Lab 4: Trilobites

Name:

Section:

AIMS:

This lab will introduce you to trilobites, the most abundant macrofossils in Lower Paleozoic marine sediments and the dominant marine arthropod clade until their extinction at the end of the Permian. You will see examples of most major trilobite groups and be introduced to the common morphotypes which convergently evolved in independent lineages multiple times. You will be introduced to the problems of resolving the ontogenetic development of long extinct organisms. By the end of this lab you should be familiar with basic trilobite morphology and have some understanding of trilobite paleobiology and evolution.

PART A: BASIC ANATOMY OF TRILOBITES.

Trilobites are an extinct group of arthropods, and so are related to familiar modern-day arthropods such as crabs, shrimps, lobsters, insects, millipedes, centipedes, horseshoe crabs, scorpions, spiders, and so on. Like all arthropods, trilobites had a hard cuticular exoskeleton for protection and support. Somewhat unusually for arthropods, the trilobite exoskeleton was mineralized with calcite for additional strength. Such mineralization gave the trilobite exoskeleton a very high chance of being preserved as a fossil (much more so than trilobite soft body parts, which soon decayed or were scavenged) once the animal died or the exoskeleton was shed off (molted) during growth.

The Trilobita takes its name from the three lobes running down the length of the body: a central, somewhat vaulted <u>axial lobe</u>, separating two <u>pleural lobes</u> on either side. Although these three lobes can be very obvious when looking at the trilobite in transverse cross-section, they can be hard to distinguish in some trilobites (particularly where the body was smooth, or "effaced").

The trilobite exoskeleton was also divided anteroposteriorly into three distinct units (tagma): the head shield (cephalon), the segmented thorax, and the tail shield

(<u>pygidium</u>). The thorax consisted of freely-articulating segments, and frequently broke apart (disarticulated) soon after the animal died or molted. Most trilobite fossils are therefore isolated cephala, pygidia, or thoracic segments. It is unusual to find complete, articulated specimens.

Trilobites first evolved during the Early Cambrian (522 million years ago) and became extinct at the end of the Permian (251 million years ago). The group was therefore around for over 270 million years of geological time! They had a high rate of evolution, and they are common as fossils, so they are ideal for biostratigraphic zonation of the Paleozoic and for studying evolution.

A1: Isotelus (Order Asaphida).

The large size of these specimens of the Ordovician trilobite *Isotelus* serve as a useful introduction to basic trilobite anatomy. However, the exoskeleton of this genus was rather effaced, so the axial and pleural lobes are not well delimited.

<u>Draw</u> a reconstruction of this trilobite (on the next page) to familiarize yourself with basic trilobite anatomy. Use Clarkson (1998, fig. 11.2) to help you identify the various body parts, and label each on your illustration. You should be able to see the cephalon, thorax, pygidium, palpebral lobes, genal spines, and the facial suture separating the fixed cheeks from the free cheeks. Also draw the hypostome, and indicate the original location of this sclerite on the animal. Careful examination will reveal the sensory ridges on the genal spines (terrace lines) and on the hypostome (fingerprint-like bertillon markings).

How many thoracic segments did *Isotelus* possess? (Beware of the "segment telescoping" in the prone specimen!)

What is the name of the suture-bound sclerite bearing the glabella and fixed cheeks?

A2: *Flexicalymene* (Order Phacopida, Suborder Calymenina).

This suite of specimens shows various stages of enrollment in this common Ordovician trilobite. Most trilobites could enroll for protection when the environment became unfavorable. This would be a deterrent for predators, which would not have had easy access to the soft underside of the trilobite. It is difficult to imagine that a trilobite enrolling for protection against a predator would remain enrolled long enough to be buried. Most enrolled trilobites preserved as fossils likely enrolled in response to sudden influxes of sediment and were buried alive. Some trilobites had complex locking mechanisms to assist in enrollment.

<u>Draw</u> and label a reconstruction of this animal as you did for *Isotelus*.

How many thoracic segments did Flexicalymene possess?

Compare the differentiation of the pygidium from the thorax in *Flexicalymene* and *Isotelus*. How does the degree of pygidial "distinctness" differ?

What features assisted in tight enrollment of this animal?

A3: Dalmanites (Order Phacopida, Suborder Phacopina).

Another relatively large trilobite, this time a species of the Silurian/Devonian trilobite *Dalmanites*. Only the cephalon is preserved here.

Draw and label the cephalon (below).

What kind of eyes does this phacopid possess?

What tells you this?

Compare the trace of the facial suture across the cephalon of *Dalmanites*, *Flexicalymene*, and *Isotelus*. How do the traces differ?

A4: *Phacops rana* (Order Phacopida, Suborder Phacopina).

This Devonian phacopid is famous for its "frog-like" cephalon (indeed, the species name of this animal means "frog"), and is an example of the phacomorph morphology (see Part B).

What kind of eyes does this phacopid possess?

How many thoracic segments did Phacops possess?

What do you notice about the facial suture in *Phacops*?

Is this condition likely to be primitive or derived in this trilobite?

Why?

PART B: TRILOBITE MORPHOTYPES.

Trilobite species inhabiting similar environments often evolved similar adaptations. When unrelated organisms evolve similar morphologies in response to common selective pressure, this is termed "convergent evolution". At least eight basic morphotypes have been recognized in trilobites, each of which was converged upon several times independently by different trilobite groups during the Paleozoic. Each morphotype is characteristic of a particular environment or mode of life.

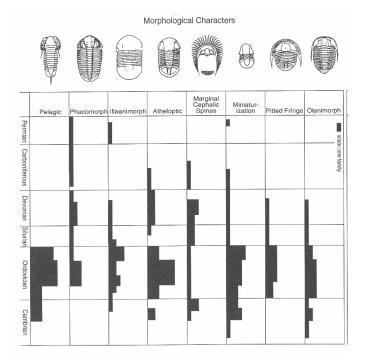


Figure B1: Stratigraphic ranges of various trilobite morphotypes.

B1: Pelagic Morphotype.

Look at the pictures of the silicified cranidia and free cheeks of *Telephina problematica*, a diminutive pelagic trilobite (from Chatterton *et al.*, 1999, *Journal of Paleontology* **73**: 219-239). Each of these sclerites is less than 1 mm in length in life.

<u>Draw</u> a reconstruction of the cephalon of *Telephina problematica*.

What feature suggests that this trilobite may have been pelagic? Why?

B2: Cephalic Marginal Spines.

Many trilobite lineages independently evolved an array of spines around the edge of the cephalon. The fringe of spines may have served as protection or as support for the cephalon when resting on the seafloor (see the paper by Clarkson, 1969).

B3: Pitted Cephalic Fringe.

Cryptolithus was an Ordovician trinucleid trilobite, a group famed for development of the bizarre pitted cephalic fringe. Trinucleids also lacked eyes and had secondarily lost the facial suture. Note the fine details of the fringe in these specimens. Trinucleid species are distinguished from each other by the arrangement and number of the pit rows. Harpetid and dionidid trilobites also independently evolved pitted cephalic fringes.

<u>Draw</u> the cephalon of *Cryptolithus*, showing the pitted fringe.

B4: Illaenimorph Morphotype.

These are specimens of the Ordovician/Silurian illaenid trilobite *Bumastus* (see also PaleoBase 1.0). Note the exaggerated vaulting of the body (especially the cephalon), and the effaced exoskeleton which are typical of such "illaenimorphs".

Why would the effaced morphology be a selective advantage in illaenimorph trilobites?

B5: Olenimorph Morphotype.

This specimen is of the Middle Cambrian ptychopariid trilobite *Elrathia kingi*. Although only known from the Drum Mountains and the House Range in Utah, this trilobite has been claimed to be the most abundant trilobite species: uncountable numbers of this animal have been found in the Wheeler Formation at these localities. *Elrathia* is a prime example of the olenimorph morphotype, possessing a thin exoskeleton and many wide but narrow thoracic segments.

What kind of environment did *Elrathia* (and olenimorph trilobites in general) typically inhabit?

What was the advantage of the olenimorph morphotype in such settings?

B6: Miniaturized Trilobites.

Miniaturized trilobites often have fewer thoracic segments than their "normal sized" ancestors. As for all trilobites, thoracic segments were released one at time (one per molt) from the front of the transitory pygidium during the meraspid period of development.

What does this suggest about the number of meraspid molts that these miniature species underwent, relative to their multi-segmented ancestors?

What might have been the selective advantage of this evolutionary change?

B7: Atheloptic Morphotype.

Atheloptic trilobites are those which reduced the size of their eyes (or lost their eyes altogether) in response to selective pressure. Ancestors of the atheloptic species had "normal sized" eyes. *Elyx* is a famous Cambrian example of an atheloptic morphotype.

What kind of environment did atheloptic trilobites typically inhabit?

Why are agnostine trilobites (see C2) not atheloptic?

PART C: SOME OTHER IMPORTANT TRILOBITES.

C1: Olenelloid trilobites.

Olenelloid trilobites were among the earliest trilobites to evolve, being entirely restricted to Lower Cambrian strata. Like the marginally older fallotaspids, olenelloids show primitive lack of a facial suture, as these specimens of *Mesonacis* demonstrate. Some olenelloids could attain a relatively huge size (over 30cm in body length).

What do you notice about the third thoracic segment in this olenelloid?

C2: Agnostine trilobites.

Agnostines are a bizarre group of trilobites. They are unusual in several respects, the most obvious being development of only two thoracic segments. Agnostines were also blind (lacking eyes) and lacked a facial suture and a calcified exoskeleton during their protaspis period of development. They range from the Lower Cambrian through Upper Ordovician, but are especially common in Middle and Upper Cambrian strata around the world. Individual species often have an almost global distribution, and are used to biostratigraphically subdivide the Cambrian. The name of the group refers to the difficulty trilobite workers have in distinguishing the cephalon from the pygidium: both sclerites are large, discoidal, and often rather smooth.

Draw an agnostine trilobite.

What mode of life do you think agnostines had? Why?

C3: Proetid trilobites.

This is a beautiful specimen of the proetid trilobite *Proetus*. The Proetida was the only group of trilobites to survive beyond the late Devonian mass extinction, and radiated in the Carboniferous to fill most of the ecological niches previously occupied by the many pre-extinction trilobite orders.

Of the other trilobites seen in this lab, which might you expect this species of *Proetus* to have been most similar to in terms of life habit?

Why?

PART D: TRILOBITE ONTOGENIES.

Silicified limestones are carbonate beds in which the entombed fossils have been replaced by silica (see Lab 1). Silicified fossils can be extracted from the surrounding matrix by dissolution of the rock in dilute acid: the carbonate dissolves away but the silicified fossils are acid-resistant and so are left in the insoluble residue. Silicified fossils are often exquisitely preserved, even down to minute sculptural details. Futhermore, silicified fossils are more resistant to compaction, and so preserve the original three-dimensional morphology of the individuals.

Silicification is the chief preservational mode permitting insight into the ontogenetic development of trilobites. Even tiny individuals less than 0.5 mm in length can be silicified. By finding conspecific specimens of a range of sizes it is possible to piece together the morphological changes a specie's went through during its ontogenetic development. This can in turn provide invaluable evidence pertaining to the

developmental biology of these long-extinct organisms, and sometimes yield insight into the processes involved in their evolution.

A major problem associated with resolving the ontogenetic development of trilobite species lies in identifying which species the juveniles belong to. The problem becomes increasingly difficult if species diversity is high: species looking quite different at maturity can look quite similar at early developmental stages. The problem would be intractable if trilobites went through a major metamorphosis during their development. However, almost all trilobite species changed their morphology only slightly at each molting event. Provided that the ontogeny is sampled with sufficient regularity, it is possible to identify even tiny specimens by tracing morphology "backwards" through development, starting from the mature morphology and identifying progressively smaller specimens.

This section of the lab introduces you to the difficulties of resolving trilobite ontogenies. It is based on a real study of Early Cambrian olenelloid trilobites from eastern Nevada. Silicified limestone beds in the Pioche Formation just below the base of the Middle Cambrian contain a rich trilobite fauna dominated by olenelloid trilobites (see figure D1). Illustrations of 30 immature specimens, representing the four species of olenelloids shown in figure D1, are provided in figure D2. Your task is to work out which specimens belong to which species! Make sure you can tell the mature cephala apart (not easy!!!) before you try to identify the juveniles. Cutting out the pictures and laying them out in front of you will help.

Results:

Ontogeny of *Nephrolenellus geniculatus*: Specimens:

Ontogeny of *Nephrolenellus multinodus*: Specimens:

Ontogeny of *Olenellus gilberti*: Specimens:

Ontogeny of *Olenellus chiefensis*: Specimens:

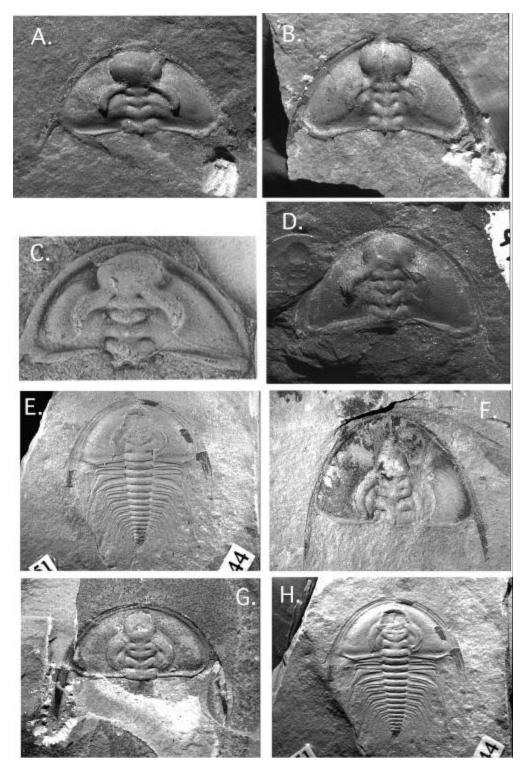


Figure D1: Mature morphology of the four species of olenelloid trilobites from the uppermost Lower Cambrian Pioche Formation of Nevada. A, B: *Nephrolenellus geniculatus*. C, D: *Nephrolenellus multinodus*. E, G, H: *Olenellus gilberti*. F: *Olenellus chiefensis*.

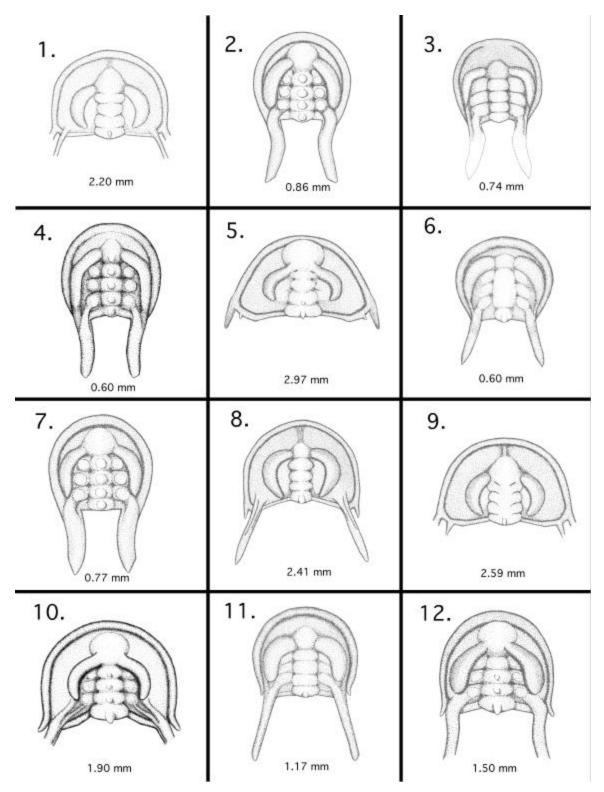


Figure D2: Illustrations of thirty silicified olenelloid trilobite cephala from the latest Lower Cambrian Pioche Formation of Nevada, representing four species.

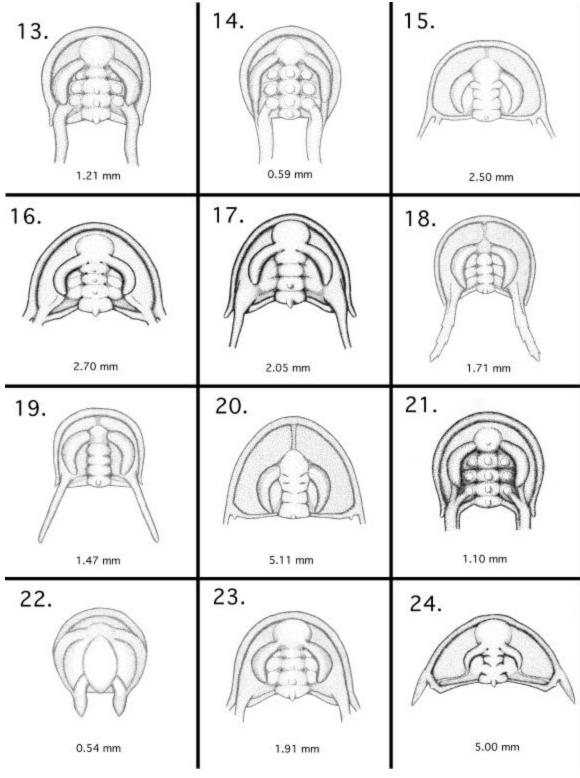


Figure D2 (continued).

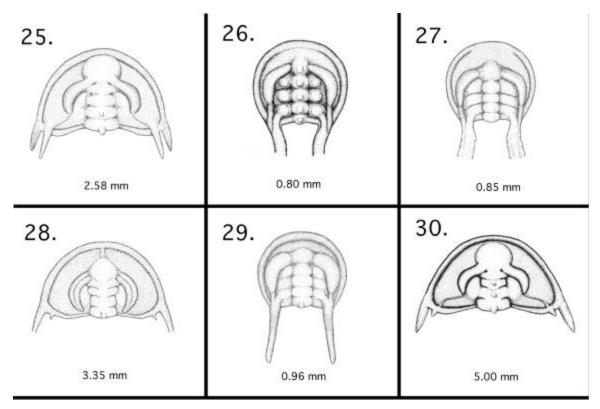


Figure D2 (continued).