



A case study of developmental palaeontology in *Stereosternum tumidum* (Mesosauridae, Parareptilia)

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Abstract. Ontogenetic series of extinct taxa are rare. However, if preserved, fossil embryos and juveniles can provide evidence of developmental plasticity as related to ecological specialization. Here, we describe articulated and isolated juvenile material found in close association with an adult mesosaurid *Stereosternum tumidum* (MB.R.2089) from Lower Permian sediments in Brazil, housed in the collection of the Museum für Naturkunde Berlin. Stylopodial, zeugopodial, and autopodial elements are not yet completely ossified in the juveniles, as indicated by compression artifacts on the surface of the bone. These correspond to internal ossification processes, which have been demonstrated in other aquatic taxa. Quantitative analysis of measurements in juvenile and adult material reveals differing growth rates between limb elements: hind limb zeugopodia, which are massive and elongate in the adult as needed for propulsion, are already comparatively larger in the juvenile than the humeri, femora, and also the zeugopodia of the forelimb. This pattern differs from that seen in another extinct aquatic reptile, *Hovasaurus boulei*. Nevertheless, we attribute the accelerated growth rate or earlier onset of ossification to be a potential developmental pathway generating limb element variation in the adult present in 280 million year old mesosaurs, which are known for their fully aquatic lifestyle, in which the hind limbs play a more prominent role than the forelimbs.

able insight into the life history of extinct taxa, as well as evolutionary trajectories. To date, ossification sequences in fossils are available for some “fish” (Cloutier, 2010), temnospondyl and lepospondyl amphibians (Fröbisch, 2008; Fröbisch et al., 2010, 2015), “younginiforms” (sensu Bickelmann et al., 2009) (Currie, 1981; Caldwell, 2002), mosasaurs (Caldwell, 2002), sauropterygians (Hugi and Scheyer, 2012), ichthyosaurs (Caldwell, 1997), sauropsids (Delfino and Sánchez-Villagra, 2010) and mammals (Sánchez-Villagra, 2010). Most of this information is derived from secondarily aquatic taxa, which is the result of a taphonomic bias (Fröbisch et al., 2010). A notable lack of published developmental data for early amniote taxa makes each incidence a valuable contribution to our knowledge of the patterns. Gaining a comprehensive picture of changes in development and growth in extinct (fossil) taxa in addition to what we know about development in modern animals, as approached in this and similar studies, contributes to our understanding of evolution, developmental trajectories, life history strategies, and more (Fröbisch et al., 2010).

Mesosauridae (Reptilia: Parareptilia) is an extinct secondarily aquatic group from the Paleozoic; notably, their fossil record also includes ontogenetic data (Rieppel, 1993; Piñeiro et al., 2012a). The clade consists of the three monospecific genera *Mesosaurus tenuidens*, *Stereosternum tumidum*, and *Brazilosaurus sanpauloensis* from Lower Permian localities in Brazil and southern Africa (Oelofsen and Araújo, 1983, 1987). Their elongate skulls, slender teeth, paddle-like limbs, and thickened (pachyostotic) trunk ribs are indicative of a secondarily fully aquatic lifestyle and distinguish mesosaurs from all other Paleozoic amniotes (Modesto, 2006). Recent studies suggest that mesosaurs, or at least *Mesosaurus*, were

1 Introduction

The study of fossilized ontogenies is largely confined to post-natal stages with ossified skeletal elements, due to preservational (taphonomic) factors. If preserved, they provide valu-

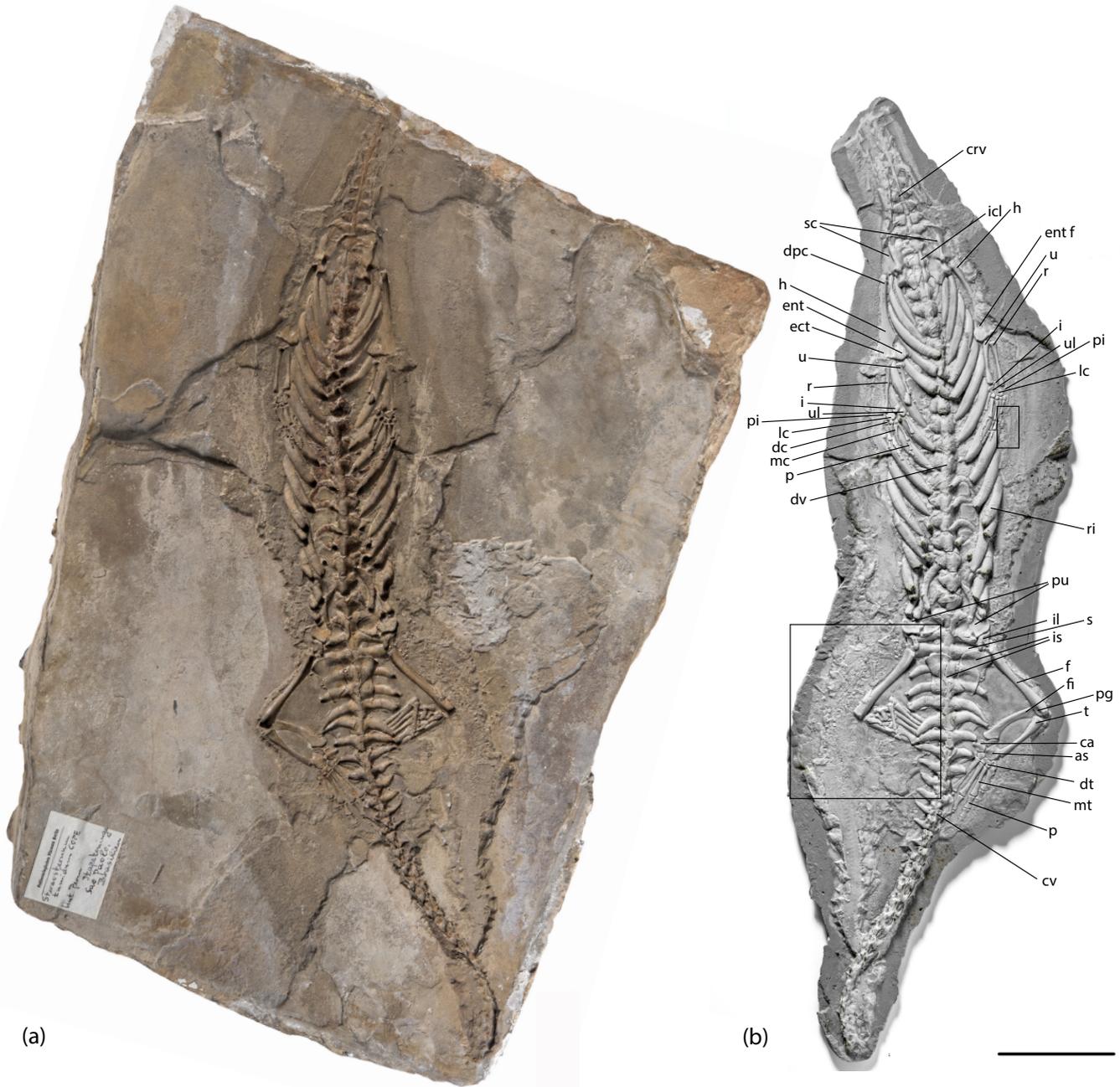


Figure 1. Overview photographs of rock slab (MB.R.2089.A, **a**) and latex cast (MB.R.2089.B, **b**) of *Stereosternum tumidum*. For detail (boxes) see Fig. 2. Scale bar equals 50 mm. For abbreviations see Material and Methods section.

slow swimmers living in shallow lagoon-like waters, possibly filter-feeding on pygocephalomorph crustaceans (Piñeiro et al., 2012b; Villamil et al., 2016). Hypothesized viviparity in *Mesosaurus* is another potential indicator of a fully aquatic lifestyle (Piñeiro et al., 2012a). Most recent studies suggest mesosaurs group basally within parareptiles; a small amniote clade that originated in the Late Carboniferous (Tsuji and Müller, 2009; Modesto et al., 2015; though see contradictory hypothesis of Laurin and Piñeiro, 2017). Evolutionary

novelties in this clade include impedance-matching hearing in nycteroleterids (Müller and Tsuji, 2007), caudal regeneration in mesosaurs (Delfino and Sánchez-Villagra, 2010), derived feeding mechanisms and bipedality in bolosaurids (Reisz et al., 2007; Berman et al., 2000), and secondarily aquatic lifestyles as well as (ovo)viviparity in mesosaurids (Modesto, 2006; Piñeiro et al., 2012a), all of which occurred in parareptiles as early as the Early Permian. The first occurrence of congenital scoliosis is also reported from mem-

bers of this clade (Szczygielski et al., 2017). Fortunately, there is some ontogenetic data available for parareptiles, such as in the pareiasaurs *Elginia* (Spencer and Lee, 2000) and *Deltavjatia* (Tsuji, 2013), procolophonids (Cisneros, 2008), and *Mesosaurus* (Rieppel, 1993; Piñeiro et al., 2012a).

Here, we describe a remarkable specimen containing an adult *Stereosternum tumidum* next to juvenile material from Lower Permian sediments in Brazil; a specimen long neglected in the fossil collections at the Museum für Naturkunde Berlin. Parent–hatchling associations in mesosaurs have thus far only been described for the sister-taxon *Mesosaurus* (Piñeiro et al., 2012a). The present finding of differing developmental stages allows for the establishment of baseline ossification sequences and growth rates. This study proposes that they relate to the adaptation of mesosaur limbs to a fully aquatic lifestyle.

2 Material and Methods

Specimen MB.R.2089 consists of a natural mold (MB.R.2089.A), preserving an articulated adult postcranium and the articulated postcranial elements of a juvenile, as well as an isolated long bone from another juvenile (Fig. 1). A latex cast (MB.R.2089.B) was prepared at the Museum für Naturkunde Berlin in 2013. In this, the adult is visible in ventral aspect. It was not until the latex cast was made that the juvenile skeleton was recognized as such, and the majority of the anatomical observations of this smaller skeleton were made directly from the cast. A historical label applied to the specimen assigned the adult to the taxon *Stereosternum tumidum*, an identification we verify using the anatomical features listed below. The close proximity of the juvenile material to the adult on the rock slab strongly suggests kinship (Piñeiro et al., 2012a).

Systematic Paleontology

Parareptilia Olson, 1947

Mesosauridae Baur, 1889

Stereosternum tumidum Cope, 1885

Type specimen: MB.R.2089

Locality and horizon: Itapetininga, Sao Paulo, Brazil. Passa Dois Group. Irati Formation. Lower Permian. Artinskian. Permian 2.

3 Results

3.1 Description of the adult

The adult consists of a well-preserved and articulated postcranium including presacral, sacral, and approximately 23 caudal vertebrae, cervical and abdominal ribs (generally

5mm thick in the midshaft region), as well as both complete fore- and hind limbs with pectoral and pelvic girdle (Fig. 1). The skull is absent (Fig. 1). All observable aspects of the postcranial anatomy conform to that of *Stereosternum tumidum*, as described by Modesto (1999, 2010). Specifically, the unfused intermedium and lateral centrale, the presence of a pisiform, and a diamond-shaped interclavicle characterize this specimen as *Stereosternum* rather than *Mesosaurus* (Fig. 1; Modesto, 1999, 2010). The fore- and hind limbs are elongate, characteristic for the aquatic lifestyle proposed for mesosaurs (Modesto, 2006; Piñeiro et al., 2012a, b; Villamil et al., 2016). Size and appearances of the fore- and hind limb stylopodia are similar, although the femora are slightly shorter. The ratio of the midshaft diameter to total length of the femur is around 9.2%, which lies between an earlier erected 11% in *Stereosternum* as compared to around 8% for *Mesosaurus* (Modesto, 1999, 2010). Zeugopodial and autopodial elements of the hind limbs are wider in the midshaft region and the proximal epiphyses compared to the ones in the forelimbs (Table 1). All limb measurements are listed in Table 1.

3.2 Description of the juvenile material

The juvenile material preserves one mostly complete individual and an isolated long bone element. Although there is considerable intraspecific variation in limb element length and shape in sub-adult mesosaurs (Rossmann and Maisch, 1999), we believe the isolated element belonging to a second individual of *Stereosternum* is most likely a femur based on size and appearance of the element compared to that of the mainly complete individual (Fig. 2a; Table 1).

The almost complete individual consists of elements of the postcranium, including vertebral column, ribs, gastralia, and fore- and hind limbs (Fig. 2b). The skull is not visible; it may be present in the rock in an underlying layer, or may have been separated from the postcranial on the missing counterpart (Fig. 2b). Body size, if measured from the approximate position of last cervical to first sacral rib, is approximately 30% of the size of the adult (Table 1). The taphonomic orientation of the skeleton cannot be attributed, as the elements are typically in close association but not completely articulated, but the axis of the skeleton is oriented in the same direction as in the adult and is “stretched out”, rather than curled into a foetal position (Fig. 2b). The mostly complete juvenile is located close to the right hind limb of the adult skeleton and does not appear to have been greatly disturbed pre or post burial, in contrast to the isolated femur, which lies close to the adult left forelimb. Although the skeletal elements are not completely articulated as can be seen in the adult, they are very closely associated and in their approximate anatomical positions.

Cervical vertebrae, located proximal to the forelimbs, are clearly diagnosable. However, dorsal and caudal vertebrae are distinguishable due only to their location in situ (Fig. 2b).

Table 1. Limb measurements of juvenile and adult material (mm). Body length is measured from the caudal end of the posteriormost cervical vertebra to the approximate position of the first sacral rib. Abbreviations: d: distal; Epiph: Epiphyses; p: proximal.

	Juvenile		Adult	
	Left	Right	Left	Right
Body length	50		185	
Humerus				
Length	11.5	11.5	37	37
Width (shaft)	2.5	2.5	3.5	3.5
Width (epiph; p, d)	3.5,3.5	3.5,3.5	3.5,14	3.5,-
Radius				
Length	7 (indet. zeugopod)		20.5	20
Width (shaft)	1.5		1.5	1.5
Width (epiph; p, d)	2.5, 2.5		3,3	3,2.5
Ulna				
Length	-	-	-	20
Width (shaft)	-	-	-	2
Width (epiph; p, d)	-	-	3,4	3.5,4
Metacarpals (I–V)				
Length	-	-	7,9,10,9.5,8	6,9,9.5,9,8
Width (shaft)	-	-	2,1.5,1.5,1.5,1.5	1,1.5,1.5,1.5,1.5
Width (epiph; p)	-	-	3,2,2,1.5,1.5	1.5,2,2,2,1.5
Width (epiph; d)	-	-	2.5,2.5,2,2,2	1.5,1.5,2,2,1.5
Femur				
Length	13	13	38	38
Length		12.5 (isolated)		
Width (shaft)	2.5	2.5	3.5	3.5
Width (shaft)		2.5 (isolated)		
Width (epiph; p, d)	-,3.5	-,3.5	5.5,6	6.5,6
Width (epiph; p, d)		3.5,3.5 (Isolated)		
Tibia				
Length	9 (indet. zeugopod)		-	24
Width (shaft)	2.5		-	2.5
Width (epiph; p, d)	4,4		-	6,3.5
Fibula				
Length	-	-	-	24
Width (shaft)	-	-	-	4
Width (epiph; p, d)	-	-	-	5.5,6
Metatarsals (I–V)				
Length	4.5,4.5 (II,III)	4.5 (indet.)	-	10,14,17,19,-
Width (shaft)	2,2	2	-	2.5,2,2,2,-
Width (epiph; p)	-	-	-	4,3.5,3.5,3.5,-
Width (epiph; d)	-	-	-	5,3.5,3.5,3.5,-

While cervical vertebrae are fully developed, the neural arch and pleurocentra of both dorsal and caudal vertebrae are not yet fully fused and are preserved in two adjacent lines, though the lack of definitive anatomy in these bones makes

it difficult to identify any individual element (Fig. 2b). Concerning length, the small skeleton retains what appears to be an almost complete tail, and at least 25 vertebrae can be recognized (Fig. 2b). Further caudally, vertebral elements are

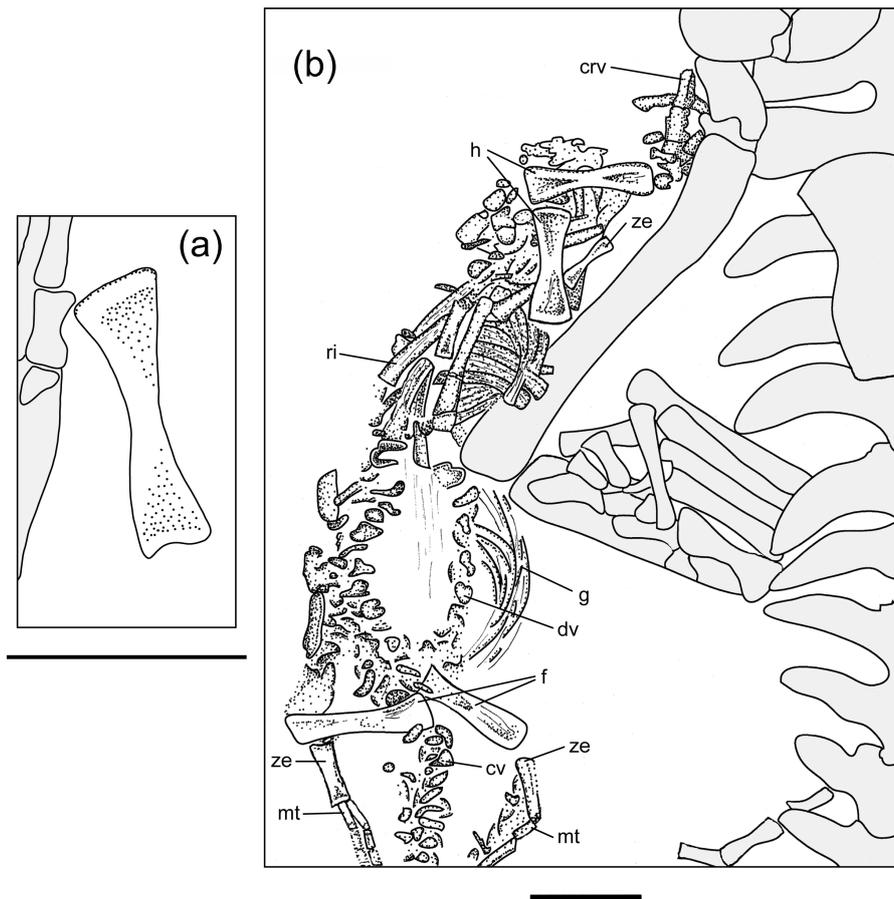


Figure 2. Detailed stippling of postcranium of an isolated femur (a) and the mostly articulated juvenile (b), based on the latex cast (MB.R.2089.B). Adult specimen is in grey. Scale bars both equal 10 mm. For abbreviations see Material and Methods section.

more difficult to discern, yet there appears to be the continuation of the outline of the soft parts of the tail with occasional bone fragments visible. Adult *Mesosaurus* and *Brazilosaurus* typically have more than 60 caudal vertebrae (Modesto, 2010), so it is reasonable to conjecture that the caudal vertebrae in this juvenile *Stereosternum* numbered more than what can be directly observed here. The ribs are already diagnostically thickened (pachyostotic; most are 2 mm thick in the midshaft) in the juvenile and are scattered throughout the thoracic region (Fig. 2b). Slender gastralia lie in the abdominal region (Fig. 2b).

Identifiable juvenile limb elements preserved in MB.R.2089 include two humeri, three femora, one indeterminate forelimb zeugopodial element, one indeterminate hind limb zeugopodial element, and three metatarsals. Due to the extreme delicacy of the juvenile skeleton, other limb elements may be preserved but obscured under those we can identify, or not differentiated enough from the “matrix” to definitively name. In the forelimb, both humeri do not exhibit characteristics such as the deltopectoral crest, ectepicondylar groove, entepicondylar foramen, and an enlarged

entepicondyle that are present in the adult (Figs. 1, 2b). Instead, they retain metaphyseal compression and epiphyseal ridges (Fig. 2b) (sensu Hugi and Scheyer, 2012), indicating low maturity similar to what is seen in pachypleurosaur juveniles (Hugi and Scheyer, 2012). In the hind limbs, all femora show reduced ontogenetic compression (sensu Hugi and Scheyer, 2012) compared with the humeri, yet also lack adult phenotypic features such as patellar groove and muscle attachment sites for trochanter (Fig. 2a, b). One of either the fibula or tibia can be identified per side (Fig. 2b, Table 1). Due to the close association of the zeugopod and the preserved metatarsals, we hypothesize that tarsals are not yet ossified (Fig. 2b), a condition also seen in other juvenile mesosaur skeletons (i.e. BSP 1979, fig. 4 from Rossman and Maisch, 1999). Two faint metatarsals can be identified in the latex cast (MB.R.2089.B). According to their location, we think these might be the middle ones (II & III; Fig. 2b, Table 1). On the other side, one indeterminate metatarsal is preserved (Fig. 2b, Table 1).

Table 2. Comparison of growth ratios in the limbs of the two distantly related *Stereosternum tumidum* (MB.R.2089; this study) and “youngini-form” *Hovasaurus boulei* (sub-adult MNHN 1908-21-8 and adult SAM 6231; after Currie, 1981, table 1).

Genus	Length	Juvenile	Adult	% of adult value
<i>Stereosternum</i>	Humerus	11.5, 11.5	37, 37	31.1
	Forelimb zeugopod	7	20.5, 20, 20	35
	Femur	13, 13, 12.5	38, 38	34.2
	Hind limb zeugopod	9	24, 24	37.5
	Metatarsals II & III	4.5, 4.5	14, 17	32.1, 26.5
<i>Hovasaurus</i>	Humerus	11	36	30.6
	Radius	7.9	21.6	36.5
	Ulna	7.2	21	34.3
	Femur	13.5	39	34.6
	Tibia	11.3	34	33.2
	Fibula	10.5	31	33.9
	Metatarsal V	5.1	17.4	29.3

3.3 Growth Rates

We calculated growth rates using limb measurements in Table 1. We find that the juvenile hind limb zeugopod, which is longer in the hind limb as compared to the forelimb in the adult, is already slightly larger (37.5% of the adult size) than all other limb elements (ranging from 26.5% in the metatarsal III to 35% in the forelimb zeugopod), indicating a faster growth rate or an earlier onset of ossification (Table 2).

Further, we compared the established growth rates in MB.R.2089 to earlier published limb growth data from another secondarily aquatic reptile, *Hovasaurus boulei* from the Upper Permian of Madagascar (Currie, 1981). *Hovasaurus* is a “youngini-form” diapsid reptile (sensu Bickelmann et al., 2009), for which, fortunately much ontogenetic material is available (Currie, 1981). It also displays enlarged hind limbs compared to the forelimbs, which are potentially useful when swimming (Currie, 1981). Comparing the ossification of limb elements in sub-adults and adults of *Stereosternum* and *Hovasaurus*, we find that the humerus, forelimb zeugopod, femur, and metatarsals show growth rates or onsets of ossification to be comparable (Table 2). However, the growth rate of the hind limb zeugopod is higher in *Stereosternum* compared to *Hovasaurus* (Table 2).

4 Discussion

The secondarily fully aquatic parareptilian clade Mesosauridae is renowned for an exceptional fossil record including the preservation of multiple growth stages, tail regeneration, along with the earliest report of (ovo)viviparity in amniotes (Rieppel, 1993; Delfino and Sánchez-Villagra, 2010; Piñeiro et al., 2012a). Here, we describe a congregation of adult and sub-adult (or potentially hatchling) material of the taxon *Stereosternum tumidum*. Parent-hatchling associations have

been previously reported in mesosaurs only in *Mesosaurus tenuidens* (Piñeiro et al., 2012a).

Ontogenetic series of fossils provide valuable insights into life history traits of organisms (Fröbisch et al., 2010). Based on the described juvenile material of *Stereosternum* we can make two observations:

1. *Ossification sequences.* Generally in tetrapods, stylopod ossification starts before that of the zeugopod and autopod, and mesopodial (wrist and ankle) ossification is significantly delayed in relation to all other limb elements (Rieppel, 1993). In the articulated juvenile mesosaur, the mesopodial elements are not yet ossified (Fig. 2b). In another isolated juvenile, attributed to *Stereosternum* (NHMUK R3521), the astragalus is ossified but not the calcaneum. Therefore, *Stereosternum* apparently follows the same ossification pattern in their mesopodia as the sister-taxon *Mesosaurus* (Rieppel, 1993).
2. *Growth rates.* Mesosaurs display aquatic specializations in their limbs, with enlarged zeugo- and autopodia in the hind limbs compared to those of the forelimbs (Rossmann and Maisch, 1999). This size variation is also present in the adult in MB.R.2089 (Fig. 1, Table 1).

First, taking the juvenile material into account, we calculated growth rates for various limb elements in *Stereosternum tumidum* (Table 2). Results show that the hind limb zeugopodia are more highly ossified, as demonstrated by the greater longitudinal length of the elements (37.5%) of the sub-adult as compared to the humeri, femora, forelimb zeugopodia, and metatarsals (ranging from 26.5 to 35%; Table 2). We associate this accelerated growth rate or earlier onset of ossification to the more robust morphology of the adult tibiae and fibulae (see epiphyseal widths in Table 1). This pattern is potentially related to stronger hind limb bones needed for propulsion during swimming. Such a phenomenon has

been demonstrated for secondarily aquatic skinks (Hugi et al., 2012). Microanatomical analyses would help shed light on its internal strength parameters, such as bone density and cortical thickness (Houssaye et al., 2016), but are not possible with the present natural mold. Unfortunately, because no metacarpals are preserved, no predictions can be made about such a pattern in the autopodia.

Secondly, in order to test for potential heterochronies, we established limb growth ratios for another fossil reptile, *Hovasaurus boulei* from the Upper Permian of Madagascar (Currie, 1981). Limb lengths and proportions in adult *Hovasaurus* are in most respects very similar to those of *Stereosternum* (MB.R.2089). However; in *Hovasaurus*, the hind limb zeugopod is not only substantially longer than that of the forelimb in this taxon, it is also longer than the hindlimb zeugopod of *Stereosternum* (Currie, 1981). In fact, growth rates of the humeri, femora, forelimb zeugopodia, and metatarsals in *Stereosternum* and *Hovasaurus* are more or less similar (Table 2). However, growth rates for the hind limb zeugopodia show a significant difference: in *Stereosternum* the juvenile elements have already reached 37.5% of the adult length, in contrast to only 33.2–33.9% in *Hovasaurus* (Table 2). This accelerated growth rate or earlier onset of ossification in *Stereosternum* is surprising given that hind limb zeugopodia in adult *Hovasaurus* are even longer than in adult *Stereosternum*. Still, we suggest that this finding of skeletal heterochrony is related to the aquatic lifestyle in Mesosauridae. In other extinct marine reptiles, hyperdactyly and hyperphalangy were other adaptations to a fully aquatic lifestyle (Caldwell, 2002). The relevant pattern in *Hovasaurus* remains to be characterized.

Heterochronies (evolutionary shifts in developmental timing) are an important tool for morphological change in the phenotype; e.g. limb allometries result from differences in the growth patterns of skeletal elements (Richardson, 1999). In *Stereosternum*, the advanced growth rate or earlier onset of ossification in hind limb zeugopodia as compared to stylopodia and forelimb zeugopodia, can be linked with longer zeugopodia and autopodia in the adult and are secondarily related to a fully aquatic lifestyle (Rossmann and Maisch, 1999). The autopodia in MB.R.2089 are not well preserved and thus can not be evaluated here. This phenomenon, in which selection for an adult trait produces crucial changes early in ontogeny, is called developmental penetrance (Richardson, 1999). In fact, differences in the phenotype are generated at a variety of ontogenetic stages (Richardson, 1999). Other mechanisms include changes at the cartilaginous level, e.g. in fossorial talpid moles in which the cartilage anlage is already a miniature of the adult phenotype including its distinct ecomorphological specializations, as related to their extreme digging behaviour (Bickelmann et al., 2014). Transcriptional heterochrony (changes in the spatial and temporal expression of developmental genes during ontogeny) is another developmental mechanism leading to morphological variation at the molecular level (Richardson et al., 2009; Bickelmann et al., 2012). Here, only subtle changes are needed to produce a significantly different phenotype (Richardson, 1999). However, these are difficult, if not impossible, to trace in the fossil record.

Our study shows evidence that differential growth rates and skeletal heterochrony are developmental trajectories that could potentially account for phenotypic variation in adult limb morphology, in this case related to adaptation to a fully aquatic lifestyle in an extinct tetrapod clade as early as 290 mya.

Data availability. No data sets were used in this article.

Appendix A: Anatomical abbreviations

as	astragalus
ca	calcaneum
crv	cervical vertebra
cv	caudal vertebra
dc	distal carpals
dpc	deltpectoral crest
dt	distal tarsals
dv	dorsal vertebra
ect	ectepicondyle
ent	entepicondyle
ent f	entepicondylar foramen
f	femur
fi	fibula
g	gastralia
h	humerus
i	intermedium
icl	interclavicle
il	ilium
is	ischium
lc	lateral centrale
mc	metacarpal
mt	metatarsal
p	phalanx
pg	patellar groove
pi	pisiform
pu	pubis
r	radius
ri	rib
s	sacral rib
sc	scapulacoracoid
t	tibia
u	ulna
ul	ulnare
ze	zeugopodial element

Appendix B: Institutional abbreviations

MB	Museum für Naturkunde Berlin, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	Natural History Museum, London, UK
SAM	South African Museum, Cape Town, South Africa

Author contributions. CB and LAT contributed equally to the study design, data analysis, and writing of the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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