



MESOSAUR TAXONOMY REAPPRAISAL: ARE *STEREOSTERNUM* AND *BRAZILOSAURUS* VALID TAXA?

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ABSTRACT – Mesosaurs are basal amniotes that lived at the beginning of the Permian or close to the Permo–Carboniferous boundary. Despite the several hundred specimens that have been found, including complete skeletons of adult and juvenile individuals, mesosaur taxonomy has been subjected to a high controversy over time. Currently, three monotypic genera, *Mesosaurus tenuidens* Gervais, *Stereosternum tumidum* Cope, and *Brazilosaurus sanpauloensis* Shikama & Ozaki are recognized, but identification of new specimens using the available diagnostic characters are arbitrary and influenced by high subjectivity. We performed anatomical and morphometric analyses to look for statistical support to these previously suggested basic diagnostic characters through an exhaustive anatomical revision of these characters and also of some new attributes discovered during the course of our study. We found a notable influence of taphonomic features in most of the diagnostic characters used to differentiate the three monotypic genera, including strong bias derived from the preservation of individuals in different ontogenetic stages, whose size and degree of ossification could have been controlled by particular environmental conditions that resulted in subtle polymorphisms of these and other few characters. Other features may even represent sexual dimorphism. After the detailed revision of the type specimens of the three currently accepted mesosaur taxa, for which we include here good-quality photographs, and considering the lack of statistical support for the most applied putative diagnostic features such as the different ratio found when comparing skull and cervical region lengths and the low or higher intensity of pachyosteosclerosis observed in dorsal ribs, which can be controlled by taphonomic and ecological conditions, we recognize *Mesosaurus* as the only mesosaurid taxon in the Paraná and Karoo basins, probably including dwarf individuals. Therefore, *S. tumidum* and *B. sanpauloensis* are suggested here as *nomina dubia* taking into account that the autapomorphies that supported these taxa cannot be confirmed to be absent in *Mesosaurus*.

Keywords: *Mesosaurus*, morphometrics, taxonomy, ?Early Permian, Gondwana.

RESUMO – Mesossauros são amniotas basais que viveram no início do Permiano ou próximo ao limite Permo–Carbonífero. Apesar das centenas de espécimes encontrados, incluindo esqueletos completos de indivíduos adultos e juvenis, a taxonomia dos mesossauros tem sido tema de muita controvérsia ao longo do tempo. Hoje, três gêneros monotípicos, *Mesosaurus tenuidens* Gervais, *Stereosternum tumidum* Cope, e *Brazilosaurus sanpauloensis* Shikama & Ozaki são reconhecidos, mas a identificação de novos espécimes utilizando os caracteres diagnósticos disponíveis é arbitrária e influenciada por alta subjetividade. Nós realizamos análises anatômica e morfométrica, tendo em vista obter um suporte estatístico para estes caracteres sugeridos como diagnósticos básicos por meio de uma exaustiva revisão anatômica destes caracteres, e de alguns novos caracteres descobertos durante o desenvolvimento de nosso estudo. Nós notamos uma notável influência de fatores tafonômicos na maioria dos caracteres diagnósticos utilizados para os três táxons monotípicos e incluindo uma forte preconceção derivada da preservação dos indivíduos em diferentes estágios ontogenéticos, cujos tamanho e grau de ossificação poderiam

ser controlados por condições ambientais que resultaram em sutis polimorfismos destes poucos caracteres. Outros aspectos podem mesmo representar dimorfismo sexual. Considerando a falta de suporte estatístico para a maioria dos putativos caracteres diagnósticos, tais como as diferentes relações entre comprimento do crânio e da coluna cervical e a pressão das condições tafonômicas e ecológicas, que podem ter controlado um menor ou maior grau de paquiosteoesclerose nas costelas dorsais, nós reconhecemos *Mesosaurus* como o único táxon de mesosaurídeo nas bacias do Paraná e Karoo, provavelmente incluindo populações anãs, e sugerimos que *S. tumidum* e *B. sanpauloensis* devem ser considerados como *nomen dubium*, levando em conta que as autapomorfias que suportam estes táxons não podem ser confirmadas como não estando presentes em *Mesosaurus*.

Palavras-chave: *Mesosaurus*, morfometria, taxonomia, ?base do Permiano, Gondwana.

INTRODUCTION

Mesosaurus are basal amniotes believed to be the first group that returned to the aquatic environment (Carroll, 1988), although recent studies suggest that they could have been semiaquatic and capable of being active on land (Núñez Demarco *et al.*, 2018). Because of their short time range and restricted geographic distribution, mesosaurus were considered good stratigraphic fossils for the Early Permian of Gondwana. However, their basal position in recent phylogenetic studies (Laurin & Piñeiro, 2017, 2018; MacDougall *et al.*, 2018) and the fact that they are part of a community in which pygocephalomorph crustaceans, insects and plants suggest a Late Carboniferous or a transitional Permo-Carboniferous age for the strata (see Huene, 1940; Calisto & Piñeiro, 2019), mesosaurus could have a ghost lineage that lead their origin to at least Late Carboniferous (Piñeiro *et al.*, 2012a). Their remains are recorded from Uruguay, Brazil, Namibia and South Africa, although some scarce and fragmentary fossils were also reported from Paraguay (Beder, 1923; Filippi, 2001; Piñeiro, 2002, 2006). This distribution was considered as one of the best paleogeographic arguments for the physic merging between South America and Africa during Late Carboniferous and Early Permian times and the establishment of a glacioeustatically-controlled sea as a nexus (Wegener, 1966; Oelofsen & Araújo, 1983).

Paradoxically, although mesosaurus are represented by thousands of specimens including almost complete skeletons, their taxonomic composition of three monotypic taxa, *Mesosaurus tenuidens* Gervais, 1865, *Stereosternum tumidum* Cope, 1885a and *Brazilosaurus sanpauloensis* Shikama & Ozaki, 1966 was subjected to debate (*e.g.* Piñeiro, 2002, 2004, 2006; Piñeiro *et al.*, 2012b). The major concerns are the poor definition and difficult identification of the diagnostic characters for each genus, even in the almost complete individuals. Therefore, this issue complicates the taxonomic assignment of the numerous articulated but fragmentary specimens available, which represent valuable evidence for reconstructing biological trends in mesosaurus and the influence of depositional environments.

It is possible that the small size and fragility of mesosaurus bones, often injured by fractures and microfractures, conspired to the incorrect recognition of the diagnostic features, which along with the influence of taphonomic traits, produce misinterpretations in the arrangement of the bones by the overlapping and fracturing observed in both cranial

and postcranial regions. Also, the preservation of specimens as molds printed as parts and counterparts (see for instance Laurin & Piñeiro, 2017), intriguingly produces virtually different morphological patterns of the bones from a single individual. Taphonomy has thus played an important role in the misidentification of the diagnostic characters and has introduced a high degree of subjectivism to the anatomical reconstructions, particularly at key skull regions.

All these issues led previous authors to even place mesosaurus as basal synspsids (Huene, 1941), basal diapsids (MacGregor, 1908) and more recently, basal anapsid parareptilians (Modesto, 1999; MacDougall *et al.*, 2018) or basal sauropsids (Laurin & Reisz, 1995; Laurin & Piñeiro, 2017, 2018). Even though appearing to be so different, all these hypotheses place the origin of mesosaurus into the Late Carboniferous, as the associated plants and invertebrates suggest (Huene, 1940; Calisto & Piñeiro, 2019).

Since the studies performed by Araújo (1977, usually cited as 1976, but actually printed in March 1977), the hypothesis of three monotypic mesosaurus taxa was the most accepted to define the family Mesosauridae. According to this hypothesis the three taxa would be easily identified because *Mesosaurus tenuidens* is mostly characterized by a long skull and a relatively short neck, while *Stereosternum tumidum* has an equivalent skull-neck length and in *Brazilosaurus sanpauloensis* the neck would be longer than the skull. That characterization was supported also by Oelofsen (1981), and more recently by Modesto (1996, 1999, 2010), and Rossmann (2000, 2001). Other characters described for identifying these mesosaurus species such as the length and section of the teeth, the pachyostosis degree of dorsal ribs, the presence/absence of an ectepicondylar foramen in the humerus, the presence of a notch or a complete foramen in the pubis (oburator foramen?), the presence of a supraneural process in dorsal vertebrae and the degree of pachyosteosclerosis in the caudal hemal arches, although ambiguous, were also evaluated as diagnostic by different authors (*e.g.* Seeley, 1892; Shikama & Ozaki, 1966; Araújo, 1977; Oelofsen, 1981; Oelofsen & Araújo, 1987; Sedor, 1994; Modesto, 1996, 1999, 2006, 2010; Soares, 1996; Sedor & Ferigolo, 2001; Rossmann, 2000, 2001; Piñeiro, 2002, 2004; Pretto *et al.*, 2014; Silva *et al.*, 2017; Laurin & Piñeiro, 2017, 2018).

At the level of the cranial anatomy, only Modesto (1996, 2006) reported differences between *Mesosaurus* and *Stereosternum*, but they were demonstrated to be taphonomically constrained by the preservation of specimens

as part and counterpart, which reproduce part of the internal surface of the bones (Piñeiro *et al.*, 2012b; Laurin & Piñeiro, 2017). Recently, well-preserved cranial materials from Uruguay assigned to *Mesosaurus* showed the presence of a small lower temporal fenestra (Piñeiro, 2004, 2006; Morosi, 2011; Piñeiro *et al.*, 2012b), thus confirming previous works by Huene (1941). The failure to determine the presence of a fenestra in all specimens assigned to *Stereosternum* and *Brazilosaurus*, and thus addressing the consideration that it may not be present in all mesosaurs, has constrained the resolution of the mesosaur phylogenetic relationships (Laurin & Piñeiro, 2017, 2018; MacDougall *et al.*, 2018).

The taphonomic features that favored the detailed preservation of isolated skulls in the Mangrullo Formation of Uruguay can be related to periodic ash falls in the basin and the installation of hypersaline and acidic bottom conditions (Piñeiro *et al.*, 2012c). This kind of preservation allows the discovery of skulls preserving complete and articulated bones, which thus retain their original anatomical position. These depositional conditions in the Konservat-Lagerstätte of the Mangrullo Formation (Piñeiro *et al.*, 2012c) are however not favorable to preserve fully articulated skeletons as they are seen in the correlative Irati Formation of Brazil. In this last country, the sedimentary bulk of rock covering the specimens is so thick that pressure fractured and dislocated the fragile skull bones.

As for the mesosaur postcranium, described in detail by several previous authors (*e.g.* Seeley, 1892; MacGregor, 1908; Huene, 1940; 1941; Araújo, 1977; Oelofsen, 1981; Sedor, 1994; Modesto, 1999, 2010), the morphological differences that would assure the recognition of the three monotypic mesosaur taxa are indeed very weak. Piñeiro (2002, 2004) and more recently Piñeiro *et al.* (2012a, b; 2016) and Laurin & Piñeiro (2017, 2018) have questioned most of such differences arguing that they are derived from taphonomy and may represent ontogenetic and intraspecific variability (probably including sexual dimorphism), in response to variable environmental conditions, thus suggesting the presence of just one mesosaur species in the Paraná and the Karoo basins. In any case, two morphotypes can be detected but they are difficult to relate to the previously proposed taxonomic categories.

The aim of this paper is to present an overview of the main diagnostic characters previously used to identify mesosaur species, specially focusing on finding a stronger characterization for *Brazilosaurus sanpauloensis* through a detailed anatomical, taphonomic and comparative morphometric study of more than three hundred of mesosaur specimens belonging to collections of Uruguay, Brazil, Germany, Japan, USA, Switzerland, South Africa, Namibia, United Kingdom and France.

MATERIAL AND METHODS

Several specimens revised and measured during this study were collected by the senior author and her students from palaeontological sites of the Mangrullo Formation of Uruguay

and are deposited in the Fossil Vertebrates Collection of the Facultad de Ciencias (**FC-DPV**), at Montevideo, Uruguay. Other studied specimens were collected by personnel of the Department of Geology of the Facultad de Agronomía and are deposited in the fossil collection of that institution (**FAGRO**). We also analysed complete individuals and partially preserved mesosaur skeletons from the following collections: **AMNH**, American Museum of Natural History, New York, USA; **BP/1**, Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa; **DNPM**, Departamento Nacional de Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **GP/2E**, Instituto de Geociências (section Palaeontology) of the São Paulo University, São Paulo, Brazil; **GSN-F**, National Earth Science Museum at the Geological Survey of Namibia, Africa; **MCN-PV**, Museu de Ciências Naturais, SEMA, Porto Alegre, Brazil; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **NHMUK** earlier **BM(NH)**, National History Museum of London, United Kingdom; **NSM-PV**, National Museum of Nature and Science, Japan; **PIMUZ**, Paleontological Institute and Museum of the University of Zurich, Switzerland; **SMF-R**, Senckenberg Forschungsinstitut und Naturmuseum Institut, Frankfurt, Germany.

We examined a total of 305 mesosaur specimens in different ontogenetic stages, 206 come from South America (Brazil and Uruguay) and 99 from Africa (Namibia and South Africa) (Table 1 and annexes in Supplementary Materials). The large sample includes unborn and several new-born individuals and specimens representing larger (mature) mesosaurs. Characters previously used to distinguish the different mesosaur taxa were revised, as well as other new skeletal features that were detected as potentially diagnostic. By applying morphometrics, we evaluated the strength of each character in articulated skeletons and the influence of ontogeny and/or taphonomy in *a priori* possible subjective interpretations.

It is worth noting that, until now, most of the studies on mesosaurs come from the analysis of specific individuals or samples from the same collection, locality or level. Our sample not only comprises a large number of specimens collected in Uruguay over more than 25 years, but it also includes the type specimens and syntypes of *Mesosaurus*, *Stereosternum*, and *Brazilosaurus*, and fossils from various additional sources as they were collected over time by different people, from different countries and from different sedimentary levels. In consequence, we can ensure that our sample is spatial and temporally representative. Thus, it is expected that it should contain representatives of all the described species.

Methods for the morphometric study

Most mesosaur specimens examined in this study (including the type specimen of *Mesosaurus tenuidens*) were revised at hand and photographed. The type specimens of *Stereosternum tumidum* and *Brazilosaurus sanpauloensis* were examined through high resolution and quality photographs, which for the first time after the description date of these taxa, are exhibited in a paper.

Then, 2D measurements were taken using the digital images. The specimens were preserved as molds, impressions, casts or permineralized half-buried bones. All the selected specimens are articulated or semi-articulated individuals, but isolated bones were also analysed for morphological reconstructions and determination of virtual intra or interspecific variability.

We measured skull length and cervical vertebral lengths in order to study the ratios between the skull and the neck length (Figure 1). This analysis could be performed in just a few specimens (23 out of 305 specimens), which preserved the skull in association with the complete cervical region.

To determine the variability in the mesosaur dentition we measured tooth length and maximum width in skulls or jaws that preserve them in place (23 out of 305 specimens). The width was measured at the tooth base, preventing any deformation produced by diagenetic compression. Moreover, the selected specimens presented other measurable characters in order to compare them with the resulting tooth length patterns. Particularly, in 18 specimens the length of the skull

or jaw could also be measured and compared. As mesosaurs change their teeth often, their dentition is made up of both old and young teeth, hence measurements can present great variability. To overcome this problem, we calculated the average length and width for each specimen measuring teeth of different sizes as they were preserved (Figure 2A). For the specimens in which teeth can be measured (18 out of 23), we also compared the mean of tooth length with the skull length (see Figure 2B). Additionally, we compared the ratio of the mean tooth length over the mean tooth width against the skull length (see Figure 2C).

We also measured pachyosteosclerosis through radius/rib ratio. Radius's width was taken in the middle of its diaphysis, and that measure would represent the minimum diameter of the bone. However, as the radius is not always preserved (because it is disarticulated and hidden), we also compared the ribs' width with measurements in the most common and recognizable long bones in mesosaur skeleton: humerus and femur. Width measurements of the humerus and femur were taken in the diaphysis (minimum width) so width between bones are more

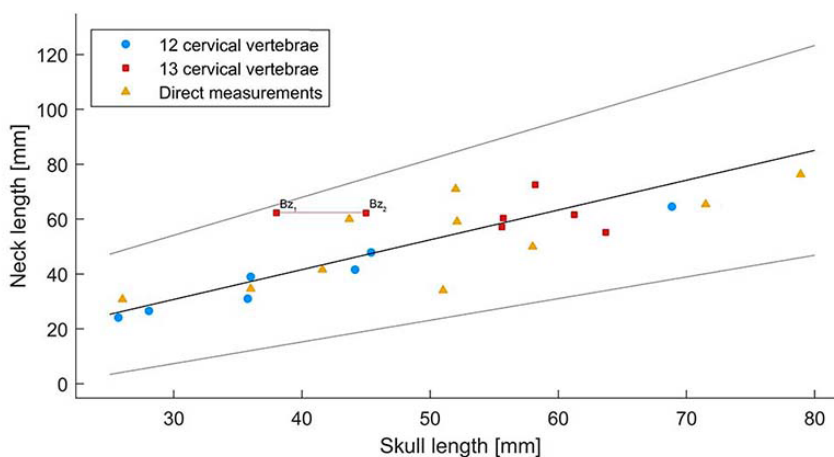


Figure 1. Plotting of skull length vs. neck length in the analyzed mesosaur specimens (NSM-PV 21867 *Brazilosaurus* type specimen; PIMUZ A III 192, 591; GP-2E 232, 284, 644, 669, 5637, 5818; AMNH 23794, 23795, 23796, 23799; SMF-R 4512, 4513, 4528, 4710, 4935, 4934; GSN-F 1636, 1640; FC-DPV 2318). Correlation coefficient: 0.97. Bz: Type specimen of *Brazilosaurus sanpauloensis* (NSM-PV 21867), Bz1: Actual length of the skull of NSM-PV 21867 with fractured snout, Bz2: Estimated total length of the skull NSM-PV 21867.

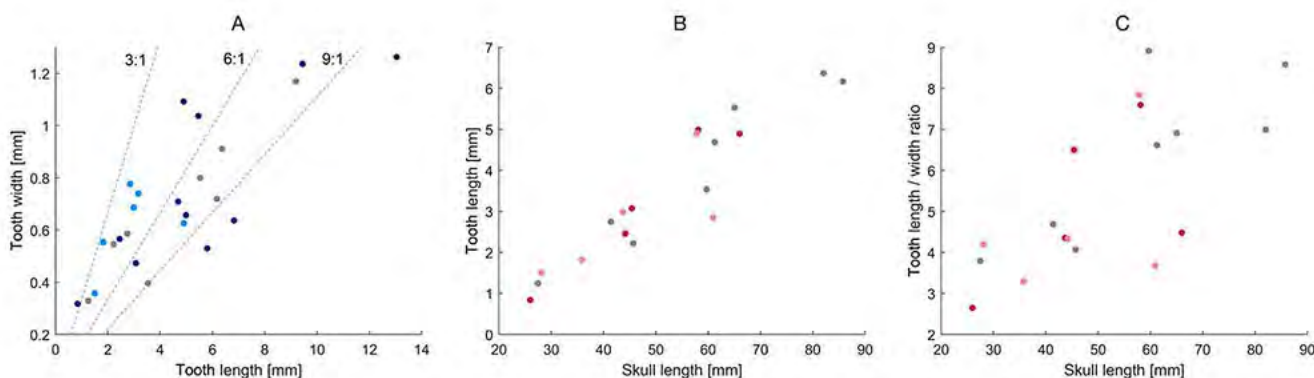


Figure 2. Tooth length in mesosaurs. **A**, mean tooth length vs. mean tooth width. Dotted lines represent the different length/width ratios indicated in the figure. **B**, mean tooth length vs. skull length. **C**, skull length vs. tooth length/width ratio. Dark colored dots are specimens that can be identified as *Mesosaurus* while light colored dots can represent specimens that can belong to other species. Grey dots correspond to specimens that cannot be assigned to any of the previous morphotypes because the lack (no preservation) of diagnostic characters.

comparable. We also calculated and used the mean of dorsal rib width because rib thickness is very variable, depending on rib number and location of the measure along the bone; error bars with three standard deviations are shown in plots (Figure 3).

Measurements were taken without consideration of the taxonomic status of the specimens. Subsequently, the characters present in each individual were analysed and (when possible) they were tentatively identified.

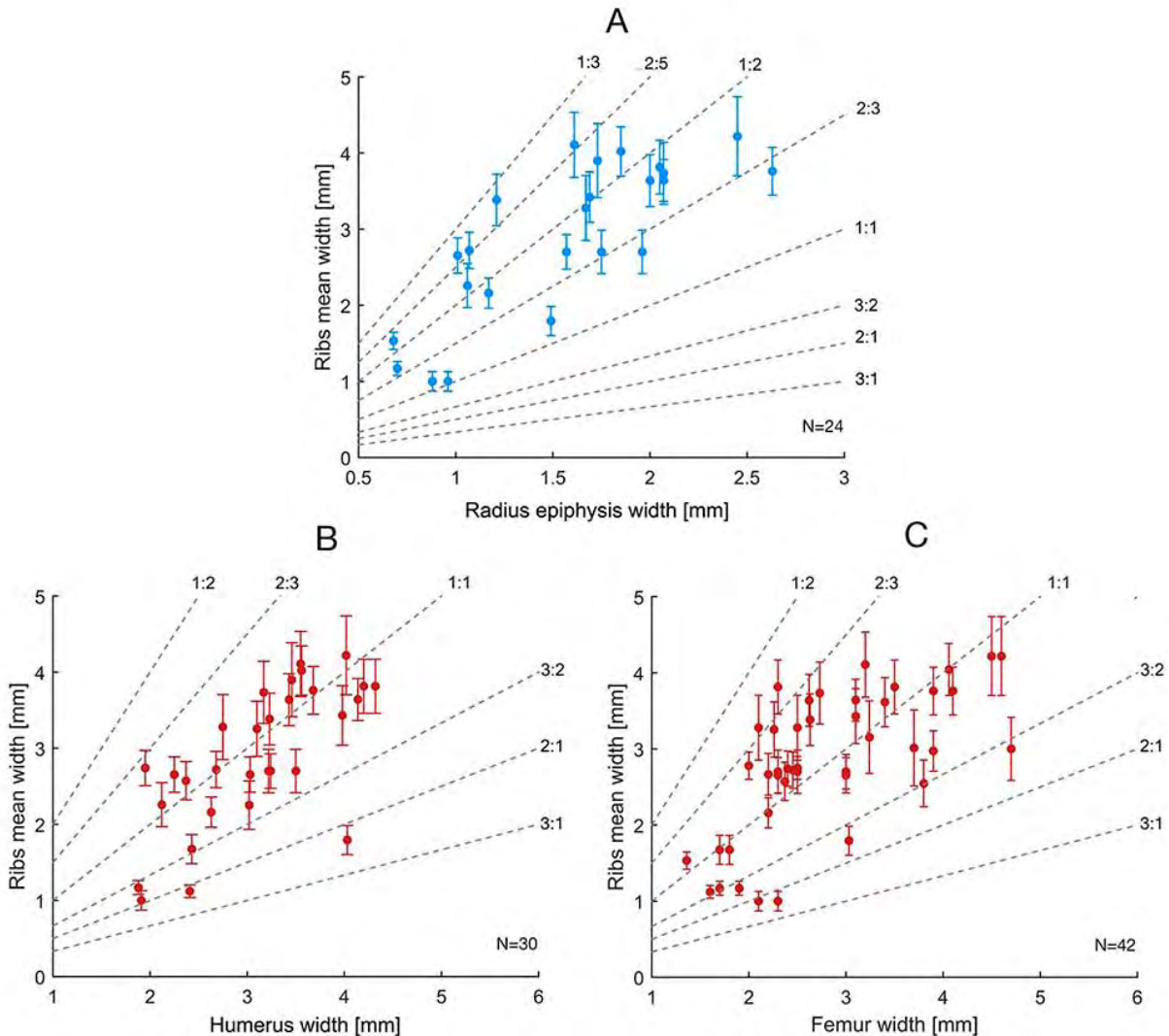


Figure 3. Rib mean width and 3σ error bars, versus the width of different mesosaur key bones. Dashed lines represent different bone/rib width ratios. Correlation coefficient: 0.97.

RESULTS

Anatomical and morphometric analyses: An overview of the main diagnostic characters previously used to identify mesosaur species

The ratio between the skull and neck length

The ratio between the skull and the neck length was originally devised to separate *Mesosaurus* from the rest of the mesosaur taxa. However, this procedure was not as useful as expected. Given the difficulty in the delimitation of the boundary between cervical and dorsal series, the alternative strategy was to use the presacral count (Araújo, 1977). Table 2 in Supplementary Materials shows the presacral vertebral count proposed for the three mesosaur taxa by different

authors. Thus, specimens assigned to *Mesosaurus* seem to have a variable range of 29 to 34 presacrals, a variability that fits in the count proposed for *Stereosternum* and *Brazilosaurus*. According to the revision that we made of more than three hundred mesosaur specimens from deposits of Uruguay, Brazil, and Africa, cervical count comprises 12 or 13 vertebrae, which added to the 21 or 22 dorsals (Villamil *et al.*, 2016; Piñeiro *et al.*, 2016) give a presacral count of 33 or 34. This result which is shown in Table 2 in Supplementary Materials is thus coincident with data provided by previous authors. Modesto (1996) for instance, argued that *Mesosaurus* has a presacral count of at least 33-34 vertebrae, very similar to the range of 34-35 that he found in casts of a few specimens that were considered to belong to *Stereosternum*.

Taking into account these difficulties, we revised the statistical support to previous hypotheses that suggested the existence of a different relation between the skull and the cervical column length, characterizing the three taxa. According to the performed morphometric studies, the skull length and cervical region length among different mesosaur specimens show a linear relationship (Figure 1) with a correlation of 0.90.

The plotted specimens having 12 or 13 cervical vertebrae were previously identified as belonging to *Stereosternum tumidum* and others to *Mesosaurus tenuidens* or *Brazilosaurus sanpauloensis* (see Table 1 in Supplementary Materials). This means that there is no consistent difference in skull/neck ratio between different mesosaur taxa. Moreover, it is worth noting that of the more than three hundred complete or partial skeletons available in museums around the world, a confident skull/neck ratio can only be measured in a few of them, where it is verified that this ratio is the same for all mesosaurs.

Tooth morphology and size

It has been suggested that the basal section of the marginal teeth in *Mesosaurus* was different from that of *Stereosternum* (Oelofsen & Araújo, 1987; but see also Modesto, 1999). This character, as well as others used to differentiate these taxa, is usually subjective and thus, very weak. We sectioned several isolated teeth from the Mangrullo Formation of Uruguay and found that the outline changes according to the place where the cut is made and thus the resulting section can be modified by taphonomic processes (Modesto, 1996; Piñeiro, 2002). For instance, in accordance with Modesto (1996), some teeth seem to be deformed by diagenetic compression, an aspect that does not guarantee that the section we are seeing is the original one. Even though, as the section is subcircular at the bases of the teeth, a measure equivalent to the width is possible to be taken. We found that some specimens seem to have wider tooth bases in relation to their length (Figure 2A).

On the other hand, Modesto (1996, 1999) suggested that the marginal teeth in specimens assigned to *Mesosaurus* are longer than those in specimens assigned to *Stereosternum* because he found that the largest teeth in *Mesosaurus* are equivalent to the length of five tooth positions, whereas in *Stereosternum*, the longest teeth would occupy the length of only three sockets. However, these comparative measures are to be taken carefully, considering that there is a great variability in the distance among tooth sockets in mesosaurs, including an important degree of deformation that occurs during fossilization processes.

According to our present analyses (Figure 2), there can be real differences in the average size of the teeth in some individuals, with an apparent reduction of the length of the largest marginal teeth present in the analyzed skulls. These studies have shown that adults have generally longer teeth than juveniles, although some specimens representing young individuals (?*Mesosaurus*-like morphotype) have a tooth length average that is equal or larger than that of adult individuals bearing relatively shorter teeth (?*Brazilosaurus*-like morphotype) (see Table 3 in Supplementary Materials and Figure 2A). Even though, when comparing tooth length with

skull length, it appears that the size of the teeth is proportional to the size of the skull but there are individuals having similar skull length but bearing teeth of different length average (see Figure 2B).

Plotting the mean tooth length/width ratio vs. skull length we can see a more variable width/length relationship (Figure 2C). Particularly, in specimens assigned to *Mesosaurus*, mean tooth width shows great variability, as can be seen in figure 2A, C. This may be due to preservation issues that particularly affect the width of the teeth, indicating that mean tooth length is less variable than mean tooth width for comparisons.

Therefore, this character should remain as unsolved by the moment and more in-depth studies from additional specimens will be necessary to get unambiguous results.

Pachyosteosclerosis of dorsal ribs and hemal arches

Increased thickness and compactness of the dorsal ribs (pachyosteosclerosis *sensu* Houssaye, 2009; 2013; Klein *et al.*, 2019) has distinguished mesosaurs from other early amniotes. *Brazilosaurus* was previously differentiated from *Mesosaurus* and *Stereosternum* for possessing thin, non pachyosteosclerotic dorsal ribs (Shikama & Ozaki, 1966). However, Timm & Araújo-Barberena (1996) discovered that a low degree of pachyostosis can be inferred from thin sections of ribs in specimens assigned to *Brazilosaurus*. This peculiarity and the fact that these specimens are often of small size, may suggest that the incipient pachyostosis in this taxon may be related to the preservation of specimens in early ontogenetic stages (Piñeiro, 2002). However, as we will see later, the type specimen (*cf.* Shikama & Ozaki, 1966) seems to be an adult (although very young), and it is feasible to find that it developed a low degree of pachyostosis (see Houssaye, 2009, s.l. intensity). This condition is in agreement to what our more recent studies have revealed, in the sense that there can indeed be some mesosaur specimens that have thinner dorsal ribs than other ones (Núñez Demarco *et al.*, 2018). That variability can be seen in Figure 3, which shows the relation between the mean dorsal ribs' width vs. the radius, humerus and femur width. Recently, Klein *et al.* (2019) argued that there would be histological differences in ribs of the mesosaurs *Stereosternum* and *Brazilosaurus*. However, they based the taxonomic identification on presacral and dorsal vertebral counts, skull / neck ratio, and the degree of pachyosteosclerosis in these bones (conditions that we discharge as useful to recognize mesosaur specimens in the present contribution). Furthermore, they did not figured the specimens analyzed and data corresponding to *Mesosaurus* for comparative purposes, were taken from previous articles where the analyzed materials come from isolated hindlimbs and "fragments" of ribs that cannot be assigned to any species due to the absence of diagnostic characters.

In most of the measured specimens, the radius/rib ratio varies between 1:1 and 1:3, with most of the plotted specimens fitting close to the 1:2 ratio (Figure 3A). Intriguingly, the smallest specimens also have variable ratios, between 2:5 and 1:1, and that may suggest that the variability can be metabolic or ontogenetic, but we have to consider that it can also be a taphonomic artifact. See for instance Figure 4, where we show



Figure 4. Variable pachyosteosclerosis intensity in mesosaur dorsal ribs. MCN-PV 2239, specimen juvenile that shows the virtual presence of thin and thick dorsal ribs in a single individual, demonstrating that the different pachyosteosclerotic degree in some mesosaurs can be a taphonomic artifact. Scale bar = 10 mm.

a single specimen possessing dorsal ribs that are virtually thin on the left side of the dorsal column, which suggests an apparent not pachyosteosclerotic condition. However, at the right side of the column, dorsal ribs are comparatively thicker, showing one of the best evidence of the influence of taphonomy in anatomic and taxonomic studies concerning mesosaurs (see Laurin & Piñeiro, 2017).

Humerus/rib measurements show more homogeneous distributions along the 1:1 ratio, and between 2:3 and 3:2 ratios, suggesting a concomitant growth of both bones during ontogeny (Figure 3B). One adult appears particularly deviated from the distribution using the humerus, but it does not show such deviation using the radius or femur ratios, suggesting a possible taphonomic artifact or intraspecific variability.

Femur/rib ratio pattern (Figure 3C) is similar to humerus/rib ratio but presenting greater dispersion. Considering all the plots, it becomes interesting that rib thickness appears to stagnate (probably related to the deceleration of growth) when they are around 4 mm thick. Younger specimens with rib width close to 1 mm, and femora between 1 and 2.5 mm, present great variation (Figures 3A and 3C), which can be verified in the histological sections (Klein *et al.*, 2019). This can be seen particularly in the femur/rib ratio (Figure 3C), where individuals have variable ratios between 1:1 and 3:1 (with the femur being thicker or similar than the rib). Curiously, individuals with more than 2 mm of rib width, but with femur sizes close to the young ones (*e.g.* 2.5 to 3 mm) change dramatically their femur/rib ratios to values between 1:3 and 1:1 (femur thinner or similar than the ribs). Larger specimens, with femur width of more than 3 mm have the radius progressively equal or thicker than ribs (Figure 5A). A similar but more subtle pattern can be observed in the radius/rib ratios. This distribution could reflect an ontogenetic and/or an intraspecific variability driven by environmental conditions. Small young specimens appear to have generally thinner dorsal ribs, compared to the femur or humerus,

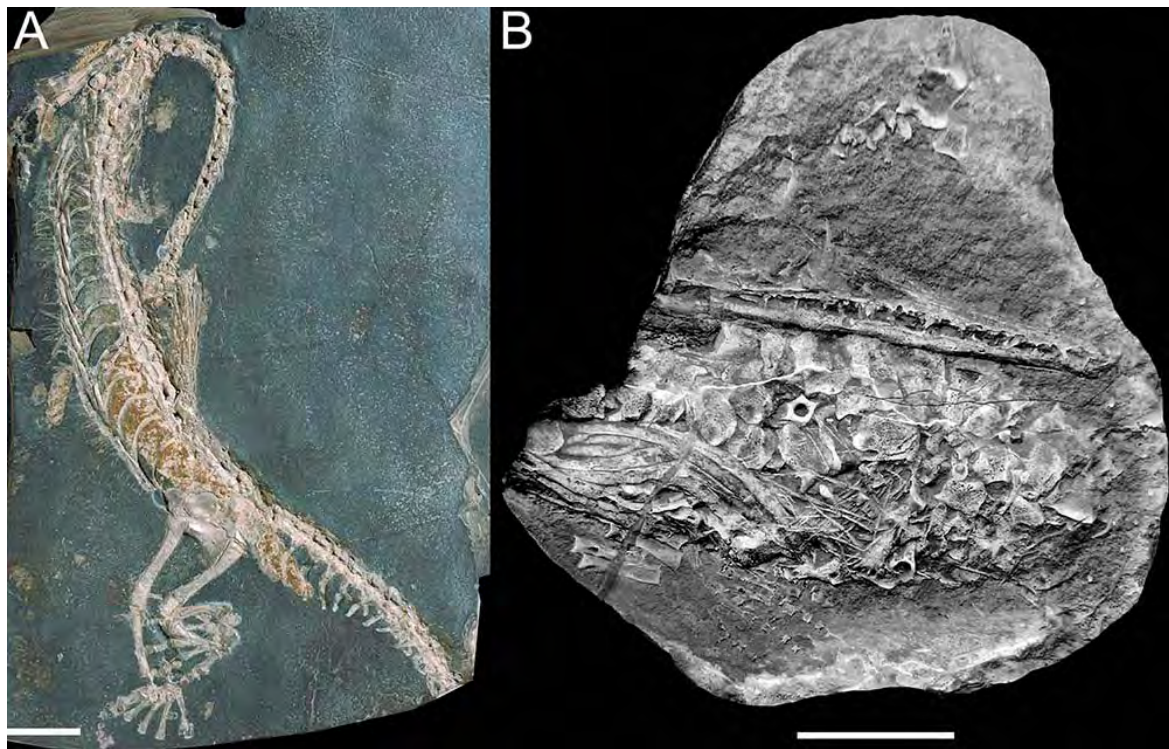


Figure 5. **A,** PIMUZ A-III-192. Almost complete young adult individual identified as belonging to *Brazilosaurus sanpauloensis* (Rossmann, 2001) showing apparently thinner dorsal ribs than other analyzed specimens of equal size. Even though, ribs are thicker than the radius. **B,** FC-DPV 2504. Unborn mesosaur embryo assigned to *Mesosaurus tenuidens*. Dorsal ribs look thick enough to equal or even overpass the width of the tibia and fibula seen in front of the superposed feet. Scale bars = 20 mm.

although they could be as wide as the radius, even in unborn mesosaurs (Piñeiro *et al.*, 2012a) (Figure 5B). Ribs suddenly grow in width, apparently faster than the femur, until they reach a maximum functional thickness (between 3 to 4 mm) related to the pachyosteosclerotic condition, but as they keep growing (as it happens in many reptile and amphibian species nowadays), the bones become thicker and thicker until the bone/rib ratios fall.

According to Houssaye (2013) who studied the dorsal rib microanatomy in *Mesosaurus*, a relatively slow growth rate of these bones can be seen, similar to that observed in terrestrial ectotherms. Additionally, mesosaur environment is characterized to have been variable across the Paraná Basin with oscillating conditions including the development of saline to hypersaline lakes in some areas (Piñeiro *et al.*, 2012c), revealing seasonal and latitudinal salinity changes. Such changes could explain the variability that mesosaurs show in the rib thickness, as was noticed to occur in other species where salinity could have affected the pachyosteosclerotic degree of bones (Chang *et al.*, 2008).

Although there can be seen high variability in the dorsal ribs width (possibly masked by taphonomic features, as we have shown above), some mesosaur specimens that appear to be adults judging by the morphology and ossification degree of the tarsus, have comparatively thinner dorsal ribs, although thicker than the radius (Figure 6A). This last relation is observed in all the articulated and most complete individuals examined, including the unborn embryo from the

Mangrullo Formation of Uruguay (Piñeiro *et al.*, 2012a), in which ribs are equal or even thicker than the stylopodial hind limb bones (Figure 5B).

Intriguingly, some authors that suggested that mesosaurs assigned to *Brazilosaurus* and *Stereosternum* have a lower degree of pachyosteosclerosis in the dorsal ribs, at the same time indicated that these specimens exhibit thick (pachyosteosclerotic) hemal arches (Oelofsen & Araújo, 1983). Thus, isolated thick hemal arches often found would be useful to recognize the presence of these taxa in the Paraná and the Karoo basins (Oelofsen & Araújo, 1983, 1987). Rather, *Mesosaurus* would have non pachyosteosclerotic and slender hemal arches (Oelofsen & Araújo, 1983).

We could not corroborate the taxonomic assessment of such different conditions of the hemal arches because we found expanded thick (U-shaped) hemal arches along with slender (V-shaped) types in the tail of a single mesosaur individual (Figure 6B). This is an observation never made before. The existence of a single individual with this character already contradicts and disables its utility as a diagnostic criterion.

Complementary accessory articulations in dorsal vertebrae

While accessory articulation structures (*i.e.* zygosphene and zygantrum-like) were described to be present in dorsal vertebrae of *Mesosaurus* (Seeley, 1892; Modesto, 1996, 1999), and *Stereosternum* (Cope, 1885a), Modesto (1996) argued that a distinct posterior extension of the neural canal roof, which he named the supraneural process is present in dorsal

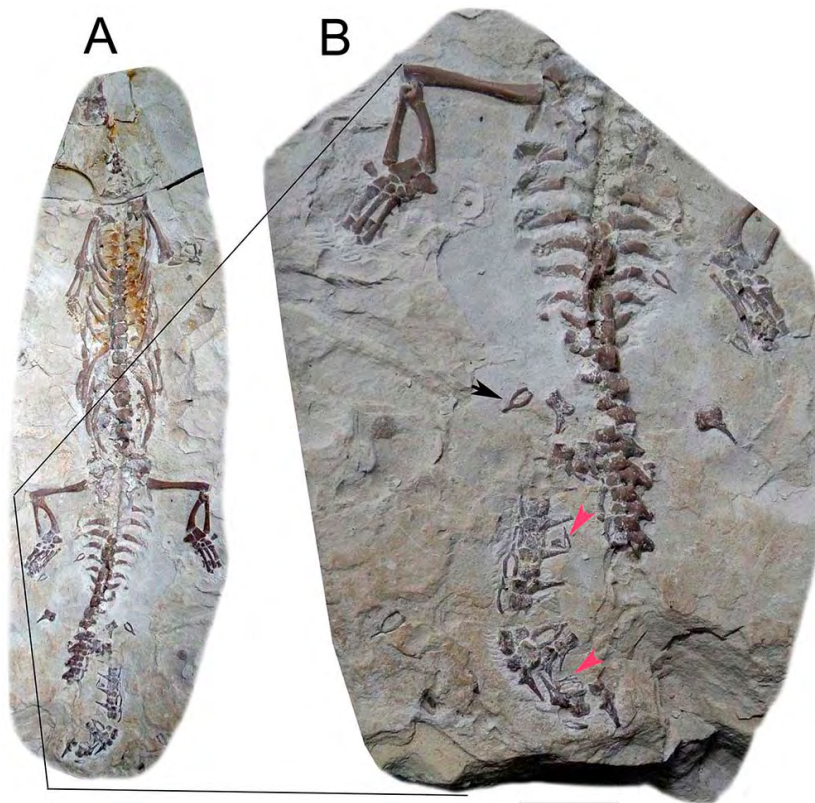


Figure 6. A, GP-2E 114A; an almost complete skeleton lacking skull and most part of the neck. The tail, although not completely preserved, displays the two morphotypes of hemal arches. B, Close up of the tail region of GP-2E 114B, showing the non pachyosteosclerotic V-shaped *Mesosaurus*-like arches (red arrows) in association to the highly pachyosteosclerotic, U-shaped *Brazilosaurus*-like ones (black arrow). Scale bar = 20 mm.

vertebrae of *Stereosternum*, thus considering this character as diagnostic for this taxon. Previously, Cope (1885a) also described the presence of a distinct projection of the neural canal roof which he called “a modified form of zygosphene”, meaning that intriguingly, he saw a projection similar to that described by Modesto (1996, 1999) but at the anterior end of the neural canal roof. Cope (1885a, p. 8) described this projection as “a roof-like projection of the neural arch above each prezygapophyses, which is applied to the superior surface of the postzygapophyses. In some of the vertebrae, this zygosphenal roof is horizontal; in others it is slightly oblique, rising outwards on each side, on the manner of a true zygosphene. It differs further from a true zygosphene in being fissured vertically, above the neural arch, but there is no

corresponding process of the adjacent vertebra to occupy it. On the contrary, there is a corresponding fossa of the posterior side of the vertebra in front. These fossae may be points of insertions of ligaments which strengthen an articulation otherwise weak”.

We studied some articulated specimens from different collections to determine the presence of the supraneural process and also looked for it in isolated dorsal vertebrae from the Mangrullo (Uruguay) and the Irati (Brazil) formations. We saw the presence of anterior accessory structures (the zygosphenes) (see Figures 7A, C, F) and paired short posterior projections of bone between the postzygapophyses; above these projections there was a shallow fossa. Thus, the posterior projection, although paired, may be a zygantrum, which by definition is a posterior extension of the roof of the neural

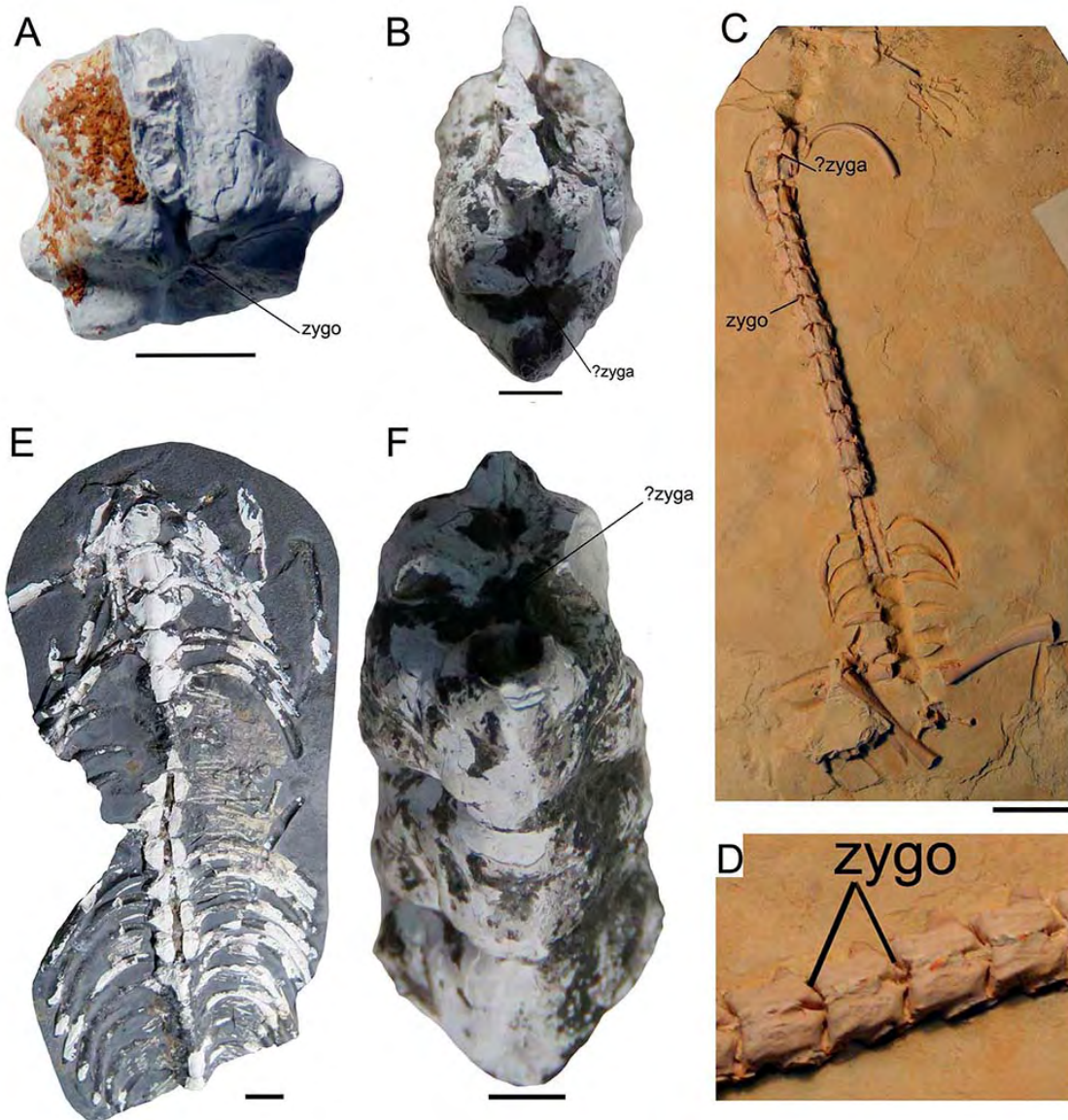


Figure 7. Mesosaur accessory articular structures. **A**, MCN-PV 0049, isolated dorsal vertebra in dorso-anterior view showing the zygosphene. **B**, MCN-PV 0048 three articulated dorsal vertebra in posterior view showing the area of possible zygantrum. **C**, photograph of specimen SMF-R 4497, a possible subadult individual showing the presence of zygosphene (zygo) and possible zygantrum (?zyga). **D**, close view of four vertebra of SMF-R 4497 showing the paired structure of the zygosphene in mesosaurs. **E**, MCN-PV 2214, specimen interpreted as a pregnant female and initially assigned to *Stereosternum*, where a longitudinally sectioned posterior vertebrae do not show the presence of a posterior projection of the neural canal roof (supraneural process *sensu* Modesto, 1999). **F**, MCN-PV 0048 in postero-ventral view showing the absence of a supraneural process. Scale bars: A, B, E = 5 mm; C = 20 mm; D = 10 mm, and F is not at scale.

canal (Romer, 1956) (Figures 7B, E). It is worth to note that Cope (1885a) alleged that there was not a zygantrum in the material that he analyzed and assigned to *Stereosternum*. Therefore, given the contradictory descriptions about these accessory articulations (from Cope, 1885a and from Modesto, 1996, 1999), and the difficulty to identify them in most of the articulated individuals (Figure 7D), it is doubtful that the supraneural process is a useful character to distinguish *Stereosternum* from other mesosaurs.

Different morphology of cervical vertebrae and ribs

In several of the analyzed mesosaur specimens the cervical region looked different from the pattern generally seen in materials assigned to *Mesosaurus*. The difference consists in the presence of a segment of the neck placed behind the atlas/axis complex and involving four or five vertebrae which apparently bear very slender, flat and long structures, three or four times longer than the corresponding centrum length that were interpreted as being posterior processes of the cervical ribs (Figure 8). However, most posterior cervicals bear more road-like broader and shorter ribs (slightly longer than the centrum length) (Figure 8A). The presence of ribs with long posterior processes has been considered by Shikama & Ozaki (1966) as diagnostic for *Brazilosaurus*, while Modesto (1996) suggested that it is a condition shared by *Brazilosaurus* and *Stereosternum*, being absent in *Mesosaurus*. However, taking into account the ability of mesosaurs to increase ossification and bone density, it would be possible that the slender posterior whip-like processes seen at the cervical region, indeed represent ossified tendons, as observed in some

long-necked sauropod dinosaurs, which was suggested to be an adaptation for stabilization of the neck and get more resistance against torsion (Taylor & Wedel, 2013). If so, we could have mesosaurs with ossified tendons (or even mineralized muscles) lying to the (normally short) posterior processes of the cervical ribs and other ones that lack them. Nevertheless, due the slenderness and delicate feature of the structures, it cannot be ruled out that they were lost during fossilization processes or that tendons were not yet ossified.

Different coossification of the mesosaur scapulo-coracoid through ontogenetic development: evidence from isolated specimens

Analyzing the anatomy of the pectoral girdle, Piñeiro (2002, 2004, 2006), suggested that there could be two morphotypes mainly based on early coossification of the scapulo-coracoid observed in some isolated small specimens, in contrast with the smooth articulation seen in comparatively larger bones (apparently from individuals still not mature) (Figure 9). The same issue was addressed by Oelofsen (1981) for specimens assigned to *Mesosaurus tenuidens* from southern Africa. This author mentioned that although there can be a tendency of both of the pectoral bones to fuse during ontogeny, some large individuals retain them still separated or united by a mild synarthrosis. According to Romer (1956), the early coossification of the scapula and the coracoid is a common condition seen in basal tetrapods and it can be an adaptation to aquatic life.

Surely, the main problem for the study of the early or late scapulo-coracoid fusion is that we have to base our



Figure 8. Possible mineralized (?calcified) tendons and muscles in mesosaurs. **A**, MCN-PV 2150, adult specimen showing possible mineralized muscle and tendons at the cervical area (arrow) along with the cervical ribs. **B**, MCN-PV 2219, enlarged and slender structures that could be ossified tendons at the anterior region of the neck (black arrows). **C**, SMF-R 4484, adult specimen showing the presence of cervical ribs with posterior long processes that may be possible ossified tendons for attachment of the long hypaxial neck muscles (black arrow). **D**, AMNH 23799, juvenile individual showing long structures on the anteriormost cervical vertebra that can be possible ossified tendons. Scale bars: A = 10 mm; B = 5 mm; C = 20 mm; D = 30 mm.

conclusions almost exclusively on isolated bones. The scapular girdle is only exceptionally preserved in articulated individuals and when it does, it is hard to reconstruct its morphology.

Intriguingly, several of the strongly fused scapulo-coracoids from the Mangrullo Formation of Uruguay are

found in the limestone levels and they are comparatively smaller than those in which the bones are just barely articulated. Only the very large specimens corresponding to very mature individuals from the shale show both bones strongly coosified (Figures 9B, E-F), representing the largest mesosaurs ever described (Piñeiro, 2004, 2006; Figure 9I).

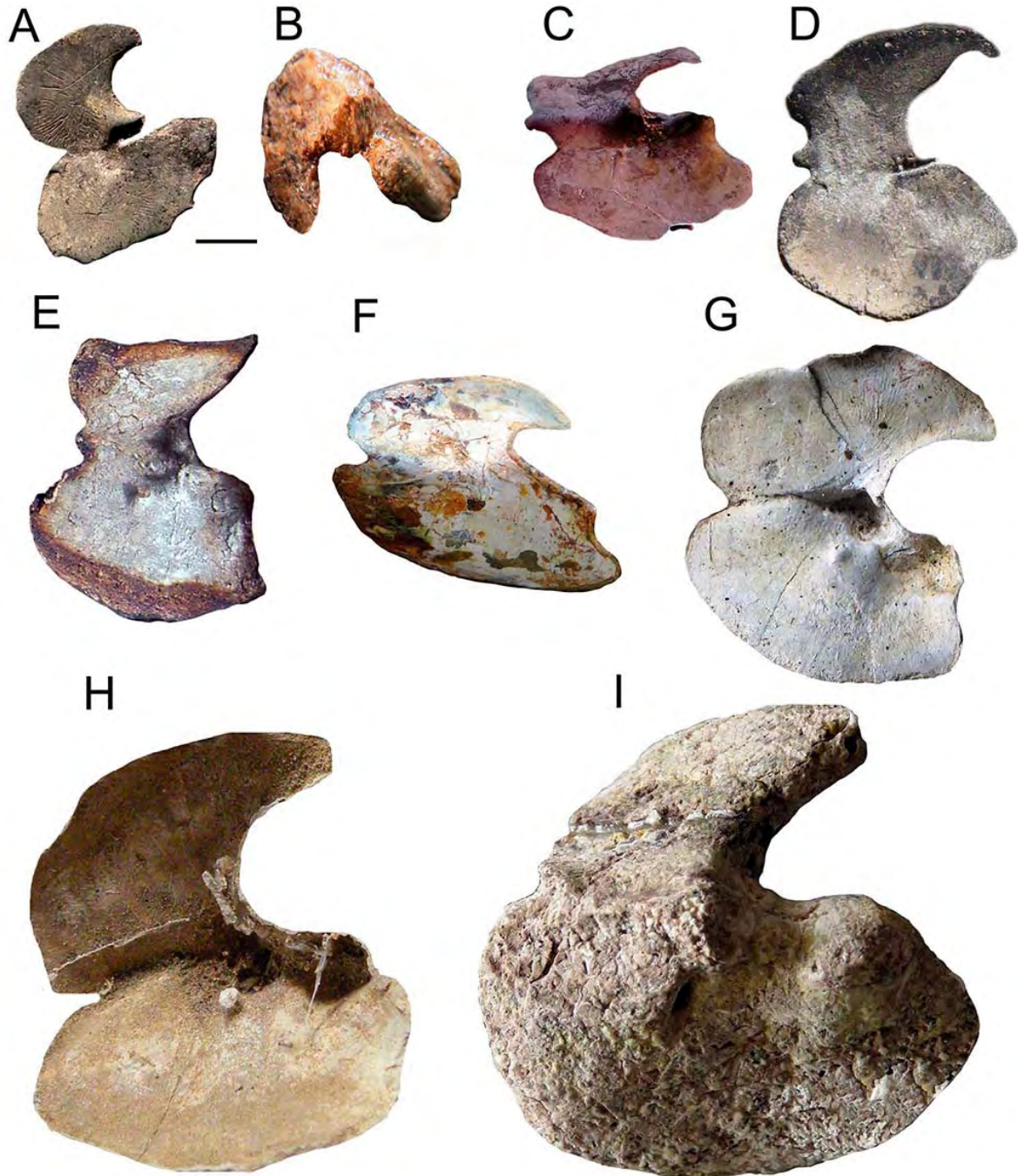


Figure 9. Scapulo-coracoid morphology. A–I, photographs of several specimens from the Mangrullo Formation (Uruguay) ordered by size (FC-DPV 2483, 1257, 1219, 2074, 1742, 1745, 2414, 2526, 2397 respectively). It can be seen that the smaller specimen (A) is clearly a juvenile where scapula and coracoid are not yet completely fused. Specimen in B is similar in size to A but both bones are already fused. C–F, specimens representing scapulae and coracoids strongly fused. G–H, scapulae and coracoids are larger but the area of articulation between both bones remains visible. I, scapulo-coracoid of a very large individual where the fusion of the bones may have been completed at a very mature ontogenetic stage. Scale bar = 5 mm.

The Mangrullo Formation (Uruguay) represents the marginal section of the basin and includes mostly coastal deposits including limestones and shales (see Bossi & Navarro, 1991; Piñeiro, 2006; Piñeiro *et al.*, 2012c). Therefore, mesosaurs coming from the limestones tend to be small, are preserved mostly disarticulated, and often as eroded bones. On the contrary, in the shale mesosaur remains are well-preserved, mostly as delicate molds, including articulated specimens. The small scapulo-coracoids should have belonged to individuals whose sizes are in the range of a subadult or young adult *Mesosaurus*. Early ossification of the pectoral girdle may be related to adaptations to a changing environment and the described polymorphic distribution of this character is perhaps controlled by changes in the dominant ecosystem (*i.e.* temperature, water level, food quality and availability) during ontogenetic development. Low temperatures for instance, reduce the development rates more than it affects the growth (Wilbur & Collins, 1973) and can produce dwarf individuals (but see below).

On the other hand, such polymorphism can be a functional consequence of their pachyosteosclerotic condition (Houssaye, 2009).

Diamond shaped versus triangular interclavicle head

Another interesting character that was previously considered as taxonomically significant for distinguishing *Mesosaurus* from *Stereosternum*, was the different shape of the interclavicle head. According to Modesto (1996) *Mesosaurus* has a triangular dorsal head whereas in *Stereosternum*, the head is diamond-shaped. We have here the same issue as the one described for the scapulo-coracoid, where the morphology of the interclavicle must be evaluated mostly from isolated specimens (Figure 10). In the present study we have just one individual in our sample preserving this bone in its original anatomical position where the morphology of the head can be assessed (Figure 10J). Other several isolated interclavicles, representing different ontogenetic stages were also studied (Figure 10).

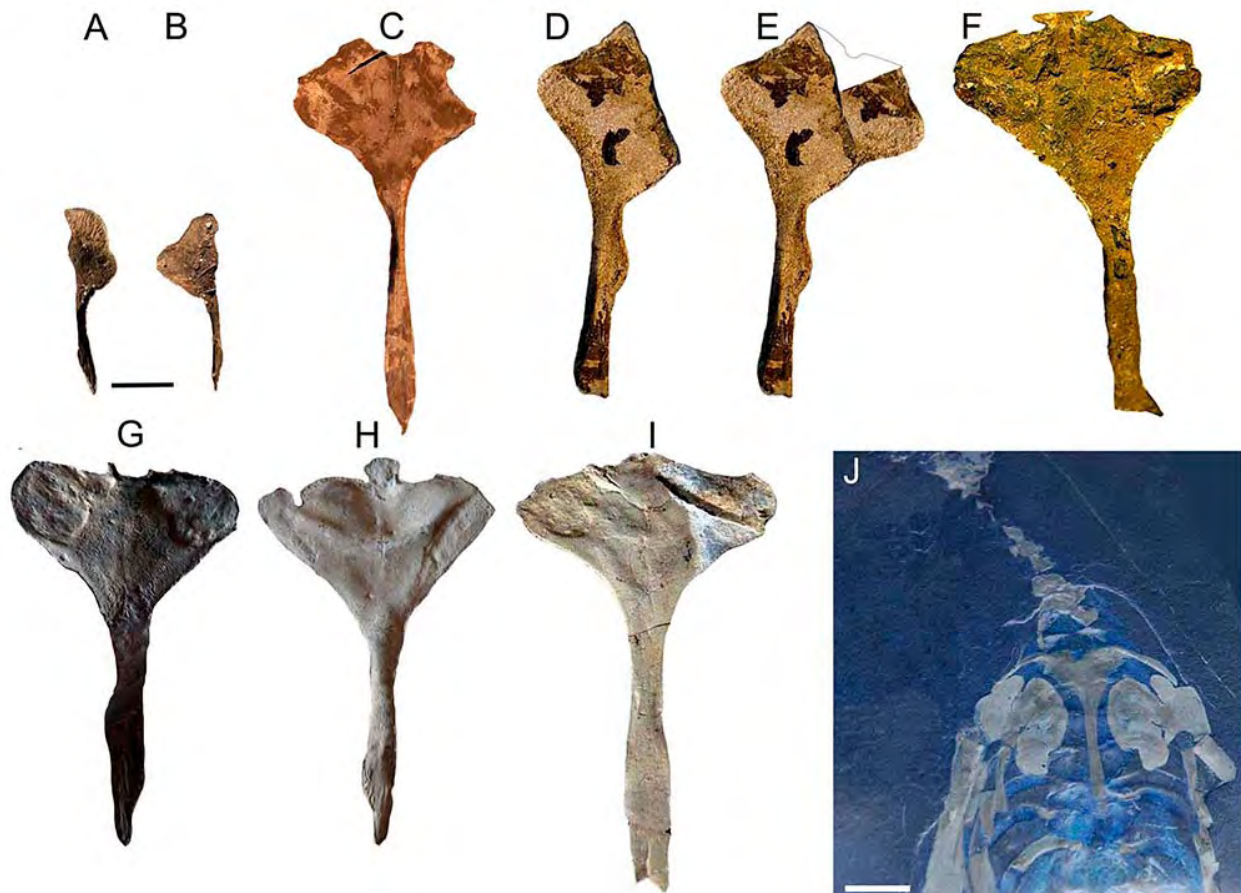


Figure 10. Interclavicle morphology. A–I, photographs of several isolated interclavicles from the Uruguayan Mangrullo Formation corresponding to different ontogenetic stages. A–B, FC-DPV 2046, part and counterpart of the interclavicle of a juvenile specimen. C, FC-DPV 2035, interclavicle of a young adult or a subadult individual showing the concave anterior border suggesting an incomplete ossification. D–E, FC-DPV 2282, represent an interclavicle with a missed part of its head (D) and its virtual restoration (E) to show how an apparently rhombic head becomes a rather triangular one. F, FC-DPV 2281, interclavicle of a mature adult individual showing the complete ossification of the anterior border. G–H, FC-DPV 2480, part and counterpart of the interclavicle of the same individual to show the different morphology of the anterior border of the head produced by taphonomic artifacts. Note the conspicuous ornamentation present in the central area of the head in ventral view (G), where also can be seen the lateral depressions for articulation of the clavicle. This morphology contrasts with the smooth surface of the dorsal view (H). I, FC-DPV 2517, dorsal view of fully ossified interclavicle of a mature mesosaur individual. J, GP-2E 5812, articulated individual from the Irati Formation (Brazil) preserving the interclavicle and the clavicles in their original anatomical position. See text for more detailed information. Scale bars: A–H = 5 mm and I = 10 mm.

The mesosaur interclavicle consists of a roughly depressed rhombic head which bears ornamentation on the central area in ventral view and a long posterior stem. Some mesosaurs retain a poorly ossified anteroventral region of the head which can be noted in specimens that correspond to immature individuals (Figures 10A–B). Thus, many of the specimens seem to have a depressed or indented area at the middle of the anterior margin of the head (Figure 10B) which is filled with bone only in very mature specimens (Figures 10D–I). This condition seems to constrain the morphology of the head, being more triangular in not completely ossified specimens and more diamond-shaped when the cartilaginous portion was already ossified. The only specimen where the interclavicle is preserved in its original anatomical position is possibly a young adult individual judging for the incomplete fusion of the scapulocoracoid and the lack of ossification of the anterodorsal interclavicle head (Figure 10J).

Concerning the preservation of the specimens as part and counterpart, which is very frequent for the Mangrullo Formation (Uruguay), we can see that both parts can look very different (see for instance Figures 10G–H), where the preservation of a more ventral view displays rounded depressed facets for clavicles at the lateral surfaces and a central area bearing fine grooved and punctuated ornamentation that extends into the elongated parasternal process (Figure 10G).

Therefore, considering the specimens available, we did not find enough evidence to corroborate the presence of two different morphotypes for the interclavicle because the differences could be due to ontogeny and taphonomy. The interclavicle head of mesosaurs is thus roughly diamond-shaped as it is in most basal amniotes.

The formation of the obturator foramen in the pubis

The presence of a notch in the pubis instead of a closed foramen was considered as a character that distinguishes *Mesosaurus* from *Stereosternum* (Seeley, 1892; MacGregor, 1908; Modesto, 1996), but the lack of in-depth anatomical studies based on a large number of specimens where the pubis is well preserved, made difficult the evaluation of this character. Indeed, we can see the two conditions in isolated bones from the Uruguayan Mangrullo Formation and initially we typically thought that they should represent the ontogenetic transition from the notch to a completely closed obturator foramen (Figure 11), as was also suggested by previous authors (*e.g.* Huene, 1941; Oelofsen, 1981; Piñeiro, 2002). However, Romer (1956) argued that the notch of the pubis seen in early amniotes at the junction of this bone with the ischium is typical for immature individuals and it will be filled with cartilage in the adults, meaning that it is not related to the other foramina present in the puboischiatic plate (*i.e.* the

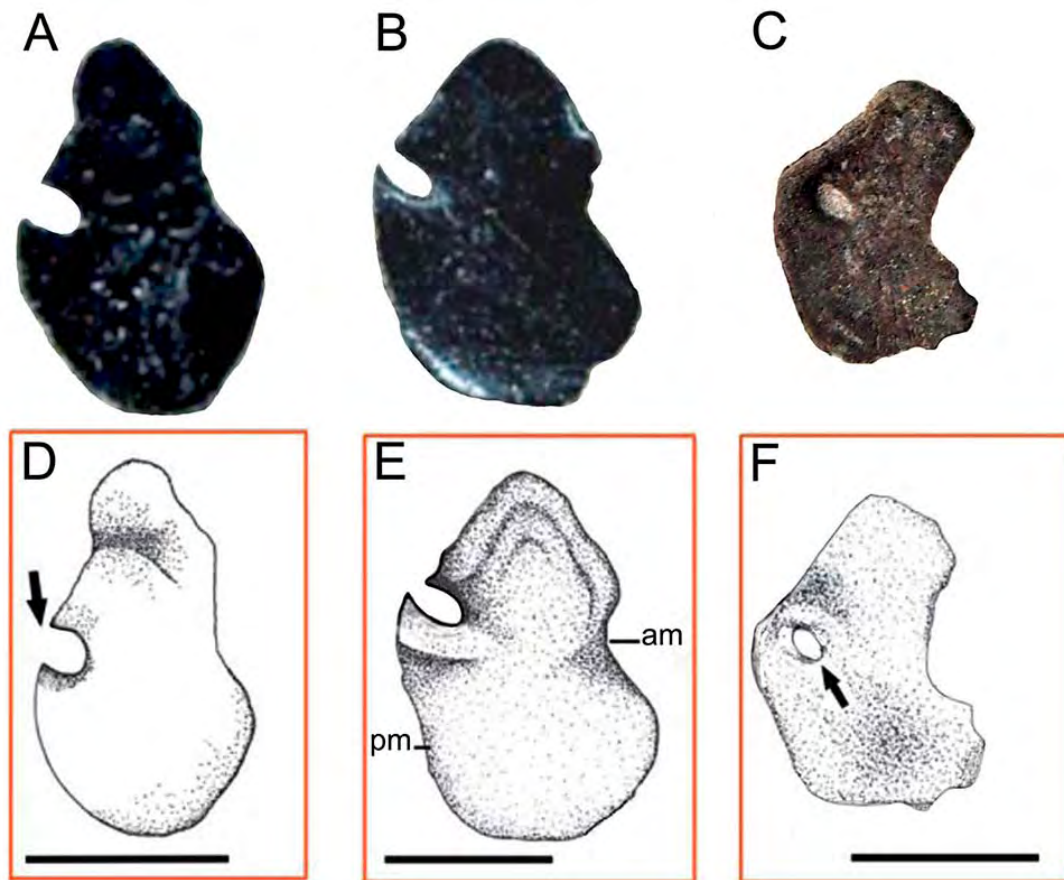


Figure 11. Morphology of the pubis. A–C: Photographs of FC-DPV 1067, 1100 and 1441 to show the process by which the pubic notch (A–B) was believed to close up to form the obturator foramen (C; black arrow). D–F. Interpretive drawings of A–C, respectively. **Abbreviations:** am, anterior margin; pm, posterior margin. Scale bars = 10 mm.

obturator foramen). In mesosaurs, the ontogenetic explanation seems to be inconsistent with what we found: large-sized pubis retaining a well open notch, and smaller specimens displaying a closed foramen piercing the bone (Píñeiro, 2002) (Figure 11). Intriguingly, none of the articulated specimens analyzed in this investigation, that were assigned to *Stereosternum* had a pubis in which a closed foramen is present; all the better preserved pubis showed a rather well distinguishable notch. Therefore, we had to evaluate the condition from isolated bones or well-preserved isolated pelvic girdles.

Interestingly, when the pubis is preserved as a mold in the shale and part and counterpart can be analyzed, the open notch observed in one of the parts appears as virtually closed in the counterpart (Figure 12), but when the foramen is present in tridimensional bones, it is not a taphonomic feature, it is real, and it seems to be formed during the coossification between the pubis, ischium and ileum, as observed in early tetrapods (Gadow, 1902; Holmes, 1984). The foramen remains near to the acetabulum, which is formed by the junction of the three pelvic bones, although there is a predominant contribution from the ileum (Figures 11C, F).

Our interpretation about this character is that the notch in the pubis is a juvenile character in mesosaurs (Figure 13A) and it will transform into a closed foramen in mature individuals, when pubis, ischium and ileum fuse together, as the pubis starts adding new bone which first closes the notch and gradually pushes the resulting foramen far away the sutured border (Figure 13B). Thus, the condition

described in mesosaurs seems to contradict the Romer's (1956) hypothesis about the formation of the obturator foramen independently of the notch present in the pubis of juvenile early amniotes.

As was already noted for the scapulocoracoid, there is a great variability concerning the ontogenetic stage when the coossification of the three pelvic bones is completed to enclose the hole.

New potentially diagnostic skeletal conditions

Morphology of the sacral ribs

All mesosaurs have two sacral vertebrae which are roughly similar in shape and fused together early in the ontogeny. Therefore, they are frequently found joined one another along with their respective ribs, even when they are preserved isolated. Despite the great variability detected in their morphology, it is possible to recognize two roughly basic morphotypes in the sacral ribs: (i) both ribs are sub-rectangular, laterally directed and only slightly expanded at the distal end, and (ii) they rather expand gradually from the suturing area with the vertebra towards their distal portion, where the anterior one or both sacral ribs flare notably to allow an intimate contact between them, including the overlapping of the posterior one, which can be narrower than its precedent (Figure 14).

The variation outside these roughly two main models may be the result of taphonomic artifacts, for instance through

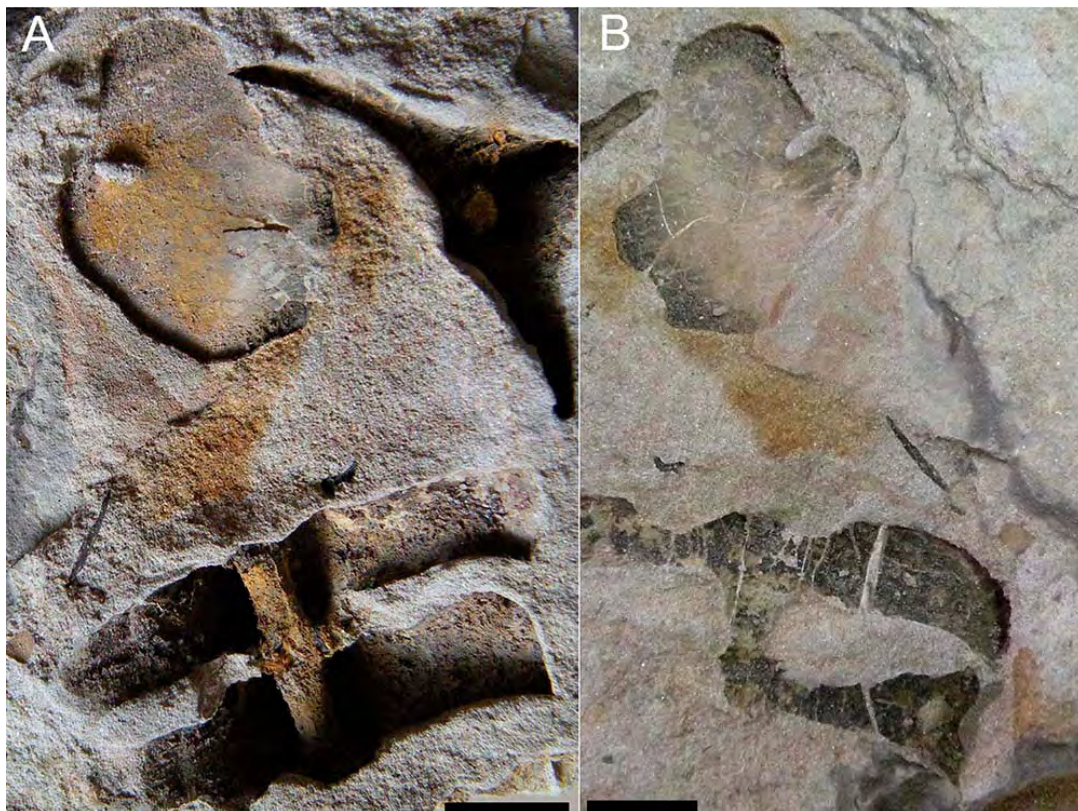


Figure 12. A–B, part and counterpart respectively of FC-DPV 2231 showing taphonomic different conditions of the pubis in a single specimen. Scale bars = 10 mm.

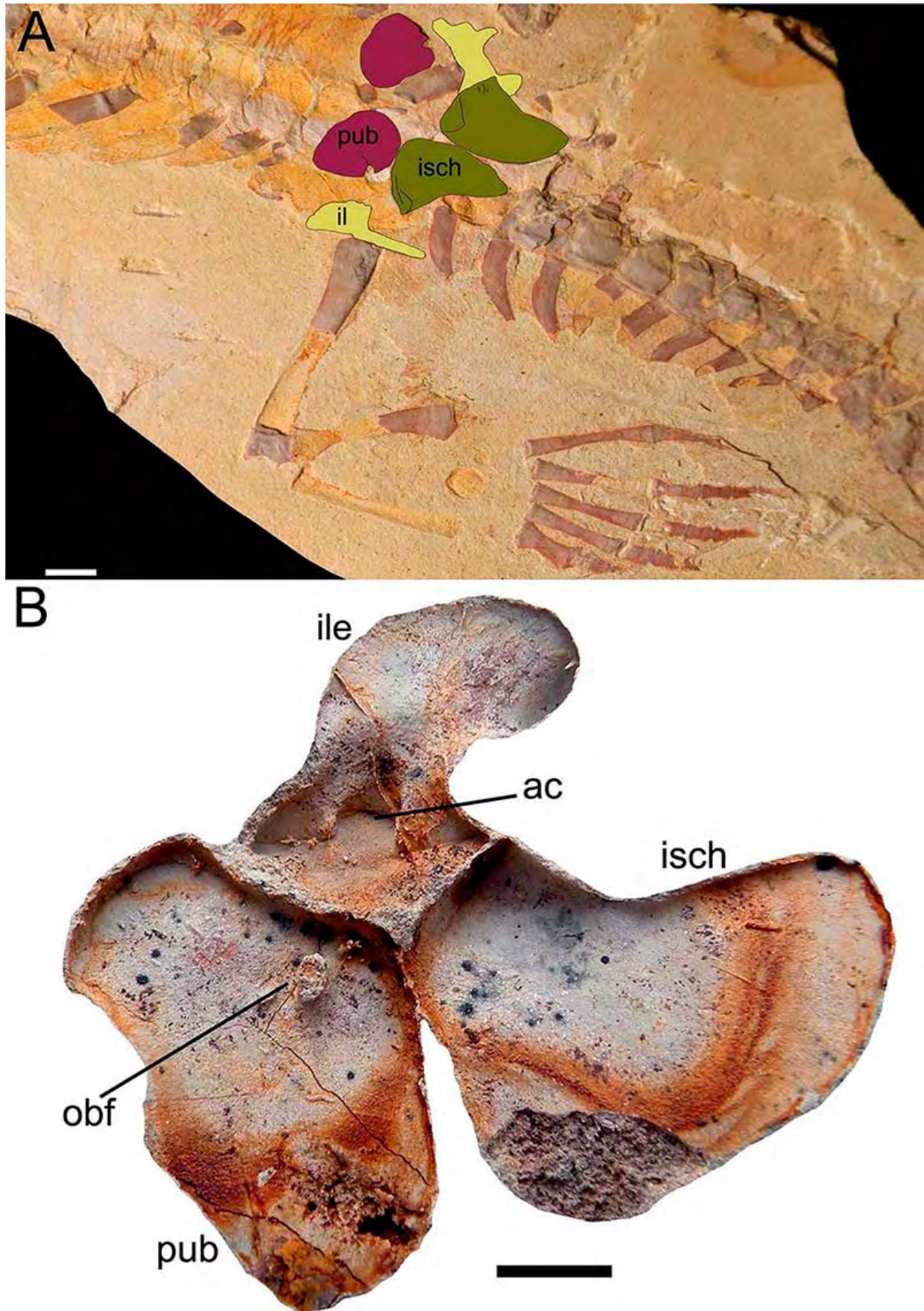


Figure 13. A, SMF-R 4490, juvenile specimen showing the anatomical position of the pelvic bones (colored) before their coossification; the pubic notch is yet superficial. B, FC-DPV 2232 showing pubis partially jointed to the ischium and the ileum (ile). The obturator foramen lays close to the acetabulum, formed by the junction of the three bones. **Abbreviations:** pub, pubis; isch, ischion; ile, ileum. Scale bars = 5 mm.

rotation of the vertebrae and their ribs producing that part of their surface remains covered by sediment. But there can also be due to intraspecific variability. It is important to note that these two morphotypes do not seem to be related with ontogenetic changes, although we could not observe their expression in an enough number of juvenile specimens

because usually the sacral area is covered by the bones of the pelvic girdle or they are not completely ossified.

For the moment, we are delighted to note that the morphotype 2 of sacral vertebrae is probably an attribute of mesosaur females as it was found in a pregnant individual (Figure 15) (see also Piñeiro *et al.*, 2012a).

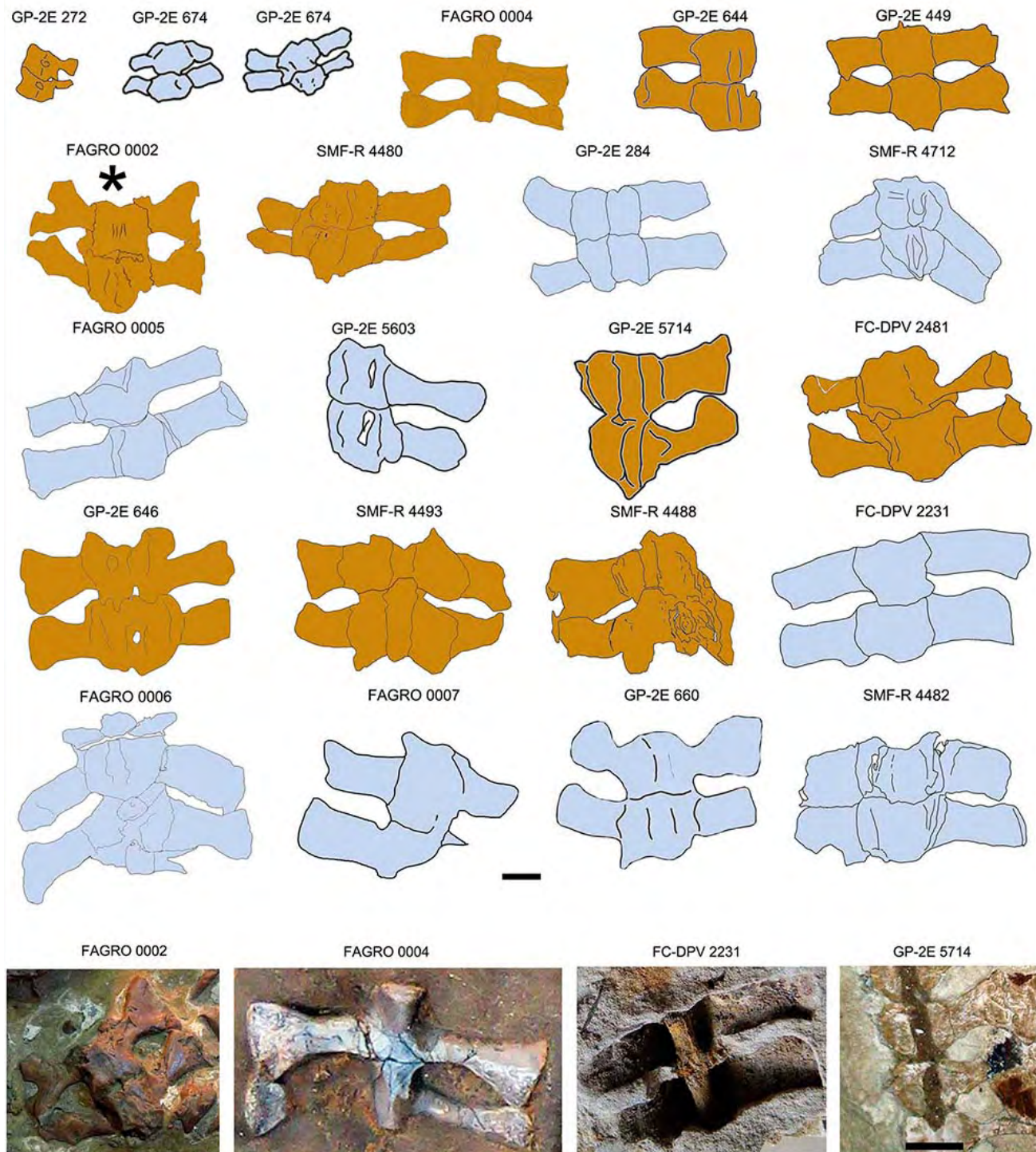


Figure 14. Morphology of the sacral ribs. The sacral vertebrae were drawn following an order according to their size; the first three in the list correspond to juvenile individuals. Morphotypes 1 and 2 described for the sacral ribs (see text) are differently colored, using grey for the former and orange for the latter. Anterior is at the top. Asterisk marks the most notable expression of morphotype 2 among the revised material. Photographs at the bottom represent the main morphotypes found. Scale bars = 10 mm.



Figure 15. Possible sexual dimorphism in mesosaurs. **A**, photograph of specimen MCN-PV 2214, a mesosaur pregnant female, containing a small embryo in the belly area. **B**, detail of the morphology of the sacral ribs (red arrows) consisting in an anterior wide rib while the posterior appears to be narrower and anteriorly directed to contact the precedent rib. Scale bar = 20 mm.

DISCUSSION

Morphological and developmental patterns in mesosaurs: the problem with the Proganosauria *sensu* Baur (1887)

With the purpose of relating mesosaurs to other groups of basal reptiles, former workers (*i.e.* Gervais, 1865; Cope, 1885a; Baur, 1887; 1889; Osborn, 1903; Broom, 1904; Huene, 1941) suggested affinities of this group to the Microsauria, Diaptosauria, Cotylosauria and Synapsida, among which the terrestrial mesosaur ancestors would be found. On the other hand, Lydekker (1889) and Ferigolo & Sedor (1998) already

had related the whole group to the aquatic Sauropterygia, the latter alleging that mesosaurs would have been descendent of an aquatic or amphibious lineage, as Romer (1957) had also previously suggested.

Baur (1887) created the term Proganosauria to include those reptiles possessing humeri with ectepicondylar foramen and five elements in the distal tarsus and Kuhn (1969) introduced the Subclass Proganosauromorpha for the mesosaurs but apparently nobody, except Karl *et al.* (2007) followed this proposal.

All mesosaurs have an ectepicondylar foramen in the humerus, but not all seem to have five distal tarsals in the foot at the same stage of development. Intriguingly, the fifth distal tarsal is absent from the well-preserved feet of some large mature individuals, but it is present in many other specimens which thus possess the complete count. As the fifth distal tarsal bone is very small, it can easily be lost during the taphonomic process. However, when four bones are observed in the distal line of the most beautifully preserved tarsi, the absent bone in that series is invariably the fifth one and no trace of its presence is left. This suggests that this bone may not have been ossified at the moment of death; even happening in adult specimens (Figures 16A, C–D). The fifth toe is also missing or badly preserved in many specimens, suggesting that perhaps it is the last that ossifies in the developmental series. According to Fröbisch *et al.* (2007) and Fröbisch (2008), condensation and chondrification patterns during early skeletal development of fingers have a postaxial dominance (IV (V), III, II, I) in anurans and amniotes, whereas there is a preaxial polarity in salamanders (II (I) III, IV, V). That means that the postaxial pattern of ossification is a characteristic of all amniotes, and the fifth toe is the first to be formed. This condition is not consistent with what we see in mesosaurs, where the distal tarsal V and possibly also the fifth toe are the last in ossify.

In salamanders (urodeles) the preaxial dominance indicates that digits IV and V are the last formed and notably, in some taxa such as *Dicamptodus ensatus*, digits IV and V of the foot and their respective distal tarsals form independently of the digital arch and they derive from the partition of the fibulare. Moreover, distal tarsal V and digit V also develop independently from the digital arch in the salamanders *Triturus* and *Salamandrella* (Fröbisch, 2008 and references therein). Therefore, although considered as a derived group, salamanders were thought to have the most ancestral pattern of limb formation (Gegenbaur, 1864), being comparable to the ossification sequence of limbs in some Paleozoic temnospondyls (Fröbisch, 2008). More interesting is that according to Vorobyeva (2000) the difference in the time of limb development is related to the reproductive strategies of the taxa and both preaxial and postaxial patterns can be observed even within a single taxon.

Whatever the mechanism that triggers the process for this condition was present in mesosaurs, it should be noted that the pedal distal tarsal V could also ossify in the normal postaxial pattern for Amniota in all individuals and its absence is just due to its very small size, which increases the possibilities to be lost before fossilization. But curiously, a reduced fifth

toe is also seen at the manus, where the distal carpal V is as well often absent.

Thus, we have shown examples of variability in the shape, size and degree of ossification of some bones that apparently do not fix with their inferred corresponding developmental degree (*e.g.* the ossification of scapulo-coracoid in small individuals, and the loose of distal tarsal V in pes and manus of adults). The condition observed in mesosaurs is yet more interesting because some adults have the complete distal tarsal count (Figure 16B) and others lack the fifth one, demonstrating the great variability present in the group

related to the different rate of ossification of certain areas of the skeleton. According to the results obtained in the present study, such variability seems to be intraspecific.

Other characters that display morphological differences (as the less or high intensity in the pachyosteosclerosis of dorsal ribs, and the early or late fusion of centralia in the pes) may also be related to ecological and developmental scenarios. Studies in salamanders have demonstrated the effect of the density of population in the resulting size of the adult individuals (Wilbur & Collins, 1973). These authors encountered that under high population densities (ecologically speaking, meaning the

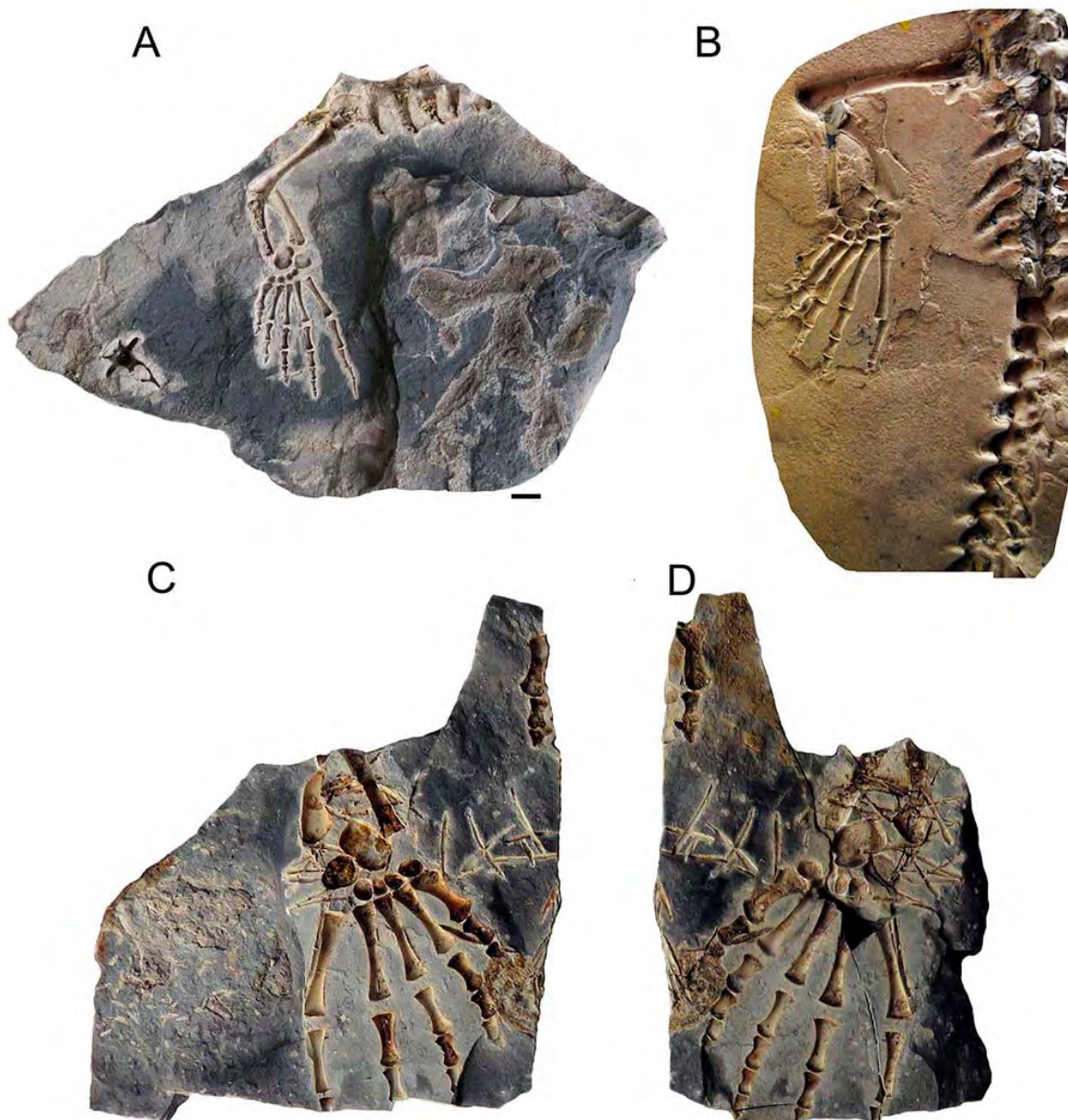


Figure 16. Possible preaxial pattern of ossification of the distal tarsals in mesosaurs. **A**, FC-DPV 1455, photograph of a young adult specimen showing no sign for the presence of a distal tarsal V. **B**, SMF-R 4528, possible adult individual although the centralia (C1+C2) is not yet completely fused to the astragalus. Even though, this specimen preserves the complete ossified series of distal tarsals, where it can be seen that the fourth is the biggest and the fifth is very small. **C–D**, FC-DPV 2531, part and counterpart respectively of the right foot of a big adult specimen (centralia is almost completely fused to astragalus) displaying an incomplete distal tarsal series, by lacking the distal tarsal V. Scale bar = 5 mm.

area used by a single species), an exponential decrease in median body size can be seen because competition for food becomes more intense and under this scenario, the differences in size become gradually magnified during development. This relation appears to be a rule in most mathematical models where growth rate is a decreasing function of density (when the population increases, the size decreases and vice versa, Tanner, 1966). Thus, considering the apparent high density of the mesosaur populations suggested by the high number of preserved individuals and the lack of potential predators in the deposits that yield the fossils, this model, along with environmental factors, can explain the decreasing growth rate seen in some mesosaurs, which even though smaller, have completed their development and reached maturity which is thus expressed in their skeletal morphology.

Mesosaurus: a well-defined mesosaur taxon; Stereosternum: a nomen dubium?

Recently, Modesto (1996, 1999, 2006, 2010) validated the three taxa previously proposed to comprise the Family Mesosauridae (*Mesosaurus tenuidens*, *Stereosternum tumidum* and *Brazilosaurus sanpauloensis*) but he mainly focused on the differences between *Mesosaurus* and *Stereosternum* at the level of both cranium and postcranium, considering *Brazilosaurus* as a taxon that needs additional information to be better evaluated. Even though, Modesto (1996, 1999) considered *Mesosaurus* and *Stereosternum* as the more closely related mesosaurids and *Brazilosaurus* as a more basal form, providing detailed diagnoses for characterizing all these taxa as follows:

“*Mesosaurus tenuidens* Gervais, 1865. Largest known mesosaur distinguished by a relatively long skull (at least 50 percent longer than cervical region), very long teeth which are curved lingually, triangular interclavicular plate, coossified manual intermedium and lateral centrale, and pisiform absent. Twentynine presacral vertebrae are usually present, of which 11 are cervicals and 18 are dorsals. However, 32 or 33 presacrals are present in some individuals, of which the first 12 are cervicals. All cervical ribs are platelike in individuals with 11 cervicals; rodlike cervical ribs are present anteriorly in individuals with 12 cervical vertebrae. An ectepicondylar groove or foramen may be present. The proximal head of the femur and the internal trochanter may be conjoined to form a single articulating surface for the acetabulum. The lateral centrale is absent. The fifth distal tarsal may be absent.

Stereosternum tumidum Cope, 1885. Medium sized mesosaur with skull equal to or slightly longer than cervical series; marginal teeth may be recurved or curved lingually; 34 or 35 presacral vertebrae are present, of which the anterior 12 are cervicals; anterior cervical ribs always possess elongate, rodlike posterior processes. An ectepicondylar groove or foramen may be present. The lateral central pedis may be either a discrete element or coossified with the astragalus. The fifth distal tarsal may be absent. Distinguished from

Mesosaurus by the presence of a supraneural process on the dorsal neural arches (indeterminate in *Brazilosaurus*).

Brazilosaurus sanpauloensis Shikama and Ozaki, 1966. Smallest known mesosaur with skull shorter than cervical series; marginal teeth relatively short; 34 or 35 presacral vertebrae are present, of which the anterior 12 are probable cervicals; cervical ribs feature elongate, rodlike posterior processes. Retains a discrete radiale. No autapomorphies are known for this taxon”.

Based on the above suggested characterizations, *Mesosaurus*, *Stereosternum* and *Brazilosaurus* seem to have roughly the same cervical count, but the length of their necks based on the presence of no more than one (or two?) additional vertebrae is relatively different when compared to the length of the skulls.

However, our present study shows that the previously considered and most diagnostic characters, including the skull/neck length ratio and the pachyosteosclerotic degree of the dorsal ribs and hemal arches, used to differentiate *Mesosaurus* from the other two proposed monotypic taxa, *Stereosternum tumidum* and *Brazilosaurus sanpauloensis*, cannot be anatomically nor statistically supported. Moreover, not only the presacral count (Table 2 in Supplementary Materials) suggests that the differences previously found are in the range of variability expected for one species, but the different morphometric and statistical analyses that we performed (see figures 1, 2 and 3) did not show the normal segregation of the plotted specimens as it would be expected if three taxa are being examined (see Yamada *et al.*, 2019 for comparison).

Other autapomorphies observed by Modesto (1996, 1999) to separate *Mesosaurus* from *Stereosternum* may be strongly influenced by taphonomy, as the shape of the interclavicular head, the presence/absence of the ectepicondylar foramen and the nature of the supraneural process. Other features, such as the pachyosteosclerotic degree of the dorsal ribs and hemal arches can be taphonomic or related to physiological and developmental processes, as it would also be the variable degree of coossification of some key skeletal bones through ontogeny (e.g. the different degree of coossification of the scapula and coracoid, the fusion of the central pedis 1 and 2 and their abutting to the astragalus, as well as the variable patterns observed in the ossification of the distal tarsal V).

Thus, it seems that *Mesosaurus* and *Stereosternum* have more similarities than real differences, and this is indeed what can be concluded after analyzing the holotype described by Cope (1885a) (Figure 17) and one plaster cast housed at the Senckenberg Institute which is a copy of the “type specimen” of *Stereosternum*, a natural external mold that remains as part of the vertebrate collection of the American Museum of Natural History (Figure 19, but see below).

On the type specimen(s) of *Stereosternum tumidum* Cope, 1885a

Before discussing the status of the type of *Stereosternum tumidum* we want to make some editorial remarks on the original publication which is often wrongly cited. The

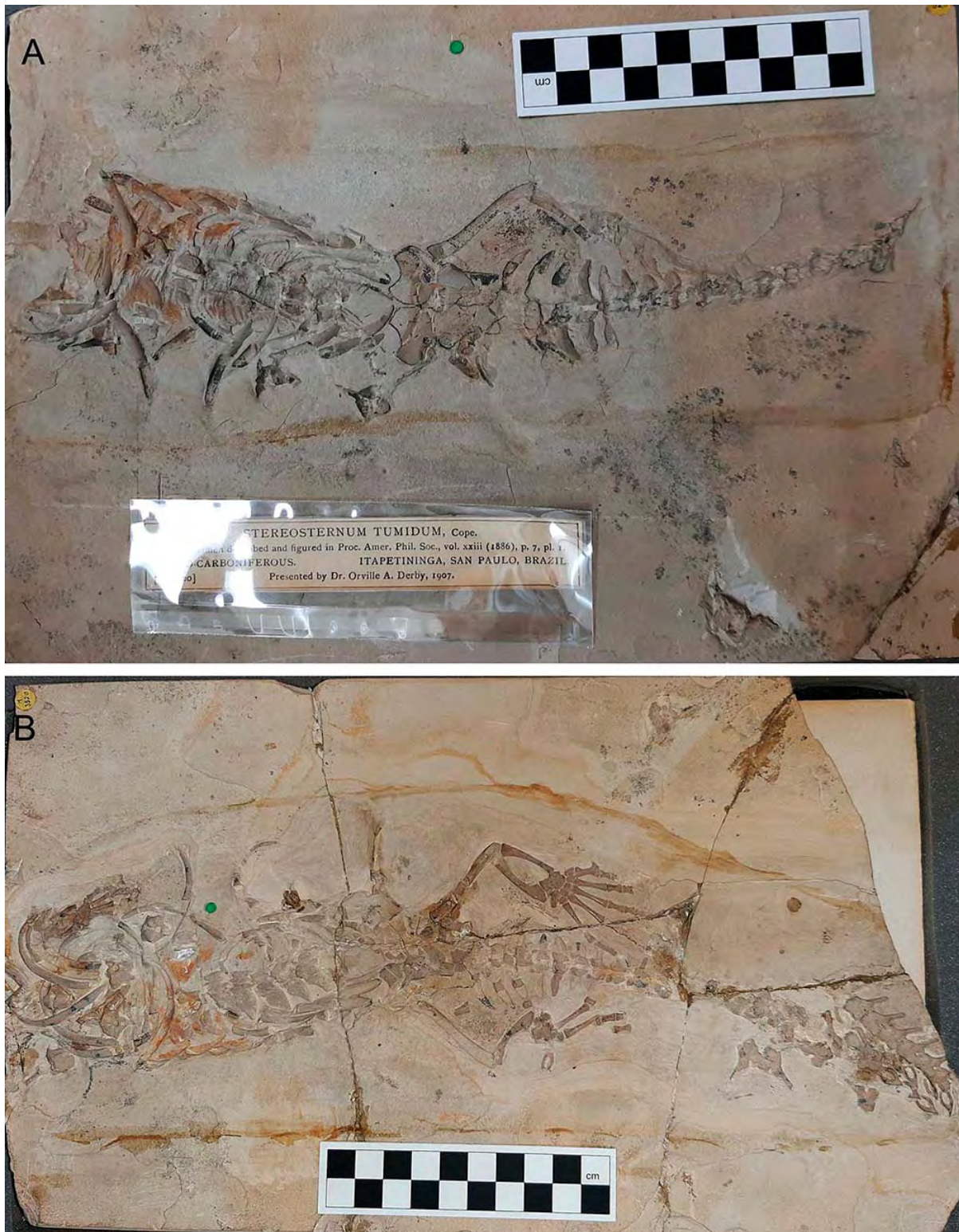


Figure 17. NHMUK R. 3520. Photographs of the syntype specimen of *Stereosternum tumidum* Cope, 1885a as preserved in A, part and B, counterpart.

original description of *Stereosternum tumidum* was published in the *Paleontological Bulletin* (Philadelphia) on July 30, 1885 (Cope, 1885a; Osborn, 1903:481, footnote 2), having a doubtless priority over the publication of the same paper in the *Proceedings of the American Philosophical Society* (Philadelphia) (Cope, 1885b). These pages of this “reprint”

were printed on September 26 (Cope, 1885b:1, 9, footers) and this date is accepted by Osborn (1929:268) but referring to the whole paper published on October 10, 1885 (Cope, 1885b:17, footer). We suppose that the date “April 17, 1885” on the headers of all pages of Cope’s paper refer to the beginning or end of the typographical composition. Adding confusion,

on page 1, in the line between “Vol. XXIII” and “No. 121” the date says “January, 1886”. Usually, this paper of identical content with that of 1885a, is mentioned as being published in 1886, surely following the date on the cover page of the volume. We conclude that although issue 121 bears the date January 1886 (year of volume XXIII of the *Proceedings*), it was actually printed in 1885 though not necessarily distributed that year. Maybe due to Christmas-New Year time, the copy of No. 121 was received at the Museum of Comparative Zoology on January 26, 1886 (see reception date on the issue’s front cover: <https://www.biodiversitylibrary.org/item/pdf/31070>). As for nomenclatural purposes in application of the Principle of Priority, the first paper (Cope, 1885a) should be cited for all the new taxa therein included.

When describing the species *Stereosternum tumidum* for the first time, Cope (1885a:7-15, unnumbered plate) did not select a holotype. His description was based on many specimens recovered from four different localities in São Paulo State, Brazil, received from geologist Orville A. Derby (Cope, 1885a:1). That means that we are dealing with an indeterminate number of syntypes, eight according to the specimens figured on the plate, numbered 1 to 8. But there are many more added by Cope (1885a:8) as “portions of several humeri”, which he briefly described but not illustrated. Except for the partially articulated skeleton (Cope, 1885a, plate figure 1) which came from a private collection (Cope, 1885a:15) (Figure 17), all other specimens belonging to *S. tumidum* should be at the MNRJ, Brazil.

Moreover, we requested information about one syntype supposedly deposited at the American Museum of Natural History (AMNH) in New York, USA, from which was made a plaster copy that rests in the Senckenberg Institute of Frankfurt, Germany. We received a response from the curator Carl Mehlin in the AMNH, who kindly provided us pictures of the specimens that are catalogued in the Museum as “*Stereosternum*”. None of them was the syntype partial skeleton described and illustrated by Cope (1885a, plate fig. 1).

It was known that after Cope’s death on April 12, 1897, the AMNH acquired his Collection of South American fossils (Osborn, 1929:140–141), but is not yet known if that included some of the syntypes of *Stereosternum tumidum* or not, or some of them were returned to their owners, *i.e.* the MNRJ and Mrs. “Madam” Ribeira de Andrada (Ribeiro de Andrade, as Araújo, 1977:110 corrected the name of the owner, *i.e.* the two slabs specimens) (Cope, 1885a:1, 15). According to Araújo (1977:110) all syntypes (she says “Holotype” as if there was only one specimen) except the Ribeiro de Andrade specimens, are located at the MNRJ, but we know now that she could have been wrong. Unfortunately, Araújo does not provide any description of neither the syntypes nor the collection numbers. It is possible that she only repeated the information given by Cope under a wrong category name (see also Karl *et al.*, 2007). Henriques *et al.* (2000), who published a listing of all fossil vertebrate types in the Museu Nacional, did not include the type material of *Stereosternum tumidum*.

With regard to the suggestion of MNRJ as the repository, we firstly have considered three possibilities: 1) Cope

returned the specimens to Derby, 2) these specimens are not identified in their collections or 3) they went lost. We know now that the one was the correct, because at least one of the specimens ended in a different repository (as for the case of *Ichthyacanthus ohiensis* Cope, 1877, as commented by Hook & Baird, 1984:697–698).

Based on the specimen BM(NH) R. 536, and not finding morphological differences with *Mesosaurus tenuidens* from Africa (“*there appear to be no characters by which this form can be specifically distinguished from the type species*”), Lydekker (1889:302) proposed the new combination *Mesosaurus tumidus* (Cope) exclusively on the basis of the geographical distance between South Africa and Brazil.

To make the issue more complicated, Rossmann (2000:16, fig. 2) illustrates a plaster cast housed at the Senckenberg Museum, Frankfurt (SMF-R 402), taken from the original specimen deposited at the AMNH identified as the “type” of *Stereosternum tumidum*. It is possible that this specimen is the same that Cope (1887) briefly described two years later, and which somebody wrongly identified as the type. As already said, the type material of *S. tumidum* is composed of at least eight syntypes. The only comparable syntype with the 1887 specimen is the slab of figure 1 (Cope, 1887). Both specimens cannot be the part and counterpart of the same individual; just a quick look at the position of the femora of both specimens is enough to reject this possibility (Figure 18).

It is also worth mentioning that the type material of *Mesosaurus brasiliensis* MacGregor, 1908 (currently a junior synonym of *Mesosaurus tenuidens*) does not belong to the American Museum of Natural History as Rossmann (2000:14) states but all seven syntypes are at the Museu Nacional, Rio de Janeiro according to Henriques *et al.* (2000:15).

Longbottom (1988) indicates that the “holotype” of *Stereosternum tumidum* belongs to the collection of the British Museum (Natural History) (now Natural History Museum) under the number NHMUK R. 3520. Unfortunately, she does not illustrate the fossil; she only remarks that “*Cope’s figure appears to be a composite of the two counterparts*”, and she was not wrong. Indeed, the type specimen described by Cope (1885a) is a combination of the two preserved slabs, perhaps it was a methodology frequently used by the drawers of that époque, but it would have had also the intention to produce a more complete interpretive drawing.

Therefore, it seems that most authors dealing with this taxon have done their research on specimens attributed to *Stereosternum tumidum*, but not on the type material, which we are now showing in Figure 17. The photographs of the specimen (which surprisingly consisted of part and counterpart as Longbottom (1988) commented) were kindly provided by curator Mike O. Day, in behalf of Marc Van den Brand.

Indeed, before receiving the news from Van den Brand and Day, we have tried to obtain information on the present repository of the syntypes supposedly deposited at the MNRJ. However, we know now that at least one of them is part of the collection of the Natural History Museum of London (NHMUK R. 3520, Figure 17). This specimen was presented

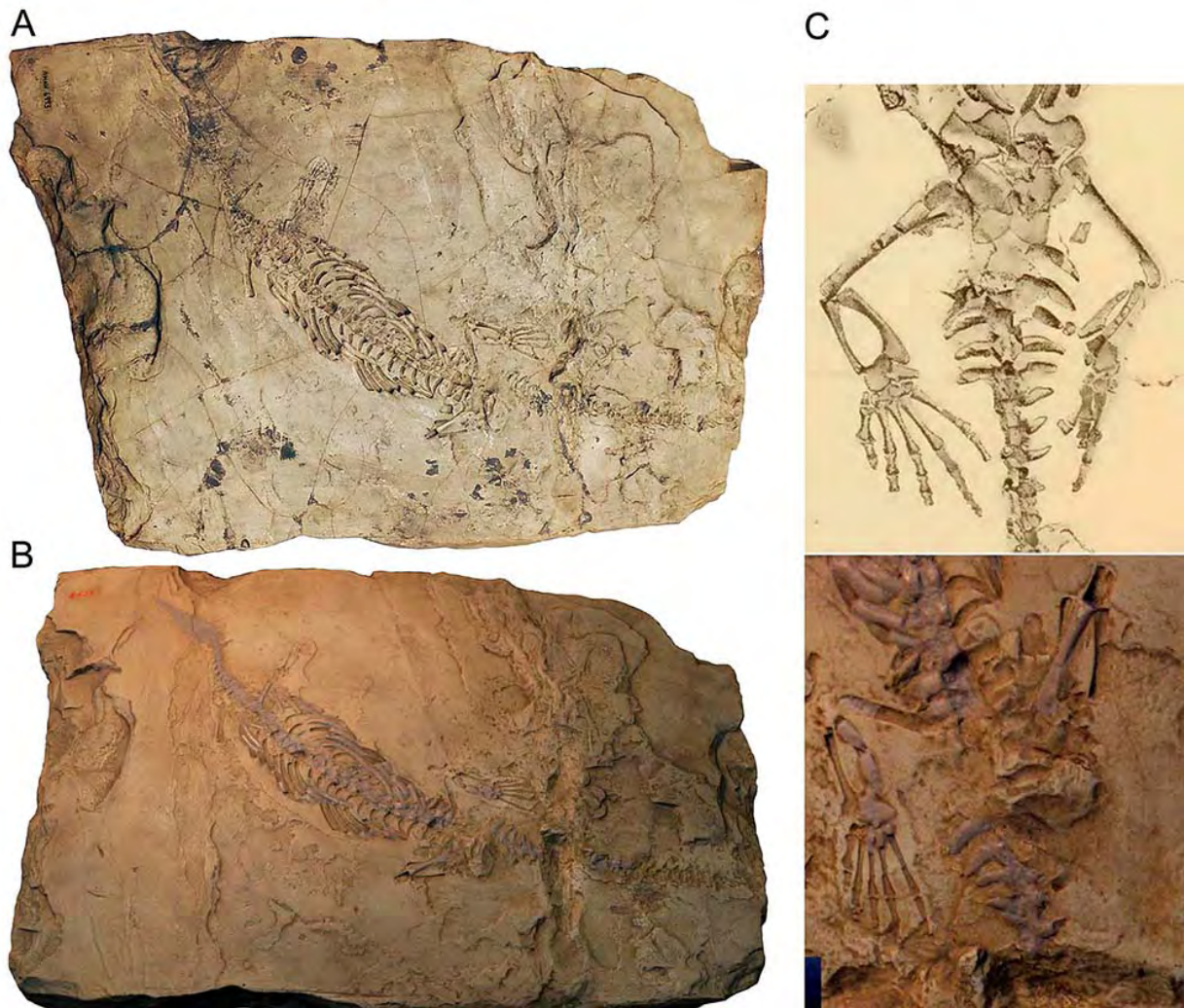


Figure 18. A, AMNH 6993. Natural cast alleged type specimen of *Stereosternum tumidum* Cope, 1885a housed at the American Museum of Natural History (New York). Photograph provided by curator Carl Mehling. B, photograph of specimen SMF-R-402, a plaster cast of AMNH 6993 housed at the Senckenberg Institute, Frankfurt, Germany. C, comparative images of the syntype of *Stereosternum tumidum* (plate from Cope (1885a, fig. 1) and the supposed holotype (AMNH 6993) and its plaster copy (SMF-R 402), to show that they are different specimens.

to the NHMUK by Derby in 1907 (see label on Figure 17A), the same person who sent the syntypes to Cope. Maybe Derby never returned the specimen to Ribeiro de Andrade or received it from her.

Leaving apart that Cope (1885a) does not ascribe any character to the new taxon *Stereosternum tumidum* that he could prove to be absent in *Mesosaurus tenuidens*, the specimen has the typical morphology expected for *Mesosaurus* and it clearly lacks the autapomorphies that supposedly characterize *Brazilosaurus* according to Shikama & Ozaki (1966) (*i.e.* lower pachyosteosclerosis intensity on the dorsal ribs). The specimen also has a typical *Mesosaurus*-like morphology of the sacral ribs, probably characteristic of the males of the species (Figure 19). Perhaps the “scarcity” of *Brazilosaurus* specimens often argued in previous works, can be explained because this last taxon has been misidentified as *Stereosternum* (see for instance Modesto 1999; Pretto *et al.*, 2014).

Considering the results of our research and our updated state of the art of our knowledge of the taxonomy of Mesosauridae it is not advisable to select the only available syntype of *Stereosternum tumidum* as lectotype. As far as we know, the remains have no diagnostic characters and the taxon should be regarded as a *nomen dubium sensu* Mones (1989) or as *species inquirenda*, if not considered a junior synonym of *Mesosaurus tenuidens* Gervais, 1865.

Assessment of the nature and taxonomic significance of the slender and elongate structures observed at the anterior region of mesosaur cervical column

Slender and long structures placed at the anterior to middle region of the cervical column have been observed on the neck of some mesosaurs whereas they are absent in the most preserved materials. This kind of structures have been described as elongated posterior processes of the cervical ribs

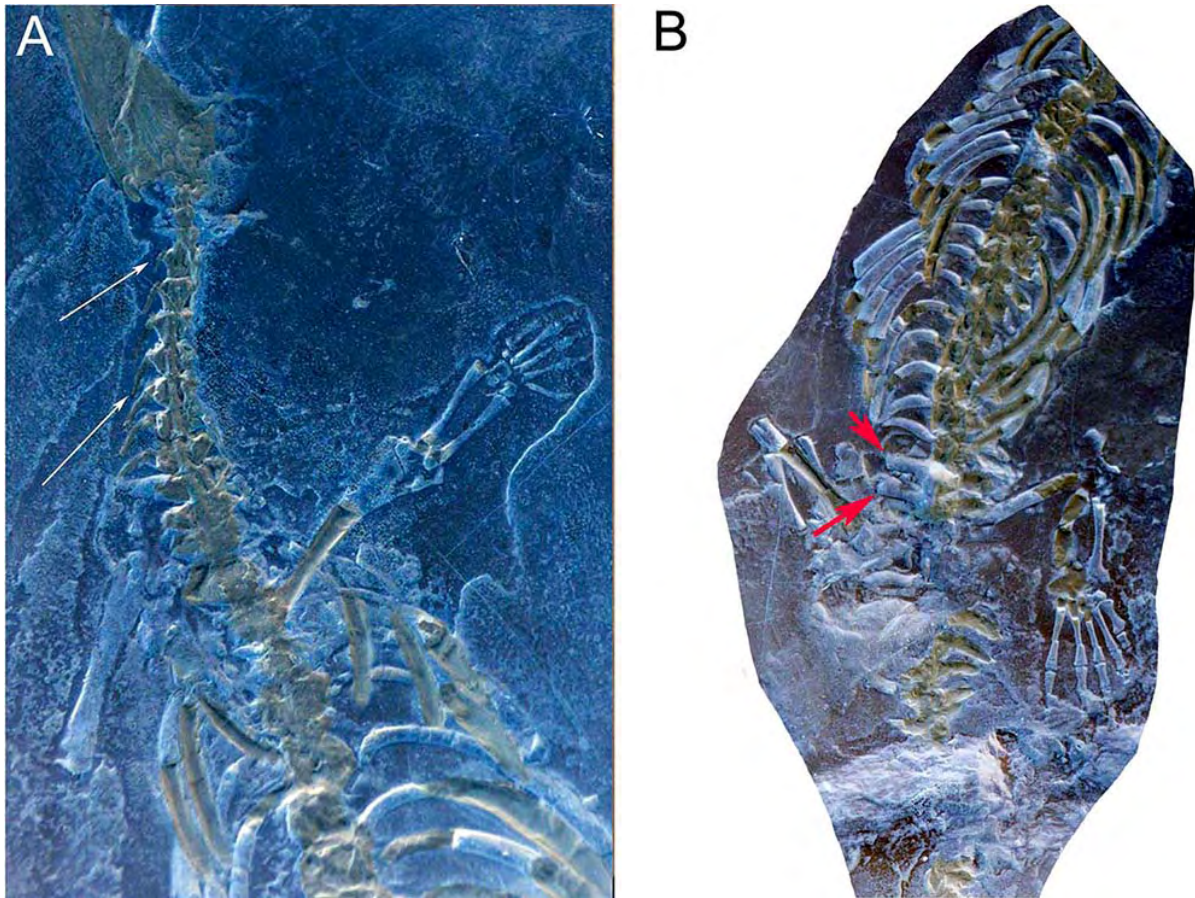


Figure 19. **A**, close up image of cast SMF-R- 402 assigned to *Stereosternum tumidum* showing the morphology of the cervical ribs (white arrows) lacking the long and slender structures. **B**, close up image of cast SMF-R- 402 showing the typical *Mesosaurus*-like morphology of the sacral ribs (red arrows). Not at scale.

in terrestrial and semiaquatic protorosaur archosauromorphs (Li *et al.*, 2004; Li, 2010; Jaquier & Scheyer, 2017) and even in archosaurs (Preuschoft & Klein, 2013), including long-necked sauropod dinosaurs (Piechowski & Dzik, 2010, but see also Klein *et al.*, 2012). These processes could have the function of strengthen the neck, keeping it almost horizontal for a rapid ingestion of the prey and possibly to allow the esophagus to widen by moving the ribs outward, such as was suggested for the protorosaur *Dinocephalosaurus* by Li (2010).

As the neck of mesosaurs may have been very muscular and possibly stiffened the slenderness of the cervical ribs may have allowed them to display smooth lateral movements (see Li *et al.*, 2004), but such delicate posterior processes may have suffered fractures when displaying such movements.

On the other hand, the long and slender structures seen in the neck of mesosaurs may be “ossified” or “mineralized” tendons of the long hypaxial neck muscles (Figure 8 A), as was suggested by Klein *et al.* (2012) for long-necked dinosaurs after examining histological sections of the long posterior processes of the cervical ribs. Such hypotheses may include the preservation of mineralized muscle fibers as shown by some mesosaur specimens in which the structures seem to be independent from the ribs (see Figures 8A, B). This condition may suggest that ventral neck muscles (probably the *musculus*

longus colli ventralis) were attached to the posterior process of the cervical rib through these mineralized tendons, allowing the neck to be lighter by reallocating the musculature towards the dorsal region, as it may have occurred in long-necked dinosaurs (Klein *et al.*, 2012). That condition may have facilitated mesosaurs to swallow large prey items, meaning pygocephalomorph crustaceans of about 10 to 20 mm in length (Silva *et al.*, 2017), but it is difficult to prove from the available materials.

The putative presence of ossified tendons in very young mesosaurs (Figure 8 D) indicates that the mineralization of muscles and tendons in the neck may have been also present in early ontogenetic stages, but histological studies will be needed to confirm the suggested hypotheses about the nature of these analyzed structures.

The absence of the long posterior processes in the cervical region of the majority of the sampled mesosaur specimens could be due to their delicate construction and very low fossilization potential, even under the favorable conditions found in the Konservat-Lagerstätte of the Mangrullo and Irati formations. But, the presence of possible mineralized soft tissues in juveniles would also suggest painful diseases that may have produced the early death of these specimens.

Therefore, taking into account the arguments presented above we consider that this character is strongly reliant on the

fossilization conditions or individual diseases and it should not be considered as a valid diagnostic character.

On the *Brazilosaurus* taxonomic characterization

According to the distribution of characters described by previous authors, and those described herein it would have been possible to justify the presence of *Brazilosaurus* as a different taxon from *Mesosaurus* in at least four autapomorphies: (1) shorter marginal teeth, (2) a segment of cervical vertebrae that bear smaller plate-like ribs bearing very long posterior processes (or ossified tendons) extending over at least three or four vertebral centrum length, (3) sacral vertebrae bearing conspicuously flared sacral ribs, (4) early ossification of the distal tarsal V, but retarded fusion of centralia to the astragalus, (5) early fusion of the scapula and coracoid in the pectoral girdle, and (6) less degree of pachyosteosclerosis in the dorsal ribs.

These features may characterize *Brazilosaurus* as a valid mesosaur taxon, because at least three of them (1, 2 and 5) were described by Shikama & Ozaki (1966) as autapomorphies for this taxon.

However, as was described above, most of these characters we interpret as speculative because their state strongly depends on the ontogenetic stage of the analyzed specimens (e.g. 1, 3, 4 and 5), can also be altered by ecological and environmental factors (5 and 6), and at least two of them (2 and 6) can be taphonomically constrained or related to diseases. Moreover, as these characters present one alternative pattern in other mesosaurs, we cannot rule out the possibility that some of these features could represent sexual dimorphism (e.g. 3).

To bring some light to this issue, we were fortunate to get some high quality photographs of the holotype of *Brazilosaurus sanpauloensis* (NSM-PV 21867) housed at the National Museum of Nature and Science, in Japan (Figure 20). Therefore, we are able to provide a brief overall description of the specimen, including a reappraisal of the diagnostic characters proposed for this taxon.

The specimen is an incomplete skeleton of a subadult individual (or possible young adult) lacking the tail, and most of the hind limbs. Its size probably reached 50 or 55 cm in total length, given that the tail of mesosaurs overpasses the length of the rest of the body. Thus, its size is at the range of subadult mesosaurs.

According to our count, the neck is formed by 13 cervical vertebrae (see figure 21, green arrow), appearing to be very large and robust (particularly at the segment from the fifth to the eight vertebrae) in comparison with the size of the specimen. The skull, which looks very short with respect to the neck length, is broken at the level of the anterior margin of the nasal bone (Figures 20B, C). Therefore, it is impossible to determine the exact length of the skull. In Figure 1, we thus plotted the exact length of the skull of the *Brazilosaurus* type specimen as it was preserved and other that was calculated according to the position of the snout fracture with respect to the position of the nares and the placement of the anterior margin of the nasal bone, at the articulation contact of nasal with the premaxilla. This area is separated from the

anteriormost margin of the skull for at least 13 or 14 tooth positions in adult or subadult mesosaur specimens. In NSM-PV 21867 there may be not more than six tooth positions, thus masking the skull as being very short (Figure 21). The contact between the anterior border of the nasal and the premaxilla should be a fragile area, as many mesosaurs show similar fractures in that place of the snout (see Figure 21H). Even though the apparent exaggerated difference between the skull and the neck lengths, both the plotted skull lengths to know the ratio between the length of the skull and the length of the neck do not segregate this specimen from the remaining analyzed mesosaurs (Figure 1).

Cervical ribs are poorly preserved as can be seen from the photographs in Figure 21 and they seem to lack the long posterior processes (or possible ossified tendons) that are well evident in a few of the studied specimens of our sample. Nevertheless, as Shikama & Ozaki (1966) described the presence of “*many fine small sized ventral costa on ventral side of third to eighth cervic vertebrae*” the condition will have to be evaluated under a direct, at hand study of the specimen, even though this feature has been discharged as diagnostic for mesosaurs.

Dorsal ribs are thin, but thicker than the radius width, measured at the middle region of the diaphysis. The specimen fits the conditions seen in other mesosaurs of equivalent stage of development, particularly evident in the ossification degree and morphology of the preserved carpal bones (Figure 20C). A possible scapulocoracoid could be preserved close to the NSM-PV 21867 skeleton and if this identification is correct, the coossification of both bones has been completed (see Figure 20A, white arrow).

Considering the hypothesis that the specimen is probably close to reaching its maturity, the presence of small disarticulated mandibular elements corresponding to a very young individual in close association with the subadult (or adult?) specimen is intriguing. These small bones were marked by red arrows on Figure 20A, and it is difficult to evaluate their significance to advise a relationship between both specimens. The association with these juvenile bones does not confirm the maturity of the larger individual nor a mother-baby relationship, given that it may have been casual. However, this kind of adult-juvenile association is present in a high number of the mesosaur specimens (including materials from Uruguay) and it was suggested to be an evidence of parental care in these early amniotes (Piñeiro *et al.*, 2012a).

If indeed this animal had reached its sexual maturity at the size and stage of development usually observed in subadult individuals, it is possible that there have been a population of dwarf mesosaurs capable of reproduction, that thus are spreading the genetic material that produce small size (although maintaining the proportion of normal individuals), low degree of pachyosteosclerosis in dorsal ribs and smaller teeth.

Nevertheless, we cannot yet prove this last hypothesis because statistically, mesosaurs like those assigned to *Brazilosaurus sanpauloensis* fit in the variability of *Mesosaurus tenuidens* as shown by specimens preserved in similar ontogenetic stages (see Figures 1–3 and 21).

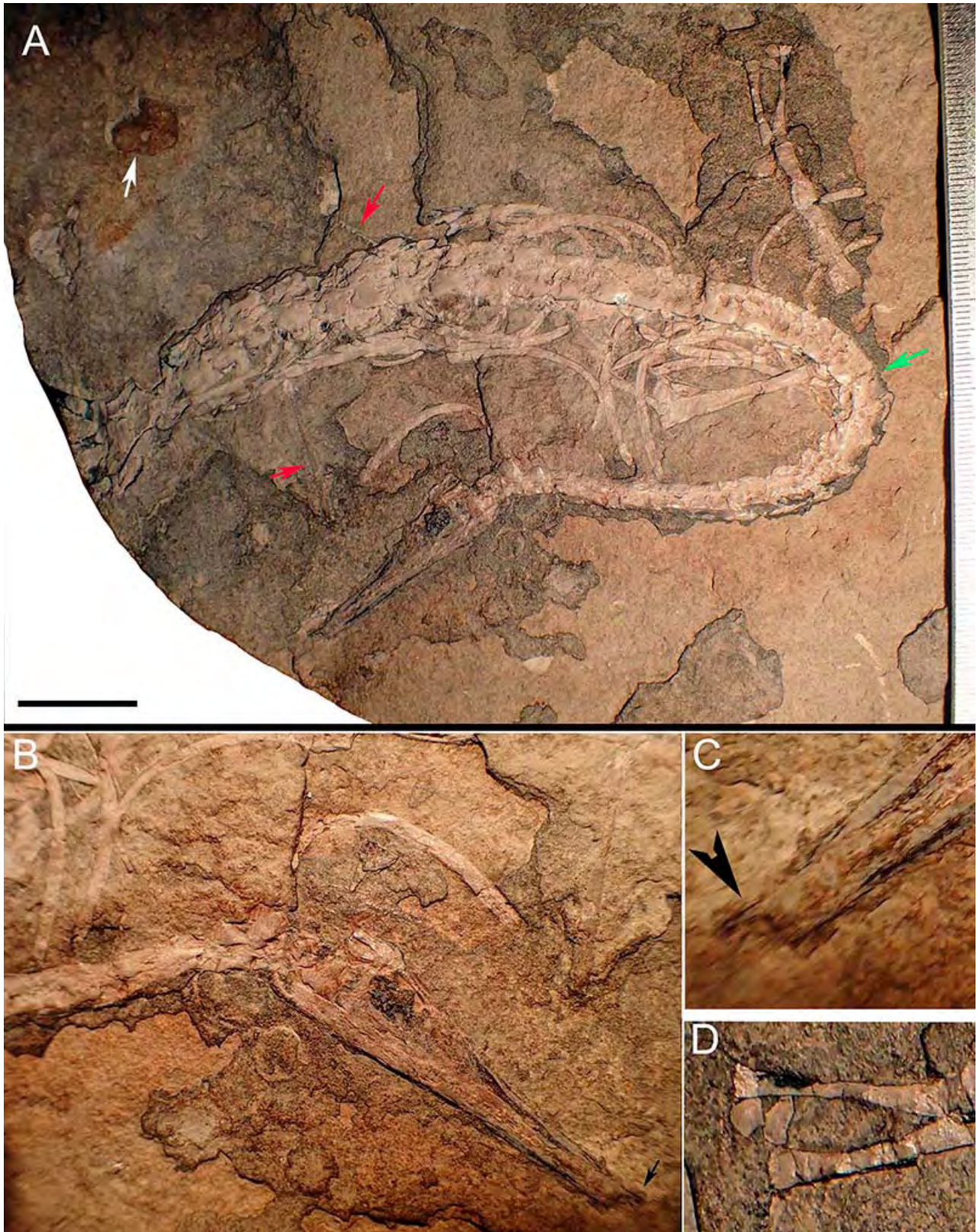


Figure 20. Reappraisal of the type specimen of *Brazilosaurus sanpauloensis* housed at the National Museum of Nature and Science, in Japan. **A**, holotype of *Brazilosaurus sanpauloensis* (NSM-PV 21867), a possible subadult (or adult) specimen as preserved. Green arrow marks the transition between last cervical and first dorsal vertebrae, white arrow shows a possible isolated scapulocoracoid that may or may not belong to the subadult (or adult) specimen, whereas red arrow points to associated mandibular remains of a juvenile specimen (approximately one half the size of the larger specimen). **B**, close up of the skull of the larger specimen showing the fracture of the snout (small black arrow) in the region anterior to the proximal margin of the nasal bone. **C**, close up of the fracture of the snout to show that it includes the premaxilla and anterior portion of the mandible. **D**, close up of the preserved carpal bones, presumed to be the intermedium (at the right) and the ulnar (at the left).

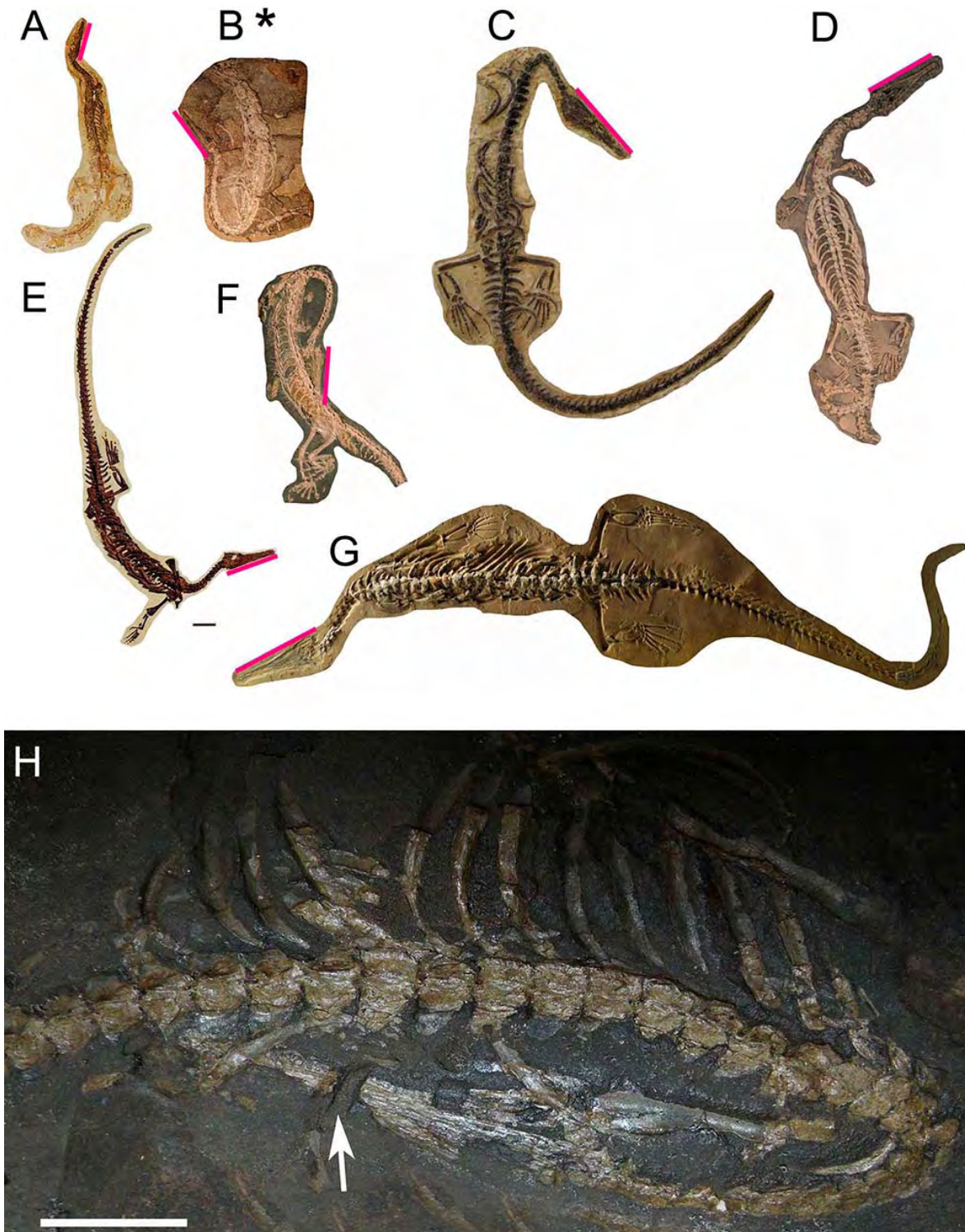


Figure 21. Size of the type specimen of *Brazilosaurus sanpauloensis* (asterisk) in comparison with other juvenile (A), subadult or young adult (C–F) and adult (G) mesosaurs. Red bars show the length of the skull in each specimen for comparison; it is worth to note that the skull length of specimen in E is even shorter than the holotype of *Brazilosaurus* (B). H, photograph of specimen MN 2196, is an example to show how much frequent is the fracture of the snout in mesosaurs, mostly at the level of the anterior margin of the nasal bone (white arrow), producing the effect of a very short skull with respect to the length of the snout. Scale bars = 20 mm.

As our results are suggesting, *Brazilosaurus sanpauloensis*, as well as *Stereosternum tumidum*, should be considered junior synonymous of *Mesosaurus tenuidens*. Figure 22 shows

the type specimens of these previously erected mesosaur taxa for comparison; they clearly demonstrate what difficult is to identify the suggested diagnostic characters for each of them.

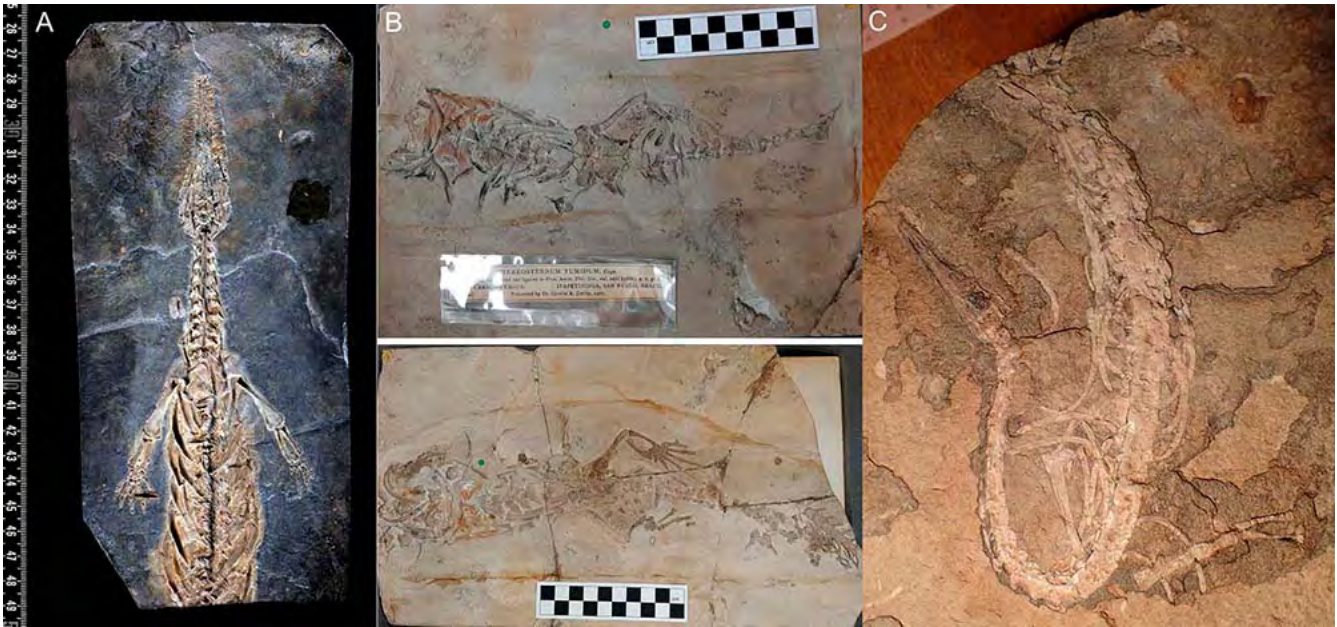


Figure 22. Type specimens of the previously erected mesosaur taxa; **A**, *Mesosaurus tenuidens* Gervais, 1865; **B**, *Stereosternum tumidum* Cope, 1885a; **C**, *Brazilosaurus sanpauloensis* Shikama & Ozaki, 1966.

Amended diagnosis for *Mesosaurus tenuidens*

After the present study, we propose the family Mesosauridae to be considered as monotypic and the amended diagnosis for *Mesosaurus tenuidens*, as the first and properly defined mesosaur taxon, is as follows:

Mesosaurus tenuidens Gervais, 1865. Small to medium sized basal amniote characterized by the presence of the following combination of characters: elongate snout bearing long and short slender teeth, recurved at the tip; nares fusiform and retracted, in communication with a small opening enclosed by the lacrimal, maxilla and nasal (the *nariale obturatum* foramen) which could be related to the release duct of a salt gland; nasal bone very long, extending anteriorly to the middle length of the snout; a small lateral temporal fenestra is present and enclosed by the jugal, the postorbital and the squamosal. 12 or 13 cervical vertebrae, similar in length or with a segment from fifth to eighth showing longer centrae (in lateral view); plate-like to rod-like cervical ribs; presacral count of 33–34 vertebrae; interclavicle head diamond-shaped; dorsal ribs displaying different pachyosteosclerotic s.l. intensity; variable sacral rib morphology, being both straight or at least one expanded at the distal end (possibly related to sexual dimorphism); scapulo-coracoid with different degree of coossification during ontogeny, even observed at early stages of development; variable ossification of the distal tarsal V, being absent even in adult individuals, variable fusion of the centralia which can appear as separated bones, fused each other or both abutting to the astragalus, depending the ontogenetic stage of the individuals.

Synonymy

Mesosaurus Gervais, 1865

Syn. *Stereosternum* Cope, 1885

Syn. *Ditrochosaurus* Gürich, 1889

Syn. *Brazilosaurus* Shikama & Ozaki, 1966

Mesosaurus tenuidens Gervais, 1865

Syn. *Stereosternum tumidum* Cope, 1885

Syn. *Ditrochosaurus capensis* Gürich, 1889

Syn. *Mesosaurus pleurogaster* Seeley, 1892

Syn. *Mesosaurus brasiliensis* MacGregor, 1908

Syn. *Brazilosaurus sanpauloensis* Shikama & Ozaki, 1966

CONCLUSIONS

One of the most contentious issues around the study of mesosaurs, beyond that about the nature of the temporal region of the skull, was without doubt, the taxonomic composition of the group. After the description of *Mesosaurus tenuidens* by Gervais (1865), several new species were proposed but all of them were synonymized to *Mesosaurus* (see Modesto, 1996, 1999).

Among the previous workers that supported the presence of just one taxon of mesosaurs in the Paraná and the Karoo basins are Friedrich von Huene (1940, 1941) and Alfred

S. Romer (1956). These brilliant anatomists considered *Mesosaurus tenuidens* as the only mesosaur species and believed that the subtle differences observed were just related to the ontogenetic stage of development of the preserved individuals.

The anatomical conditions that were previously used to support the presence of three monotypic mesosaur taxa (*apud* Araújo, 1977; Modesto, 1996, 1999, 2010) were here statistically analyzed and our results suggest that they are natural intraspecific variations produced during the individual ontogenetic growth and driven by specific environmental or ecological stress. Beyond this, many other features may be taphonomic artifacts or can represent sexual dimorphism. The preservation of natural molds of articulated, and almost complete individuals and partial skeletons or even isolated bones splitting as part and counterpart which even belonging to the same individual present subtle morphological differences, could have caused incorrect taxonomic interpretations. One clear example of this problem is the reported possible absence of an ectepicondylar foramen in the humerus (Modesto, 1999), which was demonstrated that is due to a taphonomic artifact; the foramen can be present in one of the split slabs (the part) and absent in its counterpart (see Laurin & Piñeiro, 2017, 2018). Another example is the triangular or diamond-shaped interclavicular head (Modesto, 1996; 1999), with two models that were demonstrated to be taphonomically produced. The suggested presence of only one lateral central in *Stereosternum* (by fusion of central 1 and 2) and the absence of centralia in *Mesosaurus* (Modesto, 1996, 1999) is a condition that was recently contested by Piñeiro *et al.* (2016), who demonstrated that all mesosaurs have indeed two centralia which fuse later in the ontogeny, and as Carroll (1982) has suggested previously, both of these fused bones (C1 and C2) merge to the distal border of the astragalus and abutt to and finally fuse with it in all mature mesosaur individuals.

Although taphonomy might explain many of the artifacts that we can see as factual differences among the several hundred of available mesosaur specimens, our study has revealed the presence of possible polymorphism in the population in the form of dwarfism, which may have been produced under particular developmental and ecological conditions. Also polymorphism can be found at the morphology of the sacral ribs, being straight or distally expanded at different degrees. We interpret this condition to symbolize sexual dimorphism in mesosaurs, being the distally expanded sacral ribs corresponding to females, in which this condition could offer a wider surface to the attachment of the dorsal iliac blade and a major stability on land. As evidence of this suggestion, we found the distally expanded morphotype in a specimen that carries an embryo in the abdominal area.

Unfortunately, most articulated and well preserved specimens do not include the skull, or if it is present, it is crushed and badly preserved. Thus, comparative studies on the skull morphology remain to be evaluated on a higher number of specimens. Even though, skulls studied recently by Piñeiro (2004); Morosi (2011) and Piñeiro *et al.* (2012b) have shown no reliable anatomical differences, even when they

are preserved in different planes from what the compressed specimens split (see Piñeiro *et al.*, 2012b and Laurin & Piñeiro, 2017, 2018).

Concerning the postcranial skeleton, the differences evaluated here do not give support for the presence of three mesosaur taxa in the Paraná or the Karoo Basins.

As we could not find unambiguous autapomorphies that characterize *Brazilosaurus* or *Stereosternum*, both these taxa should be considered as *nomina dubia* and junior synonyms of *Mesosaurus*.

We consider our work a progress in the taxonomic characterization of mesosaurs, now comprising only one taxon which by priority is *Mesosaurus tenuidens*. Based on this new proposal, arbitrary assignment of new studied materials will be avoided, and a better study of the evolution of each anatomical character is warranted, particularly for those that demonstrated to be ambiguous or polymorphic. These conditions are commonly found in early tetrapods being possibly associated to developmental processes in response to changing environmental factors occurring during Late Carboniferous and Early Permian (*e.g.* temperature, salinity, water level, food availability and quality and, catastrophic, tectonically controlled events). Such evolutionary plasticity, along with their phylogenetic signal, confirms *Mesosaurus* among the basalmost amniotes.

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