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On growth and form of a heteromorphic terrestrial snail: *Plectostoma concinnum* (Fulton, 1901) (Mollusca: Gastropoda: Diplommatinidae)

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The molluscan shell can be viewed as a petrified representation of the organism's ontogeny and thus can be used as a record of changes in form during growth. However, little empirical data is available on the actual growth and form of shells, as these are hard to quantify and examine simultaneously. To address these issues, we studied the growth and form of a heteromorphic and heavily ornamented land snail – *Plectostoma concinnum*. The growth data were collected in a natural growth experiment and the actual form changes of the aperture during shell ontogeny were quantified. We used an ontogeny axis that allows data of growth and form to be analysed simultaneously. Then, we examined the association between the growth and the form during three different whorl growing phases, namely, the regular coiled spire phase, the transitional constriction phase, and the distortedly-coiled tuba phase. In addition, we also explored the association between growth rate and the switching between whorl growing mode and rib growing mode. As a result, we show how the changes in the aperture ontogeny profiles in terms of aperture shape, size and growth trajectory, and the changes in growth rates, are associated with the different shell forms at different parts of the shell ontogeny. These associations suggest plausible constraints that underlie the three different shell ontogeny phases and the two different growth modes. We found that the mechanism behind the heteromorphy is the rotational changes of the animal's body and mantle edge with respect to the previously secreted shell. Overall, we propose that future study should focus on the role of the mantle and the columellar muscular system in the determination of shell form.

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25

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27

28

29 **Author Contributions**

30 LTS, ACMK, MS, and SU conceived and designed the experiments. LTS, ACMK collected data.

31 LTS, ACMK, SU analysed the data. LTS, ACMK, MS, and SU contributed

32 reagents/materials/analysis tools. LTS, SU wrote the paper. MS, ACMK commented on earlier
33 versions of the manuscript.

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49 **Introduction**

50 The physical form of organisms is central to different fields of biology, such as taxonomy,
51 evolutionary biology, ecology and functional biology. Two major themes are the way the
52 organism's form changes as it grows and the way the organism's form changes as it evolves. The
53 formal investigation of growth and form was established by Thompson (1917) in his monumental
54 *On Growth and Form*. In his book, Thompson studied the way organisms achieve their body form
55 during growth, from the viewpoint of the mathematical and physical aspects of the ontogenetic
56 processes. An extensively discussed example of these body forms are molluscan shells.

57
58 The molluscan shell, with the exception of those of bivalves, is a single structure that
59 accommodates the animal's soft body. The shell is secreted by the mantle edge, a soft elastic sheet
60 of connective tissue covered by an epithelium. Accretionary growth occurs when the mantle lying
61 inside the shell slightly extends beyond the current aperture and adds a shell increment to the
62 margin. Thus, a shell is essentially a petrified ontogeny of the aperture (i.e. the mantle edge). A
63 large amount of preserved ontogenetic information that can be used for Evo-Devo studies is
64 available from both fossilized and extant shell-bearing species (Urduy et al., 2013). In addition, the
65 molluscan shell's geometrically simple structure, resulting from a straightforward accretionary
66 growth mode makes it more popular than the body forms of other taxa in the study of theoretical
67 morphospace (Dera et al., 2008). However, it remains challenging to empirically study the actual
68 growth and form of a shell because of differences in the approaches of growth-orientated versus
69 form-orientated studies.

70
71 There have been few changes in the study of shell growth rate since Wilbur & Owen (1964). The
72 most commonly used method deals with the quantification of a shell's linear dimensions such as
73 shell length, shell width or number of whorls increment, which are then plotted against time (e.g.
74 Kobayashi & Hadfield, 1996; Sulikowska-Drozd, 2011). Although these measurements are good
75 estimators of the overall growth of the animal's soft body (measured in weight; Oosterhoff, 1977;
76 Chow, 1987; Elkarmi & Ismail, 2007; Silva, Molozzi & Callisto, 2010), they can hardly be linked
77 with the accretionary growth process and spiral geometry of the shell. In addition, shell growth may
78 be episodic because of different seasons, diurnal rhythms, or periods of activity and inactivity
79 (Linsley & Javidpour 1980). Thus, it is not easy to determine the temporal axis for shell ontogeny
80 from a shell alone.

81

82 Similarly, studies of the changes in shell form throughout ontogeny tend to be based on the same
83 morphometrics as in growth studies. These morphometrics are measured from the overall shell and
84 are plotted against whorl or rib count, or rotation angle along the shell columella (Kohn & Riggs,
85 1975; Johnston, Tabachnick & Bookstein, 1991; Checa, 1991). However, these measurements do
86 not provide an accurate record of shell form changes during ontogeny because the overall shell form
87 is an accumulation of previous growth. Moreover, whorl count depends on a single imaginary
88 coiling axis, which is missing in irregularly shaped (heteromorphic) shells.

89

90 As a consequence, seldom are growth and form of a shell analysed simultaneously because the
91 reference axes are usually not the same. For instance, a time axis may be used for shell growth, and
92 a whorl count axis for shell form. Furthermore, these shell morphometrics do not closely approach
93 the actual accretionary growth of the aperture in terms of form changes and growth trajectory
94 changes (e.g. Stone 1996; Stone 1997).

95

96 Apart from the limitations in methodology, shell growth studies have initially been biased towards
97 aquatic gastropods, and have mostly been conducted in the laboratory. For example, the chapter on
98 molluscan growth in Wilbur and Owen (1964) mentions only a single shelled terrestrial gastropod
99 species was. Although the form and structure of aquatic and terrestrial gastropod shells are very
100 similar, there are fundamental differences in the physiological and physical aspects of shell growth
101 between them (Wagge, 1951; Kado, 1960; Fournié & Chétail, 1984). In recent decades, more
102 studies on terrestrial gastropods have been conducted (e.g. Berry, 1962; Umiński, 1975; Oosterhoff,
103 1977; Baur, 1984; Ahmed & Raut, 1991; Johnson & Black, 1991; Kobayashi & Hadfield, 1996;
104 Kramarenko & Popov, 1999; de Almeida & de Almeida, 2001a; de Almeida & de Almeida, 2001b;
105 D'Avila & de Almeida, 2005; Bloch & Willig, 2009; Silva et al., 2009; Sulikowska-Drozd, 2011;
106 Kuźnik-Kowalska et al., 2013; Silva et al., 2013). It is worth mentioning that most of these growth
107 experiments used traditional morphometric methods and were conducted in the laboratory (but see
108 Oosterhoff, 1977; Johnson & Black, 1991). Because discrepancies in growth patterns exist between
109 field and laboratory experiments (Chow, 1987), further growth studies are needed from the natural
110 habitat.

111

112 All the species investigated in the above-mentioned studies have shells that grow according to a
113 regular coiling regime and with only simple calcareous sculptures on the shell surface, if any (but
114 see Berry, 1962). For shells with irregular coiling, that is, those that pass through several

115 dissociated growth stages, very little information is available as to how the growth and form
116 changes during those different shell ontogeny phases. To alleviate all these limitations, we
117 investigate the growth and form of a heteromorphic and heavily ornamented tropical land snail
118 species, *Plectostoma concinnum*, in its natural habitat.

119

120 We examined two aspects of shell growth and form: 1) the growth and form at three different whorl
121 growing phases of the *Plectostoma concinnum* shell; 2) the switching between whorl growing mode
122 and rib growing mode. First, we obtained a unified accretionary growth reference axis (hereafter
123 termed “ontogeny axis”), namely the total arc length of the shell whorl (see “Definition of ontogeny
124 axis” in Materials and Methods for more details), so that both shell growth and form data can be
125 analysed together. Second, we obtained shell growth rate information that was measured as arc
126 length of ontogeny axis (i.e. whorl length) added per day for live snails of difference growth stages.
127 Third, we quantified both the aperture form (size and shape), and the aperture growth trajectory
128 (rotation, curvature and torsion) from a series of apertures (hereafter termed “aperture ontogeny
129 profile”) that could be identified from the shells, by using 3D technology. Fourth, we explored the
130 pattern of switching between whorl growing mode and rib growing mode that determined the
131 number of ribs on the shell (see “organisms” in Materials and Methods). Finally, we examined the
132 associations between the growth and the form of the *Plectostoma concinnum* shell in all three whorl
133 growing phases and both growing modes, from developmental-biological and a theoretical-
134 morphological points of view.

135

136 **Materials and Methods**

137 **Ethics Statement**

138 The permissions for the work in the study sites were given by the Wildlife Department of Sabah
139 (JHL.600-6/1 JLD.6, JHL.6000.6/1/2 JLD.8) and the Economic Planning Unit, Malaysia (UPE:
140 40/200/19/2524).

141

142 **Organisms**

143 The tropical terrestrial micromollusc subgenus *Plectostoma* consists of 69 species that are only
144 known from limestone hills of Southeast Asia (Vermeulen, 1994; Liew et al., 2014). It is one of the
145 most diverse subgenera in the Gastropoda in terms of shell form . In this study, we selected
146 *Plectostoma concinnum* (Fulton, 1901), an endemic species in northern Borneo. This species is

147 exclusively found in limestone habitat and thus presumably not limited by calcium availability. It
148 occurs in high population densities with several millions of individuals estimated to live on
149 limestone hills of less than 0.5 km² (Schilthuizen et al., 2003).

150

151 In this study, we followed the terminology of Vermeulen (1994) in the discussion of the shell form
152 of this species, and we used the term whorl growing mode and rib growing mode in the discussion
153 of two different growth modes. At least in the case of this particular species, we think these two
154 terms are more precise than generic terms such as spiral and radial growth (e.g. Spight & Lyons,
155 1974; Vermeij, 1980). For the whorl growing mode, three growth phases can be distinguished,
156 namely, spire, constriction and tuba.

157

158 As an adult, the species has about 5.5 – 6.5 shell whorls and is about 3 mm in height and 3.5 mm in
159 width. The protoconch is smooth (Fig. 1A). The first 5 or 6 whorls of the teleoconch are regularly
160 coiled (hereafter termed “spire”) while the last half whorl (hereafter termed “tuba”) is detached
161 from the spire (Fig. 1A). The transition from the spire to the tuba is marked by a narrowing of the
162 whorl (hereafter termed “constriction”), where calcareous lamellae are formed inside the aperture
163 (hereafter termed “constriction teeth”) (Figs. 1A, 3E and 3F). The three parts are formed during the
164 whorl growing mode. It has an operculum which rests behind the constriction teeth when the
165 animal’s soft parts withdraw into the shell (hereafter “the animal” refers to the foot, the columellar
166 muscle, and the mantle). Such an extreme morphological transition between spire and tuba is also
167 known in several other extant and fossil mollusk species (e.g. Okamoto, 1988; Savazzi, 1996;
168 Vermeulen, 1994; Clements et al., 2008; Frýda & Ferrová, 2011). The shell growth of this species is
169 definite and the whorl growing mode ends with a "differentiated" peristome.

170

171 The shell exhibits regularly spaced projected commarginal ribs. As there is no standardisation in the
172 rib morphology terminology, to avoid confusion, we use the term commarginal ribs (*sensu*
173 Seilacher, 1991) for the type of ribs of *Plectostoma concinnum* because it describes the ribs with
174 reference to ontogeny and form and thus is more accurate than other terminologies (such as “radial
175 ribs” or “growth halt” *sensu* Laxton, 1970). These commarginal ribs are the product of a rib
176 growing mode, which is entered when the animal’s mantle edge expands dramatically and forms an
177 aperture that is much larger than the previous aperture produced in whorl growing mode. After shell
178 deposition stops at this rib growing mode, the subsequent whorl growing mode continues from the

179 aperture that was produced in the previous whorl growing mode. The switching between these two
180 growing modes produces the projected commarginal ribs.

181

182 **Definition of ontogeny axis**

183 To analyse the growth rate in terms of ontogeny axis growth per day and the form changes in terms
184 of aperture ontogeny profile over time, one needs to extract a set of homologous points in an
185 ontogenetic series that reflect the accretionary spiral growth. These points have to be homologous in
186 a biological sense meaning that the different growth stages of the same individual as well as those
187 of several different individuals are comparable. These landmarks can correspond to the localisation
188 of a specific structure (geometrical homology), to the temporal repetition of the same structure
189 (serial homology) or to the occurrence of a developmental event such as the onset of metamorphosis
190 or senescence (developmental homology) (Johnston, Tabachnick & Bookstein, 1991).

191

192 In *P. concinnum*, the spiral line at the anterior point of the aperture (Figs. 1C, 1G and 2A) fulfils the
193 conditions for geometrical homology since such striations are produced by particular cells at the
194 mantle edge (Salas et al., 2012). It corresponds to the point of the aperture with maximum growth
195 rate and the curvature is maximal at this point (Figs. 1F, 1G and 2A). The successive protruded
196 radial ribs fulfil the conditions for serial homology, while the protoconch-teleoconch boundary and
197 the spire-tuba constriction define developmentally homologous events. Thus, we used an ontogeny
198 axis, starting from the protoconch-teleoconch boundary (Figs. 1F and G), and obtained by
199 concatenating the arc lengths measured from the points of maximum growth rate between
200 successive protruded radial ribs. Our ontogeny axis is similar to those used by Gould (1969),
201 Vermeij (1980), Savazzi (1985), Savazzi (1990), Checa (1991) and Johnston, Tabachnick &
202 Bookstein (1991). The ontogeny axis of each shell was obtained and the growth and from variables
203 derived below were then plotted and analysed along this ontogeny axis. Different positions along
204 the ontogeny axis represent different growth stages of a shell.

205

206 **Experimental design and sampling**

207 The growth experiments were carried out at two limestone outcrops in the vicinity of Kampung
208 (Village) Sukau, Lower Kinabatangan Valley in the state of Sabah, Malaysia, between 20th April
209 and 10th May, 2011. These two isolated limestone outcrops, Batu Kampung (5°32'11"N
210 118°12'47"E) and Batu Pangi (5°31'59"N 118°18'44"E), are located 10 km apart, and thus are under
211 the same climate. Thanks to the rainy season, the microclimates were constant throughout the three

212 weeks of the experiment (Supplemental Information File S1). Six rock surfaces (*ca.* 10 m² each,
213 hereafter referred to as “plots”) with high densities of *Plectostoma concinnum* and similar
214 ecological conditions were selected. The numbers of replicated plots, growth experiment durations
215 and specimens examined are shown in Table 1.

216

217 We used a capture-mark-recapture method (CMR) in the plots. In each one-hour session, we
218 collected between 100 and 200 juveniles of *Plectostoma* at different growth stages. Then, in a field
219 lab, using a dissecting microscope, we marked each shell with a nail polish mark located on either
220 the second most recently grown rib (if the snail was at rib growing mode) (Fig. 1D) or the most
221 recently grown rib (if the snail was at whorl growing mode) (Fig. 1E). We used this marking
222 scheme instead of one in which a mark was placed on the aperture edge, to prevent the nail polish to
223 come in direct contact with the animal mantle. Our nail polish marking technique fulfilled the
224 general requirements for CMR approach (*sensu* Henry & Jarne, 2007). The marks were clearly
225 visible, persisted for at least two months under field conditions and had no noticeable effect on the
226 mantle edge. All marked individuals were released at their exact point of capture within 24 hours
227 and were recaptured between 2 and 13 days later (see table 1). All recaptured individuals were
228 killed by drying and retained. A total of 97 shells were thus obtained from both study sites, of
229 which 15 had suffered aperture damage and were discarded. All specimens were deposited as
230 voucher samples in the BORNEENSIS collection, Universiti Malaysia Sabah – BOR).

231

232 The remaining 82 shells (65 juveniles and 17 fully grown at the time of recapture) were used for the
233 following analyses. For shell growth rate analysis (Part 1), we used the 65 juvenile shells (36 from
234 Batu Pangi; collection sample BOR 5653 and 29 from Batu Kampung; collection sample BOR
235 5654). For the aperture profile analysis (Part 2), we quantified (a) aperture shape and size for five
236 representative shells (out of the 65 juvenile shells) at different growth stages; and (b) growth
237 trajectory of a fully grown shell (out of the 17 adult shells). For the analysis of whorl and rib
238 growing mode (Part 3), we examined (a) the number of switches between the two growing modes in
239 the 17 fully grown shells that collected from the same location (collection sample BOR 5652); and
240 (b) the pattern of whorl spacings between two rib growing modes of the 35 shells (out of the 65
241 juvenile shells) that had grown beyond the constriction.

242

243 **Part 1 – Shell whorl arc length growth rate along the shell ontogeny.**

244 Each of the 65 juvenile shells was photographed (with a Leica DFC495 attached to a Leica M205C
245 microscope). Photographs were taken in apical view (Fig. 1F and Supplemental Information File
246 S2). For those specimens that grew up to the tuba stage, we aligned the tuba with a plane and we
247 took additional photographs (Supplemental Information File S2). The arc length at the point of
248 maximum growth rate was calculated using the program Leica Application Suite V3.7.0. Although
249 the arc length is measured from two-dimensional images (Fig. 1F), it is a good proxy for the three-
250 dimensional arc length (Fig. 1G and Supplemental Information File S3: $r = 0.82$, $n = 251$ (3 shells),
251 $p = 0.000$). We thus obtained 5,475 arc lengths measured between successive ribs and pooled these
252 data (Supplemental Information File S4). The arc length of the ontogeny axis for each of the 65
253 shells was calculated as the sum of all the arc lengths between successive ribs of each shell.

254
255 Based on the nail polish mark on the shell, we measured the arc length before and after the growth
256 experiment. Then, we calculated growth rate as the whorl arc length (i.e. ontogeny axis) added over
257 the duration of the experiment (i.e., mm day^{-1}). We tested for the correlation between the measured
258 growth rates and the position of the specimen on the ontogeny axis prior to the growth experiment.
259 The analyses were done separately on the two growth phases of *Plectostoma concinnum*, namely,
260 spire and tuba. Spearman correlation was used since the data were not normally distributed.

262 **Part 2 – Aperture ontogeny profile changes between spire growth phase and tuba growth** 263 **phase.**

264 In this part, we examined the animal's orientation and aperture form changes along the ontogeny
265 axis. First (Part 2a), we obtained aperture forms by quantifying the traced aperture on 3D shell
266 models. Second (Part 2b), we quantified aperture growth trajectory changes by examining the
267 animal orientation with respect to its shell and by quantifying the spiral geometry of the ontogeny
268 axis in terms of curvature and torsion estimators.

269
270 We used microcomputed X-ray tomography to obtain 3D models of the various growth stages of *P.*
271 *concinnum* ($n=6$). Five of these 3D models (immature shells) were used for aperture outline analysis
272 while one 3D model of an adult shell was used for animal rotation analysis (see below). The
273 microcomputed tomography used a high-resolution micro-CT scanner (SkyScan, model 1172,
274 Aartselaar, Belgium). The scan conditions were as follows: voltage – 100kV; pixel – 1336 rows X
275 2000 columns; camera binning – 2 X 2; image pixel size – $3.42\mu\text{m}$; rotation step – 0.4° ; and rotation
276 – 360° . Next, the volume reconstruction on the acquired images was performed with the

277 manufacturer's software NRecon ver. 1.6.6.0 (SkyScan). The images were aligned to the reference
278 scan and reconstruction was done with the following settings: beam hardening correction – 100%;
279 reconstruction angular range – 360°; image conversion (dynamic range) – ca. 0.12 and ca. 20.0; and
280 result file type – BMP. Finally, 3D models were created from the reconstruction images with the
281 manufacturer's software CT Analyser ver. 1.12.0.0 (SkyScan) with the following settings: binary
282 image index – 1 to 255; and saved as digital polygon mesh objects (*.ply format). The 3D models
283 were then simplified by quadric edge collapse decimation to *ca.* 30,000 faces, with a method
284 implemented in MeshLab v1.3.0 (Cignoni, Corsini & Ranzuglia, 2008). The subsequent analyses
285 for the digital 3D shell models were done in 3D modelling open source software – Blender ver. 2.63
286 (Blender Foundation, www.blender.org).

287
288 **Part 2 (a) Aperture form changes between spire growth phase and tuba growth phase.**

289 The acquisition of aperture outlines and their trajectories was done in Blender software with its
290 embedded object-oriented programming language Python. We wrote custom Python scripts to
291 extract the outline points' coordinates for shape analysis (Supplemental Information File S5). We
292 used the “grease Pencil” tool of Blender to trace the aperture and ontogeny axis outlines on the five
293 immature shell 3D models (Figs. 1G and H). Then, we converted these traced outlines into Bezier
294 curves, where the outlines were represented by a series of points with three-dimensional Cartesian
295 coordinates. We obtained outline data of five 3D shell models with a total of 33 apertures
296 (Supplemental Information File S6), which were then analysed together with their homologous
297 ontogeny axis.

298
299 We obtained the aperture outline perimeter by summing the distances between the successive points
300 of each aperture outline. Before that, we smoothed each of the Bezier curve outlines by a three-
301 dimensional Elliptic Fourier Analysis (hereafter termed “3D EFA”; Kuhl & Giardina, 1982;
302 Godefroy et al., 2012) to minimize the possible noise coming from the digitalization process. We
303 ran the 3D EFA with the following parameterization: number of harmonics = 5, starting point =
304 anterior point, and outline orientation = clockwise. We used five harmonics because they were
305 sufficient to reliably describe the aperture outlines (Supplemental information File S7). Next, we
306 reverted 3D EFA function so that each outline was reconstructed from the same set of five
307 harmonics and by using 100 sample points along the outline. Finally, we extracted the aperture
308 perimeters from the 100 points of each outline.

309

310 We obtained principal component analysis (PCA) scores from normalized coefficients of 3D EFA
311 for each of the 33 aperture outlines (hereafter termed “shape scores”). The coefficients of the 3D
312 EFA harmonics were normalized according to Godefroy et al. (2012) so that they were invariant to
313 size and rotation. After normalization, all of the 30 normalized Fourier coefficients for each of the
314 33 aperture outlines were analysed by PCA in R statistical package 2.15.1 (R Core Team, 2012). R
315 scripts are in Supplemental Information File S4.

316

317 The aperture perimeter and shape scores of each aperture were examined together along the
318 ontogeny axis. In addition, a linear regression was performed on the spire aperture perimeter
319 changes along the ontogeny axis in R statistical package 2.15.1 (R Core Team, 2012).

320

321 **Part 2 (b) Aperture growth trajectory changes between spire growth phase and tuba growth phase.**

322 In the plots at Batu Kampung, we collected additional specimens at different growth stages to
323 examine the growth trajectory of the aperture and the orientation of the living animal with respect to
324 its shell. The living individuals were carefully picked up with a pair of soft forceps while active,
325 were immediately frozen with Freeze spray (KÄLTE, Art. Nr. 20.844.6.09.12.01) and preserved in
326 70% ethanol. The body rotation of the animals of different shell growth stages was examined with
327 scanning electron microscopy (SEM).

328

329 We found that the highest projected point of the commarginal rib corresponds to the anteroposterior
330 axis of the animal. In addition, the changes in the orientation of successive segments correspond to
331 the changes in orientation of the animal as evidenced by the homologous anterior landmark of the
332 aperture (Figs. 3A, 3B and 3C). Hence, the growth trajectory changes in terms of animal rotation
333 can be inferred directly from the shell. We therefore quantified the orientation changes of the
334 animal along the shell ontogeny from a 3D model of an adult shell with Blender. We restrict this
335 analysis to the ontogeny corresponding to the 1.5 whorls before the constriction up to maturity
336 where the most drastic changes in shell coiling direction occur (Supplemental Information File S8).

337

338 We obtained the ontogeny axis for the shell and then separated the digital 3D shell into segments
339 corresponding to successive commarginal ribs (Figs. 2A and 2B, Supplemental Information File S8).
340 We obtained changes in the rotation between two consecutive segments (hereafter termed: “NEW”
341 and “OLD” segments). The changes in animal orientations were inferred from these two segments
342 with respect to the anatomical directions of the animal. First, we aligned the anteroposterior axis of

343 the NEW shell segment with the x-axis of the global 3D Cartesian system (Fig. 2B). Second, we
344 aligned the anterior point of the OLD segment to the anterior point of the NEW segment (Fig. 2C).
345 Third, we rotated the OLD segment along the x, y and z axes until it was aligned with the NEW
346 segment (Figs. 2D, 2E and 2F). Finally, the rotation changes (in angles) were plotted along the
347 ontogeny axis.

348

349 The rotations around the three animal anatomical directions were interpreted as following. First,
350 rotation around x-axis corresponds to the aperture “inclination” with respect to the previous
351 aperture (Fig. 2D). It corresponds to the direction where the animal tilts to right or left. Second, the
352 rotation around y-axis corresponds to the rotation of the dorsoventral axis (i.e. shell growth
353 direction). Third, the rotation around z-axis corresponds to the rotation of the anteroposterior axis
354 (rotation of the aperture plane around its centroid). When the animal is viewed in dorsal view, we
355 describe this rotation as either clockwise or anticlockwise. From our observation (see above), it
356 seems the most important changes in animal orientation at different growth phases are the rotations
357 around the x-axis and the z-axis (Fig. 2B, 3A, 3B and 3C).

358

359 We are aware that the discrete rotation analysis between shell segments may not realistically reflect
360 the continuous changes of the growth trajectory. Thus, we estimated curvature and torsion, two
361 parameters that are convenient to describe a 3D spiral (Okamoto, 1988; Harary and Tal, 2011).
362 These were estimated from the same adult shell as above (Supplemental Information File S9). The
363 curvature (κ) and torsion (τ) were estimated from each sample point along the ontogeny
364 axis by a weighted least-squares fitting and local arc length approximation (Lewiner et al., 2005).
365 The calculation was done by custom written Python scripts, which were run in the Blender
366 environment (Supplemental Information File S5). The estimation was done with 100 points on the
367 left and right sides for each sample point. The value of curvature is a positive value; the ontogeny
368 axis is a straight line (i.e. shell is an orthocone) when $\kappa = 0$; and the larger the curvature, the
369 smaller the radius of curvature ($1/\kappa$). The torsion τ estimates the deviation of the curve from
370 a plane - the zero value meaning that the shell is planispiral. In addition, a negative/positive torsion
371 value corresponds to a left-handed/right-handed coiling respectively.

372

373 **Part 3 – Switching between whorl growing mode and rib growing mode; frequency and trend.**

374 We examined the variation of the number of ribs, which indicates the number of switches between
375 the two growing modes. Then we compared the switching patterns among shells varying in rib
376 number.

377

378 **Part 3 (a) Variation of total number of ribs between shells.**

379 The numbers of ribs were counted on the spire and tuba parts of each of the 17 adult shells which
380 had completed their shell growth under similar ecological conditions in our field experiment.

381 Because the number of ribs on the spire correlated with the number of ribs on the tuba (see Results),
382 in a subsequent analysis, we counted the number of ribs and arc length of the ontogeny axis on the
383 fully grown spire of 35 juvenile shells. We tested if there is a correlation between the total number
384 of ribs and the total ontogeny axis length. As all data were normally distributed, we used Pearson
385 correlation in R 2.15.1 (R Core Team, 2012); R scripts may be found in Supplemental Information
386 File S4.

387

388 **Part 3 (b) Switching trends between the whorl growing mode and the rib growing mode.**

389 We plotted 3,263 arc lengths (both spire and tuba) between successive ribs of the 35 shells along the
390 same ontogeny axis.

391

392 **Results**

393 **Part 1 – Shell whorl arc length growth rate along the shell ontogeny.**

394 The growth rates are measured in mm/day along the arc length travelled by the point of maximal
395 growth rate during ontogeny (n=65, Supporting Information File S4). The absolute shell whorl arc
396 lengths added to the shells during the growth experiments are found in Supporting Information S10.
397 Figure 4 shows the growth rate variations along the ontogeny axis for the spire and tuba growth
398 phases of 65 shells. For the growth patterns of the spire, the growth rate is positively correlated with
399 the ontogeny axis ($r = 0.45$, $n=30$, $p=0.01$). On the other hand, after the constriction, the growth
400 rate is negatively correlated the ontogeny axis ($r = -0.38$, $n=35$, $p=0.02$). These data demonstrate that
401 *O. concinnum* follows a S-shaped growth curve (with regard to time), with the maximum growth
402 rate occurring during the transitional phase (inflexion point).

403

404 **Part 2 – Aperture ontogeny profile changes between spire growth phase and tuba growth
405 phase.**

406 **Part 2 (a) Aperture form changes between spire growth phase and tuba growth phase.**

407 Figure 5A shows the changes of aperture perimeter from around 5 mm until the end of the ontogeny
408 axis. The aperture perimeter changes along the ontogeny of the five different specimens share a
409 common trend. The perimeter of the aperture increases linearly, in a constant rate ($\beta = 0.166$),
410 between 5 mm and *ca.* 11 mm at the ontogeny axis (linear regression model: (aperture perimeter) =
411 0.166 (position of ontogeny axis) + 0.457 , $R^2 = 0.97$, $F = 591.4$, $df = 1, 20$, $p=0.000$). Then, the
412 aperture size decreases during the constriction part of the ontogeny before the size increases again
413 during the tuba part of the ontogeny.

414

415 For the aperture shape analysis, the PCA reveals that the first three components accounted for
416 53.8%, 14.2%, and 9.7% of the total shape variation of all five sets of harmonics (Supplemental
417 information File S11). The correlation analysis reveals that the first component is significantly
418 correlated with 15 out of the 30 normalized Fourier coefficients, especially the Fourier coefficients
419 of the first harmonics (Supplemental information File S11). Thus, we retained the PCA first
420 component's scores as shape descriptor of aperture (due to the nature of the EFA, the first harmonic
421 contains a large part of the variation and most of the shape information ; Kuhl and Giardina, 1982).

422

423 Figure 5B shows the changes of aperture shape along the ontogeny axis. During the spire part of the
424 ontogeny, the aperture has a diamond shape with a round corner. Its perimeter is slightly convex at
425 the right anterior, left anterior and posterior sides, but slightly concave at the right posterior side.
426 Approaching the constriction part of the ontogeny, the diamond-shaped aperture becomes elongated
427 along the anteroposterior axis with slightly rounded corners. At the tuba part of the ontogeny, the
428 aperture has an ovate shape that is symmetrical along the anteroposterior axis, acute at the anterior
429 and wide at the posterior.

430

431 **Part 2 (b) – Aperture growth trajectory changes between spire growth phase and tuba growth phase.**

432 Figure 6 shows the rotational changes of each new segment with respect to the previous segment.
433 Rotation around the x-axis at the constriction and part of the last whorl shows that the changes in
434 the animal's orientation are in the opposite direction compared to most of the spire and tuba parts of
435 the ontogeny. There is no change of rotation direction around the y-axis as the shell follows a spiral
436 growth. The magnitude of rotation in the y-axis is related to the whorl length between two ribs
437 (*confer* Fig. 8). Rotations around the z-axis reveal that the rotational changes between two ribs for
438 the spire and the tuba part of the ontogeny are in opposite direction.

439

440 Figure 7 shows how the curvature and torsion values change along the ontogeny axis. The curvature
441 value decreases rather constantly from *ca.* 3 to *ca.* 1 with small fluctuations along the spire part of
442 the ontogeny. However, for the constriction to the tuba part of the ontogeny, the curvature value
443 fluctuates between 0.9 and 1.3. Torsion values along the spire decrease gradually from 0.9 to 0.1.
444 From the constriction onwards, however, torsion fluctuates wildly, becoming strongly negative
445 before returning to positive values.

446

447 **Part 3 –**

448 **Switching between whorl growing mode and rib growing mode; frequency and trend.**

449 **Part 3 (a) Variation of total number of ribs between shells.**

450 The arc lengths measured between two consecutive spines in 35 individuals of *Plectostoma*
451 *concinnum* were pooled together (3263 arc lengths in total, raw data in Supporting Information).
452 There is no significant correlation between the number of spines and the total arc length (Pearson
453 correlation, $r = -0.22$, $n = 35$, $p = 0.2$), highlighting that the number of spines varies extensively among
454 individuals exhibiting a similar total arc length. However, there is a significant correlation between
455 the number of spines before the constriction and the number of spines after the constriction
456 (Pearson correlation, $r = 0.55$, $n = 17$, $p = 0.02$). This means that there is still a consistent ontogenetic
457 pattern in this set of pooled data: the individual ontogenies do not vary to the extent that the spiral
458 and tuba phase are mixed together in the pooled data.

459

460

461 **Part 3 (b) Switching trends between the whorl growing mode and the rib growing mode.**

462 Figure 8 shows that the spacing between successive ribs increases constantly from right after the
463 protoconch (i.e. at position 0) to *ca.* 8 millimetres along the ontogeny axis. The spacing between
464 ribs then decreases until *ca.* 10 millimetres on the ontogeny axis (Figs. 1F and 8). Then, this spacing
465 increases from *ca.* 10 to *ca.* 13 millimetres on the ontogeny axis, when the shell is about to form the
466 constriction part. The spacing then decreases during the transitional constriction phase (from *ca.* 13
467 to *ca.* 14 mm on the ontogeny axis) and remains approximately constant during the tuba phase
468 (from *ca.* 14 mm to the end of the ontogeny axis). Shells with different numbers of ribs show the
469 same trend but of a different magnitude – the average rib spacing of densely ribbed shells being
470 shorter than that of sparsely ribbed shells at the same growth stage.

471

472 **Discussion**

473 **Growth and form of whorl growing mode in terms of aperture form and growth** 474 **rate.**

475 The overall shell ontogeny of *Plectostoma concinnum* does not comply at all with the ideal shell
476 growth model in which the growth parameters remain constant throughout the ontogeny. Although
477 such ideal shell growth has been an essential part in the development of gastropod theoretical
478 morphology (Moseley, 1838; Thompson, 1917; Raup, 1966), the shells of most gastropods do
479 deviate to some extent (Raup, 1966; Gould, 1968; Vermeij, 1980; Urdy et al., 2010). The shell
480 ontogeny of *P. concinnum* begins with a regular growth phase that approximates a dextral isometric
481 logarithmic spiral (spire phase, between 0 and ca. 13 mm on the ontogeny axis), followed by a more
482 variable transitional growth phase (constriction phase, ca. 13-ca. 14 mm of ontogeny axis), which
483 gives way to an open-coiling growth phase (tuba phase, from ca. 14 mm to the end of the ontogeny
484 axis). Thus, it provides a unique opportunity for us to investigate how shell form changes in relation
485 to the growth rate.

486

487 **Spire** – The spire is dextral, has a regular growth trajectory and form, and thus its curvature and
488 torsion estimators obey the 3D logarithmic spiral geometry with minor deviation (Fig. 7). During
489 the growth of the spire, the aperture ontogeny profiles either remain the same or change in a
490 constant manner. The aperture remains of almost the same shape (Fig. 5B), the aperture perimeter
491 increases linearly and constantly, the animal (i.e. the mantle) always rotates clockwise (Fig. 6C)
492 from the animal's dorsal view (e.g. Fig. 2B and 2F), and the aperture inclination declines (Fig. 6A).
493 These variables alter when the spire phase changes over to the constriction phase.

494

495 **Constriction** – The constriction part of the ontogeny breaks the simple logarithmic spiral growth
496 rule. Every aspect of the aperture ontogeny profiles changes: the aperture shape differs from the
497 spire aperture (Fig. 5B); the aperture perimeter drops, the animal (and its mantle edge) begin to
498 rotate anticlockwise (Fig. 6C) from animal's dorsal view (e.g. Fig. 2B and 2F), and the aperture
499 inclination increases (Fig. 6A).

500

501 Our data show that changes in the animal's orientation are responsible for the break in the preceding
502 growth rule (Figs. 6A, C and 7). It has been shown theoretically that the rotation of the animal
503 within the shell – which is equivalent to changing the pattern of growth rates around the aperture –

504 is the cause behind the drastic changes in the coiling pattern that are observed in heteromorph
505 ammonites (Okamoto, 1988) and cemented gastropods exhibiting distorted coiling (Vermeij, 1993;
506 Rice, 1998). Our data support this hypothesis, and suggest that the deviation is caused by the
507 continuous rotation of the mantle edge in opposite direction to that of the spire part, during the
508 accretionary growth process at the aperture.

509
510 Several studies have pointed out a general correspondence between the life position and the shell
511 morphology in recent gastropods (Linsley, 1977; Linsley et al., 1978; Morita, 1991a; Morita, 1991b;
512 Morita, 1993; Morita, 2003; Checa, Jiménez- Jiménez, & Rivas, 1998; Vermeij, 2002), indicating
513 that the life position of gastropods is almost equal to the gravitationally stable position of their
514 empty shells. These studies argued that the direction and degree of coiling, as well as aperture
515 shape are at least partly determined by the columellar muscle, the animal's living position (at the
516 time of shell secretion), and the previous whorl ('road-holding', Hutchinson, 1989; Checa, Jiménez-
517 Jiménez, & Rivas, 1998). Although some details are available regarding the structure and retraction
518 function of the columellar muscle (Brown & Trueman, 1982; Kier, 1988; Frescura & Hodson, 1992;
519 Thompson, Lowe & Kier, 1998; Suvorov, 2002), how the columellar muscle may act to affect shell
520 morphogenesis is unknown.

521 In addition to the aperture shape and growth trajectory changes at the constriction phase, the
522 aperture size also decreases along the shell ontogeny before increasing again when approaching the
523 tuba phase. This process produces a narrower shell whorl, and is unlikely to be directly involved in
524 the aperture rotation. Yet the constricted whorl might play a key role in the ontogeny of the tuba
525 part of shell. At the beginning of the tuba phase, several constriction teeth are formed inside the
526 constricted whorl. These constriction teeth are associated with the columellar muscle and thus could
527 play a role in controlling the animal's orientation with respect to the shell (Figs. 1B, 3D, 3E and 3F).
528 For example, the columellar muscle could coil around the shell columella during the spire phase
529 whereas the columellar muscle has to extend far from the shell columella during tuba phase. Hence,
530 the constriction teeth could serve as a holdfast for the columellar muscle and prevent it from
531 shifting position while under tension (e.g. Signor & Kat, 1984; Price, 2003). This kind of internal
532 structure is also common in other heteromorphic gastropods (Savazzi, 1996). So, we support
533 Suvorov's view that the constriction teeth could be important for an effective management of shell
534 orientation (Suvorov, 1993; Suvorov, 1999a; Suvorov, 1999b; Suvorov, 2002). The constriction
535 phase might therefore pave the way for the later tuba phase in forming a detached whorl.

536

537 **Tuba** – Two significant aspects of the tuba part of the shell ontogeny are its anticlockwise rotation
538 on the growth trajectory (Fig. 6C) and its detachment from the spire of the shell. At this phase, the
539 aperture shape changes rapidly (Fig. 5B) and the aperture perimeter increases again with a trend
540 similar to the spire (Fig. 5A). Here, we can show that the transition from a tightly-coiled and almost
541 isometric dextral shell to an open-coiled tube only requires a relatively small and continuous change
542 in the main growth direction. This is achieved by the continuous rotation of the animal within the
543 shell, in opposite direction as compared to the spire phase, possibly controlled by the columellar
544 muscle as discussed above.

545

546 The continuous rotation of the aperture causes the later part of the tuba to detach from the spire. In
547 the spire part, only a thin layer of shell is deposited at the right lateral part of the aperture along the
548 surface of the previous whorl, causing fusion with the previous whorl. In contrast, during the tuba
549 part of the ontogeny where the whorls are detached, thicker shell layers are deposited all around the
550 aperture.

551

552 The shell whorl overlapping at the spire part is a more economical growth strategy than detached
553 whorls (Heath, 1985; Stone, 1999; Stone, 2004). We suggest that the differences in growth rate
554 between spire and tuba might result from the detached growth of the tuba. As the aperture size of
555 the tuba and the later part of the spire is similar, and calcium is not a limiting resource for this
556 limestone-dwelling species, the formation of the detached whorl may slow down because more time
557 is required for its formation compared to the spire. However, as growth is determinate in this
558 species, we expect growth to slow anyway at the onset of maturity with the development of the
559 reproductive organs (e.g. Terhivuo, 1978; Lazaridou-Dimitriadou, 1995).

560

561 Finally, the change from tight to open coiling in *Plectostoma concinnum* could provide an
562 opportunity to revisit theoretical models on whorl overlap – the road-holding model (Hutchinson,
563 1989) and its mechanical effect on aperture shape (Morita, 1991a, b, 1993, 2003). In his
564 morphogenetic model, Morita (1991a) defines the mantle as a whole as a hydroskeleton which is
565 usually in a state of expansion resulting from internal haemolymph pressure. Consequently, the
566 mantle is simulated as a double elastic membrane connected by internal springs. Its physical state is
567 supposed to be in balance between its internal stress and the forces acting on it, such as the pressure
568 of the haemolymph, the pressure induced by the foot/columellar muscle and the boundary of the

569 shell. The deformation of the mantle is then deduced from its stress field using a finite element
570 analysis. Morita investigates the effect of a zone where the mantle cannot deform - presumably
571 because of the foot/muscle/soft parts pressing on the mantle edge. He shows that initially circular
572 walls change into elliptically elongated ones with pressure rising. In other words, the existence of a
573 fixed zone - whether that zone is large or small in size - breaks initial symmetry in the specific
574 manner: the direction of elongation is perpendicular to the fixed zone. On the contrary, all tube
575 shapes tend to converge to circular outlines when no fixed zone exists. Morita (1991b, 1993, 2003)
576 argues that this fixed zone represents whorl overlap and may explain why most open coiling or
577 minimally overlapping gastropods have circular apertures. On the other hand, outer apertural lips
578 accompanied by a distinct whorl overlap zone are either extended perpendicularly to the overlap
579 zone or are abapically inflated.

580

581 In *Plectostoma concinnum*, there are extensive shape differences between the spire and the tuba
582 apertures- notably the part of the aperture which was previously in contact with the previous whorl
583 exhibits smoothed corners in the open-coiling phase and is more symmetrical than before (Fig. 5B).
584 However, the aperture shape of the tuba is not tending towards a circle but has an ovate shape that is
585 elongated along the anteroposterior axis where the ribs are forming. Morita did not address the case
586 of ornamented specimens, so our data is not well suited to test the predictions of this model in its
587 current state.

588

589 **Number of times and trend in the switching between whorl growing mode and** 590 **rib growing mode.**

591 The total number of ribs (i.e. number of switches between whorl growing and rib growing mode)
592 can vary substantially between individuals even if they are of similar shell size (i.e. similar
593 ontogeny axis length). The number of switches between these two growing modes also does not
594 affect the final ontogeny axis length. However, we could not determine whether a shell with dense
595 ribs would need more time to become fully grown.

596

597 Despite differences in rib number, the trends in rib spacing patterns are similar. At the spire part, the
598 spacing between ribs initially increases and then decreases towards where the tuba starts to detach
599 from the spire (*ca.* 9 – 10 mm along the ontogeny axis, Fig. 1G). After that, the rib spacing

600 increases again and reaches its maximum at the constriction (*ca.* 13 – 14 mm along the ontogeny
601 axis).

602

603 A previous growth study on *Plectostoma retrovertens* showed that each rib represents a day of
604 growth (Berry, 1962). However, *Plectostoma concinnum* ribs are heavier than those of *Plectostoma*
605 *retrovertens*, and its commarginal ribs do not represent daily growth stages. Furthermore, our
606 specimens were in a cohort and collected over the same period (i.e. under similar weather
607 condition), thus the rib spacing pattern is unlikely to be caused by environmental factors.

608

609 When the trend between rib spacing (Fig. 8), aperture perimeters (Fig. 5A) and growth rates (Fig. 4)
610 are examined closely, interesting relationships among these shell parameters emerge. First, the
611 spacing between ribs is the largest, the aperture perimeter is the smallest, and the growth rate is the
612 highest at the constriction phase. Second, the rib spacing increases together with the increase of the
613 growth rate along the spire ontogeny, while rib spacing decreases with decreasing growth rates in
614 the tuba part. This suggests there might be a possible positive association between growth rate and
615 rib spacing, and hence rib density. Further studies are needed to investigate whether this association
616 is incidental or not. With limited data, we cannot decipher the ontogenetic mechanisms that produce
617 the ribs. Although several theoretical mechanisms have been proposed (e.g. Hammer, 2000;
618 Moulton, Goriely & Chirat, 2012; Chirat, Moulton & Goriely, 2013), the actual biological processes
619 responsible for the growth of commarginal ribs remain poorly understood. Hence, we suggest that
620 future studies examine the growth rates (shell deposition rate) in relation to ornamental patterns to
621 improve our understanding of the possible relationship between rib frequency and growth rates.

622

623 **Conclusion**

624 In this study, we have developed an approach which can be used to extract aperture morphological
625 changes along the ontogeny from a shell and we have found a way to analyse the growth and form
626 parameters simultaneously. By analysing growth and form in this heteromorphic shell, we have
627 shown the associations between aperture ontogeny profiles and growth rate in the determination of
628 final shell form. Our aperture ontogeny profile analysis of the shell and observations on living
629 specimens provide for the first time direct evidence for the mechanism behind the heteromorphy:
630 the rotational changes of animal and mantle edge during the shell ontogeny. Overall, we have also
631 highlighted that there is a need to improve our understanding of the developmental biology of

632 snails, especially with reference to the mantle and columellar muscular systems and their potential
633 relationship to shell morphogenesis.

634

635 Although our study provides little direct information on the developmental and genetic factors that
636 govern the shell growth and form, it already highlights some plausible constraints – related to the
637 columellar muscle and living position - underlying the three shell ontogeny phases and two different
638 growth modes of this species. As these three phases are known to occur in all of the species in this
639 genus, including those with more regularly coiled shells, our results may be generalised further in
640 the future. Our study sets the stage for future studies using mollusc species in general to address
641 issues concerning the ecology, the evolution and the development of mollusc using a mixture of
642 insights coming from aperture ontogeny profiles obtained by a 3D morphometric approach.

643

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655

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969 **Supplemental Information**

970 (<http://dx.doi.org/10.6084/m9.figshare.960018>)

971 Supplemental Information File S1. Microclimatic variation for Pangi plots.

972 Supplemental Information File S2. Raw image of 65 measured shells for Part 1 and Part 3(b).

973 Supplemental Information File S3. Correlation between 2D and 3D arc length measurement of three
974 specimens.

975 Supplemental Information File S4. Raw data for analysis in Parts 1, 2 and 3, and the R scripts.

976 Supplemental Information File S5. Python scripts for 3D aperture morphometrics and growth
977 trajectory analysis.

978 Supplemental Information File S6. Digitalised aperture outlines (n=33) of 5 specimens used in Part
979 2(a).

980 Supplemental information File S7. Comparison between raw digitised and Elliptical Fourier
981 reconstructed aperture outlines.

982 Supplemental Information File S8. Data of rotation analysis in Blender format for Part 2(b).

983 Supplemental information File S9. Digitalised 3D ontogeny axis of a shell for torsion and curvature
984 analysis in Blender.

985 Supplemental Information File S10. Absolute shell whorl arc length added during the growth
986 experiments.

987 Supplemental information File S11. PCA results of Elliptical Fourier coefficient for aperture shape
988 analysis in Part 2(a).

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1008 **Table**

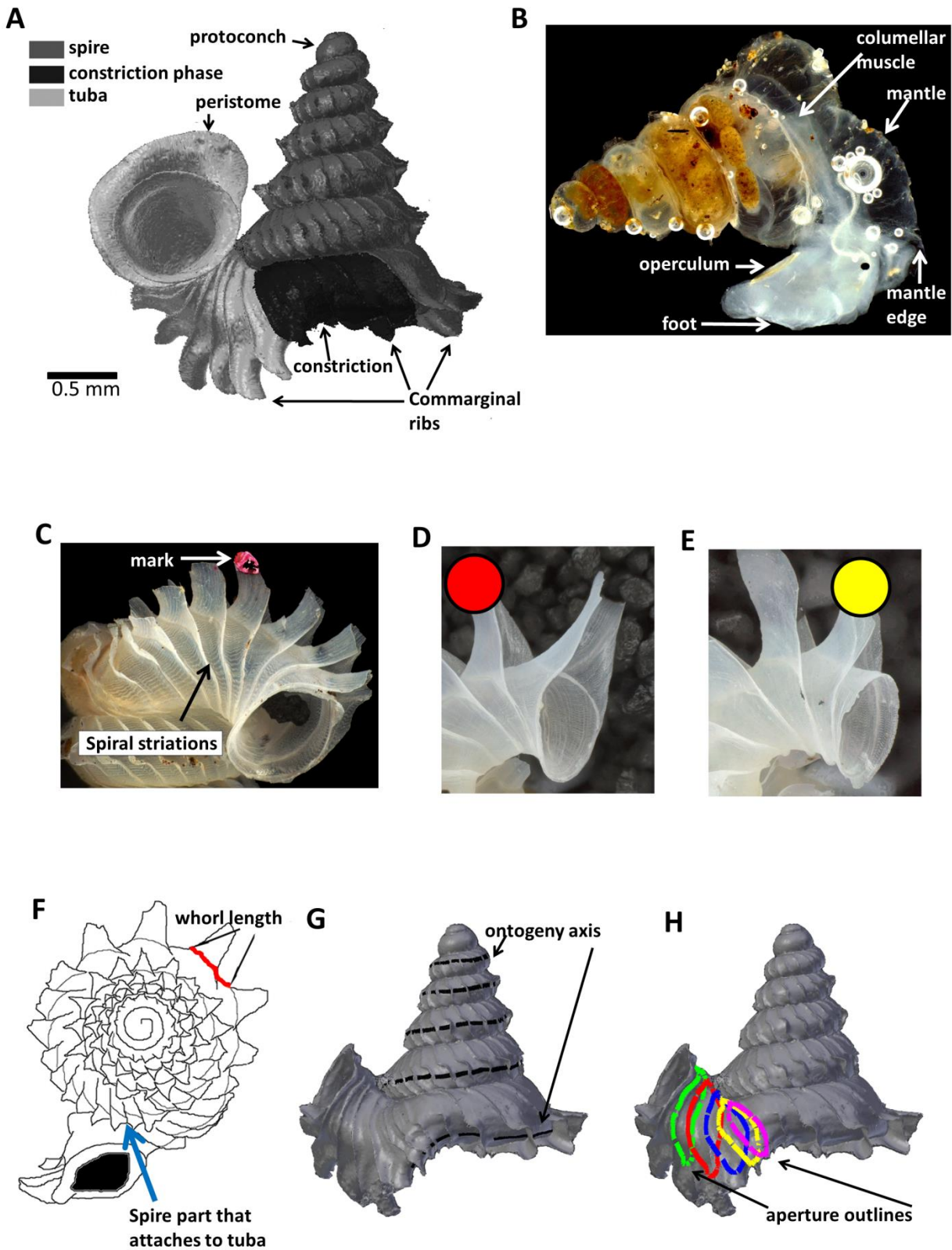
1009 Table 1. Experimental setups and number of specimens used in this study.

Dataset	Hill	Plots	Duration and date of experiment	Number of specimens
1	Kampung	1	2 days (7th May - 9th May 2011)	18
2	Kampung	2	3 days (7th May - 10th May 2011)	11
3	Pangi	1	13 days (20th April - 3th May 2011)	6
4	Pangi	2	13 days (20th April - 3th May 2011)	3
5	Pangi	3	11 days (22th April - 3th May 2011)	12
6	Pangi	4	4days (4th May- 8th May 2011)	15

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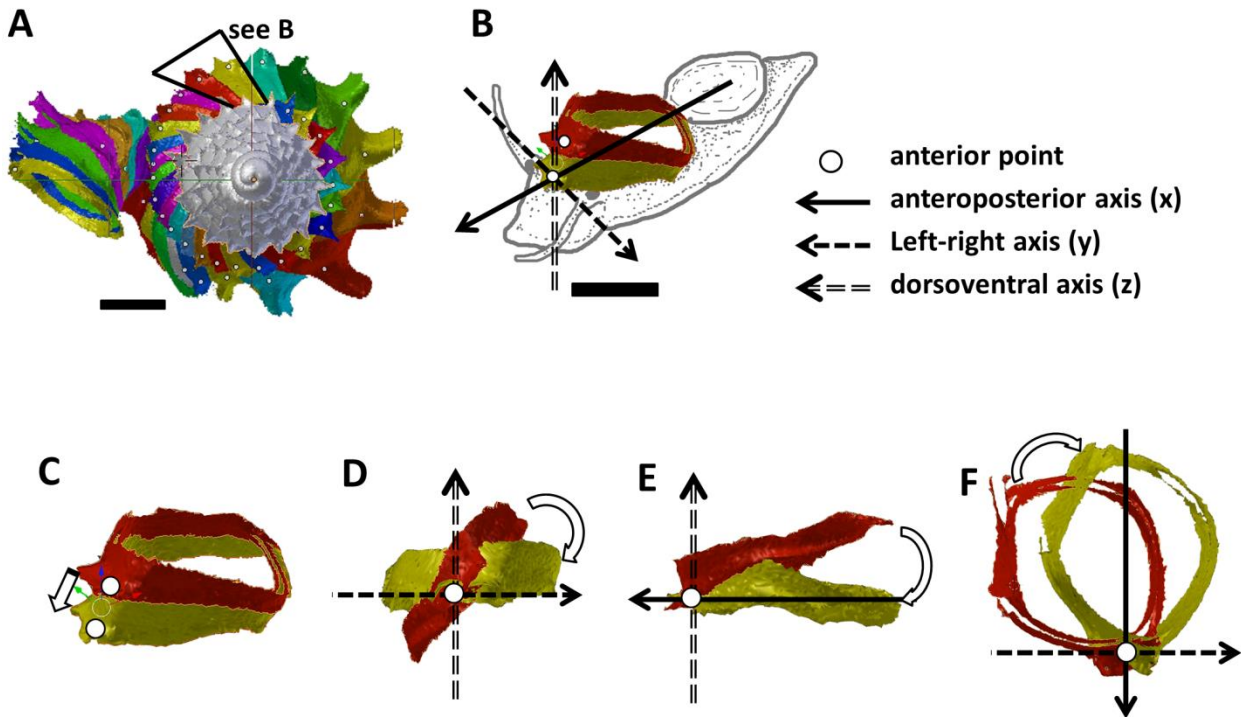
1045 **Figures**

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 1077 Figure 1. Terminology used for *Plectostoma concinnum* in this study. (A) Terminology used in the
 1078 descriptions of shell, (B) Terminology used in the descriptions of animal, (C) An example of a
 1079 shell with a nail polish mark and with the spiral striation on the shell indicated, (D) marking scheme
 1080 for a shell at rib growing mode, (E) marking scheme for a shell at whorl growing mode, (F) Whorl

1081 length measured from a specimen and the spire part that attaches to tuba, (G) Ontogeny axis
 1082 consists of a concatenation of whorl lengths of a shell, and (H) Tracing aperture outlines from a
 1083 shell.

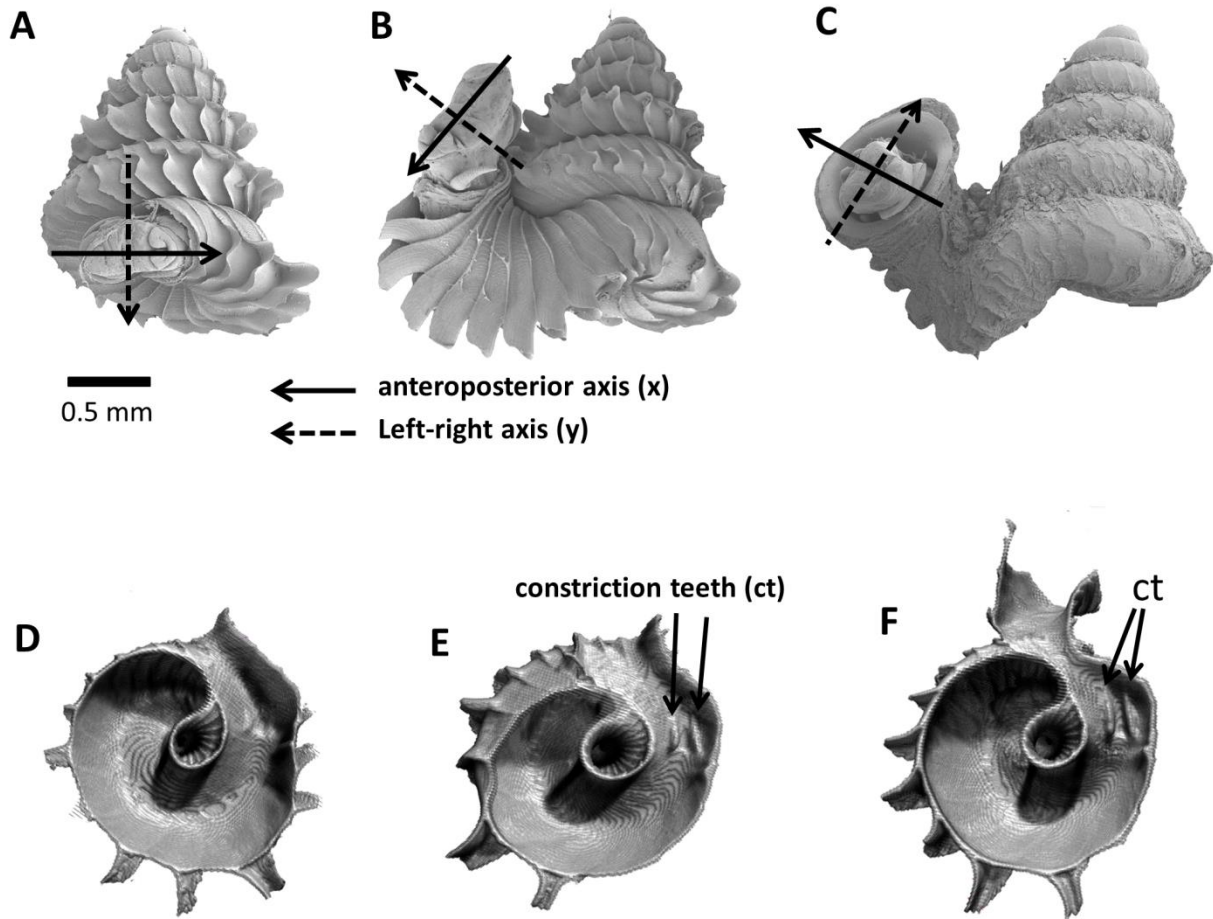


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1086 Figure 2. Steps in the analysis of aperture (i.e. animal) orientation changes. A) Segmentation: each
 1087 segment consists of whorl and rib part. For each analysis, two segments were included which
 1088 represent the two animal orientations, namely, the newly formed segment (NEW – in yellow) and
 1089 the previously formed segment (OLD – in red segment), (B) Reset the NEW segment orientation
 1090 according to the animal axes, (C) Translation: move the OLD segment to NEW segment, so that the
 1091 anterior points of the two segments were aligned, (D) Rotation of OLD segment around x-axis
 1092 corresponding animal left or right tilting from animal's anterior view, (E) Rotation of OLD segment
 1093 around y-axis corresponding to rotation of the dorsoventral axis (shell growth direction),, and (F)
 1094 Rotation of OLD segment around z-axis corresponding to rotation of the animal clockwise or
 1095 anticlockwise rotation from animal's dorsal view. Scale bar = 0.5 mm.

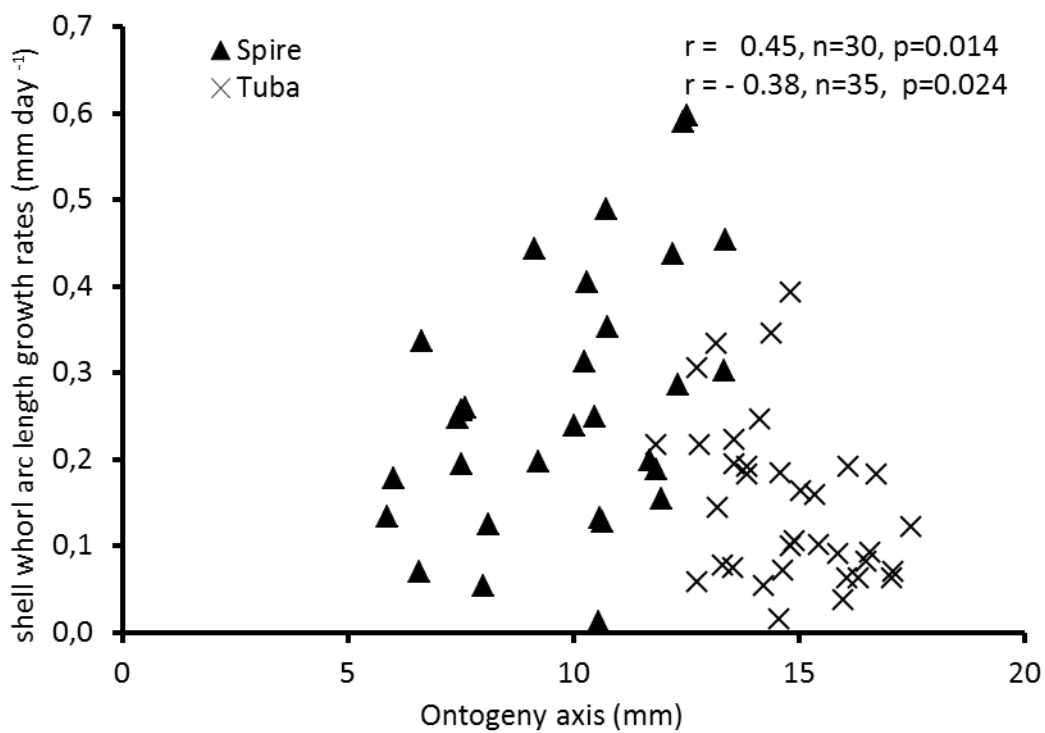
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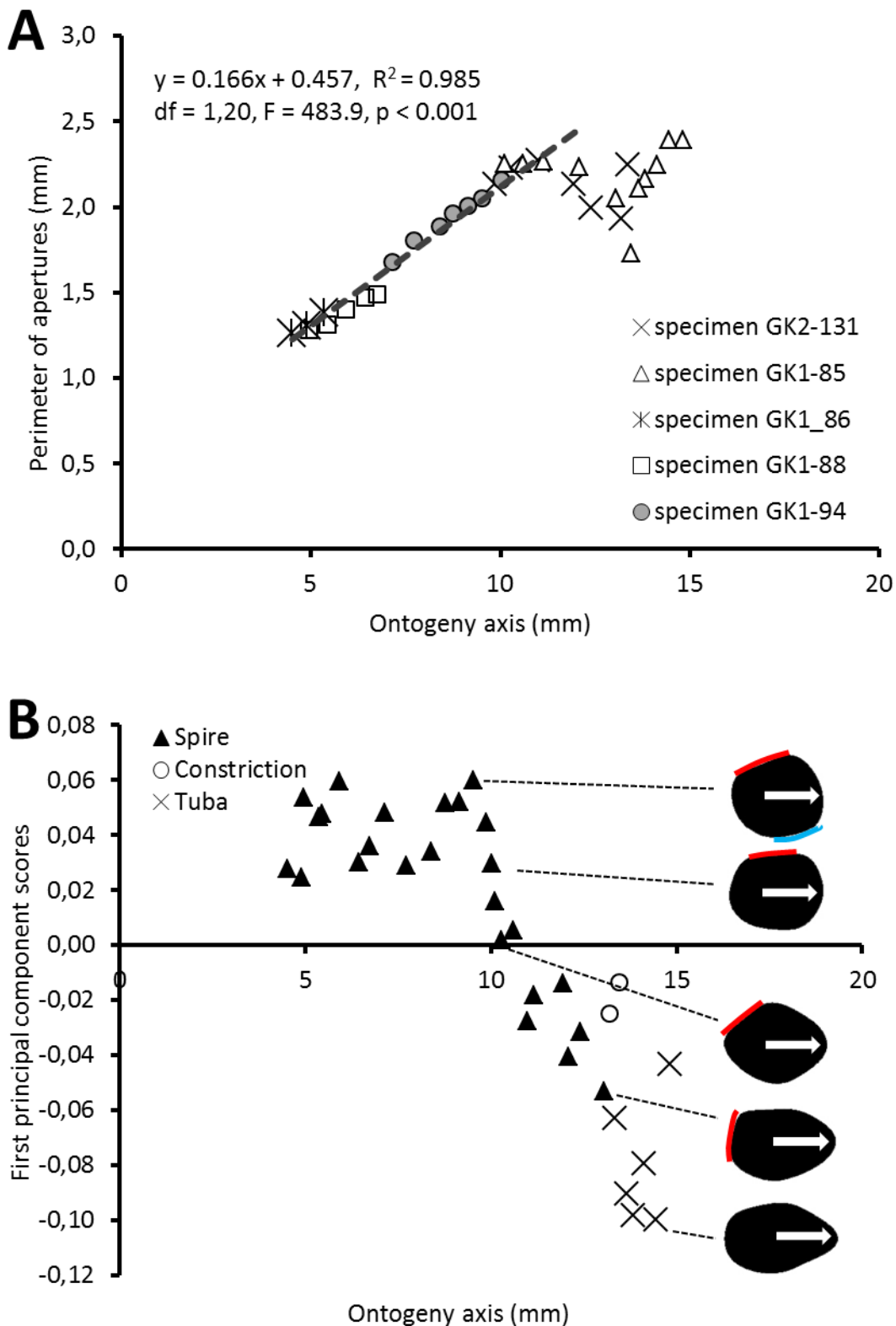
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Figure 3. Animal orientations and formation of constriction teeth of *Plectostoma concinnum* at different growth phases. (A) – (C) Orientation of animal with respect to shell at spire phase, tuba phase, and adult, (D) Constriction teeth begin to form inside the shell at the end of spire growth, (E) – (F) Constriction teeth become more prominent during the tuba growth.



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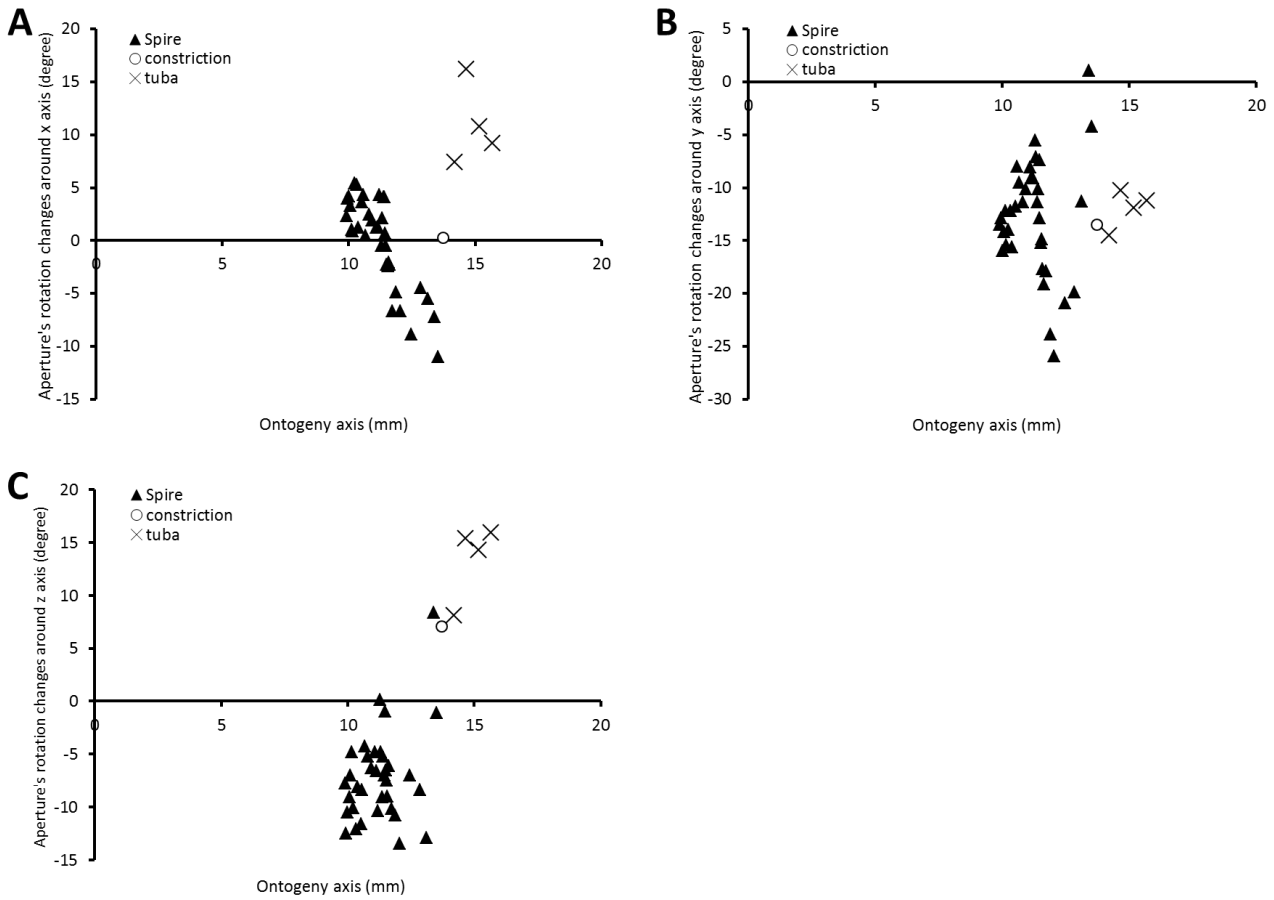
Figure 4. Growth of shell whorl arc length along the shell ontogeny for 65 specimens. Growth rate increases along the shell ontogeny for the spire part but decreases in the tuba part of the shell.



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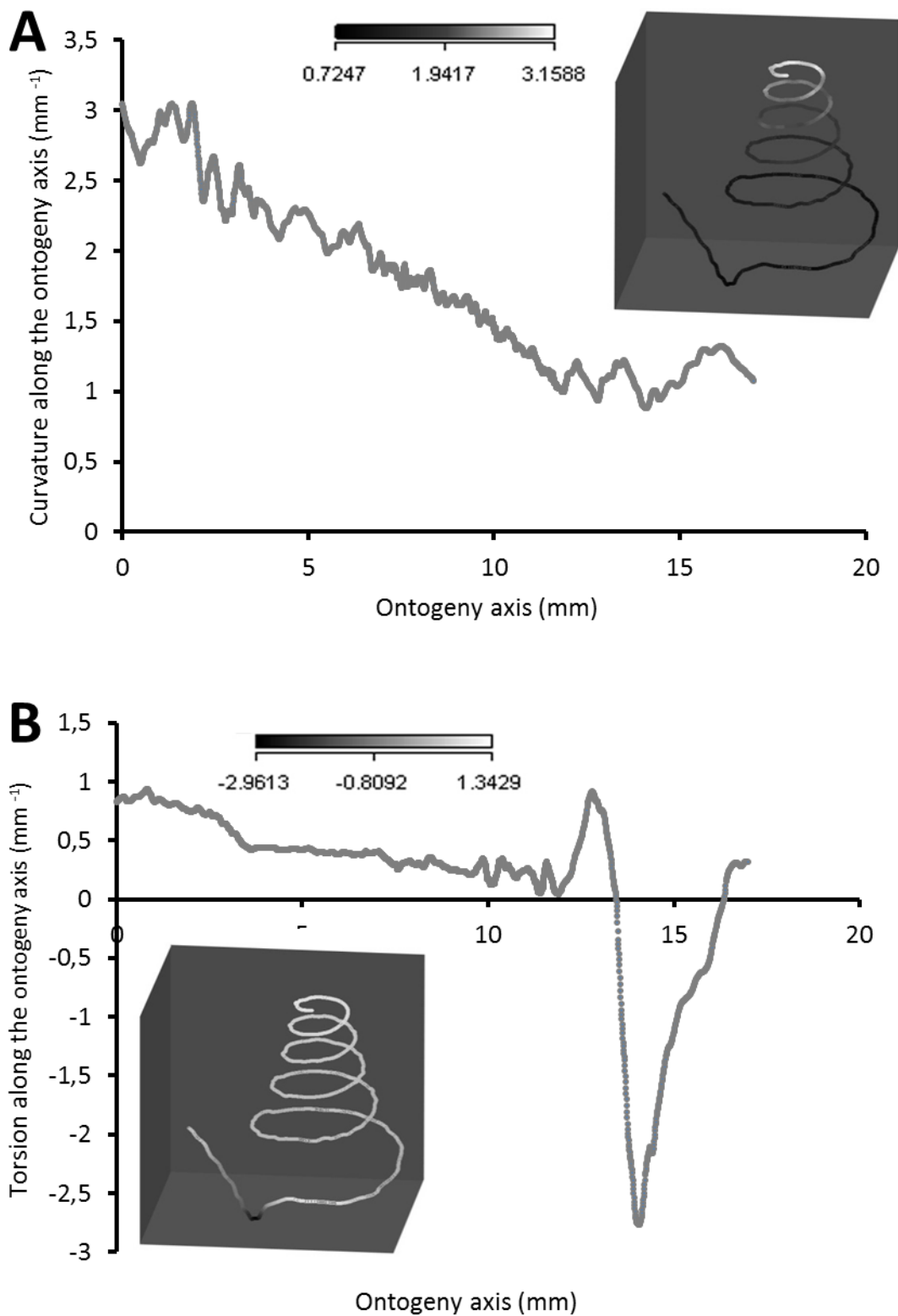
1127 Figure 5. Aperture form changes along shell ontogeny axis. (A)The apertures perimeter changes in
 1128 the five specimens show unified patterns along ontogeny axis, (B) Changes of aperture shape
 1129 (summarized in PC 1 scores, as measured from five specimens) along the ontogeny axis. Arrow
 1130 points to the anterior direction of apertures. The part of the aperture that attaches to previous whorl
 1131 (red line) and to subsequent whorl (blue line).

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Figure 6. Changes of an animal's orientation in terms of standardised rotation in angle during the growth between two consecutive segments along the ontogeny axis. (A) Rotational changes around x-axis—animal tilts to either left (negative angles) or right (positive angles), (B) Rotational changes around y-axis—shell growth direction, and (C) Rotational changes around z-axis—animal rotates either clockwise (negative angles) or anticlockwise (positive angles).



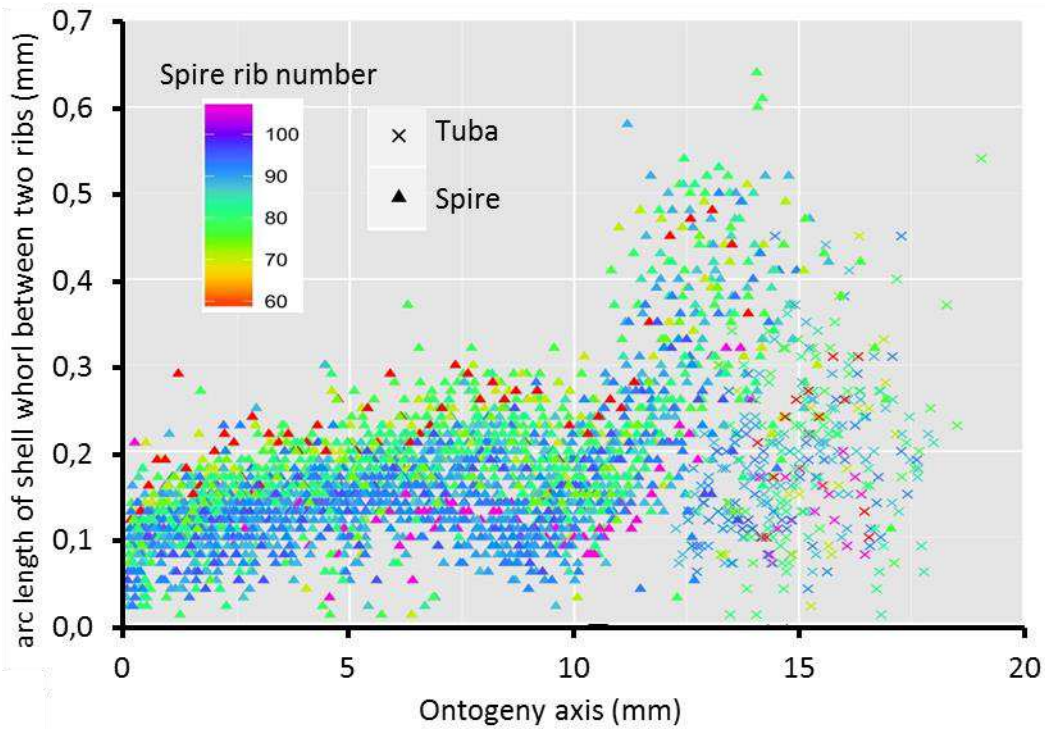
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1144 Figure 7. Curvature and torsion of a shell along the ontogeny axis. (A) curvature, inset shows

1145 curvature changes along the growth trajectory, (B) torsion, inset shows torsion changes along

1146 growth trajectory.

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Figure 8. Trends in whorl arc length between two commarginal ribs in 35 shells which vary in the number of ribs on the spire along the ontogeny axis.