

Measuring morphological complexity of segmented animals: centipedes as model systems

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Abstract

In segmented animals it is possible to define morphological complexity as the degree of morphological differentiation of segments. A quantitative method for measuring morphological complexity of segmental patterns was devised by McShea in 1992, who introduced three geometrical indices. Here, we introduce a new index of morphological complexity and emphasize the possible decoupling between segmentation and segment differentiation and illustrate different patterns of variation within segmental series and how these could affect morphological evolution and evolvability. Concepts are illustrated by contrasting the segmental models of two groups of centipedes (Chilopoda): the elongate Geophilomorpha and the short-bodied Lithobiomorpha. A preliminary application of the new metric provides no evidence of macroevolutionary increase in morphological complexity of centipede segmental organization.

Introduction

Complexity is difficult to define and to measure. Within evolutionary biology alone, several conceptually independent types of complexity have been recognized, but the corresponding metrics so far devised are seldom operational and never universal (McShea, 1996a). As in other areas of comparative biology, in the study of biological complexity it is possible to follow different methods of inquiry roughly classifiable as pattern vs. process approaches.

Within a *process approach*, complexity is meant as a function of number, heterogeneity and hierarchy of dynamic interactions among parts of biological systems (McShea, 1996a). For instance, in evolutionary perspective, some authors investigated the complexity of developmental processes by measuring the degree of developmental integration among phenotypic traits. Integration is manifested in coordinated changes in ontogeny or phylogeny, space, time, magnitude or direction (Roth, 1996). The dynamics of developmental

systems together with the topology of the mapping of genotype onto phenotype affect the evolvability, i.e. the 'propensity' to further evolution (Wagner, 1996). High levels of developmental integration may limit morphological evolution, hence the evolution of morphological complexity, because of the reduced number of morpho-functional units that can change independently (Vermeij, 1974; Lauder, 1981). Wagner & Altenberg (1996) claim that evolvability is improved by modular mapping, i.e. by a genotype-to-phenotype mapping where pleiotropic effects are virtually restricted to characters belonging to one character complex and promote character co-adaptation within the same complex.

Methods have been suggested to estimate developmental integration as correlation between morphological characters (i.e. Olson & Miller, 1958; Cheverud, 1982, 1996; Roth, 1996). A developmental biology approach to complexity stresses the interdependence of genes, developmental processes and phenotypic traits, but their relationship is neither linear nor strictly hierarchical (Minelli, 1998).

Under a *pattern approach*, complexity is a pure structural concept, based on number, heterogeneity and hierarchy of parts, thus disregarding their functionality: 'the more differentiate a system is the more complex it is' (McShea, 1996a). Differentiation itself is not a clear-cut

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concept allowing direct definitive measurements. However, it is possible to explicitly determine a set of criteria leading to consistent comparisons. Methods have been thus suggested to estimate the morphological complexity of biological structures. Cisne (1974) used both number of elements and number of kinds of appendages as a measure of morphological complexity in arthropods. Within the same logic, other authors (e.g. Bonner, 1988; Valentine *et al.*, 1993; Bell & Mooers, 1997) used the number of cell types to estimate an animal's complexity, a first step in the development of macro-evolutionary scenarios.

A study of morphological complexity focusing on the results of possibly unknown processes of development and evolution may seem poorly informative and thus unattractive. However, in so far as it generally invites for more objective measurements, it allows building a pattern data framework against which to test dynamic interpretations independently developed from a process approach. Moreover, structural patterns as a result of dynamic processes turn out to behave as boundary conditions for the further evolution of the system, i.e. they are nodal points between sequential sections of the evolutionary process. As far as we view evolution as the change of ontogeny with time (Gilbert *et al.*, 1996), structural patterns are pivotal elements of the relationship between ontogeny and phylogeny.

In this paper we deal with the morphological complexity of segmented animals. Segmentation is a conspicuous structural feature of some major animal groups (annelids, arthropods, vertebrates), and some 'metameric logic' (multiplication with differentiation) is observable at any level of biological organization (Weiss, 1990). A segmented body plan seems to be a quite effective strategy for increasing in size and specialization (Weiss, 1990; Wagner, 1996), and therefore it provides an attractive subject for investigations on complexity. Body segments, or homologous parts thereof, offer themselves as suitable units of comparison, irrespective of the peculiar mechanisms of segmentation and segment differentiation at work (Minelli & Fusco, 1995). It is necessary, however, to distinguish two 'layers of homology' (Minelli, 1998), the *origin* resp. the *patterning* of segments: different genetic cascades generally control segmentation and segment differentiation, respectively, although simultaneous effects of some gene expressions on both events may secondarily evolve in organisms with extremely condensed developmental time, as *Drosophila*.

Measuring morphological complexity

McShea's metrics

Searching for evidence of possible trends in the evolution of metazoan complexity, McShea (1996a,b) has recently reviewed the notion of complexity from the viewpoint of

evolutionary biology and the metrics thus far devised for measuring morphological complexity. In a series of previous papers, the same author presented (McShea, 1991, 1992) and used (McShea, 1993, 1994) three different metrics for measuring morphological complexity in organisms with serially homologous structures (in his study, the mammalian vertebral column). Adopting a quantitative structural approach, repetitive structures offer simplified cases for the study of complexity because for these structures it is possible to define morphological complexity as the degree of heterogeneity of a series. McShea's metrics are:

$$R = \log(X_{\max} - X_{\min}) \quad (\text{range})$$

$$C = \log(2\sum|X_i - \bar{X}|/N) \quad (\text{polarization})$$

$$Cm = \log(\sum|X_{i+1} - X_i|/(N-1)) \quad (\text{irregularity})$$

where X_i is the measurement taken from the i th element of the series, X_{\max} , X_{\min} and \bar{X} are, respectively, the maximum, the minimum and the average value of X , and N is the number of elements. A metric is a compound measure like sample statistics, but it is different from the latter because all elements are measured, instead of a sample only. Metrics are numerical values and therefore have no associated sample distribution, unless one considers measurement error. R , the range of variation along the series, gives a first measure of the magnitude of differentiation. C is the polarization of the series, expressed as the average difference from the average value of the series (a variance analogue). The average difference is doubled in the formula, so that the maximum value of C is bounded to R . C is at maximum when one half of the measures have the maximum and the other half the minimum value, irrespectively of their order. Therefore, as extreme cases, C is at maximum both in regularly alternating series and in series with one step in the middle (e.g. first half of the series at uniformly maximum value followed by the second half at uniformly minimum value). Cm , the irregularity of the series, is calculated as the sum of differences between contiguous elements; its properties will be discussed later, as more directly relevant to our analysis. These metrics are simple and based on a clear statement (McShea, 1992): the more different from each other the elements in a series, the more complex the segmental pattern.

For a more accurate evaluation of the effects of the number of elements (N) on segment differentiation, we will introduce a distinction between a *segmental pattern* (in this approach, as well as in McShea's approach, intended as a series of metric values) and what we will refer to as its *overall shape*. By definition, two segmental series (segmental patterns) of different length, i.e. with a different number of elements, cannot be *equal*. Nevertheless, if they geometrically describe the same

contour, that is, if they can be considered as samples from the same continuous mathematical function, defined in a common domain of relative segmental position (for instance (0,1)), then the two series may be regarded as *equivalent* because they share the same *overall shape*.

In practice, two series X_i and Y_j with N_X and N_Y elements, respectively, are equivalent if transforming the absolute positions of their elements in relative positions ($i \rightarrow (i - 1/2)/N_X$ resp. $j \rightarrow (j - 1/2)/N_Y$) and correcting for size with a linear transformation ($X_i \rightarrow aX_i$ resp. $Y_j \rightarrow bY_j$) the two series describe the same overall pattern.

In McShea's macroevolutionary comparisons of the segmental pattern of vertebral columns, decoupling variation in shape from variation in length was not important. Accordingly, McShea's metrics C and C_m cannot recognize equivalent patterns if these are distributed over different lengths. In other contexts, the two kinds of variation must be separated. We will show that minor adjustments can extend McShea's comparative approach to a broader set of segmented taxa, while addressing questions such as: is there a variation in complexity during the ontogeny of a given segmented animal? does the number of segments affect complexity in a segmentally polymorphic species? Macroevolutionary trends and patterns can thus be compared to microevolutionary patterns and developmental processes.

A new metric

We propose here a new metric for measuring complexity as irregularity of segmental structures. This is similar to McShea's C_m but improves it in capturing traits of the overall shape of a segmental pattern, independently from the number of segments over which it develops, and is more sensitive than C_m to differences within smooth patterns.

We call the new metric C_s because, in geometrical terms, it registers *slope* variations along the sequence of measurements describing the segmental pattern. In formula:

$$C_s = \log \left(\sum_{i=2}^{N-1} |(X_i - X_{i-1})/(1/N) - (X_{i+1} - X_i)/(1/N)| \right)$$

that simplifies to

$$C_s = \log \left(\sum_{i=2}^{N-1} |2X_i - X_{i-1} - X_{i+1}|N \right)$$

where X_i is the measurement taken from the i th element of the series and N is the total number of elements.

The different properties of C_s in respect of McShea's C_m for capturing significant aspects of morphological complexity are illustrated by the example shown in Fig. 1.

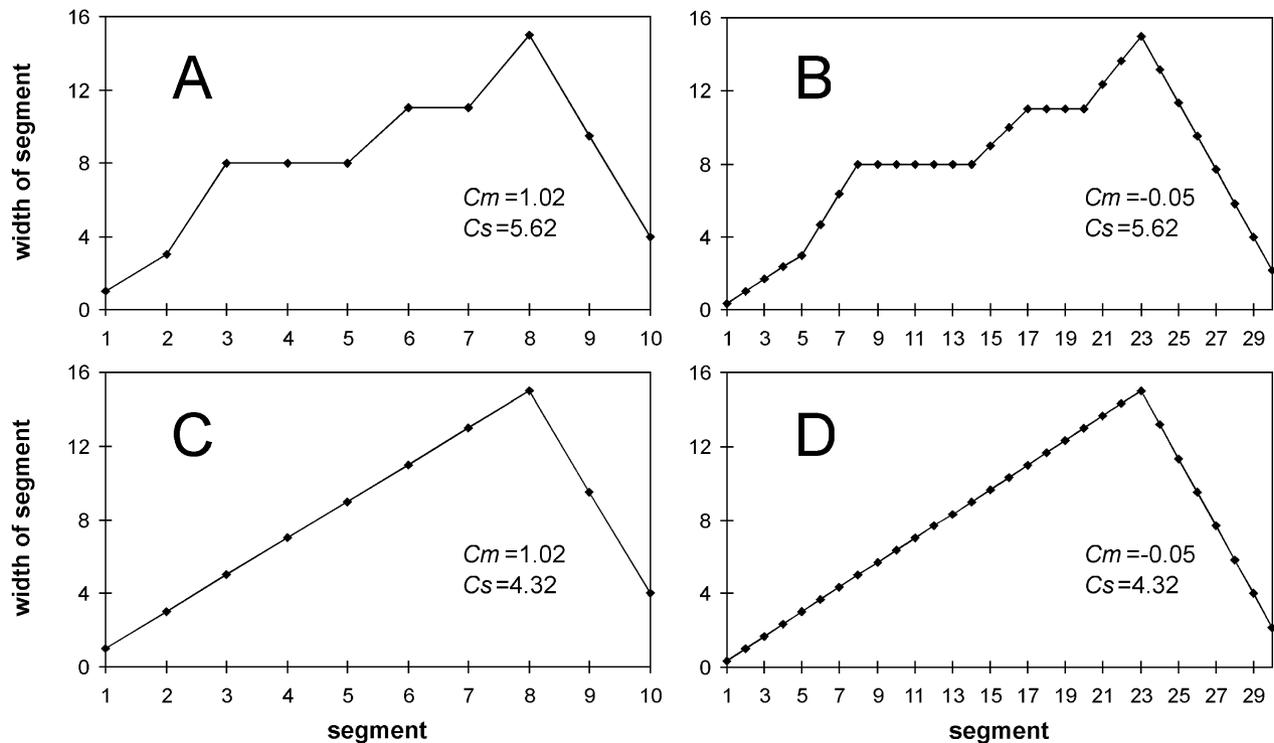


Fig. 1 Four idealized series of measurements differing in overall shape of segmental pattern (A vs. C and B vs. D) and length of segmental series (A vs. B and C vs. D) with C_m and C_s scores.

Consider the hypothetical segmental pattern for the same character in four different specimens and the complexity scores these obtain as C_m and C_s , respectively. In specimens A and B, equivalent patterns are produced by different numbers of elements (10 vs. 30). The same for C and D. Here, however, the overall shape of the segmental pattern is simpler than in A and B. In the two comparisons (A vs. B; C vs. D) the two metrics give opposite results. C_m gives a lower complexity score for B than for A (-0.05 vs. 1.02) because of the larger number of elements in the series; the same for C vs. D. Conversely, C_s is not affected by the length of the series and gives the same score for A and B (5.62) and for C and D (4.32). C_m , by measuring the sum of differences between contiguous elements, does not capture the pattern difference in that part of the series which increases monotonically and thus does not score A as more complex than C (for both, $C_m = 1.02$). In the same way, B does not get a complexity score higher than D. Instead, C_s is sensitive to the different structure of the segmental pattern along monotonic sections: A gets 5.62 while C gets 4.32 and the same for B vs. D.

Mathematically, both metrics are generated by a sum of additive terms ($N - 1$ terms for C_m , $N - 2$ for C_s), each term being 'a bit of complexity' along the pattern. C_m obtains a nonzero additive term every time there is a nonzero difference between two contiguous elements (e.g. nine nonzero terms in specimen C). For C_s a term is nonzero whenever there is a local change in the slope (e.g. one term in C). Sections of the segmental pattern that are on a straight line do not contribute to complexity, whatever the slope. C_m registers metric variations of a structural trait while C_s records variations of a morphological gradient.

C_s is not completely independent from N . If an observed segmental pattern is the discrete expression of a continuous 'signal' along the main body axis, we can expect a slight increase in complexity with N due to the fact that longer series can express the signal with greater detail. McShea (1992) has already pointed to the problem of continuous vs. discrete variation. These differences in the value of complexity are not an undesirable drawback of the metrics but *real* morphological differences due to the different number of elements in the segmental series, with possible biological significance as phylogenetic, ontogenetic or functional constraints.

Size correction

For larger animals there is a trend to systematically get higher scores of R , C , C_m and C_s because all these metrics are based on the absolute magnitude of disparity among the elements of a series. McShea (1993) tested different regression models for size correction, based on different size factors, and generally found a good agreement among the results of the different corrections.

We will show that, independently from the method of size correction adopted, the choice of *characters* used as the size factor may be critical wherever size additionally constrains the overall shape of the segmental pattern.

Segmental patterns in geophilomorph and lithobiomorph centipedes

In order to illustrate our concepts, it will be useful to compare two different segmental models exhibited by two groups of centipedes (Chilopoda) on which we have tested the applicability of McShea's metrics (Berto *et al.*, 1997), i.e. the longer worm-like Geophilomorpha and the shorter, scolopender-like Lithobiomorpha (Fig. 2).

Geophilomorphs exhibit conspicuous variability in the number (N) of leg-bearing segments. N ranges from 29 to 191 across the whole order, but never assuming any even value in this interval. This number is already present at hatching and does not change with moulting (epimorphic development). Distribution and variation of segment numbers are different in the two major clades into which Geophilomorpha split (Verhoeff, 1902–25; Foddai, 1998). One of these clades, corresponding to the traditional family Mecistocephalidae, retains two plesiomorphic features: (a) intraspecific invariance in segment number and (b) same number of segments in the two sexes. In the other clade, including all remaining families traditionally recognized in Geophilomorpha, N is lower in the males than in the females (but for a few scattered species where N is the same in the two sexes) and, generally, variable within each sex. This variation, however, is not random. In particular, the modal value of N in the female is generally 2 segments (less frequently, 4, 8 or 16 segments) higher than in the males of the same species. See Minelli & Bortoletto (1988) for an overview.

In a recent paper (Berto *et al.*, 1997) we discussed allometric patterns in ontogeny and segmental patterns of metric traits of terga, sterna and appendages in some geophilomorph species. Comparisons of segmental patterns from specimens of the same species and sex

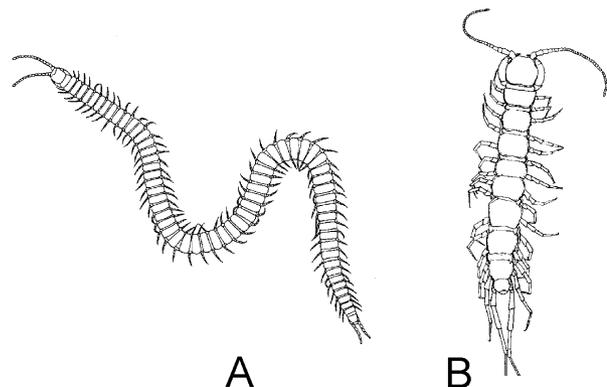


Fig. 2 Habitus of centipedes: A, geophilomorph; B, lithobiomorph.

but with a different number of trunk segments provided evidence that the overall shape of the segmental pattern is largely independent from N . This is in agreement with Minelli's (1992) observation on the segmental distribution of sternal grooves in *Sigmatogaster gracilis* (Geophilomorpha: Himantariidae). In geophilomorph centipedes segments do not behave as independent homologues. In other words, relevant features of a segmental pattern are not linked to the *absolute* ordinal position of a given segment (say, the 23rd) but rather depend on its *relative* position within the N -variable trunk region (Fig. 3). These results suggest a continuous pattern developing along the whole trunk, although mapping onto the discrete frame of N segments.

Lithobiomorph centipedes are different: the number of leg-bearing segments is constant and relatively small (15) in the adults of all species in the order and in both sexes. These centipedes develop hemi-anamorphically: the five larval stages, during which complete new segments develop posteriorly according to a specific schedule, are followed by a somehow variable number of postlarval stages, all with $N = 15$ and undergoing only minor external changes. In this group there is a precise

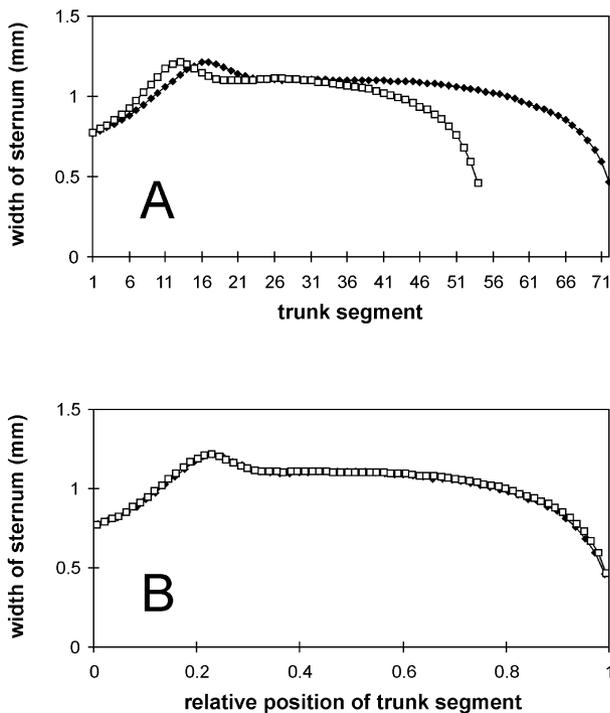


Fig. 3 Segmental patterns (width of sternum) in two geophilomorph specimens of the same species (*Clinopodes flavidus*) with different numbers of segments. A, segmental patterns represented on an axis of ordinal segmental positions; B, segmental patterns represented on an axis of relative segmental positions. For this character, the two different segmental patterns have similar overall shape.

correspondence (homology) between the i th segment of a specimen and the i th segment of any other specimen, even if the two specimens differ in N because of the different ontogenetic stadium (Fig. 4).

Irrespective of the ontogenetic or phylogenetic origin of individual differences in N , when comparing segmental series of different length, the way in which N affects the segmental pattern is completely different in the two centipede groups. In geophilomorphs the overall shape of a segmental pattern may remain the same when expressed by segmental series of different length (for instance, in intraspecific comparisons of specimens belonging to cohorts differing in N); in lithobiomorphs, the ontogenetic increase in N affects both the length and the structure of the pattern.

If segmental complexity is to be measured as a function of number and heterogeneity of elements in a segmental series, we cannot ignore that these two morphological components (number and heterogeneity) can be inter-related in different ways and degrees. Accordingly, measures of morphological complexity ought to consider their possible interactions and to evaluate these different sources of variation appropriately.

McShea (1993) corrected his metrics for body size calculating residuals from linear regression (but see below for additional comments). However, C and C_m metrics are uncritically sensitive to the number of elements in the segmental pattern. Specimens with almost equivalent pattern, but with different number of segments, yield quite different complexity scores. In particular, C_m tends to decrease when N increases. We think that equivalent segmental series should get the same complexity score. Another problem with McShea's C_m comes to light when comparing segmental patterns of the geophilomorph type with very high N . These series do sometimes show characteristic patterns also in those monotonic sections where variation between contiguous elements is smooth. In these cases, C_m is quite insensitive to pattern variations (see below).

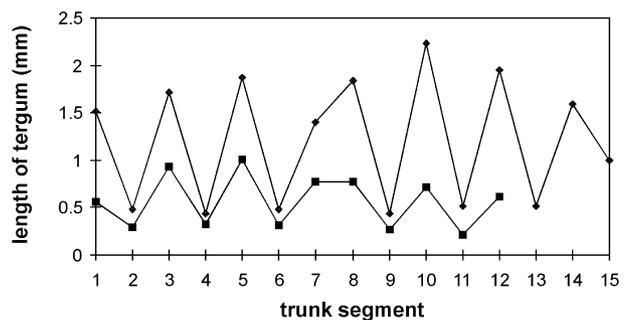


Fig. 4 Segmental patterns (length of tergum) in two lithobiomorph specimens of the same species (*Lithobius castaneus*) but with different numbers of segments, i.e. a larva IV (lower pattern) and an adult (upper pattern). For this character, the two different segmental patterns have different overall shape.

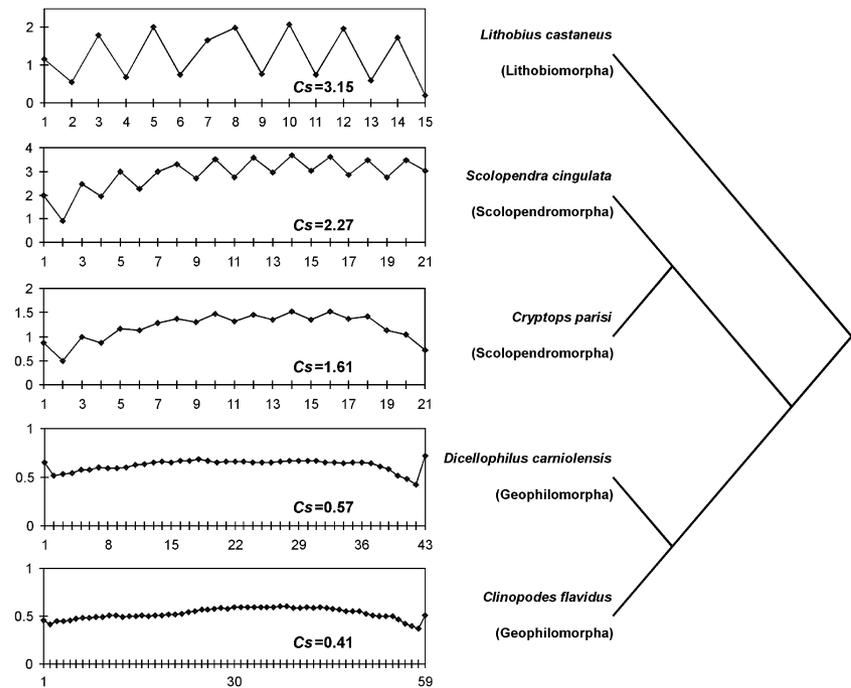


Fig. 5 Segmental patterns in five species of centipedes mapped onto their phylogenetic tree. Length of tergum (in mm, vertical axis) is plotted against absolute segmental position (horizontal axis). Segmental patterns are averaged on three specimens for each species. See text for C_s calculation.

Results

Centipedes and the evolution of segmental pattern complexity

We applied our metric to segmental patterns in five species of centipedes belonging to three different orders and five families: *Lithobius castaneus* Newport 1844 (Lithobiomorpha, Lithobiidae), *Scolopendra cingulata* Latreille 1829 (Scolopendromorpha, Scolopendridae), *Cryptops parisi* Brölemann 1920 (Scolopendromorpha, Cryptopidae), *Dicellyphilus carniolensis* (C. L. Koch 1847) (Geophilomorpha, Mecistocephalidae) and *Clinopodes flavidus* C. L. Koch 1847 (Geophilomorpha, Geophilidae). In all cases, we studied morphological complexity as reflected by the segmentally varying length of the tergum of the individual segments.

The segmental patterns shown in Fig. 5 are averages of three specimens for each species. For controlling the bias of body size (quite variable in our sample) on C_s measures, the five original segmental patterns have been standardized (linear transformation) so the sum of the elements in the series is 1 for all five species ($\sum X_i = 1$, see below for a discussion on size correction).

The five segmental patterns, mapped onto a chilopod phylogenetic tree inferred from morphological data (Shear & Bonamo, 1988) and supported by molecular evidence (complete 18S rDNA and partial 28S rDNA sequences; Giribet *et al.*, 1999), show the polymerous, almost homonomous, segmentation of geophilomorphs as apomorphic in respect to the plesiomorphic oligo-

merous and more heteronomous segmentation of lithobiomorphs.

Discussion

Size correction

For any metric based on the absolute magnitude of disparity among the elements of a series, a size correction is required to obtain meaningful comparisons of specimens of different size. A hitherto overlooked point is, however, that the choice of characters used as the size factor may be critical. Compare for instance the segmental pattern of the character 'length of sternum' in two geophilomorph specimens of the same size but with a different number of segments. If what is meant as size is the length of the whole serial structure (in our case, the length of the trunk as sum of the lengths of all individual segments), the segmental pattern of the specimen with a longer series will be flatter (Fig. 6). Therefore, on average, the individual sterna will be shorter and the complexity score derived from the segmental pattern of the length of sterna will be smaller. However, if 'size' is in some way related to the average length of sterna and the two patterns are equivalent despite any difference in N , after size correction the two patterns will obtain the same complexity score.

Quite another story is to compare the same two specimens with reference to segmental patterns of traits whose overall shape is not sensitive to N , such as the width (rather than the length) of the sterna, or to

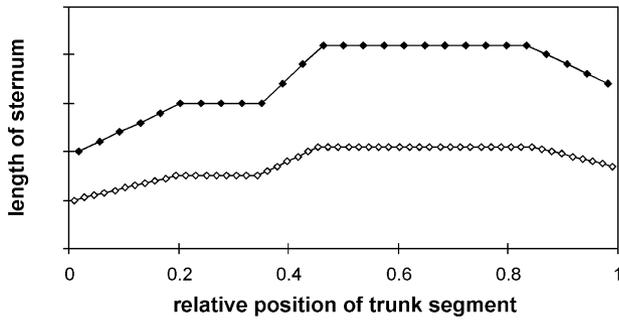


Fig. 6 Idealized segmental patterns (length of sternum) in two geophilomorph specimens with different numbers of segments and same overall shape of segmental pattern and body length.

compare specimens from species that differ widely in size, with variation in N positively correlated to variation in overall size (this may be the case in many interspecific comparisons in geophilomorphs). In these cases the choice of characters for size correction is not as critical.

The size correction we adopted in our analysis is a simple linear scaling to the same size for all specimens in the sample. This standardization precedes the calculation of C_s (or any other metric) and thus it is not a correction *a posteriori* of the metric's scores. This simple procedure makes clear that the necessary size correction is not entangled within the calculation of C_s .

There is no single correct answer to the problem of size correction, mainly because of the critical choice of the size factor, the best solution depending on the morphology of the taxa studied and on the phylogenetic level of comparison.

Pattern and noise

Measures of irregularity of a segmental pattern are quite sensitive to different sources of variation. For instance, when studying segmental patterns in some species of geophilomorphs we found individual specimens with a great local disparity between contiguous elements, these irregularities resembling random perturbations on a basic pattern. For instance, we recorded a conspicuous intraspecific variability in the segmental pattern of sternal length of *Strigamia acuminata* (Berto *et al.*, 1997). From the structural perspective of complexity, the variability of segmental patterns has at least two different components: (a) a population level polymorphism affecting segmentation or later morphogenetic processes of segment specification and (b) developmental noise, that in cases of scarce canalization may produce a developmental instability comparable with that which can be recorded by fluctuating asymmetry (Møller & Swaddle, 1997), although working, in our case, along a different axis ('fluctuating segment patterning'). The problem of developmental stability in segmental structures has been highlighted by Johnson & O'Higgins (1994), who studied

the variability of segmental pattern of some traits of the vertebral column within inbred strains of mice (*Mus musculus*).

Restricting comparison to specimens of the same age and cohort (same species, sex and N), it is possible to reduce individual variability. This is a way to avoid overestimating morphological complexity due to the confusion between different sources of segmental variation. The problem is particularly acute when segmental patterns are quite smooth, as in most geophilomorphs. For instance, in the segmental pattern of *Clinopodes flavidus* represented in Fig. 5, the value of C_s for the averaged pattern is 0.41, while the average of the three values of C_s separately calculated for the three specimens is 0.81.

Centipede segmental patterns

The alternating pattern so evident in the length of trunk terga of lithobiomorph and also, to a lesser degree, of scolopendromorph centipedes (see below) is the most conspicuous evidence of a bisegmental patterning which is a characteristic trait of the centipede ground-plan.

Two major clades are usually recognized within Chilopoda, namely Notostigmophora, corresponding to the order Scutigermorpha of traditional classifications, and Pleurostigmophora, including the three clades we considered in this paper (Lithobiomorpha, Scolopendromorpha, Geophilomorpha) as well as the little known Craterostigmomorpha (with only one species described) and the extinct Devonobiomorpha (also known after one species only). Following Shear & Bonamo (1988), these clades branched out in the following order: Lithobiomorpha, Craterostigmomorpha, Devonobiomorpha, Scolopendromorpha and Geophilomorpha.

In the Scutigermorpha, which have 15 leg-bearing segments, there are only eight terga (T1 to T8), each of which generally covers two segments, as follows: T1 (I), T2 (II, III), T3 (IV, V), T4 (VI, VII, VIII), T5 (IX, X), T6 (XI, XII), T7 (XIII, XIV) and T8 (XV).

Despite the conspicuous difference in the outlook, this segmental arrangement is very similar to that of Lithobiomorpha, where long (L) and short (S) terga alternate in the following way (slashes added to show the boundaries between terga in the corresponding segments in Scutigermorpha): L/SL/SL/SLL/SL/SL/SL/(L).

The peculiar arrangement of terga in Scutigermorpha is easily derived from that in Lithobiomorpha, if we assume that the short terga have disappeared and the two contiguous L terga (on VII and VIII) are fused together. Particularly striking is the conservation of the 'anomaly' disturbing the bisegmental pattern at midbody length. Demange (1963, 1967) explained this disturbance as due to an inhibition to develop, at least in part, a segment preceding the current VIII. We do not have a real developmental model for this hypothesis, which is only supported by the comparative morphology of skeletal

and muscular elements. At any rate, the segments within this trunk section look intriguingly like those intersected by a plane of mirror reflection as in some dramatic *bicaudal* mutants in *Drosophila* (Nüsslein-Volhard, 1977).

Similar to that in Lithobiomorpha is the segmental pattern of terga in the other clade with 15 leg-bearing segments, i.e. Craterostigmomorpha, where an additional level of morphological complexity is provided by the splitting of the longest terga in a pretergum and a metatergum (Lewis, 1981).

The extinct Devonobiomorpha, whose number of segments is unknown but higher than 16, also probably exhibited a VII/VIII singularity, although the fossil record does not allow a conclusive statement (our inference after Shear & Bonamo, 1988).

This 'anomaly' is further conserved in Scolopendromorpha, despite their larger number of leg-bearing segments, either 21 or 23. In this clade, however, the anomaly is seldom conspicuous in the length of terga, but is clearly expressed by the sequence (+ - + - + - + - + - + - + - + - + - + - + -) for a typical species with 21 leg-bearing segments) of segments bearing (+) or not (-) a pair of spiracles. Scolopendromorphs, however, show in different degrees signs of homonomization of trunk segments. This trend is most advanced in *Plutonium*, where all leg-bearing segments bear a pair of spiracles and all terga are quite similar in length.

A similar trend is present in Geophilomorpha, where all leg-bearing segments also bear spiracles and the segmental patterns of tergum length do not show any evidence of bisegmental alternation. From a functional point of view, this trend, also coupled with an increase in *N* and with several changes in their skeletomuscular organization, correlates with a change in locomotory habits, from the running locomotion of lithobiomorphs and scolopendromorphs to the borrowing locomotion or interstitial life of geophilomorphs (Manton, 1965).

Thus, the main traits of the segmental organization of centipedes are highly conserved in the whole group, despite the very early divergence (probably Devonian; Shear & Bonamo, 1988) of the major centipede lineages. This conservation suggests the presence of strong developmental constraints of centipede segmentation on the process of segment differentiation. On this topic, however, we are still at the level of pure speculation (cf. Minelli & Bortoletto, 1988; Minelli, 1993).

Segment, modules and complexity

The possibility for different body parts to evolve independently from other parts depends on the topology of the mapping of genotype onto phenotype through development (Wagner, 1996; Minelli, 1998). Wagner & Altenberg (1996) developed a model of modular mapping, where different morphofunctional units (modules) within an organism have low levels of integration among them, whereas the elements of each module have high

levels of integration and are thus expected to evolve in concert. In metameric animals, one would regard segments as (morphological) modules, but segments do not behave always as really independent units. This is also the case of centipedes.

In this respect, those indices of morphological complexity which are sensitive to singularities of a segmental series (i.e. *Cs* and *Cm* rather than McShea's *R* and *C*) seem to be better suited to studies of macroevolutionary trends of evolvability: these indices do in fact measure, specifically, some kind of interdependence between segments.

The five segmental patterns mapped onto chilopod phylogeny show the segmentation of geophilomorphs as a derived state with respect to the plesiomorphic oligomeric and more heteronomous segmentation of lithobiomorphs. This observation contradicts the so-called Williston's rule (cf. Saunders & Ho, 1984), according to which there should be a macroevolutionary trend for repetitive structures (like segments) to evolve towards fewer and increasingly specialized elements. In centipedes, we found no evidence of a macroevolutionary trend towards an increase in segmental morphological (metric) complexity (cf. also Berto *et al.*, 1997).

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