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

First revision

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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 270 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 recent hypothesis that *Mesosaurus tenuidens* is the only valid species within Mesosauridae and 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, we hypothesize that mesosaurs went through a progressive ecological shift during their growth, with juveniles being more common in shallow water deposits, whereas large adults are more frequent in pelagic sediments. 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 a better understanding of the Irati Sea fauna will be necessary to obtain a more definitive answer to the question of young mesosaur diet.

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2 **Mesosauridae**

3

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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 270 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 recent hypothesis that *Mesosaurus tenuidens* is the only valid species within Mesosauridae and 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, we hypothesize that mesosaurs went through a progressive ecological shift during their growth, with juveniles being more common in shallow water deposits, whereas large adults are more frequent in pelagic sediments. 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 a better understanding of the Irati Sea fauna will be necessary to obtain a more definitive answer to the question of young 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 deposits of what was at the time a hypersaline inland sea extending over today's eastern South America and southern Africa (Oelofsen & Araújo, 1983; Piñeiro et al., 2012b; Matos et al., 2017; Bastos et al., 2021), 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 (Carroll, 1988). Yet their affinities are controversial, their origins are poorly known, and their lineage ended with them (Laurin & Piñeiro, 2017; MacDougall et al., 2018; Ford & Benson, 2020). 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*

55 *tenuidens* to be the only valid species with "*Brazilosaurus*" and "*Stereosternum*" representing

56 junior synonyms of *Mesosaurus*.

57   All mesosaurs present a striking morphology: a slender body with a very long tail, paddle-like

58 hind limbs, a massive ribcage with thickened banana-shaped ribs, an elongated neck holding an

59 elongate but very thin skull, and a long snout bearing thin needle-like teeth (Fig. 1). This peculiar

60 appearance has resulted in conflicting hypotheses about their ecology, from amphibious (Núñez

61 Demarco et al., 2018) to fully marine (Modesto, 1999, 2010; Canoville & Laurin, 2010), from

62 undulatory (Braun & Reif, 1985; Villamil et al., 2015) to partially limb-propelled swimmers (da

63 Silva & Sedor, 2017; MacDougall et al., 2020).

64   More than other aspects of their anatomy, the long thin teeth of mesosaurs have puzzled those

65 who studied them the most. If they are somewhat reminiscent of those of other vertebrates such

66 as dolphins or gharials, mesosaur teeth are singular in their length and their needle-like

67 morphology. Consequently, they have no modern analog, which has led to contradicting attempts

68 at characterizing the feeding habits of mesosaurs. Based on cranial morphology alone,

69 MacGregor (1908) proposed a "fish"-based diet for mesosaurs. Subsequent studies discarded this

70 interpretation (Wiman, 1925; Araújo, 1976), noting that their teeth were too fragile for active

71 hunting and pointing to the absence of "fish" in mesosaur-bearing strata (Oelofsen & Araújo,

72 1983; Piñeiro et al., 2012b), although recent works show that fish were more frequent than

73 previously thought (Xavier et al., 2018). In fact, based on their tooth morphology (Pretto,

74 Cabreira & Schultz, 2012), the fauna of the Irati-Whitehill Sea (Piñeiro et al., 2012b; Chahud &

75 Petri, 2013; Xavier et al., 2018), as well as gut content and coprolite analyses (Silva et al., 2017),

76 most authors concluded that mesosaurs were filter-feeders trapping pygocephalomorph

77 crustaceans in the net of their teeth (Oelofsen & Araújo, 1983; Modesto, 1999, 2006, 2010;

78 Piñeiro et al., 2012b; Silva et al., 2017). Despite this, some authors suggested that mesosaurs

79 could have been active hunters (Pretto, Cabreira & Schultz, 2012) or even scavengers (Silva et

80 al., 2017).

81   Although interest and research effort into the paleobiology of mesosaurs has tremendously

82 increased in the last decade and some aspects of mesosaur ecology have been addressed in the

83 past, their lifestyle throughout ontogeny has not been fully investigated. Even though some

84 authors have looked at the morphometrics of mesosaurs (Araújo, 1976; Rossmann & Maisch,

85 1999; Rossmann, 2000, 2002; Núñez Demarco et al., 2018; Piñeiro et al., 2021) or at histological

86 growth marks (de Ricqlès, 1974; Canoville & Laurin, 2010; Klein et al., 2019), there have only

87 been a few studies focusing on their ontogeny (Piñeiro et al., 2012a; Piñeiro, Núñez Demarco &

88 Meneghel, 2016; Núñez Demarco et al., 2018; Bickelmann & Tsuji, 2018; Verrière, Fröbisch &

89 Fröbisch, 2021; Núñez Demarco, Ferigolo & Piñeiro, 2022). This is surprising, as mesosaurs

90 constitute a unique framework for understanding the complex links between diet and

91 morphology in the fossil record. First, they comprise one of the few comprehensive ontogenetic

92 series known in fossil amniotes (Piñeiro et al., 2012a; Piñeiro, Núñez Demarco & Meneghel,

93 2016; Bickelmann & Tsuji, 2018; Núñez Demarco, Ferigolo & Piñeiro, 2022). Second, they

94 lived in a constrained environment with greatly reduced food variety, placing considerable limits

95   on what their feeding habits could have been (Soares, 2003; Piñeiro et al., 2012b; Xavier et al.,
96   2018). Lastly, they are the first secondarily aquatic amniotes, and understanding their dietary
97   evolution has implications for the reconstruction of feeding habits in later marine amniotes.
98   Here, we provide the first quantitative assessment of ontogenetic changes in mesosaurs on
99   such a large number of specimens. With this dataset, we test the hypothesis from Núñez
100 Demarco et al. (2022) that ~~mesosaur grow~~ isometrically. Our results support the single-species
101 model of Piñeiro et al. (2021) by demonstrating that the formerly recognized species occupy
102 incomplete segments of the mesosaur size range and show very little difference between them.
103 Based on the single-species model, we do not retrieve the isometric growth measured by Núñez
104 Demarco et al. (2022) and instead show that the ontogeny of mesosaurs is marked by some
105 significant allometric transformations and environmental partitioning, likely indicating a change
106 in diet and lifestyle with growth.
107

Materials & Methods

Material investigated

110   We examined 270 articulated mesosaur specimens from collections around the world. Of
111 these, 115 were previously attributed to *Mesosaurus tenuiden*s, 96 to "*Stereosternum tumidum*",
112 13 to "*Brazilosaurus sanpauloensis*", and 46 were unidentified (Supp. Table 1). Of the identified
113 specimens, 47 had a preserved skull and teeth, with 18 attributed to *Mesosaurus*, 29 to
114 "*Stereosternum*", and only one to "*Brazilosaurus*". Earlier studies mentioned the presence of
115 teeth in "*Brazilosaurus*" (Rossmann, 2002; Modesto, 2006; Silva et al., 2017), all of them
116 relying on the average tooth length of 2 mm provided by Rossmann (2002). We find this value
117 contentious in different regards. First, Rossmann (2002) did not provide the raw measurements
118 for his calculation. Second, we reexamined the material described by Rossmann (2000, 2002) as
119 bearing teeth and noticed that elements he describes as teeth are in fact misidentified broken
120 tooth sockets from the maxilla or the dentary (Supp. Fig. 1). Finally, out of the twelve specimens
121 assigned to "*Brazilosaurus*" studied here, only ROM 28496 had some visible complete teeth. In
122 all other specimens, teeth are either missing or completely broken, in any case not in a state of
123 preservation allowing their measurement. Consequently, we must dismiss the average tooth
124 length for "*Brazilosaurus*" of 2 mm given by Rossmann (2002). For this reason, no specimens
125 previously attributed to "*Brazilosaurus*" are included in our statistical analysis of teeth.
126

Measurements

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

135   To account for cranial proportions, we measured the total skull length as well as antorbital and
136   postorbital length.
137   Likely due to dental replacement, mesosaur teeth can greatly vary in size within a single
138   specimen (Modesto, 1999, 2006; Piñeiro et al., 2021). To better account for the dimensions of
139   mesosaur teeth, we therefore chose not to use average tooth length and diameter, unlike previous
140   works (Piñeiro et al., 2021). Instead, we measured the length of the longest visible tooth and the
141   diameter of this tooth at its base.
142   Our specimens were preserved in various states of completeness, with some showing only the
143   anterior or the posterior half of the body and others missing limbs or neck while others were
144   mostly complete. Unlike Núñez Demarco et al. (2022) who studied ontogenetic variation within
145   bones, we wanted a shared proxy for specimen size to be able to model and compare variations
146   in all bones independently. Thus, we calculated the average centrum length of dorsal vertebrae
147   for each specimen, as this measurement has been shown to be a reliable estimate for body length
148   (Núñez Demarco et al., 2018).
149   All measurements were taken using a caliper directly on specimens or Fiji 1.53c on distortion-
150   corrected high-resolution photographs.
151
152   Facies
153   Mesosaur specimens can be found in various deposits that represent different sections of the
154   carbonate ramp boarding the Irati-Whitehill Sea (Xavier et al., 2018; Ng, Vega & Maranhão,
155   2019). To account for size distribution across deposit environments and potential niche
156   partitioning of ontogenetic stages in mesosaurs, we categorized our specimens into five facies: (i)
157   yellow limestone, (ii) white calcarenite, (iii) grey siltstone, (iv) grey mudstone, and (v)
158   bituminous black shales. These facies represent a gradient in depth, energy level, and
159   oxygenation of the water layers.
160
161   Statistics
162   According to Huxley (1932), simple allometry is described by the equation
163    $y = kx^{\alpha}$ or in its logarithmic form
164    $\log y = \alpha \log x + \log k$
165   The allometric coefficient α characterizes the slope of the linear relationship between the logged
166   valued of y and x and $\log k$ is the intercept of the linear relationship. Thus, an isometric growth
167   (no changes in proportion to size during ontogeny) is characterized by an allometry coefficient of
168    $\alpha = 1$ while values of $\alpha > 1$ and $\alpha < 1$ respectively reflect positive and negative allometry.
169   By transforming the simple allometry equation to express the ratio y/x rather than y as a
170   function of x, we obtain
171    $\frac{y}{x} = kx^{\alpha - 1}$ which in turns gives

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

173   In this equation we can define another allometry coefficient $\beta = \alpha - 1$. Thus, for the same values
174   of x and y, isometry is defined by $\beta = 0$ while negative and positive allometry are respectively
175   characterized by negative and positive values of β, improving readability both graphically and
176   numerically (Klingenberg, 1998). Therefore, we prefer β to α in the present study.
177   For each metric, we computed a linear regression model of the logged ratio of the metric's
178   values over size proxy value ($\log \frac{y}{x}$) as a function of logged size proxy values ($\log x$) and
179   calculated the allometry coefficient β to test for proportion changes throughout ontogeny.
180   Similarity between species was also tested for each measurement. Linear modelling and
181   statistical analyses were carried out in R 4.0.5 (R. Core Team, 2021).
182

183   **Results**
184   Three-species hypothesis
185   *Skull*
186   Skull measurements behave differently with respect to size in the three formerly recognized
187   mesosaur "species". In "*Brazilosaurus*", all three skull measurements show negative allometry,
188   albeit not significant (Table 1). In *Mesosaurus*, postorbital length is the only skull metric to
189   display a significant negative allometry, while total length and antorbital length both show a non-
190   significant positive allometry (Table 1). In "*Stereosternum*", all three skull measurements show
191   significant negative allometry but each with different allometry coefficients (Fig. 2). The
192   negative allometry is less marked for antorbital length ($\beta = -0.090$, p = 0.022) than for total
193   length ($\beta = -0.204$, p < 0.001), itself less marked than postorbital length ($\beta = -0.341$, p < 0.001).
194   For all three species, skull measurements rank similarly in terms of allometry coefficients
195   with antorbital length having the highest, followed by total length and finally postorbital length
196   last. This shows how skull elements vary differently in proportion throughout ontogeny. To
197   better account for these variations, we measured the effect of allometry in function of total skull
198   length instead of body size. In this configuration, we obtain very concordant results between the
199   three species: antorbital length shows significant positive allometry, whereas postorbital length
200   shows significant negative allometry (Table 2). Thus, over the course of ontogeny, the
201   postorbital length decreases while the snout increases relative to overall skull length (Fig. 3).
202

203   *Teeth*
204   Several authors have noted an apparent change in tooth morphology between mesosaur
205   species: "*Brazilosaurus*" and "*Stereosternum*" are described as bearing short, straight conical
206   teeth whereas *Mesosaurus* is defined by thin, curved, and elongated teeth (Oelofsen & Araújo,
207   1987; Rossmann, 2002; Modesto, 2006). Indeed, for the same body size, adult *Mesosaurus* teeth
208   are systematically longer than those of "*Stereosternum*" albeit similar in diameter (Fig. 2, 3).
209   Tooth length and diameter in *Mesosaurus* both display positive allometry, although the linear
210   relationship is not significant (Table 1). In "*Stereosternum*", both measurements show a
211   significant negative allometry, with tooth diameter showing the lowest coefficient ($\beta = -0.622$, p
212   < 0.001).

213   Since our results highlight variation in cranial dimensions throughout ontogeny, we also
214   calculated allometry coefficients for tooth measurements with respect to skull length. Surprising,
215   this shows non-significant negative allometry for tooth length in both species, whereas tooth
216   diameter exhibits negative allometry for both species, although it is only significant in
217   "*Stereosternum*" (Table 2). Thus, mesosaur teeth grow in length at the same rate as the skull,
218   meaning that they do not become proportionally longer throughout ontogeny. However, these
219   teeth keep their juvenile diameter and grow only in length in "*Stereosternum*" whereas both
220   length and diameter grow isometrically to the skull in *Mesosaurus* (Fig. 4).
221
222   *Limbs*
223   In all three species, most long bones show no significant difference in growth with isometry
224   (Table 3A-C), meaning that their proportional length with respect to body size does not change
225   throughout ontogeny. However, there are several exceptions to this.
226   In "*Brazilosaurus*", femur, tibia and metatarsal V length show significant negative allometry
227   (Table 3A). Although this might reflect a size reduction of the posterior limb during ontogeny in
228   this species, those measurements are only documented for eight adult specimens in our dataset
229   and likely do not reflect the entire ontogenetic trajectory of the species.
230   In *Mesosaurus*, most forelimb bones exhibit a significant positive allometry, aside from
231   metacarpals II, IV, and V (Fig. 2). While this suggests that the anterior autopod increases in size,
232   there are very few juveniles or subadult *Mesosaurus* in our dataset. Thus, much like for
233   "*Brazilosaurus*", *Mesosaurus* forelimb measurements are concentrated in the adult region of the
234   morphospace, and do not satisfyingly account for the entire ontogenetic variation.
235   In "*Stereosternum*", metacarpal I and metatarsal I also display a significant positive allometry,
236   but femur, tibia, fibula and metacarpal V show a significant negative allometry (Fig. 2).
237   Uniquely in mesosaur "species", the posterior autopod also shows a slight significant negative
238   allometry. This reflects a reduction in limb size with respect to the body. "*Stereosternum*" being
239   the best-documented taxon here, these results are more representative than for the two other
240   species.
241
242   *ANOVAs*
243   We measure a significant effect of species on allometry coefficients for six measurements:
244   antorbital length, tooth diameter, humerus, radius, ulna, and metacarpal III length (Table 4).
245   Rather than indicating a real difference between the species, this likely reflects a sampling bias.
246   In the near absence of *Mesosaurus* and "*Brazilosaurus*" juveniles in our dataset, values for these
247   species form a cluster concentrated in the adult–size region, which distorts linear regressions
248   (Fig. 2). Therefore, these regressions do not fully account for the ontogenetic trajectories of the
249   measurements.
250
251   Single-species hypothesis
252   In a recent study, Piñeiro et al. (2021) proposed *Mesosaurus tenuidens* to be the only valid
253   species within the clade by statistically rejecting most characters used to discriminate between

254   the three previously recognized mesosaur species. To account for this new hypothesis, we
255   reproduced our analysis with all specimens (re)assigned to *Mesosaurus*.
256
257   *Skull*
258   All three skull measurements show negative allometry when compared to body size, but the
259   linear relationship is only significant for postorbital length and total skull length (Table 1). When
260   measuring allometry with respect to total skull length, the signal is unambiguous, with antorbital
261   length showing positive allometry and postorbital length negative allometry (Fig. 3). Similar to
262   the three-species hypothesis, our results with one species point to an elongation of the snout
263   elongates and a reduction of postorbital length, while overall skull length proportionally
264   decreases with respect to the body.
265   These results differ from those of Núñez Demarco et al. (2022) who measured an isometric
266   relationship of antorbital and postorbital length to total skull length. However, this can be easily
267   explained by a difference in the statistical power of our datasets. We use a much larger dataset
268   (84 specimens vs. 19), including more juveniles and larger specimens, which refines the results
269   by producing smaller confidence intervals. It is therefore likely that the isometry in skull
270   proportion measured by Núñez Demarco et al. (2022) is a statistical artifact caused by the size of
271   their dataset.
272
273   *Teeth*
274   Under the single-species hypothesis, tooth length shows positive but non-significant allometry
275   whereas diameter shows a significant negative allometry with respect to body size. However,
276   when compared to skull size, tooth length exhibits a strong significant positive allometry and
277   tooth diameter a significant negative allometry (Table 2). In practice, tooth diameter remains the
278   same in adults as in juveniles, but teeth elongate throughout ontogeny and become more needle-
279   like.
280
281   *Limbs*
282   There is a strong trend to hind limb reduction when considering a single mesosaur taxon (Fig.
283   5). All eight long bone measurements display negative allometry coefficients in relation to body
284   size and this relationship is significant for seven of them (Table 3D). Only metatarsal I length is
285   not significantly isometric in growth. Posterior autopod length also shows a significant negative
286   allometry.
287   In contrast, forelimb long bones do not show such a reduction in size. Only metacarpals
288   display significant negative allometry, with the exception of metacarpal I that has a non-
289   significant positive allometry coefficient. Thus, while stylopod and zeugopod do not vary in
290   proportions, it appears the manus is reduced during ontogeny.
291   At first glance, it could seem that these results do not match those of Núñez Demarco et al.
292   (2022), who report isometric growth in mesosaur limbs. Nevertheless, our findings are
293   compatible with theirs. What Núñez Demarco et al. (2022) measure is that long bones grow
294   isometrically with respect to their respective stylopod, humerus length for fore limbs and femur

295 for hind limbs. What we measure is the allometry of these bones with respect to size. Here we
296 show that femur length displays a significant negative allometry with respect to size, and so do
297 most other limb bones. In sum, the isometric growth measured by Núñez Demarco et al. (2022),
298 and by extension their other results for limbs, is likely an effect of using different reference
299 frames.
300
301 Environmental distribution
302   Figure 6 shows the distribution of size classes in the main facies of the Irati-Whitehill Sea. In
303 our sample, small mesosaurs (i.e., juveniles) are overrepresented in limestone, although they also
304 occur in siltstone and black shales. Mid-sized mesosaurs are well represented in all facies despite
305 frequency variations due to sample size differences. Contrary to what has been hypothesized
306 (Núñez Demarco et al., 2018), we do not find that large specimens are only found in the marginal
307 regions of the basin. Instead, in our dataset, very large specimens (vertebral length $\geq$ 10 mm) are
308 exclusively found in mudstone and black shales, facies that correspond to deeper, more pelagic,
309 and more anoxic environments (Xavier et al., 2018; Bastos et al., 2021).
310

Discussion

312 Missing juveniles and single-species hypothesis
313   One of the most significant results of our study is not found with regards to size and
314 proportional changes in mesosaur anatomy but instead in the distribution of body size itself.
315 Despite the 270 specimens examined here, there are a number of surprising gaps in the size range
316 covered by our sample (Fig. 7). First, the few "*Brazilosaurus*" specimens studied here are
317 concentrated in the adult size range of "*Stereosternum*", but no juveniles or subadults are
318 preserved. Second, there is a clear divide between the youngest "*Stereosternum*" specimens on
319 the one hand and subadults and adults of that species on the other hand. Third, and more
320 importantly, only two specimens of *Mesosaurus* are the size of juvenile "*Stereosternum*",
321 whereas all other specimens range from the size of "*Stereosternum*" subadults to larger sizes than
322 the largest "*Stereosternum*" specimens. These gaps in size distribution have a direct effect on the
323 interpretation of allometric measurements as they alter the results of linear regressions, making
324 them less representative of ontogenetic changes.
325   Piñeiro et al. (2021) highlighted that most features employed to define mesosaur species are
326 not statistically supported or are practically unusable for identification. Characters like the shape
327 of the interclavicle, tooth length, or presacral vertebral count are highly preservation-dependent,
328 whereas others such as the degree of pachyostosis of ribs or the skull-neck length ratio are
329 subjective and ontogenetically variable (for pachyostosis, see also Klein et al., 2019). This lack
330 of reliable characters led the authors to suggest that both "*Stereosternum tumidum*" and
331 "*Brazilosaurus sanpauloensis*" are junior synonyms of *Mesosaurus tenuidens*.
332   The ontogenetic variability of supposedly taxonomic characters led to an age partitioning of
333 mesosaur specimens into the different "species". On the one hand, juvenile and subadult
334 specimens tended to be identified as "*Stereosternum*", because they bear shorter conical teeth

335   and are usually preserved complete, displaying the maximum number of presacral vertebrae.
336   Both features were formally admitted as prominent characters for mesosaur identification.
337   On the other hand, the largest mesosaur specimens bear longer, thinner teeth and have more
338   markedly pachyostotic ribs, and they tended historically to be attributed to *Mesosaurus*. As for
339   "*Brazilosaurus*" specimens, they were usually identified on the basis of their cervical vertebral
340   count, which is however a misidentification as the result of a displaced rib cage (pers. obs.). In
341   fact, even the original description of the species (Shikama & Ozaki, 1966) miscounted the
342   number of cervicals due to the posterior displacement of dorsal ribs (pers. obs.), which led to the
343   erroneous erection of this feature as a defining character. To summarize, there are several
344   reasons as to why mesosaur invalidated "species" occupy different regions of the size range.
345   Rather than a sampling bias, the size distribution gaps in our dataset more likely reflect a
346   species-identification bias. Our data shows consequent overlap in the morphometrics of all three
347   species. "*Brazilosaurus*" is virtually indistinguishable from "*Stereosternum*", whereas the old
348   definition of *Mesosaurus* seems to have mostly representatives on the higher side of the size
349   spectrum (Fig. 7). Furthermore, the low significance of allometry coefficients (Tables 1, 2, 3) is
350   also likely an effect of the small number of juveniles of the *Mesosaurus* type in our dataset,
351   although more juvenile specimens have been described that we could not include (Piñeiro et al.,
352   2012a).
353   Our results therefore corroborates the single-species hypothesis of Piñeiro et al. (2021) and
354   their discarding of the former characters as ontogenetically variable. In fact, the three previously
355   identified "species" more probably represented three artificial types: the "*Brazilosaurus*"-type is
356   a poorly preserved mesosaur with displaced ribs, the "*Stereosternum*"-type is a size class
357   encompassing juveniles to young adults, and the "*Mesosaurus*"-type represents adults with more
358   extreme sizes and morphologies. Consequently, hereafter we will only consider our results in the
359   light of the single-species hypothesis.
360
361   Environmental partitioning
362   Even when considering *Mesosaurus* as the only valid mesosaur taxon, one puzzling difference
363   between the previously distinct types cannot be explained as an effect of ontogenetic changes or
364   dubious characters alone. Some authors pointed out that the three types were not equally
365   distributed across the facies of the Irati-Whitehill Sea. Oelofsen & Araújo (1983) and Rossmann
366   (2002) noted that "*Brazilosaurus*" and "*Stereosternum*" were more commonly found in
367   limestone deposits, whereas *Mesosaurus* was more frequent in oily black shales. Since these
368   publications however, mesosaur specimens have been described in other facies and the former
369   species have been synonymized, meaning their observations must be considered with caution.
370   Nevertheless, our study demonstrate that size classes are not homogeneously distributed
371   across lithological facies: juveniles are overrepresented in limestone, and very large/old
372   specimens in black shales (Fig. 6). As argued above, flaws in the formerly admitted diagnostic
373   characters have led to juveniles and young adults being preferentially assigned to
374   "*Stereosternum*" and old adults to *Mesosaurus* (Fig. 7). Because we look at articulated

375   specimens, it is also fair to assume that the specimens were buried relatively close to their life
376   environment. Therefore, what Oelofsen & Araújo (1983) and Rossmann (2002) noticed were
377   likely the signs of ontogenetic stage partitioning rather than species partitioning.
378   The overrepresentation of juveniles and large adult in some facies suggests that mesosaurs
379   preferentially occupied some environments at different stages of their life. Juveniles were mostly
380   present in the shallower, more coastal sections of the carbonate ramp, while medium-sized
381   mesosaurs were present in all areas, and the largest and oldest individuals were restricted to
382   pelagic and anoxic regions (Fig. 6). Thus, if mesosaurs were not confined to a specific region of
383   their environment, it seems that, overall, they gradually moved away from the coast during their
384   growth.
385   The pelagic migration of mesosaurs with growth raises the question of their reproduction.
386   Associated articulated juveniles and adults, even gravid individuals, have been found in
387   limestone, siltstone, and mudstone (Piñeiro et al., 2012a; Bickelmann & Tsuji, 2018), but the
388   greater frequency of juveniles in limestone suggests that mesosaurs were mostly born near the
389   coast. If they were oviparous like most reptiles, this would have been easily explained by the
390   necessity to lay eggs on land. However, evidence suggests instead that mesosaurs were
391   viviparous, and possibly even cared for their young (Piñeiro et al., 2012a). Mesosaurs could
392   therefore have given birth anywhere in the sea, making the causes of a partitioning less clear. To
393   try to explain this, we must look at our morphometric analyses.
394
395   Ontogenetic changes and diet shifts
396   Our results show that mesosaur growth is marked by several morphological changes: an
397   elongation of the teeth relative to the skull (Fig. 3), an elongation of the snout (Fig. 4), and a
398   reduction of limbs (Fig. 5). Limb reduction throughout ontogeny hints at a difference in
399   locomotory habits between juveniles and adults. Mesosaurs are swimming reptiles, and the
400   degree of involvement of the limbs in locomotion is still debated. Some authors support the idea
401   of mainly tail-driven mesosaurs (Braun & Reif, 1985; Villamil et al., 2015) while others
402   suggested a potentially larger role of limbs in propulsion (da Silva & Sedor, 2017; MacDougall
403   et al., 2020). Yet, the ontogenetic limb reduction we expose seems incompatible with the
404   conception that limbs were crucial for locomotion. Instead, our results provide evidence for a
405   decreasing involvement of limbs in mesosaur swimming and weigh in favor of a tail-driven
406   model of mesosaur swimming throughout their ontogeny.
407   The association of limb reduction with cranial and dental modifications strongly ~~suggest~~ the
408   existence of locomotion and dietary shift in ~~mesosaur,~~ Such shifts are not rare in reptiles but are
409   usually associated with dietary partitioning between juveniles and adults, meaning they exploit
410   different food sources at different stages of their growth (Arthur, Boyle & Limpus, 2008; Gignac
411   & Erickson, 2015; Dick, Schweigert & Maxwell, 2016; Wang et al., 2017). In the case of
412   mesosaurs, a change in diet could explain the environmental migration we observe in size classes
413   (Fig. 6). As mesosaurs grew, they would have shifted from an abundant food source in the
414   coastal environment to one more prevalent in pelagic regions. Preying on different food sources

415   in different water layers would have been a way to avoid competition between ontogenetic stages
416   in a sea where resources were scarce. Different feeding habits would also explain the presence of
417   juveniles in pelagic environments, as young mesosaurs could have been born anywhere in the sea
418   but would have preferentially migrated to the coastal region looking for food. Yet, there remains
419   the question of the alternative food source.
420   Traditionally, mesosaurs are considered filter-feeders that preyed on pygocephalomorph
421   crustaceans, based on stratigraphic occurrences (Oelofsen & Araújo, 1983; Piñeiro et al., 2012b;
422   Xavier et al., 2018; Ng, Vega & Maranhão, 2019) as well as on gastric contents and coprolites
423   (Piñeiro et al., 2012b; Ramos, 2015; Silva et al., 2017). While this applies to adults, it is unclear
424   what the diet of juveniles could have been. Mesosaur-bearing strata of the Irati-Whitehill Sea
425   deposits are rich in mesosaurs and pygocephalomorphs remains but scarce in other types of
426   fossils. Only rare invertebrate traces, bivalves, and paleonisciform fish scales have been
427   described (Oelofsen & Araújo, 1983; Piñeiro et al., 2012b; Matos et al., 2017; Xavier et al.,
428   2018), although recent works have revised the abundance of paleonisciform fishes upwards
429   (Xavier et al., 2018). This raises a puzzling question: if juvenile mesosaurs did not have the same
430   diet as adults, what could they possibly have been eating?
431   Our morphometric analysis shows that young mesosaurs would have had longer limbs, shorter
432   snouts and shorter teeth than adults, a morphology better suited to active hunting than that of
433   adults. Among the known Irati-Whitehill fauna, only pygocephalomorph crustaceans and
434   paleonisciform fishes could have been the subject of active hunting. Thus, juvenile mesosaurs
435   could have actively preyed on small fish or large pygocephalomorphs, while mesosaurs would
436   have slowly filtered waters to catch smaller pygocephalomorphs or even larvae. The coastal
437   environment would have been better oxygenated and richer in nutrients, fostering the growth of
438   larger preys, whereas smaller crustaceans could have occupied the harsher pelagic waters.
439   Unfortunately, the ecology of pygocephalomorph crustaceans or paleonisciform fish is very
440   poorly known. One way of testing this hypothesis would be to examine size distribution across
441   facies for fish and crustaceans and see if there is a trend, similar to what we did for mesosaurs.
442   Another possible answer is that juvenile mesosaurs fed on animals that did not preserve well
443   under the conditions where mesosaurs were buried. For instance, young mesosaurs could have
444   eaten jellyfish or soft invertebrates with little to no mineralized tissues, which greatly reduces the
445   chances at fossilizing the latter. Although the sea's hypersaline conditions would not have
446   favored such animals (Piñeiro et al., 2012b; Bastos et al., 2021), there are occurrences of soft
447   invertebrates in hypersaline contexts (Parker, 1959; Tanner, Glenn & Moore, 1999; Gilabert,
448   2001). Yet, there are many cases of outstanding preservation in the Irati-Whitehill sediments
449   producing complete articulated fossils (Modesto, 1999, 2010; Piñeiro et al., 2012b; Núñez
450   Demarco et al., 2018), sometimes even showing soft tissue preservation (Piñeiro et al., 2012b,a;
451   MacDougall et al., 2020). With such conditions of preservation, it seems very unlikely that no
452   trace of other invertebrates would remain. It is possible, however, that soft animal fossils are yet
453   to be discovered, and that further study of the mesosaur-bearing Irati-Whitehill deposits will
454   reveal them.

455

Conclusions

456

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

464   Our results also highlight the following ontogenetic trends:
465 •   a reduction in skull length accompanied by an elongation of the snout within the skull
466 •   an elongation of teeth
467 •   a reduction in hind limb length
468 •   a reduction in manus length
469 These ontogenetic trends are associated with a partitioning of ontogenetic stages across facies
470 following a gradient of depth and distance to the coast. This suggests that mesosaurs underwent a
471 diet and lifestyle transition during their growth: juveniles had an active predatory lifestyle in a
472 coastal environment, while old adults adopted a more filter-feeding diet in more pelagic and
473 anoxic waters. Our hypothesis is that mesosaurs exploited different food sources during their
474 lifetime, but further study of the Irati-Whitehill Sea fauna will be necessary to truly test this.

475

495
496
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643

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.
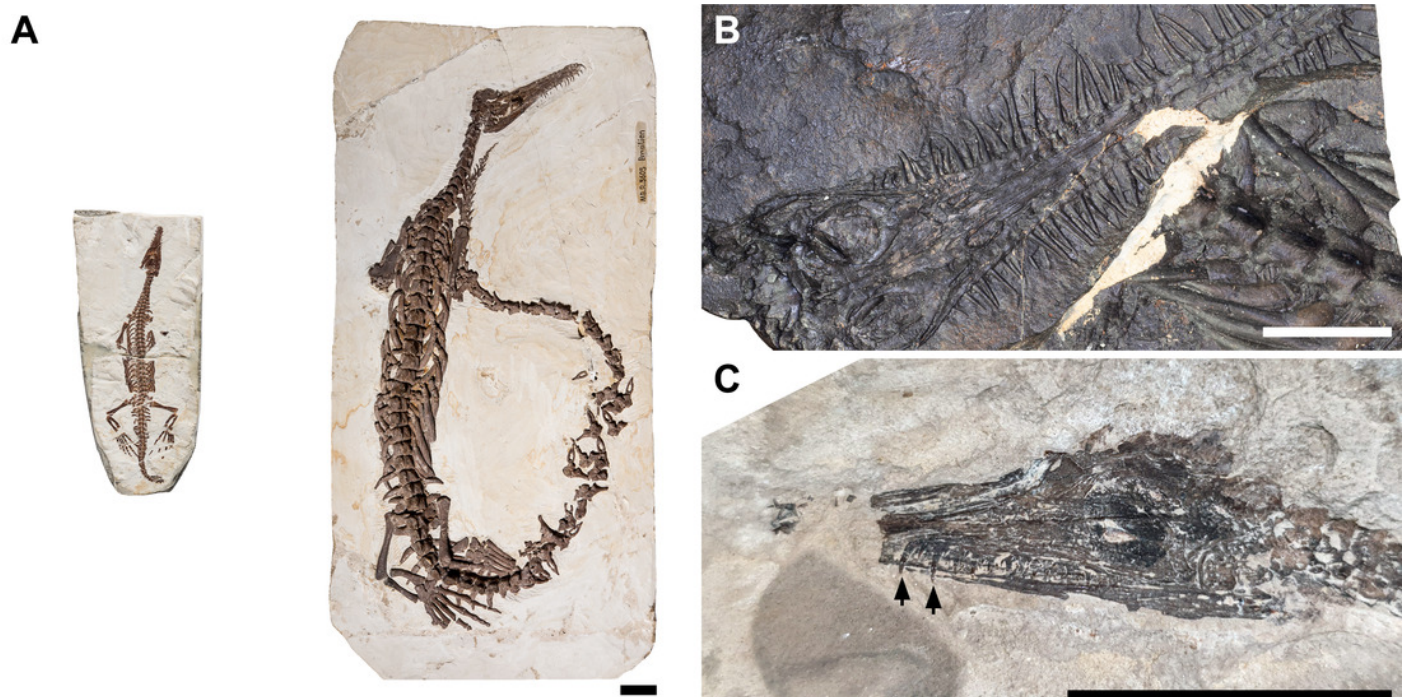
Figure 2

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

Logged scale.

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.
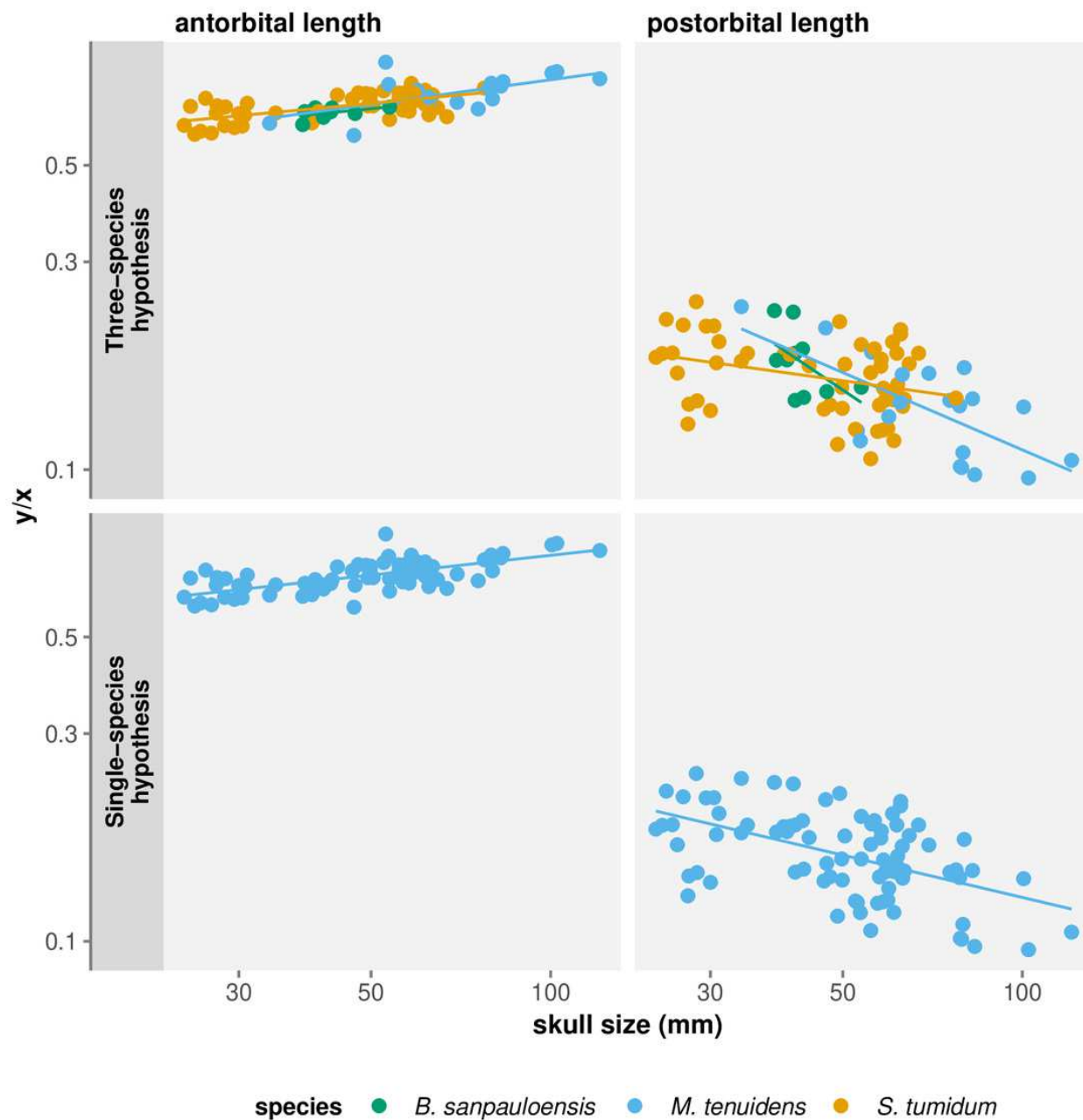
Logged scale.

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.
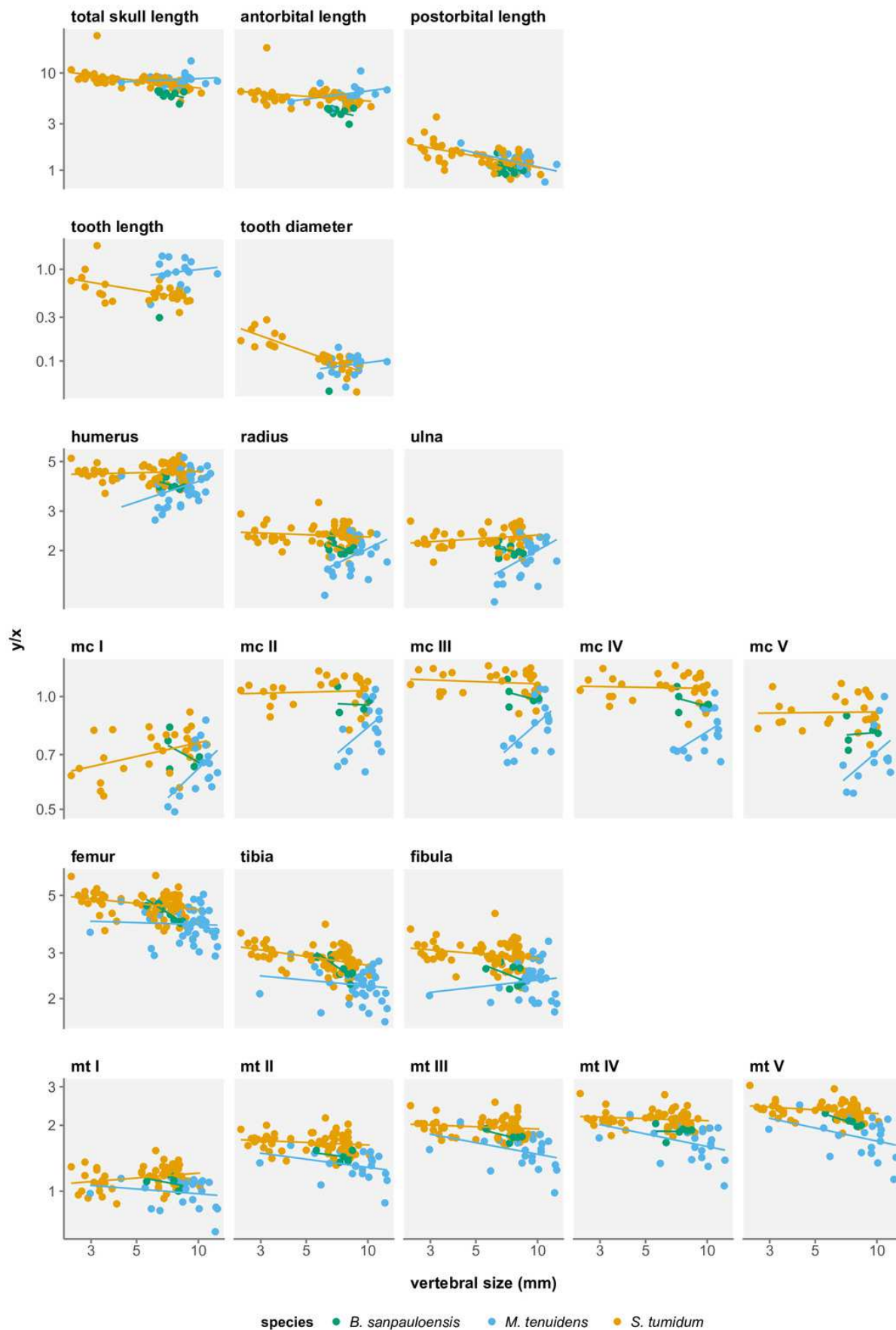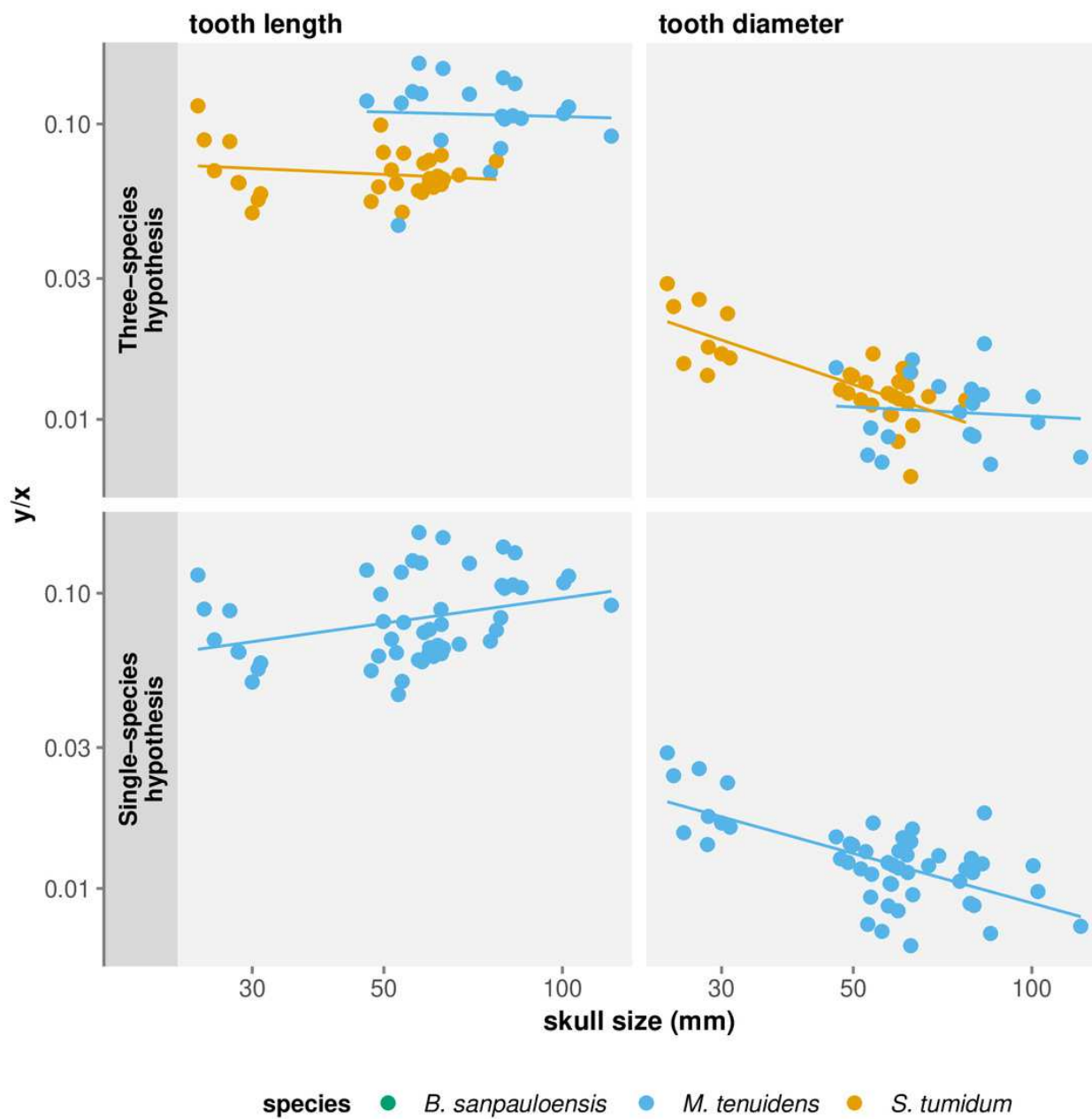
Logged scale.

Figure 5

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

Logged scale.
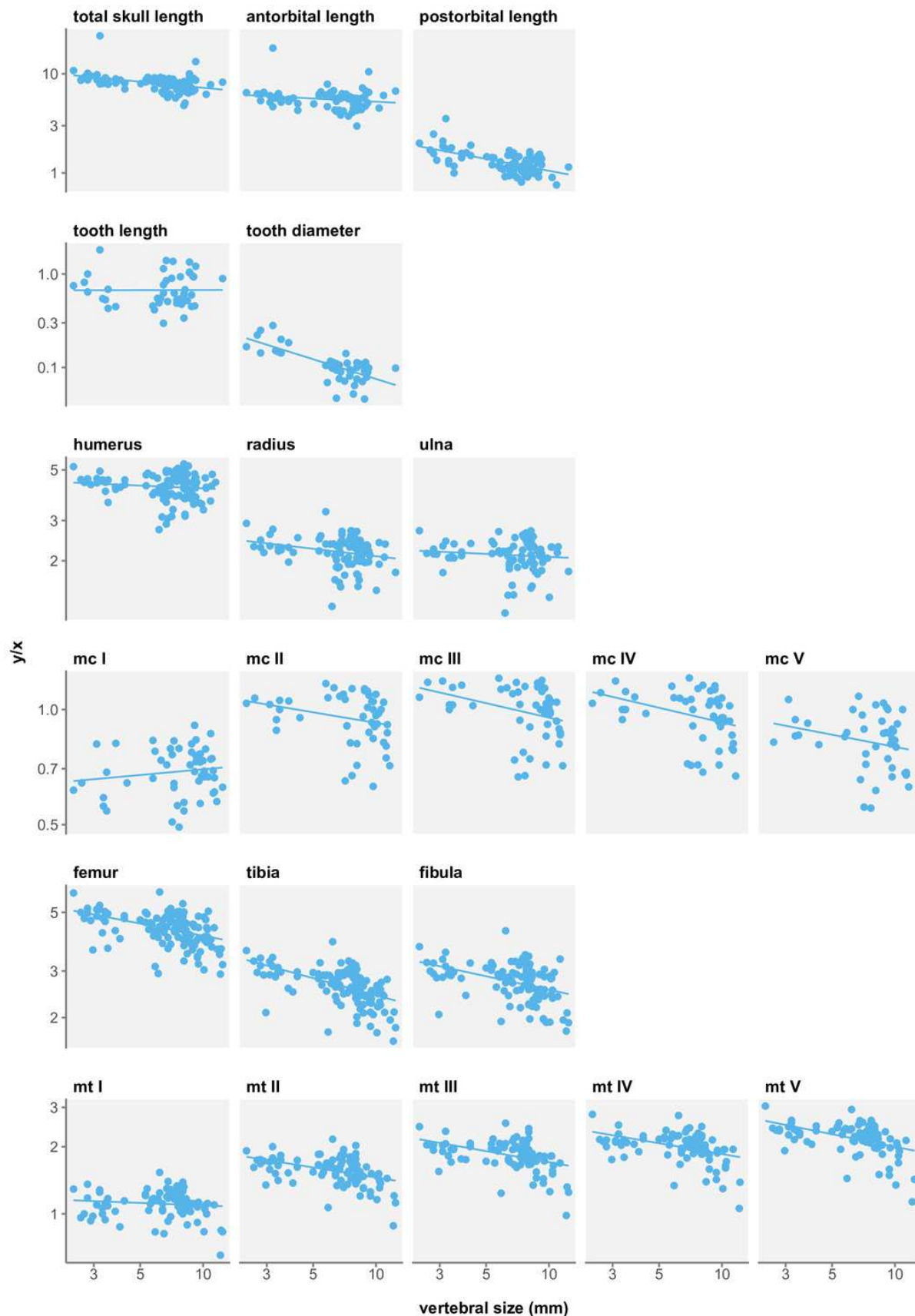
Figure 6

Size distribution of vertebral size per geological facies under the single-species hypothesis

Facies are organized top to bottom along a gradient of depth as depicted to the right, and following the deposition models from Xavier et al. (2018) and Ng et al. (2019). The energy level gradient on the right corresponds to grain size in the sediment. There is a clear overrepresentation of juveniles in limestone, as well as an overrepresentation of large specimens in black shale.
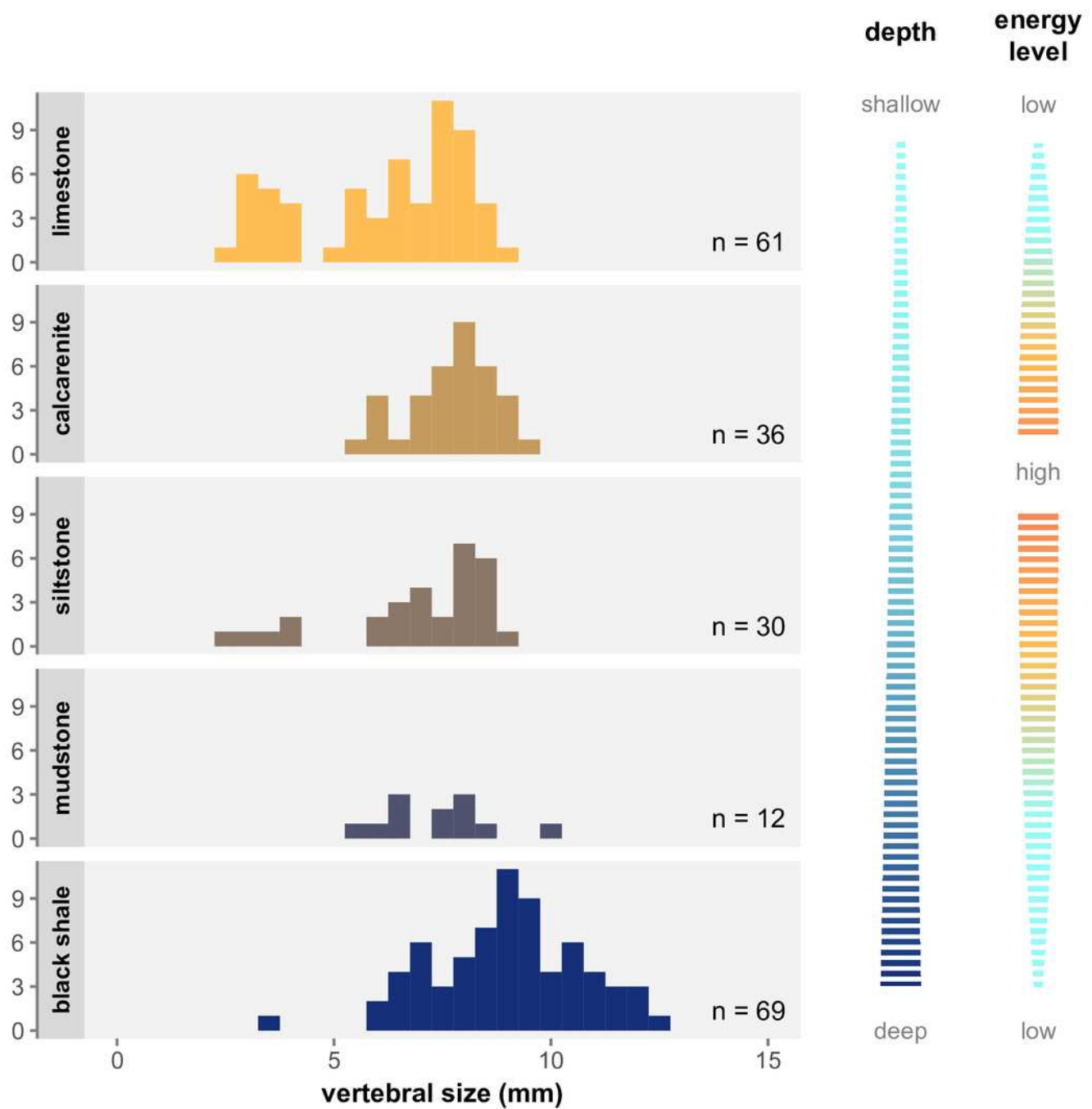
Figure 7

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

Small/juvenile specimens are notably overrepresented in the "*S. tumidum*" group, whereas large individuals are only represented in the *M. tenuidens* group.
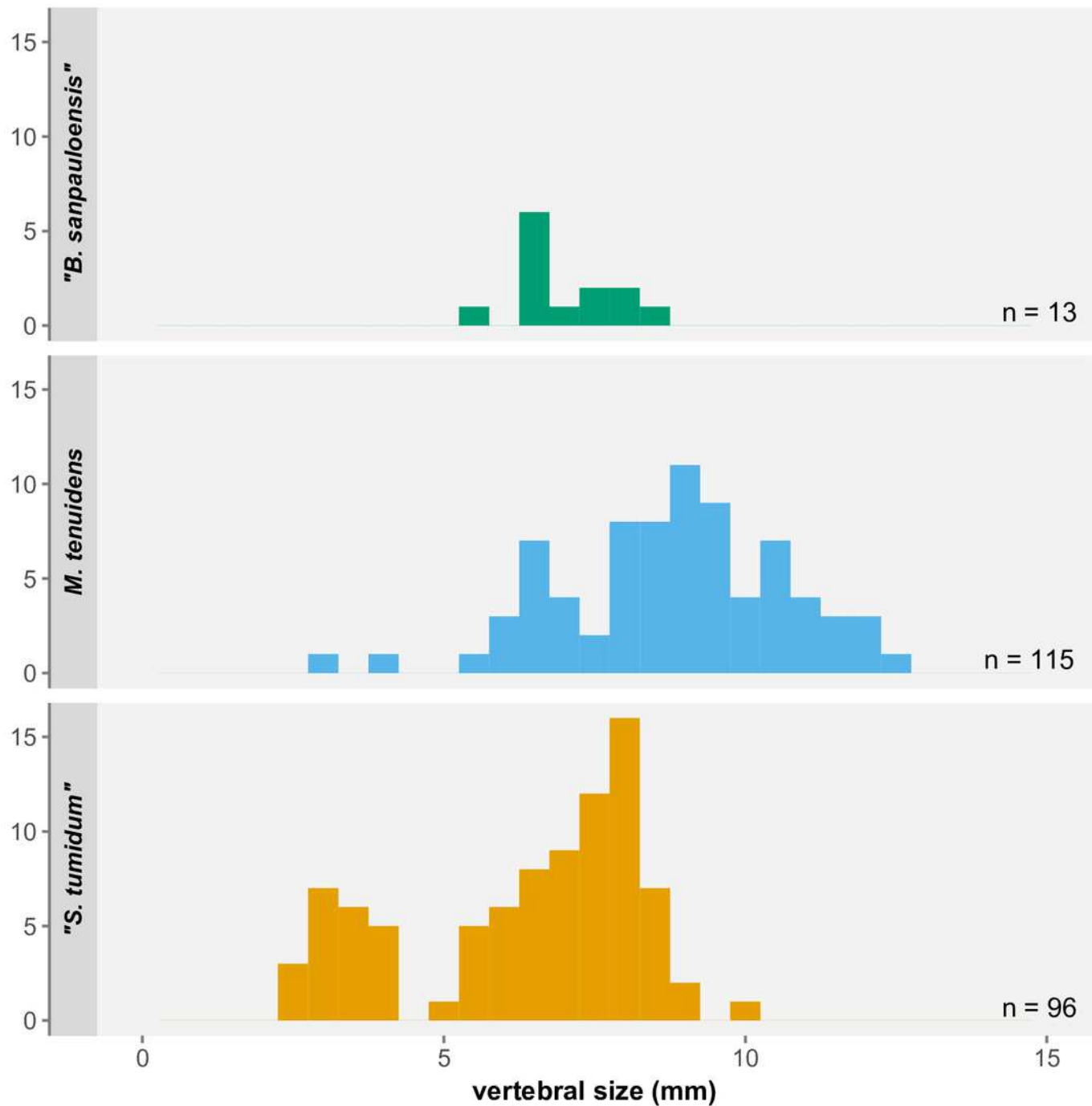
Table 1(on next page)

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

1   **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**

2
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Table 2(on next page)

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

1 **Table 2.** Allometry coefficients of logged tooth and skull measurements with respect to total
2 skull length.
3

	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**

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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

1   **Table 3**. Allometry coefficient of logged size ratios for long bone lengths.
2   **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	-	-	-	-

3
4   **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

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7 **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**

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9 **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**

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Table 4(on next page)

ANOVA results for the effect of species on measurements

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

2

	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

3