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WAS *MESOSAURUS* AN AQUATIC ANIMAL? HOW DO WE KNOW IF AN ANCIENT SPECIES WAS AQUATIC OR TERRESTRIAL?

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Mesosaurs are lizard-like reptiles that lived at the beginning of the Permian Period (280–290 million years ago) or even earlier. Mesosaurs are known from thousands of skeletons recovered in Uruguay, Brazil, and Southern Africa, including young and adult individuals and even an embryo and a pregnant female. For years, mesosaurs have been considered aquatic (water-living) animals, because they have several characteristics of species that are adapted to an aquatic life, like webbed hands and feet and the presence of thickened and compact bones. However, mesosaurs also share several features with terrestrial (land-living) species, such as the structure of the hips, the limbs, and the heels. To figure out whether mesosaurs are actually aquatic or terrestrial, we studied vertebral columns (backbones) of *Mesosaurus*

and compared them to those of other aquatic and terrestrial animals. Studying the variations in the length of the vertebrae can reveal how the animals moved and whether they were adapted to terrestrial or aquatic environments. Surprisingly, we found that *Mesosaurus* is more similar to terrestrial animals, which changes our ideas about their lifestyle.

WHAT WERE THE MESOSAURS?

During early Permian times (280–290 million years ago), life on land included several amphibians and lizard-like animals that were the ancestors of all the dinosaurs, reptiles, and mammals. *Mesosaurus* was a lizard-like animal that lived in South America and Africa during the **Permian Period**. *Mesosaurus* is considered one of the earliest aquatic relatives of reptiles and mammals [1]. The word *Mesosaurus* is Latin, and "*meso*" means "middle." Scientists describing the first *Mesosaurus* fossils believed mesosaurs were "in the middle" between amphibians and reptiles, because they had features of both. Mesosaurs had several features that suggested they lived an aquatic lifestyle: a lateral compressed tail, webbed hands and feet, and nostrils placed close to the eyes in a high position (which allowed breathing without lifting the whole head out of the water, like crocodiles do). Also, like manatees and plesiosaurs, mesosaurs had dense, thick bones that may have

PERMIAN PERIOD

The last geological period of the Paleozoic Era, extending from 299 to 251 million years before present.

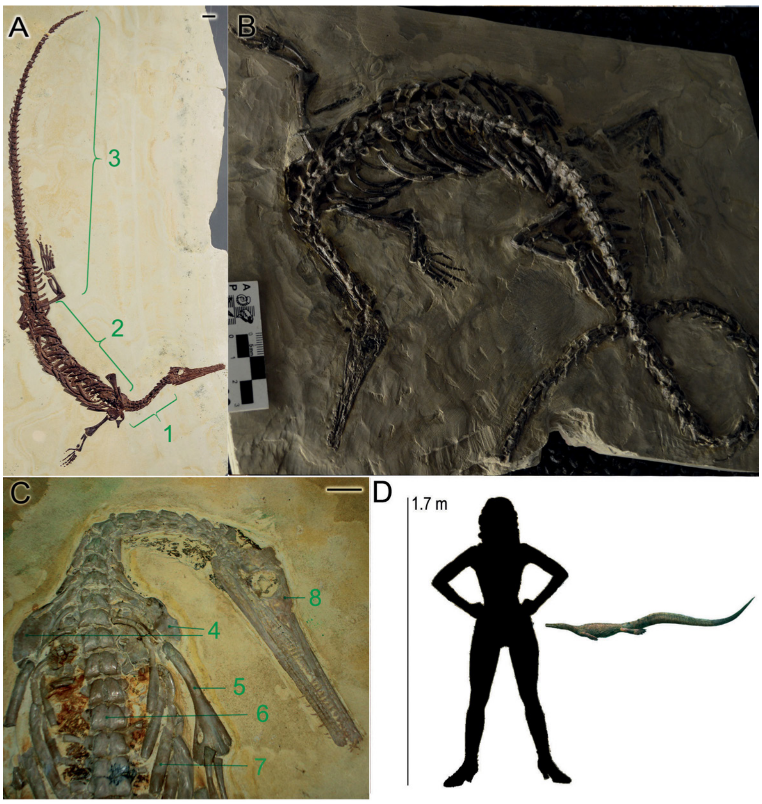

Figure 1

Figure 1

(A–C) Some mesosaur skeletons with various parts labeled: 1. cervical region, 2. dorsal region, 3. caudal region, 4. shoulder blade, 5. humerus, 6. vertebral column, 7. ribs, 8. skull. **(D)** A scaled figure showing the average size of *Mesosaurus*.

provided enable them to dive effortlessly in water (Figure 1). Because of all these characteristics, mesosaurs were considered fully aquatic and scientists believed that they rarely, if ever, came out of the water. However, mesosaurs also had certain features that were more similar to terrestrial animals, like the structure of the hip and heel [2]. Also, the environment in which mesosaurs lived was believed to have been very shallow water that was drying and shrinking, like what is happening today to the Aral Sea or Urmia Lake. So, in order to tell for sure whether mesosaurs were aquatic or terrestrial, we studied patterns in vertebral columns (backbones) and limbs (arms and legs) of mesosaurs, to see what we could determine about their lifestyle and to investigate just how aquatic they were.

MANY AQUATIC ANIMALS USE UNDULATION TO SWIM

UNDULATION

Wave-like motion.

OSCILLATION

Repeated movement. When talking about forms of swimming, it usually refers to flapping.

Most aquatic and semi-aquatic animals swim by moving their bodies or tails side to side, or up and down. This wave-like motion is called **undulation** and it is used by reptiles, whales, and fish. A few exceptions exist: turtles and penguins are aquatic animals that swim by repeatedly moving their paddles (this movement is called oscillatory movement or flapping) Animals like seals, walruses, and plesiosaurs swim using a combination of the movements of their paddles, tails, and bodies, combining undulation and **oscillation** movements.

Animals that undulate do not simply move their tails side-to-side or up and down to swim. Undulatory swimming involves movement of the whole body, because the wave-like motion passes along most of the vertebral column in order to reach the tail (Figure 2). Animals that swim with an undulatory movement have some features of their vertebral columns that allow them to make undulations of the appropriate size. For example, certain regions of the vertebral column may be reinforced, stiffened, elongated, or shortened, depending on the species.

If all the vertebrae are similar in length, the undulations will pass through the whole backbone in a similar way, from trunk to tail tip, without showing changes (Figure 2A). In contrast, differences in the lengths of certain vertebrae can produce changes in the undulations as they move along the spinal column. When an undulation passes through the body, each vertebra transmits the movement to the next one. If one vertebra is longer than the one before it, the size of the (horizontal) undulations increases in that area (Figure 2B). Similarly, if one vertebra is shorter than the one before it, a reduction in the size is produced, (Figure 2C). Over many generations, animals adapt by shortening their vertebrae in the areas where more rigidity and stability are needed or lengthening them where flexibility and enhanced mobility are needed.

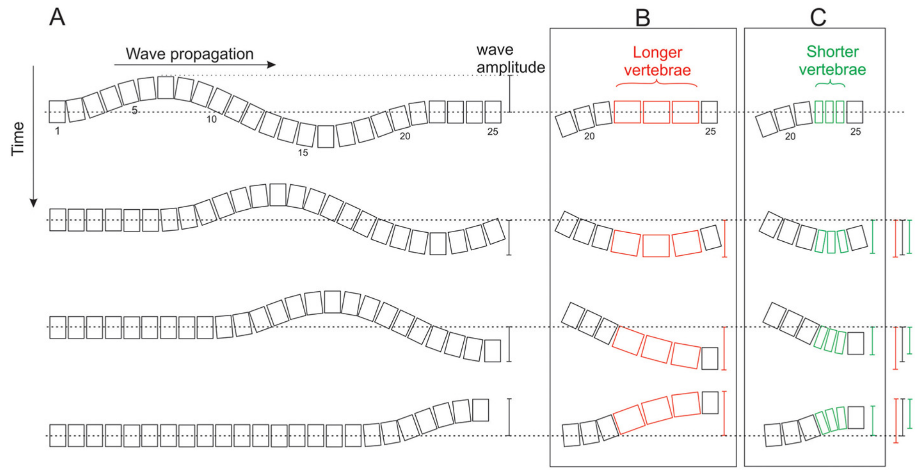

Figure 2

Figure 2

(A) How an undulation travels along the vertebral column when all vertebrae are the same length. The vertebrae are numbered from 1 to 25, with 1 being the first cervical (neck) vertebra. You can see that the wave maintains its size and shape along the vertebral column. **(B)** The amplitude (height) of the undulation increases when three vertebrae are longer than the rest. **(C)** The amplitude of the undulation is reduced when three vertebrae are shorter than the rest and the segments become more rigid. Note that the angle between the vertebrae is the same, the only difference is the segment length. Source: https://doi.org/10.3389/fevo.2018.00109.

It is expected that the vertebrae of aquatic and semi-aquatic animals should be longer in certain areas of their tails. In other areas, vertebrae should have a constant length, because these areas of the backbone allow the animals to generate and maintain wide undulations to propel themselves forward.

Terrestrial animals also undulate their vertebral columns while they walk. However, terrestrial animals need more mobility in their trunk regions, and so the vertebrae in the trunk region are the biggest ones, not the vertebrae of the tail like in aquatic animals.

A STUDY OF SKELETONS: WERE MESOSAURS ACTUALLY AQUATIC?

We examined 40 mesosaur skeletons, from museums of Uruguay, Brazil, France, Germany, Poland, Switzerland, and the USA. Some fossils were preserved as petrified bones; others were preserved as molds or casts in rock. We measured the length of each vertebra using high-resolution photographs (like in Figure 1), and we plotted the data to see how length changes along the body. Data from other extinct **semiaquatic** and terrestrial animals were also included in our study. We measured the vertebrae of other related extinct species and we collected data from other previously described animals from the literature. Then, we compared the data for *Mesosaurus* with the data from other semiaquatic and terrestrial animals. Some species that still exist were also studied, like crocodiles and iguanas, because these animals have semiaquatic lifestyles similar to mesosaurs. The extinct species were selected because they were of a similar geological age (from the Carboniferous or the Permian periods).

SEMIAQUATIC

Partially aquatic animals living or growing partly on land and partly in water or spending considerable amount of time in water. Usually, such animals live in or near water bodies, such as rivers, lakes or seas.

Because adult animals are larger than young members of the same species, comparing their data can be tricky. To solve this problem, we used a type of math called statistics to make the data for different sized individuals more valid.

We also compared, when the data was available, the relative sizes of the hind limb bones, which are different in terrestrial and aquatic animals (see Núñez Demarco et al. [3]).

MAYBE MESOSAURS WERE ONLY SEMIAQUATIC!

CERVICAL

Pertaining to the neck of an animal's body.

CAUDAL

Designates the tail or its area, the posterior part of an animal's body.

DORSAL

Related to the back of an animal's body.

We saw two patterns of vertebrae sizes; one for terrestrial and one for semiaquatic lifestyles (see Figure 3).

A. In terrestrial animals, the **cervical** (neck) vertebrae are longer than **caudal** (tail) vertebrae and in some cases can be even longer than the **dorsal** (trunk) vertebrae. The dorsal vertebrae are longer than the average, and the dorsal region of the spine displays either a peak in vertebral length or has a central region in which the dorsal vertebral length is almost constant. In some species, dorsal vertebrae are the longest ones. Caudal vertebrae decrease in length almost constantly toward the tip of the tail.

B. In semiaquatic animals, cervical vertebrae are not the longest ones; they are shorter than, or similar in size to, the caudal vertebrae. The dorsal vertebrae have a pattern that is similar to that of terrestrial animals, but the dorsal vertebrae are sometimes shorter than the average. Caudal vertebrae are sometimes the longest ones and,

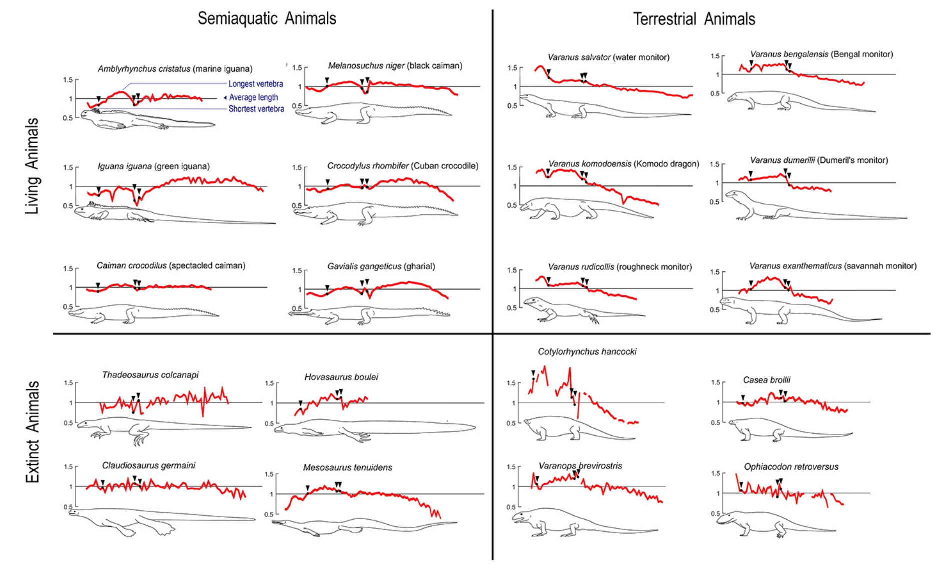

Figure 3

Vertebral length profiles for different species of semi-aquatic and terrestrial extinct and living animals related to mesosaurs. The data was created using statistical methods, so the y-axis shows the variation in length with respect to the average vertebral length. For example, a value of 1.5 means that the vertebra is 1.5 times the average. Black arrows mark the areas where the neck ends and the chest begins, and where the trunk ends and the tail begins. From this data, you can see that the vertebral length decreases continuously in the tails of terrestrial animals, but it increases or maintains its length in the tails of semiaquatic animals. Source: https://doi.org/10.3389/fevo.2018.00109.

Figure 4

Figure 4

Reconstruction of mesosaurs in their harsh environment 280 million years ago, showing closely placed volcanoes spreading ashes over the salt-water lake where they lived. You can see the likely food of mesosaurs, the pygocephalomorph crustaceans, below to the right. Note that following the results obtained in this study, *Mesosaurus* specimens are shown swimming in the lake and also walking on the ground. Credit: Roman Yevseyev, Pablo Núñez Demarco and Graciela Piñeiro.

unlike in terrestrial animals, the caudal vertebrae increase in length or keep their length constant along almost half of the tail.

Intriguingly, *Mesosaurus* has an intermediate pattern. Its cervical vertebrae are short, as in semiaquatic animals, except for four or five vertebrae in the middle of the neck observed in some individuals. However, *Mesosaurus's* caudal vertebrae have a pattern that is in between the terrestrial and semiaquatic patterns. This result is surprising, because for many years was believed that mesosaurs were aquatic, but their patterns somehow resemble those of terrestrial animals, which suggests a semiaquatic lifestyle, living partly on land and partly in the water (see Figure 4).

WHY THIS IS IMPORTANT?

Some previous studies suggested that mesosaurs laid eggs on land [4]. Thus, they could be the first known animals that laid their eggs on land. However, that theory was not universally accepted, because it was thought that mesosaurs hardly ever went ashore. Nevertheless, our study showed that mesosaurs could move on land, just as crocodiles do! This evidence will help us to understand much more about the evolution of mesosaurs and the possible causes of their eventual extinction, and might also lead us to question our ideas about other ancient species that we currently believe to be specially adapted to a particular environment.

ORIGINAL SOURCE ARTICLE

Núñez Demarco, P., Meneghel, M., Laurin, M., and Piñeiro, G. 2018. Was *Mesosaurus* a fully aquatic reptile? *Front. Earth Sci.* 6:109. doi: 10.3389/fevo.2018.00109

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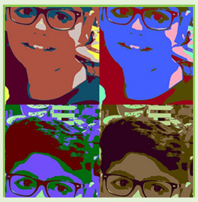

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Hello, my name is Shashi, I am 12 years old and I go to Penglais School. I enjoy playing football and basketball. My favorite subjects are Maths and Computers. I am currently studying year 7. I am a four times Guinness World Records holder in a game called Rocket League and my name is in 2018 Guinness World Record Gamers Edition.

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I am Geologist. I work as Assistant Professor at the Universidad de la República (Uruguay). Currently, I am doing my Ph.D. in Geophysics in Argentina, analyzing the magnetic field of the earth to survey the structure of the earth's crust. My work connects fields like astronomy, physics, geology, mathematics, and paleontology. Away from my studies, I am a geek, nerd, and gamer boy. *pnunez@fcien.edu.uy

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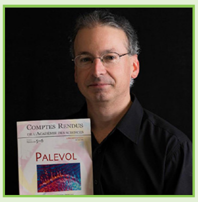
I am a Biologist, Professor, and Head of Vertebrate Zoology at the Universidad de la República in Uruguay, where I teach advanced courses in Vertebrate Zoology and Evolutive and Functional Anatomy of Vertebrates. My foremost interest is studying reptiles' biology, particularly the behavior and anatomy of poisonous snakes. My involvement with mesosaurs started some years ago, trying to interpret their anatomy and possible ways of life, using my knowledge of living reptiles as reference. In my free time I like crafting.



MICHEL LAURIN

I am a Paleontologist and Evolutionary Biologist interested in evolution of limbed vertebrates. I sometimes develop new methods (often through collaborations) and my main interests include studying how extinct animals lived, dating the Tree of Life, and how development of animals changes over time. My core expertise centers on Permo-Carboniferous limbed vertebrates and bone microanatomy. I am a Senior Research Scientist working for the CNRS in Paris, France, and I am currently one of the two Chief Editors of the Comptes Rendus Palevol.

GRACIELA HELENA PIÑEIRO

I am a Paleontologist and Evolutionary Biologist interested mainly in Late Paleozoic fossils from Uruguay. My passion and love for mesosaurs started a long time ago, when I found the first specimen of these small ancient reptiles. Now we know more about their biology, including their preferred prey, their main reproductive strategies, and their lifestyle. I would like to spend more time working with mesosaurs, but I am a Professor at the Universidad de la República (Uruguay), where I teach about the origin and evolutionary history of all vertebrate groups, from fishes to mammals. In my free time, I like to cook and spend good moments with my family. *fossil@fcien.edu.uy