A PICTORIAL GUIDE TO THE ORDERS OF TRILOBITES

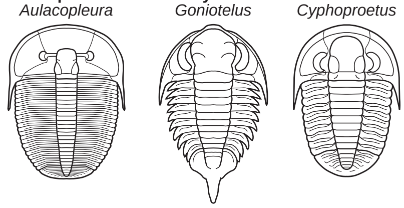
by Samuel M. Gon III, Ph.D.

ORDER PROETIDA

Superfamily Aulacopleuroidea — **Aulacopleuridae** *Aulacopleura*

Superfamily Bathyuroidea — **Bathyuridae** *Goniotelus*

Superfamily Proetoidea — **Proetidae** *Cyphoproetus*



ORDER ASAPHIDA

Superfamily Anomocaroidea — **Anomocarellidae** *Glyphaspis*

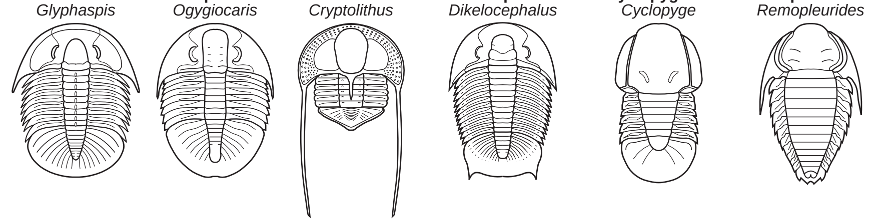
Superfamily Asaphoidea — **Asaphidae** *Ogygiocaris*

Superfamily Trinucleioidea — **Trinucleidae** *Cryptolithus*

Superfamily Dikelocephaloidea — **Dikelocephalidae** *Dikelocephalus*

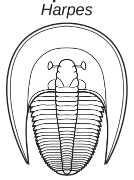
Superfamily Cyclopygoidea — **Cyclopygidae** *Cyclopyge*

Superfamily Remopleuridoidea — **Remopleurididae** *Remopleurides*



ORDER HARPETIDA

Suborder Harpetina — **Harpetidae** *Harpes*

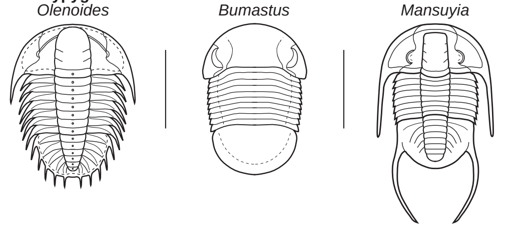


ORDER CORYNEXOCHIDA

Suborder Corynexochina — **Dorypygidae** *Olenoides*

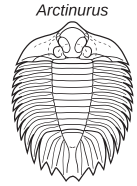
Suborder Illaenina — **Illaenidae** *Bumastus*

Suborder Leiostegiina — **Kaolishaniidae** *Mansuyia*



ORDER LICHIDA

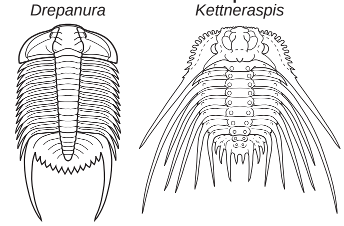
Superfamily Lichoidea — **Lichidae** *Arctinurus*



ORDER ODONTOPLEURIDA

Superfamily Dameselloidea — **Damesellidae** *Drepanura*

Superfamily Odontopleuroidea — **Odontopleuridae** *Kettneraspis*

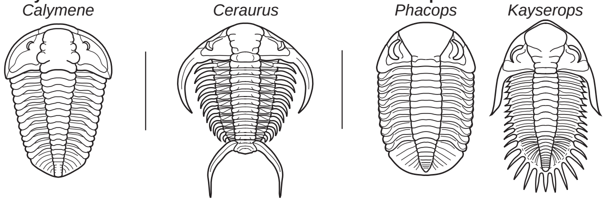


ORDER PHACOPIDA

Suborder Calymenina — **Calymenidae** *Calymene*

Suborder Cheirurina — **Cheiruridae** *Ceraurus*

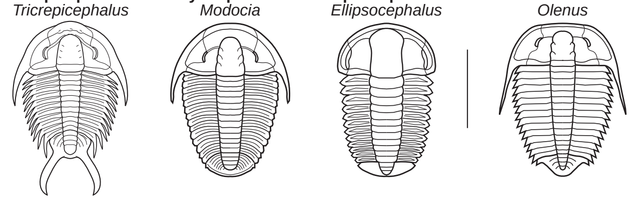
Suborder Phacopina — **Phacopidae** *Phacops*; **Acastidae** *Kayserops*



ORDER PTYCHOPARIIDA

Suborder Ptychopariina — **Tricrepicephalidae** *Tricrepicephalus*; **Ptychopariidae** *Modocia*; **Ellipsocephalidae** *Ellipsocephalus*

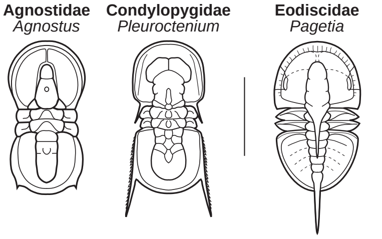
Suborder Olenina — **Olenidae** *Olenus*



ORDER AGNOSTIDA

Suborder Agnostina — **Agnostidae** *Agnostus*; **Condylopygidae** *Pleuroctenium*

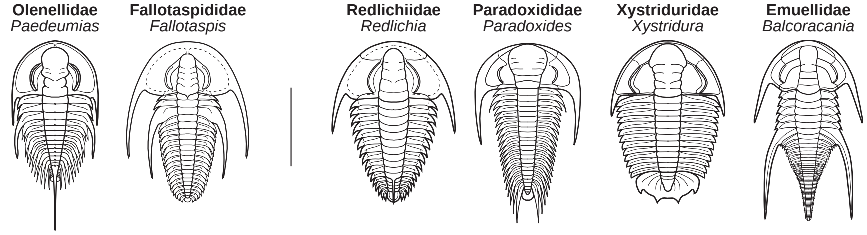
Suborder Eodiscina — **Eodiscidae** *Pagetia*



ORDER REDLICHIIDA

Suborder Olenellina — **Olenellidae** *Paedeumias*; **Fallotaspididae** *Fallotaspis*

Suborder Redlichiina — **Redlichiidae** *Redlichia*; **Paradoxididae** *Paradoxides*; **Xystriduridae** *Xystridura*; **Emuellidae** *Balcoracania*



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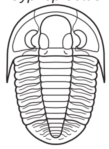
This manuscript is an adaptation of the award-winning website:

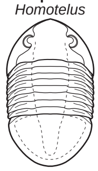
A Guide to the Orders of Trilobites

http://www.trilobites.info

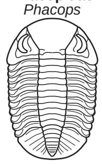
Proetidae
Cyphoproetus



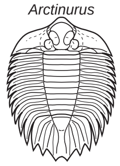
Asaphidae
Homotelus



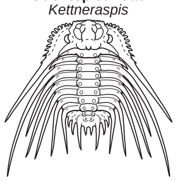
Phacopidae
Phacops



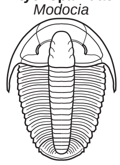
Lichidae
Arctinurus



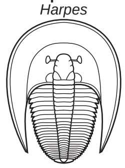
Odontopleuridae
Kettneraspis



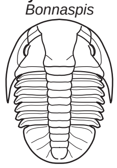
Ptychopariidae
Modocia



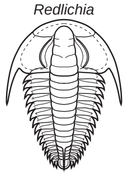
Harpetidae
Harpes



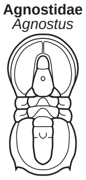
Corynexochidae
Bonnaspis



Redlichiidae
Redlichia



Agnostidae
Agnostus



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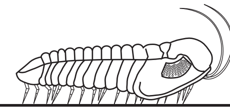
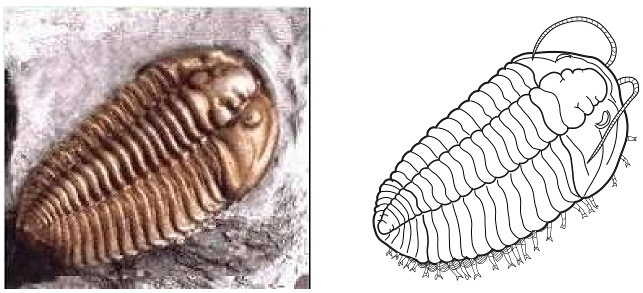
What are Trilobites?



Trilobites are hard-shelled, segmented creatures that existed over 300 million years ago in the Earth's ancient seas. They went extinct before dinosaurs even existed, and are the signature creatures of the **Paleozoic** Era, the first era to generate a diversity of complex life forms, including nearly all of the phyla of today. Although dinosaurs are the most well-known fossil life forms, trilobites are also a favorite among those familiar with **paleontology** (the study of the development of life on Earth)



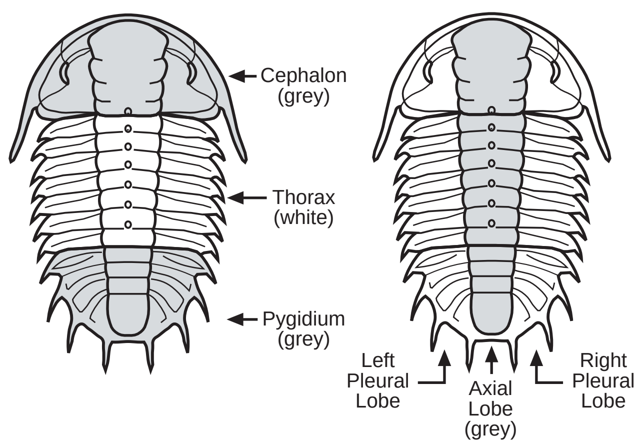
Fossil (left) and reconstruction (right) of the trilobite, *Flexicalymene meeki*

Ancient Arthropods

Trilobites were among the first of the **arthropods**, a phylum of hard-shelled creatures with multiple body segments and jointed legs. They constitute an extinct class of arthropods, the **Trilobita**, made up of nine orders, over 150 families, thousands of genera, and over 15,000 described species. New species of trilobites are unearthed and described each year. This makes trilobites the single most diverse group of extinct organisms, and within the generalized body plan of trilobites there was a great range of size and form. The smallest known trilobite is just over a millimeter long, while the largest include species from 30 to 70 cm in length (roughly a foot to over two feet long!) With such a diversity of species and sizes, thoughts on the life styles of trilobites include planktonic, swimming, and crawling forms, and we can presume they filled a varied set of ecological roles, although perhaps mostly as predators, detritivores, and scavengers. Most trilobites are about an inch long, and part of their appeal is that you can hold and examine an entire fossil animal in your hand. Try that with a dinosaur!

The 3-lobed body plan

Whatever their size, all trilobites share a similar body plan, being made up of three main body parts: a **cephalon** (head), a segmented **thorax**, and a **pygidium** (tail piece). However, the name "trilobite," meaning "three lobed," is not in reference to those three body features, but to the fact that all trilobites bear a long central axis, or **axial lobe**, flanked on each side by right and left **pleural lobes**. These three lobes that run from the cephalon to the pygidium give trilobites their name.

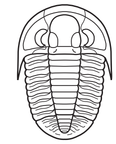


a trilobite's body can be divided into three parts both lengthwise as well as laterally.

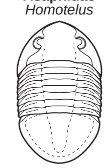
Please explore further

Trilobites are distinguished from their sister arthropods via characters thought to be unique to trilobites, including their three-lobed structure, a dorsally calcified exoskeleton, and a specialized ventral mouthpart called a hypostome. Now that you know generally what trilobites are, please explore this illustrated guide to the orders of trilobites. You'll learn about trilobite body parts, how scientists classify trilobites, when they lived, and how to tell the major groups apart. In the end, I hope you gain a better appreciation of their amazing variety. Although they are all extinct now, they were among the first explosions of biological diversity that this amazing planet of ours has produced over the eons.

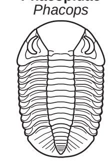
Proetidae
Cyphoproetus



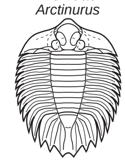
Asaphidae
Homotelus



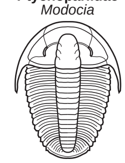
Phacopidae
Phacops



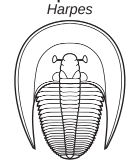
Lichidae
Arctinurus



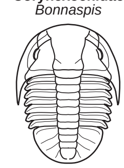
Ptychopariidae
Modocia



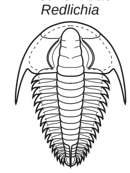
Harpetidae
Harpes



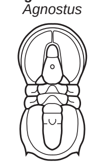
Corynexochidae
Bonnaspis



Redlichiidae
Redlichia



Agnostidae
Agnostus



Glossary of Trilobite Terms

The terms defined below appear in the descriptions of the salient characters of the trilobite orders in the fact sheets and pictorial guides. They are typically associated with a guide figure illustrating the feature.

abathochroal - eyes with compound lenses, each with separate cornea, each lens separated from others by shallow scleral walls; corneal membrane ends at lens edge. see holochroal, schizochroal.

adaxial - toward the axis (center line).

articulating facets - see facets.

atheloptic- deep water forms with absent or reduced eyes.

axial - pertaining to the axis.

axis - central lobe running the length of the trilobite body; the glabella is the main expression of the cephalic axis.

cephalic - pertaining to the cephalon.

cephalon - frontmost trilobite part; head.

coaptation - close interlocking of opposing surface during enrollment.

conterminant - hypostome attached to anterior doublure via suture. see impendent, natant.

dorsal - referring to the top or back surface, as opposed to ventral.

doublure - shell continuation under the trilobite, typically as a ventral cephalic and/or pygidial rim.

effacement - loss of detail.

enrollment - bending of the body to enclose vulnerable ventral organs in a protective clam-like or sphereoid capsule formed by the cephalon, pygidium and thoracic segments.

facets - flat surfaces, typically where two adjoining body parts meet and articulate (move); *e.g.*, articulating facets on thoracic pleural segments.

fixigena - "fixed cheek" cephalic shell surrounding glabella inside of facial sutures. see gena, librigena.

fulcrate - referring to thoracic segments with a geniculation (bend) separating a horizontal inner portion from an inclined outer portion.

gena - cephalic shell of the cephalon surrounding the glabella, usually divided by sutures into fixigena and librigena. (pl., genae)

genal angle - angle formed by the meeting of the lateral (side) and posterior (rear) margins of the cephalon; sometimes expressed as a genal spine.

genal spine - a spine anywhere on the gena (cheek) of the cephalon, typically at the genal angle.

glabella - middle (axial) portion of cephalon, typically convex and lobed.

gonatoparian - facial sutures ending at the tip of the genal angle.

granulate - bearing granules or similar sculpturing on the outer exoskeleton.

holaspis - final developmental stages beyond meraspis, attaining a certain number of thoracic segments considered typical of "adult" individuals, and typically with cephalic and pygidial characters of the adult form. (pl. holaspides) see meraspis, protaspis.

holochroal - eyes with compound lenses directly in contact, all covered by a single continuous smooth corneal surface. see abathochroal, schizochroal.

hypertrophy - grown well beyond normal size.

hypostomal - pertaining to the hypostome.

hypostome - a piece of exoskeleton on the venter (underside) of the cephalon, thought of as a mouthpart. Typically the anterior edge of the hypostome lies directly under the anterior edge of the glabella.

impendent - type of conterminent hypostomal attachment, with doublure abutting anterior hypostomal border so it is not conterminant with anterior glabellar border. see conterminant, natant.

isopygous - cephalon and pygidium similar in size. see micropygous, macropygous.

konservat-lagerstatten- fossil deposits where soft tissues or other rarely-preserved features are conserved.

librigena - "free cheek" cephalic shell to the right and left of the glabella outside of facial sutures, often lost during molting or after death. see fixigena, gena.

macropygous - pygidium larger than cephalon. see isopygous, micropygous.

meraspis - developmental stage following protaspis, bearing more than one segment, but with fewer than the adult number of thoracic segments. (pl. meraspides). see protaspis, holaspis.

micropygous - pygidium much smaller than cephalon. see isopygous, macropygous.

natant - hypostome free, not attached to the cephalic doublure.

occipital - pertaining to the occiput.

occiput - posterior portion of cephalon, the axial portion is considered part of the glabella (occipital ring).

opisthoparian - facial sutures ending along the rear margin of the cephalon adaxial to the genal angle. see gonatoparian, proparian.

opisthothorax - posterior, narrower portion of thorax when it is divided into wider, anterior prothorax and posterior opisthothorax.

palpebral lobe - portion of fixigena associated with the eye.

perrostral - along the edge of the rostrum.

pleura - lateral (side) part of thoracic segment or lateral (non axial) part of pygidium. (pl. pleurae)

pleural - referring to pleurae.

postaxial - behind the end of the axis.

preglabellar area - portion of cephalon in front of glabella.

proparian - facial sutures ending forward of the genal angle.

protaspis - earliest developmental stage, lacking segments. (pl. protaspides). see meraspis, holaspis.

prothorax - anterior and wider portion of thorax when it is divided into prothorax and narrower, posterior opisthothorax, as seen in some Redlichiida.

pygidial - pertaining to the pygidium.

pygidium - hindmost segment; tail.

pyriform - pear-shaped, typically referring to the glabella

rostral plate - middle portion of the cephalic doublure, typically defined by sutures; the hypostome typically attaches to the rostral plate; also called rostrum.

schizochroal - eyes with compound lenses, each with separate cornea, each lens separated from others by deep scleral walls; corneal membrane extends downward into sclera. see abathochroal, holochroal.

scleral - of or similar to dorsal exoskeletal shell. see sclerite.

sclerite - segment of dorsal exoskeleton.

spinose - bearing a spine or spines.

subisopygous - pygidium large, but not quite as large as cephalon.

subparallel - nearly parallel in arrangement, slightly diverging or converging.

suture - linear break in exoskeleton, typically along which parts separate during molting.

thorax - middle, segmented body portion between cephalon and pygidium. see prothorax, opisthothorax

thoracic - pertaining to the thorax.

tuberculate - bearing tubercles or similar sculpturing on the outer exoskeleton.

ventral - referring to the underside.

vincular furrow - a groove along the anterior and/or lateral cephalic doublure to accommodate the edge of the pygidium and thoracic pleurae during enrollment (*e.g.*, a feature of some Phacopida).

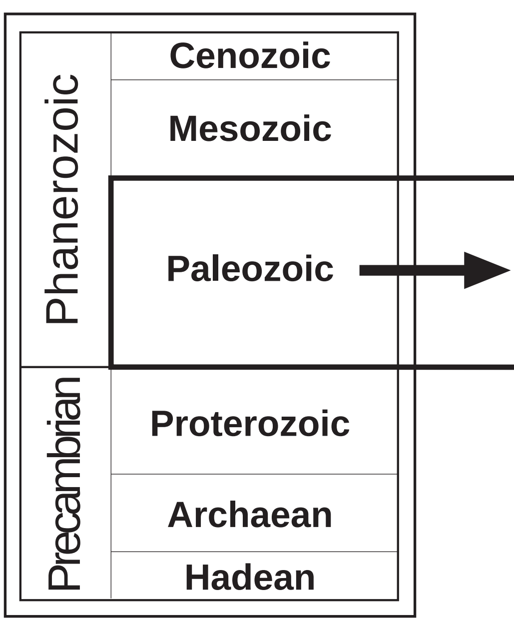
When Did Trilobites Exist?

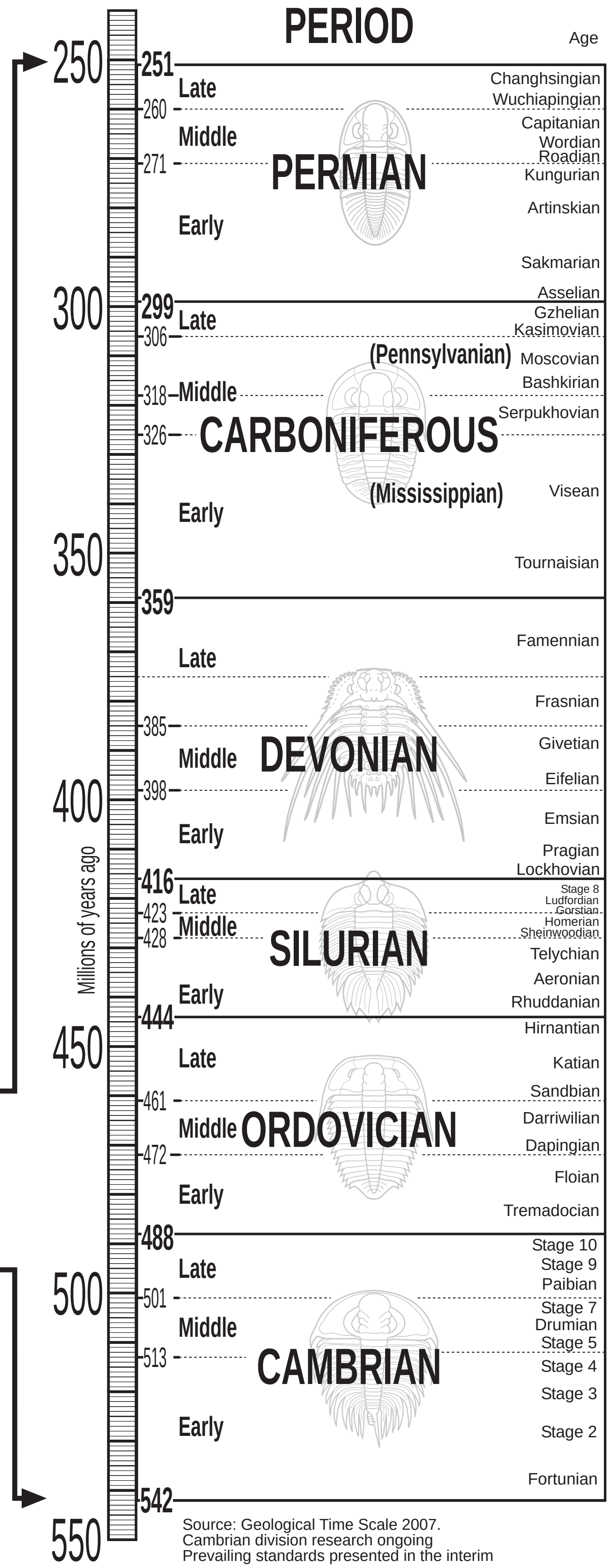
(Geological time from a trilobite's point of view)

This chart depicts the geological periods of the **Paleozoic Era**, during which trilobites lived. Trilobites are one of the diagnostic fossils of the Paleozoic Era, the earliest era of the **Phanerozoic Epoch**. The Paleozoic portion of the geological scale at bottom left is expanded on the right as geological **periods**, and the scale indicates how many millions of years ago (mya) each period spanned.

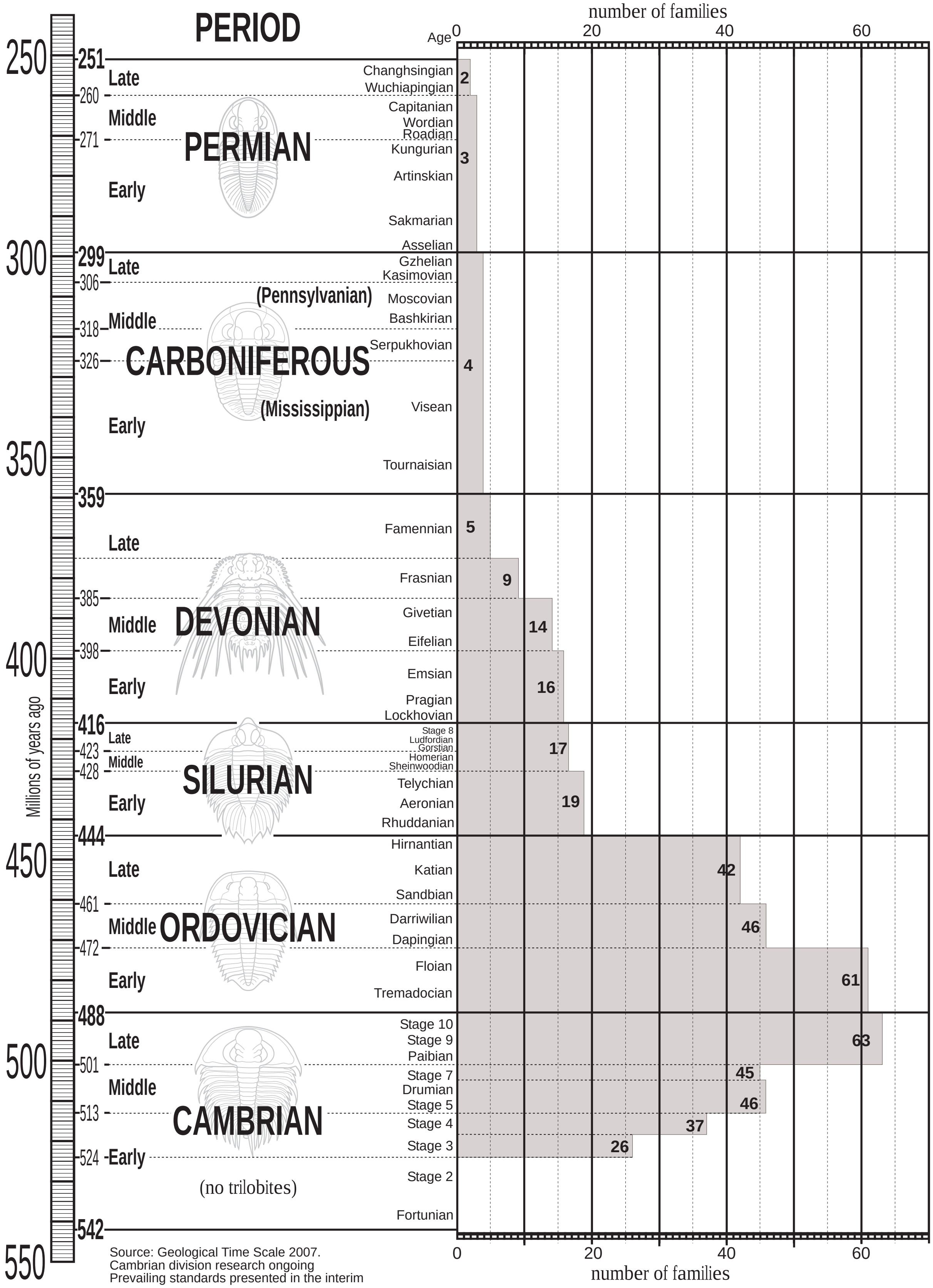
Trilobites can be found from the Early **Cambrian** period (544 mya) to the Late **Permian** (245 mya), after which trilobites (among a large number of marine organisms) went extinct in the great catastrophe that removed an estimated 90%+ of all species on earth. The **Great Permian Extinction** marks the end of the **Paleozoic** and the start of the **Mesozoic**. Trilobites are one of the few organisms that existed from the start to the end of the Paleozoic Era.

The greatest numbers of species and forms of trilobites lived during the **Cambrian** and **Ordovician** periods, after which trilobites began to decline (see Chart of trilobite family diversity over time). There were far fewer species in the **Carboniferous** and **Permian** periods. Nevertheless, to have persisted for nearly 300 million years is a testimony to the successful design and adaptability of trilobites. Some scientists even hold faint hope that in poorly explored deep sea environments, trilobites may still exist, a holdover from truly ancient times.





The Rise and Fall of Trilobites



Systematic Relationships and General Chronological Extent of the Trilobite Orders

Although higher level classification of trilobites is a contentious subject, the discussion by Fortey in the 1997 Treatise suggests an arrangement that might look something like the figure on page 8. The Redlichiida (particularly the Suborder Olenellina) is considered primitive, appearing in the Lower Cambrian, and not persisting into the Ordovician. The Agnostida also appear early and persist to the end of the Ordovician. The Redlichiida give rise to at least the Corynexochida, and the Ptychopariida (both in the Lower Cambrian). The Lichida may have arisen from early Corynexochida or Redlichiida. Both the Redlichiida and the Ptychopariida, as large primitive groups containing the ancestors of other orders, must be paraphyletic. In fact, in 2002 another order was split out of the Ptychopariida, the Order Harpetida (formerly suborder Harpina of the order Ptychopariida)

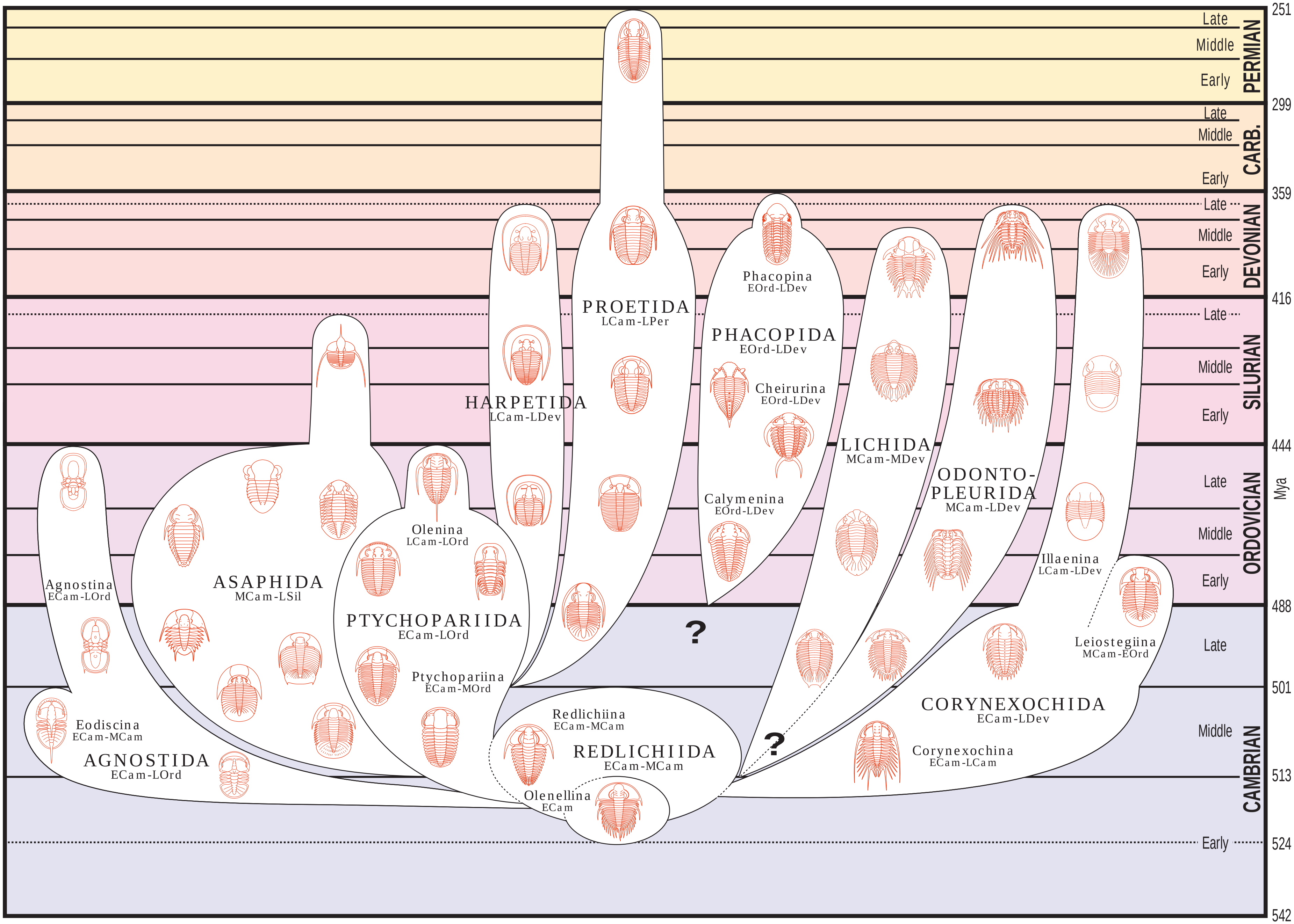
The Ptychopariida, Harpetida, Asaphida, and Proetida share (in at least the primitive forms) species with a natant hypostomal condition (leading Fortey (1990) to suggest the natural group Libristoma for these orders combined) but this has been challenged recently (Jell 2003). The recognition of Asaphida, Proetida, and Harpetida as orders is a relatively recent thing; in the 1959 Treatise they were all included in the Ptychopariida. The Ptychopariida and Harpetida maintain the natant state until their extinction at the end of the Devonian, but both the Asaphida and the Proetida develop secondarily conterminant and impendent hypostomes in their advanced forms. The great extinction event at the end of the Ordovician greatly affected trilobites, ending the Olenina, Agnostida and the vast majority of Asaphida. The remainder of the Asaphida (superfamily Trinucleioidea) are lost before the end of the Silurian, and all other orders except Proetida are lost by the end of the Devonian (most in the great extinction event between the Frasnian and Famennian ages, but one family, the Phacopidae, hangs on until the Devonian-Carboniferous transition). The Proetida persist until the end of the Permian, the last of the orders of trilobites to go extinct.

The origin of the Phacopida is uncertain. The three suborders (Phacopina, Calymenina, and Cheirurina) share a distinctive protaspis type; suggesting phylogenetic closeness. The Calymenina is perhaps the most primitive of the Phacopida, and share several characters with the Ptychopariida (including a few species with natant hypostomes), so although the hypostomal condition of the Phacopida is typically conterminant they may have had their origins with the natant Ptychopariida. Others point out the conterminant hypostomal condition, and some similarities in the exoskeleton tuberculation of Phacopida and Lichida, so the ancestral sister group of the Phacopida remains unclear.

On what basis, then, are the orders defined? Each is arguably a natural group sharing key character innovations. No single character (*e.g.*, facial suture types) dominates in higher level classification. instead, such characters as facial sutures, glabellar shape and pattern of lobation, eyes, thoracic segment number and features, pygidial shape, size and segmentation, and spinosity or surface texture and sculpture all play a role in helping define the orders. In addition, shared hypostomal conditions and patterns of early ontogeny play important roles in defining the orders of trilobites. That is why for each of the order fact sheets, as many of the above details are provided as possible.

Important note on the use of this figure: This diagram was created by Sam Gon III, based on information available in the literature, particularly the 1997 revision of the Treatise, and Fortey's 2001 synopsis of Trilobite Systematics. This figure should not be used for any purpose other than its original intent; to share with others interested in trilobites the slowly growing understanding of the relationships between the higher taxonomic units. Any similarity between this and figures published elsewhere are unintentional. I have not seen any handling of quite this sort in the literature. Any inaccuracies are entirely mine. For example, the chronological extent of the Leiostegiina is unclear (since its taxonomic status is controversial). The uncertain origins of the Phacopida and Lichida are depicted with question marks. This figure is likely to change, as our understanding of trilobite higher classification improves.

Systematic Relationships and Chronological Extent of the Trilobite Orders



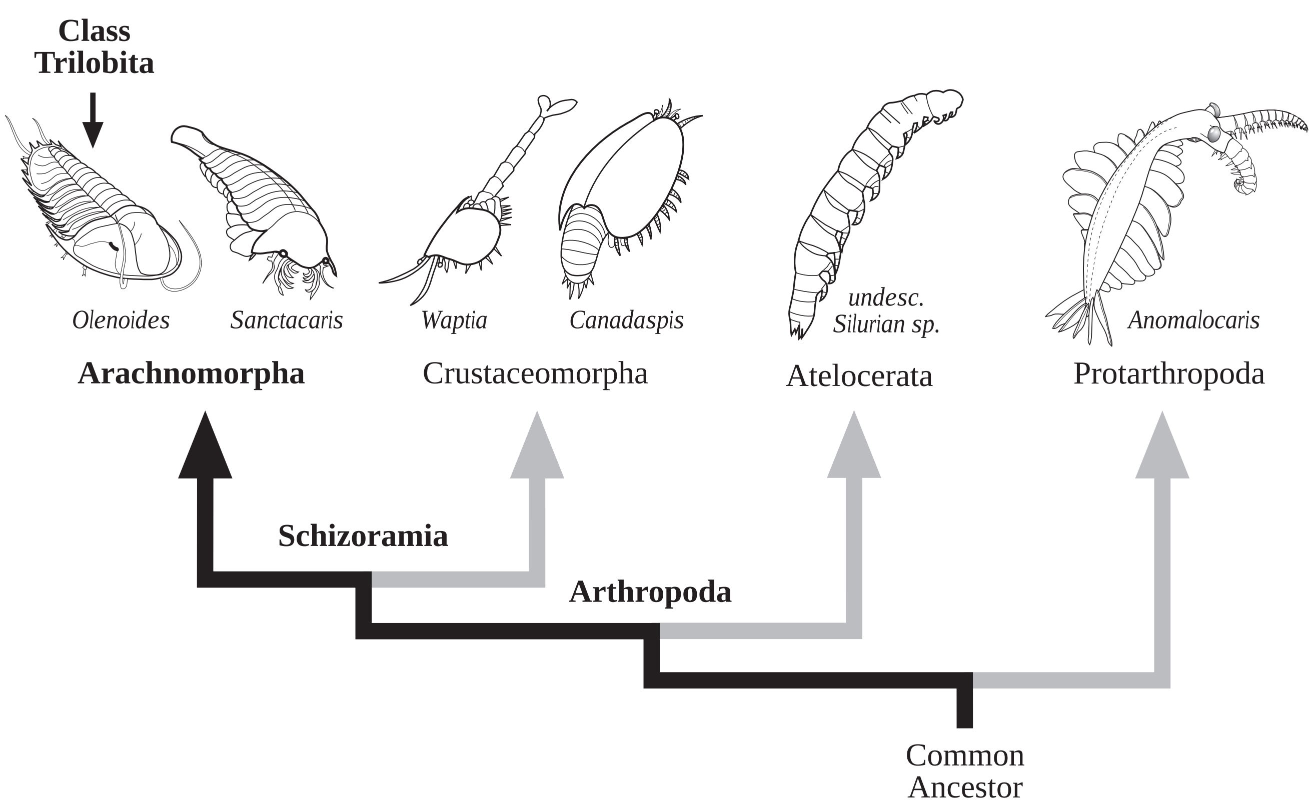
Trilobites among the Major Arthropod Groups

Trilobites had long been considered the most primitive of **Arthropods**, being among the first Cambrian arthropods discovered, but this was an artifact of preservation. When the Burgess Shales and other similar Cambrian *Konservat-Lagerstätten* deposits were discovered, large numbers of Cambrian arthropod species (that typically do not preserve well) were revealed as contemporaries of trilobites, which are now considered relatively advanced among the Paleozoic arthropods.

In the 1959 Treatise, many of the Burgess Shale animals were included in the Subphylum Trilobitomorpha. Today that subphylum is no longer considered valid. One prevalent recent classification recognizes the **Class Trilobita** sitting comfortably within the **Superclass Arachnomorpha** (an expanded concept based on the Chelicerata), alongside the **Superclass Crustaceomorpha** (based on an expansion of the Crustacea), together comprising the **Subphylum Schizoramia** (Arthropods bearing biramous limbs) contrasting with the **Subphylum Atelocerata** (insects, myriapods, and allies).

While there is certainly a great deal of diversity of form among the arthropods and near-arthropods (such as the protarthropod *Anomalocaris*), it seems reasonable that shared common ancestry in the Pre-Cambrian was the basis for the dramatic radiations of the early Cambrian, such as seen at the Burgess Shale (Canada), Chengjiang (China) and Sirius Passet (Greenland). This shared ancestry and close relationship despite seemingly great divergence of form is seen in the very similar molecular biology of modern crustaceans and insects, and suggests to some workers that the Subphylum and Superclass designations for the Arthropoda may be superfluous.

TRILOBITA AMONG THE MAJOR CLADES OF PALEOZOIC ARTHROPODA



In this classification, Trilobites are a Class within the Superclass Arachnomorpha, one of two Superclasses within the Subphylum Schizoramia of the Phylum Arthropoda.

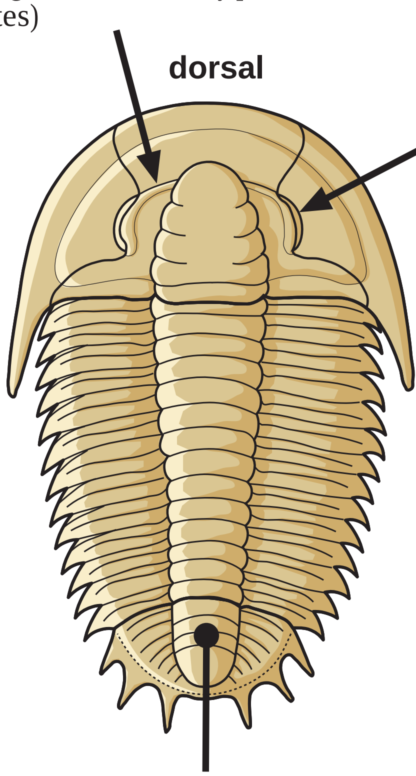
What distinguished Trilobites among Arthropods?

Trilobites are the most diverse of the extinct arthropod groups, known from perhaps 5000 genera. The classification of trilobites within the Arthropoda has generated much controversy, much of which is still not completely resolved. There are a number of characters that most workers agree distinguish trilobites from within the Arachnomorph clade, the most significant described below:

eye ridges: These are consistently present in primitive forms, connecting the front of the palpebral lobe with the axial furrow. Eye ridges are lost in many post-Cambrian trilobites)

calcitic eyes: While other compound eyes are found in Cambrian arthropods, only those of trilobites have corneal surfaces composed of prismatic calcite lenses (with the crystallographic axis perpendicular to the lens surface).

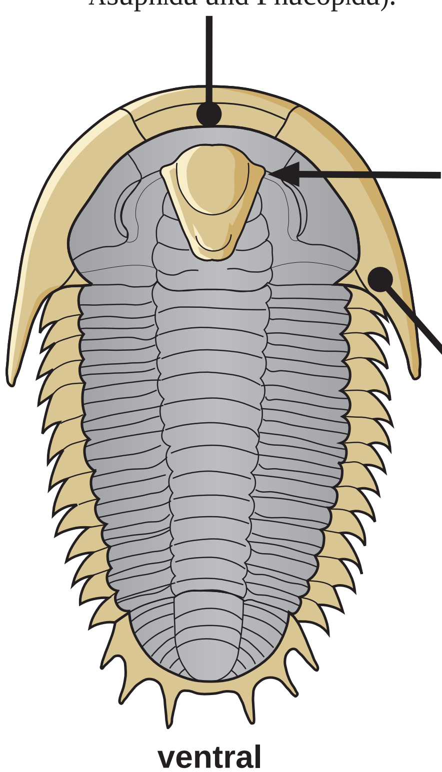
circum-ocular sutures: In Cambrian holochroal trilobite eyes, a suture around the edge of the shared corneal surface assisted in molting of holaspid trilobites. In post-Cambrian trilobites this feature is secondarily lost, leaving the corneal surface attached to the fixigena.



pygidium: The posterior tagma (body division) of >1 segment is a conspicuous feature of trilobites, primitively small (*e.g.*, in Olenellina).

rostral plate: A ventral anterior plate separated from the rest of the cephalic doublure by sutures is very well developed in primitive trilobites (*e.g.*, Redlichiida), narrower in other trilobite orders, and secondarily lost in some advanced forms (*e.g.*, Asaphida and Phacopida).

hypostomal wings: The trilobite hypostome may be homologous to the labrum in Crustacea, but only trilobite hypostoma bear anterior wings which fit in pits in the anterior axial glabellar furrows (or homologous locations).

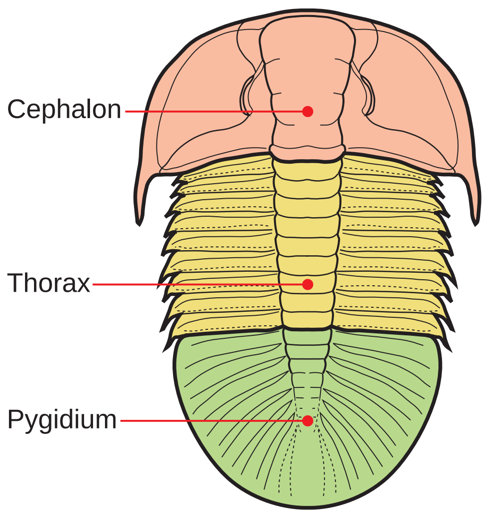


calcified cuticle: Trilobites bear a rather pure calcareous cuticle that ends ventrally at the inner edge of the doublure. Although a few other arthropod groups calcify, none do so in the same way as trilobites. Crustacea, for example, are calcified ventrally and post-orally, so their appendages are calcified.

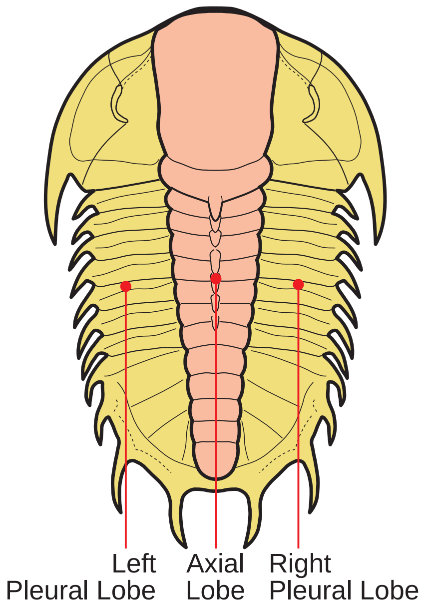
Together with the organization of the body into three anterior-posterior divisions (cephalon, thorax, and pygidium), and the three longitudinal lobes (axial lobe and two flanking pleural lobes), the body features on this page serve to readily distinguish trilobites from all other known Arthropod groups.

Major Trilobite Features

The major trilobite body features (those which generally distinguish trilobites from other Paleozoic arthropods) are summarized and illustrated here. Most of these terms figure prominently in trilobite descriptions. More detailed charts of trilobite dorsal and ventral morphological terms are presented elsewhere in this guide, as well as a glossary of terms.



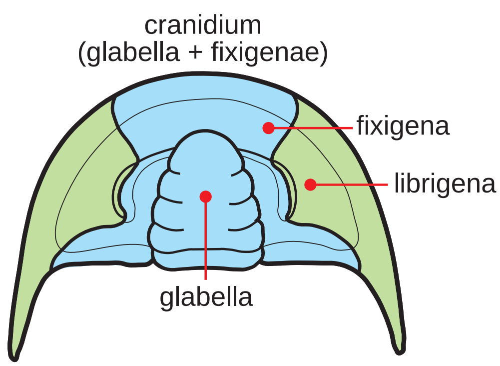
The trilobite body is divided into three major sections: a **cephalon** with eyes, mouthparts and sensory organs such as antennae, a **thorax** of multiple articulating segments (that in some species allowed enrollment), and a **pygidium**, or tail section, in which segments are fused together. These divisions are easily discerned in the dolichometopid trilobite *Bathyuriscus elegans*.

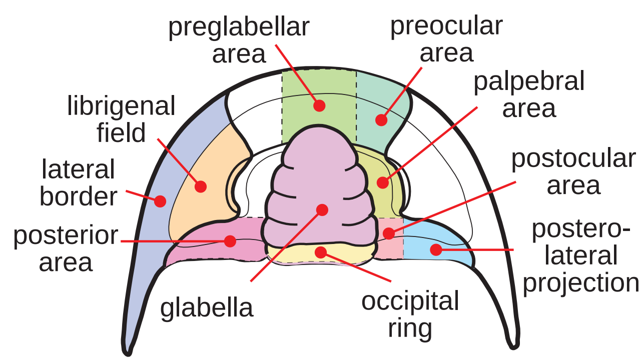


The name **"trilobite"** (meaning "**three-lobed**") is *not* based on the body sections cephalon, thorax and pygidium, but rather on the three longitudinal lobes: a central **axial lobe**, and two symmetrical **pleural lobes** that flank the axis. In the corynexochid trilobite *Dorypyge*, deep axial furrows clearly separate the axis from the two lateral lobes along the entire length of the body.

Major Trilobite Features

CEPHALIC FEATURES:
Perhaps the most important feature used to distinguish trilobite species is the cephalon, or head piece. Features of the cephalon are shown below. These are subdivisions that often assume different shapes or sizes relative to each other in different species. These are typically demarcated by the glabella, by the eyes and eye lobes, and by the facial sutures that separate the librigenae (free cheeks) from the central cranidium (see left, below).



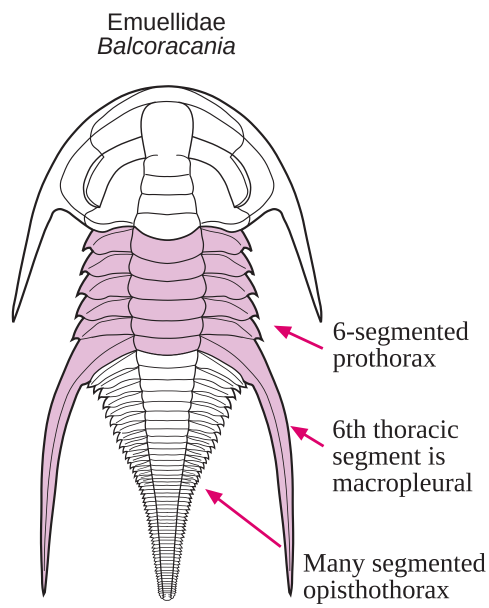


The cheeks (genae) are the pleural lobes on each side of the axial feature, the glabella. When trilobites molt or die, the librigenae (free cheeks) often separate, leaving the cranidium (glabella + fixigenae) behind.

When describing distinguishing characters between different taxa of trilobites, the presence, size, and shape of the cephalic features labeled above are often described and contrasted.

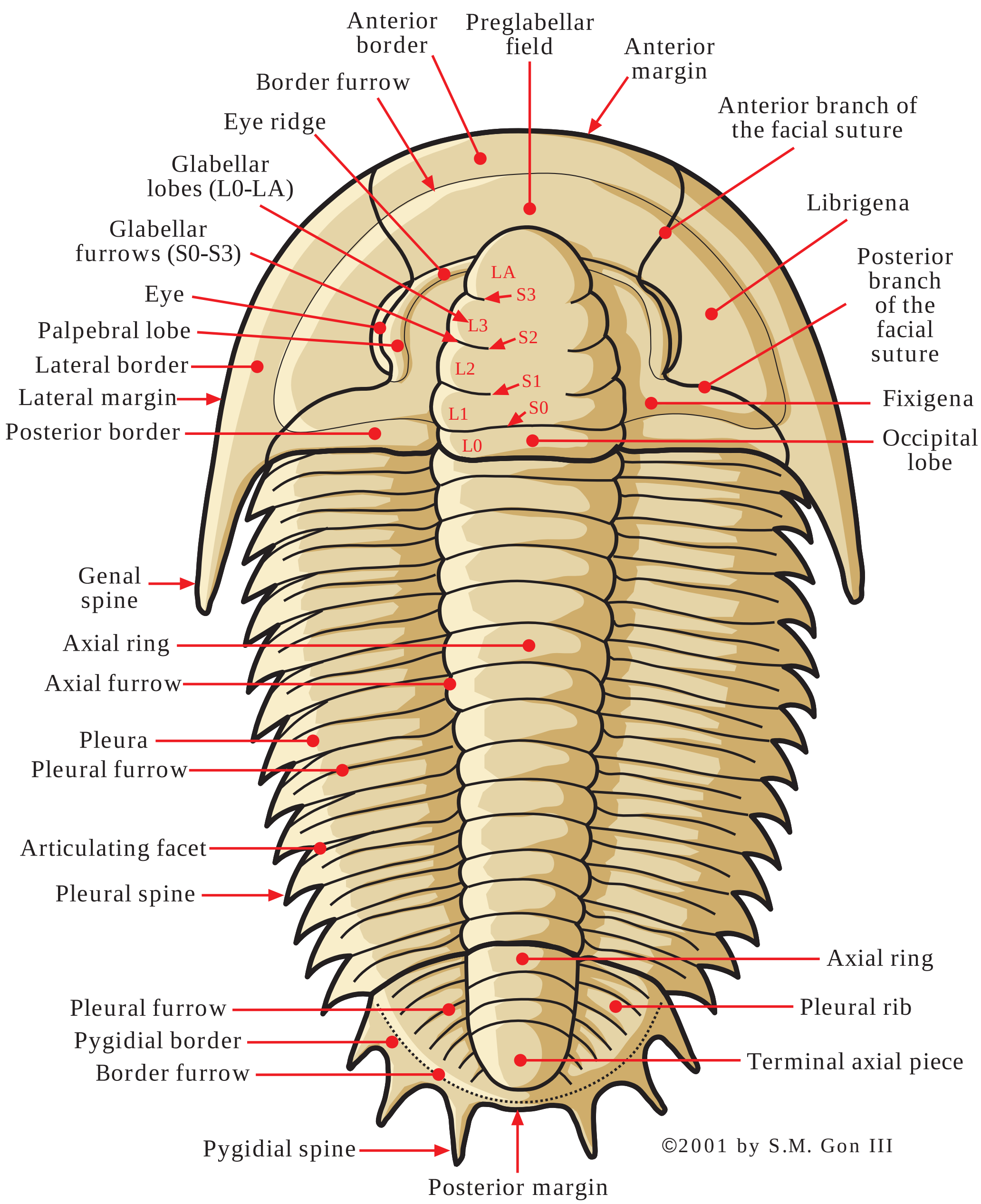
THORACIC FEATURES:
In some trilobites, the thorax may be divided into an anterior **prothorax**, followed by a posterior (often many-segmented) **opisthothorax**. This is seen in some of the Order Redlichiida, such as *Balcoracania* (see figure and image to right). Sometimes, one pleural segment is prominent in size, and is referred to as a **macropleural** segment. This is seen in many species of the suborder Olenellina of the order Redlichiida.

The majority of trilobites do not show the prothorax-opisthothorax division or the presence of macropleural segments.



Trilobite Dorsal Morphology

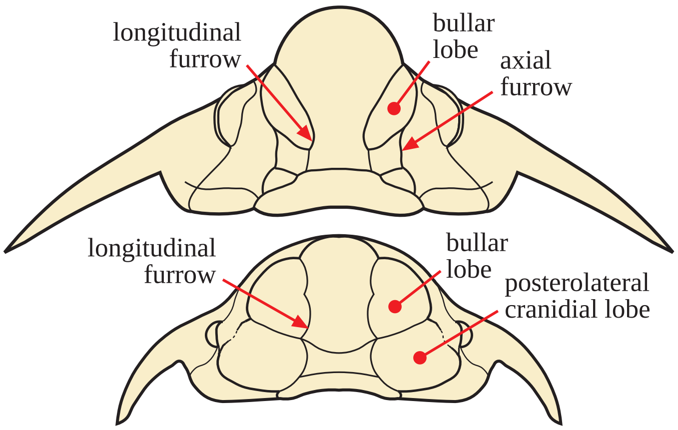
The dorsal (top) structures of a trilobite are the parts typically preserved. This is presumably because the ventral (underside) exoskeleton was either much thinner, or did not include the calcite minerals that facilitated preservation of the dorsal shell. Because of this, dorsal characters are most frequently used in trilobite classification. The image below includes most of the **dorsal morphological terms** used to define trilobite taxa. **Ventral morphology** (see page 15) can also be important. For example, there are terms describing the way the **hypostome** (a hard mouthpart on the underside of a trilobite) attaches to the rest of the cephalon. There are also broader terms that refer to **major body divisions** such as cephalon, pygidium, cranidium, axis, etc. There are some terms that relate to the relative sizes of the cephalon and pygidium. **Facial sutures** (lines along which the cephalic exoskeleton split to allow molting) are also important in classifying trilobites. There was also significant variation of trilobite eyes. We don't know very much about a trilobite's **internal anatomy**, with some exceptions! More detailed definitions of most the terms in the images below are provided in the **glossary** (page 2).



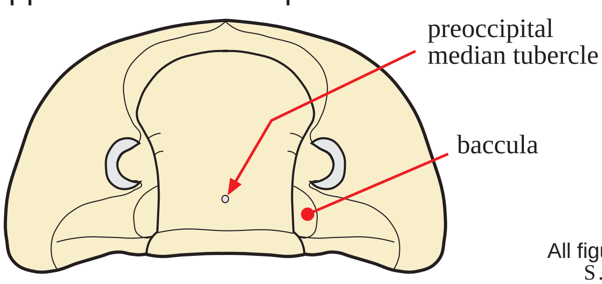
Trilobite Dorsal Morphology

Although the general terms for dorsal morphology of trilobites can be applied to all trilobites, there are some features that are only shared by specialized groups. These receive special terms designed to be used when describing these groups. Some examples of these are given below:

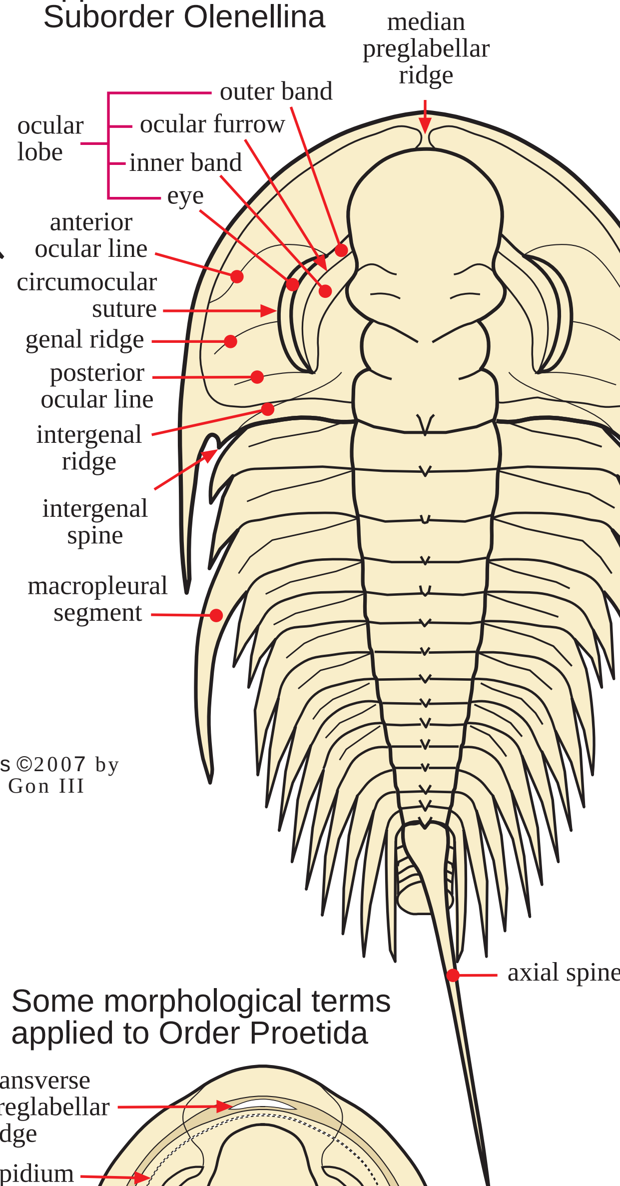
Some morphological terms applied to Order Lichida



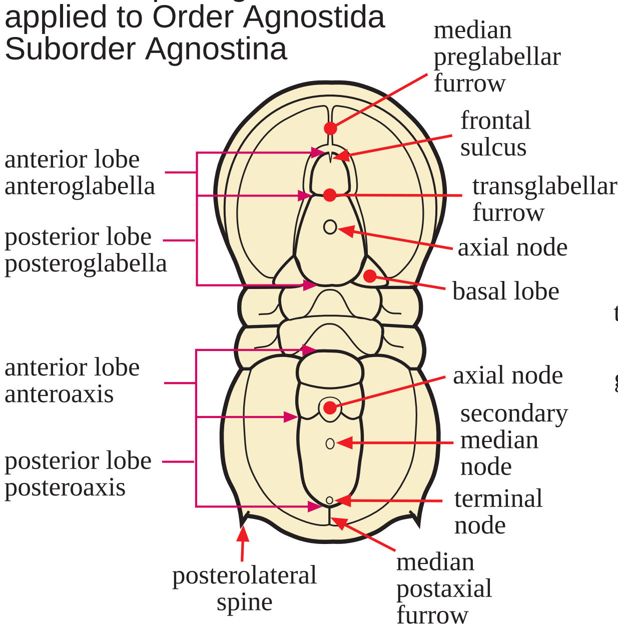
Some morphological terms applied to Order Asaphida



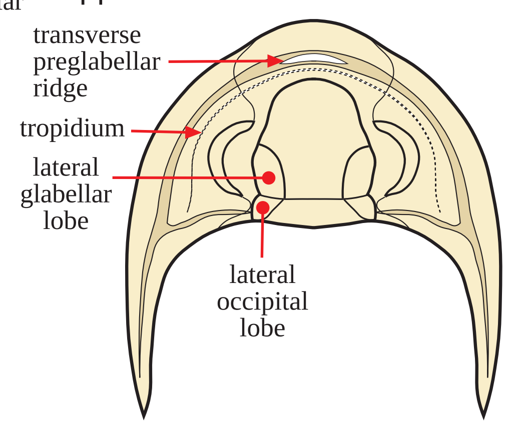
Some morphological terms applied to Order Redlichiida Suborder Olenellina



Some morphological terms applied to Order Agnostida Suborder Agnostina



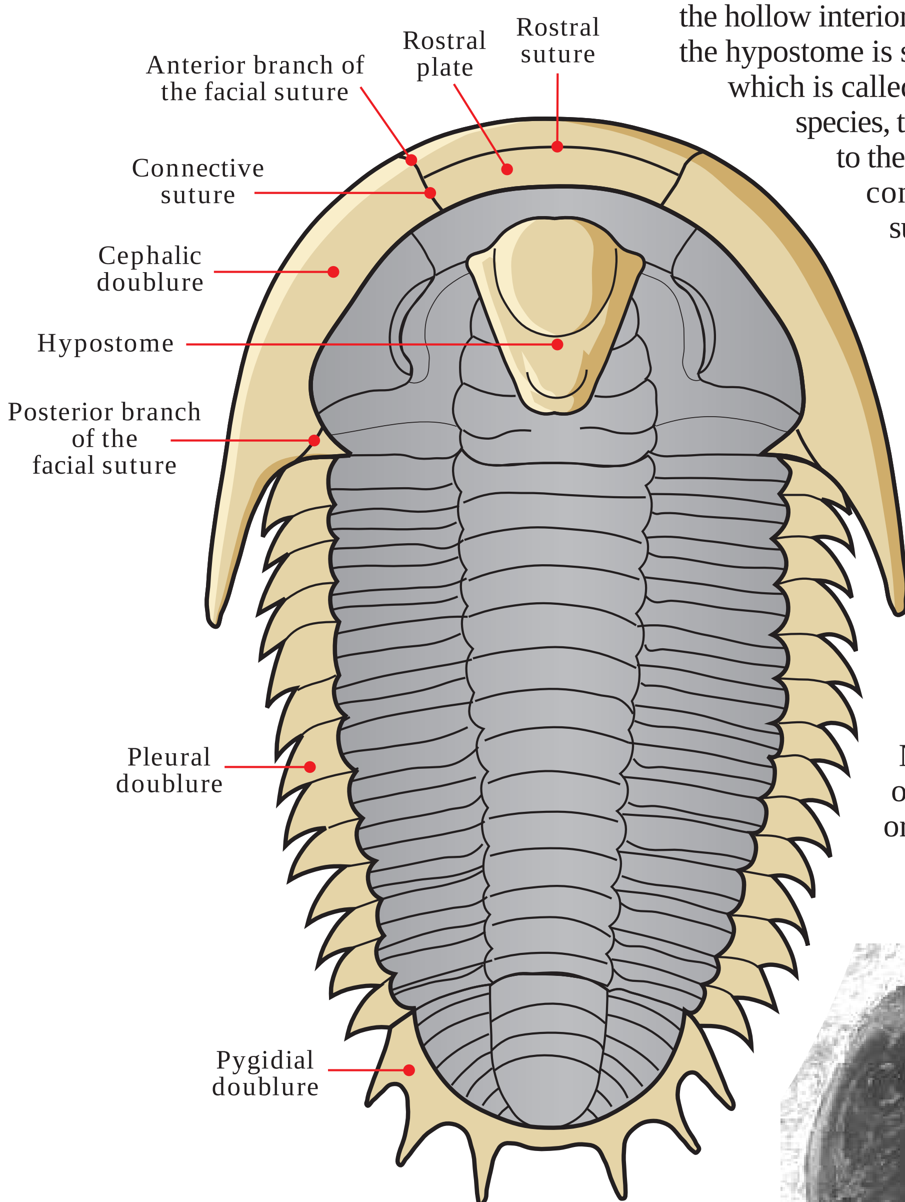
Some morphological terms applied to Order Proetida



Trilobite Ventral Morphology

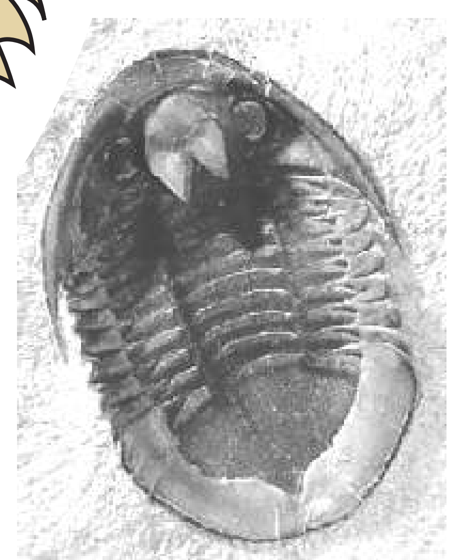
Unlike the thicker dorsal shell of a trilobite, many of the ventral (underside) features, including limbs and antennae, usually are not preserved. The portions that are typically preserved include the **doublure** (a ventral extension of the dorsal exoskeleton), a special part of the doublure, typically separated by sutures at the anterior of the cephalon, called the **rostral plate** (or rostrum), and a hard mouthpart called the **hypostome**, that typically underlies the glabella (sometimes attached to rostral plate, and sometimes free (as below).

In the figure below, the dark gray area represents the hollow interior of the dorsal shell. In this case, the hypostome is separated from the rostral plate, which is called the **natant** condition. In other species, the hypostome may be connected to the rostral plate (the **conterminant** condition), separated only by a suture, or even fused to the rostral plate. These **hypostome types** are important in trilobite classification, and are discussed in their own section elsewhere in this guide.

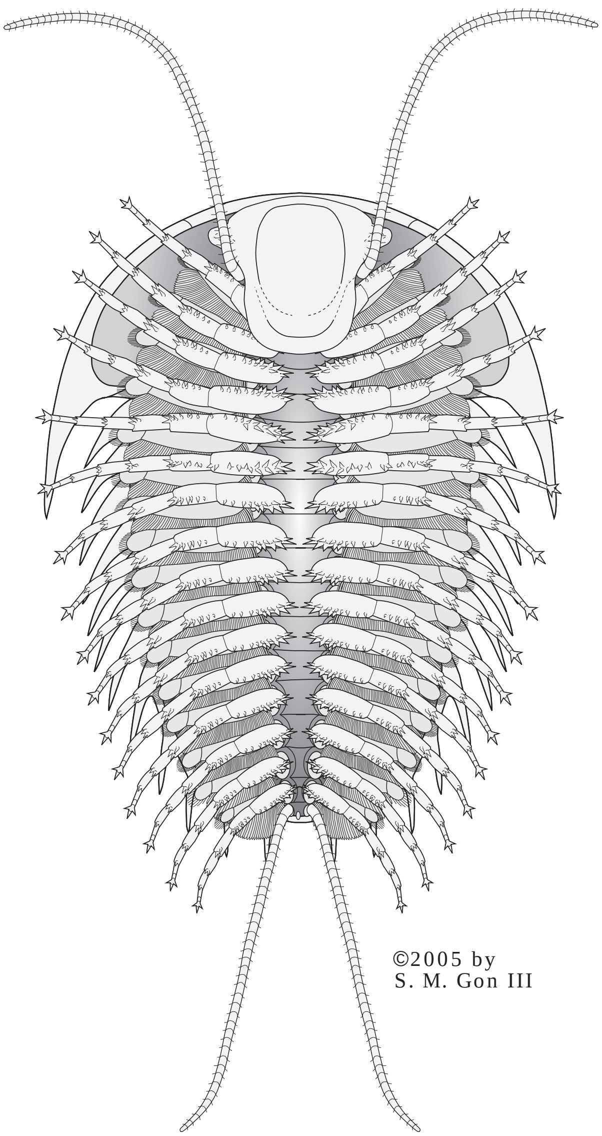


©2001 by S.M. Gon III

Below is an excellent ventral preparation of the Russian trilobite *Asaphus platyurus* from the museum website of the Saint-Petersburg Paleontological Laboratory. Note the wide pygidial doublure, often seen in members of the order Asaphida.



Trilobite Ventral Structures



In this depiction, the limbs and other ventral structures of *Olenoides serratus* are shown. As mentioned above, only rarely are these structures preserved and fossilized (other than the hypostome). Such deposits where soft-tissues are conserved are called *Konservat-Lagerstätten*, and are extremely valuable for providing a rare glimpse of not only trilobite ventral and internal structures, but taxa that do not typically preserve well.

Long, many-segmented antennae emerge from notches on the sides of the hypostome (which hides the mouth), and many pairs of legs, varying very little except in size, proceed from the cephalon to the pygidium. This primitive lack of specialization along the length of the body is one of the features of trilobite limbs.

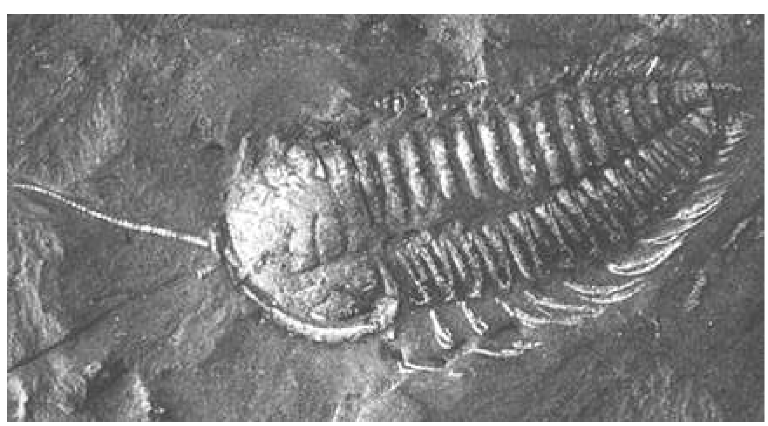
Between the crawling limbs (endopodites) and the body are pairs of finely-branched exopodites that probably served as gills. It is thought that movements of the gills and legs might have allowed at least some trilobites to swim (as similar movements provide swimming locomotion in modern marine and freshwater arthropods).

The limbs are attached to a sequential set of axial sternites (ventral segments), and each of the bases of the limbs possess jagged tooth-like structures called gnathobases that are thought to have processed food and passed food particles forward to the hypostome and mouth.

Finally, at the rear of the trilobite, two antenna-like cerci (sense organs) are depicted, although of all trilobites with preserved limbs, only *Olenoides serratus* is known to have borne them.

How do we know about the limbs and antennae of trilobites?

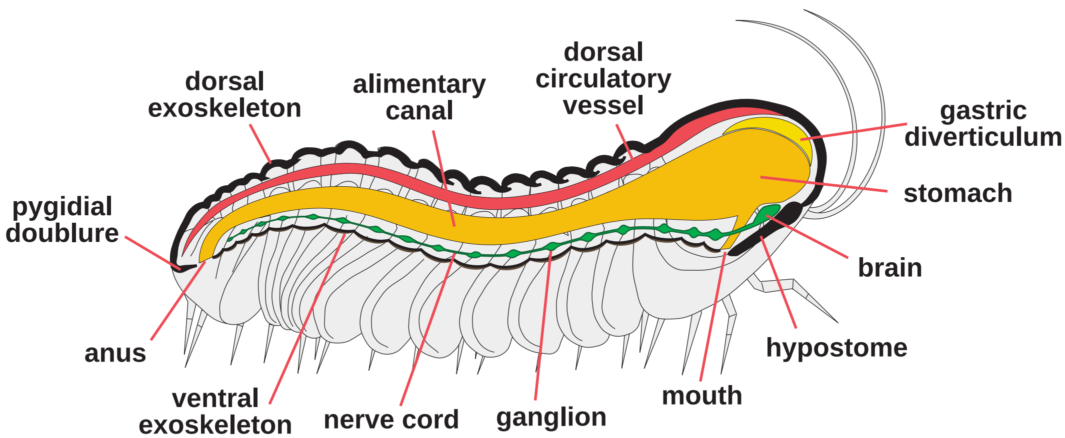
Very rarely, conditions for preservation are so good that these delicate features are preserved. To the right is an example of the olenid trilobite *Triarthrus eatoni* showing preserved antennae, legs, and gill filaments. X-ray images of these specimens reveal even more details of ventral and internal structures.



This image can be found at the website: Per Hansson's Trilobite Gallery.

Trilobite Internal Anatomy

The **dorsal morphology** of trilobites is typically well preserved, and **ventral features** such as limbs and antennae are only rarely preserved. That being the case, the **internal anatomy** of trilobites is **very poorly understood**. X-ray images of some trilobite specimens indicate a long, central structure typically considered an **alimentary canal** (intestines or gut). Only in extremely well-preserved **Agnostid** specimens has a trace of a **mouth** and **anus** been detected. The mouth is ventral to the rear edge of the **hypostome**, and the anus opens toward the rear of the **pygidium**, as might be expected. The images below are derived from several sources, including both Treatises (1959 and 1997). Most workers rely on knowledge of living arthropod anatomy and presume that trilobites had similar (if perhaps more primitive) circulatory, nervous, and muscular systems. This leads to reconstructions as below:

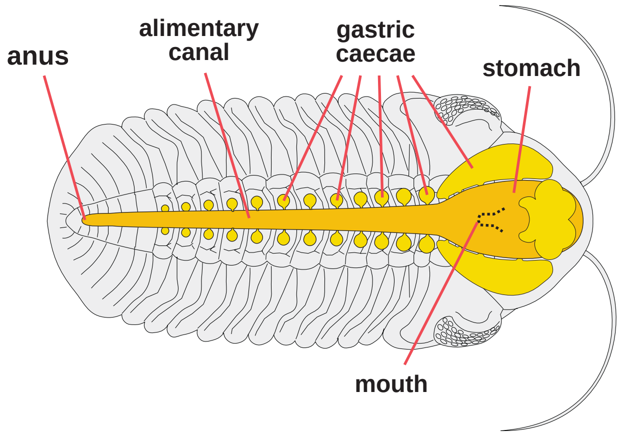


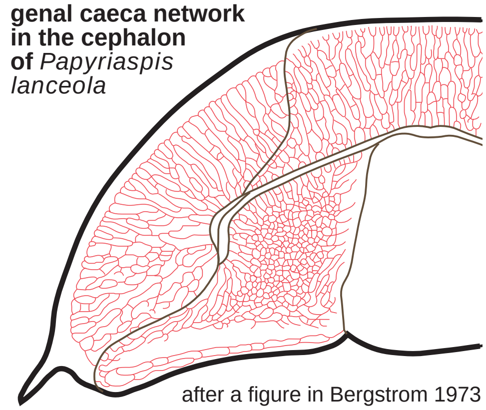
Internal features of a trilobite

In the figure above, a longitudinal sagittal section taken through the midline of the axis of a phacopid trilobite reveals some of the major systems. The thick **dorsal exoskeleton** and much thinner **ventral exoskeleton** are shown. The **dorsal circulatory vessel** (heart) underlies the exoskeleton. Modern arthropods have an open circulatory system in which internal organs are bathed in hemolymph (blood) which is circulated through contractions of the dorsal circulatory vessel. The fine branches of subcuticular blood vessels sometimes show up as fine networks in the dorsal cephalic and pygidial exoskeleton of thin-shelled trilobites, such as olenids.

The **digestive system** starts at the **mouth** (ventral and posterior to the hypostome), which feeds forward into a **stomach** which occupies most of the glabellar space. From the stomach, a long **alimentary canal** sends food backward to exit at the **anus**. Accessory digestive organs, sometimes referred to as **gastric diverticuli,** occur both above and to each side of the stomach (see another example next page).

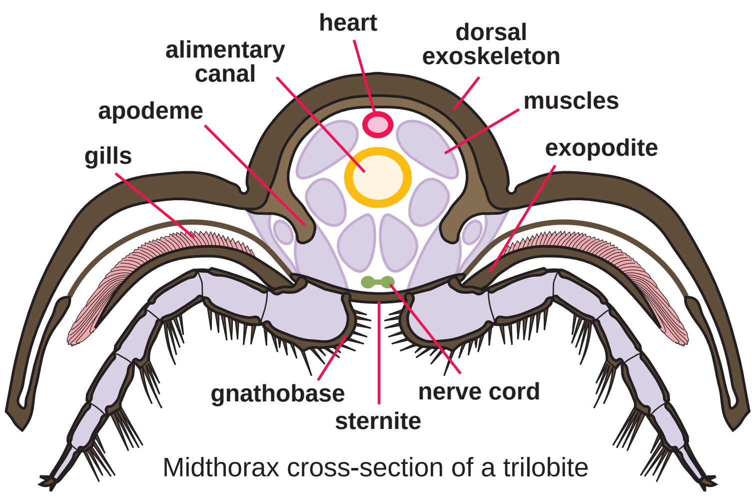
We presume that trilobites had a ventral **nervous system**, either a pair of **nerve cords** connected at segmental **ganglia**, or perhaps a single cord with segmented nodes. The **brain** would be an enlarged frontal ganglion receiving sensory input from eyes and antennae, etc. Whether it was placed in front of or behind the mouth is conjectural, although most modern arthropod brains are anterior to the mouth, with the paired central nerves passing to each side of the esophagus. In the figure above, the muscular system is not shown (see page 18). The **reproductive system** of trilobites is also very poorly understood. There is some evidence that eggs were brooded at the front of the cephalon (as they are in horseshoe crabs today), but the nature and location of copulatory organs has never been documented.





This dorsal view features the **digestive system** (dark), showing the frontal placement of the **stomach**, and the lateral and central **caecae** off the stomach (light), which were thought to have acted much as a liver. The large cephalic lobe of a phacopid wasn't occupied with its philosophical considerations, but by its most recent meal! The median **alimentary canal** ended at a posterior **anus**.

A complex network of subcuticular **genal caeca** (above) is apparent in some trilobites (*e.g.*, thin shelled Olenidae) and is probably related to **circulation** or cuticular **respiration**. Note the patterns of outward-radiating vessels and dense palpebral anastomoses. Similar **pygidial** networks occur in some species.



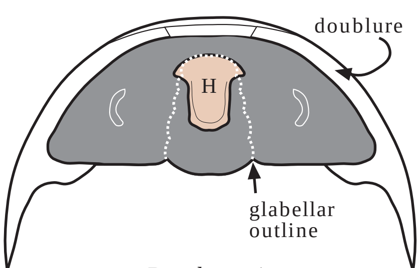
Midthorax cross-section of a trilobite

In the cross-section shown at right, through the thoracic region of a trilobite, we can see how the organ systems described above were placed centrally amidst the muscular system that worked the limbs, allowed for enrollment, and changes in body posture. The gills, borne on an extension of the limb base, are part of the circulation and respiratory system. Oxygen-rich hemolymph (arthropod blood) would enter the hemocoel (an open circulatory system bathing the internal organs and muscles) via the legs, and would be moved along the length of the animal via the long dorsal vessel (heart) shown here as a dorsal oval. Below the heart is the alimentary canal (larger oval) and the paired ventral nerve cords. The muscle masses are shown in light grey. What is probably a bit surprising is that the majority of organ systems occupies the axial lobe of the animal. Very little is held in the pleural lobes except some muscles. Some workers speculate that the excretory system of trilobites might have exited as ducts (associated with the Panderian organs) along the edge of each pleura where the pleural doublure meets the thin ventral cuticle. The pleural lobes provided protection for the limbs and gills, but the "guts" of a trilobite occupied the axial lobe. Finally, note the heavy spinose armaments on the limbs, especially on the coxae (base segment). These were thought to have acted as teeth and jaws, breaking up food before being passed forward to the hypostome and mouth. This "jaw at the base" of the leg is called a gnathobase (translating literally as "jaw base").

Hypostome Attachment and Alignment

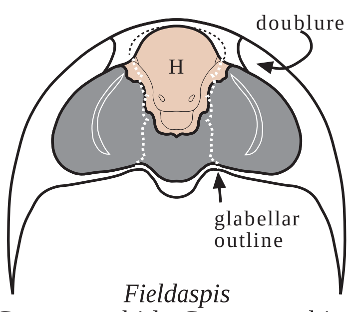
The **hypostome** of a trilobite is a calcified ventral structure that is thought to be a mouthpart. Its anterior edge is usually aligned strongly with the anterior edge of the overlying glabella (on the dorsal surface of the cephalon), and can either be separated from the anterior doublure (the **natant** condition), or attached to it (**conterminant**). Most conterminant hypostomes remain strongly aligned with the anterior glabellar edge (as in the Corynexochid example below), but there are some exceptions, in which the conterminant hypostome does not match the anterior glabella outline (the **impendent** condition). In the three examples below, the ventral cephalons of a natant, conterminant, and impendent species are shown. The hypostomes (marked H), dotted glabellar outlines, cephalic doublures and cephalic cavities (dark grey) are shown.

Natant
Hypostome free of anterior doublure, aligned with anterior edge of glabella



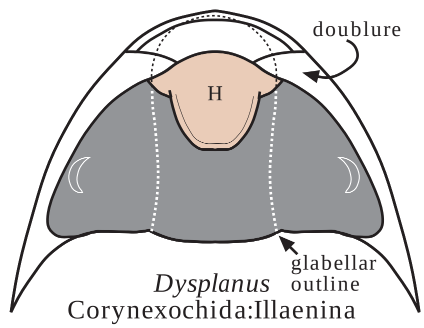
Ptychoparia
Ptychopariida:Ptychopariina

Conterminant
Hypostome attached to anterior doublure aligned with anterior edge of glabella



Fieldaspis
Corynexochida:Corynexochina

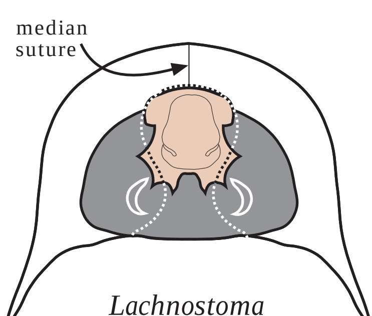
Impendent
Hypostome attached to anterior doublure but not aligned with the glabella



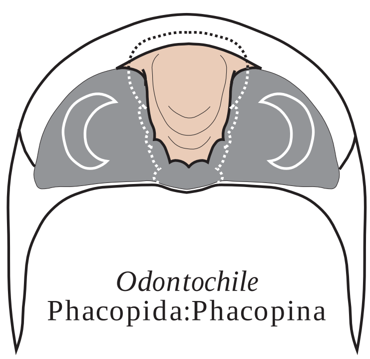
Dysplanus
Corynexochida:Illaenina

How are the hypostome types related to trilobite classification?

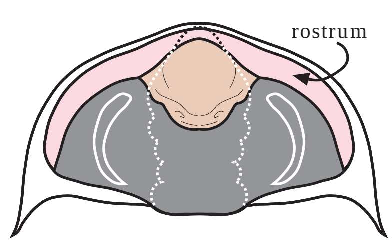
Some trilobite orders are marked by having most of its members share a certain hypostomal condition. For example, most of the order Agnostida and Ptychopariida have natant hypostomes, while most of the suborder Illaenina have impendent hypostomes. While there are certain exceptions to these patterns, the underlying shared characters provide part of the foundation for evolutionary patterns among the trilobites, important in higher level (*e.g.*, order or suborder) classification. It is worthwhile to note that combinations of ventral cephalic characters may also mark certain natural groups. Most Asaphoidea show conterminant (but aligned) hypostomes and a median suture. Most Phacopina are impendent, and bear no sutures on the anterior cephalic doublure. Most Redlichiida show a conterminant hypostome and a very wide rostrum.



Lachnostoma
Asaphida:Asaphoidea

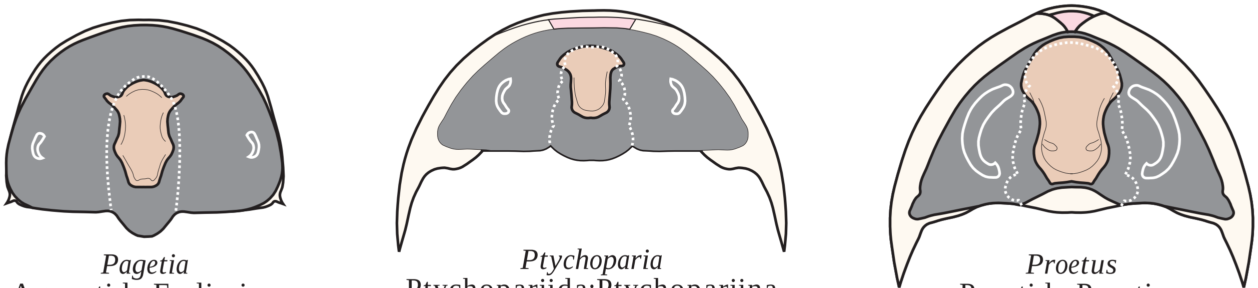


Odontochile
Phacopida:Phacopina



Kjerulfia
Redlichiida:Olenellina

Natant hypostomes:

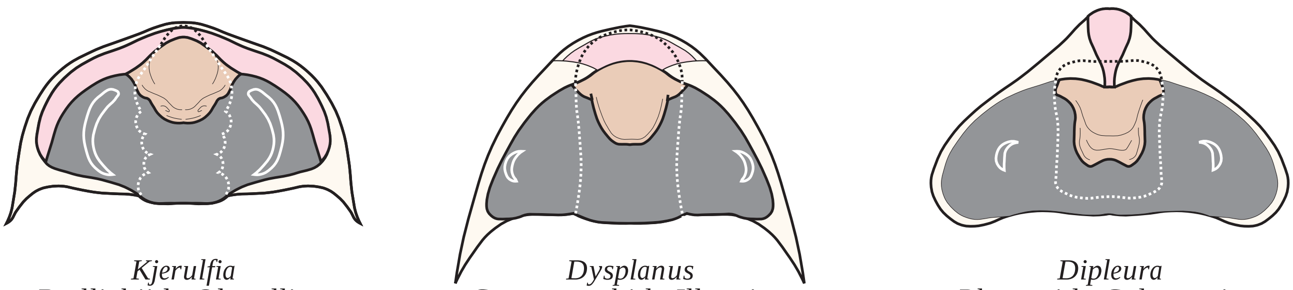


Pagetia
Agnostida:Eodiscina

Ptychoparia
Ptychopariida:Ptychopariina

Proetus
Proetida:Proetina

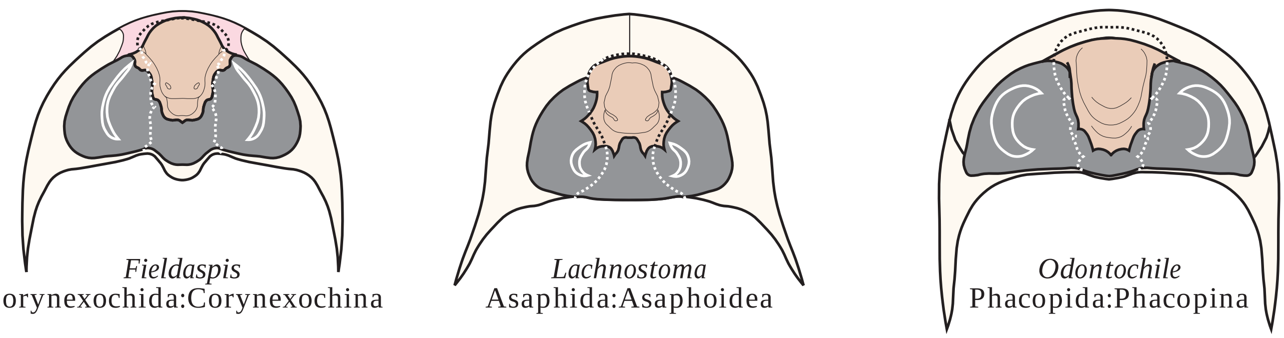
Conterminant (including Impendent) hypostomes:



Kjerulfia
Redlichiida:Olenellina

Dysplanus
Corynexochida:Illaenina

Dipleura
Phacopida:Calymenina



Fieldaspis
Corynexochida:Corynexochina

Lachnostoma
Asaphida:Asaphoidea

Odontochile
Phacopida:Phacopina

left: A ventral preparation of a Cheirurine trilobite (Phacopida) clearly shows the conterminant hypostome. Compare this with the image of the Phacopid *Odontochile* above.

right: A ventral preparation of an *Asaphus* trilobite (Asaphida) shows a forked conterminant hypostome. Compare this with the image of the Asaphid *Lachnostoma* above.

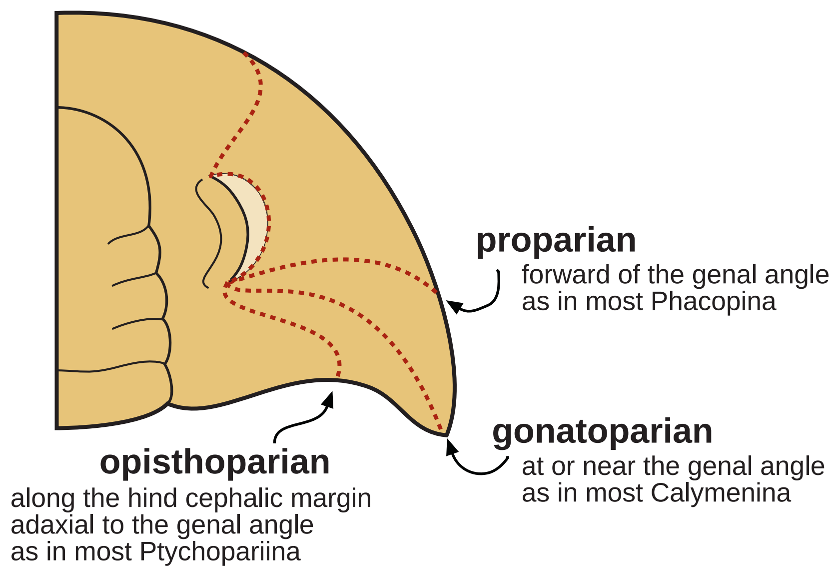
Trilobite Facial Sutures

What are facial sutures?

They are lines of weakness on the cephalic exoskeleton along which parts of the cephalon separate when the trilobite molts (sheds its exoskeleton). Facial sutures typically run from somewhere along the anterior edge of the cephalon to the anterior edge of the eye, then around the edge of the eye, continuing from there to end at either the side or rear of the cephalon. Notice that the facial sutures determine the boundary between the cranidium (cephalon and fixed cheeks) and the librigena (free cheeks). In addition to being vital for proper molting and growth of trilobites, facial sutures provide us with another character with which to help classify them. There are three main categories of facial sutures, defined in the figure below.

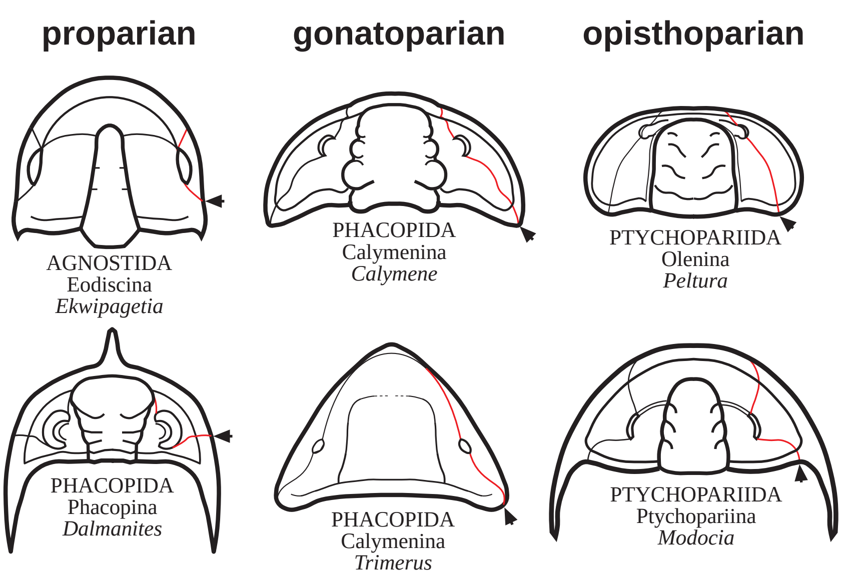
The 3 main types of facial sutures

are defined by where the suture ends, relative to the genal angle



Some examples of the three main suture types

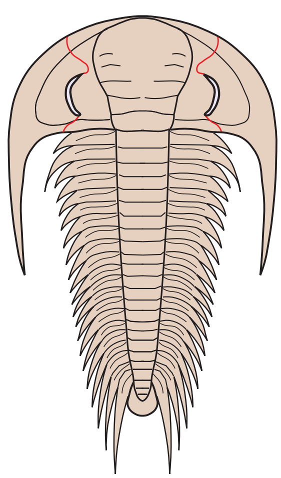
The three main suture types are shown in the examples provided below. In each case, an arrow shows where the posterior facial suture intersects the cephalic margin. Order, Suborder, and genus are provided for each. The Phacopina and Eodiscina are typically **proparian**. Calymenina are typically **gonatoparian**. Members of the Ptychopariida are typically **opisthoparian.**

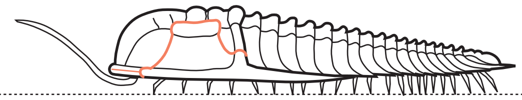


The Role of Sutures in Molting

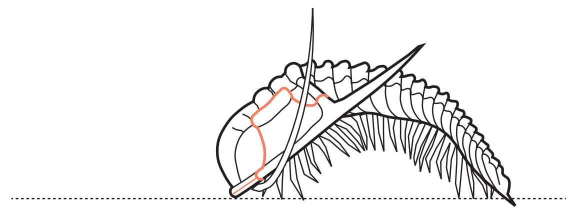
The sequence to the right depicts a *Paradoxides* trilobite molting (below left of the sequence is the animal in top view). In figure 1, the animal is shown before molting. In figure 2, the animal flexes into a curved shape, anchoring its long rear-facing pleural spines into the substrate. In figure 3, the facial sutures split, opening the cephalon (separating the cranidium from the librigenae and associated structures). This provides an exit for the molting trilobite (grey) from its exuvium (old exoskeleton), shown in figures 4-6. The arching of the body not only plants the rear pleural spines securely into the substrate, but also anchors the rostral plate at the anterior cephalic margin downward, providing an exit ramp for the emerging newly-molted animal. This sequence is consistent with fossils of *Paradoxides* in which the librigenae and rostral-hypostomal plate are found inverted beneath the axial cranidial shield. All it would take is slightly more forward tilting to have the molted librigenal assemblage flip into an inverted position, where it was preserved as an exuvial fossil.

Redlichiida
Paradoxidoidea
Paradoxididae
Paradoxides

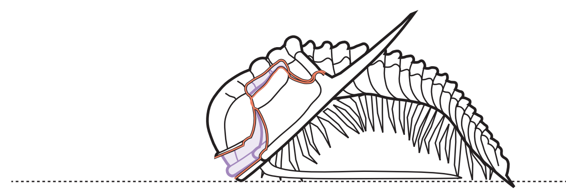




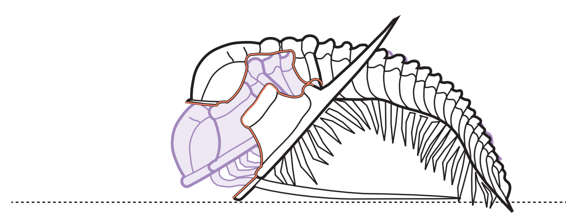
1. Animal before molting



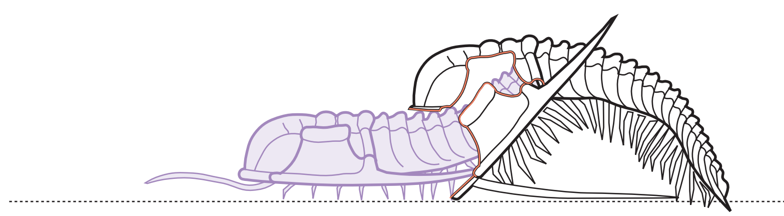
2. Arching the body anchors pygidial spines



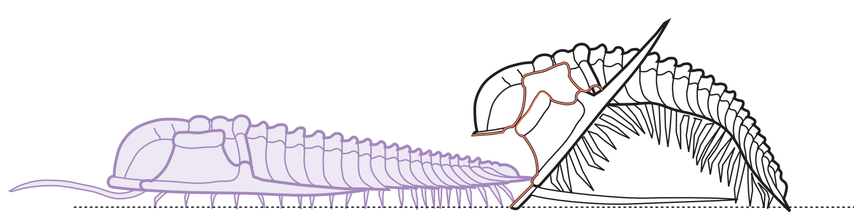
3. Facial sutures split, opening the cephalon



4. Contractions push the trilobite out of old shell



5. Freed front limbs pull the trilobite forward



6. Newly molted animal is free of its old shell

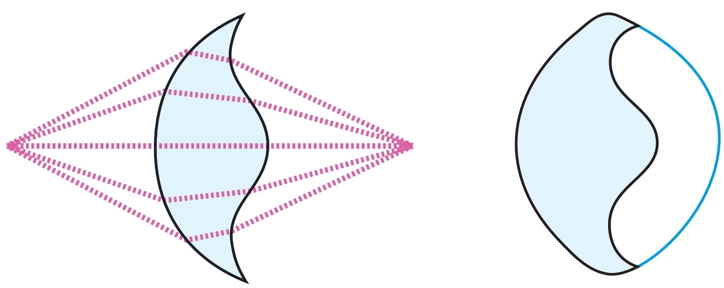
The Trilobite Eye

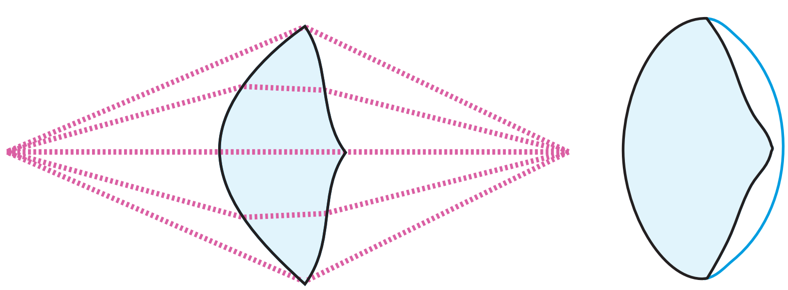

The holochroal eyes of the Asaphoid trilobite *Isotelus* were positioned high on the cephalon and provided an excellent field of vision.

Trilobites developed one of the first advanced visual systems in the animal kingdom. The majority of trilobites bore a pair of **compound eyes** (each with many lensed units). They typically occupied the outer edges of the **fixigena** (fixed cheeks) on either side of the **glabella**, adjacent to the **facial sutures**. At least one **suborder** of trilobites, the **Agnostina**,were **primarily eyeless**; none have ever been found with eyes. In contrast, a few **secondarily eyeless** species (in which a clear evolutionary trend toward reduced eye size with eventual disappearence of eyes altogether) have developed within several groups, even those known for large, well-developed eyes (*e.g.*, some Phacopina).

The advantage of good eye design

Compound eyes in living arthropods such as **insects** are very **sensitive to motion**, and they were probably similarly important for **predator detection** in trilobites. It has been suggested that **stereoscopic vision** was provided by closely-spaced, but separate lenses. **Vertebrate lenses** (such as our own) can change shape (accomodate) to focus on objects at varying distances. Trilobite eyes, in contrast, had **rigid crystalline lenses**, and therefore no accomodation. Instead, an internal **doublet structure** (two lens layers of different refractive indices acting in combination) corrected for focusing problems that result from rigid lenses. The shapes of some trilobite lenses match those derived by optical scientists over 300 million years later to answer similar needs. compare, for example, the optical designs of the 17th century physicists Descartes and Huygens shown below, with those of two trilobite species. The result is that, even without the benefit of accomodation, the rigid trilobite lens had remarkable **depth of field** (that is, allowed for objects near and far to remain in relatively good focus) and minimal **spherical abberation** (distortion of image).

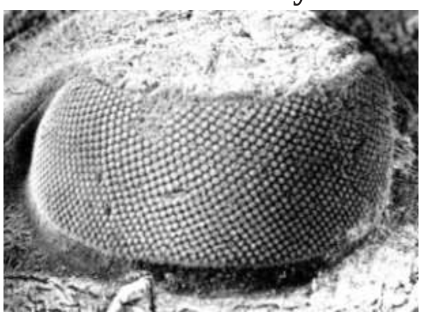

Descartes' lens design for minimal aberration (above left) is found in the lens of the trilobite *Crozonaspis* (right)
Light ray paths (dotted lines) entering the lens from the left come into focus a short distance to the right of the lens
In the eye of *Crozonaspis*, an intralensar body (white) further corrects focus after passing through the outer lens layer (grey).


Huygen's lens design for minimal aberration (above left) is found in the lens of the trilobite *Dalmanitina* (right)

Three types of trilobite eyes

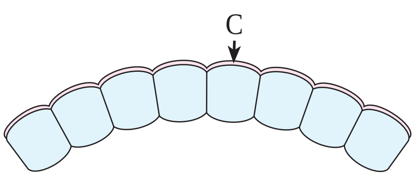
There are three recognized kinds of trilobite eyes: **holochroal**, **schizochroal**, and **abathochroal**. The first two are the major types, with the great **majority** of trilobites bearing holochroal eyes, and the distinctive schizochroal eye an innovation of the **Phacopida**. Holochroal eyes are characterized by a **close packing of biconvex lenses** beneath a **single corneal layer** that covers all lenses. These lenses are generally hexagonal in outline and range from one to more than 15,000 per eye! Schizochroal eyes in contrast are made up of few to >700 **larger, thick lenses**, each covered by **a separate cornea**. Each lens is separated from its neighbors by **sclera** (exoskeleton material) that extends deeply, providing an anchor for the **corneal membrane**, which **extends downward** into the sclera, where it is called intrascleral membrane. The abathochroal eye is seen in only a few Cambrian trilobites and is somewhat similar to the schizochroal eye, but differs in some respects: the **sclera is not thick**, and the corneal membrane does not extend downward, but ends at the edge of the lens. This table contrasts the three eye types:

Holochroal eye



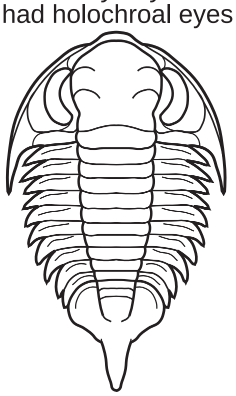
from Clarkson 1975

found in nearly all orders
few to very many (>15K) lenses
lenses typically small, numerous
one corneal layer covers all lenses
lenses in direct contact with others
no sclera between lenses
corneal membrance on surface only

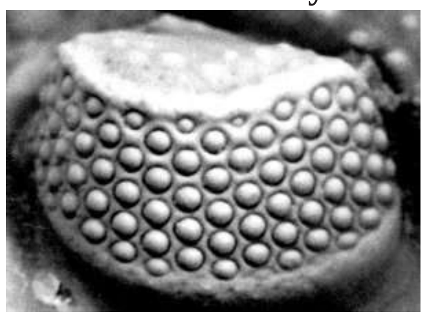


cross section reveals:
no sclera between lenses (L)
single cornea (C) covers all lenses
corneal membrane on surface only

Platyantyx
had holochroal eyes

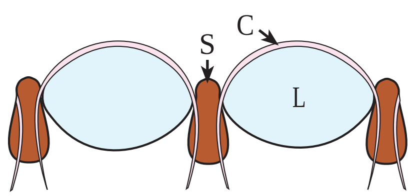


Schizochroal eye



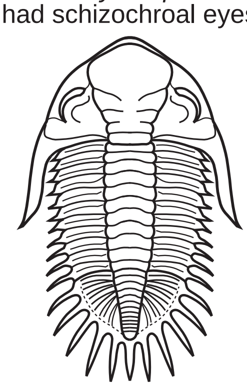
from Levi-Setti 1993

found in some Phacopida only
typically fewer lenses (to ~700)
lenses much larger, fewer
each lens bears individual cornea
lenses separated from each other
sclera between lenses very deep
corneal membrance extends into sclera

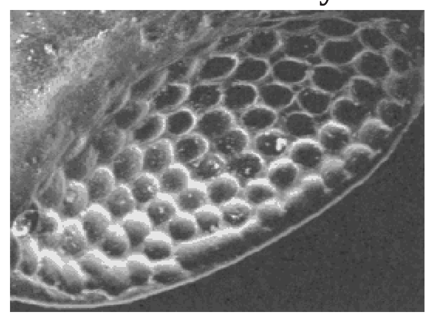


cross section reveals:
sclera (S) between lenses very deep
one cornea (C) per lens (L)
corneal membrane extends into sclera

Kayserops
had schizochroal eyes

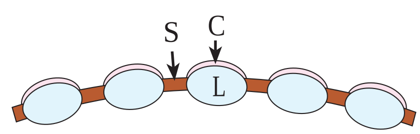


Abathochroal eye



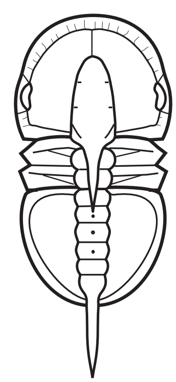
from Zhang & Clarkson 1990

found in Cambrian Eodiscina
few (to ~70) lenses
lenses small, not numerous
each lens bears individual cornea
lenses separated from each other
interlensar sclera not deep
corneal membrance ends at lens edge



cross section reveals:
sclera (S) not deeper than lenses
one cornea (C) per lens (L)
corneal membrane ends at lens edge

Pagetia
had abathochroal eyes

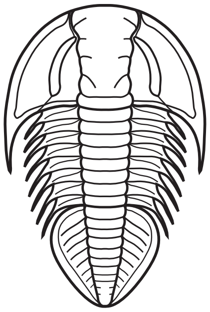


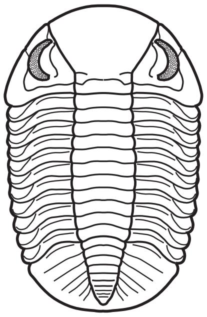
How did schizochroal eyes evolve?

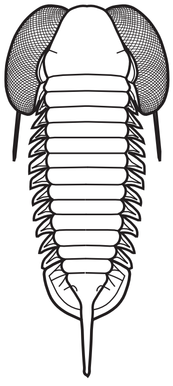
Nearly all early trilobites (Cambrian) had holochroal eyes, and it would seem hard to evolve the distinctive phacopid schizochroal eye from this form. The answer is thought to lie in ontogenetic (developmental) processes on an evolutionary time scale. **Paedomorphosis** is the **retention** of ancestral **juvenile** characteristics into **adulthood** in the descendant. Paedomorphosis can occur three ways: **progenesis** (early sexual maturity in an otherwise juvenile body), **neotony** (reduced rate of morphological development) and **post-displacement** (delayed growth of certain structures relative to others). The eyes of immature holochroal Cambrian trilobites are basically miniature schizochroal eyes. Post-displacement paedomorphosis would retain the immature form of the structures via delayed development, into the adult form.

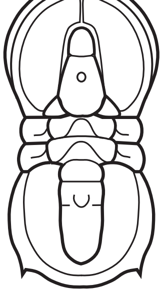
Variation in trilobite eyes

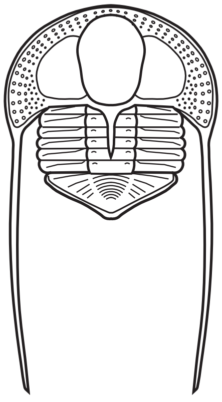
As with other aspects of the trilobite body, there was a huge variation of size and form among trilobite eyes, which in many cases seems related to the ecological life style of different species. The figures below show some of these variations. Many of the earliest trilobite eyes were cresentic, such as those of the Corynexochid *Polypleuraspis*. A conical section of schizochroal eyes gave species such as *Phacops* an excellent field of vision. In some trilobites, such as the free-swimming pelagic trilobite *Opipeuter*, the eyes were so large that they dominated the cephalon, providing a 360 degree visual field. Planktonic forms, such as *Agnostus* seem to have been entirely blind. Others, such as the Trinucleioid *Cryptolithus* were bottom filter feeders with a large, pitted sensory fringe, and eyes were reduced or lost. In species moving through a benthic layer of loose debris or algal growth, eyes raised above the body on stalks could peer about for danger, such as in the strange Russian Asaphoid *Neoasaphus kowalewski*. Species living on the bottom in deeper waters would have little need for eyes at all, and species with reduced eyes, such as *Trimerus*, and secondarily lost eyes, such as *Conocoryphe* are the result.

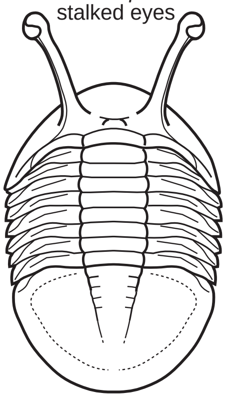


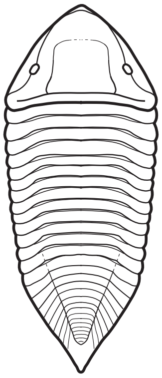


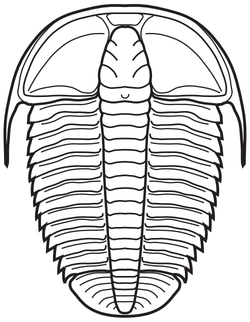








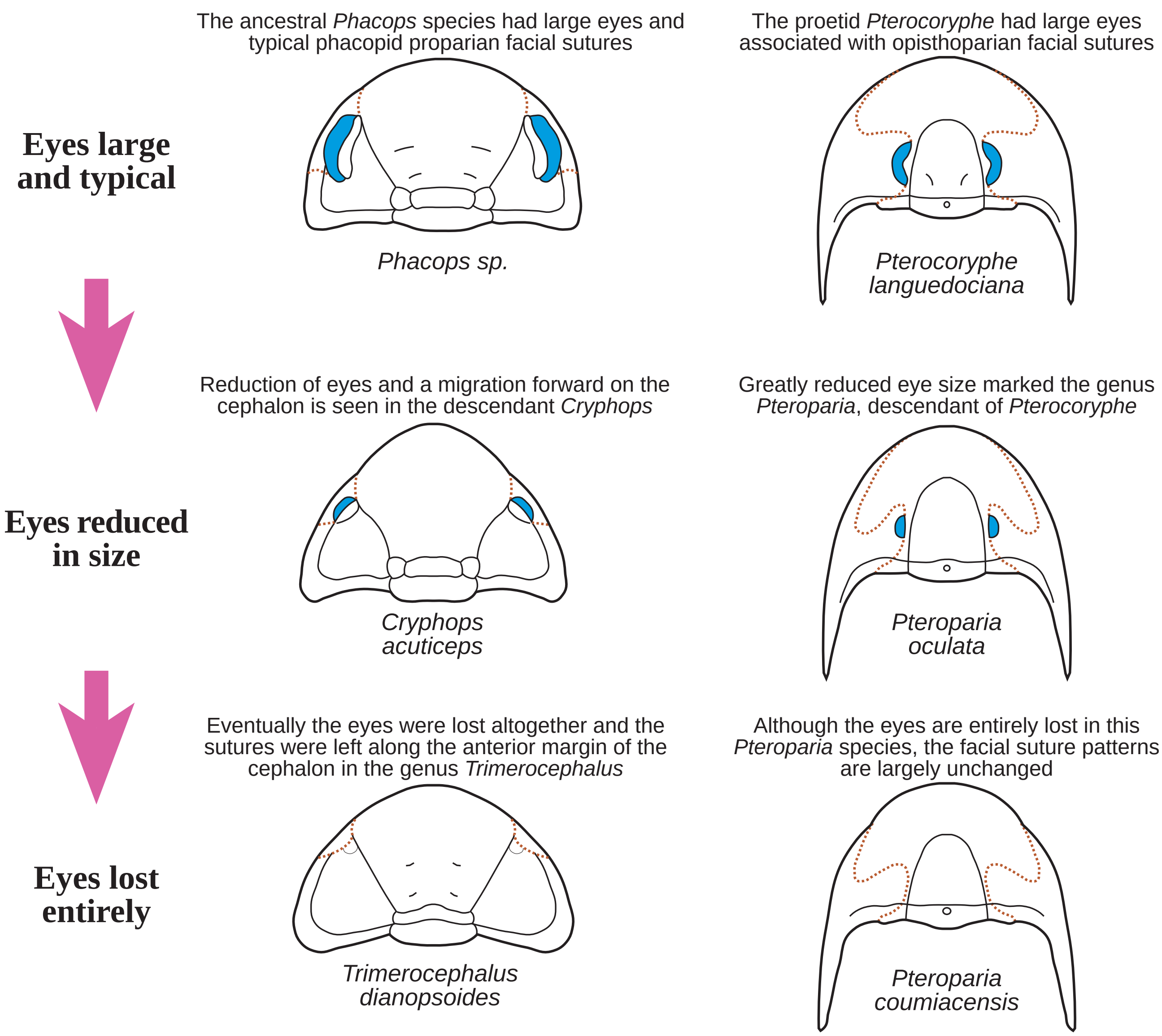




Evolutionary loss of eyes

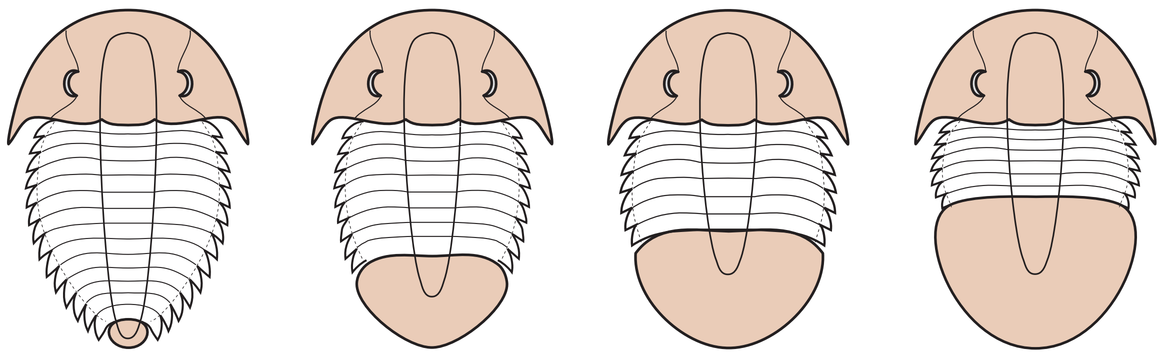
Conocoryphe is a secondarily eyeless trilobite in the Order Ptychopariida

Although eyes are normally an extremely important survival feature, there are situations under which loss of eyes might occur. For example, trilobites that took advantage of deep-water benthic habitats where light was dim or lacking might have gradually lost their eyes without suffering an adaptive disadvantage. Such eyeless trilobite assemblages are called atheloptic. Evolutionary trends are repeatedly seen in a variety of trilobite orders, and two examples are shown here. In both cases, these are Devonian trilobites that started with ancestors bearing large, functional eyes. In one sequence, eyes of a Phacopid clade were lost, and facial sutures associated with eyes were also reduced and marginalized. In the other example, involving a Proetid clade, eyes were also reduced and lost, but the basic facial suture pattern was retained. In the figures below (after Fortey & Owens 1999), the eyes are shown in dark and the facial sutures as dashed lines



Pygidium size relative to cephalon

The **pygidium** is the posterior **tagma** (body division) of a trilobite, made up of fused segments. While the **cephalon** of a trilobite is typically **wider** than the **thorax**, and one of the single largest features of a trilobite body, the **pygidium** can range from extremely small (much smaller than the cephalon) to larger than the cephalon. There are four general categories of pygidium relative size, shown below:



micropygous
pygidium much smaller than cephalon

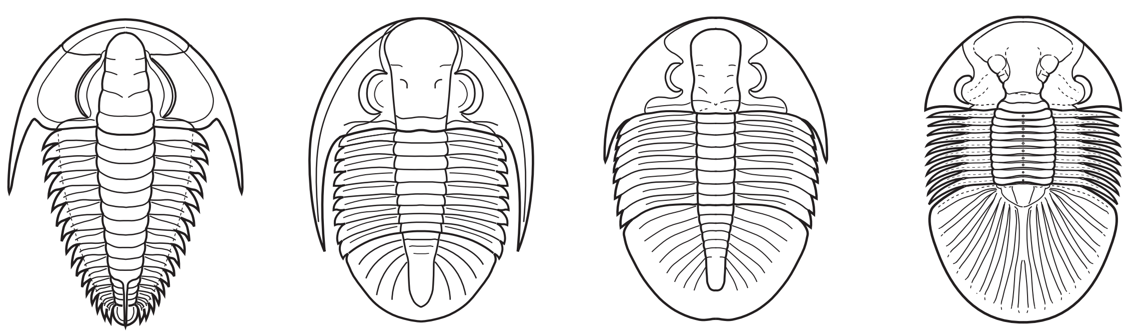
subisopygous
pygidium somewhat smaller than cephalon

isopygous
pygidium equal to cephalon

macropygous
pygidium larger than cephalon

Above are four hypothetical examples, with cephalon and pygidium tinted

The relationship between the size of the pygidium relative to the cephalon has some utility in considering trilobite classification. For example, **Redlichiida** typically have **micropygous** pygidia, while those of **Asaphida** are typically **subisopygous** to **isopygous**. Thus, these terms appear in the **Trilobite Order Fact Sheets**, elsewhere in this guide, when describing the pygidium characters of the different trilobite orders.



REDLICHIIDA
Redlichia
MICROPYGOUS

PROETIDA
Bathyurus
SUBISOPYGOUS

ASAPHIDA
Ogygiocaris
ISOPYGOUS

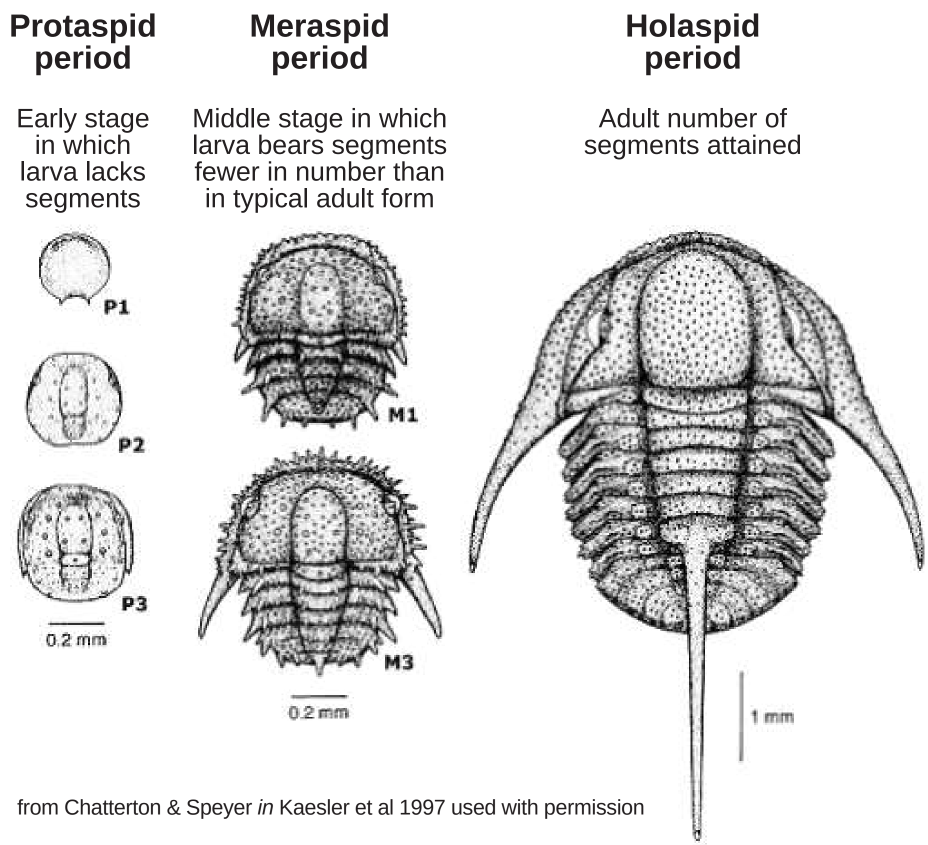
CORYNEXOCHIDA
Scutellum
MACROPYGOUS

Above are four real examples of various pygidium sizes among trilobites

Trilobite Ontogeny (Development)

Trilobites are thought to have reproduced sexually, as do nearly all arthropods today. Eggs were presumably laid (although fossilized eggs are rarely documented, as in Zhang & Pratt 1994). The embryology of trilobites is unknown, but after hatching and development of a hard exoskeleton (which presumably occurred soon after hatching) they molted their exoskeletons as they grew, as all arthropods today, leaving a record of their developmental stages.

Thus, the ontogeny (patterns of growth and development) of trilobites is known only as far as calcite exoskeletons of larval stages have sometimes been preserved, recording the progression of forms that trilobite larvae take from egg to adult. If any of the earliest larval stages lack a calcite skeleton, these would also escape our knowledge. To illustrate the ontogeny of trilobites, consider *Dimeropyge* (Proetida:Bathyuroidea), shown below (via Chatterton, in the Treatise of Invertebrate Paleontology, 1997):

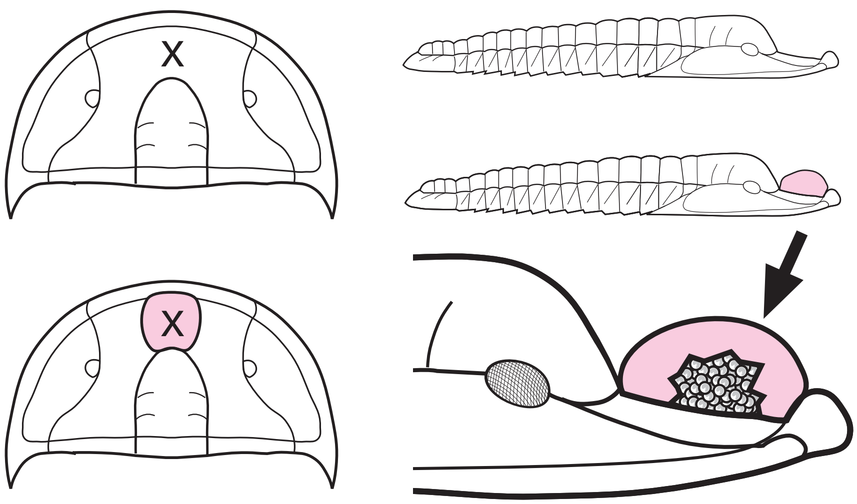


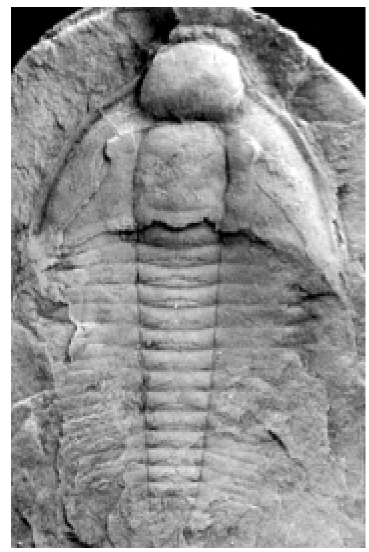
from Chatterton & Speyer *in* Kaesler et al 1997 used with permission

Three larval stages are recognized: a protaspid period, meraspid period, and a holaspid period. In the protaspid period, the larva (called a protaspis) is composed of a single segment, and often is very simple in form. It is thought that at least some early protaspid larvae were planktonic. The meraspid period is marked by a body with two or more segments, and during the meraspid stage, each molt meant the addition of usually one or two, but sometimes greater numbers of segments to the body of the growing trilobite. Several meraspid molts occurred, until the number of segments added to the meraspis achieved the typical number in the adult form of the species, and the general pattern of body morphology (shape and ornamentation) grew more similar to that of the adults of the species. At this point, the growing animal is called a holaspis, and enters into the last period of development, the holaspid period, in which the major change is not in form, but in increasing size. It is suggested that most of the increase in size in the life cycle of a trilobite occurred during the holaspid period.

Brood Pouches in Trilobites

It has recently been suggested that some trilobites may have held eggs and/or developing young within the cephalon (as horseshoe crabs do today), and anterior median swellings of the cephalon (of the preglabellar field) in some specimens are interpreted as brood pouches (*e.g.*, Fortey & Hughes 1998) because they appear only in holaspids (adults) and represent a dimorphism in which the swelling is the only morphological difference. Ostracods and some other crustaceans show similar brood pouch swellings, although not at the anterior of the body. Because specimens with brood pouches appear only in natant trilobites, it is possible that the eggs or protaspids were released ventrally, anterior of the hypostome.



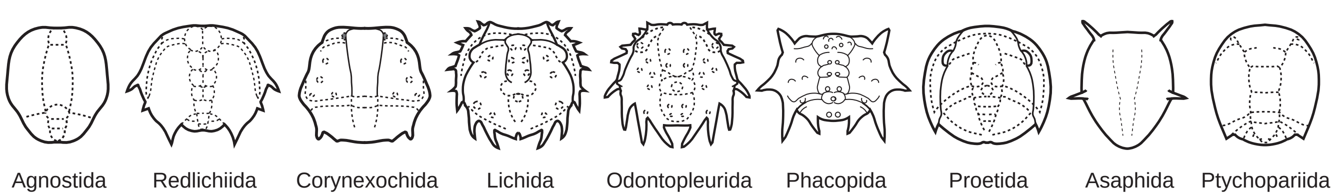


Left: dorsal view of cephalon of adult holaspid male; preglabellar field is marked "X" and brood pouch swelling in female is colored (lower left).
Right: side view of male specimen (top), brooding female (middle) and close-up cut-away showing developing eggs within pouch.

Above:
photo of specimen
showing brood pouch

Ontogeny and Classification

Recently, it has been shown that ontogeny plays an important role in assessing the higher classification of trilobites. There is a great deal of variation of form among the protaspid and meraspid larvae of the different trilobite orders, and related families and suborders show similar larval forms. For example, most of the Asaphida show a consistent protaspid form (called an *asaphoid protaspis*), and this ontogenetic similarity links groups that look quite different in mature form (for example, the Trinucleioidea and the Asaphoidea). Similarly, although the three suborders of Phacopida (Calymenina, Cheirurina, and Phacopina) are quite different in their holaspid forms, they share a number of similarities during their development that demonstrate shared derived characters indicating monophyly (descent from a common ancestor). The recent distinction of the Proetida as a class separate from the Ptychopariida was also partly based on the protaspid establishment, of adult-like cephalic characteristics, such as a tapering glabella and a preglabellar field (as in the proetid protaspid specimen depicted below). Thus, ontogeny plays an important role in assessing the higher classification and relationships of trilobites.

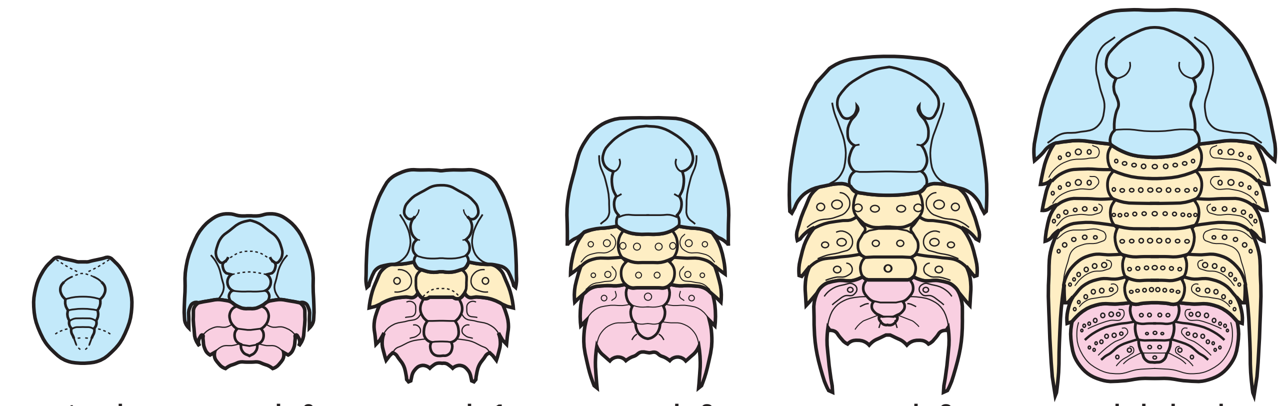


This sampler of a few protaspides of different trilobite orders merely hints at the diversity of protaspid forms

Addition of segments during larval development

When segments are added during the meraspid period, are they added to the growing larva from the cephalon or from the pygidium? In a trilobite with similar thoracic segments, it would be unclear whether new segments originate from the cephalon backward, or from pygidium forward. The ontogeny sequence of the trilobite *Shumardia pusilla* provides a clear answer, because one of the thoracic segments bears long pleural spines. This reference segment is the fourth behind the cephalon in the holaspis (see holaspid specimen at far right in the series below).

During the post-hatching development of *Shumardia*, this long-spined segment does not appear until after two meraspid molts (see meraspis 2 below), and then is followed by the addition of two more segments in subsequent molts, each added from behind the reference segment (that is, released from the pygidium into the thorax) until the six segments of the holaspid period are attained.



protaspis (no segments) — **meraspis 0** (2 thoracic segments) — **meraspis 1** (3 segments) — **meraspis 2** (4 segments) Note appearence of long-spined reference segment — **meraspis 3** (5 segments) Note release of new segment behind reference segment — **early holaspis** (6 segments) Note release of 2nd segment from pygidium forward

Selected Bibliography on Trilobite Ontogeny

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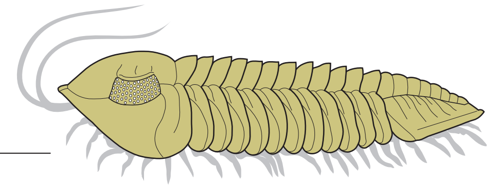
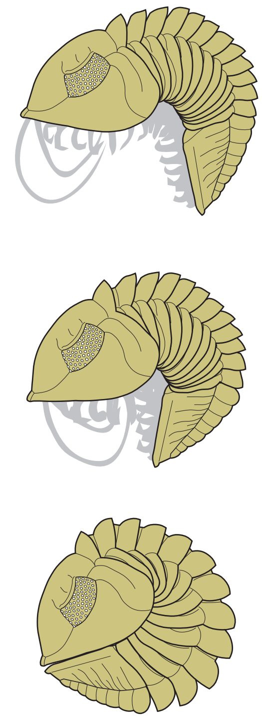
Trilobite Enrollment



What is enrollment?

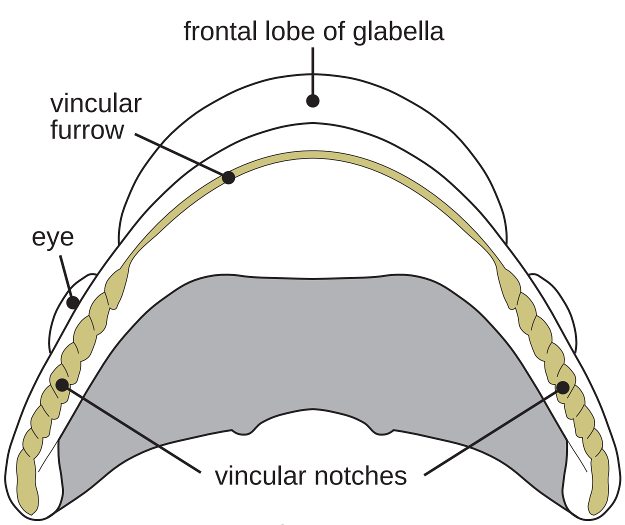
Most trilobites had the ability to enroll into a defensive ball or capsule, via the flexible articulation of the thoracic segments, bringing the cephalon and pygidium together in a tight, effective closed capsule that protected the antennae, limbs, and soft ventral surface. These specialized features are called coaptative structures, and are complementary morphological features that allow close interlocking of opposing surfaces (coaptation). For example, the cephalon and pygidium of enrolled trilobites often have similar shapes that allow a tight match, even to the point of special notches that fit the edges of the enrolled thoracic segments and the pygidial border.



Progressive enrollment
in *Acaste downingiae*

How did trilobites enroll?

In general, trilobites enroll by bending the flexible integument (shell) between each of the rigid thoracic segments so that the cephalon and pygidium are brought together and the thoracic pleurae enter an overlapping pattern. Some modern arthropods, such as crustacean isopods, are similarly able to enroll into very compact, sphereical capsules that are resistant to the typical enemies. The example to the right shows the progressive enrollment of a Phacopid trilobite: *Acaste downingiae*. Notice how the limbs and antennae are tucked in to fit within the enrolled exoskelton, and how, in the fully enrolled state, the pygidium and several thoracic pleurae contact the cephalon and no limbs or ventral surfaces are exposed at all. Where the pygidium and thoracic pleurae make contact with the cephalon, there is sometimes a specialized notch, called the vincular furrow, which matches the shape of the pygidial margin and the ends of the thoracic pleurae (see below)



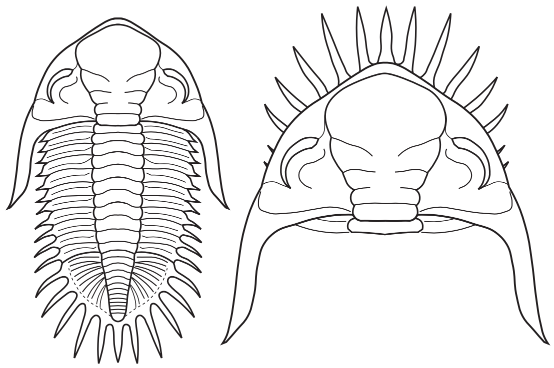
Coaptative structures
in *Paciphacops*

Vincular furrow and notches

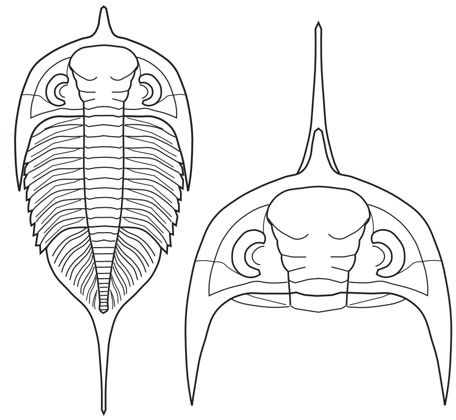
Here is the underside of the cephalon of the phacopine trilobite *Paciphacops*. When enrolled, it would appear rather similar to the enrolled *Phacops* at the bottom left of the next page. The dark grey area is the large concavity of the cephalon, where organs and front limbs would be. The narrow arch-shaped feature is the **vincular furrow**, and the **vincular notches** are arranged at the bottom left and right of the vincular furrow. The furrow accomodates the edge of the pygidium on enrollment, and the notches accomodate the rounded ends of the thoracic pleural segments, forming a perfect, tight, fit (**coaptation**).

More enrollment examples

Genal and pygidial spines are often designed to offer extra protection when the trilobite is in an enrolled state. Here is the top view of two enrolled Phacopine trilobites. Note how the cephalic and pygidial spines offer defense when the animal is in the enrolled state.



When *Kayserops* enrolls, the result is a very discouraging mouthfull to a would-be predator.

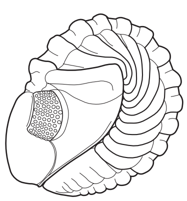


When *Dalmanites* enrolls, an unwieldy triangle of spines is presented

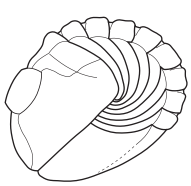
Enrollment and classification

Some trilobite workers, such as Bergstrom, suggest that the different kinds of enrollment might be useful in classification of trilobites. However, there is a great deal of variability, and other workers suggest that there is so much inconsistency that the utility of enrollment patterns among trilobites for higher level classification is relatively low, or so tied to other obvious morphological features as to be redundant.

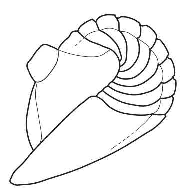
Therefore, although of uncertain value for trilobite classifcation, enrollment remains a fascinating feature of trilobite morphology and worth understanding. Here are a few more images of the enrolled forms of various species of trilobites. Notice how in the case of *Ellipsocephalus* and *Harpes*, there is not an exact fit between the cephalon and the enrolled thorax and pygidium. Faint lines show how the thorax and pygidium is tucked within the concavity of the cephalon in those cases. In *Megalaspidella*, there is an “overbite” that suggests that a portion of the pygidial venter is exposed, but in this case, a very wide pygidial doublure serves as a shield, and there are no exposed limbs or venter.



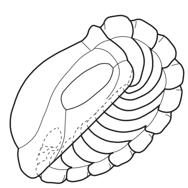
Phacops



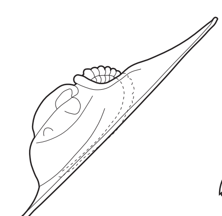
Asaphus



Megalaspidella



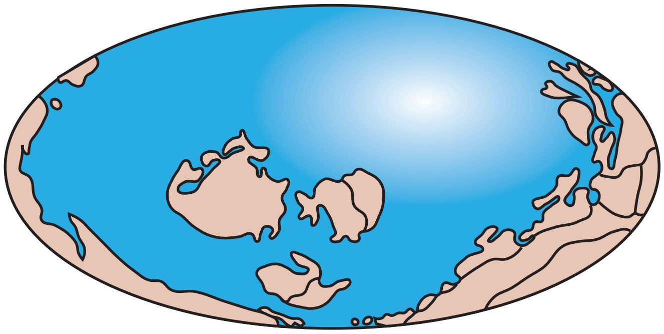
Ellipsocephalus



Harpes

Agnostus

Trilobite Ecology and Ancient Environments



The ocean basins and continents of Earth 540 million years ago bear little resemblance to the configuration of today

Half a billion years ago, the Earth's marine environment was certainly not the same as it is today. It is likely that the ocean's chemistry, including salinity, was different, and the configuration of the ocean basins and continents was entirely unlike our modern globe, because of continental drift.

Biotic environments (the living communities of plants and animals) were also different. while there were many species of marine plants and animals, many groups prominent today were missing, or poorly represented. For example, in the Cambrian and Ordovician, there were no jawed fishes, and crustaceans (crabs, shrimps, etc.) which dominate the arthropod fauna of today's oceans were not yet prominent.

A view of a Silurian reef (courtesy of the Virtual Silurian Reef). Trilobites were present in this ecosystem.

Trilobites were among the most prominent of the ancient marine arthropods, and they have only been found in oceanic fossil beds. No freshwater forms have ever been found. They occupied many different ocean environments, from shallow reef flats to deeper ocean bottoms, and even the pelagic water column, as floating plankton or free-swimming forms. Trilobites from different habitats often had specialized forms that were presumably adaptations to their environment.

Reconstruction of a Bumastoid trilobite crawling on the benthos

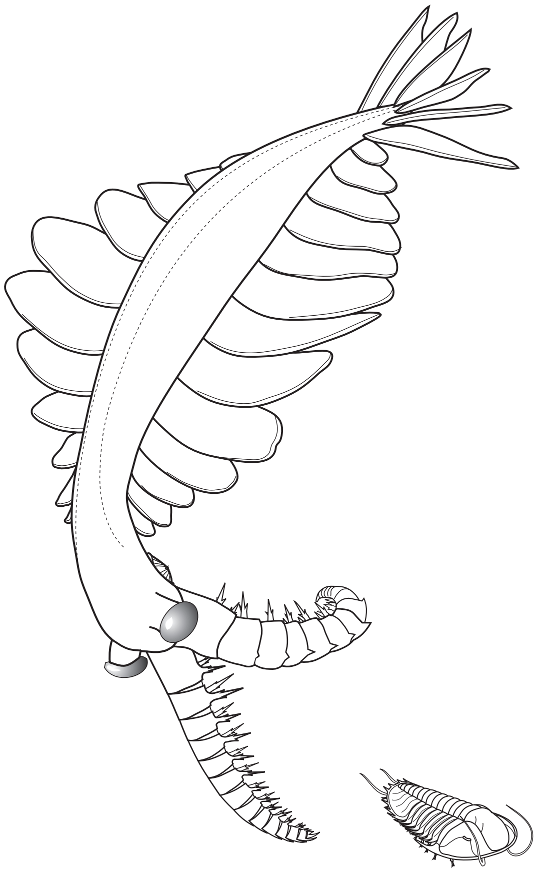
It is thought that the majority of trilobites were bottom-dwellers, crawling on the sea floor, or within complex reefs, acting as scavengers on organic debris. They were able to crawl upon and dig into the bottom sediments in search of food and to conceal themselves from predators.

Perhaps some were herbivores on beds of algae, browsers on corals, sponges, or bryozoans, or predators on smaller reef invertebrates. Some were thought to be filter feeders, facing into the current and extracting plankton and bits of organic debris.

Nautiloids were probably important predators of trilobites. Trilobites certainly were abundant and important prey for larger creatures. At first these were larger invertebrates, such as predatory worms, nautiloids, sea scorpions (eurypterids), crustaceans, and Anomalocaridids. When fishes developed and flourished in the Devonian, we can be sure that trilobites were hard pressed by these new predators. A hard exoskeleton and the ability to enroll protected trilobites from predators and sudden unfavorable environmental changes.

Reconstruction of Silurian oncocerid nautiloids that were probably among the important predators of trilobites

Trilobite predator *Anomalocaris*



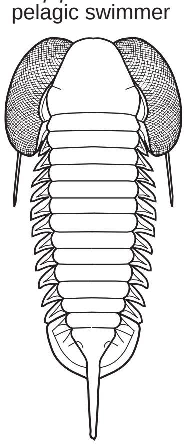
Anomalocaris closes in on *Olenoides*

Anomalocaris was the largest predator of the early Cambrian seas. At about half a meter body length it was capable of swallowing most trilobites whole, and with a ring-like mouth lined with sharp projections, could bite ragged chunks out of larger trilobites. Fossils of trilobites with wounds attributable to *Anomalocaris* have been found. An active, swimming, proto-arthropodan hunter with large eyes and grasping anterior limbs, the fossils of *Anomalocaris* and related species are found in North America, China, Australia, and other locations bearing Cambrian age strata.

In the figure to the left, I have adapted a reconstruction of *Anomalocaris* from a 1996 paper by Desmond Collins (*J. Paleontology 70(2)*:280-93) that describes the history of speculations and reconstructions of *Anomalocaris* and *Laggania* (another anomalocaridean genus). Notice how the eyes of *Anomalocaris* could swivel on flexible stalks, offering stereoscopic vision and excellent range-finding for a flexible pair of anterior limbs. Each limb was armed with spines with which to grasp and skewer victims. The round mouth is only partially shown under the head, behind the eyes. Large lateral fins probably moved in undulating waves, while rear fins provided stabilizing and turning capabilities to track swimming prey.

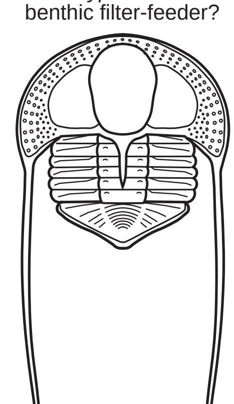
Trilobite morphology and ecology

Opipeuterella
pelagic swimmer



There is certainly a very wide range of body forms associated with trilobites. There are extremely spiny species, and ones entirely smooth and devoid of spines. There are species (such as the telephinid *Opipeuterella* shown at left) with huge eyes and narrow bodies that seem adapted to swimming in the pelagic (open ocean) water column. Other species (such as the trinucleid *Cryptolithus*, shown at right) were eyeless, with wide bodies and supporting structures such as long genal spines, that seem adapted for a dark benthic (ocean bottom) habitat. Some of the speculations on lifestyle and function of body shapes and features may never be clearly confirmed, but what we do know is that trilobites were extremely successful, found in a very wide variety of ocean habitats, and probably occupied many, if not all of the ecological niches that crustaceans do today. That being the case, we know of planktonic, free-swimming, benthic (bottom-dwellers), burrowing, reef-dwelling, and even parasitic crustaceans, and all of these life strategies have been attributed to trilobites as well.

Cryptolithus
benthic filter-feeder?



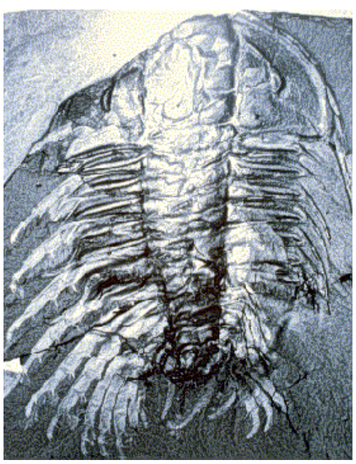
Trilobite Feeding Habits

What did trilobites eat?

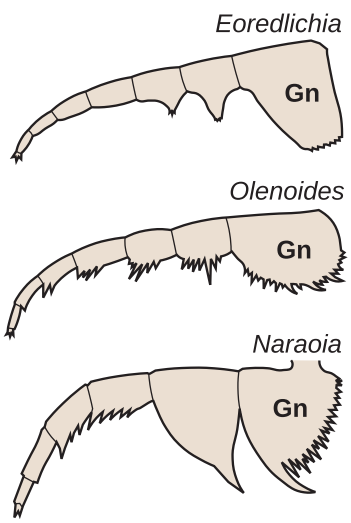
Trilobites occupied a huge set of habitats and paleolatitudes, from tropical shallows and reefs, to polar depths, and wide-ranging pelagic habitats in between. Their diversity of form suggests a complex ecology with many modes of life, including occupation of a variety of trophic (feeding) guilds. There has been a long history of speculation about the feeding habits of trilobites, ranging from predators, scavengers, filter-feeders, free-swimming planktivores, and even parasites or hosts of symbiotic bacteria. Using modern-day crustaceans as an analog, it is reasonable to suggest that the majority of trilobites may have been predator-scavengers, as the majority of marine crustaceans are today. Nonetheless, among today's crustaceans are filter-feeders (such as barnacles), planktivores (the majority of larval crustaceans fall into that category), herbivores (many small shrimp species), and parasites (a few copepods, isopods, and other taxa).

Recently (1999), Fortey and Owens (*Palaeontology 42(3)*:429-65) conducted a review of trilobite feeding habits in which several patterns were highlighted. These are discussed below, and many of the figures are adaptations of those accompanying their article:

Olenoides sp. (Corynexochida) This formidable looking trilobite was probably an active predator of benthic invertebrates such as worms.



We know about the limbs of *Olenoides* thanks to remarkable preservation at the Burgess Shales, and other *Konservat-Lagerstatten*.



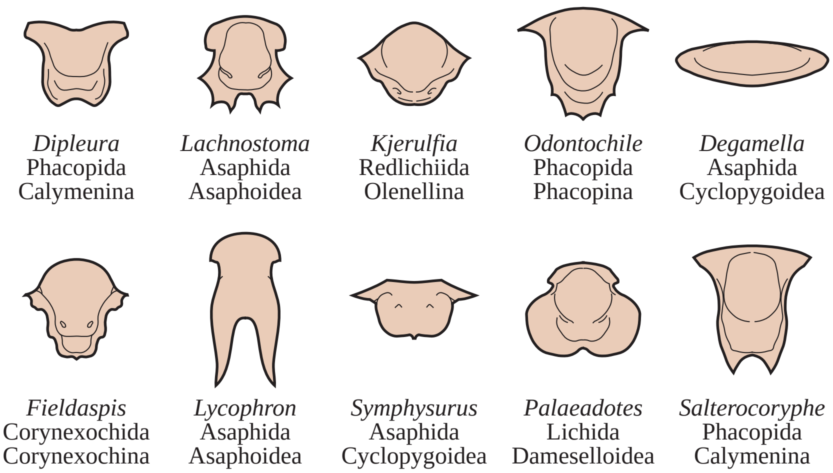
Large and/or armed gnathobases strongly suggest their use in predation.

Predator-scavengers

The majority of early trilobites were probably predators of benthic invertebrates, such as worms, and Cambrian trilobites such as *Olenoides* (far left) often bore expanded and spiny gnathobases (labeled "Gn" in the examples at left). Fossilized trilobite trails sometimes stop when they intersect worm burrows (suggesting that the trilobite was hunting for worms, and stopped to eat when it found one in its burrow). Presumably the worm was extracted, subdued and crushed or torn apart with the leg spines and strong gnathobases, then passed forward between the legs to the anterior mouth, where last processing was done against the hypostomal platform before ingestion. In crustaceans and insects, all of these functions are served by specialized anterior mouthparts on the head of the animal for processing food before ingestion. However, in trilobites, most of the processing occurred in the longitudinal medial groove between the limbs, with their repeated pairs of gnathobases, meaning that the "mouthparts" of a trilobite occupied the length of its underbody, rather than being primarily anterior. Another piece of inference on the predatory nature of early trilobites can be gained from looking at the relatives of trilobites. The sister-taxa of trilobites, such as Naraoiids, were also thought to have been predators, and indeed have very spiny and formidable looking limbs! (see the fang-bearing gnathobase of *Naraoia* above, for example).

Predatory trilobites, argued Fortey and Owens, would need to have hypostomes firmly attached to the frontal doublure (*i.e.*, conterminant), essentially stabilizing the hypostome against the cephalic exoskeleton to aid in processing prey. It is interesting to note that there is a considerable variation in the size and the shape of conterminant hypostoma, suggesting there might have been a great deal of trophic specialization. To the right are examples of this variation:

Variability in conterminant hypostomes

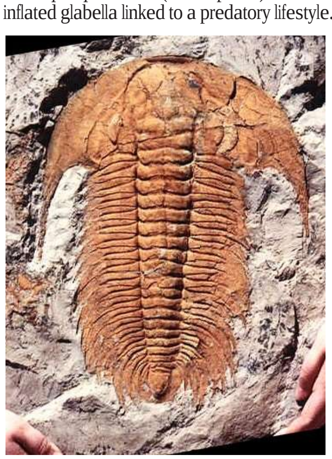


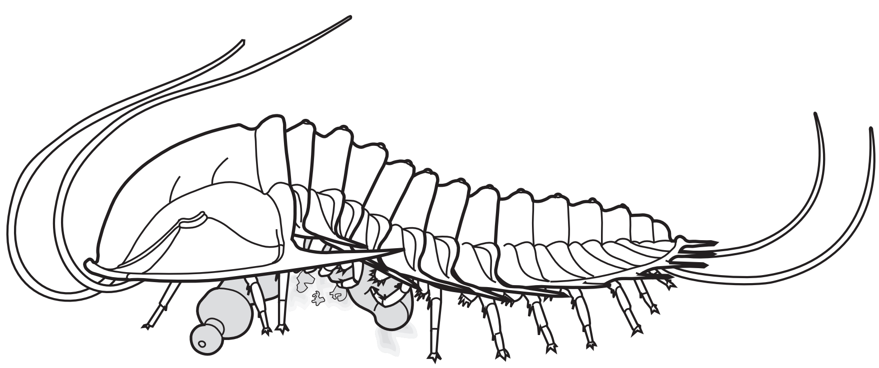

Phacops speculator (Phacopidae) has the inflated glabella linked to a predatory lifestyle.

Other predatory correlates

Fortey and Owens also suggested that species with inflated glabellae (such as Phacopina, Proetoidea, etc.) might be considered an indicator of predatory habits, with the large glabella housing a sizable digestive chamber for initial processing of large chunks of prey (vs bits of detritus). They also made the argument that the largest species of trilobites were very likely predatory, including many species of Asaphida, Lichida, Phacopida, and Redlichiida.

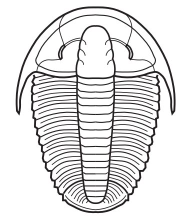
Finally, since there are few depictions of trilobites eating anything, below is a reconstruction of a large *Olenoides serratus*, subduing a small *Ottoia* (a priapulid worm) that it has just pulled from its shallow burrow. Its spiny limbs pin the hapless worm to its ventral midline, where its large gnathobases stab and tear at the worm's tough outer epidermis. Once subdued, the gnathobases will tear the worm apart and feed chunks into the mouth.


Large trilobites (such as this foot-long paradoxidid) make good candidates for a predatory lifestyle.

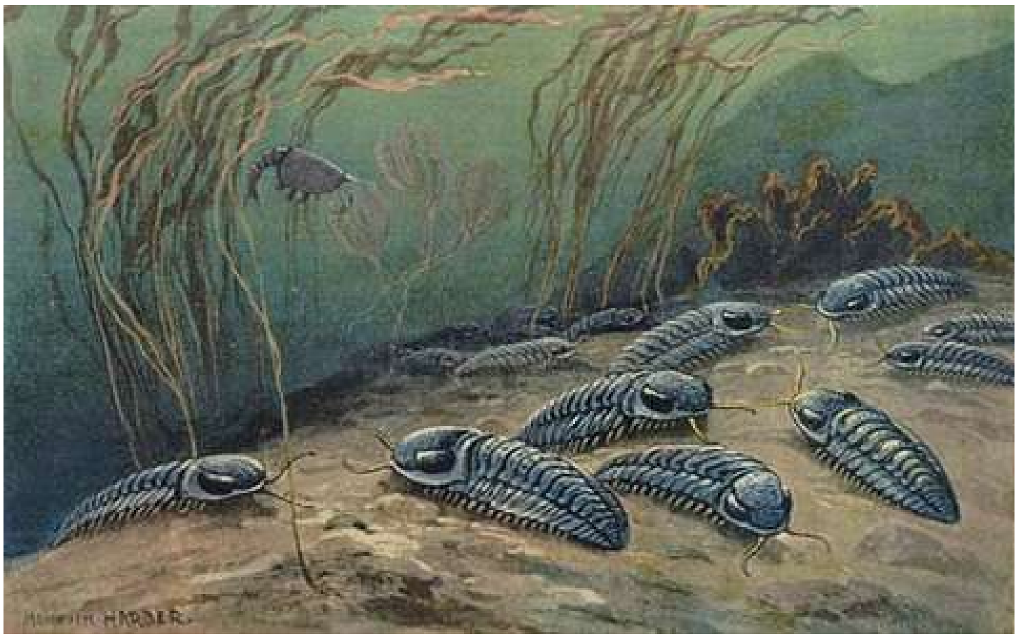

Olenoides serratus: terror of the Burgess mudflats

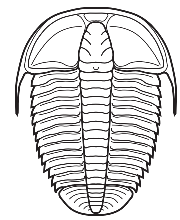
Particle-feeders

Although it is argued that trilobites with conterminant hypostomes were probably primarily predatory, a large proportion of trilobites (such as *Modocia* at right) have natant hypostomes, which Fortey and Owens suggest indicate a shift away from predation and into particle feeding, which includes scavenging for bits of benthic detritus (as the group of olenids below might be doing), or perhaps grazing on beds of algae. Trilobites are not typically depicted doing much of anything except lounging about alone or in groups!



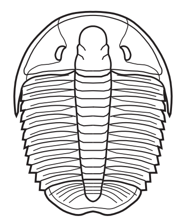
Modocia
Ptychopariida
exemplifies the general, successful Ptychoparioid form



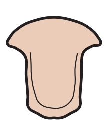


Conocoryphe
Ptychopariida
probably ate benthic detritus on deep, dark bottom habitats

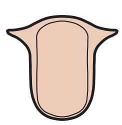
The majority of Ptychopariid trilobites would fall into the category of particle feeders, suggesting that this was a prominent trophic niche for trilobites in the Cambrian and Ordovician. There were many species that assumed the so-called "generalized ptychoparioid form" in the Cambrian and lower Ordovician, attesting to its success. The consistency of hypostome shape, size and form among natant trilobites suggests that particle feeding was a rather generalized habit that did not require much specialization of mouthparts. Indeed, through a long history, natant hypostomes tended to maintain a much more consistent form than conterminant species. Below are some examples of natant hypostomes:



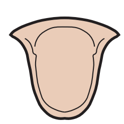
Elrathia
Ptychopariida
is found in such large numbers it must have been extremely successful



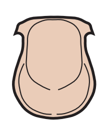
Ptychoparia
Ptychopariida
Ptychopariina



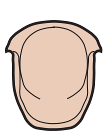
Crassifimbra
Ptychopariida
Ptychopariina



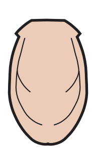
Conocoryphe
Ptychopariida
Ptychopariina



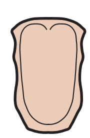
Dunderbergia
Ptychopariida
Ptychopariina



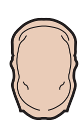
Parabolinella
Ptychopariida
Olenina



Bathyurellus
Proetida
Bathyuroidea



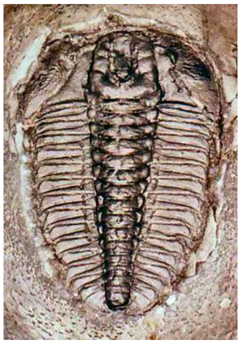
Proetus
Proetida
Proetoidea



Voigtaspis
Proetida
Proetoidea

Particle feeding as a successful lifestyle

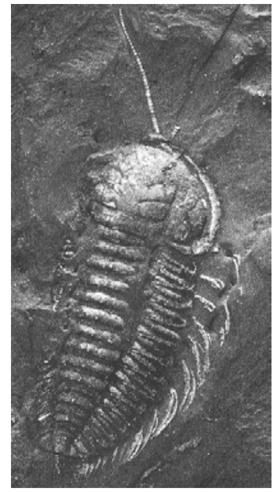
Fossil deposits that bear extremely large numbers of individuals of ptychopariids such as *Elrathia* also argue that these trilobites were near the base of the food chain (*e.g.*, herbivores), and could support much larger population numbers than less-common predatory species.



Wujiajiania sutherlandi (Ptychopariida : Olenina) lived in the dark, anerobic benthos, and may have derived nutrients from symbiotic sulphur-eating bacteria that housed in thoracic gill filaments.

Olenimorphs: symbiotic relationships?

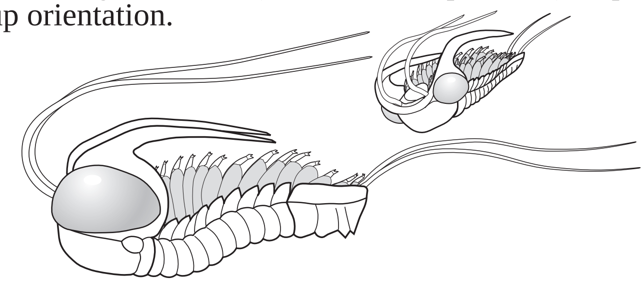
Among the Ptychopariida, the Olenina include a number of species that were known to occupy benthic, nearly anoxic substrates, high in sulphur compounds. Modern crustaceans in those situations (as at mid oceanic ridges and thermal vents) often live in a symbiotic relationship with sulphur-eating bacteria that are housed in the gill structures. Fortey suggested that this relationship may have originated with olenid trilobites in the Palaeozic. He cites the very wide thoraxic pleurae of many olenimorphs, increased numbers of thoracic segments (both traits providing ample gill surface for symbionts), and a reduced hypostome, so small that it suggests that much of the nutrient requirements for these trilobites were not being processed and ingested, but absorbed through the gills from symbiotic bacterial colonies there. Olenids are known for their well-developed gill structures, as in the image of *Triarthrus* at right.

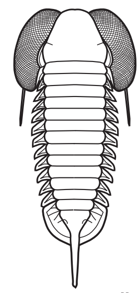


Triarthrus eatoni
Ptychopariida : Olenina

Pelagic planktivores

A number of trilobites are thought to have been able to swim freely in the water column, and had wide distributions globally. Several of these had streamlined bodies and large eyes (such as *Carolinites*, *Telephinus*, and *Opipeuterella*), which would be appropriate for either active visual hunters of zooplankton, and as a means of predator detection and avoidance for a small nectonic animal in the water column. Below is a reconstruction of the pelagic trilobite *Carolinites genacinaca* (Proetida : Telephinidae), depicted swimming in a venter-up orientation.





Opipeuterella
Proetida
Bathyuroidea

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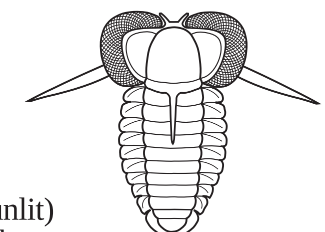
Carolinites probably hunted actively for small zooplankton in the photic (sunlit) zone, and judging from its shape, was probably a fairly fast swimmer. There are thought to be two general forms of pelagic trilobites: elongate, fast-swimming streamlined forms, and those with more squat body forms that may have been much slower swimmers.



Telephinus
Proetida
Bathyuroidea

Planktonic Agnostida?

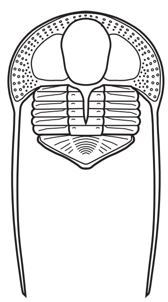
Some Agnostida were so prolific they are rock-forming,as these *Agnostus pisiformis* (Agnostida : Agnostina)

The simple form and small size of agnostid trilobites has led to speculation on their biology. The majority were eyeless, so they were not visual hunters. There have been suggestions that they were planktonic, such as ostracod crustaceans are today, hovering in swarms in the water column feeding on phytoplankton as a primary consumer. More recently it has been argued that adult Agnostida were likely benthic:Adult forms are often found extended and in the company of benthic trilobites (e.g., the association of *Elrathia* with *Peronopsis*). The global distribution of Agnostida suggests the majority were deep water benthic organisms, rather than wide-ranging planktonic species. Perhaps some larval Agnostida were planktonic, while adults settled out into a benthic lifestyle.

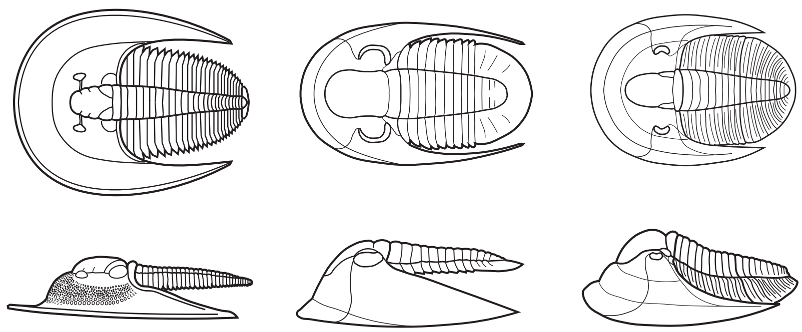
Filter feeders

Cryptolithus tesselatus
(Asaphida:Trinucleioidea)

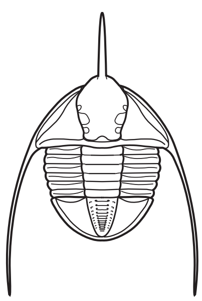
There are a number of trilobite species with large cephalic chambers, of sagitally convex form to house a filtering area, and bearing long genal spines or prolongations. The thorax and pygidium had a much less convex profile, and if extended straight back from the cephalon would be suspended significantly above the substrate. In a few of these species, the hypostome is also elevated, leaving an even larger space below for a filter chamber enclosed by the margins of the cephalon. Some good examples of this morphotype include harpetids (Ptychopariida), trinucleioids (Asaphida, such as the *Cryptolithus* at left), and perhaps some bathyurids (Proetida, such as *Uromystrum*) and brachymetopids (Proetida), such as *Cordania*. These are shown below:



Cryptolithus tesselatus
(Asaphida:Trinucleioidea)

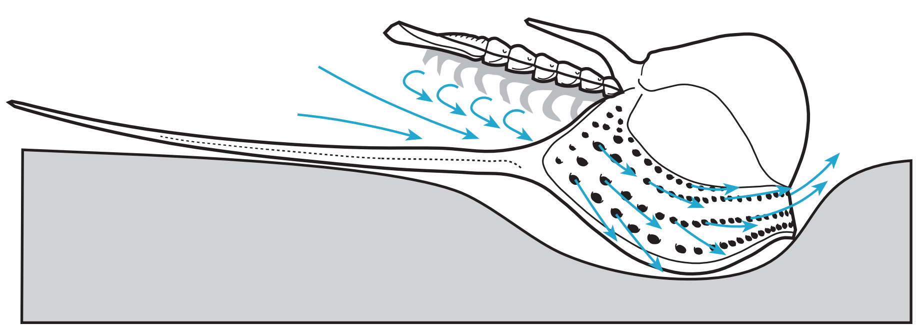


L to R: *Harpes macrocephalus* (Harpetiae), *Uromystrum validum* (Bathyuridae), and *Cordania falcata* (Brachymetopidae) all share the vaulted cephalon body form associated with possible filter-feeding habits.



Ampyx nasutus
(Asaphida:Trinucleioidea)

In trinucleioids, the cephalic filter chamber is also often marked with rows of pits that are actually fenestrae, extending all the way through the exoskeleton from dorsal to ventral. This suggests that they might have been used to allow outflow from the filter chamber, leaving edible particles behind. Fortey suggested a posture for *Cryptolithus tesselatus* in which the gill filaments on the thoracic and pygidial limbs were used to sweep sediments into the cephalic filter chamber from behind. The anterior legs were used to sort material in suspension, and processed water would exit from the pits in the cephalic fringe. The figure below illustrates this supposed filter-feeding posture:



Water flow is shown by arrows. The long genal spines help stabilize the position of the trilobite as it vigorously paddles with its legs to generate an inward current. As the limbs of *Cryptolithus* have never been observed, the size of the gill filaments (shown in gray) is conjectural.

Trophic specialization and local trilobite diversity

Considering the different feeding habits of trilobites and assessing them against the diversity of trilobite species that can be found together in a particular horizon suggests that trophic (feeding) differentiation allowed more species to occupy the same general habitat. This can help explain the sometimes large numbers of trilobite species found preserved together. One example, from the late Arenig Pontyfenni Formation in Whitland, South Wales, UK, illustrates this well. In this one location eleven trilobite species can be found in a single contemporaneous stratum. This remarkable diversity is best explained through partitioning of the trophic niches available, and when the forms of the trilobites are examined, the nature of the divisions can be hypothesized.

Pelagic forms

A first major division is to distinguish four species that appear to be pelagic, (swimming in the water column rather than moving over the benthos). These four can be further divided into two categories according to whether they appeared to be relatively fast-swimming, streamlined taxa (*Microparia* and *Degamella*), or less-streamlined and more sluggish, slower-swimming species (*Pricyclopyge* and *Cyclopyge*). Size is another diversifying attribute: while three of the four are relatively small species (ranging from 5 to 30 mm), one of the pelagic forms, *Degamella evansi*, reaches 50 - 60 mm in length, rather large for a free-swimming form.

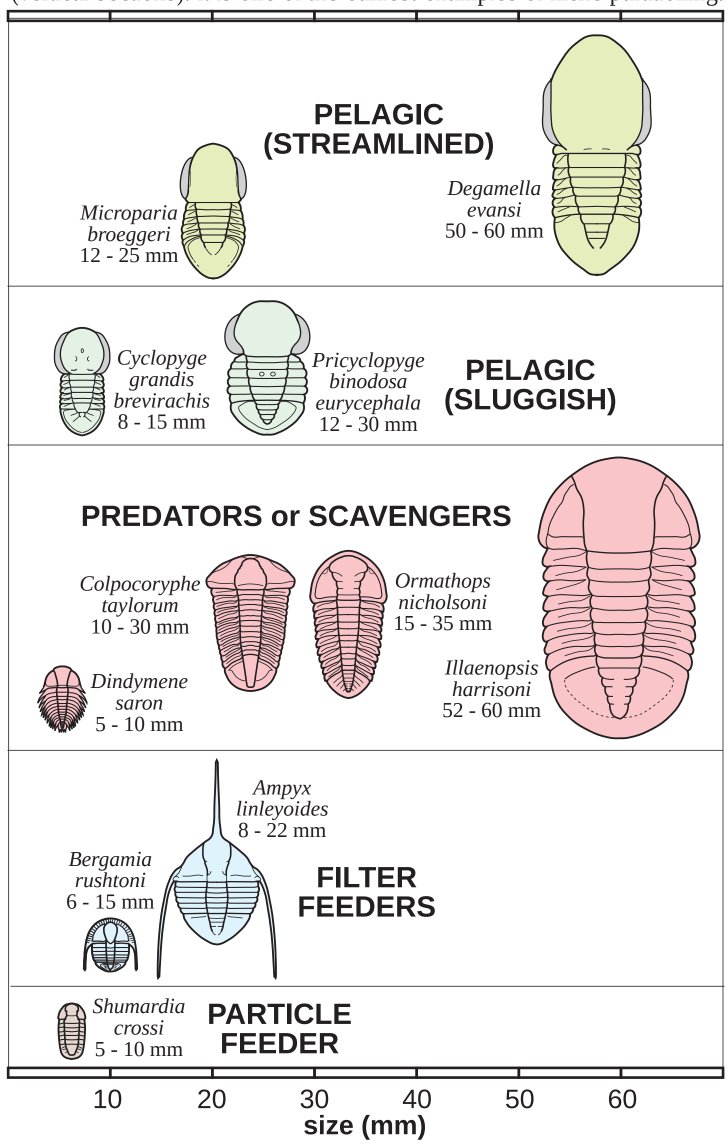
Benthic forms

The remaining majority (seven taxa) of the Pontyfenni trilobites are benthic, and occupy three major trophic guilds: a predatory-scavenging guild, a filter feeding guild, and a particle feeding guild. These also can be further subdivided according to body size, with one rather tiny shumardiid particle feeding species (*Shumardia*), and a range of small to large predator/scavengers (*Dindymene*, *Colpocoryphe*, *Ormathops*, & *Illaenopsis*). Two presumed filter-chamber feeders (*Bergamia* and *Ampyx*) complete the set of trophic specialists of the Pontyfenni trilobite fauna.

Trophic Partitioning in the Pontyfenni Trilobite Fauna

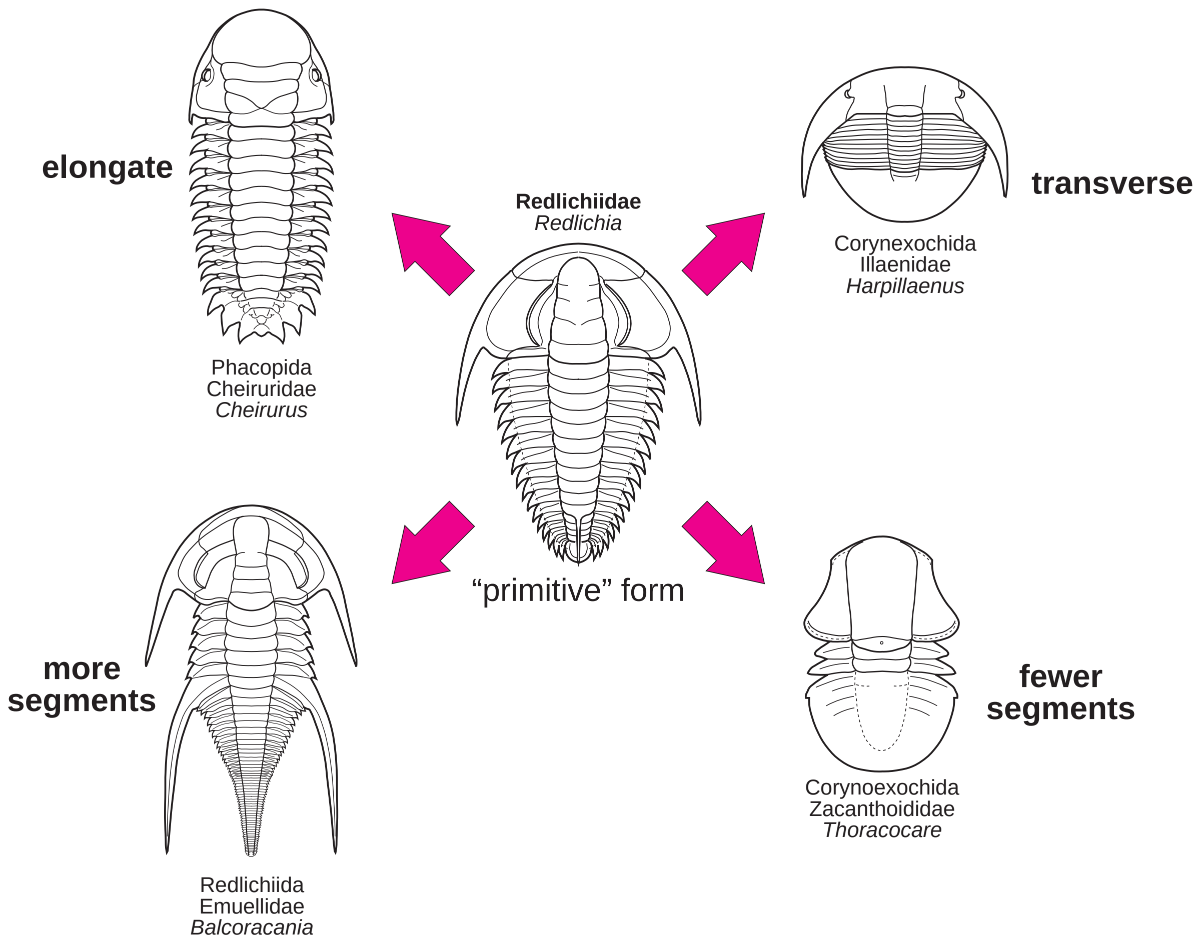
(after Fortey and Owens 1999)

The chart below categorizes the eleven trilobite species found in the Pontyfenni Formation according to size (horizontal axis) and trophic divisions (vertical sections). It is one of the earliest examples of niche partitioning.



Evolutionary Trends in Trilobites

Through the 300 million years that trilobites existed, there were many opportunities for diversification of morphology, starting from the presumed primitive morphology exemplified by a species such as *Redlichia* (shown below, center). This “primitive” morphotype had a small pygidium, well developed eye ridges, a simple, lobed glabella, several thoracic segments, and a rather flattened body form. Among the over 15,000 species of described trilobites there are species in which various aspects of morphology have diverged greatly from the primitive state. Thoracic segments were reduced to as few as two or increased to over 60, overall body shape was greatly elongated in some species, or rendered transverse (widened) in others. Examples of these trends are shown below:



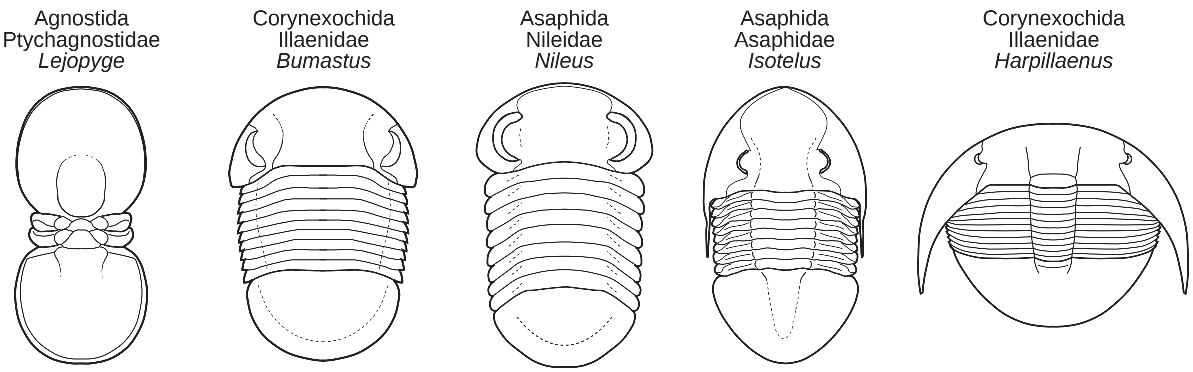
Shapes and furrow patterns of the **glabella**, and the shape and placement of **eyes and eye ridges** of course also ranged widely. An analysis of morphological diversity of trilobite forms showed that increasing from the **Cambrian**, there was a peak in morphological diversity in the **Ordovician** (which parallels a peak in overall diversity of trilobites families) that decreased as overall trilobite diversity decreased over subsequent periods, toward their extinction in the late Permian.

Within this diversification, there were a number of **evolutionary trend**s in morphology that developed in unrelated clades, creating **homeomorphy** (attainment of similar forms in unrelated groups). These homeomorphic trends, such as effacement, increased spinosity, reduction in body size, streamlined shape, and loss of eyes, can not be reliably or consistently used to assess higher systematic relationships. Instead, these features can tell us about **selective pressures** on trilobites and how similar solutions were derived in parallel by different evolutionary lineages. Each of these is discussed below, and examples are given from different orders.

Effacement

Illaenus sp.
Corynexochida:Illaenina

In several trilobite orders, but perhaps most notably among the Agnostida, Corynexochida (Suborder Illaenina), and Asaphida, effacement of cephalic, pygidial, and even thoracic furrows is not uncommon. This loss of surface detail can be confounding to systematics, since effaced features (for example loss of glabellar details) can mask evidence of relationships. Some workers suggest that effacement is an adaptation related to a burrowing lifestyle, especially in Illaenina, but such effacement might also play a role in streamlining of pelagic Asaphida, and is also seen in many Agnostida. No single selection pressure seems to have been responsible for the effaced morphotype.

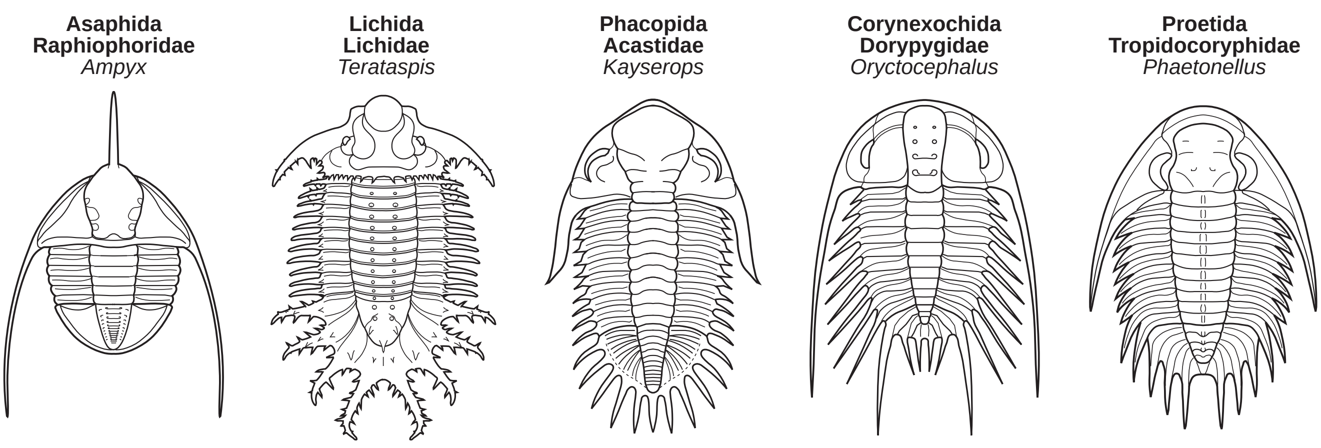


Effacement manifests in a variety of different orders, which can confound systematic determinations based on characters such as glabellar furrows.

Spinosity

Leonaspis sp. (Lichida : Odontopleuroidea)
a spiny Devonian trilobite from Morocco

The development of spines is commonly considered a defensive adaptation, and increased spinosity is seen in a wide variety of trilobite species. Alternate adaptationist hypotheses for spines include stabilization structures on a loose silty substrate (*e.g.*, the long genal spines of trinucleid Asaphida, such as *Ampyx*, below), and flotation/stabilization structures for slow-swimming taxa (*e.g.*, odontopleuroid Lichida such as *Leonaspis*, left). Spines may originate from just about any part of the exoskeleton, especially the margins. Sometimes spine patterns provide consistent and diagnostic characters for higher classification (for example, the pattern of pygidial spines is similar among odontopleuroid Lichida). However, as seen in the examples below, development of spines occurs in many orders of trilobites.

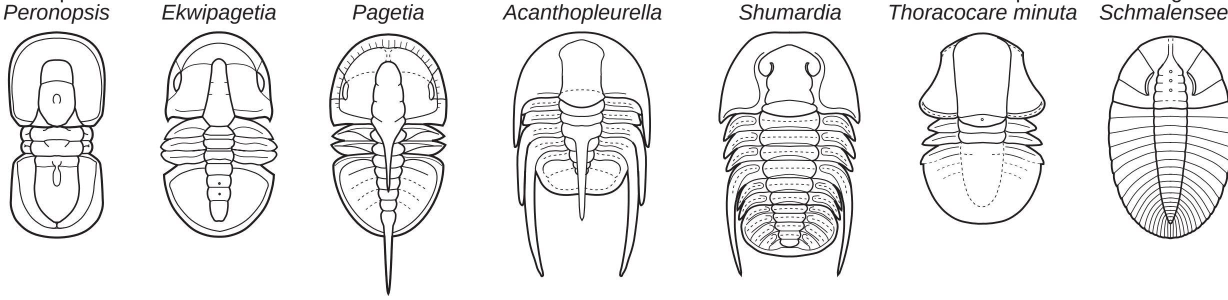


Miniaturization

Reduction in size is seen in several trilobites, such as *Acanthopleurella* (just about 1 millimeter at maturity). The general argument for evolution of small size typically evokes the numerous microhabitats of complex marine systems, coupled with a correlation of size and rapid maturity (early maturation means smaller size at adulthood). When this reduction is due to progenesis (arrested development) the trilobites may also display a reduction in the number of thoracic segments (see section on Ontogeny). *Thoracocare*, for example, has only two thoracic segments at maturity, yet is not a member of the order Agnostida (formerly thought to be the only order bearing three or fewer thoracic segments), but of Corynexochida. The entire order Agnostida is composed of small species that may have originated as a miniaturized and specialized offbranch of the Redlichiida.

Peronopsis interstricta (Peronopsidae)
Agnostida are often tiny and numerous

Agnostida / Peronopsidae / *Peronopsis*
Agnostida / Eodiscidae / *Ekwipagetia*
Agnostida / Eodiscidae / *Pagetia*
Ptychopariida / Shumardiidae / *Acanthopleurella*
Ptychopariida / Shumardiidae / *Shumardia*
Corynoexochida / Dolichometopidae / *Thoracocare minuta*
Uncertain order / Burlingiidae / *Schmalenseeia*

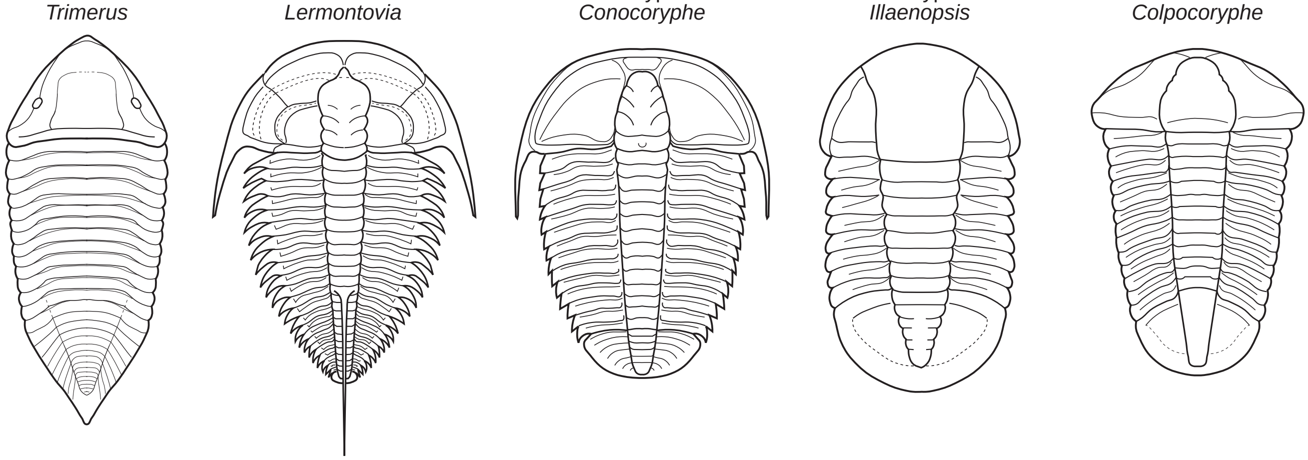


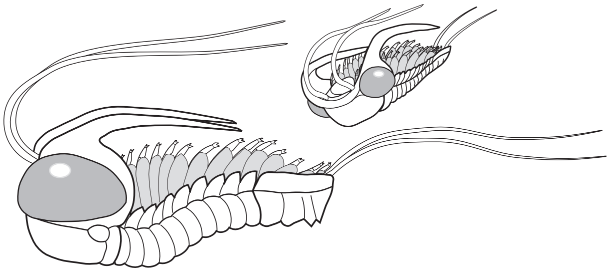
Conocoryphe sulzeri (Ptychopariida:Ptychopariina)
a pair of atheloptic trilobites, Czech Republic

Atheloptic Morphology

Secondary reduction and loss of eyes is thought to be a trend among benthic species living in deep, poorly-lit or aphotic habitats (see discussion on “The Trilobite Eye”). In these deep water biotopes, blind or nearly-blind trilobites are the dominant element. Typically, these atheloptic species have close relatives in which eyes are of normal size and function. It is interesting to note that another trend of deep bottom habitat adaptation is an increase in the number of thoracic segments (see Olenimorph section below).

Phacopida / Homalonotidae / *Trimerus*
Ptychopariida / Protolenidae / *Lermontovia*
Ptychopariida / Conocoryphidae / *Conocoryphe*
Ptychopariida / Conocoryphidae / *Illaenopsis*
Phacopida / Homalonotidae / *Colpocoryphe*





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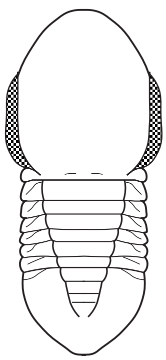
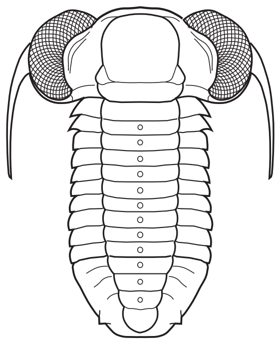
Pelagic Morphology

There are a number of trilobites that have developed extremely large eyes and elongate, streamlined body shape associated with swimming in the photic water column. The paleogeography of some of these pelagic species (for example, *Carolinites*, shown at left), suggests that their swimming abilities were good enough them to spread into a global oceanic distribution.

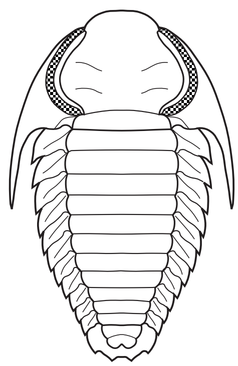
Asaphida
Cyclopygidae
Degamella



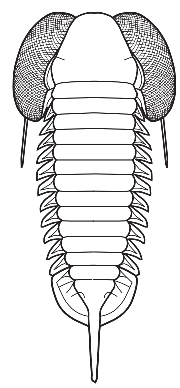
Proetida
Telephinidae
Carolinites



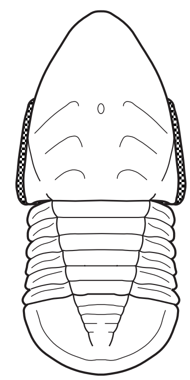
Asaphida
Remopleurididae
Remopleurides



Proetida
Telephinidae
Opipeuterella



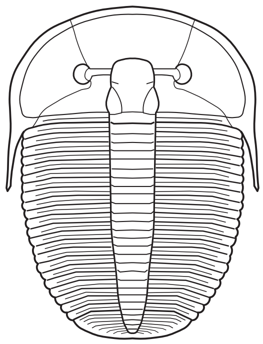
Asaphida
Cyclopygidae
Novakella



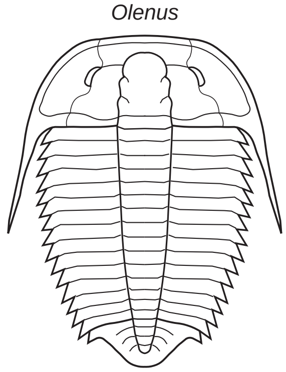
Olenimorph

Thin exoskeleton, increased numbers of thoracic segments, and a widened, flat body form is associated with benthic habitats marked by low oxygen and high sulphur compound concentrations. Fortey suggests that these **olenimorphs** (so named because many of the Ptychopariida Suborder Olenina have this form) may represent the first symbiotic relationships with sulphur eating bacteria as a feeding strategy (see section on Trilobite Feeding Habits), the numerous transverse thoracic pleurae presumeably overlaid a series of laterally expanded gill exites, maximizing oxygen absorption and providing a large surface area upon which symbiotic bacteria could live. The specimen of the olenid *Wujiajiania sutherlandi* (left) and the examples below share this olenimorph form.

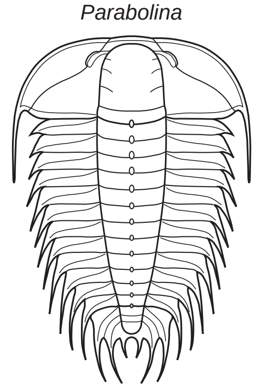
Proetida
Aulacopleuridae
Aulacopleura



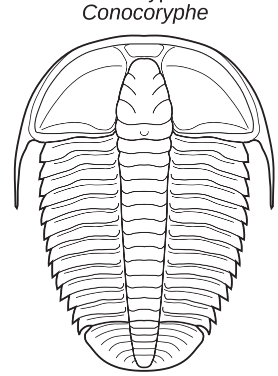
Ptychopariida
Olenidae
Olenus



Ptychopariida
Olenidae
Parabolina



Ptychopariida
Conocoryphidae
Conocoryphe

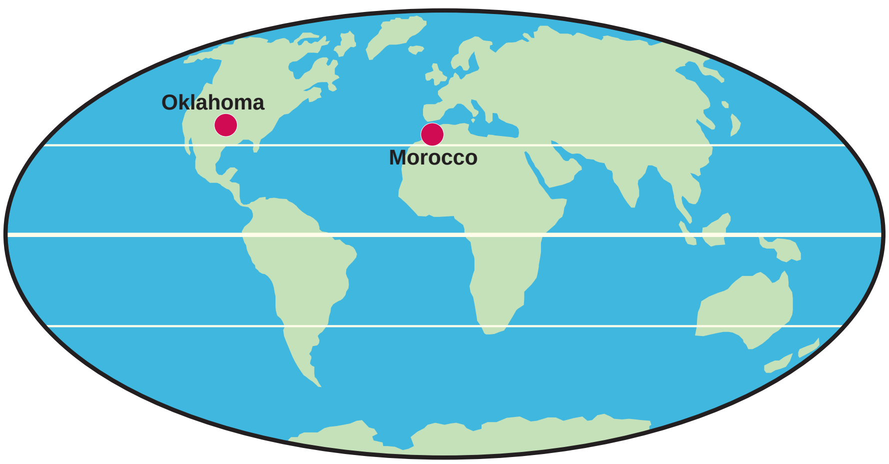


Trilobite Paleogeography

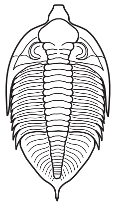
Biogeography involves the mapping and study of the **patterns of distribution** of organisms within and between the world's regions. The biogeography of plants and animals reflects their ecological requirements and the habitat niches they occupy. Some species are **widespread**, while others are **restricted** to certain regions of the globe. **Paleogeography** offers some of the same approach, but must take into account the fact of **plate tectonics**, and the changing of continental and ocean basin patterns over the course of hundreds of millions of years. The paleogeography of trilobites is particularly important because they were extremely **diverse**, were distributed all over the globe, and offer much insight on **paleoenvironments**. Trilobites occupied **marine environments** from **tropical equatorial** to **polar paleolatitudes**. Some families of trilobites were narrow in their requirements. For example, the family Bathyuridae (Proetida:Bathyuroidea) was found only in paleoequatorial regions. Trilobite marine niches ranged from **intertidal** and **nearshore** to **deep** continental slopes. Because there was very significant continental movement during the Paleozoic Era, with continents drifting apart, as well as converging and joining, the distribution and evolution of trilobites over the nearly 300 million years of their existence reflects a complex paleogeography.

Why are the trilobites from Oklahoma and Morocco so similar? One interesting example of trilobite paleogeography involves the Devonian trilobite sites of Oklahoma (such as the famous Haragan Formation), and those of Morocco (such as the prolific Hamar Laghdad Formation of the Atlas Mountains). Although on different continents today (as well as different paleocontinental systems during the Devonian), the similarities of the taxa from the two regions are amazing. Here, for example, are three of the parallel developments between the Oklahoma trilobite assemblage (top) and that of Morocco (bottom). In some cases, the same genera are found in both locations.

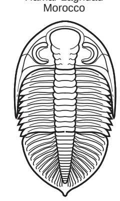
Locations of the Oklahoma and Moroccan trilobite deposits today



Dalmanitidae
Huntoniatonia
Haragan
Oklahoma



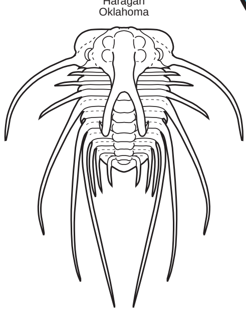
Dalmanitidae
Zlichovaspis
Hamar Laghdad
Morocco



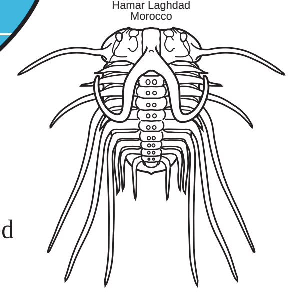
Haragan, Oklahoma and Hamar Laghdad, Morocco are widely separated today, but their trilobite assemblages are strikingly similar

Devonian continental configuration shows the connection

Odontopleuridae
Dicranurus hamatus
Haragan
Oklahoma



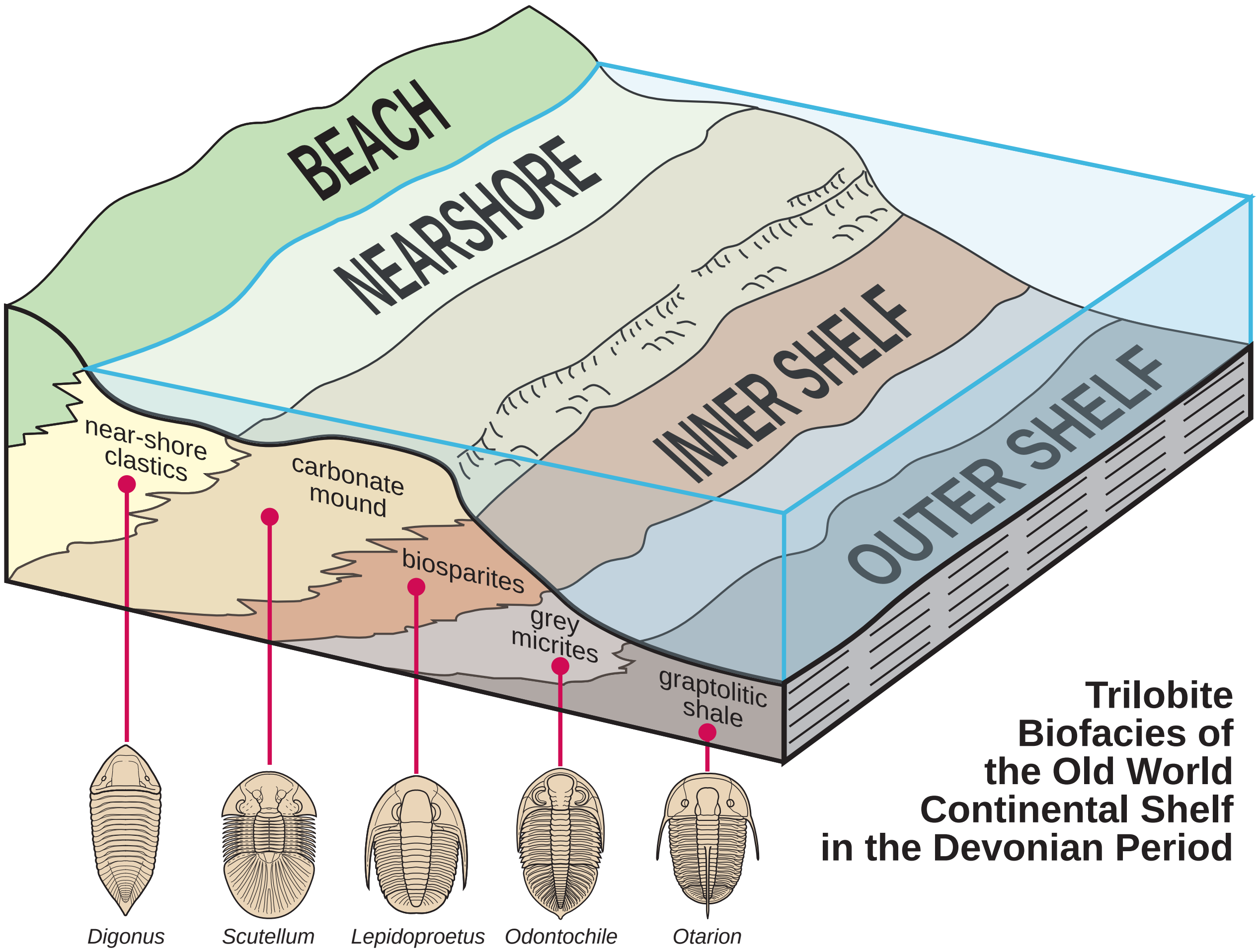
Odontopleuridae
Dicranurus monstrosus
Hamar Laghdad
Morocco



In the Devonian, Haragan and Hamar Laghdad were at similar paleolatitudes and close enough to have likely sprung from shared ancestors that then developed separately on the adjacent continental shelf systems

Deducing ancient habitats of trilobites from their surrounding matrix

Today, trilobite fossils have been found in Paleozoic formations on every continent and subcontinent, and judging from the type of sediment in which they are found, we can deduce where species were nearshore (*e.g.*, in limestones indicating shallow fringing reefs) or from deeper habitats (*e.g.*, marked by atheloptic species in continental slope sediments). While it seems that the earliest Cambrian trilobites lived in shallow habitats, by Mid-Cambrian times the entire nearshore to deep water range of biofacies was occupied by trilobites. These developed regional diagnostic genera that occupied concentric bands away from inferred shorelines, as in the example below, the Devonian shores of the Old World (Gondwana) province (today's Moroccan beds).



Trilobite Biofacies of the Old World Continental Shelf in the Devonian Period

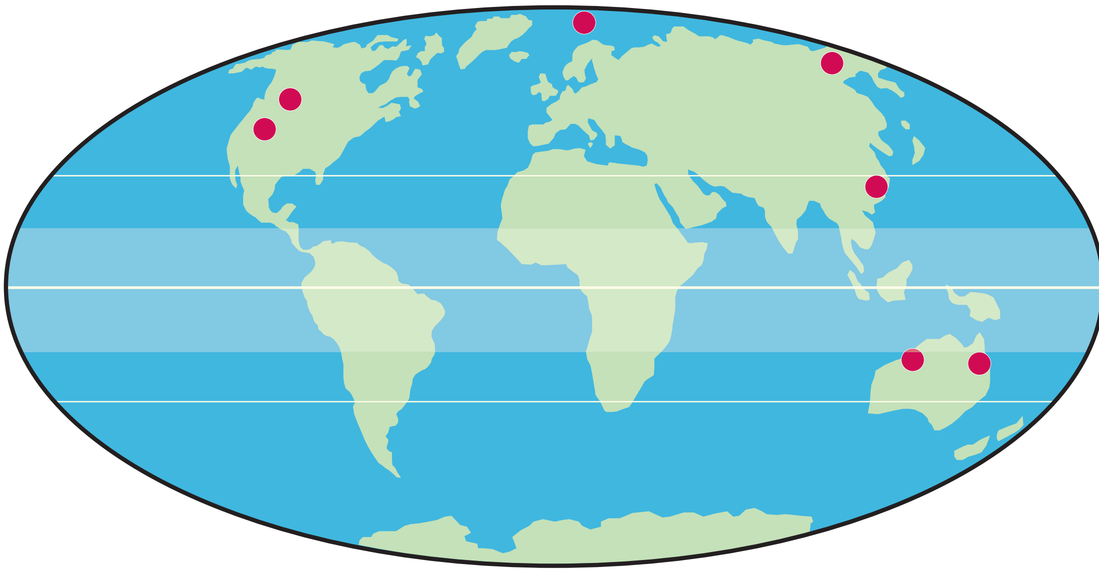
In Devonian Gondwana biofacies, the homalonotid calymenine trilobite *Digonus* (Phacopida) was diagnostic of the nearshore clastic habitat (showing wave-thrown deposits). The styginid illaenine *Scutellum* (Corynexochida) was associated with reef deposits, while the proetid *Lepidoproetus* (Proetida) was found on slopes outside the reef. The dalmanitid phacopine *Odontochile* (Phacopida) was found in grey micrite deposits still in the lower photic (sunlit) zone, but the dark, aphotic graptolitic shales of the outer continental shelf was occupied by atheloptic species, in this case, characterized by the aulacopleurid *Otarion* (Proetida).

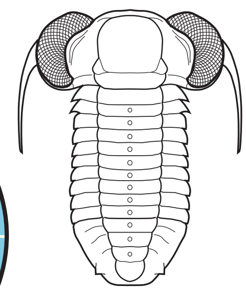
Species patterns such as the one shown above have been found in many Post-Cambrian trilobite sites in every region of the world. In many cases, the regional endemic species were found in the nearshore and carbonate mound habitats, while wider-ranging taxa were found in deeper waters, reflecting a pelagic life history and deistribution, such as shown in *Carolinites*.

Paleogeography vs modern fossil distribution

The locations of trilobite fossils on today's continents can be bewildering unless continental movement during the Paleozoic is taken into account. Indeed, trilobite fossils have told us much about the presumed locations of the paleocontinents, such as Gondwana, Laurentia, Paleosiberia, etc. For example, the trilobite *Carolinites genicinaca* (Proetida:Telephinidae) is found in far-flung and disparate places today (see top map below). However, when we examine the continental configurations during the Ordovician (when *Carolinites* lived) we see that all of those locations were tropical-equatorial, and that Carolinites was a widespread epipelagic species, It is thought to be the trilobite with the widest global distribution, past or present.

Distribution of fossils of *Carolinites genacinaca* today

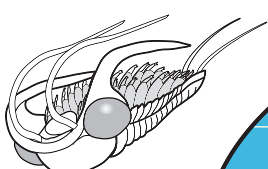




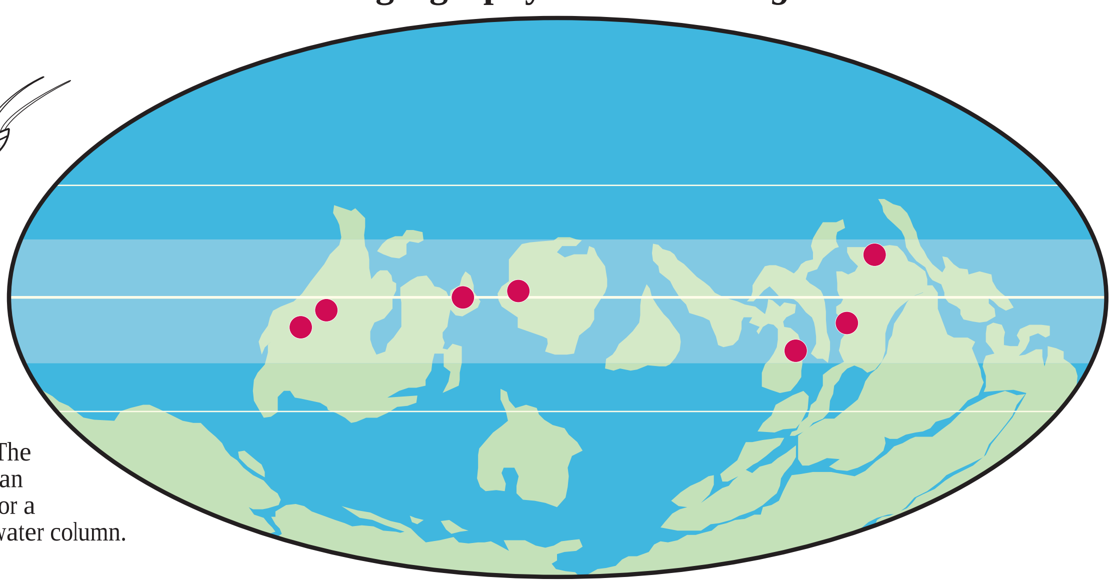
Proetida
Telephinidae
Carolinites genicinaca
has the widest global distribution of any species of trilobite

The sites where *Carolinites genacinaca* is found today range from north arctic to south subtropical

Paleozoic biogeography of *Carolinites genacinaca*



This reconstruction of *Carolinites* shows an inverted swimming posture, with limb gills serving as paddles (as in fairy shrimp today). The large eyes would offer an excellent field of view for a pelagic trilobite in the water column.



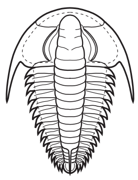
When the continents are in their Lower Ordovician configuration, the sites are all tropical-equatorial.
(both figures from McCormick & Fortey 1999)

SYSTEMATIC LISTING OF TRILOBITE FAMILIES

Source: TREATISE ON INVERTEBRATE PALEONTOLOGY

(Part O, Arthropoda 1: Trilobita, revised) 1997

The list of families below is an adaptation of the listing presented in the Treatise (1997). For the Orders Agnostida and Redlichiida, subfamilies, genera, subgenera, and species are also provided in the treatise, but since these are not yet available for the other orders, I have not included them in this listing. I hope it encourages trilobite enthusiasts to study gain insight on the classification of this diverse and fascinating group.



Redlichiidae
Redlichia

ORDER REDLICHIIDA

SUBORDER OLENELLINA

Superfamily Olenelloidea

Olenellidae
Holmiidae

Superfamily Fallotaspidoidea

Fallotaspididae
Archaeaspididae
Judomiidae
Neltneriidae
Nevadiidae

SUBORDER REDLICHIINA

Superfamily Emuelloidea

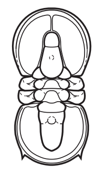
Emuellidae

Superfamily Redlichioidea

Redlichiidae
Dolerolenidae
Yinitidae
Mayiellidae
Gigantopygidae
Saukiandidae
Metadoxidae
Abadiellidae
Kueichowiidae
Menneraspididae
Redlichinidae
Chengkouaspidae

Superfamily Paradoxidoidea

Paradoxididae
Centropleuridae
Xystriduridae



Agnostidae
Agnostus

ORDER AGNOSTIDA

SUBORDER AGNOSTINA

Superfamily Agnostoidea

Agnostidae
Ptychagnostidae
Glyptagnostidae
Doryagnostidae
Peronopsidae
Diplagnostidae
Clavagnostidae
Metagnostidae

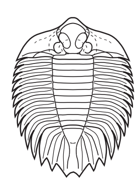
Superfamily Condylopygoidea

Condylopygidae

EODISCINA

Superfamily Eodiscoidea

Tsunyidiscidae
Hebediscidae
Calodiscidae
Weymouthiidae
Yukoniidae
Eodiscidae



Lichidae
Arctinurus

ORDER LICHIDA

SUBORDER LICHINA

Superfamily Lichoidea

Lichidae
Lichakephalidae

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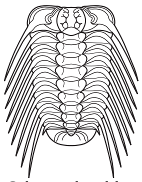
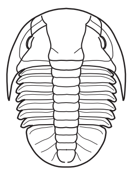


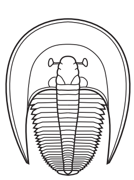
Odontopleuridae
Selenopeltis

ORDER ODONTOPLEURIDA
SUBORDER ODONTOPLEURINA
Superfamily Odontopleuroidea
Odontopleuridae
Superfamily Dameselloidea
Damesellidae



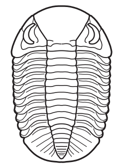
Corynexochidae
Bonnaspis

ORDER CORYNEXOCHIDA
SUBORDER CORYNEXOCHINA
Superfamily Corynexochoidea
Amgaspididae
Corynexochidae
Chengkouiidae
Dorypygidae
Oryctocephalidae
Dolichometopidae
Edelsteinaspidae
Jakutidae
Zacanthoididae
Dinesidae
SUBORDER ILLAENINA
Superfamily Illaenoidea
Styginidae (Scutelluidae)
Panderidae
Illaenidae
Tsinaniidae
SUBORDER LEIOSTEGIINA
Superfamily Leiostegioidea
Leiostegiidae
Pagodiidae
Kaolishaniidae
Cheilocephalidae
Illaenuridae
Ordosiidae
Shirakellidae (?)



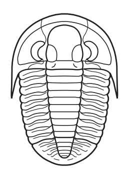
Harpetidae
Harpes

ORDER HARPETIDA
SUBORDER HARPETINA
Superfamily Harpetioidea
Harpetidae
Harpididae



Phacopidae
Phacops

ORDER PHACOPIDA
SUBORDER CALYMENINA
Superfamily Calymenoidea
Calymenidae
Homalonotidae
Pharostomatidae
Bavarillidae
Bathycheilidae
SUBORDER PHACOPINA
Superfamily Phacopoidea
Phacopidae
Pterygometopidae
Superfamily Dalmanitoidea
Dalmanitidae
Prosopiscidae
Diaphanometopidae
Superfamily Acastoidea
Acastidae
Calmoniidae
SUBORDER CHEIRURINA
Superfamily Cheiruroidea
Cheiruridae
Pliomeridae
Pilekiidae
Encrinuridae



Proetidae
Cyphoproetus

ORDER PROETIDA
SUBORDER PROETINA
Superfamily Proetoidea
Proetidae
Tropidocoryphidae
Superfamily Aulacopleuroidea
Aulacopleuridae
Brachymetopidae
Rorringtoniidae
Superfamily Bathyuroidea
Bathyuridae
Dimeropygidae
Hystricuridae
Toernquistiidae
Holotrachelidae
Telephinidae
Sharyiidae

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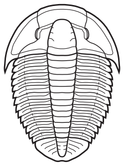
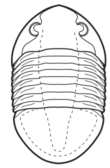


Ptychopariidae
Modocia

ORDER PTYCHOPARIIDA
SUBORDER PTYCHOPARIINA
Superfamily Ellipsocephaloidea
Bigotinidae
Yunnanocephalidae
Palaeolenidae
Estaingiidae
Ellipsocephalidae
Agraulidae
Superfamily Ptychoparioidea
Eulomidae
Antagmidae
Alokistocaridae
Ptychopariidae
Marjumiidae
Solenopleuridae
Atopidae
Holocephalinidae
Conocoryphidae
Holocephalidae
Dokimokephalidae
Nepeidae
Crepicephalidae
Tricrepicephalidae
Lonchcephalidae
Kingstoniidae
Shumardiidae
Asaphiscidae
Elviniidae
Cedariidae
Norwoodiidae
Menomoniidae
Bolaspididae
Papyriaspididae
Changshaniidae
Diceratocephalidae
Phylateridae
Conokephalinidae
Utiidae
Lisaniidae
Inouyiidae
Wuaniidae
Lorenzellidae
Proasaphiscidae
Isocolidae
Ignotogregatidae
Mapaniidae
Acrocephalitidae
Llanoaspididae
SUBORDER OLENINA
Superfamily Olenioidea
Olenidae
SUBORDER UNCERTAIN
Ithyophoridae
POLYPHYLETIC GROUPS
Catillicephalidae
Raymondinidae
Avoninidae
Plethopeltidae (near Cedariidae - Norwoodiidae?)



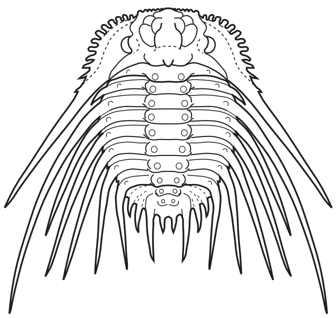
Asaphidae
Homotelus

ORDER ASAPHIDA
SUBORDER ASAPHINA
Superfamily Anomocaroidea
Anomocarellidae
Anomocaridae
Pterocephaliidae
Parabolinoididae
Aphelaspididae
Superfamily Asaphoidea
Asaphidae
Ceratopygidae
Superfamily Dikelokephaloidea
Dikelokephalidae
Andrarinidae
Saukiidae
Ptychaspididae
Eurekiidae
Superfamily Remopleuridioidea
Remopleurididae
Bohemillidae
Auritamiidae
Idahoiidae
Hungaiidae
Superfamily Cyclopygoidea
Cyclopygidae
Taihungshaniidae
Nileidae
Superfamily Trinucleioidea
Trinucleidae
Dionididae (Tongxinaspididae) (?)
Raphiophoridae
Alsataspididae
Liostracinidae
Superfamily Uncertain
Rhyssometopidae
(includes Mapaniidae, Plectriferidae)
Monkaspididae (Chelidonocephalidae) (?)

ORDER UNCERTAIN
Burlingiidae
Missisquoiidae (into Leiostegiina?)

Pictorial Guide to the Orders of Trilobites

Odontopleuridae
Kettneraspis



Introduction

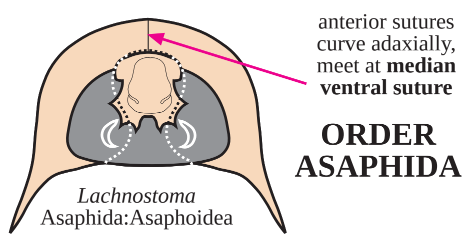
The saying goes that "A picture is worth a thousand words." Sometimes reading a description just does not have the same impact as an image that points out exactly what is being described. For example, without the image, how many words would it take to adequately describe the spiny trilobite *Kettneraspis* shown at left? The pictorial guide approach links written descriptions to an image of the specimen, pointing out the specific structure with arrows to help familiarize the user with terminology. This method is often used for natural history guides, such as field guides to birds, mammals, etc. This guide offers a pictorial approach to presenting the salient characteristics of the orders, suborders, and superfamilies of trilobites.

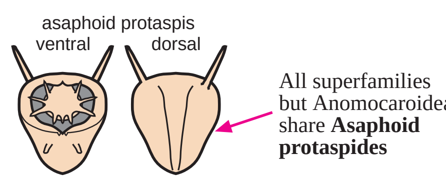
How to use the pictorial guides

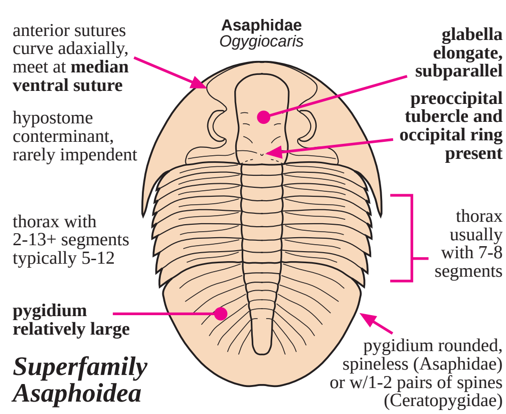
The recognized orders of trilobites are the framework for the pictorial guide. For each order there is a **narrative description** of the order, and its **constituent suborders and/or superfamilies**. For example, for the Order Agnostida, the suborders Agnostina and Eodiscina are described, and then the constituent superfamilies of these suborders are presented. An exhaustive **listing of families** is presented for each order, arranged by suborder and superfamily, so that if you know the family of a trilobite specimen, you can find its correct suborder and order. An exhaustive listing of genera is not possible, but common or **representative genera** are included, and I have attempted to list most of the genera that might typically be found in a good synoptic collection of trilobites.

One of the most useful aspects of the guide is its presentation of **diagnostic characters** (characteristics that define a particular classification). For example, one of the diagnostic characters for the Order Asaphida is the presence of a ventral median suture at the anterior ventral portion of the cephalon (see right). Related to diagnostic characters are **common features** that typically mark a group. For example, the thorax of a trilobite in the Superfamily Asaphoidea typically has 7-8 segments, and the pygidium is usually large. Where there is variability in a feature, the guide offers a **range of variation**, so you can assess the typical norms, but also the rarer exceptions. For example, a trilobite in the Superfamily Trinucleioidea typically has 5-8 thoracic segments, but only 2-3 segments in a few Raphiophoridae, and up to 30 in some Alsataspididae. Information on the characteristics of the cephalon, thorax, and pygidium are presented in this manner.

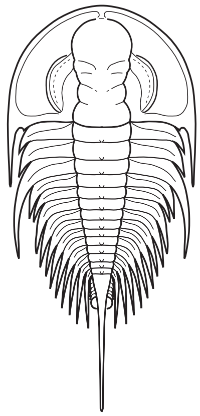
Finally, each section ends with a small gallery of trilobite drawings of complete, representative specimens that belong to that order, suborder or superfamily, so you can get a feel for the themes and variations inherent in trilobite diversity, and build your skills at assigning any complete specimen of trilobite to its likely superfamily, suborder, and order.







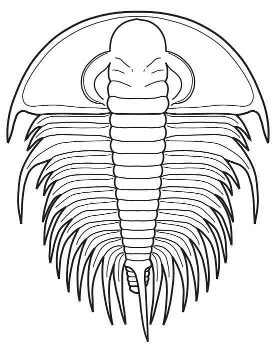
Olenellidae
Olenellus (Paedeumias)



ORDER REDLICHIIDA

Introduction: Primitive trilobites with numerous thoracic segments with spinose tips.
Cephalon: large and semicircular; glabella typically long, well-segmented, tapering or expanding forwards; genal spines typically present, strong, usually continued from a narrow, tubular cephalic border; eyes typically large, crescentic, with large, inflated palpebral lobe ridges running toward front of glabella (anterior of S3); eye ridge may be subdivided; hypostome typically conterminant, very wide rostral plate.
Thorax: with numerous segments (up to 60+), pleurae usually with spinose tips; may be subdivided into prothorax and opisthothorax.
Pygidium: typically tiny (micropygous), one or very few segments.
Occurrence: L. Cambrian to M. Cambrian.
Suborders: Olenellina and Redlichiina.

Olenellidae
Olenellus (Olenellus)



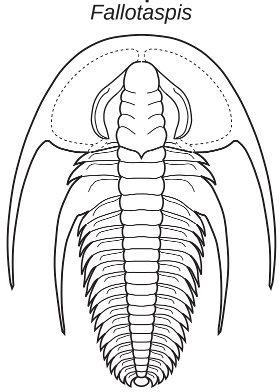
Suborder Olenellina

Cephalon: lacking facial sutures; glabella typically with rather deep lateral furrows; in some species the front glabellar lobe is an almost circular boss; conterminant hypostome, very wide rostral plate extending between genal angles, with perrostral suture (no connective sutures).
Thorax: with numerous segments, non-fulcrate; axis often spine-bearing.
Pygidium: narrow, with few segments.
Other: earliest trilobites in Cambrian stratigraphy; no calcified protaspis known; body flattened; cuticle thin.
Superfamilies: Olenelloidea, Fallotaspidoidea

Superfamily Olenelloidea

Cephalon: glabellar outline concave, anterior glabellar lobe (LA) usually enlarged, glabella narrowest at L2 or S1, L3 usually modified distally with posterolateral part bending backward and encroaching on L2; ocular lobe connects only to posterolateral part of LA.
Thorax: as in Olenellina.
Pygidium: as in Olenellina.
Families: Olenellidae, Holmiidae
Representative Genera: *Olenellus, Biceratops, Bristolia, Peachella, Nephrolenellus, Gabriellus, Laudonia, Wanneria, Holmia, Andalusiana, Cambropallas, Callavia*

Fallotaspididae
Fallotaspis



Superfamily Fallotaspidoidea

Cephalon: glabellar outline cyclindrical or slightly conical, L3 simple, similar to L2; occular lobe usually connects at anterolateral part of LA.
Thorax: as in Olenellina.
Pygidium: as in Olenellina.
Families: Fallotaspididae, Archaeaspididae, Judomiidae, Neltneriidae, Nevadiidae.
Representative Genera: *Fallotaspis, Daguinaspis, Archaeaspis, Judomia, Neltneria, Nevadia, Repinaella*

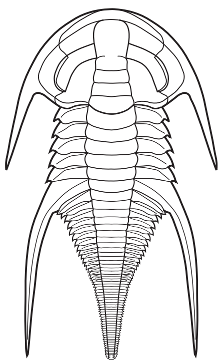
(continued next page)

ORDER REDLICHIIDA
(continued)

Suborder Redlichiina

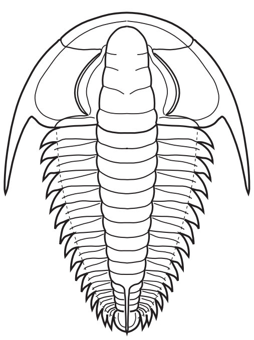
Cephalon: opisthoparian facial sutures; early forms tend to have tapering, conical glabella with furrows extending far backwards; later forms with glabella expanding forward to inflated frontal lobe; hypostome conterminant (*e.g., Redlichia*) or natant (*e.g*., *Dolerolenus*), rostral plate narrower than in Olenellina, bound by rostral and connective sutures.
Thorax: fulcrate or non-fulcrate, typically with many segments (60+ in an Emmuelid); axis infrequently spine-bearing.
Pygidium: typically small, but can be larger and with many segments.
Superfamilies: Emuelloidea, Redlichioidea, Paradoxidoidea.

Emuellidae
Balcoracania



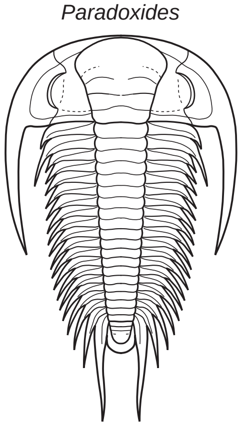
Superfamily Emuelloidea
Cephalon: cranidium subquadrate, glabella cylindrical, slightly contracted at S3, 3 pairs of glabellar furrows, preglabellar field short or absent, eye ridge wide, long, directed slightly posterolaterally, palpebral lobe cresentic, posterior area of fixigena with fulcrum, librigena with long genal spine.
Thorax: divided into prothorax of 6 segments (6th macropleural) and extremely long opisthothorax of 42-55 segments (an emuellid holds the record for greatest number of thoracic segments in a trilobite species).
Pygidium:.a minute, segmented disc.
Families: Emuellidae
Genera: *Emuella, Balcoracania, Holyoakia.*

Redlichiidae
Redlichia



Superfamily Redlichioidea
Cephalon: as in Redlichiina, but not with characters of Emuelloidea or Paradoxidoidea.
Thorax: as in Redlichiina, but not with characters of Emuelloidea or Paradoxidoidea.
Pygidium: as in Redlichiina, but not with characters of Emuelloidea or Paradoxidoidea.
Other:.largest and most diverse superfamily of Redlichiina.
Families: Redlichiidae, Dolerolenidae, Yinitidae, Mayiellidae, Gigantopygidae, Saukiandidae, Metadoxididae, Abadiellidae, Kuechowiidae, Menneraspididae, Redlichinidae, Chengkouaspidae.
Representative Genera: *Redlichia, Metaredlichia, Maopingaspis, Neoredlichia, Leptoredlichia, Eoredlichia, Wutingaspis, Kuanyangia, Dolerolenus, Paramalungia, Yinites, Drepanopyge, Paokannia, Yunnanaspis, Mayiella, Gigantopygus, Yiliangella, Saukianda, Despujolsia, Perrector, Eops, Metadoxides, Abadiella, Kueichowia, Menneraspis, Redlichina, Tungusella, Chengkouaspis.*

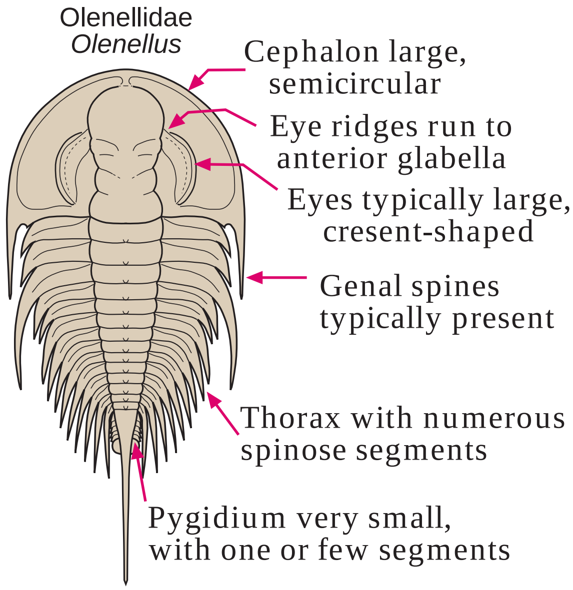
Paradoxididae
Paradoxides



Superfamily Paradoxidoidea
Cephalon: semicircular cephalon with long librigenal spine, glabella widens anteriorly to rounded or bluntly pointed LA (parallel in early forms), L1 - L4 equal or subequal, S1 generally transglabellar, but shallow medially, S2 long, may be transglabellar, S3 and S4 short (S4 strongly oblique in Centropleuridae, making large angle with S3), preglabellar field generally absent in adult, opisthoparian, anterior facial sutures divergent, transverse, to retrodivergent.
Thorax: with 14 - 21 segments, short to long pleural spines directed progressively more strongly backward from front to rear, sometimes tips bluntly truncated (Centropleuridae), 1st and 2nd segments may be macropleural.
Pygidium: generally small in Paradoxididae, tending to medium sized in Centropleuridae and Xystriduridae.
Other: often large trilobites.
Families: Paradoxididae, Centropleuridae, Xystriduridae.
Genera: *Paradoxides, Acadoparadoxides, Anabaraceps, Eccaparadoxides, Hydrocephalus, Centropleura, Anopolenus, Clarella, Zystridura.*

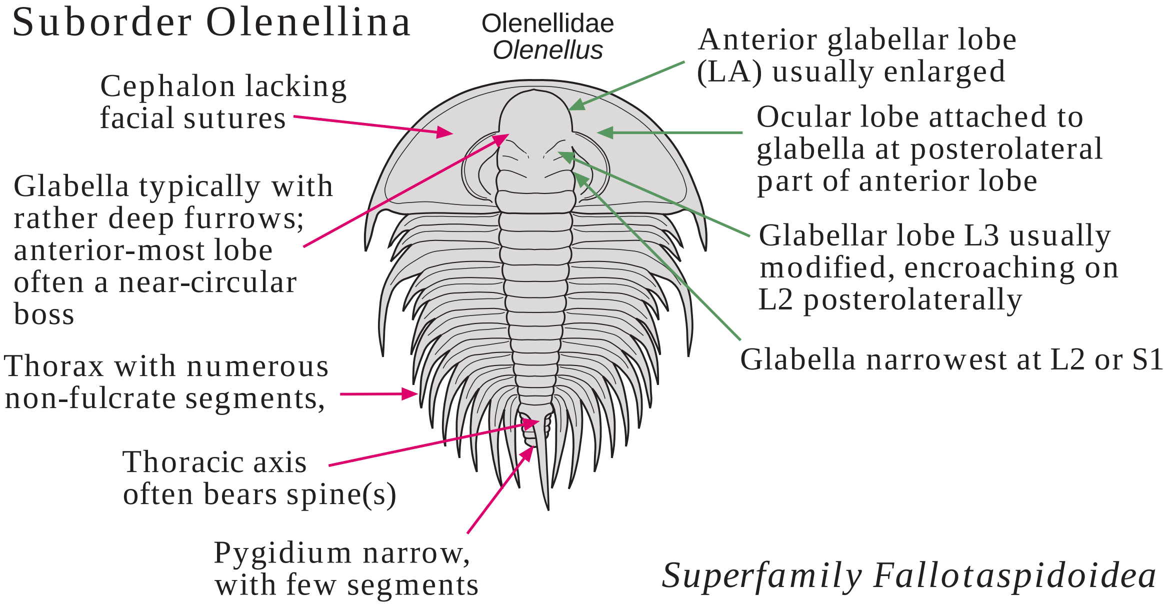
PICTORIAL GUIDE TO THE ORDER REDLICHIIDA

ORDER REDLICHIIDA

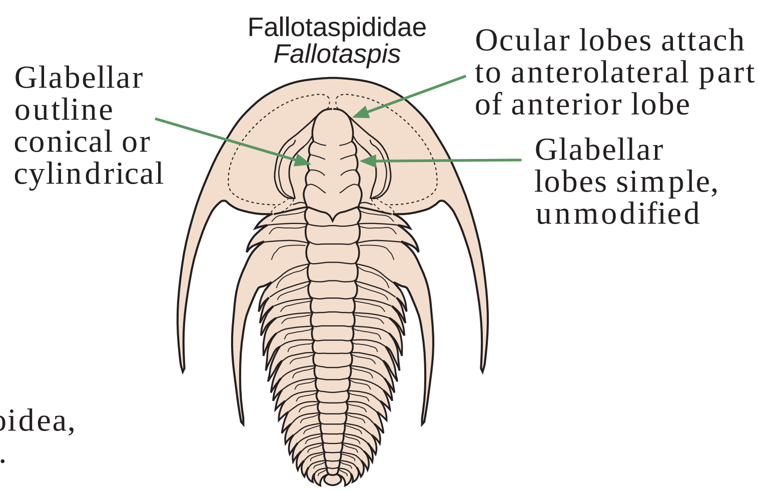


Superfamily Olenelloidea

Suborder Olenellina



Superfamily Fallotaspidoidea

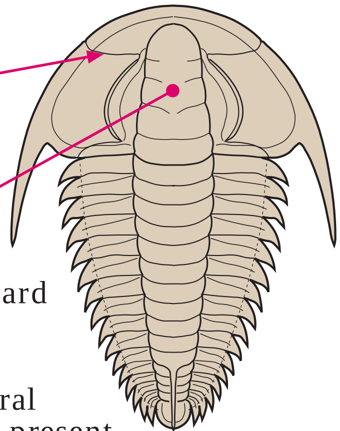


Pictorial guide to Suborder Redlichiina (Superfamilies Redlichioidea, Paradoxidoidea, and Emuelloidea) provided on next page.

PICTORIAL GUIDE TO THE ORDER REDLICHIIDA
(continued)

Suborder Redlichiina

Redlichiidae
Redlichia



Superfamily Redlichioidea

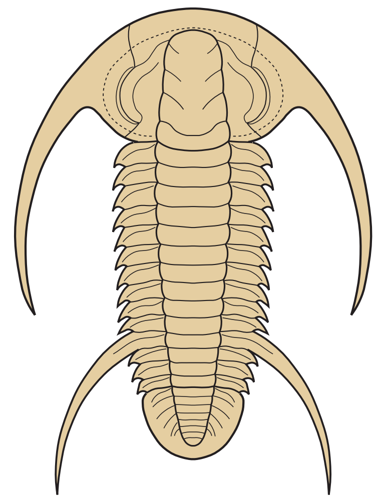
Cephalon bears opisthoparian facial sutures

Glabella tapering forward in early forms, with furrows extending far backward

Rostral plate narrower than in Olenellina; rostral and connective sutures present

Largest and most diverse superfamily of Redlichiina; hard to characterize because of significant variation of all characters

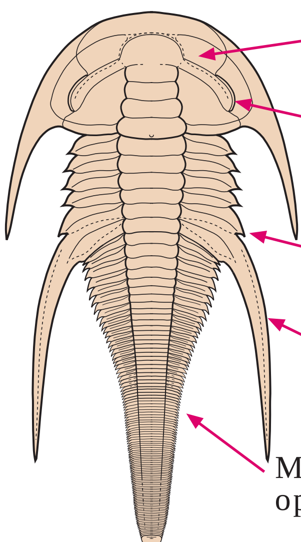
Saukiandidae
Richterops



Defined by exclusion: any Redlichiina *not* with characters of Emuelloidea or Paradoxidoidea is assigned to Redlichioidea (for example, *Richterops* at right)

Superfamily Emuelloidea

Emuellidae
Balcoracania



Cranidium subquadrate

Eye ridge wide, long, directed somewhat posterolaterally

3 or 6-segmented prothorax

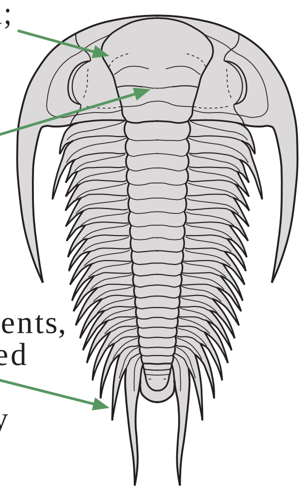
Last prothoracic segment is macropleural

Many segmented opisthothorax

Minute, discoid pygidium

Superfamily Paradoxidoidea

Paradoxididae
Paradoxides



Glabella typically expands forward; L1 - L4 subequal

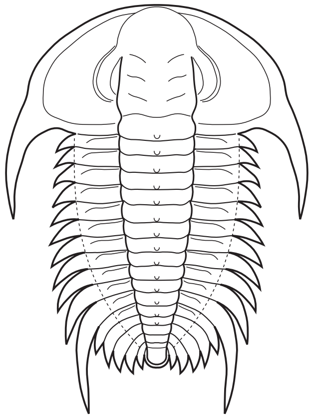
S1 generally transglabellar S2 typically long, S3 and S4 short

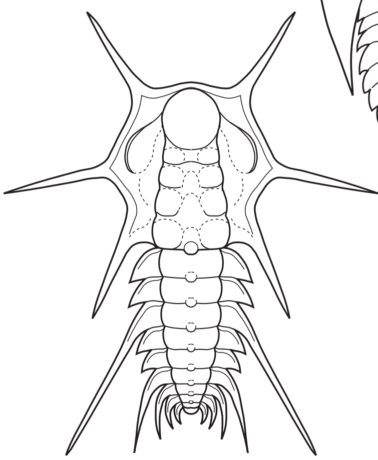
14 - 21 thoracic segments, pleural spines directed progressively more backward posteriorly

GALLERY: ORDER REDLICHIIDA

Suborder Olenellina

Neltneria
Neltneriidae

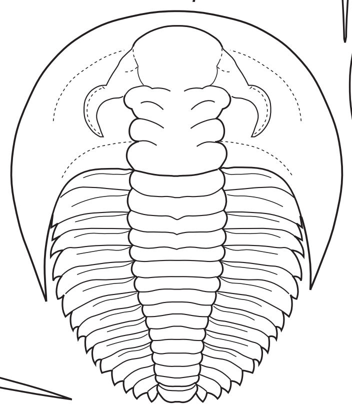




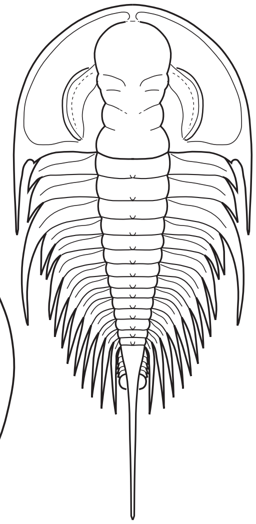
Olenellidae
Olenelloides

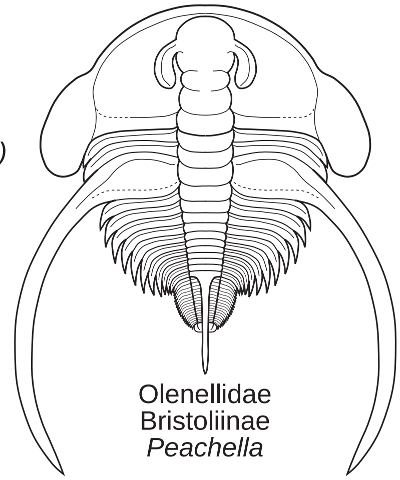
Superfamily Olenelloidea

Holmiidae
Cambropallas



Olenellidae
Olenellus (Paedeumias)

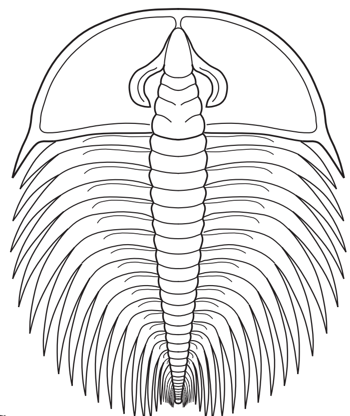




Olenellidae
Bristoliinae
Peachella

Superfamily Fallotaspidoidea

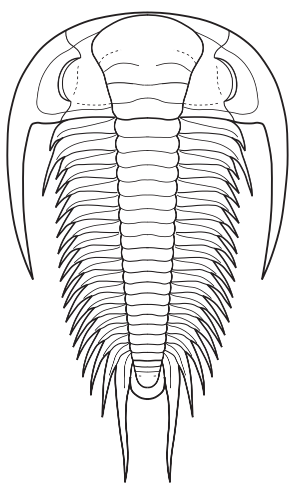
Nevadiidae
Nevadia



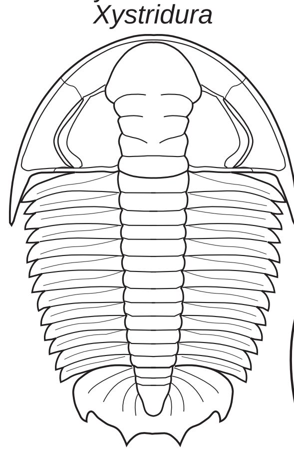
Suborder Redlichiina

Superfamily Paradoxidoidea

Paradoxididae
Paradoxides

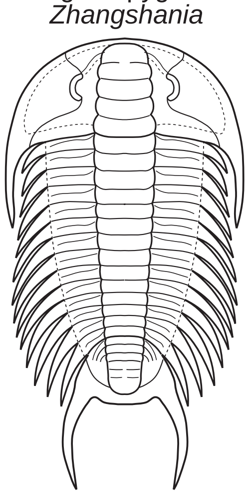


Xystriduridae
Xystridura



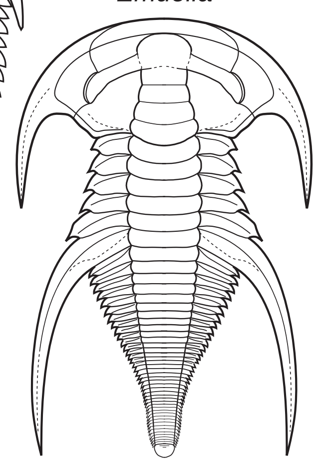
Superfamily Redlichioidea

Gigantopygidae
Zhangshania

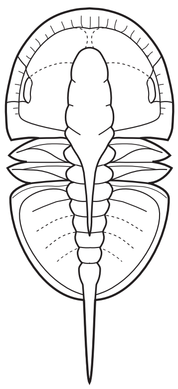


Superfamily Emuelloidea

Emuellidae
Emuella



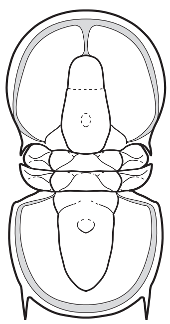
Eodiscidae
Pagetia



ORDER AGNOSTIDA

Introduction: Small trilobites (usually only a few mm long) with cephalon and pygidium similar in outline and size (isopygous); enrollment typical. It has been suggested that some Agnostina are derived from ancestors within Eodiscina.
Cephalon: cephalic shield with deeply parabolic outline, maximum width usually anterior of genal angle, sutures proparian or lacking; border convex; glabella fusiform, widest at base (except in Condylopygidae), glabellar segmentation highly variable,sometimes complex, but in some species entirely effaced; most species eyeless; hypostome natant, specialized with ribbon-like wings; rostral plate lacking (or uncalcified).
Thorax: segments 2 (Agnostina) or 3 (some Eodiscina), axis typically broad, short fulcrate pleurae.
Pygidium: strongly isopygous; pygidial margin typically closely matching cephalic margin.
Occurrence: L. Cambrian to U. Ordovician (Ashgill).
Suborders: Agnostina and Eodiscina.

Agnostidae
Agnostus



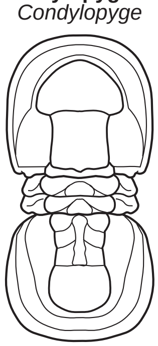
Suborder Agnostina

Cephalon: no facial sutures or eyes; cephalothoracic aperture present.
Thorax: 2 thoracic segments bearing distinctive articulating structures, but no articulating half-ring on anterior thoracic segment.
Pygidium: axis usually wide, inflated, 3 or fewer segments, one of which usually carries a tubercle; pygidial margin often bearing posterolateral spines. Cuticle thin.
Superfamilies: Agnostoidea and Condylopygoidea (each described below).

Superfamily Agnostoidea

Cephalon: with basal glabella lobes anteriorly directed, no clear occipital structure present, anterior glabellar lobe typically subequal in width to posteroglabella, or narrowing forward (not laterally expanded).
Thorax: as in typical Agnostina.
Pygidium: variable within bounds of typical Agnostina.
Representative Families: Agnostidae, Clavagnostidae, Diplagnostidae, Doryagnostidae, Glyptagnostidae, Metagnostidae, Peronopsidae, Ptychagnostidae
Representative Genera: *Agnostus, Ammagnostus, Arthrorachis, Aspidagnostus, Clavagnostus, Diplagnostus, Poryagnostus, Glyptagnostus, Goniagnostus, Hypagnostus, Metagnostus, Oidalagnostus, Peronopsis, Phalagnostus, Pseudagnostus, Ptychagnostus, Spinagnostus*

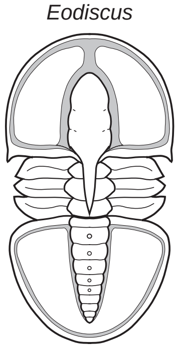
Condylopygidae
Condylopyge



Superfamily Condylopygoidea

Cephalon: with transversely oriented basal glabella lobes, separated by medial plate, together forming a clear occipital structure, anterior glabellar lobe laterally expanded around anterior end of posteroglabella, sometimes separated by a median sulcus.
Thorax: as in typical Agnostina.
Pygidium: axis with triannulate anteroaxis; broad, posteriorly rounded posteroaxis.
Representative Families: Condylopygidae
Representative Genera: *Condylopyge, Pleuroctenium.*

Eodiscidae
Eodiscus



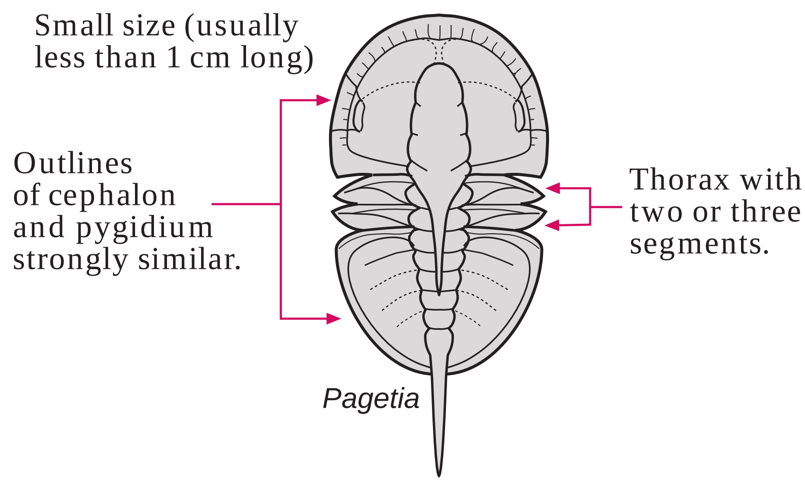
Suborder Eodiscina

Superfamily Eodiscoidea

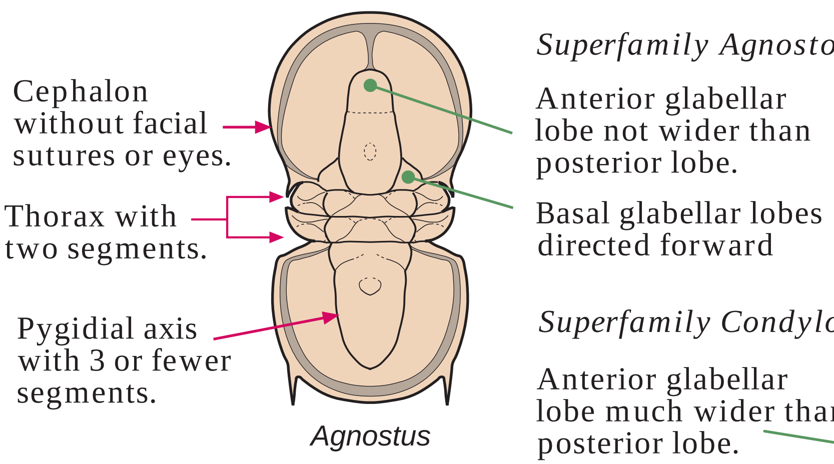
Introduction: Eodiscina provide the bridge connecting Agnostida with “typical” trilobites. Presence of eyes, sutures, and typical thoracic structure suggest that Eodiscina are akin to Ptychopariida, but placement in Agnostida prevails in the 1997 Treatise.
Cephalon: with proparian sutures, when present; some retain eyes; glabella usually simple, narrow and tapering.
Thorax: 2 or 3 thoracic segments of normal trilobite form, with articulating half-rings.
Pygidium: axis can be long and narrow, extending close to margin, generally distinctly divided into more than 3 ringlike segments; pleural region segmented in some species, sometimes pygidial segmentation effaced; border furrows often very deep; axis sometimes spinose.
Families: Calodiscidae, Eodiscidae, Hebediscidae, Tsunyidiscidae, Weymouthiidae, Yukoniidae.
Representative Genera: *Calodiscus, Eodiscus, Hebediscus, Tsunyidiscus, Weymouthia, Yukonia.*

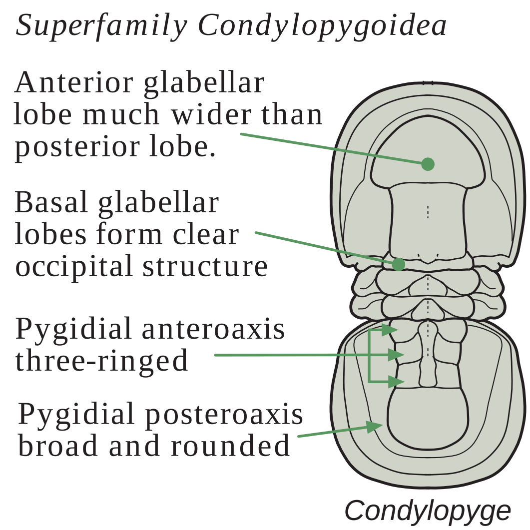
PICTORIAL GUIDE TO THE ORDER AGNOSTIDA

ORDER AGNOSTIDA

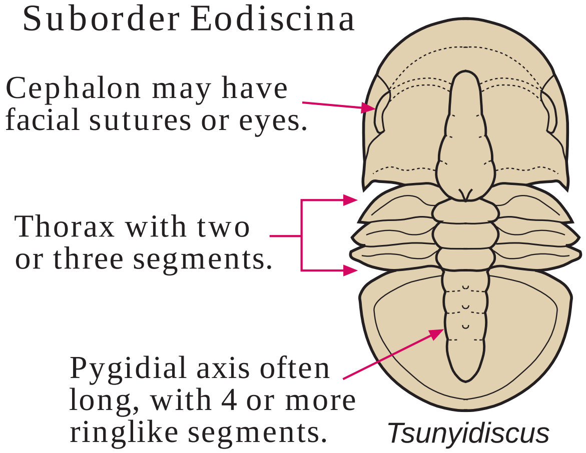


Suborder Agnostina





Suborder Eodiscina

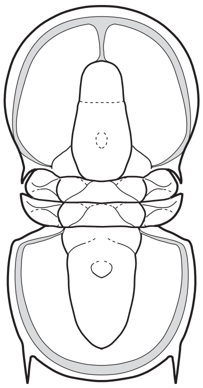


GALLERY: ORDER AGNOSTIDA

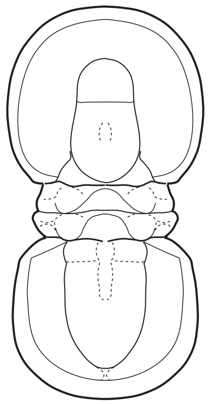
Suborder Agnostina

Superfamily Agnostoidea

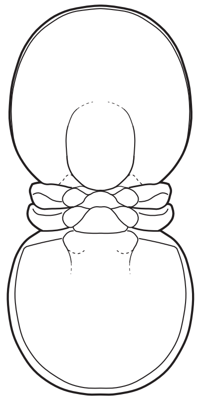
Agnostidae
Agnostus



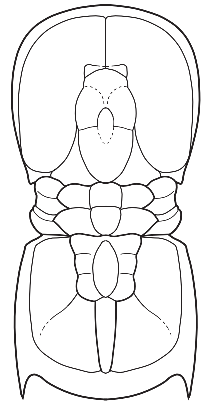
Peronopsidae
Peronopsis



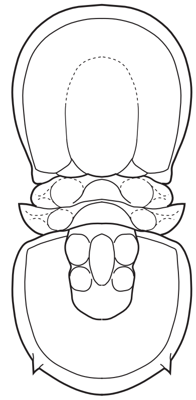
Ptychagnostidae
Lejopyge



Diplagnostidae
Machairagnostus



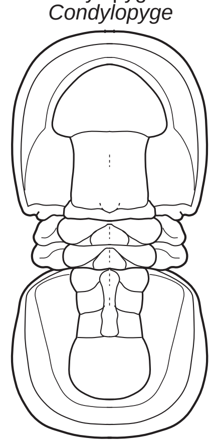
Metagnostidae
Arthrorhachis



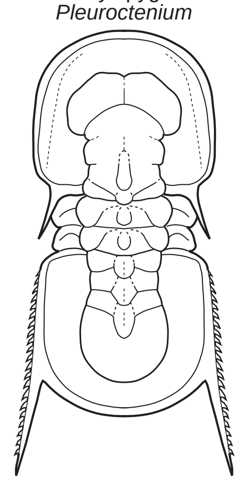
Suborder Agnostina

Superfamily Condylopygoidea

Condylopygidae
Condylopyge

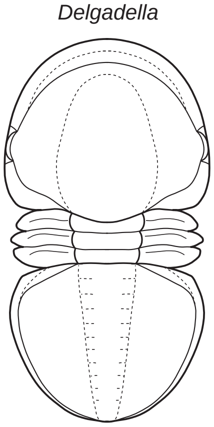


Condylopygidae
Pleuroctenium

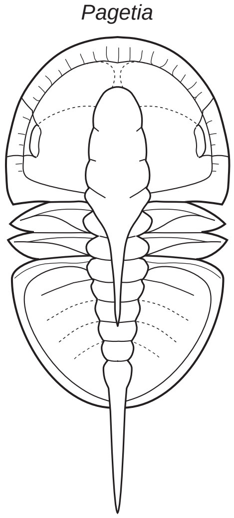


Suborder Eodiscina

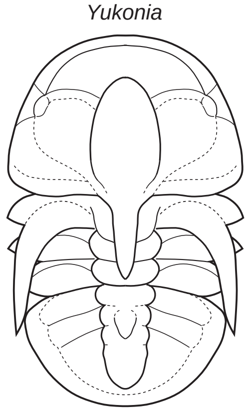
Hebediscidae
Delgadella



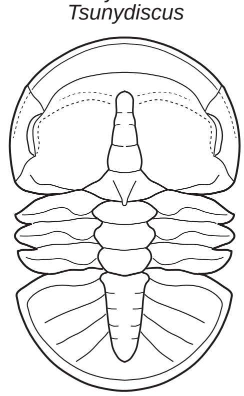
Eodiscidae
Pagetia



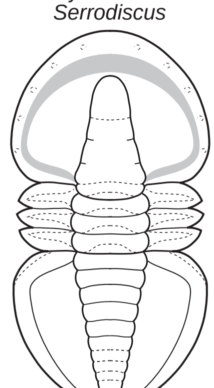
Yukoniidae
Yukonia



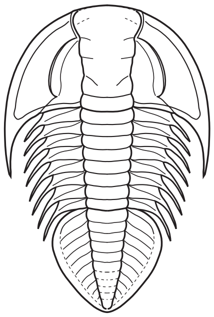
Tsunydiscidae
Tsunydiscus



Weymouthiidae
Serrodiscus



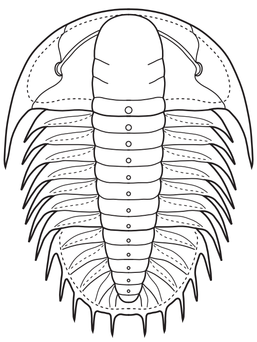
Dolichometopidae
Polypleuraspis



ORDER CORYNEXOCHIDA

Cephalon: opisthoparian sutures; glabella elongate, sides often concave (pestle-shaped), furrows (when not effaced) typically with splayed arrangement, the hind pair pointing sharply backwards, and anterior pairs tending more and more forward directed; sometimes furrows pit-like; cranidial borders often ledgelike; hypostomal attachment conterminant or (in derived forms) impendent; eyes typically large, in some gently arcuate.
Thorax: typically with 7-8 segments (but range for order is 2-18), pleural tips often spinose
Pygidium: typically large (isopygous or subisopygous), of variable form, some spinose.
Other: Metaprotaspis hexagonal, glabella expanding forward, anterior pits, posterior spines.
Occurrence: Lower Cambrian – Middle Devonian
Suborders: Corynexochina, Illaenina, Leiostegiina

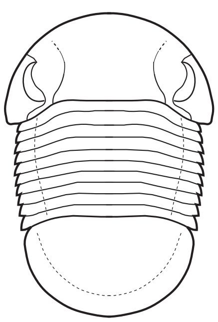
Dorypygidae
Olenoides



Suborder Corynexochina

Cephalon: cephalic sutures opisthoparian, anterior sutures generally subparallel; glabella long, subparallel, or expanding anteriorly; eyes typically elongate, narrow; hypostome typically fused with rostral plate (conterminant); genal spines often present.
Thorax: typically 7-8 segments, but up to 18 and as low as 2, pleurae typically spine tipped.
Pygidium: variable, typically large and spinose, some with smooth border.
Superfamilies/Families: Corynexochoidea/Amgaspididae, Corynexochidae, Dinesidae, Dokimocephalidae, Dolichometopidae, Dorypygidae, Edelsteinaspididae, Jakutidae, Oryctocephalidae, Zacanthoididae.
Representative Genera: *Albertella, Amgaspis, Amphoton, Athabaskia, Bathyuriscus, Bonnaspis, Changaspis, Dinesus, Dokimocephalus, Dorypyge, Edelsteinaspis, Glossopleura, Jakutus, Kootenia, Lancastria,Ogygopsis, Olenoides, Oryctocephalus, Zacanthoides*.

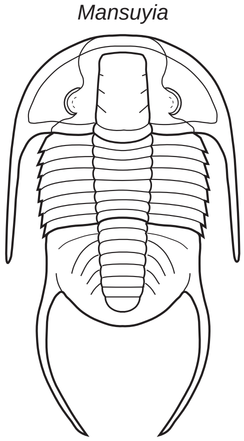
Illaenidae
Bumastus



Suborder Illaenina

Cephalon: typically effaced, opisthoparian facial sutures, but sutures distinctly divergent anteriorly; glabella expands forwards, lateral furrows often faint or absent; hypostome impendent (variant of conterminant); extra-axial cephalic muscle impression (lunette) present; doublure broad.
Thorax: typically 8-10 segments (but 6 in Phillipsinellidae).
Pygidium: isopygous or subisopygous, rounded posteriorly, usually with short axis.
Superfamily/Families: Illaenoidea/Illaenidae, Panderiidae, Styginidae, Tsinaniidae.
Representative Genera: *Bumastus, Ectillaenus, Hemibarrandia, Illaenus, Panderia, Paralejurus, Phillipsinella, Scabriscutellum, Shergoldia, Tsinania*.

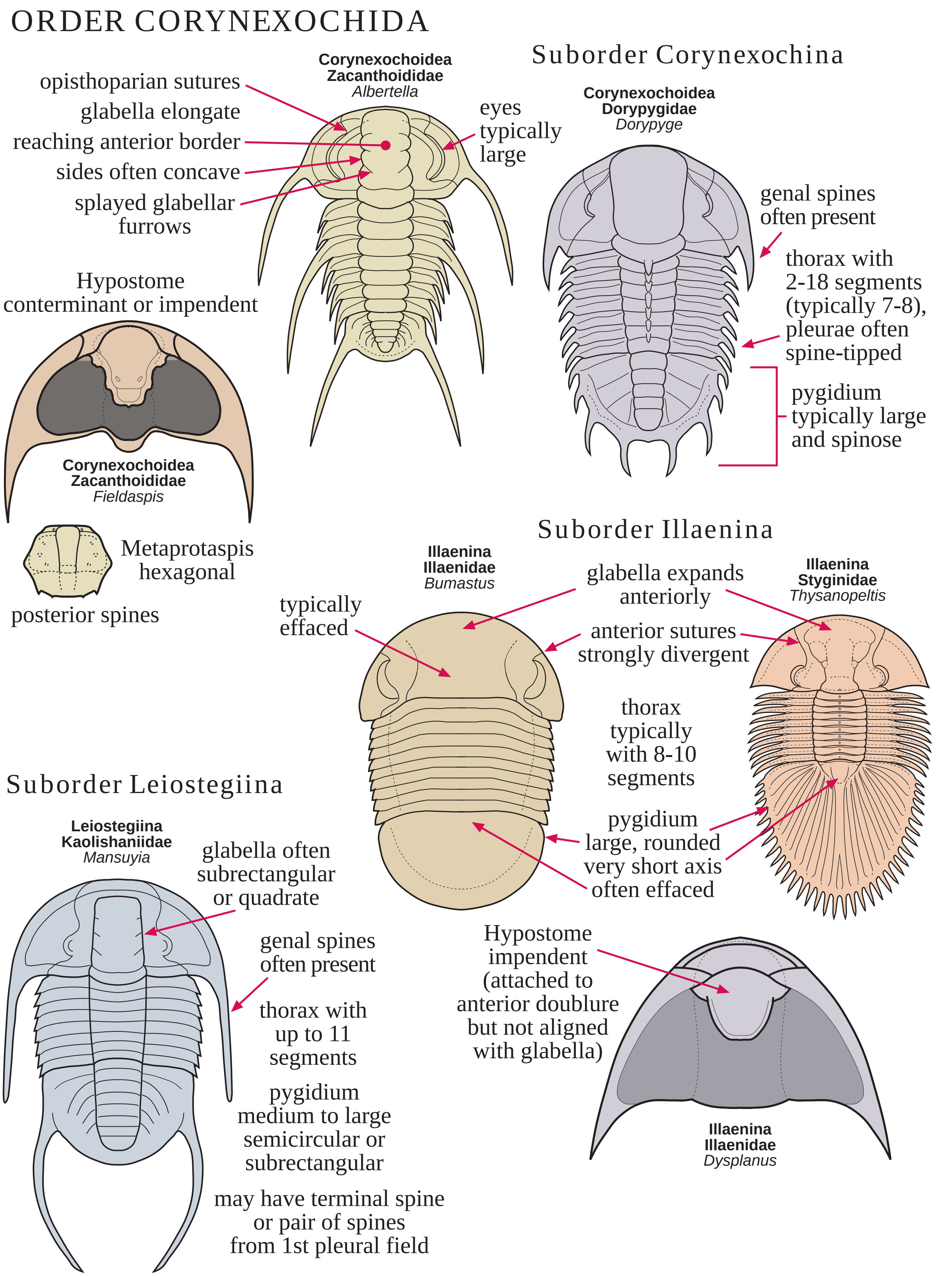
Kaolishaniidae
Mansuyia



Suborder Leiostegiina

Cephalon: opisthoparian, glabella variable, many with Corynexochoid form, others subrectangular or quadrate, sometimes broad base, tapering forward, lateral furrows on glabella often faint or absent; palpebral furrows and eye ridges often present; eyes often medium sized, but variable; genal spines typically present.
Thorax: variable, up to 11 segments.
Pygidium: medium to large, broadly transverse, semicircular, subrectangular, or subtriangular; furrows often faint or absent; axis often persist along nearly full length, sometimes extending into terminal spine, or a pair of lateral spines extending from 1st and 2nd pleural field (Kaolishaniidae)
Other: ontogeny more similar to Ptychopariida than other Corynexochida; relationship of the Leiostegiina to the other two suborders not yet determined.
Superfamily/Family: Leiostegioidea/Cheilocephalidae, Kaolishaniidae, Lecanopygidae, Leiostegidae, Pagodiidae, Missisquoiidae?, Ordosiidae, Shirakiellidae.
Representative Genera: *Cheilocephalus, Illaenurus, Kaolishania, Komaspidella, Lecanopyge, Leiostegium, Lloydia, Mansuyia, Ordosia, Pagodia, Shirakiella, Szechuanella*.

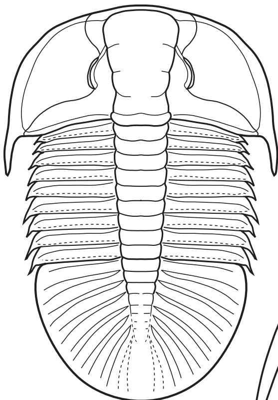
PICTORIAL GUIDE TO THE ORDER CORYNEXOCHIDA



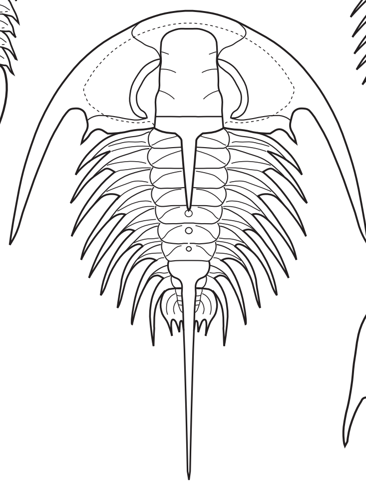
GALLERY: ORDER CORYNEXOCHIDA

Suborder Corynexochina

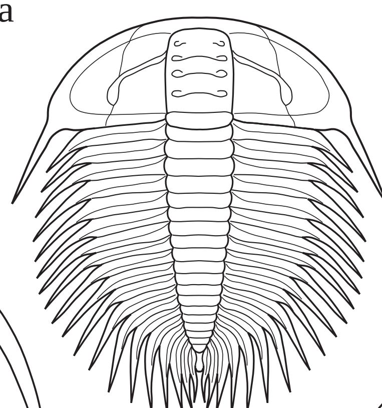
Dolichometopidae
Bathyuriscus



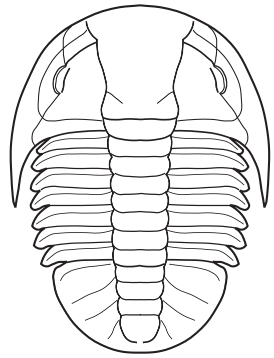
Zacanthoididae
Zacanthoides



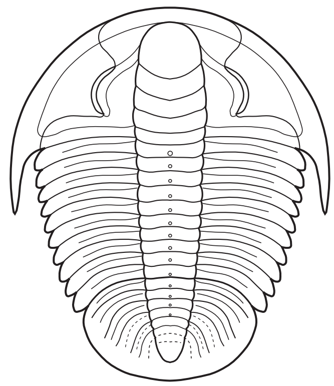
Oryctocephalidae
Lancastria



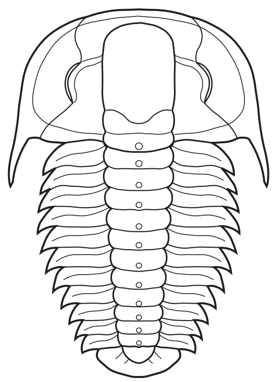
Corynexochidae
Bonnaspis



Edelsteinaspididae
Edelsteinaspis

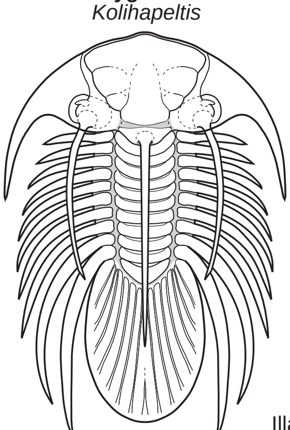


Dinesidae
Dinesus

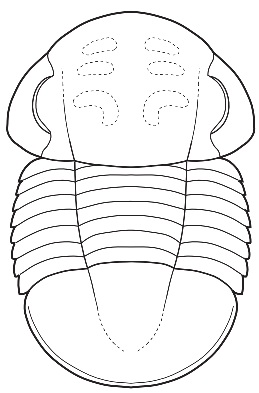


Suborder Illaenina

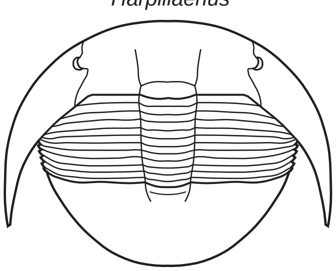
Styginidae
Kolihapeltis



Panderiidae
Panderia

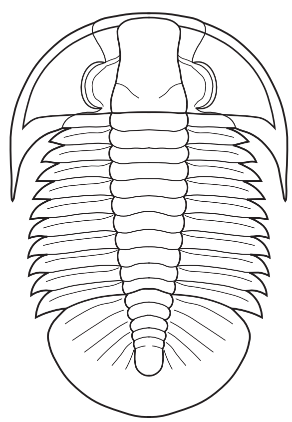


Illaenidae
Harpillaenus

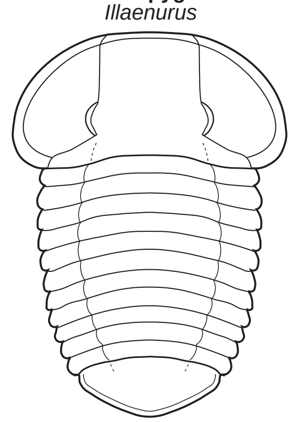


Suborder Leiostegiina

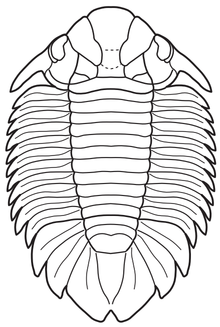
Leiostegiidae
Paraszechuanella



Lecanopygidae
Illaenurus



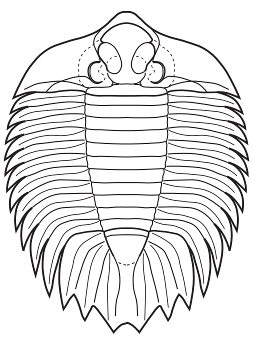
Lichidae
Dicranopeltis



ORDER LICHIDA

Introduction: typically spiny with densely granulate or tuberculate exoskeletons.
Cephalon: opisthoparian sutures; glabella broad, large, extending to anterior border, lobation simple (Odontopleuroidea) to complex, with fused lateral and glabellar lobes (Lichoidea); eyes typically present, holochroal, usually not large; conterminant hypostome.
Thorax: variable, 8-13 segments, usually spine-tipped, sometimes with distinctive spines (*e.g.*, Odontopleuroidea).
Pygidium: typically isopygous to macropygous, but sometimes short (*e.g.*, Odontopleuroidea), often longer than wide, often with 3 pairs of furrowed pleurae, typically ending in spinose tips.
Occurrence: Late Middle Cambrian to Devonian (Frasnian).
Superfamilies: Lichoidea, Odontopleuroidea, Damesselloidea

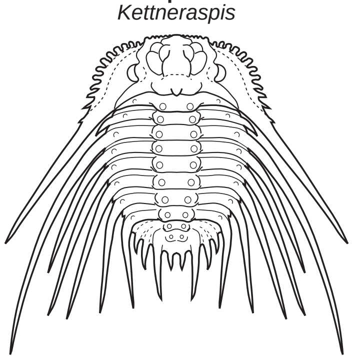
Lichidae
Arctinurus



Superfamily Lichoidea

Introduction: medium to large trilobites, typically surface sculpturing involves two size classes of granules or tubercles.
Cephalon: opisthoparian sutures, glabella broad, extending to anterior border, with unique complex structure (lateral glabellar and occipital lobes often fused with each other and with cranidium).
Thorax: 10-11 segments, pleurae initially horizontal, bend retrograde at fulcrum, end in free points.
Pygidium: large, usually flattened, often with 3 pleural pairs of leaflike or spinose structures.
Families: Lichidae, Lichakephalidae
Representative Genera: *Arctinurus, Ceratarges, Dicranopeltis, Eoacidaspis, Hemiarges, Hoplolichas, Lichas, Lichakephalus, Lobopyge, Platylichas, Terataspis, Uralichas.*

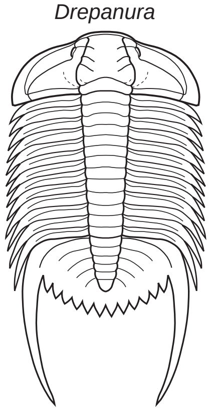
Odontopleuridae
Kettneraspis



Superfamily Odontopleuroidea

Introduction: typically very spinose and densely sculptured trilobites.
Cephalon: convex; glabella tapering forward or subparallel, extending to anterior margin or nearly so, less complex lobation than in Lichoidea; eye ridges run from anterior end of glabella to palpebral lobe; opisthoparian sutures (fused in a few species), when present, often placed on sutural ridges; distinct notch in margin of free cheek adjacent to where anterior sutures cut cephalic margin; short genal spines typically present.
Thorax: 8 – 10 segments; tips of each bear 2 – 3 pairs of spines (anterior pair often difficult to see, ventrally directed); often with symmetrical row arrangements of pleural spines or tubercles.
Pygidium: micropygous, short, transverse, with 2 – 3 axial rings (3rd often faint), one or more pairs of tubular border spines, the largest of which connected to first axial ring by prominent ridge.
Families: Odontopleuridae
Representative Genera: *Acidaspis, Ceratonurus, Diacanthaspis, Dicranurus, Kettneraspis, Leonaspis, Miraspis, Odontopleura, Selenopeltis.*

Damesellidae
Drepanura



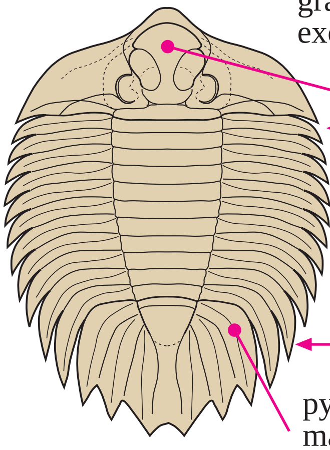
Superfamily Damesselloidea

Introduction: similar to Odontopleuroids, surface finely to coarsely granulose.
Cephalon: opisthoparian sutures; glabella narrow or broad based, tapering forward, less complex lobation than in Lichoidea; genal spines typically present.
Thorax: with up to 13 segments, less specialized than in Odontopleuroidea, more as in Lichoidea.
Pygidium: longer pygidia than in Odontopleuroidea, with more axial segments; tapering axis, thicker-set marginal spines, 1-7 pairs of pleural pygidial spines of varying length
Family: Damesellidae
Representative Genera: *Blackwelderia, Damesella, Drepanura, Palaeadotes, Stephanocare.*

PICTORIAL GUIDE TO THE ORDER LICHIDA

ORDER LICHIDA

Lichidae
Arctinurus



spiny trilobites with granulate or tuberculate exoskeletons

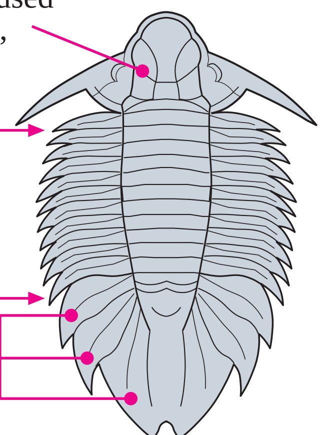
glabella broad, large, extending to anterior border, glabellar lobation may be complex

thorax 8-13 segments, usually spinose

pygidium often spiny may bear paired leaflike lobes

Superfamily Lichoidea

Lichidae
Dicranopeltis



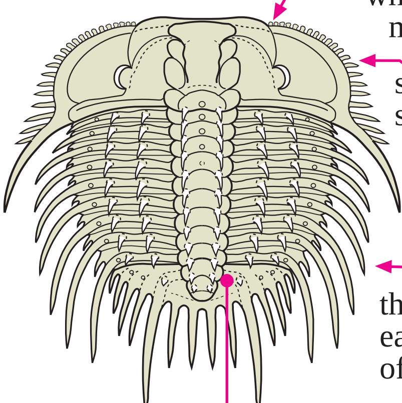
glabellar structure complex, with fused lateral, occipital, and cranidial lobes

thorax 10-11 segments, with spinose points

pygidium large, often flattened, often with 3 pairs of leaflike or spinose pleural structures

Superfamily Odontopleuroidea

Odontopleuridae
Odontopleura



distinct notch in margin where anterior sutures meet anterior border

several short genal spines typically present

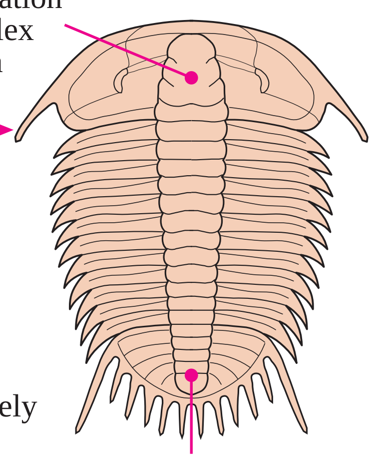
exoskeleton very spinose and densely sculptured

thorax 8-10 segments, each with 2-3 pairs of spines

pygidium micropygous, transverse, bearing one or more pairs of spines, largest of which connected to first axial ring via prominent ridge

Superfamily Dameselloidea

Damesellidae
Damesella



glabella tapering forward, lobation not as complex as Lichoidea

genal spines typically present

thorax with up to 13 segments, more as in Lichoidea than Odontopleuroidea

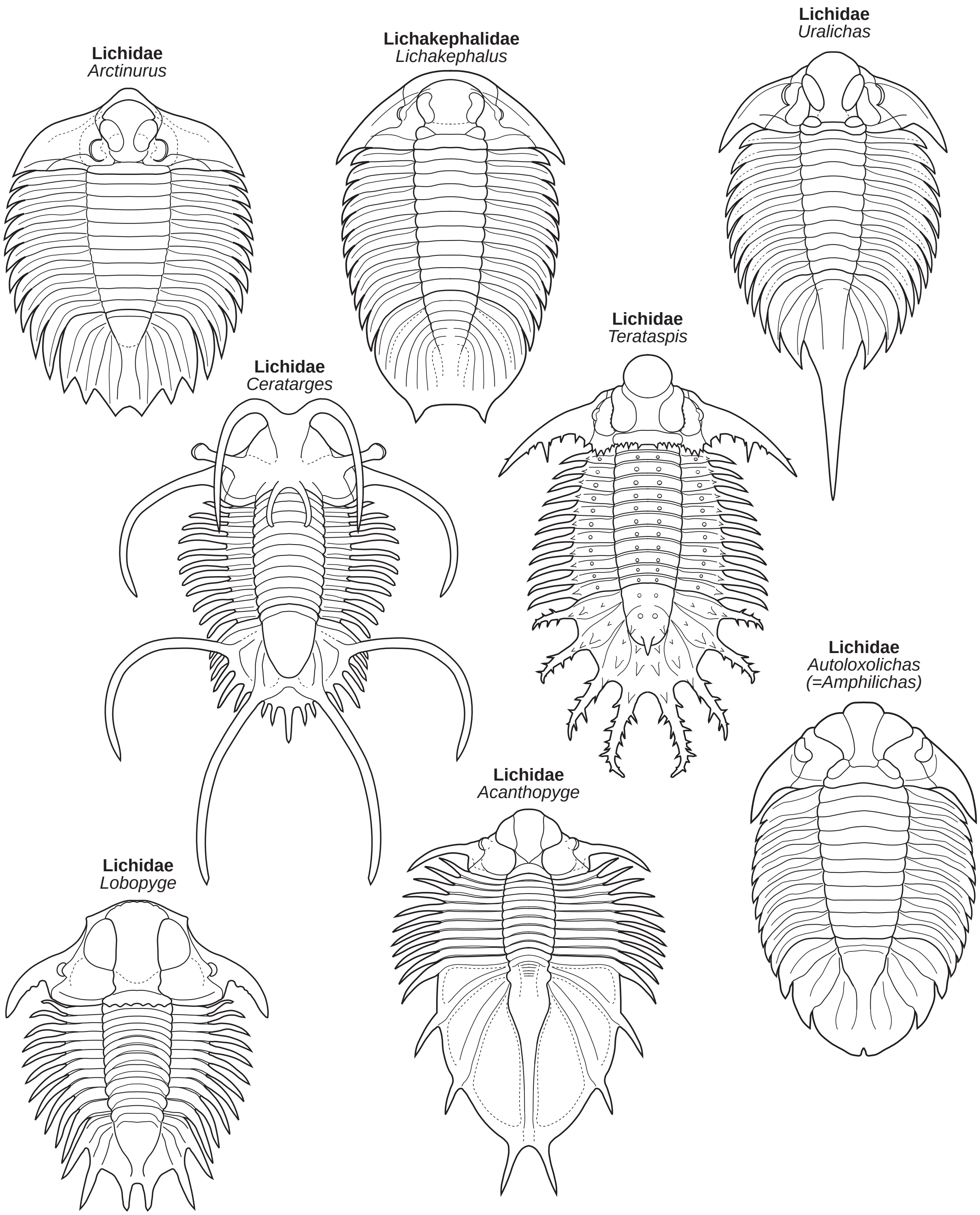
exoskeleton finely to coarsely granulose

longer pygidia than Odontopleuroidea, 1-7 pairs of pleural marginal spines of varying length

CLASSIFICATION NOTE: Recent publications recognize Order Odontopleurida as a separate sister taxon to Order Lichida. It contains the Superfamilies Odontopleuroidea and Dameselloidea.

GALLERY: ORDER LICHIDA

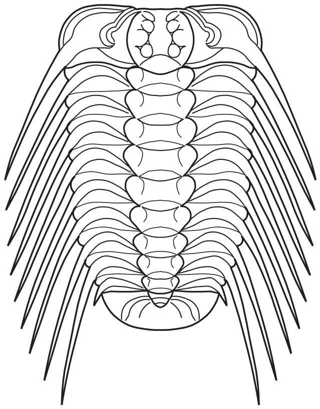
Superfamily Lichoidea



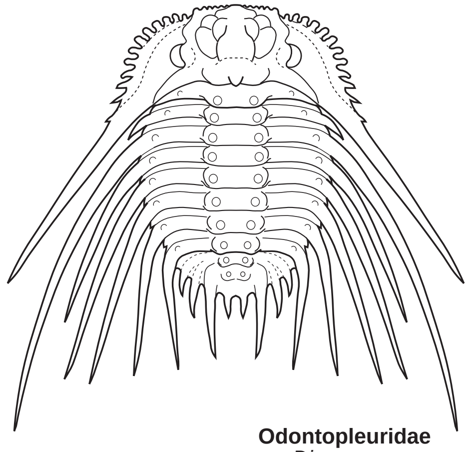
GALLERY: ORDER ODONTOPLEURIDA
(continued)

Superfamily Odontopleuroidea

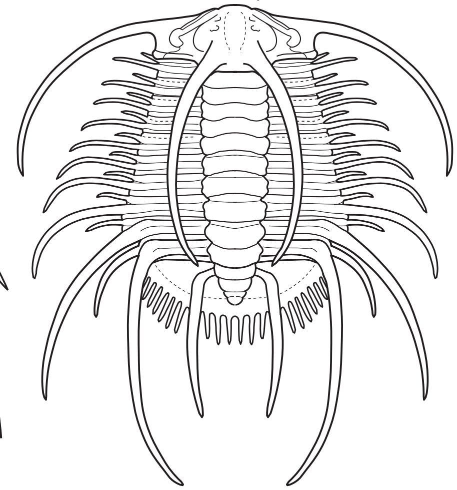
Selenopeltidae
Selenopeltis



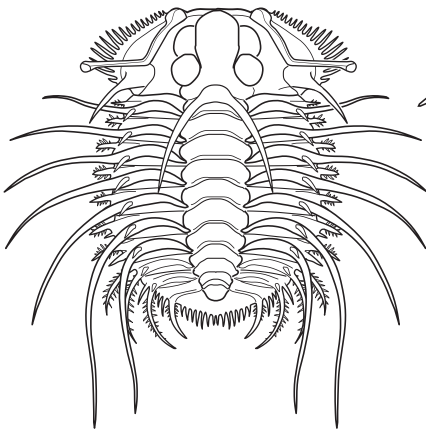
Odontopleuridae
Kettneraspis



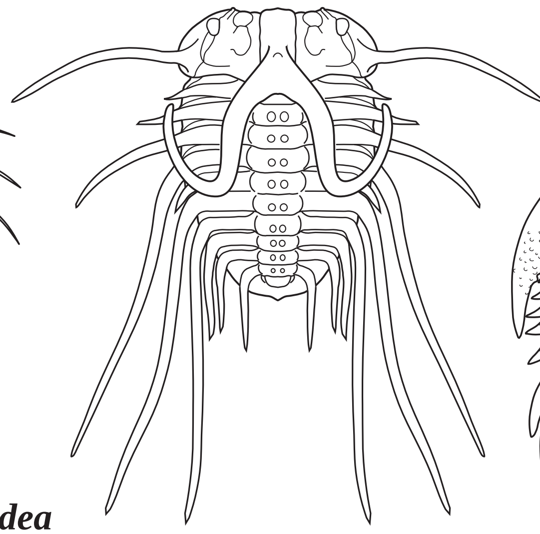
Odontopleuridae
Boedaspis



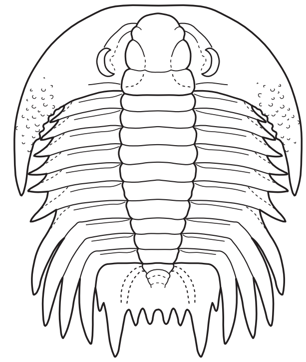
Odontopleuridae
Miraspis



Odontopleuridae
Dicranurus

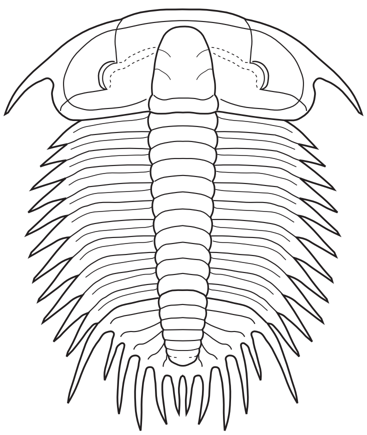


Odontopleuridae
Stelckaspis

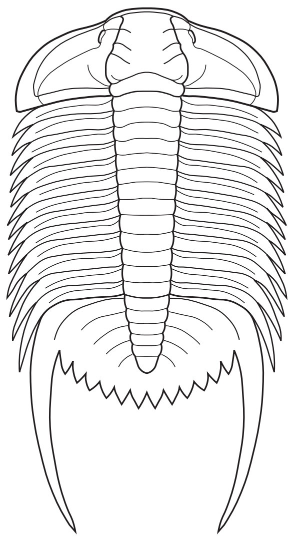


Superfamily Dameselloidea

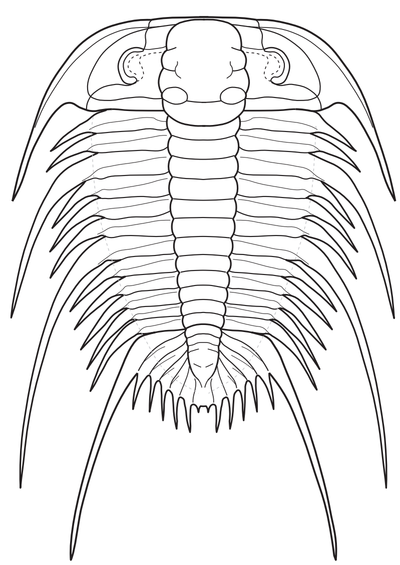
Damesellidae
Damesella



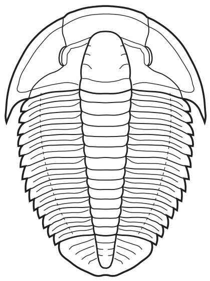
Damesellidae
Drepanura



Damesellidae
Palaeadotes



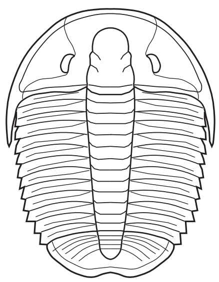
Ptychopariidae
Modocia



ORDER PTYCHOPARIIDA

Introduction: A very large, heterogenous order, classification problematic, with specialized offshoots that are hard to frame within a general diagnosis.
Cephalon: typically with opisthoparian facial sutures, with gently forward-tapering simple glabella bearing a broad, rounded front (e.g., Olenina), 3 pairs of rather narrow parallel glabellar furrows; natant hypostome.
Thorax: typically large with 8+ thoracic segments.
Pygidium: quite variable, but typically with a small pygidium bearing a border (Cambrian) or a larger pygidium with or without border (post-Cambrian).
Occurrence: Lower Cambrian to Upper Ordovician.
Suborders: Ptychopariina, Olenina.

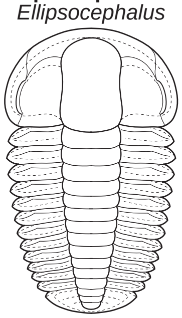
Ptychopariidae
Elrathia



Suborder Ptychopariina

Introduction: Primitive Ptychopariida, a large and extremely varied group.
Cephalon: glabella usually tapering with 3 pairs of glabellar furrows, sutures typically opisthoparian, but some proparian, and blind forms marginal; anterior sutures usually convergent to slightly divergent, posterior sections moderately to highly divergent; eyes usually present, medial, and near glabella; usually blade-like genal spines present.
Thorax: generally long, relative to pygidium.
Pygidium: variable, but typically smaller than thorax.
Occurrence: Cambrian
Superfamilies: Ellipsocephaloidea and Ptychoparioidea (see below)

Ellipsocephalidae
Ellipsocephalus



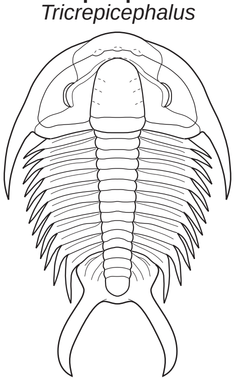
Superfamily Ellipsocephaloidea

Cephalon: glabella tapering forward, or subparallel or slightly expanding forward; up to 5 pairs of lateral furrows, eye ridges present.
Thorax: generally 12-16 thoracic segments.
Pygidium: small, unremarkable.
Families: Agraulidae, Aldonaiidae, Bigotinidae, Ellipsocephalidae, Estaingiidae, Palaeolenidae, Yunnanocephalidae.
Representative Genera: *Agraulos, Aldonaia, Bergeroniellus, Bigotina, Ellipsocephalus, Ellipsostrenua, Estaingia, Lermontovia, Palaeolenus, Protolenus, Pseudolenus, Yunnanocephalus.*

Superfamily Ptychoparioidea

Cephalon: typically with well-defined border, glabella tapering forward, preglabellar field present, opisthoparian sutures, natant hypostome, and genal spines; but exceptions include eyeless forms (Conocoryphidae), proparian forms (Norwoodiidae), rounded genal angles and gonatoparian sutures (Menomoniidae).

Tricrepicephalidae
Tricrepicephalus



Thorax: typically 12-17 segments, but reduced to 4 in a Shumardiid.
Pygidium: typically micropygous, transverse, pleural field nearly flat, with distinct pleural grooves; but exceptionally isopygous (*e.g.*, some Asaphiscidae, Cooselidae).
Families:, Eulomidae, Antagmidae, Alokistocaridae, Ptychopariidae, Marjumiidae, Solenopleuridae, Atopidae, Holocephalinidae, Conocoryphidae, Holocephalidae, Dokimokephalidae, Nepeidae, Crepicephalidae, Tricrepicephalidae, Lonchcephalidae, Kingstoniidae, Shumardiidae, Asaphiscidae, Elviniidae, Cedariidae, Norwoodiidae, Menomoniidae, Bolaspididae, Papyriaspididae, Changshaniidae, Diceratocephalidae, Phylateridae, Conokephalinidae, Utiidae, Lisaniidae, Inouyiidae, Wuaniidae, Lorenzellidae, Proasaphiscidae, Isocolidae, Ignotogregatidae, Mapaniidae, Acrocephalitidae, Llanoaspididae.
Representative Genera: *Alokistocare, Asthenopsis, Atops, Bailiella, Bolaspidella, Carolinites, Conocoryphe, Densonella, Diceratocephalus, Dokimokephalus, Elrathia, Holanshania, Holcacephalus, Irvingella, Marjumia, Mexicella, Modocia, Nepea, Norwoodia, Ptychoparia, Sao, Shumardia, Solenopleura, Tricrepicephalus.*

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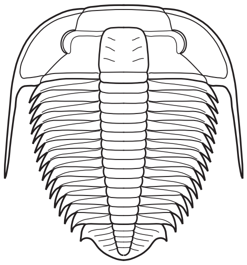
ORDER PTYCHOPARIIDA
(continued)

Olenidae
Olenus



Suborder Olenina

Cephalon: with narrow border, opisthoparian sutures (exceptionally proparian), genal angle rounded or spined, glabella tapering forward with simple, sigmoid, or bifurcate furrows (furrows absent in some forms); librigenae typically fused; eyes small to medium, usually with distinct eye ridges.
Thorax: 9-24 segments.
Pygidium: micropygous to subisopygous, with or without marginal spines.
Occurrence: Lower Cambrian to Upper Ordovician
Family: Olenidae (subfamilies Oleninae, Triarthrinae, Pelturinae, Leptoplastinae, Balnibardiinae)
Representative Genera: *Balnibarbi*, *Bienvillia*, *Ctenopyge*, *Leptoplastus*, *Olenus*, *Parabolina*, *Peltura*, *Triarthrus*, *Wujiajiania.*

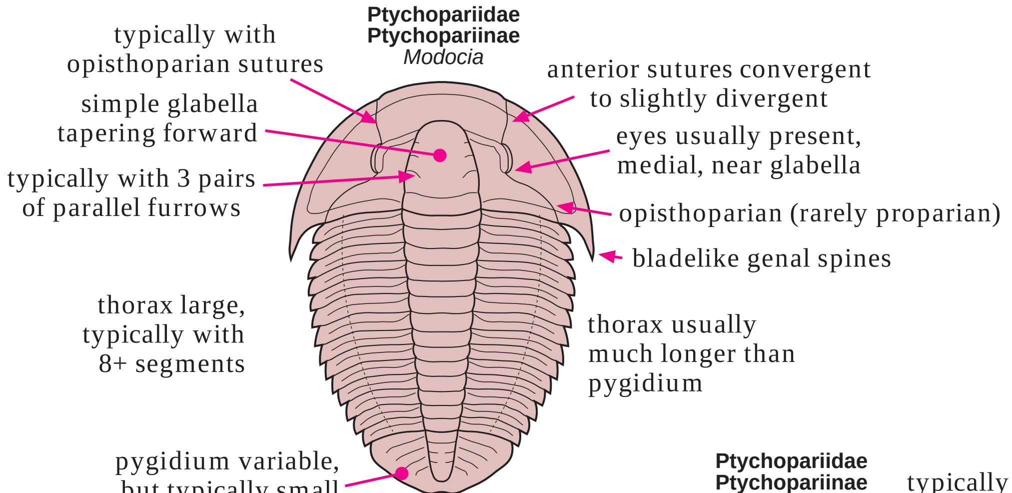
PICTORIAL GUIDE TO THE ORDER PTYCHOPARIIDA

ORDER PTYCHOPARIIDA

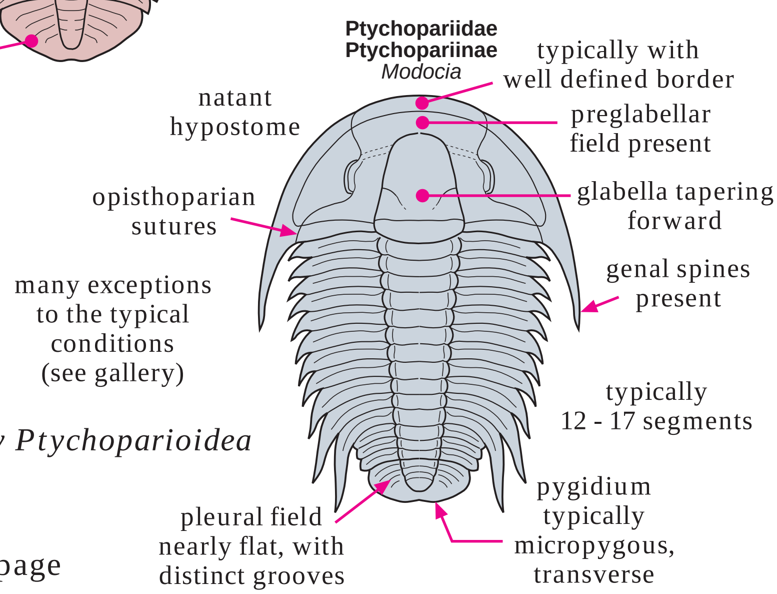
a large and variable order, with specialized offshoots difficult to reconcile in a single characterization

Suborder Ptychopariina

primitive Ptychopariida; a large and extremely varied group (see Gallery)



Superfamily Ptychoparioidea

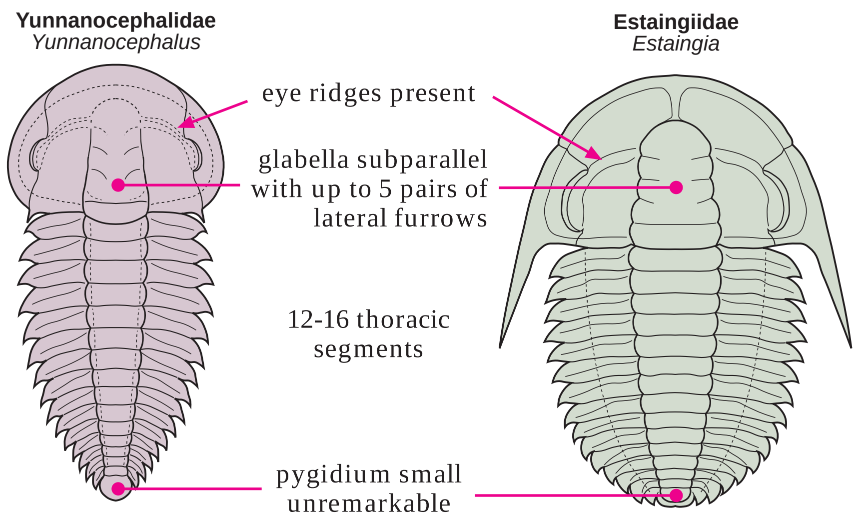


Pictorial guide continues on next page

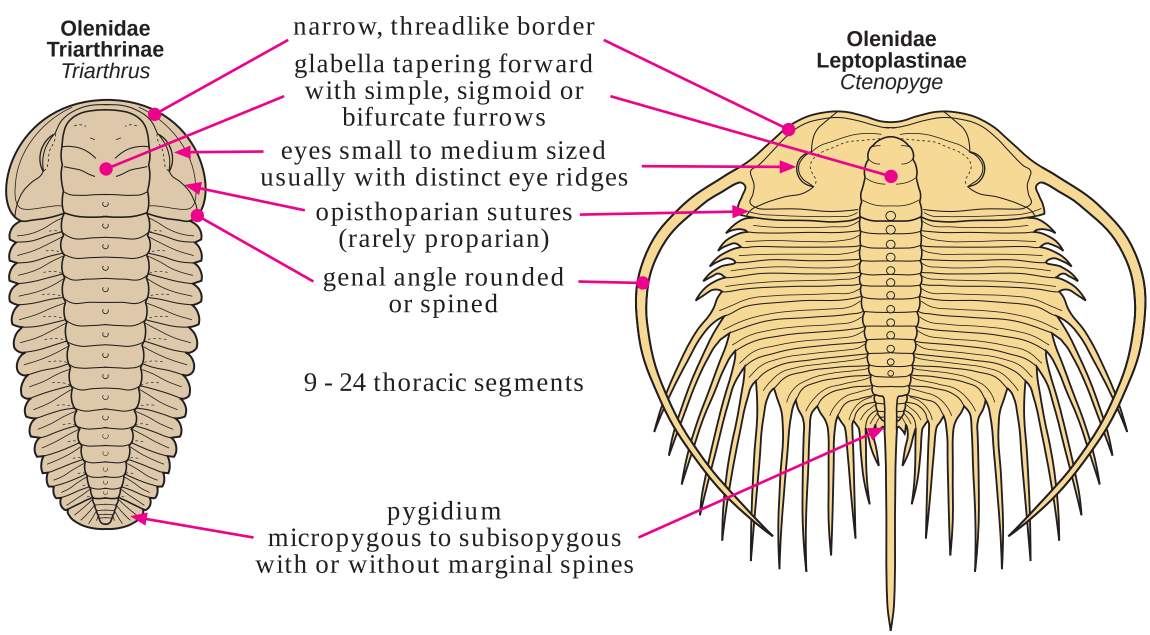
PICTORIAL GUIDE TO THE ORDER PTYCHOPARIIDA
(continued)

Suborder Ptychopariina

Superfamily Ellipsocephaloidea



Suborder Olenina

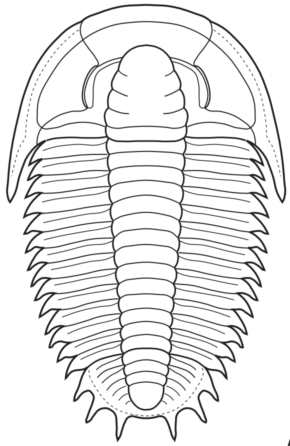


GALLERY: ORDER PTYCHOPARIIDA

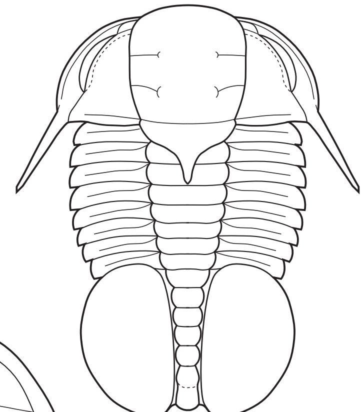
Suborder Ptychopariina

Superfamily Ptychoparioidea

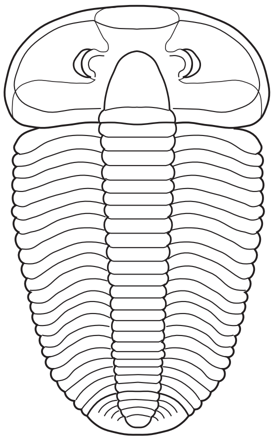
Marjumiidae
Marjumia



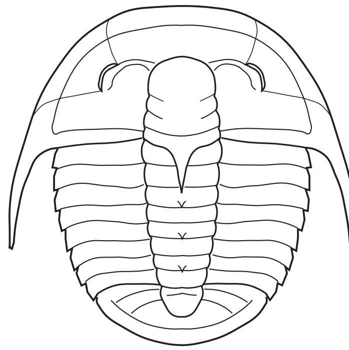
Catillicephalidae
Pemphigaspis



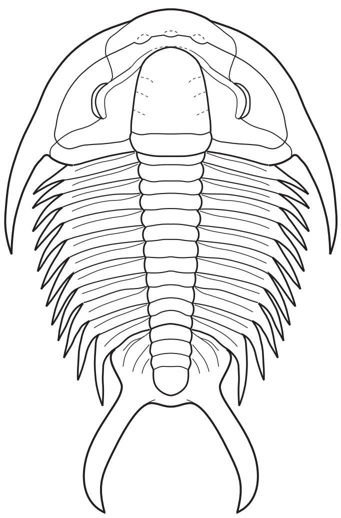
Menomoniidae
Densonella



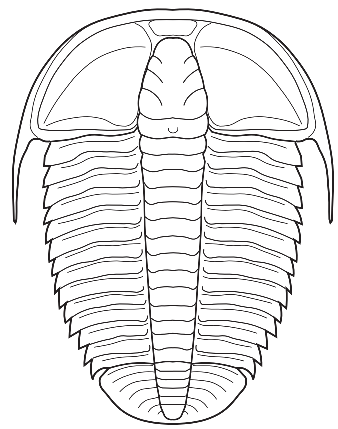
Norwoodiidae
Holcacephalus



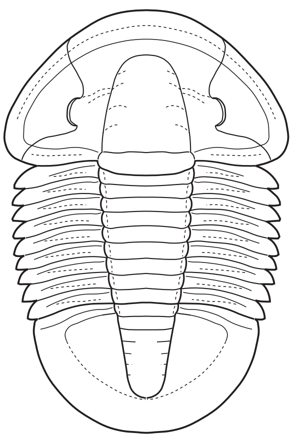
Tricrepicephalidae
Tricrepicephalus



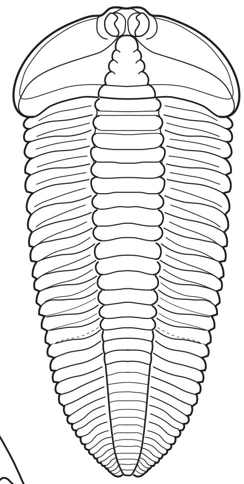
Conocoryphidae
Conocoryphe



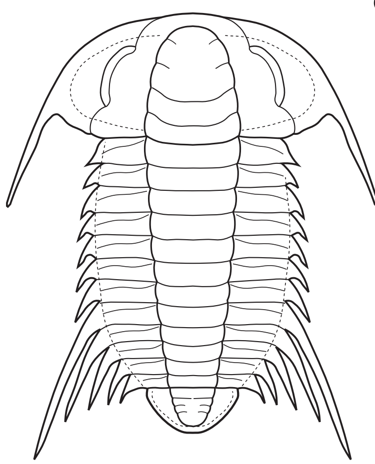
Asaphiscidae
Asaphiscus



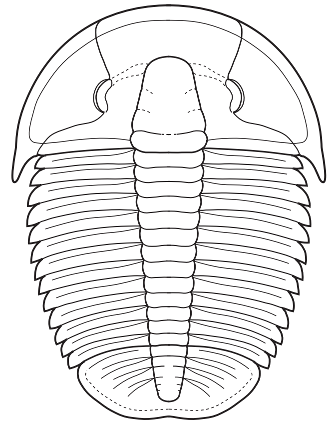
Menomoniidae
Dresbachia



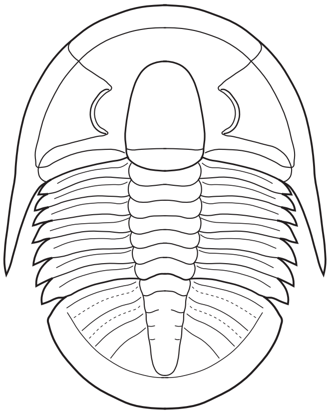
Elviniidae
Irvingella



Ptychopariidae
Elrathia



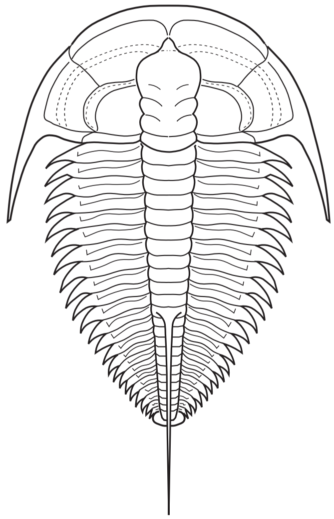
Cedariidae
Cedaria



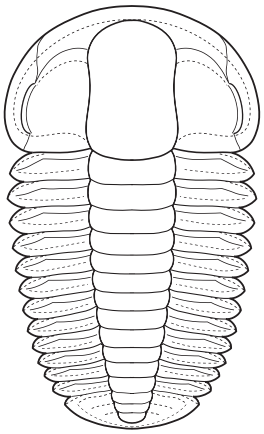
GALLERY: ORDER PTYCHOPARIIDA
(continued)

Superfamily Ellipsocephaloidea

Protolenidae
Protoleninae
Lermontovia

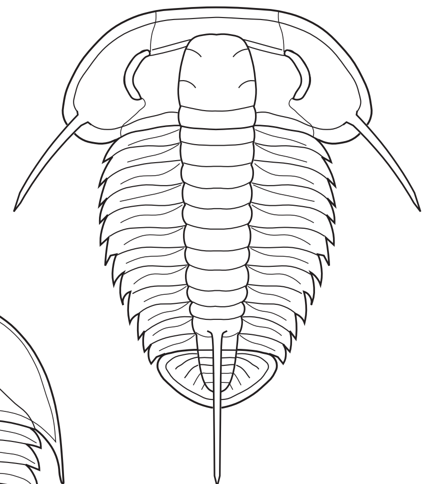


Ellipsocephalidae
Ellipsocephalinae
Ellipsocephalus

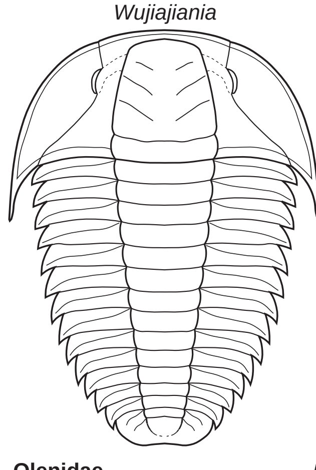


Suborder Olenina

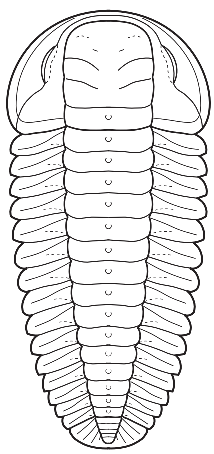
Olenidae
Leptoplastinae
Leptoplastus



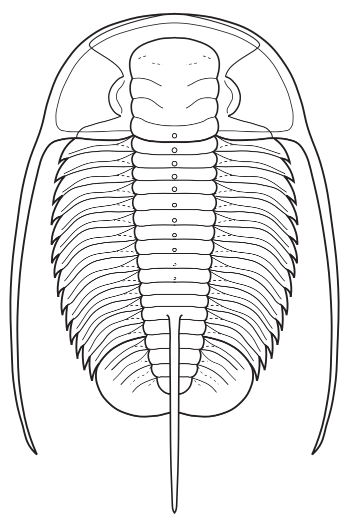
Olenidae
Oleninae
Wujiajiania



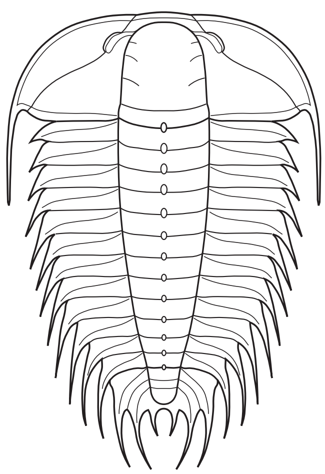
Olenidae
Triarthrinae
Triarthrus



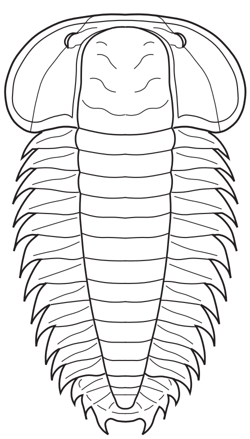
Olenidae
Balnibarbiinae
Balnibarbi



Olenidae
Oleninae
Parabolina

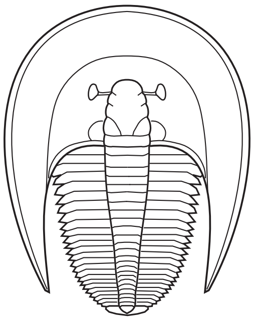


Olenidae
Pelturinae
Peltura



ORDER HARPETIDA

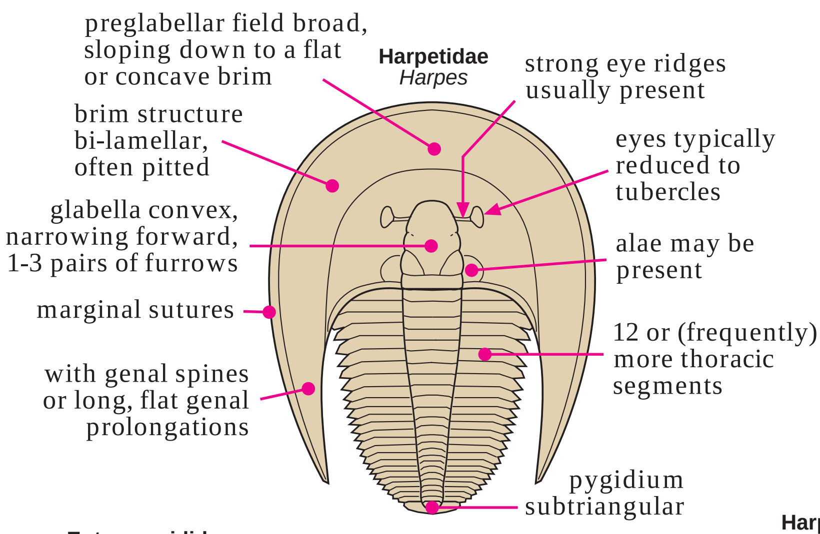
Harpetidae
Harpes



Introduction: A small order of three families, split from the Ptychopariida in 2002, easily distinguished by marginal sutures and lack of rostral plate, as well as the presence of the "harpetid brim."
Cephalon: semicircular to ovate; fringe inclined, consisting of vaulted inner genal roll, which is convex or flat, and an outer bilaminar brim, either flat, convex or concave, extending posteriorly to long, flat genal prolongations; facial sutures marginal, in Entomaspididae involving the eyes, but with anterior and posterior sections running close together toward otherwise marginal sutures; glabella convex, narrowing forwards, with 1 to 3 pairs of furrows, posterior pair isolating triangular basal lobes; occipital ring convex; alae typically present; preglabellar field broad, sloping down to flat or upwardly concave border; eyes commonly reduced to prominent tubercles, centrally located on genae, strong eye ridges present; external surface of cephalon may be tuberculose or granulose.
Thorax: with 12 or (frequently) more segments, pleurae flattened, with broad axial furrows.
Pygidium: subtriangular, elongate to short.
Families: Entomaspididae, Harpetidae, Harpididae (=Loganopeltidae).
Occurrence: Upper Cambrian to Late Devonian (Frasnian).
Representative Genera: *Bohemoharpes, Dolichoharpes, Entomaspis, Eoharpes, Harpes, Harpides, Loganopeltis, Hibbertia (formerly Paraharpes),Scotoharpes (formerly Aristoharpes)*

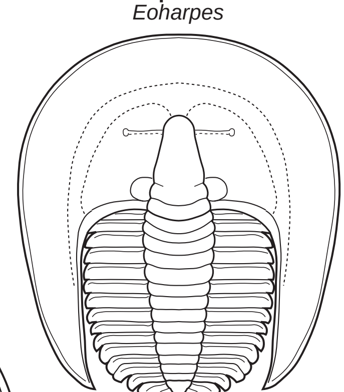
PICTORIAL GUIDE TO THE ORDER HARPETIDA

ORDER HARPETIDA

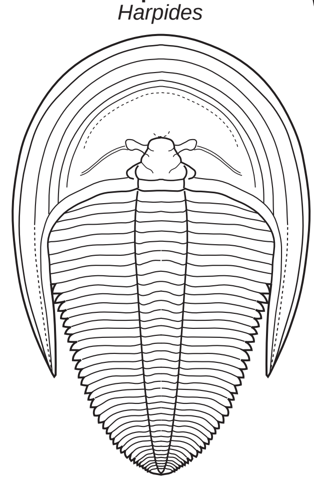


GALLERY: ORDER HARPETIDA

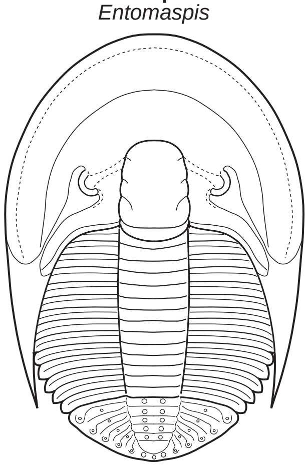
Harpetidae
Eoharpes



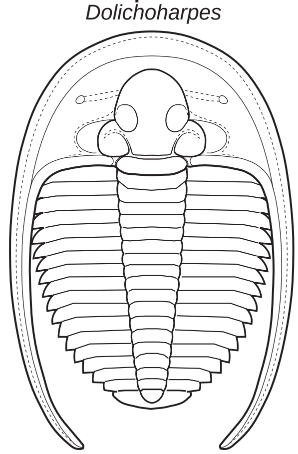
Harpididae
Harpides



Entomaspididae
Entomaspis

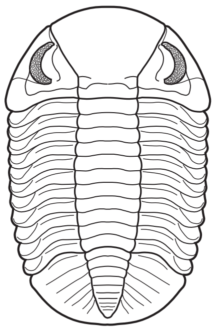


Harpetidae
Dolichoharpes



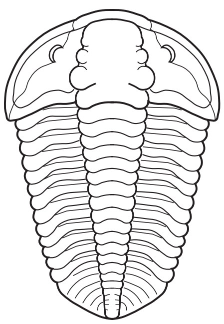
ORDER PHACOPIDA

Phacopidae
Phacops



Introduction: large and variable group of related suborders.
Cephalon: typically proparian (Phacopina and Cheirurina) or gonatoparian (Calymenina), preglabellar field often very short or absent, 4 or fewer pairs of glabellar furrows (these sometimes fused); eyes, when present, schizochroal (Phacopina) or holochroal (Cheirurina and Calymenina); with rostral plates (Calymenina and Cheirurina) or without (Phacopina); hypostome conterminant (all suborders) to impendent (some Phacopina).
Thorax: 8 – 19 segments, may be distinctly furrowed, axis may be broad (*e.g.*, Homalonotidae).
Pygidium: typically micropygous (most Calymenina and Phacopina), but variable (subisopygous in Dalmanitoidea), may be lobed or spiny (*e.g.*, Cheirurina, some Dalmanitoidea), or smooth-margined, with round or subtriangular outline (*e.g.*, Calymenina, Phacopoidea).
Other: All suborders share similar ontogeny (the “Phacopoid” protaspis) that in particular link the otherwise rather distinctive Calymenina to other Phacopida.
Occurrence: Lower Ordovician (Tremadoc) to Upper Devonian (Famennian)
Suborders: Calymenina, Phacopina, Cheirurina.

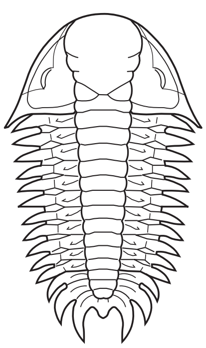
Calymenidae
Calymene



Suborder Calymenina

Cephalon: semicircular to subtriangular, typically with gonatoparian sutures (a few opisthoparian, *e.g.*, Bathycheilidae, primitive Homalonotidae); glabella narrowing forwards; eyes holochroal, often small; hypostome conterminant, rostral plate present.
Thorax: 11 – 13 (typically 13), segments with rounded tips.
Pygidium: semicircular or triangular, without spinose margin.
Occurrence: Lower Ordovician -
Families: Bathycheilidae, Bavarillidae, Calymenidae, Homalonotidae, Pharostomatidae.
Representative Genera: *Bathycheilus, Bavarilla, Calymene, Diacalymene, Dipleura, Flexicalymene, Homalonotus, Neseuretus, Prionocheilus, Pharostomina, Trimerus.*

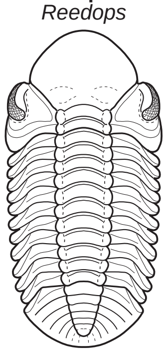
Cheiruridae
Cheirurus



Suborder Cheirurina

Cephalon: proparian sutures (a few opisthoparian), glabella usually expanding forwards or barrel-shaped, up to 4 pairs of furrows; holochroal eyes, often small; gena often with fine pitting; with rostral plate; hypostome conterminant, anterior wing with prominent process.
Thorax: variable numbers of distinctive segments within Phacopid range of 8-19, often spine-tipped.
Pygidium: often highly modified with 2-16 distinct pairs of ribs, lobed or spinose margin.
Other: often with tuberculate exoskeleton.
Occurrence: Lower Ordovician -
Superfamilies/Families: Cheiruroidea/Cheiruridae, Encrinuridae, Pilekiidae, Pliomeridae.
Representative Genera: *Actinopeltis, Ceraurus, Cheirurus, Coronocephalus, Cybeloides, Cyrtometopus, Encrinuroides, Encrinurus, Pilekia, Placoparia, Pliomera, Pseudocybele, Staurocephalus, Xylabion*.

Phacopidae
Reedops

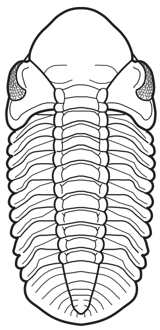


Suborder Phacopina

Cephalon: proparian sutures (sometimes fused), schizochroal eyes; glabella expands forwards; librigenae typically yoked as single piece; hypostome conterminant to impendent, no rostral plate; some with genal spines (*e.g.*, Dalmanitoidea, Some Acastoidea).
Thorax: 10 to (typically 11) segments, pleurae furrowed, articulating facets distinct, rounded, angular, or spinose tips. **Pygidium**: typically smaller than cephalon (but subisopygous in Dalmanitoidea and Acastoidea), smooth or spinose.
Occurrence: Middle Ordovician - Upper Devonian
Superfamilies: Phacopoidea, Dalmanitoidea, Acastoidea (See next page)
Representative Genera: See Superfamily descriptions, next page.

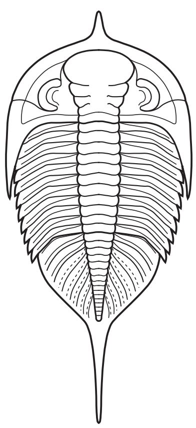
ORDER PHACOPIDA
(continued)

Superfamilies of the Suborder Phacopina



Superfamily Phacopoidea

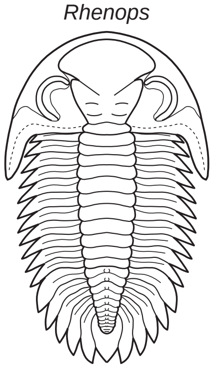
Cephalon: generally with strongly divergent axial furrows (glabella greatly expanding anteriorly), anterior glabellar lobes fused into single anterior tri-composite lobe, frontal area generally lacking (obliterated by large glabella), eyes (when present) typically anterior; genal angle typically rounded, without genal spines (exceptions among Pterygometopidae), vincular furrow generally present.
Thorax: variable, but often with rounded tips.
Pygidium: typically micropygous (Phacopidae) to subisopygous (some Pterygometopidae), not spinose.
Families: Phacopidae, Pterygometopidae
Genera: *Ductina*, *Kainops, Phacops*, *Pterygometopus, Reedops*



Superfamily Dalmanitoidea

Cephalon: typically bearing genal spines, generally with well-developed preglabellar field, median region of glabella bearing muscle scars; eyes tend to mesial or posterior, true vincular furrows lacking.
Thorax: variable, but often with spinose tips.
Pygidium: typically subisopygous, often spinose (terminal or marginal spines); axial ring furrows of consistent depth along length of pygidial axis, axial furrows with consistent angle of convergence posteriorly.
Families: Dalmanitidae, Diaphanometopidae, Prosopiscidae
Genera: *Crozonaspis, Dalmanites, Dalmanitina, Diaphanometopus, Eudolatites, Huntoniatonia, Mucronaspis, Odontocephalus, Odontochile, Ormathops, Prosopiscus, Synphoroides, Zeliskella.*

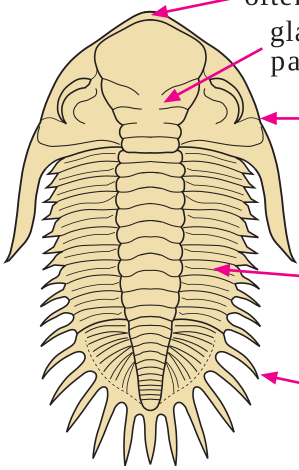
Superfamily Acastoidea



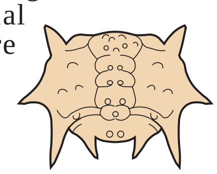
Cephalon: axial furrows slightly to moderately divergent, anterior glabellar lobes and furrows usually not fused (although furrows may be indistinct), eyes typically distant from posterior border furrows, but not strongly anterior (as in Phacopoidea); frontal glabellar lobe auxilliary impression system triangular in outline, maximum width adjacent to preglabellar furrow, median glabellar region devoid of muscle scars; cephalic margin “shouldered,” laterally convex course of genal margin topographically distinct from curvature of axial margin.
Thorax: pleural endings blunt, rounded, or angular, not spinose.
Pygidium: micropygous to subisopygous, many spinose (expressed as marginal spines); pygidial axis with deep, apodemal anterior ring furrows, abrupt transition to shallow posterior ring furrows, with coincident decrease in angle of axial furrow convergence.
Other: some species similar in general body form to Phacopoidea, but cephalic (especially glabellar) and other differences as noted above.
Families: Acastidae, Calmoniidae.
Genera: *Acaste, Acastoides, Asteropyge, Calmonia, Coltraneia, Comura, Cryphina, Eldredgeia, Erbenochile, Greenops, Heliopyge, Hollardops, Kayserops, Metacanthina, Odontocephalus, Pennaia, Phacopina, Psychopyge, Quadrops, Rhenops, Treveropyge, Walliserops.*

PICTORIAL GUIDE TO THE ORDER PHACOPIDA

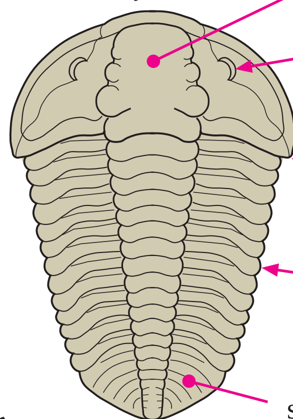
ORDER PHACOPIDA

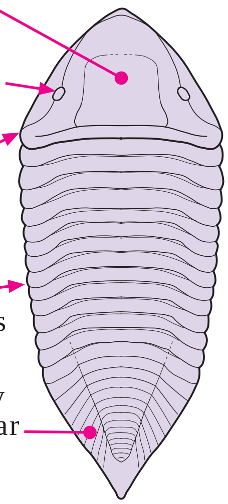


similar protaspid larval stage among all suborders, including 3 pairs of prominent marginal spines, only two of which are cephalic:

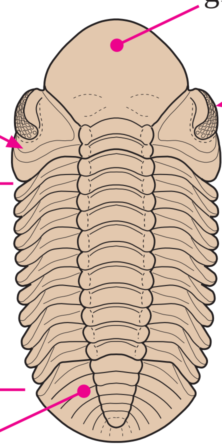


Suborder Calymenina



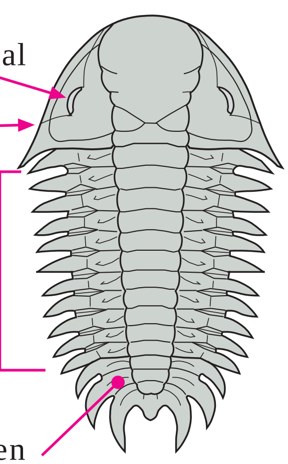


Suborder Phacopina



Pictorial guides to the three Superfamilies of Phacopina: Phacopoidea, Dalmanitoidea, and Acastoidea, are provided on the next page

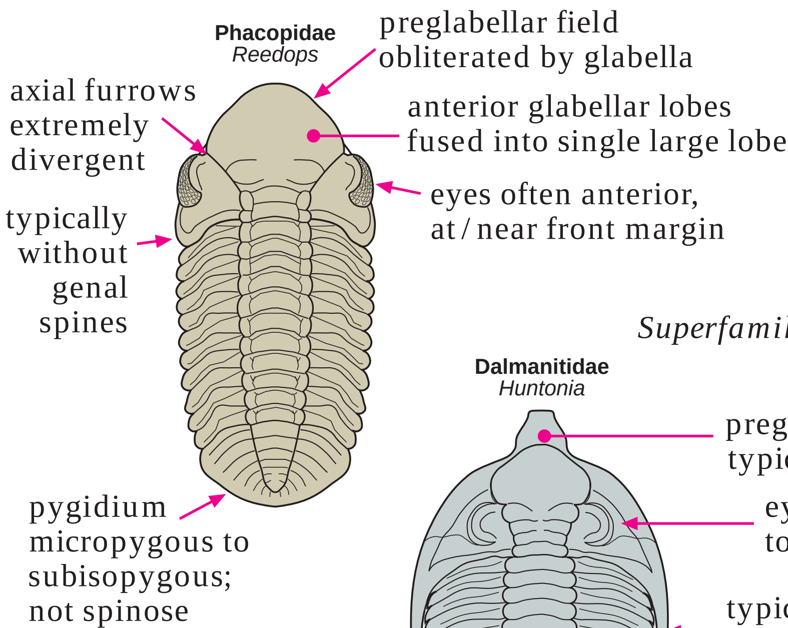
Suborder Cheirurina



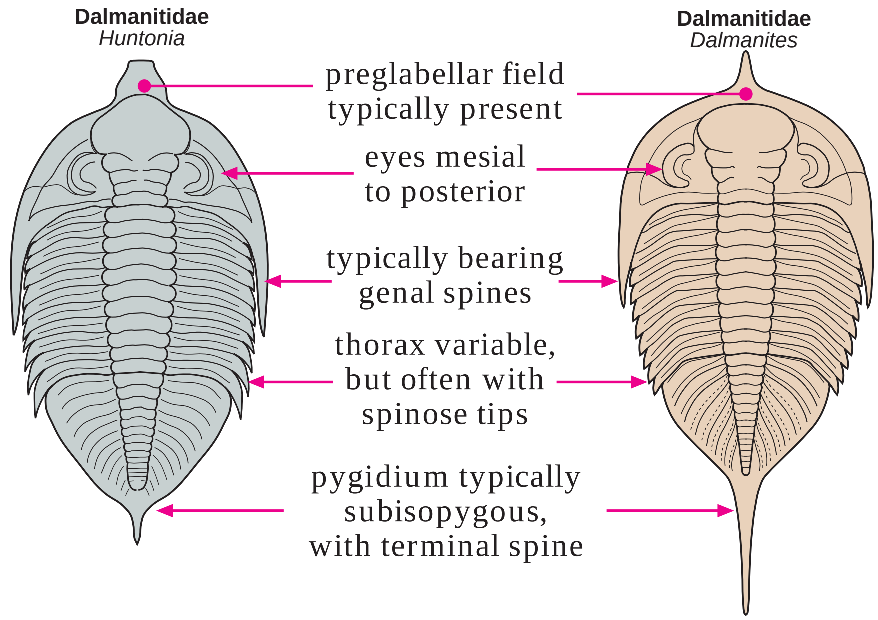
PICTORIAL GUIDE TO THE ORDER PHACOPIDA
(continued)

Suborder Phacopina

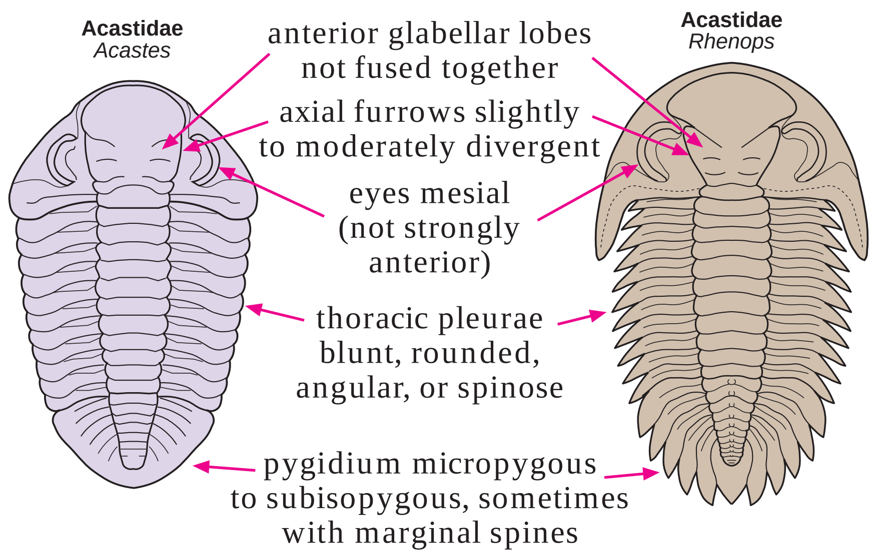
Superfamily Phacopoidea



Superfamily Dalmanitoidea



Superfamily Acastoidea

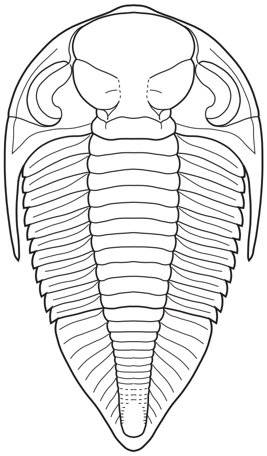


GALLERY: ORDER PHACOPIDA

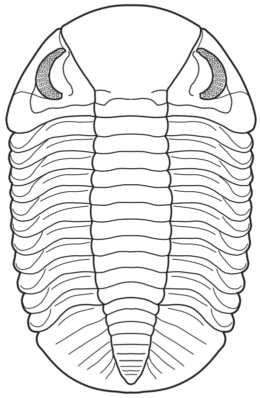
Suborder Phacopina

Superfamily Phacopoidea

Pterygomatopidae
Sceptaspis

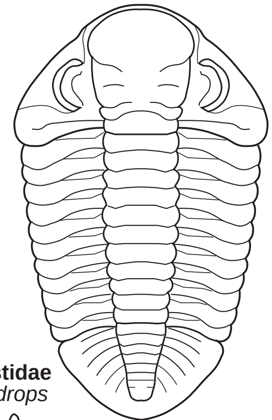


Phacopidae
Phacops

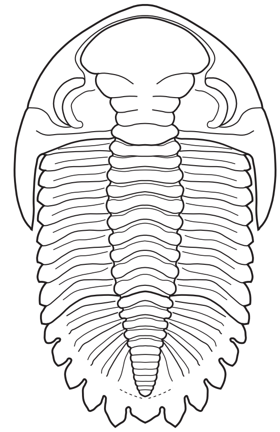


Superfamily Acastoidea

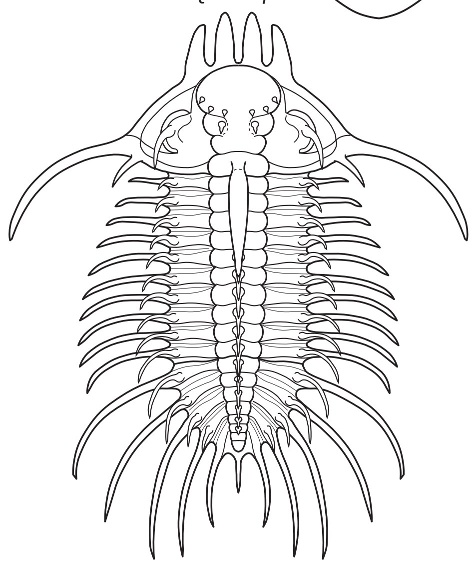
Acastidae
Acastes



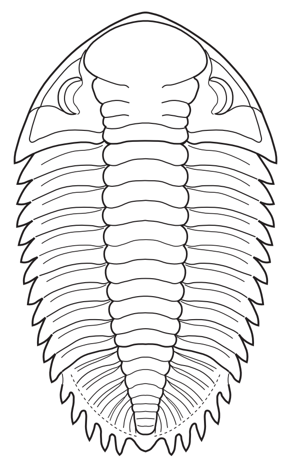
Acastidae
Hollardops



Acastidae
Quadrops

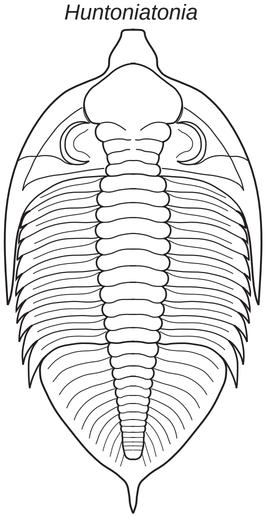


Calmoniidae
Metacryphaeus

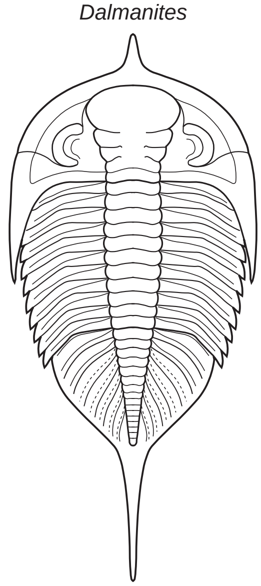


Superfamily Dalmanitoidea

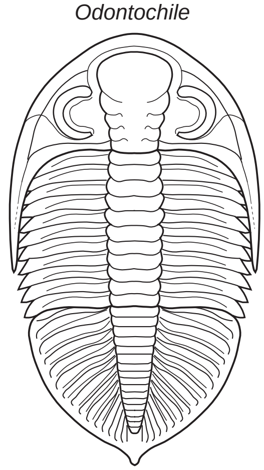
Dalmanitidae
Huntoniatonia



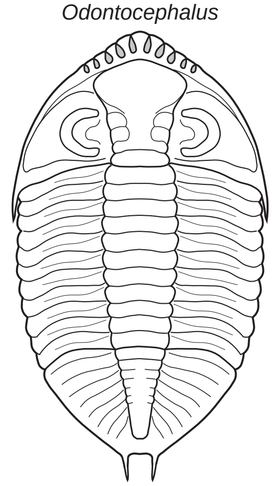
Dalmanitidae
Dalmanites



Dalmanitidae
Odontochile



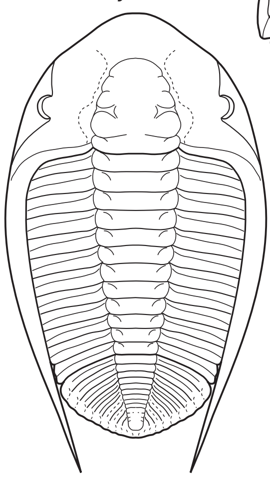
Dalmanitidae
Odontocephalus



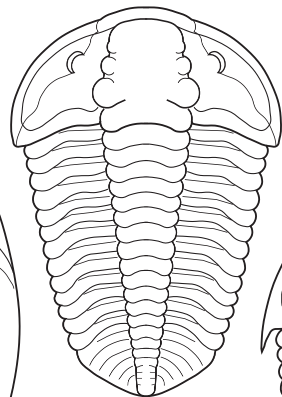
GALLERY: ORDER PHACOPIDA
(continued)

Suborder Calymenina

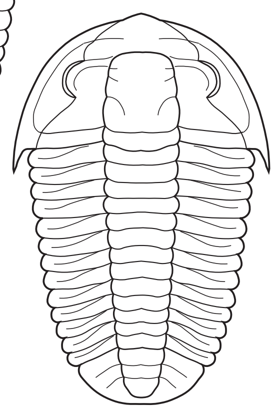
Bathycheilidae
Bathycheilus



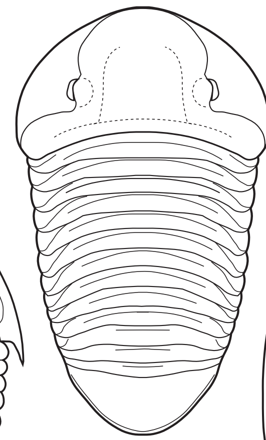
Calymenidae
Calymene



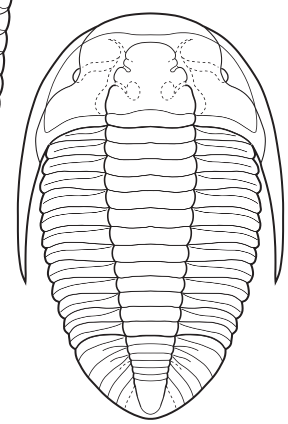
Homalonotidae
Bavarilla



Homalonotidae
Parahomalonotus

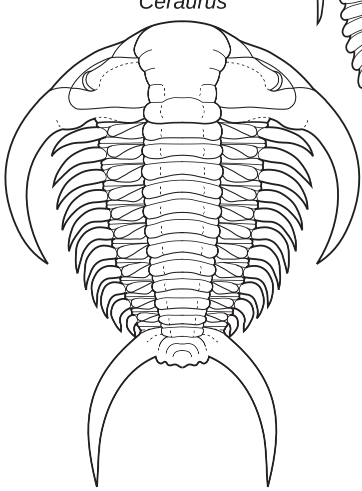


Pharostomatidae
Prionocheilus

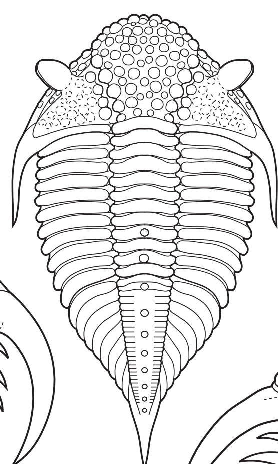


Suborder Cheirurina

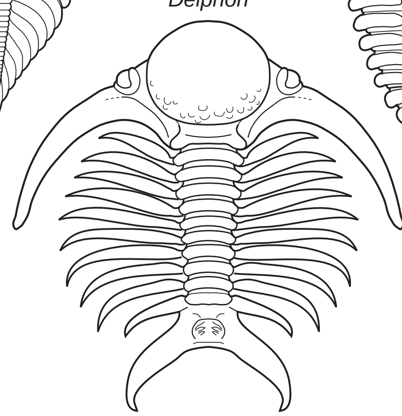
Cheiruridae
Ceraurus



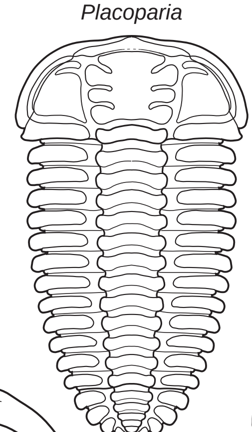
Encrinuridae
Encrinurus



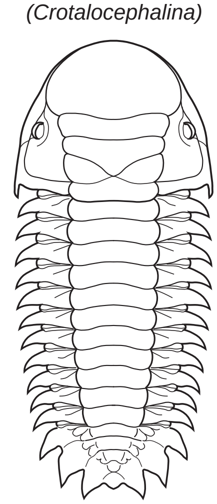
Cheiruridae
Deiphon



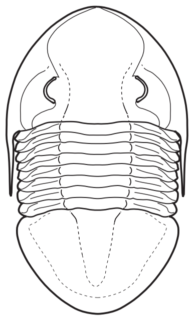
Pliomeridae
Placoparia



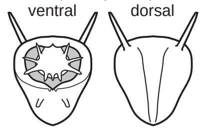
Cheiruridae
Cheirurus
(Crotalocephalina)



Asaphidae
Isotelus



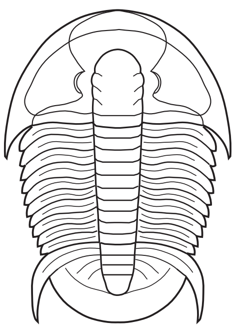
asaphoid protaspis
ventral dorsal



ORDER ASAPHIDA

Introduction: A large (comprising ~20% of trilobite species), morphologically diverse order of trilobites, most advanced families united by similar ontogeny (the ovoid, effaced **"asaphoid" protaspid** form with enrolled doublure); most members with a median ventral suture (secondarily lost via fusion in two advanced families).
Cephalon: often equal/subequal to pygidium (*e.g.*, Asaphoidea), but some not so (*e.g.*, Trinucleioidea); usually with a high degree of cephalic effacement so glabellar furrows are faint or not visible; eyes usually large (some forms secondarily blind); preoccipital glabellar tubercle in advanced forms; cephalic doublure often wide, with terrace ridges; librigena are typically separated by a **median ventral suture**; dorsal anterior facial sutures often curve adaxially to meet in front of the glabella; sutures opisthoparian; hypostome conterminent or impendent, with only primitive forms (*e.g.*, the Anomocaroidea) natant.
Thorax: typically 5 - 12 segments, but 2 - 3 in a few Trinucleioidea, 13+ in some Anomocaroidea, and up to 30 in an Alsataspidid (Trinucleioidea).
Pygidium: **typically large** (subisopygous to macropygous), with a wide doublure.
Occurrence: Middle-Upper Cambrian boundary to upper Ordovician-lower Silurian.
Suborders: None (or nominate Asaphina).
Superfamilies: Anomocaroidea, Asaphoidea, Dikelokephaloidea, Remopleuridoidea, Cyclopygoidea, Trinucleioidea. (see below)

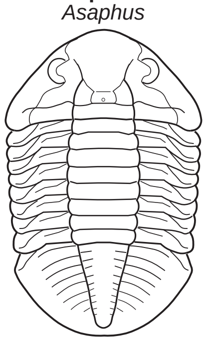
Pterocephaliidae
Housia



Superfamily Anomocaroidea

Introduction: Primitive Asaphida (possibly ancestral to some other asaphine groups), including families retaining the **natant hypostomal condition**, as well as other ptychoparioid features; **protaspides resembling those of Ptychopariida** (not "asaphoid"); not all families included may be monophyletic (*i.e.*, Anomocaroidea as described here is likely a paraphyletic group of families).
Cephalon: preglabellar field wide; glabella typically parallel or gently tapering, with 3 or 4 pairs of furrows more or less of ptychoparioid type, palpebral lobes long, sickle-shaped; median ventral suture; **natant hypostome**, some approaching conterminant.
Thorax: 10-13+ segments.
Pygidium: typically large, with broad, usually concave border, 2-10 axial rings.
Families: Andrarinidae, Anomocarellidae, Anomocaridae, Aphelaspididae, Pterocephalidae, Parabolinoididae.
Representative Genera: *Andrarina, Anomocare, Aphelaspis, Glyphaspis, Housia, Labiostria, Litocephalus, Parabolinoides, Pterocephalia.*

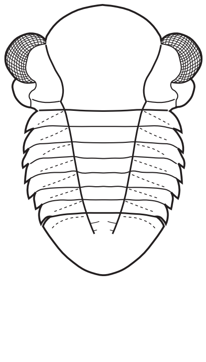
Asaphidae
Asaphus



Superfamily Asaphoidea

Introduction: As in typical Asaphida with the following additional defining characteristics:
Cephalon: bearing **preoccipital glabellar tubercle**; glabella elongate, subparallel to tapering forward, with **defined occipital ring**, curved, apostrophe-like pair of **basal glabellar furrows isolated** within glabella; hypostome conterminant (rarely impendent)
Thorax: typically 8 segments (6 to 9 in some Ceratopygidae), with petaloid facets (as in Cyclopygoidea).
Pygidium: typically rounded and without spines, but sometimes with a terminal spine or pair of spines (*e.g.*, Thysanopyginae).
Families: Asaphidae, Ceratopygidae.
Representative Genera: *Asaphus, Basilicus, Ceratopyge, Hedinaspis, Isotelus, Megalaspidella, Neoasaphus, Niobella, Ogyginus, Ogygiocaris, Pseudogygites, Ptychopyge, Ptyocephalus.*

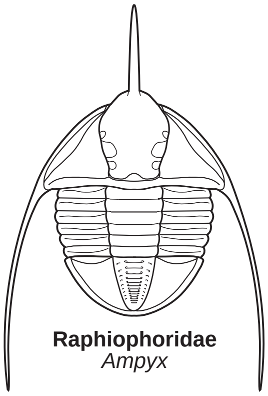
Cyclopygidae
Cyclopyge



Superfamily Cyclopygoidea

Cephalon: **glabella expanding forward to anterior margin**, effaced in later cyclopygids, may be fused with occipital ring; fixigenae reduced (except in primitive Taihungshaniidae), **palpebral lobes lack distinct rims, and contact axial furrows at anterior ends**, librigenae fused (Cyclopygidae and Nileidae) or with anterior median suture (Taihungshaniidae); **hypostome relatively transverse, impendent, often with tripartite posterior margin**; eye various sized (may be hypertrophied and convex (Cyclopygidae), typically closely adjoined to glabella.
Thorax: 5-8(9?) segments, with petaloid facets (as with Asaphoidea).
Pygidium: medium to large (subisopygous in Nileidae), axis usually with 2-5 rings (but up to 20+ in advanced Taihungshaniidae), may be smooth or with indistinct furrows; margin smooth (except paired spines in Taihungshaniidae).
Families: Cyclopygidae, Isocolidae? Nileidae, Taishunghaniidae
Representative Genera: *Asaphopsis, Cyclopyge, Illaenopsis, Nileus, Novakella, Taihungshania*

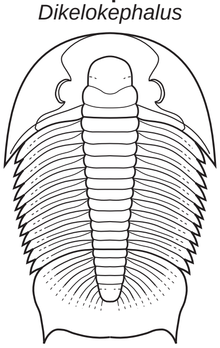
ORDER ASAPHIDA
(continued)



Raphiophoridae
Ampyx

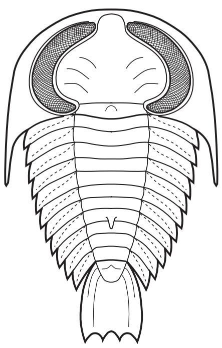
Superfamily Trinucleioidea
Cephalon: Opisthoparian or marginal facial sutures, generally eyeless; glabella typically **convex and pyriform**, with 3 or fewer pairs of furrows, preoccipital glabellar tubercle sometimes present; usually long genal spines.
Thorax: usually 5 – 8 segments, but only 2-3 segments in progenetic Raphiophoridae, and up to 30 in *Seleneceme* (Alsataspididae), with **long, narrow adaxial pleurae**, .
Pygidium: wide, **typically triangular**, narrow axis extending to posterior margin, border strongly declined, **doublure very narrow**.
Other: Asaphoid protaspis shows common ancestry; *Raphiophorus* is the only Trinucleioid (indeed the only representative of the order Asaphida) that continues beyond the Ordovician-Silurian boundary.
Families: Alsataspididae, Dionididae, Lisaniidae, Raphiophoridae, Trinucleidae,
Representative Genera: *Ampyxina, Bergamia, Cryptolithus, Dionide, Hapalopleura, Jegorovaia, Lisania, Onnia, Orometopus, Protolloydolithus, Raphiophorus, Seleneceme, Taklamakania, Trinucleus.*

Dikelokephalidae
Dikelokephalus



Superfamily Dikelokephaloidea
Cephalon: with opisthoparian sutures, **glabella typically truncate anteriorly and squat, bulging transversely anterior of occipital ring** (shared feature with sister group Remopleuridoidea), 1-4 pairs of lateral furrows, 1p may be transglabellar; preglabellar field variable, sometimes absent, **palpebral ridge typically well-defined, but separate from axial furrow** (compare to sister group Remopleuroidea); genal spines typically present, of various length, **with posterior border furrow persistent into basal part of genal spine**; median ventral suture rarely lost to secondary fusion; hypostome conterminant
Thorax: 8-12 segments, axis convex, pleurae typically wider than length of axis, typically with short, pointed ends (longer in Loganellidae).
Pygidium: micropygous to isopygous, variable shape, axis often extends majority of length, sometimes with post-axial ridge, posterior margin smooth or spined (1-5 pairs of marginal spines)
Families: Dikelocephalidae, Saukiidae, Ptychaspididae, Eurekiidae.
Representative Genera: *Dikelocephalus, Eurekia, Loganellus, Ptychaspis, Saukia, Tellerina.*

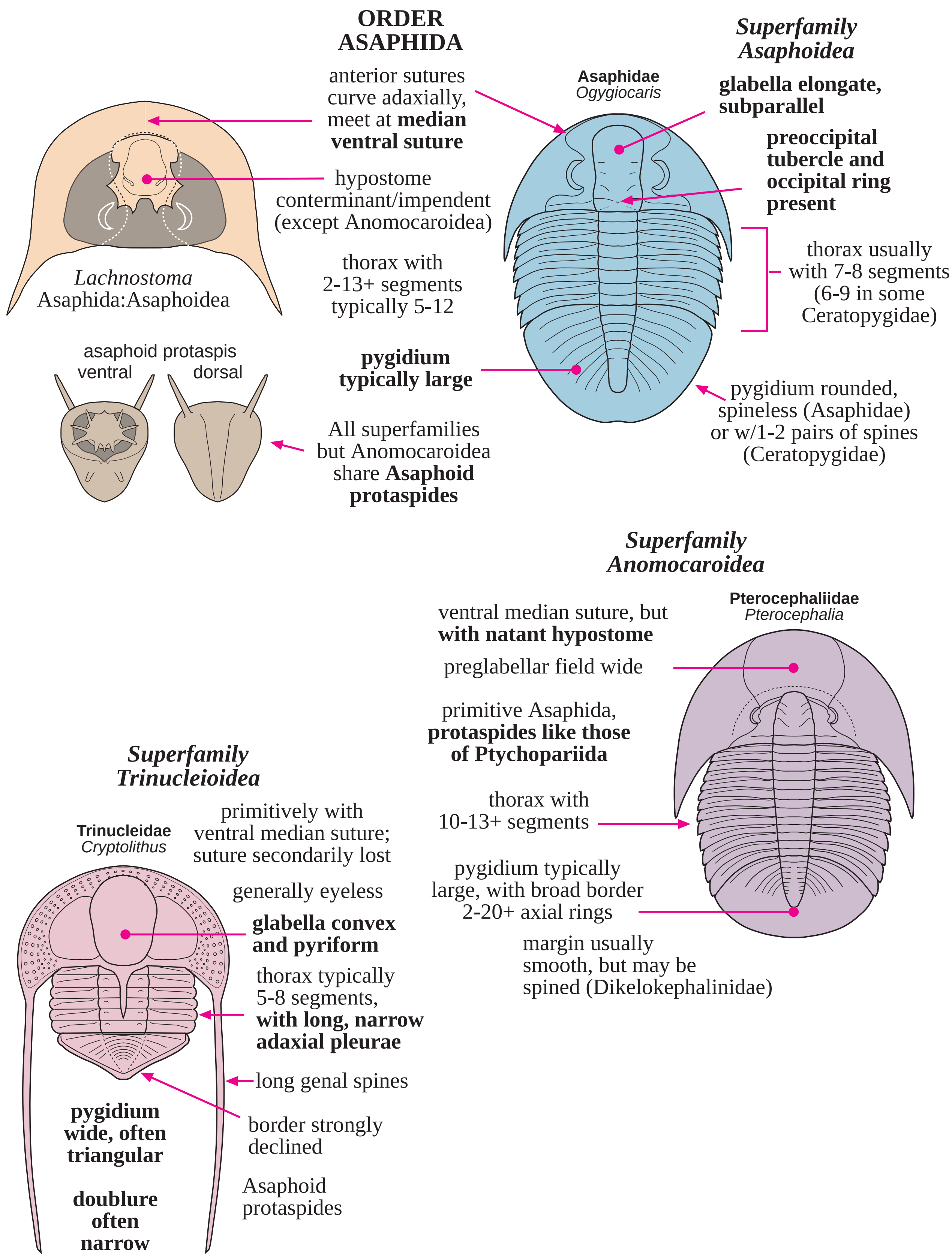
Remopleurididae
Amphitryon



Superfamily Remopleuridoidea
Cephalon: with opisthoparian sutures, **glabella bulges tranversely anterior of occipital ring** (as in sister group Dikelokephaloidea), with up to 3 pairs lateral furrows, eyes medium to very large, with **narrow, wire-like socle, palpebral rims inflated, deep rim furrows, extending into axial furrows anteriorly**; genal spines present.
Thorax: 9-12 segments, axis convex, pleural furrows diagonal, pleural tips typically point backward.
Pygidium: with **spinose margin, spines flattened, conjoined at bases**, extending to axis; convex axis not extending to posterior margin, pleural field flat, typically furrowed and backward curving. Surface variously sculptured or granulose.
Families: Remopleurididae, Bohemillidae, Auritamiidae, Idahoiidae, Hungaiidae.
Representative Genera: *Amphitryon, Apatokephalus, Auritamia, Bohemilla, Hungaia, Hypodicranotus, Kainella, Loganellus, Macropyge, Pseudokainella, Remopleurides, Richardsonella, Robergia.*

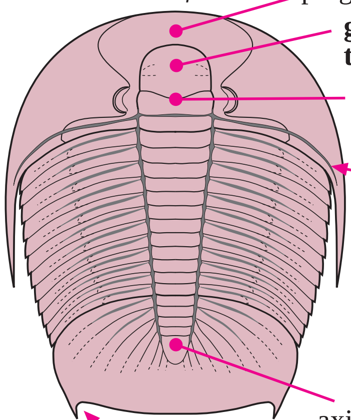
Superfamily Uncertain
Families: Monkaspididae, Rhyssometopidae.
Representative Genera: *Liaonigaspis, Monkaspis, Plectrifer, Rhyssometopus, Walcottaspidella.*

PICTORIAL GUIDE TO THE ORDER ASAPHIDA

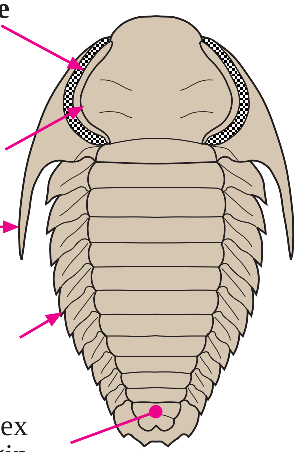


PICTORIAL GUIDE TO THE ORDER ASAPHIDA
(continued)

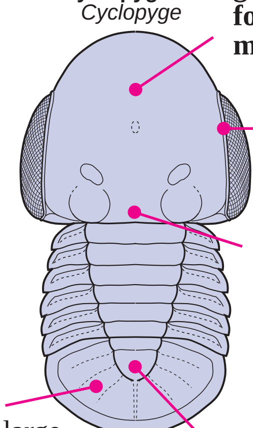
Superfamily Dikelocephaloidea



Superfamily Remopleuridoidea



Superfamily Cyclopygoidea

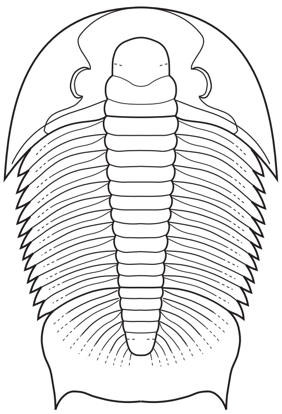


GALLERY: ORDER ASAPHIDA

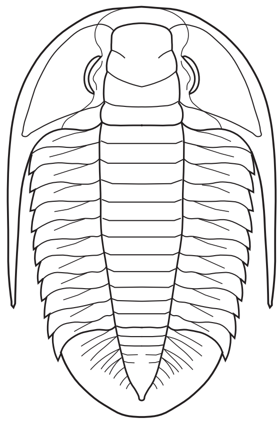
Suborder Asaphina

Superfamily Dikelokephaloidea

Dikelokephalidae
Dikelokephalus

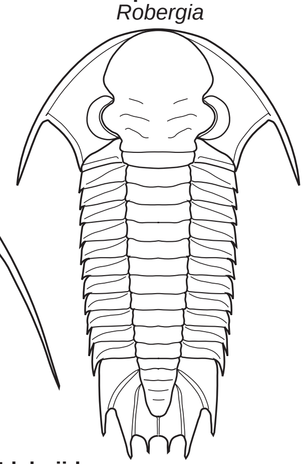


Saukiidae
Saukia

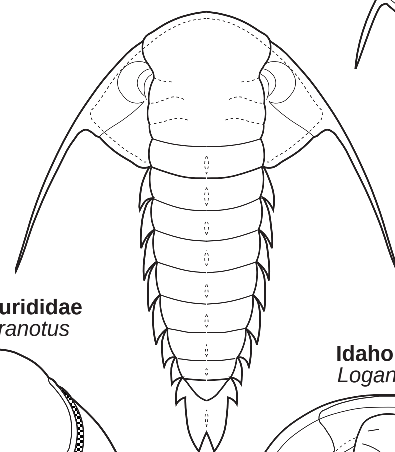


Superfamily Remopleuridoidea

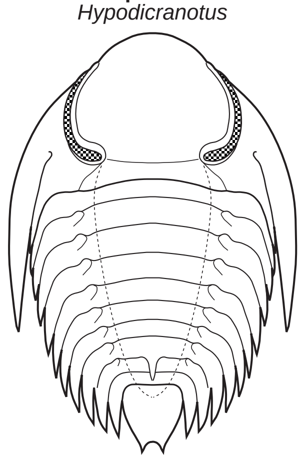
Remopleurididae
Robergia



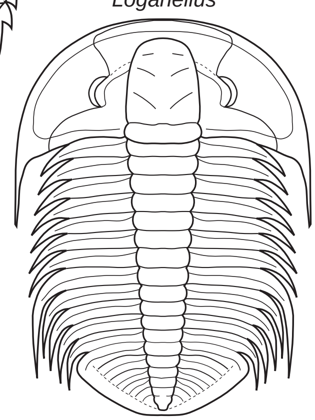
Bohemillidae
Bohemilla



Remopleurididae
Hypodicranotus

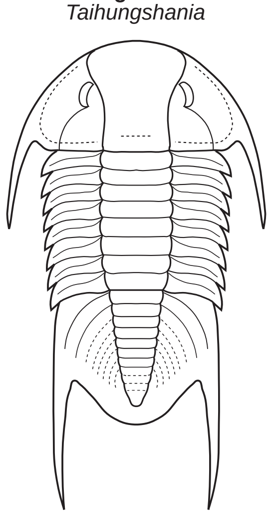


Idahoiidae
Loganellus

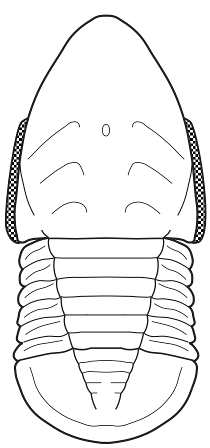


Superfamily Cyclopygoidea

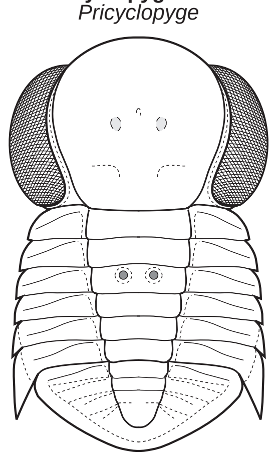
Taihungshaniidae
Taihungshania



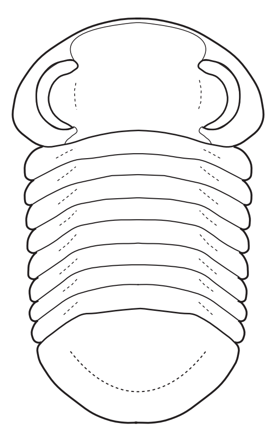
Cyclopygidae
Novakella



Cyclopygidae
Pricyclopyge



Nileidae
Nileus

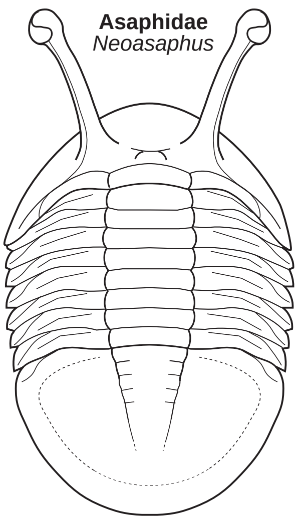


GALLERY: ORDER ASAPHIDA

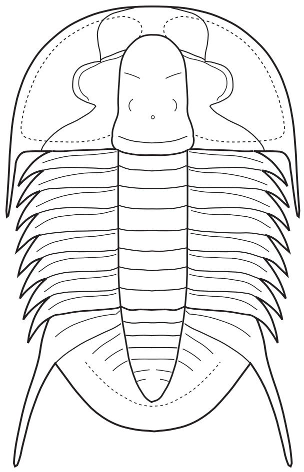
(continued)

Superfamily Asaphoidea

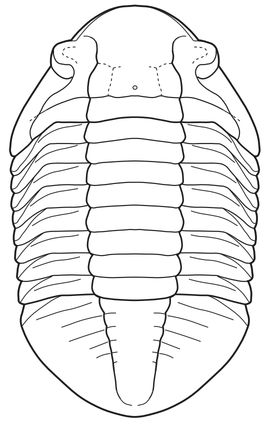
Asaphidae
Neoasaphus



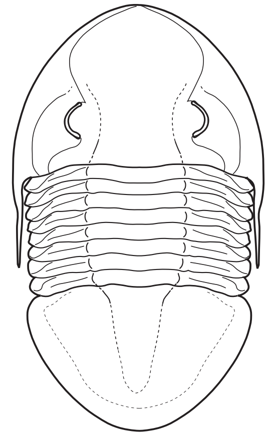
Ceratopygidae
Proceratopyge



Asaphidae
Asaphus

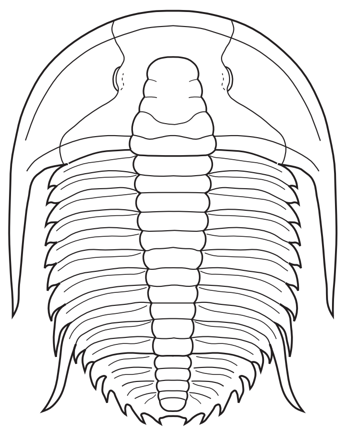


Asaphidae
Isotelus

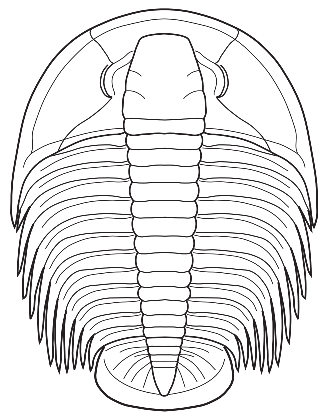


Superfamily Anomocaroidea

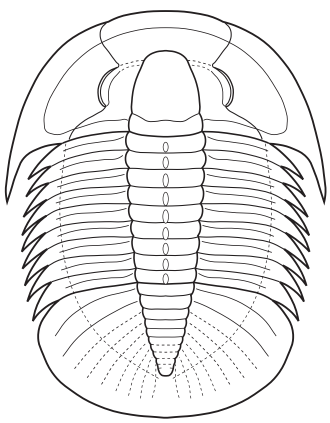
Parabolinoididae
Orygmaspis



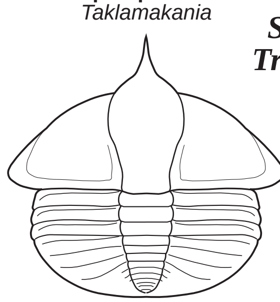
Aphelaspididae
Aphelaspis



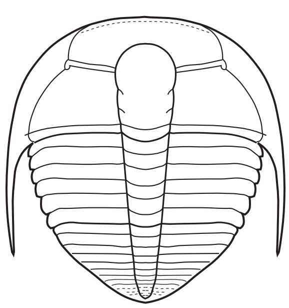
Anomocarellidae
Glyphaspis



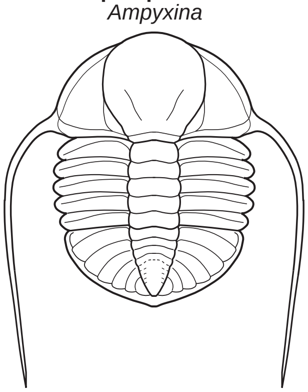
Raphiophoridae
Taklamakania



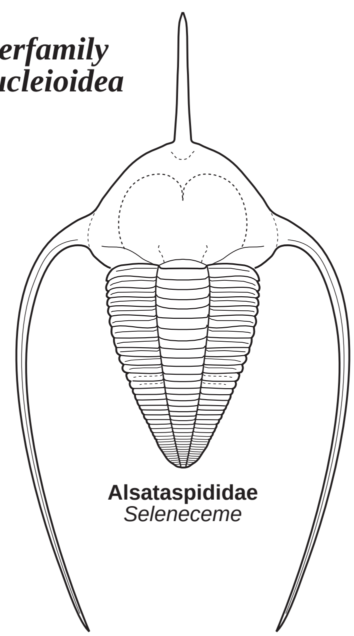
Hapalopleuridae
Araiopleura



Raphiophoridae
Ampyxina



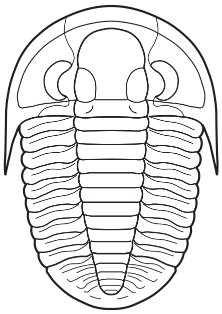
Superfamily Trinucleioidea



Alsataspididae
Seleneceme

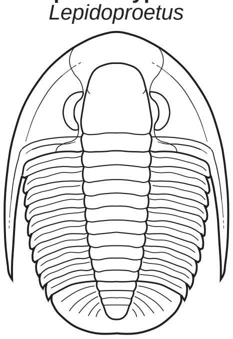
ORDER PROETIDA

Proetidae
Cyphoproetus



Introduction: Typically small trilobites, near Ptychopariida. Protaspid growth stages of the two orders similar, but late protaspides of Proetida show tapering glabella andpreglabellar field (a meraspid development in Ptychopariida); Proetida achieve natant hypostome early in ontogeny; one of the Libristomate (natant hypostomal derived) orders, possibly derived from early Ordovician Hystricurinae. Exoskeleton sometimes with pits or small tubercles.
Cephalon: opisthoparian sutures, glabella large, vaulted, well-defined, narrowing forwards, typically 4 pairs of glabellar furrows, posterior-most pair longest and deepest, those anterior shorter and fainter, medium occipital tubercle usually present; eyes usually present, holochroal, often large, convex; rostral plate narrow and backward tapering; long hypostome, most species natant, some secondarily conterminant (e.g., late Proetidae); typically with genal spines.
Thorax: 8 – 22 (typically 10) segments, tips variable, blunt to long-spined.
Pygidium: micropygous to subisopygous, often spineless, usually with 4 to 10+ distinct pleural furrows.
Occurrence: Ordovician (Tremadoc) to Permian (Tartarian)
Suborders: None (or nominate Proetina)
Superfamilies: Proetoidea, Aulacopleuroidea, Bathyuroidea

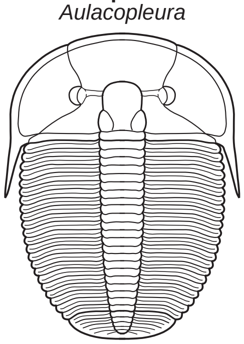
Tropidocoryphidae
Lepidoproetus



Superfamily Proetoidea

Cephalon: opisthoparian sutures; glabella tapering or inverse pyriform, mostly suboval, with 3-4 pairs of lateral furrows, sometimes indistinct (Proetidae), or glabella long, expanding forward to anterior border furrow or beyond, with lateral preoccipital lobes present (Phillipsidae); eyes, when present, typically holochroal, convex; fixigenae narrow, librigenae broad, except in blind species; hypostome typically natant, but secondarily conterminent in advanced Proetidae; genal angle spined or blunt rounded.
Thorax: 8-10 segments, typically 10 in Proetidae, 9 in Phillipsiidae, pleurae furrowed, tips blunt or spined.
Pygidium: typically semicircular, with few segments, but some large, long, parabolic, with up to 33 axial segments; margin typically smooth, but some with terminal axial spine or pleural spines.
Families: Proetidae, Tropidocoryphidae
Representative Genera: *Ameura, Astycoryphe, Basidechenella, Bollandia, Cornuproetus, Cummingella, Cyphoproetus, Dechenella, Ditomopyge, Gerastos, Griffithides, Koneprusites, Neogriffithides, Paladin, Phillipsia, Prantlia, Proetus, Pseudophillipsia, Pteroparia, Warburgella, Xiphogonium.*

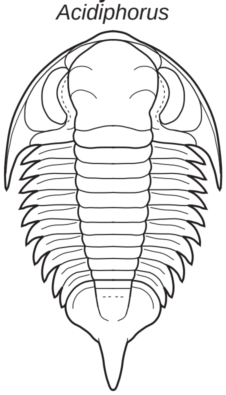
Aulacopleuridae
Aulacopleura



Superfamily Aulacopleuroidea

Cephalon: semicircular or semielliptical, with border and preglabellar field present; opisthoparian sutures; glabella typically short; genal spines present; hypostome natant (primitive condition); exoskeleton pitted, or with small tubercles.
Thorax: 11-22 segments, pleural ends usually rounded.
Pygidium: may be small, short, with even margin (Aulacopleuridae), or longer, with spines (some Brachymetopidae).
Families: Aulacopleuridae, Brachymetopidae, Rorringtoniidae
Representative Genera: *Aulacopleura, Brachymetopus, Cordania, Cyphaspis, Cyamella, Harpidella, Maurotarion, Namuropyge, Otarion, Paraaulacopleura, Radnoria, Rorringtonia.*

Bathyuridae
Acidiphorus



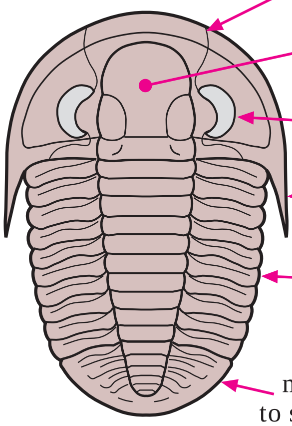
Superfamily Bathyuroidea

Cephalon: convex, with distinct border of varying width, opisthoparian sutures; glabella well defined, subparallel or gently expanding/tapering forward, with 3 or fewer lateral furrows, sometimes faint or absent; eyes medium to large, placed opposite or behind center of glabella; genal spines typically present, sometimes broad; hypostome typically natant, but secondarily conterminent in advanced Bathyuridae.
Thorax: 8-12 segments, pleurae typically with distinct furrows.
Pygidium: subisopygous to micropygous, gently to moderately convex, no border furrow, axis of varying length (absent in Celmidae), sometimes prolonged into post-axial ridge or axial spine, often 3 axial rings + terminal.
Other: exoskeleton sometimes ornamented variously with pits, tubercles, small spines, or terraces.
Families: Bathyuridae, Dimeropygidae, Holotrachelidae, Hystricuridae, Raymondinidae, Telephinidae, Toernquistiidae.
Representative Genera: *Acidiphorus, Bathyurus, Carolinities, Celmus, Dimeropyge, Glaphurus, Holotrachelus, Hystricurus, Lecanopyge, Opipeuter, Platyantyx, Raymondina, Telephinus, Toernquistia*.

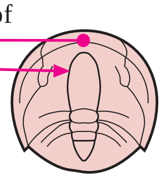
PICTORIAL GUIDE TO THE ORDER PROETIDA

ORDER PROETIDA

Recently split from Ptychopariida, persisting through the Permian

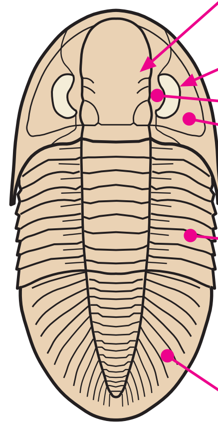
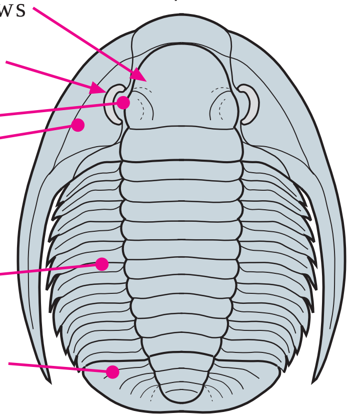


most species natant, but some are secondarily conterminant (*e.g.*, late Proetidae and Bathyuridae)

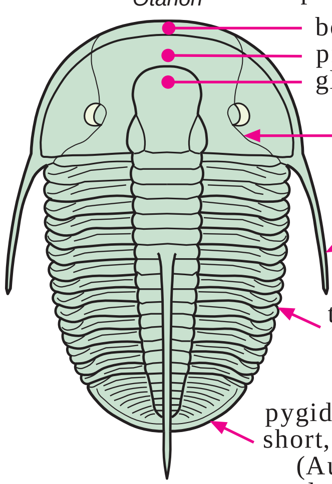


Proetus
protaspis

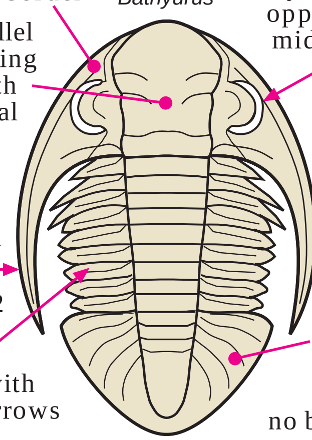
Superfamily Proetoidea

Superfamily Aulacopleuroidea



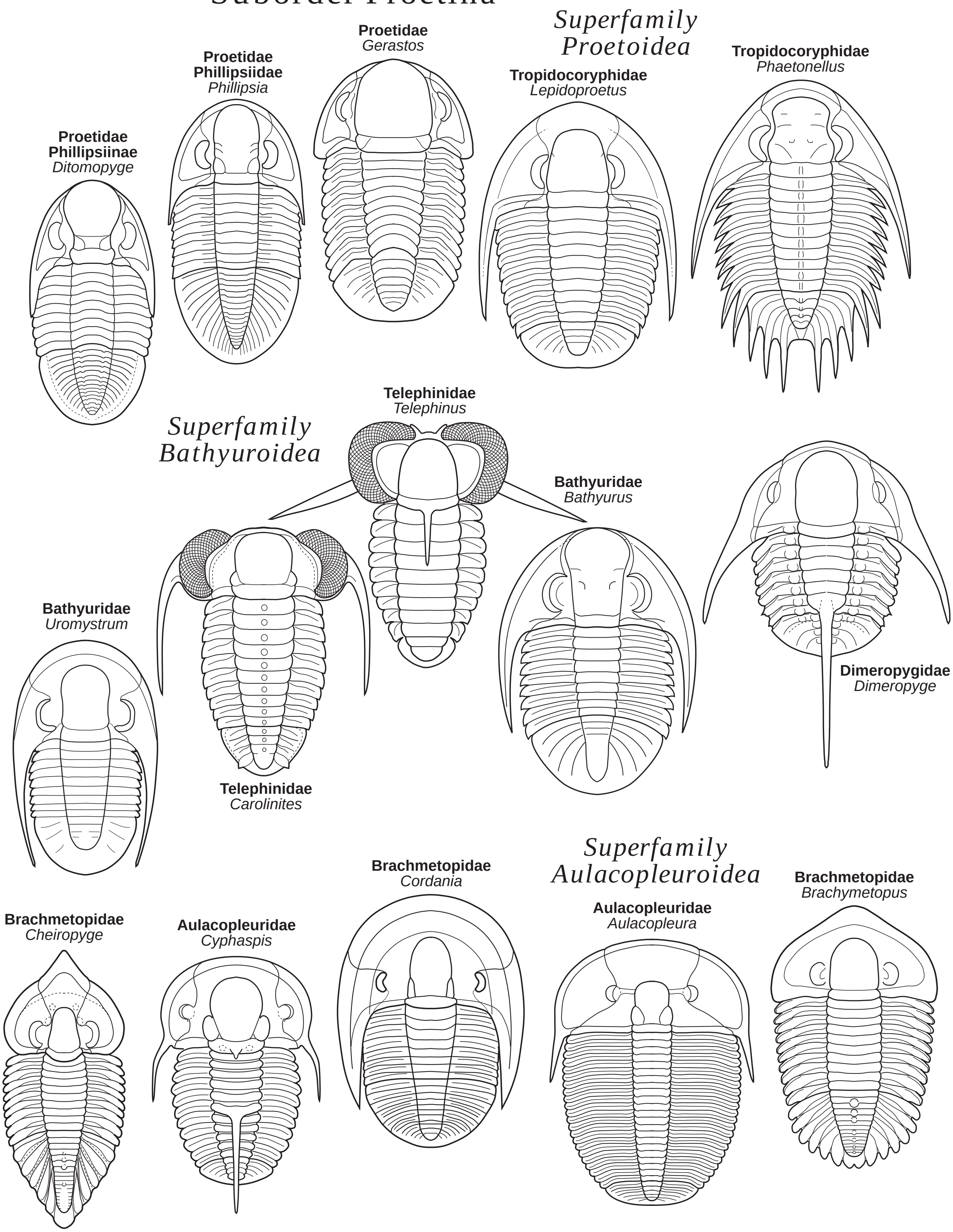
Superfamily Bathyuroidea



axis often 3 rings + terminal segment sometimes extending into axial spine

GALLERY: ORDER PROETIDA

Suborder Proetina



SELECTED SOURCES ON TRILOBITE ORDERS

The selected bibliography below includes a few sources I found helpful in my exploration of trilobite biology and taxonomy. I hope it encourages trilobite enthusiasts to gain insight on the classification of this diverse and fascinating group of organisms. Reviews and general sources that I found particularly helpful I have marked with an asterisk (*).

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* Moore, R.C., ed. 1959. *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1*. Geological Society of America & University of Kansas Press. Lawrence, Kansas & Boulder, Colorado. xix + 560 pp., 415 figs.

Whittington, H.B. 1988a. Hypostomes of post-Cambrian trilobites. *New Mexico Bureau of Mines and Mineral Resource, Memoir* 44:321-39, 26 figs.

Whittington, H.B. 1988b. Hypostomes and ventral cephalic sutures in Cambrian trilobites. *Palaeontology* 31:577-610.

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