



Morphological nomenclature, between patterns and processes: segments and segmentation as a paradigmatic case*

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Abstract

The words we use for describing biological systems and their transformations through development and evolution can recurrently perform as ‘conceptual traps’, i.e. as representations that limit the possibilities of improving our understanding of the very processes they are called to describe. The main focus of this contribution is on the paradigmatic case of segmentation. Limits and drawbacks of the concept of ‘segment’ are critically discussed. Its value as a descriptive unit does not entitle it as a sensible unit for other uses, as for instance investigating the evolution of the developmental process of segmentation.

Key words: Arthropods, Development, Evo-devo, Evolution, Parasegments, Re-segmentation, Segmental mismatch

Introduction

Developmental biology and evolutionary biology are sciences of change through time. Formulating and testing hypotheses within these two disciplines, or at their interface (the so called evolutionary developmental biology, or evo-devo), needs sound names. Names are essential to describe organism features, both (anatomical) patterns and (physiological) processes, but also to describe the changes of these features along ontogeny and across generations, the two processes that produce developmental and evolutionary patterns, respectively. Thus, although the question of names is not a distinctive aspect of this area of biology, it is nonetheless deeply entangled with scientific investigation and communication.

Some issues related to the use of names in morphology are well known and universally acknowledged by specialists. One is that the use of the same name for two structures, or two features, in two different organisms is easily taken as an implicit declaration of homology (see Edgecombe 2008). Attempts to avoid this over-interpretation generates an over-proliferation of morphological and anatomical terminology. However, this is generally accounted for in systematics, for instance in compiling data matrices for phylogenetic reconstruction, although paradoxes remain, such as that of the segmentally patterned animals (e.g., kinorhynchs, rotifers, cestodes) that are usually qualified as non-segmented (Minelli & Fusco 2004). Another issue is that scientific progress is not just accumulation of new knowledge, with its specific new nomenclature. There is a continuous revision and refinement of what we already know, where the original meaning of words tends to be stretched, or the words are variably qualified through adjectives, prefixes and suffixes, to fit the new state of knowledge. This process is often a source of terminological confusion. Think for instance of the changing attitudes in respect to the concept of homology, starting with its meaning in pre-Darwinian times, to go throughout the new synthesis, the advent of cladistics, and the so called genomics era (Minelli 2003). Names are undoubtedly in dynamic relationship with knowledge, and continuous vigilance is thus in order.

However, this is just the tip of the iceberg. Names and name usage can exhibit more sly drawbacks. The words we use for describing biological systems and their transformations risk continuously to perform as 'conceptual traps', i.e. as concepts that limit our capability to ask and address sensible questions. There are many examples in descriptive morphology ('tagma', 'body axis', 'body plan'), in development ('embryo', 'larva', 'adult'), and in evolution ('heterochrony', 'novelty', 'adaptation') (see Minelli and Fusco 1995, Minelli *et al.* 2006).

The main focus of this article is on segmentation and its evolution, both as morphological pattern and developmental process, as it represents a paradigmatic case of a 'false friend' in biology. The term 'segmentation' is used to describe both a morphological feature (a form of body symmetry) and the developmental process that generates it. The two concepts are obviously related, but in some way they are independent from each other, and can be analyzed separately.

Segmentation pattern: from structures to axis to structures

Segmentation is a form of body symmetry, in particular it is a type of translational symmetry. A segmental pattern can be defined as the serial occurrence of homologous structures along an axis of the body, for instance along the main body axis.

The scolopender is a good example of a segmented animal, and its body architecture can easily be described on the basis of its symmetry. An introductory textbook description might start as follows: "The body of a scolopender consists of a head and a trunk. The first trunk segment bears a pair of poisonous maxillipedes; this is usually followed, depending on the species, by 21 or 23 leg-bearing segments, followed in turn by a limbless genito-anal region." Onto this 'segmental frame' it is easy to add further anatomical details, to specify, for instance, that "dorsal sclerites of leg-bearing segments II, IV, VI, IX, XI, XIII, XV, XVII, XIX are relatively shorter with respect to the contiguous segments", or that "spiracles, the openings of the tracheal system, are usually borne on pleural sclerites limited to segments III, V, VII, X, XII, XIV, XVI, XVIII, XX".

The value of such a descriptive framework will not be questioned. But let's reflect a moment on its implications. More or less consciously, the periodic pattern is thus intended to apply to the whole trunk, rather than to a specified series of serially homologous structures, such as legs, sclerites, or spiracles. The scolopender is qualified as a segmented animal because its body is comprised of a certain number of segments, rather than because its body presents one or more series of segmental (repetitive) structures. When the segmental pattern is attributed to the whole body axis, rather than to a specific set of repetitive structures along it, the idea of a body 'comprised of' a certain number of 'body-blocks' or 'modules' will inescapably result (Budd 2001).

This unnecessary, apparently harmless, conceptual (or semantic) shift, from ‘a segmented animal is one with segmental structures’ to ‘a segmented animal is made of segments’, conveys a number of drawbacks.

For instance, descriptive complications arise when different serial structures along the same axis show discordant serial arrangements. Similar occurrences are traditionally referred to as cases of ‘segmental mismatch’, a label that with a body-block concept of segment is clearly an oxymoron, because if the body is comprised of segments, there are no distinct segmental series that can either match or not. Segmental mismatch is not rare, nor is it taxonomically confined to a single clade. Many myriapods exhibit segmental mismatch: in symphylans and craterostigmomorph centipedes there are more tergites than leg pairs, whereas in scutigero-morph centipedes and tetramerocerate pauropods the number of tergites is smaller than the number of leg pairs (review in Fusco 2005). In millipedes, for the most part of the trunk, there are two leg pairs for each tergal plate, but the first three or four tergal plates correspond to one leg pair each. Still more, in some taxa the number of dorsal sclerites is not predictive of the number of leg pairs (and vice-versa), as there is only a statistical correlation between the two numbers (Enghoff *et al.* 1993).

Adopting a body-block concept of segment, the evolution of segmentation reduces to a limited set of evolutionary options. Beyond changing the number of segments, variation is just produced by fusion and/or splitting of pre-existing segmental structures. Thus, even in case of segmental mismatch, it seems sensible to ask which is the exact correspondence between different segmental series. For instance, in the case of millipedes, on the basis of what seemed to be the obvious correspondence between dorsal and ventral segmental structures in those species, as the julids, where these elements form a continuous ring, the same correspondence was extended to non ring-forming species. But, descriptive embryology of the pill millipede *Glomeris marginata* suggests a different correlation between dorsal and ventral segmental units (review in Janssen *et al.* 2006). More recently, studying the expression of some segmentation genes, in *Glomeris* again, it finally turned out that dorsal and ventral serial structures are independently established in the embryo, and that the antero-posterior boundaries of the prospective dorsal sclerites do not correlate with either the antero-posterior boundaries of the anlagen of ventral or dorsal structures (Janssen *et al.* 2004). Expression patterns of segmentation genes in the prospective ventral and dorsal tissues are different as well (Janssen *et al.* 2008).

The evolution of segmental mismatch can occur through pathways of change that are other than those resulting from the abstract logic of fusion or splitting of pre-existing segmental structures. Beyond providing developmental genetic basis for dorso-ventral mismatch, Janssen *et al.*'s studies (2004, 2008) showed that, for millipedes at least, the body-block segment is at best a descriptive or a functional body unit (Minelli 2004). But its value as a descriptive unit does not entitle it as a sensible unit for other uses, as for instance to investigate the evolution of the developmental process of segmentation.

Segmentation and re-segmentation

A pattern that presents translational symmetry can be easily described as the periodic occurrence of a repeating motif of a given length (period). However this does not imply that this motif is unique. The number of possible motifs in a periodic pattern is indeed infinite (Fig. 1). The arbitrary choice of which one is the most appropriate for a given task is either a question of convenience or a mere convention. In a linear periodic pattern, a motif can be characterized by anterior and posterior boundaries, but these boundaries, as such, are not inherent elements of the pattern.

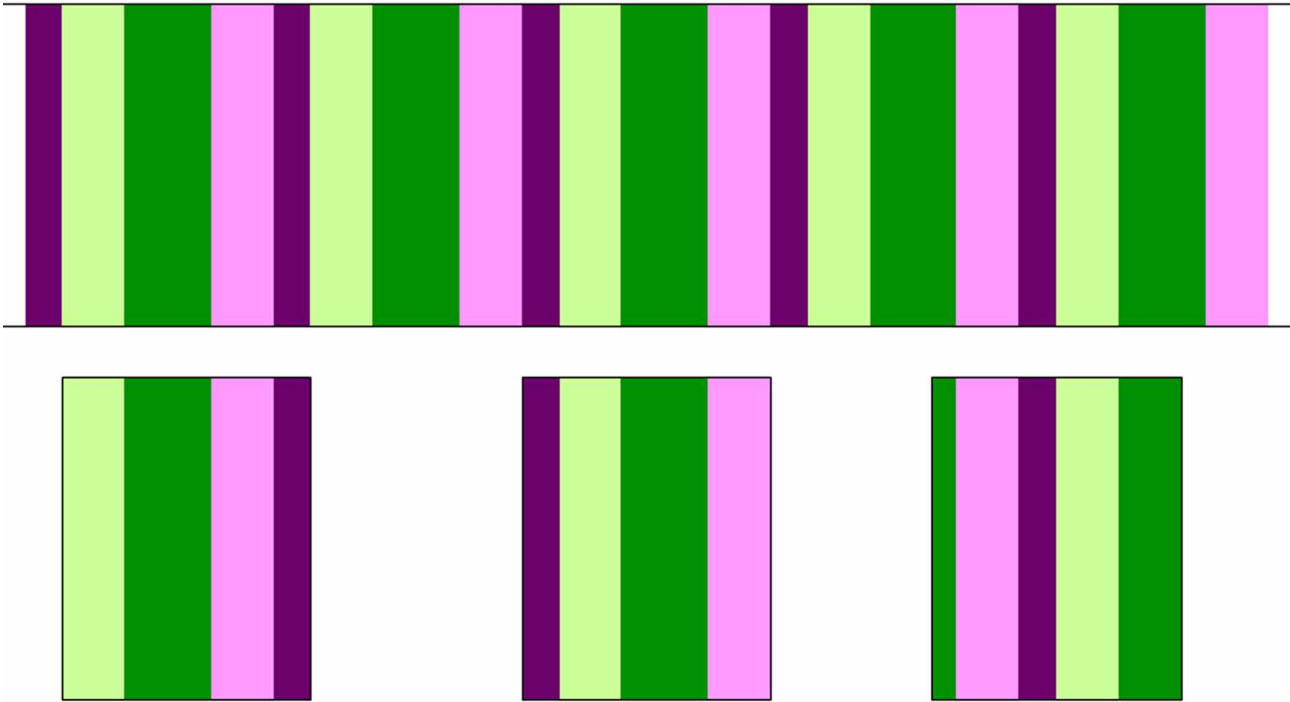


FIGURE 1. A periodic pattern with three of the infinite repeating motifs that can be used for describing it.

These almost trivial geometrical considerations are evidently not as obvious in studying animal segmental patterns. In standard descriptions of gene expression patterns, it is common practice to use a reference system based on segmental units delimited by segmental boundaries, as if these could be established univocally. However, while anatomical elements (e.g. sclerites), cell domains (e.g. compartments, i.e. cell populations of (poly)clonal origin), or gene expression domains, can have objective boundaries, segments, that is the units (sections) into which the axis is subdivided, have only the boundaries given by their definition, for the simple geometrical reasons mentioned above.

Developmental genetic studies, in *Drosophila* first (Martinez-Arias & Lawrence 1985), and later in other arthropods (review in Damen 2007), showed that in the early embryo the functional segmental unit is different from the functional segmental unit in the later embryonic, larval and adult stages. In the early embryo, segment-polarity genes (like *engrailed* or *wingless*) define parasegmental boundaries. These are limits of clonal restriction and often limits of expression domain for later regulatory genes, like the *Hox* genes. Parasegments are out of phase with respect to the later segments, as defined on the basis of trunk articulation. For some authors (e.g., Lawrence 1992), only parasegments are real entities, i.e. “units of internal description” of the embryo, whereas segments, being mere anatomical outcomes, as developmental units “may only exist in the mind of scientists”. Other authors (e.g., Deutsch 2004) consider the passage from the parasegment to the segment reference system as an important ontogenetic shift in segmental organization. This has sometimes been called re-segmentation (e.g., Prud’homme *et al.* 2003), in analogy to a similar process described for vertebrate somitogenesis (e.g., Saga & Takeda 2001). My opinion is that neither parasegments nor segments are necessary developmental units. Paraphrasing Lawrence (1992), what might be only in the mind of the scientists is the embryo’s need for ‘units of internal description’. If the initiation/localization of a morphogenetic process producing a segmental structure (e.g., the insect leg) needs a pre-existing specific periodic signal (e.g., *wingless* expression), this does not entail that there is also a need for an early subdivision of a body domain (e.g., the thorax) into a number of abstract ‘units of internal description’, either parasegments or segments.

Re-segmentation is not a process per se. It comes to life only in virtue of the arbitrary definitions of two

different (and out of phase) descriptive units. Simply, different morphogenetic processes, in early and later development, in different ectodermal and mesodermal tissues, exploit the same framework of positional information provided by the expression of a pool of segmentation genes. It is true that in *Drosophila* early embryogenesis, during germ-band retraction, parasegmental grooves disappear and the segmental ones start to form, but this does not require a shift in the ‘internal reference systems’.

In the arthropods where it has been investigated, re-segmentation does not involve in the same way all the segmental structures of the body, thus the ‘segmental organization’ of the adult exoskeleton can be associated to the ‘parasegmental organization’ of its nervous system (Deutsch 2004). This differential ‘frame shift’ has been interpreted as an adaptation for permitting movement and for improving motor control in animals with an articulated exoskeleton, as arthropods are. Although along the main body axis there are indeed many segmental structures (sclerites, myomers, neuromers) reciprocally out of frame (for very good functional reasons), this does not require the presence of two (or more) segmental ‘reference systems’. For segmental structures with the same period, one will suffice. Pattern formation needs positional information, but ‘units of internal description’ are not indispensable. In *Glomeris* it is sensible to distinguish between dorsal and ventral *segmentation*, or dorsal and ventral segmental patterns, but there is no need to define dorsal and ventral *segments* (Janssen *et al.* 2008).

Similarly to the concept of segment as a body block, the idea of the segment (or parasegment) as a necessary developmental unit is a descriptive heredity that constraints the way in which we can conceive the evolution of development. In this case, it imposes to the embryo a developmental logic based on repeated units, apparently necessary to obtain the whole segmental pattern. Evolution of developmental pathways hardly feel this constrictions, which only emerge from the geometry of our descriptions.

Segmentation process: producing segments or not

There are good reasons for not taking segments too literally, and these reasons can be found in the way in which segmentation develops and evolves. This is certainly a semantic issue, but it is not a ‘mere semantic issue’, since the meaning associated with these words conditions investigation and understanding of real biological process, both in development and evolution.

To understand the evolution of these developmental pathways we should keep segmental patterns (that sometimes can be easily described as a series of segments) well distinct from segmentation processes (that can produce segments or not). In absence of direct observational data, segments should be considered just as epiphenomenal units (Fusco 2005). The overall aspect of a segmented animal depends on the level of concordance between different segmental series of structures. When many structures occur with the same periodicity, the effect of a body comprised of a series of segments is obtained. To some extent, this could be the case of the scolopender. On the contrary, when different structures are patterned on the basis of distinct discordant regulative signals, the result is a body affected by segmental mismatch, as in the case of the millipede.

The diversity of arthropod segmental patterns fits suitably with segmentation evolving through ‘segment-free’ pathways of change.

Conclusions

If morphological nomenclature hides insidious ‘conceptual traps’ that can bias the investigation of biological patterns and processes, is there a general method to avoid them? The problem, evidently, is one of identifying such fallacies. Clues of the presence of a conceptual trap might be a logically inconsistent nomenclature or an ineffectually complex terminology. For instance, descriptive systems based on the depiction of a ‘general rule’

(‘the trunk of an arthropod is made of a series of segments’) followed by a list of ‘exceptions’ (‘not all segments are exactly the same’, ‘not all structures present a segmental arrangement’, or ‘not all structures present the same segmental arrangement’) are very common. This practice, beyond being logically unsatisfactory and leading to an uncontrolled proliferation of morphological nomenclature, tends to hide the fact that we are probably missing some relevant aspect of the pattern (or process) under consideration.

Without the intention of advancing a radical solution (if there is one) to this weakness of morphological nomenclature, here is a short list of simple rules of thumb that can perhaps help avoiding at least the most macroscopic fallacies.

- i. Try to disregard, as much as possible, the burden of non-declared meanings and implications that the usage of a given term has produced and accumulated along its history. Segmentation is not an ‘all or nothing’ condition. Arthropods, annelids and vertebrates are segmented just up to a point. And, there are many non-arthropod, non-annelid, non-vertebrate animals that are segmented animals, up to a point.
- ii. Acknowledge and accept the non-resolvable approximate nature of morphological nomenclature. It always depends on the level of description. Any periodic pattern can disappear at an enough close scrutiny. Think of the actual variation of any biometric variable along the main axis (for instance, in an arthropod, a cuticle parameter varying from sclerite to arthrodistal membrane), it is never periodic in the strict sense with which this word is used in mathematics. Periodicity emerges only at a convenient level of description (for instance just considering the alternation of sclerites (0) and arthrodistal membranes (1): 0101010...). Segmentation exists just up to a point.
- iii. Keep always in mind the distinction between the level of description from the level of reality. A model M can be defined as a representation of the system S that can be usefully employed for answering questions on S . Any model has its range of application, beyond that it is only an inadequate representation. As a general rule, a descriptive model cannot be used as the starting point for addressing questions of development and evolution of the modelled system. Segments are elements of a representation.

In short, before usage, ask what that name is for.

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