

The Paleontograph

A newsletter for those interested in all aspects of Paleontology
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From Your Editor

Well, we made through another year. We are all older and wiser. It was a wild year in America with lots happening. I'll just leave it at that.

Hopefully, you read Bob's note in our last issue. We've decided to make a couple more issues and come to an end. I'm not sure how many back logged articles I have but I will have a better idea after this issue. Time will tell.

I hope you all have a safe, healthy and happy New Year! If any of you go to Tucson, I'll be at the Days Inn on the highway, around back in room 140 stop in and say hello.



The Paleontograph was created in 2012 to continue what was originally the newsletter of The New Jersey Paleontological Society. The Paleontograph publishes articles, book reviews, personal accounts, and anything else that relates to Paleontology and fossils. Feel free to submit both technical and non-technical work. We try to appeal to a wide range of people interested in fossils. Articles about localities, specific types of fossils, fossil preparation, shows or events, museum displays, field trips, websites are all welcome.

This newsletter is meant to be one, by and for the readers. Issues will come out when there is enough content to fill an issue. I encourage all to submit contributions. It will be interesting, informative and fun to read. It can become whatever the readers and contributors want it to be, so it will be a work in progress. TC, January 2012

Edited by Tom Caggiano and distributed at no charge

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The Rise and Reign of the Mammals—A Review

Bob Sheridan July 28, 2022

Popular books on prehistoric mammals are becoming more common, whereas once they were very rare compared to books on dinosaurs. Today's review is for "The Rise and Reign of the Mammals" (TRAROTM) by Steve Brusatte. Brusatte is an American paleontologist at the University of Edinburgh. He has written a number of popular articles and books, in particular "The Rise and Fall of the Dinosaurs," which I reviewed for the Paleontograph in 2018. (Brusatte switched his academic attention from dinosaurs to mammals fairly recently.)

Mammals have a number of unique features compared to other amniotes:

1. Single skull opening behind the eye (the synapsid condition).
2. Teeth of different types. The back teeth can occlude and there are only two sets of teeth per lifetime. Mammals are especially known for their specialized molars.
3. Mandible made of a single bone. Three other bones that were part of the reptilian jaw joint ended up tiny and in the middle ear.
4. Large brains.
5. Warm-blooded. The presence of hair.
6. Give live birth (except for a few egg-layers, the monotremes).
7. Feed their young on milk.

Because mammals are now the dominant animal group (and we are one of them), they are too familiar and almost boring, but if they were extinct, according to the author, they would be regarded as wondrous, akin to how we feel about dinosaurs, especially since the largest animals ever (i.e. the whales) are mammals.

Of course, not all the characteristics listed above evolved at once. Synapsids with multiple tooth types appeared as early as the Pennsylvanian. There was a long period of synapsids dominating animal flora, and reaching large sizes and extreme diversity, until the Late Permian. These animals would have looked very reptile-like to our eyes (hence the old name "mammal-like reptile"); it was not recognized until a few decades ago that these were mammal ancestors. The first true mammals (with most above characteristics, or at least the ones that fossilize) appeared in the Triassic about the same time as the origin of the dinosaurs. There is evidence for hair at that time, or at least whiskers. Although there was a

fairly good diversity of mammals in the Mesozoic (with analogs of beaver, mole, flying squirrel, etc.), it is after the dinosaurs died that mammals dominated as land animals. Big brains are a recent characteristic (somewhere in the Eocene). Some of the most extreme mammals (e.g. the whales) originated very recently (Miocene).

Now, to talk about this book in particular. Popular works in paleontology seem to be a mixture of the following:

1. Personal experiences of the author in the field.
2. Discussion of the history of thought on the specific topic.
3. In depth discussion of specific specimens.
4. Summary of current findings.
5. Conversations with contemporary paleontologists.
6. (Speculative) stories describing the experiences of an individual animal. (What I call the "you are there" style.)

Sometimes the particular mixture the author takes can be entertaining and informative to us amateur paleofans, sometimes not. For example, I think Thomas Halliday's "Otherands" went too far in the direction of "you are there," whereas I usually prefer a more fact-based or historical approach. TRAROTM has a little bit of everything, and that worked for me. Another feature of books on popular paleontology is that they can aim to be a comprehensive treatise on the subject without exhaustive detail (like Donald Prothero's "Princeton Field Guide to Prehistoric Mammals") or a be compendium of "special topics" (like Elsa Panciroli's "Beasts Before Us"), each of which is covered in depth.

TRAROTM covers many topics (ranging from the origin of synapsids to the putative "sixth extinction" of the present day), so there is some approximation of being comprehensive, but does go into depth for many topics. He does this in a very clear manner. For example, in the past, I would find discussions of mammal molar types (docodont, triconodont, symmetrodont, multituberculate, tribosphenic, etc.) bewildering. Now I have a pretty good idea what these are, and what the tooth shapes imply about diet, how the jaw moved, and relatedness among mammal groups. (BTW most living placental mammals, including humans, are tribosphenic).

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Mammals Cont'd

One unfortunate effect of following paleontology as a hobby by reading the primary sources is that popular books seem to contain only "old news." That is not the case here. TRAROTM is very current. For instance, it covers the work (published in April 2022) where relative size of the brains of placental mammals is seen to shrink somewhere between the Paleocene and Eocene.

Illustrations in this book are life restorations of animals in pencil sketch format (mostly by Todd Marshal, a professional paleoartist) and black-and-white scientific diagrams (mostly by Sarah Shelley, a former PhD student of Brusatte). There are also black and white photographs of fossil specimens. I wouldn't say this was a densely illustrated book, but there always was an illustration when needed.

I can give this book a very high recommendation.

Sources:

Brusatte, S.

"The Rise and Reign of the Mammals. A New History, from the Shadow of the Dinosaurs to Us."
HarperCollins Publishers Inc. NY 528 pages \$25 (hardcover).

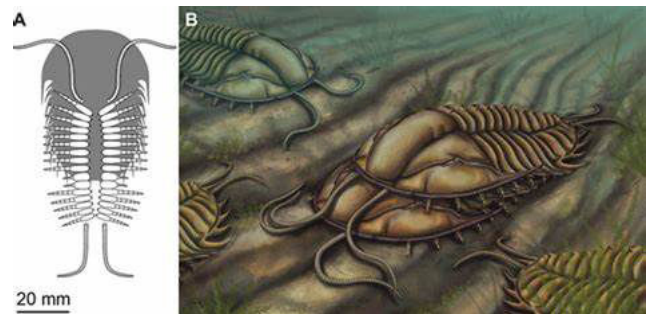
Trilobite Claspers?

Bob Sheridan June 8, 2022

Claspers are male anatomical structures that are used for mating. They can act as hooks to hold the female in the correct position, and they can have an additional function of transferring sperm. Claspers are found in vertebrates and invertebrates. In the case of arthropods, which have many pairs of legs, some of the legs may be modified into claspers. Typically these are smaller than walking legs and have some kind of grasping appendage.

Losso et al. (2020) describe a specimen (ROMIP 66299) of the trilobite *Olenoides serratus* from the Burgess Shale (Early Cambrian). *Olenoides* is typically a few inches long. There are hundreds of known specimens, and the authors selected 13 for study. The special aspect of ROMIP 66299 is that

some legs on the right side of the animal (probably pair 7-16) are visible, and pairs 10 and 11 are different from the rest. The terminal appendages on these pairs are much smaller than normal. Since they occur about two-thirds of the way toward the back of the animal they are unlikely to be for feeding, and the authors assign them as claspers. Analogy is made with horseshoe crabs, presumably the closest living relatives to trilobites, which have claspers on the front pair of legs, and lobsters which have claspers on their abdomen.



Legs are not often visible in trilobite specimens, so having ROMIP 66299 is important. However, I have my doubts about the "clasper hypothesis". Remember, we only see one of each pair of legs in this specimen. One could be more confident if both the left and right side showed reduced legs. Also, the authors admit that this specimen is the only one out of the 13 they studied that showed the reduced legs. That would imply all 12 of the other specimens to be female, which seems unlikely. Also, if horseshoe crab claspers were in the front, wouldn't we expect that in trilobites also. It is hard to eliminate an alternative hypothesis, such as: this specimen lost its legs accidentally and we are seeing the stumps grow back. Only more trilobite specimens with reduced legs in the same or analogous positions will be convincing.

Sources:

Losso, S.R.; Ortega-Hernandez, J.

"Claspers in mid-Cambrian *Olenoides serratus* indicate horseshoe crab-like mating in trilobites."
Geology 2022, 50, 897-901.

Did Dinosaurs Survive the End-Triassic Extinction Because they Were Cold-Adapted?

Bob Sheridan August 8, 2022

The dinosaurs originated in the Late Triassic. There was a mass extinction (one of the “Big Five”) 202 Myr. ago called the End Triassic Extinction (ETE) that eliminated a large fraction of land- and water-based animals. However, the dinosaurs did not seem particularly reduced, and became the dominant land animal thereafter. The cause for the extinction is not clear, although it appears that it might have been a time of increased vulcanism. There is much uncertainty about the duration of the extinction; it may have been the concatenation of several separate events.

Olsen et al. (2022) propose a mechanism by which the dinosaurs could have escaped extinction at the ETE. The key is the discovery of “ice-rafted debris” in marine deposits from the Late Triassic to the earliest Jurassic in the Junggar Basin, which is now northeastern China. (The Junggar Basin has deposits that span from the Carboniferous to the Quaternary.) Ice-rafted debris consists of gravel that is transported from land on glaciers and that is deposited in sea sediments when the ice melts. The size distribution of the gravel from the Junggar Basin is comparable to debris from known Ice Age glaciers. The paleolatitude at the time was ~71N, i.e. well within the arctic circle. The implication is that there was at least some freezing at the poles at the end of the Triassic.

Here is the overall reasoning:

1. The end-Triassic was cold enough to have ice at the poles (from the above observation).
2. There are fossils (including footprints) of dinosaurs at higher paleolatitudes at the end of the Triassic, whereas fossils of other types of reptiles are closer to the equator.
3. The reason dinosaurs were near the poles was because they were adapted to cold.
4. It appears that all types of later dinosaurs might be feathered. If being feathered is a primitive trait for dinosaurs, Triassic dinosaurs probably had them.
5. The dinosaurs survived a “volcanic winter” at the ETE because they were insulated with feathers. The same thing could be said for mammals and their fur.

This is a reasonable speculation that has some weak spots. The biggest issue is that the End-Triassic had a very high level of carbon dioxide, which would normally cause warming. The authors have to argue that the volcanic eruptions at the end of the Triassic caused cooling because they emitted sulfur aerosols (which reflect sunlight), and this more than compensated for the carbon dioxide. This is not implausible; we have observed “volcanic winters”, even in historic times. There is some evidence from plant fossils and ocean isotope ratios that the ETE was a cooling rather than a warming event. However, many paleontologists feel there is equally good evidence for warming. (Or there could have been both cooling and warming at different times—currently we cannot be sure.) Another difficulty is that the earliest evidence we have for feathered Dinosaurs is in the Late Jurassic, so while we might infer feathered dinosaurs in the Triassic, it cannot be confirmed that the feathers were good enough to provide insulation.

The authors point out that our prejudice for dinosaurs is that they are associated with warmer climates, and that they are arguing the opposite, at least for the ETE. That is an interesting point. Some of this prejudice could be our association of modern reptiles with warmer climates. Also we do know the later, larger dinosaurs (Jurassic and Cretaceous) lived at times that are much warmer than today. Sources:

Olsen, P.; Sha, J.; Fang, Y.; Chang, C.; Whiteside, J.H.; Kinney, S.; Sues, H.-D.; Kent, D.; Schaller, M.; Vajda, V.

“Arctic ice and the ecological rise of the dinosaurs.” *Science Advances* 2022, 8, eabo6342.

The Amazing Shrinking Brain (Relatively Speaking) of Paleocene Mammals

Bob Sheridan August 10, 2022

Among crown mammals, brain volume (or weight) depends on body size, and a straight line can be drawn through most mammals on a plot of log(brain weight) vs. log(body weight) plot. This relationship is allometric, i.e., as body weight increases the brain weight increases, but not as fast, i.e., the slope of such lines is less than 1.0.

A metric EQ (encephalization quotient) can be calculated as the ratio of the weight observed for a species and the weight expected for an average mammal of that weight (the average mammal would fall exactly on the line). Some mammals have large EQ's: for example apes (with humans being the most exceptional at ~7), cetaceans, and elephants. Opossums are on the less brainy side (EQ~0.2). It is generally assumed that EQ corresponds to cognitive ability.

Modern mammals have very large brains per size compared to modern reptiles, but that has not always been the case. It is generally assumed that the earliest mammals started off with relatively small brains like their synapsid ancestors, and brain size rose steadily after the end of the Mesozoic. Bertrand et al. (2022) study body size, brain size, and the ratios for a 138 mammals and mammaliamorphs from the Triassic to the Eocene. For this study to be done, CT-scans needed to be taken for uncrushed mammals skulls, which is rare at some time periods. Since the CT-scans generate the volume of brains instead of weights, volume is used in this analysis; weight is proportional to volume since brains have constant density. These authors use PEQ as a metric of encephalization. PEQ is EQ that is "phylogenetically adjusted". That is not well explained, but for the purposes of this paper, it means dividing the mammals into four groups (mesozoic, paleocene, eocene stem, and eocene crown—the last contain modern mammals) and having a separate line in the log (brain volume) vs. log(body weight) for each. Information can be gotten from the intercepts and slopes of the lines. The same information can be gotten by looking at box plots of the log(body weight) and log(brain volume) of the same groups. In addition to treating animals in groups, the authors also look at these parameters as a function of time divided into 10 Myr. intervals.

In terms of groups: Mesozoic mammals are small (e.g., median 100 grams) while the other mammal groups are larger and about the same (median 6300 grams). For comparison, a rat is a few hundred grams, and a cat can be as heavy as 6000 grams. Mesozoic mammals have small brains in absolute size (median 0.6 cubic centimeter), and the brains get larger in the order paleocene, eocene stem, and eocene crown. In eocene the eocene crown group the median 18 cubic centimeters. Of course these are just medians, half the mammals are bigger and half are smaller, and some can be very large. If we look at the PEQ, paleocene mammals are slightly less brainy than mesozoic mammals on the average. This is also reflected in the slopes of the lines for the

groups. The paleocene group shows less growth of brains relative to the body than the crown eocene group.

In terms of time: Mean body weight starts small at 190 Myr (~10 grams), reaches a peak at 130 Myr. (~600 grams), falls again at 80 Myr. (~30 grams), and after 66 Myr. reaches 10,000 grams and plateaus there. This is an expected trend. We know the first mammals were very small, and we know only small mammals survived the K-P extinction and grew in size once the dinosaurs were gone. The brain volume goes through a similar trend with time. However, the timing of the body weight trend and the brain volume trend are not completely in synch and this is reflected in the PEQ. At 190 Myr. PEQ~0.1, plateaus at ~0.18 for the rest of the Mesozoic, then falls to 0.10 at 60 Myr., and rises again, and hits a maximum of 0.4 at 40 Myr. Basically this means that Paleocene mammals had smaller brains per body size than Mesozoic mammals, consistent with the "group view" in the previous paragraph.

These results are generally not consistent with the traditional idea that mammals have been steadily getting brainier over time. The authors speculate that after the death of the dinosaurs, in the Paleocene bodies grew to fill a number of vacant ecological niches, but braininess was not required until much later when the niches were full and mammals had to compete against each other.

Specific parts of the brain can be discerned in the CT-scans. These authors note that the ratio of volume of the olfactory lobe relative to the total volume of the brain is steady until the K-P extinction, after which it falls off. On the other hand, the ratio of the cerebrum to the total volume of the brain rises steadily after the K-P extinction. This might imply less of a dependence on smell and more on advanced cognition.

Sources:

Bertrand, O.C.; Shelley, S.L.; Williamson, T.E.; Wible, J.R.; Chester, S.G.B.; Flynn, J.J.; Holbrook, L.T.; Lyson, T.R.; Meng, J.; Miller, I.M.; Püschel, H.P.; Smith, T.; Spaulding, M.; Tseng, Z.J.; Stephen L. Brusatte, "Brain before brains in placental mammals after the end-Cretaceous extinction." *Science* 2022, 376, 80-85.

Smith, F.A.
"The road to a larger brain."
Science 2022, 376, 27-28.

Injuries in Dickinsonia

Bob Sheridan August 15, 2022

Ediacaran fauna (named for the Ediacara Hills in Australia where they were first identified) are a group of Precambrian fossil organisms that lived world-wide 600-545 Myr. Most of the fossils are only sediment-filled impressions in sandstone, and preserve no hard parts. Most appear to have very simple symmetrical structures, resembling “fronds”, “air-mattresses”, “spirals”, etc. A few have more complex structures, but these appear fractal in nature, i.e. tubular branches coming off larger branches, which come from even larger branches. Linking the Ediacaran fauna to any type of later organism by anatomy has been very difficult so far. There have been a number of suggestions as to their identity: early forms of animals seen later in the Cambrian, a form of animal life no longer living, giant protozoa, lichens, algal mats, etc.. Of course, the Ediacaran fauna are diverse in form, and all of those identities could be true for some subset of the fossils.

Today's story concerns a specific type of Ediacaran fossil Dickinsonia. This was named by Reg Sprigg, discoverer of the Ediacaran formations, after his employer Ben Dickinson, Director of Mines in South Australia. There are many species of Dickinsonia, and fossils are found in Asia, Eastern Europe, and Australia. Dickinsonia is a flat bilaterally symmetric oval or egg-shape (up to 1.4 meters long) impression with a large number of “ribs” extending from its periphery to a line along its long axis. At one end of the oval is a place with wider spacing of the ribs. This is called the “deltoid.” The opposite side of the oval is called the “antideltoid.” One segment containing a “rib” is often called a “unit” or “module,” and there are 11-58 units on each side in a given individual.

There is nothing around like Dickinsonia today, it has been variously interpreted (as with any Ediacaran species) as a segmented worm, a sponge, a jellyfish, lichen, bacterial mats, etc.. It is not even clear that Dickinsonia lived in water and/or could move. For example, some interpret Dickinsonia as a sessile organism (like a sea pen) and the deltoid as a “holdfast” rather than a “head.” It is not even clear that what we call “Dickinsonia” is the entire organism, and not just a piece of something larger.

Recently, the interpretation of Dickinsonia has tilted toward some kind of primitive “bilateran,” which is

usually interpreted as a multi-cellular “animal.” In 2017 Hoekzema et al. noted that the number of units and the length of the oval are proportional over a set of specimens, suggesting Dickinsonia grows by adding units. The more units a specimen has, the smaller the deltoid region, which could suggest units are being generated at the deltoid end until the deltoid end is “used up.” To the authors, the growth pattern suggests they are early animals, perhaps like modern placozoans or cnidarians.

Bobrovskiy et al. (2018) attempted to measure steranes (degraded products of cholesterol-like molecules) in Dickinsonia fossils. The type of sterane in the fossils seemed more consistent with those of animals and less with algae or fungus (and therefore less with lichen).

Most recently Retallack (2022) reinterpreted a few specimens of Dickinsonia described by the same authors a few years earlier (Ivantsov et al., 2020) where there was some kind of apparent damage to the living organism that was being repaired. The thought is that the appearance of the regrowth would offer clues about what kind of organism Dickinsonia was. Most of the regrowth is confined to the anti-deltoid end. In a few specimens, that end seems to be partitioned off from the rest of the units and/or doubled, giving the appearance of two “tails.” These authors compare a number of types of current organisms, the types of injuries they suffer, and what the regrowth looks like. They conclude that the regrowth in Dickinsonia more closely resembles that of fungi (including lichens) or plants. This is in contradiction to the previous “animal” interpretations.

Any interpretation of Ediacaran biota depends on analogies with present day fauna and flora, but it is very hard to tell whether these analogies hold up, or that the assumptions behind them are valid.

Sources:

Bobrovskiy, I.; Hope, J.M.; Ivantsov, A.; Nettersheim, B.J.; Hallmann, C.; Brocks, J.J.
“Ancient steroids establish the Ediacaran fossil Dickinsonia as one of the earliest animals.”
Science 2018, 361, 1246-1249.

Hoekzema, R.S.; Brasier M.D.; Dunn, F. S. and Liu, A.G. 2017
“Quantitative study of developmental biology confirms Dickinsonia as a metazoan.”
Proc. R. Soc. B. 2017 **284**: 20171348.
Ivantsov A.; Zakrevskaya M.; Nagovitsyn, A.; Krasnova, A.; Bobrovskiy, I.; Luzhnaya, E.; (2020)

"Intravital damage to the body of *Dickinsonia* (Metazoa of the late Ediacaran)." Journal of Paleontology 94: 1019–1034. Retallack, G.J.

"Damaged *Dickinsonia* specimens provide clues to Ediacaran vendobiont biology."

PLoS ONE 2022, 17:e0269638.

Archosaur Orbits

Bob Sheridan August 17, 2022

"Orbit" is the name given to the opening of the skull containing eyeball. If nothing else were known, one might expect that the orbit would be circular, just fitting the outside of eyeball. However, in many fossil skulls, there is a deviation from circular. In the most extreme examples, for example in *Tyrannosaurus*, the orbit can be a tall "keyhole" shape (a very tall oval shape pinched in the middle), with the eye occupying the upper opening. Is there an explanation for the variety of orbit shapes?

Lautenschlager (2022) does a morphological analysis of 404 orbits of Mesozoic archosaurs: dinosaurs, pterosaurs, crocodylians, dinosauromorphs (archosaurs ancestral to dinosaurs), archosauromorphs (reptiles that are diapsids, but not quite archosaurs), and pseudosuchians (diverse archosaurs, which are closer to crocodylians than birds, but not actually crocodylians). The universe of orbit shapes is projected into two dimensions by principal components analysis. The first dimension (PC1) is basically "constriction along the long axis of the skull" vs. "compression perpendicular to the axis of the skull". The second dimension (PC2) is "compression along the axis of the skull." In this plot, most orbits are circular and this is represented by a large cluster of points in the center. Dinosaurs are the most variable group with many orbits extending left on PC1, i.e., toward extreme "keyhole" shapes. However, pterosaurs, and archosauromorphs also show some big departures from circular. That is, the "vertical oval" or "keyhole" shape has appeared independently several times among archosaurs.

There are two additional levels of complication. First, the groups may expand or contract the diversity in orbit shapes with time. For example, the pseudosuchia and archosauromorphs are more diverse in the Early Triassic than the Late Triassic

(and they are basically extinct after that). Dinosaurs have low diversity in the Triassic but reach maximum diversity in the Late Cretaceous. Pterosaurs reach peak diversity in the Early Cretaceous. Second, orbital shapes can change with ontogeny. For example, juvenile *tyrannosaurs* have round orbits, but mature *tyrannosaurs* have keyhole orbits. A similar phenomenon is seen with *Proterosuchus*, an archosauromorph.

What is the explanation for the orbit shape? The fact that similar extreme orbits appeared convergently among several groups of archosaurs suggests an adaptive explanation. A large clue is that the most extreme keyhole examples are for large animals (skull over a meter long) who are also carnivores. The converse is not true; some large carnivores have round orbits. The authors test the idea that bite stresses are important using finite element analysis. This computational technique is borrowed from mechanical engineering and is meant to determine areas of stress in structures like bridges. The authors examined virtual *Tyrannosaurus* skulls with different orbit shapes and monitored the forces on the skull when forces are applied to the teeth. They feel that the keyhole or "tall oval" orbital shape dissipates forces from the upper teeth and causes less distortion to the top of the skull, including the orbit itself. I wouldn't say the differences in stresses between orbit shapes is very large, but I wouldn't necessarily expect it to be. Remember in all archosaurs, the teeth are all in front of the orbit, so forces on the teeth would not transmit directly through the orbit, but only via the snout.

I am not yet convinced of the "bite force" explanation, since finite element analysis was tested only on a virtual *Tyrannosaurus* skull. Granted that *Tyrannosaurus* is an "extreme orbit" case, but to be convincing, the same analysis would need to be done on a variety of skulls of various sizes and orbit shapes. Also it is not clear why some large carnivores, with presumably strong jaws, get by with a round orbit, and it is also not clear why smaller carnivores would not need to protect their skulls from bite stresses.

Sources:

Lautenschlager, S.

"Functional and ecomorphological evolution of orbit shape in mesozoic archosaurs is driven by body size and diet."

Communications Biology 2022, 5:754.

The Pitfalls of “Speciation” as Applied to *Tyrannosaurus rex*

Bob Sheridan August 19, 2022

How do we know individual specimens are of the same species. For extant organisms, the primary definition of species has to do with whether individuals can breed and generate fertile offspring. A secondary definition depends on comparing the two specimens on a number of characteristics and seeing whether they are sufficiently similar to each other and sufficiently different from other known species. For extinct organisms, only the secondary definition is possible, and the characteristics are limited to the shape and size of bones (or other hard parts), and not color, biochemistry, etc.. Even if two specimens differ somewhat, they still could be the same species, but represent different sexes, different ages, different geographical varieties, or just show individual variation? In paleontographic practice, determination of species has been mostly subjective and handled at the discretion of the discoverer. There have always been “lumpers,” who see fewer species (or genera), and “splitters,” who see more species (or genera). For example, in recent years there is some discussion whether the genera *Torosaurus* and *Triceratops* represent different ages of the same animal, or whether “*Brontosaurus*” is distinct from *Apatosaurus*.

There are statistical approaches to help determine whether two specimens are the same species, but it is necessary to know, for instance, what the variation among individuals of the same species looks like, whether characteristics fall into a bimodal distribution, or how characteristics vary with time. This in turn requires us to have enough (and complete enough) specimens. Most dinosaurs (or any large vertebrate) species fall into the “not enough specimens” category. However, there are enough specimens of *Tyrannosaurus* (>40), the most popular dinosaur, to make statistical analysis possible.

Any paper about *Tyrannosaurus* will get the attention of the popular press, no matter how esoteric the study. In March, Paul et al. (2022) suggested that a dozen or so *Tyrannosaurus rex* specimens from the Hell Creek Formation actually represent three species: *T. imperator* (robust, 2 incisors), *T. rex* (robust, 1 incisor), and *T. regina* (gracile, 1 incisor). The first lived earlier, and the last two lived to the end of the Cretaceous. That paper is behind a paywall, so I was not able to read it. However, I gather that the distinctions are based on

the robustness of the femur (e.g. circumference vs. length) and the number of small teeth in the front of the lower jaw (incisors). Two bits of background help to put this into historical context:

1. In the 1990’s a suggestion was made that robustness of the femur was an indication of sexual dimorphism, with the robust form being “female.” Here the suggestion is that “robust” is a different species rather than a different sex.
2. There are still arguments whether *Tyrannosaurs* (North America) and *Tarbosaurus* (Asia) are different genera, different species, or just a geographical variation of the same species. Paul et al. make even finer distinctions about a geographically local set of specimens.

You always expect pushback on claims like this, and Carr et al. (2022) make the case that the evidence is not adequate to disprove the simpler idea that there is only one species *T. rex*. Their criticisms are the following:

1. One should not consider only two characteristics of *Tyrannosaurus*, but all available characteristics.
2. Paul et al. used *Allosaurus* from Cleveland-Lloyd Quarry for determining how variable the robustness of the femur can be among individuals of the same species. Those individuals are probably too homogeneous. Other standards show much more variability.
3. The “incisor tooth” is defined by its diameter relative to that of nearby teeth. The criterion for making the distinction of “incisor” from other teeth is not clear, and teeth are lost during growth, so that probably cannot be used to distinguish species.
4. The clustering method Paul et al. used for grouping the specimens is subject to artifacts, i.e. seeing groupings that are not there.
5. There are other very good *Tyrannosaurus* specimens that do not fall into any of the three proposed groups.
6. Some of the specimens used by Paul et al. are in private hands and should not be included because they are not guaranteed to be available for examination.

When Carr et al. reconsider the robustness of *Tyrannosaurus* femurs using more specimens, they find the variation among specimens is not larger than among individuals of the some extant bird species or some other theropods species.

Cont’d

In clustering femurs, they find that statistically there is only one cluster and not two or more, i.e., the distribution of robustness is a continuum rather than bimodal. Similarly with incisors. Carr et al. seem focused on refuting the specific claims of Paul et al. on femur robustness and incisor teeth. It would have been informative to cluster known *Tyrannosaurus* specimens using all more characteristics to see if the specimens naturally fall into groups.

This is just another example of common arguments in paleontology (or actually pretty much any science). One party says "Here is an interesting observation, which has the following taxonomic/lifestyle consequence." Another party asks "Is it beyond a reasonable doubt that the observation cannot be explained by a simpler hypothesis?"

Sources:

Carr, T.D.; Napoli, J.G.; Brusatte, S.L.; Holtz, T.R.Jr.; Hone, D.W.E.; Williamson, T.E.; Zanno, L.E. "Insufficient Evidence for Multiple Species of *Tyrannosaurus* in the Latest Cretaceous of North America: A Comment on The Tyrant Lizard King, Queen and Emperor: Multiple Lines of Morphological and Stratigraphic Evidence Support Subtle Evolution and Probable Speciation Within the North American Genus *Tyrannosaurus*"

Evolutionary Biology 2022, 49, 327-341.

Paul, G. S., Persons, W. S., & Van Raalte, J. (2022). "The tyrant lizard king, queen, and emperor: Multiple lines of morphological and stratigraphic evidence support subtle evolution and probable speciation within the North American genus *Tyrannosaurus*." *Evolutionary Biology* 2022, 49, 156-179.

We Suspected Megalodon Was a Badass—Now We Have Good Evidence

Bob Sheridan August 21, 2022

Megalodon (of which there may be up to four species) is the name we give to the giant shark that lived 23-3.5 Myr. ago. Knowledge of Megalodon is almost entirely based on isolated teeth, which are large (up to 6 inches long), triangular, and serrated. Since sharks have mostly cartilaginous skeletons, denticles, teeth, and jaws are the only preserved

parts in most shark fossils. On the other hand, since sharks shed teeth continuously, any individual may leave thousands of fossil teeth. Megalodon teeth are found along the coasts of North and South America, Africa, Asia, and Australia in what would be tropical or temperate regions. The genus name applied to Megalodon has changed with the years. Originally it was *Charcharodon*, then others suggested it should be *Carcharocles*, but today the preferred genus is *Otodus*. These changes are due to our shifting idea about how living sharks are related, and which living shark Megalodon is likely related to.

Estimates of the length of Megalodon (anywhere from 40-70 feet) can be made by a number of methods, mostly based on the teeth. One method is based on scaling up a great white shark so the great white's largest teeth (which have roughly the same shape) would be the same size as Megalodon's. There is a great deal of uncertainty in this kind of estimate. Teeth length and shark body length are not necessarily linearly related between species, any individual shark will have teeth of different sizes, adult sharks may vary in length, the great white may not a good analog for Megalodon in terms of shape, etc.

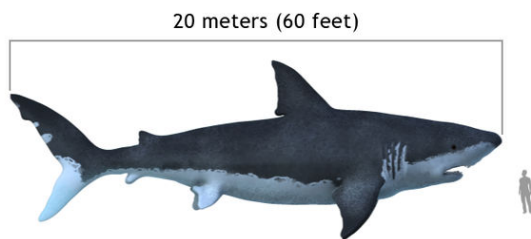
Fortunately, we occasionally find ossified shark parts as fossils. An exceptional set of ~140 disconnected partially ossified fossil vertebrae was discovered in Belgium in the 19th Century. These have the appearance of disks about 9 inches in diameter but with varying thickness. These were more thoroughly studied in 2021 by Shimada et al.. One can distinguish growth rings by CT-scanning, giving the specimen an age of ~46 years and an estimated length of ~30 feet. It must be a Megalodon since nothing else is as large. They estimate that if it had lived, this specimen could have attained an age of up to 100 and a length of 50 feet.

Cooper et al. (2022) attempt a virtual 3D model of Megalodon by scaling up a CT-scan of a great white shark so that its vertebrae would best match the fossils discussed above, and then replacing the great white jaws with Megalodon jaws. It is admitted that great whites and Megalodons may not be related, but the great white is probably the best living analog, and the one for which there is already CT-scanned data. This model incorporates assumptions, but is based on more data points (i.e., using multiple vertebrae) than would using only a few teeth.

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Given a 3D model, a number of estimates can be made. The total length of the model is around 50 feet (as opposed to the estimate of ~30 feet in the previous paragraph). The weight would be close to 28 tons. The cruising speed would be 3 miles per hour, extrapolated from the speed of living sharks as a function of size. This is faster in absolute speed than any living shark, and would mean that Megalodon could travel great distances. (However it is a middling speed in units of body lengths.) The stomach volume would be enough to accommodate an entire killer whale, and Megalodon could swallow a killer whale in 5 bites, given its gape. Given the energy requirements of living sharks, such a meal should be good for a few months.



We already know that Megalodon were “macropredators” that attacked big prey like whales, because there are tooth marks and even embedded teeth in whale skeletons from the same time period. Another term to be aware of is “trophic level,” i.e. an organism with a high trophic level is “at the top of the food chain” or an “apex predator.” There is a technique to estimate trophic level in living animals, by measuring the abundance of a rare isotope of nitrogen N-15 relative to the most common isotope N-14. Apparently, as protein is metabolized, N-14 is eliminated faster than N-15, and so animals that eat other animals accumulate more N-15. So the more N-15, the higher in the food chain the animal is. This technique can be used in fossil organisms as long as enough protein is preserved in bones or teeth (the protein usually collagen because that is the most stable). Kast et al. (2022) study the presence of N-15 in teeth. They consider two sources of nitrogen: 1. collagen in dentin 2. organic material in enameloid part of the tooth. The N-15 in enameloid seems to be proportional to N-15 in dentin for living sand sharks, indicating that enameloid measurements could substitute for dentin measurements. They also measured enameloid N-15 in shark teeth from the Late Cretaceous to the present. It is assumed the sharks with narrow teeth

(“piscivorous”—or fish-eating) are lower in the food chain that sharks like Megalodon with triangular teeth (“macropredators”). As expected the N-15 in later Megalodons is fairly constant over time from the Eocene to the Pliocene, constant among all locations (North America, Japan, etc.), greater than for the piscivorous sharks, and greater than for modern great white sharks. This is consistent with Megalodon being very high in the food chain. It also appears that the (small) Paleocene *Otodus* had a lower N-15 than larger and later (Eocene after) *Otodus*, hinting that the trophic level increased as the size increased. However, even though the size of *Otodus* continued to increase after the Eocene, the trophic level did not, indicating that being extremely large was not necessary to being an apex predator. Instead, the authors suggest, being able to eat anything allowed Megalodon to reach large sizes.

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Cushioning for the Feet of Sauropods

Bob Sheridan August 24, 2022

Sauropods were very heavy animals, reaching in some cases masses of 50 metric tons. We can see that sauropods are already “graviportal” in the sense that their feet and toes are very short compared to most dinosaurs, and their legs are more upright. We know of many sauropod trackways. The hand prints tend to be oval or horseshoe shaped, with the long axis of the footprint perpendicular to the direction of travel. The foot prints are more or less round with a flat bottom, and only a hint of toes in front. Since all dinosaurs walk on their toes, with their metatarsals held in the air, and only their phalanges on the ground, it has usually been assumed from the foot prints that sauropods had some kind of rounded soft tissue pad under their metatarsals, very much like those seen in the feet of elephants.

Jannel et al. (2022) analyze the usefulness of a “pedal pad” through finite element analysis. This computational technique, borrowed from structural engineering, measures the local stresses in materials under the application of an outside force. In this particular case, the authors are looking at the stresses in a sauropod foot given the estimated weight that is applied through the legs. The following are under study: Plateosaurus (a bipedal sauropod ancestor), and the sauropods Rhoetosaurus, Diplodocus, Camarasaurus, and Giraffatitan. The weight of the animals goes up in this order. The modern elephant is used for comparison; it is lighter than every sauropod, but heavier than Plateosaurus. As a sensitivity check, the authors try three varieties of “digitigrade” stance, with the angle of the metatarsals relative to the ground varying (from nearly flat to tip-toe).

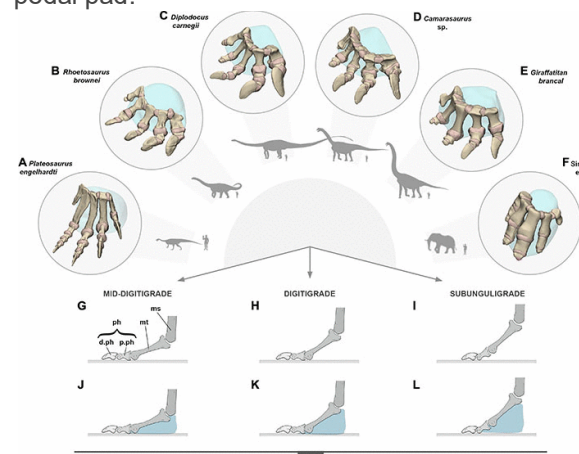
Two questions are being asked here:

1. How much stress is in the five individual metatarsals in the presence and absence of a pedal pad, assuming that it is composed of soft tissue like modern collagen?
2. Without a pedal pad, would the stresses in the metatarsals be enough to break them, given a reasonable estimate of the strength of modern bone?

In this study, it is assumed that there are no other structures (ligaments, muscles, etc.) relieving the stresses on the bones.

Not surprisingly, the pedal pad reduces stress on all the metatarsals for all animals for no other reason

that the weight is spread out over a larger area. (Interestingly, for the elephant the stress on the middle toe is not reduced.) Without a pedal pad, all the sauropods would be in serious danger of breaking at least two of their metatarsals. This effect is modulated by the angle of the metatarsals. As expected, in a more tip-toe position there is less risk, because bones are harder to break by compression along their axes, and easier to snap sideways. Even Plateosaurus shows a lesser, but not zero, possibility of breakage without a pedal pad. According to this analysis, the elephant is never in danger of breaking metatarsals with or without a pedal pad.



The authors speculate about a soft tissue pedal pad being “incipient” in the ancestral Triassic Plateosaurus (its foot print does show a wide “heel” as well as long toes) and growing into a “full” pedal pad in all subsequent sauropod descendants, starting in the Jurassic. This is probably accompanied by a more tip-toe stance of the metatarsals, which helps relieve sideward stress on the metatarsals, as well as allowing the pedal pad to expand in thickness.

This study does not address the question of why the front feet of sauropods do not show evidence of pads even though they probably bore a reasonable fraction of the total weight. Also the modern elephant, as simulated here, is never in danger of breaking its metatarsals, so there must be at least one more reason to have a pedal pad than avoiding this risk.

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Jannel, A.; Salisbury, S.W.; Panagiotopoulou, O. “Softening the steps to gigantism in sauropods through the evolution of a pedal pad.” *Science Advances* 2022, 8: eabm8280.

Using Trackways to Determine the Gait of Sauropods

Bob Sheridan September 3, 2022

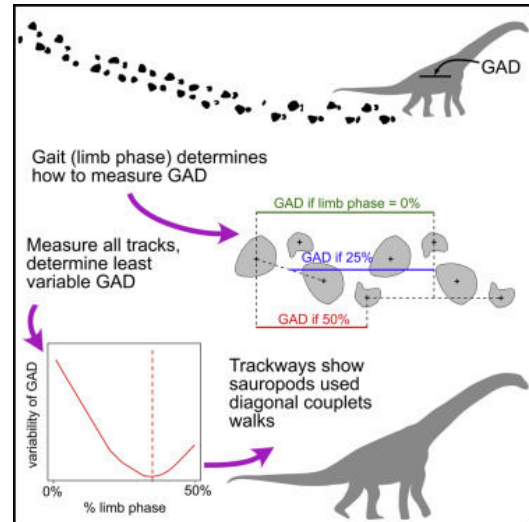
Quadrupeds walk or run in a number of modes or “gaits”. These have various names: walking, pacing, trotting, etc. The gaits are “symmetric” in the sense that anything that happens on the left will be eventually echoed on the right. Any given quadruped may have more than one gait, for the purpose of moving at different speeds, for saving energy, etc. Horses, for example, can walk, trot, canter, and gallop. Gaits are defined by the order and timing of how the feet move. For instance a walk is BL->FL->BR->FR, where “BL” is “back left”. The gait cycle is the time between, say, BL is planted and the time that it is planted again. The gait phase is the fraction of the gait cycle after the BL is planted in a forward step and the FL is planted in a forward step. The phase is reported in terms of a fraction of the cycle. So a phase 50% (trot) means when the BL is planted forward, the FL is pointed backward about to leave the ground. A phase of 0% (pace) means the BL and FL are both planted forward at the same time. A phase of 20% (walk) means when the BL is planted forward, the FL is leaving the ground. A phase of 40% (diagonal-couplet) means the BL and FR are planted forward almost at the same time.

Sauropods are the largest land animals ever to live, so it is interesting to know how they moved. The largest living animal is the elephant and it moves in a walk, even when at top speed.

We do have many sauropod trackways. In a trackway, the feet and hands would move both in front and behind the hips and shoulders and it might be possible to discern from the trackway the order in which this happens for the feet and hands. However, it is generally thought that it is too hard to determine gaits from sauropod trackways because we did not know in advance for the animal that made the tracks the distance between the shoulders and hips (called the “glenoid-acetabular distance” or GAD), the length of the legs, etc.

Lallensack and Falkingham (2022) propose a method of determining gait from trackways that does not need knowing those things in advance. They idea is to assume that the GAD for an individual animal does not change as it walks. One varies the theoretical phase, predicts where the footprints would fall, and finds the phase where the variation in estimated GAD during the walk cycle is minimum (ideally zero) according to the observed footprints. They claim that they can do this with only

half a cycle’s worth of footprints. This idea was tested on the trackways of three dogs, two horses, a fox, a raccoon, a camel, and an elephant, some of these animals in more than one gait (e.g. walk, trot, etc.). The idea generally holds up for the living animals.



The authors applied the methods to three sauropod trackways from the Early Cretaceous of Arkansas: Briar Site Q1 and Q2 and Certain Teed. These are “wide-guage” tracks, with a large distance between left and right footprints, i.e. probably from titanosaurs, as opposed to “narrow-guage” tracks, from, for example, diplodocids. The estimated phase of these trackways is 31-44%. This is close to a diagonal-couplet, i.e. the BL and FR are planted forward at the same time. This is close to how a rhinoceros moves, but not at all like an elephant. The argument is that the diagonal-couplet maximizes the support on both sides at all parts of the cycle such that the center of gravity does not shift side-to-side (presumably this would be an issue for an animal with wide-guage tracks), and allows a faster motion than a walk.

The “constant GAD” idea can clearly be applied to any type of quadruped trackways where the torso is fairly rigid, so the reach of this approach is potentially very great. There are certainly many ornithomimid and sauropod dinosaur trackways that could be studied. The “diagonal-couplet for maximum support” argument here clearly needs to be tested on narrow-guage sauropod footprints.

Sources:

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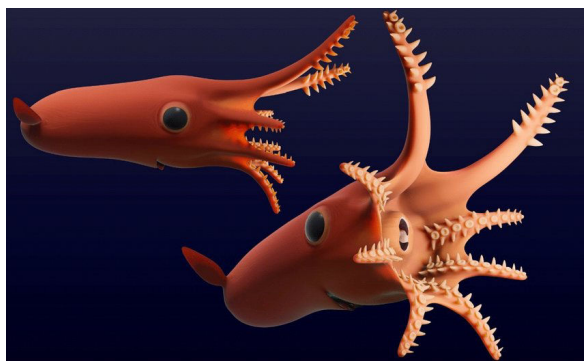
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Current Biology 2022, 32, 1635-1

Jurassic Vampire Squid

Bob Sheridan September 9, 2022

First a word about vampire squids. These are small (up to 1 foot) squids with plump bodies and short arms and tentacles. There are two small fins at the back of the animal. There is only one extant species, *Vampyroteuthis infernalis* ("vampire squid from hell"). The name "vampire" comes from the fact that their adjacent arms are connected to each other over their full length by a webbing that somewhat resembles a cape (or to my eyes a partly folded umbrella), and they tend to be a dark red in color. They have small suckers only on the distal part of the arms in a single row, and the arms have fleshy spikes called cirri on the inner surface. They have two retractable "tendrils" between the dorsal arms (presumably analogous to squid tentacles). Vampire squids live in the very deep ocean, i.e., more than 2000 feet, and are adapted in at least three ways: the ends of their arms are bioluminescent, they have very large eyes for their size, and they can get by with very little oxygen because they have a very slow metabolism. They also lack an ink sac; this presumably makes sense because a squirted ink cloud can't act as a distraction in the dark. It is thought that the vampire squid eats detritus or plankton-size animals.



Except for the "pen" (also called the "gladius") and "beak," squids are mostly made of soft parts that are seldom preserved as fossils. There are vampire squid fossils, however. An isolated pen (given the genus *Necroteuthis*) was discovered in 2021 from the Oligocene of Hungary. This pen more closely resembles that of the modern vampire squid than any other known squid. The fossil foraminifers (microscopic shelled ameba) surrounding the pen are similar to foraminifers that inhabit very deep environments today. Also, oxygen isotope ratio of the foraminifer shells are suggestive of a deoxygenated environment. This implies that

vampire squids were in their present deep sea environment since the Oligocene. More interesting, there is a much older fossil vampire squid named *Vampyronassa rhodanica* from La Voulte-sur-Rhône, which is a Middle Jurassic marine Lagerstätte in France. Fossils from this location tend to be preserved in three dimensions and have the soft parts preserved.

Rowe et al. (2022) describe a CT-scan of three specimens of *V. rhodanica* from La Voulte-sur-Rhône. The anatomy of *V. rhodanica* is very similar to that of the modern vampire squid, including the absence of an ink sac and the details of how the suckers are attached to the arms, which is unique among cephalopods. However, the authors note the following differences:

1. *V. rhodanica* does not have dorsal filaments. However, the dorsal pair of arms are elongated and have enlarged suckers.
2. the suckers on the other arms are more numerous and closer together
3. the cirri are larger.

The authors suggest that the ancestral vampire squid (as exemplified by *V. rhodanica*) is likely to have been more of a predator than *V. infernalis*, much like most modern squid. This implies the current detritus-eating deep-water form split off between the Jurassic and the Oligocene.

Sources:

Rowe, A.J.; Kruta, I.; Landman, N.H.; Villier, L.; Fernandez, V.; Rouget, I.
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Scientific Reports 2022, 12:8292

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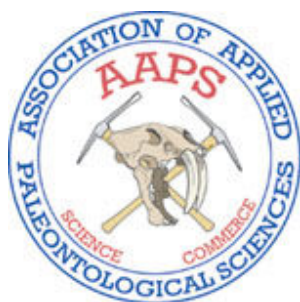
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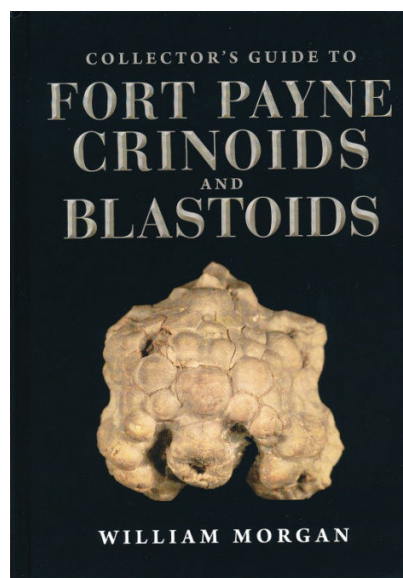
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The Paleontograph back issues are archived on the Journal Page of the AAPS website.

<https://www.aaps-journal.org/>



LostWorldFossils.com



The focus of this book is on the Fort Payne Formation and the fossil crinoids and blastoids, which are found there. Although, it is not widely known outside of academic programs in geology and/or paleontology, the Fort Payne is one the largest Mississippian-age formations in the middle and southeastern United States.

Unlike the crinoids found in the Edwardsville Formation, which are world-renown for their completeness and aesthetic qualities, crinoids from the Fort Payne are rarely complete. Therefore, the first chapter of the book introduces the anatomy and the descriptive terminology essential for identifying crinoids collected from the Fort Payne.

The second chapter of the book introduces the ongoing revision of the classification of crinoids. This process was still ongoing at the time that is book was written.

The third chapter briefly reviews the better known of the fossiliferous formations found in the Mississippian. More detail is provided for the geology and paleontology of the Fort Payne.

Collections of crinoids and blastoids from the Fort Payne are rarely publically displayed. Therefore, Chapter four proves high quality color photographs of some the best preserved specimens curated at major museums in the United States. In almost every case there are two photographs of each specimen, one unlabeled and a second with key features labeled and identified.

The fifth chapter reviews the morphology of blastoids and discusses the blastoids species currently known from the Fort Payne.

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