LETTERS

Ecologically distinct dinosaurian sister group shows early diversification of Ornithodira

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The early evolutionary history of Ornithodira (avian-line archosaurs) has hitherto been documented by incomplete (*Lagerpeton*[1]) or unusually specialized forms (pterosaurs and *Silesaurus*[2]). Recently, a variety of *Silesaurus*-like taxa have been reported from the Triassic period of both Gondwana and Laurasia, but their relationships to each other and to dinosaurs remain a subject of debate[3–5]. Here we report on a new avian-line archosaur from the early Middle Triassic (Anisian) of Tanzania. Phylogenetic analysis places *Asilisaurus kongwe* gen. et sp. nov. as an avian-line archosaur and a member of the Silesauridae, which is here considered the sister taxon to Dinosauria. Silesaurids were diverse and had a wide distribution by the Late Triassic, with a novel ornithodiran bauplan including leaf-shaped teeth, a beak-like lower jaw, long, gracile limbs, and a quadrupedal stance. Our analysis suggests that the dentition and diet of silesaurids, ornithischians and sauropodomorphs evolved independently from a plesiomorphic carnivorous form. As the oldest avian-line archosaur, *Asilisaurus* demonstrates the antiquity of both Ornithodira and the dinosaurian lineage. The initial diversification of Archosauria, previously documented by crocodilian-line archosaurs in the Anisian[6], can now be shown to include a contemporaneous avian-line radiation. The unparalleled taxonomic diversity of the Manda archosaur assemblage indicates that archosaur diversification was well underway by the Middle Triassic or earlier.

By the Middle Triassic, Archosauria had diverged into two lineages: the crocodilian line (Pseudosuchia) and the avian line (Ornithodira, including dinosaurs). During the early evolutionary history of these two clades, pseudosuchians were both numerically abundant and morphologically diverse. In contrast, the avian lineage only became dominant during the Early Jurassic, roughly 35 million years after the origin of Dinosauria[4,7].

Triassic deposits have recently begun to yield a diversity of close dinosaur relatives from around the world, whereas records were previously restricted to a single locality from the Middle Triassic of Argentina[8]. New records include lagerpetids, a clade of small forms with long, gracile hindlimbs[4,9], and a number of taxa similar to the unusual dinosauriform *Silesaurus*[2]. These groups included contemporaries of dinosaurs, and they persisted well into the Late Triassic, at least until the mid-Norian[4]. *Silesaurus*, from the late Carnian/early Norian of Poland, is unusual among early dinosauromorphs in possessing a beaked lower jaw and a gracile, quadrupedal stance. Here we demonstrate the antiquity, diversity and wide distribution of the clade containing *Silesaurus* and its relatives by introducing a new avian-line archosaur from the Anisian (early Middle Triassic) of Tanzania. The discovery of this well represented taxon demonstrates that early ornithodiran lineages (pterosaurs, various basal dinosauromorphs, and the lineage leading to Dinosauria) had diverged by the late Anisian.

Archosauria Cope, 1869 (*sensu* Gauthier and Padian, 1985)
Ornithodira Gauthier, 1986 (*sensu* Sereno, 1991)
Dinosauriformes Novas, 1992
Silesauridae clade nov.

Definition: the most inclusive clade for Silesauridae contains *Silesaurus opolensis* Dzik, 2003 but not *Passer domesticus* Linnaeus, 1758, *Triceratops horridus* (Marsh, 1889) and *Alligator mississippiensis* Daudin, 1801.

Diagnosis. Silesauridae differs from all other archosaurs in possessing the following unique combination of character states: rugose ridge on the anterolateral edges of the supraoccipital; notch ventral to femoral head; straight transverse groove on the proximal surface of the femur; and ilium has a straight ventral margin of the acetabulum (see Supplementary Information).

Asilisaurus kongwe gen. et sp. nov.

Etymology. From *asili*, Swahili for ancestor or foundation, and *sauros*, Greek for lizard; *kongwe*, Swahili for ancient.

Holotype. NMT RB9 (National Museum of Tanzania, Dar es Salaam, Tanzania), the anterior portion of a left dentary with associated tooth (Fig. 1a–d).

Paratype. Material found associated with the holotype, but derived from multiple individuals (Fig. 2 and Supplementary Information). Anterior cervical vertebra (NMT RB21), left scapulocoracoid (NMT RB10), sacrum (NMT RB11), proximal portion of an ischium (NMT RB12), ilium (NMT RB13), proximal portion of a pubis (NMT RB14), anterior portion of a skull (NMT RB15), proximal portion of a left humerus (NMT RB16), left astragalus (NMT RB17), right calcaneum (NMT RB18), proximal portion of a left femur (NMT RB19), right tibia (NMT RB20). Additional material from the type locality referable to *Asilisaurus* is under preparation.

Locality and horizon. Most of the specimens derive from a fluviolacustrine mudstone–sandstone sequence in the Lifua Member of the Manda Beds[10], near the town of Litumba Ndyosi, Ruhuhu Basin, Tanzania. The type locality preserves the remains of at least fourteen individuals (based on the number of the second sacral vertebra). Cynodonts (*Aleodon brachyrhamphus* and *Scalenodon angustifrons*), dicynodonts (*Sangusaurus* and *Angonisaurus*), archosauromorphs (*Stenaulorhynchus* and pseudosuchians) and stereospondyl amphibians occur in the immediate area[11–15]. On the basis of comparison with the tetrapod fauna of the subzone C of the *Cynognathus* assemblage zone of

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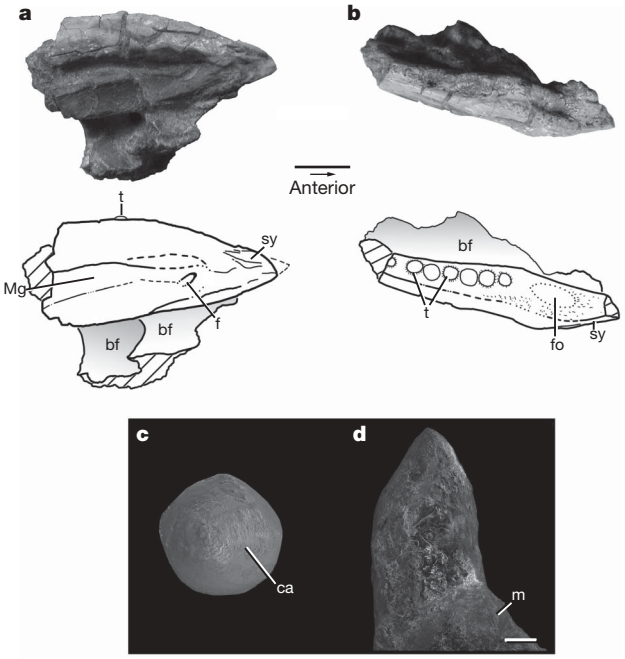

Figure 1 | New silesaurid from Tanzania, *Asilisaurus kongwe* (NMT RB9). **a**, Anterior portion of the holotypic dentary in medial view. **b**, Anterior portion of the holotypic dentary in occlusal view. **c**, **d**, Scanning electron micrographs of a dentary crown in occlusal (**c**) and lateral (**d**) views. Scale bars: 1 cm (**a**, **b**); 100 μm (**c**, **d**). bf, bone fragments; ca, carina; f, foramen; fo, fossa; m, matrix; Mg, Meckelian groove; sy, symphysis; t, tooth.

South Africa[16–18], the Lifua Member is considered to be late Anisian in age[18].

Diagnosis. *Asilisaurus* differs from all other archosaurs in possessing the following unique combination of character states: anterior portion of the dentary tapers to a sharp point; teeth absent from the anterior portion of the dentary; teeth ankylosed into the alveoli; distinctly convex dorsal margin of the dentary; Meckelian groove positioned at the dorsoventral midpoint of the medial surface of the dentary; peg-like teeth with extremely small, poorly developed serrations (see Supplementary Information for differential diagnosis using additional characters preserved on the paratypes).

Description. Nearly the entire skeleton of *Asilisaurus* is known from an accumulation of isolated elements and partially articulated individuals at a single locality. Only portions of the skull and manus remain unknown. Most individuals were probably juveniles because the majority of femora are 60–80% of the maximum size recovered. We estimate that the largest individuals of *Asilisaurus* would measure 2–3 m in length, based on femoral length comparisons with *Silesaurus*.

The skull has similar proportions to that of *Silesaurus*[2]. The anterior portion of the dentary (NMT RB9) tapers to a point like that of both *Silesaurus* and *Sacisaurus*[19], but possesses a convex dorsal edge unlike other silesaurids. Small foramina cover the lateral surface of the anterior portion of the dentary, indicating that it was covered by a rhamphotheca. Medially, the prominent Meckelian groove is positioned at the dorsoventral midpoint of the dentary, in contrast to the more ventral position of *Silesaurus*, *Sacisaurus* and Hayden Quarry specimens[4]. A fossa (Fig. 1b) on the occlusal margin separates the tip of the dentary from the tooth row. The closely packed and socketed teeth are ankylosed to the dentary, a synapomorphy uniting *Silesaurus*, *Sacisaurus*, *Asilisaurus* and specimens from the Hayden Quarry[4]. The two preserved teeth are peg-like, but the tip of each crown bears tiny serrations on its carinae.

The anterior cervical vertebrae are significantly longer than both the axis and the posterior cervical vertebrae, similar to *Lewisuchus*[20]. The rhomboidal cervical vertebrae lack epipophyses, in contrast to the inferred ancestral condition for Dinosauria[21]. Hyposphene–hypantra articulations are present in the dorsal vertebrae. *Asilisaurus* possesses only the two primordial sacral vertebrae. The sacrals are not co-ossified; however, sacral rib one extends onto the body of the last presacral vertebra, a character also present in *Silesaurus*.

The scapula is tall and narrow like that of *Silesaurus*. The glenoid is directed posteroventrally as in dinosaurs, suggesting that the forelimbs were directed underneath the body. The coracoid bears an enlarged biceps tubercle that is separated from the glenoid by a gap. The proximal portion of the humerus is mediolaterally

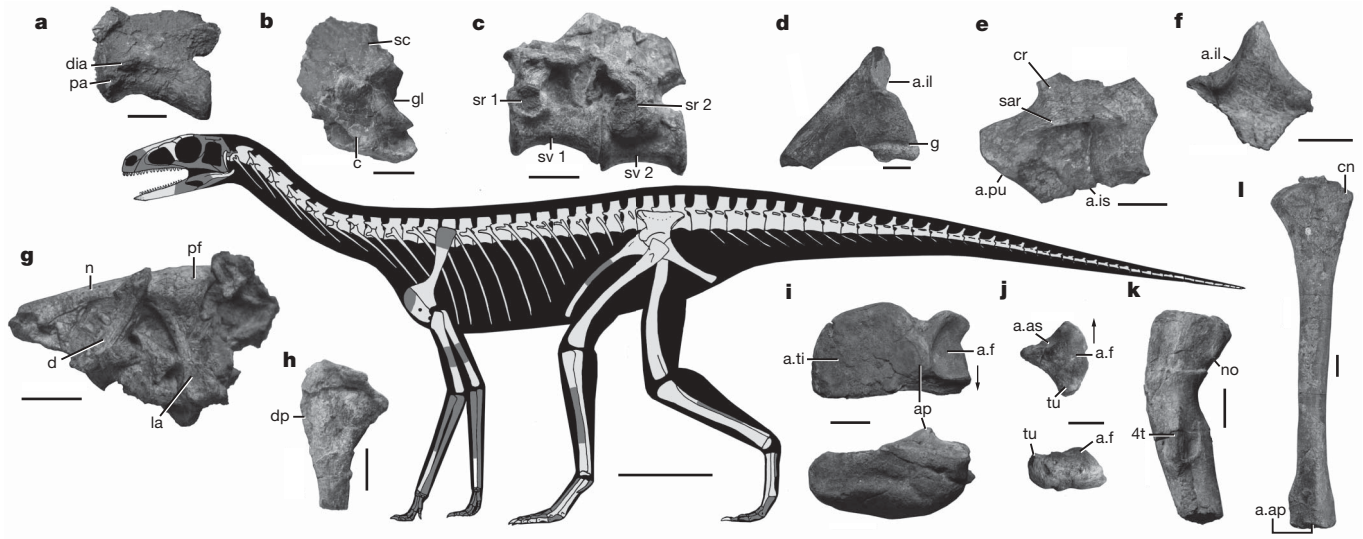

Figure 2 | Skeletal anatomy of *Asilisaurus kongwe*. **a**, Anterior cervical vertebra (NMT RB21). **b**, Left scapulocoracoid (NMT RB10). **c**, Sacrum (NMT RB11) (reversed). **d**, Proximal portion of the pubis (NMT RB14) (reversed). **e**, Ilium (NMT RB13) (reversed). **f**, Proximal portion of the ischium (NMT RB12) (reversed). **g**, Anterior portion of the skull (NMT RB15) (reversed). **h**, Proximal portion of the left humerus in posterior view (NMT RB16). **i**, Left astragalus in proximal (top) and anterior (bottom) views (NMT RB17). **j**, Right calcaneum in proximal (top) and lateral (bottom) views (NMT RB18). Arrows in **i** and **j** indicate the anterior direction. **k**, Proximal portion of a left femur in posteromedial view (NMT RB19). **l**, Right tibia in lateral view (NMT RB20). Panels **a**–**f** are shown in lateral view. Scale bars: 1 cm (**a**–**l**); 10 cm for the skeleton. Dark grey bones represent missing elements and missing portions of the skeleton based on *Silesaurus*[5]. 4t, fourth trochanter; a., articulates with; ap, anterior process; as, astragalus; c, coracoid; cn, cnemial crest; cr, crest; d, dentary; dia, diapophysis; dp, deltopectoral crest; f, fibula; g, groove; gl, glenoid; il, ilium; is, ischium; la, lacrimal; n, nasal; no, notch; pa, parapophysis; pf, prefrontal; pu, pubis; sar, supra-acetabular rim; sc, scapula; sr, sacral rib; sv, sacral vertebra; ti, tibia; tu, tuber.

expanded like that of *Euparkeria*, and the apex of the deltopectoral crest of the humerus is located at the proximal surface. Although incomplete, the estimated lengths of the humerus and radius indicate that *Asilisaurus* had elongate forelimbs like *Silesaurus*.

The acetabulum of *Asilisaurus* was closed, as with all non-dinosaurian ornithodirans. A distinct crest on the ilium extends dorsally from a well-developed supra-acetabular rim to the pre-acetabular process, as in *Pseudolagosuchus*[22], *Silesaurus* and *Sacisaurus*. The postacetabular process of the ilium lacks a brevis shelf. The pubis is anteroventrally directed and terminates as a thick, mediolaterally wide sheet of bone. A groove on the proximal surface of the pubis separates the articular facet with the ilium from the articular facet of the ischium, as in *Silesaurus* and dinosaurs such as *Saturnalia*[4]. The ischial shafts are closely appressed to one another for their entire length and terminate in a posterodorsal expansion.

The femur of *Asilisaurus* possesses a distinct notch ventral to its head. The proximal surface is incised by a straight sulcus similar to that in many basal archosaurs, and like all dinosauriforms, both anteromedial and posterior proximal medial tubera are developed and a distinct facies articularis antitrochanterica is present. Like other basal dinosauromorphs[9], a distinct anterior trochanter is connected to the shaft for the length of the trochanter and bears a poorly developed trochanteric shelf. The crista tibiofibularis is poorly expanded and is separated from the lateral condyle of the femur by a slight groove. The popliteal fossa between the posterior condyles of the femur expands proximally to greater than one-third of the femoral length, a character also present in *Silesaurus*, *Eucoelophysis* and *Sacisaurus*. The tibia bears a well-developed, straight cnemial crest with two equally sized posterior condyles of the proximal portion, similar to other basal dinosauriforms. The distal surface possesses a poorly developed slot for the ascending process of the astragalus.

The astragalus and calcaneum are separate elements, unlike the co-ossified condition in pterosaurs, lagerpetids and theropod dinosaurs. The distinct anterior ascending process of the astragalus is low and poorly developed compared to those of dinosaurs and *Silesaurus*, but nearly identical to the condition in *Pseudolagosuchus*[22]. A posterior groove is clearly present on the astragalus. The articulation between the astragalus and the calcaneum is much like that of pseudosuchians: the astragalus has a convex surface whereas the calcaneum has a corresponding concave surface. Furthermore, the calcaneum bears a small posterolaterally directed tuber, like that of *Pseudolagosuchus*[22] and *Marasuchus*[23]. Additionally, the articular facet for the fibula is convex, in contrast to the concave facet of *Silesaurus*[2] and Dinosauria.

Our phylogenetic analysis (34 taxa, 290 characters; see Supplementary Information) of *Asilisaurus*, representative pseudosuchians, a diversity of basal ornithodirans, and early dinosaurs recovers *Asilisaurus* in a monophyletic Silesauridae containing *Lewisuchus*/*Pseudolagosuchus* (see Supplementary Information), *Eucoelophysis*[3,4,24], *Sacisaurus*[19] and *Silesaurus*[2]. Silesauridae is supported by four unambiguous synapomorphies (Supplementary Information), whereas the unnamed clade containing *Asilisaurus*, *Eucoelophysis*, *Sacisaurus* and *Silesaurus* is supported by the following synapomorphies: anterior extent of the dentary tapers to a sharp point; teeth absent in the anterior portion of the dentary; maxillary and dentary crowns short and subtriangular; straight medial articular facet of the proximal portion of the femur; and popliteal fossa of the distal end of the femur extends proximally between one-fourth and one-third the length of the shaft. These synapomorphies allow the placement of more fragmentary specimens from western North America into Silesauridae using unambiguous synapomorphies (Supplementary Information), thus demonstrating that the clade had a Gondwanan distribution during the Middle Triassic and became more widely distributed by the Late Triassic (Fig. 3).

Notably, Silesauridae is well supported as the closest sister taxon of Dinosauria (see Supplementary Information), conclusively demonstrating that *Silesaurus* and *Silesaurus*-like forms are not basal members

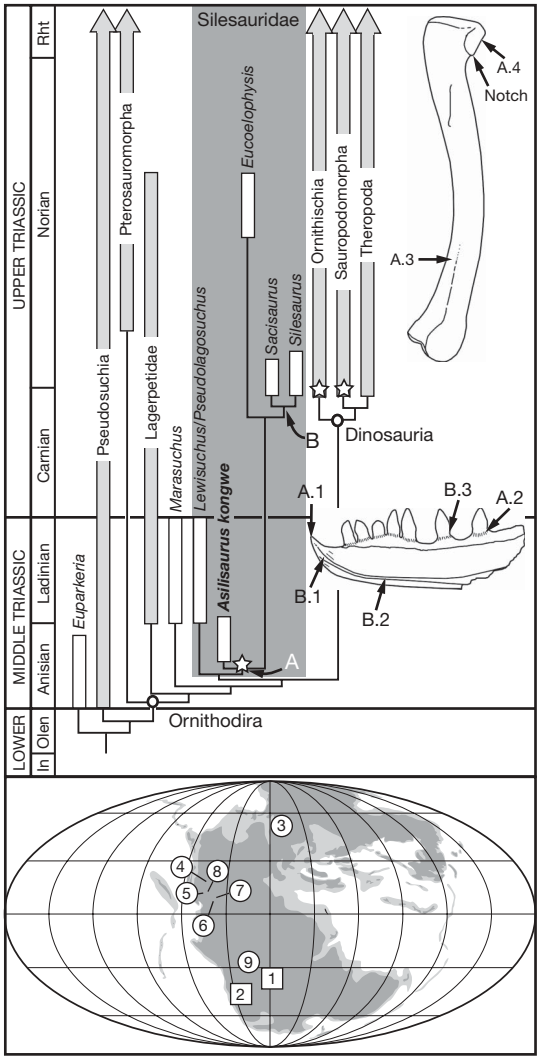

Figure 3 | Phylogenetic relationships of *Asilisaurus kongwe* within Archosauria and silesaurid biogeography. Strict consensus of six trees of an analysis with 33 taxa and 290 characters (Supplementary Information). Pseudosuchia, Ornithischia, Sauropodomorpha, Theropoda, Pterosauromorpha and Lagerpetidae have been collapsed for clarity. Stars indicate lineages with herbivorous or omnivorous diets. The length of the white bars indicates stratigraphic imprecision. Important synapomorphies for *Asilisaurus* plus *Silesaurus* illustrated on a left femur of *Silesaurus* in posteromedial view (top) and a right dentary of *Silesaurus* in medial view (bottom): A.1, anterior portion of dentary tapers to a point; A.2, teeth fused to the bone of attachment; A.3 division of the distal condyles of the femur divided for more than one-quarter length of the element; A.4, flat articular facet of the femur. Important synapomorphies for *Sacisaurus* plus *Silesaurus* (B): B.1, Meckelian groove extends through dentary symphysis; B.2, Meckelian groove restricted to the ventral margin of dentary; B.3, teeth with constricted roots. In, Induan; Olen, Olenekian; Rht, Rhaetian. Middle Triassic (squares): 1, *Asilisaurus*; 2, *Lewisuchus*/*Pseudolagosuchus*. Late Triassic taxa (circles): 3, *Silesaurus*; 4, Eagle Basin specimens; 5, Petrified Forest N.P. taxon; 6, Otis Chalk taxon; 7, *Technosaurus*; 8, *Eucoelophysis*; 9, *Sacisaurus*. Palaeogeographic globe after http://jan.ucc.nau.edu/~rcb7/globaltext2.html. See Supplementary Information for further discussion of occurrences.

of the ornithischian dinosaur lineage[5]. All silesaurids lack classical dinosaurian character states such as a laterally open acetabulum, an elongate deltopectoral crest of the humerus, and an extension of the supratemporal fossa onto the posterodorsal surface of the frontal. Thus, features present in *Silesaurus*, such as the ornithischian-like dentition and a theropod-like ankle, represent independent acquisitions (homoplasies) and are not synapomorphies shared with Dinosauria, because these features are not present in the most basal members of Silesauridae (that is, *Asilisaurus* and *Lewisuchus*/*Pseudolagosuchus*).

Silesaurids possess an unexpected bauplan previously unknown among basal ornithodirans. All known silesaurid taxa represented by adequate material possess an elongate neck, elongate forelimbs and a robust pes. Perhaps the most striking feature of all silesaurids (except *Lewisuchus*) is the presence of teeth with sub-triangular crowns and a constricted root, and dentaries with a beak-like anterior tip, indicating that these taxa were specialized for an omnivorous and/or herbivorous diet[25,26]. Similar specializations are present among ornithischian, sauropodomorph and some coelurosaurian[26] dinosaurs. Because some of the earliest members of these clades lack characters suggestive of a omnivorous and/or herbivorous diet (for example, *Lewisuchus*[20] and *Panphagia*[27]), our analyses suggest that these specializations were independently acquired in at least the silesaurid and sauropodomorph lineages, and possibly in ornithischians as well, and that the shift towards omnivory/herbivory in these three lineages comprised overlapping but distinct suites of morphological characters (Supplementary Information).

The phylogenetic position of *Asilisaurus* within avian-line archosaurs indicates that the radiation of ornithodirans commenced by the early Middle Triassic. Indeed, pterosauromorph, lagerpetid, *Marasuchus*, silesaurid and dinosaurian lineages must have all diverged by the late Anisian (Fig. 3). Moreover, the ghost lineage (see Fig. 3) inferred from our phylogeny predicts that taxa closer to Dinosauria than to Silesauridae will be discovered in Middle Triassic strata. Ornithodiran diversification was part of a more inclusive archosaur radiation as evidenced by the diversity of crocodilian-line archosaurs co-occurring in the Manda beds of Tanzania. The Manda archosaur assemblage includes 'rauisuchians'[13,28], an *Erpetosuchus*-like taxon[29], *Hypselorachis*[30], and other undescribed pseudosuchians[15]. The minimum of six archosaur lineages represented within the Manda beds is unmatched in similarly aged deposits[18] and foreshadows the taxonomic composition of archosaur-dominated assemblages later in the Triassic. Thus, *Asilisaurus* and other coeval archosaurs from the Manda beds preserve direct evidence that archosaur diversification commenced by the Middle Triassic, but that the group as a whole did not come to dominate terrestrial ecosystems until the Late Triassic.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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