

Segmental units and shape control in Chilopoda

DIANA BERTO, GIUSEPPE FUSCO & ALESSANDRO MINELLI

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In geophilomorph centipedes, the overall shape invariance does not mirror the widespread variability in segmental composition (intra- and interspecific, linked or not with sex differences). We have developed a morphometric approach to this puzzling mismatch by studying allometric patterns in ontogeny and segmental patterns of metric traits of sterna and appendages, as well as through a comparative evaluation of morphological complexity. Comparisons of segmental patterns from individuals with different number of body segments (N) show that both the overall shape of the trunk and the segmental distribution of morphological markers are independent from N . Therefore, segments *per se* are of little significance as homologues. In *Clinopodes flavidus* C.L. Koch, 1847 (Geophilidae), size and shape of the leg-bearing trunk are in allometric relationship to the size of the N -invariant terminal body parts; this relationship is independent from N , that is, size and differentiation of trunk structures are independent from the number of segments. In a macroevolutionary perspective, a quantitative approach to morphological complexity of metameric structures reveals both increases and decreases in complexity of centipede trunk structures.

Keywords: centipede, Chilopoda, segments, complexity, homology, allometry.

D. Berto, G. Fusco & A. Minelli, Dipartimento di Biologia, Università degli Studi di Padova, Via Trieste 75, I-35121 Padova, Italy. E-mail: almin@cribi1.bio.unipd.it.

Introduction

It is difficult to describe a centipede without reference to segments or to the more or less regular pairing of trunk segments in bisegmental units. However, we are very far from an understanding of the morphogenetic control responsible for body shape. Two points are particularly puzzling.

First, the major facets of the body organisation of a centipede are the same across the class, in spite of major differences in post-embryonic developmental schedules, either epimorphic or (hemi)anamorphic.

Second, within Geophilomorpha (and, to a much lesser degree, within Scolopendromorpha), extremely similar body plans are obtained with different number of segmental units. In particular, if this plasticity is limited, in Scolopendromorpha, to having related species walking on 21 rather than on 23 pairs of legs, in Geophilomorpha the plasticity in segment number is shown in all ways and degrees:

- intraspecific variation (from a mere 2-segment difference between short and long specimens up to something between 87 and 179 segments

in *Himantarium gabrielis* (Linnaeus, 1767); but also, sometimes, no variation at all, as in the species of Mecistocephalidae);

- sexual dimorphism (modal differences between male and female sometimes lacking, but usually of 2 or more segments, up to 16);
- and also modal differences between closely related species.

In addition to the old notion of centipede morphology, that only odd numbers of leg pairs are possible in (adults of) these arthropods, more elaborated (“octonary”) patterns have been described in recent times (Minelli & Bortoletto 1988). Nevertheless, we are still in the realm of comparative anatomy or, at most, of “rational” morphology. Unexplained is, in particular, the fact that the lower number of leg-bearing segments usually found in males is not due to the development of sex-specific leg-less segmental structures corresponding to one or more 2-segment leg-bearing units in females. Also extraordinary is the “fixation of number fixation” in Mecistocephalidae, a point about which

some theoretical speculations have been offered already (Maynard Smith 1960; Minelli & Bortoletto 1988).

The mismatch between the widespread variability in segmental composition and the overall shape invariance raises some questions. Are segments non-trivial morphogenetic units? How far are size and differentiation of trunk structures dependent on the number of segments? How far do centipedes follow the so-called Williston's rule, i.e. a macroevolutionary trend towards less numerous and more specialised elements in a series, e.g. of segments? We have addressed these questions by studying, in Geophilomorpha and other centipedes, allometric patterns in ontogeny and segmental patterns of metric traits of sterna and appendages, and trying a comparative evaluation of morphological complexity sensu McShea (1992).

Material and methods

Because of the intraspecific variability in the number of body segments, an acute problem of homology arises when looking for correspondence between metameric structures occurring in different number in different specimens. Therefore, we decided to analyse the body parts variable in segment number independently from the segment-invariant ones. Accordingly, we adopted a subdivision of the geophilomorph body in three regions. Two of them, suitable for representing size, shape and their ontogenetic co-variation, have fixed segmental composition. These are the *anterior region* with the head and the forcipular segment and the *posterior region* with the last leg-bearing segment with specialised appendages and the genital segments. The third region – the *intermediate region* i.e. the leg-bearing trunk segments without the last one – is comprised of a variable number of segments.

In the following, the term cohort is used to designate the set of specimens of a given species and sex which have the same number of leg pairs.

We did not hesitate to regard as homologous features belonging to the anterior or posterior regions

in different specimens of different species, sex and cohort. Therefore, we felt confident in comparing corresponding features of these parts (e.g., head length) across species, sexes and cohorts.

On the other hand, our analysis of segmental patterns *within* a given specimen could rest on the serial homology relationship (homonymy) existing between corresponding structures in the individual segments of the intermediate segmentally variable region.

We did not take for granted an homology between the intermediate regions of specimens of different cohorts taken as wholes; this homology however came out *from* our morphometric analysis.

Material and measurements

To investigate the role of intraspecific variation of the number of trunk segments in post-embryonic growth patterns, Italian specimens of two species were compared: one with fixed number of segments (*Dicelophilus carniolensis* (C. L. Koch, 1847), Mecistocephalidae: $N = 43$ in all specimens of both sexes), another with a sizeable difference between the sexes, and intra-sex variability (*Clinopodes flavidus* C.L. Koch, 1847, Geophilidae: $N = 55-75$ in females, $N = 51-71$ in males). Basing on a preliminary study on Italian populations of *C. flavidus* (Zanon et al., unpubl.), we assumed the males with N segments to be cohort-equivalent to females with $N+2$ segments.

We performed parallel analyses on six different data sets, each set representing an ontogenetic series (from early adolescens to adult specimens) of the same species, sex and cohort. These are (sample size in brackets): *C. flavidus*, males, $N = 59$ ($n = 38$); *C. flavidus*, males, $N = 63$ ($n = 30$); *C. flavidus*, females, $N = 61$ ($n = 22$); *C. flavidus*, females, $N = 65$ ($n = 37$); *D. carniolensis*, males, $N = 43$ ($n = 34$); *D. carniolensis*, females, $N = 43$ ($n = 28$). Nine measurements were taken on the segmentally invariant regions on each specimen (see legend to Tab. 2).

To perform the morphometric analysis of the leg-bearing trunk, from each of the original six

groups, a subgroup of 3 young specimens and a subgroup of 3 fully adult specimens were taken, thus forming a total of 12 data sets homogeneous for species, sex, cohort and age. To evaluate size and shape variation in body parts affected by variability in the number of segments, three morphological characters were used (see legend to Fig. 1).

Seven male *C. flavidus* with $N = 59$ and ten male *C. flavidus* with $N = 63$ (specimens of different age in each series) were finally used to study the influence of metameric arrangement in the allometric relationship between trunk size and overall size.

Furthermore, in order to estimate morphological complexity, we studied materials from 11 species in four orders: *Scutigera coleoptrata* (Linnaeus, 1758) (Scutigermorpha); *Lithobius castaneus* Newport, 1844 (Lithobiomorpha); *Scolopendra cingulata* Latreille, 1829, *Cryptops hortensis* Leach, 1815, *Cryptopsparis* Brölemann, 1920, *Cryptops punicus* (Silvestri, 1896), and *Plutonium zwierleinii* Cavanna, 1881 (Scolopendromorpha); *Himantarium gabrielis*, *Dicelophylus carniolensis*, *Strigamia acuminata* (Leach, 1815), and *Strigamia transilvanica* (Verhoeff, 1928) (Geophilomorpha).

Eight morphological characters were measured for each segment of the leg-bearing trunk (see legend to Fig. 3).

Data analysis

A multivariate analysis of ontogenetic allometry was done by principal component analysis (PCA) on the covariance matrix of log-transformed measures of the nine characters from the segmentally invariant body parts. The first principal component (PC1) is the normalised linear combination of the log-transformed variables which maximises the proportion of total variance accounted for, and can therefore be seen as a line of best fit to the data points. PC1 coefficients define the direction of the growth vector of the group of specimens, i.e. its ontogenetic trajectory in the morphospace defined by the morphological characters investigated. The individual scores of each specimen on PC1 is a logarithmic measure of its overall size. *t* tests were

performed on allometric coefficients to evaluate size and shape variation during ontogeny and to assess possible influences of species, sex and cohort on allometric growth.

Patterns of metameric variation for the three morphological characters of the leg-bearing trunk were investigated in the 12 small data sets. Diagrams representing the variation of each character along the main body axis were graphically compared after suitable linear geometric transformations (see legend to Fig. 1), to assess the dependence of segmental patterns on species, age, sex and cohort.

The sum of lengths of all sterna was used as a proxy for the length of the intermediate region.

As to a quantitative measure of complexity of metameric structures, we followed McShea's geometrical approach (1993). This author introduced three indices of complexity: *R* (range), *C* (global differentiation) and *C_m* (local differentiation or irregularity):

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

$$C = \log(2 \sum |X_i - X_m| / N)$$

$$C_m = \log[\sum |X_{i+1} - X_i| / (N-1)]$$

where X_i is the measurement taken from the *i*th element, X_{max} , X_{min} , X_m are, respectively, the maximum, the minimum and the average value of X , and N is the number of elements. Our approach differs from the original one in introducing a correction to avoid the bias on estimates of complexity due to N . Graphical evaluation of segmental patterns within a species (see Results, below) had demonstrated the segmental behaviour of several characters to be N -invariant. Therefore, at least for centipedes, it would be misleading to get different scores for morphological complexity in those cases in which one and the same segmental pattern develops on segmental series with different N . On the other hand, our computer simulations demonstrated that McShea's indices are not N -independent. Hence, our correction for multiplicity.

Following McShea, we introduced a *size correction* to avoid bias from overall size differences

Tab. 1. Male-female comparisons of frequency distributions of leg pair numbers for several species of Geophilomorpha. Geographical origin of the samples, when not specified in the table, is given in the source papers; for the unpublished data, details can be obtained from the present authors. Sample size for males resp. females is given in columns with headings n_M , n_F respectively. The following columns give the value of the parameter D of Kolmogorov-Smirnov's test for different hypotheses (0, 2, 4, 6, 8, 10, 12, 14, 16, 18 segments) of female/male shift. D is calculated as $(\max|S_M(x) - S_F(x)|) / (n_M n_F) / (n_M + n_F)$ where $S_M(x)$ and $S_F(x)$ are the cumulated frequencies of the samples and n_M and n_F are their respective sizes. An asterisk (*) marks those comparisons where the hypothesised amount of shift can be accepted at the 0.1 level of significance (two-tail test). The last column (r) refers to the data sources: 1, Minelli et al. 1984; 2, Simonato, unpubl.; 3, Demange 1963; 4, Demange 1961; 5, Pereira et al. 1994; 6, Zanon, unpubl.; 7, Minelli, unpubl.; 8, Tortani, unpubl.; 9, Meidell 1984. — In all cases but two (*Ribautia centralis* and *Orya panousei* from Tunisia) the most likely shift is for a number of segments equalling a power of 2.

	n_M	n_F	0	2	4	6	8	10	12	14	16	18	r
<i>Himantarium gabrielis</i> (Linnaeus, 1767)	101	114	1.22*	0.85*	0.82*	0.97*	1.16*	1.37	-	-	-	-	1
<i>Stigmatogaster gracilis</i> (Meinert, 1870)	40	27	0.69*	1.28	2.02	-	-	-	-	-	-	-	2
<i>Henia vesuviana</i> (Newport, 1845)	50	104	1.18*	0.68*	1.63	-	-	-	-	-	-	-	2
<i>Lamotteophilus spinosus</i> Demange, 1963	24	25	-	-	-	-	-	-	-	1.39	1.08*	2.48	3
<i>Orya panousei</i> Demange, 1961 (Morocco)	437	567	-	-	-	3.14	1.77	3.69	-	-	-	-	4
<i>Orya panousei</i> Demange, 1961 (Tunisia)	40	22	-	-	-	-	1.83	0.52*	1.18*	-	-	-	4
<i>Pectiniunguis ascendens</i> Pereira et al., 1994	558	626	16.94	0.08*	17.07	-	-	-	-	-	-	-	5
<i>Ctenophilus amieti</i> (Demange, 1963)	8	15	-	1.43	0.36*	1.07*	-	-	-	-	-	-	3
<i>Ctenophilus oligopodus</i> (Demange, 1963)	115	175	2.90	0.57*	3.91	-	-	-	-	-	-	-	3
<i>Ctenophilus pratensis</i> (Demange, 1963)	26	42	2.84	0.71*	3.09	-	-	-	-	-	-	-	3
<i>Schendyla nemorensis</i> (C.L. Koch, 1835)	17	52	0.87*	1.29	1.92	-	-	-	-	-	-	-	2
<i>Schendylurus pumicosus</i> Demange, 1963	48	43	2.26	0.18*	2.36	-	-	-	-	-	-	-	3
<i>Ballophilus smaragdus</i> Demange, 1963	31	32	-	1.69	0.49*	2.47	-	-	-	-	-	-	3
<i>Clinopodes flavidus</i> C.L. Koch, 1847	22	13	1.10*	0.26*	1.24	2.34	-	-	-	-	-	-	6
<i>Geophilus carpophagus</i> Leach, 1815	49	67	1.94	0.47*	2.43	-	-	-	-	-	-	-	2
<i>G. t. truncorum</i> Bergsøe & Meinert, 1866	33	53	3.15	0.09*	3.06	-	-	-	-	-	-	-	7
<i>G. t. ribauti</i> Brölemann, 1908	83	130	3.24	0.32*	3.45	-	-	-	-	-	-	-	7
<i>Hyphydrophilus adisi</i> Pereira et al., 1994	551	679	17.36	0.05*	17.41	-	-	-	-	-	-	-	5
<i>Ribautia campestris</i> Demange, 1963	78	99	0.90*	1.95	-	-	-	-	-	-	-	-	3
<i>Ribautia centralis</i> (Silvestri, 1907)	367	428	4.39	6.61	-	-	-	-	-	-	-	-	5
<i>Ribautia cribellata</i> Demange, 1963	44	41	0.30*	1.99	-	-	-	-	-	-	-	-	3
<i>Strigamia acuminata</i> (Leach, 1815)	65	58	5.35	0.11*	5.45	-	-	-	-	-	-	-	8
<i>Strigamia maritima</i> (Leach, 1817)	718	712	16.66	0.75*	15.77	-	-	-	-	-	-	-	9

between the individuals to be compared: the values of C were replaced with the residuals from a linear regression between C and the logarithm of a size factor, while R and C_m were replaced with the

residuals from the same regression line computed for C .

It is only after this size correction that we introduced (for C and C_m) the correction for

multiplicity: the size-corrected C and C_m where replaced with the residuals from the regression on $\log(N)$ for C and $\log(N-1)$ for C_m .

Finally, as in McShea (1993), we applied a third run of linear regressions, to remove redundancy between the three indices. R values (corrected for size) were replaced with their residual from a linear regression of R (corrected for size) on C (corrected for size and multiplicity): the new index is R' or range relative to C . Redundancy in C_m was removed in the same way giving C_m' or irregularity relative to C .

We will only report here on a preliminary evaluation of R' , C and C_m' data in a macro-evolutionary perspective. To that end, we adopted a simplified representation, by ranking the eleven species, for each character studied, following the increasing series of values for each complexity index.

Results and discussions

A revisit of segment numbers in Geophilomorpha

New speciographic work confirms $N=29$ as the lowest number of leg-bearing segments in Geophilomorpha. At present, we know 4 species in 2 families with 29 pairs of legs, i.e. three members of Geophilidae (*Dinogeophilus oligopodus* Pereira, 1984, *Geophilus richardi* Brölemann, 1904 and an undescribed species from a cave in France) and one of Schendylidae (*Schendylurus oligopus* Pereira et al., 1995). At the moment, there is also no evidence of geophilomorphs with more than 191 pairs of legs, the maximum known since long for this group (*Gonibregmatus plurimipes* Chamberlin, 1920).

Overall, our current database for the number of segments in Geophilomorpha is not much better than that used by Minelli & Bortoletto (1988) to propose their octonary model. We stress here, however, some methodological problems requiring attention.

First, differences in N between closely related species are difficult to interpret, due to the lack of reliable phylogenetic scenarios. More meaningful

Tab. 2. PC1 coefficients for the six data sets (ontogenetic series). See text for details on specimens and PCA. The nine characters considered are: CshL, length of the cephalic shield; CshW, width of the cephalic shield; CxtL, length of the forcipular coxosternum; CxtW, width of the forcipular coxosternum; ForL, length of the femoroid of the forcipule; LstL, length of the last leg-bearing sterna; LstW, width of the last leg-bearing sterna; TibL, length of the tibia of the last leg-bearing segment; TibW, diameter of the tibia of the last leg-bearing segment.

	<i>Clinopodes flavidus</i>				<i>Dicelophilus carniolensis</i>	
	m 59	m 63	f 61	f 65	m 43	f 43
CshL	.264	.267	.261	.282	.307	.316
CshW	.294	.293	.311	.319	.289	.302
CxtL	.331	.332	.342	.328	.339	.347
CxtW	.323	.329	.337	.351	.319	.338
ForL	.312	.318	.344	.322	.334	.344
LstL	.358	.350	.383	.390	.339	.361
LstW	.377	.353	.375	.364	.373	.357
TibL	.358	.379	.365	.376	.366	.387
TibW	.365	.363	.257	.240	.326	.232

are therefore, at the moment, comparisons within the species.

Second, intraspecific variability is difficult to evaluate and interpret because of the usually scarce knowledge we have about the variability between different local populations. The only good evidence for an octonary pattern from the bimodal frequency distribution of N in a local sample of the same species and sex is still the *Ribautia campestris* material described by Demange (1963).

Instead, a statistical analysis of differences between the sexes, on a database of about 20 species, confirmed that these differences are, in most cases, powers of 2, i.e. 0, 2, 4, 8 or 16 (Tab. 1).

Ontogenetic allometry of invariant regions

In all six groups, principal component analysis

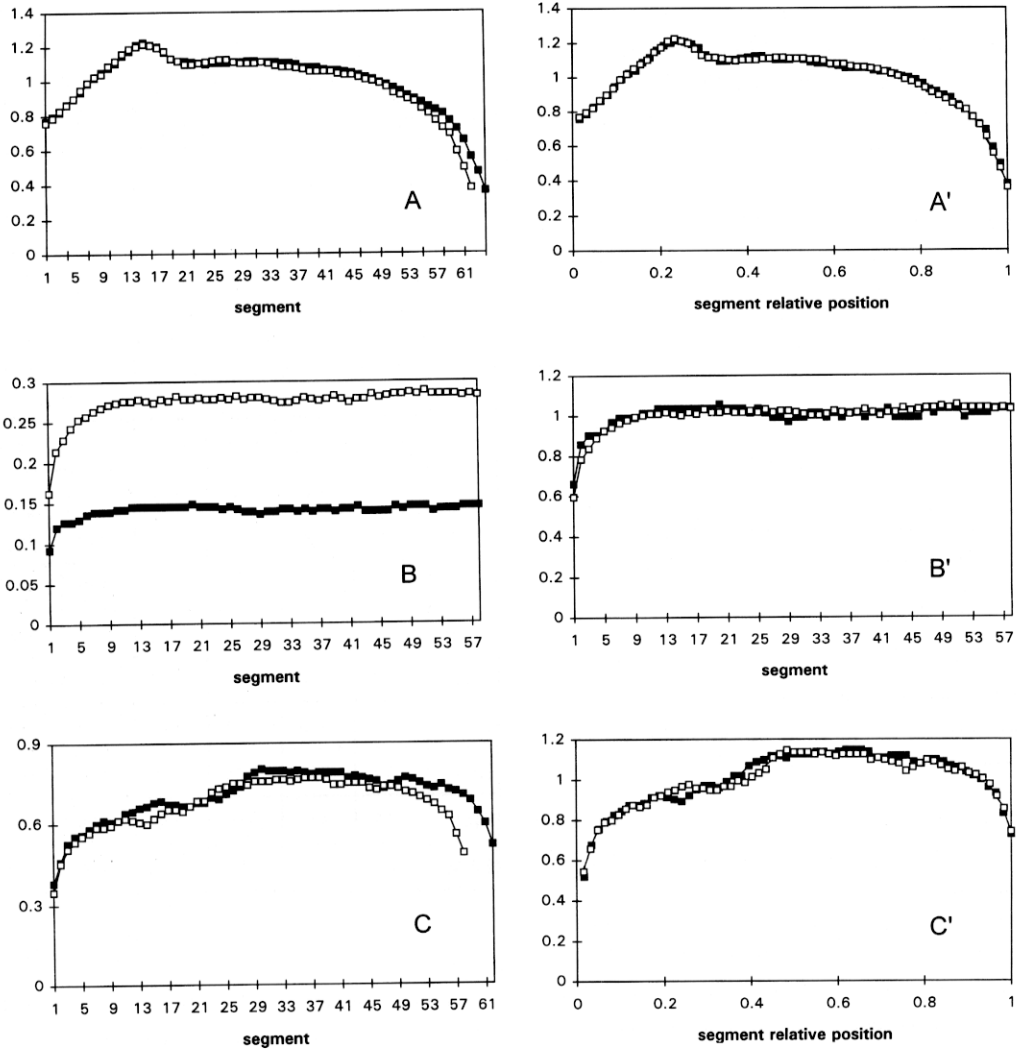


Fig. 1. Examples of segmental patterns (segmentally variable intermediate region) for *Clinopodes flavidus* specimens of different sex (A, A' - width of the sternum), age (B, B' - length of the femur) and cohort (C, C' - length of the sternum): on the left column (A, B, C) the untransformed pattern, on the right column (A', B', C') the corresponding pattern after linear geometric transformation. In these transformations Y_i is replaced by Y_i/Y_m , where Y_i is the value of the character in the i th segment and Y_m the average value over all segments. Moreover, in A' and C', X_i is replaced by X_i/N , where X_i is the ordinal value of the segment and N the total number of segments in the region. In A, A': empty squares, adult males with 63 pairs of legs; solid squares, adult females with 65 pairs of legs. In B, B': empty squares, adult males with 59 pairs of legs; solid squares, juvenile males with 59 pairs of legs. In C, C': empty squares, adult males with 59 pairs of legs; solid squares, adult males with 63 pairs of legs.

reveals that PC1 always accounts for over 95% of the total variation. This means a good fit with the multivariate generalisation of the classical allometric model where character co-variation behaves as power law relationship. These high eigenvalues support the interpretation of PC1 as a "growth

vector" and therefore the use of a multivariate relative size as a proxy for age.

PC1 coefficients are generally similar between the data sets of the same species (Tab. 2), revealing similar ontogenetic trajectories in morphospace. Only for the coefficients of the diameter of the last

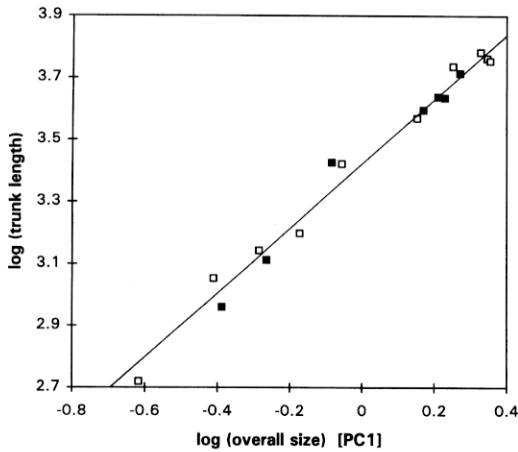


Fig. 2. Bivariate scattergram of trunk length (natural logarithm of the sum of sterna lengths in mm) vs. body size (PC1 scores). Solid squares, males with 59 pairs of legs; empty squares, males with 63 pairs of legs. The same regression line fits both groups of records.

pair of legs did we register, in the females of both species, a strong negative allometry to the rest of the body (coefficient conspicuously lower than 0.33, the value for isometry in a set of 9 variables), while the same character in males was more or less isometric. These results were expected, the shape of the last pair of legs being conspicuously sexually dimorphic.

Allometric coefficients for the traits of the anterior region are generally lower than those of posterior region. This difference reveals a slight variation during growth of the relative proportions between the foremost and the hindmost part of the body (see below).

Are segments non-trivial morphogenetic units?

To answer this question we compared graphically segmental patterns between data sets of the same species differing in sex (6 comparisons), age (6 comparisons) or cohort (4 comparisons (examples in Fig. 1)).

In no instance did we obtain sizeable differences between the segmental patterns thus compared. This result points to a quite early achievement of the definitive species-specific distribution over the trunk

R'

StL	1	4	3	4	9	8	11	2	9	6	7
StW	3	7	8	6	4	1	5	9	10	2	11
TeL	6	4	9	7	10	2	8	1	4	11	3
TeW	1	6	5	7	3	4	2	10	8	9	11
PrL	3	5	10	11	9	4	8	1	2	6	7
FeL	3	6	9	11	8	2	5	1	4	7	10
TiL	3	6	9	10	7	1	5	2	4	8	11
TaL	1	8	10	11	9	6	3	2	4	7	5

C

StL	11	1	4	5	8	2	7	6	10	9	2
StW	9	10	2	1	4	4	6	8	11	7	3
TeL	1	11	7	9	8	1	4	6	10	5	3
TeW	9	1	5	6	3	10	4	1	11	7	8
PrL	4	3	6	9	8	2	7	5	11	9	1
FeL	4	7	5	10	7	2	3	6	11	9	1
TiL	9	5	6	8	7	1	3	4	11	10	2
TaL	8	11	4	5	6	1	3	7	9	9	1

Cm'

StL	9	9	7	7	11	2	5	6	10	3	3
StW	2	2	11	7	8	1	2	4	9	10	4
TeL	9	9	6	3	5	11	10	8	1	7	4
TeW	11	11	8	5	1	2	3	4	9	7	6
PrL	5	5	8	11	6	3	2	10	1	7	4
FeL	9	9	6	11	7	1	4	5	2	9	8
TiL	8	8	7	11	6	2	3	5	1	9	10
TaL	7	7	7	10	5	3	2	9	1	4	11

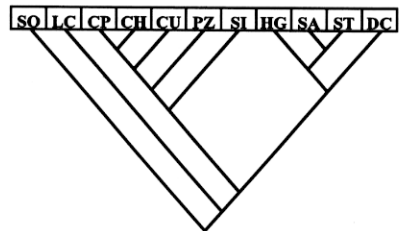


Fig. 3. Rank scores for the indices of morphological complexity R', C, Cm' (see text) for the following characters and species. Characters: StL, length of sternum; StW, width of sternum; TeL, length of tergum; TeW, width of tergum; PrL, length of praefemur; FeL, length of femur; TiL, length of tibia; TaL, length of tarsus. Species: SO, *Scutigera coleoptrata*; LC, *Lithobius castaneus*; CP, *Cryptops parisi*; CH, *Cryptops hortensis*; CU, *Cryptops punicus*; PZ, *Plutonium zwierleinii*; SI, *Scolopendra cingulata*; HG, *Himantarium gabrielis*; SA, *Strigamia acuminata*; ST, *Strigamia transilvanica*; DC, *Dicelophorus carniolensis*. The tree at the bottom of the figure reproduces the traditional view of phylogenetic relationships between the species studied.

of local differentiations, but the latter are only identified in respect to a global framework. That is, the position of any specific marker is not linked to a given numbered segment, but only to the relative position within the N-variable region (Minelli 1992; Turcato et al. 1995).

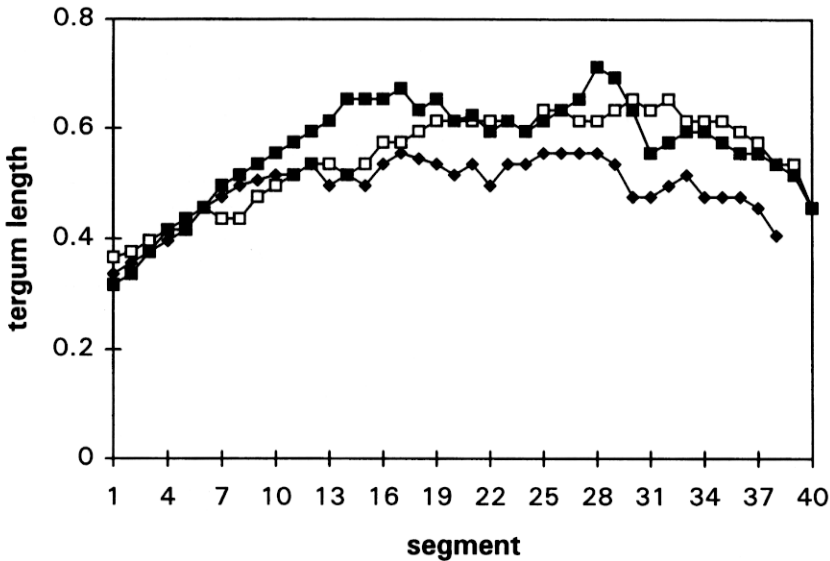


Fig. 4. Irregular segmental patterns for the tergum length in three specimens of *Strigamia acuminata* (diamonds: male; squares, females).

How far are size and differentiation of trunk structures dependent on the number of segments?

We considered the influence of the segment number on the average size of trunk segments. Allometric analysis of the relationship between length of the trunk vs. overall size (expressed as PC1 score) in two samples (ontogenetic series) of *Clinopodes flavidus* of the same sex but belonging to different cohorts (males with 59 leg-bearing segments and males with 63 leg-bearing segments, respectively) resulted in non-significantly different allometric coefficients (both slope and intercept) (Fig. 2). In other words, a specimen of *C. flavidus* of a given size, with 59 pairs of legs, will have on average the same trunk length as a specimen of the same species and size that walks on 63 pairs of legs. The segments of the latter will be slightly shorter on average than those of the former specimen. Because of the slight difference in the number of segments between the two groups under comparison we checked the robustness of our test with an alternative hypothesis. We compared the allometric coefficients for the relationship between average length of the sterna and overall size in the two groups of males. We found that the intercepts of the regression lines

were different enough to discard the hypothesis that cohorts with more segments have longer trunks in direct proportion to the number of their leg-bearing segments.

The slopes of both regression lines were not significantly different from unity, that is, there is an isometric relationship (or scale invariance), also confirmed by preliminary observations on *Strigamia acuminata*, between the size of the trunk and the size of the invariant regions. Because of the different allometric behaviour of anterior and posterior region, the trunk shows a growth coefficient intermediate between the anterior (smaller) and the posterior region (bigger). This results in a kind of antero-posterior growth gradient. This is a common feature of animal growth (Huxley 1932) but, in these opisthogoneate arthropods, it may be related to the development and differentiation of the posterior (subterminal) genital structures.

How far do centipedes follow Williston's rule?

A common fate of so-called macroevolutionary "laws" is that they are subsequently found only to be applicable to restricted samples of complaisant

organisms. The same may probably be true for the so-called Williston's rule, i.e. a macroevolutionary trend towards less numerous and more specialised elements in a series, e.g. of segments (cf. Saunders & Ho 1984). As for segmentation, geophilomorphs may superficially look little more advanced than homonomous annelids, therefore a good candidate for primitive condition within Chilopoda. However, on Dohle's (1985) tree, geophilomorphs come out as a relatively young branch, thus suggesting that the (apparent) homonymy of the trunk of these centipedes is not a feature of the centipede ground-plan. In a similar vein, Enghoff's (1990) ground-plan of chilognathan millipedes shows a relatively short animal, less worm-like than many modern juliform Diplopoda.

Recently, McShea (1993) approached the study of macroevolutionary trends in metameric structures through a quantitative approach to the morphological complexity of the vertebral column of mammals. He did not observe a consistent trend; instead, increases and decreases of complexity were equally frequent.

We followed the same approach, but for the minor technical details explained before.

We found no coherent, species-specific behaviour for all measured traits.

In some species (e.g., *Cryptops* spp.) the traits of the trunk and those of the appendages have distinct behaviour, with some consistency within the traits of the trunk and also, but in a different range of scores, within the traits of the appendages.

In other instances, length of terga and length of sterna show concordant trends, and the same holds true for width of terga and width of sterna, whereas the two measures (length and width) do not show concordance either for terga or for sterna.

Matching the results of the analysis of complexity and the phylogeny we adopted (Fig. 3), we could not identify a clear trend. There is no consistent increase or decrease of complexity scores along the lineages. Even within the same order (Geophilomorpha, Scolopendromorpha) the behaviour of the complexity scores is quite erratic. That means that Williston's

rule does not apply here.

In so far as we focus on interspecies (intertaxon) comparisons, individual differences in segmental patterns are just noise, comparable to the fluctuating asymmetries we usually disregard when describing "the" morphology of a given species. In order to recover a species-specific pattern from the rough individual data, we choose to work with average segmental patterns extracted from samples of specimens of the same species and sex. However, we noticed that the individual behaviour may differ from the calculated average in different ways and degrees. In particular, pronounced irregularities of some individual patterns were conspicuous in some species, such as *Strigamia acuminata*, but not uniformly over all characters, the length of terga and sterna being often, in this species, severely affected (Fig. 4). We wonder how far these individual erratic heteronomies can be dependent on stressful events during development, as currently suggested for fluctuating asymmetry (Clarke 1992, Parsons 1992).

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