features of a closed contour. *Computer*
427 *Graphics and Image Processing* 18, 236–258.
- 428 Lestrel, P.E. (Ed.). 1997: *Fourier Descriptors and their Applications in Biology*, 484 pp.
429 Cambridge University Press, United Kingdom.
- 430 La Perna, R., Mandic, O. & Harzhauser, M. 2017: Systematics and Palaeobiogeography of
431 *Megacardita* Sacco in the Neogene of Europe (Bivalvia, Carditidae). *Papers in Palaeontology*
432 3, 111–150.

- 433 Leanza, H.A. 1981: Una nueva especie de *Myophorella* (Trigoniidae-Bivalvia) del Cretácico
434 Inferior de Neuquén, Argentina. *Ameghiniana* 18, 1–9.
- 435 Lomovasky, B.J., Brey, T., Morriconi, E., & Calvo, J. 2002: Growth and production of the
436 venerid bivalve *Eurhomalea exalbida* in the Beagle Channel, Tierra del Fuego. *Journal of Sea*
437 *Research* 48, 209–216.
- 438 Marshall, P. & Murdoch, R. 1919: Some new fossil species of Mollusca. *Transactions of the*
439 *New Zealand Institute* 51, 253–258.
- 440 Maunz, M. & German, R. Z. 1997: Ontogeny and limb bone scaling in two New World
441 marsupials, *Monodelphis domestica* and *Didelphis virginiana*. *Journal of Morphology* 231,
442 117–130.
- 443 McKinney, M. 1984: Allometry and heterochrony in an Eocene echinoid lineage: morphological
444 change as a by-product of size selection. *Paleobiology* 10, 407–419.
- 445 Meek, F.B. 1876: A report on the invertebrate Cretaceous and Tertiary fossils of the upper
446 Missouri country. In Hayden, F.V. (ed.): *Report of the United States Geological Survey of the*
447 *Territories. Invertebrate Paleontology* 9, 1–629.
- 448 Mitteroecker P., Gunz P., Bernhard M., Schaefer K. & Bookstein F.L., 2004: Comparison of
449 cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution*
450 46, 679–698.
- 451 Mitteroecker, P., Gunz, P. & Bookstein, F. L. 2005: Heterochrony and geometric morphometrics:
452 a comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*. *Evolution &*
453 *Development* 7, 244–258.

- 454 Monteiro, L.R., Benedetto, A.P., Guillermo, L.H. & Rivera, L.A. 2005: Allometric changes and
455 shape differentiation of sagitta otoliths in sciaenid fishes. *Fisheries Research* 74, 288–299.
- 456 Olsson, A.A. 1932: Contribution to the Tertiary paleontology of northern Peru: Part 5, the
457 Peruvian Miocene. *Bulletins of American Paleontology* 19, 1–272.
- 458 Pannella, G., & Maclintock, C. 1968: Biological and environmental rhythms reflected in
459 molluscan shell growth. *Journal of Paleontology* 42, Supplement 2, 64–80.
- 460 Pérez, D.E., Alvarez, M.J. & Santelli, M.B., 2017: Reassessment of *Neovenericor* Rossi de
461 García, Levy & Franchi, 1980 (Bivalvia: Carditidae) using a geometric morphometric
462 approach, and revision of planicostate carditids from Argentina. *Alcheringa* 41, 112–123.
- 463 Rossi de García, E., Levy, R. & Franchi, M.R., 1980: *Neovenericor* n. gen. (Bivalvia) su
464 presencia en el Miembro Monte León (Formación Patagonia). *Revista de la Asociación*
465 *Geológica Argentina* 35, 59–71.
- 466 Rudwick, M.J.S. 1968. Some analytic methods in the study of ontogeny in fossils with
467 accretionary skeletons. *Journal of Paleontology* 42, 35–49.
- 468 Sacco, F., 1899: *I Molluschi dei terreni terziarii del Piemonte e della Liguria. Part XXVII*
469 *(Unionidae, Carditidae, Astartidae, Crassatellidae, Lasaeidae, Galeommidae, Cardiidae,*
470 *Limnocardiidae e Chamidae)*, 102 pp. Carlo Clausen, Turin.
- 471 Santelli, M.B. & del Río, C.J. 2014: Revisión de la subfamilia Crassatellinae (Bivalvia:
472 Crassatellidae) del Paleógeno–Neógeno de Argentina. *Ameghiniana* 51, 311–332.
- 473 Savazzi, E. & Yao, P. 1992: Some morphological adaptations in freshwater bivalves. *Lethaia* 25,
474 195–209.

- 475 Schumacher C.F. 1817: *Essai d'un nouveau système des habitations des vers testacés*, 288 pp.
476 Schultz, Copenhagen.
- 477 Shea, B. 1983: Allometry and heterochrony in the African apes. *American Journal of Physical*
478 *Anthropology* 62, 275–289.
- 479 Stanley, S.M. 1970: Relations of shell form to life habits in the Bivalvia (Mollusca). *Geological*
480 *Society Memoir* 125, 1–296.
- 481 Stanley, S.M. 1975: Why clams have the shape they have: an experimental analysis of
482 burrowing. *Paleobiology* 1, 48–58.
- 483 Stanley, S.M. 1977: Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves.
484 *Palaeontology* 20, 869–899.
- 485 Stenzel, H. B. & Krause, E. K. 1957: In Stenzel, H.B., Krause, E.K. & Twining, S.T. (eds.):
486 *Pelecypoda from the type locality of the Stone City beds (Middle Eocene) of Texas*. Texas
487 *University Publication* 5704, 1–237.
- 488 Stewart, R.B. 1930: Gabb's California Cretaceous and Tertiary type lamellibranchs. *Special*
489 *Publications of the Academy of Natural Sciences of Philadelphia* 3, 1–314.
- 490 Suter, H., 1913: New species of Tertiary Mollusca. *Transactions of the New Zealand Institute* 45,
491 294–297.
- 492 Tashiro, M., & Matsuda, T. 1988: Mode of life in Cretaceous trigonoids. *Fossils* 45, 9–21.

- 493 Tomašových A, Carlson Sandra J, & Labarbera M. 2008. Ontogenetic nice shift in the
494 brachiopod *terebratalia transversia*: relationship between the loss of rotation ability and
495 allometric growth. *Palaeontology* 51, 1471–1496.
- 496 Urdy, S., Goudemand, N., Bucher, H. & Chirat, R. 2010. Growth-dependent phenotypic
497 variation of molluscan shells: Implications for allometric data interpretation. *Journal of*
498 *Experimental Zoology* 314B, 303–326.
- 499 Wingard, G.L. 1993: A detailed taxonomy of Upper Cretaceous and Lower Tertiary
500 Crassatellidae in the Eastern United States – an example of the nature of extinction at the
501 boundary. *United States Geological Survey, Professional Paper 1535*, 1–131.
- 502 Zelditch, M.L., Bookstein, F.L. & Lundrigan, B.L. 1992: Ontogeny of integrated skull growth in
503 the cotton rat *Sigmodon fulviventer*. *Evolution* 46, 1164–1180.

504

505 **Explanations of figures**

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

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

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

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

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

526 Figure 5. Overlapping of extreme outline configurations. A. *Claibornicardia paleopatagonica*.
527 B. *Crassatella kokeni*. Red outline = juvenile specimens. Blue outline = adult specimens.
528 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) 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.

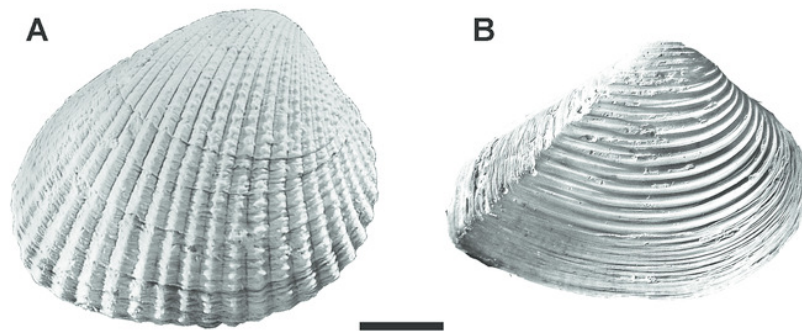


Figure 2

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.

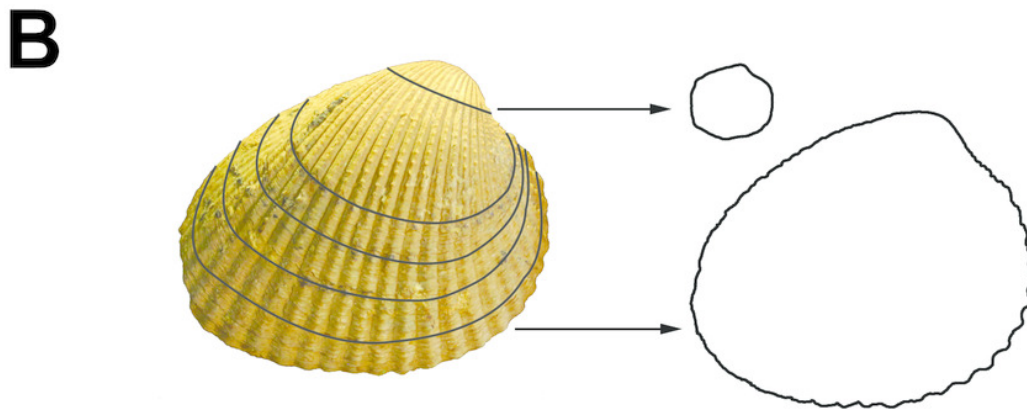
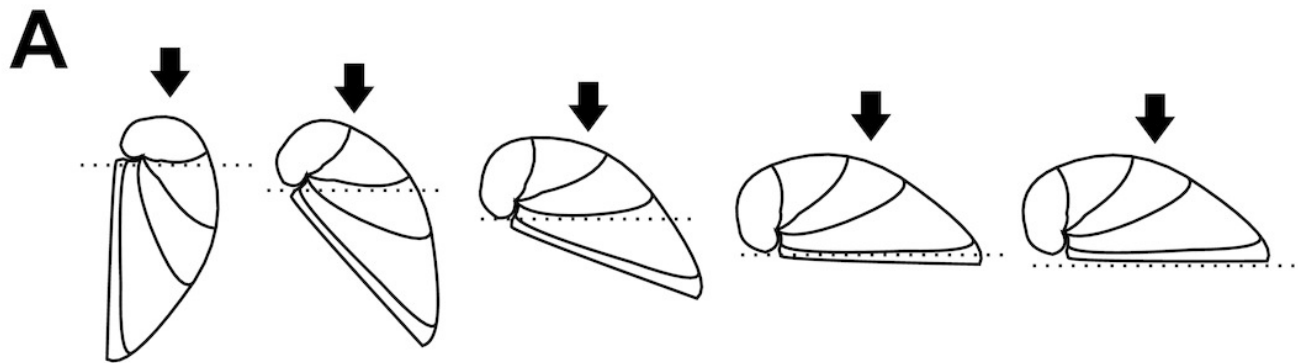


Figure 3

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 precedence. 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 camacho* and squares indicate specimen previously assigned to *Crassatellites patagonicus*.

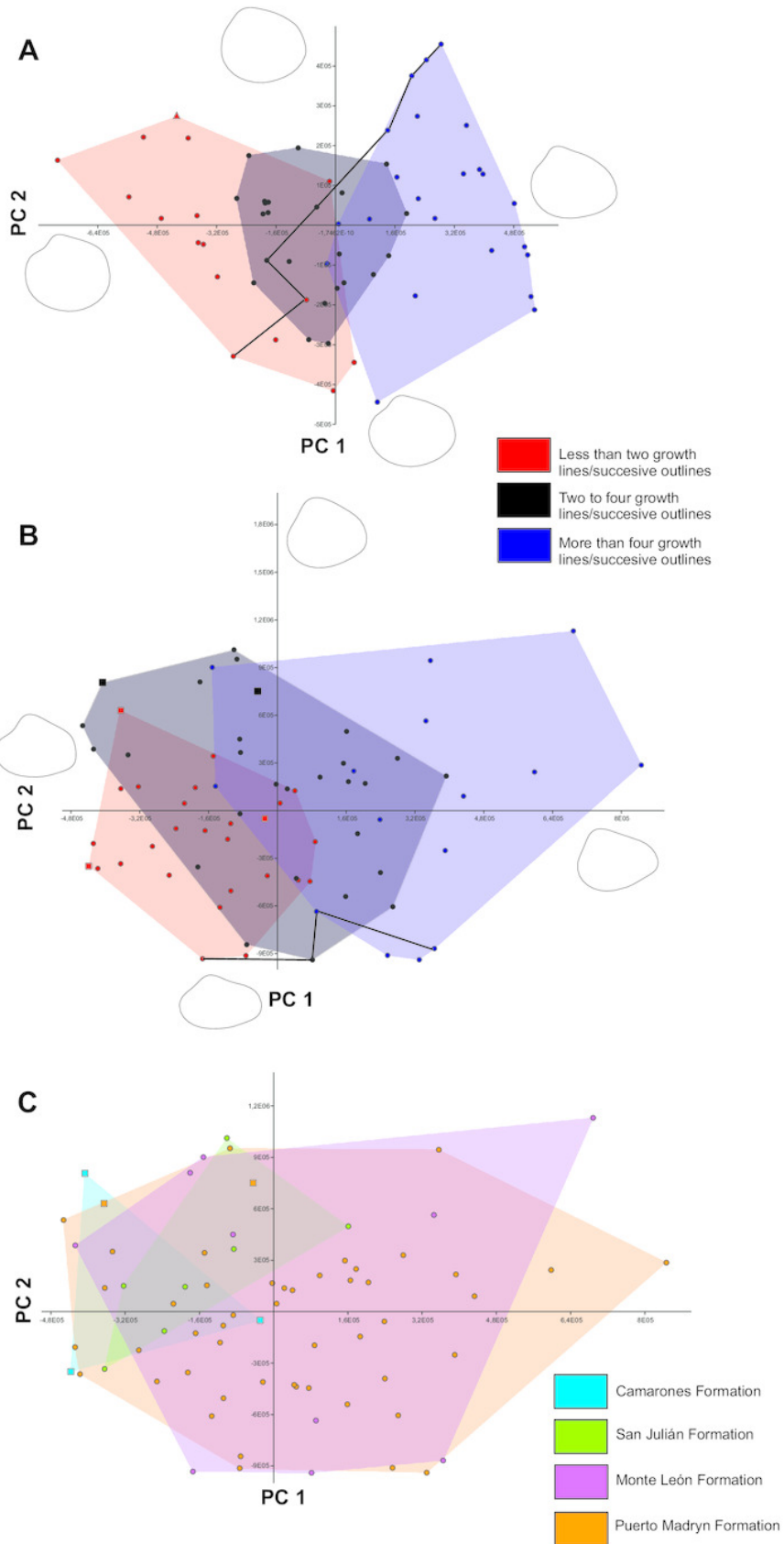


Figure 4

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.

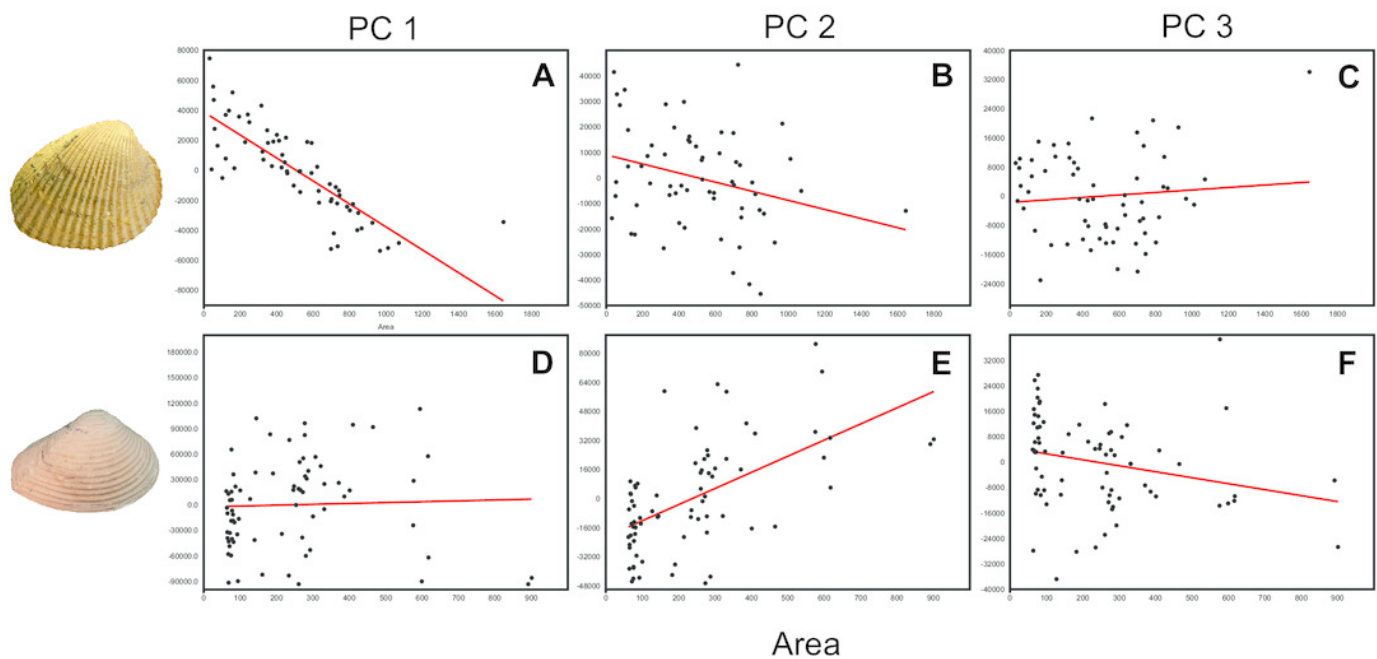


Figure 5

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.

