



## The Pattern of Variation in Centipede Segment Number as an Example of Developmental Constraint in Evolution

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The range of animal morphologies observed in nature is partly determined by natural selection. However, there is no agreement yet regarding whether it is also partly determined by developmental constraint. Testing for the effects of constraint has been difficult due to the lack of both an appropriate null model and a sufficiently simple system capable of yielding unambiguous results regarding the model's plausibility. Here we examine the case of variation in segment number in geophilomorph centipedes. Curiously, while this ranges between 29 and 191, there are no species in which an even number of segments is observed, in contrast to about 1000 species with odd numbers of segments. It seems unlikely that this distribution of character values is determined by selection alone. Using an approach based on Bayesian inference, we attempt to quantify the probability of obtaining the observed distribution of values given a null model in which developmental constraint is absent. Since this probability is in the region of  $10^{-20}$ , we conclude that constraint must be involved. We discuss various implications of this conclusion, and comment on the unexpected absence of neoteny and progenesis in centipede evolution.

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### 1. Introduction

Why do animals take the forms they do, and not others? Why, as Raff (1996) has asked, are all land vertebrates “tetrapods”—except for cases of secondary loss, for example snakes—while none have six, eight, or many legs? Why is the situation precisely reversed for land arthropods? In general, why are certain areas of multicellular morphospace densely populated with many representative species, while other areas, apparently characterizing viable designs, are unoccupied by any extant or extinct animals?

There are two very different answers to these questions, representing two opposing schools of

thought on the relative importance of natural selection and developmental constraint in determining the actual distribution of morphologies that we observe—either now, or at any point in evolutionary history, or cumulatively. One is the “pan-selectionist” view that variation is potentially available in all directions from any given phyletic starting-point, and that selection determines which subset of variants prevails. The alternative is the “developmental constraint” view that many of the gaps we observe between different morphologies do not arise from the non-adaptiveness of the absent forms but rather from the difficulty of making them through an ontogenetic process.

The pan-selectionist view can be traced back to Wallace (1870), who considered variation to be

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omnipresent and available in all phenotypic directions imaginable, apparently without even a quantitative bias in any direction. He refers (p. 290) to “Universal variability—small in amount but in every direction”, and Mayo (1983, p. 104) boldly states that “The major constraint on natural selection as an agent of change is natural selection as a stabilizing force”, apparently relegating any kind of *developmental* constraint to a minor role at best.

In contrast, Gould & Lewontin (1979) argue that organisms are “so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting the pathways of change than the selective force that may mediate change when it occurs”. Goodwin (1994) makes a similar point but in a specific context, namely the arrangement of leaves (phyllotaxis) in angiosperms. He points out that more than 80% of the quarter-million or so extant species have a spiral arrangement, and suggests that “the frequency of the different phyllotactic patterns in nature may simply reflect the relative probabilities of the morphogenetic trajectories of the various forms and have little to do with natural selection”.

It is necessary, at this point, to clarify the nature of the debate. There are probably no evolutionary biologists left who deny a role of some sort for natural selection. So there is no “pan-constraintist” school of thought. Also, while the pan-selectionists criticized by Gould & Lewontin (1979) do indeed deny any role for developmental constraint, most neo-Darwinians are not pan-selectionists. The relationship between neo-Darwinism and developmental constraint is best expressed by Wagner (1988) as follows. “It is true that the concept of developmental constraints is implicitly contained in neo-Darwinian theory. Nevertheless, it is also true that this concept has almost never had an influence on the main stream of research that was done by neo-Darwinists.” There are now some signs that the situation may be changing: see the recent work of Guerra *et al.* (1997) and Pezzoli *et al.* (1997).

In the past, much debate about the importance of developmental constraint in evolution has been diffuse and inconclusive. This is partly due

to the lack of an agreed definition, partly to the lack of a clear question regarding the role of constraint for which we can seek an unambiguous answer, and partly to the lack of a “model system” which encapsulates a form of constraint that is sufficiently simple and unidimensional that it can be dealt with productively. We attempt to rectify all three of these problems below.

## 2. What is “Constraint”?

There is a great danger that discussions of any form of “constraint” in evolution degenerate into a “hopeless exercise in semantics” (Antonovics & van Tienderen, 1991). Various authors have attempted definitions and categorizations in attempt to avoid this danger, notably Maynard Smith *et al.* (1985) and Resnik (1995). We will make use of these definitions, and a criticism of the former authors by Williams (1992), to make clear exactly what we mean by developmental constraint in this article.

We adopt a definite strategy here: we deliberately choose a narrow, *sensu stricto*, definition. We do this not because it corresponds best to the predominant usage in the literature (which it does not) but because (a) it increases the clarity of the argument and (b) it is “conservative”: if we can show that narrowly defined developmental constraint is important, then it follows that any more broadly defined counterpart must be at least equally important, if not more so.

Our starting point is the rather broad definition of Maynard Smith *et al.* (1985) which is as follows: “A developmental constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition or dynamics of the developmental system.” Narrowing down from this, we will deal only with what both Maynard Smith *et al.* (1985) and Resnik (1995) call local (as opposed to universal) constraints. We are focusing herein on centipedes, and on questions specific to a segmented body plan. We are thus not interested, in the present context, in the fact that all animals find it hard to produce wheels (Gould, 1983, chapter 12), interesting though this is, because it is an example of a universal constraint. Also, we will include only the

TABLE 1

*The six orders of centipedes (class Chilopoda), together with their segment numbers, species numbers and mode of development. (LBS = leg-bearing segments; ana- and epimorphic are explained in the Discussion; Devonobiomorpha is an extinct group—see Shear & Bonamo, 1988)*

Order	No. of LBS	No. of extant species	Development
Scutigermorpha	15	130	Anamorphic
Lithobiomorpha	15	1100	Anamorphic
Craterostigmomorpha	15	2	Anamorphic
Devonobiomorpha	?	0	?
Scolopendromorpha	21 or 23	550	Epimorphic
Geophilomorpha	29–191*	1000	Epimorphic

\* Odd numbers only throughout this range.

complete non-production of certain variant phenotypes rather than a restriction in (or “bias” against) their production, even though the broader “bias” definition is useful in a more general way as a counter-view to Wallace’s (1870) notion of effectively unbiased variation in all directions.

We will try, as far as possible, to divorce developmental from selective constraints, though this is in fact very difficult. We are following Williams’ (1992) advice here that “including fitness costs as developmental constraints” is not sensible, because “If selection is listed among the constraints, then what is it that is being constrained?” However, the problem is that while the complete absence of (for example) centipedes with 20 pairs of legs (see Table 1) *appears* to be a case of non-production rather than selective elimination, since no such centipedes have ever been observed, the possibility of selective elimination of embryos with 20 leg-pairs before egg-hatching cannot be excluded on the basis of the limited number of observations on centipede embryology conducted to date (Heymons, 1901; Johannsen & Butt, 1941; Whittington *et al.*, 1991). If selection is involved here, it is probably “internal selection”—see Discussion.

We have now arrived at a narrow definition which encapsulates only a subset of the phenomena that would be included in Maynard Smith *et al.*’s (1985) broader definition. Ours reads as follows: *Developmental constraint is the non-production of variant phenotypes caused by*

*the nature of the developmental system.* Let us now put this definition to work.

### 3. Questions and Models

The question we pose in this article is as follows: is the distribution of “segment number” in centipedes such that it can only be explained by invoking developmental constraint? The way we proceed towards an answer is (a) to construct a model or hypothesis of what the distribution should look like under the assumption that all variants are possible and the range actually found is determined entirely by selection; and (b) to examine the plausibility of this model. This is the approach advocated by Antonovics & van Tienderen (1991) who put it as follows. “A constraint seems to have little relevance without a specific reference to a null model. ... We therefore strongly urge that authors should state the null model explicitly; usually this null model describes what phenotypic variation to expect given a set of assumptions”.

The “null” description derives from the fact that developmental constraint is presumed absent. What we need is some means of measuring the strength of evidence (see below) with respect to the null model. If the null model is sufficiently implausible, an alternative model incorporating developmental constraint is favoured, though of course there are many possible such models and there is no way, as yet, of distinguishing between them. (For examples of the null model approach

in community ecology, where it has been more widely utilized, see Strong *et al.*, 1984.)

#### 4. A Null Model for Centipede Segment Number

##### 4.1. BAYESIAN INFERENCE

The approach we take here uses Bayesian inference (see, for example, O'Hagan, 1994) where the starting point is the identification of a "prior" probability distribution for the variable "segment number", given a limited knowledge of centipede morphology on the part of an observer. The argument in favour of a Bayesian approach seems particularly strong in this case where the evidence consists of the observed results of the evolutionary process rather than any repeatable experiment. However, since many readers may be more familiar with the frequentist approach to statistical inference, we give a brief outline of the relevant ideas as follows.

Probability is used to represent "degree of belief". Hence, if there are  $J$  competing hypotheses  $H_1, \dots, H_J$ , each is assigned a probability to measure the certainty attached to it. The usual rules of probability apply so, for example, if  $H_1, \dots, H_J$ , are mutually exclusive and exhaustive and the probability of  $H_j$  is  $P_j$ , then  $\sum P_j = 1$ . Before observing the data  $D$ , we have *prior* probabilities  $P_{01}, \dots, P_{0J}$ . When the data are observed these are converted to *posterior* probabilities  $P_{11}, \dots, P_{1J}$  using Bayes' theorem to calculate the conditional probabilities of the hypotheses given the data. That is

$$P_{1i} = \frac{P_{0i} \Pr(D|H_i)}{\sum_{j=1}^J P_{0j} \Pr(D|H_j)}, \quad (1)$$

where  $\Pr(D|H_j)$  is the conditional probability of the data given the hypothesis  $H_j$ . In the case of *simple* hypotheses which do not involve unknown parameters,  $\Pr(D|H_j)$  is called the *likelihood* and depends only on the hypothesis and the data. In the case of *composite* hypotheses, its calculation may involve prior probabilities specified for unknown parameters.

The *prior odds* in favour of  $H_j$  over  $H_1$  are  $P_{0j}/P_{01}$  and similarly the *posterior odds* are

$$\frac{P_{1j}}{P_{11}} = \frac{P_{0j}}{P_{01}} \frac{\Pr(D|H_j)}{\Pr(D|H_1)}. \quad (2)$$

The ratio  $\Pr(D|H_j)/\Pr(D|H_1)$  is called a *Bayes factor*.

##### 4.2. A SIMPLE ANALYSIS

Now, we will attempt to apply these ideas for measuring the evidence from the numbers of leg-bearing segments of known species of centipedes. For simplicity, we will discuss only the Geophilomorpha (see Table 1). One hypothesis is  $H_1$ : there is no developmental constraint. If there is developmental constraint, then, before we observe the data, it could take any one of many different forms and these are represented by  $H_2, H_3, \dots$ . We need to be able to identify what it might have been reasonably imagined that these would be, before the data had been seen. We might imagine that we had not counted the leg-bearing segments of centipedes before but had, at least, some idea of what the animals would look like and roughly how many segments they would have. We can then ask whether the evidence, when we see it, should convince us that only odd numbers of leg-bearing segments are possible, which is the curious pattern actually observed—see Fig. 1. (Odd numbers of leg-bearing segments may correspond to even total numbers of segments (Minelli & Bortoletto, 1988), though there is some difficulty in interpreting the segmental basis of the head and genital regions.) More rigorously, we are really considering how convinced we should be that any new species discovered would also have an odd number of leg-bearing segments.

For simplicity, let us, at least initially, only consider constraints which take the form of periodicities in the possible numbers of leg-bearing segments. That is, only every  $j$ th number is possible. E.g., if  $j = 2$ , then either only odd numbers are possible or only even numbers are possible. If  $j = 3$  then only 1,4,7, ... or only 2,5,8, ... or only 3,6,9, ... are possible. We might reasonably restrict our attention to fairly small values of  $j$  as confirmation of large values would require observation of species with implausibly large numbers of segments.

If we label the hypotheses as  $H_j$ : there is periodicity with period  $j$ , then it is immediately apparent from the data that  $\Pr(D|H_j) = 0$  and hence  $P_{1j} = 0$  for  $j > 2$ . Determining  $\Pr(D|H_1)$

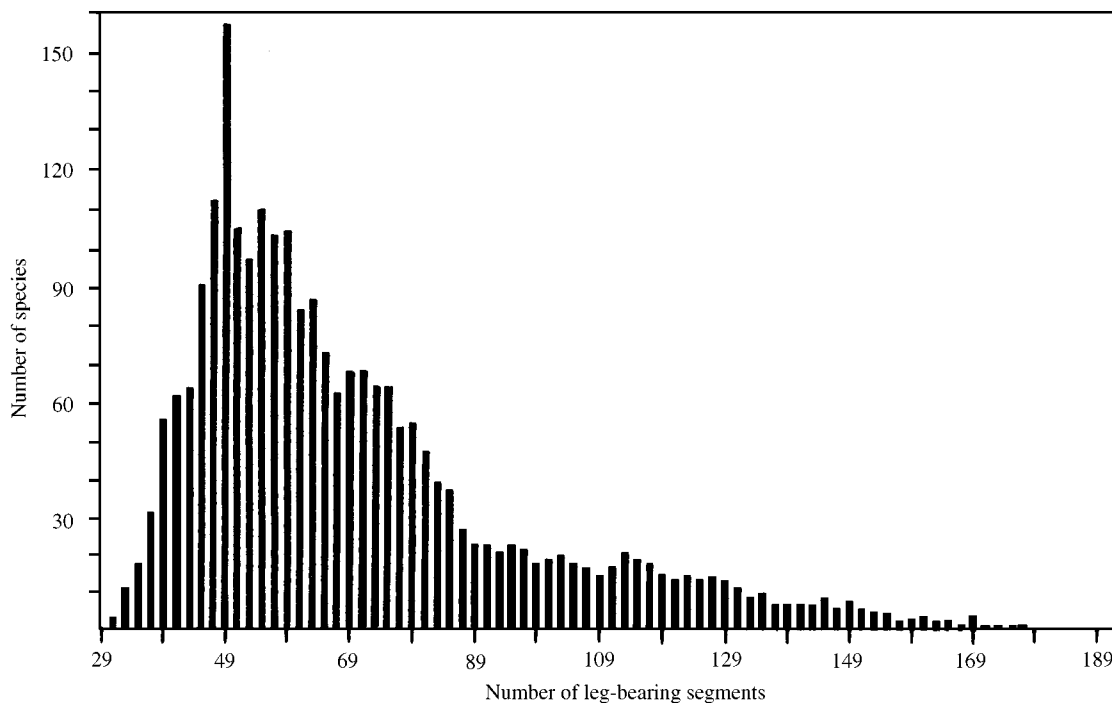


FIG. 1. The distribution of the number of leg-bearing segments among all known species of geophilomorphs. Note that variable species contribute to several adjacent bars, while fixed species (family Mecistocephalidae) contribute to a single bar. From Minelli & Bortoletto (1988), with permission.

and  $\Pr(D|H_2)$  is not so straightforward. However, we present a very simple argument and argue that our conclusions are likely to be conservative compared to those from more detailed analyses.

The data consist of the numbers  $X$  of leg-bearing segments in the known species. We make a number of simplifying assumptions here, all of which should cause our approach to be “conservative”. First, we ignore the intraspecific component of the variation, even though this is itself strongly suggestive of developmental constraint. In the following,  $X$  values can be taken to be the precise number of trunk segments for invariant species and the modal number for variable ones. Second, it does not seem reasonable to consider the species to be independent. It could be, for example, that many of the species with  $X = 69$  have evolved from a common ancestor with  $X = 69$ . This means that the weight of evidence from the number of species with  $X = 69$  is less than it would be if they were independent. The limit of how small it can be is given when we treat all species with a given  $X$  value as a single

observation. We will do this to obtain a conservative value for the Bayes factor.

Third, it is also likely that neighbouring segment numbers are not independent. We might expect the observed numbers to be clustered together, as in fact they are. That is, if we discovered a species with  $X = 69$  this might lead us to expect to find other species with similar  $X$  values. This point is reinforced by a recent cladistic analysis of the Geophilomorpha by Foddai (1998). We might also expect some of the numbers to be spread by the effects of competition, through the co-evolutionary process of character displacement (Brown & Wilson, 1956), though in fact, the evidence for such a process is rather weak (Arthur, 1982). Similarly, there may be some values of  $X$ , for example very large ones, which are less likely *a priori* than others. Such considerations would have a similar effect to reducing the number of available segment numbers. If we ignore this, then again we will obtain a conservative value for the Bayes factor.

Taking this extremely simplistic, conservative, approach we argue as follows. Suppose that there

are  $2n$  possible values of  $X$  from which to choose. Under  $H_1$  the number of the possible selections of  $m$  values is

$$\binom{2n}{m} = \frac{(2n)!}{m!(2n-m)!}. \quad (3)$$

Under  $H_2$  selections containing only odd numbers and selections containing only even numbers are possible, but not selections containing both odd and even numbers. Thus, the number of possibilities is

$$2 \binom{n}{m} = \frac{2n!}{m!(n-m)!}. \quad (4)$$

Assuming, conservatively, that all selections are equally likely, the probability of any given selection is the reciprocal of the number of possible selections. To obtain  $\Pr(D|H_j)$  this probability must be multiplied by the probability of the value of  $m$ , the number of different  $X$  values, given  $H_j$ . If only odd numbers are possible then we might reasonably expect only half as many different values of  $X$ , therefore giving each value of  $m$  approximately twice the probability. However, it could be argued that this is not so and, even if both odd and even numbers were possible, we might not expect to observe all of the possible  $X$  values in a range. Therefore, we again take the conservative choice and assume that the probability for a given value of  $m$  does not differ between  $H_1$  and  $H_2$ . In this case it cancels out in the Bayes factor.

The Bayes factor in favour of  $H_2$  over  $H_1$  is thus

$$\begin{aligned} B &= \frac{\binom{2n}{m}}{2 \binom{n}{m}} \\ &= \left(\frac{1}{2}\right) \left(\frac{2n}{m} \frac{2n-1}{m-1} \dots \frac{2n-m+1}{1}\right) \\ &\quad \times \left(\frac{n}{m} \frac{n-1}{m-1} \dots \frac{n-m+1}{1}\right)^{-1} \\ &= \left(\frac{1}{2}\right) \left(\frac{2n}{n} \frac{2n-1}{n-1} \dots \frac{2n-m+1}{n-m+1}\right). \end{aligned} \quad (5)$$

So, as  $n \rightarrow \infty$ ,  $B \rightarrow 2^{m-1}$ . For  $n < \infty$ ,  $B > 2^{m-1}$ . For the Geophilomorpha  $m = 76$  so, bearing in mind our discussion above, we conclude that  $B$  should be at least  $2^{75} \approx 3.8 \times 10^{22}$ .

In order to see how this Bayes factor turns into a posterior probability, we need to introduce some prior probabilities. At first glance, this appears to be difficult as there are many possible patterns which we could observe. However, we can argue as follows. Suppose that the probability that there is constraint of some sort is  $\alpha$ . Let  $\beta$  be the conditional probability that, given that there is constraint, this takes the form of a simple periodicity as described above. Let  $\gamma$  be the conditional probability that, given that there is constraint and that it is a simple periodicity, the period is 2. Then the prior probability of  $H_1$  is  $1 - \alpha$  and the prior probability of  $H_2$  is  $\alpha\beta\gamma$ . The prior odds in favour of  $H_2$  over  $H_1$  are therefore  $\alpha\beta\gamma/(1 - \alpha)$ . Readers may supply their own values for  $\alpha$ ,  $\beta$  and  $\gamma$  but, if we are willing to state, for example, that  $\alpha \geq 0.1$ ,  $\beta \geq 0.1$  and  $\gamma \geq 0.1$ , this leads to the conclusion that the prior odds are at least  $10^{-2}/9$ . This in turn leads to posterior odds of greater than  $4 \times 10^{19}$  and a posterior probability of no constraint of around  $10^{-20}$ .

This analysis has been very simple and unsophisticated. However, we put it forward to show the kind of approach that might be taken and to stimulate discussion. We acknowledge that many refinements could be made to the argument. For example, we have not discussed the possibility of a system where even numbers are possible but, for some reason, very unlikely to be observed. We hope to have the opportunity to present a more detailed analysis in a future paper.

## 5. Discussion

Our conclusion is clear: some mixture of selection and constraint determines the observed pattern of variation in centipede segment number. At this stage, attempts to evaluate the relative importance of the two processes are probably futile; it would be more productive to focus on the *nature* of these and other developmental constraints—that is, to ask what cellular mechanisms underly the difficulty of producing certain forms. This question can be asked in both molecular and “systems” terms, and much of the ongoing

work on the molecular basis of development will eventually help to elucidate the nature of constraints. One model of how mechanisms of segment production might lead to constraint in this particular context is given by Minelli & Bortoletto (1988). These authors propose a multiplicative system of segment production in which pairs of segments are derived from single "eosegments" in early embryogenesis.

Centipedes are sometimes divided into two sub-classes based on the way segments are produced in ontogeny (Lewis, 1981): Anamorpha (a paraphyletic group that includes the lithobiomorphs—see below) in which segment number increases from egg-hatching to adulthood by posterior addition of segments through progressive juvenile stages; and Epimorpha (a derived monophyletic group including the geophilomorphs) in which the adult segment number is established during embryogenesis, and does not increase after the egg hatches. Ironically, the longest centipedes are epimorphic while the shortest are anamorphic, which seems counter-intuitive and is itself an intriguing problem.

Two interesting points emerge from this anamorphic/epimorphic distinction. First, consider the juvenile anamorphic centipede *Lithobius variegatus* shown in Fig. 2, which has 12 pairs of legs. Its existence demonstrates (a) that a centipede with an even number of trunk segments and leg pairs can be a perfectly viable, well-adapted entity capable of moving, feeding, and generally surviving, in a natural environment; and (b) that what is "prohibited" in developmental terms is not the production of an even-segment-number centipede, but rather an ontogeny that *culminates* in an even number of segments. In fact, it is quite remarkable that throughout the evolution of the Lithobiomorpha (currently more than 1000 species—see Table 1) there appears not to have been a single heterochronic change (neither neoteny nor progenesis) that has resulted in a species in which an even-segment-number juvenile becomes reproductively mature and the ancestral 15-segment adult stage is lost. Heterochronic processes are common in other taxonomic groups (reviewed by Gould, 1977 and McKinney & McNamara, 1991), suggesting that the developmental-genetic

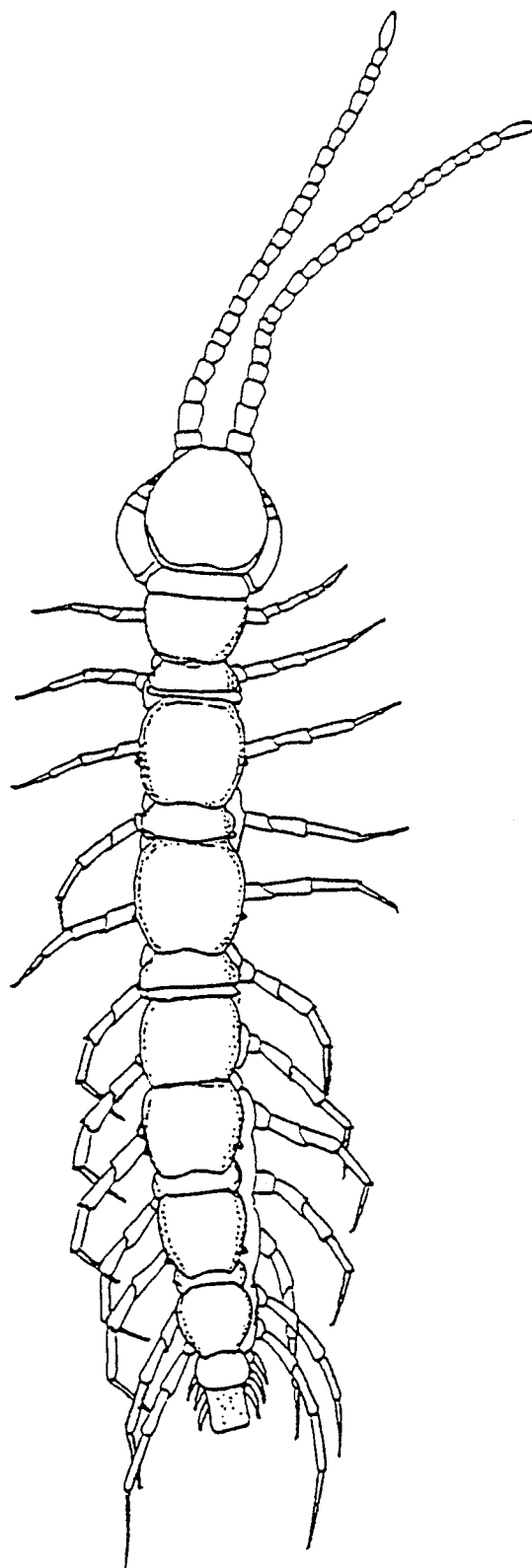


FIG. 2. A juvenile *Lithobius variegatus* with 12 leg-bearing segments. Note also the three pairs of limb buds (posterior) which will give rise to leg-pairs at the final sub-adult moult. From Eason (1964), with permission.

basis of such changes is widespread and that this kind of evolution is relatively “easy” for natural selection to produce, along with its spatial equivalent, heterotopy. So why it has not occurred here is a mystery.

Second, consider the embryonic development of an epimorphic centipede, *Scolopendra morsitans*. Although this is the most-studied species of centipede from an embryological perspective (see Heymons, 1901; Johannsen & Butt, 1941; Gilbert & Raunio, 1997), it is uncertain whether embryos with even segment numbers, destined to be even-numbered hatchlings and adults, are simply never produced, or alternatively are produced occasionally but always die before hatching. If the latter, then it is a moot point whether this is more appropriately considered as developmental constraint or selection. Perhaps, in such a case, the choice of stance should depend on the cause of mortality. If embryos with even numbers of segments are more susceptible to mortality caused by an external agent such as an egg-predator, then this is clearly selection. However, such a scenario seems most unlikely. Alternatively, if these embryos die due to internal “scrambling” of the developmental process, then this could be considered to be developmental constraint, or, perhaps better, “internal selection”. Indeed, these two can be hard to separate—see Whyte (1965) and Arthur (1997). (Note that “developmental selection” or “clonal selection” is an entirely different process to internal selection—see Buss, 1987, Frank, 1997).

The pattern of variation in segment number also has an implication for the size of morphological step involved in directional evolutionary change. The ancestral “stem species” centipede probably had 15 trunk segments (see Shear & Bonamo, 1988; Borucki, 1996; Giribet *et al.*, 1999, but, for a counter-view, Shultz & Regier, 1997). If so, then to get to the next largest number observed—21 segments—the *smallest* step possible is two segments at a time. Since even well-preserved fossil centipedes are rarely complete (see Mundel, 1979 for an exception), it is hard to get direct evidence concerning whether steps were 2/2/2, 2/4, 4/2 or 6. Also, if Minelli & Bortoletto’s (1988) “octonary” model is correct, it may be that evolution took a path 15 → 23 → 21, in which case the first step was +8 segments.

Even the smallest possible addition of two segments to 15 is a sizeable proportional change (13%), while adding eight segments is a change of 53%. This does not, of course, mean that we should all become neo-Goldschmidians believing in the preponderance of saltations (see Goldschmidt, 1940). However, it does indicate that a view of morphological evolution wherein individual mutations always cause only imperceptible shifts of the value of a character such as “body length” is too extreme in the other direction. Evolution must also involve what Dawkins (1986) calls “stretched DC8” mutations (as opposed to those that turn DC8’s into 747’s), of which a mutationally elongated centipede is a classic example.

Finally, it is important to distinguish between demonstration of the existence of developmental constraint and demonstration of its importance. Wagner (1988) makes a link between highly constrained basic body plans and the evolution of high degrees of phenotypic complexity and functional integration. (He uses the insects as an example of this link.) It seems likely that some forms of constraint do indeed “accidentally” facilitate the evolutionary production of morphological complexity, while others have no such effect. The apparent prohibition of centipede ontogenies that culminate in an even number of trunk segments may well be an example of the latter.

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