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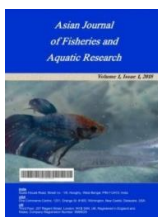
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Unexpected Covariances between Shell Growth Parameters are Controlling the Range of Interspecific Variations of Shell shape in the Deep-Sea Clams Genus *Calyptogena* (Bivalvia: Veneroida)

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Author's contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

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ABSTRACT

In Bivalves, shell shape descriptors (in particular, elongation E, dissymmetry D, ventral convexity K) are considered functionally-relevant parameters, each of them likely being exposed to specific selective pressures, according to environmental conditions. Indeed, previous investigations, have repeatedly confirmed that different types of constraints do apply to the respective ranges of interspecific variations of E, D, K: in particular, a trend for a substantially extended range of interspecific variation of shell-elongation E (likely attributed to niche differentiation) and, on the contrary, a trend for a severely restricted range of interspecific variation of ventral-convexity K (closely centered at an optimum for mechanical resistance of valves). In turn, due to rigid geometrical relationships linking shell-shape to shell-growth, this pattern of constraints on shell-shape variations implies, mathematically, the occurrence of specifically associated covariances between shell-growth parameters, the occurrence of which were, indeed, repeatedly observed within all groups of *shallow-waters* clams examined so far. Yet, the fairly different environmental conditions prevailing at bathyal / abyssal depths invite addressing comparatively some typically *deep-sea* clams; hereafter the genus *Calyptogena*. Contrary to expectation, the same types of

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covariances between shell-growth parameters are reported in deep-sea *Calypptogena* as those reported in shallow-waters clams, thus suggesting less dissimilar patterns of constraints than expected between shallow waters and deep-sea conditions.

Keywords: *Mollusk; shell contour; growth parameters; functional parameters; ecological constraint selective pressure; morphospace.*

1. INTRODUCTION

Shell shape in Bivalves, especially the overall profile of valves' contour, arguably has functional implications for the animal (list of references below). As such, shell-shape may be subjected to various selective pressures according to environmental conditions. For example, niche differentiation according to a given functional shell-shape trait, likely promoted by interspecific competition, may induce a *significant enlargement* of the range of interspecific variation of this functional trait while, on the contrary, the necessity to remain in the vicinity of some functional optimum may induce the *narrow restriction* of the range of interspecific variation for the corresponding functional trait.

Now, beyond such conceptual propositions, the occurrence of selective pressures actually at work, in order to expand or restrict one particular shell-shape parameter or another, is not so easy to demonstrate in practice. Such demonstration would normally call for long and complex experimentations to test the corresponding issues. An alternative solution, however, may arise from the thorough analysis of crude field data. Due to rigid geometrical relationships between shell-growth parameters and shell-shape parameters in bivalves, it has been demonstrated [1-2] that any significant *modification of amplitude* of the range of variations of a given shell-shape parameter (either expansion or restriction) mathematically implies the appearance of a specific kind of *covariation* between shell-growth parameters. Conversely, the unexpected occurrence of a given covariance between shell-growth parameters calls for the likely existence of a constraint, that either expands or contracts the range of variation of one or another shell-shape parameters ("unexpected occurrence" being understood in the sense that no other alternative origin for this covariance – developmental in particular [3] – might arguably be admitted). To make things more concrete, Table 1 (reproduced from reference [2]) highlights the pattern of correspondence between (i) the different types of possible covariances between shell-growth parameters and (ii) the different possible

combinations of expansion / contraction of the ranges of variations of each of the shell-shape parameters.

Based on this procedure, a series of investigations conducted on a variety of groups of clams ([1,2] and also still *unpublished data*) have provided evidence for the repeated occurrence of either expansion or restriction of the interspecific ranges of variation of several functionally-relevant shell-shape traits ("expansion or restriction" being understood as compared to what would be the amplitudes of these ranges of variation in the absence of covariance). More precisely, the following trends have been highlighted [2] as regards three major, functionally-relevant shell-shape traits (more precisely defined below, in section Methods):

- Statistically significant *enlargements* of the interspecific range of variation of shell *elongation* E ;
- Statistically significant *restrictions* of the interspecific range of variation of the *ventral convexity* of shell contour K ;
- Statistically significant *restrictions* of the interspecific range of variation of *shell dissymmetry* D (yet essentially for the domain of *highest* dissymmetry levels).

All these investigations (and the corresponding results) were addressing common groups of clams essentially distributed in relatively *shallow waters*. Now, it is conceivable that the strongly different environmental conditions of *deep-sea* contexts may induce partly different selective pressures on bivalves, thus influencing differently the ranges of interspecific variations of the functionally-relevant shell-shape parameters E, K, D.

Hereafter, I consider the interspecific variations of the shell-shape within the *deep-sea* genus *Calypptogena* (Dall, 1891) [Bivalvia: Veneroida], an important component of bathyal and abyssal bivalves' fauna, in particular around many hydrothermal vents, cold seeps, whale falls. According to the procedure described above, I seek, at first, for the possible occurrence of significant unexpected covariances between shell-growth parameters (defined below). Then, I

examine which of *developmental* constraint or *selective* constraint is more likely involved in the occurrence of these covariances and I confirm, accordingly, the likely existence of selective constraints controlling shell shape in *Calyptogena*. At last, I test whether these selective constraints, prevailing under *deep-sea* conditions, substantially differ from those recorded in clams under *shallow waters*. The degree of consistency of the conclusions drawn from the present investigation is then discussed, in the light of the functional relevance admittedly attributed [4 to 25] to E, D, K, the three major parameters describing the shape of shell contour in Bivalves.

2. MATERIALS AND METHODS

2.1 Definition of Shell Growth Parameters and Shell shape Parameters and Their Mutual Geometrical Linkage

In a *growth-based* approach of shell shape, the sagittal outline of shells may be appropriately characterised synthetically using three indices associated to three “typical growth vectors” V, V', V'' (Fig. 1), each of them extending from the valve umbo A. The umbo (or “apex”) being defined, here, as “the extreme dorsal side near the umbo itself, as quoted in reference [26], see also [14]. Segment BC being the valve length L, then vectors V', V'' respectively join the apex A to the shell outline at the extremities B, 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', the parallel through F to BC. Three *growth-related* indices are defined as:

- * the *apical angle* ‘ α ’ (angle BÂC);
- * the *differential growth index* ‘ ρ ’ identified to the ratio between axial (dorso-ventral) growth and mean lateral growth, $\rho = V / (\frac{1}{2} (V' + V''))$;
- * the *dissymmetric growth index* ‘ δ ’ identified to 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 contour may be synthetically characterised by (i) the shell elongation, i.e. 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 the umbo. Three indices are defined correspondingly (Fig. 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 . The functional relevance of each of these three shell-shape parameters have been argued in references [4 to 25] with special attention to shell dissymmetry D in reference [25].

As for the three growth-related parameters α , ρ , δ above, these three functionally-relevant parameters E, D, K, are, intrinsically, free from any geometrical constraint *a priori* and thus *mutually independent also*. Yet, E, D, K are entirely dependent, *a posteriori*, upon α , ρ , δ , according to three, *geometrically-based equations*, provided in Appendix: equations A.1, A.2, A.3 and Table A.2 (see references [1-2] for the derivation of these equations and further details).

A general consequence of this set of geometrical relationships, linking the functionally-relevant parameters E, D, K, to the growth-related parameters α , ρ , δ , is that the respective *amplitudes of the ranges of variations* of E, D, K are substantially affected by the occurrence of *covariance(s)* between α , ρ , δ [2].

As shown in Table 1, covariations between growth-parameters (according to their sign and the couple of growth parameters involved) may either widen or narrow the ranges of variations of one or the other among the three functionally-relevant parameters E, D, K (as compared to what would be the magnitudes of these ranges in the absence of covariation between α , ρ , δ).

Accordingly, *unveiling such covariances* between α , ρ , δ , (unexpected geometrically) point to the likely occurrence of either (i) *developmental* constraints acting *directly* on α , ρ , δ , or *selective* constraints on the amplitudes of interspecific variations of shell-shape parameters E, D, K (in turn, generating *indirectly* the recorded covariances between α , ρ , δ).

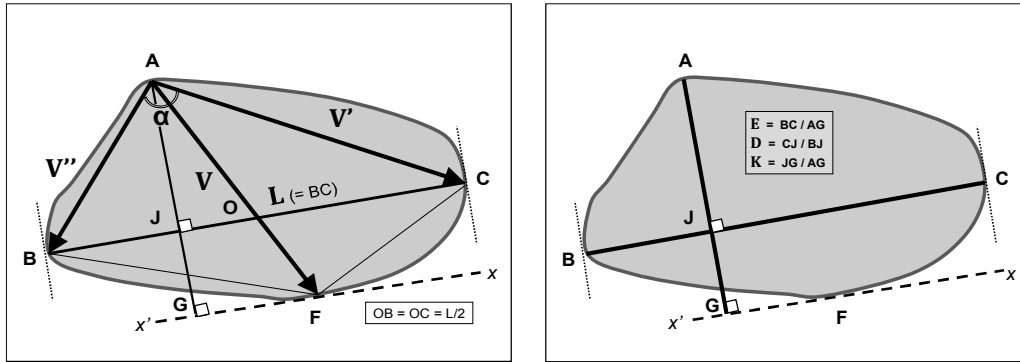


Fig. 1. Definition of two alternative sets of descriptors of the shell outline: (left) the three growth-related parameters: apical angle α ($= \widehat{BAC}$) ; differential growth index $\rho = V/1/2(V' + V'')$; dissymmetric growth index $\delta = V'/V''$; (right) the three functionally-relevant parameters: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

Table 1. Consequences of the occurrence of significant covariations between growth-related parameters α , ρ , δ , on the magnitude of the ranges of variation ΔE , ΔK , ΔD of the functionally relevant parameters E, K, D [as compared to what would be the magnitudes ΔE , ΔK , ΔD , in the absence of any covariations between α , ρ , δ]. Arrows pointing upward (resp. downward) stand for a widened (resp. a narrowed) range of variation; the sign '=' stands for a non-affected range of variations

Patterns of co-variation of shell-growth parameters	ΔE	ΔK	ΔD
Covariance $\rho - \delta$ positive	↓	↓	=
Covariance $\rho - \delta$ negative	↑	↑	=
Covariance $\alpha - \rho$ positive	↓	↑	=
Covariance $\alpha - \rho$ negative	↑	↓	=
Covariance $\alpha - \delta$ positive	↑	↓	↓
Covariance $\alpha - \delta$ negative	↓	↑	↑

It is in that sense that *unveiling statistically significant covariances* between α , ρ , δ , may serve as a tool to *highlight the existence of either developmental or environmentally-related selective constraints* on shell shape. While, the existence of such constraints would, indeed, be *far more difficult to demonstrate otherwise* [3].

2.2 Data Recording and Statistical Analysis

Shell measurements (L, V, V', V'' according to Fig. 1) were made available from published works [27 to 34] for a set of thirty species within the genus *Calypptogena*. Shell-growth parameters α , ρ , δ and shell-shape parameters E, D, K were then computed as indicated above. Quantitative data is summarized in Appendix at Table A.1.

Statistical analysis (linear correlations) were carried out using the software available in 'Excel'.

3. RESULTS

Two statistically significant covariances are recorded within *Calypptogena*, between shell-growth parameters α , ρ , δ ; depending on the range of value of the growth-dissymmetry index δ : (i) a *negative covariance* between the apical angle α and the differential growth index ρ , when δ is less than 2.2 ($r = 0.62$, $n = 12$, $df = 10$, $t = 2.50$, $p = 0.02$) ; (ii) a *positive covariance* between the apical angle α and the growth-dissymmetry index δ , when δ is larger than 2.2 ($r = 0.50$, $n = 18$, $df = 16$, $t = 2.30$, $p = 0.02$): Figs. 2 and 3.

According to Table 1, each of these two covariances is enough to make compatible (i) a *wider range* of interspecific differentiation of shell elongation E and (ii) a *narrower range* of interspecific differentiation of ventral convexity K (as compared to what would be the amplitudes of these ranges in the absence of covariance).

For higher values ($\delta > 2.2$) of the growth-dissymmetry index δ , the positive covariance between α and δ makes also compatible, in addition, a *narrower range* of interspecific differentiation of the dissymmetry of the shell outline D (as compared to what would be this range in the absence of covariance): Table 1.

Indeed, the comparison of the standard deviations (or the coefficients of variation) between the recorded results and the corresponding simulated situation for mutually independent growth-parameters (500 replicates) confirms these expected trends: Table 2. A

graphical representation of the same results is provided by Figs. 4 and 5. These graphical representations highlight the deformations of the actually occupied shell morphospace $\{E, D, K\}$ - induced by the negative covariance α - ρ and the positive covariance α - δ - as compared to what the situation would be if these covariances did not exist, i.e. if the variations of α , ρ , δ were mutually independent. These deformations of the actually occupied morphospace comprise, as already mentioned, a *widening of the range of variation of the elongation E* and a *restriction of the ranges of variation of the dissymmetry D and especially of the ventral convexity K*.

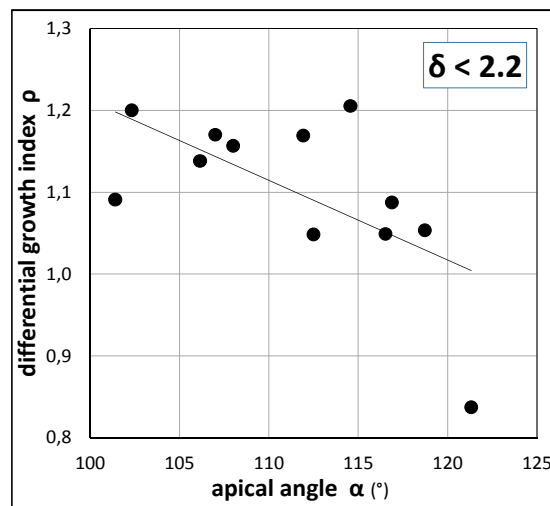


Fig. 2. Covariances between shell-growth parameters: negative covariance between α and ρ for $\delta < 2.2$. Details in text

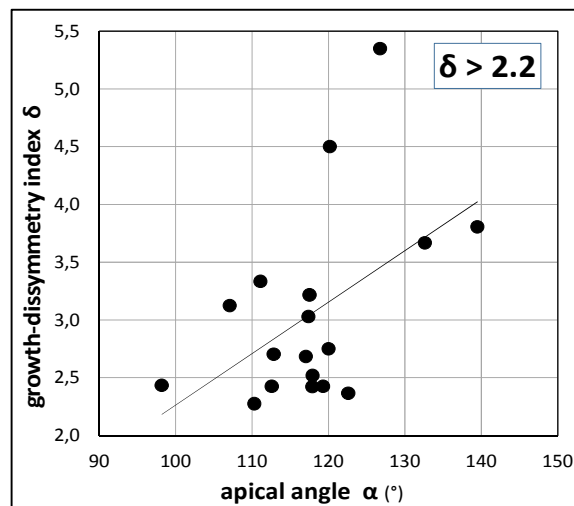


Fig. 3. Covariances between shell-growth parameters: positive covariance between α and δ for $\delta > 2.2$. Details in text

Table 2. The differences between actual results and simulated situations for mutually independent growth-parameters (500 replicates), are significant for both shell elongation E (Bartlett test on standard deviations, $n = 30$ & 500 , $\chi^2 = 4.72$, $p < 0.05$) and ventral convexity of shell outline K (Bartlett test on standard deviations, $n = 30$ & 500 , $\chi^2 = 8.02$, $p < 0.01$). For D the comparison is considered for $\delta > 2.2$, when the regulation involving the positive covariance between α and δ actually occurs; yet, due to the smaller number of species ($n = 18$ instead of 30), statistical significance is less easily reached (Bartlett test on standard deviations, $n = 18$ & 500 , $\chi^2 = 2.82$, $p < 0.10$)

	coeff. of var. E	coeff. of var. K	coeff. of var. D
as-recorded results	0.39	0.13	0.29
growth-parameters independent	0.31	0.21	0.39
ratio as-recorded / independent	1.26	0.62	0.74

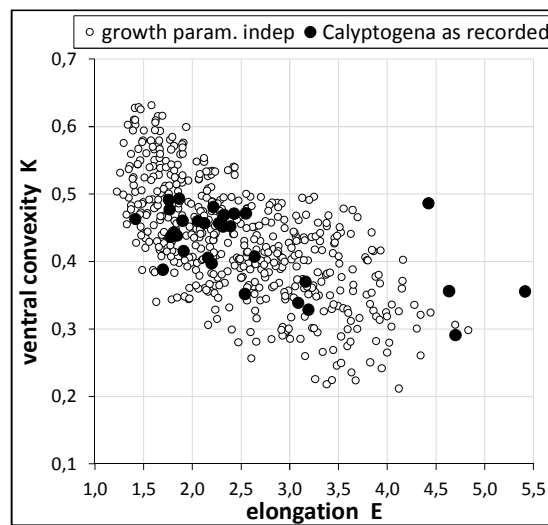


Fig. 4. The ranges of interspecific variations of shell-shape parameters E and K, as recorded in deep-sea *Calypptogena* and compared to the computed corresponding ranges if the growth parameters were mutually independent (simulation with 500 replicates). Comments in the text

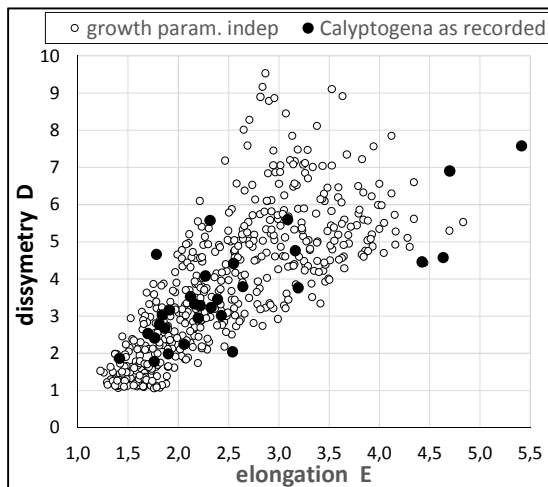


Fig. 5. The ranges of interspecific variation of shell-shape parameters E and D, as recorded in deep-sea *Calypptogena* and compared to the computed corresponding ranges if the growth parameters were mutually independent (simulation with 500 replicates). Comments in the text.

The range of interspecific variations of shell-elongation E is *extended* (ratio 1.26) while the range of interspecific variation of ventral convexity K of shell outline is *restricted* (ratio 0.62).

As expected also, the range of interspecific variation of the dissymmetry D of shell outline is *restricted* (ratio 0.74) for those species having high dissymmetrical growth ($\delta > 2.2$), although the smaller number of species involved in that case contributes to make statistical significance more difficult to reach.

4. DISCUSSION

Three functionally-relevant parameters, the shell elongation E, the shell dissymmetry D, and the ventral convexity K of shell contour, are strictly geometrically dependent upon the growth-related parameters α , ρ , δ , defined above, according to the system of three equations (A.1, A.2, A.3) provided in Appendix. The signs of the dependences of each of E, D, K, upon each of α , ρ , δ are respectively specified in Appendix, Table A.2. Due to this tightly entangled pattern of dependences, the respective ranges of variation of parameters E, D, K, not only depend on the amplitudes of variation of each of the growth parameters α , ρ , δ , but they *depends also* on the occurrence of (geometrically unexpected) *covariations* (either positive or negative) between these growth parameters, according to a pattern specified in Table 1 above.

Previous studies analysing the interspecific variations of shell shape within a series of bivalves genus (*Tellina*, *Donax*, *Gari*, *Abra*, *Macoma*) [1,2] have shown that, among the six types of covariances that may exist *a priori* between the three growth-related parameters α , ρ and δ , *only* the negative covariance between α and ρ was systematically recorded. In addition, recent (unpublished) work on interspecific variations within Mactridae, including clams species with high levels of shell-growth dissymmetry (δ up to 3.1) also confirms the occurrence of the negative covariance between α and ρ . The latter being, yet, symptomatically replaced by a positive covariance between α and δ for higher degrees of growth dissymmetry (an exception which, indeed, confirms the general “rule”, as shown below.

Accordingly, the following scheme accounts for the whole set of previously investigated groups of clams, prevailing in shallow waters:

- * The systematic occurrence of a *negative covariance between the apical angle α and the differential growth index ρ* , within the more common range of values of shell-growth dissymmetry δ ($\delta < 2.2$ in the studied series of clams);
- * The occurrence of a *positive covariance between the apical angle α and the growth-dissymmetry index δ* , for those species only, having high levels of growth dissymmetry δ ($\delta > 2.2$ in the studied series of clams).

As a result, one or the other of these two particular covariances suffice to make compatible:

- a significant *enlargement* of the range of interspecific variations of *shell elongation* E (as compared to what would be this range if the three growth parameters were varying independently, with unchanged amplitudes) ;
- with a severe *narrowing* of the range of inter-specific variations of the *ventral convexity* K of shell contour (as compared to what would be this range if the three growth parameters were varying independently, with unchanged amplitudes) ;
- and (specifically for *large levels of growth dissymmetry*) with a significant *narrowing* of the range of interspecific variations of the *dissymmetry of the shell contour* D (once more, as compared to what would be this range if the three growth parameters were varying independently, with unchanged amplitudes).

The next question to be considered now is whether these covariances between growth parameters would arguably result:

- From *developmental* constraints (other than the purely geometrical constraints which do not exist, as already mentioned, see [1,2]) applying directly on the growth process and then, controlling only *indirectly* the achieved shell shape, or,
- From *selective* constraints applying now *directly* to functionally-relevant shell shape parameters, resulting in the selective sorting of the more appropriate, best adapted shell shapes, according to the preferred *environmental* contexts of each species (the recorded covariances between growth parameters being, thus,

the indirect result of these selective pressures applying directly to shell-shape).

As already emphasised, distinguishing between *developmental* and *selective* constraints often reveals far from being easy [3]. Yet, considering the results reported above, one of these two options may tentatively be selected, based on the consistency and the parsimony of argumentations.

The “*developmental*” option apparently lacks of relevant arguments to explain the systematic occurrence of *only* one or the other of the two recorded types of covariations (among the six, *a priori* equally possible types) and, accordingly, would require *ad hoc* justifications; thus providing less parsimonious and less likely explanation.

The “*selective*” option profits by a series of seemingly more convincing arguments.

First, the pervasive trend for *widening* of the range of interspecific variations of shell elongation E, which is recorded in all the currently tested groups of bivalves, makes sense in the perspective of clear niche differentiation between species, given the functional importance attributed to shell elongation [4 to 24].

Second, if *intra*-specific variations, instead of interspecific, were addressed, it is a restriction of the range of variations of E, instead of an expansion, that would be expected. Accordingly, at the scale of *intra*-specific variations, a positive covariance between ρ and δ (which makes compatible a restriction of the ranges of variations of both the elongation E and the ventral convexity K: see Table 1) would be expected, instead of the negative covariance between α and ρ . *Interestingly*, on-going investigations on the *intra*-specific variations in fresh water bivalves (*Anodonta cygnea* and *Unio pictorum*) do actually *confirm the preceding expectation*, i.e., the occurrence of a significant positive covariance between ρ and δ [2].

Third, it seems logical that a selective pressure against excessive values of shell dissymmetry, if any, be mainly operational for those clams already showing high levels of dissymmetry, in order to limit extreme values of dissymmetry D. And this, indeed, is the case for highly dissymmetric species, within Mactridae and within *Calypptogena* as well. A positive covariance between α and δ specifically occurs in that case, which makes compatible, not only the expansion

of the range of E and the restriction of the range of K, but also, in addition, the restriction of the range of variations of D. Excessive growth dissymmetry δ means excessive values of shell dissymmetry D, which, in turn, may possibly become disadvantageous [25].

Fourth, the systematic trend for narrowing the range of variations of the ventral convexity (both intra- and inter-specific variations) may receive plausible explanations based on both shell mechanical resistance and valves-closing efficiency, as already argued previously [1,2].

All these facts, indeed, feature consistent and make sense with the hypothesis of selective pressures applying to shell-shape parameters. Even if none of these arguments might be considered totally demonstrative by itself; yet, taken altogether, they are gaining additional consistency and comply, as a whole, with the idea that the recorded interspecific covariations between shell-growth parameters may well result, indirectly, from environmentally-related, selective pressures, widening or narrowing the ranges of interspecific variations of the functionally-relevant, shell-shape parameters E, D, K.

Coming back to the focused genus *Calypptogena*, one particular question of interest, in the present context of study, was whether or not *deep-sea conditions* may be substantially less harsh to bivalves than conditions prevailing at more shallow depths, especially in terms of mechanical stresses upon shells, resulting from either predators or abiotic solicitations. As an optimal answer of bivalves shells to severe mechanical stresses is suspected to be the main cause of the restricted range of variation of the ventral convexity K, around its optimal value (near 0.4, according to [1,2]), hypothetically less harsh solicitations on shells in deep sea would then likely result in a relaxed control of the amplitude of variations of K. Thus leading, in turn, toward less strong covariances $\alpha - \rho$ and $\alpha - \delta$, since the occurrence of these covariances is only required to make compatible a significant expansion of the variability of E with a severe restriction of the variability of K.

Yet, on the contrary, the significant levels of covariances reported above for *Calypptogena*, (both negative covariance $\alpha - \rho$ and positive covariance $\alpha - \delta$), suggests that a selective pressure against excessive variations of the ventral convexity K, apart from its presumably

optimal value, *still holds for this group of deep-sea clams*. And, probably as well, for other groups of deep-sea bivalves, since similar conclusions merge from on-going analysis within the genus *Bathymodiolus*.

In fact, the aforementioned hypothesis of reduced environmental stresses under deep-sea conditions may well be inappropriate: the necessity of efficient structural defense against predators in *Calyptogena* has already been reported [35,36]. Predatory fishes and crabs are reported being found in high densities around hydrothermal vents [37] and cold-seep communities [38,39].

5. CONCLUSION

The respective amplitudes of interspecific variations of functionally-relevant parameters describing shell shape (elongation E, dissymmetry D, ventral convexity K) are mathematically connected to the degree and sign of covariances that may occur between shell-growth related parameters (apical angle α , differential growth index ρ , growth-dissymmetry index δ), due to the *rigid geometrical linkage* between the latter $\{\alpha, \rho, \delta\}$ and the former $\{E, D, K\}$, in Bivalves. Previous results from a series of investigations on interspecific variability of shell parameters within several groups of clams, characteristic of relatively *shallow waters* (*Tellina*, *Donax*, *Gari*, *Abra*, *Macoma*, *Mactra*, *Lutraria*, all belonging to Veneroidae) consistently reveal the occurrence of specific covariances between growth-related parameters (either a negative covariance $\alpha - \rho$ or a positive covariance $\alpha - \delta$), making compatible both enlarged interspecific variations of the shell elongation E and severely restricted interspecific variations of the ventral convexity K.

Here, in the *deep-sea* clams' genus *Calyptogena*, the same combination of interspecific covariations is recorded (among a series of others that would yet be *a priori* equally possible). This suggests, accordingly, that a similar combination of selective constraints, controlling the amplitudes of interspecific variations of the functionally-relevant shell shape parameters E, D, K, is operational within deep-sea *Calyptogena* as well as among shallow-waters clams. Thus, although shallow and deep waters appears strongly different environments, the selective pressures that likely apply to functionally-relevant aspects of shell shape in Bivalves do not seem so different.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX

**Table A.1 - Growth and size parameters of shell contour
for the thirty species of *Calyptogena* (s.l.) considered in this study**

	L	V	V'	V''	$\alpha(^{\circ})$	ρ	δ	E	D	K
<i>Calyptogena birmani</i> Domaneschi & Lopes, 1990	78,5	54,0	63,0	36,0	101	1,09	1,75	1,70	2,54	0,39
<i>Calyptogena costaricana</i> Krylova & Sahling, 2006	61,5	37,5	44,5	27,0	117	1,05	1,65	1,90	1,99	0,46
<i>Calyptogena diagonalis</i> Barry & Kochevar, 1999	80,0	49,5	70,0	21,0	111	1,09	3,33	3,08	5,60	0,34
<i>Calyptogena elongata</i> Dall, 1916	62,0	38,5	51,0	19,0	117	1,10	2,68	2,64	3,80	0,41
<i>Calyptogena extenta</i> Krylova & Moskalev, 1996	152,0	82,5	126,5	34,5	133	1,02	3,67	4,63	4,58	0,36
<i>Calyptogena fausta</i> Okutani, Fujikura & Hashimoto, 1993	71,0	43,5	56,5	26,5	113	1,05	2,13	2,20	2,96	0,40
<i>Calyptogena fossajaponica</i> Okutani, Fujikura & Kojima, 2000	65,0	49,5	49,0	33,5	102	1,20	1,46	1,41	1,87	0,46
<i>Calyptogena gallardoi</i> Sellanes & Krylova, 2005	61,0	43,0	49,5	24,0	107	1,17	2,06	1,84	3,03	0,44
<i>Calyptogena goffrediae</i> Krylova & Sahling, 2006	65,0	45,5	50,5	25,0	115	1,21	2,02	1,86	2,68	0,49
<i>Calyptogena kaikoi</i> Okutani & Métivier, 1986	69,5	48,5	57,0	23,5	113	1,20	2,43	2,12	3,53	0,46
<i>Calyptogena kawamurai</i> Kuroda, 1943	103,5	72,0	82,5	42,0	108	1,16	1,96	1,81	2,78	0,44
<i>Calyptogena laubieri</i> Okutani & Métivier, 1986	68,0	46,5	54,5	22,5	118	1,21	2,42	2,21	3,28	0,48
<i>Calyptogena magnifica</i> Boss & Turner, 1980	119,0	56,5	85,5	49,5	121	0,84	1,73	2,54	2,05	0,35
<i>Calyptogena magnocultellus</i> Okutani, Kojima & Iwasaki, 2002	70,0	42,5	59,5	18,5	118	1,09	3,22	3,16	4,76	0,37
<i>Calyptogena makranensis</i> Krylova & Sahling, 2006	65,5	39,5	48,5	26,5	119	1,05	1,83	2,06	2,25	0,46
<i>Calyptogena nankaiensis</i> Okutani, Kojima & Ashi, 1996	71,0	54,5	62,5	20,0	107	1,32	3,13	2,31	5,58	0,45
<i>Calyptogena nautili</i> Okutani & Métivier, 1986	81,0	53,0	65,5	26,0	118	1,16	2,52	2,39	3,46	0,45
<i>Calyptogena novacula</i> (Krylova, Sahling & Janssen 2010)	66,0	37,5	58,5	13,0	120	1,05	4,50	4,70	6,91	0,29
<i>Calyptogena okutanii</i> Kojima & Ohta, 1997	71,5	47,0	57,0	23,5	119	1,17	2,43	2,32	3,24	0,47
<i>Calyptogena pacifica</i> Dall, 1891	63,5	51,0	56,0	23,0	98	1,29	2,43	1,78	4,67	0,44
<i>Calyptogena packardana</i> Barry, Kochevar, Baxter & Harrold, 1997	71,0	50,5	59,5	22,0	113	1,24	2,70	2,27	4,08	0,46
<i>Calyptogena phaseoliformis</i> Métivier, Okutani & Ohta, 1986	69,0	43,0	61,5	11,5	127	1,18	5,35	5,41	7,58	0,36
<i>Calyptogena rectimargo</i> Scarlato, 1981	62,0	39,0	48,5	20,5	123	1,13	2,37	2,43	3,02	0,47
<i>Calyptogena similis</i> Okutani, Kojima & Ashi, 1997	74,0	39,5	60,5	22,0	120	0,96	2,75	3,19	3,77	0,33
<i>Calyptogena solidissima</i> Okutani, Hashimoto & Fujikura, 1992	72,0	49,5	59,0	28,0	106	1,14	2,11	1,91	3,17	0,42
<i>Calyptogena southwardae</i> (Krylova, Sahling & Janssen 2010)	63,0	45,0	53,0	17,5	117	1,28	3,03	2,55	4,42	0,47
<i>Calyptogena soyoe</i> Okutani, 1957	71,0	46,0	58,0	25,5	110	1,10	2,27	2,16	3,34	0,41
<i>Calyptogena starobogatovi</i> Krylova & Sahling, 2006	64,0	40,5	45,0	29,5	117	1,09	1,53	1,76	1,79	0,49
<i>Calyptogena tsubasa</i> Okutani, Fujikura & Kojima, 2000	71,5	47,0	59,0	15,5	140	1,26	3,81	4,42	4,47	0,49
<i>Calyptogena valdiviae</i> (Thiele Jaekel, 1931)	60,0	41,5	46,0	25,0	112	1,17	1,84	1,76	2,42	0,48
				aver	115	1,14	2,57	2,55	3,653	0,426
				S.D.	8,74	0,10	0,89	1,00	1,421	0,055
				C.V.	0,076	0,09	0,346	0,392	0,389	0,130

**The geometrical linkage between the growth-based parameters α , ρ , δ
and the functionally-relevant parameters E, D, K,**

According to references [2,3]:

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

$$D = (\delta^2 - \delta \cdot \cos(\alpha)) / (1 - \delta \cdot \cos(\alpha)) \quad [A.2]$$

$$K = 1 - E \cdot \{ (X / (E \cdot \cos(\theta)))^2 - 0,25 \cdot [1 + (X / (E \cdot \cos(\theta)))^2] \}^{0.5} \quad [A.3]$$

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.

Table A.2 – The signs of the dependence of each of three *functionally-relevant* parameters E, D, K, upon each of three *growth-based* parameters α , ρ , δ , according to the system of equations above

	E	D	K
α	+	–	+
ρ	–	0	+
δ	+	+	–

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