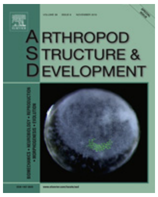
Arthropod Structure & Development 39 (2010) 468–477

Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd



Multi-scale relationships between numbers and size in the evolution of arthropod body features

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ARTICLE INFO

Article history:
Received 4 March 2010
Accepted 28 June 2010

Keywords:
Allometry
Body patterning
Evolvability
Eye
Segmentation

ABSTRACT

Size-related changes of form in animals with periodically patterned body axes and post-embryonic growth discontinuously obtained throughout a series of moulting episodes cannot be accounted for by allometry alone. We address here the relationships between body size and number and size of appropriately selected structural units (e.g., segments), which may more or less closely approximate independent developmental units, or unitary targets of selection, or both. Distinguishing between units fundamentally involving one cell only or a small and fixed number of cells (e.g., the ommatidia in a compound eye), and units made of an indeterminate number of cells (e.g., trunk segments), we analyze and discuss a selection of body features of either kind, both in ontogeny and in phylogeny, through a review of current literature and meta-analyses of published and unpublished data. While size/number relationships are too diverse to allow easy generalizations, they provide conspicuous examples of the complex interplay of selective forces and developmental constraints that characterizes the evolution of arthropod body patterning.

1. Introduction

Change in organism size is generally accompanied by changes in structure. This happens both in ontogeny, along an individual's trajectory of growth, and in phylogeny, when evolutionary modification is reflected, among others, by change in size at a comparable developmental stage, most obviously or most conspicuously at the adult stage.

The most common form of change in structure linked to a change in size is allometry. This is true of arthropods as it is true of animals belonging to other phyla. However, insects and crustaceans have often provided research objects and textbook examples in the study of allometry, since Huxley's (1932) classic *Problems of Relative Growth*. However, allometry, in the form of a function of shape change with size, is far from exhausting the scope of the size-correlated changes of form. In animals like arthropods, with a periodic patterning of the body axes and where the post-embryonic increase in size is discontinuously obtained throughout a series of moulting episodes, allometry fails to capture prominent features of the relationship between form and size.

A complementary approach is provided by the study of the relationships between body size and number and size of body units (e.g., body segments, or articles of appendages), which may more or less closely approximate independent developmental units, or unitary targets of selection, or both.

2. Taxonomic and morphological framework

2.1. Body size

Were it not for three successful lineages of mostly tiny forms, i.e. mites, copepods and ostracods, we could certainly say that the vast majority of arthropods are at least one millimeter long. Smaller adults, however, have independently evolved in many arthropod lineages (Table 1), often repeatedly within each of them, as exemplified by beetles and hymenopterans (Supplementary material 1). A detailed analysis of these evolutionary transitions in body size are beyond the scope of this paper and, indeed, would require for any relevant group a detailed phylogenetic hypothesis, which in many cases is not yet available. Nevertheless, it is a reasonable guess that in many cases a very small size evolved long or very long ago, while within other groups the smallest representatives are the result of a recent, often marked reduction in size. A first rough indication derives from the overall size range of the members of a taxon (Table 1). For example, the prevalence and phylogenetic (or taxonomic) distribution of very small species among the living mites (e.g., Lindquist, 1984; Bernini, 1986; Evans, 1992; Dunlop and Alberti, 2008) suggests that their characteristic small size was

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doi:10.1016/j.asd.2010.06.002

Table 1
A list of arthropod taxa whose smallest members are less than 1 mm in length, with approximate size (in mm) of the smallest and the largest species thus far recorded (figure precision depends on the source; data from McLaughlin, 1980; Schram, 1986; Naumann et al., 1991; Gruner et al., 1993; Dathe, 2003).

0.09–30	Acari
0.1–8	Podocopa
0.1–10	Collembola
0.1–34	Myodocopa
0.11–320	Copepoda
0.15–60	Hymenoptera
0.2–6	Anomopoda
0.25–180	Coleoptera
0.3–1	Tantulocarida
0.35–11.8	Phthiraptera
0.37–90	Araneae
0.4–1	Mystacocarida
0.4–20	Acrothoracica
0.5–2	Pauropoda
0.5–4	Cumacea
0.5–5.4	Bathynellacea
0.5–8	Aphidiina
0.5–10	Psocoptera
0.5–14	Thysanoptera
0.5–30	Branchiura
0.5–60	Diptera
0.5–110	Heteroptera
0.5–400	Isopoda
0.65–1.8	Palpigradi
0.8–2.6	Protura
0.86–12	Pseudoscorpiones

acquired long ago. This is also supported by fossils, of which the admittedly scanty record (Bernini, 1986; Selden, 1992) includes a precious, tiny *Protacarus crani* from the Early Devonian Rhynie Chert (Hirst, 1923). The same can be said of copepods, within which groups of parasites of exceptionally large size have repeatedly evolved, more or less recently, from ancestors likely around 1 mm long (e.g., Huys and Boxshall, 1991; Ho, 1994).

In other cases, as in isopods and amphipods, phylogeny shows that both the lowest and the highest values in the size range are quite likely the result of opposite trends, towards miniaturization (related for example to interstitial life) or towards gigantism. An overall message we can derive from this variegated pattern of size values and size changes is that the size of an arthropod is likely prone to major change in a relatively short time span, although this will not apply in the case a given size is of major selective value *per se*. The latter condition is found, for example, in the specialized parasitoids that complete their growth within one host egg, whose size obviously constrains the size of the eventually developing adult wasp. Interestingly, many chalcidoids (e.g., Yoshimoto, 1975) and mymarommatids (Fursov et al., 2002) are known from Cretaceous ambers, and even a proctotrupid-like fossil from the early Jurassic strata (Rasnitsyn, 1983). In addition, some of these million years-old specimens of tiny parasitoids have been found not to differ from their closest living relatives on morphological characters currently regarded as diagnostic at the species level. These include a mymarid and a mymarommatid hymenopteran from Baltic amber, dated 45 million years BP (Bakkendorf, 1948; Doutt, 1973), and another mymarid and a scelionid wasp from 20 million years-old Mexican amber (Masner, 1969; Doutt, 1973).

At the opposite end of the range of size changes, the fairly old age of these lineages of tiny hymenopterans is mirrored by the giants among mites, i.e. the ticks, which probably originated sometimes during the Cretaceous (Nava et al., 2009), as by mid-Cretaceous their sub-clades Argasidae (de la Fuente, 2003) and Ixodidae (Poinar and Brown, 2003) are both recognizable in the fossil record.

Lack of phylogenetic studies invites not to venture into excessive speculations, nevertheless we can confidently state that extremely small or extremely large sizes have evolved, in some lineages, in quite recent times (Schütt, 2003). This probably applies, for example, to some at least of the tiniest of spiders, e.g. in the Ochyroceratidae, Symphytognathidae, Oonopidae and Telemidae, several of which are less than 1 mm long (see the phylogenetic position of these groups within the spider radiation; e.g., Coddington and Levi, 1991; Ramirez, 2000). One of us (Minelli, 2003) advanced the hypothesis that a likely correlate of recent miniaturization is perhaps the loss of symmetry in the distribution of the slit sensory organs in *Comaroma bertkaui*, a tiny spider 1.6 mm long (Kropf, 1998), in strong contrast with the regular patterns of the sensory setae of mites, including those much smaller than *Comaroma*. Along their very long history as miniature arthropods, mites have possibly adjusted their body patterning mechanisms to their tiny size, something that has not been obtained yet in lineages of recent miniaturization.

2.2. Morphological correlates of miniaturization

Structural changes accompanying a strong reduction in body size (miniaturization) are often limited by the fixed, or variable but not indefinitely compressible size of pattern units (Hanken and Wake, 1993). Examples are provided by unit structures corresponding to one cell or very few cells, such as cuticular scutes, or insect and crustacean ommatidia, but also by the units (either structural or pigmentary) of body colour patterns. We cannot expect the complex black-and-yellow livery of hornets to be reproduced in full on the back of a tiny parasitoid wasp less than 1 mm long, or a dozen of well-defined black spots to occur on orange or red background on the elytra of a tiny beetle of the same size, only because this pattern is known to occur in (substantially larger) ladybirds. In either case, the area available on the miniature insects would not be sufficient to accommodate so many elements of a necessarily coarse-grain colour pattern.

A strong reduction in size is often accompanied by the lack, or at least the fading out, of the boundaries between elements which are otherwise well distinct, or more clearly articulated, in larger-size relatives (e.g., Polilov and Beutel, 2009, 2010). In ontogenetic terms, this effect results from the loss of a developmental phase during which the corresponding parts would be otherwise produced or articulated, but in comparative/phylogenetic terms we might be tempted to describe this effect of miniaturization as a 'fusion' of previously distinct elements.

Strong reduction in body size can affect the segmentation both of the limbs and the main body axis, as observed in the Ptiliidae, Corylophidae and Myxophaga, the smallest of beetles (Beutel et al., 1999; Grebennikov and Beutel, 2002; Polilov, 2005, 2008; Polilov and Beutel, 2009). Two of the three main subtaxa of the Collembola show extensive 'segment fusion' involving most of both thorax and abdomen, and this condition is likely related to their small and often very small size, the body length of the Symphypleona spanning between 0.1 mm and 5 mm, while the Neelipleona are confined to the 0.3 to 0.7 mm interval. Fading body segmentation and reduced limb segmentation are also typical of several of the smallest mites, for example the eriophyids.

Among these numerous occurrences of non-disjoined structural elements among miniaturized arthropods there are also those caused by the reduced transversal dimension of the animals. This condition can determine reduction and eventually loss of laterality. In the very small spiders of the family Symphytognathidae, the chelicerae are medially fused, at the base at least, and often along the entire length (Moritz, 1993). In cladocerans, a 'cyclopia' effect is apparent, as in these tiny crustaceans one median compound eye replaces the usual lateral pair.

2.3. Units of structure or pattern

In the vast majority of arthropods there is no shortage of multiple, often serially arranged, features whose number and/or size varies with changes in body size. Among these there are body segments, limb articles, sensory bristles and units of pigmentary or structural colour patterns, just to mention the more obvious.

From the perspective of the present analysis, the most sensible categorization is perhaps distinguishing between units fundamentally involving only one cell or a fixed set of very few cells (as is often the case for sensilla and epidermal glands), and units made of an indeterminate number of cells. In ontogeny as well as in phylogeny, the units of the first kind will likely vary in number rather than in size, while those of the other kind are in principle free to change both in number and size with changes in the animal's overall size. We will consider a selection of units of either kind.

3. One-cell vs. many-cell units of structure

3.1. Cell size and cell number

Variation in size, either of the whole animal or of a given body part, is mainly provided by variation in cell number, itself a consequence of differences in the rate and/or timing of mitotic activity. However, an additional factor affecting body or organ size is the average cell size. In *Drosophila*, reduction in average cell size accounts for 32% of the remarkable reduction in wing area, compared to the wild type, in the small-size *chico* mutant. The remaining 68% is explained by reduction of cell number, and similar results were recorded for the eye (Böhni et al., 1999). Similarly, in the wing, eye and basitarsus of several Hawaiian *Drosophila*, cell size contributes between one third and two thirds to interspecies differences in organ size (Stevenson et al., 1995).

The contribution of cell size to changes in organ size and the resilience of cell size to overall variations in body size can be studied easily by comparing samples of the polygonal areas (scutes) often quite conspicuous in surface view on the cuticle of many arthropods. Fusco et al. (2000) showed that in the centipede *Lithobius* the polygonal surface pattern of the cuticle reproduces faithfully the shape of the external side of the hypodermal cells at the stage of deposition of the very first layers of the cuticle. In geophilomorph centipedes the polygonal pattern is detectable on most cuticular districts. In a sample of 29 species, representative of a wide range of sizes (from 6 mm dwarf species to gigantic species more than 200 mm long), we found no correlation between the average size of the scutes on the cephalic shield and the animal's body size (Fig. 1; Moretto et al., in prep.)

3.2. Modularity and size/number relationships: the case of arthropod eyes

Structures composed of a high and flexible number of cells can keep in pace with variation in body size by varying themselves in size, usually by an increase in cell number. On the opposite, the size of structures composed (or produced) by a single cell, or a very small (usually fixed) number of cells, is practically independent from body size, while the number of these structures may remain open to change across moults.

However, the distinction between these two classes of features is not necessarily a definitive one. Evolutionary changes from variable to fixed composition (in terms of number and specialization of cells) may cause a number-invariant and size-variable body feature to evolve into a feature with opposite relationship with body size. In the following lines we will present an example of such an evolutionary transition. The opposite trend, starting from features with constant cellular composition whose number increase with body size, is quite less likely, but its possible occurrence cannot be ruled out.

Our example is provided by arthropod lateral eyes. Two main types can be contrasted. One of these types, probably the most primitive condition within the Euarthropoda (Harzsch et al., 2007) is the lateral eyes of the chelicerates. Here the number of eyes remains constant throughout the whole post-embryonic development, while the number of cells in each eye, and thus the size of the organ, increases at each moult. The other type is offered by the compound eyes of crustaceans and insects, which are composed of a variable number of units (ommatidia), all of which have identical cellular composition, with two corneagenous cells, four crystalline cone cells and eight retinula cells; some variation is only admitted for the surrounding pigment cells. The peculiar and phylogenetically very conservative structure of crustacean and insect ommatidia is a convincing apomorphy of this arthropod clade (Melzer et al., 2000; Paulus, 2000; Dohle, 2001; Richter, 2002), aptly fixed in the name Tetraconata (Dohle, 2001), often used as an alternative to Pancrustacea (Zrzavý and Štys, 1997) as the name of this monophyletic group.

The size of the individual ommatidia is strictly constrained by their fixed cellular composition. As a consequence, the increase in size of a compound eye along the post-embryonic development is only obtained by addition of new ommatidia, externally to the cluster of the existing ones (e.g. Hafner and Tokarski, 2001). Another consequence of this fixed size and structure of the ommatidia is the presence of eyes with a very small number of normal-size ommatidia in miniaturized insects, e.g. ptiliid beetles (Polilov and Beutel, 2009).

These two types of arthropod eyes are obvious examples of the two types of structures (respectively invariant in number or in size with changing body size), but, with respect to the topic of our review, more interesting are the conditions found in myriapods. Myriapods are indeed the most diverse among the main arthropod

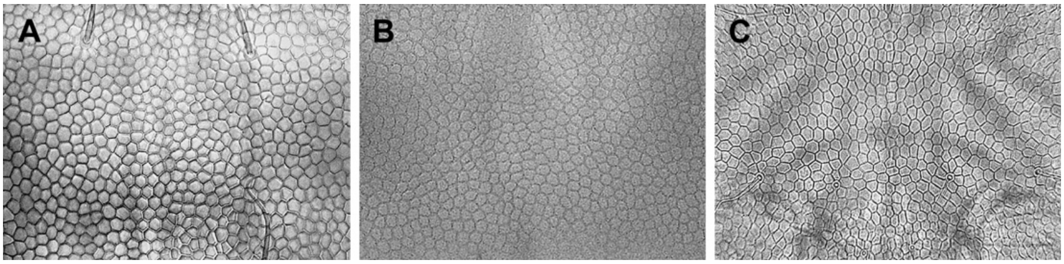

Fig. 1. Examples of scute patterns in the cephalic shield of three geophilomorph species. A. *Geophilus alpinus*. B. *Ribautia proxima*. C. *Orya barbarica*. Each area is 240 × 180 μm.

lineages from the point of view of eye morphology and morphogenesis (e.g., Harzsch et al., 2007). We will briefly contrast here two conditions of major relevance with respect to our discussion, but it is fair to remark, in passing, both the unique architecture of the compound eye of *Scutigera* (Müller et al., 2003) and the existence of large myriapod groups exclusively composed of blind species, e.g., the Polydesmida among the millipedes and the Geophilomorpha among the centipedes, this anatomical condition not being reasonably explained by the animals' life style.

The first condition, as exemplified by *Scolopendra*, consists in an ontogenetically invariant number of eyes, each of which increases in size as a consequence of continuing mitotic activity involving all parts of the eye, i.e. the distal retinula, the proximal retinula, the sheath cells and the pigment layer (Harzsch et al., 2007).

The second condition is found in lithobiomorph centipedes and in the millipedes provided with eyes, e.g. the pill millipedes, the julids and the spirostreptids. Here, at each side of the head there is a field of units (traditionally called ocelli, but interpreted as ocellar ommatidia by Harzsch et al., 2007), whose number increases regularly at each moult (e.g., Enghoff et al., 1993), thus providing a good quantitative trait on which to determine the stadium to which an individual belongs. The regular addition of new units in anterodorsal direction with respect to the single, 'founding' ocellus (or ommatidium) present at hatching, is strongly reminiscent of the regular, marginal addition of new ommatidia in the growing compound eye of the Tetraconata. Indeed, virtually all papers describing the post-embryonic development of millipede eyes seem implicitly to accept that the visual units whose number increases at each moult (ocelli) are individually non-growing units, as are the ommatidia of the Tetraconata (e.g., Peitsalmi and Pajunen, 1991, 1992). However, the cellular composition of these 'ocellar ommatidia' is not fixed at the time these units first appear on the millipede's head. For example, in the blaniulid *Nopoiulus kochii* the average diameter of the ocellar ommatidia increases from 17 to 20 to 24 μm moving from stadium III to IV to V, respectively (pers. observations). This is probably just an example of a general, but hitherto virtually overlooked phenomenon in millipede eye development. At last, in their comparative study on mechanisms of eye development in myriapods, Harzsch et al. (2007) have reported evidence of mitotic activity in a ring surrounding mature ocellar ommatidia in *Archispirostreptus gigas*, suggesting persistent intercalary growth, at least within the layer of retinula cells. Thus, in these ocellar ommatidia of millipedes we have evidence of body structures which change both in size and in number as a function of age and body size.

4. Size and trunk segmentation

4.1. The size-segmentation morphospace

In the panorama of arthropod segmentation, the number of trunk segments is generally stable within high-rank clades, although exceptions are found (e.g., centipedes, millipedes, branchiopods, remipedes). Therefore, to a certain degree, it could be argued that evolutionary change in body size is quite independent from changes in segmentation pattern, as it is independent from tagmosis.

However, inter- and intraspecific variation in segment number has independently evolved in two myriapod clades, accompanied by an evolutionary change towards considerably higher numbers of segments when compared to the respective sister clades (Fusco, 2005). These two clades are the geophilomorph centipedes (compared to the scolopendromorphs, within which variation in segment number is very limited; but see Chagas et al., 2008; Minelli et al., 2009) and helminthomorph millipedes (compared to pill millipedes where, again, trunk segment number is much more stable; Enghoff, 1984; Edgecombe et al., 1999; Sierwald et al., 2003; Edgecombe and Giribet, 2004). Evolutionary transitions towards very polypodous forms have elaborated on two different developmental modes of segmentation: geophilomorphs are epimorphic, i.e., the full complement of segments is produced during embryogenesis, while millipedes are anamorphic, i.e., new trunk segments are added during post-embryonic life.

For these two myriapod clades, we present below a meta-analysis of data on the relationship between body size and number of trunk segments based on available published and unpublished data.

Data on the number of trunk segments needs two remarks. The first is about what to count as a segment. A segmental pattern can be defined as the serial occurrence of homologous structures along a specified body axis (Fusco, 2005). In cases of concordance between several series of periodic structures (e.g., leg pairs, tergites, sternites, spiracles, etc.), the body appears as comprised of a certain number of 'segments', here intended as modular partitions (units) of the main body axis (Minelli and Fusco, 2004). However, there are cases, as in the millipedes (Enghoff et al., 1993), where the segmental series of different periodic structures repeated along the main body axis show discordant arrangement ('segmental mismatch'). In these cases delimitation of segments is at least arbitrary (if meaningful) and their count questionable. Pragmatically, as we are interested here in comparing segmental patterns among related taxa, segment counts are based on the segmental units traditionally recognized by descriptive morphology within each taxon, as generally defined by the pattern of a 'leading' series of periodic structures (e.g., tergites), thus disregarding more complex developmental aspects of segmentation (Fusco, 2008).

A second remark is about the nature of segment number variation. For some records, different sources of variation (interspecific differences and different kinds of intraspecific variation) cannot be disentangled. Although unsuitable for statistical hypothesis testing about variation, this set of data nevertheless allows at least to trace an approximate area of occupancy in a defined morphospace. We considered a simple two-dimensional morphospace, characterized by two variables, body size and number of trunk segments, heretofore indicated as the *size-segmentation morphospace*. Sources providing data in the form of ranges of variation for each of the two variables for taxa above the species level tend to produce a pattern of occupancy where the area is estimated by excess (as extreme values of one variable do not necessary co-occur with any value of the other variable, as a rectangular area would suggest). On the opposite side, incomplete knowledge for some taxa will produce a pattern of occupancy where the area is estimated by defect (as a result of an underestimation of the actual range of variation). For our meta-analysis, we assume that neither effect is strong enough to sensibly affect the general picture.

4.2. Trunk size and segmentation in geophilomorph centipedes

Within Geophilomorpha, body length of full-grown specimens varies between less than 10 mm to more than 200 mm, while the number of leg-bearing segments varies between 27 and 191 though, as a rule, only odd numbers occur (but see Leśniewska et al., 2009). Along with interspecific variation in segment numbers, often there is also intraspecific variation, both within and between sexes (the main exception being the majority of mecistocephalids). The number of leg-bearing segments is fixed since hatching (or in the very first instars), thus individual differences in adult segment numbers are not due to age differences (Fusco, 2005).

Across the whole clade, occupation of the size-segmentation morphospace indicates a direct relationship between trunk length and the number of leg-bearing segments (Fig. 2; data from Bonato, in press), and a similar relationship is also found within less inclusive clades, as in the highly variable genera *Stenotaenia* (Fig. 3), *Henia* and *Ribautia* (Bonato and Minelli, 2008). Both sensible reduction and extreme increase in adult body size have evolved independently in several lineages within Geophilomorpha, the former trend being often coupled with a derived reduction in the number of trunk segments, while the latter is always coupled with the highest number of segments found in the respective lineage (Foddai et al., 2003).

On the other hand, among specimens of the same species and sex, but with a variable numbers of trunk segments, there is no evidence of a correlation between size and number of trunk segments. In the very few cases studied (*Clinopodes flavidus*; Berto et al., 1997; *Strigamia maritima*; Kettle and Arthur, 2000), the length of the trunk is not correlated with the number of trunk segments, i.e. specimens with more segments tend on average to have shorter segments (Fig. 4). This 'primacy of tagmata over segments' is also reflected in the patterning of the segmental structures (e.g. tergites and sternites) along the trunk. In a given species, the longitudinal (segmental) pattern of quantitative (e.g., width of tergites; Berto et al., 1997) and qualitative (e.g., presence/absence of a given morphological mark on sternites; Minelli, 1992) traits of the segmental structures does not depend on the absolute ordinal position of the segments along the trunk, but rather on their relative position (i.e., with respect to the total number of trunk segments) (Fusco, 2005).

This different behaviour of interspecific and intraspecific relationship between size and segmentation in geophilomorphs is not easy to explain. A recent paper on the geophilomorph model species *S. maritima* contributes evidence of an environmental component of intraspecific variation in segment number (Vedel et al., 2008, 2010). This plastic effect could in principle bear on the difference between intraspecific and interspecific size/segmentation relationships. However, as the estimated environmental variation is only a small fraction of the observed phenotypic variation in the species, phenotypic plasticity cannot explain it in full.

4.3. *Trunk size and segmentation in helminthomorph millipedes*

In many Helminthomorpha (and Diplopoda in general), because of the marked dorso-ventral mismatch in segmental arrangement, segment count is not straightforward (Enghoff et al., 1993). For the sake of comparison, we counted functionally articulating trunk units as they appear dorsally, ignoring the question of what is a development-based segmental unit in these animals (see Fusco, 2008). Moreover, as many helmintomorph millipedes are euanamorphic (i.e., the addition of new segments continues until the last moult the animal undergoes, without any evidence of a targeted, fixed number eventually reached), for many species, the increase of the number of segments during adult life does not easily permit disentangling static (i.e., within stage) variation from ontogenetic variation in segment numbers. For this reason, and for homogeneity with the teloanamorphic and hemianamorphic species in the group (for which anamorphosis leads to a species-specific, targeted number of segments), the dataset is based on the maximum values for both body length and the number of trunk segments recorded for each species, thus disregarding intraspecific individual differences (data from Hoffman, 1982 and Enghoff et al., 1993).

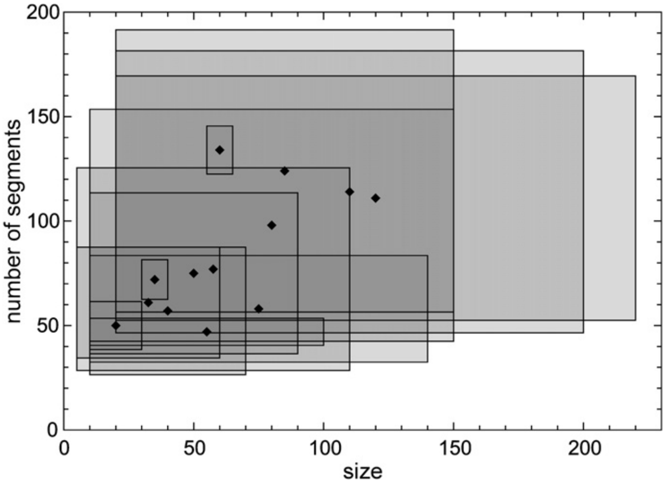

Fig. 2. Size-segmentation morphospace occupation in geophilomorph centipedes. Rectangles are morphometric variable ranges for each of the 13 traditionally recognized families, diamonds are variable averages (rectangle centers). Size is body length (mm) for full-grown adults, and number of segments is the number of leg-bearing segments. Data from Bonato (in press).

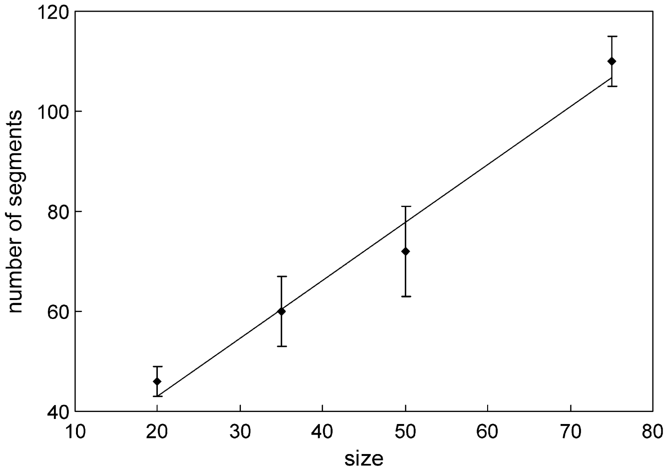

Fig. 3. Linear regression analysis on size and number of segment variation in four *Stenotaenia* species (Chilopoda: Geophilomorpha: Geophilidae). For each species, size is body length (mm) for full-grown adults, number of segments (diamonds) is the central value of the intraspecific range of variation (bars). Regression coefficient is significant ($P < 0.012$, T test). Data from Bonato and Minelli (2008).

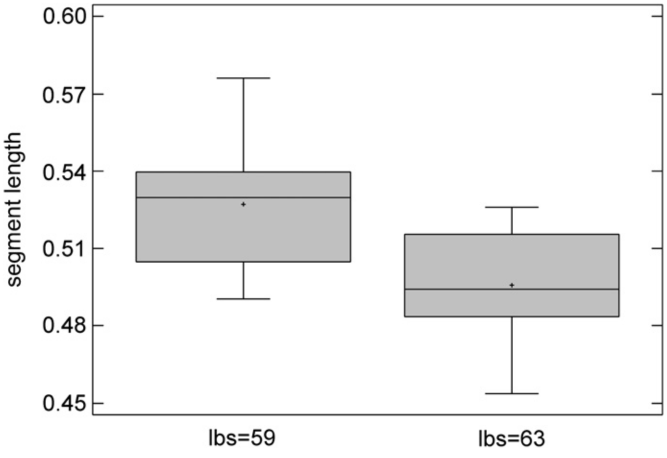

Fig. 4. Comparison of trunk segment length between two female cohorts of *Clinopodes flavidus* with 59 and 63 leg-bearing segments (lbs), respectively. Segment length was normalized with respect to body size. This is calculated as the ratio between the average segment length for the specimen and body size (principal component analysis scores based on 9 metric characters of the cephalic and the genito-anal regions). In ontogeny, trunk length is isometric with body size. Difference is significant ($P < 0.036$, Mann–Whitney test on the medians), and close to the value expected for a trunk length independent from the number of trunk segments. Boxes represent the interval between lower and upper quartiles, with median (transverse line) and mean (small cross); vertical lines are ranges of variation. Data from Berto et al. (1997).

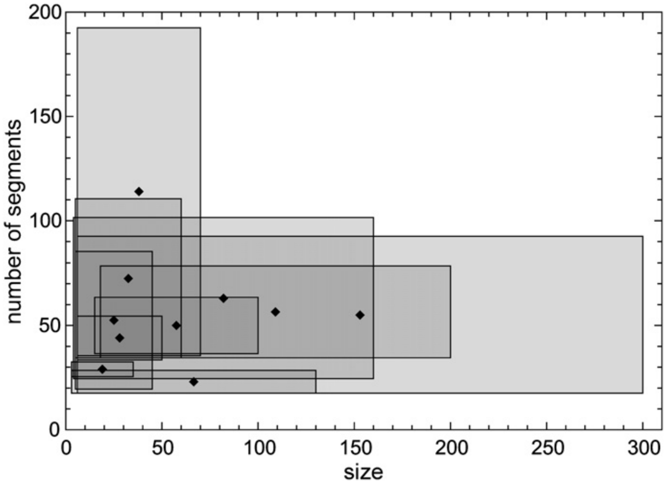

Fig. 5. Size-segmentation morphospace occupation in helminthomorph millipedes. Rectangles are morphometric variable ranges for each of the 10 traditionally recognized orders, diamonds are variable averages (rectangle centers). Size (body length, in mm) and the number of segments (number of dorsal segmental units, i.e. rings, tergites, or pleurotergites, depending on the taxon) are maximum values recorded for full-grown adults in the species, thus disregarding intraspecific individual differences. Data from Hoffman (1982) and Enghoff et al. (1993).

In the whole clade, in full-grown specimens, body length varies between less than 2 mm to some 300 mm, while the number of trunk segments varies between 18 and 192. Accordingly, the number of leg pairs varies from 28 to some 380.

Across the whole clade Helminthomorpha, morphospace occupation does not suggest a simple relationship between size and number of segments (Fig. 5). The occupied region of the morphospace is characterized by two orthogonal directions with an opposite variational pattern. Some clades, e.g., Siphonophorida, have evolved large segment numbers without a significant increase in size, while, vice versa, other clades, e.g., Spirostreptida have evolved large sizes without a comparable increase in segment number. This pattern of morphospace occupation contrasts with the pattern of interspecific variation in Geophilomorpha.

However, similarly to Geophilomorpha, inspecting variation at another taxonomic level reveals a different relationship between the two morphometric variables. In two well documented datasets, relative to two Macaronesian species flocks of julid millipedes, within the genus *Cylindroiulus* (Enghoff, 1982) and the genus *Dolichoiulus* (Enghoff, 1992) respectively, there is a significant correlation between size and number of trunk segments (Fig. 6).

4.4. Covariation of size and trunk segmentation

The relationship between body size and segmental pattern is neither simple nor univocal, as it varies between clades and at different taxonomic level within clades. Although data presented here are not suitable for rigorous quantitative analysis and hypothesis testing, some generalizations are nonetheless possible, as conspicuous differences in the covariation of the two morphometric variables are qualitatively appreciable, if not quantitatively measurable.

There is a marked contrast both between the two main clades under comparison, Geophilomorpha and Helminthomorpha, and between clades at different taxonomic level within each main clade. These different patterns of covariation of size and segmentation have emerged through evolutionary processes taking place on very different time scales, or are the result of events of very different age in the geological scale, the Lower Palaeozoic for the divergence between geophilomorphs and helminthomorphs, and virtually the Recent for intraspecific variation within the two geophilomorph species considered above (*C. flavidus* and *S. maritima*). Moreover, variation at high level is significantly more conspicuous than variation at lower taxonomic level. For instance, the range of segment number variation in the whole of Geophilomorpha is more than 150 trunk segments, while the intraspecific range of variation for the two aforementioned species is less than 10 trunk segments.

One can speculate that these diverse patterns of variation reflect the predominance of different evolutionary 'forces' along the evolutionary history of myriapods. Natural selection is an obvious candidate as a major factor to explain interspecific relationships between size and segmentation at intermediate taxonomic level (i.e, 'middle age', in terms of the evolutionary history of the whole clade), while both older and more recent patterns (including intraspecific patterns) may witness to the effects of constraints on the developmental system ('historical developmental constraints' vs. 'local developmental constraints', *sensu* Resnik, 1995).

Complex relationships between size and segmentation seem to have characterized arthropod morphology since early phases of their evolutionary history. Adults of the Silurian proetid trilobite *Aulacopleura konincki* exhibited marked variation in the number of thoracic segments, with five morphs with 18–22 thoracic segments, while trunk segmentation, as characteristic of the Trilobita, was hemianamorphic (Fusco et al., 2004). In *A. konincki* there is a significant inverse relationship between the average length of thoracic segments and their number, i.e. specimens with more thoracic segments have, on average, shorter segments (Fig. 7). This intraspecific relationship between the two morphometric variables is similar to that found in Geophilomorpha, however, while variation

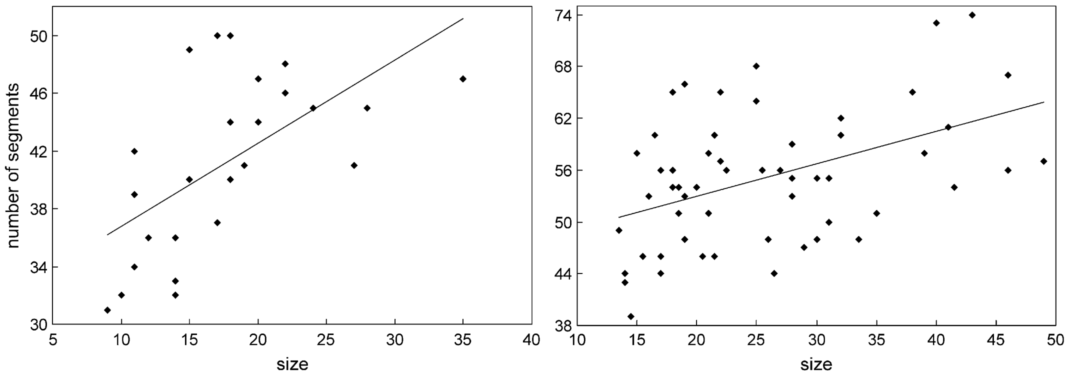

Fig. 6. Linear regression analysis on size and number of segment variation in *Cylindroiulus* species from Madeira ($n = 25$, left panel), and in *Dolichoiulus* species from Macaronesia ($n = 57$, right panel). For each species, size is maximum body length (mm) for full-grown adults, number of segments is maximum number of pediferous rings for full-grown adults. Regression coefficients are both significant ($P < 0.001$, T test). Data from Enghoff (1982) for *Cylindroiulus* and Enghoff (1992) for *Dolichoiulus*.

in segment length in the geophilomorph *C. flavidus* approximately matches the value expected for a trunk length independent from the number of trunk segments (Fig. 4), in the trilobite segment length compensates the effect of segment number only for about 40%, thus, on average, individuals with more thoracic segments, although having shorter segments, have a longer thorax nevertheless.

5. Size and limb segmentation

5.1. Early vs. late limb segmentation

Depending on the species and/or the limb type, segmentation (division into articles) of the limb axis is either a) fully established during embryogenesis, b) exclusively developed post-embryonically, or c) set in during embryogenesis and then completed post-embryonically. In case of post-embryonic segmentation, the segmental pattern can emerge either with a single moulting event, e.g., at metamorphosis, or through several moults. In the latter case, change in article number co-occurs with the growth of the individual and is thus in some way associated with its size, while in the other cases this is not necessarily so.

Indeed, among those limbs whose segmental pattern is largely or totally completed during embryonic development, the effect of size on limb segmentation seems very limited or even nonexistent, as within each of the major arthropod groups the segmentation of these limbs is fairly constant, irrespective of the enormous size variation within those groups (see Boxshall, 2004). Few exceptions are found, and these interestingly involve limb parts that in more or less closely related species show some degree of post-embryonic article addition. For instance, the endopod (inner ramus) of thoracic limbs of malacostracan crustaceans usually has five articles and no post-embryonic increase in their number; some euphausiids and some penaeid decapods, however, show a small post-embryonic increase in article number and in bathynellids, which are the smallest malacostracans (body length, 0.5–5.4 mm), the thoracopodal endopod is divided into four articles only (Schminke, 1981). Another exception is found in the tarsus of insect legs, as in the smallest species this is often divided into a smaller number of articles with respect to their closest, larger relatives (Rensch, 1959; Polilov and Beutel, 2009, 2010). Leg segmentation does not generally change post-embryonically in insects, but in few hemimetabolous insects, e.g., in the hemipteran *Oncopeltus fasciatus*, it is precisely the tarsus that acquires new articles during post-embryonic development (Shaw and Bryant, 1974).

To further investigate the possible effect of body size on limb segmentation we discuss here in more detail two different limb models, representative of limb types with limited and extensive post-embryonic article addition, respectively.

5.2. The forelegs of whip spiders

Tibia and tarsus of the forelegs (whips or antenniform legs) of whip spiders (Amblypygi) are subdivided into many articles, from a few to several tens. Number of tibial and tarsal articles varies to some extent intraspecifically and to a much greater extent interspecifically. The number of these articles, however, increases post-embryonically only with the first moult, from protonymph to nymph (Igelmund, 1987; Weygoldt, 1996). Analysis of a dataset (see Supplementary material 2) of 52 species (out of about 120 described; Weygoldt, 2000) with representatives from 15 whip spider genera (out of 20 according to traditional taxonomy; see Weygoldt, 2000) shows a significant relationship between body size and number of tibial and tarsal articles (Fig. 8).

In all amblypygid species for which data on limb regeneration are available, regenerated whips have more articles than normal (Weygoldt, 1984; Igelmund, 1987). In *Heterophrynus elaphus*, Igelmund (1987) noted that regenerated whips from older (and thus larger) specimens have more segments than those regenerated from younger individuals. This size-related limb 'over-regeneration' in whip spiders is in line with the interspecific direct relationship between size and segmentation.

5.3. The second antennae of isopod crustaceans

The second antennae of isopods are usually composed of a proximal peduncle, divided into articles with intrinsic musculature, and a distal flagellum, also divided into articles but completely devoid of muscles (Wege, 1911; Imms, 1939). The peduncle is usually divided into 5 or 6 articles (Wägele, 1983; Brusca and Wilson, 1991) and this number is usually invariant within each of the major isopod groups (Brusca and Wilson, 1991) and post-embryonic article

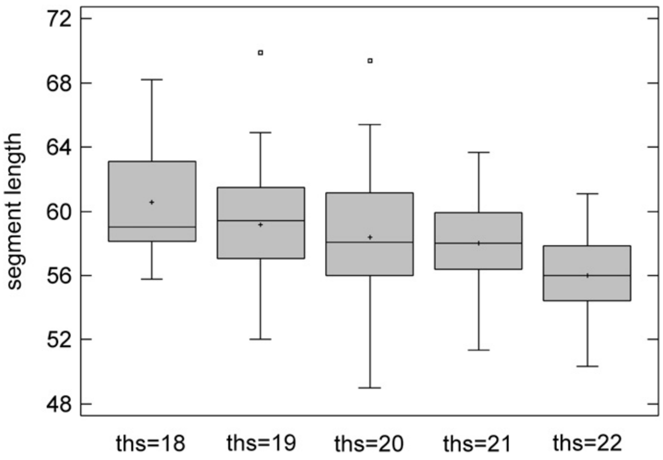

Fig. 7. Comparison of segment lengths in five morphs of *Aulacopleura konincki* with 18–22 thoracic segments (ths). Segment length was normalized with respect to size by calculating the ratio between the specimen average segment length and the size of the cephalon (Cephalic Centroid Size, based on 15 landmarks, see Fusco et al., 2004). Differences are significant ($P < 0.013$, ANOVA). Boxes' symbols as in Fig. 4, small squares are outliers. N. Hughes' unpublished data from the materials of Fusco et al. (2004).

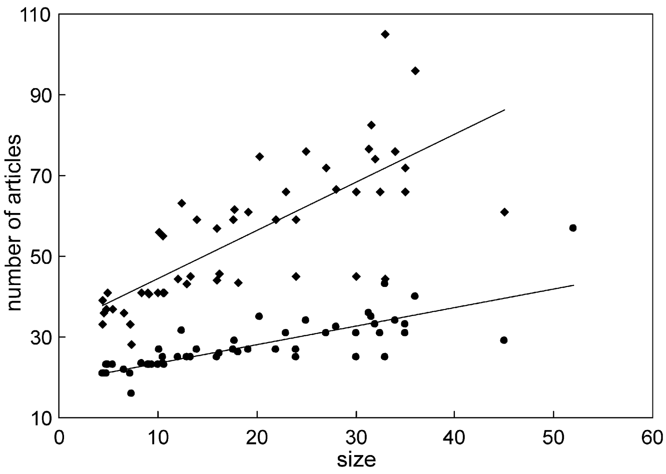

Fig. 8. Linear regression analysis on size and number of articles variation in tibia (dots) and tarsus (diamonds) of the forelegs (whips) of 52 species of whip spiders (Amblypygi). Size is body length (mm) for full-grown adults. Regression coefficients are both significant ($P < 0.001$, $P < 0.003$, T test). Data sources in Supplementary material 2.

addition has never been reported. In contrast to the peduncle, in many isopod species the number of articles in the flagellum increases along the animal's whole life, thus segmentation is correlated here with body size. An example is *Asellus aquaticus*, where there is even no fixed maximum number of flagellar articles (Maruzzo et al., 2007).

The ontogenetic schedule of segmentation can vary phylogenetically, as shown by comparisons between isopod species with markedly different body size. For example, in the huge *Bathynomus* species, the number of flagellar articles is usually comparable to that of normal-size asellids, or even smaller. Undamaged antennal flagella of *Bathynomus pelor* (body length between 50 and 130 mm at maturity) have 43 to 49 articles (Thompson et al., 2009), while *A. aquaticus* (body length between 7 and 10 mm in full-grown specimens) has 50–80 flagellar articles (Verovnik et al., 2009). Variation in the ontogenetic relationship between body size and number of flagellar articles has been reported also for very closely related taxa. For instance, this relationship differs between different subspecies of *A. aquaticus* (see Turk et al., 1996). In other cases, however, the ontogenetic relationship between body size and segmentation is phylogenetically conservative. For example, the ontogenetic relationship between body size and article number is basically the same in all of the seven *Idotea* species studied by Naylor (1955).

Addition of flagellar articles at each moult during the whole life is probably the primitive condition among isopods, as it is widespread in this group and recorded in other peracarids as well (e.g., amphipods: Geisler, 1944; Page, 1979; Williams, 1987). Derived conditions, however, are also found. Oniscideans exhibit a variable number of flagellar articles, but the truly terrestrial species usually have only 2 or 3 articles, and this extreme degree of reduction has been likely acquired several times independently (Hoese, 1989; Schmalfuss, 1998). In the species with reduced flagellar segmentation there may be limited post-embryonic addition (e.g., one article in *Atlantoscia floridana*; Araujo et al., 2004), and the size/segmentation relationship is obviously lost. Species of Arcturidae (*sensu* Poore, 2001) have relatively long, highly modified, second antennae. However, most of the limb length is provided by the peduncle, which is divided into 5 articles as expected, while the flagellum is reduced to just 2 or 3 articles with a terminal claw (e.g., Castelló, 1997; Castelló and Poore, 1998; King, 2000, 2003; King and Poore, 2001; Stransky and Svavarsson, 2006; Menioui and Poore, 2008). In other isopod groups (e.g., Gnathiidae, Paramunnidae) the number of flagellar articles is usually fixed, although exceptions are found. Most gnathiid species, for example, have 7 flagellar articles and no post-embryonic segmentation has been reported (e.g., Smit et al., 1999; Smit and Van As, 2000; Smit and Basson, 2002; Svavarsson and Jörundsdóttir, 2004; Tanaka, 2005; Golovan, 2006; Shimomura et al., 2008; Coetzee et al., 2009; Ferreira et al., 2009) but species with less (Shimomura and Tanaka, 2008) or more (Shimomura et al., 2008) articles are known. The ectoparasitic bopyroideans exhibit a still different derived condition. While their larvae have second antennae with still recognizable peduncle and a flagellum of few articles (e.g., Hartnoll, 1966; Shimomura et al., 2005), in the adults the second antennae are further reduced and the distinction between peduncle and flagellum is unclear, sometimes these appendages are completely lacking (e.g., Hartnoll, 1966; Boyko, 2004; Shimomura et al., 2005).

5.4. Size and limb patterning

Although based on a limited sample of segmental patterns, the analysis presented here shows that against the background of a wide variation in the processes of limb segmentation, body size and/or growth is sometimes highly influential on the segmental pattern of arthropod limbs. This is in agreement with what developmental genetic studies have shown for the legs of *Drosophila*, where the development of tarsal articles differs in many respects from the development of the other leg articles (e.g., Kojima, 2004), and a specific growth-dependent model of tarsus segmentation has been proposed (de Celis and Bray, 2003). However, while on one hand these cases contribute evidence for a relationship between size and segmentation in the arthropod limb, on the other hand the relationship seems not to be so consistent as to suggest the existence of underlying general constraints, showing instead to be prone to evolutionary change in several directions.

6. Final remarks

Allometry alone is unable to capture some key features of the relationship between size and form in arthropods. We have taken here a complementary approach to the study of change of form, both in ontogeny and in phylogeny, based on the size dependence of a hierarchy of serially homologous structures within the body or its parts.

In principle, a neat boundary can be expected to divide arthropod body features whose size increases with increasing body size, from those whose number, rather than size, varies as a function of overall size. This difference applies to comparisons between subsequent ontogenetic stages of the same animal as well as to comparisons between adult or otherwise equivalent conspecifics with different body size, or to representatives of related taxa. However, this is not always the case, as there are structures which share properties of both kinds of features. The ocellar ommatidia of millipedes are an example of body structures which change both in size and in number with age and body size, and the eyes of lithobiomorph centipedes probably behave the same way. To some extent, the eyes of myriapods are structurally intermediate between those of chelicerates and those of the Tetraconata (Harzsch et al., 2005, 2007). Thus, their peculiar way to vary with body size could be interpreted as reflecting an ongoing transition from an 'open' system dominated by poorly localized mitotic activity in a growing (in this case, ocular/ommatidial) field to a highly structured system dominated by the continuous (e.g., malacostracans, hemimetabolous insects) or one-step (holometabolous insects) 'freezing' of small, highly specialized clusters of cells whose size and shape are definitely fixed for the remaining of the animal's life.

Structures that cannot be easily qualified according to their growth mode with respect to changes in overall size are not the only element of complexity for size/number relationships, as complex patterns emerge also from the analysis of arthropod body features that fit quite well within one or the other of the two aforementioned categories.

This is the case of the relationship between body size and segmental pattern, either in the trunk or along the appendages. It varies widely between clades, at different taxonomic level within a clade, and sometimes even between different districts of the same body part in one and the same animal. This diversity possibly reflects variation in the relevant evolutionary processes along the history of the group, where the tension between constructional constraints and functional requirements of the biological systems has certainly played a key role. Indeed, as exemplified by the ontogeny of the trilobite *A. konincki*, complex relationships between size and segmentation seem to have characterized the body organization of arthropods since early phases of their evolutionary history.

Far from providing a general tool for investigating variation in form, this analysis makes evident nonetheless the need for a multiple approach to the study of evolution of arthropod morphological patterns.

Acknowledgements

Thanks are due to Angelika Stollewerk for inviting us to contribute a paper to the Special Issue of Arthropod Structure & Development on ‘Evolution of Patterning Mechanisms’, to Rolf Beutel, Lucio Bonato, Henrik Enghoff, Leandro Drago, Nigel Hughes, Richard Palmer, Frederik Schram and two anonymous referees for their suggestions and comments on our ms. L. Bonato and N. Hughes kindly provided unpublished data.

Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.asd.2010.06.002.

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