



A large-bodied silesaurid from the Lifua Member of the Manda beds (Middle Triassic) of Tanzania and its implications for body-size evolution in Dinosauromorpha[☆]

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ABSTRACT

Many dinosaur lineages were characterised by wide ranges of body-size, ranging from taxa that were <1 m in length to the largest of all terrestrial vertebrates. On the other hand, the closest relatives of dinosaurs, the non-dinosaurian dinosauriforms, such as *Marasuchus* and *lagerpetids*, were small-bodied animals with little variation in body-size. Here, we describe a partial femur of an unexpectedly large-bodied silesaurid (non-dinosaurian dinosauriform) from the Lifua Member of the Manda beds (?late Anisian) from southwestern Tanzania. This specimen (NHMUK R16303) is estimated to have had a femoral length of approximately 345 mm, which exceeds that of many Triassic and Lower Jurassic dinosaurs, and is either a large individual of the contemporary *Asilisaurus kongwe* or represents a new and otherwise unknown silesaurid taxon. In either case, it shows that body-size increases were more prevalent among early dinosauriforms than realised previously. Moreover, silesaurid size increase occurred in parallel with that in early dinosaurs, alongside the convergent acquisition of other features related to locomotion and herbivory. However, Late Triassic faunas including large-bodied sauropodomorph and theropod dinosaurs lack similarly-sized non-dinosaurian dinosauriforms, whereas the Lifua Member fauna includes both a large silesaurid and the early ?dinosaur *Nyasasaurus*, which overlapped in size.

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1. Introduction

One of the most conspicuous features of many non-avian dinosaurs is their large body-size, with modal body masses for this group of approximately 1000 kg (Farlow et al., 1995; O'Gorman and Hone, 2012). Nevertheless, the first dinosaurs were relatively small animals, ranging in length from 1 to 6 m, and it was only subsequently that various lineages independently acquired large size (Carrano, 2006; Irmis, 2011; O'Gorman and Hone, 2012; Sookias et al., 2012; Turner and Nesbitt, 2013). Increased body-size is often cited as a key adaptation underpinning dinosaur success due to the numerous benefits it confers, including increased range size, behavioural and physiological buffering against adverse local environmental conditions, predator avoidance, digestive efficiency, etc. (Sander et al., 2011; O'Gorman and Hone, 2012). By contrast, other dinosauriform taxa, such as *lagerpetids*, *Marasuchus*, and early diverging silesaurids, retained the plesiomorphic condition of small body-size with little variation from the hypothesised size of the

last common ancestor of crocodylians and birds (Irmis, 2011; Langer et al., 2013; Turner and Nesbitt, 2013).

Silesauridae is a recently recognised, paucispecific clade that is either the sister-group to Dinosauria (e.g., Irmis et al., 2007; Nesbitt et al., 2009; Brusatte et al., 2010; Langer et al., 2010; Nesbitt et al., 2010; Nesbitt, 2011; Langer et al., 2013), the sister-group of *Nyasasaurus* + Dinosauria (Nesbitt et al., 2013a), a paraphyletic group just outside Dinosauria (Ezcurra, 2006), or a paraphyletic group including sister-taxa to both Dinosauria and Ornithischia (Langer and Ferigolo, 2013). The earliest known silesaurids are from the Middle Triassic (Anisian) of eastern and central Africa (*Asilisaurus* and *Lutungutali*; Nesbitt et al., 2010; Peacock et al., 2013) and the clade persisted into the mid-Norian (*Eucoelophysis*) and possibly the ?Rhaetian (*Agnosphitys*, if a silesaurid; see Langer et al., 2013), and extended its geographic distribution into northern Africa, the Americas, and Europe through this interval (Langer et al., 2013). Most silesaurids appear to have been omnivorous or herbivorous (Dzik, 2003; Nesbitt et al., 2010; Langer and Ferigolo, 2013), although the basal-most member of the clade, *Lewisuchus*, may have been a carnivore (Romer, 1972; Nesbitt et al., 2010). *Silesaurus* was likely quadrupedal (Dzik, 2003), though facultative bipedality has also been suggested (Piechowski and Dzik, 2010), but silesaurid locomotion has yet to be studied in detail and the stance of other taxa has not been addressed. On the basis of current phylogenies,

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many silesaurid characteristics associated with omnivory/herbivory, quadrupedality, and growth strategies evolved in parallel with those in early dinosaurs (Nesbitt et al., 2010; Langer et al., 2013).

Reported femoral lengths of silesaurids range from 87 to 200 mm (Table 1) representing individuals with estimated maximum body lengths of up to approximately 2–3 m (Dzik, 2003; Nesbitt et al., 2010). Here, we report a partial femur of a potentially new silesaurid taxon from the Middle Triassic (?late Anisian) Lifua Member of the Manda beds of Tanzania. This specimen indicates that not only did silesaurids reach considerably larger body-sizes than known previously, but that they also exceeded many early dinosaurs in size. We discuss the implications that this specimen has for understanding dinosauromorph body-size evolution.

2. Material and methods

2.1. Specimen history

NHMUK R16303 was collected in 1963 during a joint Natural History Museum (then British Museum [Natural History])/University of London expedition to what was Tanganyika Territory, and is now southwestern Tanzania (see Attridge et al., 1964). This expedition collected abundant material from the Middle Triassic mudstones and sandstones of the Manda beds of the Ruhuhu Basin, including dicynodonts, cynodonts, rhynchosaurs, and archosauriforms, complementing earlier collections made in the region during the 1930s by teams led by G.M. Stockley and F.R. Parrington (e.g., Stockley, 1932; Charig, 1956). The archosauriform material from the 1963 expedition was passed to A.J. Charig for further study, but this work was never completed. Indeed, many specimens from this expedition remain unregistered in the NHMUK collections (P.M.B. and S.J.N., pers. obs.). To date, the only archosaurs reported from this expedition are the often mentioned (e.g., Nesbitt et al., 2013b), but still undescribed, large-headed archosauriform taxon '*Pallisteria augustimentum*' (NHMUK R36620), which Charig (in Appleby et al., 1967) named without diagnosis or description (and is therefore

a nomen nudum), and the ctenosauriscid *Hypselorhachis mirabilis* (NHMUK R16586; Butler et al., 2009). Recent reappraisal of other archosauriform material in the NHMUK has also led to the recognition of a new non-archosaurian archosauriform, *Asperoris mynyama* (Nesbitt et al., 2013c), and the silesaurid femur described herein.

The proximal and distal ends of a right silesaurid femur were recognised during a survey of the 1963 collection by S.J.N. It was part of a collection of fragmentary material associated with the partially in situ specimen of '*Pallisteria*,' which was obtained from field locality U15 (this mixed collection was designated U15/1 in the field: A.J. Charig, unpublished field notes). Nearly all of the collection made from U15/1 belongs to a large archosauriform and these fragments likely represent more skeletal elements of '*Pallisteria*'; no other fragments clearly belong to the silesaurid found at the same locality. The original extent of locality U15 is unknown, but the proximal and distal ends of the silesaurid femur were found in the same canvas bag, are compatible in size, and have identical preservation: this suggests that the two fragments were found close to each other and pertain to the same element. The silesaurid femur has now been registered separately (NHMUK R16303) to avoid confusion with the material assigned to '*Pallisteria*' (NHMUK R36620).

2.2. Size estimation criteria

In order to estimate the complete femoral length of NHMUK R16303, a multivariate linear regression was performed on a dataset including complete femoral lengths (l), maximum proximal femoral widths (w_1), and maximum distal femoral widths (w_2) for a range of Triassic–Lower Jurassic dinosauromorph taxa (see Fig. 1 for measurements). Data were fitted to the following equation:

$$l = a + b_1 w_1 + b_2 w_2$$

where a is a constant and b_1 and b_2 are the respective regression coefficients. The regression was implemented in R (R Core Development

Table 1

Measurements (all in mm) of selected early dinosaur, silesaurid, and basal dinosauromorph taxa used in the multiple regression analysis. Abbreviation: Prox. = proximal.

Taxon	Specimen	Length	Prox. long axis	Distal long axis	Source
<i>Asilisaurus kongwe</i>	NMT RB159	144	28	28	S.J.N., pers. obs.
<i>Asilisaurus kongwe</i>	NMT RB169	74	15	15	S.J.N., pers. obs.
<i>Asilisaurus kongwe</i>	NMT RB171	137	29	28	S.J.N., pers. obs.
<i>Asilisaurus kongwe</i>	NMT RB172	96	18	19	S.J.N., pers. obs.
<i>Chindesaurus bryansmalli</i>	PEFO 10395	265	41	36	S.J.N., pers. obs.
<i>Diodorus scytobrachion</i>	MHNM-ARG 37	92	23	22	Kammerer et al. (2013)
<i>Dromomeron gregorii</i>	TMM 31100-764	60	12	14	S.J.N., pers. obs.
<i>Dromomeron gregorii</i>	TMM 31100-1306	96	21	23	S.J.N., pers. obs.
<i>Dromomeron gregorii</i>	TMM 31100-1308	84	16	16	S.J.N., pers. obs.
<i>Dromomeron gregorii</i>	TMM 31100-464	95	22	20	S.J.N., pers. obs.
<i>Eoraptor lunensis</i>	PVSJ 407	152	28	23	S.J.N., pers. obs.
<i>Herrerasaurus ischigualastensis</i>	PVSJ 373	353	37	72	S.J.N., pers. obs.
<i>Lesothosaurus diagnosticus</i>	NHMUK RU B17	104	19	24	P.M.B., pers. obs.
<i>Marasuchus lilloensis</i>	PVL 3870 (right)	42	6	6	Sereno and Arcucci (1994)
<i>Sacisaurus agudoensis</i>	MCN PV10009/R	87	14	10	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10010/R	92	17	15	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10011/R	97	16	9	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10012/R	102	18	13	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10013/R	99	16	13	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10014/R	97	16	15	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10015/R	103	16	15	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10017/R	110	16	12	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10018/R	89	15	16	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10019/R	93	15	17	Langer and Ferigolo (2013)
<i>Sacisaurus agudoensis</i>	MCN PV10063/R	88	14	17	Langer and Ferigolo (2013)
<i>Silesaurus opolensis</i>	ZPAL AbIII/361	200	35	33	Dzik (2003)
<i>Syntarus kayentakatae</i>	MNA 43688-1	228	39	37	S.J.N., pers. obs.
Unnamed Ntawere taxon	NHCC LB45/46	160	23	28	B.R.P., pers. obs.
Unnamed Otis Chalk taxon	TMM 31100-185	142	21	26	S.J.N., pers. obs.
Unnamed Otis Chalk taxon	TMM 31100-1303	151	25	24	S.J.N., pers. obs.
Unnamed Otis Chalk taxon	TMM 31100-1304	155	25	28	S.J.N., pers. obs.

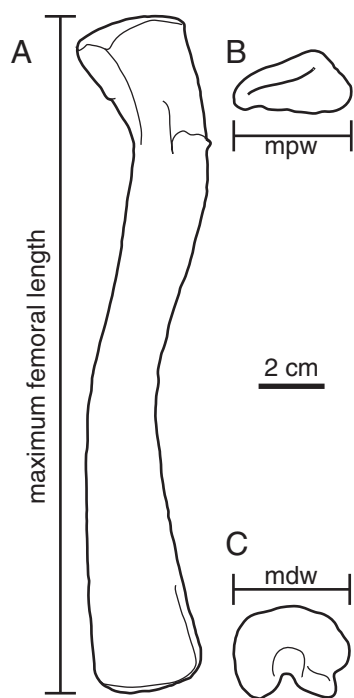


Fig. 1. Outlines of a left silesaurid femur in A, anterolateral, B, proximal, and C, distal views to show the measurements taken for the multiple linear regression of femoral dimensions. Based on *Silesaurus opolensis* (redrawn from Dzik, 2003). Abbreviations: mdw maximum distal width; mpw maximum proximal width.

Team, 2011) and we also report the coefficients calculated (R^2) and 95% confidence limits on the calculated femoral length.

Measurements (in mm) were taken directly from original material or obtained from the literature (Table 1): all were rounded to the nearest millimetre. The dataset includes 32 femora representing 13 taxa, which span the phylogenetic transition from early dinosauiromorphs (lagerpetids) to early dinosaurs. Multiple femora are known for several taxa (e.g., *Asilisaurus*, *Sacisaurus*) and these were included to incorporate the influence of possible ontogenetic variation into the analysis.

2.3. Specimen preparation

Both fragments were encased in a thin (~2 mm) calcium carbonate coating. However, the bone surface is generally well preserved and the matrix easily separated in most cases. One of us (S.J.N.) removed the calcium carbonate coating on both fragments using an ARO Marxall pneumatic aircscribe modified with an HW-10 (Hardy Winkler Co.) microtip adaptor. Butvar B-76 dissolved in acetone was applied with a small brush to protect the surface following detailed surface preparation. The specimens were moulded and cast.

2.4. Institutional abbreviations

MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MHNM, Museum d'Histoire Naturelle de Marrakech, Marrakech, Morocco; MNA, Museum of Northern Arizona, Flagstaff, U.S.A.; NHCC, National Heritage Conservation Commission of Zambia, Lusaka, Zambia; NHMUK, Natural History Museum, London, U.K.; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PEFO, Petrified Forest National Park, Arizona, U.S.A.; PVL, Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; SAM, Iziko South African Museum, Cape Town, South Africa; TMM, Vertebrate Paleontology Laboratory, Texas Natural Science Center, The University of Texas Austin, Austin, Texas, U.S.A.; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

3. Systematic palaeontology

Dinosauiromorpha Benton, 1985

Dinosauriformes Novas, 1992

Silesauridae Langer et al., 2010

Gen. et sp. indet. (Fig. 2)

3.1. Specimen

A partial right femur (NHMUK R16303) represented by its proximal and distal ends, but lacking the shaft.

3.2. Locality, age, and horizon

Field locality U15/1, east of the Mkongleko River, northwest of Songea, Ruhuhu Basin, southern Tanzania (A.J. Charig, unpublished field notes); Lifua Member of the Manda beds, Middle Triassic, ?late Anisian (Abdala et al., 2005; Catuneanu et al., 2005).

3.3. Identification

NHMUK R16303 can be referred to Silesauridae on the basis of the following suite of synapomorphies (after Nesbitt et al., 2010; Nesbitt, 2011): i) presence of a notch ventral to the proximal head of the femur; ii) presence of a straight transverse groove on the femoral proximal surface; and iii) straight medial articulation facet of the proximal portion of the femur. The distal end of the femur does not have any unambiguous silesaurid synapomorphies as none have yet been identified. However, the distal end of the femur is consistent with that of other silesaurids in that: i) the distal surface bears a transversely-oriented depression, ii) the distal epicondyles are sub-equal in size and are weakly expanded relative to the preserved distal portion of the shaft; and iii) the lateral distal (= fibular) condyle is nearly absent and is continuous with the crista tibiofibularis. Given the consistency of size, proximity when found (see above) and similarity of morphology with other silesaurids, we hypothesise that the proximal and distal ends are from the same individual, although we cannot confirm this definitively. Additionally, NHMUK R16303 does not pertain to '*Pallisteria augustimentum*' (NHMUK R36620) because the proximal portion of NHMUK R16303 bears silesaurid synapomorphies and the size of NHMUK R16303 is far too small to belong to the preserved remains of the likely archosaur '*Pallisteria augustimentum*'.

4. Description and comparisons

The proximal end of the femur is broken ventrally at the level of the anterior (= lesser) trochanter. In proximal view, it has an elongate, subtriangular outline that is widest medially and tapers laterally. There is no clear separation between the femoral head and the greater trochanter and a fossa trochanterica is absent. The proximal surface bears a deep, prominent, mediolaterally-extending groove, which is slightly offset towards the anterior margin of the femur, and that traverses almost the entire width of the proximal end. A similar groove is present in other silesaurids (e.g., *Asilisaurus kongwe*, NMT RB159; *Silesaurus opolensis*, Dzik, 2003) and is present in some other archosaurs (e.g., poposauroids, early theropods: (Nesbitt, 2011)). The anteroposteriorly narrow facies articularis antitrochanterica is restricted to the proximal surface of the femoral head and does not extend ventrally around the lateral, anterior, or posterior margins of the proximal end, although it does extend for a small distance ventrally along its medial margin. A reduced facies articularis antitrochanterica is also present in *A. kongwe* (NMT RB159); the facies articularis antitrochanterica is completely absent in stratigraphically younger silesaurids (e.g., *S. opolensis*, Dzik, 2003). This short ventral extension is separated from the medially facing articular surface of the femoral head by a distinct bony rim and break in slope.

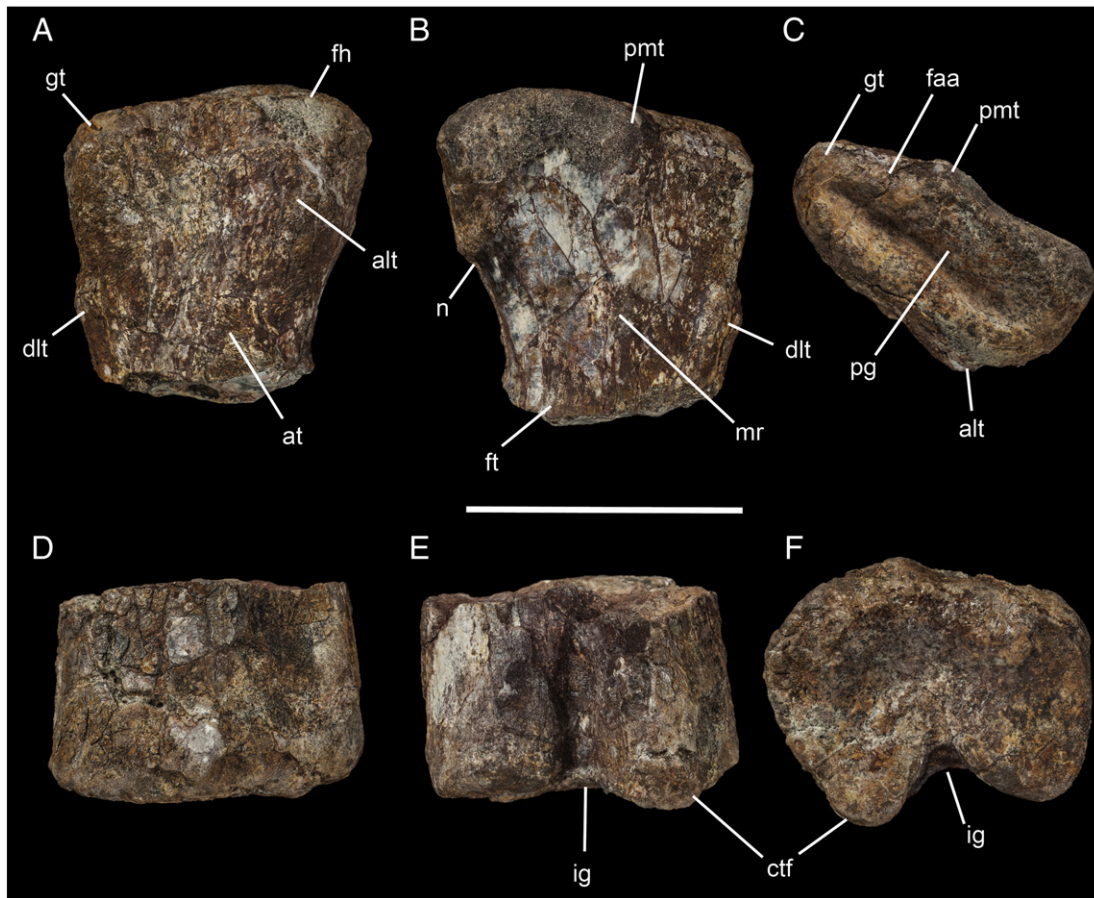


Fig. 2. Right femur of an indeterminate silesaurid (NHMUK R16303) from the Lifua Member (?late Anisian) of the Manda beds, southwestern Tanzania. Proximal part in A, anterolateral, B, posteromedial, and C, proximal views. Distal part in D, anterior, E, posterior, and F, distal views. Abbreviations: alt anterolateral tuber; at anterior trochanter; ctf crista tibiofibularis; dlt dorsolateral trochanter; faa facies articularis antitrochanterica; fh, femoral head; ft fourth trochanter; gt greater trochanter; ig posterior intercondylar groove; mr medial ridge; n notch; pg proximal groove; pmt posteromedial tuber; scale bar = 50 mm.

In anterolateral view, the dorsal margin of the proximal end is almost straight. An angle of approximately 80° separates the dorsal and medial margins of the femoral head and a slight constriction marks the junction between the medial articular surface of the head and the femoral shaft. The medial articular surface of the femoral head forms a flat, sub-vertically inclined plane. A prominent tuberosity, the anterolateral tuber (sensu Nesbitt (2011) = craniomedial crest of Langer and Ferigolo (2013)), is positioned on the anterolateral surface of the femoral head, just lateroventral to its dorsomedial apex. The degree of expansion of the anteromedial tuber is likely the result of slight deformation of the proximal femur. The rest of the anterolateral surface of the proximal end is flat to very gently convex, with the exception of a low, trapezoidal rugosity, which is slightly medially offset from the midpoint of the shaft and positioned ventrolateral to the anterolateral tuber. This rugosity probably represents the proximal-most part of the anterior trochanter. The apex of the anterior trochanter is confluent with the surrounding proximal end surface and is not finger-like as in some early dinosaurs (e.g., *Coelophysis bauri*, Colbert, 1989). The lateral margin of the proximal femur is slightly stepped in anterior view, with a distinct notch situated approximately 30 mm below the greater trochanter. This notch is defined ventrally by the swollen and rugose dorsolateral trochanter, which is also visible in posterior view.

In posteromedial view, the dorsal margin of the femoral head (= anteromedial tuber of Nesbitt (2011)) is gently convex, whereas that of the greater trochanter is flat and slopes gently ventrolaterally. A distinct notch separates the medial articular surface of the femoral head from the shaft as in other silesaurids, such as *A. kongwe* (NMT RB159), *S. opolensis* (Dzik, 2003), and *Sacisaurus agudoensis* (Langer and Ferigolo, 2013). A small but distinct tuberosity, the posteromedial

tuber (= medial tuber of Langer and Ferigolo (2013)), is positioned at the midpoint of the femoral dorsal margin. The presence of a posteromedial tuber is plesiomorphic for Silesauridae as it is present in the early diverging form *A. kongwe* (NMT RB159), but absent or nearly absent in stratigraphically younger silesaurids such as *S. opolensis* (Dzik, 2003). The anteromedial and posteromedial tubera are approximately the same size. A low, sharp medial ridge extends ventrally from the posteromedial tuber subdividing the posterior surface of the proximal portion of the femur into two gently concave portions. This ridge is more prominent proximally and attenuates ventrally, merging into a possible muscle scar dorsal to the level of the break. This muscle scar is also present in *A. kongwe* (NMT RB159). A low swelling at the ventromedial corner of the preserved posterior surface represents the dorsal-most part of the fourth trochanter. In distal view, the proximal femoral shaft has an ovate outline at the level of the break, with the long axis of the oval oriented mediolaterally.

The articular surface of the distal end of the femur is shallowly concave with a weakly defined mediolaterally trending depression. The anterior margin of this concavity is defined by a thick rim, whereas posteriorly the surface flattens and is continuous with the ventral surfaces of the medial and lateral (= crista tibiofibularis) epicondyles. A deep intercondylar groove separates the two epicondyles in distal view. We identify the medial condyle as the tibial condyle and the more lateral condyle as a combination of the crista tibiofibularis and the lateral condyle (= fibular condyle) of other archosaurs. Both epicondyles have subtriangular outlines with bluntly rounded apices, though the medial epicondyle is anteroposteriorly shorter and mediolaterally wider than the lateral epicondyle. The greater posterior projection of the lateral epicondyle is accentuated by slight asymmetry

of the distal femur, which exhibits greater anteroposterior expansion in its lateral part.

In posterior view, each epicondyle is continuous with a robust ridge that extends dorsally: these two ridges define a deep groove on the posterior surface of the femur. Due to breakage, however, it is unclear if the intercondylar groove separates these epicondylar ridges as far proximally as in some silesaurids (Nesbitt et al., 2010). The medial and lateral surfaces of the distal femur are gently convex anteroposteriorly and each is separated from the anterior surface by a distinct break in slope. The anterior surface bears a very shallow longitudinal concavity close to its medial margin, whereas the area adjacent to the medial surface is gently convex. In dorsal view, the broken femoral surface has a sub-ovate outline, which is anteroposteriorly widest laterally and with its long axis oriented transversely.

5. Body-size results

The multiple linear regression recovered a strong, statistically significant relationship between femoral length (l), proximal femoral width (w_1), and distal femoral width (w_2):

$$l = -5.37 + 2.94(w_1) + 3.17(w_2) \quad (p = 0.000, R^2 = 0.91)$$

Substituting the values of w_1 and w_2 for those of NHMUK R16303 ($w_1 = 57$ mm; $w_2 = 58$ mm) yields a calculated femoral length of 345.8 ± 50 mm for this animal (95% confidence limits). This value far exceeds the femoral lengths of all other known non-dinosaurian dinosauromorphs and those of several early dinosaurs (Table 1: see Discussion, below).

6. Discussion

6.1. Taxonomic implications

The type locality of *Asilisaurus kongwe* has produced thousands of partially articulated and isolated skeletal elements of silesaurids and a few other vertebrates, including cynodonts (Nesbitt et al., 2010). To date, all of the silesaurid remains from the type locality have been attributed to *A. kongwe* (Nesbitt et al., 2010) based on similar size (~within a 15% size range) and morphology (with no major differences with the sample of each element) (S.J.N., pers obs). Within this sample, most femora range in length from 90 to 130 mm as estimated based on partial proximal or distal segments. Silesaurid remains are also common throughout the Lifua Member across the Ruhuhu Basin and the size range of silesaurid femora from this unit ranges from 74 to 144 mm (Table 1). Fragments of larger silesaurid femora possibly extend the upper size of these silesaurids to ~180 mm (e.g., SAM-PK-10598). Our estimated length for NHMUK R16303 is therefore nearly twice that of the largest silesaurid femur and approximately three times the length of the modal femoral length at the type locality. However, the preserved morphology of NHMUK R16303 is essentially identical to that of *A. kongwe*. The combined presence of an anterior trochanter with a proximal apex that is poorly developed and completely attached to the shaft, a poorly-developed facies articularis antitrochanterica, and a muscle scar just proximal to the proximal portion of the fourth trochanter is found only in *A. kongwe* and NHMUK R16303 among silesaurids.

Using these data, we envision two taxonomic scenarios based on the differently-sized silesaurid material from the Lifua Member: i) that there are potentially two silesaurids in the Lifua Member, the smaller *A. kongwe* and a larger, currently unnamed form; or ii) that *A. kongwe* is a juvenile or subadult of the larger form and that the majority of known *A. kongwe* specimens represent individuals that are maximally half grown or even smaller.

Other unresolvable issues further complicate these two scenarios. For example, it is unclear whether the small (*A. kongwe*) and large

forms were contemporaries. The vegetated, low-lying outcrops of the Lifua Member are difficult to correlate, so the precise stratigraphic relationships of the various vertebrate localities are currently unknown. This situation is also exacerbated by the lack of detailed information on the precise location and stratigraphy of locality U15. Consequently, we refrain from referring NHMUK R16303 to either *A. kongwe* or to a new taxon on the basis of current data, and we retain it as a silesaurid of uncertain affinities. Histological work on *A. kongwe*, in combination with discoveries of additional large silesaurid specimens, will be necessary in order to choose between these alternate scenarios. Unfortunately, we cannot evaluate the ontogenetic status of NHMUK R16303 due to the incompleteness of the material.

6.2. Palaeobiological implications

The large Manda silesaurid stands apart from all other Middle and Late Triassic non-dinosaurian dinosauromorphs in terms of body-size. NHMUK R16303 is estimated to have had a body length of at least ~3 m based on comparison with *Asilisaurus kongwe* (Fig. 3). Specimens of lagerpetids, *Marasuchus lilloensis*, most other silesaurid taxa, and other non-dinosaurian avemetatarsalians like *Scleromochlus taylori* all likely had body lengths of approximately 1.5 m or less (Table 1; (Sereno and Arcucci, 1994; Benton, 1999; Dzik, 2003; Nesbitt et al., 2010)). Alongside *A. kongwe* and *Nyasasaurus parringtoni*, also from the Lifua Member, and *Lutungutali sitwensis* of the upper Ntawere Formation in Zambia, NHMUK R16303 is one of the oldest known body fossils pertaining to a bird-line archosaur. *N. parringtoni* was also estimated to be between 2 and 3 m in length based on vertebral dimensions (Nesbitt et al., 2013a). Together NHMUK R16303 and *N. parringtoni* argue for an immediate expansion in body-size early in bird-line archosaur evolution relative to the small body-size that is inferred to be plesiomorphic for Ornithodira, although the latter taxa do not reach the far larger sizes attained by contemporary pseudosuchians (Sookias et al., 2012; Turner and Nesbitt, 2013).

As the basal-most silesaurid, *Lewisuchus admixtus*, is a relatively small animal (Romer, 1972), NHMUK R16303 likely indicates that increased body-size was gained convergently in silesaurids and early dinosaurs. This increase occurred in concert with the convergent acquisition of many other features in these clades, including craniodental characters associated with herbivory (e.g., coarsely serrated and leaf-shaped teeth, presence of a beak) and various postcranial characteristics, including the presence of increased numbers of sacral vertebrae and possible quadrupedality (Dzik, 2003; Nesbitt et al., 2010; Langer et al., 2013). The estimated femoral length of NHMUK R16303 exceeds that of many early dinosaurs (see Table 1), but is comparable to that of some individuals of *Herrerasaurus ischigualastensis* (Novas, 1994) and was clearly smaller than that of many Late Triassic sauropodomorphs (e.g., (Yates and Kitching, 2003)). However, there was little spatiotemporal overlap in the distributions of large-bodied silesaurids and similarly-sized (or larger) early dinosaurs. In faunas where these clades co-occur, as in the Ischigualasto Formation of Argentina (Carnian–early Norian) and the Chinle Formation (Norian) of the southwestern U.S.A., known silesaurids are small animals that do not reach the largest sizes attained by some of their dinosaurian contemporaries (Irmis et al., 2007; Martínez et al., 2013). One possible exception comes from the Lifua Member of the Manda beds: if *N. parringtoni* is a dinosaur (Nesbitt et al., 2013a), then this fauna potentially included contemporary, similarly-sized silesaurids and early dinosaurs. Even if *N. parringtoni* is a non-dinosaurian dinosauriform, the presence of this taxon and NHMUK R16303 indicate that body-size increases among early ornithodirans were more prevalent than recognised previously. Nevertheless, it appears that dinosaurs rapidly increased in size beyond the range occupied by non-dinosaurian dinosauriforms, with a variety of larger sauropodomorphs (e.g., *Antetonitrus*, *Plateosaurus*, *Riojasaurus*), and theropods (*Zupaysaurus*) appearing in the Norian.

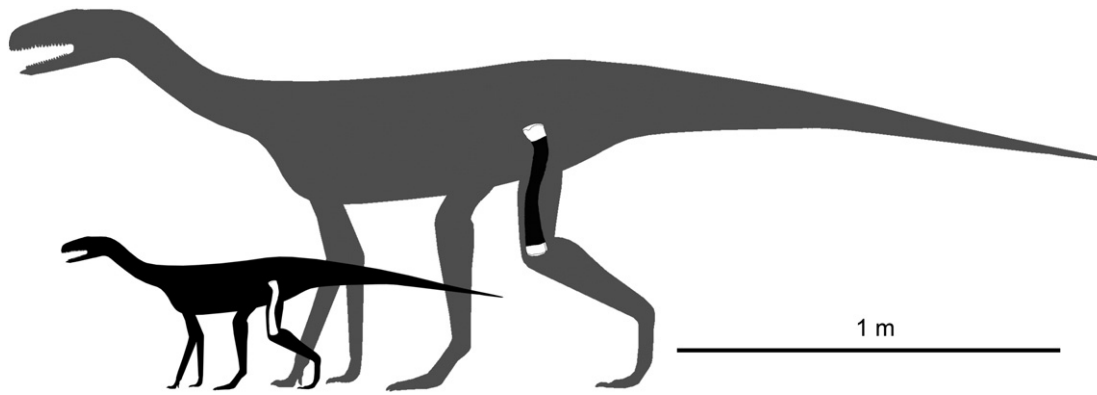


Fig. 3. Reconstructed outlines of Lifua Member silesaurids (modified from Nesbitt et al., 2010), scaled by femoral length. A, large taxon represented by NHMUK R16303. B, largest specimen of *Asilisaurus kongwe* from Table 1 (NMT RB159; femoral length: 144 mm).

If two silesaurids were present in the ?late Anisian Lifua Member (see discussion in Section 6.1, above), then this, in combination with the presence of *N. parringtoni*, would imply a higher than expected taxonomic diversity of dinosauriforms in the early Middle Triassic than might have been expected in such early archosaur faunas. Moreover, if these taxa were distinguished by differences in body-size, this might also suggest some form of ecological partitioning between them, though we currently have no direct evidence for dietary preferences in either *N. parringtoni* or NHMUK R16303. To date, all other silesaurid material from the Lifua Member has been assigned to *A. kongwe* (Nesbitt et al., 2010); however, if NHMUK R16303 does represent a distinct taxon it is possible that other isolated elements from these deposits might also be referable to this taxon, rather than *A. kongwe*. This has implications for understanding the skeletal anatomy of *A. kongwe*, current knowledge of which relies in part on the referral of isolated specimens (Nesbitt et al., 2010).

Alternatively, if NHMUK R16303 proves to be a large-sized individual of *A. kongwe*, a literal reading of the available fossil record would imply that almost all of the known elements of this taxon pertain to skeletally immature individuals. This might further suggest that *A. kongwe* lived mainly in groups of small-sized individuals, and that adult survivorship was low, at least if the available sample is representative of the original population demographics. Similar life history characteristics are also thought to characterise various dinosaur clades (Varricchio, 2011), raising the possibility that either the same behavioural repertoires were also present in the common ancestor of silesaurids and dinosaurs, or that this may represent another convergence between the two groups. Finally, although NHMUK R16303 is the largest known silesaurid specimen from the Lifua Member, it should be noted that this does not necessarily record the maximum size possible for these animals.

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