

Adult Shell-size Regulation in Conspirally-coiled Shells: Evidence for a Widespread Negative Covariance between Whorls Growth-rate and the Final Number of Whorls in Land Snails

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Author's contribution

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

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ABSTRACT

As shown, in particular, by the late S.J. Gould, the involvement of a regulation process, aiming at limiting the range of intraspecific variations in adult shell size, in those land snail species with determinate growth, can be indirectly, but conveniently, diagnosed by highlighting a negative covariance between the whorls growth-rate and the whorls number reached at adulthood. However, up to now, such kind of regulation had only been demonstrated in very few cases among land snails and shelled Gastropods in general. Accordingly, quite more extensive checking is required, across both the taxonomic spectrum and the geometrical range of shell profiles. The present report is a very preliminary contribution addressing these issues, which have been neglected for too long. Considering a still limited number of eight species, yet largely encompassing both taxonomic range and shell profiles, it is shown that strong negative covariances between whorls growth-rate and whorls number are systematically highlighted, thereby supporting the involvement of an efficient regulation process of adult shell size and shape in each eight species. Moreover, the degree of regulation of the adult shell size has been quantified and this regulation proves being remarkably effective as a whole, while yet remaining highly species-specific, with very significant disparities among species – and this, somewhat surprisingly, being quite irrespective of the type of geometrical profiles of shells, among the studied species.

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1. INTRODUCTION

Many animals exhibit determinate-growth, that is the adult body size of individuals belonging to a given species is usually constrained to remain within a more or less narrow, definite range of values, proper to the species. Many species of conispirally-coiled shelled Gastropods, in particular land snails, show determinate growth. Although shell volume not necessarily strictly identifies to soft body volume in land snails, the former usually tightly reflects the latter. And in particular, the overall shell morphometry (either shell height or shell diameter) exhibits a determinate growth as well, directly answering the determinate growth of its dweller.

In typically conispirally coiled shells, the overall shell size depends on the combination of three main factors: (i) the size of the first whorl, (ii) the expanding ratio of the section of the (exponentially growing) successive whorls and (iii) the achieved number 'n_a' of whorls at adult stage ("fully blown" shell) [1].

One may conveniently combine the two first contributions in a "shell growth parameter" here labelled as 'γ' (see Appendix for its definition and computation method). So that a given overall shell size may be achieved by various – negatively covariant – combinations of n_a and γ values. What GOODFRIEND [1] comments in more literal terms as "a given size may be achieved by few whorls which expand rapidly or by numerous whorls that expand slowly". GOULD [2] said substantially the same when pointing out that "shell may reach larger size either by growing more whorls or by growing larger whorls".

This implies, in turn, that a *negative covariance* is expected to occur between n_a and γ if a regulation process is involved. The latter aiming at constraining the overall shell-size to remain within a limited – species specific – range. Accordingly, actually recording a *negative covariance* between n_a and γ would thus support the involvement of such a regulation process. And would thus aptly serve as a *diagnostic criterium* for this regulating process, as GOULD had shown for the land snail genus *Cerion* [2-5].

It does not appear, however, that the issue has been addressed much further, following the seminal investigations of GOULD and coworkers (but yet see punctual reports [6-8]). And this

neglect despite the interest that there would be to verify that, beyond the case of *Cerion*, the tendency to such negative covariances would, in fact, be quite more widespread among land snail species, as can be expected.

The present work aims at contributing to such desirable further investigations, by considering eight land snail species, more or less commonly encountered in France.

2. MATERIALS AND METHODS

Eight populations were sampled for the eight following species, among which three have globular shells, one has discoidal shell and four have more or less elongate shells:

* *Cepaea nemoralis* (Linneaus 1758) : 103 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Cornu aspersum* (O.F. Müller 1774) : 33 sampled adult individuals, located at Salins-les-Bains (Jura department, Franche-Comté);

* *Monacha cartusiana* (O.F. Müller 1774) : 115 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Helicodonta obvoluta* (O.F. Müller 1774) : 83 sampled adult individuals, located at Blois-sur-Seille (Jura department, Franche-Comté);

* *Pomatias elegans* (O.F. Müller 1774) : 110 sampled adult individuals, located at Saint Vallerin (Saône & Loire department, south Burgundy);

* *Chondrula tridens* (O.F. Müller 1774) : 51 sampled adult individuals, located at Germagny (Saône & Loire department, south Burgundy);

* *Ena montana* (Draparnaud 1801) : 28 sampled adult individuals, located at Val-Suzon (Côte d'Or department, central Burgundy);

* *Zebrina detrita* (O.F. Müller 1774) : 43 sampled adult individuals, located at Le Parrotier (Vaucluse department, Provence).

For each examined shell, both the number of whorls n_a and the shell size (diameter D_a or height H_a) were measured:

- the shell size by using a numeric calliper (to the precision of 1/10 mm);
- the number of whorls by careful examination of the shell, examined from the apex, according to the procedure prescribed by KERNEY & CAMERON [9], using a stereo-microscope at moderate magnification, a procedure which typically allows reaching a precision at the level of 1/10 whorl revolution. Subsequently, the differential growth parameter 'γ' is measured according to the procedure originally described in BÉGUINOT [6,7] and briefly recalled below, in the Appendix.

Besides the number of whorls n_a and the overall shell size at adulthood (i.e. shell diameter D_a for globular or discoidal shells or shell height H_a for elongate shells), the growth parameter γ (which, together with n_a , determine the adult shell size) is thus conveniently and easily made available for each individual shell in the population under study.

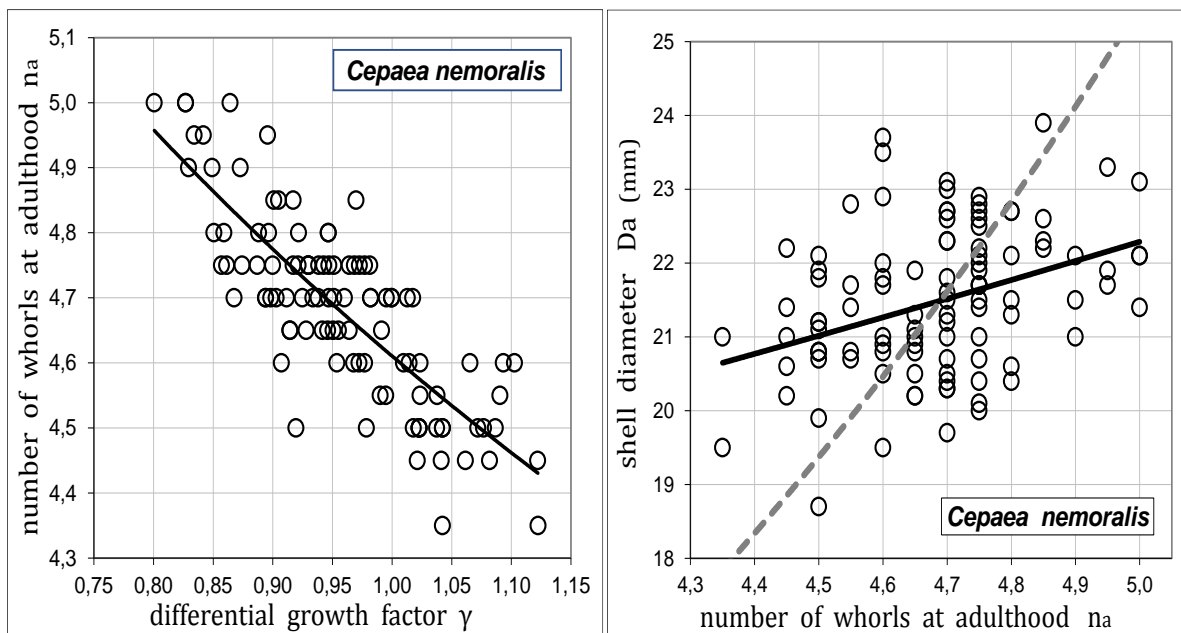
As regards the estimations of the statistical significance of the reported results, the *Student t-test* was used to characterize both:

- the degree of significance of the reported negative correlation between n_a and γ and
- the degree of significance of the reported reduction of the slope of the dependence of the shell size (D_a or H_a) upon the number of whorls n_a , as compared to what this slope would be in the absence of regulation. Reduction which thereby highlights the degree of efficiency of the regulation of adult shell size

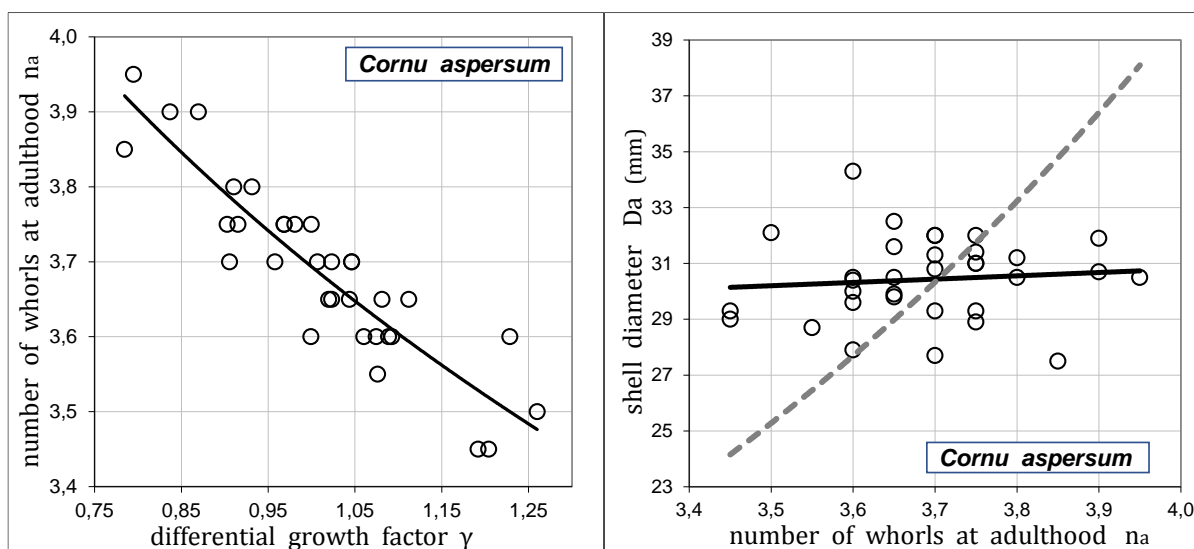
3. RESULTS

For each of the eight studied species, the series of Figs. 1 to 16 provide:

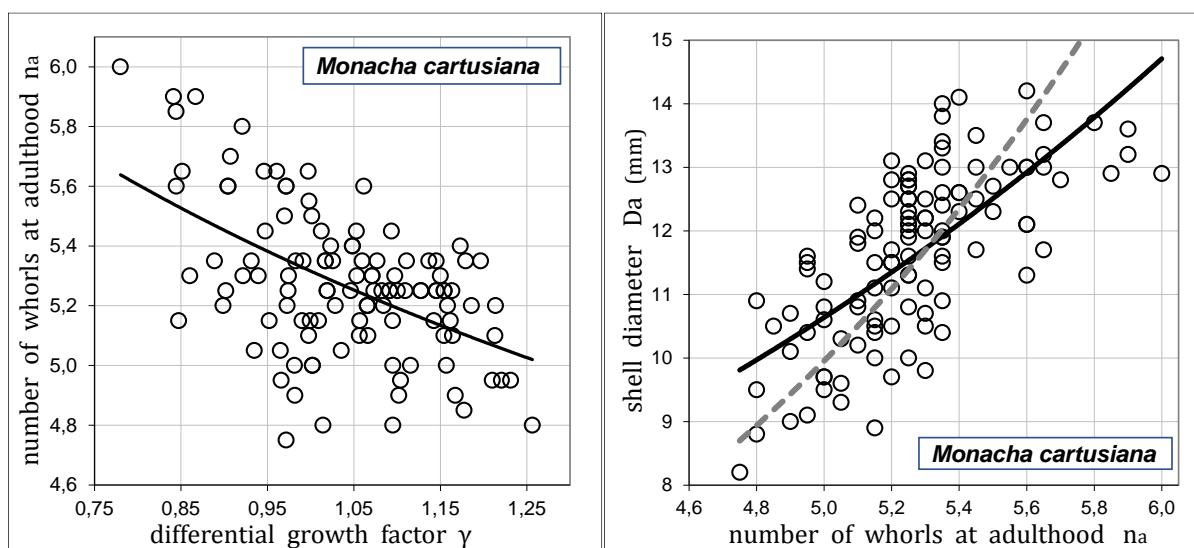
- on the *left*, the regression of the number of whorls at adult stage n_a against the differential growth parameter γ , computed as described in Appendix. Allowing thus to check for the occurrence of a statistically significant negative covariance between both parameters n_a and γ – as such symptomatic of the involvement of a regulation process limiting the range of variation of the overall shell size at adulthood;



Figs. 1 & 2. Shell size regulation in a population of 103 individuals of the land snail *Cepaea nemoralis*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.82$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell diameter plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 4.73 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 14.5$, d.d.l = 101, $p < 0.0001$.



Figs. 3 & 4. Shell size regulation in a population of 33 individuals of the land snail *Cornu aspersum*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.90$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell diameter plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be **24.3 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 11.8$, d.d.l = 31, $p < 0.0001$.**



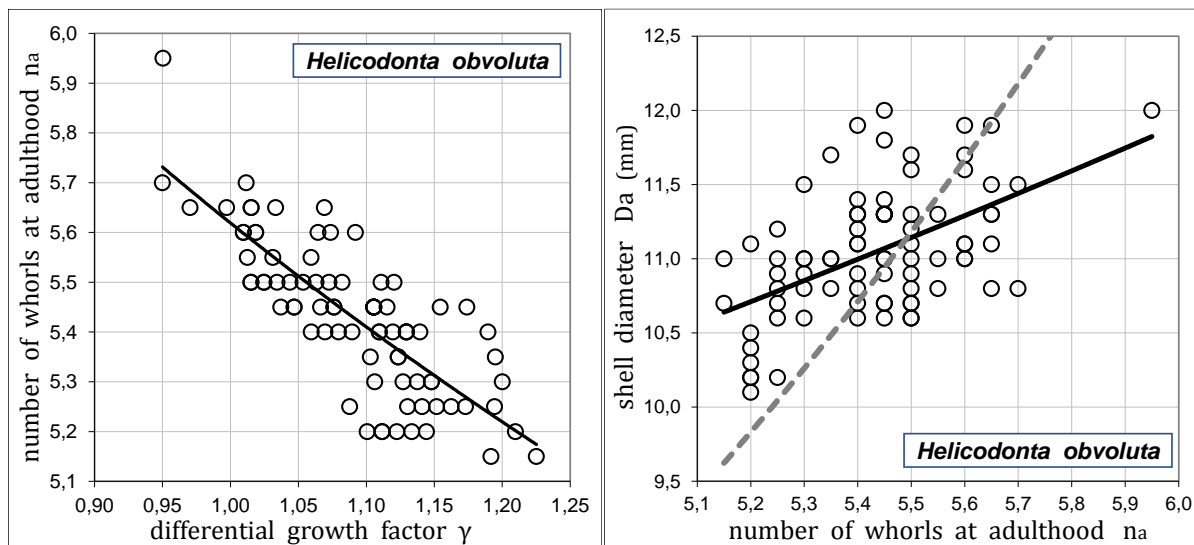
Figs. 5 & 6. Shell size regulation in a population of 115 individuals of the land snail *Monacha cartusiana*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.53$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell diameter plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be **1.75 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 7.59$, d.d.l = 113, $p < 0.0001$.**

– on the *right*, the overall shell size (D_a or H_a) plotted against the number of whorls at adult stage n_a . For comparison, is also provided in the same Figure, the variation of the overall shell size with n_a , computed for a single individual of

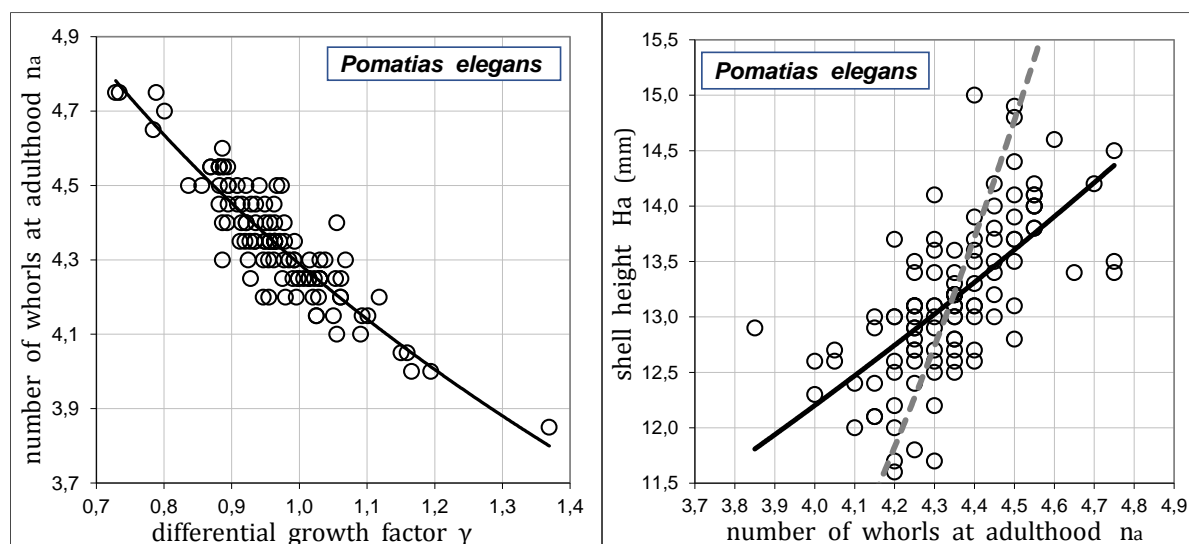
the species (dashed grey line), which is representative of the trend of variations of shell sizes with n_a if no regulation had taken place. Accordingly, the highlighted reduction of the slope of the dependence of shell size (solid line)

– as compared to what would be this slope in the absence of regulation (dashed grey line) – thus allows to appreciate the *degree of efficiency* of the process actually involved in the regulation of

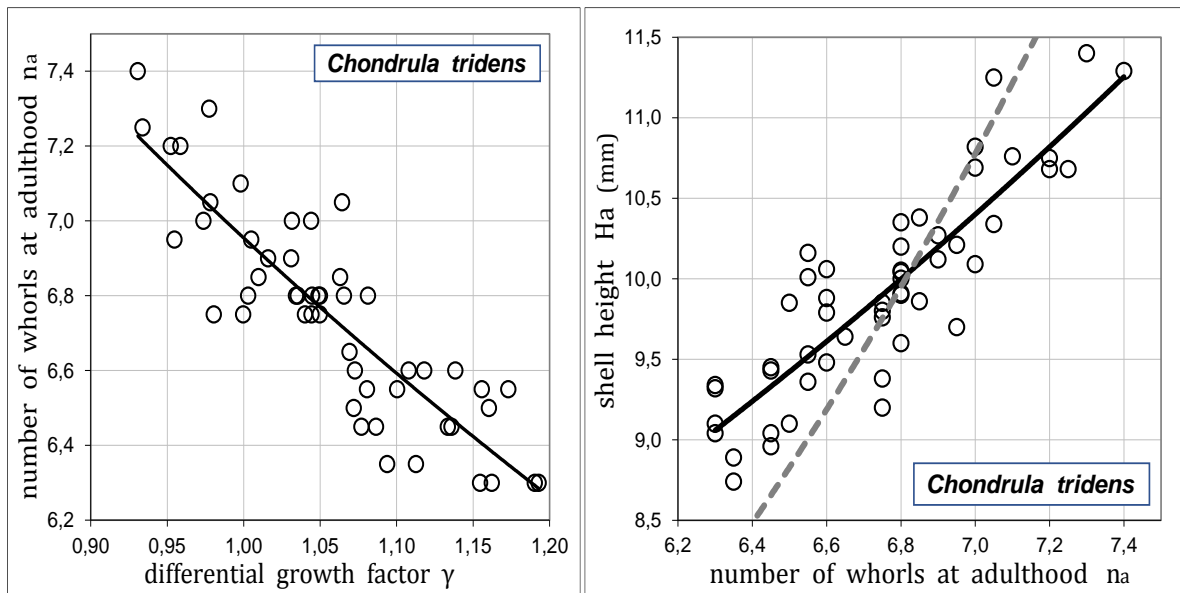
adult shell size. Being understood that an ideally perfect regulation would have led to a perfect invariance of the overall shell size with the number of whorls at adult stage.



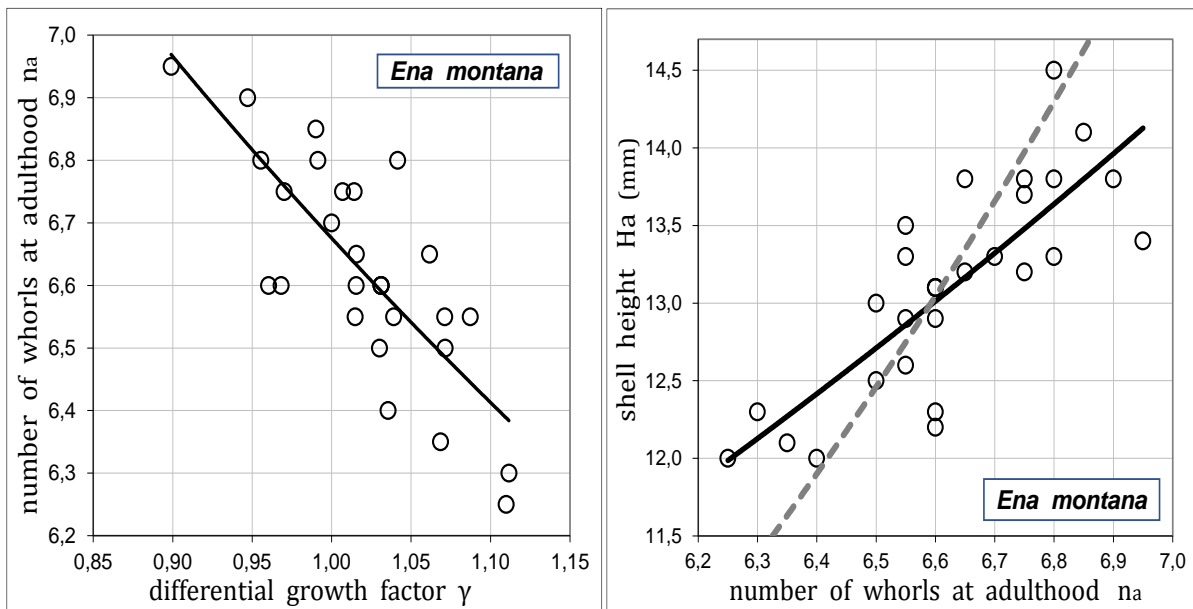
Figs. 7 & 8. Shell size regulation in a population of 83 individuals of the land snail *Helicodonta obvoluta*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.81$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell diameter plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 3.24 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 12.1$, d.d.l = 81, $p < 0.0001$.



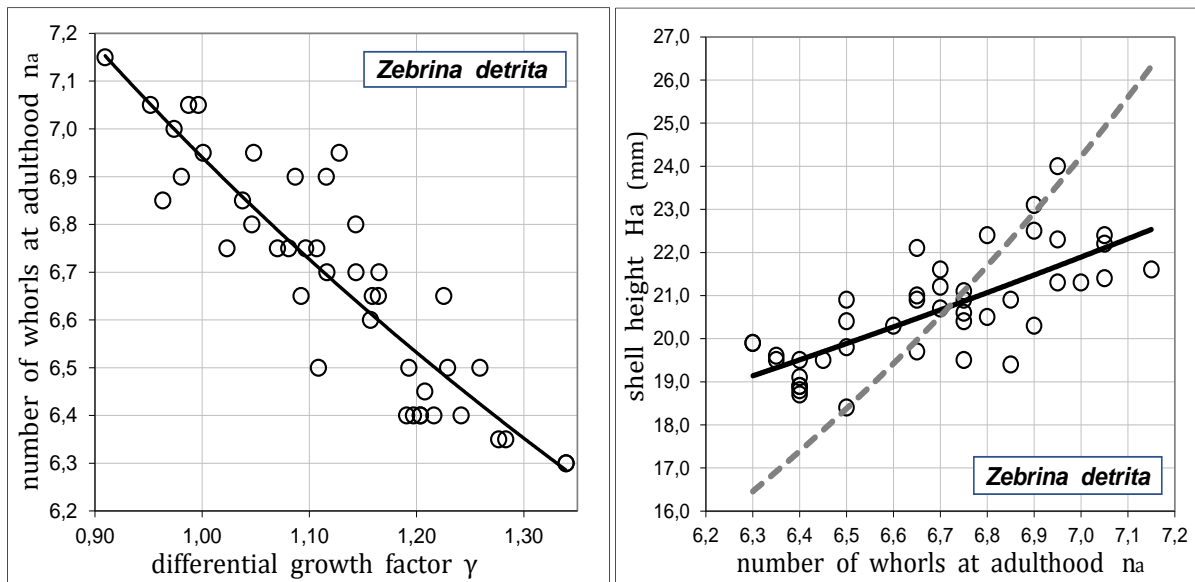
Figs. 9 & 10. Shell size regulation in a population of 110 individuals of the land snail *Pomatias elegans*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.90$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell height plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 3.43 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 22.1$, d.d.l = 108, $p < 0.0001$.



Figs. 11 & 12. Shell size regulation in a population of 51 individuals of the land snail *Chondrula tridens*. **Left:** negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.87$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. **Right:** shell height plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 2.00 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 12.5$, d.d.l = 49, $p < 0.0001$.



Figs. 13 & 14. Shell size regulation in a population of 28 individuals of the land snail *Ena montana*. **Left:** negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.79$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. **Right:** shell height plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 1.97 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 6.5$, d.d.l = 26, $p < 0.0001$.



Figs. 15 & 16. Shell size regulation in a population of 43 individuals of the land snail *Zebrina detrita*. Left: negative covariance between the number of whorls at adulthood n_a and the differential growth factor γ ($r = -0.90$, $p < 0.0001$), symptomatic of the resulting regulation of shell size. Right: shell height plotted against the number of whorls n_a ; the slope of the regression (solid line) turns out to be 2.85 times lower than it would be if no regulation of the shell size had actually occurred (dashed line): $t = 12.8$, d.d.l = 41, $p < 0.0001$.

4. DISCUSSION

Body size is, perhaps, the most straightforwardly apparent characteristic of an organism [10]. And, for those species with determinate growth, as is the case for many land snail species, this stands more particularly for the *adult body size* and, by extension, stands as well for the shell size reached at adulthood (i.e., the size of “fully blown” shell). Generally speaking, for species with determinate growth, the adult body size is regulated by mechanisms that both control: (i) the *rate of growth* and (ii) the *duration of growth* [11].

Now, as regards fully grown conispirally-coiled shells, having reach the adult stage, it goes natural (and it is far more convenient in practice) to reformulate the preceding assertion as: “the size reached by adult conispirally-coiled shells, is regulated by mechanisms that both control: (i) the *whorls’ growth* parameter (here measured by the index γ) and (ii) the *number of whorls* n_a .”

And this, independently of whether or not the number of whorls n_a indeed results of growth duration (as is often admitted but is, yet, unlikely to be always the case).

Still generally speaking, it is considered quite common, in studies of life-history plasticity, to

find a *negative relationship* between the age of transition to adulthood and the growth conditions under which individuals are developing, with, in particular, higher growth rate typically resulting in earlier access to adulthood [12]. Accordingly, returning once again to conispirally-coiled shells, a *negative covariance* is expected to occur between *whorls growth rate* all along shell development and the number of whorls of fully blown shells. As already emphasized, such kind of negative covariance was highlighted in particular in the seminal reports by GOULD for the land snail genus *Cerion*. It seems logical to speculate that a same kind of negative covariance is to be encountered – more or less strong – in most, if not all, conispirally-coiled shells, among land snails. This seems, however, having been checked only in very few cases [6-8] as already mentioned. So that there is need to expand investigations to quite a larger range of land snail taxa – and this all the more that there may be some suspicion that the rule could possibly met some exceptions. For example, BAUR [13] reports that in the minute land snail species *Chondrina clienta*, the individuals of a given size all had the same whorl number, which would imply that either (i) no variability in growth rate actually takes place within populations of *Chondrina clienta* (which would seem rather unusual and unlikely) or, alternatively, that in

fact, no negative covariance occurs between γ and n_a in this particular species.

Hence, a still further incentive to investigate more widely and deeply on the subject. Which was the purpose of this preliminary contribution in this respect.

The eight investigated species studied above were therefore chosen as:

(i) covering a broad taxonomic spectrum (including one species of Prosobranchia, which are comparatively very few among land snails);

(ii) extended to the whole range of conspirally-coiled profiles, from globular, then discoid, up to more or less elongate shells, - thereby attempting to derive more general deductions;

(iii) corresponding to rather common species, in order to gain easier access to relatively numerous local populations of individuals, so as to identify statistically significant trends.

As regards the *negative covariance* between the differential growth index γ and the number of whorls n_a at adult stage (considered as being symptomatic of the involvement of a regulation process controlling the adult soft-body size of land snails and thus resonating upon the regulation of fully blown shell size), *highly statistically-significant confirmations of such involvement* is obtained for each of all eight species ($p < 0.0001$ in all cases).

However, if the indirect evidence has thus been provided of the implication of a regulatory process being operational in each of the eight species, it still remains to evaluate the degree of efficiency of this regulation, in terms of the degree of limitation of the range of variation of the adult shell size within a same population of a same given species. The reported results in Figs. 2, 4, 6, 8, 10, 12, 14 and 18 show that the average slope of the regression of the adult shell size against the number of whorls is always *markedly lower* than would be expected in the absence of regulation. With, as a consequence, *quite a narrower scatter* of fully blown shell sizes than if no regulation had actually occur. The slopes, however, never fall to zero, that is to an ideally-perfect regulation. Thus, the regulation, however strong as it can be, yet remains only partial. But nonetheless rather significant since – as compared to inoperative regulation – the slopes are reduced by a factor comprised

between 1.75 (for *Monacha cartusiana*) and 24.3 (for *Cornu aspersum*) with an average factor of reduction of 5.53 (arithmetically) or 3.54 (geometrically, which is more relevant for a ratio). Thus, with an average trend for the shrinkage of the regression slope by *more than a factor 3*, the efficiency of the regulation of the adult shell size in these eight investigated species proves being globally very determinant, although remaining not ideally perfect. Besides, reaching ideal perfection (i.e., the regression slope falling to zero) would not, in fact, so markedly improve the efficiency because the corresponding gain would be partly buffered by the unavoidable residual scatter of individual shell sizes at any given value of n_a , as apparent in all cases.

In addition, it seems that the efficiency of the regulation process might well be higher when *combining both* the shell height *and* the shell width (for example via the [computed shell-volume]^{1/3}), rather than by uniquely involving *either* the height *or* the diameter, as considered above (unpublished results with the land snails *Pomatias elegans*, *Chondrula tridens* and *Ena montana*). This, indeed, is not surprising but would nevertheless require further investigations.

Now – as efficient as shell-size regulation turns out to be – it yet remains that the level of regulation efficiency can *differ very significantly, depending on species identity*, as clearly exemplified when comparing the eight studied species with each other.

5. CONCLUSION

Beyond the demonstration of the likely systematic occurrence of an efficient regulation process constraining adult shell-size variations within species in land snails (which indeed was expected), it is the markedly *species-specific* character of the *degree of efficiency* of this regulation which features as the main lesson of the present study – as highlighted by the rather *strong disparity* between the degrees of regulation efficiency reported above among the eight studied species.

In addition, it turns out, also, that the types of profile of shells do not seem to be discriminant in this respect, contrary to what might have been hypothesized. Thus, the two species exhibiting respectively the higher and the lower degrees of regulation efficiency, *Cornu aspersum* and *Monacha cartusiana*, both belong, yet, to the *same type* of globular profiles, while the shells

with discoid or more or less elongated profiles are in intermediate positions as regards the degrees of regulation efficiency.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX

Disentangling and quantifying the respective contributions of growth parameters 'n_a' and 'γ' to the overall shell-size in conispirally-coiled shells

For those gastropod species with shell coiling geometry fairly approaching a conispiral profile and approximately answering the ideal exponential growth model (i.e. logarithmic spiral coiling), the contribution, δ_i , of whorl number 'i' to the overall shell dimensions Δ (shell height or shell width) is, according to [14-21]:

$$\Delta_i = \delta_1 \cdot \varepsilon^{(i-1)}$$

where:

- δ_1 is the contribution of whorl number one;
- ε is the rate of whorl expansion (and, as well, the ratio between the contributions of two successive whorls: $\varepsilon = \delta_{i+1}/\delta_i$).

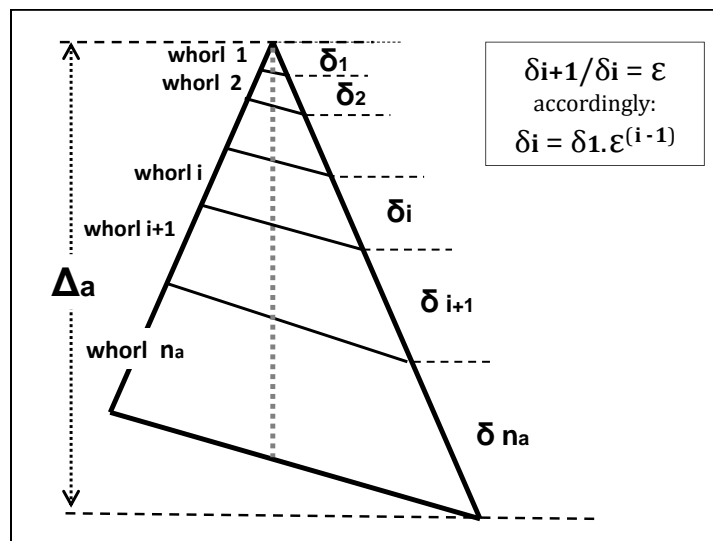


Fig. A1. Schematic sketch of the section of an ideally conispirally coiled shell, showing the morphometric parameters involved in this study: n_a the number of whorls at adult stage; δ_i the contribution to shell-height of the ith whorl; ε the ratio of expansion of whorl section per revolution; Δ_a the final, adult shell size. Here, for an elongated shell shape, the overall shell size Δ_a is identified to shell height. While, a globular or discoidal shell shape would answer a similar schematic sketch with, accordingly, the overall shell size taken as the shell diameter.

Then, for a shell with n whorls, the shell size is the sum of these n successive contributions:

$$\Delta(n) = \sum_{i=1 \text{ to } n} (\delta_i) = \sum_{i=1 \text{ to } n} (\delta_1 \cdot \varepsilon^{(i-1)}) = [\delta_1 / (\varepsilon - 1)] \cdot (\varepsilon^n - 1) \quad (\text{A1})$$

$$\Delta(n) = c \cdot (\varepsilon^n - 1) \quad (\text{A1 bis})$$

with $\sum_{i=1 \text{ to } n}$ designating the summation extended to the n whorls of the shell and $c = [\delta_1 / (\varepsilon - 1)]$

The size of a shell having reached its adult stage, with a corresponding number n_a of whorls, is thus $\Delta_a (= \Delta(n_a))$ defined as follows:

$$\Delta_a = c \cdot (\varepsilon^{n_a} - 1) = [\delta_1 / (\varepsilon - 1)] \cdot (\varepsilon^{n_a} - 1) \quad (\text{A2})$$

Some more or less limited discrepancies may exist, of course, between the specific reality and the idealised, classical conispiral model involving whorls contributions *regularly increasing exponentially* with the whorl numbering label. Yet, here, focus is placed on the inter-individual *variability* and we are dealing with *variations* of shell size rather than with the estimates of size itself. As *first order* discrepancy regarding the *absolute* values taken by a parameter have only *second-order* influence upon the inter-individual *variations* of this parameter, it follows that using the idealised classical model remains appropriate to the subject under study here.

Defining a synthetic parameter ‘ γ ’ accounting for the combined contributions of growth parameters $\bar{\delta}_1$ and ε

The parameters $\bar{\delta}_1$ and ε govern together the *geometry of progressive shell development* (equation A2). Either or both parameters are subjected to intra-specific (i.e. inter-individual) variability, inducing in turn, an inter-individual variability of the shell size reached at any *given* number of whorls. As for any other phenotypic character, the intra-specific variability of shell growth parameters may conveniently be considered by reference to a conventionally defined “type specimen” (characterised by the referential values $\bar{\delta}_1^*$ and ε^* of parameters $\bar{\delta}_1$ and ε respectively, for the species under consideration).

The consequence on the adult-shell size of the intra-specific variability of growth parameters $\bar{\delta}_1$ and/or ε may then be quantified by the variations of the ratio:

$$\gamma = \Delta_a / \Delta_a^* \quad (\text{A3})$$

where:

- Δ_a is the adult size of the shell under consideration;

- Δ_a^* is the size that the *type specimen* (or any specimen having the same parameters $\bar{\delta}_1^*$ and ε^*) would take for a number of whorls *equal* to the number of whorls n_a of the adult-shell under consideration. The value of Δ_a^* is provided by equation (A2) with $\bar{\delta}_1 = \bar{\delta}_1^*$ and $\varepsilon = \varepsilon^*$:

$$\Delta_a^* = c^* \cdot (\varepsilon^{*n_a} - 1), \text{ with } c^* = \bar{\delta}_1^* / (\varepsilon^* - 1) \quad (\text{A4})$$

Thus defined, the parameter γ *integrates* the influence of $\bar{\delta}_1$ and ε on the geometrical development of the shell *all along* its ontogeny (*via* ε) and since its very beginning (*via* $\bar{\delta}_1$). Parameter γ may thus be designed as “*individual growth factor*” or, focussing here upon the intra-specific variability, as “*differential growth factor*”. Although there is, of course, no possibility of disentangling the respective contributions to γ of parameters $\bar{\delta}_1$ and ε , it remains that γ conveniently accounts for the *combined* contributions of $\bar{\delta}_1$ and ε to the overall shell size Δ , at any given value of the number of whorls, by reference to a freely chosen type specimen of the corresponding species.

A.3 – Practical procedure

Consider a population of adult individuals (belonging to a same species having been previously typified with a referential “*type specimen*”, in terms of the values of $\bar{\delta}_1^*$ and ε^*) submitted to a morphometric study. For each individual, both the number of whorls n_a and the shell size Δ_a are measured, the later by using a numeric calliper and the former by careful examination from shell apex (according to procedure by KERNEY & CAMERON [9] under stereo-microscope at moderate magnification, typically allowing a precision at a level of 1/10 whorl revolution. Now, introducing the measured values $\bar{\delta}_1^*$ and ε^* in equation (A4) provides the value of Δ_a^* . Then, introducing the measured value of Δ_a in equation (A3) provides the values of the differential growth index γ for each of the individual shells under study. Thus, the growth components n_a and γ (that have together determined the adult shell size Δ_a) are thus *conveniently and easily made available for each member individual* of the population under study.

We thus dispose of a tool to give a more “quantitative turn” to the adage by GOULD, already quoted in Introduction: that is, conispirally-coiled Gastropods “may reach larger size either by growing more whorls (*i.e.* by growing larger n_a) or by growing larger whorls (*i.e.* by exhibiting larger γ)”.

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