The Paleontograph

A newsletter for those interested in all aspects of Paleontology
Volume 3 Issue 4 October, 2014

From Your Editor

It's rainy and cool here in New York today. That makes it a good day to sit at my computer and get out this latest issue. The collecting season, for me at least, is over, although, I hope to squeeze in a couple more small trips. This year did not stand as a great year of collecting for me, as many of my plans went bad for one reason or another despite a lot of driving. The year went very fast for me. But that is the way it is as you get older.

I took my business to the Denver Coliseum Show this year. With the closing of one of the Zinn shows, the Coliseum is now Denver's big show and getting better each year. I met many cool people and saw some pretty nice fossils. I know most of you don't attend shows but I've found them to be a good source of information and friendships of the kind you can't get over the internet.

Remember, I'm always looking for articles so don't be shy.
Well, I leave you to read onto the great articles we have for you.

TC

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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Low-tech vs. High-tech in Measuring the Distal Femur of Mammals

Bob Sheridan, April 1, 2014

This is a question that frequently comes up in my own line of work: I have a simple method of doing something, and a more complex method of doing the same thing. Usually the claim is that the complex method gets better results. Is the complex method better enough that it justifies the extra time and expense?

A recent paper (Gould, 2014) asks the question about competing methods of “morphometrics”, i.e. measuring the size and shape of something and linking the measurements to something of biological interest. Specifically, the something we are measuring is the distal femur of mammals. Typically the distal end of a femur looks like a pair of half-cylinder knobs (“condyles”) separated by a notch. There is an inner (toward the midline of the body) and outer condyle, and a front and a back.

The something of biological interest is the type of lifestyle the mammal lives in terms of locomotion:
1. arboreal (stays in trees)
2. scansorial (moves on the ground and climbs trees)
3. terrestrial (slow-moving ground dweller)
4. semi-aquatic (moves on the ground and swims)
5. semi-fossorial (dig burrows)
6. cursorial (ground-dwelling and runs swiftly).
For this exercise, 44 mammal genera were assigned one of these categories.

The two methods being considered are:
1. Using calipers to measure 6 distances on the distal femur and taking four ratios. Taking the ratios separates the effect of shape from the effect of size. This is takes a minute per femur, and requires very little equipment. This is called "linear measurement."
2. Scanning the femur with a laser scanner. Obviously, this takes special equipment. It is necessary to orient the femurs in the same way before the scan and some editing on the computer is necessary to isolate the distal femur from the rest of the femur. This might take one or two hours per femur. Software is used to find landmarks on the distal femur and a large number of distances are calculated automatically. This is called "geometric morphometrics."

The questions being asked here are:
1. Do the methods agree on which aspects of the distal femur are predictive of the lifestyle?
2. Is one method more predictive of the lifestyle if the same statistical methods are used?

The answer to the first question is yes. Both methods agree one what features distinguish the mammal lifestyles. For example arboreal and scansorial mammals have distal femurs that are wider from side-to-side than they are deep from front to back. The authors feel these differences are consistent with the range of motion and type of forces that are seen in each lifestyle.

The answer to the second question is yes. Geometric morphometrics better separates the lifestyles from each other. This is clearly because it includes information that the linear method does not. For example, semi-aquatic, arboreal and scansorial mammals show an asymmetry in the rearward projection of the condyles, something that cannot be captured in the ratios.

Linear measurement depends critically on which measurements the investigator decides to make beforehand. If there is some important feature that the investigator did not consider, it will not be included. On the other hand, geometric morphometrics automatically includes a large amount of information independent of preconceptions. Therefore, geometric morphometrics has an edge.

I really like this study. However, as I have found in my own field, one example is not enough to tell whether one method is consistently better. I look forward to more.

Sources:

Gould, F.G.H.
"To 3D or not 3D, that is the question: Do 3D surface analyses improve the ecomorphological power of the distal femur in placental mammals?"
PLoS ONE 2014, 9, e91719.

One Trackmaker, Many Kinds of Tracks

Bob Sheridan, April 21, 2014

It is just common sense that the morphology of animal footprints is dependent on the firmness of what the animal is walking on. If the animal is walking through firm mud, the footprint is more or less the same as a mold of the bottom of the foot. If you are walking through very wet mud, the mud squishes over the top of the foot (producing "displacement rims"), and this mud falls down after the foot is removed and obscures the outline of the foot, and the walls of the footprint fall inward ("wall collapse"). The animal is walking on almost solid ground, only parts of the foot may make an impression. Trace fossils such as dinosaur footprints are classified based on their shape, and there is a good possibility that some tracks that appear different may be made by the same type of animal on different types of ground. This is widely recognized as a possibility, but a new paper shows an example where this is clearly demonstrated.

Razzolini et al. (2014) describe the El Frontal tracksite in northern Spain. Several mudstone and siltstone layers are present. They probably date from the Early Cretaceous. A digital record of the tracksite was made by laser scanning and photogrammetry. There are 45 separate trackways consisting of 200 tridactyl tracks (i.e. footprints) characteristic of theropods. A typical theropod track would show the impression of three digits (II, III, IV) with III being the longest. One can sometimes see the impression of the hallux (e.g. toe I).

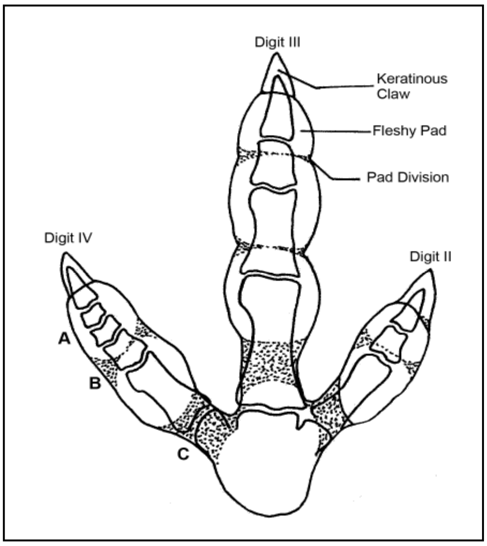
Some of the El Frontal trackways are quite short (2 to 5 tracks), and some are long (20 or more tracks) The individual tracks are between 17 and 34 cm long and anywhere between 0.1 and 5 cm deep. Aside from the overall length and maximum depth, other measures were taken of each track: track width, angle between the toes, height of displacement rims, etc. For trackways one can measure the "pace length", i.e. the distance between sequential tracks.

Four of the longer trackways (F4, F5, F7, F17) were studied for variation between the individual tracks. It is possible that F17 was made by a different type of theropod (or perhaps an older one) because the tracks are about 10 cm longer. There can be a big variation in appearance among tracks even in the same trackway. Some of the tracks are typical good tridactyl impressions, some are more or less collapsed. There are some correlations among measurements within a single trackway. For instance, the depth of a track and the height of the displacement rims are correlated. This is not surprising, if the mud is soft, the animal will sink further and the mud will tend to squish further upward. On the other hand, the length of the track and the depth are not correlated within a single trackway. However, not surprisingly, the larger animal F17 makes the deepest tracks on the average.

One can also graph individual track measurements with sequence number (step 1, step2, etc.) within a single trackway. Not unexpectedly, in F4, F5, F7, and F17 the pace length and track length are more or less constant, as would be expected for a single animal walking steadily for a time. In contrast, the depth can vary markedly between on adjacent track and the next, and not monotonically. Most satisfying is that the trends in trackways correlate with each other where they intersect. For instance, trackway 17 gets deeper on the same part of the surface that trackway 7 gets deeper. Trackway 5 gets deeper on the same part of the surface that Trackway 4 gets deeper. The simplest explanation is that the softness of the mud the animals are walking through varies and it was softest where both tracks are deepest.

Sources:

Razzolini, N.L.; Vila, B.; Castanera, D.; Falkingham, P.L.; Barco, J.L.; Canudo, J.I.; Manning, P.L.; Galobart, A.
"Intra-trackway morphological variations due to substrate consistency: the El Frontal dinosaur tracksite (Lower Cretaceous, Spain)."
PLoS ONE 2014, 9, e93708.



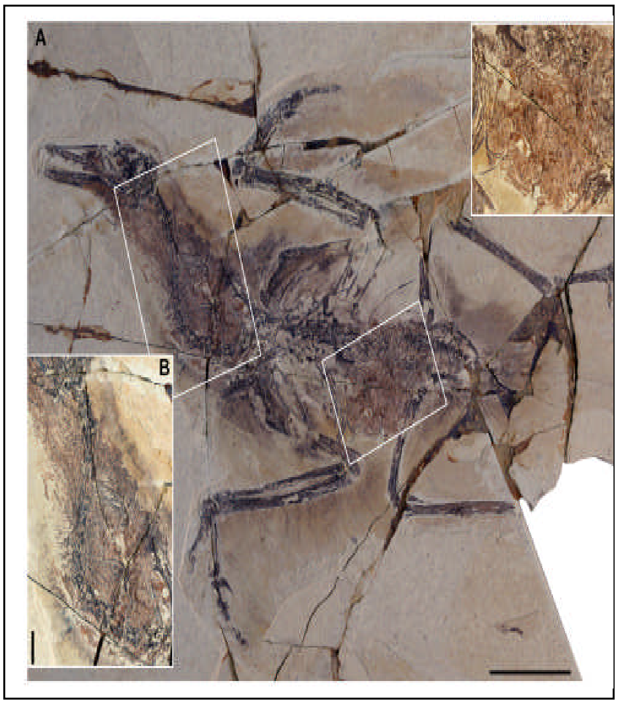
Ed Note; This is generic footprint diagram not from the referenced article.

Yanornis,
the Cretaceous Bird Ate Fish

Bob Sheridan, April 26, 2014

Since the mid-1990's China has been the source of an incredible number of well-preserved fossils of feathered dinosaurs and true birds from the Early Cretaceous. The variation among Mesozoic birds is very large due to the fact that they are mosaics of primitive and advanced features: teeth vs. no teeth, long bony tails vs. tiny tails, light vs. heavy skulls, etc. The preservation of these fossils is good enough that outlines of feathers (and the feathers themselves in many cases) are almost always present. We can also examine the stomach contents in many specimens to determine the diet of these birds.

New specimens of Yanornis with preserved stomach contents are reported by Zheng et al. (2014). Yanornis is a fairly advanced Early Cretaceous bird, modern in almost every way except that it retains teeth. It would be about chicken-size when alive. Ten specimens described by Zheng et al. have the remains of fish bones and scales in the alimentary canal. In some cases the genus of fish can be identified from the scales, e.g. Jinanichthys and Protopsherus. All the specimens preserve a whole or partial fish in the neck, which in a modern bird would be the crop. (A crop is an expanded muscular pouch in the esophagus that allows some birds to temporarily store food, which can be digested later in a safe location.)



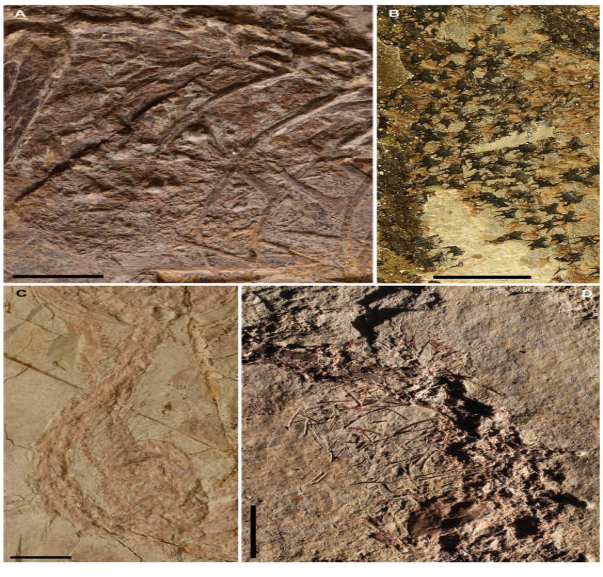
There are other macerated fish bones in the abdomen where a modern bird would have a gizzard. One can infer that Yanornis swallowed fish whole, despite having teeth. Also that it had a crop like many modern birds. (Crops have been inferred in other Mesozoic birds like Jeholornis). Finally, it must have had a gizzard-like organ for mashing the bones.

One question that needs to be addressed is why many previous specimens of Yanornis seemed to have gastroliths in their abdomen, so that previously it was thought that Yanornis might be a herbivore or ate otherwise tough foods. One explanation is that the diet of Yanornis varied.
The authors suggest a simpler explanation: the "gastroliths" were stones swallowed accidentally or that they were compacted sand that is often swallowed with fish.

Sources:

Zheng, X.; O'Conner, J.K.; Huchzermeyer, F.; Wang, X.; Wang, Y.; Zhang, X.; Zhou, Z.
"New specimens of Yanornis indicates a piscivorous diet and modern alimentary canal."
PLoS ONE 2014, 9, e95036.

FIGURE 3 FROM THE ARTICLE SHOWING CONTENTS



LEFT, FIGURE 1: *Yanornis* STM9-15 preserving whole fish in the crop and macerated fish bones in the ventriculus: (A) full slab, scale bar equals five cm; (B) detail of the crop, scale bar equals one cm; (C) detail of the ventriculus.

Dinosaurs Without Bones- -A Review

Bob Sheridan, June 7, 2014

Ichnology is the study of trace fossils (footprints, tooth marks, burrows, etc.) The most interesting thing about trace fossils is that they record the behavior of a living anima, as opposed to body fossils which tell you everything about anatomy, but are effectively mute about behavior. Also, trace fossils can be very abundant; an animal only has so many bones, but can leave thousands of tracks in a lifetime. As you probably know, there are a number of frustrations connected with linking the two types of fossil: The formations that preserved footprints, for instance, are seldom the same formations that preserve bones. Also, although one can with some confidence assign which broad type of animal made which trace fossil, narrowing it down to a specific genus is sometimes impossible. Therefore one needs to have a separate system of nomenclature, with "ichnospecies" (types of traces) and "real" species, with no absolute way of linking the two.

As with any field in paleontology, popular books on ichnology concentrate on dinosaurs. In the 1990's most books about dinosaur trace fossils were by Martin Lockley: "Tracking Dinosaurs" (1991), "Dinosaur Tracks and Traces" (1991), "The Eternal Trail" (1999), etc.
After a two decade gap in popular books on ichnology, I was pleased to see a new book "Dinosaurs Without Bones" by Anthony J. Martin. Martin is a paleontologist at Emory University who specializes in trace fossils, with emphasis on the Southern Hemisphere.

The chapter headings are:

1. Sleuthing Dinosaurs
2. These Feet Were Made for Walking, Running, Sitting, Swimming, Herding, and Hunting
3. The Mystery of Lark Quarry
4. Dinosaur Nests and Bringing Up Babies
5. Dinosaurs Down Underground
6. Broken Bones, Toothmarks, and Marks on Teeth
7. Why Would a Dinosaur Eat a Rock?
8. The Remains of the Day: Dinosaur Vomit, Stomach Contents, Feces, and Other Gut Feelings
9. The Great Cretaceous Walk
10. Tracking theDinosaurs Among Us
11. Dinosaurian Landscapes and Evolutionary Traces

Two things you can immediately tell from the headers:

1. This book expands the notion of trace fossils beyond the usual footprints, tooth marks, and burrows, and includes anything that records some kind of behavior.
2. The book is written in a very humorous style, with a lot of word-play.

I will dip into some of these topics to give you a flavor. Obviously, there is a lot of interesting material.

From Chapter 3: Paleontologists tend to be story tellers (in my mind a little too much, speculating far beyond the facts in some cases), and ichnologists are even more extreme in this trait because their objects of study preserve behavior. Lark Quarry (in Australia) preserves ~3300 dinosaur footprints and seems to tell a compelling story. There are a few medium size three-toed footprints, presumed from some ornithopod, many three-toed footprints of some small theropods all moving in the same direction and running at high speed (because the tracks are widely spaced in the direction of travel). Some of the small tracks overstep the medium-sized prints. There are also a line of very large three-toed prints, presumably of a large theropod). The story is "dinosaur stampede", where the large theropod panics a herd of smaller theropods who want to avoid being eaten. Presumably this inspired the Tyrannosaurs chasing a herd of Gallimimus in "Jurassic Park." Unfortunately further work puts this exciting story into doubt. It is not necessarily straightforward to tell the three-toed tracks from ornithopods (like hadrosaurs) from the tree-toed tracks of theropods. The proportions of the very large tracks are more like that of an ornithopod, than a theropod. In fact there are no known very large theropods from Australia 95 Myr., but there is a very large ornithopod, Muttaburrasaurus. So whatever the small dinosaurs were running from, it probably was not from being eaten.

From Chapter 5: Martin is famous for studying the only known case of a burrowing dinosaur. A spiral burrow (6ft long and 1 ft in diameter) was excavated from Montana in 2005. It contained three disarticulated skeletons of Oryctodromeus, a small herbivore, one adult and two juveniles. This would be a very tight fit, but not unusual for a burrowing animal. The completeness of the skeletons makes a pretty good case that the animals died in the burrow and were not washed in later.

Cont'd

Trace Fossils Cont'd

From Chapter 7: The classic explanation of the rounded pebbles found associated with the abdomen of dinosaurs (gastroliths) is that they were deliberately swallowed and acted as substitute teeth for grinding plant matter. This is often applied specifically for sauropods. The real situation is more complicated. Many herbivorous dinosaurs with no grinding teeth have never shown any gastroliths, and surprisingly many meat-eating dinosaurs have gastroliths. One can never be certain that the gastroliths were deliberately or accidentally swallowed, nor can one always eliminate the possibility that stones were washed into the burst abdominal cavity of a dinosaur long after death.

From Chapter 10: Birds are living dinosaurs, and much of their behavior leaves traces: beak marks, nests, bowers, etc. It is speculative, but once we know what bird-caused traces look like, we can look for the same features in Mesozoic sediments.

From Chapter 11: Many individual animals working together leave traces on their environment. For instance, overgrazing of vegetation allows for faster erosion, which can change the course of rivers. Dinosaur flatulence could cause global warming. Mobile dinosaurs could distribute seeds and parasites across continents. I found this a very eye-opening discussion. Unfortunately, while one can detect things like erosion and global warming in the fossil record, it is very hard to assign the behavior of specific animals as a cause.

I enjoyed "Dinosaurs Without Bones" overall. It contained much information of which I was not previously aware, and it was an easy read. On the other hand, if you are looking for more technical information on dinosaur traces, you will have to look elsewhere. One thing I did miss is helpful diagrams embedded with the text to illustrate certain points. All photographs of trace fossils, and a few diagrams (the most amusing of which is "Brachiosaurus projectile vomiting"), are together in the center of the book.

Sources:

Martin, A.J.
"Dinosaurs Without Bones. Dinosaur Lives Revealed by Their Trace Fossils."
Pegasus Books, NY, 2014, 460 pages; $30 (hardcover)

Feathers on all Dinosaurs?

Bob Sheridan July 25, 2014.

I have lost count of the number of feathered dinosaurs. Almost all of them have been discovered in China, the famous exception is Archaeopteryx from Solnhofen in Germany. The vast majority of these are maniraptorans, the subgroup of theropod dinosaurs from which birds arose. There are many types of feathers found in these animals, ranging from short filaments to long plumes with central shafts. Different types of feathers are often found in the same animal. By now it is widely accepted that feathers originated for a purpose other than flight (e.g. insulation or display), and were adapted for flight later.

You will remember that dinosaurs come in two major groups: the Saurischians (to which theropods belong) and the Ornithischians. There have been hints that interesting integumentary structures can occur in Ornithischians. Psittacosaurus (a sister group to the ceratopsians, which includes the famous Triceratops) has some kind of bristles on its tail. Another ornithischian Tianyulong (which is a heterodontosaur) also seems to have some kind of rigid filaments on its neck, back, and tail. Some pterosaurs (which are archosaurs, but not dinosaurs) show "hairs" on the wings. It has not been clear whether these structures are the same as the feathers in theropods. If they are the same, it seems likely that protofeathers evolved in an archosaur ancestor and all dinosaurs (and pterosaurs) inherited them. If they are not the same, it is more likely that the branches of dinosaur evolved their integumentary structures separately.

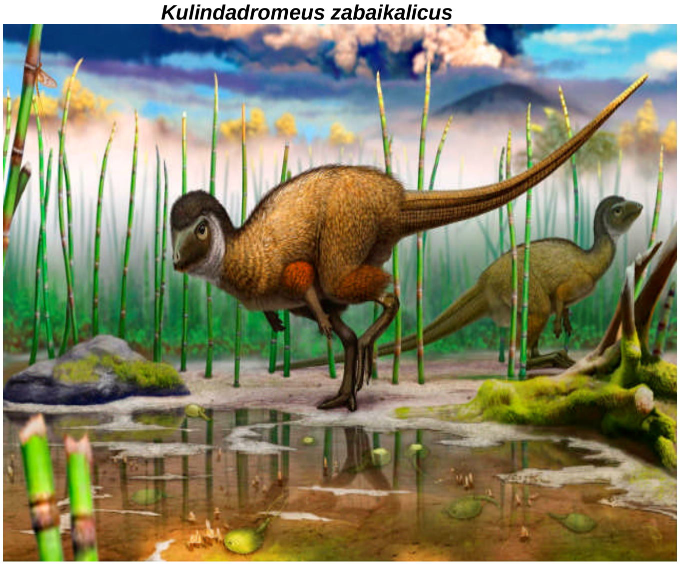
A close up of the feathers

Cont'd

Feathers and Scales Cont'd

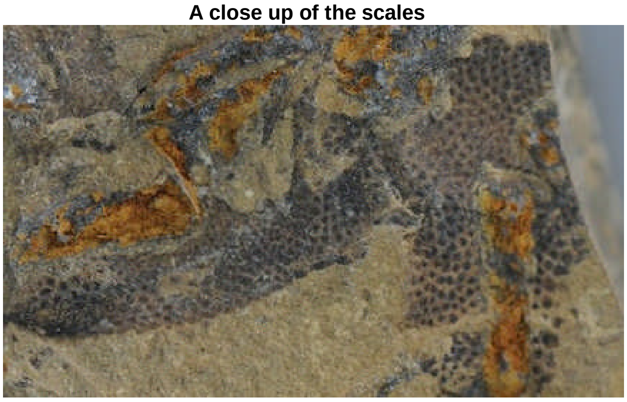
A new ornithischian with feather-like structures has been described in this week's Science by Godefroit et al. (2014). Specimens of a new dinosaur called *Kulindadromeus zabaikalicus* ("runner from the Kulinda locality") were found in a monospecific bone bed in southeastern Siberia. The bonebed contains several hundred disarticulated skeletons. Kulindadromeus appears to be a basal bipedal ornithiscian about 1.5 meters long. The degree of preservation is unusual for a specimen outside China. Kulindadromeus contains three types of scales and three types of feather-like structures. The three types of scales are:
1. Rounded and and hexagonal scales (<3.5 mm long) on the legs (similar to those found on modern birds).
2. Smaller (< 1mm) rounded scales on the arms and feet.
3. Arched scales (20mm long) on the tail.
The three types of feathers-like structures are:
1. Short and thin monofilaments (10-15mm long, 0.15 mm wide) on the thorax, back and head (similar to those found on theropods).
2. Branched filaments on the humerus and femur (resembling down feathers).
3. Ribbon shaped elements made of parallel filaments at the top of the lower leg (20mm long and 1.5-3mm wide). This type of integument has not been seen before.

Kulindadromeus zabaikalicus



The fact that an ornithischian has multiple "feather" types and that some of these types look very much like the "feathers" on theropods, makes it more likely that the "feathers" are the same in ornithischian and theropods.

A close up of the scales



I was puzzled by the authors' emphasis on the fact that Kulindadromeus has both feathers and scales, since this is not unusual. Modern birds do also. However, they point out that many feathered theropod dinosaurs (e.g. microraptor) have feathers on their lower legs and feet and there has been a trend for the feathers to be reduced and scales to appear on the feet as feathered dinosaurs evolved to modern birds. The fact that an ornithischian is showing the same trend might suggest that ornithischians and theropods have a common mechanism for feather formation, which would further support the idea that the apparent "feathers" are the same in both groups.

Sources:

Godefroit, P.; Sinitsa, S.M.; Dhouailly, D.; Bolotsky, Y.L.; Sizov, A.V.; McNamara, M.E.; Benton, M.J.; Spagna, P.
"A Jurassic ornithischian dinosaur from Siberia with both feathers and scales."
Science 2014, 345, 451-454.

The Eleventh Specimen of Archaeopteryx

Bob Sheridan, July 4, 2014

Since its discovery in the 1860, Archaeopteryx has been considered one candidate for the "First Bird." This is not at all surprising, given at the time it was the only known feathered animal from the Mesozoic, and appeared to be an intermediate between dinosaurs and birds in that it has teeth and a long bony tail. Now that we know many dozens of feathered dinosaurs and dozens of early birds, Archaeopteryx is looking more like a feathered dinosaur than like a bird.

Up to very recently there have been only 10 specimens of Archaeopteryx known, all from Solnhofen limestone. Since the specimens seem to come in a variety of sizes, from crow- to raven-sized, and some details about the skull are slightly different, it has been suggested that perhaps there is more than one species or even more than one genus. Most specimens show some feather impressions, but in three specimens (London, Berlin, and Thermopolis) the impressions are extremely clear. Archaeopteryx as very modern appearing "pennaceous" feathers, especially on the wings and tail: a central shaft surrounded by asymmetrical vanes. The asymmetry in feathers is associated with flight in modern birds.

This week in "Nature" Foth et al. (2014) report an eleventh specimen of Archaeopteryx. The exact date of discovery is not known, and this specimen resides in a private collection, although it is on loan to a museum in Munich, and is available for scientific study. The specimen is missing most of the skull (the mandible is preserved) and one wing. However, the feather impressions are excellent. In previous specimens one could see the wing and tail feathers clearly, but not the body, neck, or leg feathers. In this new specimen, one can see those feathers more clearly. The surprise is that all the body feathers (torso, neck, legs, etc.) are long pennaceous feathers: they have a central shaft and symmetric vanes. This is very different than in modern birds, in other feathered dinosaurs, and in early birds.

The authors do a phylogenetic analysis of feather types among maniraptoran theropods. Feather types vary a great deal between these animals. The authors conclude that, since they are present in animals that could not fly, and they are present in places of the body that are not used for flight, pennaceous feathers originally had a purpose other than flight. Probably they were used for display. (Insulation is a less likely use because insulation wouldn't require a complex structure.) Pennaceous feathers were probably adapted for flight later, by becoming stronger and asymmetric.

Some investigators have argued that the feather shafts in Archaeopteryx wing feathers are very thin and would too easily bend if force was applied. The implication of this is that Archaeopteryx could not fly. The authors graph shaft thickness per feather length as a function of weight of the bird for the new specimen, early birds, and modern flighted birds. Archaeopteryx falls about in the middle of modern birds on this plot, so shaft thickness cannot be used to rule out flight in Archaeopteryx.

Sources:

Foth, C.; Tischlinger, H.; Rauhut, O.W.M. "New specimen of Archaeopteryx provides insights into the evolution of pennaceous feathers." Nature 2014, 511, 79-82.

Dinosaurs as Mesotherms

Bob Sheridan, June 21, 2014

Those of us old enough can remember the "Warm-Blooded" vs. "Cold-Blooded" debates of the Dinosaur Renaissance. That is, the classical view of dinosaurs as slow, plodding, behaviorally uninteresting reptiles (like lizards) was replaced by the idea of fast, social, behaviorally interesting animals (like birds?). The impetus for this was the discovery of Deinonychus by John Ostrom in the late 1960's. Not only did Deinonychus have bird-like skeleton, but it apparently had to be able to stand on one leg (and/or jump) in order to use its foot claws. Robert Bakker revived this issue in the 1980's, arguing that the behavior of dinosaurs and their bone histology argued that they were warm-blooded.

Since then, it has been recognized that the situation is more complicated than having only two extreme categories. Body temperature, metabolic rate, growth rate, bone histology, agility, posture, presence of nasal turbinates, presence of air sacs, number of heart chambers, etc. are not necessarily correlated, and an animal can be warm-blooded by one criterion and cold-blooded by another. Even for the "body temperature" criterion, there can be a middle-ground. Today, there are clearly warm-blooded animals (birds, mammals) that maintain a high constant body temperature (endotherms). There are clearly cold-blooded animals (most fish, reptiles, amphibians) that have a body temperature close to that of the environment (ectotherms). Then there are animals that maintain a body temperature above that of the environment, but not necessarily a constant temperature.

The suggestion has been made several times that dinosaurs were not exactly like today's warm-blooded birds nor like today's cold-blooded lizards, but something different. Today's story is further evidence of that. Grady et al. (2014) compared the growth rate of dinosaurs to several classes of modern animals. We can produce a growth curve for dinosaurs by examining a set of different sized of dinosaurs of the same species. The mass of the dinosaur is estimated from the size of the bones. The age of the dinosaur can be estimated from the number of LAGS in their long bones (very much like counting tree rings). This can be done for only about twenty dinosaurs for which we have a series of sizes, but that is enough for this study. This study uses only one number derivable from the growth curve, the rate of fastest growth, measured in grams per day. The maximum growth rates in living animals are known. The authors divided the living animals into several classes: altricial birds, precocial birds, placental mammals, sharks, fish, squamates (lizards and snakes), and crocodilians. (The ectotherm growth rates were taken only for animals living in moderate to tropical conditions.)

One can graph the log of maximum growth rate vs. log of the adult mass of the animal. The classes of animals fall on a straight line, each with a different slope and intercept. Birds have the highest growth rate, followed by placental mammals, followed by dinosaurs, followed by sharks, squamates, and crocodilians. That is, dinosaurs as a class are intermediate between the classic categories of warm-blooded and cold-blooded. Interestingly, the larger dinosaurs had growth rates similar to mammals and smaller dinosaurs had growth rates similar to squamates. Even dinosaurs closely related to birds, including Archaeopteryx appear to have an intermediate growth rate. (This is consistent with a study a few years ago that showed the bone histology of Archaeopteryx is indicative of slow growth.)

The authors created an equation that links growth rate with size and metabolic rate for living animals. Given this equation, dinosaurs fall into a middle category of metabolic rate expected for their size. There are a handful of modern animals that seem to have a metabolic rate higher or lower than most similar animals: among them the Echidna (a primitive mammal), tuna, a laminid shark, and the leatherback sea turtle. These animals maintain a temperature above that of the environment, but not necessarily a high constant temperature. The inference is that dinosaurs were similar. The evolutionary significance is that dinosaurs had an advantage over their more torpid reptile cousins by being more agile; on the other hand, they did not have to spend energy maintaining a high body temperature.

Sources:

Balter, M.
"Dinosaur metabolism neither hot nor cold, but just right."
Science 2014, 344, 1216-1217.

Grady, J.M.; Enquist, B.J.; Dettweiler-Robinson, E.; Wright, N.A.; Smith, F.A.
"Evidence for mesothermy in dinosaurs."
Science 2014, 344, 1268-1272.