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**

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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

19   conducted using a geometric morphometric approach (Elliptic Fourier Analysis), obtaining

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.

Introduction

27

28   According to the Gould-Mosimann school (defined by Klingeberg, 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 (Urdy *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

Materials & Methods

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 statment 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 equivalve 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 stablished 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 procedence of shells. Nevertheless, the result of MANOVA test for the regression

219 analysis is significant (p-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 instraspecific 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

334

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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 procedence. 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.
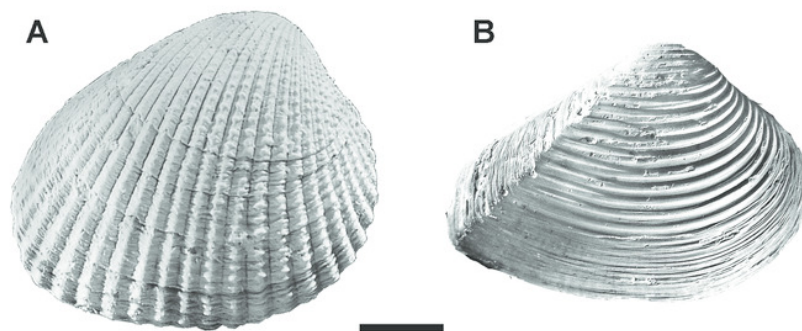
A

B

Figure 2

Applied methodology to obtain successive outlines of a single valve.

A. One valve oriented in different angles. Dotted lines indicate the parallel position of valves regarding to surface, arrows indicate position of digital camera. B. Example of successive outlines captured in one specimen (MACN-Pi 5197). First and last outline illustrated. Photo credit: the authors.
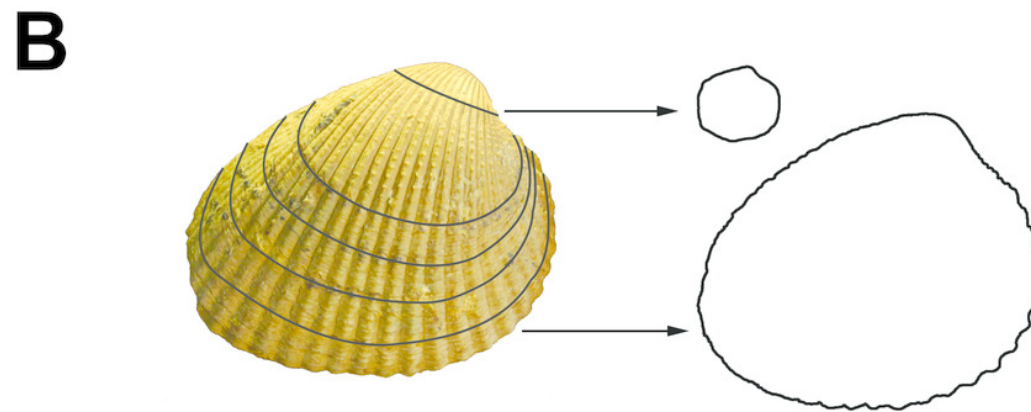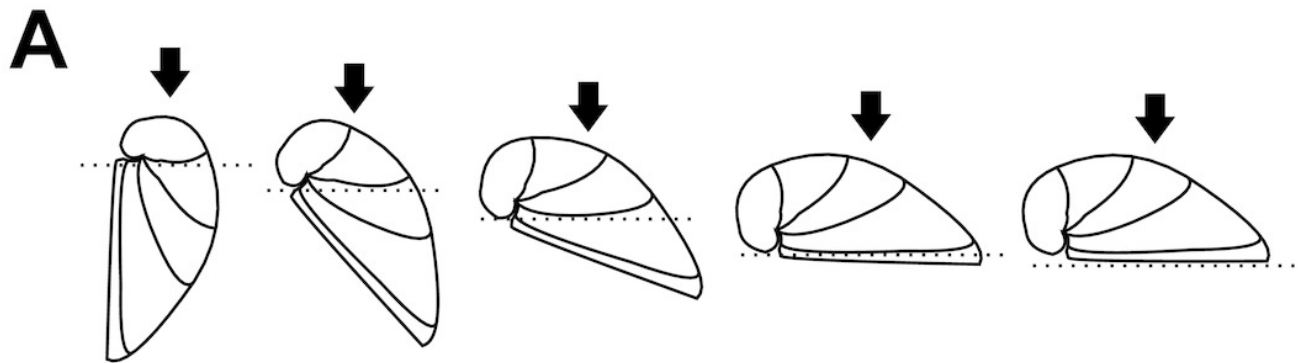
Figure 3

Results of Principal Component Analyses.

A. *Claibornicardia paleopatagonica* arranged by ontogenetic stage. B. *Crassatella kokeni* arranged by ontogenetic stage. C. *Crassatella kokeni* arranged by stratigraphic procedence. Color legends and the extreme morphologies of each principal component are illustrated in the graph. Black lines in A and B show ontogenetic trajectories of a selected specimen. Triangles indicate specimen previously assigned to *Venericardia camachoi* and squares indicate specimen previously assigned to *Crassatellites patagonicus*.
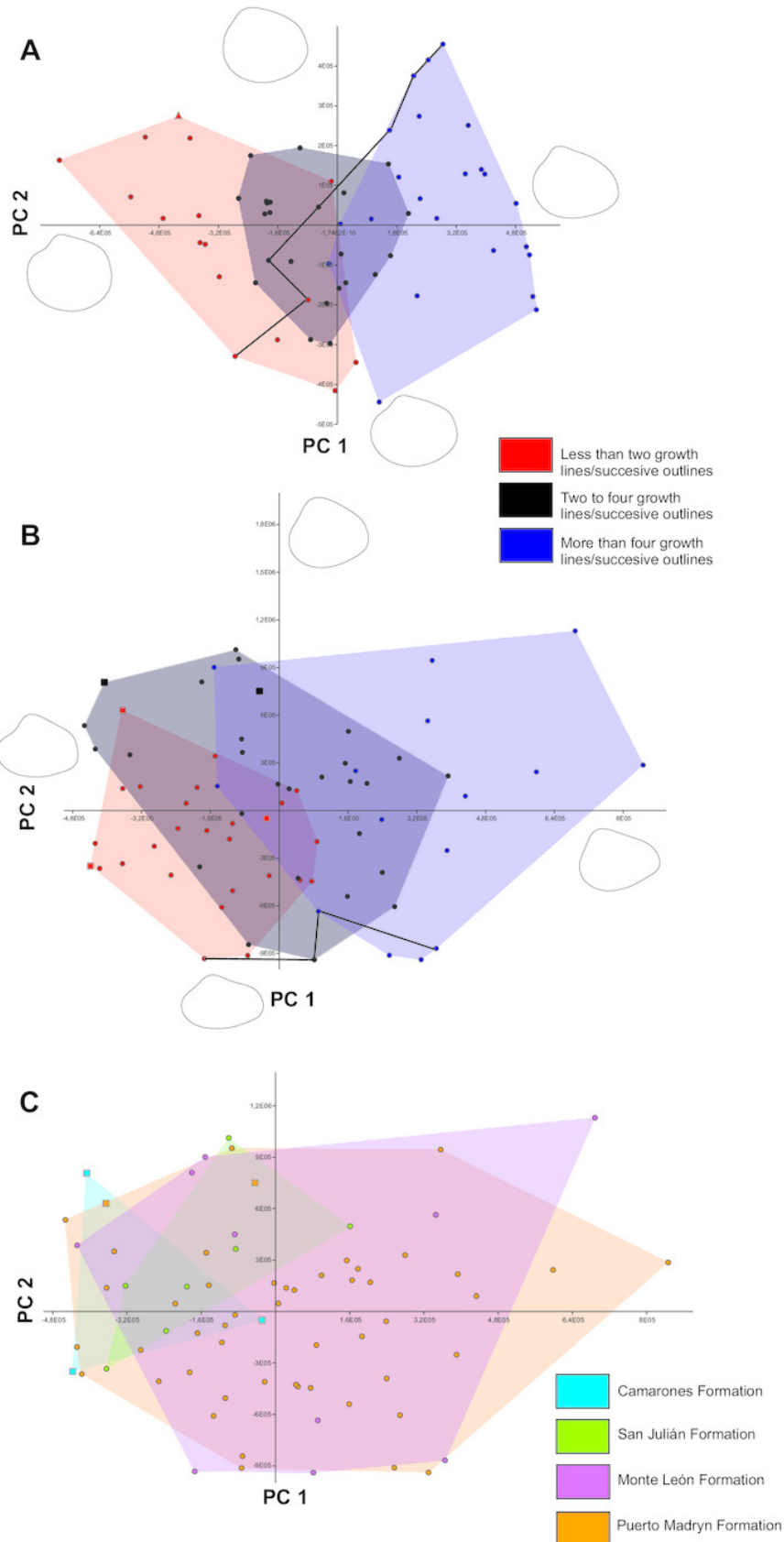
Figure 4

Results of Multivariate Regression Analyses, between area (size) and three first principal components (shapes).

A–C includes principal components obtained from *Claibornicardia paleopatagonica*, and D–F those obtained from *Crassatella kokeni*. Red line indicates trend line. Photo credit: the authors.
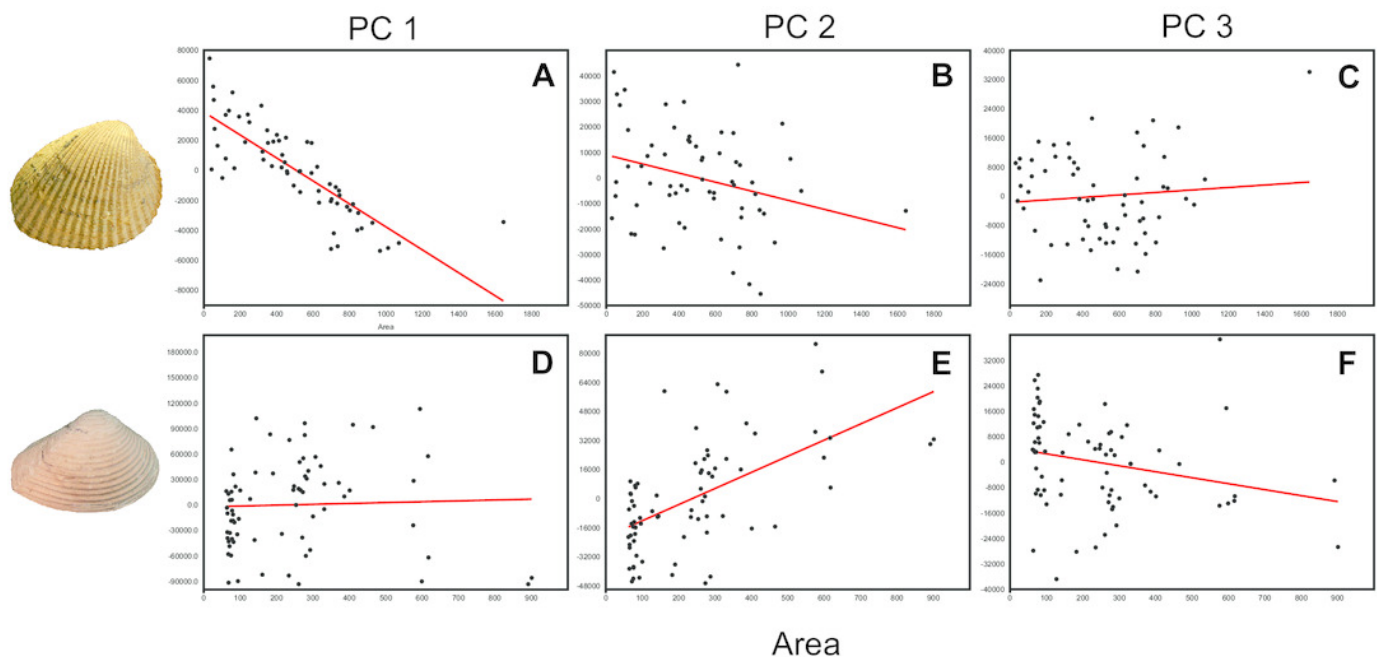
Figure 5

Overlapping of extreme outline configurations.

A. *Claibornicardia paleopatagonica*. B. *Crassatella kokeni*. Red outline = juvenile specimens.

Blue outline = adult specimens. Arrows indicate positive or negative allometry.