



Evolution of morphological allometry

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Evolution of morphological allometry

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Abstract

Allometry refers to the power-law relationship that often occurs between body parts and total body size. Whether measured during growth (ontogenetic allometry), among individuals at similar developmental stage (static allometry) or among populations or species (evolutionary allometry), allometric relationships are often surprisingly tight, and relatively invariant. Consequently, it has been suggested that allometry could constrain phenotypic evolution, that is, force evolving species along fixed trajectories. Alternatively allometric relationship may result from selection. Despite nearly a century of active research on allometry, distinguishing between these two alternatives remains difficult partly due to the use of a broad sense definition of allometry where the meaning of relative growth was lost. Focusing on the original narrow-sense definition of allometry, we review evidence for and against the “allometry as a constraint” hypothesis. Although the low evolvability of the static allometric slopes observed in some studies suggests a possible constraining effect of this parameter on phenotypic evolution, the nearly complete absence of knowledge about selection on allometry prevents any firm conclusion.

Keywords: adaptation, microevolution, macroevolution, evolutionary constraint

Abstract: 166 words; Main text: 5565 words ; 1 table; 5 figures; 2 boxes

42 Introduction

43 Allometry is the study of the relationship between body size and other organismal traits.
44 Allometry is important because variation in a wide variety of morphological, physiological
45 and life history traits are highly correlated with organism size [1,2,3]. These relationships
46 generate intuitive hypotheses for understanding trait variation; for example, the fact that
47 humans are larger than mice can be used to explain why the basal metabolic rate of a human
48 is much higher than the basal metabolic rate of a mouse. In most cases, traits show a non-
49 linear relationship with size that is accurately captured by a power relationship of the form $z =$
50 ax^b , where the trait value is z , the organism size is x , and a and b are parameters of the
51 relationship. If $b = 1$, the relationship between the trait and size is linear, a condition referred
52 to as isometry. When $b \neq 1$, the relationship is non-linear on the arithmetic scale. For
53 example, the basal metabolic rate in mammals scales with body mass with a coefficient $b \approx$
54 0.71 [4]; as a result, for every unit increase in mass, a larger organism will have a smaller
55 increase in basal metabolic rate than a smaller organism. Consequently, humans have a basal
56 metabolic rate 5 to 10 times smaller than a mouse when corrected for body size. The ubiquity
57 of these power-law relationships has led biologists to refer to them as allometric relationships.
58 Analyzed on log-transformed data these relationships become linear: $\log(z) = \log(a) +$
59 $b \times \log(x)$, where $\log(a)$ and b represent the allometric intercept and slope, respectively.
60 Because size varies during growth, among individuals of similar age, or among populations or
61 species, three types of allometry have been defined. Ontogenetic allometry refers to the
62 allometric relationship when size varies during growth. Static allometry refers to the
63 relationship when size varies among individuals measured at a similar developmental stage
64 and evolutionary allometry refers to the allometric relationship when size varies among
65 population or species means.
66 Allometric relationships often fit very precisely when the range of sizes is large, which

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is usually the case at the ontogenetic and evolutionary levels. Furthermore, ontogenetic and static allometric slopes usually vary little among closely related species. These observations have led several authors to suggest that allometric slopes most likely reflect strong physical, physiological or biological mechanisms that somehow constrain the rate and direction of evolution [5,6,7]. For example, the scaling of metabolism with body size, referred to above, may be explained by the limits of diffusion through the limited surface area per volume of the larger human than the smaller mouse [8]. Accordingly, allometric relationships have been taken as prime evidence against the dominance of natural selection as an evolutionary force [9]. This constraint hypothesis has been widely accepted for physiological and life history traits [10,11], but has become more controversial for morphological traits.

The alternative to the constraint hypothesis of allometry is that natural selection persistently favors the particular power relationships between traits and size that are observed. This hypothesis is at least implicitly widely accepted in the traditional studies of functional allometry [2]. For example, the relationship between the cross-sectional area of the skeleton with body mass may be explained in terms of optimal allocation, balancing the chances of breakage – favoring a robust skeleton – with the costs of locomotion – favoring a lighter skeleton. Accordingly, several authors have suggested that allometric slope could evolve under selection [12,13,14,15]. In this context, the evolution of the static allometry of sexually selected traits has been a particularly popular topic. Secondary sexual displays have been predicted to evolve particularly steep slopes (i.e. positive allometry: $b > 1$) under handicap models [12,13,16,17,18], while genitalia are expected to show negative allometry ($b < 1$) due to stabilizing selection on trait size [14, 19, 20].

Optimally, it should be possible to distinguish between the constraint and selective explanations for allometry by quantifying both the selection forces and the evolvability of allometry (i.e. its capacity to evolve) and compare the predicted and observed patterns of

evolution in allometry. The general prediction is that a constrained slope will either be incapable of evolving (an absolute constraint, [21]), or that fitness will decrease so rapidly when moved away from the optimal value that the possible advantages of the altered slope would not outweigh the fitness costs. Unfortunately, despite renewed interest in allometry in the last two decades, progress in understanding the evolution of morphological allometry has been slow. A key reason for this is the rise of a ‘broad sense’ definition of allometry as any monotonic relationship between trait size and body size [22, 23] (Box 1). This divorces the study of scaling from the prevalence of power relationships (Box 2), and in particular from the centrality of the slope as the essence of allometry [24]. The result is a body of literature that has measured quantities that cannot be interpreted as parameters of a power relationship.

Our aim in the current contribution is therefore to define clear predictions concerning the constraint and selection hypotheses on morphological allometries and review the recent literature in the light of these predictions.

Evolutionary constraint and allometry

Evolutionary constraints are defined as any processes that preclude a trait from reaching a phenotypic optimum, or slow down its evolution towards this optimum [25]. Depending on the perspective and processes involved, many types of constraint have been defined [25,26]. Initially, allometry has been classified as developmental constraint, that is, constraint imposed by the developmental architecture in the production of variant phenotypes [27]. Although developmental constraints may themselves result from selection [28,29], they may still limit the direction of phenotypic evolution. Such perspective of allometry as developmental constraint corresponds to the view defended by early students of allometry and heterochrony [5, 6, 7, 30, 31], who explained patterns of species divergence by changes in timing or rate of development along constant ontogenetic processes.

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117 The introduction of the quantitative genetics framework in the study of allometry [32,
118 33, 34, 35] has shifted the hypothesis of allometry as a constraint from a developmental to a
119 genetic perspective. Genetic constraints occur when the amount or pattern of genetic variation
120 limits or channels the response to selection. Although these two perspectives are intimately
121 linked because genetic constraints often result from developmental constraints, this change in
122 perspective may have weakened the constraint hypothesis, given the ubiquity of genetic
123 variation generally found [36]. But more recently, the hypothesis of constraint due to low
124 genetic variation has been refueled by the realization that genetic correlations among traits
125 due to pleiotropy could seriously influence the direction of phenotypic evolution [21, 37, 38,
126 39, 40, 41, 42, 43], allometry being a perfect example of such a constraint.

127 Importantly, the quantitative genetics approach of allometry underlines the fact that
128 understanding the evolution of allometry, and testing whether allometry represents an
129 evolutionary constraint requires quantifying the evolvability of allometry and comparing the
130 observed evolutionary patterns with those patterns expected under specific selection
131 pressures. If we are to test the “allometry as a constraint” hypothesis, we should therefore
132 answer the following questions; 1) Is allometry evolvable? 2) Does allometry constrains
133 patterns of phenotypic evolution? Static allometry represents the pivotal level at which these
134 questions should be asked. Indeed, it is the level at which developmental constraints will be
135 expressed, and patterns of static allometry will allow us to make predictions about phenotypic
136 evolution.

137

138 Is static allometry evolvable?

139 Testing whether a trait is evolvable or not may be achieved by quantifying either its
140 propensity to vary (i.e. its evolvability; [44]), or its evolution, that is, quantifying the changes
141 in the trait when selected. In the following, after considering the possible sources of constraint

and selection acting on static allometry, we review evidence for both the evolution of static allometry at the microevolutionary scale and its evolvability.

Sources of constraint

Evolution of static allometry depends on the evolution of the static allometric slopes and intercepts. One key challenge is that an individual organism expresses neither a slope nor an intercept. Therefore, if these parameters represent quantitative traits, estimating their genetic variation requires clonal organisms where genetically similar organisms of different size can be measured, measurement of "allometries" across relatives in family groups, or across modules in modular organisms. Alternatively, because ontogenetic, static and evolutionary allometries of morphological traits all result from a single process, namely growth, testing the evolvability of static allometry could be achieved by estimating the evolvability of the growth processes that generate covariance among traits. Several growth models have been suggested to explain how static allometry is generated from simple growth patterns [5, 16, 31, 45, 46]. Using these models one can identify possible constraints on the variation of static allometry.

From Huxley's (1932) [5] model of relative growth (Box 1), it can be shown that when two traits present an ontogenetic allometry such as $z = a + bx$, with x and z varying during growth, the static allometric slope at any specific time t can be expressed as:

$$b_s = \bar{b} + \frac{Cov(x_t, a) + \bar{x}_t Cov(x_t, b)}{Var(x)}, \tag{1}$$

where \bar{b} is the ontogenetic allometric slope averaged across all individuals, (i.e. the mean ontogenetic allometry of the population), and \bar{x}_t , the mean body size at time t [47]. This shows that the static allometric slope is affected by both the average slope of the ontogenetic

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allometry and the covariance between the parameters of the ontogenetic allometry (slope and intercept) and body size. Similarly, parameters of the ontogenetic allometry will affect the average value of the trait over the entire range of sizes. This effect can be expressed in terms of the mean trait at the population mean body size, \bar{x}_t , in the following way:

$$\bar{z}_t = \bar{a} + E(bx_t) = \bar{a} + \bar{b}\bar{x}_t + \sigma(b, x_t), \quad (2)$$

where \bar{a} is the average ontogenetic intercept across all individuals. Therefore a positive covariance between the ontogenetic slope and body size at stage t will increase the mean value, while a negative covariance will decrease it. This model illustrates how variation in the static allometric slope and intercept can be generated by variation of the ontogenetic parameters. Importantly, it also shows that when ontogenetic and static allometries are different ($Cov(x_t, b) \neq 0$ or $Cov(x_t, a) \neq 0$), invariance of static allometry across populations with different mean body size implies changes in the ontogenetic parameters. Comparing ontogenetic and static allometries and estimating the variation of the ontogenetic parameters should therefore provide valuable insight in the possibility for static allometry to evolve.

Different body parts do not always grow simultaneously; some traits grow most rapidly early in development (e.g. mammalian brain, [48]) while others continue to grow after body mass has stopped increasing (e.g. appendages in holometabolous insects, secondary sexual traits in vertebrates [49], and see [50] for the special case of deer antlers). Ontogenetic allometry resulting from this type of growth pattern is necessarily non-linear [e.g. 45, 46], and sometimes the link between ontogenetic and static allometry can be difficult to establish. Nevertheless, even in such cases the overall growth of the trait may be coordinated with the expected body size, despite the difference in the timing of growth. Static allometry could then be interpreted as the reaction norm of a trait to changes in body size which represents the

growth environment (see [16] for such a model). Variation in the allometric slope could then have a component due to variation in the trait sensitivity to the growth state of the whole organism. Lack of genetic variance in trait growth sensitivity to the size of the body or the sharing of a large proportion of the developmental pathway therefore seem the most likely sources of constraint on changes in static allometry. Importantly, such constraints would affect the allometric slope, but not necessarily the intercept.

Sources of selection

Selection on trait and body size – Change in the allometric slope may occur as a side effect of directional selection on trait or body size. This type of selection probably represents the most common selection in the wild, as demonstrated by variation in size among populations and closely related species. Following the model described above (Eq. 1 and 2), in absence of covariance between body size and the ontogenetic parameters, ontogenetic and static allometry should be similar, and changes in body size should not affect the static allometric slope (Fig. 1; scenario A), except if the ontogenetic allometry is non-linear. If one of the covariance terms between body size and the slope or the intercept of the ontogenetic allometry is different from zero and constant, changes in body size should generate changes in static allometric slope (Fig. 1; scenario D). Finally, changes in the mean trait (\bar{z}_t) are expected to affect either the mean ontogenetic intercept (\bar{a} , Fig. 1 scenario C), the mean body size (\bar{x}_t , Fig. 1 scenario A), the mean ontogenetic slope (\bar{b}), the covariance between these last two terms $\sigma(b, x_t)$, or any combination of these parameters. Changes in static allometric slope with increasing body size may also occur if the sensitivity of trait growth to the growth environment is non-linear. In presence of threshold or saturation effects, one can predict that changes in body size may result in changes in the static allometric slope.

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216 *Selection on the slope* – Alternatively the static allometric slope can evolve as a result of
217 selection on the slope itself, with no change in \bar{x}_i or \bar{z}_i (Fig. 1, scenario B), which is
218 equivalent to assuming correlated selection on size and the trait. With correlated selection,
219 there will be an adaptive ridge that links the bivariate distribution of the traits to fitness (Fig.
220 2A). We can completely separate selection on the allometric slope from selection on trait
221 means by imagining an adaptive landscape that selects on trait (co)variances but not on trait
222 mean (i.e. no directional selection). We generally expect that trait means will evolve more
223 rapidly than trait variation, so when a change in selection regime affects both means and
224 (co)variances, we will rapidly approach the situation where only the (co)variances continue to
225 be selected. A simple example of such changes would be selection for a decrease in trait
226 variance combined with either an increase or constant variance in body size, which would
227 decrease the allometric slope. Selection for increasing variance in trait size combined with a
228 decreasing variance in body size should generate an increase in the allometric slope. Figure
229 2B shows a case of disruptive selection favoring extreme combinations of trait and body size
230 over those near the means. This type of selection maximizes selection on variances and
231 covariances, and therefore should lead to the maximum rate of response in the allometric
232 slope. Strong disruptive selection balanced precisely to lead to no directional selection is
233 probably an extremely rare event in nature, however. In theory, the presence of a selective
234 ridge should be sufficient to favor a particular slope in the absence of disruptive selection, but
235 the strength of selection on the slope will be quite weak, because many individuals the center
236 of the distribution (i.e. with non-informative genotype) will be selected (Compare Fig. 2A and
237 B).

238 Verbal models of selection on allometric slope have been proposed to explain the
239 positive allometry often observed in sexually selected traits [12,13, 17, 18, 51]. In these
240 models, positive allometry evolves either because large males, presumably in better condition,

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are able to invest more in costly traits, or because the benefits of large traits increased with body size. By applying various selection regimes on an allocation model of growth, Bonduriansky and Day (2003) [16] showed that the conditions under which positive allometry evolved were more restrictive than previously thought, but that an increase in the relative fitness gain for larger traits with an increase in body size should select for positive allometry. Canalizing selection on trait size, on the other hand, has also been suggested to affect static allometry by generating negative allometries as for example for male copulatory organs in insects [14, 19].

The variational properties that generate variance and covariance among traits are pivotal to the evolution of static allometry. Although selection experiments have suggested that variation may respond to selection [52] it remains unclear how efficiently selection can mold genetic and environmental variation [53, 54, 55, 56]. The evolution of covariance between trait size and body size directly links the evolution of the static allometric slope with the evolution of the phenotypic and genetic covariance matrices (**P** and **G** on log scale). Much theoretical and empirical work shows that genetic covariances do evolve [54, 57, 58, 59, 60], but it remains unclear what forces drive these changes, and how rapidly they can take place. The various hypotheses listed here suggest that, in many cases, selection on the allometric slope is rather weak and indirect. If combined with a low evolvability, this may result in slow evolutionary change in allometry.

Evolvability and evolution in static allometry

Because changes in ontogenetic allometry are expected to provoke changes in static allometry (Eq. 1), we first consider here evidence for the evolution of ontogenetic allometry. Such evidence is provided by several studies comparing ontogenetic allometries among species [e.g. 61, 62, 63, 64]. However, few studies have tested the relationship between ontogenetic

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and static allometry [34, 65, 66, 67, 68], and fewer have analyzed how variation in the parameters of ontogenetic allometry affected static allometry. The only study, to our knowledge, that compared the relationship between ontogenetic and static allometry among populations [47], showed that static allometry between caudal fin length and body length in female Guppies (*Poecilia reticulata*) was steeper than the ontogenetic allometry, but was similar among three populations with different adult female length. This was achieved, among other things, by differences in the average ontogenetic allometric slope among populations. The relevance of these results regarding the rate at which ontogenetic allometry evolve is unclear, however, because guppy populations from different drainages may have been separated for hundred thousands of generations [69]. Furthermore, although individual variation in ontogenetic allometry has been observed [47], the genetic basis of this variation remains unknown, and overall we found only one study that reported heritability of ontogenetic slopes of chest circumference ($h^2 = 0.25 \pm 0.07$) and tail length ($h^2 = 0.39 \pm 0.08$) on body weight within six laboratory strains of rats selected for larger or smaller weight [70].

Microevolutionary changes in phenotypic covariances among traits are suggested by studies reporting rapid changes in the **G**- or **P**- matrices within populations [71, 72, 73]. These observations are difficult to interpret in terms of evolution of allometry, however, because traits are not always strongly correlated in the first place and **G**-matrices are rarely analyzed on log scale. Furthermore, studies analyzing changes in the **P**-matrix cannot distinguish between environmental and genetic changes in the patterns of covariation among traits.

Estimates of genetic variance in static allometric slopes are scarce, and we found only one study reporting heritabilities of allometric slopes measured on log scale [74]. In this study, heritabilities of the static allometric slope between the length of several bones and the cubic root of body weight, and between the weight of internal organs and body weight were all statistically significant but relatively small (all $h^2 < 0.13$) despite being measured in the lab.

Alternatively, artificial selection can be used to uncover genetic variation and covariation in quantitative traits [75]. During the last two decades, several authors have claimed to have altered patterns of static allometry by artificial selection. In addition, a few artificial selection studies on size have shown changes in the covariance patterns between the size of some traits and body size. Unfortunately, most of these studies have adopted the broad-sense definition of allometry, seriously hampering our ability to interpret their results in terms of the evolution of allometry [23]. For example, in a study on a stalk-eyed fly (*Cyrtodiopsis dalmanni*), selection exerted on the ratio between eye span and body length significantly affected the covariance between the two traits when measured on arithmetic scale [76]. Reanalysis of the regression line on the log scale shows that changes in the allometric slope are still present but much weaker than those reported in the original study (Table 1). A similar selection procedure was used in two experiments on the butterfly *Bicyclus anynana* [77, 78]. In both experiments, the intercepts of the relationships on arithmetic scale were strongly affected by selection, but the slopes were apparently not, although no formal tests of change in slope were reported. What were the consequences of the selection on the allometric slope remains unknown.

The only artificial selection experiment on narrow-sense allometry conducted so far combined stabilizing and disruptive selection on body area and caudal fin area to select for a change in static allometric slope (procedure similar as the one described in Fig. 2B; [79]. Selection to increase and decrease the intercept was also applied on two separate lines. Results suggested that the allometric slopes had very little capacity to vary compared to the allometric intercepts. This conclusion, however, was weakened by the small number of generations of selection.

Two studies investigating the effects of artificial selection on body size on correlated traits provide some evidence for rapid change in static allometric slope. In a selection

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experiment to increase or decrease body mass in the moth *Manduca sexta*, static allometry between wing mass and body mass became steeper in the line selected for smaller body mass and shallower in the line selected for larger body mass after 10 generations of selection ([80]; and see [23] for reanalysis using standard regression). Similarly, estimation of the static allometric slopes in the different lines of a selection experiment to increase body size in *Drosophila melanogaster* [81] reveals that allometries between wing length and thorax length or between wing length and tibia length increased in the line selected for smaller thorax length, and decreased in the line selected for larger thorax length (Table 1). Additionally, Cayetano et al. (2011) [82] while relaxing sexual selection for ca. 21 generations in the seed beetle *Callosobruchus maculatus* observed a change in the allometry between two traits of the genital apparatus in males and elytron length. The reanalysis of the data from this last experiment showed, however, a very poor fit of the traits with the allometric model and casted doubt on the validity of the interpretation of the results [23].

One factor that has not been considered in these experiments, however, is the possibility of plasticity in the allometric slope. Plasticity in allometric relationships has been little studied, but one study clearly shows that static allometry varies in response to different environmental treatments [83]. Similarly, a selection experiment on *Drosophila* wings in which selection was performed on the relative position of some veins [55, 84, 85] shows erratic but sometimes statistically significant variation in static allometry (Fig. 3). The differences in slope apparent in Figure 3, could, if observed in isolation, be misinterpreted as change in allometry due to selection. To avoid such problem we strongly recommend following the changes in allometry from generation to generation, and experiments that fail to do so should be interpreted with caution.

The dissection of the insulin/IGF signaling pathway that controls trait size in animals provides a nice illustration of how the growth of specific traits responds to changes in the

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growth environment, that is, changes in body size [86, 87]. Interestingly, recent experiments have uncovered mutations at specific loci that could affect the organ sensitivity to variation in the growth environment and therefore affect the slope of the static allometry [74, 88]. Although these studies provide clear evidence for genetic variation in allometric slope, they also suggest that this variation results from complex genetic architecture [74] that may not easily respond to selection.

Neither inter-population variation nor quantitative genetics experiments provide conclusive evidence for genetic variation in the allometric slope. For the intercept, quantitative genetic studies provide clear evidence for high evolvability.

Does static allometry constrain phenotypic evolution?

Theoretical considerations

Micro-evolutionary studies reviewed in the last section suggest that the evolvability of the allometric slope is low relative to the evolvability of the intercept. At the macro-evolutionary level, reviews on allometry of secondary sexual characters clearly show that allometry of homologous traits can vary among sexes from the same species or among species [89, 90]. Such information is by itself, not very informative about the constraint hypothesis because we do not know anything about the strength of selection on the allometric relationships, and the time scale for divergence can be very long. Therefore, it remains unclear whether there are meaningful evolutionary constraints due to allometry.

In the absence of empirical knowledge regarding selection on allometry, we are left with the option of generating predictions based on scenarios where static allometry constrains phenotypic evolution under various hypothetical selection regimes. In this context, a general prediction is that, if static allometric parameters represent evolutionary constraints they

should strongly shape patterns of populations and species divergence. This was initially suggested by Gould [6, 7] and placed in a quantitative genetic framework by Lande [32, 33] who showed that, under constant patterns of covariance between traits (constant **G**-matrix), selection acting only on the body size (x), will generate a correlated response on the trait size (z). In this case, the evolutionary allometric slope (b_e) along which populations and species evolve, will correspond to the ratio of the correlated response in z divided by the direct response in x , that is, the slope of the genetic regression between the two traits: $b_s = \sigma_A(x,z) / \sigma_A^2(x)$, where $\sigma_A^2(x)$ and $\sigma_A(x,z)$ are the additive genetic variance in x and the covariance between x and z , respectively (Fig. 4 scenario A).

Because static allometry is defined at the phenotypic level, the static allometric slope (b_s) combines both additive genetic and residual variances and covariances: $b_s = [\sigma_A(x,z) + \sigma_R(x,z)] / [\sigma_A^2(x) + \sigma_R^2(x)]$, where R denotes all other residual components of the variance, including environmental and non-additive genetic variance. Static and evolutionary regression coefficients, b_s and b_e , will be similar when the relative contributions of the residual variance and covariance are similar to the relative contributions of their additive genetic counterparts. In this case, the genetic and phenotypic variance-covariance matrices, **G** and **P**, will be proportional for these elements. If this condition is not fulfilled, evolutionary allometry will not follow the trajectory defined by the static allometry, contrary to previous claims by Gould [91] and others (Fig. 4 scenarios B and C; [33]). Furthermore, if the additive genetic and residual contributions to static allometry are different but remain constant, the static allometric slope should remain constant across populations and species while the intercept will change with changing mean size (Fig. 4 scenario B and C).

It is important to realize that when Lande's model [33] is generalized to allow selection on the trait and both size, and there is at least some additive genetic variation in both, the means obtained in the long term depend only on the selective optima for size and the

trait, and not at all on the patterns of covariance among them [35]. If this is the case, and if selective optima are spread more or less randomly in the bivariate morphospace, we would expect no relationship between evolutionary and static allometry (Fig. 4 Scenario C and D). Scenario C represents a situation where the slope is an absolute constraint but the trait and body size means can evolve more or less freely in the morphospace (Fig. 4 Scenario C). This provides the other major explanation for evolutionary allometry: it is not the pattern of genetic variation, but the pattern of natural and sexual selection that dictates allometry.

These considerations underline the problem we have of testing the allometry as a constraint hypothesis without knowing the selection patterns acting on allometric relationships, and in most cases, only speculative interpretation of the macro-evolutionary patterns can be achieved. Although specific predictions have been suggested regarding the effect of selection on allometric slope for genitals and secondary sexual characters, these predictions only concerned the type of allometry expected (positive or negative allometry), but not the strength of selection. Furthermore, in the case of secondary sexual characters, it has been shown that positive allometry was only expected under specific selection pressures [16], and a later review [89] confirmed that static allometric slopes in this type of character was not necessarily larger than one.

Empirical patterns

Although many studies have compared relationships between trait size and body size among populations and species, Voje et al. [23] identified only 10 studies that allowed estimation of the variation in static allometric slope and intercept (studies on log scale with sufficient information about the allometric parameters). Excluding genital traits, their analysis revealed inter-specific variation in static allometric slope within genera (median standard deviation corrected for sampling error: SD = 0.27). Within species, the static allometric slope varies

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among populations but this variation is more limited (median SD = 0.07). For the allometric intercept, patterns of variation were similar with higher variation among species (median SD = 0.15) than among populations (median SD = 0.02).

Because the slope and intercept are on different scales, their level of variation is not directly comparable. Using the concept of conditional variance [39, 41], Voje et al. [23] estimated the influence of changes in size or in allometric slope and intercept in the evolution of trait size. This method allowed them to compare variation in slope and intercept on a common scale (variance in trait size). At the interspecific level, 74% of the variation in trait size was associated with changes in species mean size. The contribution of the changes in static allometric slope or intercept were more limited (13% and 29% of the log trait variance explained, respectively, e.g. Fig. 5A). The contributions of these three parameters to trait diversification at the among-population level were similar, with size variation explaining 71%, slope explaining 36%, and intercept variation explaining 40%. However, as previously mentioned, much less variation in static allometry was observed among populations, and the evolutionary allometry was often very similar to the pattern of static allometry (Fig. 5B).

Finally, Voje et al. [23] showed that within species, the average static allometry across populations was a good predictor of the evolutionary allometry, while across species within genera the average static allometry was poorly correlated with the evolutionary allometry.

These results are compatible with the “allometry as a constraint” hypothesis if selective optima were spread more or less randomly in the bivariate morphospace. Indeed, morphological evolution more constrained along static allometric trajectories at the within-species level than at the among-species level could be interpreted as signature of evolutionary constraint.

In an attempt to estimate the rate of morphological evolution towards a predicted optimum, Voje and Hansen [92] reanalyzed data on the evolution of the static allometry

between eye-span and body length in various species of stalk-eyed fly (Diopsidae). Using sexual size dimorphism as a measure of the strength of sexual selection in order to estimate optima, they showed that the static allometric slope in male trait was tracking these optima, but this took millions of years to accomplish.

The “one size fits all” hypothesis

The various studies analyzing static allometry of genital traits in arthropods and vertebrates showed consistently shallow static allometric slopes ($\beta < 1$) for these traits, as expected from the “one size fits all” hypothesis [14, 19]. Eberhardt [19] reported few exceptions to this pattern. However, all these exceptions came from studies where static allometry was estimated using major axis regression, a method that will over-estimate the slope for relationships with low r^2 . Accordingly, for all exceptions reported, the relationship between the genitalia and the measure of body size was poor (range r^2 : 0.0 – 0.58). In all cases where data were reanalyzed using standard regression methods, genital traits showed negative ($b < 1$) static allometry [23, 93].

The “one size fits all” hypothesis has also been extended for reproductive organs in flowering plants with insect pollination, where the fit between pollen donor and pollen receiver organs and pollinators of relatively constant size and behavior is expected to produce stabilizing selection [94]. Several studies have provided clear evidence for the relative invariance of floral traits compared to vegetative traits [95, 96] and the two studies that have tested the effect of pollination accuracy on the allometry of the pollen transport organs both reported shallow allometry for these traits [97, 98].

If results from studies on the “one size fits all” hypothesis provide clear evidence of a possible effect of selection on static allometry, they do not provide evidence for high evolvability of the allometric slope. Indeed, intraspecific comparison of static allometry in

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insect genitalia show that variation in the allometric slope explains only a small proportion of the variation in genitalia size, 92% of the variance of log-size genitalia being independent of the variation in allometric slope [23]. This is particularly clear when observing the allometric slope between genitalia size and body size in various populations of the beetle species *Dorcus titanus* (Fig 5C).

Conclusions

Despite the huge interest morphological allometry has focused among evolutionary biologists for nearly a century, we are left with a limited understanding of its evolution. Key observations such as genetic variation in ontogenetic allometry or in the static allometric slope are surprisingly scarce. Although micro- and macroevolutionary patterns seem to point at a constraining effect of morphological allometry on phenotypic evolution, the complete lack of data on the nature of direct or indirect selection on allometry, and the near absence of data on genetic variation in allometric parameters precludes the interpretation of these patterns as evidence for or against the constraint and adaptation hypotheses. Until such data are obtained the evolution of allometry will remain a mystery.

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Table 1: Changes in arithmetic slope and allometric slope (log scale) in two artificial selection experiments. In the experiment on the stalk-eyed fly (*Cyrtodiopsis dalmanni*) [76] selection was exerted for 13 generations to change the ratio between eye-span and body length. We estimated the slope on the arithmetic scale from Fig. 3 in the original paper by estimating the values of the extreme points of the regression lines. These data were subsequently log-transformed to obtain the allometric slopes. In the experiment on *Drosophila* [81], selection to increase or decrease thorax length was conducted for 23 generations. Estimates of the allometric slopes were obtained from the variance and covariance parameters scaled by the trait mean (male and female combined). Standard errors of the estimates are not available.

Species	Trait	Body size	Sex	Line	Arithmetic slope	Allometric slope
<i>Cyrtodiopsis dalmanni</i>	Eye-span	Body length	♀ rep1	Down	0.71	0.87
				Up	1.00	1.10
			♂ rep 1	Down	1.37	1.19
				Up	1.73	1.38
			♀ rep2	Down	0.56	0.68
				Up	0.66	0.74
			♂ rep 2	Down	1.10	0.98
				Up	1.43	1.10
<i>Drosophila melanogaster</i>	Wing length	Thorax length	♀+♂	large	0.49	0.30
			♀+♂	Small	0.68	0.38
			♀+♂	Control	0.42	0.24
	Tibia length	Thorax length	♀+♂	large	0.39	0.58
			♀+♂	Small	0.65	0.93
			♀+♂	Control	0.40	0.60

Figure 1. Evolution of static allometry. The scenarios considered here correspond to the expected evolution of static allometry from an ancestral state depending on the constraining parameter (i.e. the parameter that is not evolvable). Vertical and horizontal dash lines represent the mean trait value and body size. Body size is mean centered, so the allometric intercept represent the trait value at the population mean (i.e. elevation of the allometric regression). In the scenario A, both the slope and the intercept are constraining parameters. Any change in body size will generate a change in trait size and vice versa. In the scenario B, only the allometric slope changes while the intercept (elevation) does not change. In the scenario C, the slope is the constraining parameter while the intercept can change. In the scenario D, slope and intercept can evolve. This pattern may be also generated by the effect of a negative covariance between body size and the ontogenetic slope when selection on body size occurs (see Eq. 1).

Figure 2. Selection to change allometric slope via correlated selection on the trait and body size. A) Selection is generated by the difference in the direction of the phenotypic regression and the adaptive ridge. Black dots represent individuals and the blue dots represent the selected individuals (with the highest fitness). B) Saddle fitness landscape that generates disruptive selection on one of the two traits. This selection regime is more efficient to change the slope because individuals in the middle of the distribution are not selected.

Figure 3. Phenotypic plasticity in static allometry. The figure presents the variation in the slope of the static allometry between wing size (estimated by the centroid size) and the inter-landmark distance 2 - 12 (see diagram for landmarks number) in two populations of *D. melanogaster* selected to increase (grey arrows) or decrease (back arrows) a selection index. Selection was performed for 26 generations. Idiosyncratic variation of the slope (estimated on

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100 males at each generation) generates statistically significant differences between selection lines at generation 4, 9 and 11. The data presented here correspond to the LHM 1 replicate, but similar results were observed for the other three replicates, LHM 2 and IV 1 and 2 (see [55] for more detail).

Figure 4. Static allometry as an evolutionary constraint. The various scenarios represent the effect of constraining parameters of the static allometry on the evolutionary allometry, assuming that selective optima are spread more or less randomly in the bivariate morphospace. In scenario A, neither the slope nor the intercept vary. The divergence of population means follow the genetic allometric regression (see text). If the slopes of the genetic and phenotypic allometry are similar, evolutionary allometry will follow the patterns of static allometry. In scenario B, the intercept is allowed to change but not the slope. Although such a pattern may result from the evolution of the intercept itself, it may also result from the difference between the phenotypic and genetic allometry (see text). Scenario C presents a similar pattern but where selection does not favor any particular direction in the morphospace. In scenario D, both intercept and slope can evolve (no constraint).

Figure 5. Example of variation in static allometric and effect on evolutionary allometry A) among population within species B) among species within genus C) among species genitals (Figure from [23] Voje et al. 2014).

Box 1 – Narrow sense and broad sense allometry: conceptual and methodological issues

In the recent years, the term allometry has been used for any type of monotonic relationships between two morphological variables, independently of the scale on which these variables were expressed. This broad definition of allometry is inconsistent with the biological interpretation of morphological allometry originally suggested by Huxley [5, 99]. Huxley [5] showed that if an arbitrary trait Z and body size X , grow at different rate but under the control of a common growth parameter G , such that $dX/dt = \alpha XG$, and $dZ/dt = \beta ZG$, where α and β are specific constants for X and Y , respectively, and t the time during growth, the relationship between Z and X follows a power law $Z = AX^{\beta/\alpha}$, where A is a constant that depends on the initial values of Z and X . On a log scale, this relationship is linear $z = a + bx$, where $z = \log(Z)$, $x = \log(X)$, $a = \log(A)$. Savageau [100] generalized this model and showed that whenever two or more variables are connected in a dynamic synergistic system controlled by one variable, their relationship follows an allometric relationship. Therefore, allometry, in its narrow sense is defined by two parameters of a power relation that can be expressed as the intercept a and the slope b of a linear regression on log scale. When the explanatory variable (x) is mean centered, the intercept, a , becomes the elevation of the static allometry, that is, the trait size at the population mean body size [101, 102, 103].

Which statistical model should be used to estimate these parameters has been the subject of long debates. First, it has been suggested that the best estimation of these parameters should be done from a power relationship fitted on arithmetic scale [104, 105]. This approach would be justified if the processes producing the error would act in an additive manner. Although this may be the case for measurement error, it is most likely that the biological error will be generated by multiplicative processes similar to those responsible for the growth of the trait [106]. Because most of the error on the response variable is likely to be

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of biological origin, estimates produced by linear regression on log scale should be better than those produced by a power model fitted on arithmetic scale. Both approaches are valid, however, and should ideally be conducted with proper modeling of both biological and measurement error.

It has been repeatedly suggested that major-axis or reduced major-axis regression should be used in place of ordinary least-squares regression to estimate allometric parameters in order to account for the effect of observational error in the predictor variables. However, neither of these models provides sensible estimates of allometric regression slopes when there is biological ‘error’ (i.e. biological deviations from the allometric line) in the model [107, 108]. These models provide estimates of slopes, but these slopes are not proper estimates of the exponent b in the narrow-sense allometric relation. A dramatic consequence of the reduced major-axis regression is that, even in absence of covariance between the two traits, an “allometric” slope can be estimated and its statistical significance tested [e.g. 82].

Finally, we notice that ignoring the consequences of trait dimension on the allometric slope has led to some erroneous statements in the recent study of allometry. For example, a positive allometry between testes size and body length has been reported in Hottentot golden mole (*Amblysomus hottentotus*) as an exception to the “one size fits all” hypothesis [109]. However, this positive allometry is most likely generated by the difference in dimension between the traits (body length – length vs. testes mass - volume).

Box 2: From bivariate to multivariate allometry: drifting away from the Huxley’s model

Jolicoeur [110] suggested analyzing multivariate relative growth using the first principal component (or eigenvector) of the variance-covariance matrix of log-scaled trait values (herein PC1). He showed the relation between this approach and the Huxley model [5] arguing that the trait’s loadings on PC1 are equivalent to their allometric exponents. This approach formalized multivariate isometric variation as a PC1 vector with all elements or loadings equal to $1/\sqrt{k}$, where k is the number of traits measured. Variation along such a $\{1/\sqrt{k}, \dots, 1/\sqrt{k}\}$ vector is associated to variation in organism size while its proportions remain constant. Group difference in multivariate allometry is commonly estimated as the angle between two within-group PC1 in the multivariate space [67]. This approach has been used to describe the plasticity of static multivariate allometry of *Drosophila* exposed to different environmental conditions [83], or to investigate the evolutionary diversity among species [111, 112].

However, the biological meaning of the PC1 loadings in this approach is not equivalent to the one of the standard regression estimates (i.e. Huxley’s allometric exponent). Instead, these estimates are the slopes of the standard regressions of trait variables on size, as defined by PC1. Importantly, the ratios of the loadings do not correspond to the “variables’ bivariate allometric coefficient” [67], at least not if they are properly estimated with a standard regression (Box 1), but these correspond to the ratio of their respective covariances with PC1. This can be interpreted as the relative change in the two traits for a given change along PC1. However, the orientation of the PC1 vector in the morphospace can vary with an increase in trait(s) variance even if covariances are kept constant.

This raises the problem of the use of an adequate definition of size in the study of its relation with shape (see [113] for review). The two most commonly used approaches for

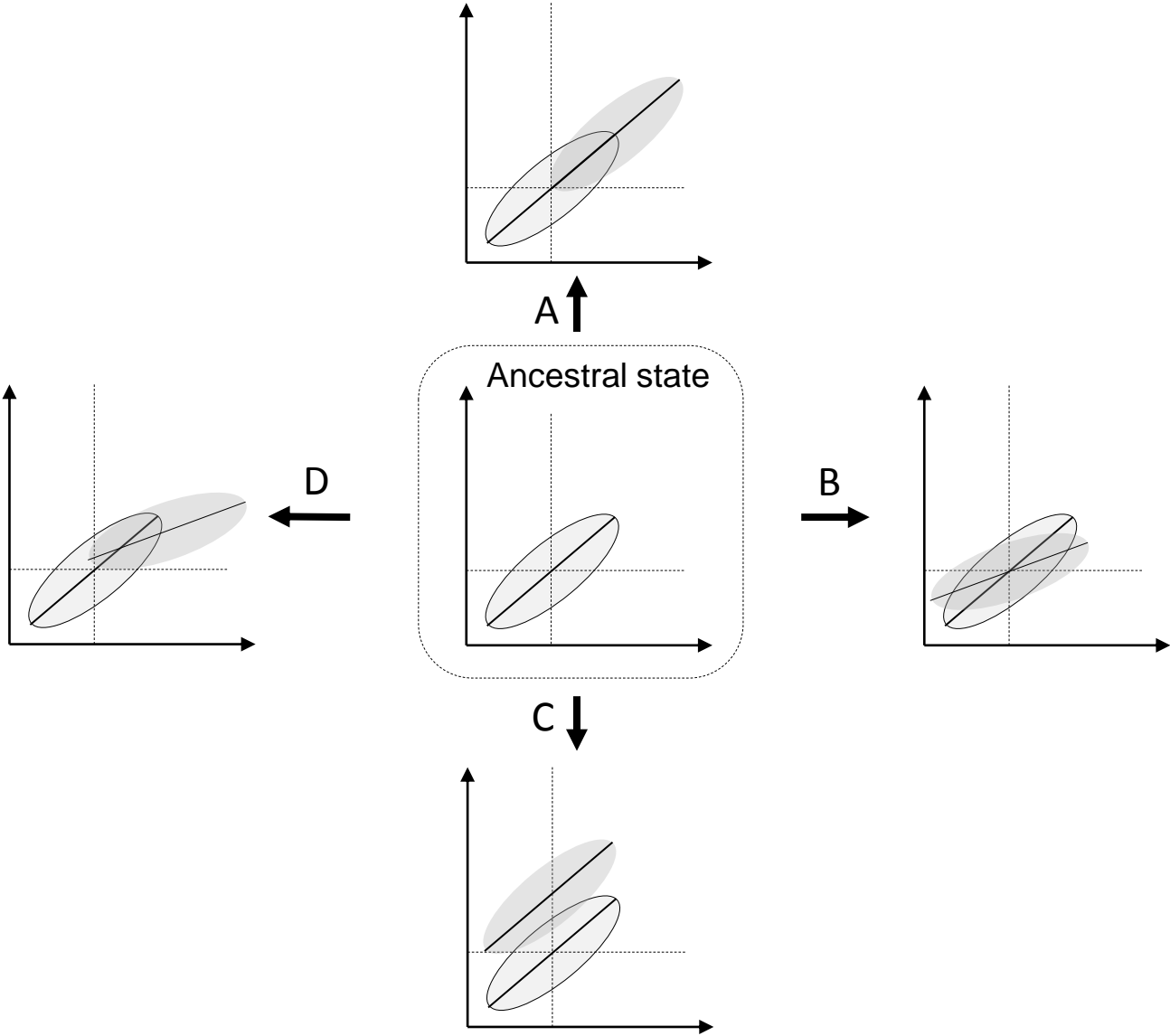
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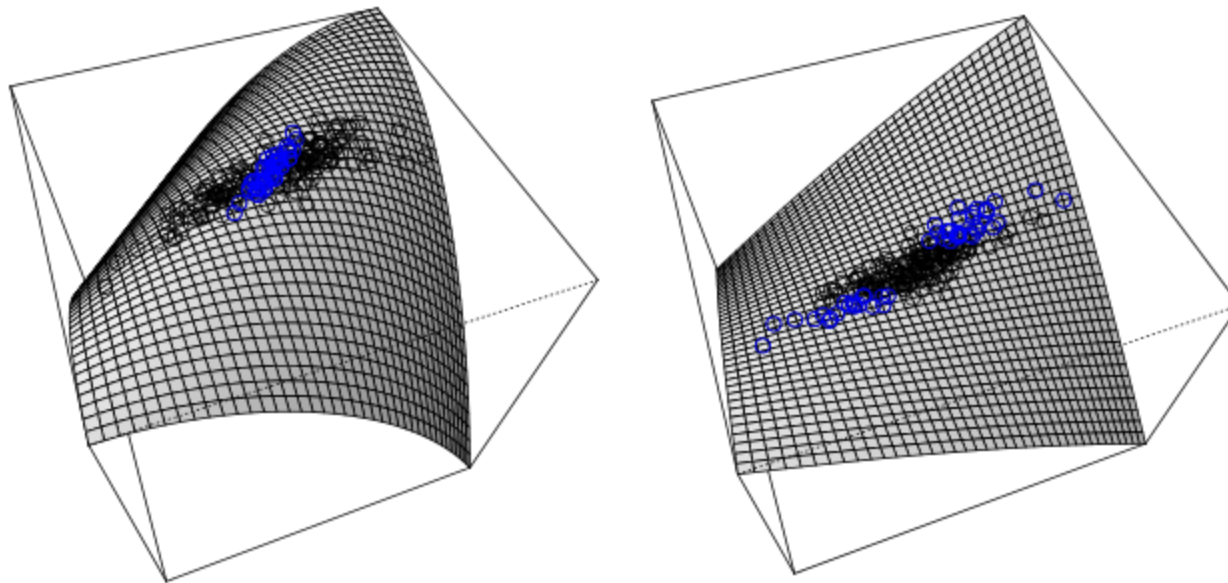
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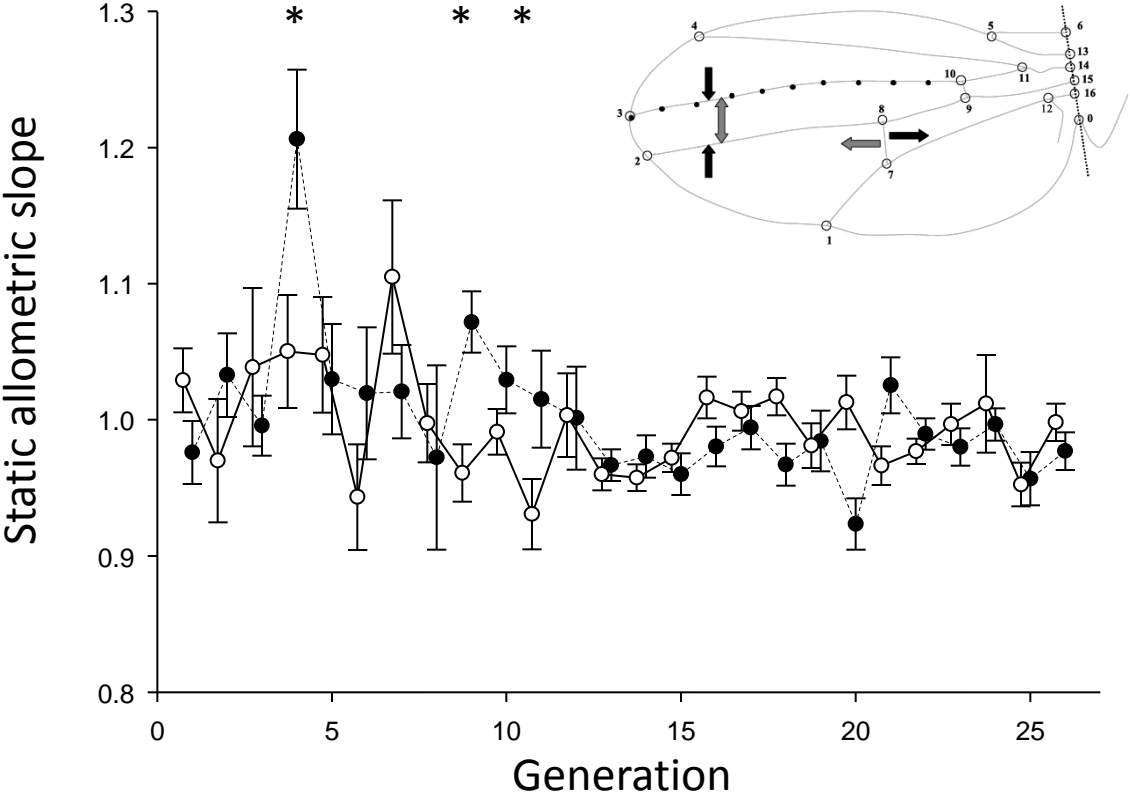
estimating size are the PC1-as-size approach described above and Mosimann's [114] definition. Mosimann [114] defined size as any function G of the measurement vector \mathbf{x} that satisfies the property: $G(a\mathbf{x})=aG(\mathbf{x})$, $G(\mathbf{x})$ having the same dimension than any element of \mathbf{x} . Indeed, shape being on a ratio scale, multiplication of each element of the ratios by a constant a does not change shape and G is uncorrelated with any ratios under fully isometric multivariate variation. It is worth noticing that Huxley [5] already defined traits' growth rate as affected by a common growth factor (" G ") that vanishes when the growth rates of the traits are put in relation in the exponential relationship.

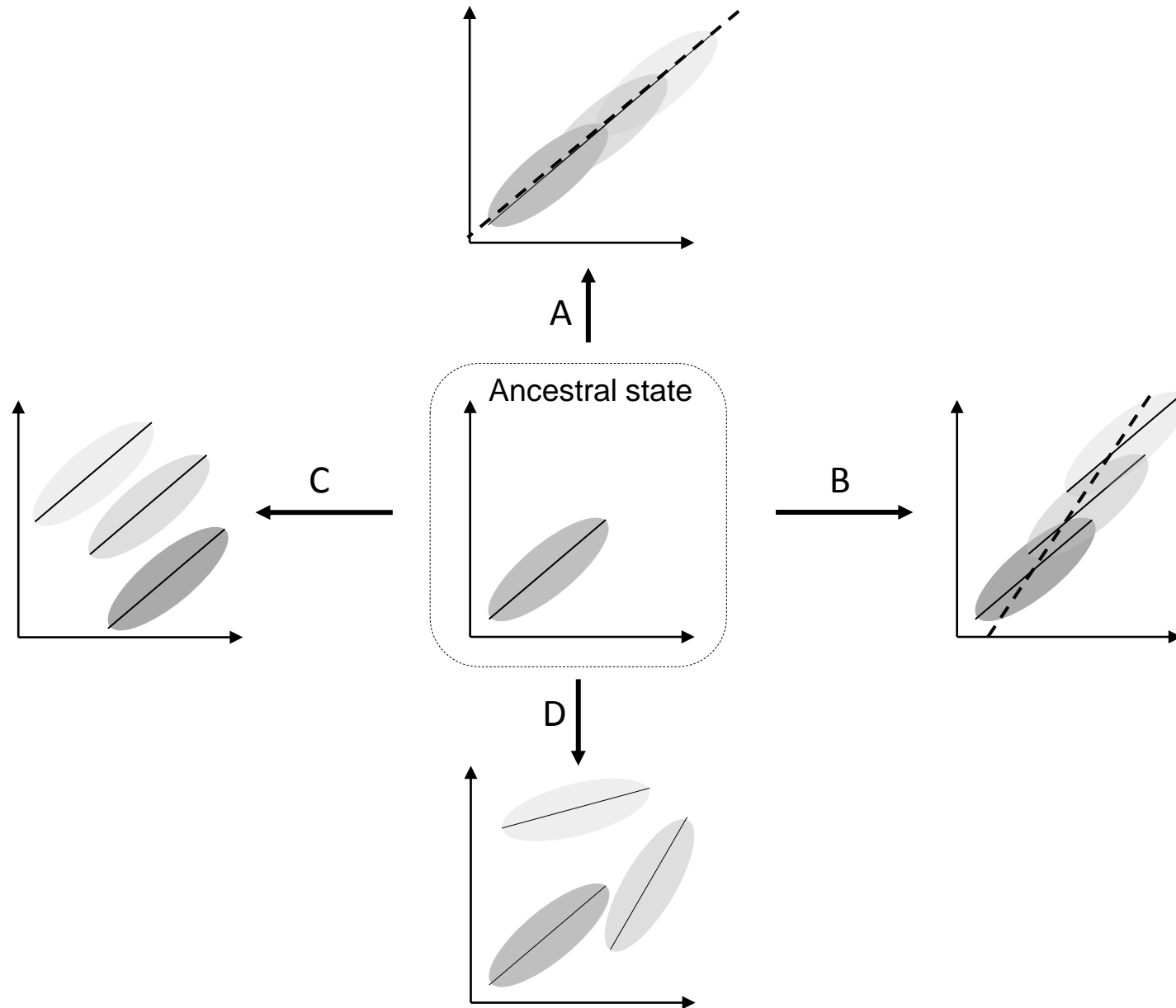
Contrary to the PC1 approach, this geometric definition of size is not directly dependent of the variance-covariance properties of the studied samples. As a measure of size, geometric morphometrics conventionally use centroid size (CS), the square root of the sum of squared distances of a set of landmarks from the centroid of the entire landmarks configuration. Although this choice does not generally rely on biological arguments, centroid size corresponds to a size vector according to Mosimann's definition. The Procrustes superimposition algorithm scales landmark coordinates with CS, providing Mosimann's shape vectors. The effect of CS on remaining shape variation therefore corresponds to multivariate allometry. The effect of size variation on shape can be graphically depicted in computing the product $\mathbf{y}\beta'(\beta\beta')^{-0.5}$ [115] where \mathbf{y} is the shape variables and β the multivariate regression coefficients, allowing to compare multivariate allometric patterns across different groups [116, 117].

Under specific conditions, a multivariate regression of shape on size certainly represents the multivariate approach the most closely related to the original bivariate model from Huxley. On the other hand, the broadly used geometric morphometric approach abandons the notion of trait for a notion of shape analyzed as a whole, and hampers interpretations of allometry in a context of relative growth.

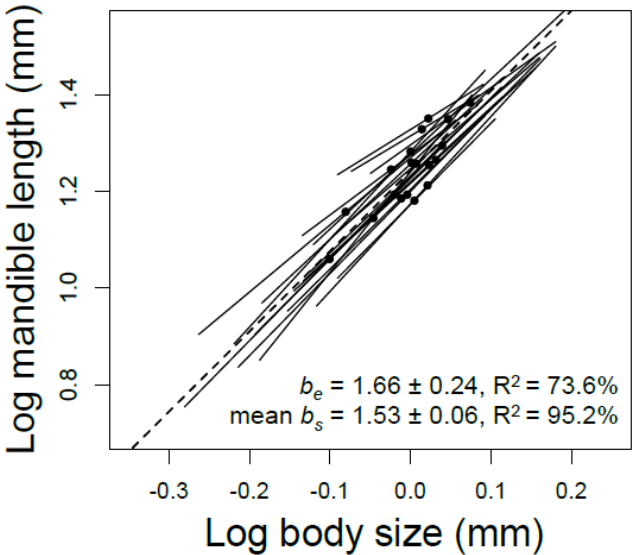




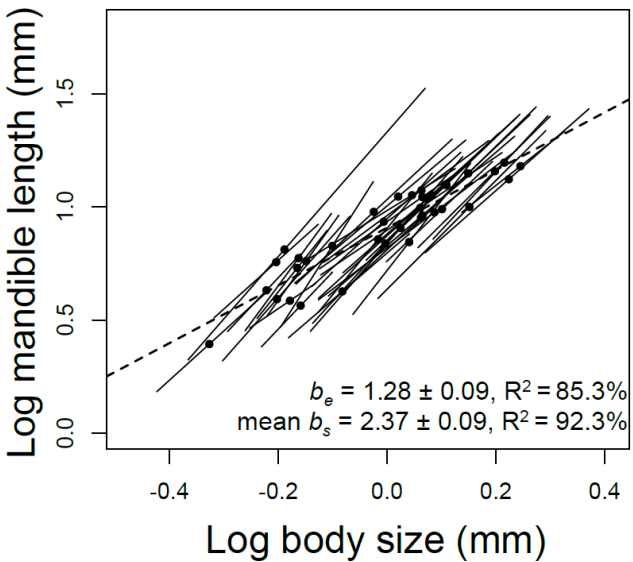




Dorcus titanus
(males) N = 19



Dorcus (males) N = 37



Dorcus titanus
(males) N = 19

