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History of the Concept of Allometry[1]

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Synopsis. Allometry designates the changes in relative dimensions of parts of the body that are correlated with changes in overall size. Julian Huxley and Georges Teissier coined this term in 1936. In a joint paper, they agreed to use this term in order to avoid confusion in the field of relative growth. They also agreed on the conventional symbols to use in the algebraic formula: $y = bx^{\alpha}$. Julian Huxley is often said to have discovered the "law of constant differential growth" in 1924, but a similar formula had been used earlier by several authors, in various contexts, and under various titles. Three decades before Huxley, Dubois and Lapicque used a power law and logarithmic coordinates for the description of the relation between brain size and body size in mammals, both from an intraspecific, and an interspecific, point of view. Later on, in the 1910s and early 1920s, Pézard and Champy's work on sexual characters provided decisive experimental evidence in favor of a law of relative growth at the level of individual development.

This paper examines: (1) early works on relative growth, and their relation to Huxley and Teissier's "discovery"; (2) Teissier and Huxley's joint paper of 1936, in particular their tacit disagreement on the signification of the coefficient "b"; and (3) the status of allometry in evolutionary theory after Huxley, especially in the context of paleobiology.

INTRODUCTION

Julian Huxley and Georges Teissier coined the term “allometry” in 1936. In a joint paper, simultaneously published in English and in French (Huxley & Teissier 1936a, 1936b), they agreed to use this term in order to avoid confusion in the field of relative growth. They also agreed on the symbols to be used in the algebraic formula of allometric growth: $y = bx^{\square}$. My paper proposes a large-scale history of the concept of allometry over approximately 70 years, before and after Huxley’s and Teissier’s adoption of the contemporary standard terminology. The history of allometry can be illustrated by the image of an hourglass. In the top part of the hourglass, various lines of research, belonging to different areas of biology, converge towards the law of constant differential growth (Huxley 1924b). The middle part represents the time when the modern terminology and treatment of allometry was invented (1924 through 1940 approximately). The lower part of the hourglass corresponds to the period after 1945, when biologists, especially evolutionary biologists, realized that both the term and the equation of allometry were equivocal.

Before telling the story, it is necessary to define the term “allometry”, even though the emergence of the modern conventional definition is part of the problem. In its broadest sense, allometry designates the changes in relative dimensions of parts of an organism that are correlated with changes in overall size. Or, more concisely: “the relationship between changes in shape and overall size” (Levinton 1988: 305). Today, at least four different concepts of allometry are usually distinguished: (1) ontogenetic allometry, which refers to relative growth in individuals; (2) phylogenetic allometry, which refers to constant differential growth ratios in lineages; (3) intraspecific allometry, which refers to adult individuals within a species or a given local population; (4) interspecific allometry, which refers to the same kind of phenomenon among related species (Gould 1966). Categories (1) and (2) are commonly characterized as “dynamic” or “truly temporal”; categories (3) and (4) as “static” (Gould 1966). Although it is no longer use, I will refer occasionally to these various modes of allometry in my reconstitution of the origins of the concept. This will help in understanding the historical continuity of the studies discussed here.

ALLOMETRY BEFORE HUXLEY AND TEISSIER (1897-1924)

Brain/Body Studies: Interspecific and Intraspecific Comparisons

Frédéric Cuvier probably gave the first example of relative growth. Cuvier observed that in closely related mammals the bigger the animal the smaller the relative size of the brain. However, it is only at the end of the 19^{th} century that a quantitative formula was proposed for this strange phenomenon. In 1897, Eugène Dubois (1858-1940), the Dutch naturalist who coined the expression “pithecanthropus”, published a remarkable article on the relation between the weight of the brain and the weight of the body in mammals. Dubois wanted to develop a quantitative tool that could discriminate between two factors that determine the brain volume: (1) the “degree of cephalization” (reflecting the position of a given species on scale of evolutionary progress); (2) size since, in related species, the brain will be relatively smaller in a bigger species of animal.

These two requirements are reflected in his final formula (Dubois 1897: 368) for the expression of the relation between the weight of the brain “e” (for *encephalon*) and “s” (for *soma*):

$$e = c.s^{r}$$

where:

c: “coefficient of cephalization

r: coefficient relation (Dubois thought that the relative size of the brain was in fact more or less proportional to the surface of the body, that is $r \approx 0,66$)

This was obviously a power function. Moreover, “e” and “s” were easily measurable, and “r” could be inferred from comparisons between related species[2]. From these comparisons, Dubois calculated the value of r as being between 0,51 and 0,55.

One year later, a young French physiologist, Louis Lapicque (1866-1952) applied Dubois’ formula to the comparison of the relative weights of brains between individuals belonging to a single species, the Dog. He obtained a value for the coefficient of relation 0,25. In the following decade, Lapicque wrote a number of other articles on the relative weight of the brain both within and among species. He systematically obtained coefficient of relation values that were close to 0,25 for intraspecific comparisons, and close to 0,5-0,6 for interspecific comparisons.

In 1907, Lapicque gave an impressive graphic representation of what he called Dubois’ formula, in the case of interspecific comparisons (Lapicque 1907). This representation is based upon the fact that the power function $e = c.s^r$ is strictly equivalent to the logarithmic equation $\log e = r \log s + \log c$. With logarithmic coordinates, comparisons between related species obeying Dubois’ law will lie on a straight line. Because Lapicque accepted Dubois’ conclusion that the coefficient of relation was always equal to approximately 0.55, his graphic representation of the relative weight of the brain in related mammals consists of a series of parallel straight lines (bold lines on fig. 1). Lapicque called these lines “isoneural lines”. The equations have the same “exponent of relation” r (that is the same slope); the only difference between them is the coefficient of cephalization c. On the same diagram, Lapicque also drew a series of dashed lines with a 45° slope. These lines were purely theoretical. They corresponded to what would happen to a series of animals in which the absolute ratio between brain and body weight was maintained. Lapicque did not comment further on this representation, but it should be noted that this is exactly the kind of graphic representation that was the basis of S.J. Gould’s reflection on allometry sixty years later (see fig. 6 and comments below).

This leads us to our first conclusion. Around 1900, Dubois and Lapicque’s research on the relation between brain size and body size involved a mathematical and graphical tool that exactly corresponded to what was later called allometry (inter– and intraspecific allometry, or Gould’s “static allometry”). This tool was then commonly applied to interspecific and intraspecific comparisons of adults. Lapicque tried to apply this tool to a small number of other nervous or sensory organs (medulla, or eye size; see e.g. Dhéré & Lapicque 1898, Lapicque 1910). Neither Dubois nor Lapicque was interested in individual growth. It should be observed that they were convinced that the slope of the logarithmic curves was always the same: 0,25 for intraspecific comparisons, and 0,5-0,6 for interspecific comparisons. They thought that this was an empirical law, with no clear theoretical basis.

Relative Growth in Individual Organisms

Dubois and Lapicque’s line of research was biometrical. The following approach was experimental. From the early 1900s onwards, a number of biologists observed that in many animals, secondary sexual characters grew relatively larger over an individual’s lifetime. Albert Pézard (1875-1927) made the first experimental and quantitative study of the subject. In a doctoral dissertation that was completed before teh beginning of WWI (1914) but published only in 1918, Pézard studied the development of sexual characters in cockerels. Plotting the lengths of spurs and comb against overall body size, he showed that there was an obvious “discordance” between the curves of body size and comb size, whereas the growth of the spurs approximately followed the bird’s general development. Pézard provided many diagrams illustrating this phenomenon. Figure 2 reproduces the first of them. He also proposed a new terminology: “Growth that follows the general development of the organism can be termed *isogonic growth*, and growth that is special or conditioned can be called *heterogonic* *growth*"(Pézard 1918: 23). "Heterogonic growth" remained the commonest expression for individual relative growth until the introduction of "allometry" in 1935, especially in the English literature. Pézard's monograph was a remarkable experimental study, which influenced many people working in a wide range of areas: the physiology of sex of course, but also embryology, endocrinology, biometry. It showed clearly that the relevant variable was not time, but body size. Furthermore, his use of graphs made the significance of the data particularly clear. There was, however, an important absence in Pézard's work. He did not propose any hypothesis about the algebraic form of the law of heterogonic growth of the comb.

In 1924, in a book entitled *Sexuality and Hormones*, Christian Champy, another French physiologist, proposed such a formula. In this book, he coined the expression "Dysharmonic growth" for "an extremely general phenomenon", which he claimed to have discovered: the continuous increase of the relative size of secondary sexual characters as a function of body size (Champy 1924). The book provided impressive illustrations of this phenomenon, especially in insects (fig. 3). Champy explained this phenomenon by a sexual hormone causing an increase of the rate of mitotic cell divisions in certain parts of the body. For this reason, he argued that the relative growth process was adequately described by a parabolic curve. “Disharmonic growth” followed thus a law of the form:

$$V = at^2$$

where V is a measure of the secondary sexual character, *t* is body size, and *q* a constant. In this formula, the relative growth of an organ is obviously a function of body size. This equation is not exactly similar to a power law, but it is a special case of it. Later on, in 1931, Teissier observed that Champy’s law was indeed a good approximation for the insects he had used to verify his formula. In *Dynastes*, the power law is indeed a parabolic law.

Neither Pézard nor Champy referred to the classical biometrical works of Dubois, Lapicque and others on the relation between brain and body size. But their work on individual relative growth was crucial to the emergence of the general concept of allometry.

HUXLEY AND TEISSIER (1924-1936)

Huxley (1887-1975) and Relative Growth

Huxley’s first paper on relative growth appeared in 1924. It tried to answer to a question raised by Thomas H. Morgan, a year earlier, on the abdominal width of female fiddler crabs

(*Uca pugnax*). Morgan was puzzled by the very large abdomen of some of these animals, and wondered whether this character resulted from their genetic make-up or from the law of growth. Working on Morgan's data, Huxley argued in favor of the second hypothesis, and, on this occasion, used for the first time Pézard's terminology of "heterogonic" and "isogonic" growth. Although this paper does not provide the law of heterogony which made him famous a few months later, it did provide a simple method for detecting heterogonic growth: "The best method of detecting and analyzing heterogonic growth-rate is by plotting the percentage size of the part in question against the absolute size of some dimension of the whole body" (Huxley 1924a: 475).

In the case of Morgan's data on the fiddler crab, this meant plotting the ratio abdomen breadth/carapace breadth (A/C) against carapace breadth (C). If A/C does not vary as C increases, the character is isogonic; if it varies, this means that the growth-rate of the abdomen varies. Huxley provided a sketched graph (fig. 4). The curves on the left and right represent the law of growth of two classes of crabs. The curve in the middle represents the mean growth of all crabs. The left curve shows a typically isogonic growth (A/C varies continuously and regularly). The right curve shows an isogonic, then heterogonic, growth. The middle curve describes the whole population *en masse*.

Nevertheless, this paper did not say anything about the law of heterogonic growth. This was the object of a second paper, published a few months later in *Nature*. This was a short note, not much more than a page, but it is certainly Huxley's most significant scientific contribution in terms of empirical research.

In this paper, Huxley (1924b) stated a law of heterogonic growth for the chelae of fiddler crabs. This law is a power law of the form:

$$y = bx^{k}$$

Where:

y: magnitude of the differentially growing organ;
x: body size;
k: constant differential growth-ratio;
b: constant (origin index).

The essential theoretical feature of this formula is the following: what is constant (*k*) is not a ratio of two sizes but a ratio between two growth-rates. Furthermore, Huxley said, the power law can equally well be expressed as a logarithmic equation:

$$\log y = k \log x + \log b$$

Under this form, it provides a remarkably easy method for detecting and proving the existence of heterogonic growth: with logarithmic coordinates, the heterogonic growth of an organ will appear as a straight line of slope $\neq 1$.

At this point it is worth asking what was Huxley's debt towards the various authors discussed above. In his 1924 paper, Huxley quotes Pézard and Champy, but there is no allusion whatsoever to the brain/body studies. In his 1932 synthetic book on Relative Growth, he occasionally quotes some late papers by Dubois and Lapicque, but never the crucial papers I discussed here. Moreover he does not allude to them when he solemnly introduces his mathematical formulation of the notion of "constant differential growth-ratio" at the beginning of the book. On the contrary, he says: "Champy and others have pointed out that certain organs increase in relative size with the absolute size of the body which bears them; but so far as I am aware, I [Huxley 1924B] was the first to demonstrate the simple and significant relation between the magnitudes of the two variables" (Huxley 1932: 4). Then follows the exposition of the formula. There is something puzzling here. In his first 1924 paper on relative growth, Huxley manifestly failed to raise the possibility of using a power law to solve his problem. In the second one, he used it. Where did he get the idea? Many of his friends, such as D'Arcy Thompson or Haldane might have helped him. I have no evidence for this. What is certain, however, is that he never mentioned that he was influenced by the classical use of a power function in the domain of brain/body studies. Thus the real story of how Huxley discovered the power law is uncertain. But his constant unwillingness to acknowledge the priority of those who had used it in the context of studies on the relative increase of brain size raises doubts about his intellectual honnesty.

Teissier (1900-1972) and Relative Growth

We find exactly the reverse in Georges Teissier’s early work on relative growth. Teissier was fifteen years younger than Huxley. Mathematically trained, he was interested both in systematics and biometry. When Huxley discovered his law of heterogony, Teissier was only 24, and had not yet written anything on biometry. He published first paper on relative growth in 1926. This paper dealt with the size of ommatidia as a function of body size in various insects. Using a power law, this paper showed that “in a given species... the bigger the insect is, the bigger the facets of the eye”. Teissier did not refer to Huxley, but to Lapicque, who had compared the size of the eye with body size in vertebrates just three years earlier (Lapicque & Grioud 1923). Like Lapicque, Teissier proposed a formulation of this phenomenon of relative growth with the aid of a power law.

In his following papers on differential growth (1928a, 1928b, 1928c, 1929), Teissier continued to refer to Lapicque. But he also began (1928a) to refer to Huxley and to use a differential growth formula, which was formally identical to Huxley’s. Still he never said that Huxley had discovered it. Finally, in his doctoral dissertation of 1931, Teissier devoted a full paragraph to the history of relative growth. There he acknowledged the important role of Huxley, but denied that Huxley had discovered the method of describing differential growth with the aid of a power law and logarithmic coordinates. He said that this method of description of relative growth had been discovered in 1897 and 1898 by Dubois and Lapicque (Dutch and French respectively), and that they had applied it to the study of the variation of characters such as brain size or the area of the retina, as a function of body size in vertebrates (Teissier 1931: 88-93). Did Teissier deliberately quote Lapicque instead of Huxley in his first paper, in order to avoid recognizing Huxley's priority? This is possible, but I do not think it is the case. More simply, Teissier was biometrically oriented, he was originally interested in inter– and intraspecific comparisons in adults, and it was only a little later (in his doctoral dissertation) that he came to be interested also in individual growth. Whatever the case, the lesson of this story is that the discovery of the concept of constant differential growth ratio is a complex one. Huxley certainly played a major role in it, in interpreting individual growth in terms of a power law. But he did not discover a formula that had never been previously thought to apply to differential growth in general.

This being said, at the end of the 1920s and in the 1930s, a veritable industry of differential growth rapidly developed.

The power law was verified on innumerable examples, and became a standard tool for the study of simple as well as complex patterns of development, with different parameters for simultaneous allometric curves in the same animal, critical points, etc. Many examples of this kind of study can be found in Huxley’s and Teissier’s synthetic books published in 1932 and 1934.

Huxley’s and Teissier’s Joint Paper (1936)

In 1935, Huxley and Teissier decided to agree on a common terminology for relative growth. Over a space of a few months, they exchanged letters and negotiated various compromises regarding the designation, vocabulary and symbolic notation of the law of relative growth. In 1936, two joint papers were published in French (*Comptes rendus de la Société de biologie*) and in English (*Nature*). The two authors decided to abondon the terms they had each previously used: “allometry” replaced Huxley’s “heterogony” and Teissier’s “dysharmony”; “isometry” replaced “isogony” and “harmony”. They also agreed on a common symbolic formulation of the law: $y = bx^{□}$

The comparison of the French and the English version, and the correspondence between the two authors show that most differences are unimportant. There is however one major difference. It concerns the constant *'b'*. For Huxley, this constant had no biological significance whatsoever. *'b'* was no more than the value of *y* when $x = 1$. This constant was therefore arbitrary, and depended only of the choice of the measuring-unit. Since this unit could be such that the allometric relation did not exist for a given value of *x*, the "b" parameter had no biological signification. Teissier did not agree. He felt that 'b' could be given a biological meaning if attention was paid to the statistical nature of the data. For this reason, he introduced into the French version the following sentence: "From a statistical point of view, [*b*] represents the mean value of the ratio *y/x* for all the observed individuals" (Huxley & Teissier, 1936a: 936. For a more elaborate justification, see also Teissier 1935: 301). Huxley did not put this sentence in the English version.

In another paper published in 1936, Teissier provided a remarkable example of the biological meaning of the coefficient 'b'. He showed that local populations of a given species could have allometric equations for a certain organ that differed only by the coefficient "b". If for example the growth of the chelae of a lobster could be described by two successive allometric equations, and if the only difference between the two local races was in the "b" coefficient of the second equation, this meant that one of the races initiated the second phase of growth earlier, in younger animals (fig. 5).

This disagreement between Huxley and Teissier proved extremely important for the further history of allometry, as I will show.

ALLOMETRY AND THE MODERN SYNTHESIS (1949-1970)

In the last section of this paper, I will focus on problems generated by allometry in modern evolutionary theory. Other areas of research might be considered. As shown by a recent review article published in *Development*, a lot of work has been done in the 1980s and 1990s on the physiological and embryological mechanisms that act as proximate causes of allometry (Stern and Emlen 1999). This would be a fascinating subject, but I will leave it aside to concentrate on the question of evolution.

It is frequently argued that the Modern Synthesis neglected morphology and embryology. This is partly true, and thus partly false. What I will try to show here is that allometry was a major opportunity for those responsible for the Modern Synthesis to take into account morphology and embryology. Allometry was certainly not a major theme in the early phase of the modern synthesis (1940s), but it became quite important in the 1950s and 1960s among biologists who were obviously working within the paradigm of the modern synthesis. I will take (young) Stephen Jay Gould as an exemplary model of this attitude. A complete historical description would obviously include many other authors. However Gould can be seen as the person who most aptly recapitulated and renewed the subject. Thus, to be clear, I will show how Gould, insofar as he worked on allometry, played a major role in the completion of the Modern Synthesis.

Strangely enough, Huxley, in his Evolution: The Modern Synthesis, did not say much about allometry. The nine pages he devoted to this subject are essentially a compilation. No clear idea emerges as to the possible important theoretical problems raised by allometry for the modern synthesis. Huxley, like many others involved in the Synthesis, was probably embarrassed by the idea that, if allometry was really a very important phenomenon in evolution, then it challenged the overall adaptationist orientation of the synthesis.

In 1949, however, Norman Newell, an invertebrate paleontologist who later tutored Stephen Jay Gould, published an important article on phyletic size in invertebrates in the journal Evolution. A few passages are devoted to allometry. They were sketchy, but obviously important for the author. Basically, Newell rejected the common view according to which allometry implies non-adaptive, or orthogenetic evolution. Newell used three arguments, all related to the so-called constant parameters of the allometric equation. Firstly, he claimed that the □ parameter (the constant differential growth-ratio) is in fact modifiable by natural selection. Secondly, the constancy of □ (which Newell calls 'k') can in certain cases be attributed to natural selection. Following Simpson, Newell mentions the example of the relatively wider limb bones of larger land vertebrates. Here we have an allometric curve with an exponent approximately equal to 1.5. This is obviously due to natural selection: "Large animals without a proper relation between limb and body size would not survive" (Newell 1949: 105). Thirdly, the 'b' parameter can also change as a consequence of natural selection. Newell takes the example of suture length in certain lineages of Ammonoidea. Commenting on the allometric curves represented in figure 6, he writes: "… the regressions of successively younger genera apparently shift to the left. I interpret this to mean that natural selection has established ammonites with progressively decreasing values of b in the allometric relationship. This causes acceleration in development" (Newell 1947: 115). In this article, however, Newell did not systematically delve into the adaptive meaning of allometry. He just gave examples. But it seems clear to me that the kind of argument he proposed there was crucial for Gould.

I now turn to Gould. Gould's major papers on allometry were published between 1965 and 1971 (White and Gould 1965, Gould

1966, 1969, 1971). These early papers are no doubt a major, and perhaps underestimated contribution to modern evolutionary biology. All of them are long monographs. I will not try to summarize them, even superficially. I will merely point out the main lines threads of Gould's approach, as they emerge from the bulk of his major monographs. These approaches are as follows:

(1) Clarification of the meaning of the constant b in the allometric equation.

(2) Clarification of the relation between allometry and adaptive evolution.

(3) Clarification of the relations between the various modes of allometry.

Although this was not clear from the outset, these three themes were in fact closely related.

Concerning the 'b' parameter, Gould, like Teissier, whom he significantly quotes in his papers, thinks that it has a biological significance, and indeed a major one. In interspecific or intraspecific allometry, changing 'b' means generating a new regression line, which is parallel to the previous line, but shifted one way another. Gould's question is thus: from a dynamic point of view, how are certain species able to transcend of their allometric curve, and jump to another one? In particular, how can they preserve their overall shape, that is the absolute value of the ratio between one particular organ and the global size of the organism when size increases? From a mathematical point of view, such a process means that a certain lineage would be able to shift from one allometric curve to another along a line of slope 1. Gould provided an algebraic analysis of this problem in his first paper with White in 1965, but it is only in 1971 that he gave a graphical illustration of it (fig. 6). From a formal point of view, the essential idea can be stated as follows: what is the law of change of “b” that will preserve shape?

There are two possible evolutionary mechanisms that could accomplish such a change. Eugène Dubois, whom I referred to at the beginning of this paper, proposed the first one. Note that Gould’s 1971 diagram is very similar to Lapicque’s representation of 1907, with its theoretical lines of slope 1 going from one allometric curve to another (see fig. 1). For Dubois, moving from one “isoneural” line to another could be accomplished by a sudden change in the ontogeny. Dubois thought that mammals had increased the absolute brain/body ratio by successive doubling of the number of neurons in early embryogenesis. The second possible mechanism is acceleration or retardation of development in the course of phyletic evolution. In contrast with Dubois’ schema, this hypothesis does not imply sudden change, but a gradual evolution that involves intraspecific selection or selection between closely related species. Fig. 7 is a plausible example of such a process. Gould favors this second hypothesis, which is typically gradualist, adaptationist and selectionist. Note also that this reflection on the meaning of the coefficient ‘b’ involves a subtle articulation between the four modes of allometry: allometry of growth, phyletic allometry, static intraspecific and static interspecific allometry.

There is another aspect of Gould’s reflection on the relation between allometry and adaptation. For Gould, allometry, when it exists, is most often a non-adaptive source of evolutionary change. Such a change is a mechanical consequence of the increase in size, an increase that is itself adaptive. Thus allometry will most often be a source of biological diversity. But once the increase of size has taken place, organisms have to compensate for the non-adaptive effects of allometry. In constant environments in particular, allometric parameters (‘b’ as well as ‘▯’) will be subject to natural selection.

I cannot go further in the analysis of Gould’s view of allometry, but I think that I have showed how he tried to define the appropriate meaning of this phenomenon in the framework of the modern synthesis. All Gould’s work on relative growth is characterized by his systematic use of any biometrical method that could help solve the problems he addressed. This explains the fascinating relations between his own work and that of early biometrical studies of the brain/body relation at the turn of the 20th century. It also explains the reason why he thought that allometry was less important and challenging in the 1970s than two or three decades previously. The treatment of allometry relies on bivariate analysis. In contrast, modern analysis of the evolution of shape relies on extensive use of multivariate analysis. This in turn raises new questions, which are beyond the scope of this paper.

I would like to add a final comment. When I went through Gould's papers on allometry, I was impressed by the precision of his knowledge about Dutch, German and French pioneers on the subject of relative growth, especially in the case the 19th century work on the relationship between brain and body size. This cannot be a surprise if one thinks of Gould's later work on heterochrony and other paelobiological subjects. However, I take it as a good example of the close connection that can sometimes relate inventive scientific work to historical awareness.

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White and S. J. Gould, 1965. Interpretation of the coefficient

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[1] From the Symposium on…

[2] According to the formula $r = \log E - \log e / \log S - \log s$. (E and e : weights of the two brains; S and s: weight of the two bodies. Dubois 1897 : 363).