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Caudal autotomy in *Mesosaurus tenuidens* Gervais, 1865 under scrutiny and a surprising new pattern of vertebral organization in the mesosaur tail

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ABSTRACT

Mesosaurs are basal amniotes that lived in an extended epicontinental sea resulting from Devonian and Carboniferous glaciations reported in Southern Gondwana. Previously considered to be marine animals, this interpretation is not supported by their skeletal anatomy, and was updated to a more semiaquatic style, prompting increased interest for mesosaur studies. Recently, transverse fractures

and weak ossified areas at the subcentral surface of some caudal vertebrae have been interpreted as fracture planes related to a putative capability of autotomy in mesosaurs. We reassess the data used in support of caudal autotomy and identify the constraining morphological features of the involved vertebrae that contradict the development of such ability in mesosaurs. Moreover, we analyze the physiological and behavioral negative consequences that the loss of part of the tail would represent for aquatic and semiaquatic animals. The fact that no extant taxa living in these environments developed caudal autotomy supports our interpretations. We present an alternative hypothesis that suggests the presence of multipartite caudal centra represented by pleurocentrum and intercentrum arranged in the way expected for a reverse embolomerous pattern, previously undescribed for early stegocephalians or amniotes. However, a rapid revision of specialized literature suggests that the pattern could have been present in other basal amniotes and the possibility deserves additional studies, mainly in juvenile individuals. Our reinterpretation of the structure of mesosaur caudal vertebrae supports the proposed morphological plasticity observed in many clades of basal stegocephalians and amniotes and would match the recently suggested phylogenetic affinities of mesosaurs with respect to taxa that are close to, or part of the amniote stem under some phylogenies.

KEY WORDS

Mesosauridae,
vertebral patterns,
caudal vertebrae,
autotomy,
Gondwana.

RÉSUMÉ

Étude de l'autotomie chez Mesosaurus tenuidens Gervais, 1865 et un nouveau modèle surprenant de vertèbres caudales dans la queue des mésosaures.

Les mésosaures sont des amniotes basaux qui vivaient dans une mer épicontinentale étendue résultant des glaciations du Dévonien et du Carbonifère signalées dans le sud du Gondwana. Pendant longtemps, ils ont été interprétés comme des animaux marins, mais cette interprétation, non étayée par leur anatomie squelettique, a été abandonnée par certains auteurs qui proposent un style davantage semi-aquatique, ce qui a généré une recrudescence d'intérêt notable pour les études sur les mésosaures. Récemment, des fractures vertébrales dans la zone sous-centrale de certaines vertèbres caudales ont été interprétées comme des plans de fracture liés à une capacité putative d'autotomie chez les mésosaures. Nous réévaluons l'hypothèse proposée et retrouvons plusieurs facteurs contraignant la morphologie des vertèbres impliquées dans le processus autotomique, en plus des conséquences négatives physiologiques et comportementales que la perte d'une partie de la queue représenterait pour des animaux aquatiques et semi-aquatiques. Le fait qu'aucun taxon vivant dans ces environnements n'ait développé d'autotomie caudale soutient nos interprétations. Par conséquent, nous présentons une hypothèse alternative qui suggère la présence de centres caudaux multipartites représentés par un pleurocentrum et un intercentrum disposés de la manière attendue pour un motif embolomère inverse, précédemment inédit chez les premiers stégocéphales ou amniotes. Notre réinterprétation des vertèbres caudales du mésosaure fournit de nouvelles preuves de la plasticité morphologique proposée observée dans de nombreux clades de stégocéphales basaux et correspond aux affinités phylogénétiques récemment suggérées entre les mésosaures et des taxons qui sont proches de la souche des amniotes ou qui en font partie dans certaines phylogénies.

MOTS CLÉS

Mesosauridae,
modèles vertébraux,
vertèbres caudales,
autotomie,
Gondwana.

INTRODUCTION

Since its discovery about two centuries ago, *Mesosaurus tenuidens* Gervais, 1865 has been considered as a transitional taxon. Described by Gervais (1865) for the first time, *Mesosaurus* Gervais, 1865 puzzled early amniote researchers such as Cope (1886) who considered mesosaurs as possessing a unique skeletal morphology consisting of a mixture of anatomical features characteristic of both aquatic and terrestrial reptiles and who placed them tentatively in the “Batrachia”. He based this relationship on the distinctive

small size of the centrum of dorsal vertebrae relative to the swollen neural arch, a feature more commonly observed in seymouriamorphs and diadectomorphs rather than in reptiles and other basal amniotes (Carroll & Baird 1972; Clark & Carroll 1973; Carroll 1982). However, the vertebral morphology and other osteological characters used in early paleontological studies that sought to establish the affinities of mesosaurids to diapsids or synapsids, were ignored in recent phylogenetic studies that instead linked them to the stem sauropsids or to the parareptiles (e.g. Gauthier *et al.* 1988a, b, c; Laurin & Reisz 1995; Modesto 1996, 1999; Laurin &

Piñero 2017, 2018; MacDougall *et al.* 2018, among others). Their specialized (although not yet completely known) cranial morphology, with a long snout bearing slender and thin teeth, posteriorly placed nares, and pachyosteosclerotic ribs and vertebrae, were considered as adaptations for a marine environment (Araújo 1977; Oelofsen 1981; Oelofsen & Araújo 1983; Modesto 1996, 1999, 2010), which implied that mesosaurids were the first amniotes to return to water. However, these hypotheses were not universally accepted, and some workers proposed that mesosaurids were semiaquatic animals that may have retained this lifestyle from their ancestors (see Romer 1947; Piñero *et al.* 2016, 2021; Núñez Demarco *et al.* 2022).

To confidently infer the lifestyle of an ancient extinct species, detailed anatomical studies of the skeleton in individuals representing different ontogenetic stages are necessary. These studies can be complemented with paleoenvironmental interpretations of the geological setting of their fossilization. The reliability of these inferences also depends on the size of the studied sample and the quality of preservation. Other associated fossils from the surrounding matrix and from the entire stratigraphic sequence can help constrain paleoenvironmental conditions as well as the establishment of biostratigraphic correlations. These data sources have long been available for studying the lifestyle of mesosaurs and have been used to support the aforementioned hypotheses, although many of them remain controversial.

A recent study by MacDougall *et al.* (2020) reassessed previously suggested hypotheses that mesosaurids retained caudal autotomy as a defensive response against predators, a controversial possibility that is revisited in the present contribution. As we argue below, this mechanism is not as plausible in aquatic, tail-propelled animals (see Villamil *et al.* 2015) as in terrestrial ones that rely on limbs for locomotion.

Caudal autotomy is the voluntary shedding of the tail through specialized vertebrae that develop fracture planes and/or areas of bone weakness, and a series of muscles and blood vessels that automatically constrict to limit the loss of soft tissues. Among reptiles, this phenomenon is unknown in crocodiles and turtles but widespread within squamates where it serves as a defensive behavior that favors escape from predators (i.e., Gordeeva *et al.* 2020). The splitting can be either intravertebral or intervertebral; the first pattern is the most common in squamates, except in agamids, which have developed intervertebral caudal autotomy (Ananjeva *et al.* 2021).

Romer (1956) initially suggested that some lines of fracture and poorly ossified areas observed in the centrum of some mesosaurid caudal vertebrae implied a potential capability for caudal intravertebral autotomy. This hypothesis was followed by MacDougall *et al.* (2020) as a possible condition characterizing mesosaurids based on the fact that other Paleozoic amniotes, such as the captorhinid *Captorhinus aguti* (Cope, 1882) (LeBlanc *et al.* 2018) and *C. laticeps* (Williston, 1909) (“*Eocaptorhinus*” in Heaton 1979; Dilkes & Reisz 1986), show similar lines of fractures in the centrum of some vertebrae, interpreted as evidence for autotomy (Romer 1956; Heaton & Reisz 1980; LeBlanc *et al.* 2018).

For captorhinids, which are often suggested to have been terrestrial, autotomy is a plausible explanation for the fracture planes observed in isolated caudal vertebrae. However, for aquatic or semiaquatic taxa for which the tail plays an essential role in swimming, tail loss can be disadvantageous (Fleming *et al.* 2013). The absence of fracture planes in all the extant aquatic taxa, including marine mammals and snakes, and also their absence in the caudal vertebrae of the marine iguana (*Amblyrhynchus cristatus* Bell, 1825), which remains capable of land incursions, supports this point (Arrivillaga & Brown 2020). The only exception may be the water anole (*Anolis aquaticus* Taylor, 1956) which is indeed a semiaquatic dactyloid squamate, in which autotomy was related with the exacerbated boldness of the males. Although individuals of both sexes have the capability to autotomize their tail, the strategy was observed mainly in the males, which drop their tails to avoid intraspecific predation during polygynous matings (Talavera *et al.* 2021).

The mesosaurid tail is almost completely preserved in many specimens, with putative fracture planes observed in nearly all of the caudal vertebrae. Thus, if autotomy did occur in mesosaurids, more than half of the tail could have been lost. This would represent a significant physiologic cost as the tail served as the main swimming organ for mesosaurids (Modesto 1996; Villamil *et al.* 2015). MacDougall *et al.* (2020) acknowledged this issue and suggested that the role of the tail in mesosaurid locomotion had been previously exaggerated, and that propulsion in the water could have been achieved by their paddle-like limbs. In addition, MacDougall *et al.* (2020) concluded that autotomy cannot be definitively proven in mesosaurids, and the presence of fracture planes could be a relic condition.

The aim of this contribution is to review the morphological, physiological and behavioral implications of tail autotomy in extinct aquatic forms such as *Mesosaurus tenuidens* by contrasting previous hypotheses about its lifestyle as a marine or semiaquatic amniote. We also provide a new interpretation of the putative fracture planes reported in the mesosaurid caudal centra. Whereas the autotomous vertebrae in recent taxa are generally peculiar and persistent caudal segments characterized by splitting produced by a fracture that runs across the centrum and the neural arch, and this structural pattern does not change through ontogeny, in mesosaurids, on the contrary, the “fracture planes” only affect the centrum of the vertebra, and they are present in all the vertebrae posterior to the “pygal” segment.

MATERIAL AND METHODS

MATERIAL

To assess the biological significance of the observed fracture planes in some mesosaurid caudal vertebrae, a comparative morphological analysis was conducted across a large dataset comprising over 700 specimens. This dataset includes both isolated elements representing various positions in the tail and articulated tails containing the complete caudal series.

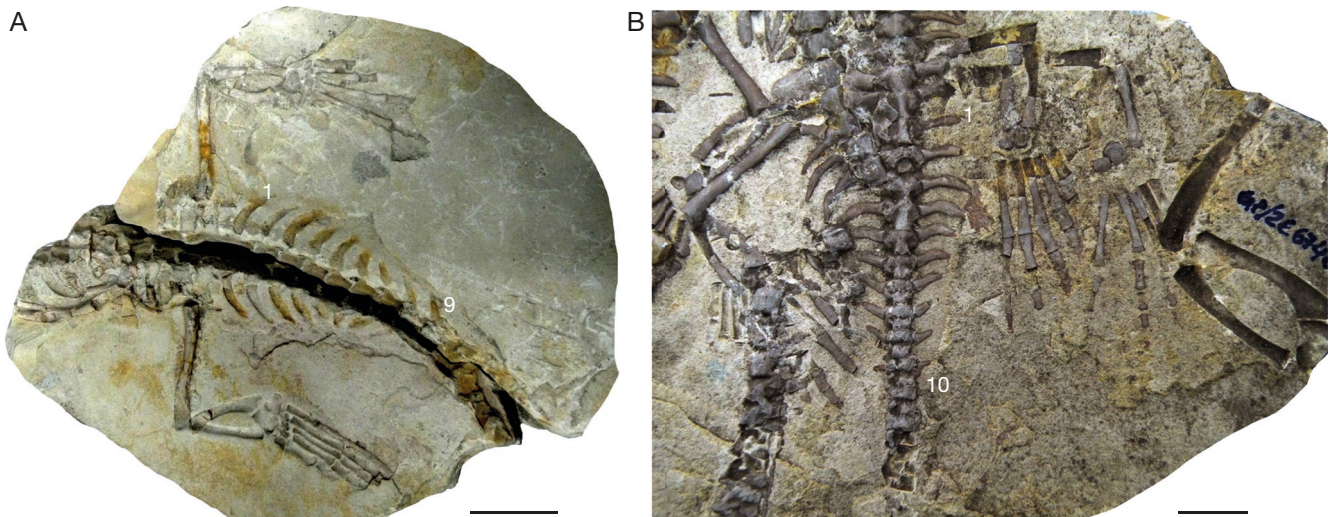


FIG. 1. — *Mesosaurus tenuidens* Gervais, 1865 specimens showing the morphology of the “pygal-like” segment: **A**, GP-2E 653a, posterior region of presacral series, pelvic girdle and hind limbs, and anterior part of the tail showing only nine caudal vertebrae carrying ribs, which decrease in size posteriorly; **B**, GP-2E 674b showing aggregation of juvenile and adult individuals. The whole “pygal-like” segment (ten vertebrae) is preserved. Scale bars: A, 30 mm; B, 10 mm.

A parasagittal histological slide of the caudal vertebrae from specimen MCN-PV-20.007-P was prepared. Due to the exceptionally thin nature of the fossil material, which matches the thickness of the diamond saw employed, only one section was produced. Subsequently, images were captured using a magnifying glass and microscope in both normal and polarized light.

Piñeiro *et al.* (2021) recently proposed that Mesosauridae Baur, 1889 includes a single taxon, *Mesosaurus tenuidens*, a conclusion that was also supported by Verrière & Fröbisch (2022) and that is accepted here. Therefore, throughout this study, the terms “mesosaurid” or “mesosaur” are used to refer exclusively to this taxon.

ABBREVIATIONS

The analyzed *Mesosaurus* specimens are from the following collections:

- FC-DPV Departamento de Paleontología, Facultad de Ciencias, Montevideo;
- DNPM Departamento Nacional de Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro;
- GP-2E Instituto de Geociências (section Palaeontology) of the São Paulo University, São Paulo;
- MCN-PV Museu de Ciências Naturais, SEMA, Porto Alegre;
- BP/1 Evolutionary Studies Institute, University of Witwatersrand, Johannesburg;
- GSN-F National Earth Science Museum at the Geological Survey of Namibia;
- AMNH American Museum of Natural History, New York;
- NSM-PV National Museum of Nature and Science;
- PIMUZ Paleontological Institute and Museum of the University of Zurich;
- SMF-R Senckenberg Forschungsinstitut und Naturmuseum Institut, Frankfurt;
- SMNS Staatliches Museum für Naturkunde, Stuttgart (Table 1).

This diverse sample encompasses caudal vertebrae and tails from both adult and juvenile individuals, preserved at different ontogenetic stages.

METHODS

Specimens of different sizes and attributable to different stages of development were analyzed under a NIKON HFX-DX stereoscopic microscope equipped with camera lucida and Infinity Analyze software for the analysis. This setup facilitated the capture of photographs and the creation of drawings to document the anatomical features of the studied vertebrae. In some instances, more time-intensive methods were utilized, involving the careful removal of surrounding sediment from 3D-preserved specimens. One of these 3D specimens was sectioned to produce a thin section along a longitudinal, parasagittal plane of mid-distal caudal vertebrae, allowing for the study of their microstructure and ossification processes. All specimens from Uruguayan (FC-DPV), and Brazilian (GP-2E, DNPM and MCN-PV) collections, as well as those from the SMF-R collection in Germany, were examined directly, whereas specimens from other collections were studied using photographs kindly provided by the respective curators (refer to the Acknowledgements section for further details).

RESULTS

MESOSAUR VERTEBRAE ANATOMY: IMPLICATIONS FOR THE “AUTOTOMY” HYPOTHESIS

To compare with both extant and extinct taxa for which autotomy has been suggested or observed, we provide a concise description of the anatomical characteristics and structural arrangement of the vertebral segments that can be identified in the mesosaurid tail.

The “pygal” caudal segment of Mesosaurus

The first seven to ten caudal vertebrae (observed intraspecific numerical variations may reflect sexual dimorphism; see Shine *et al.* 1999) constitute a specialized string characterized by the presence of ribs firmly attached to the short transverse



FIG. 2. — *Mesosaurus tenuidens* Gervais, 1865 from the Mangrullo Formation of Uruguay. Morphology of the last caudal vertebrae of the pygal-like segment: **A, B**, FC-DPV 2206; **C**, FC-DPV 2467; **D**, FC-DPV 2231. These specimens show the presence of transverse processes and associated ribs (**yellow arrowheads**), as well as a haemal arch (**red arrowheads**) in the preserved vertebrae. They must consequently be part of the last of the “pygal-like” series because the anterior portion of that segment lack chevrons, whereas in the postpygal vertebrae, transverse processes are very poorly developed, if at all. Scale bars: 10 mm.

TABLE 1. — List of studied specimens in this work.

SMF-R 391	GP/2E 444	FC-DPV 1467
SMF-R 387	GP/2E 449	FC-DPV 1461
SMF-R 396	GP/2E 480	FC-DPV 2534
SMF-R 397	GP/2E 486	FC-DPV 2037
SMF-R 402	GP/2E 5423	FC-DPV 2061
SMF-R 4470	GP/2E 5603	FC-DPV 2116
SMF-R 4473	GP/2E 5610	FC-DPV 2242
SMF-R 4476	GP/2E 5633	FC-DPV 2280
SMF-R 4477	GP/2E 5637	FC-DPV 2318
SMF-R 4478	GP/2E 5647	FC-DPV 2481
SMF-R 4479	GP/2E 5714	FC-DPV 2506
SMF-R 4480	GP/2E 5740	FC-DPV 2504
SMF-R 4482	GP/2E 5764	FC-DPV 1006
SMF-R 4484	GP/2E 5796	FC-DPV 1100
SMF-R 4485	GP/2E 5812a	FC-DPV 1441
SMF-R 4488	GP/2E 5862	FC-DPV 2231
SMF-R 4490	GP/2E 596	FC-DPV 2232
SMF-R 4493	GP/2E 62	FC-DPV S/N
SMF-R 4496	GP/2E 63 big	FC-DPV S/N
SMF-R 4497	GP/2E 63 little	FC-DPV S/N
SMF-R 4512	GP/2E 639	FC-DPV S/N
SMF-R 4513 1 adult	GP/2E 644	FC-DPV 2483
SMF-R 4513 1 young	GP/2E 646	FC-DPV 2489
SMF-R 4528	GP/2E 65	FC-DPV 1219
SMF-R 4710	GP/2E 653a	FC-DPV 2074
SMF-R 4712	GP/2E 657b	FC-DPV 1742
SMF-R 4921	GP/2E 660	FC-DPV 1745
SMF-R 5040c	GP/2E 666	FC-DPV 2414
SMF-R-4934	GP/2E 664	FC-DPV 2526
SMF-R-4935	GP/2E 669a, b, c	FC-DPV 2307
AMNH 23794	GP/2E 670	FC-DPV 2046
AMNH 23795	GP/2E 674a	FC-DPV 2035
AMNH 23796	GP/2E 674b	FC-DPV 2282
AMNH 23799	GP/2E 675	FC-DPV 2281
PIMUZ A-III 192	GP/2E 680	FC-DPV 2480
PIMUZ A-III 513	GP/2E 683	FC-DPV 2517
PIMUZ A-III 591	GP/2E exhibition S/N A	FC-DPV 3622
PIMUZ A-III 801	GP/2E exhibition S/N B	FC-DPV 3623
MN 4741	GP/2E exhibition S/N C	FC-DPV 3620
MCN-PV 0048	GP/2E exhibition S/N D	FC-DPV 1427
MCN-PV 0049	GP/2E exhibition S/N E	FC-DPV 2397
MCN-PV 2158	GP/2E exhibition S/N F	FC-DPV 3621
MCN-PV 2214	GP/2E exhibition S/N G	FC-DPV 2396
MCN-PV S/N	GP/2E exhibition S/N H	FC-DPV 1061
DNPM 4816	GP/2E S/N	FC-DPV 1347
GP/2E 114a	GP/2E S/N	FAGRO 0004
GP/2E 232	GP/2E S/N	FAGRO 0002
GP/2E 26639	MG 9639	FAGRO 0005
GP/2E 272	PF 3530	FAGRO 0006
GP/2E 284	PF IPL 220011/04 770	FAGRO 0007
GP/2E 296	PF (0407)-3528	
GP/2E 3579	PF_3529	

processes, the lack of haemal arches (chevrons) and also the absence of “fracture/suture planes”. However, in mesosaurs the last vertebrae of the pygal segment can carry an haemal arch.

This configuration follows the previously documented trait of basal stegocephalians, in which all presacral vertebrae, as well as the first caudals, bear ribs (Romer 1947).

The ribs of the first five caudal vertebrae are long, stout and bent posteriorly, as is also observed for instance in captorhinids (Heaton & Reisz 1980; Berman & Reisz 1986), diadectids (Berman & Henrici 2003) and seymouriamorphs (Berman *et al.* 1987). From the sixth to the ninth or tenth vertebrae, the ribs abruptly decrease in size with the last three either bent anteriorly or pointing laterally (Fig. 1). These anterior-

most nine to ten caudal vertebrae may be considered as the “pygal-like” segment, which in extant squamates possessing intravertebral autotomy, is associated with the insertion of the caudofemoralis longus muscle, and thus autotomy cannot occur in vertebrae of this segment which is typically characterized by the absence of fracture planes (Ritzman *et al.* 2012).

Due to the presence of long and firmly fused ribs, a condition which is morphologically similar to that observed in the posterior dorsal vertebrae (Fig. 1), the ribs of the first ten caudal vertebrae of mesosaurs are often preserved parallel to the stratification, and thus, the vertebrae are mostly exposed in ventral or dorsal view, or in a frontal or antero/postero-lateral view on rare occasions. This makes it challenging to confirm the existence of potential “fracture planes” (from now on referred to as “fracture/suture planes”) within these anteriormost caudal vertebrae. However, some fortuitous isolated vertebrae recognized as part of the “pygal segment” because they bear short transverse processes carrying a rib, show that there are no central fractures in these vertebrae at the mid-centrum area. The presence of haemal arches in the last vertebrae of the “pygal-like” segment can also be confirmed by examining these isolated vertebrae (Fig. 2C, D).

The postpygal caudal segment of Mesosaurus

The putative “fracture/suture planes” described by MacDougall *et al.* (2020) as evidence for autotomy in mesosaurs are present in vertebrae placed posterior to the last vertebra of the pygal segment. This vertebral segment will be known as the postpygal string and is characterized by vertebrae with diminutive transverse processes in the cranialmost segments (or none whatsoever, farther caudally), and are predominantly preserved in lateral view (Fig. 3).

The mesosaurid “postpygal” segment is formed by at least 56 vertebrae, some of which articulate with short ribs, if at all, but this condition is gradually lost in caudal direction. Most of them also bear haemal arches (chevrons); and only the last five or six vertebrae near to the tip of the tail are simplified and lack neural spines or haemal arches (Fig. 3B, C).

This distribution indicates that *Mesosaurus* possessed a long tail consisting of more than 60 vertebrae, a length similar to what has been suggested for *Captorhinus* Cope, 1895 and all the basalmost stegocephalians (Romer 1947). Moreover, based on the described general pattern for mesosaur caudal vertebrae, it is possible to identify the relative position of isolated caudal vertebrae in the tail, and also determine if it is part of the “pygal-like” or the “post-pygal” series through the orientation of the transverse processes and ribs and by the presence/absence of haemal arches (Fig. 3).

A review of the pygal and postpygal vertebral morphology in extant and extinct reptiles

The described morphological pattern of these regions in mesosaurs is notably different from that observed in most extant reptiles that can autotomize their tails, where haemal arches are almost always absent from the pygal segment. The anole *Anolis carolinensis* Voigt, 1832 (in Cuvier & Voigt 1832) is an exception, because of the presence of chevrons

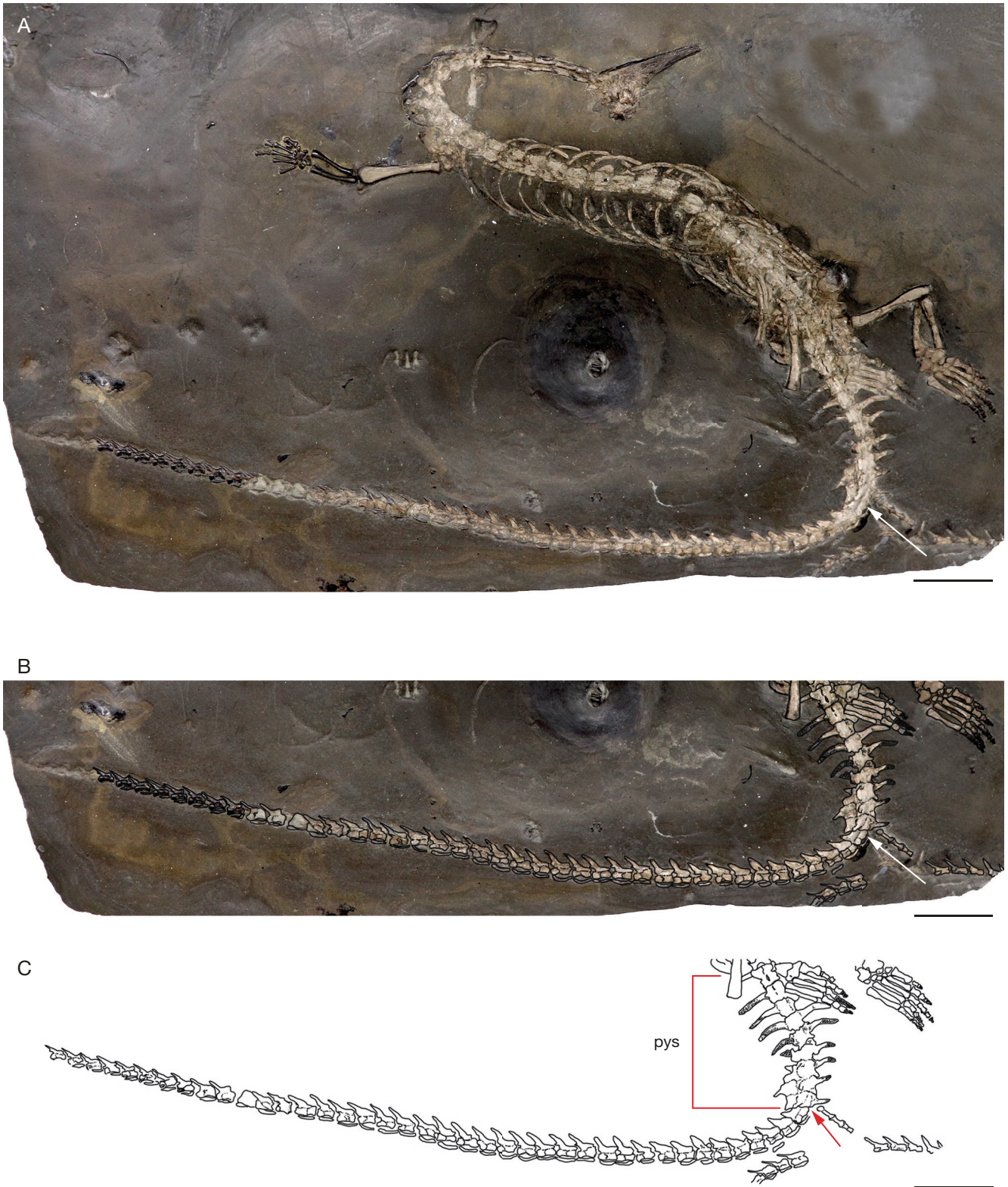


FIG. 3. — *Mesosaurus tenuidens* Gervais, 1865 “fracture/suture lines” present in all the vertebrae forming the “postpygal” segment of the tail: **A**, SMNS 51560. Photograph of an almost complete skeleton of a subadult specimen showing the very long tail of mesosaurs, which exceeds the length of the skull plus the thoracic region. The end of the “pygal” segment and the beginning of the postpygal region (**white arrows**) is identified by the presence of vertebrae showing the centrum divided in two areas by a subcentral “fracture/suture line”; **B**, detailed view of the tail of SMNS 51560 with the outline of bones highlighted; **C**, interpretive drawing of **B**; the pygal segment (**pys**) and the limi with the postpygal vertebrae are delimited by **bracket** and **arrow** respectively, in **red color**. Scale bars: 30 mm.

in the posteriormost vertebrae of the pygal segment characterized by the lack of transverse processes and the absence of fracture planes, although in some other squamate species, the posterior vertebrae of the series may exhibit both features (Ritzman *et al.* 2012).

The number of vertebrae in the pygal series varies among taxa, but a pygal region is always retained in taxa that undergo tail autotomy, as these vertebrae do not develop fracture planes. Therefore, autotomy is produced through fractures present in just a few vertebrae in the postpygal series and the split occurs immediately posterior to the short transverse processes (Gilbert *et al.* 2013).

Autotomy in Captorhinidae Case, 1911? For extinct taxa, one of the few suggested cases of autotomy is found among the captorhinids. However, the presence of autotomy in this taxon is uncertain, both because function is never known with certainty in extinct taxa (it is inferred, rather than observed) but more specifically because in *Captorhinus*, some of the vertebrae forming the “pygal” series seem to have fractures, whereas most of the components of the “post-pygal” series lack them (see Heaton & Reisz 1980; Dilkes & Reisz 1986; LeBlanc *et al.* 2018).

This is not the expected pattern, but it can be possibly influenced by the fragmentary nature of the studied materials. This prevents morphological comparisons between transitional presacrals, sacrals and the first caudals, which hampers establishing the position of the vertebrae bearing the fracture planes, along the tail. Many conclusions in this regard, like the interpretation of a “pygal” segment composed of five vertebrae (LeBlanc *et al.* 2018), are based on articulated fragmentary remains which putatively included vertebrae from the eighth to the fourteenth out of an estimated total of 60 or more caudal vertebrae (Heaton & Reisz 1980).

The case of *Captorhinus* also reveals the difficulties that commonly exist in reconstructing morphological and physiological patterns in extinct taxa; and because mesosaurs are an outstanding exception for the abundant and well-preserved materials that are available at the different paleontological collections around the world, it is possible to discriminate between hypotheses.

Potential autotomy in microsaurian lepospondyls. Within lepospondyls, autotomy and tail regeneration have been reported in the microsaurian *Microbrachis pelikani* Fritsch, 1875 from the Upper Carboniferous of Czech Republic (Carroll & Gaskill 1978; Milner 2008; Olori 2015; Fröbisch *et al.* 2015; Vos *et al.* 2018). Unlike recent salamanders that exhibit intervertebral splitting, in *Microbrachis pelikani*, it is intravertebral, as suggested by histological studies of thin serial sections of the caudal segments. There seems to be a decrease in ossification degree of the caudal vertebrae from anterior to posterior, very similar to what is observed in the juvenile mesosauroids. However, the fracture planes and the fine morphology of the splitting area in the *Microbrachis* specimens where the autotomy and regeneration were suggested are not clear from the interpretive drawings provided in Vos

et al. 2018. Olori (2015) shows photographs of *Microbrachis pelikani* and the two specimens that were thought to display autotomy and regeneration following the 11th vertebra, seem to be a taphonomic feature common in vertebrae preserved in ventral view, where only the central part of the centrum is visible; the rest of the skeleton is covered by sediment. Therefore, the available images do not allow making definitive conclusions. The images provided by Milner (2008) are similarly inconclusive; that study investigated if the length of the tail in *Microbrachis* can be associated with the capacity of regeneration of damaged segments of the tail in this taxon. The author warned that the last terminal vertebrae of the tail remain unossified in most *Microbrachis* specimens and thus, regeneration is not easy to determine. It is possible that the delayed ossification of terminal vertebrae in the tail and the long tail is due to the addition of vertebrae through the ontogeny, as seen in some extant salamanders such as Ambistomatidae Gray, 1950 and Plethodontidae (Gray, 1850) (Milner 2008). Interestingly, the haemal arches figured in Vos *et al.* (2018: fig. 6) are drawn as fused to the posterior region of the vertebral centrum, suggesting the presence of a reversed position of the intercentrum in the microsauroid *Microbrachis* as occurs for mesosauroids.

Potential autotomy in marine early diapsids? In the literature on marine mosasauroids, ichthyopterygians and sauropterygians, there is no mention of caudal vertebral structures (i.e., fracture planes) suggesting autotomy. The pygal segment appears to be formed by more than five vertebra in several of the revised sauropterygian taxa (e.g. Liu *et al.* 2021; Wolniewicz *et al.* 2023). The anteriormost transverse processes are relatively short and laterally directed in the pygals but they become wider and shorter in the postpygal series to gradually transform into short nubbins in the posteriormost vertebrae. The information on the nature of the haemal arches in ichthyopterygians and sauropterygians is scarce and ambiguous. Within mosasauroids, the pygal segment seems to be short in many species, and the haemal arches, when preserved in the postpygal string, seem to be articulated or fused to the posterior end of the vertebral centrum, as could be observed from many described taxa (see Williston 1898; Osborn 1899; Bell & Polcyn 2005; Kear 2006; Druckenmiller & Russell 2009; Konishi *et al.* 2012; Carpenter 2017; among others).

FUNCTIONAL SIGNIFICANCE OF THE “FRACTURE/SUTURE” PLANES IN THE “POSTPYGAL” MESOSAUR VERTEBRAE
All the vertebrae within the “postpygal” series display a distinctive “fracture/suture” line or a weakly ossified area crossing the centra (Fig. 3), which has been interpreted as “fracture plane” for a potential development of autotomy in mesosaurs (Romer 1956; MacDougall *et al.* 2020). This structure resembles an incompletely closed suture that separates two regions of different sizes within the centrum, with the anteriormost part being slightly larger (Fig. 4). Conversely, some partial strings of the mesosaur tail have fortuitously split sagittally or parasagittally, creating taphonomic counter-

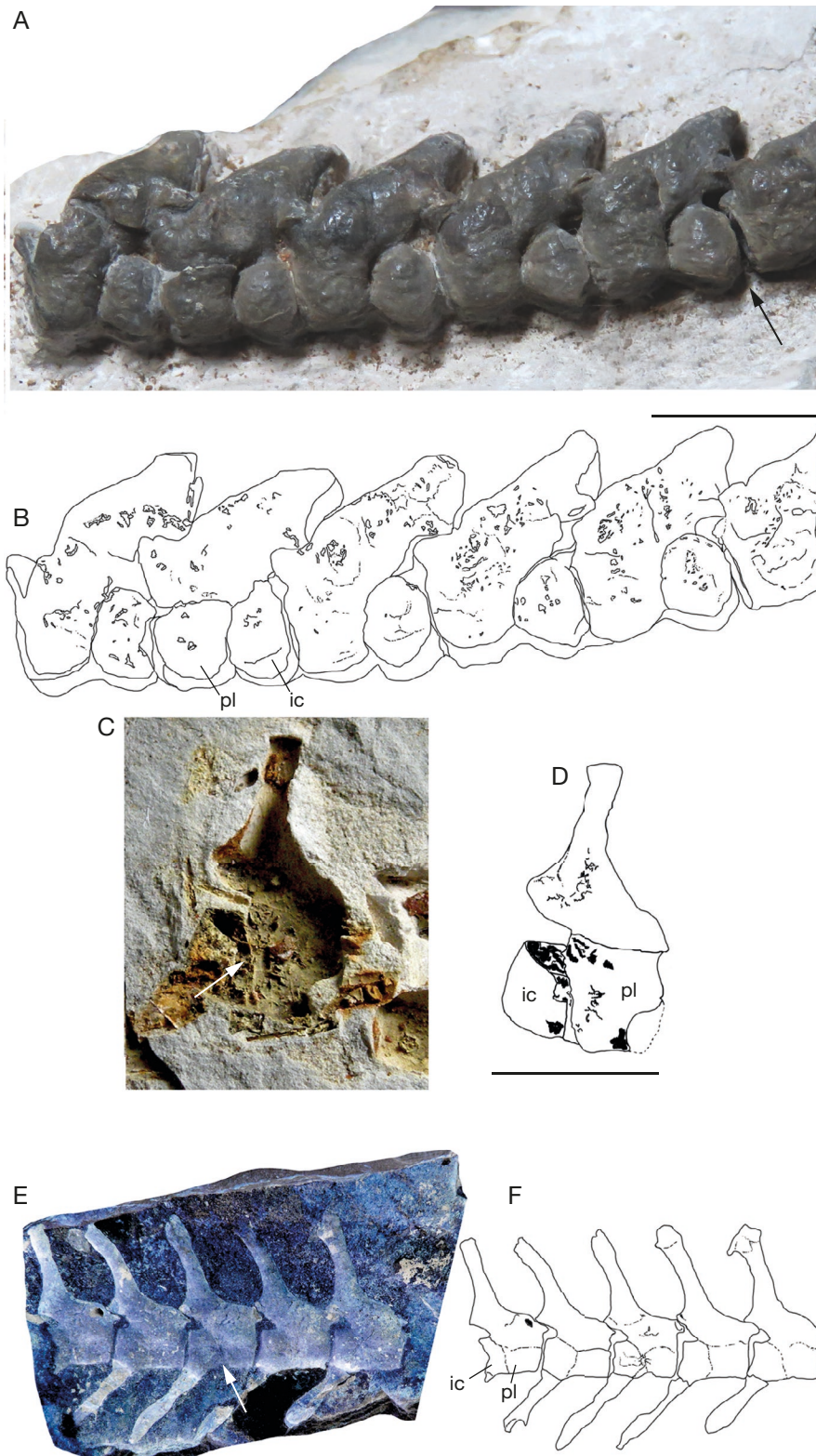


FIG. 4. — *Mesosaurus tenuidens* Gervais, 1865 “fracture/suture planes” in caudal vertebrae from the “postpygal” region of the tail: **A**, MCN-2242, caudal fragment of six articulated vertebrae showing the conspicuous fracture/suture lines dividing the centrum into two consecutive regions (**black arrow**) that look like distinct bones. In this specimen, the morphology of the vertebrae indicates that they are from the middle region of the tail (see MacDougall *et al.* 2018); **B**, interpretive drawing of the specimen in **A**, indicating the bones that form the caudal centrum in the post-pygal region; **C**, FC-DPV 2094. Isolated caudal vertebra from the postpygal segment of the tail of a mature mesosaur. Note that the taphonomic dislocation between the anterior and posterior parts of the centrum (**white arrow**) was produced following the “fracture/suture line” that characterizes these vertebrae; **D**, interpretive drawing of **C** showing the bones involved in the dislocation; **E**, FC-DPV 2205. Caudal fragment consisting of five articulated vertebrae bearing their respective haemal arches. The “fracture/suture” area (**white arrow**) is not as noticeable as in **A**, but it is still fairly obvious; **F**, interpretive drawing of **E**, indicating the bones present in the mesosaur caudal centrum. Abbreviations: **ic**, intercentrum; **pl**, pleurocentrum. Scale bars: 10 mm.

parts that reveal their internal anatomy. These counterparts expose structures such as what we prove by SEM analyses to be phosphatized remains of the notochordal tissues and the neural chord preserved within the neural canal (Figs 5; 6). The notochord is visible as a continuous structure along the dorsal vertebral series (Fig. 5E, F), although it appears as to have been interrupted at the middle of the caudal vertebrae, just where the “fracture/suture” line separates anterior and posterior central areas (Fig. 5A-D, G, H). This apparent interruption of the notochord may be related to the presence of the two primitive bones in the centrum formation, in vertebrae of the postpygal caudal series of mesosaurs. The thin section suggests that the notochord could remain continuous, although reduced to a thin thread at the level of the fracture plane area of each vertebra, which is probably a condition that was reestablished during ontogeny after the fusion between pleurocentrum and intercentrum was completed (Figs 5; 6).

PHYSIOLOGICAL AND BEHAVIORAL CONSTRAINTS PREVENTING AUTOTOMY IN MESOSAURS

Among extant amphibians and reptiles that have evolved tail autotomy, a series of morphological adaptations minimize trauma for the involved tissues (Gilbert *et al.* 2013).

The fracture planes and areas of bone weakness in some caudal vertebrae indicate the location where the split occurs if the animal perceives threat from a predator. The “fracture/suture” planes observed by MacDougall *et al.* (2020) in mesosaurs are similar to each other; they occur in most, if not all postpygal vertebrae, and do not affect the neural arch, contrary to what is typically observed in all extant vertebrates adapted to caudal autotomy to avoid predation, where the fracture plane penetrates the neural arches (Silva *et al.* 2021).

The mesosaurid tail is a very important organ of the body, since it is longer than the remaining body length and it presumably had an important propulsive function during swimming (Modesto 1996; Villamil *et al.* 2015; Núñez Demarco *et al.* 2018, but see MacDougall *et al.* 2020).

Another factor to take into account is the morphology and orientation of the zygapophyses, which also play a crucial role in conferring stability to the vertebral column during locomotion. In mesosaurs, the trunk vertebrae have laterally placed and almost horizontal prezygapophyses and posteroventrally inclined postzygapophyses at the base of swollen neural arches, which allow significant lateral movement while restricting rotation of the vertebral column (Olson 1976).

A notable morphological change occurs at the beginning of the “postpygal segment” of the tail, where the vertebrae become laterally constricted, and the articular facets of the pre- and post-zygapophyses are positioned close to the sagittal plane, with the prezygapophyses oriented dorsomedially and the postzygapophyses facing ventrolaterally. This arrangement likely permits only moderate lateral movements while limiting rotation (Olson 1976), a pattern that is typical of taxa performing anguilliform movements, which presumably occurred also in mesosaurs (Villamil *et al.* 2015). This morphology is favorable to an

ambush-like predation strategy on fast prey like the juvenile pygocephalomorph crustaceans fossilized within the same beds as mesosaurids (Silva *et al.* 2017).

The loss of a long tail like that of mesosaurs would also alter the body mass distribution, affecting the balance and stability during locomotion (Gillis & Higham 2016). The incidence of these effects has been studied, for instance, in terrestrial and aquatic *Desmognathus* Baird, 1850 urodeles, revealing that the loss of part of the tail is more dangerous for the latter (Marvin 2010).

Furthermore, the biomechanical changes resulting from the tail loss could lead to isolation of the animals due to the inability to maintain a normal locomotion. This would not only affect aspects such as feeding, self-protection and reproductive strategies (Shine *et al.* 1999), but might also influence their social behavior (Gillis & Higham 2016). In the case of mesosaurs, gregarious and/or parental care behaviors have been proposed, perhaps during the reproductive season and shortly after birth when adults and their offspring are found together (Piñeiro *et al.* 2012a, b).

ECOLOGICAL CONSTRAINTS – PREDATION HYPOTHESIS

MacDougall *et al.* (2020) tentatively suggested that “autotomy” may have been functional in juvenile individuals, and that it may have become more difficult in adults.

Indeed, the hypothesis of autotomy as a defense mechanism that is more developed in juveniles (Savvides *et al.* 2018) could have been advantageous in mesosaurs if cannibalism occurred, but this may have been lost during ontogeny as it occurs in recent reptiles, especially considering that no predator of adult mesosaurs is known to occur in their environment.

Intriguingly, “fracture/suture” lines seem to be less prominent in very young mesosaurs with respect to what is shown in adult or subadult individuals (see Fig. 7). This may be due to the fact that the skeletons of juveniles are poorly ossified and the preservation potential is low (Fig. 7A-C); this therefore would prevent the retention of some features with the same detailed precision as in more ossified specimens. Perhaps as previously suggested, fracture-suture planes may be acquired later in the ontogeny (Williston 1925), but most probably it is due to a taphonomic influence giving some fortuitous findings of isolated caudal vertebrae of juvenile mesosaurids from the Mangrullo Formation of Uruguay, where the fracture planes are perfectly observed, as shown in Figure 7D.

Mesosaurs have no known predators and this conclusion may not be related to collecting biases, as all the organisms cohabiting with mesosaurs in the Mangrullo Formation had the potential to be preserved, including insect and plant soft tissues as wings and leaves (Piñeiro 2006). Even though, parental care has been previously suggested for mesosaurs based on the high number of fossils that show a hatchling-early juvenile-adult association. These are particularly well-documented in areas that may have been breeding grounds, such as the Mangrullo Formation Konservat Lagerstätte, where a mesosaur egg containing a foetus has appeared (Piñeiro *et al.* 2012a).

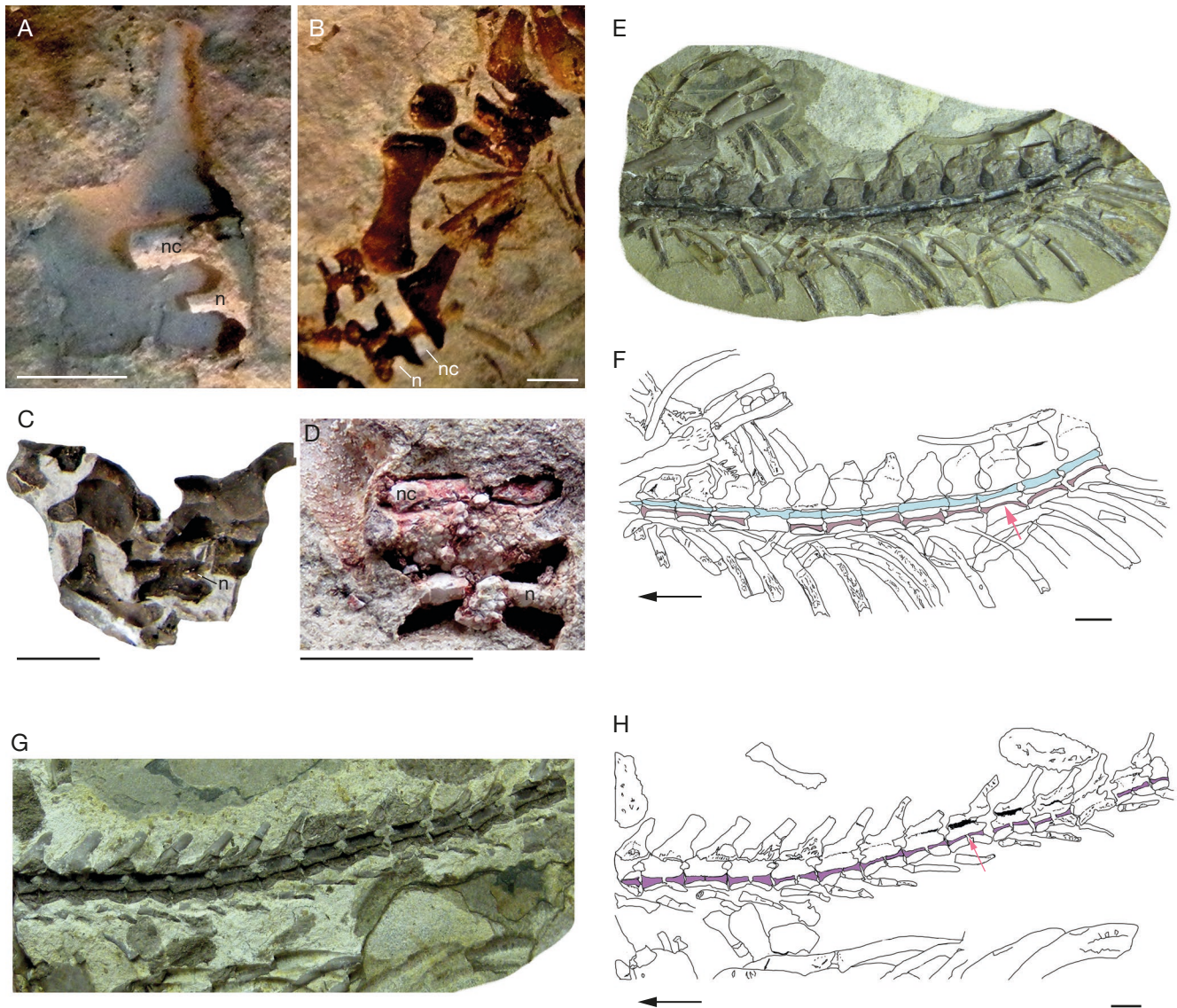


FIG. 5. — *Mesosaurus tenuidens* Gervais, 1865 dorsal and caudal vertebrae showing exceptionally preserved phosphatized notochord and neural chord: **A-D**, photographs of isolated caudal vertebra belonging to vertebrate collection of Facultad de Ciencias, Montevideo, Uruguay (FC-DPV), showing the preserved space for the neural canal (**nc**) and the discontinued notochord at the middle of the vertebral centrum (**n**) in all of them; **E**, isolated string of MCN-PV 2158 A-A', consisting of twelve dorsal vertebrae showing phosphatized notochordal tissues. Note that the notochord is clearly continuous through the complete sequence (**red arrow**); **F**, interpretive drawing of **E**, showing the notochord detached in pink and the neural chord in blue, the **black arrow** indicates the cranial direction; **G**, isolated string including at least seven caudal vertebrae from the medio-distal region of the tail of MCN-PV 2158 A-A'. Some discontinuities (**red arrow**) can be clearly seen in the notochord throughout the tail elements; **H**, interpretive drawing of **G**, showing the notochord detached in pink and the neural chord in blue. The **black arrow** indicates the cranial direction. Scale bars: A-D, 5 mm; E-G, 10 mm.

DISCUSSION

A REVISION OF THE MAIN VERTEBRAL CENTRUM PATTERNS DESCRIBED FOR PALAEOZOIC TETRAPODS

One of the many taxonomically relevant characters of Palaeozoic tetrapods or stegocephalians, depending on the nomenclature used (Laurin 2020a, b), is the morphology of the vertebral column. Although three basic patterns were recognized for basal tetrapods, a great variability exists among and within the different taxa, which has been attributed to substantial morphological plasticity in early vertebrates (Herbst & Hutchinson 2018) (Fig. 8). Thus, in addition to the vertebral types: 1) rhachitinous (large

intercentrum and smaller dorsal paired pleurocentra); 2) embolomerous (pleurocentrum and intercentrum present but the former is dominant); and 3) stereospondylous (one element is dominant, normally the intercentrum (Laurin 1998; Witzmann *et al.* 2013; Konietzko-Meier *et al.* 2014), other vertebral morphologies have been described, such as the gastrocentrous vertebrae (pleurocentrum is much larger than the intercentrum), monospondylous (a single holospondylous segment) and diplospondylous (a variation of the embolomerous type, with both disk-shaped intercentrum and pleurocentrum perforated by the notochord) (Gadow 1896; Romer 1947, 1956; Holmes 1989; Pierce *et al.* 2013; Danto *et al.* 2017).

Whereas the rhachitomous construction is usually considered the ancestral condition by most authors (e.g. Laurin 1998; Pierce *et al.* 2013), a few other studies have suggested the embolomerous type as the vertebral pattern from which all other were derived (Romer 1947). Moreover, although the rhachitomous type is characteristic of temnospondyls, and the embolomerous pattern is closer to either amniotes (under the “Temnosponyl Hypothesis”, abbreviated as TH below; Ruta & Coates 2007), or Tetrapoda (under the “Lepospondyl Hypothesis”, abbreviated LH below; Marjanović & Laurin 2019), both patterns can be found in some taxonomically diverse clades (Romer 1947). Furthermore, the monospondylous type is more frequently found in most lepospondyls, but some “microsaurs” have a small intercentrum and an embolomerous condition appears to be present in *Archerontiscus* (Carroll 1969). Additionally, Shishkin (1989) and Pierce *et al.* (2013) described a reverse rhachitomous pattern where the pleurocentrum occupies an anterior position in the centrum, whereas the intercentrum is posterior. According to Pierce *et al.* (2013), this last pattern is present in *Acanthostega* Jarvik, 1952 and *Pederpes* Clack, 2002, indicating that this could be the primitive condition. Alternatively, this atypical morphology could reflect developmental plasticity in basal tetrapods.

AN ALTERNATIVE HYPOTHESIS TO EXPLAIN THE MORPHOLOGY OBSERVED IN THE MESOSAUR CAUDAL VERTEBRAE

Taking into account the counter-arguments against the hypothesis that suggests tail autotomy for mesosaurs when facing predation danger, and considering the unconservative traits of mesosaurs, as well as their aquatic (or semiaquatic) lifestyle in which the tail plays a crucial role in locomotion (Villamil *et al.* 2015), it is worth exploring alternative explanations for the presence of “fracture/suture” lines in their caudal vertebrae.

According to Gadow’s (1933) classical contribution about the “evolution of the vertebral column”, which continues to inspire research on vertebral evolution and structure (e.g. Wake & Wake 2000; Danto *et al.* 2017), the changes observed in vertebral construction within the evolutionary history of vertebrates are reflected in some ontogenetic stages, variability along the vertebral column, and may also reflect selective pressures. For instance, the tail may retain plesiomorphic characters that are eliminated in other parts of the skeleton, so that the tail appears to be “more primitive” than the trunk (Gadow 1933). The centrum and the entire vertebra develop from sclerotomes that divide themselves into two halves; the posterior half fuses to the anterior one of the immediately more caudal sclerotome, and this recombined unit develops into a vertebra (Turner & Sidor 2018). Therefore, the diplospondylous vertebrae are formed by parts of two sclerotomes in the way that their anterior part comes from the posterior half of a sclerotome and the posterior part is formed by the anterior half of the next (caudal) esclerotome. According to Gadow (1933), the anterior part of the vertebra reduces in size during tetrapod evolution, while the posterior becomes dominant. In mesosaurs, the centrum of most caudal vertebrae

seems to be divided into two parts of different sizes, with the posterior being smaller. Therefore, the “fracture/suture line” seen in the mesosaur caudal centra that splits them into anterior and posterior halves might represent the suture between the large, anterior element (pleurocentrum) and the smaller posterior one (intercentrum).

This new hypothesis is consistent with the presence of pleurocentrum and intercentrum in the postpygal caudal series of mesosaurs, but their spatial arrangement may differ from a more conventional pattern of some other amniotes. If we accept the premise that the bone articulating with the haemal arch is the intercentrum, while the one supporting the neural arch is the pleurocentrum (Romer 1956), then the mesosaur centrum is composed of an intercentrum in a posterior position and a pleurocentrum in an anterior position (Fig. 8G), which until now appeared to be an unusual configuration for Amniota (Figs 4; 8), but see below.

It might be suggested that mesosaur caudal vertebrae exhibit a reverse rhachitomous condition as described by Shishkin (1989). However, in the rhachitomous condition, neither the intercentrum nor the pleurocentrum form closed ossified rings. Thus, the mesosaur caudal vertebrae are better interpreted as displaying an embolomerous condition reversed from the conventional pattern that occurs in long-tailed Upper Carboniferous or early Permian stegocephalians (Gadow 1933). Therefore, such a configuration is plausible, and our observations support this suggestion (Fig. 4). Indeed, it is unclear if embolomerous or rhachitomous vertebral organizations represent the ancestral condition in the phylogenetic hypotheses proposed for basal tetrapods (e.g. Romer 1947; Danto *et al.* 2017), although the rhachitomous morphotype has been most recently accepted (e.g. Laurin 1998). This pattern is otherwise unknown among amniotes, but it has been described for Devonian and Early Carboniferous stem-tetrapods and may be plesiomorphic for stegocephalians (Pierce *et al.* 2013).

The puzzling aspect of the two central elements in vertebrae of the “postpygal” segment of the mesosaur tail is seen as a putative reversal in the anatomical arrangement, with the intercentrum articulating most tightly with the pleurocentrum cranial to it. However, as noted in previous studies (i.e., Gadow 1933), intercentra are usually more closely integrated to the preceding vertebra than to the succeeding. This is reminiscent of the pattern found in *Proterogyrinus* Romer, 1970, where it is unclear with which pleurocentrum the intercentrum is most tightly integrated (Holmes 1984). The condition in *Mesosaurus* could be similar to that in *Proterogyrinus* but in the latter, it can be seen only in articulated specimens. When each vertebra is studied in isolation, we clearly see one anterior “bone” supporting the neural arch which is articulated or partially fused to a posterior “bone” bearing a long chevron bone. The arrangement in mesosaurs can be most easily recognized in an isolated vertebra where the intercentrum is placed posterior to a larger pleurocentrum, and we can argue that the intercentrum is in the process of fusion to the posterior part (pleurocentrum) of the preceding vertebra. These elements can always be assembled in the conventional pattern (intercentrum with a chevron bone anterior to the

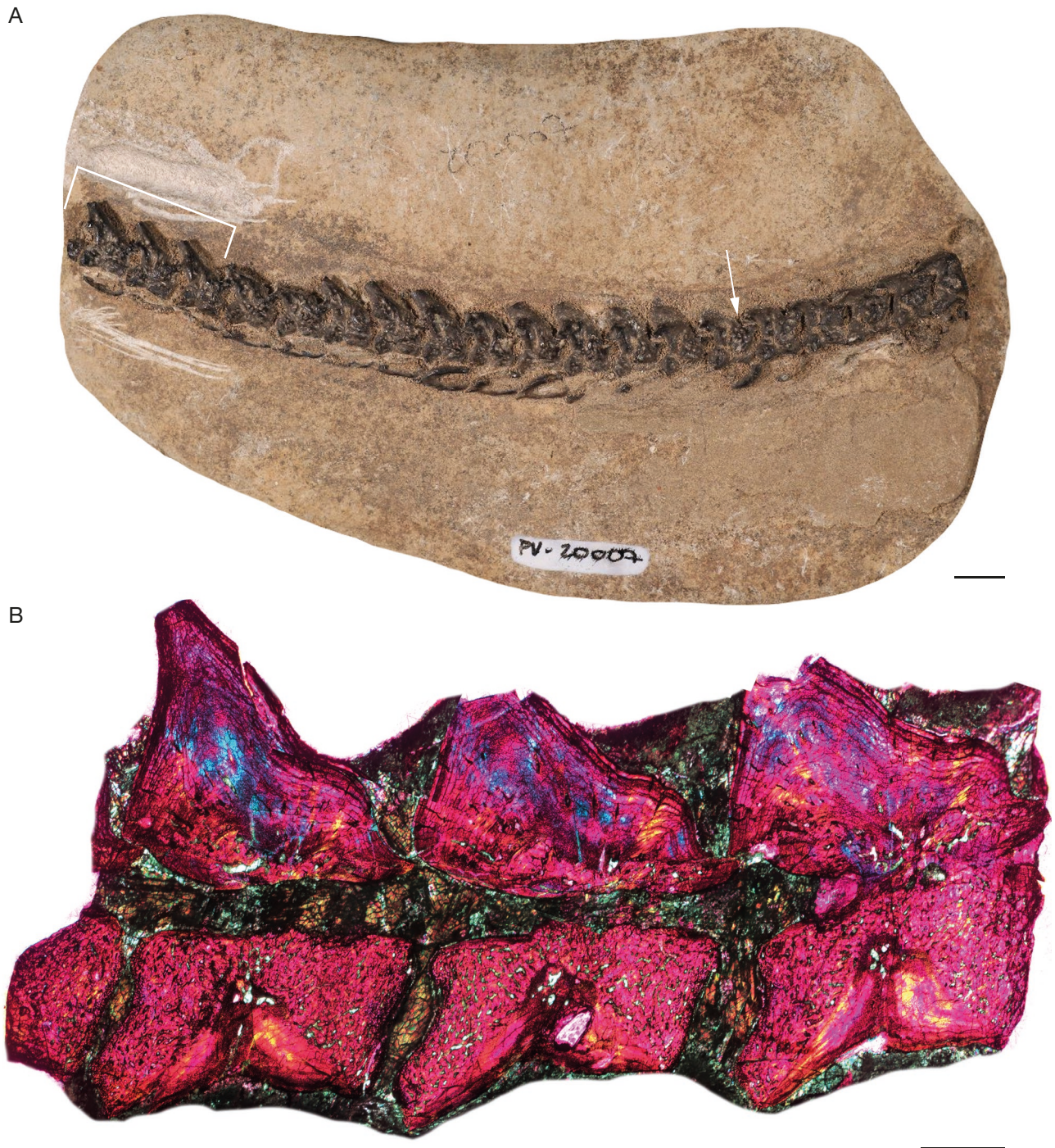


FIG. 6. — *Mesosaurus tenuidens* Gervais, 1865, microanatomy of the postpygal caudal vertebrae: **A**, MCN-PV-20007. Photograph of the complete specimen consisting in a caudal series that includes part of the pygal-like vertebrae (**black arrow** indicating the last of these vertebrae) and part of the postpygal series. The vertebrae used for the thin section are the three enclosed by a white bracket on the left side; **B**, picture of the thin section under polarized light. The integration of the two bones into a single element can be seen at the roughly central area of the centrum. Scale bars: A, 5 mm; B, 1 mm.

pleurocentrum), but we consider that mesosaurid specimens with caudal vertebrae suggest that the intercentrum is most tightly and functionally integrated with the pleurocentrum located anterior to it.

This interpretation reinforces the ancestral variability observed in vertebral centrum types (Fig. 8), which has been widely accepted as a characteristic of early stegocephal-

ians and early reptiles (e.g. many “adult” procolophonids as well as protorothyridids possess sutured but unfused intercentra and pleurocentra, at least in the trunk vertebrae, as indicated in a personal comment of anonymous reviewer 1) (see also Gadow 1896; Carroll 1968, 1989; Shishkin 1989; Pierce *et al.* 2013; Danto *et al.* 2017; among many others).

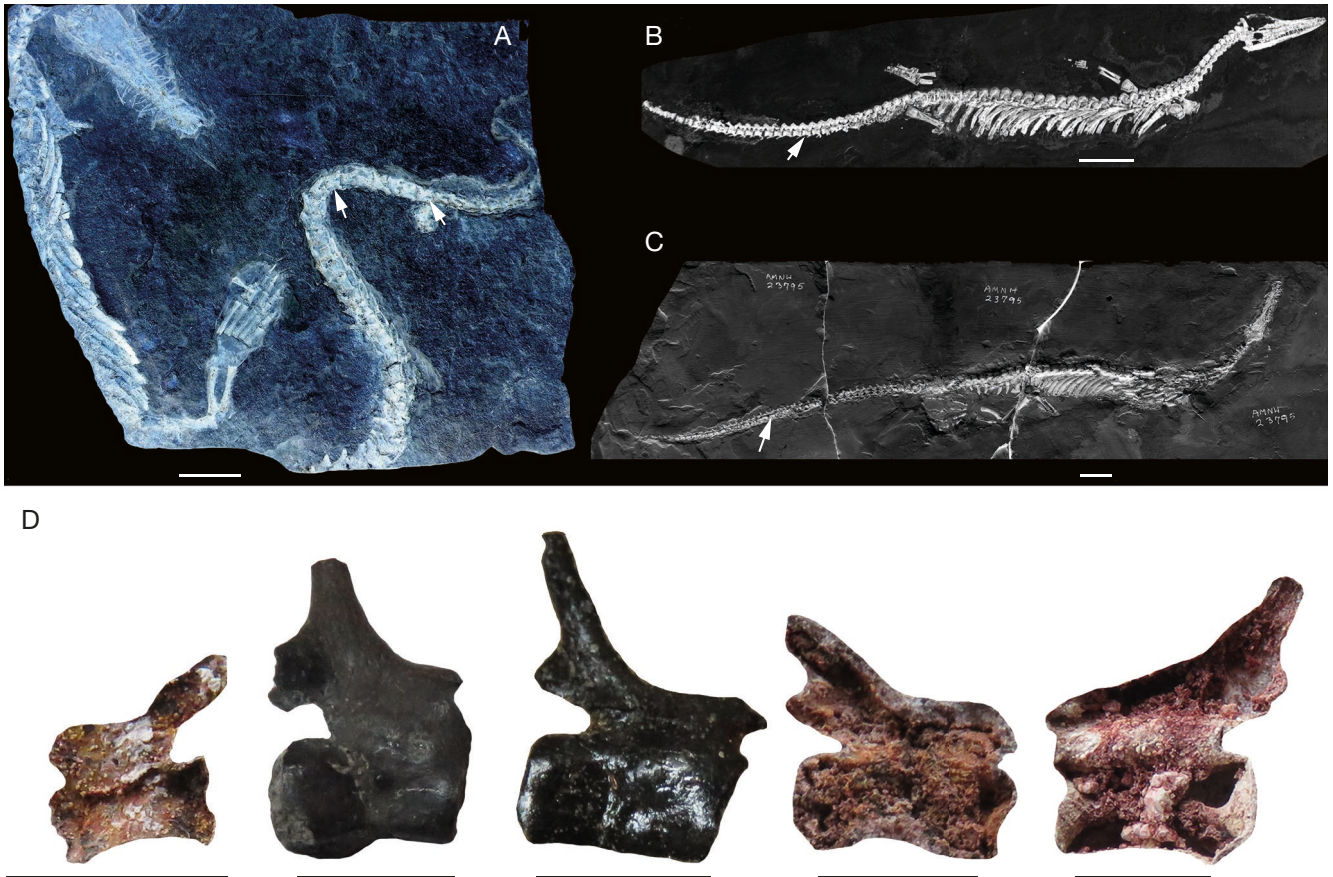


FIG. 7. — *Mesosaurus tenuidens* Gervais, 1865 early juvenile specimens showing the morphology of the pygal and postpygal regions of the tail: **A**, FC-DPV 2318, almost complete right part of a skeleton (the left part was cut by a caterpillar machine) from the Mangrullo Formation of Uruguay. It can be appreciated that the suture-fracture plane (arrows) is not as obvious in these vertebrae as it is seen in adult mesosaurs from the same location; **B**, SMF-R 4512, almost complete very young individual from the Irati Formation of Brazil. Despite the apparent good preservation of the skeleton, the typical fracture plane is only observed in some of the caudal vertebrae (arrow); **C**, AMNH 23795, an early juvenile mesosaur from the Irati Formation of Brazil showing the same unnoticeable suture-fracture plane in vertebrae from the postpygal segment; **D**, photographs of several isolated caudal vertebrae belonging to very young (juvenile) mesosaur specimens. Note that they are not part of the last caudal segment of adult mesosaurs because in such vertebrae the dorsal spine is bent posterior to almost remains in contact with the dorsal surface of the neural arch, or it is absent, a feature that is not present in the specimens shown herein. Scale bars: A-C, 20 mm; D, 5 mm.

MICROANATOMY

To further test our hypothesis about the multipartite configuration of the mesosaur caudal centra, we produced a parasagittal thin section of three postpygal caudal vertebrae, possibly from the middle-posterior region of the column (Fig. 6A).

The vertebrae are very compact, based on comparisons with extant taxa (de Buffrénil *et al.* 2021), as expected for mesosaurs (Villamil *et al.* 2015). Most of the neural arch and bone bordering the purported fracture/suture line is compact bone (see also MacDougall *et al.* 2020: fig. 3), but the bone is more spongy (but still fairly compact) in the middle of the centrum and at the base of the neural arch (Fig. 6A, B). The fracture/suture line is present in all three sectioned vertebral centra. The posterior element in each centrum is smaller (shorter) and it bears the haemal arch (chevron). The notochordal canal is partially preserved in all three vertebrae, and is visible especially in the first one on the left side of Figure 6B.

The mesosaur first caudal vertebrae, here referred as the “pygal-like” segment, are holospondylous, a condition that is common in Amniota, where the pleurocentrum is the dominant bone and the intercentrum has been reduced in

size, lost or fused to the pleurocentrum, and the centrum becomes as formed by a single element, which presumably is a pleurocentrum (Carroll 1968, 1989). The presence of a single central bone is a condition known as holospondylous or monospondylous; thus, both terms can be used.

Our observations suggest that the holospondylous condition in trunk and pygal mesosaur vertebrae could derive from, or it is equivalent to a reverse embolomerous condition, which is seen in the tail of mesosaurs and may reflect the ancestral condition. However, as demonstrated above in the previous section, the functional integration between intercentrum and pleurocentrum in juvenile specimens of early amniotes deserves to be re-examined.

The gastrocentrous pattern, typical of many amniotes, also characterizes the vertebrae of some lepospondyls (Holmes 1989; Laurin 1998; Danto *et al.* 2017). Among lepospondyls, tuditanomorph microsaur retain intercentra, while *Archerontiscus* displays a vertebral embolomerous configuration (Carroll 1969; Danto *et al.* 2017). This variability in vertebral centrum pattern supports the high plasticity suggested by Pierce *et al.* (2013) for Carboniferous tetrapods (or stegocephalians), and

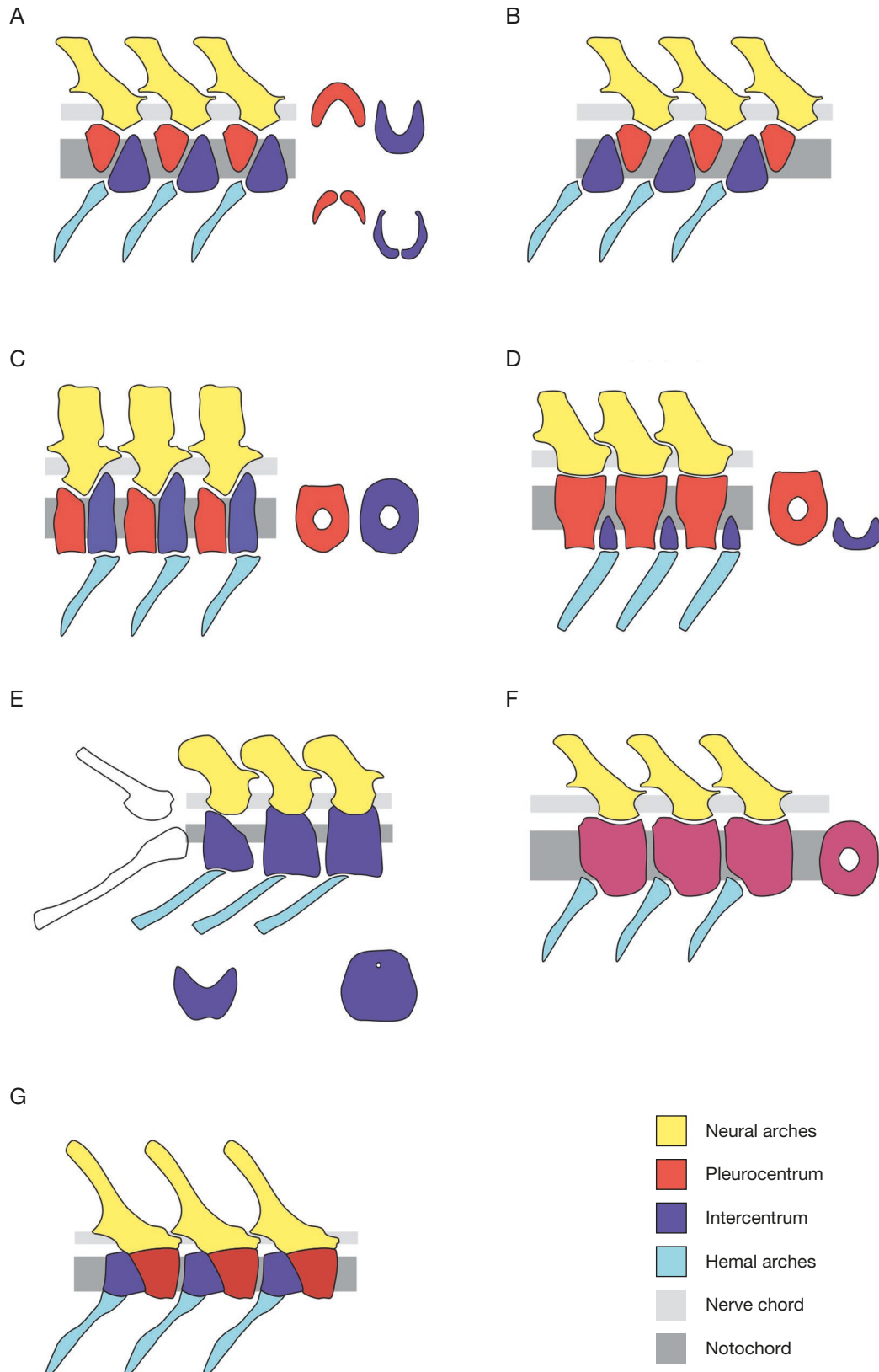


FIG. 8. — Schematic drawings of the caudal vertebral morphotypes described for various stegocephalians, including amniotes: **A**, rhachitomous; **B**, reverse rhachitomous; **C**, embolomerous (*Eogyrinus* Watson, 1926); **D**, gastrocentrous (*Discosauriscus* Kuhn, 1933); **E**, stereospondylous (*Metoposaurus* Lydekker, 1890); **F**, holospondylous; **G**, reverse embolomerous? (*Mesosaurus* Gervais, 1865). Rhachitomous and reverse rhachitomous vertebrae follow Shishkin (1989); Embolomerous vertebrae are modeled after *Eogyrinus* Watson, 1926 following Panchen (1966); gastrocentrous vertebrae are modeled after *Discosauriscus* Kuhn, 1933 according to Klembara & Bartik (1999); stereospondylous vertebrae are based on *Metoposaurus* Lydekker, 1890 following Sulej (2007).

our interpretation of the mesosaurid caudal vertebral configuration suggests that this evolutionary lability extended into basal amniotes.

Our microanatomical results compared with those from MacDougall et al. (2020)

Our data on the structure of caudal vertebrae of mesosaurs is congruent and complementary with those provided by MacDougall *et al.* (2020), given that the views are slightly different; the section shown by MacDougall *et al.* (2020: fig. 3) appears to be slightly parasagittal, or slightly oblique, with the left part showing the notochordal canal, which is not visible to the right. Thus, both reports show a core of trabecular bone covered by compact bone, and an unossified zone that separates a cranial and a caudal part of the centrum for more than half of its height.

Our observations are also reminiscent, but to a lesser extent, of the caudal centra of *Captorhinus* described by LeBlanc *et al.* (2018) and plausibly interpreted as adapted for caudal autotomy. *Captorhinus* appears to lack the combination of compact bone bordering the presumed fracture plane, with dense spongy bone located further from that plane. Instead, it has a thin, fairly compact cortex on either side of the fracture plane, with a much less compact cortex further from that plane. Other comparisons are hampered by differences in shape of the vertebrae. Notably, the notochordal canal seems to be much wider and of more irregular width in *Captorhinus* than in *Mesosaurus*. This is obvious in sagittal section (LeBlanc *et al.* 2018: fig. 1f), but even in longitudinal, horizontal sections (LeBlanc *et al.* 2018: fig. 2; erroneously called “transverse sections” in the legend).

However, while our anatomical observations are broadly congruent, our functional and evolutionary interpretations differ rather sharply. We do not interpret these structures of the mesosaur caudal vertebrae as adaptations for autotomy (although this is a plausible interpretation for *Captorhinus*). In addition to arguments presented above, and the absence of known potential predators for mesosaurs, which was already mentioned by MacDougall *et al.* (2020: 5), three points militate against autotomy in mesosaurs.

First, the girdles (notably, the pelvic girdle, which is most relevant to this argument) are relatively small in mesosaurs (no larger than in Cisuralian terrestrial amniotes) (Modesto 2010). Marine reptiles that rely only or mostly on limbs for aquatic locomotion have expanded girdles, which serve for attachment of the appendicular muscles. This is especially obvious in Plesiosauria (O’Keefe 2002), which had a relatively small tail and obviously relied mostly on limbs to swim. The unexpanded girdles of mesosaurs do not suggest particularly powerful limbs.

Second, the negative allometry of the limb growth pattern compared to overall length reported by Verrière & Fröbisch (2022) militates for a decreasing role of limbs in aquatic locomotion through ontogeny. This also suggests that the limbs were not the primary thrust providers, although it is likely that they were involved in steering and may have provided additional thrust in some situations.

Third, disadvantageous or even simply unneeded adaptations for autotomy should be eliminated fairly quickly by natural selection. MacDougall *et al.* (2020: 2) suggested that “mesosaurs would have been theoretically capable of caudal autotomy, but likely did not utilize the behaviour.” We find this unlikely. Bone is a metabolically costly tissue to produce, and it is typically optimized to resist mechanical strain to which it is exposed through normal physical activity (de Buffrénil *et al.* 2021). Rupture planes weaken bones (vertebrae, in this case) and are detrimental if they are not required, especially because in that case, additional bone must be deposited to compensate for the weakness induced by this suboptimal structure.

Our observations support this conclusion to an extent, given that the caudal vertebrae of mesosaurs are very compact (Fig. 6), although this could also simply reflect the pachyosteosclerosis found in much of the mesosaur skeleton. Nevertheless, the contrast with the much less compact *Captorhinus* caudal vertebrae (LeBlanc *et al.* (2018) is startling. Thus, if a putative terrestrial ancestor of mesosaurs had such fracture planes, these planes would have been quickly eliminated by natural selection. It is unlikely that the highly specialized morphotype of mesosaurs (most notably in their skull and long, slender teeth) arose without a similar optimization of vertebral structure for their lifestyle. Eliminating unneeded weakness (fracture planes) would presumably have occurred early in that process because that would have been a very cost-effective solution and given that mesosaur presacral vertebrae lacked fracture planes, all the required genes would have been present.

This last counter-argument begs the question of the function of this strange vertebral structure. Did it allow additional flexibility, notably between the pleurocentrum linked to the neural arch, and the intercentrum linked to the hemal arch, especially in young mesosaurs? Such flexibility might have been accomplished by relative movement between elements as long as they remained unfused, and by slight bending of bone (to a much reduced extent), after such a fusion occurred. This question deserves additional scrutiny, but will require additional ontogenetic and anatomical data, as well as biomechanical modeling to solve.

The enigmatic structure of caudal vertebrae of mesosaurs could also reflect a primitive condition as suggested above (which is not mutually exclusive of the hypothesis that it conferred additional flexibility).

Less probable, its presence in this taxon could also perhaps reflect the reduction of ossification that often accompanies a return to an aquatic lifestyle in tetrapods (Laurin *et al.* 2004), a pervasive phenomenon that was noticed long ago (Williston 1911). However this hypothesis is unlikely given the pachyosteosclerotic condition of most of the axial skeleton of mesosaurs, even from the earliest post-hatching stages (Piñero *et al.* 2012b).

If early developmental stages of early amniotes retained such a vertebral structure (a hypothesis that would require exceptional preservation of unmineralized tissues of embryos

or potentially early juveniles to test), the adaptation for caudal autotomy in captorhinids may have involved retention of this early developmental structure.

COULD THE REVERSED EMBOLOMEROUS CONDITION HAVE BEEN PRESENT (ALTHOUGH MASKED) IN OTHER EARLY AMNIOTES THAN *MESOSAURUS*?

Despite the reverse embolomerous condition described herein for the mesosaur caudal vertebrae, the architectural construction of the tail does not differ substantially from that observed in most groups of early amniote taxa. For instance, the caudal region, when preserved, is composed of vertebrae possessing an intercentrum positioned anterior to the pleurocentrum, as also occurs in the dorsal vertebral segment. Moreover, the intercentrum of vertebrae positioned posterior to the proximal string (pygal) with a variable number of elements, carries the haemal arches even near the tip of the tail (Heaton & Reisz 1980). However, a rapid revision of the available previous literature (old and more recent) shows that the mesosaur configuration could have been present in the caudal vertebrae of other basal tetrapod taxa. Starting with the study of Everett Olson (1936) on the axial musculature in early tetrapods, we can see some clues: caudal vertebrae assigned to *Diadectes* Cope, 1878 and *Dimetrodon* Cope, 1878 are drawn in figure 8 of Olson (1936: 280) and their haemal arches are fused to the posterior end of the centrum. The same condition is apparently present in the synapsid *Varanosaurus acutirostris* Broili, 1904, according to Sumida (1989: 155, fig. 4) and could have been developed in earlier taxa such as the seymouriamorphs, as documented by Laurin (1996: 658, fig. 5) for *Ariekanerpeton sigalovi* (Tatarinov, 1968), where four haemal arches are positioned (although not articulated) close to the posterior end of the respective centra. The fact that all four arches display the exactly same position with respect to the centra, makes it improbable that it results from a taphonomic process.

In basal diapsids, there seems to be an anterior “pygal segment”, although it is shorter than that observed in *Mesosaurus*. In *Petrolacosaurus* Lane, 1945, however, intercentra are described in this anteriormost caudal segment, as well as the corresponding haemal arches associated to the third or fourth vertebrae (Peabody 1952; Reisz 1981). Furthermore, the possibility of development of autotomy was suggested for *Araeoscelis* Williston, 1910, although it was only based on the presence of an isolated ossified, roughly conical structure of uncertain identity, bearing strongly marked ribs as a kind of superficial ornamentation, a morphology very similar to what is observed in regenerated tails of some squamates (see Vaughn 1955: pl. 2).

Another interesting case is that of *Dolabrosaurus aquatilis* Berman & Reisz, 1992, a drepanosaurid diapsid from the Upper Triassic of North America, where the haemal arches can be fused to both the posterior and the anterior end of the caudal vertebrae (Berman & Reisz 1992). This suggests a reverse embolomerous condition in the more anterior vertebrae, but a return to the normal configuration at the posterior region. More recently, *Hypuronector limnaios* Colbert

& Olsen, 2001, another related drepanosaurid, was shown to display the reverse embolomerous condition. In this last taxon, the fusion of the haemal arches to a trapezoid-like intercentrum is more evident, and a putative fracture plane can be also observed at the middle of the centrum in some of the preserved caudal vertebrae (see Colbert & Olsen 2001: fig. 9C). The hypothesis of autotomy suggested for captorhinids (i.e., LeBlanc *et al.* 2018) is difficult to ascertain because of the fragmentary nature of the analyzed specimens, as explained above. But taking into account the obvious presence of fracture-suture lines in most of the caudal vertebrae shown by LeBlanc *et al.* 2018) and the articulation of the haemal arches to the posterior end of the centrum observed in the string of caudal vertebrae belonging to a juvenile individual shown (LeBlanc *et al.* 2018: fig. 4b), it may be not surprising that captorhinids, diadectids, seymouriamorphs and some synapsids may have had the reverse embolomerous condition, but it was not previously detected.

THE INTENSE CONTROVERSY ABOUT MESOSAUR RELATIONSHIPS IS NOT OVER

Although mesosaurs are most frequently considered to be specialized aquatic amniotes (Araújo 1977; Oelofsen 1981; Modesto 1996, 1999; among others), they display a combination of primitive and derived characters, perhaps associated to a progressive although incomplete adaptation of an aquatic lifestyle (Núñez Demarco *et al.* 2018). However, the extent of such an adaptation in mesosaurs is not completely clear. It is true that some of the mesosaur features reveal limited capability for terrestrial locomotion, a trait also observed in numerous Carboniferous stegocephalians, such as *Gephyrostegus* Jaekel, 1903 and *Westlothiana* Smithson & Rolfe, 1990 (Smithson 1989; Piñeiro *et al.* 2016; Herbst & Hutchinson 2018). The last two taxa, despite being outside Amniota, exhibit terrestrial specializations like the development of an amniotic tarsus with precursor bones arranged in the normal position of the astragalus and calcaneum but showing different stages of fusion with the intermedium and the fibulare (see figure 10 in Piñeiro *et al.* 2016). But mesosaurs may not have developed capabilities to an exclusively fully aquatic lifestyle, and they presumably inhabited shallow, plausibly hypersaline water. This is suggested by the presence of pachyosteosclerosis in this taxon, a condition which was suggested to be developed in animals adapted to shallow aquatic environments (Houssaye 2009; Canoville & Laurin 2010). This hypothesis could be linked to the progressive draught of the Mangrullo and Irati seas, as was suggested in previous papers based on solid evidence suggesting an increasing of the water salinity and the deposition of evaporitic gypsum crystals (Piñeiro *et al.* 2012b, 2025; Petri *et al.* 2022).

Transitional features in mesosaurs have been interpreted as suggestive of possible affinities with other aquatic to semi-aquatic taxa, such as the recumbitrostran microsauros lepospondyls (Piñeiro *et al.* 2016; Núñez Demarco *et al.* 2022), which were recently considered by some authors as being part of the stem of Amniota (Pardo *et al.* 2017). However, affinities

between mesosaurs and recumbirostran microsaurians may be unlikely given that extensive phylogenetic analyses recovered the former as amniotes, close to the base of Sauropsida or at the base of Parareptilia. Furthermore, the position of recumbirostran microsaurians has been far more controversial; they are stem-amphibians according to Marjanović & Laurin (2019), but crown-amniotes according to Pardo *et al.* (2017) and Mann *et al.* (2023), among others.

However, mesosaurs have retained many ancestral characters, including: 1) the presence of five phalanges in the fifth pedal toe, whereas just four or three are observed in most tetrapods and basal amniotes (*Hylonomus* Dawson, 1860 pes, for instance, is reconstructed with three phalanges at the V toe; Clack *et al.* 2022); 2) a longer metatarsal V. Among basal stegocephalians, a long toe V, which is the longest of the pedal series, is a condition only present in the anthracosaur *Silvanerpeton miripedes* Clack, 1994 (Clack 1994; Ruta & Clack 2006) and the embolomerous *Archeria* Case 1915 (see Clack *et al.* 2022). While this character can be autapomorphic for mesosaurs or it can be an adaptation to an aquatic (or semi-aquatic) lifestyle, it is only shared with basal taxa; and 3) mesosaurs displayed an isometric growth pattern, a condition that could be considered of uncertain polarity, given that it is documented in few taxa, but that currently is only observed in basal or stem amniote taxa. The isometry is particularly marked at the level of limbs, as observed in microsaurians and other lepospondyls, sharply contrasting with the allometric pattern characterizing other early amniotes (Núñez Demarco *et al.* 2022).

According to a recent taxonomic review of Mesosauridae, *Mesosaurus tenuidens* is the only valid species (Piñeiro *et al.* 2021; but see also Verrière & Fröbisch 2022), reducing even more the already low diversity in early tetrapods observed during the lifespan of mesosaurs in Southern Gondwana. Whereas mesosaur phylogenetic affinities remain controversial, a putative relationship between mesosaurs and the basalmost amniote groups seems possible, even at the level of the amniote stem group (Piñeiro *et al.* 2016; Núñez Demarco *et al.* 2022, but see also Pardo *et al.* 2017).

Other hypotheses have suggested a position on the reptilian stem (Laurin & Reisz 1995; Laurin & Piñeiro 2017) or at the base of Parareptilia (Modesto 2006), but they would have to be revised by including recently published new data about mesosaur anatomy, ontogeny, taxonomy and physiology.

Indeed, mesosaurs have always appeared as a very basal group in the main known phylogenetic trees on amniote relationships, either as basal sauropsids or as basal parareptiles (regarding that the later are also basal sauropsids), and that signal should be taken into account in future studies.

CONCLUSIONS

In this study, we reassess the proposed hypothesis that mesosaurs had developed caudal autotomy. Our investigation focuses on examining the biomechanical and behavioral consequences of tail loss in aquatic or semiaquatic taxa, demonstrating that no extant taxa with these lifestyles display autotomy, which

appears to be restricted to terrestrial tetrapods. Our analysis reveals that mesosaurs may display a previously undocumented vertebral type in their caudal vertebrae consisting of a multipartite centrum formed by an intercentrum partially fused to the pleurocentrum, which is surprisingly located anterior (cranial) to it. The identification of these bones relies on the fact that the intercentrum carries a long chevron, while the pleurocentrum supports the neural arch. This novel vertebral arrangement is consistent with a reverse embolomerous type, which possibly occurred in other basal amniotes, as we preliminarily demonstrated in this work, but it may not have been detected because of taphonomic biases (the tail is incomplete or absent in most fossil tetrapods), and because it is often unclear to which pleurocentrum the intercentrum is functionally most tightly linked. These results support the plasticity and variability suggested to characterize the vertebral centrum configuration in basal tetrapods, which may have extended into basal amniotes, and which needs to be better documented to improve our understanding of vertebral evolution (Buckley *et al.* 2013). This study also makes one wonder if there has been overgeneralizations in whether the amniote centrum is primarily pleurocentral in nature, especially in the early amniote members (Reviewer 1, personal communication).

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