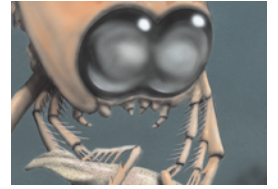


# Fossils explained 65



## Thylacocephalans

Thylacocephalans are an extinct group of arthropods of an uncertain systematic position. Originally considered phyllocarid crustaceans, they have since been classified within their own class, the Thylacocephala Pinna, Arduini, Pesarini and Teruzzi, 1982 on the basis of the exceptionally preserved Lower Jurassic (Sinemurian) species *Ostenocaris cypriformis* from Osteno, Italy. Since that time, the membership of the Thylacocephala has grown as a number of new species have been discovered, as well as previously known species moved into the group.

Thylacocephalans are characterized by a body almost entirely enclosed within a bivalved-carapace, often with a prominent anterior rostrum-notch complex. Typically, thylacocephalans also have large, compound eyes; three pairs of large, subchelate appendages on the anterior part of the body; at least eight pairs of lamellate gills on the middle part of the body, and a posterior series of small, paddle-like limbs. The central problem in Thylacocephalan taxonomy is the affinity of carapace-only fossils that lack the key synapomorphies that reside in the soft-parts. The oldest known putative representative (*Zhenghecaris*) is known from the Lower Cambrian Maotianshan shales of China, while the oldest unequivocal thylacocephalan (*Thylacares brandonensis*) comes from the Silurian of Wisconsin, USA. The last of the thylacocephalans occur in the Upper Cretaceous limestones of Lebanon. Although common in many different localities of different ages in the world (e.g. Devonian of Europe and Australia), the best-known and preserved species come from the Triassic and Jurassic of Italy and France. Over 20 genera of thylacocephalans have been recognized so far.

### Morphology and anatomy

Thylacocephalans are highly unusual arthropods. The main body, consisting of an unknown number of tagma, is covered by a bivalve carapace (usually oval in outline and possibly originally phosphatic in some species). The surface sculpture may be ornamented by various ridges and folds; the surface may also be covered by tiny, polygonal microstructures. The carapace may possess both anterior and posterior

spines (Fig. 1), but the anterior spine (rostrum) above the eyes is generally more prominent (Fig. 1A–B, D).

Some specimens, especially from the Triassic and Jurassic, also bear distinctive looped lines of pores or spheres, which penetrate the dorsal region of the carapace. It is possible that they are remnants of additional chemoreceptors or even photophores, but more research (including thin-section studies) is needed to decipher their true function. The photophore hypothesis is provocative, because it gives an opportunity to speculate on the thylacocephalan mode of life. However, it is probably impossible to unambiguously determine the function of these structures when we are left with only fossilized material.

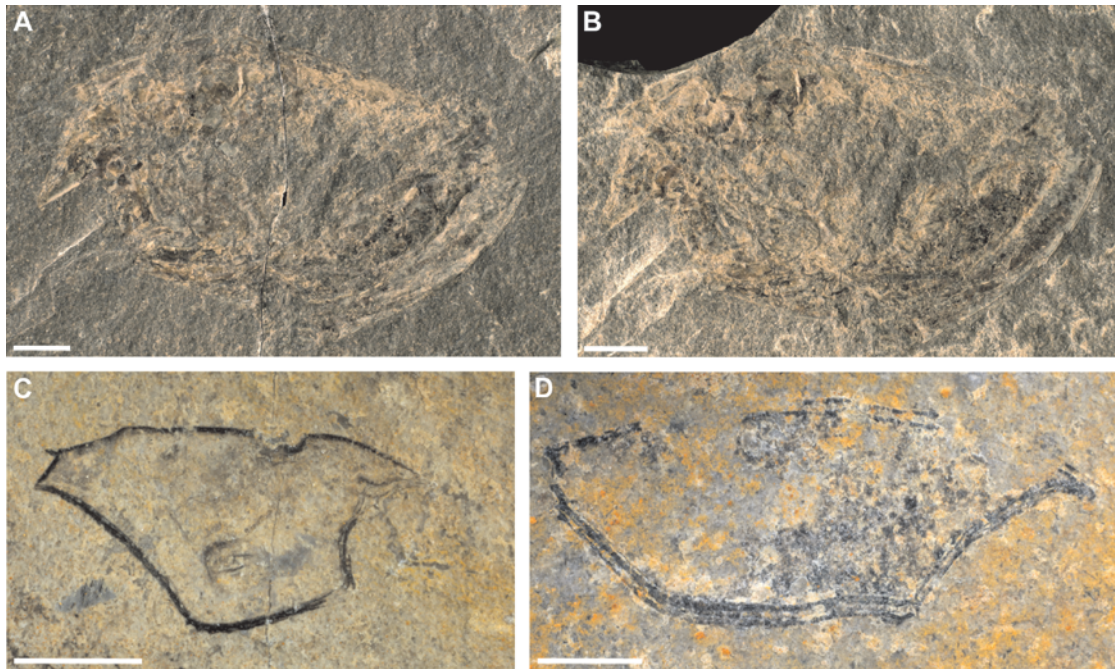
In some completely preserved specimens, the anterior part of the carapace, just below the rostrum, holds two eyes (Figs 2–3). In the oldest, putative representatives from the Lower Cambrian, the eyes are small, drop-shaped (possibly stalked), while in some of the Jurassic forms, they are large and prominent (possibly fused, Fig. 3), with numerous small ommatidia. The large eyes occupy the distinct concavity in the anterior edge of the carapace, the so-called optic notch. The posterior part of the body is strongly reduced and rarely visible.

The body and appendages of thylacocephalans are rarely preserved, probably due to their light-to-absent mineralization as compared to the carapace. What is known about their non-carapace anatomy is extrapolated from exceptionally preserved specimens. Their tagmosis is the subject of debate. Earlier workers saw their anatomy as consistent with division into a head, thorax and abdomen, found in

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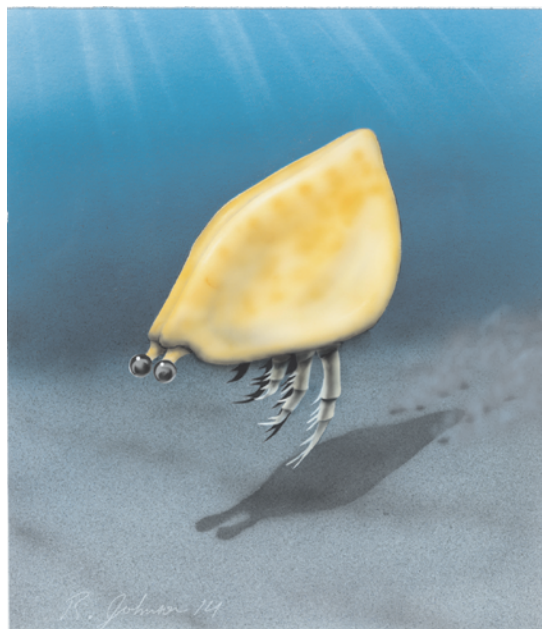


**Fig. 1.** Examples of Devonian (A–B) and Cretaceous (C–D) thylacocephalans. A–B. Carapaces of *Concavicularis* sp., lower Famennian, Poland; anterior to the left. C. *Victoriacaris muhiensis* Hegna, Vega & González-Rodríguez, Albian–Cenomanian, Mexico; anterior to the left. D. *Polzia eldoctorensis* Hegna, Vega & González-Rodríguez, Albian–Cenomanian, Mexico; anterior to the right. Scale bars 5 mm.

other crustaceans. This interpretation assumes that the raptorial appendages are part of the thorax and the posterior pleopod-like appendages are part of the abdomen. However, if true, then either the thorax is exceedingly short (just three, limb-bearing segments), or we have no knowledge of the rest of the thoracic appendages. Furthermore, the raptorial appendages seem to insert too far forward on the thorax—possibly on to part of the head. A more recent interpretation sees the three raptorial appendages as representing the two maxillae of the crustacean head, and the posterior-most one representing a maxilliped. The rest of the body would be comprised of an undifferentiated trunk with a variable number of pleopod-like swimming appendages (see Fig. 3).

The head region, in addition to their eyes, seems to have had two pairs of antennae, as based on *Clausocarid* from the Jurassic of Germany (Fig. 3) and *Thylacocephalus* from the Cretaceous of Lebanon. The preservation of other head appendages (e.g. mandible) has been suggested in some specimens. The boundary between the head and trunk is difficult to discern. Somewhere in that region are three, typically large, subchelate raptorial appendages. These appendages, where known, seem to increase in size posteriorly. The spine-bearing raptorial limbs are long and protrude beyond the ventral margin of the carapace (Figs 2, 3). They are superficially similar to those of the Recent mantis shrimp (Stomatopoda) and also likely played a role in predatory activity. As indicated above, these raptorial appendages may fit the pattern of maxillipedes observed in other crustaceans, and, thus, may imply a similar shift in HOX genes. The

trunk region has eight pairs of lamellar gills in some species (*Dollocaris*) held under the carapace—but these are not easily observed or interpreted in other species. The posterior part of the trunk (i.e. behind the raptorial appendages) has eight or more pairs of pleopod-like appendages. The pleopod-like appendages are much smaller than the raptorial appendages and largely enclosed within the posterior part of the carapace; only their distal, filamentous parts may protrude beyond the carapace posteriorly (Fig. 3). Their role is enigmatic but it is quite likely that they had a swimming function. The telson is small, but its exact nature is unknown.



**Fig. 2.** Artist's reconstruction of the Silurian thylacocephalan, *Thylacares*. Note the small, stalked eyes and spine-bearing raptorial appendages. Putative antennae were omitted from the reconstruction (drawing by Robert Johnson).

## Taxonomy, diversity and extinction

Controversy has long surrounded the thylacocephalans. The presence of jointed appendages and compound eyes cements their position within Arthropoda; however, their relationship with regards to arthropod groups is unclear. At present, they are allied with the Crustacea on the basis of one synapomorphy present in a couple of species: the presence of two pairs of antennae. Recently, it has been suggested that the presence of up to five pronounced endites with numerous setae on the raptorial appendages of Silurian Thylacocephala supports their eucrustacean affinity.

Circumstantial evidence supports the crustacean hypothesis: the crustacean lineage is the only lineage that has evolved a bivalve-style carapace—which it has done multiple times, independently. Several different positions within the crustacean crown group have been proposed, but a stem-group crustacean position cannot be excluded either. Recently, similarities between the tagmosis of remipede crustaceans and thylacocephalans have been noted—only raising more questions about both of these enigmatic lineages.

Two orders of Thylacocephala are currently discerned: Concavicularida and Conchyliocarida (Table 1). However, the majority of thylacocephalans are preserved as carapace-only remains, lacking appendages and other soft-body anatomical features. As a result, for most species, this division functionally rests on one characteristic—the relative prominence of the optic notch (paradoxically, the more prominent the eyes are, the less pronounced the optic notch is from the frontal margin of the carapace). This order-level division was not recovered in explicit, character-based phylogenetic analyses, but was displayed graphically as the favored hypothesis of Schram (2014).

Several potential synapomorphies have been pointed out by several individuals. These are: (1) huge, anterior compound eyes; (2) a large carapace almost completely enclosing the body; (3) three pairs of anterior raptorial appendages; (4) a trunk region with eight lamellar gills; and (5) a set of small pleopod-like limbs posteriorly. Any list of thylacocephalan synapomorphies suffers from a preservation problem—the all-important non-carapace characteristics are only preserved in a handful of species. This raises an important question—how reliable are our criteria for differentiating carapace-only fossils as belonging to either thylacocephalans or phyllocarids?

Until recently, there were only two described thylacocephalan families: Austriocarididae and Clausocarididae. These families both have very restricted memberships, and thus failed to encompass all thylacocephalans. The majority of thylacocephalans were, as a result, family-less.



**Fig. 3.** Artistic reconstruction of the Jurassic thylacocephalan, *Clausocaris* capturing a coleoid cephalopod. Note the large, fused eyes, spine-bearing raptorial appendages at the front, and tiny, pleopod-like appendages at the posterior part of the carapace (drawing by Robert Johnson).

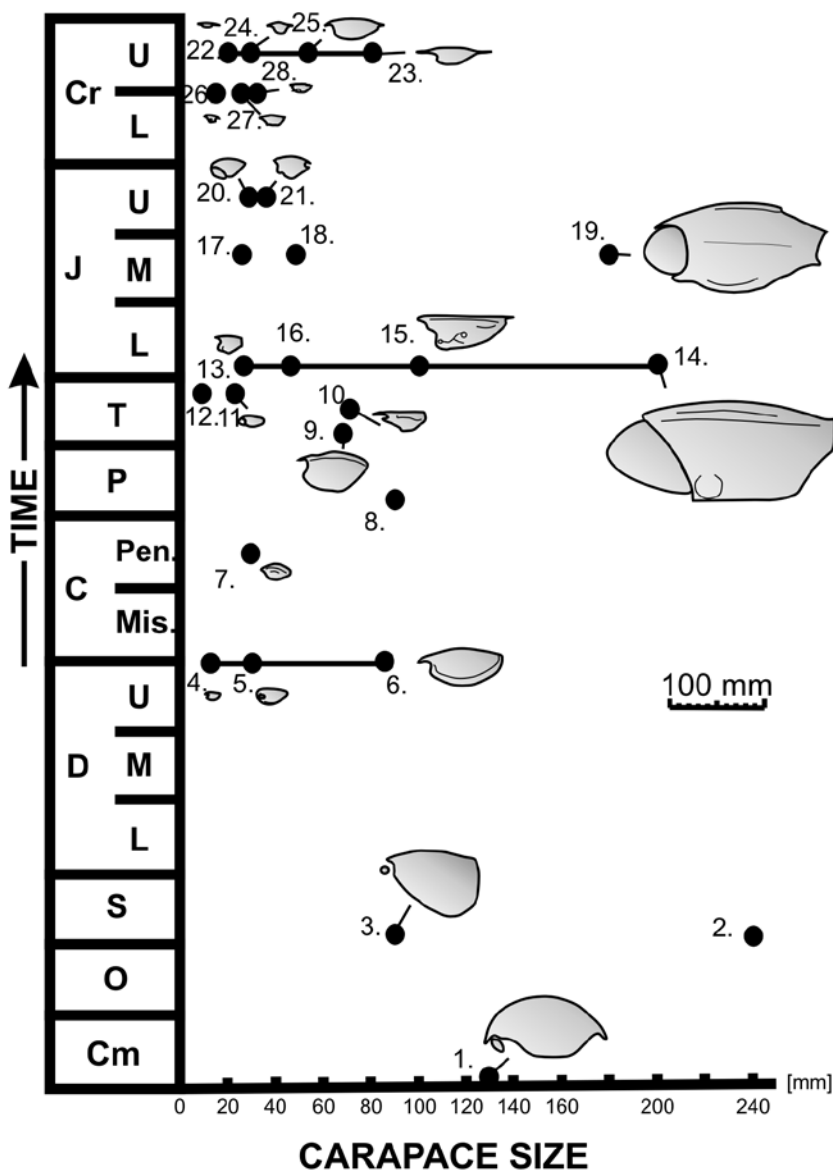
Recently, a new, complete system of familial-level taxonomy for thylacocephalans was proposed. It utilized the two existing families (Austriocarididae and Clausocarididae) and added five more families: Concavicularididae, Microcarididae, Protozooidae, Dollocarididae and Ostenocarididae (see Table 1).

*Zhenghecaris* from the Lower Cambrian Maotianshan Shale is the oldest putative thylacocephalan, but the character support for such an assignment remains weak. Other Cambrian taxa have also been allied with the Thylacocephala, but, for the most part, have subsequently been rejected. The oldest, universally accepted thylacocephalan is a recently described species from the Silurian of Wisconsin, USA. The stratigraphically youngest members are from the Upper Cretaceous of Lebanon (see Fig. 5 for stratigraphical ranges of taxa and carapace sizes).

Though thylacocephalans occasionally achieve

**Table 1.** Thylacocephalan generic diversity within currently distinguished Conchyliocarida and Concavicularida orders (based on Schram, 2014).

Conchyliocarida	Concavicularida
<b>Dollocarididae</b> <i>Dollocaris, Mayrocaris, Paraostenia, Victoriacaris</i>	<b>Austriocarididae</b> <i>Austriocaris, ?Yangzicaris</i>
<b>Ostenocarididae</b> <i>Killianocaris, Ostenocaris</i>	<b>Concavicularididae</b> <i>Ankitokazocaris, Concavicularis, Harrycaris</i>
	<b>Clausocarididae</b> <i>Clausocaris, Convexicaris</i>
	<b>Microcarididae</b> <i>Atropicaris, Ferrecaris, Microcaris, Polzia, Thylacocephalus</i>
<b>Order &amp; family</b> <i>Insertae sedes</i> <i>Ainiktozoon, Rugocaris, Thylacares</i>	<b>Protozooidae</b> <i>Protozoa, Pseuderichthus</i>



**Fig. 4.** Size range of thylacocephalans (Lower Cambrian to Upper Cretaceous). 1. *Zhenghecaris*; 2. *Ainiktozoon*; 3. *Thylacares*; 4, 5. *Concavicularis* (two different species); 6. *Harrycaris*; 7. *Convexicularis*; 8. *Coreocar*; 9. *Ankitokazocaris*; 10. *Yangzicaris*; 11. *Atropicaris*; 12. *Microcaris*; 13, 14. *Ostenocaris* (two different species); 15. *Austriocaris*; 16. *Rugocaris*; 17. *Paraostenia*; 18. *Kilianocaris*; 19. *Dollocaris*; 20. *Clausocar*; 21. *Mayrocaris*; 22, 23. *Protozoa* (two different species); 24. *Pseuderichthus*; 25. *Thylacocephalus*; 26. *Victoriacaris*; 27. *Polzia*; 28. Undetermined species of Hegna *et al.* (2014). Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; Mis, Mississippian; Pen, Pennsylvanian; P, Permian; T, Triassic; J, Jurassic; Cr, Cretaceous; L, Lower; M, Middle; U, Upper (modified after Vannier *et al.*, 2006).

high abundances locally, they tend to be low abundance components of fossil deposits. In most cases, they also have a low alpha diversity—usually just a single species known from a given locality. This low abundance and diversity, coupled with the fact that they are typically only found in fossil lagerstätten, makes it difficult to draw firm conclusions about their biogeographic and diversity patterns. If

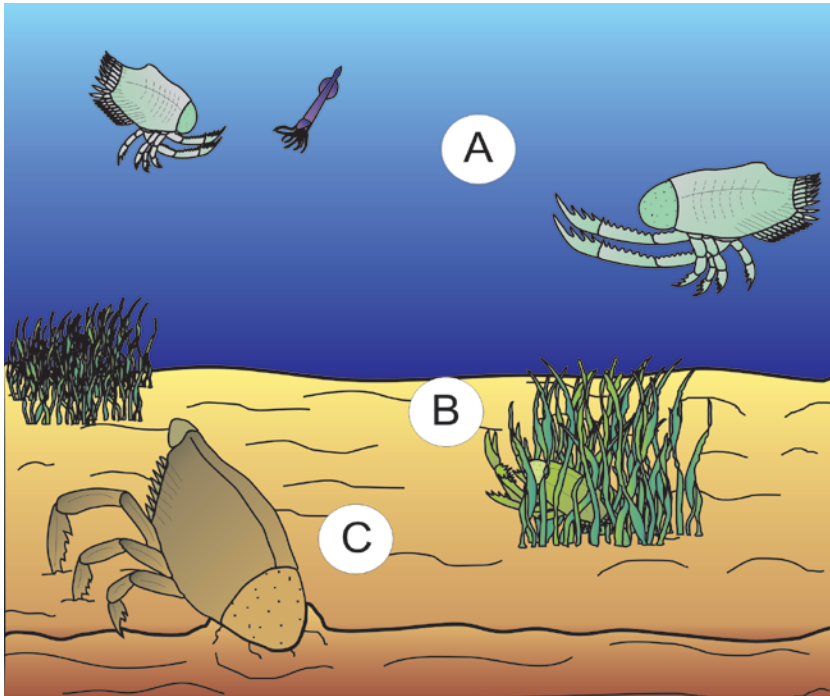
the entirety of their geological range is considered, they occur on all continents except Antarctica and South America—but, one occurrence (for example, the thylacocephalans from the Devonian Gogo Formation in Australia) does not mean necessarily that the taxon inhabited the given continent for the entirety of the Palaeozoic and Mesozoic. It has been pointed out that their known diversity patterns at the end of the Mesozoic are consistent with a possible range constriction and extinction prior to the end-Cretaceous event, but more sampling is needed to confirm these patterns.

### Ecology and mode of life

The occurrence of thylacocephalans in deposits of various ages representing different facies indicate that these animals inhabited a variety of marine palaeoenvironments. It is certain, however, that at least some forms (as Jurassic *Dollocaris*) lived in deep, dark environments, which is supported by the presence of large eyes and their occurrence in deep-water facies. However, the enigmatic morphology of thylacocephalans makes interpreting their mode of life difficult. Preserved gut contents in some of the specimens, in the form of cephalopod arm hooks and carapace fragments of different arthropods, indicate that some were carnivorous (as suggested by their appendage morphology). The presence of thylacocephalan carapaces and their fragments within the body cavity of Palaeozoic sharks and coprolites indicate that they were preyed upon by larger predators.

Currently, three hypotheses concerning their mode of life prevail (Fig. 5).

- 1 The benthic scavenger hypothesis states that long limbs of thylacocephalans had a walking rather than hunting purpose. In that case, they would have fed on organic matter scattered on the seafloor.
- 2 The necto-benthic predator hypothesis states that pleopod-like appendages enabled only short jumps and not active swimming. In this case, thylacocephalans would have been ambush predators, hiding among the algae on the seabottom, and hunting with the aid of their long, spiny, raptorial limbs used to stab the potential prey. This hypothesis may be supported by the similarity of their raptorial limbs to those in mantis shrimp crustaceans that hunt in a similar manner.
- 3 The nektonic predator hypothesis states that the thylacocephalan oval carapace and a battery of pleopod-like appendages allowed them active swimming in the water column. According to this hypothesis, they hunted in deep, dark waters, maybe even luring the prey by its own luminescence, similarly to the modern hyperiid



**Fig. 5.** Hypothetical modes of life of thylacocephalans, as: **A.** a benthic scavenger, **B.** necto-benthic ambush predator and **C.** nektonic predator.

crustaceans.

There is also a possibility, that all three hypotheses contain some truth—different species may have had different modes of life or they may have occupied different niches during different parts of their ontogeny. However, in order to better understand their palaeoecology and mode of life, more exceptionally preserved specimens from various facies and ages are needed.

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