

Research Article

Covarying Shell Growth Parameters and the Regulation of Shell Shape in Marine Bivalves: A Case Study on Tellinoidea

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Specific parameters characterising shell shape may arguably have a significant role in the adaptation of bivalve molluscs to their particular environments. Yet, such *functionally relevant* shape parameters (shell outline elongation, dissymmetry, and ventral convexity) are not those parameters that the animal may directly control. Rather than shell shape, the animal regulates shell growth. Accordingly, an alternative, *growth-based* description of shell-shape is best fitted to understand how the animal may control the achieved shell shape. The key point is, in practice, to bring out the link between those two alternative modes of shell-shape descriptions, that is, to derive the set of equations which connects the *growth-based* shell-shape parameters to the *functionally relevant* shell-shape parameters. Thus, a preliminary object of this note is to *derive* this set of equations as a tool for further investigations. A second object of this work is to provide an illustrative example of implementation of this tool. I report on an unexpected negative covariance between growth-based parameters and show how this covariance results in a severe limitation of the range of interspecific variability of the degree of ventral convexity of the shell outline within the superfamily Tellinoidea. Hypotheses are proposed regarding the constraints possibly at the origin of this limitation of interspecific variability.

1. Introduction

Since Réaumur [1] at least, the shape of molluscs shells is relevantly understood, not simply as a geometrical figuration *per se*, defined at the outset, but also as the result of a cumulative growth process (of biomineral accretion). Accordingly, molluscan shells are one among those “archetypal” examples favoured by Thompson [2], where *growth* process definitely rules the resulting *form* which, indeed, would not make any sense being separated from its generating pathway.

Defining more precisely the geometrical relationships relating the achieved shell shape to the involved shell-growth parameters is more recent however and was first developed in the framework of approximately conispirally coiled gastropod shells [3–7]. In bivalves, the shell-growth process has frequently been schematised using a set of vectors diverging from the valve umbo and rejoining the valve margin [8–10], the length of each vector thus representing the relative growth progress in the corresponding direction. This *growth-based* approach of shell-shape description is

especially appropriate when addressing how the animal actually controls shell growth, so as to achieve a definite shell shape. Alternatively, when focus is put upon the *functional role* of shell shape, another kind of shape descriptors is preferentially required, typically including shell elongation, the degrees of dissymmetry, and of ventral convexity of shell outline [9, 10]. Thus, while providing alternative descriptions of the same reality (the shell shape), these two distinct approaches, respectively, address different, complementary contexts, in terms of the animal concerns. In other words, while the animal survival success may partially depend upon the (presumably) *functionally relevant* set of shell-shape parameters [9–29], the animal control upon this category of shell-shape parameters is only indirect, readily operating only *via* the accretionary growth process of shell, which is best accounted for by the set of *growth-based* shape parameters (defined below).

Accordingly, a rational understanding of how a functionally adequate shell outline is achieved through the animal's direct control of the shell-growth process requires deriving,

at first, the relationships between both sets of descriptive parameters of the shell outline. Hence, the derivation of the system of equations linking the *functionally relevant* set and the *growth-based* set of parameters describing shell outline is a preliminary object of this work.

Then, in practice, these equations may serve as a tool to investigate how the *growth-based* parameters (and, as it happens, the existence of specific covariance between these parameters) can ultimately control the ranges of variation of each of the *functionally relevant* parameters. An illustrative example is proposed, within the marine bivalves superfamily Tellinoidea (Blainville 1814), demonstrating how a strong negative covariance between two specific *growth-based* parameters (“ α ” and “ ρ ,” defined below) results, in particular, in a substantial limitation of the range of interspecific variation of one of the *functionally relevant* shell-shape parameters, the degree of ventral convexity of the shell outline. This covariance and the resulting restriction of the range of interspecific variation of ventral convexity arguably answer ecological constraints applying to bivalve shell shape. Interestingly, it is worth noting that regulating processes purposely involving negative covariances between growth parameters are already known, in both gastropods [30, 31] and bivalves [32], as a means to limit excessive *intraspecific* variations of the adult-shell size (while, here, the regulation aims at limiting *interspecific* differences regarding shell shape).

2. Relating the *Functionally Relevant* Shell Shape Parameters to the *Growth-Based* Shell Shape Parameters

In a *growth-based* approach of shell shape, the sagittal outline of shells may be appropriately parameterised synthetically using three indices associated to three “typical growth vectors” (Figure 1), each of them extending from the valve umbo A . The umbo (or “apex”) is defined, here, as “the extreme dorsal side near the umbo itself,” as quoted by Galtsoff [8]; see also [9]. BC being the valve length L , then vectors V' and V'' , respectively, join the apex A to the shell outline at the extremities B and C of the segment BC and vector V joins the apex A to the shell outline at point F via the middle O of segment BC . Finally, the segment AG is perpendicular to xx' , parallel through F to BC .

Three *growth-based* indices are defined as follows:

- (i) the *apical angle* “ α ” (angle $B\hat{A}C$);
- (ii) the *differential growth index* “ ρ ” identified as the ratio between axial (dorsoventral) growth and mean lateral growth, $\rho = V/(1/2)(V' + V'')$;
- (iii) the *dissymmetric growth index* “ δ ” identified as the ratio of the larger to the smaller lateral growth vectors, $\delta = V'/V''$.

These three parameters are *geometrically independent* factors, in the sense that no mutual dependence between α , ρ , and δ is compelled by purely geometric constraint: the direction and/or module of each vector may, indeed, freely

be changed independently of the two others, in a purely geometric perspective.

These three parameters thus account schematically for the *growth pattern* of valves.

Alternatively, in a *functionally relevant* approach, the main traits of the shape of shell outline may be synthetically characterised by (i) the shell elongation, that is, the ratio of contour length to contour height, (ii) the valve dissymmetry, namely, the degree of dissymmetry of the position of the umbo versus the anterior and posterior extremities of shell, and (iii) the ventral convexity, that is, the degree of prominence of the ventral side of the shell outline, opposite to umbo. Three indices are defined correspondingly (Figure 1): the “shell elongation” index “ E ” as the ratio $BC/AG = L/(V \cdot \cos(G\hat{A}F))$, the “shell dissymmetry” index “ D ” as the ratio CJ/BJ , and the “ventral convexity” index “ K ” as the ratio JG/AG .

Note that choosing, in both approaches, a limited number of parameters to describe the shell outline, rather than implementing more refined approaches, such as Fourier analysis of shell contour, is deliberate. As the shell outline in bivalves is generally relatively simple, the main traits of shell outline may be fairly well captured by even a limited number of appropriately chosen parameters [33]. Moreover, a major advantage of limiting the number of parameters is that the equations linking growth-based and functionally relevant shape parameters may be derived under an explicitly *analytical* form, as more appropriate to readily bring out and highlight the rationale behind the equations.

As for the three growth-based parameters α , ρ , and δ above, these three functionally relevant parameters E , D , and K , are, intrinsically, free from any geometrical constraint *a priori* and thus mutually independent. Yet, E , D , and K are entirely dependent *a posteriori* upon the growth parameters α , ρ , and δ , according to the three geometrically based equations below (see Appendix for further details and a demonstration):

$$E = f(\alpha, \rho, \delta), \quad (1)$$

$$D = g(\alpha, \delta), \quad (2)$$

$$K = h(\alpha, \rho, \delta). \quad (3)$$

The way each of the three parameters E , D , and K depends upon each of the three governing parameters α , ρ , and δ may be quantified by considering the corresponding partial derivatives: $\partial E/\partial\alpha$, $\partial E/\partial\rho$, $\partial E/\partial\delta$, $\partial D/\partial\alpha$, $\partial D/\partial\delta$, $\partial K/\partial\alpha$, $\partial K/\partial\rho$, and $\partial K/\partial\delta$. In short:

- (i) the shell elongation E is (as expected) monotonously increasing with the apical angle α and monotonously decreasing with the differential-growth index ρ ; the dependence of E upon the growth-dissymmetry index δ is less intuitive but is also monotonously positive;
- (ii) the shell dissymmetry D is strongly increasing with the growth-dissymmetry index δ and, less intuitively, is decreasing with the apical angle α ;

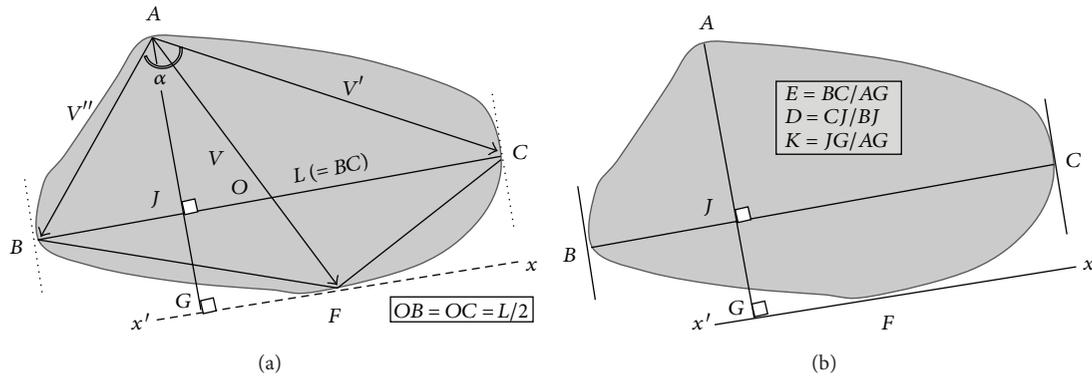


FIGURE 1: Definition of two alternative sets of descriptors of the shell outline: (a) the three growth-based parameters: apical angle α ($=\widehat{BAC}$); differential growth index $\rho = V / (1/2)(V' + V'')$; dissymmetric growth index $\delta = V' / V''$; (b) the three functionally relevant parameters: elongation E , dissymmetry D , and ventral convexity K .

- (iii) the ventral convexity K of the shell outline is strongly increasing with both the apical angle α and the differential-growth index ρ and weakly decreasing with the growth-dissymmetry index δ .

An overview of the variations

- (i) of the shell elongation E and ventral convexity K , according to α , ρ , at given δ , is provided in Figures 2(a) and 2(b);
- (ii) of the shell dissymmetry D , according to α , δ , is provided in Figure 2(c).

3. A Negative Covariance between Growth-Based Parameters α and ρ and the Consequences upon the Ranges of Interspecific Variations of the Shell Elongation E and the Ventral Convexity K , in Tellinoidea

The modules of growth vectors V , V' , V'' and the apical angle α between V' and V'' were measured for 85 species belonging to the two larger genera within the superfamily Tellinoidea, distributed worldwide: 36 species of *Donax*, 49 species of *Tellina*, using iconographic data by Robin [34]. Parameters α , ρ , δ and E , D , K were then computed according to the definitions and equations above.

One particular, unexpected feature emerging from this study is a negative covariance occurring between the differential growth index ρ and the apical angle α (Figure 3). The trend is statistically highly significant ($r = 0.74$, $n = 36$, $P < 0.0001$ for *Donax*; $r = 0.91$, $n = 49$, $P < 0.0001$ for *Tellina*; no explanation is suggested as to why the strength of covariance seems stronger for *Tellina* than for *Donax*). No or weakly significant covariances occur between the index of growth dissymmetry δ and each of the two other growth parameters, α and ρ ($r[\rho - \delta, \text{Donax}] = 0.04$, $P = 0.81$; $r[\alpha - \delta, \text{Donax}] = 0.26$, $P = 0.13$; $r[\rho - \delta, \text{Tellina}] = 0.003$, $P = 0.98$; $r[\alpha - \delta, \text{Tellina}] = 0.13$, $P = 0.37$).

The occurrence of a strong covariance between growth factors (here between α and ρ) was unexpected since, as mentioned above, these factors are mutually independent *a priori*, free from any prior geometrical constraint. This, in turn, suggests the involvement of another kind of constraint, of arguably biological origin as discussed later on.

In turn, this strong negative covariance between the growth-based parameters α and ρ has direct consequences upon how the functionally relevant parameters, especially E and K , are actually dependent upon α and ρ . Theoretically, any given value of the shell elongation E (or of the ventral convexity K) may be obtained by an infinity of different combinations of values of α and ρ (see (1) and (3) or Figures 2(a) and 2(b)). In fact, the strong covariance between α and ρ strongly constrains the pattern of dependence of both E and K upon α and ρ , as highlighted by Figures 4(a) and 4(b) and Figures 5(a) and 5(b). For example, the lowest values of shell elongation E are systematically associated with both the highest values of ρ and the lowest values of α and the reverse stands for the highest values of E . This is particularly striking for *Tellina* (Figure 4(b)) due to the especially strong negative covariance within this genus (Figure 3). The rationale behind this pattern is easily understood from the fact that $\partial E / \partial \alpha > 0$ and $\partial E / \partial \rho < 0$ in (1) (graphically presented in Figure 2(a)). The pattern is different for the ventral convexity K , in accordance with $\partial K / \partial \alpha$ and $\partial K / \partial \rho$ being both > 0 in (3) (graphically presented in Figure 2(b)).

4. Discussion

4.1. Linking the Main Traits of Shell Outline to the Growth-Based Parameters. Reducing the morphological description of bivalve shell outline to a set of only three (mutually independent) parameters may seem excessive reductionism, a rather schematic approach. Yet, as is often the case (at least for simple shapes), even a few, but adequately selected, parameters may already capture much of the displayed data [33]. Moreover, focusing upon a few (major) parameters allows keeping a convenient analytical form to the equations

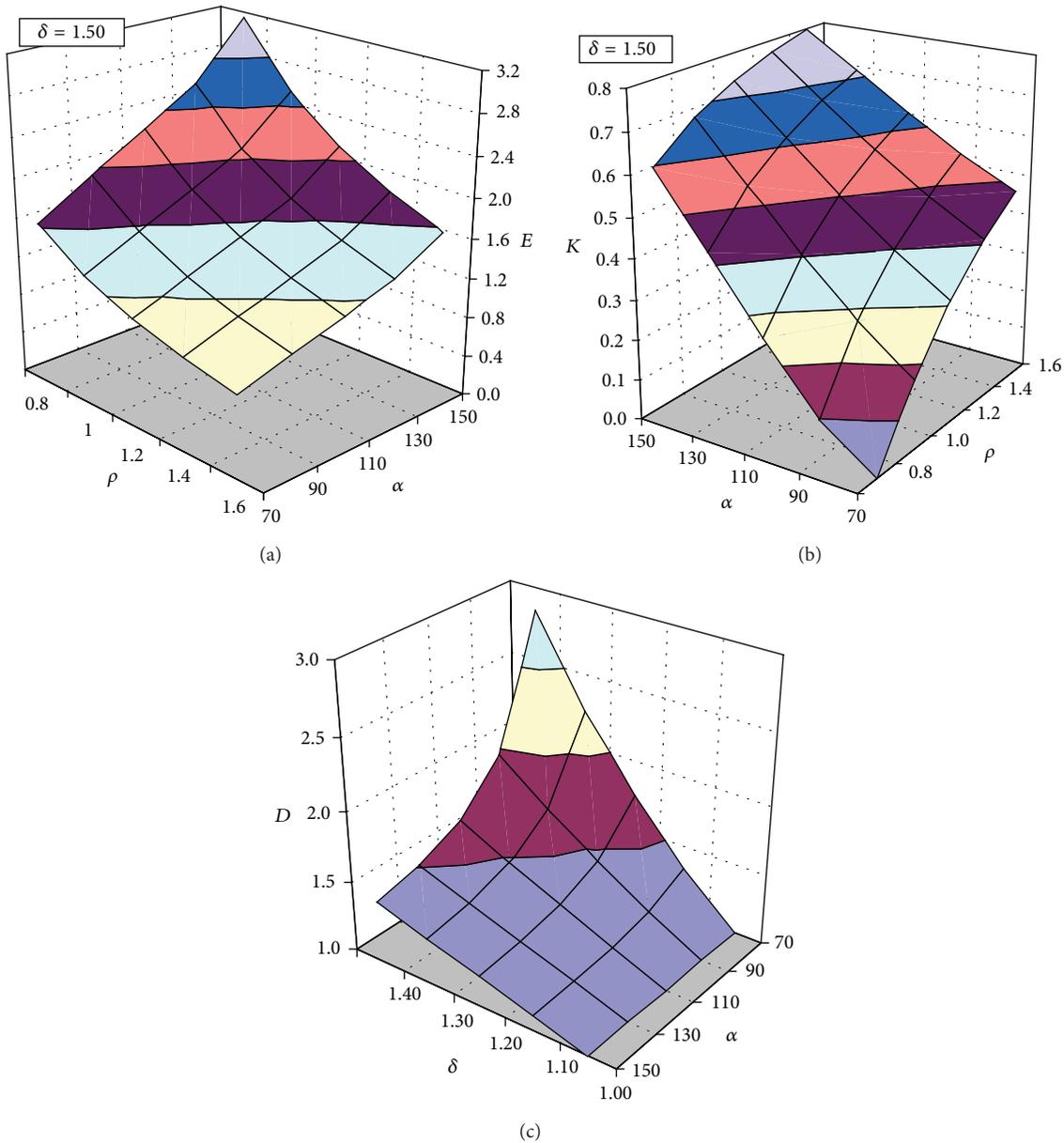


FIGURE 2: The elongation E , the ventral convexity K , and the dissymmetry D of shell outline computed against growth-based parameters ((1), (2), and (3)). Ventral convexity K is increasing with both α and ρ , while the elongation E increases with α but decreases with ρ . The dissymmetry D increases with δ and decreases with α .

linking the shell shape to the growth development and thus helps highlight the rationale behind these equations.

In bivalves, the shell elongation E , the shell dissymmetry D , and the ventral convexity K (defined in Figure 1) would likely be the main traits of the shell outline captured at first glance. Also, these parameters may arguably quantify some traits of shell contour *potentially* having significant functionalities, relevant to the animal survival success (E and/or K : [9–28]; D : [29]). Parallel to these three *functionally relevant* parameters E , D , and K , three *growth-based* parameters α , ρ , and δ provide an alternative description of the shell outline, deliberately focused, this time, upon the developmental process which, finally, generate this particular shell

outline. The *functionally relevant* parameters are related to the *growth-based* parameters by a set of geometrically based governing equations (1), (2), and (3). These equations rule the sign and degree of dependence of each functionally relevant parameter, E , D , K , upon each growth-based parameter, α , ρ , and δ . Their *analytical* mode of expression opportunely allows an easy derivation of the trends of variations of E , D , K according to α , ρ , and δ , as summarized in Table 1.

4.2. *The Regulation of the Ranges of Variation of Functionally Relevant Parameters via Appropriate Covariances between the Growth-Based Parameters.* If a given functionally relevant

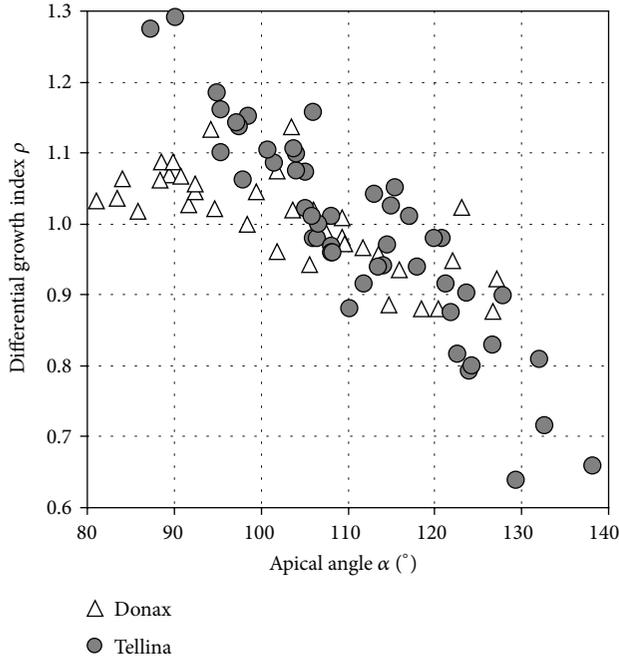


FIGURE 3: The differential growth index ρ plotted against the apical angle α : a strong negative covariance is recorded within each of the two studied bivalves genera, *Donax* and *Tellina*. (N.B.: similar patterns of negative covariation between α and ρ are observed, as well, within the other, smaller genus belonging to Tellinoidea: *Arcopecten*, *Gari*, *Macoma*; Béguinot, unpublished results).

TABLE 1: The signs of the variations, $\partial E/\partial\alpha$, $\partial E/\partial\rho$, $\partial E/\partial\delta$, $\partial D/\partial\alpha$, $\partial D/\partial\rho$, $\partial D/\partial\delta$, $\partial K/\partial\alpha$, $\partial K/\partial\rho$, and $\partial K/\partial\delta$ of the functionally relevant parameters E , K , and D , according to variations of the growth-based parameters α , ρ , and δ (according to Section 2).

	∂E	∂D	∂K
$\partial/\partial\alpha$	>0	<0	>0
$\partial/\partial\rho$	<0	=0	>0
$\partial/\partial\delta$	>0	>0	<0

parameter has dependences of the *same* sign (either >0 or <0) upon two growth-based parameters, then a *positive covariance* between these two growth-based parameters will tend to *increase the range* of variation of the considered functionally relevant parameter (as compared to what would be this range of variation if there was no covariance between these two growth-based parameters). And, conversely, a *negative covariance* between these two growth-based parameters will tend to *decrease the range* of variation of the considered functionally relevant parameter.

If a given functionally relevant parameter has dependences of *opposite* signs upon two growth-based parameters, then a *positive covariance* between these two growth-based parameters will tend to *decrease the range* of variation of the considered functionally relevant parameter. And, conversely, a *negative covariance* between these two growth-based parameters will tend to *increase the range* of variation of the considered functionally relevant parameter.

TABLE 2: The relative variations $(\partial E/E)/(\partial\alpha/\alpha)$, $(\partial E/E)/(\partial\rho/\rho)$, $(\partial E/E)/(\partial\delta/\delta)$, $(\partial D/D)/(\partial\alpha/\alpha)$, $(\partial D/D)/(\partial\rho/\rho)$, $(\partial D/D)/(\partial\delta/\delta)$, $(\partial K/K)/(\partial\alpha/\alpha)$, $(\partial K/K)/(\partial\rho/\rho)$, and $(\partial K/K)/(\partial\delta/\delta)$ of the functionally relevant parameters E , D , K , according to variations of the growth-based parameters α , ρ , δ .

(a) for the genus <i>Donax</i>			
	$\partial E/E$	$\partial D/D$	$\partial K/K$
$\partial\alpha/\alpha$	+0.72	-0.73	+1.80
$\partial\rho/\rho$	-0.99	0.00	+1.72
$\partial\delta/\delta$	+0.35	+1.60	-0.18
(b) for the genus <i>Tellina</i>			
	$\partial E/E$	$\partial D/D$	$\partial K/K$
$\partial\alpha/\alpha$	+0.65	-0.23	+1.87
$\partial\rho/\rho$	-0.98	0.00	+1.35
$\partial\delta/\delta$	+0.13	+1.46	-0.08

Based on information provided in Table 1 for the signs of the dependence of E , D , K upon α , ρ , and δ in bivalves, it is thus possible to predict how the range of variation of each of the three functionally relevant parameters, E , D , K , is either *enlarged* or *restricted* according to the occurrence and sign of any *particular covariance* between the growth-based parameters α , ρ , and δ .

4.3. *Covariance between Growth Parameters and the Resulting Pattern of Regulation of Shell Shape in the Superfamily Tellinoidea.* Moving now from theoretical preliminaries to practical applications, one important and unexpected feature emerges from a survey of the interspecific variations of growth-based parameters within *Donax* and *Tellina*, the two larger genera of bivalves belonging to the superfamily Tellinoidea: a strong *negative covariance* is recorded between the apical angle α and the differential growth ratio ρ (Figure 3). This covariance was rather unexpected since, as already mentioned, the *growth-based* parameters α , ρ , and δ are geometrically independent. In other words, this covariance draws attention upon some biologically relevant *constraining* process. From a *functional* point of view, the occurrence of this negative correlation between α and ρ results in conformity with Section 4.2 and Table 2:

- (i) in a *restriction* of the range of variation of the ventral convexity K (as compared to what would be this range of variation if there was no covariance between α and ρ), since the opposite variations of α and ρ tend to mutually cancel their respective effects upon K , due to both $\partial K/\partial\alpha$ and $\partial K/\partial\rho$ having the same sign (>0) in (3);
- (ii) conversely, in an *extension* of the range of variations of the elongation E , due to $\partial E/\partial\alpha$ and $\partial E/\partial\rho$ having opposite signs in (1).

Thus, the negative correlation which actually constrains the variations of α and ρ allows a large range of interspecific variations of the shell elongation E with, yet, limited collateral influence upon the ventral convexity K . Specifically, for the

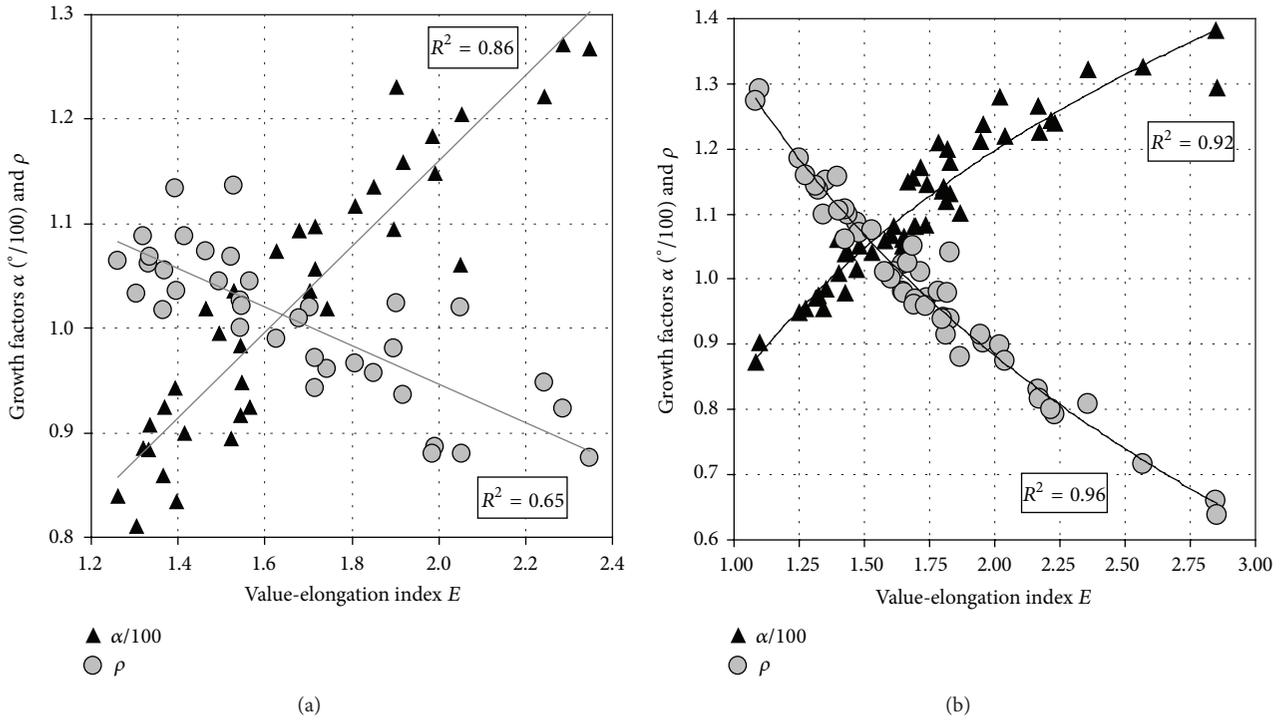


FIGURE 4: The shell elongation E plotted against the growth-based parameters α and ρ , for 36 species within the genus *Donax* (a) and 49 species within the genus *Tellina* (b)—black triangles: apical angle α ($^{\circ}/100$); grey dots: differential growth index ρ . The increase of α and decrease of ρ with growing E are both highly significant ($P < 0.0001$ in all cases).

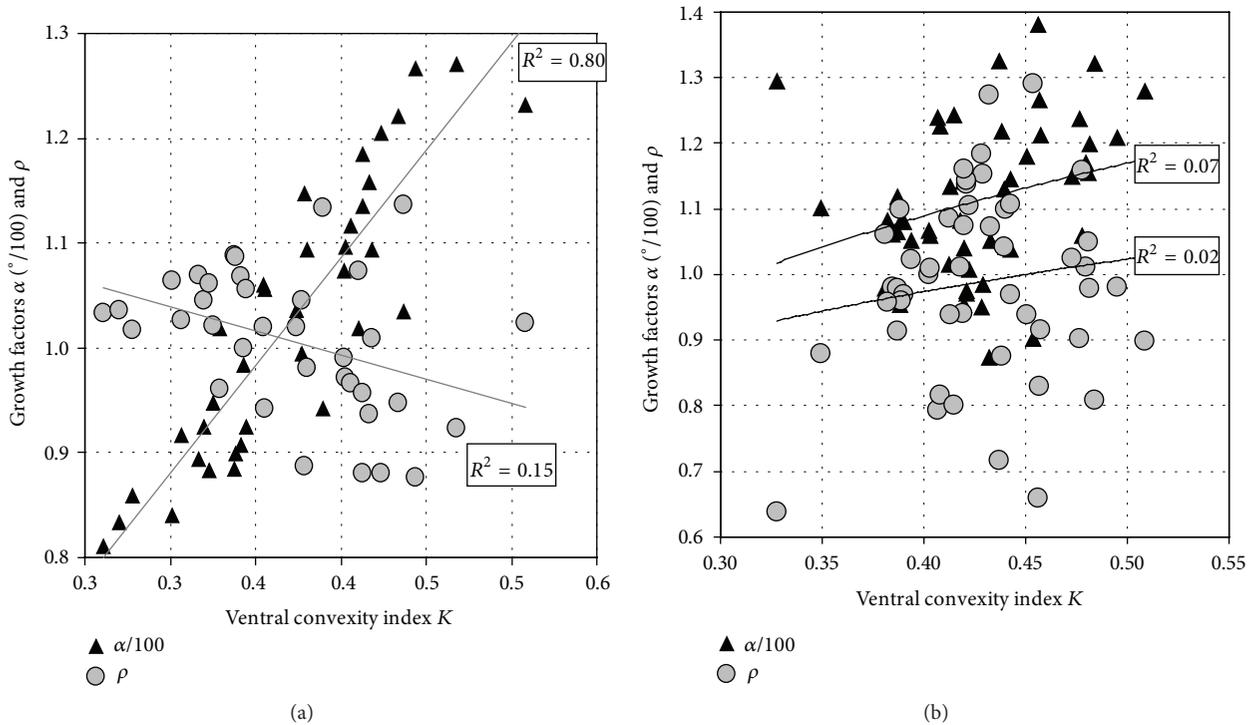


FIGURE 5: The ventral convexity K plotted against the growth-based parameters α and ρ , for 36 species within the genus *Donax* (a) and 49 species within the genus *Tellina* (b)—black triangles: apical angle α ($^{\circ}/100$); grey dots: differential growth index ρ . The increase of α and decrease of ρ with growing K for *Donax* are highly significant ($P < 0.0001$) and significant ($P = 0.02$), respectively. For *Tellina*, the trends are not significant ($P > 0.05$ for both).

same variation of valve elongation E (say from 1.2 to 2.2), the resulting computed variation of K is 2.23 times *smaller* due to the negative covariance recorded between α and ρ than it would be if the elongation would proceed, for example, from the variation of α alone.

4.4. Discussing the Possible Origins of the Negative Covariance between the Growth-Based Parameters α and ρ . The constraining covariance between growth-based parameters α and ρ reported within the superfamily Tellinoidea may have either

- (i) a *developmental* origin, as *directly* operating on the orientations and respective sizes of the “growth vectors” V, V', V'' and thus on α and ρ , or
- (ii) an *adaptive* origin, as the result of a selective process, more readily involving one or several of the functionally relevant parameters E, D, K .

Distinguishing between these two hypotheses, however, is far from being easy [35]. Yet, a comparison of the present results with the data obtained for the intraspecific variations recorded within *Donax trunculus* (Linné, 1758) and *Donax vittatus* (da Costa, 1778) may possibly help to cast some light on the question. At the intraspecific level, a positive covariance between ρ and δ is recorded in both *Donax trunculus* and *Donax vittatus* (Béguinot, *unpublished data*), instead of the negative covariance between α and ρ observed at the interspecific level within Tellinoidea. This positive covariance between ρ and δ results, accordingly (Section 4.2 and Table 1), in a restriction of the ranges of intraspecific variation of *both* the elongation E and the ventral convexity K of shell outline.

These contrasted patterns between the intraspecific and the interspecific levels, regarding both the type of covariance and the associated consequences, should likely make more sense in an “adaptive” perspective than according to a “developmental” point of view. The logic is not easy to understand, indeed, behind a hypothetical *developmental constraint* applied directly to growth-based parameters and which moves—seemingly somewhat arbitrarily—from a positive covariance between ρ and δ at the intraspecific level to a negative covariance between α and ρ at the interspecific level. The associated consequences, in terms of the extension of the range of variation of the presumably functionally related parameters E and K , would be more readily understandable. A regulation makes sense, which tends to reduce the ranges of variations of functionally relevant phenotypic characters at the intraspecific level and, on the contrary, contributes to enlarge these ranges of variations at the interspecific level. And this is the case, here, for the shell elongation E —although the range of variation of the ventral convexity K remains restricted at both intra- and interspecific levels. Now, what might be the selective advantage of restraining the variability of ventral convexity K , inclusively at the interspecific level? Some tentative arguments may be suggested. The ventral portion of valves is often the weakest and, thus, more at risks [13], since the ventral part of the shell, especially the posteroventral sector, is ordinarily less thick and thus less resistant than the dorsal part. Increasing ventral convexity,

that is, ventral prominence, would thus enlarge the corresponding weakened zone. Also, a larger convexity would tend to reduce the sealing pressure along the ventral margin (at given unchanged positions of insertion of the adductor muscles) and thus would make easier the shell opening by predators. Accordingly, a sufficient level of shell mechanical resistance to various kinds of environmentally induced stresses might preclude too high values of ventral convexity. Conversely, a sufficient value of ventral convexity might well be dictated by the avoidance of excessively acute profiles of valves contour at the anterior and posterior extremities (i.e., around C and B , Figure 1) which would inevitably result from too weak a convexity. Such acute portions would be at still greater risks and more prone to suffer local breakage.

An optimally centred and size-limited range of values for the ventral convexity of shell outline would thus arguably be selected.

Admittedly, the “adaptive” perspective remains to be more firmly confirmed. Extending investigations, combining both the *functionally relevant* and the *growth-based* approaches of shell shape and applied to quite a wider range of bivalves groups would probably help to clarify the point.

Appendix

The Equations Relating the Valve Shape Parameters E, D, K to the Growth Parameters α, ρ , and δ

Consider the following:

$$E = \frac{\left[(\delta^2 - 2\delta \cdot \cos(\alpha) + 1) \cdot (4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2) \right]^{0.5}}{\rho \cdot (\delta + 1) \cdot \delta \cdot \sin(\alpha)}, \quad (\text{A.1})$$

$$D = \frac{\delta^2 - \delta \cdot \cos(\alpha)}{1 - \delta \cdot \cos(\alpha)}, \quad (\text{A.2})$$

$$K = 1 - E \cdot \left\{ \left(\frac{X}{E \cdot \cos(\theta)} \right)^2 - 0.25 \right. \\ \left. * \left[1 + \left(\frac{X}{E \cdot \cos(\theta)} \right)^2 \right. \right. \\ \left. \left. - \left(\frac{X}{\delta \cdot E \cdot \cos(\theta)} \right)^2 \right]^2 \right\}^{0.5}, \quad (\text{A.3})$$

with $X = 2\delta/(\rho \cdot (\delta + 1))$; $\cos(\theta) = 2\delta \cdot \sin(\alpha)/(4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2)^{0.5}$ and E defined above.

N.B.: for the specific case where shells are (sub-) symmetric ($\delta = 1$), the three equations are simplified as

$$E = \frac{[2(1 - \cos(\alpha))]^{0.5}}{\rho};$$

$$D = 1; \quad (\text{A.4})$$

$$K = 1 - \frac{[(1/2)(1 + \cos(\alpha))]^{0.5}}{\rho}.$$

In other words, this system of three equations (A.1), (A.2), and (A.3) expresses the tensor relationship linking the two alternative sets of parameters describing the shell outline, α , ρ , δ and E, D, K .

Demonstration of (A.1), (A.2), and (A.3). The following, classical relationships between angles, sides, and height in triangles are applied here within the triangle ABC (see Figure 1):

$$BC = L = (V'^2 + V''^2 - 2V'V'' \cos(\alpha))^{0.5}, \quad (\text{A.5})$$

$$JC = \frac{L^2 + V'^2 - V''^2}{2L}, \quad (\text{A.6})$$

$$AJ = \left[V'^2 - \left(\frac{L^2 + V'^2 - V''^2}{2L} \right)^2 \right]^{0.5}. \quad (\text{A.7})$$

Valve Elongation. Consider

$$E = \frac{BC}{AG} = \frac{L}{AG} = \frac{L}{AF \cdot \cos(\theta)}$$

$$= \frac{L}{V \cdot \cos(\theta)}, \quad \text{with } \theta = \text{angle } \hat{G}\hat{A}\hat{F}. \quad (\text{A.8})$$

Accounting for the definitions of $\rho = V/(1/2)(V' + V'')$ and $\delta = V'/V''$, it comes that

$$V'' = \frac{2V}{\rho \cdot (\delta + 1)}. \quad (\text{A.9})$$

Equation (A.5) yields then

$$\frac{L}{V''} = (\delta^2 - 2\delta \cdot \cos(\alpha) + 1)^{0.5}. \quad (\text{A.10})$$

From (A.9) and (A.10)

$$\frac{L}{V} = \frac{2(\delta^2 - 2\delta \cdot \cos(\alpha) + 1)^{0.5}}{\rho \cdot (\delta + 1)}. \quad (\text{A.11})$$

Now, $JO = JC - L/2$ and, from (A.6) and (A.7), it follows that

$$tg(\theta) = \frac{JO}{AJ} = \frac{V'^2 - V''^2}{(4L^2 \cdot V'^2 - (L^2 + V'^2 - V''^2)^2)^{0.5}} \quad (\text{A.12})$$

and, as $\delta = V'/V''$,

$$tg(\theta) = \frac{\delta^2 - 1}{(4\delta^2(L/V'')^2 - ((L/V'')^2 + \delta^2 - 1)^2)^{0.5}}. \quad (\text{A.13})$$

Substituting L/V'' by its expression in (A.10) yields $tg(\theta) = (\delta^2 - 1)/(2\delta \cdot \sin(\alpha))$ and then

$$\cos(\theta) = \left(\frac{1}{1 + tg^2(\theta)} \right)^{0.5} = \frac{2\delta \cdot \sin(\alpha)}{(4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2)^{0.5}}. \quad (\text{A.14})$$

Finally, (A.11) and (A.14) yield for the elongation $E = L/(V \cdot \cos(\theta))$

$$E = \frac{\left[(\delta^2 - 2\delta \cdot \cos(\alpha) + 1) \cdot (4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2) \right]^{0.5}}{\rho \cdot (\delta + 1) \cdot \delta \cdot \sin(\alpha)}. \quad (\text{A.15})$$

Valve Dissymmetry. $D = JC/JB = JC/(L - JC)$ and, according to (A.5) and (A.6), $D = (\delta^2 - 1 + (L/V'')^2)/(1 - \delta^2 + (L/V'')^2)$. With (L/V'') defined at (A.10), it comes that

$$D = \frac{\delta^2 - \delta \cdot \cos(\alpha)}{1 - \delta \cdot \cos(\alpha)}. \quad (\text{A.16})$$

Convexity K of the Ventral Contour of Valve. The convexity K of the ventral contour of valve is defined by the ratio $K = JG/AG = 1 - AJ/AG$.

From (A.7) and accounting for $E = L/AG$, it comes that

$$K = 1 - \left[V'^2 - \left(\frac{L^2 + V'^2 - V''^2}{2L} \right)^2 \right]^{0.5} \left(\frac{E}{L} \right),$$

$$K = 1 - E \cdot \left\{ \left(\frac{V'}{L} \right)^2 - 0.25 \left[1 + \left(\frac{V'}{L} \right)^2 - \left(\frac{V''}{L} \right)^2 \right]^2 \right\}^{0.5}. \quad (\text{A.17})$$

According to (A.9), $V''/L = 2/(E \cdot \rho \cdot (\delta + 1))$ and $V'/L = 2\delta/(E \cdot \rho \cdot (\delta + 1))$.

Substitution of V'/L and V''/L by their expressions above yields finally

$$K$$

$$= 1 - E \cdot \left\{ \left(\frac{X}{E \cdot \cos(\theta)} \right)^2 - 0.25 \right.$$

$$\left. \times \left[1 + \left(\frac{X}{E \cdot \cos(\theta)} \right)^2 - \left(\frac{X}{\delta \cdot E \cdot \cos(\theta)} \right)^2 \right]^2 \right\}^{0.5} \quad (\text{A.18})$$

with $X = 2\delta/(\rho \cdot (\delta + 1))$; $\cos(\theta) = 2\delta \cdot \sin(\alpha)/(4\delta^2 \sin^2(\alpha) + (\delta^2 - 1)^2)^{0.5}$ according to (A.14) and E defined by (A.15).

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

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