Ontogenetic, dietary, and environmental shifts in Mesosauridae (#70265)

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Ontogenetic, dietary, and environmental shifts in Mesosauridae

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Mesosaurs are the first secondarily aquatic amniotes and one of the most enigmatic clades of reptiles from the early Permian. They have long puzzled paleontologists with their unique morphologies: possessing an elongated skull with thin needle-like teeth, a long neck, large webbed hindlimbs, banana-shaped pachyosteosclerotic ribs, and a long tail. Here, we look at a large dataset of morphometric measurements from 265 mesosaur specimens in collections around the world. These measurements characterize skull, tooth, and limb proportions and their variation with size. This data presents evidence of surprising ontogenetic changes in these animals as well as new insights into their taxonomy. Our results support the recently proposed idea that *Mesosaurus tenuidens* is the only valid species within Mesosauridae. They suggest that "*Stereosternum tumidum*" and "*Brazilosaurus sanpauloensis*" represent immature stages or incomplete specimens of *Mesosaurus* by showing that all three species occupy an incomplete portion of the overall size range of mesosaurs. Under the single-species hypothesis, we highlight a number of ontogenetic trends: (1) a reduction in skull length accompanied by an elongation of the snout within the skull, (2) an elongation of teeth, (3) a reduction in hind limb length, and (4) a reduction in manus length. Concurrent with these changes, mesosaurs go through an ecological shift during their growth, with juveniles being more common in limestone characteristic of shallow waters, whereas adults are more frequent in black shales deposited in an anoxic pelagic environment. These parallel changes suggest that mesosaurs underwent a diet and lifestyle transition during ontogeny, from an active predatory lifestyle as juveniles to a more filter-feeding diet as adults. We propose that this change in lifestyle and environments may have been driven by the pursuit of different food sources, but isotope analyses and a better understanding of the Irati Sea fauna will be necessary to obtain a more definitive answer to the question of mesosaur diet.

Ontogenetic, dietary, and environmental shifts in Mesosauridae

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Abstract

Mesosaurs are the first secondarily aquatic amniotes and one of the most enigmatic clades of reptiles from the early Permian. They have long puzzled paleontologists with their unique morphologies: possessing an elongated skull with thin needle-like teeth, a long neck, large webbed hindlimbs, banana-shaped pachyosteosclerotic ribs, and a long tail. Here, we look at a large dataset of morphometric measurements from 265 mesosaur specimens in collections around the world. These measurements characterize skull, tooth, and limb proportions and their variation with size. This data presents evidence of surprising ontogenetic changes in these animals as well as new insights into their taxonomy. Our results support the recently proposed idea that *Mesosaurus tenuidens* is the only valid species within Mesosauridae. They suggest that "*Stereosternum tumidum*" and "*Brazilosaurus sanpauloensis*" represent immature stages or incomplete specimens of *Mesosaurus* by showing that all three species occupy an incomplete portion of the overall size range of mesosaurs. Under the single-species hypothesis, we highlight a number of ontogenetic trends: (1) a reduction in skull length accompanied by an elongation of the snout within the skull, (2) an elongation of teeth, (3) a reduction in hind limb length, and (4) a reduction in manus length. Concurrent with these changes, mesosaurs go through an ecological shift during their growth, with juveniles being more common in limestone characteristic of shallow waters, whereas adults are more frequent in black shales deposited in an anoxic pelagic environment. These parallel changes suggest that mesosaurs underwent a diet and lifestyle transition during ontogeny, from an active predatory lifestyle as juveniles to a more filter-feeding diet as adults. We propose that this change in lifestyle and environments may have been driven by the pursuit of different food sources, but isotope analyses and a better understanding of the Irati Sea fauna will be necessary to obtain a more definitive answer to the question of mesosaur diet.

Introduction

Mesosaurs are small marine parareptiles from the early Permian and one of the most enigmatic clades of early amniotes. Although they are exclusively found in the successional black shales and limestone deposits of what was at the time an inland sea extending over today's Brazil, Uruguay, South Africa, and Namibia (Oelofsen & Araújo, 1983), and despite their short period of existence (Soares, 2003), mesosaurs represent a key snapshot in amniote evolutionary history. Indeed, they are the first secondarily aquatic amniotes, i.e., the first fully terrestrial tetrapods to have return to live in water. Yet their affinities are controversial (Laurin & Piñeiro, 2017; MacDougall et al., 2018; Ford & Benson, 2020), their origins are poorly known, and their lineage ended with them. Until recently, three monotypic genera were recognized: *Mesosaurus tenuidens* (Gervais, 1869), *"Stereosternum tumidum"* (Cope, 1886), and *"Brazilosaurus sanpauloensis"* (Shikama & Ozaki, 1966). Although these three taxa were originally supported by a number of diagnostic characters (Shikama & Ozaki, 1966; Araújo, 1976; Oelofsen & Araújo, 1987; Modesto, 1999, 2006, 2010), a recent review (Piñeiro et al., 2021) deemed these characters arbitrary and suggested *Mesosaurus tenuidens* to be the only valid species with *"Brazilosaurus"* and *"Stereosternum"* representing *nomina dubia*.

All mesosaurs present a striking morphology: a slender body with a very long tail, paddle-like hind limbs, a massive ribcage with thickened banana-shaped ribs, an elongated neck holding an elongate but very thin skull, and a long snout bearing thin needle-like teeth (Fig. 1). This peculiar appearance has resulted in conflicting hypotheses about their ecology, from amphibious (Nuñez Demarco et al., 2018) to fully marine (Modesto, 1999, 2010; Canoville & Laurin, 2010), from undulatory (Braun & Reif, 1985; Villamil et al., 2015) to partially limb-propelled swimmers (da Silva & Sedor, 2017; MacDougall et al., 2020).

More than other aspects of their anatomy, the long thin teeth of mesosaurs have puzzled those who studied them the most. If they are somewhat reminiscent of those of other vertebrates such as dolphins or gharials, mesosaur teeth are singular in their length and their needle-like morphology. Consequently, they have no modern analog, which has led to contradicting attempts at characterizing the feeding habits of mesosaurs. Based on cranial morphology alone, MacGregor (1908) proposed a "fish"-based diet for mesosaurs, but subsequent studies discarded this interpretation (Wiman, 1925; Araújo, 1976), noting that their teeth were too fragile for active hunting and pointing to the absence of "fish" in mesosaur-bearing strata. Instead, based on their tooth morphology, the fauna of the Irati Formation, as well as gut content and coprolite analyses, most authors concluded that mesosaurs were filter-feeders trapping pygocephalomorph crustaceans in the net of their teeth (Oelofsen & Araújo, 1983; Modesto, 1999, 2006, 2010; Piñeiro et al., 2012b; Silva et al., 2017). Despite this, some authors suggested that mesosaurs could have been active hunters (Pretto, Cabreira & Schultz, 2012) or even occasionally cannibalistic (Silva et al., 2017).

Although interest and research effort into the paleobiology of mesosaurs has tremendously increased in the last decade and some aspects of mesosaur ecology have been addressed in the past, their lifestyle throughout ontogeny has not been fully investigated. Even though some authors have looked at the morphometrics of mesosaurs (Oelofsen & Araújo, 1987; Rossmann & Maisch, 1999; Rossmann, 2002; Piñeiro et al., 2021) or at histological growth marks (de Ricqlès, 1974; Canoville & Laurin, 2010; Klein et al., 2019), studies focusing on their ontogeny remain rare (Piñeiro et al., 2012a; Piñeiro, Núñez Demarco & Meneghel, 2016; Bickelmann & Tsuji, 2018; Verrière, Fröbisch & Fröbisch, 2021). This is surprising, as mesosaurs constitute a unique framework for understanding the complex links between diet and morphology in the fossil record. First, they comprise one of the few comprehensive ontogenetic series known in fossil amniotes (Piñeiro et al., 2012a; Bickelmann & Tsuji, 2018). Second, they lived in a constrained environment with greatly reduced food variety, placing considerable limits on what their feeding habits could have been (Soares, 2003; Piñeiro et al., 2012b). Lastly, they are the first secondarily aquatic amniotes, and understanding their dietary evolution has implications for the reconstruction of feeding habits in later marine amniotes.

Here, we provide the first quantitative assessment of ontogenetic changes in mesosaurs on such a large number of specimens. Our results highlight very few significant differences in osteological and dental proportions between "*Brazilosaurus*", *"Stereosternum"*, and *Mesosaurus*. We also show important gaps in the size range of each supposed species. However, when considering them to represent a single mesosaur species, we show that the ontogeny of mesosaurs is marked by morphological transformations and niche partitioning, likely indicating a change in diet and lifestyle with growth.

Materials & Methods

Material investigated

We examined over 265 mesosaur specimens from collections around the world. Of these, 109 were previously attributed to *Mesosaurus tenuiden*s, 94 to *"Stereosternum tumidum"*, and 12 to *"Brazilosaurus sanpauloensis"* (Supp. Data 1). Of these specimens, 47 had a preserved skull and teeth, with 18 attributed to *Mesosaurus*, 29 to *"Stereosternum"*, and only one to *"Brazilosaurus"*. Earlier studies mentioned the presence of teeth in *"Brazilosaurus"* (Rossmann, 2002; Modesto, 2006; Silva et al., 2017), all of them relying on the average tooth length of 2 mm provided by Rossmann (2002). We find this value contentious in different regards. First, Rossmann (2002) did not provide the raw measurements for his calculation. Second, we reexamined the material described by Rossmann (2000, 2002) as bearing teeth and noticed that elements he describes as teeth are in fact misidentified broken tooth sockets from the maxilla or the dentary (Supp. Fig. 1). Finally, out of the twelve specimens assigned to *"Brazilosaurus"* studied here, only ROM 28496 had some visible complete teeth. In all other specimens, teeth are either missing or completely broken, in any case not in a state of preservation allowing their measurement. Consequently, we must dismiss the average tooth length for *"Brazilosaurus"* of 2 mm given by Rossmann (2002). For this reason, no specimens previously attributed to *"Brazilosaurus"* are included in our statistical analysis of teeth.

Measurements

For each specimen, we measured the length of most preserved long bones: humerus, radius, ulna and metacarpals in the forelimb; femur, tibia, fibula, and metatarsals in the hind limbs. When possible, we also measured autopod length, from the proximal edge of the intermedium to the distal tip of digit III for the forelimb, and from the proximal edge of the astragalus to the distal tip of digit V in the hind limb, as digit III and V are the longest digits in the anterior and posterior autopod, respectively. In juveniles where carpals and tarsals were not ossified, the distalmost portions of the ulna or fibula were taken as most proximal extent of the autopodium. To account for cranial proportions, we measured the total skull length as well as antorbital and postorbital length.

Likely due to dental replacement (Modesto, 1999, 2006; Piñeiro et al., 2021), mesosaur teeth can greatly vary in size within a single specimen. To better account for the maximum dimensions of mesosaur teeth, we measured the length of the longest visible tooth and the diameter of this tooth at its base.

Our specimens were preserved in various states of completeness, with some showing only the anterior or the posterior half of the body and others missing limbs or neck while others were mostly complete. In order to obtain a common and reliable proxy for specimen size, we calculated the average length of dorsal vertebrae for each specimen.

All measurements were taken using a caliper or Fiji 1.53c on distortion-corrected high-resolution photographs.

Statistics

According to Huxley (1932), simple allometry is described by the equation

$y = kx^{\alpha}$ or in its logarithmic form

$$\log y = \alpha \log x + \log k$$

The allometric coefficient α characterizes the slope of the linear relationship between the logged valued of y and x and $\log k$ is the intercept of the linear relationship. Thus, an isometric growth (no changes in proportion to size during ontogeny) is characterized by an allometry coefficient of $\alpha = 1$ while values of $\alpha > 1$ and $\alpha < 1$ respectively reflect positive and negative allometry.

By transforming the simple allometry equation to express the ratio y/x rather than y as a function of x, we obtain

$\frac{y}{x} = kx^{\alpha - 1}$ which in turns gives

$$\log \frac{y}{x} = (\alpha - 1) \log x + \log k$$

In this equation we can define another allometry coefficient $\beta = \alpha - 1$. Thus, for the same values of x and y, isometry is defined by $\beta = 0$ while negative and positive allometry are respectively characterized by negative and positive values of β, improving readability both graphically and numerically (Klingenberg, 1998). Therefore, we prefer β to α in the present study.

For each metric, we computed a linear model of the logged ratio of the metric's values over size proxy value ($\log \frac{y}{x}$) as a function of logged size proxy values ($\log x$) and calculated the allometry coefficient β to test for proportion changes throughout ontogeny. Similarity between species was also tested for each measurement. Linear modelling and statistical analyses were carried out in R 4.0.5 (R. Core Team, 2021).

Results

Three-species hypothesis

Skull

Skull measurements behave differently with respect to size in the three mesosaur species. In "*Brazilosaurus*", all three skull measurements show negative allometry, albeit not significant (Table 1). In *Mesosaurus*, postorbital length is the only skull metric to display a significant negative allometry, while total length and antorbital length both show a non-significant positive allometry (Table 1). In "*Stereosternum*", all three skull measurements show significant negative allometry but each with different allometry coefficients (Fig. 2). The negative allometry is less marked for antorbital length ($\beta = -0.090$, p = 0.022) than for total length ($\beta = -0.204$, $p < 0.001$), itself less marked than postorbital length ($\beta = -0.341$, $p < 0.001$).

For all three species, skull measurements rank similarly in terms of allometry coefficients with antorbital length having the highest, followed by total length and finally postorbital length last. This shows how skull elements vary differently in proportion throughout ontogeny. To better account for these variations, we measured the effect of allometry in function of total skull length instead of body size. In this configuration, we obtain very concordant results between the three species: antorbital length shows significant positive allometry, whereas postorbital length shows significant negative allometry (Table 2). Thus, over the course of ontogeny, the postorbital length decreases while the snout increases relative to overall skull length (Fig. 3).

Teeth

Several authors have noted an apparent change in tooth morphology between mesosaur species: "*Brazilosaurus*" and "*Stereosternum*" are described as bearing short, straight conical teeth whereas *Mesosaurus* is defined by thin, curved, and elongated teeth (Oelofsen & Araújo, 1987; Rossmann, 2002; Modesto, 2006). Indeed, for the same body size, adult *Mesosaurus* teeth are systematically longer than those of "*Stereosternum*" albeit similar in diameter (Fig. 2, 3).

Tooth length and diameter in *Mesosaurus* both display positive allometry, although the linear relationship is not significant (Table 1). In "*Stereosternum*", both measurements show a significant negative allometry, with tooth diameter showing the lowest coefficient ($\beta = -0.622$, $p < 0.001$).

Since our results highlight variation in cranial dimensions throughout ontogeny, we also calculated allometry coefficients for tooth measurements with respect to skull length. Surprising, this shows non-significant negative allometry for tooth length in both species, whereas tooth diameter exhibits negative allometry for both species, although it is only significant in "*Stereosternum*" (Table 2). Thus, mesosaur teeth grow in length at the same rate as the skull, meaning that they do not become proportionally longer throughout ontogeny. However, these teeth keep their juvenile diameter and grow only in length in "*Stereosternum*" whereas both length and diameter grow isometrically to the skull in *Mesosaurus* (Fig?).

Limbs

In all three species, most long bones show no significant difference in growth with isometry (Table 3A-C), meaning that their proportional length with respect to body size does not change throughout ontogeny. However, there are several exceptions to this.

In *"Brazilosaurus"*, femur, tibia and metatarsal V length show significant negative allometry (Table 3A). Although this might reflect a size reduction of the posterior limb during ontogeny in this species, those measurements are only documented for eight adult specimens in our dataset and likely do not reflect the entire ontogenetic trajectory of the species.

In *Mesosaurus*, most forelimb bones exhibit a significant positive allometry, aside from metacarpals II, IV, and V (Fig. 2). While this suggests that the anterior autopod increases in size, there are very few juveniles or subadult *Mesosaurus* in our dataset. Thus, much like for "*Brazilosaurus*", *Mesosaurus* forelimb measurements are concentrated in the adult region of the morphospace, and do not satisfyingly account for the entire ontogenetic variation.

In "*Stereosternum*", metacarpal I and metatarsal I also display a significant positive allometry, but femur, tibia, fibula and metacarpal V show a significant negative allometry (Fig. 2). Uniquely in mesosaur "species", the posterior autopod also shows a slight significant negative allometry. This reflects a reduction in limb size with respect to the body. "*Stereosternum*" being the best-documented taxon here, these results are more representative than for the two other species.

ANOVAs

We measure a significant effect of species on allometry coefficients for six measurements: antorbital length, tooth diameter, humerus, radius, ulna, and metacarpal III length (Table 4). Rather than indicating a real difference between the species, this likely reflects a sampling bias. In the near absence of *Mesosaurus* and "*Brazilosaurus*" juveniles in our dataset, values for these species form a cluster concentrated in the adult–size region, which distorts linear regressions (Fig. 2). Therefore, these regressions do not fully account for the ontogenetic trajectories of the measurements.

Single-species hypothesis

In a recent study, Piñeiro et al. (2021) proposed *Mesosaurus tenuidens* to be the only valid species within the clade by statistically rejecting most characters used to discriminate between the three previously recognized mesosaur species. To account for this new hypothesis, we reproduced our analysis with all specimens (re)assigned to *Mesosaurus*.

Skull

All three skull measurements show negative allometry when compared to body size, but the linear relationship is only significant for postorbital length and total skull length (Table 1). When measuring allometry with respect to total skull length, the signal is unambiguous, with antorbital length showing positive allometry and postorbital length negative allometry (Fig. 3). Similar to the three-species hypothesis, our results with one species point to an elongation where the snout elongates and postorbital length reduces, while overall skull length decreases with respect to the body.

Teeth

Under the single-species hypothesis, tooth length shows positive but non-significant allometry whereas diameter shows a significant negative allometry with respect to body size. However, when compared to skull size, tooth length exhibits a strong significant positive allometry and tooth diameter a significant negative allometry (Table 2). In practice, tooth diameter remains the same in adults as in juveniles, but teeth elongate throughout ontogeny and become more needle-like.

Limbs

There is a strong trend to hind limb reduction when considering a single mesosaur taxon. All eight long bone measurements display negative allometry coefficients in relation to body size and this relationship is significant for seven of them (Table 3D). Only metatarsal I length is not significantly isometric in growth. Posterior autopod length also shows a significant negative allometry.

In contrast, forelimb long bones do not show such a reduction in size. Only metacarpals display significant negative allometry, with the exception of metacarpal I that has a non-significant positive allometry coefficient. Thus, while stylopod and zeugopod do not vary in proportions, it appears the manus is reduced during ontogeny.

Discussion

The case of the missing juveniles

One of the most significant results of our study is not found with regards to size and proportional changes in mesosaur anatomy but instead in the distribution of body size itself. Despite the 265 specimens examined here, there are a number of surprising gaps in the size range covered by our sample (Fig. 6). First, the few "*Brazilosaurus*" specimens studied here are concentrated in the adult size range of "*Stereosternum*", but no juveniles or subadults are preserved. Second, there is a clear divide between the youngest "*Stereosternum*" specimens on the one hand and subadults and adults of that species on the other hand. Third, and more importantly, only two specimens of *Mesosaurus* are the size of juvenile "*Stereosternum*", whereas all other specimens range from the size of "*Stereosternum*" subadults to larger sizes than the largest "*Stereosternum*" specimens do. These gaps in size distribution have a direct effect on the interpretation of allometric measurements as they alter the results of linear regressions, making them less representative of ontogenetic changes.

Piñeiro et al. (2021) highlighted that most features employed to define mesosaur species are not statistically supported or are practically unusable for identification. Characters like the shape of the interclavicle, tooth length, or presacral vertebral count are highly preservation-dependent, whereas others such as the degree of pachyostosis of ribs or the skull-neck length ratio are subjective and ontogenetically variable (for pachyostosis, see also Klein et al., 2019). This lack of reliable characters led the authors to suggest that both "*Stereosternum tumidum*" and "*Brazilosaurus sanpauloensis*" are misidentified junior synonyms of *Mesosaurus tenuidens*.

The ontogenetic variability of supposedly taxonomic characters led to an age partitioning of mesosaur specimens. On the one hand, juvenile specimens tended to be identified as "*Stereosternum*", because they bear shorter conical teeth and are usually preserved complete, displaying the maximum number of presacral vertebrae. Both features were usually admitted as prominent characters for mesosaur identification. On the other hand, the largest mesosaur specimens bear longer, thinner teeth and have extremely pachyostotic ribs, and they tended to be attributed to *Mesosaurus*. As for "*Brazilosaurus*" specimens, they were usually identified on the basis of their cervical vertebral count, which is however a misidentification as the result of a displaced rib cage (pers. obs.). In fact, even the original description of the species (Shikama & Ozaki, 1966) miscounted the number of cervicals due to rib displacement (pers. obs.), which led to the erroneous erection of this feature as a defining character. To summarize, there are several reasons as to why mesosaur species occupy different regions of the size range.

Rather than a sampling bias, the size distribution gaps in our dataset more likely reflect a species-identification bias. Our data shows consequent overlap in the morphometrics of all three species. "*Brazilosaurus*" is virtually indistinguishable from "*Stereosternum*", whereas *Mesosaurus* seems to have mostly representatives on the higher side of the size spectrum (Fig. 6). Furthermore, the low significance of allometry coefficients (Tables 1, 2, 3) is also likely an effect of the lack of juvenile *Mesosaurus*. Our data therefore corroborates the single-species hypothesis of Piñeiro et al. (2021). In fact, the three previously identified "species" more probably represent three types: the "*Brazilosaurus*"-type is a poorly preserved mesosaur with displaced ribs, the "*Stereosternum*"-type is a size class encompassing juveniles to young adults, and the "*Mesosaurus*"-type represents adults with more extreme sizes and morphologies.

Niche partitioning

Even when considering "*Stereosternum*" and "*Brazilosaurus*" as size classes of *Mesosaurus*, one fundamental difference between the previously distinct types cannot be explained as an effect of ontogenetic changes or dubious characters alone. Namely, the three types usually occur in different geological strata: "*Brazilosaurus*" and "*Stereosternum*" are more commonly found in limestone deposits characteristic of a shallow coastal environment, whereas *Mesosaurus* is more frequent in oily black shales representing deep anoxic and stratified waters (Oelofsen & Araújo, 1983; Rossmann, 2002). This environmental segregation of types highlights a form of niche partitioning of mesosaurs between limestone and black shales environments.

Several morphological variations seem associated with this niche partitioning. The "*Brazilosaurus*" and "*Stereosternum*" types have proportionally smaller teeth and larger limbs than *Mesosaurus* (Fig. 2). At first glance, the presence of different morphologies in different environments could suggest that the types of mesosaurs recognized so far correspond indeed to different species. Each environment would have been populated by a particular mesosaur taxon with specific feeding habits and locomotory mode. However, the differences we observe are not statistically significant between species and are not sufficient to compensate for the shaky foundation on which mesosaur species were erected. In summary, mesosaur types are too similar to justify maintaining distinct mesosaur species, even when niche partitioning is considered.

In contrast, if all mesosaurs are considered to belong to a single species, the morphological differences observed between specimens from the two environments can be interpreted as ontogenetic changes. Individuals found in the limestone environment, distinguished by smaller sizes (Fig. 6), would correspond to juveniles and subadults, whereas mesosaurs from the black shales correspond to larger, older individuals. As they aged, mesosaurs would have moved from shallow coastal waters to deeper anoxic waters. This transition would have been accompanied by an elongation of the teeth relative to the skull (Fig. 3), an elongation of the snout (Fig. 4), and a reduction of limbs (Fig. 2).

Limb reduction throughout ontogeny hints at a difference in locomotory habits between juveniles and adults. Mesosaurs are swimming reptiles, and the degree of involvement of the limbs in locomotion is still debated. Some authors support the idea of mainly tail-driven mesosaurs (Braun & Reif, 1985; Villamil et al., 2015) while others suggested a potentially larger role of limbs in propulsion (da Silva & Sedor, 2017; MacDougall et al., 2020). Yet, the ontogenetic limb reduction we expose seems incompatible with the idea that limbs were crucial for locomotion. Instead, our results provide evidence for a decreasing involvement of limbs in mesosaur swimming and weight in favor of a tail-driven model of mesosaur swimming throughout their ontogeny.

Ontogenetic niche shifts and morphological variations are not rare in reptiles but are usually associated with dietary partitioning between juveniles and adults, meaning they exploit different food sources at different stages of their growth (Arthur, Boyle & Limpus, 2008; Gignac & Erickson, 2015; Dick, Schweigert & Maxwell, 2016; Wang et al., 2017). Yet, in the case of mesosaurs, available food sources were extremely limited. Traditionally, mesosaurs are considered filter-feeders that preyed on pygocephalomorph crustaceans, based on stratigraphic occurrences (Oelofsen & Araújo, 1983; Piñeiro et al., 2012b) as well as on their gastric contents and coprolites (Piñeiro et al., 2012b; Ramos, 2015; Silva et al., 2017). But another important argument in favor of the crustacean diet hypothesis is the lack of alternative food sources. Mesosaur-bearing strata of the Irati and Whitehill formations are scarce in fossils other than mesosaurs and pygocephalomorphs. Other than these, only fragmentary fish scales and bones and traces of annelids have been reported (Oelofsen & Araújo, 1983; Soares, 2003; Piñeiro et al., 2012b). This raises a puzzling question: given the absence of alternative food sources, if juvenile mesosaurs did not have the same diet as adults, what could they possibly have been eating?

One possible answer is that juvenile mesosaurs fed on animals that did not preserve well under the conditions where mesosaurs were buried. For instance, young mesosaurs could have eaten jellyfish or soft invertebrates with little to no mineralized tissues, which greatly reduces the chances at fossilizing the latter. This would partly explain the morphological changes between juveniles and adults, as juveniles might have needed different hunting strategies to catch their prey, perhaps involving longer limbs for better maneuvering. However, while some strata of the Irati Formation do reflect turbulent taphonomic conditions and only contain disarticulated skeletons and broken up crustaceans (Soares, 2003), others show outstanding preservation and produce complete articulated fossils (Modesto, 1999, 2006, 2010; Piñeiro et al., 2012b), sometimes even showing soft tissue preservation (MacDougall et al., 2020). With such conditions of preservation, it seems very unlikely that no trace of other invertebrates remain. It is possible, however, that soft animal fossils remain to be discovered, and that further study of the mesosaur-bearing Irati strata will reveal them.

A second potential explanation would be that juvenile mesosaurs preyed on adult pygocephalomorphs, but that adult mesosaurs fed on pygocephalomorph larvae. Young mesosaurs would have needed longer limbs and shorter snouts and teeth for active hunting, while adults would have filtered waters to catch larvae using a slower swimming style. This hypothesis would explain the absence of any other fossils in the strata. Unfortunately, the life cycle of pygocephalomorph crustaceans and their ecology in general is very poorly known, and our hypothesis remains speculative at this point. To answer the question of juvenile mesosaur feeding habits more substantively, isotope markers would have to be compared across different growth stages of mesosaurs.

Conclusions

After examining a large sample of mesosaur morphometric measurements, we present evidence of ontogenetic changes in these animals as well as insights into their taxonomy. First, our results demonstrate that the three previously identified species occupy incomplete portions of the size range of mesosaurs and show very minor differences in body proportions otherwise. This supports the proposition of Piñeiro et al. (2021) that *Mesosaurus tenuidens* is the only valid species and indicates that “*Stereosternum tumidum*” and “*Brazilosaurus sanpauloensis*” likely represent immature stages or incomplete specimens of *Mesosaurus*. Our results also highlight the following ontogenetic trends:

- a reduction in skull length accompanied by an elongation of the snout within the skull
- an elongation of teeth
- a reduction in hind limb length
- a reduction in manus length

These ontogenetic trends are associated with an environmental partitioning of the different growth stages, which suggests that mesosaurs underwent a diet and lifestyle transition during their growth: juveniles had an active predatory lifestyle in a coastal limestone environment, while adults adopted a more filter-feeding diet in a pelagic anoxic black shale environment. Our hypothesis is that mesosaurs exploited different food sources during their lifetime, but isotopic analyses and a deepening of our knowledge of the fauna of the Irati Sea will be necessary to truly test this.

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Figure 1

Comparison of morphologies in juvenile and adult mesosaurs.

Scale bars equal 20 mm. **A.** Side-by-side comparison of a juvenile (BSPG 1979 I 37, on the left) and an adult *"Stereosternum tumidum"* (MB.R.5605, on the right) showing the ontogenetically changing proportions. **B.** Close-up of the skull of adult *Mesosaurus tenuidens* NRM PZ R 207c showing the characteristic needle-like teeth of mesosaurs. **C.** Close-up of juvenile *"Stereosternum tumidum"* GP/2E 9233 with arrows showing the shorter teeth of immature individuals.

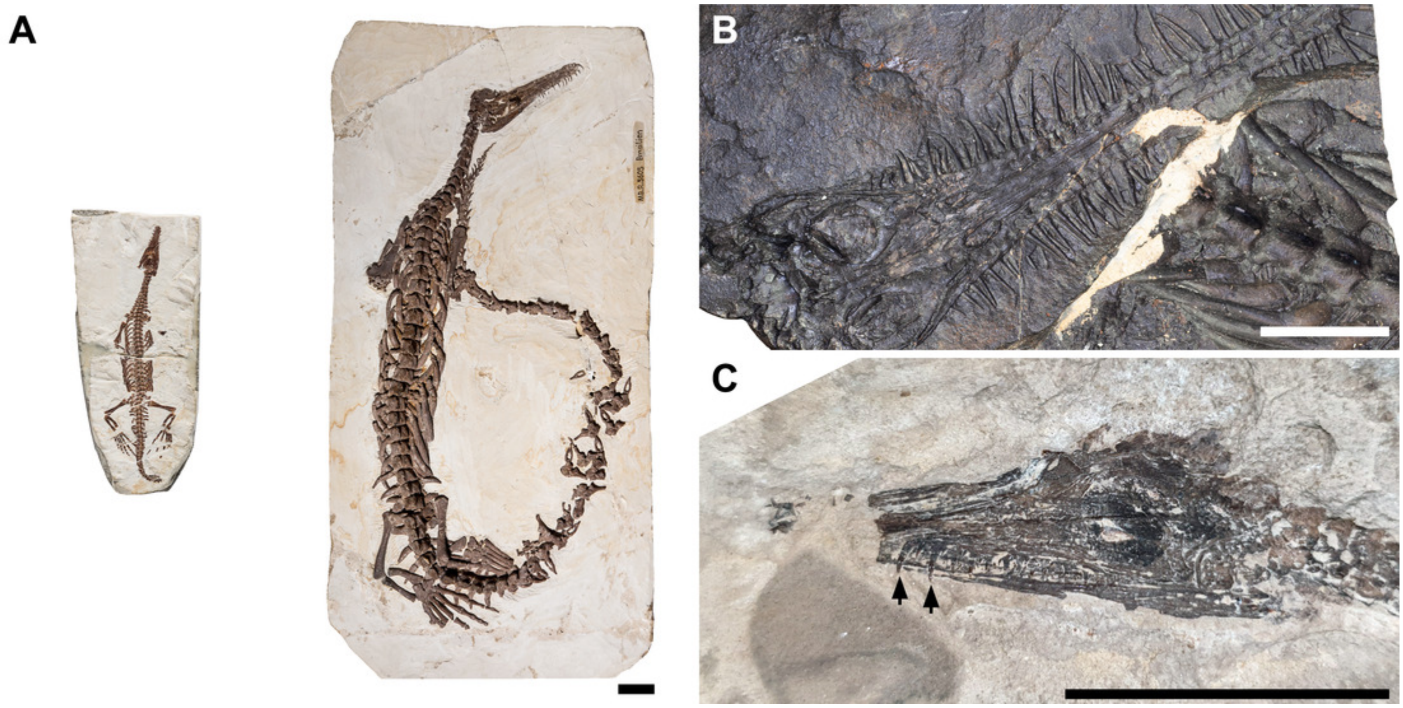

Figure 2

Measurement/size ratios in function of size under the three-species hypothesis.

Logged scale.

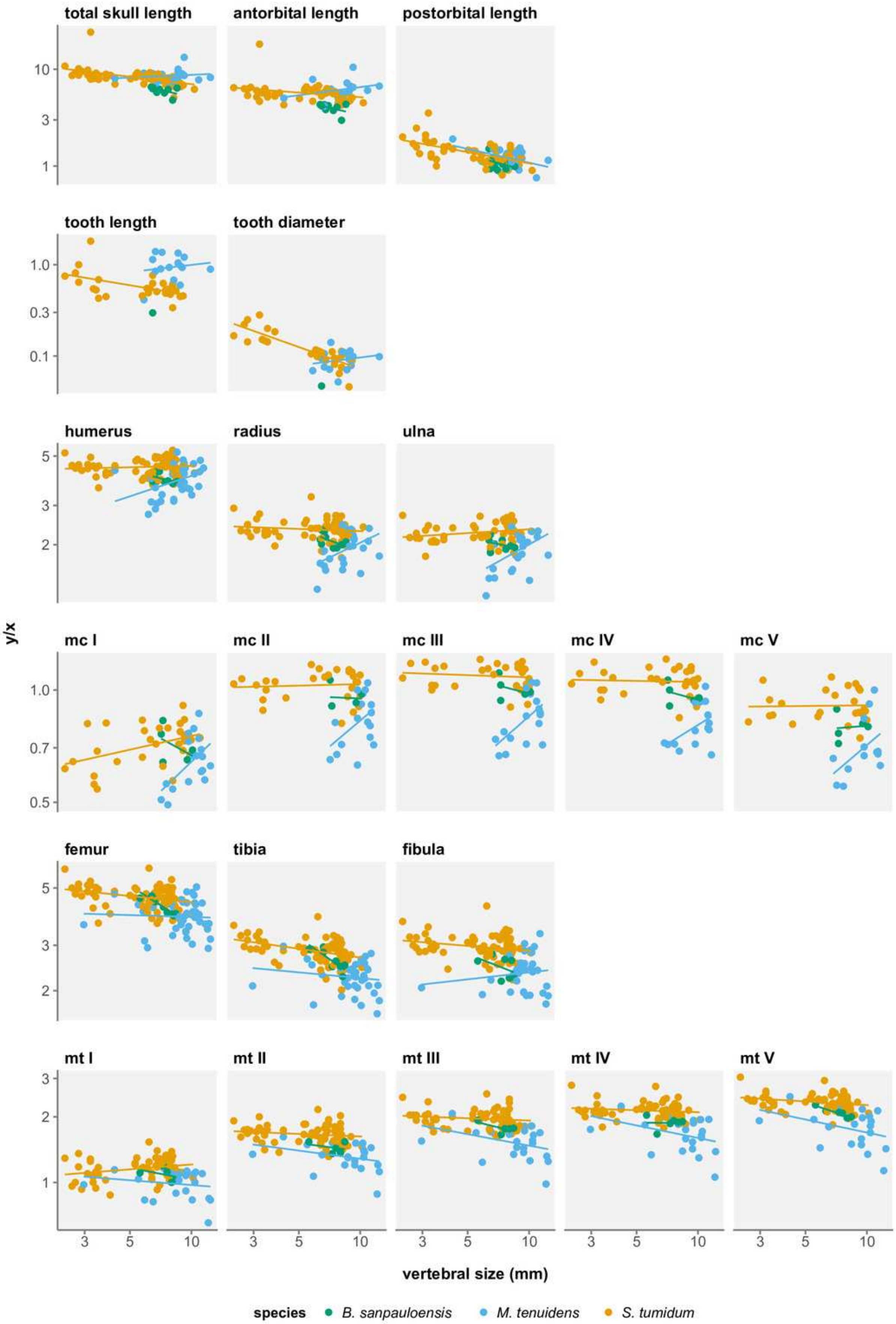
total skull length
antorbital length
postorbital length
tooth length
tooth diameter
humerus
radius
ulna
mc I
mc II
mc III
mc IV
mc V
femur
tibia
fibula
mt I
mt II
mt III
mt IV
mt V
y/x
10
3
1
1.0
0.3
0.1
5
3
2
1.0
0.7
0.5
5
3
2
3
2
1
3
5
10
vertebral size (mm)
species
B. sanpauloensis
M. tenuidens
S. tumidum

Figure 3

Comparison of skull measurements/total skull length ratios in function of total skull length under the three-species and the single-species hypothesis.

Logged scale.

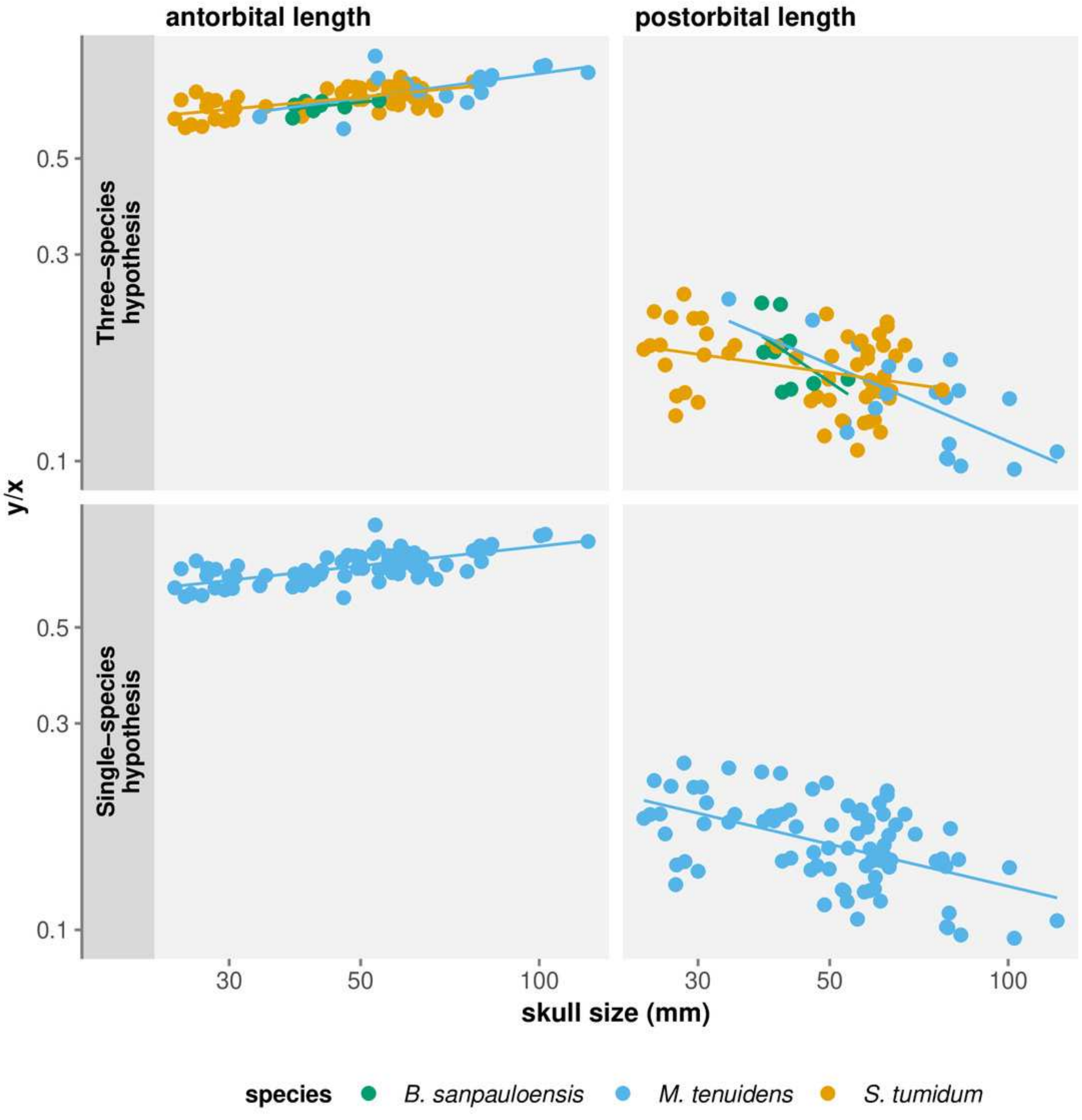
antorbital length
postorbital length
Three–species hypothesis
Single–species hypothesis
y/x
0.5
0.3
0.1
0.5
0.3
0.1
30
50
100
30
50
100
skull size (mm)
species
B. sanpauloensis
M. tenuidens
S. tumidum

Figure 4

Comparison of tooth measurements/total skull length ratios in function of total skull length under the three-species and the single-species hypothesis.

Logged scale.

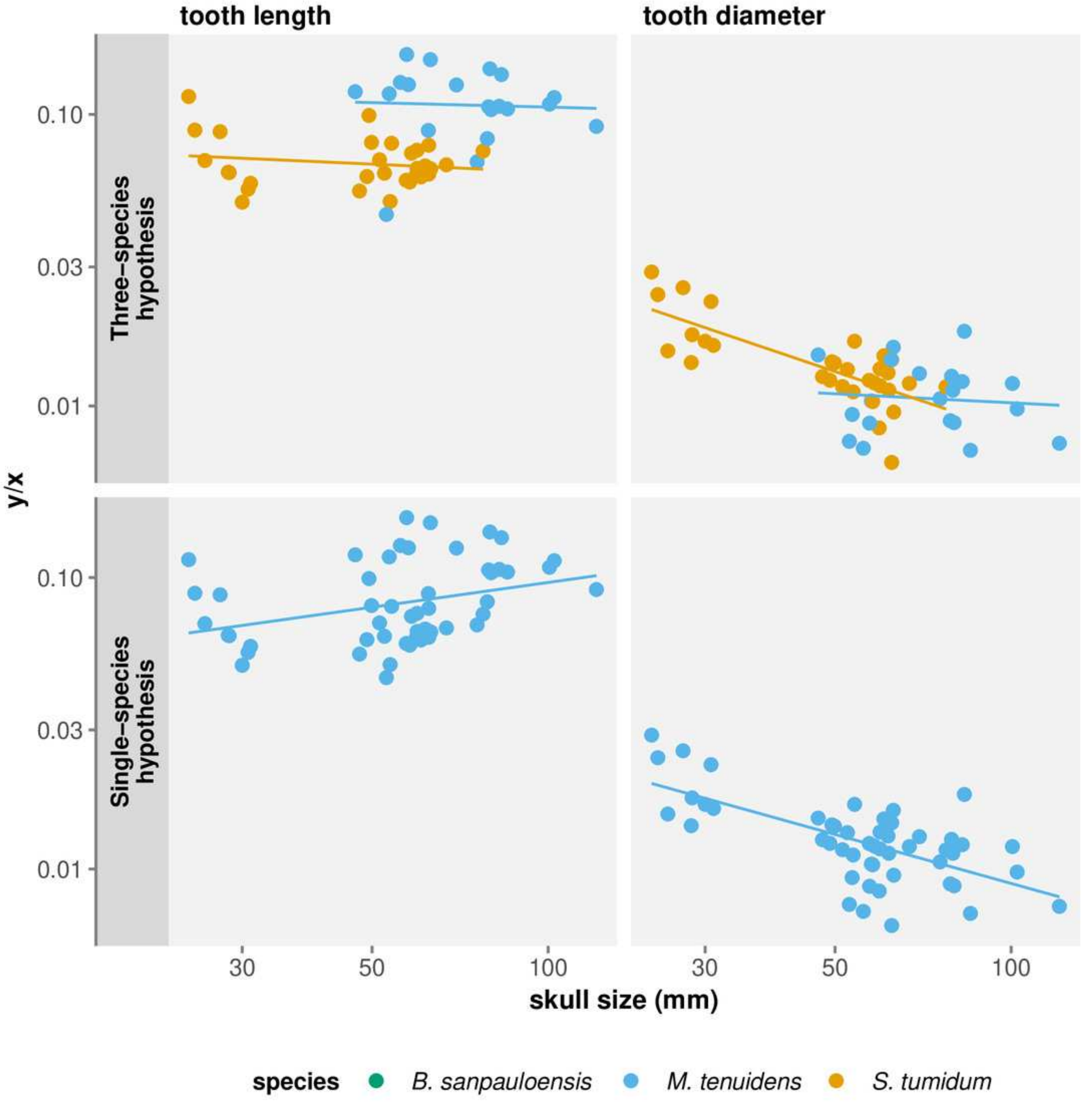
tooth length
tooth diameter
Three–species hypothesis
Single–species hypothesis
y/x
0.10
0.03
0.01
0.10
0.03
0.01
30
50
100
30
50
100
skull size (mm)
species
● B. sanpauloensis
● M. tenuidens
● S. tumidum

Figure 5

Measurement/size ratios in function of size under the single-species hypothesis.

Logged scale.

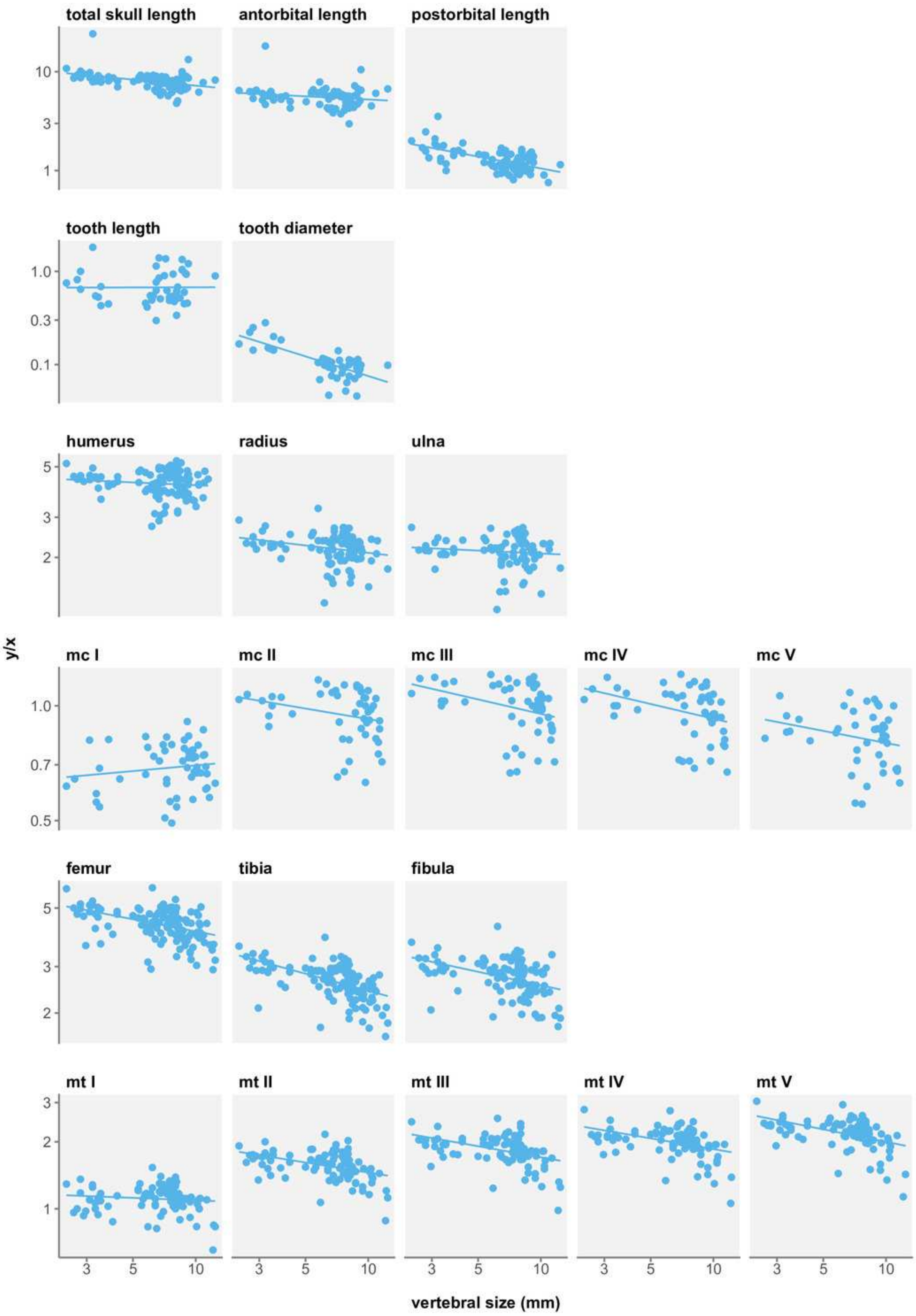
total skull length
antorbital length
postorbital length
10
3
1
tooth length
tooth diameter
1.0
0.3
0.1
humerus
radius
ulna
5
3
2
y/x
mc I
mc II
mc III
mc IV
mc V
1.0
0.7
0.5
femur
tibia
fibula
5
3
2
mt I
mt II
mt III
mt IV
mt V
3
2
1
3
5
10
vertebral size (mm)

Figure 6

Histogram of average vertebral size under the three-species hypothesis.

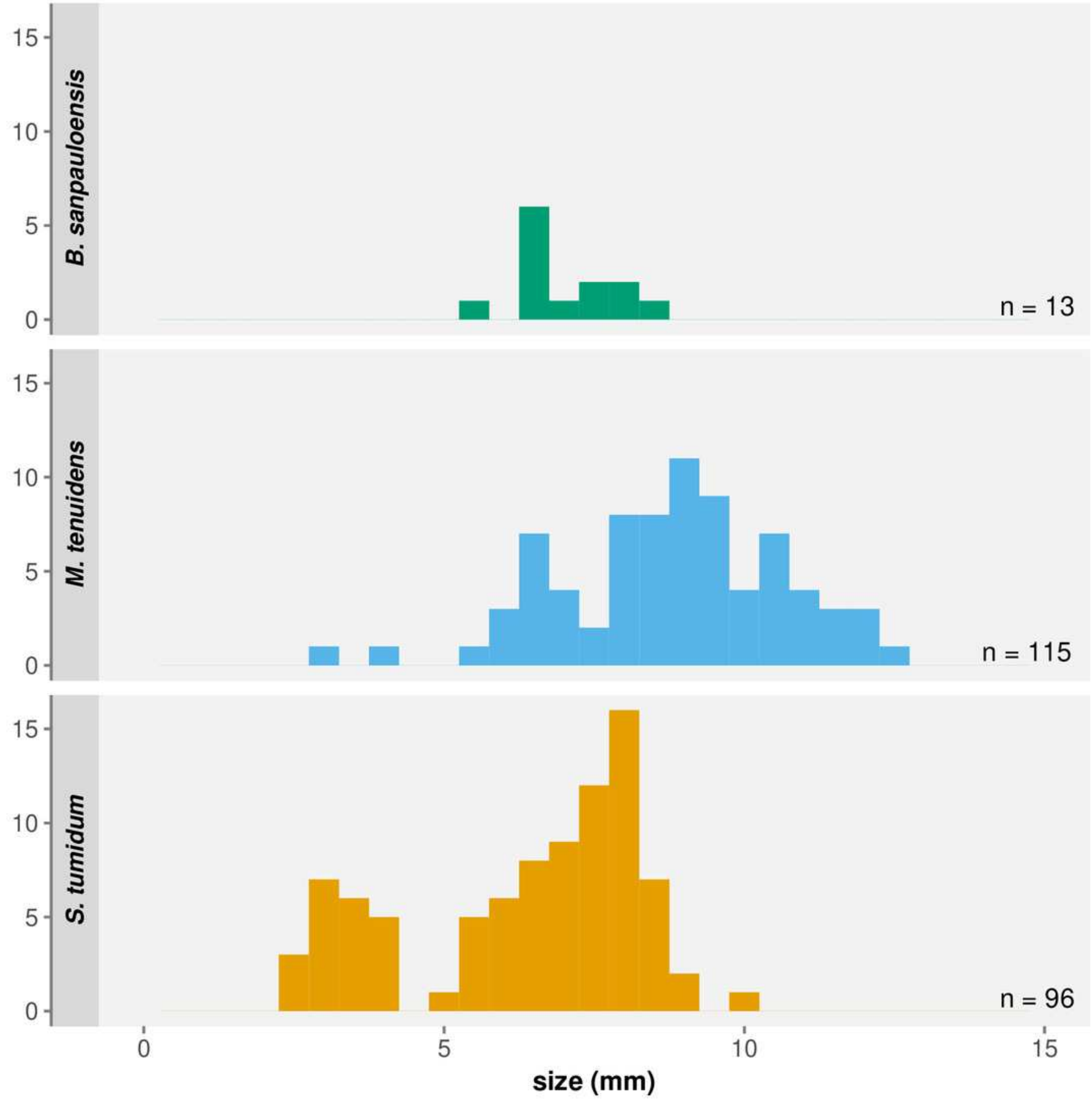

Table 1(on next page)

Allometry coefficient of logged size ratios for teeth and skull measurements.

Table 1. Allometry coefficient of logged size ratios for teeth and skull measurements.

	Allometry coefficient β	**SE**	**t-value**	**p-value**
“B. sanpauloensis”				
tooth length	-	-	-	-
tooth diameter	-	-	-	-
skull total length	–0.505	0.299	–1.688	0.135
skull antorbital length	–0.549	0.382	–1.436	0.194
skull postorbital length	–0.626	0.525	–1.193	0.272
M. tenuidens				
tooth length	0.237	0.431	0.550	0.591
tooth diameter	0.464	0.354	1.309	0.212
skull total length	0.026	0.097	0.268	0.792
skull antorbital length	0.204	0.160	1.279	0.222
skull postorbital length	–0.511	0.275	–2.308	**0.037**
“S.” tumidum				
tooth length	–0.241	0.090	–2.665	**0.013**
tooth diameter	–0.622	0.104	–5.995	**< 0.001**
skull total length	–0.204	0.031	–6.505	**< 0.001**
skull antorbital length	–0.090	0.038	–2.356	**0.022**
skull postorbital length	–0.341	0.064	–5.315	**< 0.001**
Single-species hypothesis				
tooth length	0.124	0.142	0.877	0.385
tooth diameter	–0.515	0.110	–4.685	**< 0.001**
skull total length	–0.168	0.036	–4.636	**< 0.001**
skull antorbital length	–0.067	0.048	–1.390	0.168
skull postorbital length	–0.342	0.059	–5.806	**< 0.001**

Table 2(on next page)

Allometry coefficients of logged tooth and skull measurements with respect to total skull length.

Table 2. Allometry coefficients of logged tooth and skull measurements with respect to total skull length.

	Allometry coefficient β	**SE**	**t-value**	**p-value**
"B. sanpauloensis"				
tooth length	-	-	-	-
tooth diameter	-	-	-	-
skull antorbital length	0.134	0.086	1.563	0.157
skull postorbital length	–0.925	0.522	–1.771	0.114
M. tenuidens				
tooth length	–0.051	0.276	–0.186	0.855
tooth diameter	–0.103	0.260	–0.398	0.696
skull antorbital length	0.187	0.058	3.206	**0.005**
skull postorbital length	–0.590	0.156	–3.785	**0.001**
"S. tumidum"				
tooth length	–0.091	0.097	–0.936	0.357
tooth diameter	–0.678	0.107	–6.336	**< 0.001**
skull antorbital length	0.129	0.021	6.220	**< 0.001**
skull postorbital length	–0.191	0.074	–2.573	**0.013**
Single-species hypothesis				
tooth length	0.282	0.115	2.456	**0.018**
tooth diameter	–0.558	0.092	–6.082	**< 0.001**
skull antorbital length	0.151	0.017	8.913	**< 0.001**
skull postorbital length	–0.323	0.058	–5.583	**< 0.001**

Table 3(on next page)

Allometry coefficient of logged size ratios for long bone lengths.

A. “*B. sanpauloensis*". **B.** *M. tenuidens.* **C.** "*S.* tumidum" **D.** Single–species hypothesis

Table 3. Allometry coefficient of logged size ratios for long bone lengths.

A. “*B. sanpauloensis*”

	Allometry coefficient *β*	SE	t-value	p-value
humerus	–0.044	0.033	–1.321	0.189
radius	–0.081	0.054	–1.497	0.137
ulna	–0.083	0.057	–1.449	0.151
mc I	0.062	0.058	1.078	0.285
mc II	–0.122	0.062	–1.988	0.052
mc III	–0.159	0.063	–2.509	0.015
mc IV	–0.173	0.063	–2.728	0.009
mc V	–0.146	0.081	–1.809	0.077
anterior autopod	0.050	0.212	0.236	0.852
femur	–0.154	0.030	–5.078	**< 0.001**
tibia	–0.212	0.035	–6.119	**< 0.001**
fibula	–0.167	0.039	–4.268	**< 0.001**
mt I	–0.026	0.036	–0.709	0.480
mt II	–0.142	0.035	–4.068	**< 0.001**
mt III	–0.163	0.040	–4.108	**< 0.001**
mt IV	–0.157	0.039	–4.042	**< 0.001**
mt V	–0.185	0.040	–4.630	**< 0.001**
posterior autopod	-	-	-	-

B. *M. tenuidens*

	Allometry coefficient *β*	SE	t-value	p-value
humerus	0.308	0.125	2.473	**0.018**
radius	0.445	0.171	2.599	**0.016**
ulna	0.515	0.199	2.588	**0.016**
mc I	0.646	0.244	2.650	**0.017**
mc II	0.569	0.282	2.018	0.062
mc III	0.590	0.218	2.713	**0.016**
mc IV	0.417	0.217	1.923	0.077
mc V	0.573	0.308	1.859	0.090
anterior autopod	0.527	0.607	0.867	0.450
Femur	–0.024	0.077	–0.31	0.758
Tibia	–0.074	0.077	–0.952	0.347
Fibula	0.089	0.112	0.799	0.431
mt I	–0.073	0.09	–0.812	0.425
mt II	–0.124	0.082	–1.524	0.143
mt III	–0.175	0.096	–1.828	0.082
mt IV	–0.192	0.105	–1.816	0.084
mt V	–0.199	0.115	–1.728	0.101
posterior autopod	–0.122	0.053	–2.293	0.262

C. “*S. tumidum*”

	Allometry coefficient *β*	SE	t-value	p-value
humerus	0.021	0.027	0.771	0.444
radius	–0.034	0.036	–0.936	0.353
ulna	0.057	0.034	1.698	0.095
mc I	0.150	0.056	2.683	**0.012**
mc II	0.017	0.045	0.366	0.717
mc III	–0.024	0.039	–0.616	0.543
mc IV	–0.012	0.041	–0.279	0.782
mc V	0.007	0.058	0.124	0.902
anterior autopod	–0.025	0.066	–0.370	0.716
femur	–0.081	0.029	–2.779	**0.007**
tibia	–0.113	0.03	–3.773	**< 0.001**
fibula	–0.065	0.034	–1.875	0.065
mt I	0.074	0.034	2.173	**0.033**
mt II	–0.038	0.029	–1.304	0.197
mt III	–0.035	0.031	–1.114	0.269
mt IV	–0.031	0.028	–1.089	0.280
mt V	–0.056	0.027	–2.069	**0.043**
posterior autopod	–0.140	0.061	–2.310	**0.028**

D. Single–species hypothesis

Single species hypothesis	Allometry coefficient *β*	SE	t-value	p-value
humerus	–0.041	0.035	–1.184	0.239
radius	–0.109	0.043	–2.502	**0.014**
ulna	–0.044	0.046	–0.949	0.346
mc I	0.061	0.057	1.074	0.288
mc II	–0.113	0.062	–1.831	0.073
mc III	–0.154	0.064	–2.411	**0.020**
mc IV	–0.157	0.062	–2.522	**0.015**
mc V	–0.130	0.082	–1.589	0.120
anterior autopod	–0.120	0093	–1.281	0.212
femur	–0.153	0.029	–5.303	**< 0.001**
tibia	–0.215	0.031	–6.875	**< 0.001**
fibula	–0.170	0.037	–4.6	**< 0.001**
mt I	–0.037	0.035	–1.06	0.292
mt II	–0.150	0.034	–4.47	**< 0.001**
mt III	–0.166	0.038	–4.405	**< 0.001**
mt IV	–0.161	0.038	–4.247	**< 0.001**
mt V	–0.187	0.039	–4.774	**< 0.001**
posterior autopod	–0.152	0.053	–2.863	**0.007**

Table 4(on next page)

ANOVA results for the effect of species on measurements

Table 4. ANOVA results for the effect of species on measurements

	df	**F**	**p-value**
total skull length	2	2.993	0.056
antorbital length	2	3.170	**0.048**
postorbital length	2	0.413	0.663
tooth length	1	2.141	0.151
tooth diameter	1	14.504	**< 0.001**
humerus	2	4.822	**0.010**
radius	2	6.340	**0.003**
ulna	2	5.040	**0.009**
mc I	2	3.109	0.054
mc II	2	3.069	0.056
mc III	2	6.483	**0.003**
mc IV	2	3.020	0.059
mc V	2	2.743	0.077
femur	2	1.425	0.244
tibia	2	1.224	0.298
fibula	2	1.551	0.217
mt I	2	1.816	0.169
mt II	2	0.745	0.478
mt III	2	1.724	0.184
mt IV	2	2.126	0.126
mt V	2	1.887	0.158