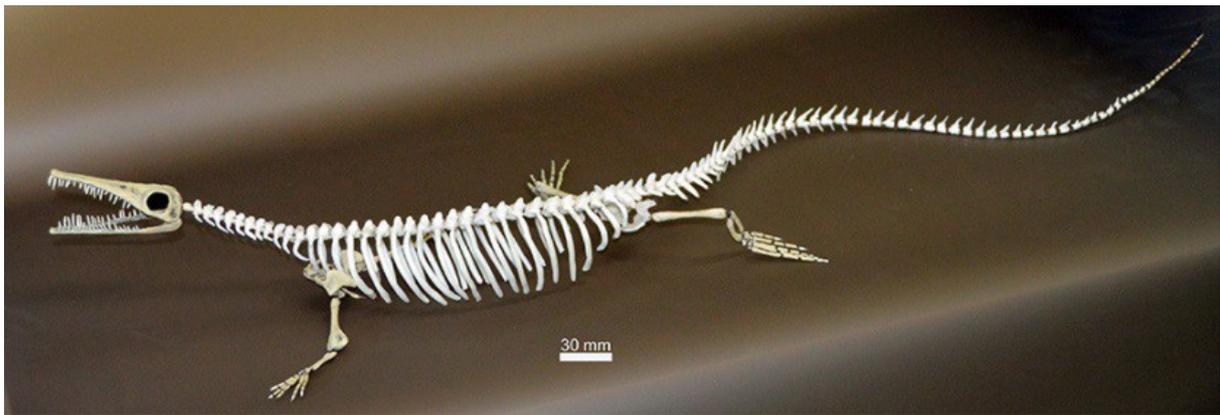


6 MARCH, 2017

The feeding habits of mesosaurs

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*Skeletal reconstruction of a young adult mesosaur (*Mesosaurus tenuidens*) from the Early Permian of Uruguay and Brazil (reproduced from Silva et al., 2017).*

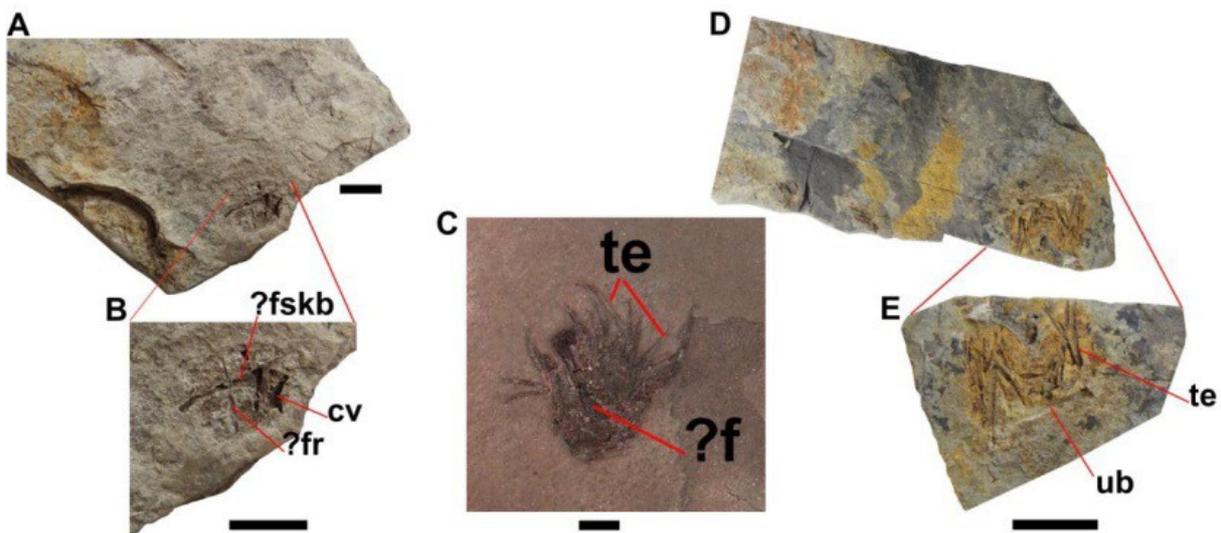
Mesosaurs and the Early Amniote Evolution

Mesosaurs represent the most amazing animals of the distant past. They are the oldest known amniotes that developed adaptations to aquatic environment. By the Early Permian, mesosaurs inhabited cold and salty water bodies resulting from the drought of an originally large inland sea that extended over what is now South America and Africa (Piñeiro et al., 2012b). Mesosaurs are represented by several species and a myriad of specimens, including well-preserved skeletons from the Lower Permian of Uruguay, Brazil, and southern Africa, which have been studied for a long time since the 19th century. Thanks to the specific geographic distribution of their remains, mesosaurs have even helped Alfred Wegener to formulate the theory of continental drift.

The study of mesosaurs is indeed important for a number of reasons. First of all, they represent so-called basal amniotes. It means that mesosaurs were quite close in the evolutionary tree to the last common ancestor of all sauropsids (a group including reptiles, their ancestors and relatives) and synapsids (a group including mammals, their ancestors and relatives). For instance, the discovery of well-preserved mesosaur embryos curled as within an egg, and one pregnant female has recently yielded clues

about the reproductive biology of early amniotes (Piñeiro et al., 2012a). Interestingly, mesosaurs were viviparous or they laid eggs in advanced stages of development. Finds from Uruguay even suggest that there perhaps existed some kind of parental care in mesosaurs due to common associations of remains of adults with newborns.

Such data can be better understood when interpreted in a broader paleoecologic context. Therefore, our team composed of four researchers from Uruguay, Brazil, and Poland (R.R. Silva, J. Ferigolo, P. Bajdek, and G. Piñeiro) and lead by Graciela Piñeiro, has recently published a new paper on the biology of mesosaurs (Silva et al., 2017), which largely expands our knowledge about these animals. Here, we'd like to briefly sum up our conclusions regarding the feeding habits, physiology, and environment of mesosaurs of Uruguay and Brazil.



Putative mesosaur regurgitalites (fossil vomit) from the Mangrullo Formation, Uruguay; scale bars 1 cm (reproduced from Silva et al., 2017).

Unusual Finds from the Lower Permian of Uruguay and Brazil

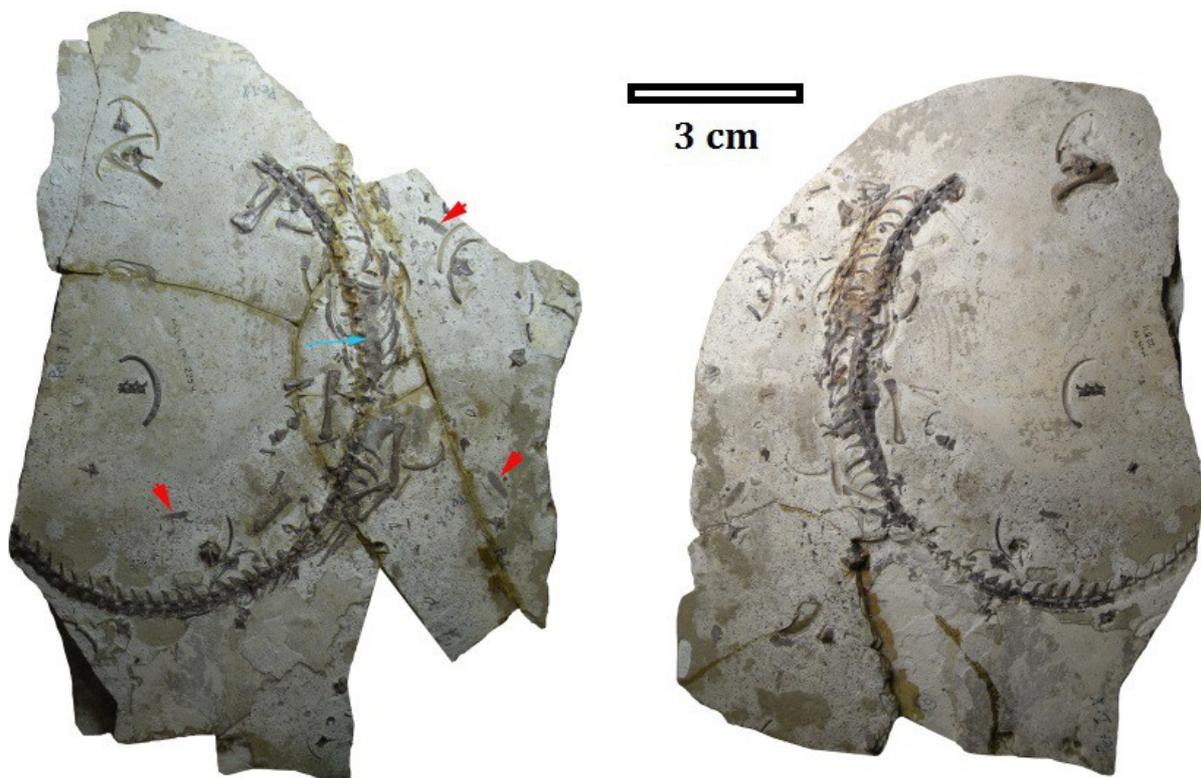
Preserved gastric contents, cololites (fossil intestine matter), coprolites (fossil feces), and regurgitalites (fossil vomit) of mesosaurs that we have studied, tell us a lot about the feeding habits, physiology, and life conditions of mesosaurs. These fossils come from the Mangrullo Formation of Uruguay and the Iratí Formation of the State of Goiás, Brazil. Mesosaurids lived in an inland hypersaline water body, with exceptional preservation conditions that justified describing mesosaur-bearing strata as a Fossil-Lagerstätte.

First of all, our study represents an exceptional case where gastric contents, cololites, coprolites, and regurgitalites (i.e., all the “basic” bromalite types) of a single animal

species are described. It gave us an uncommon opportunity to make certain observations on all these fossil types, such as to compare their general form of preservation and even the degree of digestion of swallowed remains in different stages of the digestive process.

Paleontologists hardly ever are able to link fossil feces to their producer. This case is different. No other tetrapod is found in the mesosaur-bearing strata. The coprolites have a non-spiral morphology that is typical for tetrapods, in contrast to all fish of the Permian Period. Finally, the content of the coprolites is comparable to that found in mesosaur stomach and intestine contents. Alternatively, the smallest of the coprolite specimens would have been produced by large crustaceans.

Such an uncommon opportunity to take a look at the feeding habits of an extinct animal must not be wasted. Previously, the diet of mesosaurs was only inferred from indirect evidence, what is in fact a kind of 'educated guess'. For over a hundred years, various hypotheses have been proposed for determining mesosaur feeding habits: fish-eating, sludge filter-type habit, or crustacean-based diet. Now, let's look deep into mesosaur stomachs...



Mesosaur skeleton (Brazilosaurus sanpauloensis) showing a preserved cololite (blue arrow) and several coprolites surrounding it (red arrows), from the Iratí Formation, Brazil (modified from Silva et al., 2017).

Cannibals and Scavengers under Environmental Stress

We found out that mesosaur diet included crustaceans as the main food item, corroborating some of the hypotheses. On the other hand, no fish remains were recognized in mesosaur gastric contents, cololites, coprolites, and regurgitalites, as no fish are found in the mesosaur-bearing strata. More surprisingly, acid-etched mesosaur bones and teeth are found in mesosaur bromalites.

The presence of mesosaur remains in mesosaur stomach content, regurgitalites, and other bromalites, is particularly interesting. Yet, easy assumptions in the study of bromalites are sometimes misleading. Were mesosaurs cannibalistic predators? Well, the jaw aperture in an average-sized mesosaur was much too small to allow even newborn mesosaurs to be swallowed whole, meanwhile mesosaur teeth seem not to be adapted to powerful biting. A predatory scenario would be hence a little surprising to us. Instead, we note that mesosaurs fed on crustaceans generally not exceeding 2 cm in length. Taking a close look at the gastric contents we can recognize no articulated skeletal elements, which would be expected to be still present in the earliest stage of the digestive process.

Explanation of the mystery requires a comment on the environment which the mesosaurs lived in. Mesosaur remains are found in rocks formed in a hypersaline water body and such environments are famous for extreme severity. The stress conditions might have been also caused by the extended volcanism and ash spread into the water body during the Early Permian. The environmental conditions and the faunistic poverty of the mesosaur-bearing 'salty sea' are the first key to the mystery. There were no fish in water, nearly nothing to eat for mesosaurs but crustaceans and... mesosaur dead bodies.

Cannibalistic behavior and scavenging are quite common under environmental stress, overcrowding and insufficient food resources. Mesosaurs probably ingested elements of mesosaurid carrion in partial decomposition. It seems possible that also the largest of the crustacean remains were scavenged from the bottom, as they often appear to be very weathered.

Mesosaurs regurgitated the biggest of bone fragments as well as seemingly crustaceans, which were too large to pass through the gastrointestinal tract. Various amniotes, as for example raptor birds, crocodiles, and probably ichthyosaurs, regurgitate most of the indigestible or hard-to-digest remains. Some of the objects might have been ingested accidentally, or were mesosaurs so hungry living in this harsh environment? Regurgitation might also have been caused by the environmental stress itself. Because digestion efficiency depends on body temperature, in extant reptiles undigested food remnants may be regurgitated during periods of unfavorable environmental temperature. Disease may also cause regurgitation.

Bone elements in the mesosaur coprolites are intriguing too. Reptiles are characterized by a strong digestion and many of them digest the swallowed bones practically completely. However, mesosaurs were fairly small and their period of digestion was not necessarily very long. Also, the presence of poorly digested remains in feces, caused by short digestion, may have to do with fluctuating food availability.

Epilog of the Mesosaur Story

Fossilization of the mesosaur remains and their bromalites was facilitated by microbial mats on the bottom of the water bodies and the volcanic events and ash spread. It gave us a fascinating, but also a little terrifying opportunity to investigate enigmas of the biology of some of the earliest amniotes. The study of mesosaurs has just begun!

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