Introduction to the Trilobites: Morphology, Macroevolution and More

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Undergraduate laboratory exercise for sophomore/junior level paleontology course

Learning Goals and Pedagogy

This lab is intended for an upper level paleontology course containing sophomores and juniors who have already taken historical geology or its equivalent; however it may be suitable for introductory biology or geology students familiar with geological time, phylogenies, and trace fossils. This lab will be particularly helpful to those institutions that lack a large teaching collection by providing color photographs of museum specimens. Students may find previous exposure to phylogenetic methods and terminology helpful in completing this laboratory exercise. The learning goals for this lab are the following: 1) to familiarize students with the anatomy and terminology relating to trilobites; 2) to give students experience identifying morphologic structures on real fossil specimens, not just diagrammatic representations; 3) to highlight major events or trends in the evolutionary history and ecology of the Trilobita; and 4) to expose students to the study of macroevolution in the fossil record using trilobites as a case study.

Introduction to the Trilobites

The Trilobites are an extinct subphylum of the Arthropoda (the most diverse phylum on earth with nearly a million species described). Arthropoda also contains all fossil and living crustaceans, spiders, and insects as well as several other solely extinct groups. The trilobites were an extremely important and diverse type of marine invertebrates that lived during the Paleozoic Era. They were exclusively marine but occurred in all types of marine environments, and ranged in size from less than a centimeter to almost a meter. They were once one of the most successful of all animal groups and in certain fossil deposits, especially in the Cambrian, Ordovician, and Devonian periods, they were extremely abundant. They still astound us today with their profusion of body forms (see Fig. 1). Trilobites are well represented in the fossil record because of their mineralized (usually calcium carbonate and thus of similar basic mineralogy to a clam shell), sturdy exoskeleton, which would have been much thicker and stronger (and harder to break) than the shell of a modern crab. Further, being arthropods, they molted as they grew, such that every single trilobite was capable of leaving behind many, many skeletons that could become fossilized. Most of what we know about trilobites comes from the remains of their mineralized exoskeleton, and in fact the external shell does provide a lot of information about what the trilobite animal inside the shell looked like. Most notably, the eyes are preserved as part of the skeleton so we have an excellent idea about how trilobite eyes looked and operated. In addition, there are a few rare instances in trilobites when not only the exoskeleton but also their soft tissues were preserved including their legs, gut, and antennae. Interestingly, while the external shell differs quite a lot across the different trilobite species the internal anatomy was more conserved. In any event, in this lab we will provide extensive information about their external shells as well as their internal anatomy. Further, here we will focus not only on the general type and appearance of trilobites. We will also pay special attention to their significance for our understanding of evolution and the nature of ecology in the distant past, while providing both exercises and numerous illustrations.

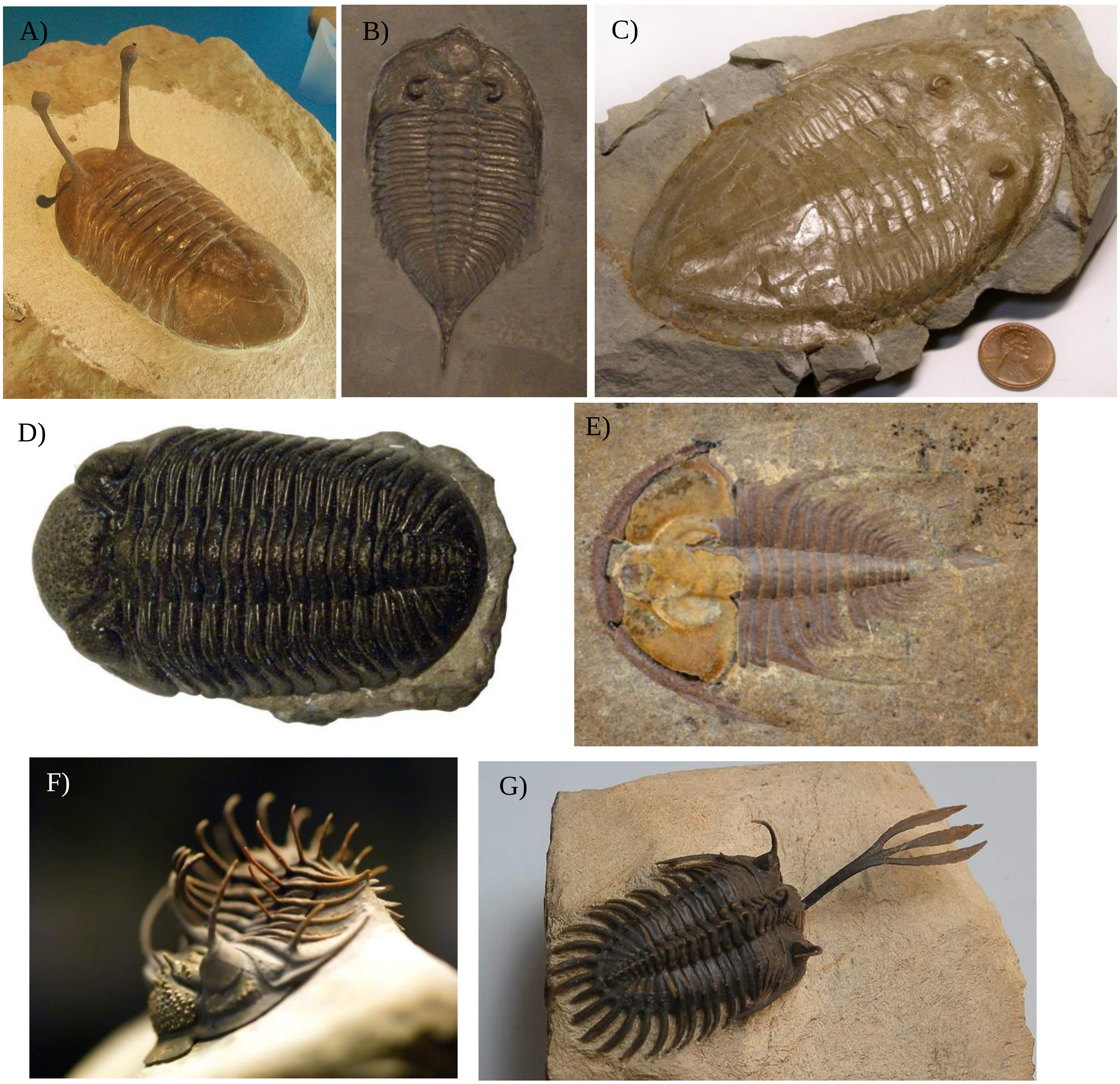


Figure 1: A) *Asaphus kowalewskii*, by Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, B) *Dalmanities limulurus* University of Kansas Museum, on exhibit, C) *Isotelus iowensis* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 294608, D)*Phacops milleri* University Of Kansas Museum, on exhibit, E) *Olenellus sp.* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 369418, F) *Comura* sp., by Wikipedia Loves Art participant "Assignment_Houston_One" [CC-BY-SA-2.5 (http://creativecommons.org/licenses/by-sa/2.5)], via Wikimedia Commons*;* G) *Walliserops trifurcates*, by Arenamontanus (Own work) [CC-BY-2.0 (http://creativecommons.org/licenses/by/2.0/)], via Flickr.

Sheer Numbers

The sheer variety of trilobites is impressive. As mentioned above, they belong to the most diverse phylum, the arthropods, and when it comes to total variety and diversity trilobites were no slouches themselves. They have been divided into:

10 Orders that include
150 Families assigned to
~5,000 Genera that contain perhaps more than
20,000 Species

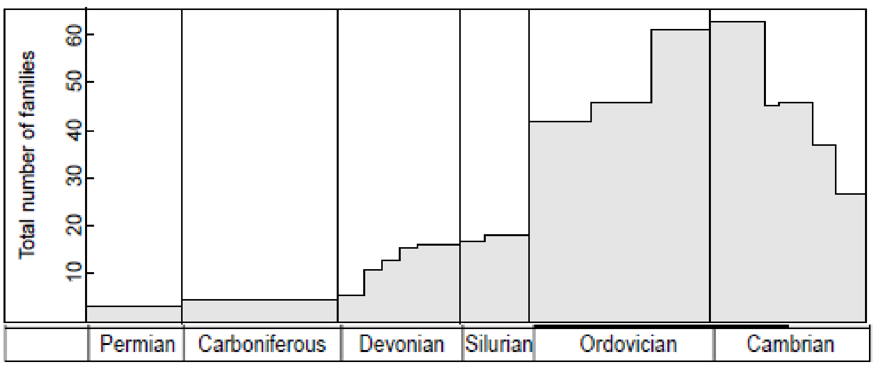


Figure 2: Diversity of trilobites, number of families, through time from the *Treatise on Invertebrate Paleontology*, used with permission.

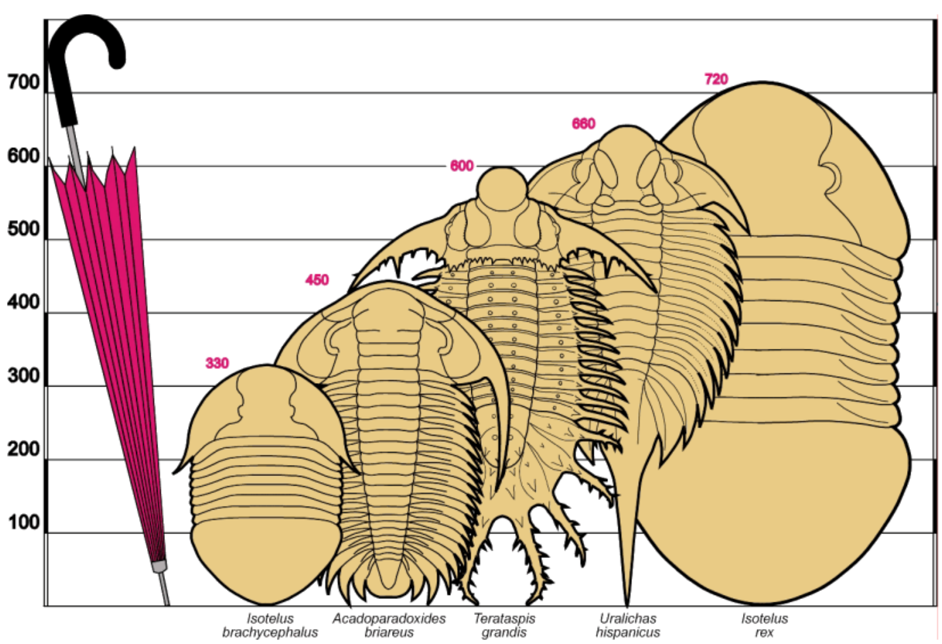


Figure 3: Size range of the largest trilobites, from Sam Gon, http://www.trilobites.info/lgtrilos.htm, used with permission.

As already mentioned, trilobites show an impressive variation in size, from under 1 mm to over 70 cm in length, although the average trilobite was probably around 5-6 cm. Figure 3 nicely illustrates the sizes of the very largest known trilobites.

Temporal and Spatial Distribution

521 Ma (Cambrian) to 251 Ma (Permian) ≈ 300 million year history
Greatest numbers in Cambrian and Ordovician
Worldwide distribution

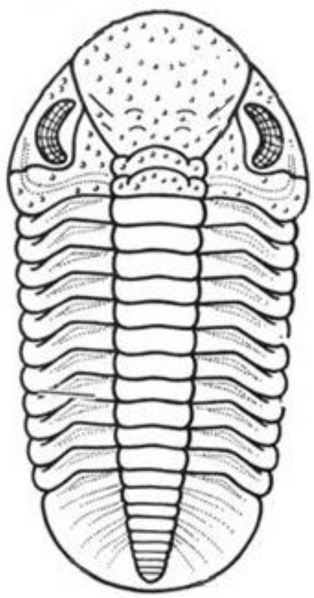
The earliest trilobites appear suddenly in rocks of Early Cambrian age (522-530 Ma) from present day Scandinavia and eastern Europe. Soon afterwards trilobites also appeared in China, North America, Antarctica, and Australia and within the Early Cambrian are found throughout the world. The early history of trilobite evolution shows a pattern of biogeographic differentiation which taken with other evidence suggests that there may have been some significant period of trilobite evolution before they actually appeared in the fossil record. Current estimates suggest that although the earliest trilobites appeared in the fossil record around 525 Ma they may have originated 550-600 Ma (Lieberman and Karim, 2010). Paleontologists continue to investigate this trend looking for evidence of older trilobites and working to better constrain the timing of their origins. The reasons why the earliest relatives may have been absent from the fossil record remain unclear but may include the fact that they were small, lacked a hard shell, or they were very rare and restricted to environments where they were unlikely to fossilize.

The trilobites continued to diversify into the Ordovician, but were hit particularly hard by the end Ordovician mass extinction. Trilobites were able to partially recover after the end Ordovician mass extinction, only to be hit again by the Late Devonian mass extinction. Trilobite diversity failed to rebound after the Late Devonian event and the group was eventually wiped out during the largest mass extinction of all time at the end of the Permian. Indeed, as we shall discuss more fully below, scientists are exploring the possibility that part of the reason trilobites are no longer with us today has to do with the fact that they fared particularly poorly during times of mass extinction (Lieberman and Melott, 2013).

General Anatomy

In small groups, identify at least 5 morphological features of trilobites that you think are important for anatomical description. Mark the features on the trilobite diagram below, with lines pointing to them.

Consider the variety of body forms shown in Figures 1 and 3. Can you identify any additional morphological features that may be important for distinguishing groups of trilobites from one another? Add as many as you can identify to your diagram.



The name trilobite refers to fact that their body is made up of three longitudinal (along the length of the body) sections: the central section, known as the **axial lobe**; and the two lobes on either side of the axial lobe, known as the **pleural lobes** (Figure 4 and 5). Trilobites are also separated into three sections from front to back known as tagmata: the **cephalon,** or head; the middle section made up of multiple segments known as the **thorax;** and the posterior section, or **pygidium** (plural = pygidia) (Figures 4 and 5). Some trilobites have spines originating at the genal angle, in which case they are called **genal spines**.

How does the commonly accepted anatomical regions of trilobites compare with the important anatomical features identified by your group?

Did you identify the longitudinal sections as important features? Did you identify the tagmata as an important feature?

Use the diagram and descriptions provided in Figures 4 and 5 to label the anatomical elements highlighted in this photograph of the trilobite *Phacops*.

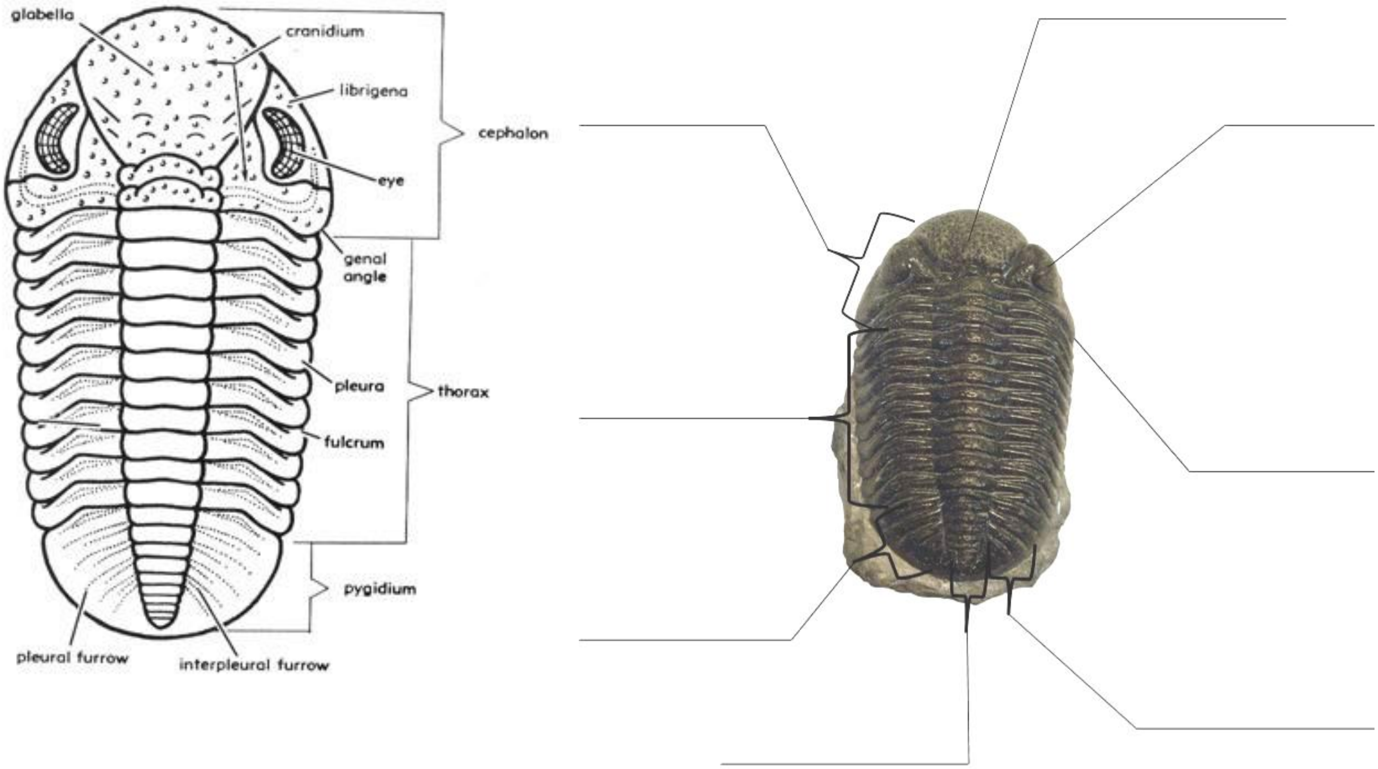
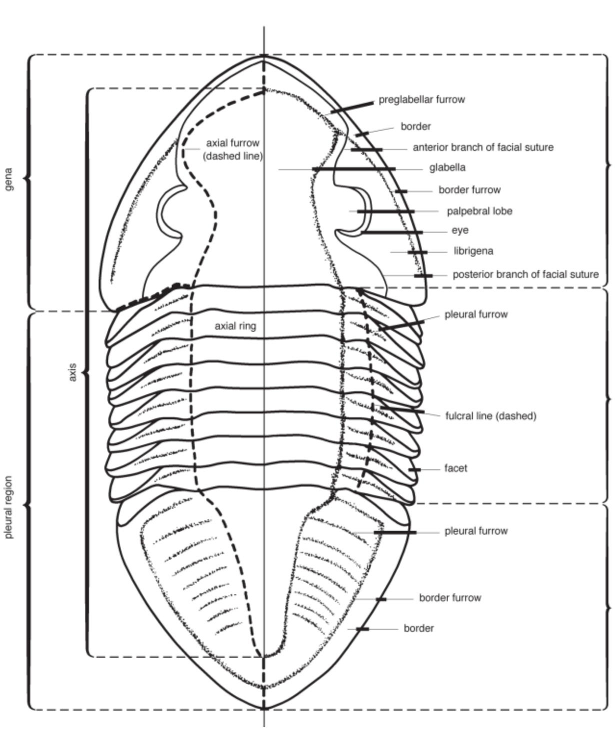


Figure 4: External trilobite anatomy. A) Diagram of *Phacops* from the *Treatise on Invertebrate Paleontology*, used with permission. B) Photo of *Phacops milleri* specimen from the University of Kansas Museum, on exhibit.

Use the diagram and descriptions provided in Figures 4 and 5 to label some of the same anatomical elements in this photograph of the morphologically distinct *Isotelus iownesis*.



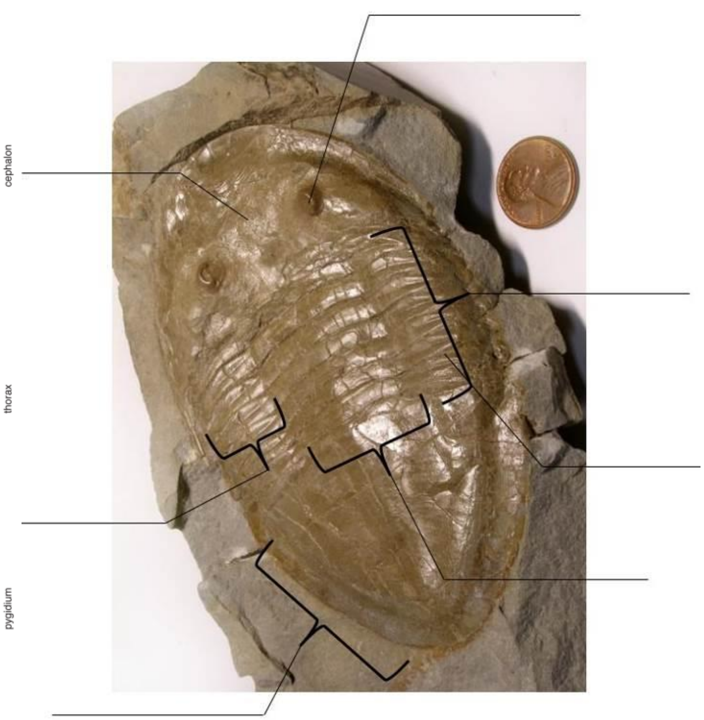


Figure 5 (previous page): External trilobite anatomy continued. A) Diagram of the Ordovician trilobite, *Isotelus* from *the Treatise on Invertebrate Paleontology*, used with permission. B) *Isotelus iowensis.* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 294608.

Now that you are familiar with general trilobite anatomy, choose one of the trilobites from Figure 1. Spend 2 minutes writing a description of your trilobite, but do not write down which one you chose. Try to be detailed in your observations and use the correct anatomical terminology where possible.

Once you are finished recording your observations, switch lab handouts with your neighbor and try to determine which trilobite they described based on their recorded observations. You may <u>not</u> ask your neighbor for clarification and must rely solely on their written description.

Were you able to match their description with the correct trilobite? Were they able to identify which trilobite you described?

What was difficult about identifying you neighbor's trilobite from their description? What made the task easier? How might you change your own description after this exercise?

The above photos and diagrams depict the **dorsal** (upper or backside) surface of the trilobite. Below is a diagram of the **ventral** (underbelly) morphology of a trilobite.

An important ventral morphological feature of trilobites is a calcified plate near the mouth known as the **hypostome**.

The hypostome is thought to have been used in feeding. It may be rigidly or flexibly attached to the shell of the cephalon, and can display a variety of shapes including points or fork-shaped projections.

Figure 6: Ventral view of a *Ceraurus whittingtoni* cephalon from the *Treatise on Invertebrate Paleontology*, used with permission.

The shells of trilobites are frequently preserved as fossils due to their mineralized exoskeletons hardened with calcite. Trilobite limbs, however, are rare in the fossil record because they lacked a hard mineralized coating of calcite. To reconstruct limb morphology, we must rely on exceptionally preserved trilobites, those preserving both hard and soft tissues as fossils. This *Triarthus eatoni* specimen (Fig. 7) from the Ordovician Beecher's trilobite bed locality in upstate New York is an example of a pyritized trilobite (the limbs are substituted by the mineral pyrite which contains Iron and Sulfur) that preserves soft tissues such as antennae and appendages. Trilobites have **biramous** appendages: each appendage is made up of two branches. These branched appendages are found along the length of the body occurring in repeating pairs, with multiple pairs on the cephalon, one pair per thoracic segment, and several small pairs on the pygidium. Unlike many modern arthropods with many specialized limbs, the limbs of trilobites are essentially the same from front to back, varying only in size. The upper branch, or **gill** branch, is a soft, filamentous structure used to obtain oxygen from the water. The lower branch is a jointed walking leg used for locomotion. The gill branches are located directly under the trilobite shell.

Please answer the following questions using the diagrams and photos provided in Figure 7.

A) B)

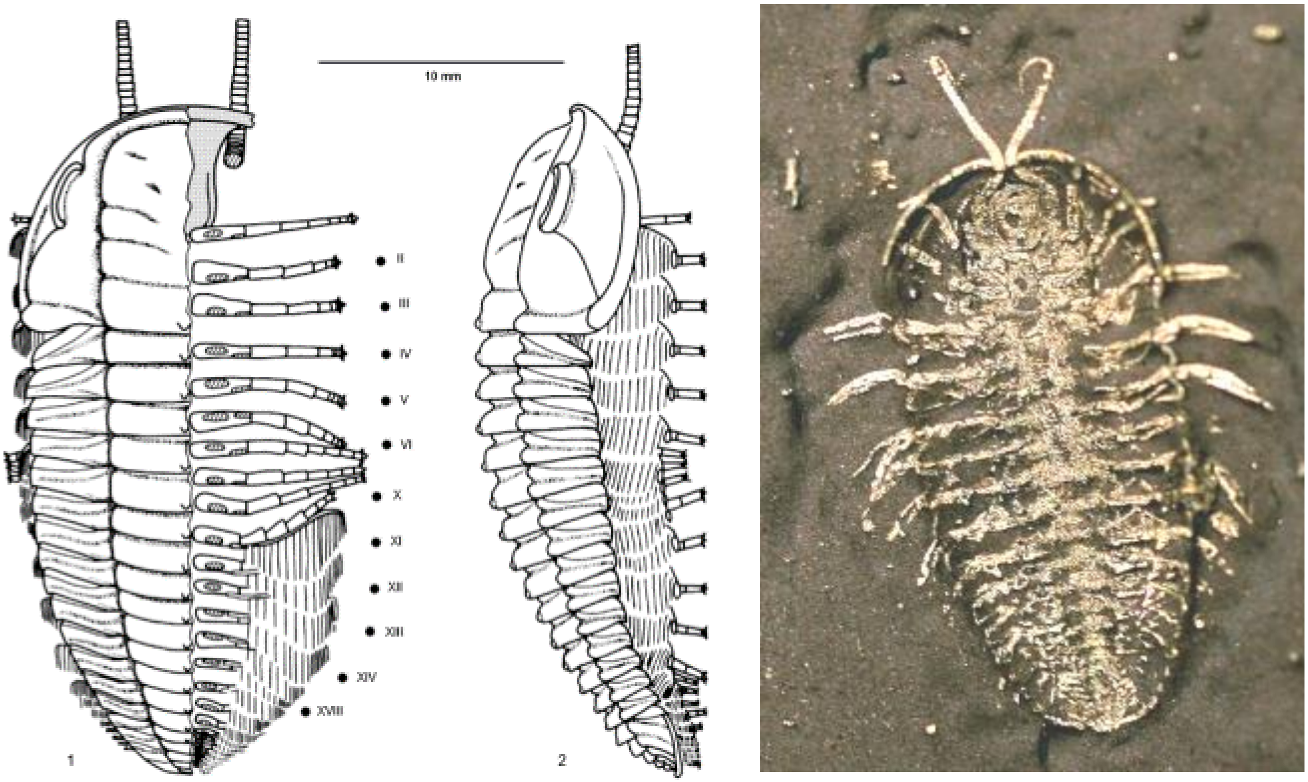


Figure 7: Limb morphology. A) Diagram of the limbs of *Triarthus eatoni* from the *Treatise on Invertebrate Paleontology*, used with permission. B) Photograph of a pyritized specimen of *Triarthus eatoni* YPM 219 from the Yale Peabody Museum collections, by Bruce Lieberman, used with permission.

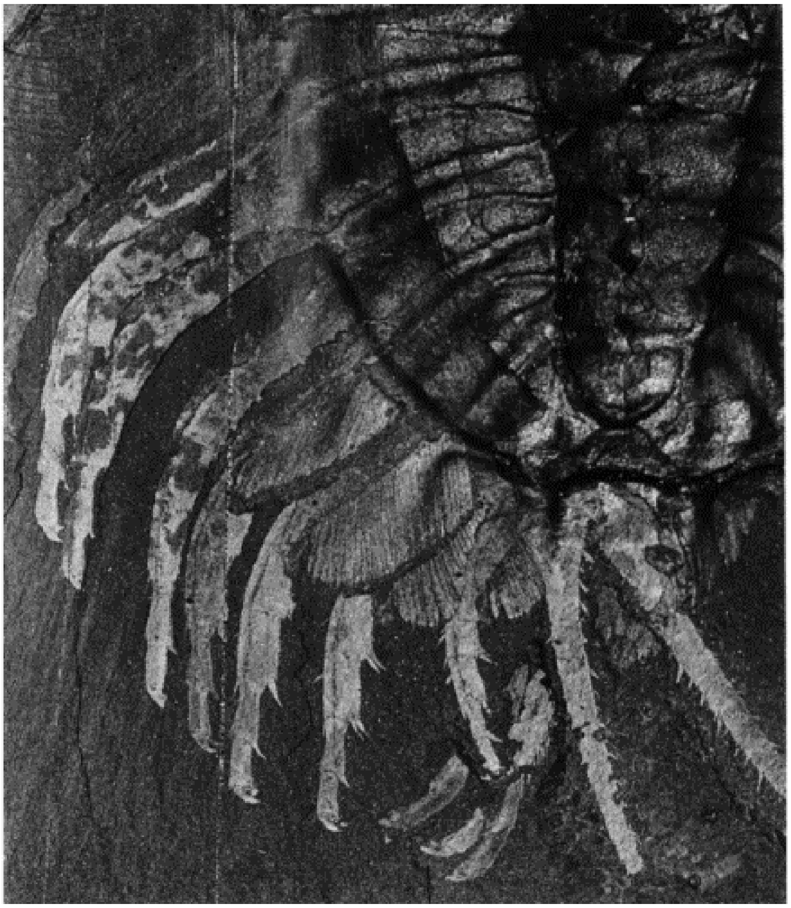
How many pairs of limbs does the cephalon have?

How many pairs of limbs does the thorax have (hint, there are 14 thoracic segments)?

On the diagrams or photo above (Fig. 7), draw a line separating the thorax from the pygidium (hint, the diagram showing the side view may be the most helpful for this task).

Does the pygidium have limbs?   Y/N

A) B)



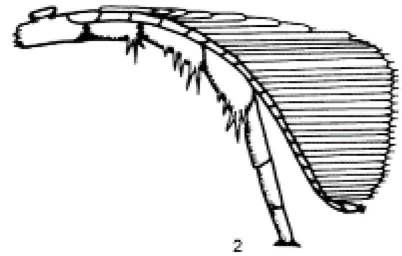


Figure 8: Enlarged view of trilobite biramous limb morphology showing the jointed walking leg and filamentous gill branch. A) Close up of Middle Cambrian *Olenoides serratus* from *Treatise on Invertebrate Paleontology*, used with permission. B) Limb reconstruction from the *Treatise on Invertebrate Paleontology*, used with permission.

Using the diagram as a guide, circle and label a walking leg and a gill branch on the close-up photo provided in Figure 8.

What was the gill's function? How did the gill's feathery construction help it perform this function?

What factors constrain the placement of the gills? For instance, would gills placed under the walking leg be more or less effective? Why?

Many different clades of trilobites are capable of flexing the thoracic segments to rest the cephalon on the pygidium. The process of flexing into a ball is known as **enrollment**. Some trilobites even have structures that allow the cephalon and pygidium margins to interlock for a tight fit.

Figure 9: Fully enrolled trilobites, *Flexicalymene meeki* (Upper Ordovician) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 241339-241344 and University of Kansas Museum, Invertebrate Paleontology (KUMIP) 241347-241349.

Given what you just learned about the structure of trilobite limbs, what do you think the benefit of enrollment was? What might cause a trilobite to roll up into a ball?

Looking at the range of morphologies illustrated in Figure 1, what other structures can you see in the photos that likely served the same function as enrollment?

Trilobites had compound eyes, made up of numerous calcite lenses. Eyes in which individual lenses are not separated are known as holochroal (Fig. 10A). All of the lenses in a holochroal eye share a single cornea or covering. Eyes in which individual lenses were separated by exoskeleton material are known as schizochroal (Fig. 10B). In a schizochroal eye, each lens had its own cornea. Holochroal and schizochroal eyes may have been equally adept at allowing trilobites to see static objects, but schizochroal eyes were more adept at detecting movement.

A) B)

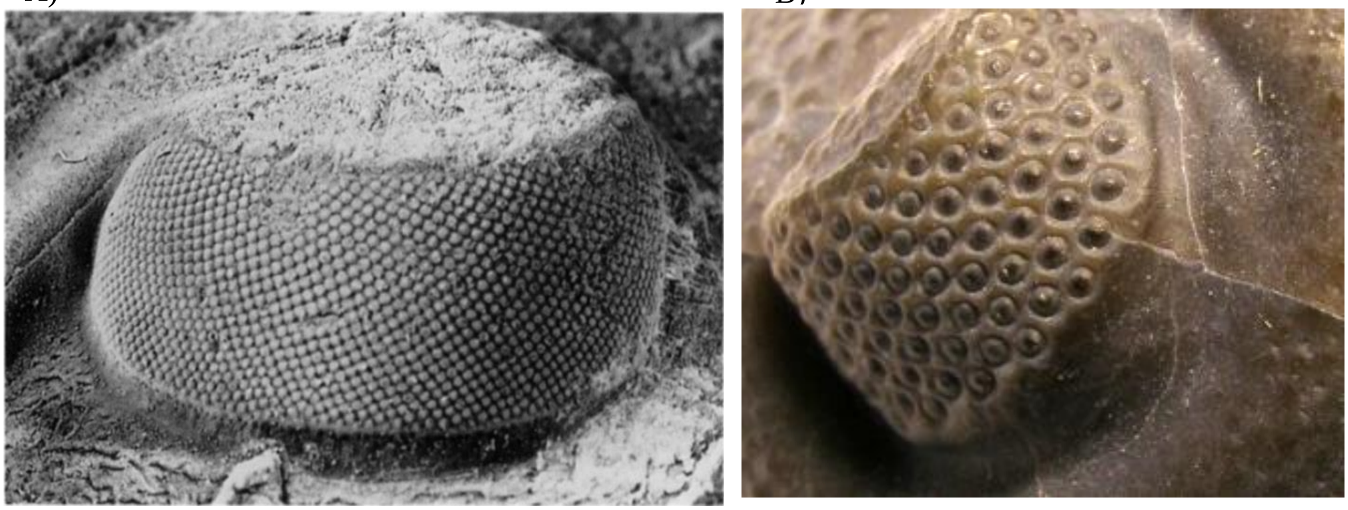


Figure 10: A) Holochroal eye of *Paralejurus brongniarti*, Devonian, Bohemia; lateral view, ×7 (Clarkson, 1975, pl. 1, fig. 1) from the *Treatise on Invertebrate Paleontology*, used with permission. B) Schizochroal eye of *Phacops rana* University of Kansas Museum, Invertebrate Paleontology (KUMIP) 240295.

The holochroal style of eyes evolved first, whereas the schizochroal style of eyes evolved in only one group of trilobites, the Order Phacopida, and presumably evolved sometime in the Late Cambrian.

A) B) C) D)

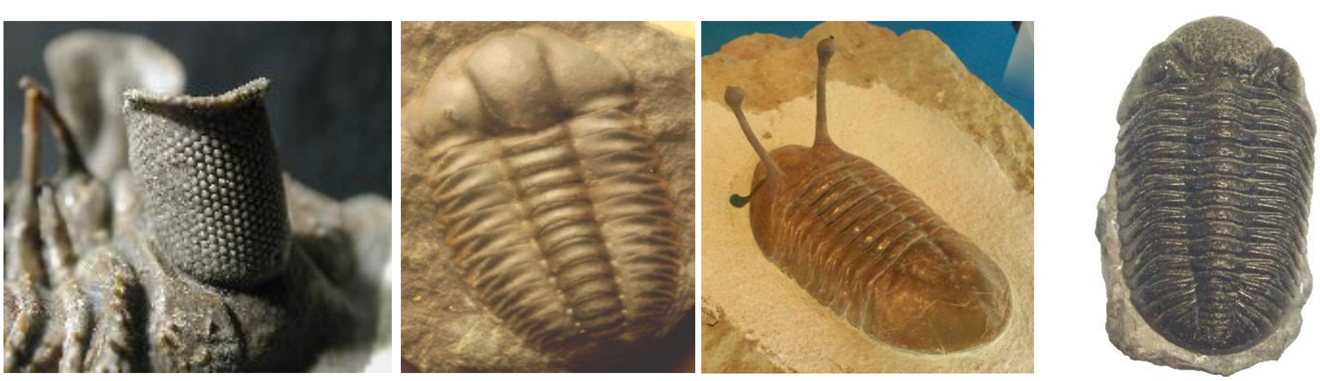


Figure 11: A) *Erbenochile erbenii*, by Moussa Direct Ltd. (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, B) *Ellipsocephalus hoffi*, by TheoricienQuantique (Own work) [Public domain], via Wikimedia Commons, C) *Asaphus kowalewskii*, by Smokeybjb (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, D) *Phacops milleri* University of Kansas Museum, on exhibit.

Describe the visual capabilities of the trilobites in Figure 11. Things to consider: presence or absence of an eye; the size of the eye; the position of the eye on the cephalon; the field of vision the trilobite may have had (in which directions can the trilobite see); whether the eye is schizochroal or holochroal?

A)

B)

C)

D)

Ecological Niches

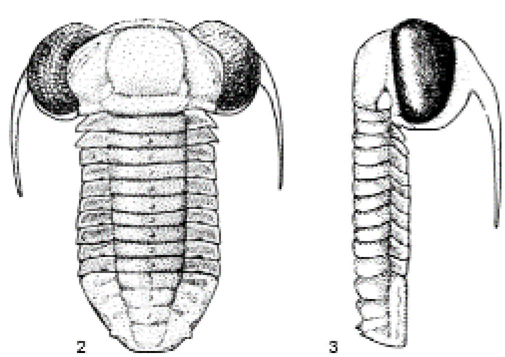
As mentioned above, trilobites are only found in rocks representing marine environments, but they were present at all depths and in all marine environments. Trilobites filled many different ecological niches and were capable of a wide range of behaviors. Paleontologists reconstruct these behaviors and modes of life using a combination of evidence including morphology, occurrence with other organisms, types of sediments in which trilobites are preserved (yielding information on the types of environments in which trilobites lived), and trace fossils or trackways made by trilobites. Below are some examples of morphological traits exhibited by trilobites, scientific interpretations of those traits, and the lifestyle or behavior inferred from the interpretations.

Fossil Evidence	**Interpretation**	**Inferred Lifestyle or Behavior**
Reduced thorax and pygidium; smoothed cephalon; downward projecting spines; facies independence	Light, streamlined body allows fast swimming. Spines prohibit effective movement on the sediment surface. Distribution controlled by water column characteristics rather than sediment characteristics.	Pelagic Lifestyle/Swimming
Smooth exterior, broad & flat axial lobe Larger muscle attachments	Reduce friction Stronger limb motions to move sediments	Burrowing
Eyes reduced or absent Wide bodies, genal spines	Darker conditions, less need/no need for keen eyesight Added support for soupy substrate	Living in Deep Water
Well-developed limbs, flexible hypostome, *Cruziana* feeding traces	Food passed anteriorly towards the mouth during the course of movement, flexible hypostome used as a scoop.	Particle Feeding
Unusual occipital angle, pitted fringe	Pits allow water to flow through cephalon from leg-generated currents	Filter Feeding
Rigid, strongly braced hypostome; forked hypostome projections	Ability to process relatively large food particles	Predatory, feeding on soft bodied worms

Matching exercise. Now that you have the criteria for recognizing different lifestyles, classify the body or trace fossils in Figure 12 by matching their respective letters with their inferred lifestyle listed below (numbers 1-6).

A) *Lloydolithus lloydi*

B) *Carolinites genacinaca*



C) *Asaphus lepidurus*

D) *Cruziana* trace fossil

E) *Ampyx priscus*

F) underside *Asaphus expansus*

1) Pelagic ______________ 2) Burrowing ______________

3) Deep water ______________ 4) Particle feeding ______________

5) Filter feeding ______________ 6) Predatory ______________

Figure 12: A) *Lloydolithus lloydi*, by Tomleetaiwan (Own work) [CC0], via Wikimedia Commons, B) *Carolinites genacinaca*, from the *Treatise on Invertebrate Paleontology*, used with permission, C) *Asaphus lepidurus*, by DanielCD (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, D) *Cruziana* trace fossil, by Luis Fernández García (Own Work) [CC-BY-SA-2.1-Es (http://creativecommons.org/licenses/by-a/2.1/es/deed.en)], via Wikimedia Commons, E) *Ampyx priscus*, by Dwergenpaartje (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons, F) Ventral view of *Asaphus expansus*, by Dwergenpaartje (Own work) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons.

Review of Selected Trilobite Orders

Order Agnostida (Fig. 13) – Early Cambrian to Late Ordovician, abundant and widespread. Agnostoids are typically small (only a few mm long) and **isopygous**, having a cephalon and pygidium that are similar in both outline and size. Agnostid trilobites are frequently blind. Their thorax consists of only 2-3 segments. The limbs of Agnostoids, known only from juveniles, are morphologically very different from the limbs of other trilobites. This major difference in limb morphology has cast doubt on the placement of the Agnostoids within the class Trilobita and several authors believe the Agnostoids should lie just outside of the Trilobita. The agnosticism about their true relationship to trilobites explains their distinctive name.

Figure 13: Photo of the Agnostoid trilobite *Anglangostus* from the *Treatise on Invertebrate Paleontology*, used with permission.

Order Redlichiida (Fig. 14) – Early to Middle Cambrian, the earliest order of trilobites including the suborders Olenelloidea, Emuelloidea, Redlichioidea, and Paradoxidoidea. Redlichiids possess primitive morphological characters including numerous thoracic segments, spiny tips at the end of their thoracic segments, and **micropygy** – a small pygidium relative to body size made up of a small number of fused segments. The order Redlichiida is paraphyletic given the fact that it is very basal (thought to be the ancestor of multiple later trilobite groups) and linked together by primitive morphologies.

A) B)

Figure 14: *Olenellus sp.* specimens, A) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 86258 and B) University of Kansas Museum, Invertebrate Paleontology (KUMIP) 369418.

Order Phacopida (Fig. 15) – Early Ordovician to Late Devonian. Phacopoids are large bodied and extremely diverse in their morphology. Members of the Phacopida are united by traits they share early in development and also their distinctive, schizochroal eyes. Suborders include Calymenina, Phacopina, and Cheirurina. This order also includes the subfamily Asteropyginae shown below (Fig. 15A).

A)

B)

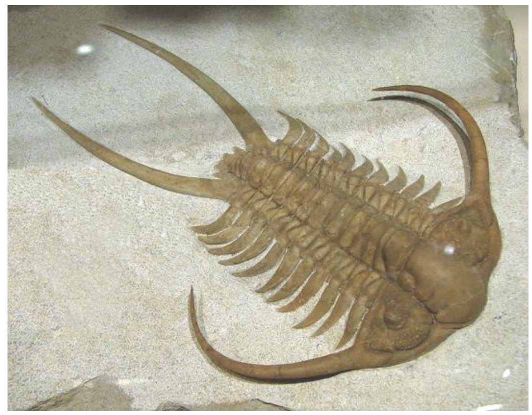


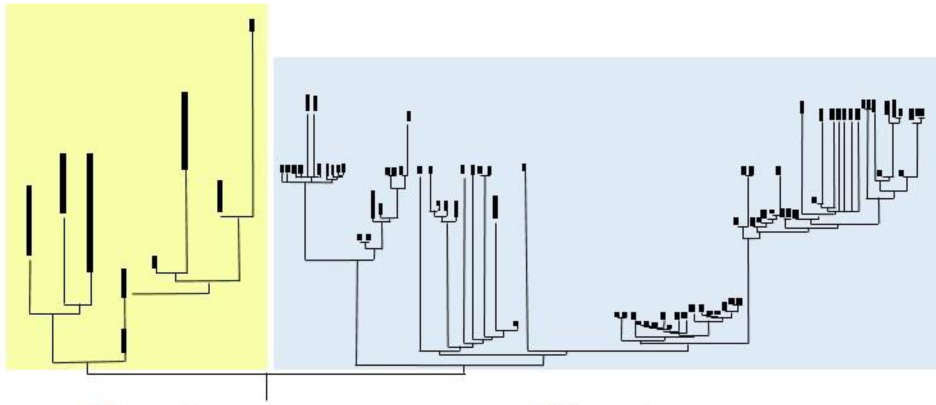
Figure 15 (previous page): A) *Walliserops n. sp*., by Moussa Direct Ltd. (Moussa Direct Ltd. image archive) [CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons. B) *Paraceraurus*, by Vassil (Alias Collections.) [GFDL (http://www.gnu.org/copyleft/fdl.html) or CC-BY-SA-3.0 (http://creativecommons.org/licenses/by-sa/3.0)], via Wikimedia Commons.

For more information about trilobite ecology, morphology, or the various orders of trilobites please visit Sam Gon's comprehensive website at http://www.trilobites.info/

Macroevolution of the Trilobites

Macroevolution is the study of the patterns and processes that affect the birth, death, and persistence of species. For instance, scientists who study macroevolution might wonder when and why new species arise or why some groups speciate rapidly while others give rise to new species very slowly. Ultimately, macroevolution is the study of evolution at the grand scale and this is an area studied by paleontologists, evolutionary biologists, and systematists. Examples of macroevolutionary patterns include: similar changes in trait evolution across multiple groups within a given lineage and pulses of evolution in response to climate change (Vrba 1996; Congreve 2013).

Figure 16 (next page): Two lineages (yellow and blue) within the same group that show very different patterns of diversity. The yellow lineage has few long lived species while the blue lineage has many more short lived species.



~ 10 species ~ 100 species

Questions of interest to scientists studying macroevolution might include:

1) Why are some groups of organisms (or clades) diverse while others have only a few species within them?
2) What are the dominant trends in the evolution of a particular group over time?
3) How are clades differentially affected by mass extinctions?

For example, the trilobites appear to be harder hit by mass extinctions than their contemporaries (Lieberman and Karim, 2010). In spite of their high levels of diversity, trilobites suffered major losses during the end Ordovician (Melott et al., 2004) and Late Devonian mass extinctions (McGhee, 1996). After the Late Devonian biodiversity crisis, trilobite diversity failed to fully recover (Brezinski, 1999) and the group was wiped out completely during the largest mass extinction of all time at the end of the Permian (Fortey and Owens, 1997).

Why do the trilobites thrive in normal background conditions yet remain more susceptible to mass extinctions than other types of organisms? To evaluate this question we need to consider the following:

Origination is the appearance of new species. Origination rate is measured as the number of new species appearances over a period of time.

Extinction is the permanent and global disappearance of a species. Extinction rate is measured as the number of species disappearances over a period of time.

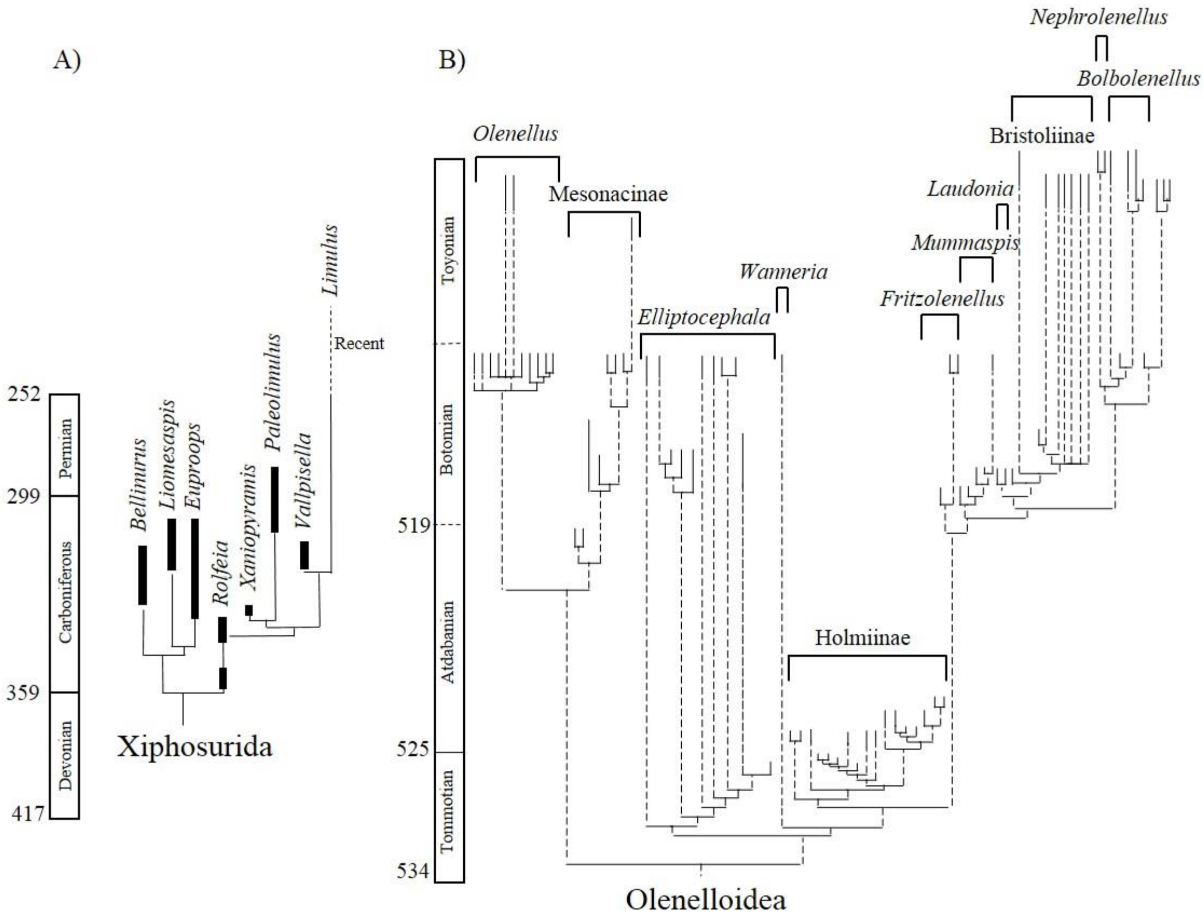
Originations and extinctions constantly occur throughout geologic history. The small and relatively consistent rate of extinction happening under normal conditions is known as **background extinction**. When the extinction rate spikes, resulting in a large number of species going extinct at the same time, these events are identified as **mass extinctions**. Under normal conditions, groups that show high rates of speciation over time (many originations) are likely to also have high rates of extinction (Eldredge, 1979; Stanley, 1979; Vrba, 1980). This correlation leads us to our next concept, volatility.

Volatility is a measure of a group's stability through time and is a function of background origination and extinction rates. High volatility clades have high rates of background extinction and origination, which can lead to the frequent turnover of species within the group. Low volatility groups have low rates of origination and extinction, leading to a stable clade made up of the same species over long periods of time. Volatility has been decreasing across all taxa throughout the Phanerozoic because high volatility groups have an increased probability of their diversity falling to zero, a value from which they can never recover (Lieberman and Melott, 2013). Lieberman and Melott (2013) describe this increased risk of clade-wide extinction as resulting in a "survival of the blandest" pattern as high volatility clades are weeded out over time while low volatility clades persist. The impacts of volatility seem to be particularly important during times of mass extinction, with high volatility clades, like ammonites and trilobites, suffering greater losses than their low-volatility contemporaries (Lieberman and Karim, 2010). Interestingly, the reason trilobites, and also ammonites are no longer with us today, is likely because they evolved rapidly. It was the same factors that made them evolve rapidly, however, that made them prone to extinction.

At this point it may be helpful to consider an analogy between the longevity of fossil groups and the performance of stock prices through time, provided by Lieberman and Melott (2013). In this analogy, stock market volatility is a measure of how a stock changes price relative to changes in the market as a whole. High volatility stocks are those that experience dramatic increases or decreases in price unpredicted by the greater market trend, while low volatility stocks are more likely to change their price congruently with the overall market trend. Research has shown that low volatility stocks yield the best returns for long-term investors; adjusting for inflation, an initial $1 investment in 1968 yields $10.28 in 2008 if invested in low volatility stocks and only $0.64 if invested in high volatility stocks (from Baker et al. 2011).

Examine the origination and extinction rates over time for the following groups.

Figure 17 (next page): Phylogenetic relationships plotted against geologic time on the y-axis. A) Xiphosurida (horseshoe crabs) modified after Anderson and Selden (1997), with permission from John Wiley and Sons, license 3326071282933. B) The trilobite family Olenelloidea from Lieberman (1999), copyright Yale University.



Which group has the highest rates of origination over time?

Which group has the highest rates of extinction over time?

Which group is the most stable (least volatile)? Does the most stable group also have the longest history?

Based on the above readings, which group do you expect to have survived the longest? Explain your choice.

Using the hypothetical trees on the following page (Fig. 18) as guides, draw a **high** volatility clade. You may include a brief description of your clade's attributes. Things to keep in mind: How diverse is a high volatility clade likely to be? Is the clade likely to be long lived? What can you say about species turnover in this group?

Using the hypothetical trees on the following page (Fig. 18) as guides, draw a **low** volatility clade. You may include a brief description of your clade's attributes. Things to keep in mind: How diverse is a low volatility clade likely to be? Is the clade likely to be long lived? What can you say about species turnover in this group?

Is it possible to build up high diversity in a low volatility clade? If so, how might it occur?

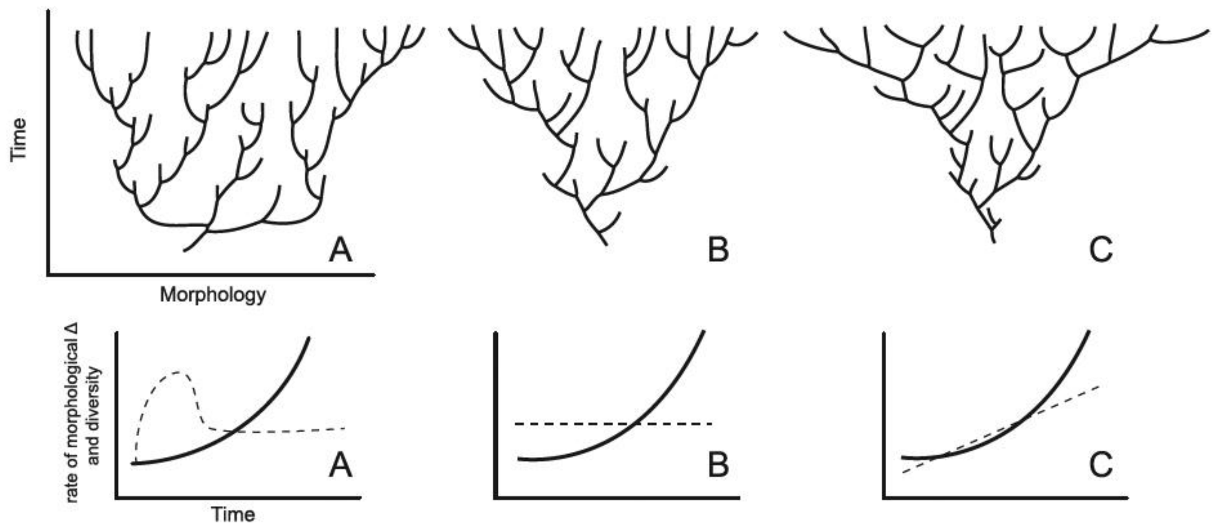


Figure 18: Schematic representations of lineage evolution with varied rates of morphological change and diversity increase. The bottom graphs show the relationship between time and rates of morphological change (the dashed line) and diversity increase (the solid line). The top row of graphs show the number of species (number of branches) present at any given time (along the y-axis) and the range of morphologies represented by those species (width along the x-axis). All three scenarios (A,B, and C) show increasing diversity over time. In case A, the rate of morphological change peaks early and then returns to an average rate (dashed line). This is reflected in the corresponding tree which has similar widths (range or morphologies present) at the bottom (early in the clade's history) and the top (late in the clade's history). Reproduced from Abe and Lieberman (2012), copyright The Paleontological Society.

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References

Abe, F.R and Lieberman, B.S. (2012). Quantifying morphological change during and evolutionary radiation of Devonian trilobites. *Paleobiology*, 38, 292-307.

Anderson, L.I. and Selden, P.A. (1997). Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia*, 30, 19-31.

Baker, M., Bradley, B. and Wurgler, J. (2011). Benchmarks as limits to arbitrage: understanding the low-volatility anomaly. *Financial Analysts Journal*, 67, 40–54.

Brezinski, D.K. (1999). The rise and fall of late Paleozoic trilobites of the United States. *Journal of Paleontology*, 73, 164–175.

Congreve, C. R. (2013). Cladal turnover: the end Ordovician as a large-scale analogue of species turnover. *Palaeontology*, 56, 1285-1296.

Eldredge, N. (1979). Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History*, 13, 7–19.

Fortey, R.A. and Owens, R.M. (1997). Evolutionary history. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, O (Arthropoda 1, Trilobita, Revised). Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. 249–287.

Gon, S.M., III. (2014). A guide to the orders of trilobites. http://www.trilobites.info/

Lieberman, B.S. (1999). Systematic Revision of the Olenelloidea (Trilobita, Cambrian). *Bulletin of the Peabody Museum of Natural History*, 45, 1-150.

Lieberman, B.S. and Karim, T.S. (2010). Tracing the trilobite tree from the root to the tips: A model marriage of fossils and phylogeny. *Arthropod Structure and Development*, 39, 111-123.

Lieberman, B.S. and Melott, A.L. (2013). Declining volatility, a general property of disparate systems: From fossils, to stocks, to the stars. *Palaeontology*, 56, 1297-1304.

Melott, A.L., Lieberman, B.S., Laird, C.M., Martin, L.D., Medvedev, M.V., Thomas, B.C., Cannizo, J.K., Gehrels, N. and Jackman, C.H. (2004). Did a gamma-ray burst initiate the late Ordovician mass extinction? *International Journal of Astrobiology*, 3, 55–61.

On the Cutting Edge - Professional Development for Geoscience Faculty (2013). Teaching Paleontology in the 21st Century. http://serc.carleton.edu/NAGTWorkshops/paleo/index.html#coursedesign. Accessed 18 December 2013.

Padian, K. (2008). Trickle-down evolution: an approach to getting major evolutionary adaptive changes into textbooks and curricula. *Integrative and Comparative Biology*, *48*(2), 175-188.

Padian, K. (2010). How to Win the Evolution War: Teach Macroevolution! *Evolution: Education and Outreach*, *3*(2), 206-214.

Stanley, S.M. (1979). *Macroevolution*. W.H. Freeman, San Francisco.
Vrba, E.S. (1980). Evolution, species, and fossils: how does life evolve? S*outh African Journal of Science*, 76, 61–84.
Vrba, E.S. (1995). The fossil record of African Antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C. and Burckle, L.H. (Eds.), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven, CT, pp. 385–424.
Weissert, W. (2013). Evolution debate again engulfs Texas Board of Ed. AP. http://bigstory.ap.org/article/evolution-debate-again-engulfs-texas-board-ed. Accessed 10 January 2013.