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Patterns in Palaeontology: The development of trilobites

by [Lukáš Laibl](#)^{*1}

Introduction:

[Trilobites](#) are an iconic group of ancient animals, with a fossil record that dates back more than 500 million years and consists of some 17,000 species. These extinct [arthropods](#) are characterized by a hard, mineralized exoskeleton, which greatly enhances their chances of being preserved as fossils. The exoskeleton is thought to have been mineralised soon after they hatched from eggs, and so we can find various growth stages of trilobites in the fossil record, including individuals less than half a millimetre long. That makes it possible to study the entire post-embryonic development (that is, the development after they hatch from the egg) of numerous species. This is important because [work on the development of ancient organisms](#) provides data crucial for our understanding of their palaeobiogeography, evolution and relationships with other organisms.

The first description of trilobite development was published more than 160 years ago by the French palaeontologist [Joachim Barrande](#), in the first volume of his great work, *Système Silurien du Centre de la Bohême* (Silurian system of central Bohemia), published in 1852 (Fig. 1). Since then, many palaeontologists have studied the development of trilobites, and today post-embryonic development has been characterized for hundreds of species from all over the world.

Traditionally, the post-embryonic development of trilobites is divided into three successive periods – the protaspid, meraspid and holaspid period (Fig. 2). The protaspid period is made up of the earliest mineralized post-embryonic stages (but see Box 1), during which the [cephalon](#), or head shield, and [trunk](#) were joined as one piece. The meraspid period began when the first joint between the cephalon and the trunk developed. During the meraspid period, new segments were progressively released from the front edge of the [pygidium](#), or tail shield, into the thorax. Finally, in the holaspid period, the organism had the complete number of segments in its thorax that is characteristic of its species. Trilobites, however, continued to increase in size even during the holaspid period.

Box 1: Phaselus

In 1978, the palaeontologists Richard Fortey and Samuel Morris described tiny [sclerites](#) preserved in the mineral apatite that were associated with early developmental stages of trilobites. These sclerites are oval, about 0.2 mm long and convex. Fortey and Morris named these structures phaselus and suggested that they represent a calcified pre-protaspid stage of trilobites, comparable to the earliest larval stages of [crustaceans](#). Since their initial discovery, these phaselus larvae have been reported from various localities. However, several authors have questioned whether phaselus stages are actually trilobites, mainly because the structures that characterize them are not unique to trilobites. The debate about the nature of the phaselus persists to this day.

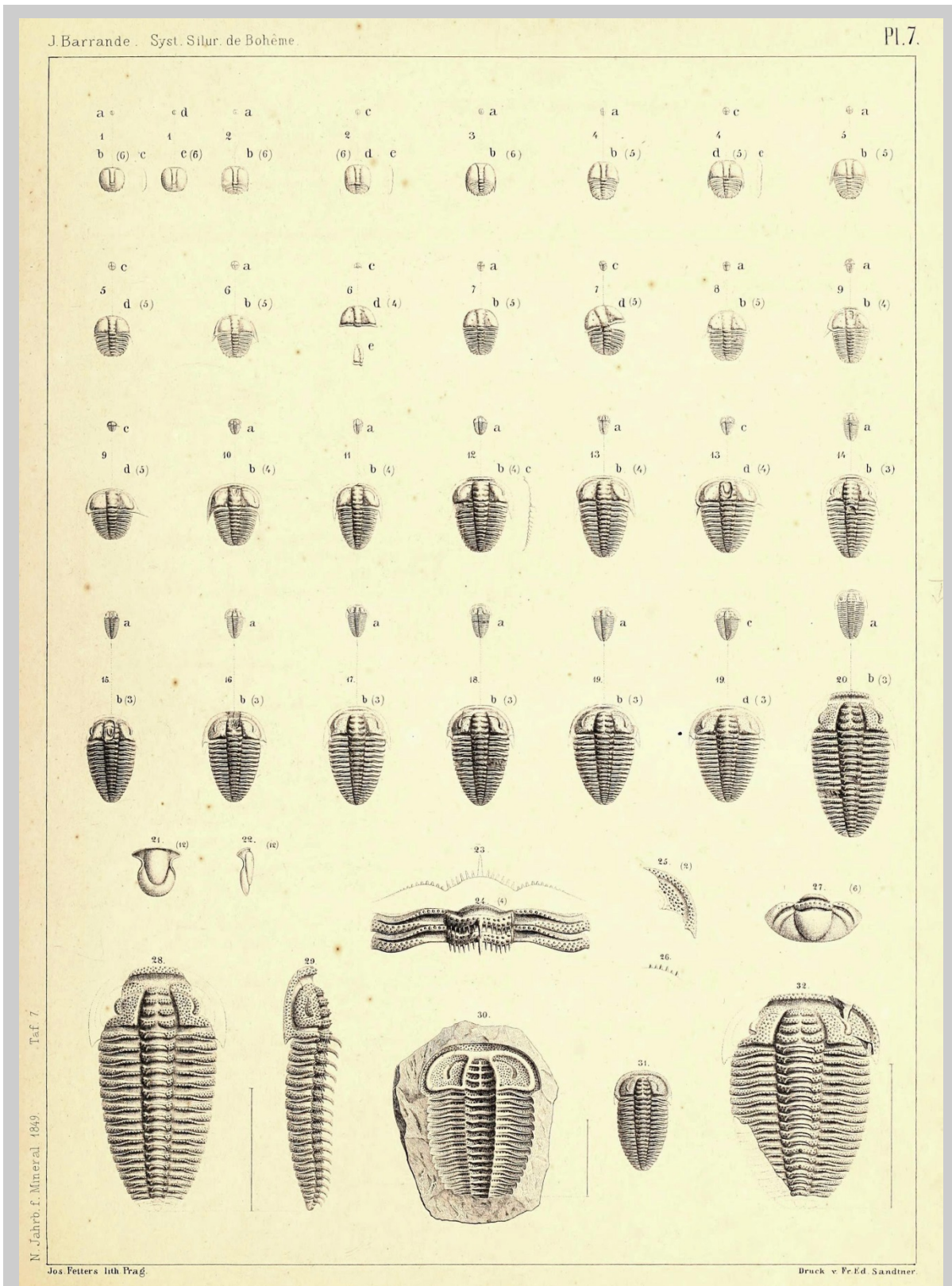
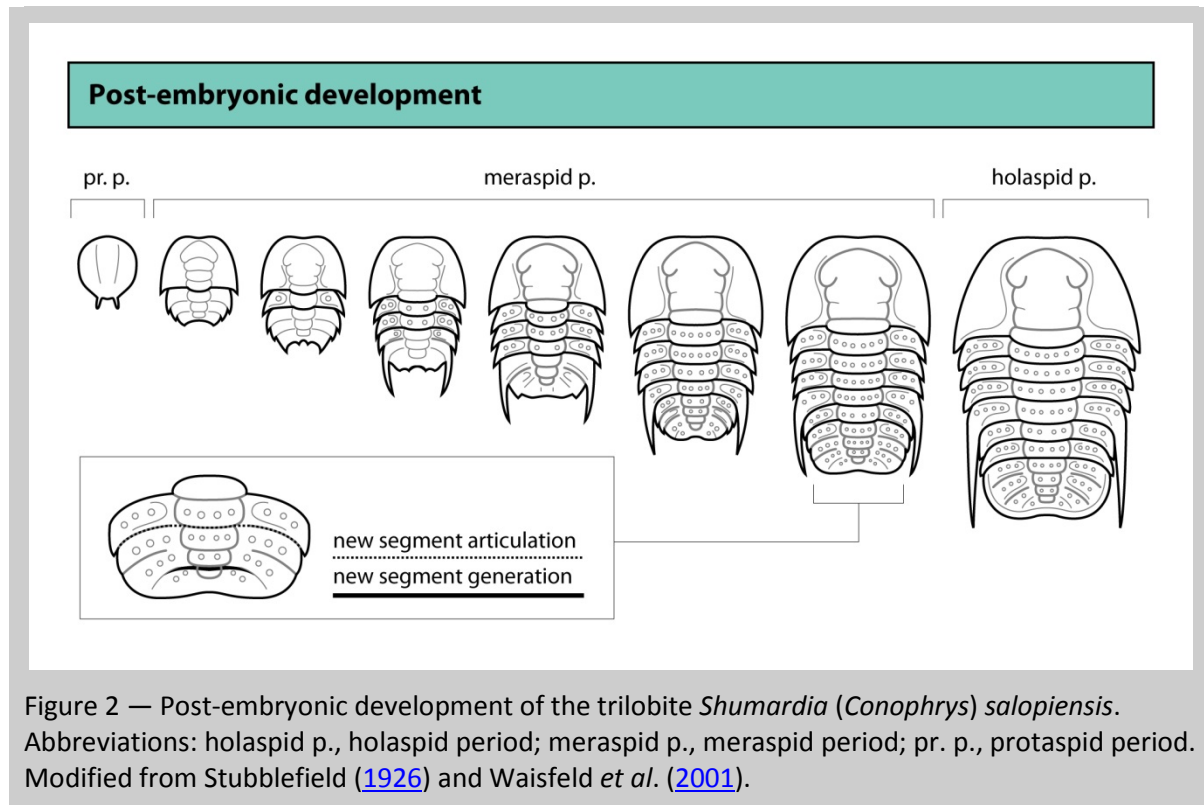


Figure 1 — Plate from Joachim Barrande's first volume of *Système Silurien du Centre de la Bohême* showing the post-embryonic development of the trilobite *Sao hirsuta* (compare with Fig. 6F–H). Source: Barrande ([1852](#)).



How did trilobites grow?

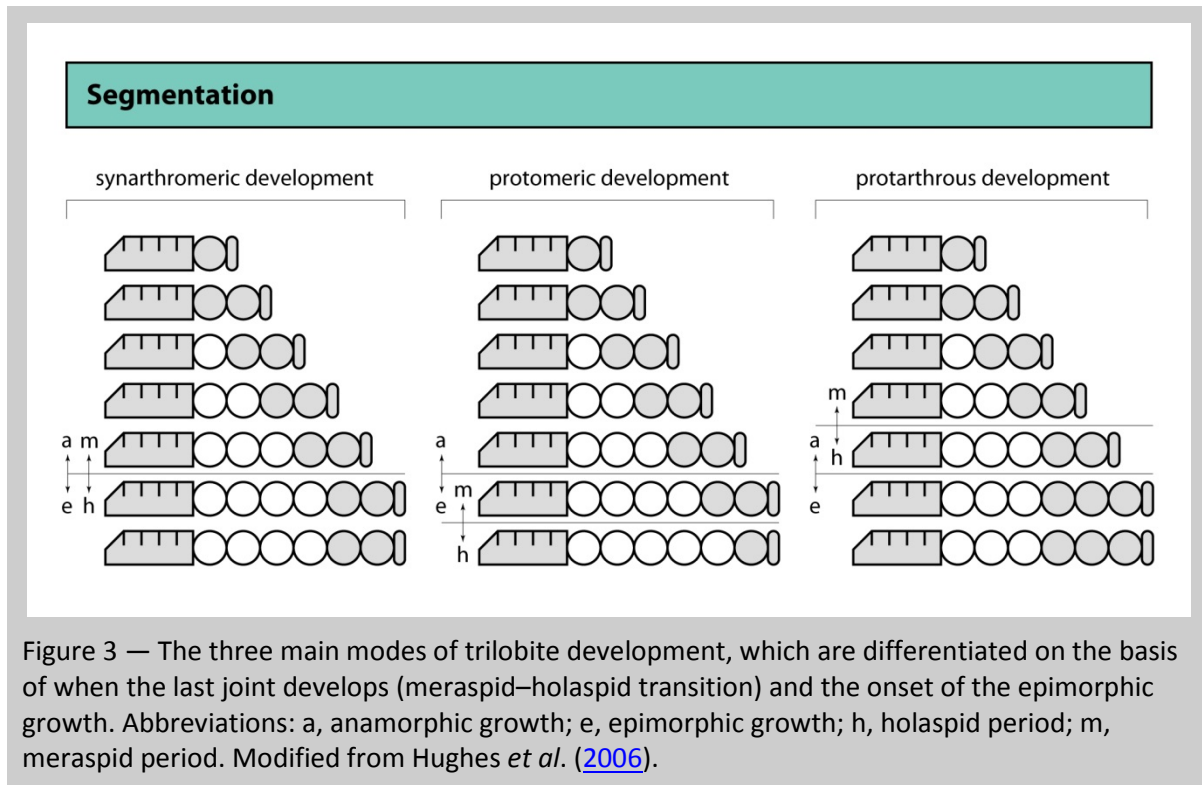
The trilobite exoskeleton, like that of other [ecdysozoans](#) (all animals that shed their exoskeleton, including arthropods), grew in stages through a series of [moulting events](#). The amount of growth between individual moults of any given species was more or less constant during development. Only in the case of radical metamorphosis (see below) was the growth increment slightly higher than in the rest of the development. The growth increments in trilobites are similar to those of living arthropods.

The most striking pattern during the early post-embryonic development of all trilobites is the sequential addition of segments behind the cephalon. This addition (called anamorphic growth) occurred during early development. Later in the development, the production of new segments halted, but trilobites continued to increase in size (epimorphic growth). This type of development, where anamorphic growth is followed by epimorphic growth, is called hemianamorphic development and it is also seen in modern millipedes, sea spiders and some centipedes and crustaceans.

During anamorphic growth, new segments of the trunk originated from the growth zone near the rear part of the body. This is especially well documented in trilobites with segments that are [morphologically](#) distinct from other parts of the body, meaning that they are different in appearance or shape. For example, the Ordovician trilobite *Shumardia (Conophrys) salopiensis* bears long spines on the fourth segment behind the head (Fig. 2). Once these spines developed, they remained on the fourth segment throughout ontogeny.

From the development of *S. (C.) salopiensis* it is also evident that newly generated segments were originally fused together and formed a structure called the meraspid or transitory pygidium (Fig. 2). On the front end of the meraspid pygidium, the segments were progressively released into the thorax. Functionally, the meraspid pygidium resembled a conveyor belt of segments that were generated near

its back end and released in its front end. By comparing when the last segment was released with when epimorphic growth begins, we can recognize three modes of trilobite development: protomeric, synarthromeric and protarthrous (Fig. 3).

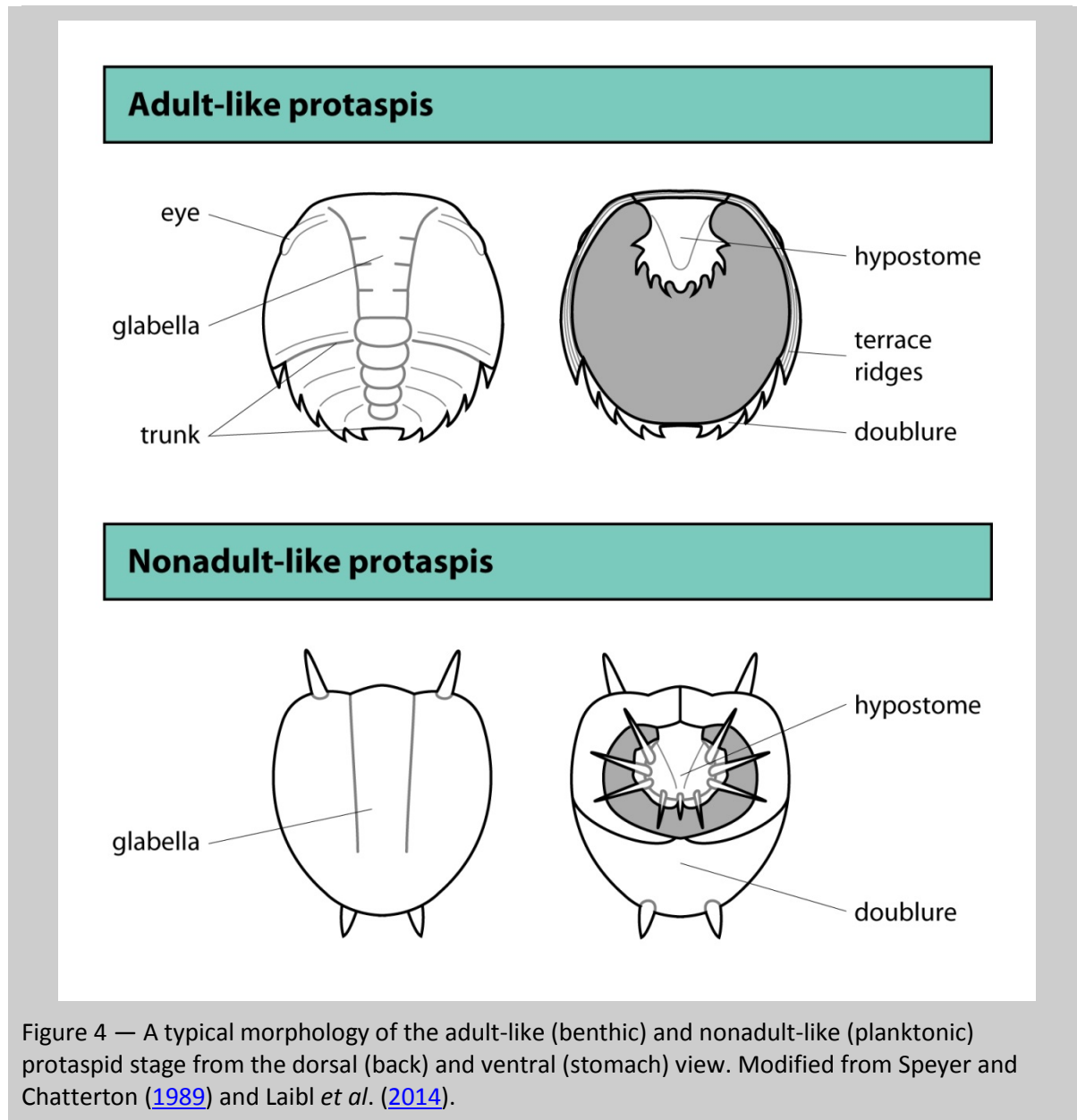


Bulbous and saucer-shaped larvae:

With some exceptions, most adult trilobites were [benthic](#) scavengers — hunting the sea floor for scraps — or deposit feeders. But what about the tiny protaspides, the youngest trilobites? Originally, trilobite workers considered all early developmental stages of trilobites to be [planktonic](#), usually just because they were so small. A detailed study about the modes of life of early stages of developing trilobites was published by Brian Chatterton and Stephen Speyer in 1989. They established two general types of trilobite protaspides, based on the overall similarity to later developmental stages: adult-like and non-adult-like protaspides (Fig. 4).

Adult-like protaspides look a bit like adult (holaspid) trilobites. They are flattened from top to bottom, with a flat stomach (ventral) surface (shaped like an inverted saucer) and sharply folded [doublure](#), which often bears structures called terrace ridges. On the ventral side of the exoskeleton, they have a large opening (part of the exoskeleton) and a comparatively small [hypostome](#), a section of exoskeleton near the trilobite mouth. These protaspides can have numerous spines along their edges, and these generally stick out horizontally.

Non-adult-like protaspides are, by contrast, usually bulbous or globular and do not resemble adult trilobites at all. The ventral opening is often small and is mostly covered by a comparatively large hypostome with needle-like spines forming a structure similar to a ‘crown of thorns’. Unlike adult-like forms, the non-adult-like protaspides can have spines projecting in all three dimensions. The surface of



the exoskeleton of non-adult-like protaspides can bear structures such as pits, polygonal ridges or tiny ridges that resemble fingerprints.

It is believed that non-adult-like protaspides were probably planktonic, whereas adult-like ones were mostly benthic. All trilobites with non-adult-like protaspides went through a radical metamorphosis when they changed their lifestyle from planktonic to benthic. This occurred in an early stage of trilobite development, usually after one, two or three moultings.

Trilobites from the [Cambrian](#) period (541 million to 485 million years ago) generally have adult-like protaspides (unless they lack protaspis stages at all, as do members of the suborders Olenellina and Agnostina). The typical non-adult-like protaspides evolved independently in several trilobite groups at the end of the Cambrian period or during the [Ordovician](#) period (485 million to 444 million years ago). This independent evolution of planktonic developmental stages in various trilobite lineages close to the Cambrian–Ordovician boundary could be related to increasing ecological pressure with the onset of the [Great Ordovician Biodiversification Event](#).

Trilobites with a long planktonic period of development were quite successful during the Ordovician period. However, at the end of this time, most of these forms went extinct. The extreme climatic changes at the end of this period and the glaciation of the supercontinent Gondwana were probably responsible for changes in production of [phytoplankton](#), and might also have resulted in the extinction of certain trilobites, given that the protaspides would have spent long periods of time drifting in the water column.

Plankton eaters and yolk eaters:

We have seen that early developmental stages of trilobites could be either planktonic or benthic, but what did they feed on? Larvae of recent marine crustaceans (and plenty of other animals) consume two different kinds of food. The majority of them feed on plankton or small organic particles; they are called planktotrophic (plankton eaters) or detritotrophic (detritus eaters). These forms are common in lower latitudes along the equator, where the production of phytoplankton is relatively stable throughout the entire year. The other type of larva is nourished by a large yolk store and is called lecithotrophic (yolk eater). The lecithotrophic larvae are common in places where the production of plankton is limited or seasonally unstable, such as in high latitudes or in freshwater environments.

Generally, the feeding strategies of early developmental stages of many extinct marine animals can be inferred from the size of their earliest stage, because this should reflect the egg size and therefore the amount of yolk present. If this is correct, we can infer that most trilobites with comparatively small protaspides (about 0.2 to 0.6 mm long) were planktotrophic or detritotrophic, as in the majority of recent marine crustaceans. However, some protaspide stages reach quite large or even gigantic (more than 1.5 mm long) dimensions (Fig. 5). Could these extraordinary large stages be lecithotrophic? Answering this question may be harder than expected, because in trilobites we never know whether the stages we find in the fossil record are actually the earliest ones that hatched from the egg.

We can, however, look for some other developmental traits that are typical for recent lecithotrophic groups. In crustaceans, lecithotrophy is frequently associated with short duration of their early development. Species with planktotrophic development can have five, ten or even more larval stages; by contrast, species with lecithotrophic development have only two or three. A similar pattern can be seen in some of the giant protaspides. Whereas most trilobites added one or two segments during each moult, the genus *Eccaparadoxides* (Fig. 6D) added four and the genus *Hydrocephalus* (Fig. 6C) added six segments during one moult. Metaphorically they skipped several stages. This pattern is called accelerated development and leads to a shorter duration of early development.

Another prominent feature of these giant protaspides is an inflated [glabella](#), the axial portion of the head shield (Figs 5F,G & 6C,D). Recent crustaceans whose larvae or juveniles are lecithotrophic usually store yolk or lipids from the yolk in the digestive system, under the carapace. In some cases, the amount of yolk can cause a prominent inflation of the carapace. Trilobites had the front of their digestive system under the glabella. Therefore, the inflation of glabella in some trilobite protaspides may represent a similar adaptation for lipid storage.

Protaspid size comparison

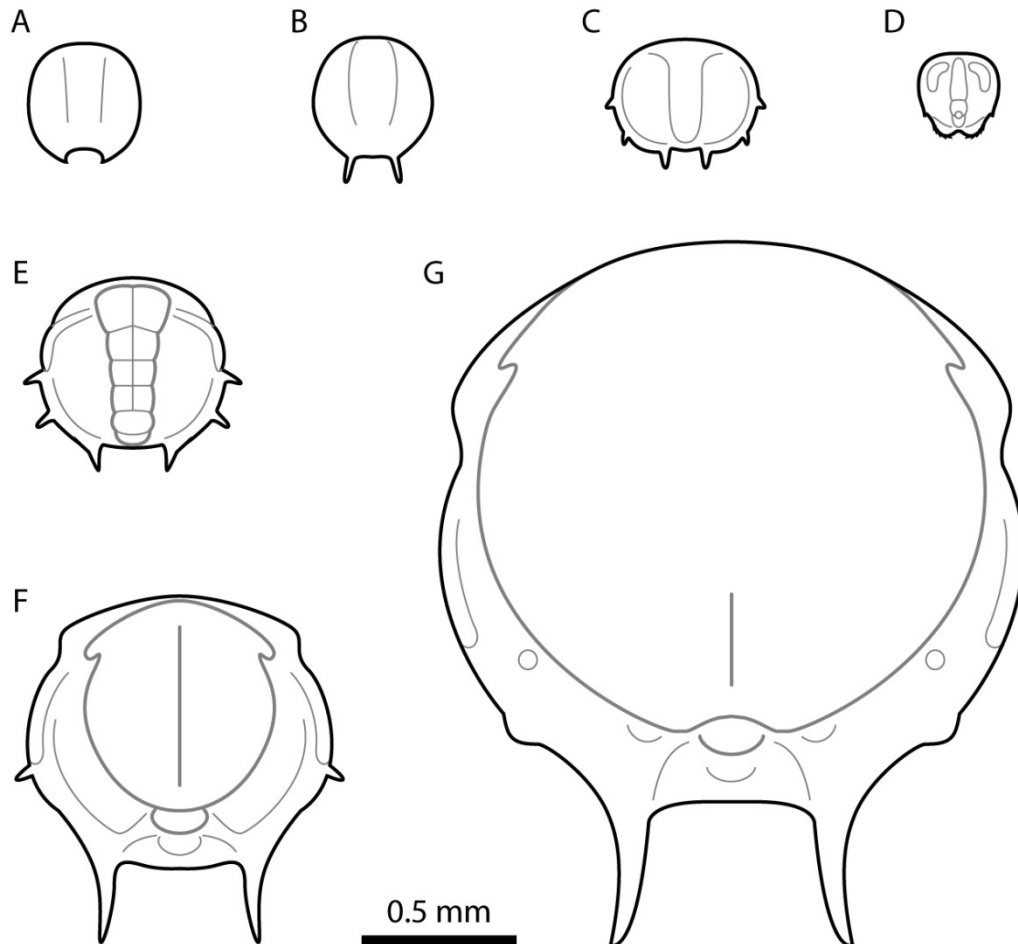


Figure 5 — A size comparison of the earliest-known protaspid stages in some Cambrian trilobites. A, *Bolaspidella*; B, *Tsinania*; C, *Aphelaspis*; D, *Shizhudiscus*; E, *Metaredlichia*; F, *Eccaparadoxides*; G, *Hydrocephalus*. Modified from Dai and Zhang (2012), Laibl *et al.* (2017), Lee and Chatterton (2005a,b), Park and Choi (2009) and Zhang and Clarkson (1993).

When we compare the size of the earliest protaspid stages with the species' [palaeogeographic](#) distribution, we can see an interesting pattern. The species that lived along the equator have rather small protaspides, whereas the species with giant protaspides are restricted to high-latitude areas, nearer Earth's poles. If the protaspid size really reflects the feeding mode, then this distribution is compatible with what we know from modern species: that giant lecithotrophic larvae are more common in higher latitudes, where the production of phytoplankton is seasonally unstable.



Figure 6 — A hodgepodge of early developmental stages of trilobites. A, meraspid stage of *Fritzolenellus* (about 4 mm long), Cambrian, Newfoundland; B, protaspid stage of *Ellipsostrenua* (about 0.6 mm long), Cambrian, Sweden; C, protaspid stage of *Hydrocephalus* (about 2 mm long), Cambrian, Czechia; D, protaspid stage of *Eccaparadoxides* (about 1.3 mm long), Cambrian, Czechia; E, meraspid stage of *Condylopyge* (about 2 mm long), Cambrian, Czechia; F, protaspid stage of *Sao* (about 1 mm long), Cambrian, Czechia; G, early meraspid stage of *Sao* (about 1.5 mm long), Cambrian, Czechia; H, late meraspid stage of *Sao* (about 6 mm long), Cambrian, Czechia; I, early holaspid stage of *Ellipsocephalus* (about 5 mm long), Cambrian, Czechia; J, meraspid stage of *Triarthrus* (about 3.6 mm long), Ordovician, USA; K, protaspid stage of an unidentified species of *Asaphida* (about 1 mm long), Ordovician, USA; L, meraspid stage of *Deanaspis* (about 1.5 mm long), Ordovician, Czechia; M, protaspid stage of *Remopleurides* (about 1 mm long), Ordovician, USA; N, meraspid stage of *Dalmanitina* (about 1.8 mm long), Ordovician, Czechia; O, meraspid stage of *Ectillaenus* (about 9.5 mm long), Ordovician, Czechia; P, meraspid stage of *Aulacopleura* (about 2.5 mm long), Ordovician, Czechia. Specimens from the National Museum, Prague (D, E, G–H, L, N–P), Czech Geological Survey, Prague (C, F, I), Museum of Comparative Zoology, Cambridge, Massachusetts, USA (J), Natural History Museum, London (K, M) and Lund University, Lund, Sweden (B). Credit: L. Laibl.

Summary:

Studies focused on the post-embryonic development of trilobites are important for our understanding of their palaeobiogeographic distribution, their survival during extinction events and their evolutionary relationships. This article briefly summarizes the current knowledge of the post-embryonic development of trilobites. Trilobites show a multistage development with addition of new segments during early ontogeny and a stable number of segments during late ontogeny. The earliest stages of trilobites have two basic types, the adult-like (benthic) and nonadult-like (planktonic) morphology. Extremely large early stages of trilobites with accelerated development and inflated glabella might have fed on stored yolks.

Suggestions for further reading:

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