Trace Fossils

- A trace fossil is indirect evidence of ancient life (exclusive of body parts) that reflects some sort of behavior by the organism. Examples of trace fossils are tracks, trails, burrows, borings, gnawings, eggs, nests, gizzard stones, and dung.
- In contrast, a body fossil is direct evidence of ancient life that involves some body part of the organism.

paleoichnology

- Dinosaurs left trace fossils represented by tracks, tooth marks, eggs, nests, gastroliths (stones in the stomach for grinding), and coprolites (fossilized poop).
- Body fossils of dinosaurs include bones and skin impressions. As an example of the distinction between dinosaur body fossils and trace fossils, skin impressions are not trace fossils unless they were made while the dinosaur was still alive, such as the skin impressions that might be associated with a footprint.

Types of Dinosaur Trace Fossils

- Tracks and Trackways
- Eggs and Nests
- Tooth Marks
- Gastroliths
- Coprolites

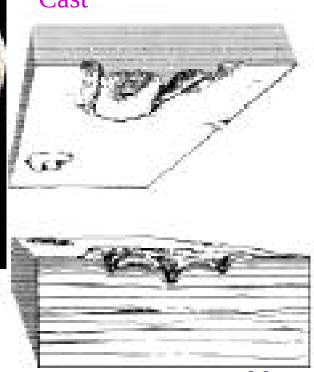
Tracks

- A track is the impression left by a foot in a sediment or other substrate, although some two-legged dinosaurs also made "hand" (forelimb) impressions, which are also considered as tracks. Tracks are preserved in two main ways:

(1) as **impressions** (negative relief), which are molds of the original foot; and

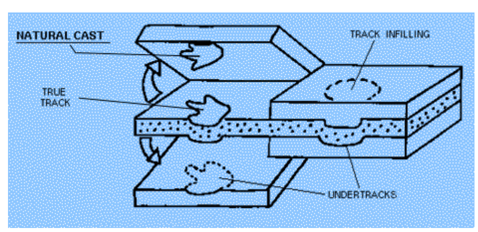
(2) as **casts** (positive relief) made by overlying sediments into the original impressions.

Cast



Impression or Mold

- Some dinosaurs were also heavy enough to deform layers of sediment below the surface; such impressions (and their overlying casts) are called **undertracks** because they were under the original track surface.



This track, in the Entrada Formation (Jurassic) of eastern Utah, shows only a partial impression and is probably an undertrack.

However, a deep claw impression is visible on the far left toe, probably indicating a shift of the theropod's weight to the left.

- A **trackway** is two or more consecutive tracks made by the same animal. Many mammals and birds leave a walking trackway that shows an angle between the footprints from a midline of travel; some trackers refer to this progression as diagonal walking. All dinosaurs seemingly were diagonal walkers.

- Dinosaur trackways show no evidence of either tail or belly dragging, meaning that dinosaurs walked erect with their limbs underneath their bodies, rather than sprawled to the sides of the body.

- Dinosaurs either traveled on two rear feet (bipedal) or four feet (quadrupedal).
- If a dinosaur was obligated to walk on two feet (such as humans) for most of its life, then it was an obligate biped; an obligate quadruped spent most of its life on four feet.
- If a dinosaur could walk on two feet (similar to modern bears) but spent most of its time on four feet, it was a facultative biped but an obligate quadruped. Accordingly, a normally bipedal dinosaur that could have gone onto all four limbs was a facultative quadruped.

- Because actual body remains are only very rarely associated with trackways - tracks have their own unique taxonomy that is not associated with the taxonomy of the dinosaur body fossils.

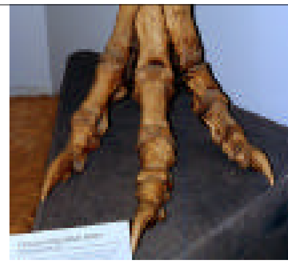
- Different types of dinosaurs left distinctive tracks that can be attributed to general classifications (ceratopsians, theropods, ornithopods, sauropods) but tracks rarely give enough detail to identify the genus or species of the trackmaker (e.g., Tyrannosaurus, Apatosaurus, Triceratops).

Bipedal Trackways

- The first dinosaurs are thought to have been bipedal descendants of archosaurs that evolved during the Triassic Period. Dinosaur tracks from the Late Triassic, which show bipedalism, support this hypothesis. These tracks have a three-toed shape (with narrow-width toes) that is characteristic of theropods from the Late Triassic through the Late Cretaceous Periods.

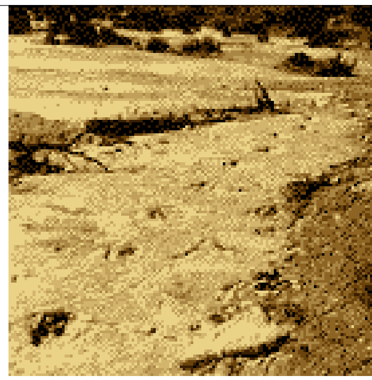
- All theropods were obligate bipeds, although some rare examples of trackways show that they went down onto all fours, meaning some of them were facultative quadrupeds. Some tracks show claw impressions at the ends of toes. Theropods trackways show little deviation from the midline of travel, as if they were walking on a tightrope.

- This foot belongs to Allosaurus, a large Jurassic theropod. Notice the three toes with a relatively narrow width. The skeleton is mounted at Dinosaur National Monument, northeastern Utah, USA.



- This foot belongs to Tyrannosaurus, a large Cretaceous theropod. Although separated by millions of years, both Allosaurus and Tyrannosaurus would have left similar footprints that were attributable to large theropods. Foot is from a replica mounted in Western Colorado's Dinosaur Valley, Grand Junction, Colorado.

- This theropod track is in the Morrison Formation (Jurassic) of eastern Utah. Notice the greater depth of the track in the toe region, which suggests a horizontal posture for the dinosaur while it was walking.



theropod trackway

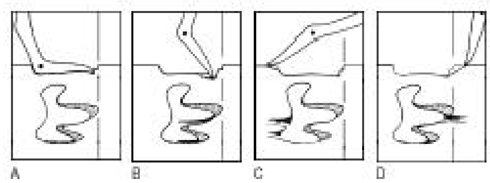
- **Ornithopods** were also capable of leaving bipedal trackways but were mostly facultative bipeds. Their tracks are similar to those of theropods in that they frequently show a three-toed pattern;
- they differ from theropod tracks in the width of the individual toe prints, which are greater than those of theropods.
- Theropod tracks also show distincitive claw impressions and lack the “heel” impressions featured in ornithopod trackways.

- Ornithopod tracks are present in deposits from the Jurassic through the Late Cretaceous but are particularly common in Late Cretaceous deposits. Hadrosaurs are probably the best known ornithopods that left tracks attributable to the trackmaker.

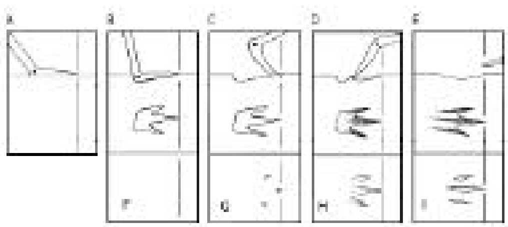
- This is a typical ornithopod foot (a hadrosaur), showing the widely splayed three-toed anatomy. Skeleton is in the Museum of Western Colorado's Dinosaur Valley, Grand Junction, Colorado.

- This ornithopod track was cast in the bottom of a sandstone bed, hence you are looking at the bottom of the footprint in positive relief. Track is in the Museum of Western Colorado's Dinosaur Valley, Grand Junction, Colorado.

- The large size attained by some ornithopods late in the Mesozoic Era is shown by this Late Cretaceous ornithopod print, with my sandaled foot (size 9, men's) for scale. This track is also preserved as a sandstone cast, so you are looking at the bottom of the footprint.



The making of typical ornithopod tracks: (A) impact of foot into muddy surface. (B) Kick-off causing initial toe-drag inside footprint. (C) Kick-off with toe-drag behind footprint. (D) Kick-off with toe-drag in front of footprint.



The making of typical [illegible]

Quadrupedal Trackways

- Most dinosaurs were obligate quadrupeds; well-known groups of dinosaurs that normally walked on all four legs include prosauropods, sauropods, ceratopsians, ankylosaurs, and stegosaurs. Although sauropods have been shown in some books, the Jurassic Park movies, and museum displays as capable of standing on their hind limbs (thus becoming facultative bipeds), **no trackway evidence exists to corroborate such an assertion.**

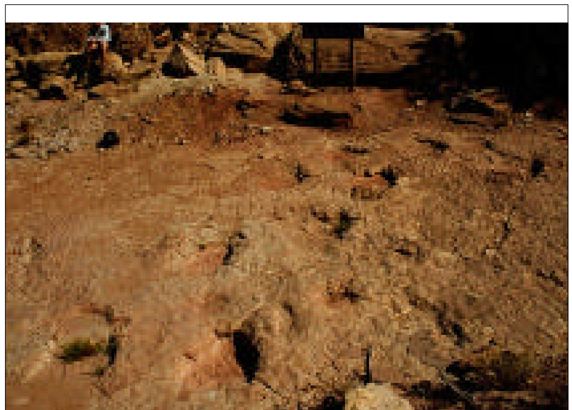
- The front foot of a quadrupedal animal is called the manus, whereas the back foot is called the pes.
- Quadrupedal dinosaurs seemingly walked like most diagonal walkers do nowadays, by moving the right manus and left pes at about the same time, alternating with the left manus and right pes. Trackways show the manus print slightly in front of the pes print on each side of the trackway.

- Prosauropods, ceratopsians, ankylosaurs, and possibly stegosaurs left four-toed impressions in their tracks, both for the manus and pes.
- Sauropods have five-toed tracks for their pes impressions but do not show toes in manus impressions.
- Some quadrupedal ornithopods have three-toed tracks for their pes impressions but manus prints do not show obvious toes, either.

- The large padded footprint left by the hind foot of a sauropod dinosaur. The print shows the curved claw marks typical of this type of dinosaur. The print which is on a fallen block is on the base of a sandstone unit.

- This sauropod print is of a right pes and is one track in a trackway. The tip of a field boot is the scale in the lower lefthand corner. The mud "push-ups" in the front of the track (toward the top of the image) and to the right indicate the shifting of the sauropod's weight forward and to the right. Locality is in eastern Utah, Morrison Formation (Jurassic).

- The following trackway, to which the previously depicted sauropod print belongs, registers a rarely recorded event; a sauropod that changed its direction of travel abruptly to the right. The progression of the sauropod was from the lower lefthand corner to the upper righthand corner of the picture. Both manus and pes prints are visible in the image. (If you look closely to the lower right, a theropod track is pointed in a direction perpendicular to the sauropod trackway.)



- Trackways may indicate specific behaviours or social interactions. Any interpretations must, of course, be made with caution.
- A site with many trackways may not necessarily indicate herding or other social groupings, especially if the hiatus between deposition was particularly lengthy.

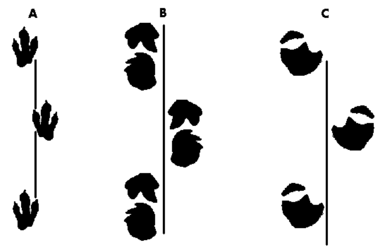
- However, there is evidence that, for at least some of the time, brontosaurs traveled in herds. At Davenport Ranch, Texas "the limestone records the passage of two dozen brontosaurs in a compact mass, the very largest prints at the front periphery, the very smallest in the middle of the group. So brontosaur bulls or maybe senior cows must have guarded their young." (Bakker, 1986).

- This interpretation has been modified by Martin Lockley (1986), who inferred from this and other Colorado tracks that larger sauropods ranged in front of smaller members of the herd and "were probably walking in some type of staggered or spearhead formation" (Lockley et al.,1986).
- "There is evidence of predation, of solitary hunters stalking their prey, and of opportunists and scavengers roaming in packs“ (Thulborn, 1990).

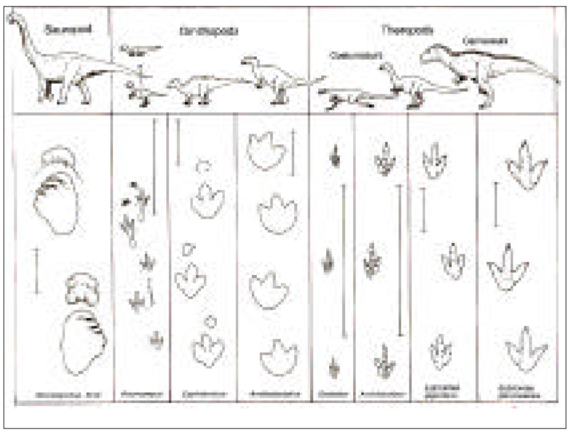
- Trackways can also indicate swimming, stampeding or even limping dinosaurs (Thulborn & Wade, 1984 in Thulborn, 1990).
- Any inferences about dinosaur behavior will always be limited. We can never know the real complexities of dinosaur behavior.

- The previously shown set of trackways from Colorado shows two things about sauropods and helps in our understanding of a third. Firstly it shows that these large animals did move in herds. Secondly it proves that these dinosaurs (and indeed, probably all others) did not drag their tails along the ground. And thirdly is suggests that eggs were abandoned and juveniles were not nurtured. It generally appears to be the case that tracks such as these were all made by well-grown individuals together and are not accompanied by young.

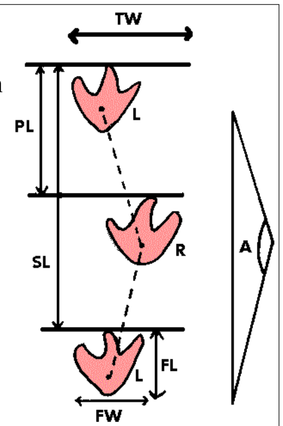
- In the film Jurassic Park we saw Velociraptors attacking their prey simultaneously from several directions after hiding quietly in the bushes. Such particular behaviors would be very hard to find or interpret from the fossil track record.
- Furthermore if they were represented, it is likely that several, equally-plausible behavioral explanations could be suggested.

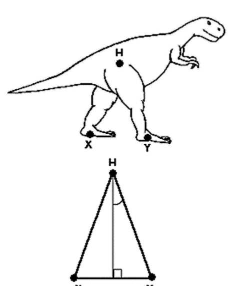


- A = Theropod - habitually bipedal
- B = Sauropod - habitually quadrupedal
- C = Iguanadont - quadrupedal
- Drawings not to scale. Drawing by Myles McLeod after Paul (1987)



- TW = Trackway Width
- SL = Stride Length
- PL = Pace Length
- FL = Footprint Length
- FW = Footprint Width
- A = Pace angulation
- L = Left print
- R = Right print





Geometric Method

Drawing by M McLeod after Avnimelech (1966) in Thulborn (1989)

DINOSAUR EGGS AND NESTS

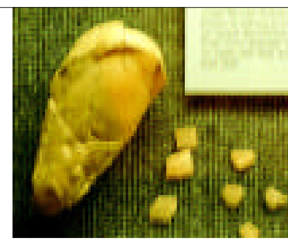
- Dinosaurs reproduced through eggs laid on land, just like most modern reptiles and birds, rather than giving live birth (such as most mammals). Dinosaur eggs are either represented in the geologic record as individuals or are arranged in definite patterns, indicating the former presence of nests.

- An egg is an enclosed, mineralized structure containing an amniote (yolk sac) that helps to nourish the developing embryo. The structure is a type of protection for the embryo that also keeps all of its nutrients in a restricted space. In contrast, amphibians require a water source for their eggs, hence times of drought (and consequent shrinkage of aquatic habitats) can be detrimental to amphibian reproduction. Amniotic eggs also have a porous and permeable structure that allows the developing embryo to "breathe," thus offering protection but also allowing an exchange with the surrounding environment.

- Dinosaur eggs are preserved as oblate to semispherical structures that also show distinctive shell microstructures. In some cases, dinosaur eggs have preserved parts of embryonic dinosaurs, which can help to correlate a dinosaur egg with a species of dinosaur, such as Maiasaurus and Oviraptor.

- However, the egg itself is the trace fossil, whereas any bodily remains of an embryo constitute a body fossil.

- An assemblage of eggs in close association with one another in the fossil record is often regarded as part of a clutch, meaning that these eggs represent one egg-laying episode.



- This dinosaur egg, attributed to the theropod Oviraptor, is partially crushed but still shows the asymmetrical and oval shape associated with this species' eggs. Shell fragments are to the right of the egg. Samples are in Western Colorado's Museum of Dinosaur Valley, Grand Junction, Colorado, USA.

- This pair of partially preserved dinosaur eggs come from the Late Cretaceous Nanxiong Basin of southeastern China, a locality that has yielded thousands of dinosaur eggs. The specimens are in the Löwentor Museum, Stuttgart, Germany.

Hadrosaur Egg

Hadrosaur Eggs

Sauropod Egg

Sauropod Egg

Oviraptor Egg

- A nest is a biogenic structure typically containing a clutch and commonly represented by an arrangement of eggs in a semicircular or spiraled pattern.
- In some instances, a raised area surrounding the eggs will denote the border of the nest.
- Dinosaur nests were on the ground, like some modern reptiles and a few birds (i.e., penguins), rather than in trees, like many modern birds.
- No evidence exists indicating that any dinosaurs lived in trees, let alone built nests in trees.

- Nests are sometimes found containing hatchlings or other remains of juveniles, which assists in the identification of the parental species.
- Community structures and social interactions for some dinosaurs, such as Maiasaurus, are indicated by multiple nests preserved on the same sedimentary horizon. The significance of this inferred interaction is that certain dinosaurs behaved much more like birds, rather than like most reptiles.

- This dinosaur nest shows a spiraled arrangement of the eggs, which were probably oriented in the nest by the mother dinosaur after they were laid. Specimen is in the Fruita Paleontogical Museum, Fruita, Colorado, USA.

- One of the more spectacular dinosaur fossil finds of recent years was of a Late Cretaceous specimen of Oviraptor that was found in a sitting position directly over its nest. This find, a wonderful combination of trace fossils and a body fossil, represents one of the most compelling pieces of evidence for brooding behavior in dinosaurs.

- **ALL** dinosaur eggs are basketball-sized or smaller: **NO** dinosaur hatched from eggs the size of people!!

- **ALL dinosaurs came from small babies!**

  (Differs from the mammalian condition, where baby elephants etc. are BIG animals!)

DINOSAUR TOOTHMARKS

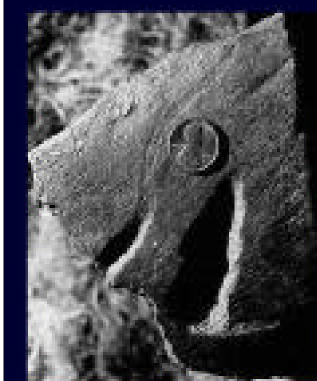
- All animals with teeth have the capability of leaving tooth marks on any solid substance that they bite, whether these substances are plants, animals, or (who knows why) rocks. A tooth mark is the impression left by a biting animal with teeth, regardless of what was being bitten.

- Dinosaurs who fed on other dinosaurs left distinctive tooth marks on bones, indicating feeding habits for some types of dinosaurs. In some cases, these tooth marks perfectly match the "dental records" of teeth from known dinosaurs and are preserved in bones of an identifiable species of dinosaur.

- An example of this direct correlation between "dinner" and "diner" is Tyrannosaurus tooth marks in Triceratops bones. However, such tooth marks do not necessarily mean that Tyrannosaurus preyed upon and killed Triceratops, because the specimen of Triceratops may have been already dead when munched by Tyrannosaurus (thus leaving open the possibility of scavenging behavior, rather than predation).

- This tail vertebra from Apatosaurus shows a few tooth marks on the left transverse process, indicating that some carnivorous dinosaur (probably Allosaurus) fed on Apatosaurus. Specimen is in the Museum of Western Colorado's Dinosaur Valley,Grand Junction, Colorado.

- The end of this limb bone (looks like a tibia) from Apatosaurus has parallel toothmarks on it. The spacing of the tooth marks, as well as the individual marks themselves, help to identify what dinosaur was feeding on this apatosaur.



Part of a pelvic bone with tooth marks. Notice especially the "bite-and-drag" mark to the left.

LEFT: A *T. rex* tooth. RIGHT: A mold made by pouring silicone rubber into one of the bite marks.

- Bite marks that show healing have been discovered in some dinosaurs, and in one a very few instances (Tyrannosaurus again and a Sinraptor from China) can be attributed to intraspecific competition. In other words, a healed tooth mark on a specimen of Tyrannosaurus was inflicted by another individual Tyrannosaurus, indicating that two individuals of the same species were fighting with one another. Thus, dinosaur toothmarks can indicate feeding habits and other interactions between or within species.

DINOSAUR GASTROLITHS

- Some modern birds will swallow stones, which then reside in their gizzards and aid in digestion of food by helping to grind tough food material. Because birds do not have teeth, they need their gizzards to grind their food, which helps to increase the surface area of the food for easier digestibility.

- Stones used to help in the mechanical breakdown of food within a digestive tract are called gastroliths ("gastro" = "stomach" and "lith" = "stone") and a colloquial term for gastroliths is "gizzard stones."
- Apparently dinosaurs also swallowed stones for the same reason as birds; numerous polished stones are associated with some dinosaur remains and are especially convincing when found within the thoracic regions of a skeleton. These stones are typically smooth, polished, and oblate to semispherical.

DINOSAUR COPROLITES

- One of the byproducts of digestion is waste material, which is conveniently excreted from the body at an end of the body opposite from the mouth region in most animals. This waste material can be in the form of a gas, liquid, or solid, but when preserved as a solid is politely called feces. A socially acceptable colloquial synonym for fecal material used by modern trackers is "scat," and these same people will refer to the study of scat as "scatology."

- **Coprolites** are fossilized feces, and dinosaurs were no different from other animals in leaving such deposits after digesting their meals.

- Dinosaur coprolites are valuable trace fossils for figuring out the paleodiets (or feeding behavior) of dinosaurs. Coprolites can show either body fossils of plant material (indicating an herbivorous diet) or bones (indicating a carnivorous diet).

- Modern grizzly bears of North America (Ursus horribilis) will leave scat containing both plant and animal matter (indicating an omnivorous diet), but **no dinosaur coprolites have demonstrated an omnivorous diet** by choice for dinosaurs (as far as I know).

- Herbivorous dinosaurs almost certainly would have ingested plant-dwelling insects and other arthropods while feeding, thus making them "accidental“ insectivores.

- Coprolites also provide information about habitats and the presence of dinosaurs in areas otherwise lacking dinosaur body fossils or other trace fossils (such as tracks). Preservation of coprolites is dependent on their original organic content, water content, where they were deposited, and method of burial. For example, coprolites made by carnivorous dinosaurs (theropods) were more likely to be preserved than those made by herbivores because of the high mineral content provided by bone material of the consumed prey animals.

- An good preservational environment would have been a floodplain associated with rivers, where the feces deposited on a dry part of the floodplain dehydrated slightly before rapid burial by a river flood. Other environments where coprolites were likely to have been preserved include "watering holes" (ponds), swamps, streams, and muddy areas associated with estuaries or lakes.

- This coprolite is most likely from a sauropod, owing mainly to its large size (about 40 cm diameter), and age (Jurassic); it is from the Morrison Formation in eastern Utah and the specimen was in the Löwentor Museum of Stuttgart, Germany.

- A coprolite this large probably does not represent one single pellet but an amalgamation of several pellets that merged together (indicating an originally high fluid content to the pellets). Individual dinosaur coprolites actually can be quite small (< 10 cm length) compared to the body size of the tracemakers. An example of this seemingly anomalous correlation can be observed in modern mule deer (Odocoileus hemionus) and elks (Cervus canadensis) of North America, animals that can weigh more than 100 kg but leave many individual pellets less than 1 cm in diameter.