



# The Development of Arthropod Segmentation Across the Embryonic/Post-embryonic Divide – An Evolutionary Perspective

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In many arthropods, the appearance of new segments and their differentiation are not completed by the end of embryogenesis but continue, in different form and degree, well after hatching, in some cases up to the last post-embryonic molt. Focusing on the segmentation process currently described as post-embryonic segment addition (or, anamorphosis), we revise here the current knowledge and discuss it in an evolutionary framework which involves data from fossils, comparative morphology of extant taxa and gene expression. We advise that for a better understanding of the developmental changes underlying the evolution of arthropod segmentation, some key concepts should be applied in a critical way. These include the notion of the segment as a body block and the idea that hatching represents a well-defined divide, shared by all arthropods, between two contrasting developmental phases, embryonic vs. post-embryonic. This eventually reveals the complexity of the developmental processes occurring across hatching, which can evolve in different directions and with a different pace, creating the observed vagueness of the embryonic/post-embryonic divide.

**Keywords:** anamorphosis, comparative analysis, development, evolvability, fossils, hatching, gene expression, phylogeny

## INTRODUCTION

In many arthropods, production and differentiation of new segments are not completed by the end of embryogenesis but continue, in different form and degree, well after hatching, in some cases up to the last post-embryonic molt.

The post-embryonic addition of new segments is called *anamorphosis* and the taxa that present this mode of development are said to exhibit *anamorphic development*. Alternative to this developmental mode is *epimorphic development*, where the number of segments remains constant throughout the whole post-embryonic life. Completing the spectrum of options for the ontogenetic variation in the number of segments, there is the much less common process of *desegmentation* (or *regressive segmentation*), where the number of segments decreases at some point of the post-embryonic development; this is limited to a few holometabolous insects (Minelli and Fusco, 2013). Post-embryonic segment addition is not necessarily limited to a reproductively immature condition or to a larval phase, when present.

## Anamorphosis: Numbers and Modes

Segmentation is a combination of multiple developmental processes that span from the first expression of segmentation genes to the complete display of all the morphological features of a mature segmental body unit. Since segmental units undergo developmental patterning (which may involve size, shape, limb formation, etc.), the “segmental stage” at which a segment can be considered “laid down” is an arbitrary choice. For instance, in the anostracan crustacean *Artemia*, this was identified either with the “segmental stage c,” at which the segment has the shape of a short cylinder (Weisz, 1946), or with the appearance of a stripe of Engrailed protein at the prospective posterior boundary of the segment (Williams et al., 2012).

For our comparative purposes, we count as developmental addition of a new segment the first morphological appearance of a segmental unit as traditionally recognized by descriptive morphology (not necessarily the same for all taxa), irrespective of how close it is to its final morphology (e.g., disregarding presence/absence of limb buds). We calculated a *degree of anamorphosis* as the percentage of segments that are added during post-embryonic life, from 0% in epimorphic taxa, to >95% in the longest millipedes (see **Supplementary Table 1** for details on segment count).

Independent from the degree of anamorphosis, three main *modes of anamorphosis* are recognized, as first proposed by Enghoff et al. (1993) for millipedes. In *euanamorphosis*, segment number increases at each molt throughout the whole post-embryonic life, to terminate only with the death of the animal. In *teloanamorphosis*, segment number also increases throughout the animal's life, but both the number of molts and the schedule of segment addition at each molt are fixed for a given species and sex. Finally, in *hemianamorphosis*, the post-embryonic development includes a first anamorphic phase, through a first batch of stages (instars) separated by molts, followed by an epimorphic phase where molts take place without further increase in the number of body segments.

## TAXONOMIC SURVEY

### Anamorphosis in Extant Arthropods

The distribution of anamorphosis and epimorphosis in the main groups is shown in **Figure 1** (reference to source data in **Supplementary Table 1**).

In Chelicerata, hemianamorphosis is found among the Pycnogonida, which are sister to all the other Chelicerata, the Euchelicerata; these are all epimorphic to the exclusion of the Acariformes. Within the Pycnogonida and Acariformes, a few lineages have independently evolved epimorphic development (Lindquist, 1984; Brenneis and Arango, 2019).

Most myriapod lineages are hemianamorphic. Epimorphic development only occurs in the centipede clade rightly named Epimorpha, which includes the Scolopendromorpha and Geophilomorpha. Euanamorphosis and teloanamorphosis are found among the Helminthomorpha millipedes exclusively, where both modes may have evolved once or several times independently (Miyazawa et al., 2014).

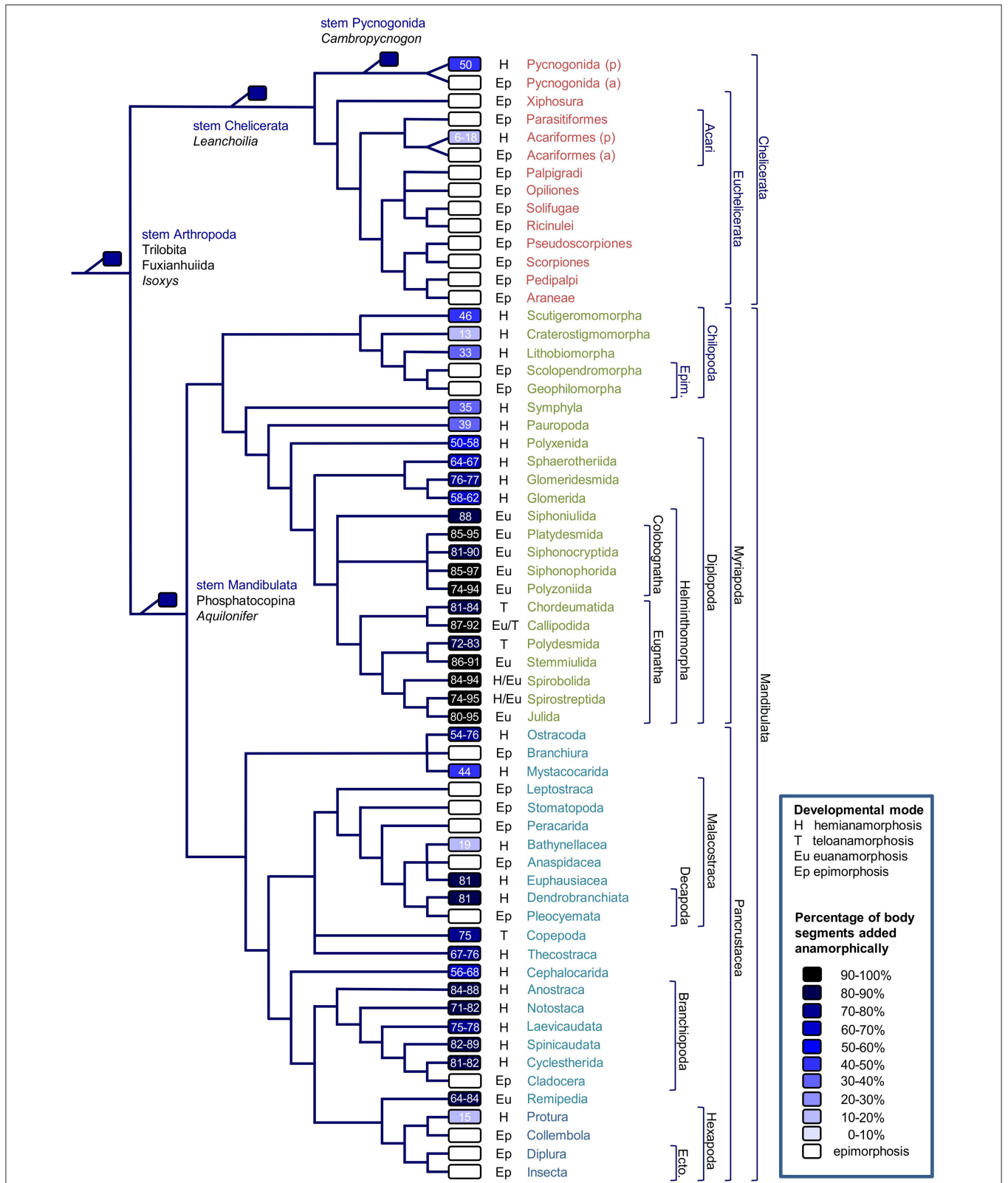
Within the Pancrustacea, hemianamorphosis is the most common developmental mode among the “crustacean” (non-Hexapoda) lineages, but epimorphic development has evolved in some lineages, in association with direct development, whereas teloanamorphosis has possibly evolved in Copepoda (Huys, 2014) and euanamorphosis in Remipedia (Koenemann et al., 2009). Within the Hexapoda, only the Protura are hemianamorphic, while the Collembola, Diplura, and Insecta are epimorphic.

### Anamorphosis in Fossil Arthropods

Ontogenetic series are available for several fossil arthropods, both stem- and crown-group. Many of these show anamorphic development and hemianamorphosis seems to be the most common mode of segmentation among stem-group taxa (e.g., Fu et al., 2014, 2018). However, segmentation in these ancient forms also exhibits some distinctive features with respect to extant taxa. Many Phosphatocopina, interpreted either as stem-group Pancrustacea (Haug and Haug, 2015) or stem-group Mandibulata (Chipman and Edgecombe, 2019), were anamorphic with indirect development (Haug and Haug, 2015), hatching as so-called *head larva*. In contrast to modern anamorphic taxa, no segments were added with the first few molts, that is, anamorphosis was in some way delayed. Another peculiar feature of anamorphosis in these early forms was that, similar to trilobites, segments first emerged as dorsally non-articulated units forming a single shield, the pygidium. The most anterior pygidial segments developed articulation in successive stages, in a process that in trilobites is called *segment release*. Trilobita, variably assigned to stem-group arthropods, stem-group chelicerates or stem-group mandibulates (Giribet and Edgecombe, 2019), mostly developed hemianamorphically (Hughes et al., 2006). However, some Emuellidae, with more than 100 trunk segments as adults, were possibly euanamorphic (Paterson and Edgecombe, 2006), whereas Zhang and Clarkson (2009) made the case for an epimorphic eodiscoid species. Delayed anamorphosis might have characterized trilobite post-embryonic development as well. Evidence for an even earlier phase of cephalic segment addition (during the so-called phaselus stage, if this was actually a phase of trilobite ontogeny), is weak (Hughes et al., 2006).

### Phylogenetic Patterns

Phylogenetic distribution of anamorphosis in extant taxa and information from extinct forms concur to indicate hemianamorphic development as the primitive condition in arthropods (Hughes et al., 2006; Minelli and Fusco, 2013; Miyazawa et al., 2014; Haug and Haug, 2015; Brenneis et al., 2017). Uncertainties on key nodes of arthropod phylogeny and incomplete information on post-embryonic segmentation in several taxa prevent a formal analysis of the evolution of this developmental character at the level of the whole clade. However, starting from the hypothesis of hemianamorphosis as the plesiomorphic condition and complementing the phylogenetic distribution of the character in **Figure 1** with some available information at lower taxonomic level, four different evolutionary transitions can be recognized.



**FIGURE 1 |** Phylogenetic distribution of segmentation modes in arthropods. Phylogeny based on Giribet and Edgecombe (2019), Chipman and Edgecombe (2019) (fossils), Howard et al. (2020) (Chelicerata), Fernández et al. (2016) (Myriapoda), and Schwentner et al. (2018) (Branchiopoda and Malacostraca). p, plesiomorphic (Continued)

**FIGURE 1** | condition; a, apomorphic condition; H, hemianamorphosis; T, teloanamorphosis; Eu, eunanamorphosis; Ep, epimorphosis; Epim., Epimorpha; Ecto., Ectognatha. Color of boxes and figures inside each box (percentage of body segments added post-embryonically) express the degree of anamorphosis (quantified only for extant taxa). In case of variation at lower taxonomic level, data refers to the most common or to the hypothesized plesiomorphic condition in the taxon. Details in **Supplementary Table 1**.

**(i) Partial embryonization of segmentation** (less anamorphic segments), with a consequent reduction in the degree of anamorphosis, seems to have occurred frequently. Millipedes usually have four trunk segments at hatching, but several species from different clades (Polyzoniida, Platydesmida, Julida, Stemmiulida, Spirobolida) hatch with more, up to 38 segments (Minelli, 2015; **Supplementary Table 1**). In centipedes, interpretation of the phylogenetic pattern crucially depends on the identity of the taxon that is sister to Epimorpha, either Lithobiomorpha or Craterostigmomorpha. In the first case, mainly supported by molecular data, from the primitive condition represented by Scutigermorpha, there would have been a conspicuous embryonization of segmentation in Craterostigmomorpha firstly, followed by an opposite change in Lithobiomorpha and complete embryonization in Geophilomorpha. In the second case, mainly supported by morphological data (other than segmentation mode), a progressive embryonization from Scutigermorpha to Epimorpha would have occurred. Among crustaceans, from a primitive condition of hatching as a nauplius larva, many lineages have independently evolved shorter anamorphic development, hatching as a more advanced-stage larva (e.g., metanauplius in Cephalocarida and Mystacocarida). This cannot generally be interpreted as a systemic heterochronic change, because different aspects of segmentation (segment appearance, segment patterning, or limb formation) and development of larval features (autonomous nutrition, locomotion, muscular, and nervous systems) are not necessarily associated (Fritsch et al., 2013; Haug and Haug, 2015; Jirikowski et al., 2015). Segmental patterning can even progress in the opposite direction with respect to segment addition, i.e., from posterior to anterior (Minelli, 2003, p. 162).

**(ii) Complete embryonization of segmentation** (epimorphosis) has evolved several times independently: at least in one trilobite species (Zhang and Clarkson, 2009), in some lineages of Pycnogonida (Brenneis et al., 2017), in Euchelicerata, in Epimorpha among the centipedes, in several lineages of Malacostraca (but see below), in Cladocera and twice among the Hexapoda, i.e., in Collembola and Ectognatha. In some cases, this process is associated with the evolution of direct from indirect development (many crustaceans) and a shortening of the metameric trunk (e.g., Branchiura and Cladocera). However, the opposite is observed in Geophilomorpha, where epimorphosis is associated with the most segment-rich trunks among the arthropods. It must also be noted that epimorphosis can evolve from anamorphosis not only by embryonization of the addition of most posterior segments, but also from the suppression of the addition of those segments (*suppressed anamorphosis*), as

suggested for some lineages of Acariformes (Bochkov, 2009; Bolton et al., 2017).

**(iii) Partial de-embryonization of sequential segmentation from an anamorphic condition** (more segments produced by anamorphosis), with a consequent increase in the degree of anamorphosis, is apparently less common. Stem-group Pancrustacea hatched as head larvae of five segments, whereas the primitive condition for crown-group Pancrustacea is thought to be a four-segment nauplius (Haug and Haug, 2015). According to Scholtz (2000), Euphausiacea and Dendrobranchiata would have evolved a “new” nauplius secondarily (and in parallel) from primitive Malacostraca with shorter anamorphosis, but this has been questioned more recently (Akther et al., 2015; see also below). In centipedes, if Lithobiomorpha are actually sister to Epimorpha (see above), the former would have extended anamorphosis from a shorter Craterostigmomorpha-like condition.

**(iv) Partial de-embryonization of embryonic sequential segmentation from epimorphosis** (*secondary anamorphosis*), seems to be even more rare, and putative cases are uncertain. In Pycnogonida, some Nymphonidae might have returned to anamorphosis (Brenneis et al., 2017), but uncertainties on the phylogeny of epimorphic pycnogonids do not allow to resolve this transition with confidence. If Euchelicerata are primitively epimorphic, Acariformes would have evolved anamorphosis secondarily. However, due to the persisting instability of phylogenetic hypotheses about the major clades of Euchelicerata (Giribet and Edgecombe, 2019), it is not unparsimonious to hypothesize that the Acariformes simply retained the plesiomorphic chelicerate condition (Bochkov, 2009; Bolton et al., 2017). The phylogeny in **Figure 1** would support epimorphosis as plesiomorphic for the Malacostraca, with secondary independent transition to anamorphosis in some derived taxa, compatible with the presence of a zoea-like larva as the plesiomorphic condition for the group (Jirikowski et al., 2015). However, in consideration of the similarities between the nauplii in anamorphic malacostracans and non-malacostracans and the differences in the direct development of epimorphic malacostracans, other authors have put forward the opposite hypothesis, i.e., the retention of the primitive condition of malacostracan anamorphic larval development in Bathynellacea, Euphausiacea, and Dendrobranchiata and its independent loss in the other malacostracan groups (Akther et al., 2015; Haug and Haug, 2015).

Anamorphosis and epimorphosis are not fundamentally distinct developmental modes, the latter being only the lower extreme degree of the former. This is more than an arithmetic truism. In several clades, e.g., in decapod crustaceans, segment number is the same in anamorphic and epimorphic lineages. Among the most polymeric



epimorphic clade, the Geophilomorpha, Brena and Akam (2013) discovered a minimal leftover of anamorphosis in the species *Strigamia maritima*, where 2–3 terminal segments (out of 48–54 trunk segments) are added after hatching, during the first embryoid stages (see below). However, the opposite evolutionary transitions, embryonization vs. de-embryonization of segment formation, might not have the same evolvability, the former having apparently occurred more often than the latter.

## Genetics of Anamorphosis

In anamorphic development, as well as in embryonic sequential segmentation, the new segments appear sequentially in anteroposterior progression from a subterminal region referred to as “segment addition zone” (SAZ; Janssen et al., 2010). This is also often referred to as the proliferative (or generative, or growth) zone, but SAZ is to be preferred because it makes no assumption of localized and continuous cell proliferation in the posterior of the body (Clark et al., 2019; see also Fusco, 2005). However, information about morphogenesis and gene expression associated with anamorphosis is scarce, and current investigations are mainly concerned with the evolution of embryonic simultaneous segmentation from embryonic sequential segmentation in insects.

Evidence of a conserved role of the segment polarity gene *engrailed* during anamorphosis was found in the anostracan crustaceans *Artemia* and *Thamnocephalus* (Manzanares et al., 1993; Constantinou et al., 2020), in the thecostracan crustacean *Sacculina* (Gibert et al., 2000) and in the centipede *Lithobius* (Bortolin et al., 2011).

The involvement of Notch signaling is increasingly emerging as a common feature of sequential segmentation throughout the Bilateria. Williams et al. (2012) showed that blocking Notch signaling causes a specific, repeatable effect on segmentation in *Artemia franciscana* and *Thamnocephalus platyurus*, although the observation that loss-of-function Notch phenotypes differ significantly across arthropods suggests some variation in the role of Notch in the regulation of sequential segmentation.

Despite the paucity of experimental data on the developmental genetics of anamorphosis, some indirect information can be obtained from comparative studies on embryonic segmentation. In a certain way, the evolutionary embryonization of anamorphosis can be seen as a natural experiment, where post-embryonic segmentation, a process not easily accessible to current molecular methodologies, is brought under the eye of the investigator. The extended similarities found in embryonic sequential segmentation in lineages that independently evolved either complete or partial embryonization of segmentation can perhaps indicate a common basic mechanism among lineages with different degree of anamorphosis up to epimorphosis. This could be based on the same clock-and-wavefront mechanism inferred from data on embryonic segmentation in a small number of model species, and hypothesized to be ancestral and conserved among arthropods (Clark et al., 2019).

## ANAMORPHOSIS IN CONTEXT

Beyond the arbitrariness of what to count as the appearance of a new segment, the previous descriptions might suggest that anamorphosis is a well-defined phenomenon, and that its evolution can be confidently traced whenever reliable developmental and phylogenetic information is available. However, this is only a superficial view that can serve only broad comparative purposes. On a closer inspection, seeking for mechanistic explanations, anamorphosis remains surrounded by uncertainties that can be locally resolved only by overcoming the idealizations hidden in the traditional concepts of hatching, larva, and segment.

## The Blurry Event of Hatching

It is not always the case that hatching separates embryonic from post-embryonic phases neatly. More or less embryo-like (embryoid) hatchlings are described for many arthropod groups, under a variety of taxon-specific terms (Minelli et al., 2006; Minelli and Fusco, 2013; Fritsch and Richter, 2015; Haug, 2020; **Supplementary Table 1**).

Focusing on taxonomic distribution and morphological and functional characteristics of these embryoid stages, three facts highlight the evolutionary flexibility of arthropod developmental schedules. First, conditions at hatching are often different between closely related taxa (e.g., in many spiders there is a pronymph with incompletely articulated appendages, but not in all). Second, this diversity is associated with a diversity in the number of molts the animal undergoes before and after the beginning of its active life. In most pterygote insects, three embryonic cuticles are shed before hatching, but only two in the cyclorrhaphous flies (Konopová and Zrzavý, 2005). Third, the condition at hatching is not necessarily correlated to segmentation schedule. For example, epimorphic hexapod hatchlings are anything between an active juvenile and a vermiform pronymph, while anamorphic myriapods hatch in conditions so different as the very active larva I of *Lithobius* and the motionless pupoid of *Pauropus* (Minelli et al., 2006).

Situated at one extreme of both embryonic and post-embryonic phases, where the methodologies used in the study of each phase are less effective, development around hatching time is little investigated, and recent work is disclosing unsuspected situations. For example, two embryoid stages were traditionally reported for the geophilomorph centipedes, whereas a recent closer scrutiny in *Strigamia maritima* revealed five stages (Brena, 2014).

## The Multifaceted Larva

Many arthropods, in particular among the Pancrustacea, begin post-embryonic life as larvae. However, the term larva has been applied to immatures with very different, although non-mutually exclusive characteristics. These include forms that differ morphologically from the adult, have different ecological niches than the corresponding adult, or transform into an adult by a metamorphosis (see Haug (2020) for a detailed account), thus the qualification of development as either direct or indirect is somehow a matter of degree or requires qualitative specification

(e.g., for some intermediate cases Fritsch et al. (2013) introduced the term *pseudo-direct development*). The evolution of post-embryonic segmentation, although potentially independent from other developmental features of juvenile stages, can be found to be variably associated to larval evolution, as for instance when the evolution of direct development coincides with a transition to epimorphosis.

## The Complex Segment

Description and comparative analysis of anamorphosis assume that we are dealing with unambiguously countable units, the segments. However, not all putatively segmental structures (especially those of internal anatomy) are in register, as they can have different period or phase. Thus, a more realistic depiction of arthropod body organization is obtained by dissociating the serial homology of individual periodic structures (e.g., legs or sclerites), or *segmentation*, from the concept of the *segment as a body module* (e.g., Budd, 2001; Minelli and Fusco, 2004; Fusco, 2005, 2008; Fusco and Minelli, 2013; Hannibal and Patel, 2013). This accounts for the occurrence of so-called “segmental mismatch,” i.e., the discordance between different segmental series within the same animal, and of a number of segmental abnormalities (Leśniewska et al., 2009), but also for the high disparity in arthropod segmental patterns. The study of anamorphosis cannot disregard the complexity and the disparity of the segmentation process (Minelli, 2020).

## CONCLUSIONS

We advise that for a better understanding of the developmental changes underlying the evolution of arthropod segmentation, some key concepts should be applied in a critical way.

The putative embryonic/post-embryonic divide suffers the same shortcomings shown by the traditional periodization of development (articulation in temporal units for comparative purposes) within each of the two main phases of arthropod development (Minelli et al., 2006). During embryonic development, periodization can either be based on absolute time from egg laying, on the fraction of elapsed embryonic time, or with reference to a series of events such as blastoderm formation, gastrulation, etc. During post-embryonic development, periodization is mainly based on temporal units delimited by molts, generally referred to as stages or instars. In both phases, some developmental events are employed to give temporal order to other events, but there is no biological foundation for one series of events to be recognized as “ordinator” and all other events as “ordered.” Periodization cannot be other than a relative

framework, and the same is true for the passage from embryonic to post-embryonic life.

Evolutionary developmental biology seems to be over-preoccupied with boundaries, both in space (e.g., those between segments) and time (e.g., those between stages). However, these boundaries can easily hide both the continuity of many co-occurring developmental processes and the independence exhibited to a different degree by the same set of processes (Minelli et al., 2006). As an alternative, for instance, rather than defining embryonic development on the basis of its putative boundaries (fertilization, when the case, and hatching), it seems more sensible to define it based on “what it is,” that is as a special context for early developmental events, characterized by the fact that the latter run protected by the body of a parent (or a host) or by a shell, that are stabilized in physical parameters, occur in relatively small-size living systems, are supplied with energy and materials from the parent, etc. None of these features is necessary, nor sufficient for defining the embryonic phase, and each one can change in evolution with different direction and pace, creating the observed vagueness of the embryonic/post-embryonic divide. From this stance, recurrent embryonization and (although less frequently) de-embryonization of segmentation in evolution reveal the robustness of the developmental processes involved, able to work in contexts so different as an embryo and an active animal, where in many cases these processes can go on for years.

Evolution is about change, and to study evolutionary change we need flexible conceptual frameworks and data formats.

## AUTHOR CONTRIBUTIONS

Both authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.622482/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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