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Fossil Focus: Trilobites

by Mark Bell*¹

Introduction:

Trilobites make up one of the most fascinating and diverse groups in the fossil record. Over the course of their long history — which dates back to near the beginning of the [Cambrian](#) period, around 520 million years ago — they have inhabited a wide range of marine environments, from [reefs](#) to [abyssal](#) depths. In addition, trilobites have evolved several different life strategies, from burrowing to swimming; these are reflected in their varied appearances, or [morphologies](#) (Fig. 1). Several species, famously those from the [Devonian](#) period of Morocco (about 420 million to 360 million years ago), developed a rich array of protective spines, which has made them a popular choice among fossil collectors and dealers.

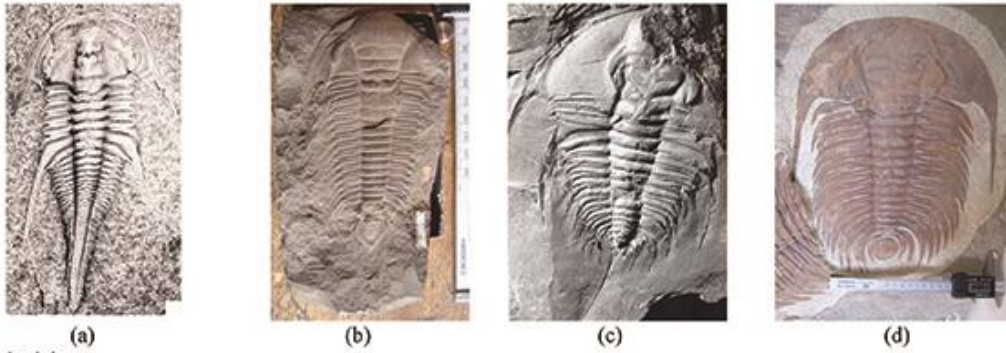
The earliest scientific report of a trilobite fossil was by Reverend Edward Lhwyd in 1698. This specimen was collected near Llandeilo in South Wales, and was originally described by Lhwyd as “some kind of flat fish” (Fig. 2a). Later, following more and more fossil discoveries, trilobites were recognized as [arthropods](#), more closely related to crabs, spiders and lobsters than to fish. In the past 200 years, more than 17,000 species have been described, and trilobites have become increasingly important in the formulation of geological and evolutionary ideas. Historically trilobites were primarily used in the dating of rock strata and in the 19th century geologists including Adam Sedgwick and Roderick Murchison used different species of trilobites (as well as other groups) to define sections of the Cambrian and Silurian respectively. Variation in the number of lens in the eyes of the genus *Phacops* was used by Niles Eldredge and Steven J. Gould as evidence for the theory of punctuated equilibrium, whereby species evolve with little net morphological change (stasis) which is occasionally interrupted by short periods of sudden change associated with speciation events (cladogenesis).

In some countries, trilobites have even taken on importance as cultural icons. During the nineteenth century, the French geologist Joachim Barrande described in detail many fossils from what is now the Czech Republic, including assorted trilobites (Fig. 2c). The Czech city of Prague is very proud of its rich palaeontological heritage and trilobites can today be seen in many unusual places, including restaurants (Fig. 2b), and are also commonly used as the focus for the carvings and sculptures seen in walls and paving stones.

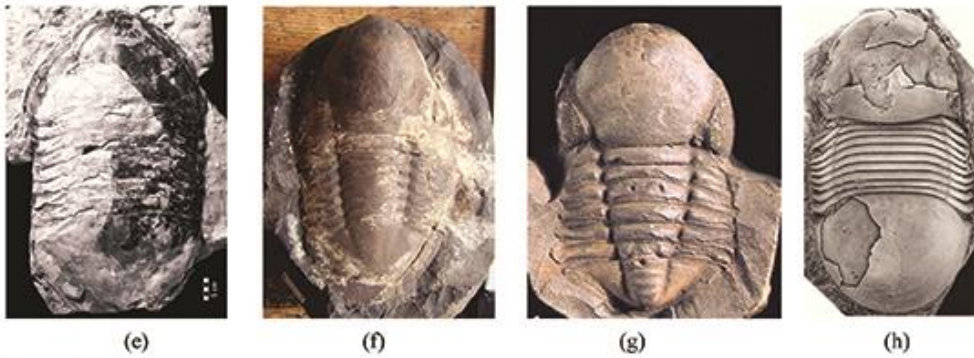
Trilobite diversification:

The oldest trilobites come from the lower Cambrian of North America, Siberia and Morocco. The fossil record shows that the number of trilobite species rapidly increased during the Cambrian, with the group reaching its peak [diversity](#) in the middle to upper Cambrian, around 500 million years ago (Fig. 3). Following this high point, trilobite diversity generally declined for about the uppermost [Permian](#) period, when the last remaining species went extinct. This fall in diversity was punctuated by two pulses of rapid [diversification](#). The first of these was the ‘[Great Ordovician Biodiversification Event](#)’, which occurred from about 485 million to 460 million years ago and saw the innovation of forms that would be common for the rest of trilobite history (asaphids (Fig. 1e-g),

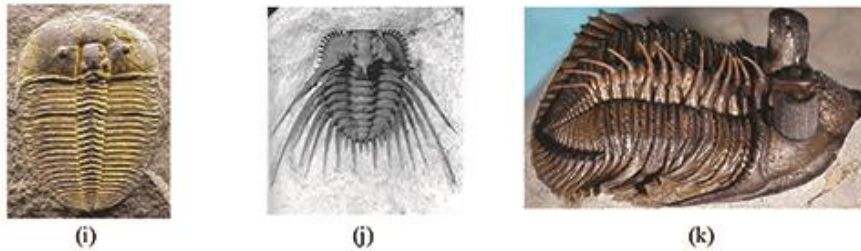
Cambrian:



Ordovician:



Silurian and Devonian:



Post-Devonian:

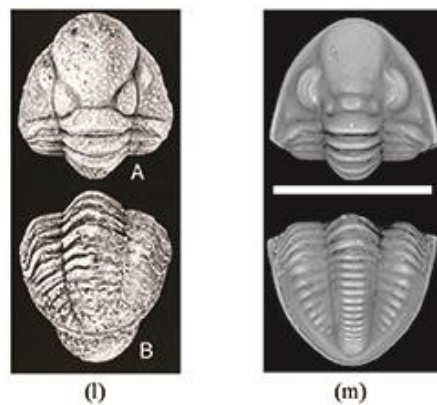


FIGURE 1 — KEY TRILOBITE SPECIES DISCUSSED IN THE TEXT. (A) *BALCORACANIA DAILYI* (~10MM), (B) *PARADOXIDES GRACILIS* (110MM), (C) *OLENELLUS* (~20MM); (D) *ACADOPARADOXIDES BRIAERUS* (300MM) (E) *ISOTELUS REX* (720MM), (F) *PARABARRANDIA BOHEMICA* (120MM), (G) *PRICYCLOPYGE BINODOSA BINODOSA* (20MM), (H) *CYBANTYX ANAGLYPTOS* (50MM), (I) *AULACOPLEURA KONINCKI* (20MM); (J) *LEONASPIS* (10MM), (K) *ERBENOCHILE ERBENI* (50MM), (L) *KATHWAIA CAPITOROSA* (~30MM), (M) *DITOMOPYGE* (~30MM). SOURCES: (A) PATERSON AND EDGECOMBE, 2006; (C,J) LEVI-SETTI, 1993; (E) RUDKIN ET AL., 2003; (G) FORTEY, 1985; (H) WHITTINGTON, 1997; (I) [HTTP://ALTURL.COM/J58TK](http://alturl.com/J58TK) (K) CHATTERTON AND GIBB, 2010; (L) OWEN, 2003; (M) [HTTP://ALTURL.COM/A8GIQ](http://alturl.com/A8GIQ).

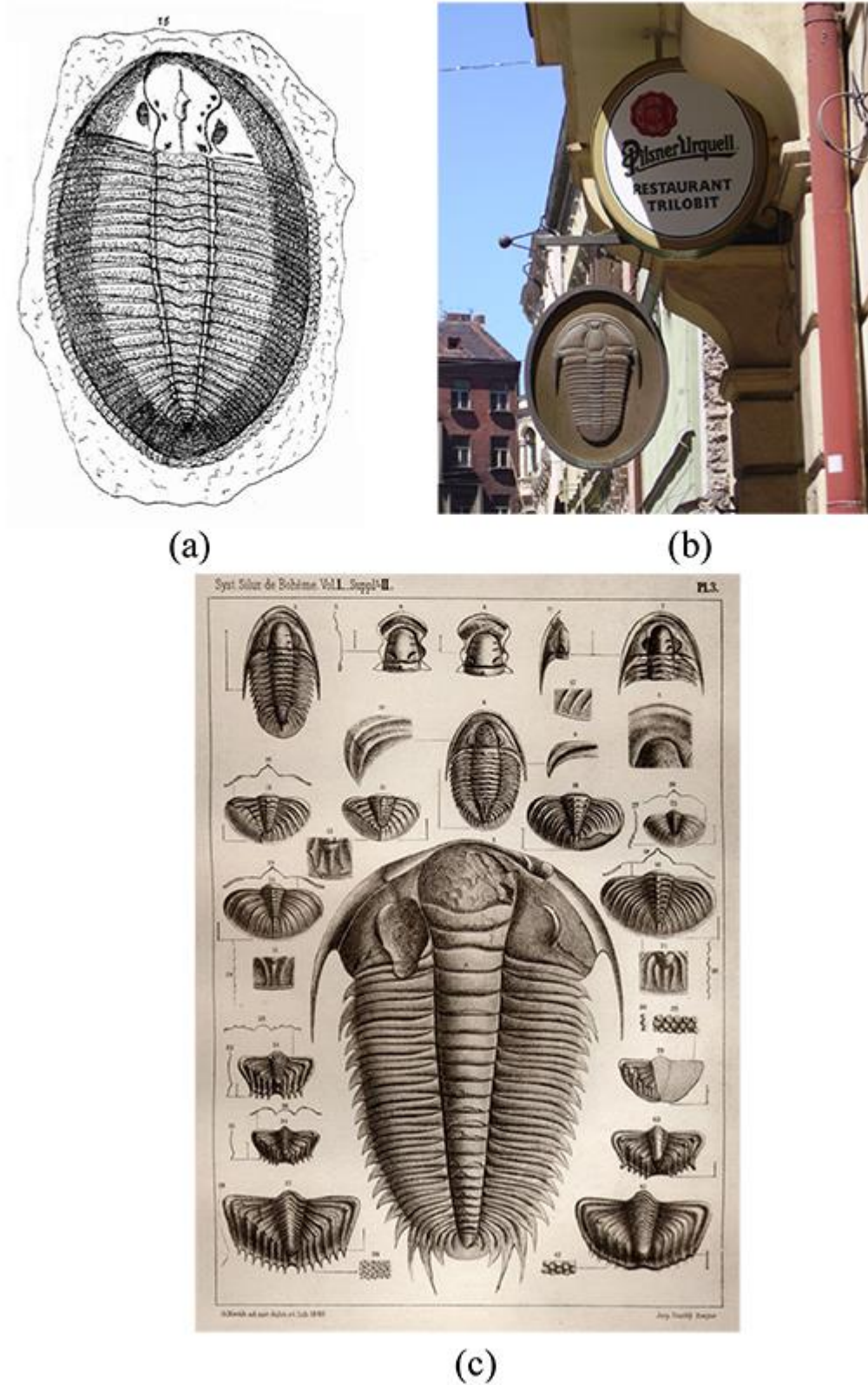


FIGURE 2 — (A) REVEREND EDWARD LHWYD'S "FLAT FISH". SOURCE: [HTTP://ALTURL.COM/9S5O9](http://alturl.com/9s5o9) (B) TRILOBITE BAR IN PRAGUE. CREDIT: DAVID BRESSAN. (C) CAMBRIAN TRILOBITES DESCRIBED BY JOACHIM BARRANDE IN 1852. SOURCE: [HTTP://ALTURL.COM/O7CK9](http://alturl.com/o7ck9).

phacopids (Fig. 1k) and proetids (Fig. 1i,l,m)), whereas the typical Cambrian (redlichiids and olenellids; Fig. 1a-d) forms became extinct. The second and last major rise in diversity occurred in the Lower to Middle Devonian (about 419 million to 382 million years ago) and was shorter-lived. This period was characterized by the evolution of very spiny forms (such as that in Fig. 1i-j); the development of these structures and the simultaneous increase in diversity could be the result of the trilobites being preyed on by other invertebrate groups, especially cephalopods such as orthocones, which are related to the modern nautilus. An increase in diversity due to predation pressure might sound counterintuitive, but is in fact very common in the natural world. Organisms develop adaptations to avoid being eaten, in this case through strengthening their defensive capabilities, which in turn drives a diversity increase in the group being predated upon; this evolutionary ‘arms race’ effect was named the escalation hypothesis by palaeontologist Geerat Vermeij in the 1980s.

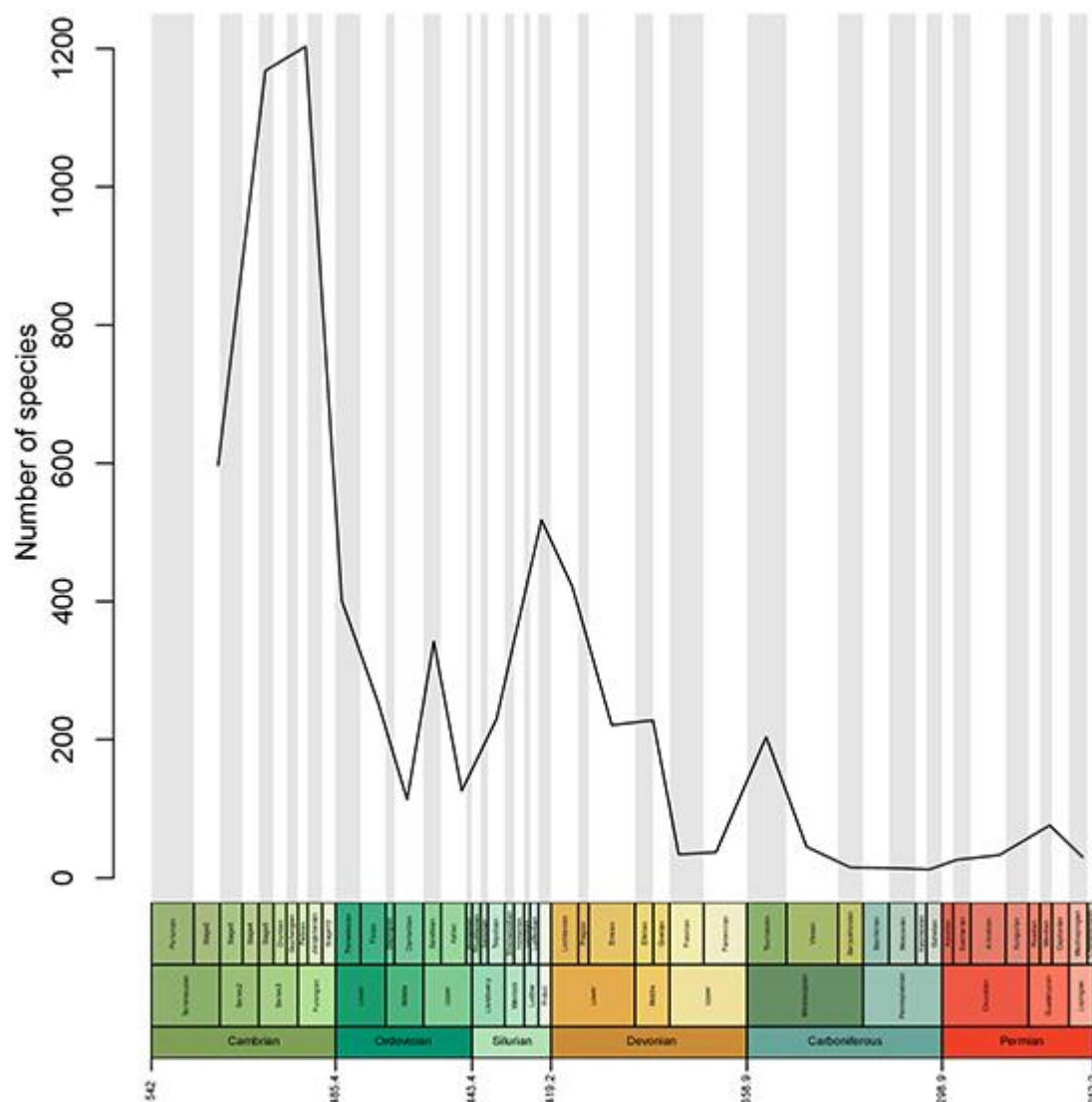


FIGURE 3 — SPECIES DIVERSITY OF TRILOBITES. BASED ON OCCURRENCES FROM THE PALEOBIOLOGY DATABASE: KIESSLING, W., M. FOOTE, A. I. MILLER, M. E. PATZKOWSKY, P. J. WAGNER, S. M. HOLLAND, M. J. HOPKINS, M. E. CLAPHAM, AND P. M. NOVACK-GOTTSHALL. 2013. TAXONOMIC OCCURRENCES OF TRILOBITA. PALEOBIOLOGY DATABASE. [HTTP://PALEODB.ORG](http://paleodb.org).

Morphology and ontogeny:

The name 'trilobite' (Latin for "three-lobed") comes from the way that the [exoskeleton](#) is divided into a central axis with lobes (left and right pleural lobes) on either side (Fig. 4a). However, trilobites are also divided into three sections (called tagmata) from front to back. These are a head shield (the cephalon); a body made of articulated segments (the thorax); and a tail shield consisting of multiple fused segments (the pygidium) (Fig. 4b). From this seemingly simple arrangement comes an incredible plethora of form with species evolving a wide range of features from smooth, effaced exoskeletons (Fig. 1e-h), high spinosity (Fig. 1j,k) or smaller (or complete loss of) eyes (Fig. 1f). Trilobites show excellent examples of convergent evolution, whereby morphological characters such as these are independently evolved in unrelated species e.g. effaced exoskeletons occur in both the families Asaphidae (Fig 1. e) and Illaenidae (Fig 1. h). An interesting example of convergence is *Aulacopleura konincki* (Fig 1. i) from the Silurian of the Czech Republic that evolved features common to basal trilobites species including a narrow thoracic axis, large (and variable) number of thoracic segments and a small pygidium. This is likely associated with the adaptation towards life in low oxygen, high sulphur environment, known as the olenimorphic type; this was common in the Cambrian.

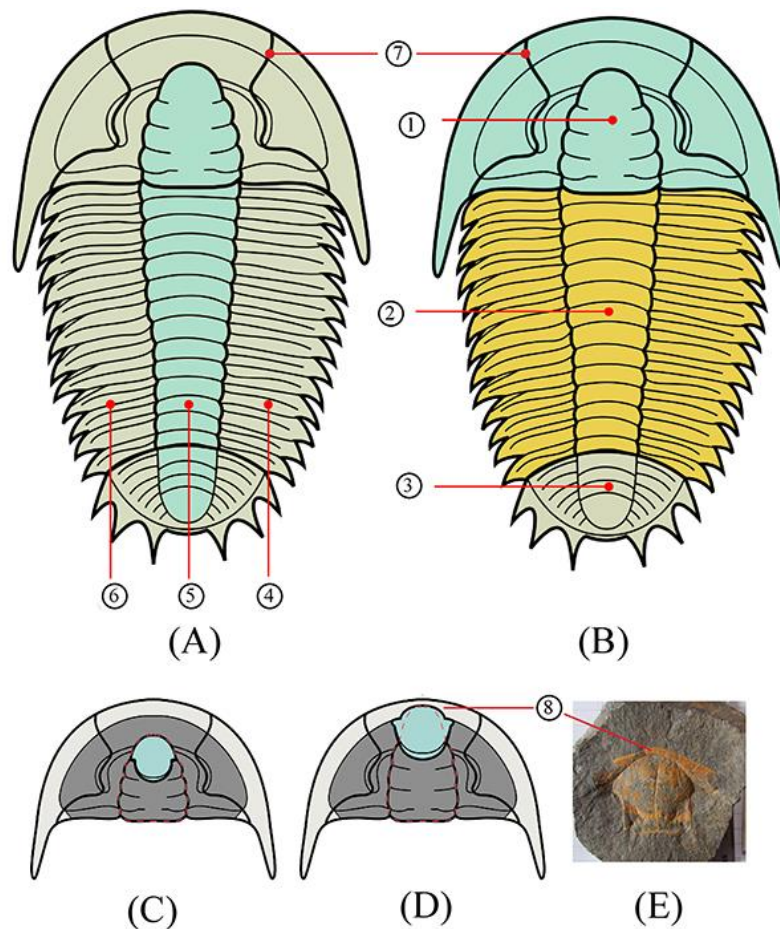


FIGURE 4 — TRILOBITE MORPHOLOGY. (A) UPPER (DORSAL) AND (B) LOWER (VENTRAL) VIEWS. 1, CEPHALON; 2, THORAX; 3, PYGIDIUM; 4, RIGHT PLEURAL LOBE; 5, AXIAL LOBE; 6, LEFT PLEURAL LOBE; 7, FACIAL SUTURES; 8 DOUBLURE. (C) CONTERMINANT AND (D) NATANT HYPOSTOME ATTACHMENT CONDITION; THE HYPOSTOME IS MARKED IN BLUE AND THE OUTLINE OF THE GLABELLA IN RED, (E) HYPOSTOME AND DOUBLURE OF *HYDROCEPHALUS CARENS*. SOURCES: (A-D) COPYRIGHT SAM GON III 1999–2005.

As with other arthropods, trilobites grew by moulting, passing through a series of distinct developmental stages or [instars](#). During moulting, the exoskeleton broke across joints, or sutures, between the segments, such as the facial sutures, which join the free cheeks to the rest of the cephalon (Fig. 4a,b). After moulting, the individual took on water to swell its body size before growing a new exoskeleton.

Moulting was an important part of the trilobite life cycle. In the early stages of development, this process was used to increase the number of thoracic segments, as well as the overall size of the animal. Trilobite development can be broadly divided into three main stages: protaspid, meraspid and holaspid (Fig. 5). The protaspid and meraspid phases involve moulting followed by an increase in segment number (anamorphic growth pattern). In the protaspid stage is represented by a circular disc with facial sutures but with no division between body sections. The meraspid stage begins when the first segment between the cephalon and the pygidium develops. During the following moults of the meraspid stage, segments are released from the front of the pygidium into the thorax. This continues until a stable number of segments is reached. After that, the holaspid stage begins, and the individual increases only in size after each instar (epimorphic growth pattern). The stable number of thoracic segments varies across the group, ranging from two in agnostids to more than 100 in *Balcoracania dailyi*. This has led some researchers to suggest that some species continued to add segments throughout their entire lives.

Trilobites have one of the largest size ranges of any [Palaeozoic](#) arthropod group — with the notable exception of the [eurypterids](#). Adult, holaspid trilobites typically range from less than 1 centimetre up to around 10 centimetres long. The largest known complete trilobite, *Isotelus rex*, from the Upper Ordovician of Canada, measures 72 centimetres. Although large trilobite fossils are found in regions that were around the equator when trilobites were alive, they seem to be more abundant in areas that were located close to the South Pole, especially during the Cambrian and Ordovician. The trilobite species *Acadoparadoxides briareus*, which is found in rocks called the Jbel Warmast Formation in the Middle Cambrian of Morocco (Fig. 1d) typically reach around 30 centimetres. In addition, the Valongo Formation in the Middle Ordovician of Portugal contains a highly diverse variety of giant trilobite species including *Hungioides bohemicus* and *Ogyginus forteyi*, the latter of which is estimated to have reached around 90 centimetres.

Lifestyle and feeding strategies:

It is difficult to reconstruct the life habits or ecologies of wholly extinct groups such as trilobites, but we can make some inferences based on their exoskeletal morphology, comparisons with extant relatives and the types of rocks they are preserved in.

Trilobites can be broadly separated into two categories: predators and deposit feeders. One feature used to recognize these categories is how the hypostome, a plate on the lower surface of the exoskeleton, is attached (Fig. 4c,d). The hypostome was generally lined up with the back of the glabella, a dome that covered the stomach and mouthparts. In predatory trilobites, the hypostome was rigidly fixed to a rim around the underside of the trilobite, called the doublure (Fig. 4), allowing the trilobite to process prey such as worms and small crustaceans. This is called the conterminant condition. By contrast, in deposit-feeding species the hypostome was less tightly fixed to the

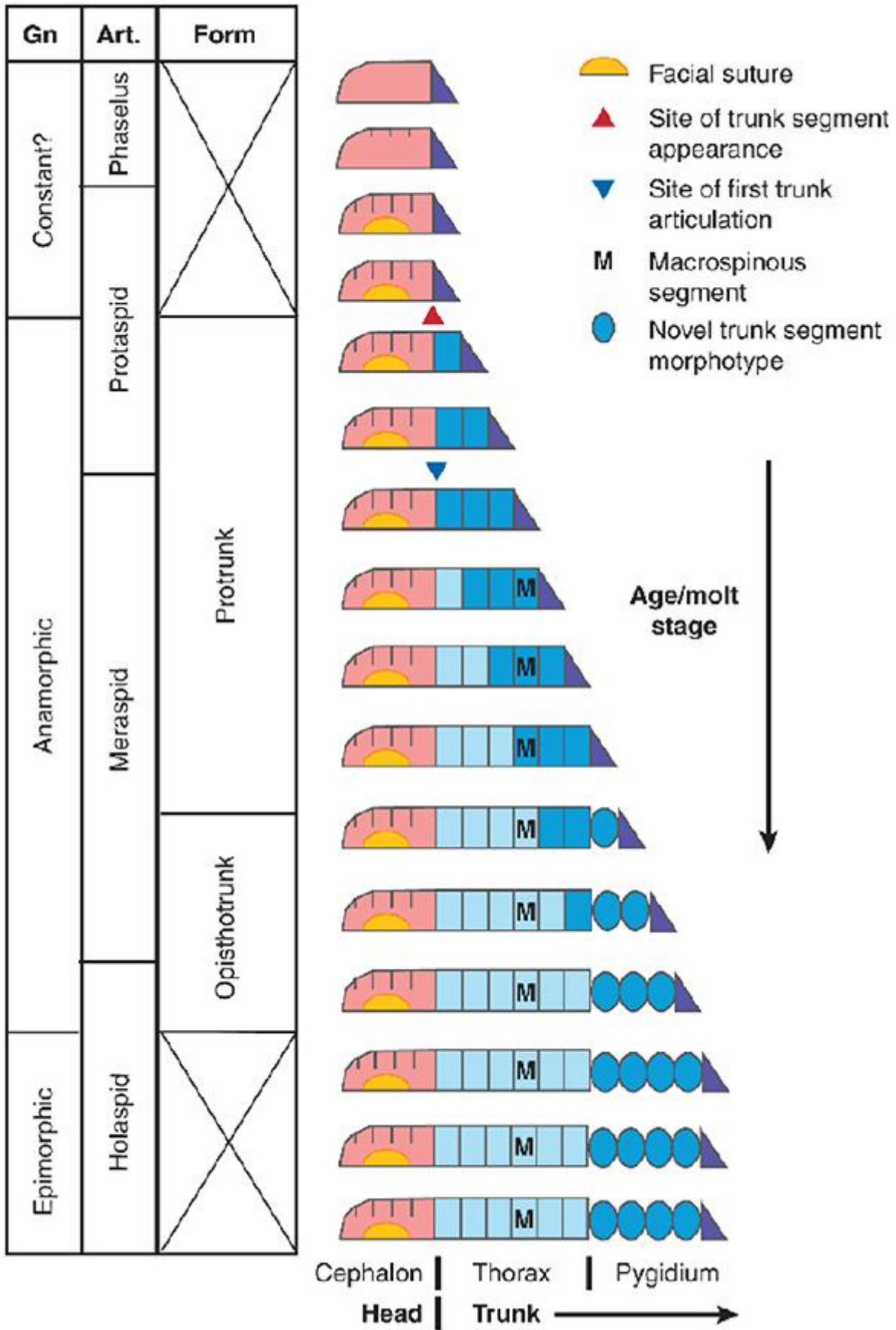


FIGURE 5 — TRILOBITE ONTOGENY. SOURCE: HUGHES, 2007.

doublure (the natant condition), and would have been used mainly for sieving through mud on the sea floor for food particles. Predatory trilobites have other characteristics that further differentiate them from deposit feeders, including much greater variability in overall form, a more arched exoskeleton and a generally greater size range. These species appeared with the first trilobites in the lower Cambrian, but became extinct in a mass extinction during the Late Devonian period, with only the deposit-feeding proetids surviving until the end of the Permian.

Most trilobites are thought to have been [benthic](#), living on or just below the sea floor; however, during the Ordovician, another life strategy became dominant. Several groups evolved morphologies consistent with an active, free-swimming lifestyle in the open ocean. The families Telephinidae and Cyclopygidae are typical of this life style, having developed a more streamlined body and a wider thoracic axis, presumably due to the need for stronger swimming muscles (Fig. 1f,g). They also developed greatly inflated eyes, which allowed for 360-degree vision. These species tend to be found in rock layers that formed in a deep marine environment that was penetrated by only a small amount of sunlight, and so usually contain blind trilobite species. This suggests that the swimming animals lived higher in the water column, falling into the depths only after their death.

Phylogeny:

Despite being one of the best-studied fossil groups, trilobites still cause a number of phylogenetic controversies. These mainly revolve around their relationships in the Euarthropoda (arthropods defined by a cephalon with conjoined segments, antennae and three pairs of limbs that each branch into two parts) and the relationships of groups within trilobites. Current evidence suggests that trilobites are closely related to chelicerates (a group containing spiders, scorpions, mites and horseshoe crabs), mandibulates (crustaceans, myriapods and insects) or both. Another issue concerns the relationships of the suborder Agnostina, which consists of small, blind species with only two thoracic segments. Many researchers place the group as a close relative of the eodiscid trilobite group, but others exclude it from the trilobites entirely, thinking instead that the organisms are crustaceans.

Summary:

Despite certain areas of uncertainty the study of trilobites shows no sign of abating, even after more than two centuries of collecting. New species are continually being discovered and described, illuminating previously unknown features and in turn increasing our understanding of the evolutionary history of this fantastic fossil group.

Further Reading:

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www.trilobites.info — A fantastic website created and maintained by Sam Gon III, covering everything you always wanted to know about trilobites but were afraid to ask.

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