

*Basal euarthropod development: a fossil-based
perspective*

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The morphological gap between Euarthropoda (the crown group that contains all extant arthropods) and living arthropod-like animals such as onychophorans, tardigrades and pentastomids is bridged by a number of fossils known primarily from rocks some 520 to 490 million years old (e.g. *Fuxianhuia*, *Chengjiangocaris*, *Shankouia*, see Figure 15.1; cf. Waloszek *et al.* 2005). These centimetre-scale fossil animals illuminate critical steps in early arthropod evolution (particularly head and limb development) but provide a limited amount of developmental information because of a lack of early ontogenetic stages. Small individuals that might represent premature stages are scarce or absent, and the degree of allometry among the available individuals is generally modest. A limited number of early arthropod taxa do show more substantial ontogenetic information (Waloszek and Maas 2005). This chapter reviews the morphological development of early arthropods from two perspectives. The first is that provided by ontogenetic series based on the well-preserved biomineralised exoskeletons of trilobites, the best represented arthropod taxon in Palaeozoic rocks, but one whose development is seldom considered in broader comparative context. The second is that provided by ‘Orsten’-type preserved faunas, in which the entire cuticle of numerous post-embryonic specimens of various species, mainly representatives of the crustacean evolutionary lineage (stem derivatives and Labrophora with phosphatocopines and members of the Eucrustacea; see Maas and Waloszek 2005) was replaced with spectacular fidelity by calcium phosphate in the absence of any compaction (Müller 1985). Such preservation has permitted detailed reconstruction of portions of the ontogeny of several late Cambrian euarthropods normally absent from the fossil record. Patterns of segment generation common to these different sources may provide insight into the developmental mode of basal Euarthropoda, and thus into the evolution of arthropod ontogeny.

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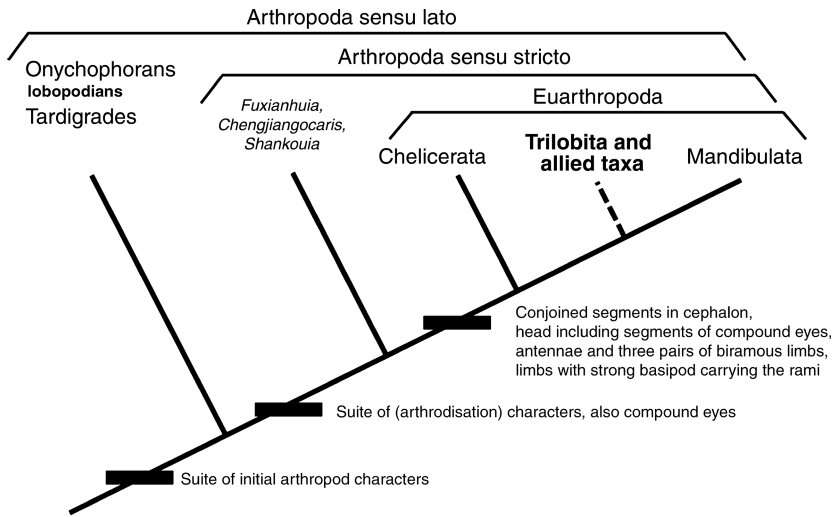


Figure 15.1 Phylogenetic relationships among major groups of living and fossils arthropod taxa (modified from Waloszek *et al.* 2005). We use the informal term ‘allied taxa’ to refer to a group of euarthropods with slim, long and feeler-like antennae and subsequent serial appendage pairs being biramous with lamellae-bearing exopods in cephalon and trunk, with a cephalic shield that covered basically three pairs of biramous limbs, and a trunk composed of largely homonomous exoskeletal segments commonly divided into an anterior region of freely articulating segments and a pygidium-like structure posteriorly.

TRILOBITE STRUCTURE AND DEVELOPMENT

This discussion of trilobite segmentation focuses on the development of the segmentation of the biomineralised exoskeleton. Although appendages are known in some 20 species (see Hughes 2003a, Table 1, for a review) and there was a direct correlation between appendage pairs and dorsal exoskeletal segments in the non-terminal regions of the anterior–posterior (A-P) axis, ontogenetic information about trilobite development is almost entirely restricted to the development of the biomineralised exoskeleton. This was divided into two principal regions along the A-P axis, the cephalon and the trunk (Figure 15.2). Within the cephalon exoskeletal segmentation was most evident in the axial region. The number of cephalic segments remained constant during the ontogenies of individual species, although in some cases adjacent segments differed markedly in shape. The number of segments within the cephalon (at least four) also appears to have been approximately constant throughout the Trilobita. It is not known whether these segments were specified simultaneously or sequentially. In

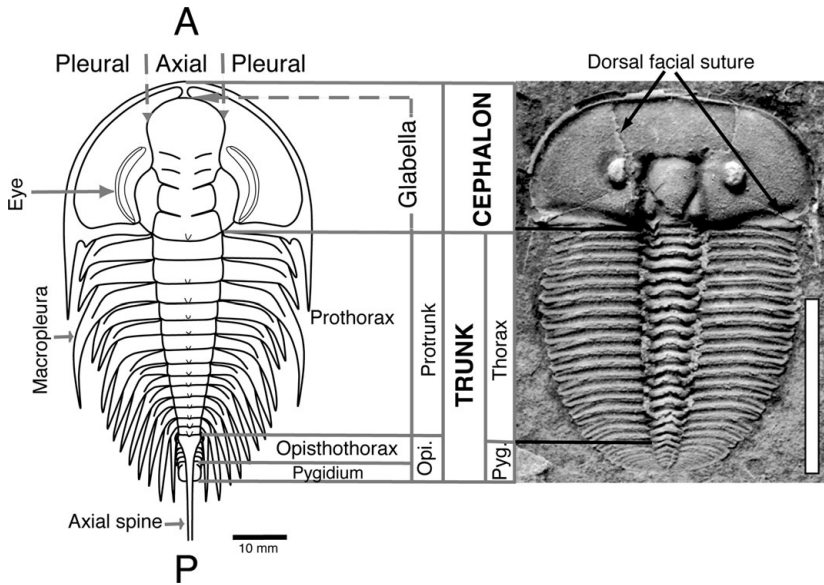


Figure 15.2 Basic dorsal morphology of two trilobites. A is anterior, P is posterior, Pyg. is the pygidium. Figure on the left, based on a generalised olenelloid trilobite, had a boundary between two distinct batches of segments located within the thorax, dividing the protrunk from the opisthotrunk. *Aulacopleura konincki*, on the right, displayed the homonomous trunk condition in which all segments shared a similar morphology.

striking contrast, the number of segments in the trunk region evidently varied both ontogenetically within species and phylogenetically among them. Trunk segmentation was expressed in both axial and pleural (lateral) regions, and displayed several different attributes whose variation was partially independent of one another. Such attributes include: (1) the number of trunk segments in the mature, segment invariant (epimorphic) phase of postembryonic development; (2) the number and development of functional articulations within the trunk region; (3) the form of trunk segments.

THE NUMBER AND GENERATION OF TRUNK SEGMENTS

The site at which new trunk segments were generated was a subterminal generative zone. This was located by studies of segments that were individualised from their first appearance, commonly by a unique axial or pleural spine (e.g. Stubblefield 1926, Chatterton 1994), which first appeared

adjacent to the posterior end of the trunk, just as in the great majority of those arthropods in which segment expression is sequential (including those classified as having 'short germ-band' embryonic development). The development of trilobite trunk segmentation is also comparable to that of many other (eu)arthropods in that new trunk segments appeared sequentially through a series of postembryonic instars, a pattern that is termed anamorphic development.

In all species of trilobite in which ontogeny is well known, anamorphic instars were succeeded by an ontogenetic phase during which moulting and size increase continued, but which was invariant in the number of segments expressed in the biomineralised exoskeleton. This biphasic accretive-invariant segmentation pattern seen in trilobites, some myriapods and some crustaceans is termed 'hemianamorphic' development (Enghoff *et al.* 1993). In trilobites, following the general usage of specialists on myriapod biology, the second, 'segment invariant' phase is known as the 'epimorphic' phase (Hughes 2003b, Hughes *et al.* 2006). Hemianamorphic development evidently characterised the vast majority of the over 15 000 trilobite species known. It is not clear whether those rare trilobites with over 100 trunk segments (Paterson and Edgecombe 2006) achieved an epimorphic phase, and it is possible that some trilobites continued to add segments throughout life. The range in mature trunk segment numbers among trilobites varied widely, from forms bearing fewer than 10 trunk segments to those with over 100. Such a range of variation was evident even amongst early Cambrian species.

The rate of production of segments during the anamorphic phase was variable both ontogenetically within species and phylogenetically among them, and phases in which successive instars maintained a stable number of segments intercalated within other phases of anamorphic segment production have been reported (McNamara *et al.* 2003). Nevertheless, the number of segments expressed between successive instars was generally one or two segments, not the much larger numbers seen between instars in some derived myriapods (Fusco 2005) and crustaceans (Walossek 1993). Such a pattern of regular and gradual segment generation greatly aids in the reconstruction of trilobite ontogenies which are based on sclerites derived from multiple individuals and gives the impression that trilobite growth was 'track-like' (Hughes and Chapman 1995), i.e. channelled along a trajectory of progressive, modest change. Nevertheless, more striking ontogenetic changes have been recognised between particular instars and have been labelled as 'metamorphosis' in trilobites (Evitt 1961, but see Hughes *et al.* 2006). There are also cases in which juveniles cannot be linked with any co-occurrent mature forms, perhaps suggesting morphological changes

too extreme to permit such association in the absence of the sequential instars of any individual (Chatterton and Speyer 1997).

ARTICULATIONS BETWEEN TRUNK SEGMENTS

In later ontogenetic stages, the trilobite trunk was divided into the thorax, an anterior set of segments each with a functioning joint along its entire anterior and posterior margins, and the pygidium, a posterior set of conjoined segments that did not functionally articulate with one another. The similarity of form in thoracic and pygidial segments partially reflected their common site of origin at the subterminal growth zone. An important aspect of trilobite development is that at first appearance all trunk segments were conjoined to segments immediately anterior to them. During early post-embryonic development all segments, whether part of the cephalon or trunk, were dorsally conjoined. The appearance of a functional joint between the rear of the cephalon and the anterior of the trunk marked the transition from the protaspid to the meraspid ontogenetic stages (Figure 15.3). At this stage the dorsal exoskeleton was a two-part, hinge-like structure made up of two units each comprising conjoined segments: the cephalon and the trunk. New segments accreted anamorphically near the rear of the trunk. New articulations between segments resulted in the progressive construction of the thorax, via the sequential release into it of trunk segments previously conjoined in the meraspid pygidium. Hence the construction of the trilobite thorax was a gradual and prolonged process with the thorax recognisable as a distinct region several instars after the segments that came to constitute it first appeared near the rear of the trunk.

Traditionally the trilobite pygidium has been considered homologous to the abdomen of other (eu)arthropods (Burmeister 1846, Cisne *et al.* 1980), but this pattern of the exchange of segments between the 'abdomen' and thorax is unlike that in almost all other (eu)arthropods (see below, and for distinction between limb-bearing thorax and limb-less abdomen, see Walossek and Müller 1998). All trilobites in which ontogenies are well known reached an instar in which segments ceased to be released into the thorax. Attainment of that state marked the transition from the meraspid stage to the holaspid stage. Like the anamorphic generation of trunk segments, the construction of the trilobite thorax was a gradual process, although it could depart from the regular release of one segment per instar. Cases in which more than one segment may have been released simultaneously, or two conjoined segments were released into the thorax

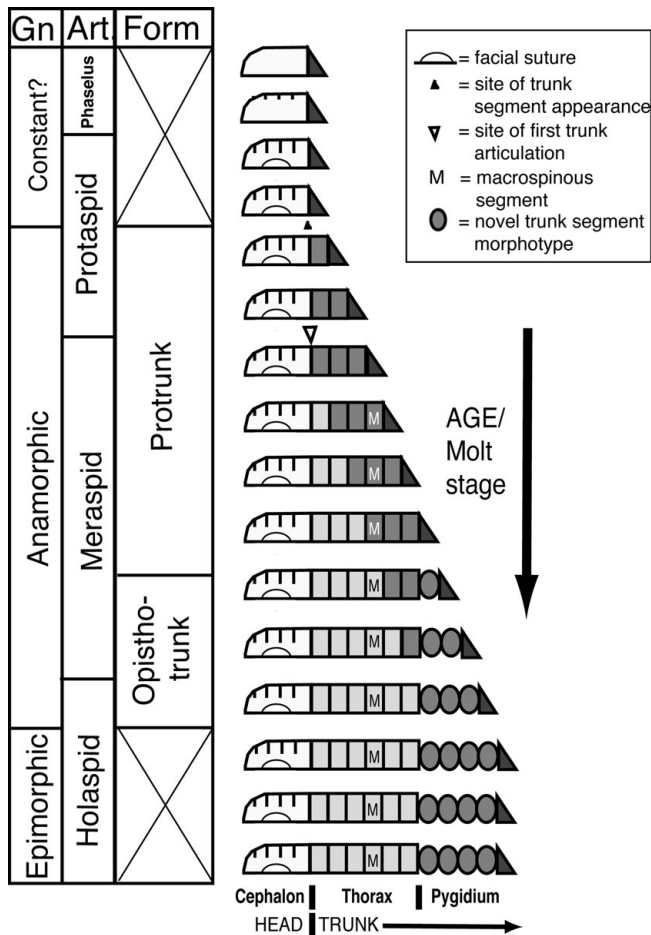


Figure 15.3 Generalised trilobite ontogeny showing the boundaries of ontogenetic stages based on three aspects of the development of segments: generation, articulation and morphology (see Hughes *et al.*, 2006, fig. 3). 'Gn' refers to stages based on segment generation and contains a poorly known initial stage that may have had a constant set of cephalic segments, the anamorphic phase during which new segments appeared in the trunk, and the epimorphic phase after which the segment number was constant despite continued moulting. 'Form' refers to the morphology of newly generated trunk segments that in some trilobites are divided into discrete batches of anterior (protrunk) and posterior (opisthotrunk) segments. 'Art' refers to developmental stages based on dorsal sclerite articulation pattern and includes the stages previously applied in studies of trilobite ontogeny. Site of the appearance of new trunk segments is shown for the first trunk segment only. Solid grey triangle is the terminal piece, darker grey segments are conjoined and part of the pygidium. Lighter grey segments are thoracic. Individualised segments, such as those that bore unusually large axial or pleural spines (i.e. a 'macrospinous' condition), retained the same position relative to the cephalic margin following first appearance, indicating that the site of appearance of new segments was subterminal, and that the boundary between articulating and conjoined segments migrated posteriorly during the meraspid phase (Stubblefield 1926). The functional significance of this segment was considered by Hughes (2003a).

together, are known but are rare. Other cases in which there may have been two or more instars for every segment released are also known but are uncommon.

THE FORM OF TRUNK SEGMENTS

Recognition of distinct body regions in arthropods is generally based on the morphology of segments, rather than their pattern of articulation. What little is known of trilobite trunk appendages does not indicate major differences in appendage morphology along the trunk: changes, where they do occur, tend to be mainly size differences, or relatively minor morphological modifications (Hughes 2003a). Nevertheless, the trilobite trunk exoskeleton did show marked differences in segment morphology in some cases (Hughes 2005). Examples include individual segments marked by unique features such as axial or pleural spines, or the grouping of segments into batches, each of which had a broadly uniform segment morphology that was distinct from that of other batches. The later case is more comparable to the traditional tagmatic boundaries recognised along the anterior–posterior axis of other arthropods. Indeed, trilobites present an interesting case in which the evolution of a morphologically distinct posterior tagma apparently occurred independently several times within the group. In trilobites in which all trunk segments, whether thoracic or pygidial, are homonomous arguments for recognising the holaspide pygidium as a distinct tagma are weak (Minelli *et al.* 2003). However, where the trunk is heteronomous, and divided into batches of distinct segments, it is more reasonable to consider the trunk to comprise two tagmata, particularly where the boundary in segment morphotype coincides with the mature thoracic/pygidial boundary (Hughes 2003a,b, 2005).

The freedom to vary segment morphology within the trunk was strongly constrained in the trilobite thorax because in that region segments were required to articulate with one another. This constraint also apparently applied to the segments in the juvenile trunk that would eventually become thoracic: ultimately they had to achieve a form that permitted articulation. Trilobite trunk segments did not apparently change radically in shape as they were released from the pygidium into the trunk. This is evident in the early ontogenies of those trilobites in which segments that would ultimately become thoracic and those ultimately part of the mature pygidium are differentiated within the meraspide pygidium (Chatterton 1971, Hughes 2003a). Interestingly, peripheral features, such as marginal spines, seem to vary ontogenetically independently of their ultimate identity

as thoracic or pygidial segments. However, variation in axial features, such as the courses of furrows marking segment boundaries, and in the relationship between axial and pleural segmentation, could be markedly different in the two regions, with tight covariation in these features in those segments that would become thoracic, and more independent variation in those that would remain pygidial throughout life.

DIVERSITY IN THE SEGMENTATION PROCESS
AMONG TRILOBITES

Each of the three attributes of trunk segmentation discussed above reached a mature phase after which, although growth via moulting continued, each state remained invariant (Figure 15.3) (Hughes *et al.* 2006). In the case of segment generation this was the onset of a stable number of segments (epimorphic phase); for articulation, it was the attainment of a constant number of thoracic segments (holaspid stage); and with respect to segment form, it was the onset of production of the distinct set of posterior trunk segments (the opisthotrunk) in those trilobites with a heteronomous, two-batch trunk (Figures 15.2 and 15.3). Given the rather regular and progressive development of the trunk segmentation, we might expect that transitions to the mature phases of each of these attributes would be strongly coordinated. In some cases this was so, and particularly in those trilobites in which the mature thorax and pygidium represent distinctly different structures, each presumably with a distinctly different function (Figure 15.4). Nevertheless, trilobites showed a surprising diversity in the relative developmental timing of the transitions to the mature phases of these attributes. Cases in which transition to a stable number of segments coincided with onset of the holaspid phase are termed *synarthromeric*, those in which segment generation was completed prior to the termination of trunk articulation are *proteromeric*, and those in which articulation was completed prior to onset of a stable number of segments are *protarthrous* (Hughes *et al.* 2006).

A review of such cases shows a variety of patterns (Hughes *et al.* 2006). For example, the numbers of trunk segments in the Silurian aulacopleurid trilobite *Aulacopleura konincki* varied, apparently intraspecifically, over a range of five segments, but each of the five morphs apparently showed synarthromeric growth (Fusco *et al.* 2004). On the other hand, two putative intraspecific morphs of the early Cambrian eodiscid trilobite *Neocobboldia chinlinica* ultimately apparently achieved the same total number of trunk segments. A suggested explanation for this is that one may have developed

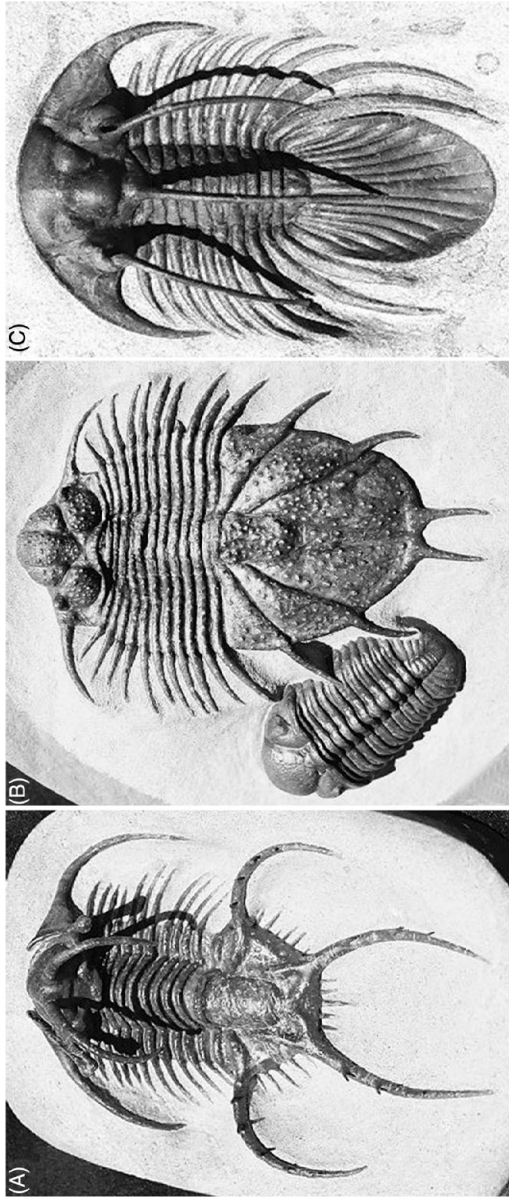


Figure 15.4 The 'two-batch' heteronomous trunk condition in which the mature thoracic and pygidial segments had very different morphologies occurred in a variety of major trilobite taxa, as illustrated by the large specimens in each of the three figures. All specimens are from the AM Limestone of the Devonian of Morocco. A, *Ceratarges* sp. (Order Odontopleurida), length 8.4 cm. B, The larger specimen is the lichiid trilobite *Acanthopyge* (*Acanthopyge*) cf. *haueri* (Order Odontopleurida), length 8.4 cm. The smaller trilobite (Order Phacopida, species undescribed) shows the homonomous trunk condition. C, *Kolibhapeltis* sp. (Order Corynexochida), length about 5 cm. Note that the boundary in segment morphology coincides with the mature thoracic–pygidial boundary in each of these cases. Modified from Hughes (2007).

synarthromerically, the other proteromerically (Hughes *et al.* 2006). A comprehensive review of trunk trilobite development has yet to be attempted, but it appears that variation in developmental mode commonly occurred at low taxonomic levels, although some taxa may be characterized by a particular mode. One case is known in which the epimorphic stage was achieved prior to the onset of trunk articulation: the late Cambrian *Schmalenseeia fusilis* never developed joints in the trunk and thus remained a permanent protaspid (Peng *et al.* 2005, Hughes *et al.* 2006).

The principal value of the developmental record of trilobites is the ability to explore how these different aspects of the segmentation process map onto the phylogeny of the group, and to consider the evolutionary trade-offs between the flexibility to vary aspects of the trunk independently, and the advantages of increasingly integrated covariation. Key to exploring this is the delay during development between the appearance of segments and the attainment of their final functional role in the thorax. Thorough exploration of the developmental record of trilobites will require a combination of careful phylogenetic and functional analyses and detailed individual studies of growth mechanics, and firm conclusions are not yet warranted. Nevertheless, those trilobites that varied trunk segment numbers at low taxonomic levels do appear to be those in which the trunk consisted of homonomous segments, while those with a highly tagmatized trunk were invariant in segment numbers (Hughes 2005). The fact that the tendency toward a more highly integrated, segment invariant trunk occurred independently among several trilobite taxa (and possibly also some allied taxa often referred to as 'trilobitomorpha') offers promise for exploring the functional context of such a transition.

DEVELOPMENTAL PATTERNS AMONG 'ORSTEN' ARTHROPODS

Several 'Orsten' (eu)arthropods are preserved with multiple developmental stages, the ontogeny of the eucrustacean *Rehbachella kinnekullensis* being by far the best known (Walossek 1993) (Figure 15.5B). The earliest larva of this possible stem branchiopod was a true nauplius, a short-headed larva that is autapomorphic for Eucrustacea. This larva bore only three pairs of appendages, one pair of uniramous antennulae and two pairs of biramous limbs, the so-called antenna and mandible. Altogether, four 'naupliar' and 26 'post-naupliar' stages have been distinguished in *R. kinnekullensis*. During this phase, the trunk segments were added progressively at the rate of one segment for every two moults. This sequence led to a trunk with 13 limb-bearing segments, while the posteriormost trunk limbs

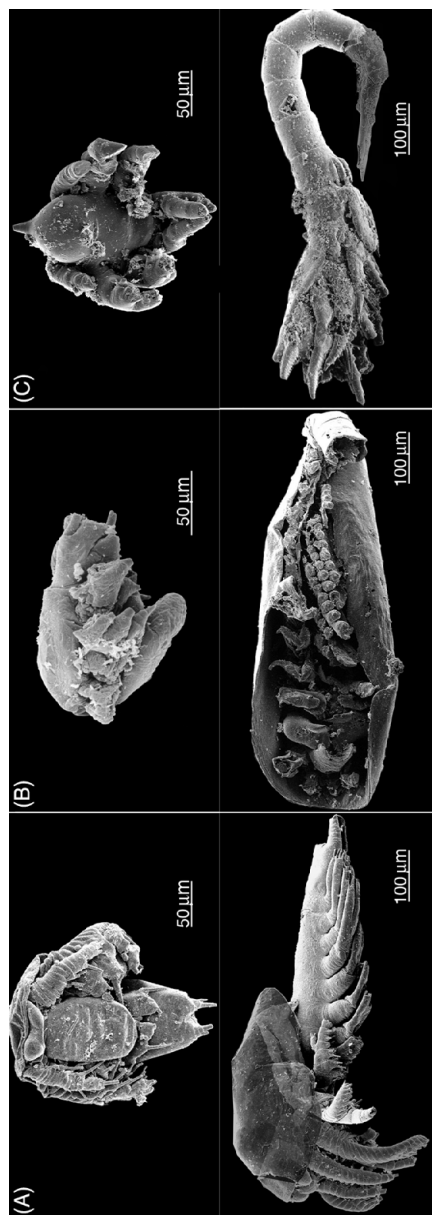


Figure 15.5 Three crustaceans from the 'Orsten' fauna. Top row shows early larvae, bottom row latest known stages. A, *Bredocaris admirabilis* (lower picture composed of different specimens). B, *Rebbachiella kinnekullensis*. C, *Martinsonia elongata*. All specimens illustrate the exceptional three-dimensional preservation.

remained of larval shape and the hind body remained unsegmented (Walossek 1993).

The extant brine shrimp *Artemia salina* adds one trunk segment per moult, and after that phase the abdominal segments are added successively, while the appendages are modified into adult shape. Comparison with *Rebbachiella* indicates that even the latest stages of the fossil (size- and developmentally correlated with that of the latest larva of the first phase of *Artemia*) were still immature. Likewise, *Rebbachiella* would have required additional moults to develop the segmentation of the abdomen. Isolated limbs and body fragments also hint at older developmental stages, some being twice the size of the largest complete specimen. The 30-stage sequence of *Rebbachiella* is, therefore, far from being complete.

The strictly anamorphic developmental pattern exhibited by *Rebbachiella* has been used as a reference for the developmental patterns of other Crustacea (Figure 15.6A, B), serving to highlight deviations from such a regular system. It can even enable us to predict the size of a larva of a taxon based on its segmental stage via the correlation between the number of clearly expressed segments and overall size. This applies between moults that show large developmental 'jumps' between stages, with addition of several segments in one step (Figure 15.6C for penaeid decapod malacostracans).

As compared to the regular developmental pattern in *R. kinnekullensis*, the 'Orsten' eucrustacean, *Bredocaris admirabilis* (Figure 15.5A), exhibited a derived mode of development. The first larva was already a metanauplius having a vestigial maxillula in the form of a bifid lobe and corresponding to a L₃ *Rebbachiella* larva. In the four next stages, the segments of the second maxillae and the thorax were added anamorphically, but were not separated on the undivided hind body and can be recognised only through five ventral and progressively appearing limb buds, which remain as such during the entire phase (in a strict anamorphic sequence, limbs develop progressively and also add setae). With the next known stage, presumably a single moult further, the now fully developed trunk bore the developed maxilla and seven thoracopods. Hence *B. admirabilis* deviated from the scheme of development seen in *R. kinnekullensis*, still adding segments at each moult, but delaying trunk and limb development until a final step toward another instar, which might have been either a juvenile or the adult. This specific ontogenetic pattern is represented by extant barnacles, identifying *B. admirabilis* as a stem-lineage member of the taxon Thecostraca (cf. characterisation by Müller and Walossek 1988), which embraces cirripeds and a set of small-sized crustaceans such as ascothoracids and facetotectans (Høeg and Kolbasov 2002).



Figure 15.6 Schematic diagram of the developmental stages of various fossil and recent crustaceans. Numbers denote successive stages: 1–4 for early larvae, Ts 1 to n are for stages with developed postcephalic segments. Bars indicate stages expressed in the ontogenies of each taxon. Ad: adult, Ts: trunk segment. A, *Rebbachiella kinnekullensis*. B, *Artemia salina*. C, Example of a penaeid decapod malacostracan. *Rebbachiella* shows the most strictly anamorphic pattern. Deviation from the pattern is exemplified by large ‘jumps’ (gaps comprising missing stages) in the development of penaeid decapod malacostracans (cf. Wålössek 1993).

'Orsten' larval evidence is also available for a few non-eucrustacean taxa, including phosphatocopines, the sister taxon of Eucrustacea, derivatives of the stem lineage of Labrophora = Eucrustacea and Phosphatocopina, taxa like *Agnostus pisiformis* and a stem representative of the sea spiders, Pycnogonida (Müller and Walossek 1986a, Waloszek and Dunlop 2002). Investigations of the developmental patterns of more derivatives of the stem crustaceans are still in progress, but we can state that all of them started their ontogenies with an early larva with antennae and three pairs of functional head limbs, a condition named the 'head larva' by Walossek and Müller (1990, 1998) that characterised the ground pattern of the Euarthropoda.

Martinssonina elongata (Figure 15.5C) is the only species of the labrophoran stem-lineage derivatives with a larval series described in detail although this series is incomplete (Müller and Walossek 1986b). The first three stages were all head larvae, bearing three post-antennular biramous limbs and not adding further segments but changing proportions and developing a mouth and anus (they hatched as lecithotrophic larvae). The next known stage already had a head with an additional pair of limbs, a trunk with five ring-shaped segments and an elongate caudal end bearing the anus ventral-subterminally. Further addition of segments in the trunk region did not increase the number of limbs, nor change their developmental status – at least in the next stage, which bore seven trunk portions plus the caudal end.

The ontogeny of *Agnostus pisiformis* is also well known from the 'Orsten' (Müller and Walossek 1987). The phylogenetic relationships of *A. pisiformis* and the other agnostids traditionally assigned to trilobites are still controversial (Walossek and Müller 1990, Stein *et al.* 2005; but see Cotton and Fortey 2005). Agnostids lack several trilobite autapomorphies, such as the dorsal location of their compound eyes (*A. pisiformis* may have had remains of ventral compound eyes in the form of small soft humps in front of the hypostome; Müller and Walossek 1987, their Plate 11), or a multi-annulated, flagellum-like and possibly sensorial antenna (antennula in crustaceans) (*A. pisiformis* bore a leg-like antenna/antennula for food gathering; Müller and Walossek 1987). Furthermore, *A. pisiformis* had two pairs of post-antennular/antennular limbs that were specialised for swimming (Stein *et al.* 2005), a feature known otherwise only in Crustacea. Yet, the dorsal shield features, such as the glabellar lobes, may rather link agnostids with trilobites, and agnostids showed a developmental pattern that is similar to trilobites – the progressive release of trunk segments (Figure 15.7; see paragraphs above).

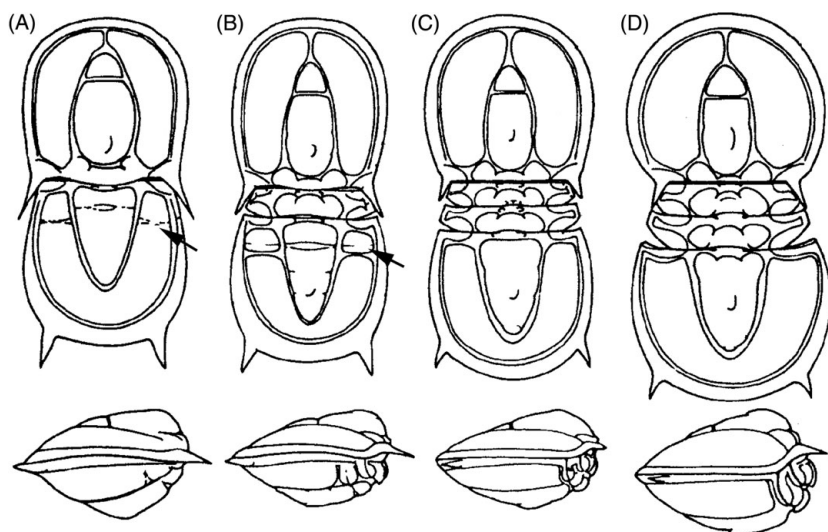


Figure 15.7 Developmental stages of *Agnostus pisiformis*. Top row: dorsal, outstretched view (probably not living position), bottom row: enrolled lateral view. A, First meraspis stage 0.327–0.43 mm; B, second meraspis stage 0.52–0.82 mm; C, first holaspis stage 0.9 mm; D, late holaspis stage *c.* 2 mm (modified from Müller and Walossek 1987). Arrows indicate future thoracic segments before being released. This developmental pattern is similar to the one known from trilobites.

TRILOBITE AND 'ORSTEN' ARTHROPOD DEVELOPMENT COMPARED, AND THAT OF OTHER ARTHROPODS

The records of trilobite and 'Orsten' arthropod ontogenies contrast markedly in preservational style. The value of phylogenetic and temporal richness of the record of trilobite ontogeny is tempered by its limitation to exoskeletal information alone. 'Orsten' preservation is incomparably richer in morphological detail but, although occurring in several sites worldwide, is currently restricted to a handful of taxa. Given these differences, the fact that both data sources show broadly consistent patterns is likely to be of some significance. Although the appendages of unequivocal juvenile trilobites are unknown, those of the cephalon of mature trilobites, which bore a pair of uniramous antennae followed by three pairs of biramous appendages (Hughes 2003a) support the idea that the 'head larva' was the basal euarthropod condition. Furthermore, Waloszek's hypothesis (Walossek 1993) that crustaceans, as exemplified by *Rebbachiella*, basically show an extended phase of anamorphic development, with morphological change at each moult limited

in scope, is consistent with the pattern seen in the development of the trilobite exoskeleton, in which change was generally progressive, track-like and incremental (Hughes *et al.* 2006). The degree of allometric shape change between instars was comparatively modest and generally gradual, especially at later phases of ontogeny. Even when so-called 'metamorphoses' occurred in trilobites they were not such radical reorganisations of the body as seen in the development of some derived arthropods. It is notable that hemianamorphic development is also basal condition in myriapods (Fusco 2005), raising the possibility that gradual, anamorphic development characterised basal mandibulates and their closest relatives (Hughes *et al.* 2006).

Interpretation of fossil ontogeny in functional terms is often difficult, but the fact that each trilobite instar had to function effectively in the external environment (as opposed to those arthropods that attained the mature form within the egg) may have placed a functional constraint on the ability to achieve dramatic morphological transitions between instars (Hughes 2003a). However, other free-living arthropods have been able to modify their life cycles (and accompanying morphologies) radically and examples of this kind of development were already present among the 'Orsten' arthropods discussed above, so this cannot account completely for the relative conservatism of trilobite ontogeny. Nevertheless, gradual, anamorphic development apparently occurred widely among early euarthropods and so this pattern need not require a trilobite-specific explanation. Perhaps food sources in the early Palaeozoic marine ecosystems were not partitioned into discrete, heterogeneous size classes, and this permitted early consumers to maintain a similar form, and presumably also similar feeding mode, across a wide range of absolute size.

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REFERENCES

- Burmeister, H. 1846. *The Organization of Trilobites*. London: The Ray Society.
Chatterton, B. D. E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica, Abteilung A* 137, 1-108.

- Chatterton, B. D. E. 1994. Ordovician proetide trilobite *Dimeropyge*, with a new species from northwestern Canada. *Journal of Paleontology* **68**, 541–556.
- Chatterton, B. D. E. & Speyer, S. E. 1997. Ontogeny. In H. B. Whittington (ed.) *Treatise on Invertebrate Paleontology*, Part O, *Arthropoda 1. Trilobita, revised*. Boulder, CO: The Geological Society of America and Lawrence, KS: The University of Kansas, pp. 173–247.
- Cisne, J. L., Chandlee, G. O., Rabe, B. D. & Cohen, J. A. 1980. Geographic variation and episodic evolution in an Ordovician trilobite. *Science* **209**, 925–927.
- Cotton, T. J. & Fortey, R. A. 2005. Comparative morphology and relationships of the Agnostida. In S. Koenemann & R. A. Jenner (eds.) *Crustacea and Arthropod Phylogeny. Crustacean Issues 16*, Boca Raton, Florida: CRC Press, pp. 95–136.
- Enghoff, H., Dohle, W. & Blower, J. G. 1993. Anamorphosis in millipedes (Diplopoda). The present state of knowledge and phylogenetic considerations. *Zoological Journal of the Linnean Society* **109**, 103–234.
- Evitt, W. R. 1961. Early ontogeny in the trilobite family Asaphidae. *Journal of Paleontology* **35**, 986–995.
- Fusco, G. 2005. Trunk segment numbers and sequential segmentation in myriapods. *Evolution & Development* **7**, 608–617.
- Fusco, G., Hughes, N. C., Webster, M. & Minelli, A. 2004. Exploring developmental modes in a fossil arthropod: growth and trunk segmentation of the trilobite *Aulacopleura konincki*. *American Naturalist* **163**, 167–183.
- Høeg J. T. & Kolbasov, G. A. 2002. Lattice organs in Y-cyprids of the Facetotecta and their significance in the phylogeny of the Crustacea Thecostraca. *Acta Zoologica* **83**, 67–79.
- Hughes, N. C. 2003a. Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative and Comparative Biology* **41**, 185–206.
- Hughes, N. C. 2003b. Trilobite body patterning and the evolution of arthropod tagmosis. *BioEssays* **25**, 386–395.
- Hughes, N. C. 2005. Trilobite construction: building a bridge across the micro and macroevolutionary divide. In D. E. G. Briggs (ed.) *Evolving Form and Function: Fossils and Development*. New Haven: Peabody Museum of Natural History, Yale University, pp. 138–158.
- Hughes, N. C. 2007 The evolution of trilobite body patterning. *Annual Reviews of Earth and Planetary Sciences* **35**, 401–434.
- Hughes, N. C. & Chapman, R. E. 1995. Growth and variation in the Silurian proetide trilobite *Aulacopleura konincki* and its implications for trilobite palaeobiology. *Lethaia* **28**, 333–353.
- Hughes, N. C., Minelli, A. & Fusco, G. 2006. The ontogeny of trilobite segmentation: a comparative approach. *Paleobiology* **32**, 602–627.
- Mass, A. & Waloszek, D. 2005. Phosphatocopina – ostracode-like sister group of Eucrustacea. *Hydrobiologia*, **538**, 139–152.
- McNamara, K. J., Yu, F. & Zhou, Z. 2003. Ontogeny and heterochrony in the oryctocephalid trilobite *Arthricocephalus* from the Early Cambrian of China. *Special Papers in Palaeontology* **70**, 103–126.

- Minelli, A., Fusco, G. & Hughes, N. C. 2003. Tagmata and segment specification in trilobites. *Special Papers in Palaeontology* **70**, 31–43.
- Müller, K. J. 1985. Exceptional preservation in calcareous nodules. *Philosophical Transactions of the Royal Society of London B* **311**, 67–73.
- Müller, K. J. & Walossek, D. 1986a. Arthropod larvae from the Upper Cambrian of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **77**, 157–179.
- Müller, K. J. & Walossek, D. 1986b. *Martinssonina elongata* gen. et. sp. n., a crustacean-like euarthropod from the Upper Cambrian 'Orsten' of Sweden. *Zoologica Scripta* **15**, 73–92.
- Müller, K. J. & Walossek, D. 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils and Strata* **19**, 1–124.
- Müller, K. J. & Walossek, D. 1988. External morphology and larval development of the Upper Cambrian maxillopod *Bredocaris admirabilis*. *Fossils and Strata* **23**, 1–70.
- Paterson, J. R. & Edgecombe, G. D. 2006. The Early Cambrian trilobite family Emuellidae Pocock, 1970: Systematic position and revision of Australian species. *Journal of Paleontology* **80**, 496–513.
- Peng, S., Babcock, L. E. & Lin, H. 2005. *Polymerid Trilobites From the Cambrian of Northwestern Hunan, China*, Vol. 2. *Ptychopariida, Eodiscida, and Undetermined Forms*. Beijing: Science Press.
- Stein, M., Waloszek, D. & Maas, A. 2005. *Oelandocaris oelandica* and the stem lineage of Crustacea. In S. Koenemann & R. A. Jenner (eds.) *Crustacea and Arthropod Phylogeny, Crustacean Issues 16*, Boca Raton, Florida: CRC Press, pp. 55–71.
- Stubblefield, C. J. 1926. Notes on the development of a trilobite, *Shumardia pusilla* (Sars). *Zoological Journal of the Linnean Society of London* **35**, 345–372.
- Walossek, D. 1993. The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea. *Fossils and Strata* **32**, 1–202.
- Walossek, D. & Müller, K. J. 1990. Upper Cambrian stem-lineage crustaceans and their bearing on the monophyletic origin of Crustacea and the position of *Agnostus*. *Lethaia* **23**, 409–27.
- Walossek, D. & Müller, K. J. 1998. Cambrian 'Orste'-type arthropods and the phylogeny of Crustacea. In R. R. Fortey & R. Thomas (eds.) *Arthropod Relationships (Systematics Association Special Volume 55)*. London: Chapman & Hall, pp. 139–153.
- Waloszek, D., Chen, J., Maas, A. & Wang, X. 2005. Early Cambrian arthropods – new insights into arthropod head and structural evolution. *Arthropod Structure & Development* **34**, 189–205.
- Waloszek, D. & Dunlop, J. A. 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian 'Orsten' of Sweden, and the phylogenetic position of pycnogonids. *Palaeontology* **45**, 421–446.
- Waloszek, D. & Maas, A. 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. *Evolution & Development* **7**, 515–527.