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The age of the Tashinga Formation (Karoo Supergroup) in the Mid-Zambezi Basin, Zimbabwe and the first phytosaur from mainland sub-Saharan Africa

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ABSTRACT

Correlations between continental sequences within the Karoo-aged basins of southern and eastern Africa are difficult due to the dearth of shared index fossils and a lack of radioisotopic dates for key formations. Here we describe four sites along the southeastern shoreline of Lake Kariba, Zimbabwe, within the Mid-Zambezi Basin, that yield material of phytosaurs (Archosauromorpha: Phytosauria) from within the informal Tashinga Formation (Upper Karoo Group). These phytosaur remains are the first to be recovered from sub-Saharan mainland Africa, representing a major geographic range extension for this group into high southern latitudes. Furthermore, an LA-ICPMS maximum depositional age of 209.2 ± 4.5 Ma (late Norian/early Rhaetian) derived from detrital zircons provides the first absolute age estimate for any of these sites. The phytosaurs are associated with lungfish and metoposaurid amphibians, forming part of a terrestrial-aquatic dominated biota, a previously undocumented biome from the Late Triassic of southern Africa.

1. Introduction

The Karoo-aged basins of southern and eastern Africa have provided fossils of critical importance in shaping our understanding of Permo-Triassic vertebrate evolution, shedding light on the emergence of crocodiles, dinosaurs, mammals and turtles, among many other groups (Kitching and Raath, 1984; Rubidge, 2005). Most of this material has been collected from within the main Karoo Basin, but important collections have also been made in other areas, including the Ruhuhu Basin of Tanzania and the Luangwa Basin of Zambia (e.g., Sidor and Nesbitt, 2018).

Collections have also been made in several Karoo-aged basins within Zimbabwe, although many of the outcrops have not been explored extensively for decades (e.g., Attridge, 1963; Bond et al., 1970; Raath et al., 1970; Bond, 1973). Here, we report on several new fossil vertebrate localities on the shores of Lake Kariba, Zimbabwe, which is positioned within one of the larger Karoo-aged basins, the Mid-Zambezi Basin. This basin represents a series of en-echelon rift structures whose formation was associated with Permo-Carboniferous crustal extension and Triassic strike-slip movements (De Wit et al., 1988; Catuneanu et al., 2005). The Mid-Zambezi Basin preserves sedimentary deposits that correlate with those in the main Karoo Basin and the neighboring Cabora Bassa Basin (De Wit et al., 1988; Smith et al., 1993; Johnson et al., 1996; Zerfass et al., 2004; Catuneanu et al., 2005; Abdala et al., 2013). The underlying geology in and around Lake Kariba

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also consists of sediments that correlate to and are contemporaneous with the main Karoo Basin's Dwyka, Ecca and Beaufort groups (Lower Karoo Group) and the Stormberg and Drakensberg groups (Upper Karoo Group) (Fig. 1).

The sediments of the main Karoo Basin in South Africa have been studied intensively and a well-established biozonation exists for these deposits, parts of which have been correlated with the international geochronologic timescale on the basis of radioisotopic dates obtained from primary tuffs and detrital zircons (Rubidge et al., 2013). Following from this work, there have been many attempts to correlate the sediments of the smaller Karoo-aged basins, such as those of the Mid-Zambezi and Cabora Bassa basins of Zimbabwe, the Ruhuhu Basin of Tanzania and the Luangwa Basin of Zambia, with those of both the main Karoo Basin and other basins in the region (e.g., Smith et al., 1993; Johnson et al., 1996; Rogers et al., 2004; Zerfass et al., 2004; Catuneanu et al., 2005; Bordy et al., 2010; Abdala et al., 2013; Peecook et al., 2018; Wynd et al., 2018). However, the regional and global correlations of the upper Karoo Group units contained within these basins are poorly supported due to a dearth of shared index fossils and the lack of radioisotopic dates from these thick terrestrial sequences (Dubiel et al., 1991; Rogers et al., 1993; Luo and Wu, 1994; Arcucci et al., 2004; Irmis et al., 2011; Riese et al., 2011).

Phytosauria is an extinct clade of semi-aquatic archosauromorphs that is regarded as either the sister-group of Archosauria (Sereno and Arcucci, 1990; Sereno, 1991; Nesbitt, 2011) or as an early diverging lineage of pseudosuchian archosaurs (Chatterjee, 1982; Benton and Clark, 1988; Parrish, 1993; Ezcurra, 2016). The clade consists of approximately 30 genera of superficially crocodile-like animals with narrow, elongated snouts and heavily armored bodies, which can reach up to 10 m in length (e.g., Stocker and Butler, 2013). Phytosaurs lived exclusively in the Late Triassic (late Carnian–Rhaetian: Buffetaut, 1993; Lucas, 1998; Stocker and Butler, 2013) and their remains are common in central Europe and North America (see review in Stocker and Butler, 2013), with rare occurrences in other Laurasian continents (e.g., Buffetaut and Ingavat, 1982; Morales and Ash, 1993; Renesto and Lombardo, 1999; Heckert et al., 2005; Brusatte et al., 2013). By contrast, the group is rare in Gondwana, with occurrences limited to Brazil, India, Madagascar and Morocco (e.g., Chatterjee, 1978; Dutuit, 1978; Jalil, 1999; Kischlat and Lucas, 2003; Burmeister et al., 2006). Nevertheless, phytosaurs are regarded as important index fossils and have been used in defining a series of ‘Land Vertebrate Faunachrons’ throughout the Norian and Rhaetian epochs, based primarily on their North American record (e.g., Lucas, 1998; Parker and Irmis, 2005; Rayfield et al., 2009; Martz and Parker, 2017).

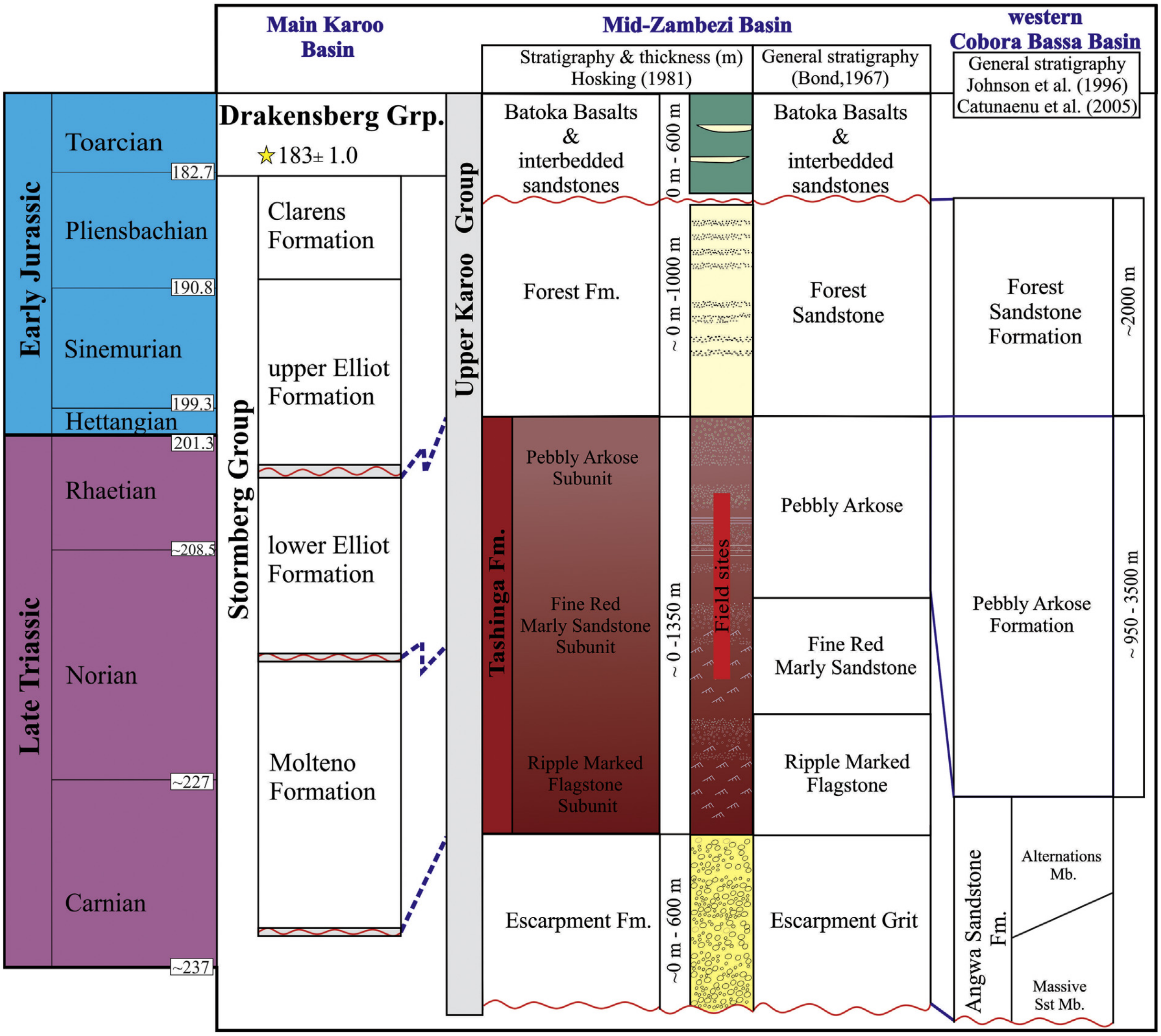


Fig. 1. General lithostratigraphic subdivisions and correlation of the Upper Triassic–Lower Jurassic Stormberg Group (Karoo Supergroup, main Karoo Basin, South Africa) to similar-aged units from the Mid-Zambezi and Western Cabora Bassa basins (Zimbabwe and Zambia). Correlations are tentative, based on shared fossil assemblages and adapted from Smith et al. (1993), Johnson et al. (1996) and Catuneanu et al. (2005). Note the changes in lithostratigraphic nomenclature within the Mid-Zambezi Basin. The distribution of the current field sites is demarcated within the generalized stratigraphic log for the Mid-Zambezi Basin.

Here, we report the discovery of the first definitive phytosaur material from sub-Saharan mainland Africa, from the Tashinga Formation of the Mid-Zambezi Basin, Zimbabwe. We also provide context to reported upper Karoo sites in the Lake Kariba area and present the first radioisotopic date recovered from the upper Karoo sediments of this basin. This new information provides critical biostratigraphic and radiometric calibration points that will facilitate stratigraphic correlations between the sediments of the Mid-Zambezi Basin and those of other basins across southern Africa. It also indicates a major range extension in phytosaur geographic distribution and furnishes new insights into the Late Triassic paleoecology of the Mid-Zambezi Basin.

2. Materials and methods

2.1. Mapping and logging

Standard field techniques were used to document and record macroscopic observations of the host sedimentary rocks at and around the phytosaur-bearing sites. The lithology, sedimentary structures, vertical and lateral grain size variations were described as per Miall (1996) and sedimentary logs created thereafter.

2.2. Radioisotopic dating

Radioisotopic dating was carried out using detrital zircon grains (field sample MS-17-6) that were isolated from a sandstone unit 7.5 m below 'The Dentist' phytosaur site.

Approximately 2 kg of sandstone was collected from fresh outcrop face to comprise the detrital zircon sample. This sample was coarsely broken up using a jaw crusher and then reduced to powder using a disc mill, after which it was sieved, and the <500 μm fraction retained for further separation. For mineral separation of the sieved powder we used a Wilfley Table, retaining the heavy and medium components. These components were washed in acetone and then dried in a low-temperature oven for 24 h. The dried sample was subjected to heavy liquid separation using bromoform (density 2.88 g/cm^3). After drying, the dense fraction was finally subjected to magnetic separation on a Frantz Isodynamic Magnetic Separator set with a forward slope of 25° and a side tilt of 15°. By gradually increasing the amperage of the separator, zircon separates were concentrated in the most non-magnetic component at around 1.2 amps.

Once separated, a representative subset of zircon grains was randomly split and mounted on a 1″ acrylic disc using double-sided sticky tape. Samples were analyzed using an ESI 193 nm Excimer laser ablation system attached to a Thermo iCAP Q-ICP-MS at the Trace Element and Radiogenic Isotope Lab at the Department of Geosciences, University of Arkansas, USA. In total, 171 zircon grains were analyzed during two analytical sessions. Zircon grains were selected randomly for analysis provided that the grain was large enough to accommodate a 25 μm ablation spot and was free of obvious defects such as inclusions and surface cracks. Analysis of whole grains allows depth profiling of the grain from the surface inward (e.g., Kelly et al., 2014) and insures that the outermost (i.e., youngest) part of the grain is included in the analysis. Twelve grains displayed distinct age domains during ablation where a younger rim age transitioned inward to an older core age.

Data reduction was conducted using Iolite and the UPbGeochronology4 data reduction scheme (Paton et al., 2010). During the first analytical session, Plešovice (337 Ma; Sláma et al., 2008) was used as a primary zircon standard with R33 (417 Ma; Black et al., 2004) as a secondary standard. The weighted mean ^{206}Pb/^{238}U age for the R33 secondary standard was within 1% (2σ internal error) of the expected value for this analytical session. During the second analytical session, 91,500 (1065 Ma) was used as a primary standard with Plešovice and R33 as secondary standards. The weighted mean ^{206}Pb/^{238}U age of both secondary standards was within 0.3% (2σ internal error) of the accepted ages. Grain analysis integration windows were manually adjusted in some cases to avoid highly discordant or ^{204}Pb contaminated zones. The ^{206}Pb/^{238}U age was selected for analyses with a ^{206}Pb/^{238}U age < 1300 Ma; the ^{207}Pb/^{206}Pb age was used for all other, older analyses. Analyses with a ^{206}Pb/^{238}U age < 1300 Ma were filtered from the dataset if discordance between the ^{206}U/^{238}U and ^{207}U/^{235}U ratios exceeded 15% or if the 2σ internal error of the age exceeded 10%. Analyses with a ^{206}Pb/^{238}U age > 1300 Ma were filtered from the dataset if ^{206}U/^{238}U and ^{207}Pb/^{206}Pb discordance was >30% or if reverse discordance was >15%. In total, nine analyses were filtered from the dataset, representing ~5% of the total data collected. Calculation of age distributions (probability density plots [PDPs] and kernel density estimations [KDEs]) and maximum depositional ages follows Dickinson and Gehrels (2009), Sharman et al. (2018) and Coutts et al. (2019).

2.3. Fossil material

Specimens described in this paper were accessioned at the Natural History Museum of Zimbabwe, Bulawayo (NHMZ). They were photographed using a Canon 760D body fitted with a Canon L-series 24–105 mm lens. Three-dimensional models of some of the phytosaur jaw fragments described below were produced from still photographs using AgiSoft Pro v 1.2.2. Measurements of specimens were taken using sliding callipers with 0.1 mm precision.

3. Geologic setting and sedimentology

The four new phytosaur sites, nicknamed 'Steve's Phytosaur Site', 'The Dentist' (due to its abundance of fossil teeth), 'Coprolite Hill' and 'Phytosaur Gully' lie in northern Zimbabwe, east of Tashinga on the southern shore of Lake Kariba, within Matusadona National Park (Fig. 2). Following the stratigraphic scheme outlined in the unpublished dissertation of Hosking (1981), the phytosaur localities are located stratigraphically within the upper part of the Tashinga Formation. The informal Tashinga Formation is the consolidation of three lithostratigraphic units: the lowermost 'Ripple Marked Flagstone', the 'Fine Red Marly Sandstone' and the uppermost 'Pebbly Arkose'. These three units, together with the underlying 'Escarpment Grits'/Escarpment Formation and overlying Forest Formation (=Forest Sandstone) and Batoka Basalts form part of the informal 'Upper Karoo' (Late Triassic–Early Jurassic; Bond et al., 1970; Hosking, 1981). Currently, there is some variation in the nomenclature used to describe the 'Upper Karoo' stratigraphy in the Mid-Zambezi Basin. This is likely due to the lack of formalized lithostratigraphic descriptions (Bond, 1973; Hosking, 1981; Oesterlen and Millsteed, 1994; Oesterlen, 1999; Catuneanu et al., 2005).

The informal 'Ripple Marked Flagstone' subunit of the Tashinga Formation, as described by Hosking (1981), is not currently exposed at any of our field sites. This subunit has been correlated with the Molteno Formation of the main Karoo Basin (Late Triassic: Carnian) based on the shared occurrence of the seed-fern *Dicroidium* and *Dicroidium*-bearing assemblages (Bond, 1973; Hosking, 1981; Barale et al., 2005). The 'Fine Red Marly Sandstone' and the overlying 'Pebbly Arkose' subunits were both exposed in our field areas. The descriptive titles of these subunits, i.e., marly, pebbly and arkosic, were not strictly encountered in our field mapping, and 'marly' appears to be a misnomer. Furthermore, the sedimentological ambiguity of the 'Fine Red Marly Sandstone' and to a lesser extent the 'Pebbly Arkose' subunit is compounded by the lack of a formal description. Additional mapping and sedimentological description of both vertical and lateral outcrop are necessary to establish beyond doubt the relationships between the various exposures along the Lake Kariba shoreline. In general, the 'Fine Red Marly Sandstone' has been neglected in terms of sedimentological or paleontological descriptions. Hosking's (1981) 'Ta facies' best describes the 'Fine Red Marly Sandstone' and is considered to be composed of red/maroon fine-grained sandstones, siltstones and mudstones bearing primary sedimentary structures ranging from ripple cross-lamination to desiccation

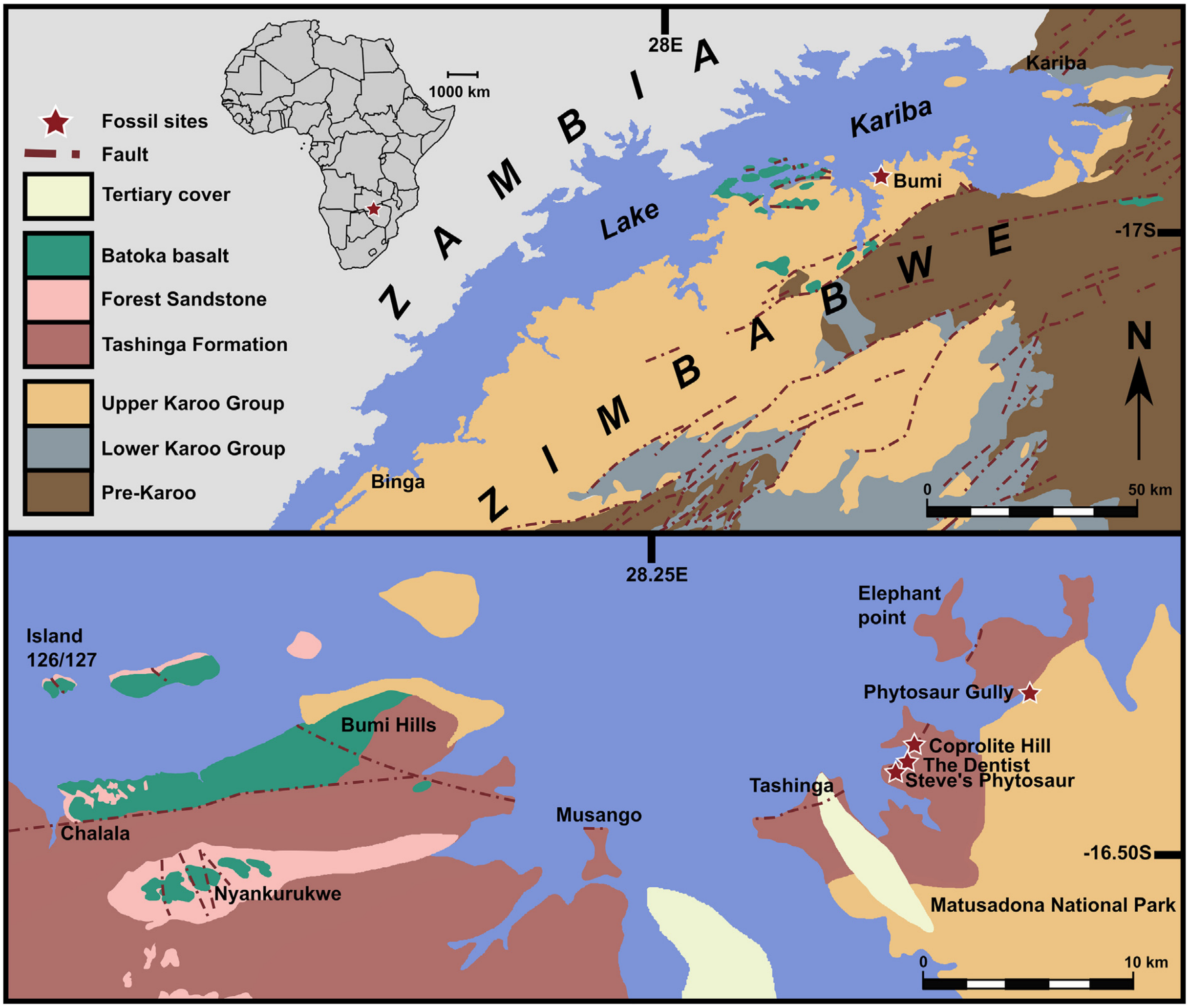


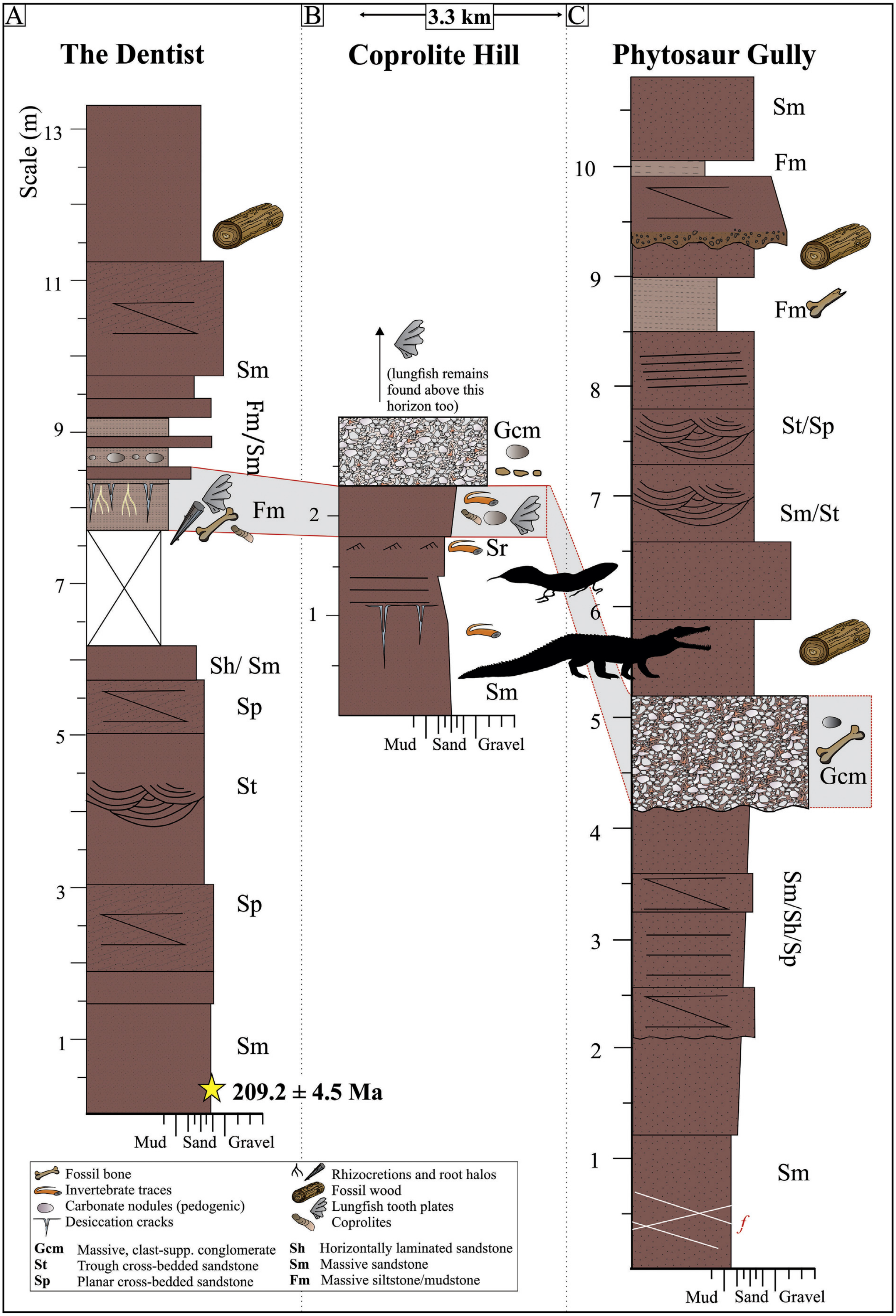
Fig. 2. A, geologic map showing the regional geology of northern-most Zimbabwe and Lake Kariba. Star indicates the position of the complex of sites under investigation. B, close-up of the local geology of the 'Steve's Phytosaur Site', 'The Dentist', 'Coprolite Hill' and 'Phytosaur Gully' sites near Tashinga, within Matusadona National Park. Geological map adapted from Marsh and Jackson (1974) and field mapping by TJB (Zimbabwe Geological Survey).

cracks and intense bioturbation. Importantly, a defining feature of the 'Fine Red Marly Sandstone' is the occurrence of pedogenic nodule conglomerates, as noted by Macgregor (1941), Bond (1973) and Hosking (1981).

By contrast, the 'Pebbly Arkose' subunit is considered a coarse-grained facies composed of fine to very coarse-grained sandstones and conglomerates and it contains 'typically' Late Triassic taxa including fossil woods (e.g., *Rhexoxylon africanum* and *Dadoxylon* spp. – the latter now recognized as a junior synonym of *Agathoxylon* Hartig; Rößler et al., 2014; Marsh and Jackson, 1974), lungfish tooth plates (Bond, 1973) and rhynchosaur remains (the latter in the Western Cabora Bassa Basin: Raath et al., 1992). Oesterlen and Millsteed (1994) proposed that the 'Pebbly Arkose' subunit was deposited by braided fluvial systems with interchannel floodplains that were dominated by ephemeral lakes, crevasse splays and vegetation. The 'Pebbly Arkose' is generally considered to be contemporaneous with the Elliot Formation in the main Karoo Basin. From our preliminary field mapping, we infer that these two subunits may be laterally gradational with an interfingering relationship between the upper boundary of the 'Fine Red Marly Sandstone' and the overlying 'Pebbly Arkose'.

All of the phytosaur localities lie within the upper part of the Tashinga Formation but represent slightly different stratigraphic levels (Fig. 3). Three of the four phytosaur-bearing sites described herein, 'Steve's Phytosaur Site' (16°48′35.03″S; 28°28′4.98″E), 'The Dentist' (16°48′33.79″S, 28°28′5.71″E) and 'Coprolite Hill' (16°48′27.57″S; 28°28′12.34″E), were discovered by SFE and are almost immediately adjacent to each other. The fourth locality, 'Phytosaur Gully', is approximately 3 km NE of the other sites (16°47′10.80″S, 28°29′16.38″E) and was discovered during fieldwork in March 2018. The majority of the material described below was collected from either 'Steve's Phytosaur Site' or 'The Dentist' locality, all as surface float (material from 'Coprolite Hill' was also surface collected). In situ material was present in large fallen blocks of reworked pedogenic nodule conglomerate within 'Phytosaur Gully', although many of these could not be collected due to the lack of appropriate equipment.

The sedimentological context of the fossiliferous unit at both the 'Steve's Phytosaur Site' and 'The Dentist' localities is a pedogenically overprinted red to grey muddy-siltstone (Fig. 3A, Fm) with a well-developed pedogenic assemblage of rhizocretions (diameters 0.4–2 cm), coprolites (~2–4 cm in length), small in situ pedogenic nodules (1–5 cm in length) and sandstone-filled desiccation cracks. This fossiliferous muddy-siltstone is interbedded with thin (<20 cm), laterally discontinuous very fine- to fine-grained sandstone beds that are tabular and massive to horizontally laminated. The laterally associated 'Coprolite Hill' contains fossils within a paleo-pedogenically overprinted fine-grained sandstone with pedogenic nodules, vertebrate coprolites (1–7 cm in length; Fig. 3B) and intensive bioturbation. This overlies a fine-


A
B
3.3 km
C
The Dentist
Coprolite Hill
Phytosaur Gully
Scale (m)
13
11
9
7
5
3
1
Sm
Fm/Sm
Fm
Sh/ Sm
Sp
St
Sp
Sm
209.2 ± 4.5 Ma
Mud
Sand
Gravel
(lungfish remains found above this horizon too)
Gcm
2
Sr
1
Sm
Mud
Sand
Gravel
10
9
8
7
6
5
4
3
2
1
Sm
Fm
Fm
St/Sp
Sm/St
Gcm
Sm/Sh/Sp
Sm
f
Mud
Sand
Gravel
Fossil bone
Invertebrate traces
Carbonate nodules (pedogenic)
Desiccation cracks
Rhizocretions and root halos
Fossil wood
Lungfish tooth plates
Coprolites
Gcm Massive, clast-supp. conglomerate
St Trough cross-bedded sandstone
Sp Planar cross-bedded sandstone
Sh Horizontally laminated sandstone
Sm Massive sandstone
Fm Massive siltstone/mudstone

grained ripple cross-laminated sandstone (showing ripple drift) and is overlain by a locally constrained mud-chip and pedogenic nodule conglomerate. This conglomerate is clast-supported with clasts ranging between 0.5 and 1 cm in size. The logged section indicates the waning of energy, followed by a period of non-deposition and then periodic denudation and the accumulation of floodplain by-products (i.e., nodules, lungfish tooth plates and bone). Overlying the fossiliferous succession are channel sandstones (Fig. 3, Sm, Sp, Sh) and overbank deposits (Fig. 3, Fm) that contain abundant fossil wood.

At 'Phytosaur Gully' (Fig. 3C) fossil remains are found within an intraformational, reworked mud-chip and pedogenic nodule conglomerate that overlies massive to horizontal and planar cross-bedded sandstones. The pedogenic nodule conglomerate is ≤1 m thick, massive, poorly-sorted and clast-supported with clast sizes ranging between ≤1 to ≥20 cm. Clasts are of various compositions (e.g., mudstone, sandstone, pedogenic carbonate nodules, bone fragments) and range from rounded to sub-angular. The lower contact is an undulating erosional surface.

4. Radioisotopic age of 'The Dentist' site

Fig. 4 presents a summary of the detrital zircon U-Pb ages obtained from sample MS-17-6. Major age peaks occur at 262, 458, 553, 966 and 1055 Ma, with smaller peaks at 741, 831 and 1712 Ma. Eighty percent of analyses fall between 400 and 1200 Ma, with an additional 11% being Permian or Triassic in age. Two Late Triassic grains were the youngest identified (206.3 ± 6.6 and 211.9 ± 3.2 Ma; Fig. 4; Supplementary Table S1). The younger of these two grains is 8.3% discordant with an approximate U concentration of ~1100 ppm, suggesting the possibility of Pb loss. However, the slightly older, but more precise, grain was only 3.2% discordant with a U concentration of ~120 ppm (Supplementary Table S1). The next nine youngest analyses fall between 260 and 240 Ma (Fig. 4).

Many methods have been proposed for calculating the maximum depositional age from detrital zircons (Dickinson and Gehrels, 2009; Coutts et al., 2019). Following these workers, and Sharman et al. (2018), we consider seven methods: the youngest single grain (YSG), youngest cluster overlapping at 1σ with at least two grains (YC1σ[2+]) or overlapping at 2σ with at least three grains (YC2σ[3+]), the youngest three detrital zircons (Y3Za) or the youngest three that overlap within error (Y3Zo), the youngest statistical population (YSP), and the τ method (see Coutts et al., 2019 for a review of these different approaches). Both the YSG and the YC1σ(2+) methods yield Late Triassic maximum depositional ages: 206.3 ± 6.6 and 209.2 ± 4.5 Ma, respectively (Fig. 4). The remaining metrics yield older (225.6 ± 3.2 to 250.2 ± 1.6 Ma) Triassic maximum depositional ages. Because use of the YSG has been discouraged due to the potential for Pb loss and/or contamination in any given sample (Dickinson and Gehrels, 2009), we use the more conservative YC1σ(2+) age of 209.2 ± 4.5 Ma (2σ) as an estimate of the maximum depositional age of the sandstone unit 7.5 m below the phytosaur site.

5. First phytosaur material from sub-Saharan Africa

5.1. Systematic paleontology

Archosauriformes Gauthier et al., 1988
Phytosauria von Meyer, 1861
Gen. et sp. indet. (Figs. 5–9)

5.1.1. Material

Mandibular fragments (NHMZ 2418, 2419, 2428, 2429, 2444, 2445), isolated teeth (NHMZ 2422–2425, 2440, 2443) and osteoderms (NHMZ 2420).

5.1.2. Locality and horizon

The 'Steve's Phytosaur Site', 'The Dentist', 'Coprolite Hill' and 'Phytosaur Gully' localities east of Tashinga, Matusadona National Park, southern shoreline of Lake Kariba, Zimbabwe (see Fig. 2); upper part of the Tashinga Formation, Karoo Supergroup (late Norian/early Rhaetian, Upper Triassic).

5.1.3. Remarks

Although the material recovered exhibits several phytosaur synapomorphies, it is too fragmentary to identify to lower taxonomic levels and synapomorphies of phytosaur subclades (e.g., Stocker and Butler, 2013; Jones and Butler, 2018) are absent.

5.2. Mandible

Six lower jaw sections have been collected from the 'Steve's Phytosaur Site' and 'Coprolite Hill' sites. Three of these are very fragmentary and so the following description is based on the three most complete specimens (NHMZ 2418, 2419, 2444; Figs. 5, 6A–C; see 3D model in Supplementary material). Two of these sections (NHMZ 2418, 2419; Fig. 5) are from 'Steve's Phytosaur Site' and the third (NHMZ 2444: Fig. 6A–C) is from 'Coprolite Hill'. NHMZ 2418 and 2419 represent individuals of similar size. Each of the latter comprises the same region of the lower jaw from different individuals, which due to breakage or abrasion captures both the internal and external splenial/dentary contact. Each includes ~nine alveoli; in NHMZ 2418 these are almost entirely represented by the medial alveolar margin only, as all but two alveoli are missing their lateral border (Fig. 5A, B). NHMZ 2418 has a maximum width of 80 mm due to the loss of the lateral alveolar border on one side of the specimen whereas that of NHMZ 2419 is 101 mm; in NHMZ 2418 the distance from the intersplenial suture to the preserved lateral alveolar border is 50 mm, suggesting a total width similar to NHMZ 2419.

The unabraded surface of NHMZ 2418 is identified as the dorsal section of a mandible as the single interalveolar plate and those portions of the lateral alveolar margin that are preserved do not appear to be broken or abraded, suggesting that these alveolar openings are genuine, rather than an intramandibular cross-section (Fig. 5A). On the reverse side of this section, the alveoli slope medially, giving them a ventromedial/dorsolateral orientation, consistent with other phytosaurs (Fig. 5B). The medial section of NHMZ 2418 is also consistent with the dorsal mandibular morphology of phytosaurs, being slightly expanded dorsally, with respect to the alveoli, in a shallow curve. All alveoli preserved in NHMZ 2419 appear on the dorsal broken surface, with most representing cross-sections (Fig. 5D); the lateral border of the right alveolar row may represent the original bone-surface, but this is difficult to ascertain. The unabraded surface of NHMZ 2419 preserves the ventral section of the mandible from the same region as NHMZ 2418, displaying a dentary-splenial suture of very similar size and morphology (Fig. 5E). It is difficult to assess the maximum width of NHMZ 2444 due to breakage (Fig. 6A–C), but the distance from the intersplenial suture to the labial edge of the dentary is 70 mm, suggesting a maximum width of 140 mm. NHMZ 2418 and 2419 both consist of the anterior parts of articulated lower jaws, including parts of both dentaries and both splenials (Fig. 5). By contrast, NHMZ 2444 is a lower jaw section from a more posterior position than the other two specimens, consisting of portions of the right dentary, right splenial and a small portion of the

Fig. 3. Measured stratigraphic sections from phytosaur-bearing localities along the shoreline of Lake Kariba at A, 'The Dentist' site, B, 'Coprolite Hill' site and C, 'Phytosaur Gully' site. 'Phytosaur Gully' lies 3.3 km north-north-east of 'Steve's Phytosaur Site', 'The Dentist' and 'Coprolite Hill'. Star indicates the source of the U-Pb detrital zircon sample with its maximum depositional age of 209.2 ± 4.5 Ma. The grey bar and associated lungfish and phytosaur outline indicate the phytosaur- and lungfish-bearing fossiliferous horizons.

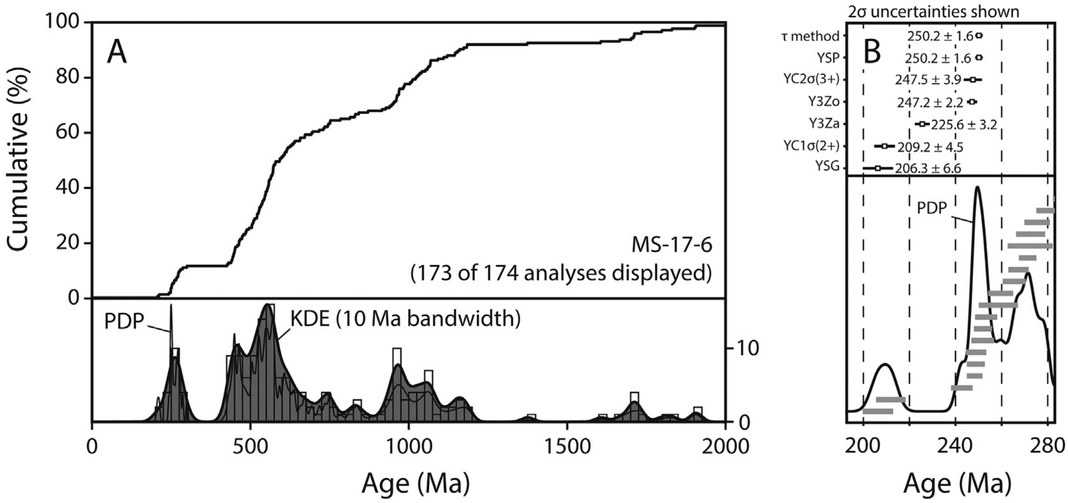


Fig. 4. A, detrital zircon U-Pb ages from sample MS-17-6 displayed as cumulative (above) and relative (below) age distributions. B, maximum depositional age calculation following seven different approaches described by Dickinson and Gehrels (2009) and Coutts et al. (2019). Horizontal grey bars on the lower plot represent individual U-Pb analyses.

left splenial (Fig. 6A–C). Another dorsally positioned bone lies lingual to the alveolar margin and dorsal to the splenials.

In anterior or posterior view, the mandibles are wide and shallow, producing a broad, 'U'-shaped cross-section. The mandibles are widest posteriorly and taper in width anteriorly. Two parallel rows of small, elongate, elliptical foramina extend for the entire length of the dentary in lateral view in both specimens, extending just ventral to and parallel with the alveolar margin (Fig. 5C, F). Ventral to these foramina, the lateral and ventral surfaces of the mandibles are separated by a clear break in slope. In dorsal view, the mandibles lack the majority of the lateral alveolar border; however, the abraded section shows the alveoli to be sub-circular in outline, angled ventromedially and clearly separated from each other, extending deep into the body of dentary, terminating close to the splenial contact. Several partial tooth roots with sub-circular cross-sections are preserved within the alveoli in both specimens (Fig. 5). The dorsal surface of the mandible is slightly convex at its medial section between the alveolar rows and displays many small foramina along the entire length of the preserved fragment, but primarily concentrated on the dentaries around the anterior-most extent of the dentary-splenial suture. The ventral surface of the mandible is slightly convex mediolaterally and is ornamented with numerous small circular to elliptical pits and some smaller foramina.

In ventral view, the splenials form an elongate, triangular wedge that separates the dentaries along the posterior midline of the mandible (Fig. 5B, E). Their broken posterior surfaces reveal that the suture between the splenials is complex and interdigitated, whereas that between the splenials and dentaries is simpler, but still displays a degree of interdigitation posteriorly in dorsal view. In dorsal and ventral views, the splenial extends anteriorly approximately halfway along each preserved fragment; although the external dentary-splenial suture shows relatively little sign of interdigitation, the internal suture, identifiable on the broken dorsal surface of NHMZ 2419, is complex. The mandibular symphysis is almost indistinguishable in both dorsal and ventral views, however, close inspection of the preserved bone surface and the broken surfaces reveal a heavily interdigitated suture.

NHMZ 2445 includes nine pieces of lower jaw (likely dentary) that are essentially identical to NHMZ 2418 and 2419, but that are broken, less well preserved and potentially represent fragments from several different individuals (Fig. 6D–H). Finally, NHMZ 2428 and 2429 represent fragments of lower jaw that were positioned close to its anterior terminus. In many respects they are similar to the specimens described above, but each bears a large corrugated area that formed the articulation for the mandibular symphysis.

The mandibular material can be referred to Phytosauria unambiguously, based on the presence of several character states considered to be synapomorphic for the clade, including an elongate mandibular symphysis (Sereno, 1991; Nesbitt, 2011; Ezcurra, 2016), the relatively constant dorsoventral height of the symphyseal region (Hungerbühler, 2001), the presence of a symphyseal platform (Hungerbühler, 1998, 2001), a strongly interdigitating mandibular symphysis (Holliday and Nesbitt, 2013) and a double row of grooves/foramina extending posteriorly from the anterior tip of the dentary (Maisch and Kapitzke, 2010; Ezcurra, 2016). These characters are discussed further in Supplementary Appendix S1.

A possible phytosaur premaxillary terminal rosette was found at Phytosaur Gully, preserved in conglomerate (Fig. 7). The preserved section of bone measures approximately 100 mm anteroposteriorly by 75 mm mediolaterally and includes four large tooth alveoli and the remnants of tooth roots displaying thecodont implantation. Each of the enlarged alveoli measures approximately 15–20 mm labiolingually, and possible remnants of a pair of smaller posterior alveoli are also present. Although the bone is poorly preserved and badly weathered, the presence of four large terminal alveoli rather than six suggests this element is part of the premaxillary rosette rather than the dentary, if it belongs to a phytosaur. The alveoli are distributed evenly across the midline of the element, representing two left and two right alveoli; however, the midline suture is indiscernible. The two anterior alveoli are located extremely close to the midline, while the large posterior alveoli are shifted slightly more laterally, as is usually the case in the premaxillary terminal rosette of phytosaurs.

The pattern of tooth placement displayed by the large anterior alveoli is unusually narrow for phytosaurs. This may be due to preservation and weathering: on the exposed surface, the alveoli appear to be directed slightly medially as they exit the preserved portion of bone and shallow sulci leading upward and medial from the alveoli hint at the continuation of each alveolus into material that has been lost to erosion. It therefore seems possible that the exposed part of the terminal rosette is a weathered cross-section, part way through the tip of the snout in dorsal view (Fig. 7). Based on this assessment, the probable direction of each alveolus is consistent with the direction and angle of teeth in the terminal rosette of phytosaurs, i.e. the anterior-most teeth project almost straight ventrally, with the roots curving posterodorsally, and the second set of terminal teeth project ventrolaterally, with the roots

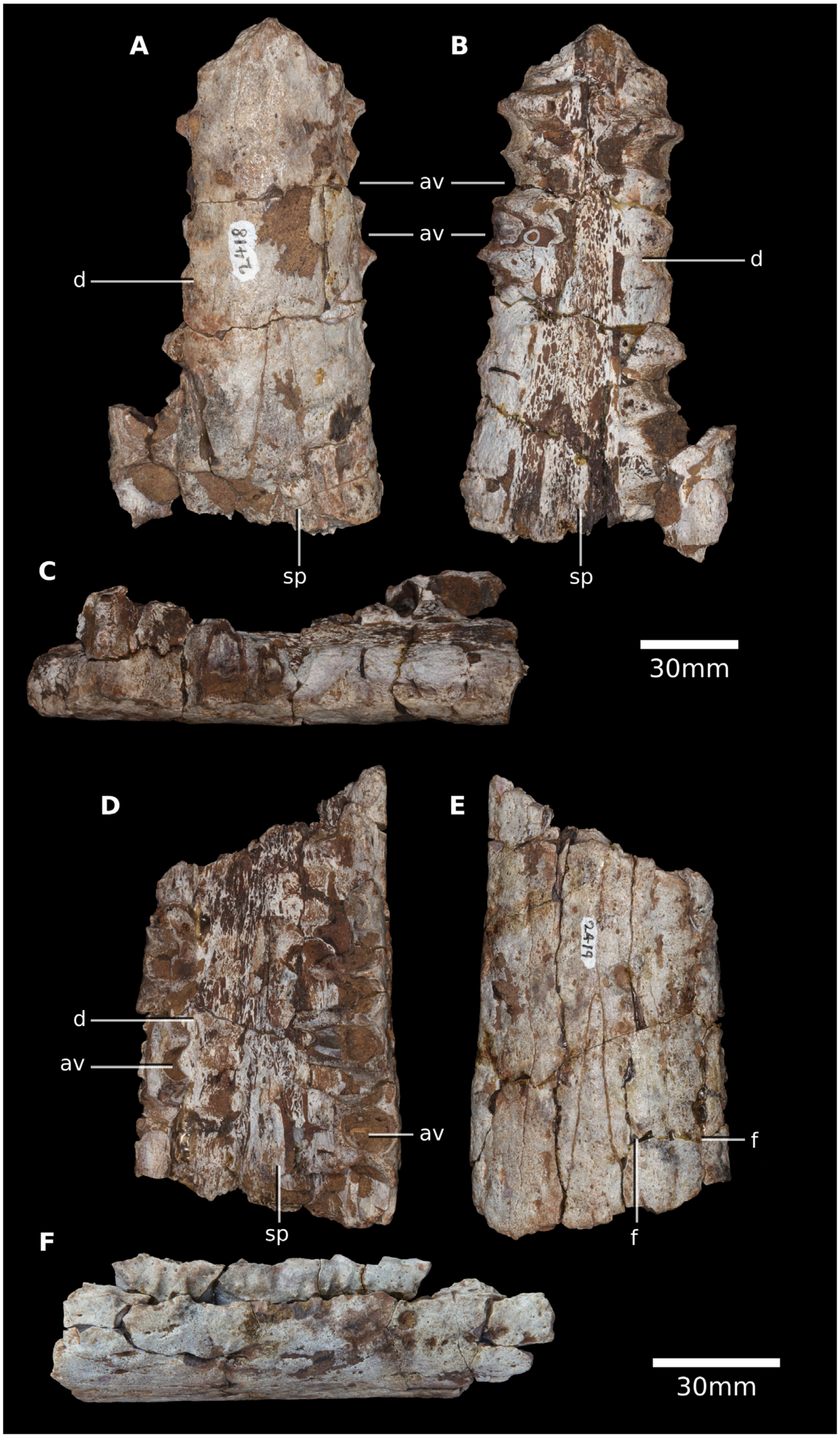


Fig. 5. Partial mandibles of a taxonomically indeterminate phytosaur collected from the Tashinga Formation of 'Steve's Phytosaur Site'. A–C, NHMZ 2418 in dorsal (A), ventral (B) and right lateral (C) views. D–F, NHMZ 2419 in dorsal (D), ventral (E) and right lateral (F) views. Abbreviations: av, alveolus; d, dentary; f, parallel rows of foramina; sp, splenial.

curving dorsally and posteromedially. The narrowness of the rosette may therefore be due to the dorsomedial direction of the posterior pair of enlarged alveoli, and the exposed face being a cross-section dorsal to the actual alveolar openings.

The presence of a set of four enlarged anterior teeth, and the possible presence of a much smaller pair of posterior teeth are suggestive of a phytosaurian origin for this fragment. There is no sign of a terminal external naris, which would also be consistent

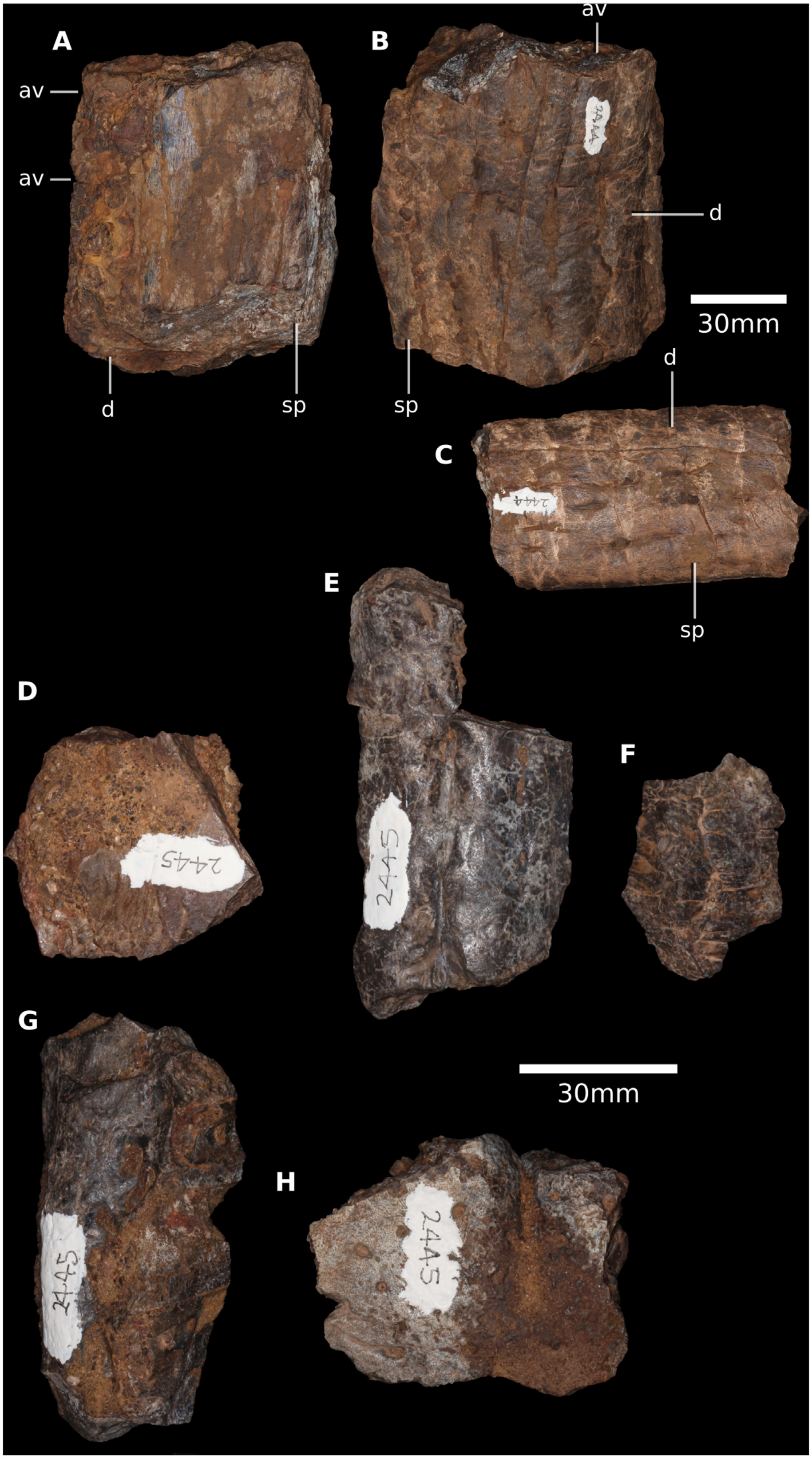


Fig. 6. Partial mandibles of a taxonomically indeterminate phytosaur collected from the Tashinga Formation of the 'Coprolite Hill' site. A–C, NHMZ 2444, consisting of a right dentary, right splenial and a small portion of the left splenial in dorsomedial (A), ventrolateral (B) and right lateral (C) views. D–H, NHMZ 2445, various dentary fragments, potentially representing more than one individual. Abbreviations: av, alveolus; d, dentary; sp, splenial.

with a phytosaur; however, it remains possible that any narial material that was present was weathered away, alongside the rest of the dorsal surface of the snout. Therefore, although a phytosaur origin for this terminal rosette seems most likely, it is not currently possible to rule out other archosauromorph affinities for this specimen.

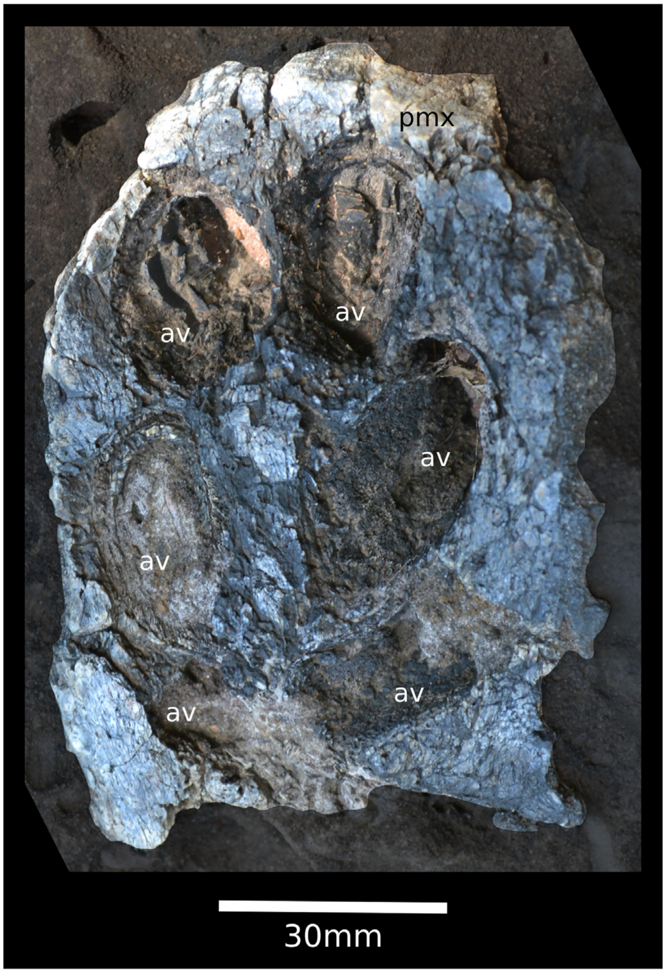


Fig. 7. Terminal rosette of a ?phytosaur premaxilla in ventral view, photographed in situ in the Tashinga Formation at the 'Phytosaur Gully' locality. Anterior is towards the top of the figure. This specimen was not collected. Abbreviations: av, alveolus; pmx, premaxilla.

5.3. Teeth

At least 100 teeth collected from all four localities can be attributed to phytosaurs (NHMZ 2422–2425, 2440, 2443), although the majority have been collected from 'The Dentist' site. Two tooth crown morphologies are present in the sample: elongate, conical and recurved crowns versus those that are laterally compressed and phylloform (Fig. 8). Both tooth types are approximately equal in abundance. None of the teeth are complete: all lack roots and many lack parts of the crown. Many of the teeth are abraded and lack enamel. Conical teeth range in size considerably, with apicobasal lengths of approximately 35–100 mm and basal diameters of 10–32 mm, whereas the phylloform teeth are more uniform in size, with apicobasal lengths of 45 mm and maximum mesiodistal widths of approximately 25 mm.

In labial/lingual view, the phylloform tooth crowns taper apically, are mesiodistally expanded with respect to their bases and have subtriangular outlines (Fig. 8A). In mesial/distal view, the tooth apex is inclined slightly medially. They are almost symmetrical about their long axes in labial/lingual view, though the tip is slightly offset distally to produce a very slight recurvature. Both the mesial and distal margins bear sharp carinae, which are sometimes very finely serrated, with a high serration density and forming a right angle perpendicular to the carinae. Where present, the enamel is usually smooth and unornamented, but short, apicobasally extending ridges are sometimes present close to the crown base, and these are only a few millimetres in length. The labial crown surfaces are mesiodistally and apicobasally convex, while the lingual surface is weakly convex mesiodistally and shallowly concave apicobasally, to produce a narrow, 'D'-shaped cross-section. The teeth have elongation indices (of tooth apicobasal height/tooth mesiodistal width) of approximately 2.0 (Fig. 8A).

By contrast, many of the conical teeth are more strongly recurved distally (and weakly curved lingually also) and are substantially more elongate with minimum elongation indices of 3.0–5.0 (Fig. 8B). As with the phylloform teeth, they have strongly convex labial margins and weakly concave/convex lingual margins, producing a 'D'-shaped basal cross-section. Prominent carinae are present on the mesial and distal margins, extending from the crown apex basally, but they do not reach the crown base terminating a short distance apical to it. The enamel surfaces are generally smooth, but sometimes bear faint wrinkles close to the carinae on both the lingual and labial surfaces, and short apicobasally extending ridges are occasionally present near the crown base. The carinae bear serrations identical to those of the phylloform teeth.

The dentition, when taken as a whole, exhibits features characteristic of phytosaurs that distinguish them from those of other Mesozoic reptiles (Fig. 8). The array of tooth morphologies found corresponds well with the pattern of heterodonty displayed by almost all phytosaur taxa (Hungerbühler, 2000; Nesbitt, 2011; Ezcurra, 2016). In the anterior terminal rosette, phytosaurs possess large, robust and elongated conical teeth, followed posteriorly by smaller, elongate, conical and recurved teeth that may or may not possess carinae. Posteriorly the dentition becomes more phylloform and blade-like, with strong carinae and labiolingual asymmetry. In addition, the possession of both carinae bearing small serrations set at 90° to the tooth-edge and longitudinal apicobasal striations are also characteristic of the group (Nesbitt, 2011; Ezcurra, 2016).

5.4. Osteoderms

NHMZ 2420 includes a number of unassociated partial osteoderms, collected from 'Steve's Phytosaur Site' (Fig. 9). All of the osteoderm fragments are broken along their margins, so their original outlines cannot be determined. Several of these have prominent pyramidal bosses that are offset from the centre of the osteoderm, towards the lateral(?) margin (e.g., Fig. 9C, E). One of these osteoderms possesses a series of strong, radiating ridges that extend from the boss towards the margins along the external surface (Fig. 9C). Other osteoderms have a relatively smooth external surface with a series of small pits that surround the boss (Fig. 9E). Two osteoderms are sub-symmetrical in outline with a midline keel, and one of these has an extremely rugose external surface (Fig. 9B). In all four osteoderms the internal surface is smooth and bears a few small nutrient foramina (Fig. 9A–C). The curvature of this surface varies: in some it is shallowly convex, while in others it is mildly concave.

6. Discussion

6.1. Paleoenvironment of the phytosaur localities

The upper part of the Tashinga Formation is a continental red-maroon succession that can be subdivided into two facies associations. The first, the fine-grained facies, contains the phytosaur material and is represented by sandstones, siltstones and mudstones defined by paleo-pedogenic alteration, e.g., invertebrate trace fossils, pedogenic nodules, desiccation cracks and rhizocretions, with subordinate pedogenic nodule conglomerates. These features conform to 'Facies Ta' as described by Hosking (1981). In contrast, the coarse-grained facies is dominated by massive or trough cross-bedded, medium- to coarse-grained sandstones and conglomerate beds. This coarse-grained facies typically bears fossil wood clasts ranging in size from 2 cm to >2 m in length.

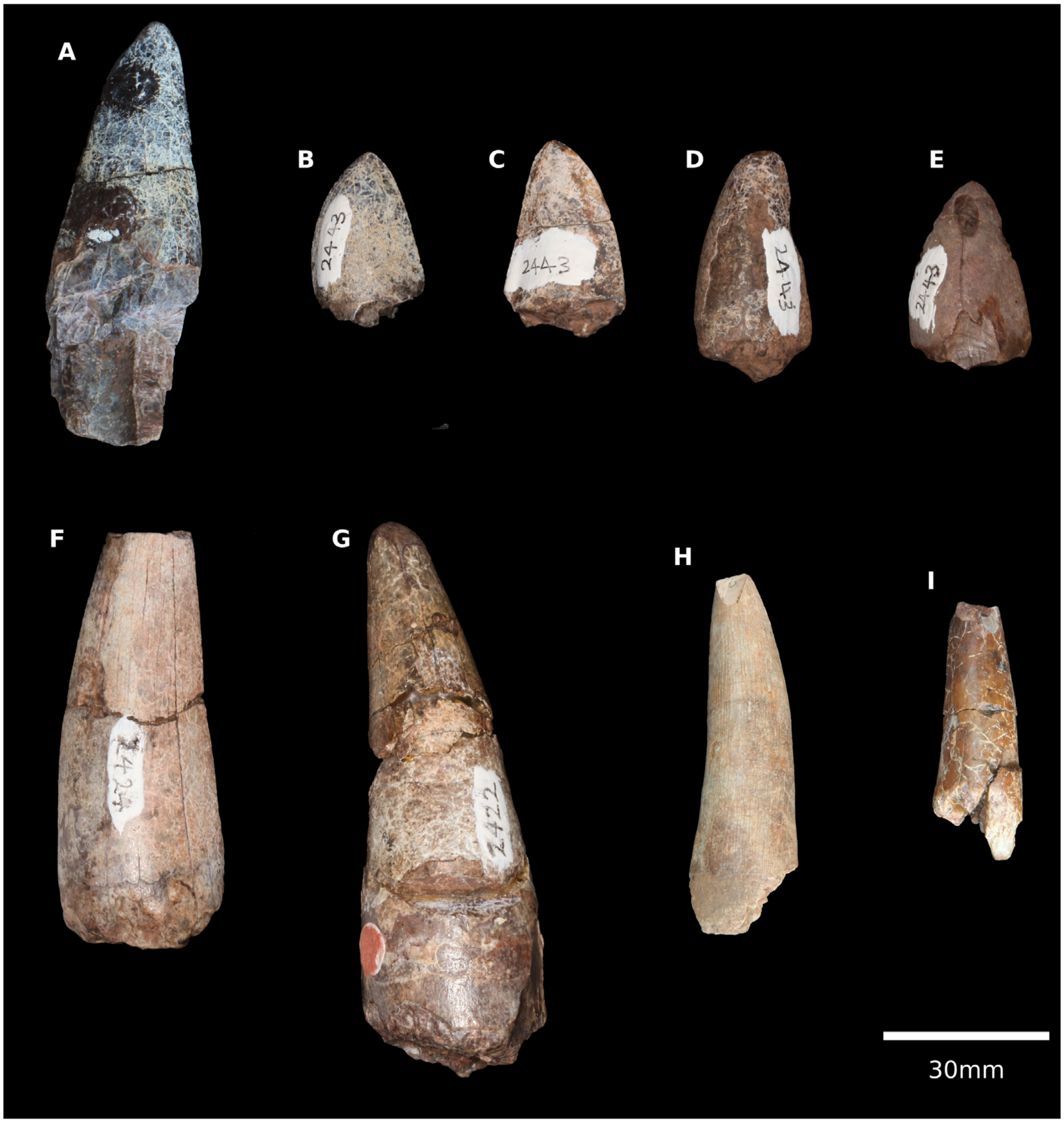


Fig. 8. Isolated teeth of a taxonomically indeterminate phytosaur from the Tashinga Formation of 'The Dentist' site. A–E, examples of phylloform tooth morphotypes (NHMZ 2443); F–I, examples of conical tooth morphotypes (F, NHMZ 2424; G, NHMZ 2422; H, I, NHMZ 2424). NB, these isolated teeth were registered collectively under a small series of batch numbers, but this does not imply that they were found associated and it is unlikely that they are from the same individuals.

In general, the four phytosaur-bearing sites are situated in horizons that are associated with a paleo-pedogenically altered fine-grained facies indicative of lower energy conditions. These facies associations are suggestive of a vegetated floodplain (e.g., rhizocretions, paleo-pedogenic overprinting and pedogenic nodules) that experienced periodic quiescence, allowing for intensive bioturbation, vegetation development and the concentration of fossil remains (e.g., body fossils and coprolites). The interbedded thin, massive, very-fine grained sandstone beds (Fig. 3A) provide evidence for increasing frequency of higher energy events. These sandstone beds become increasingly thicker and coarser-grained up-section (Fig. 3A) and form stacked, multistory units. The fine-grained facies features are congruent with short-lived flood events followed by seasonal flooding in a fluvio-lacustrine environment. The reworked pedogenic nodule conglomerate (Fig. 3B, C) indicates high energy events capable of locally denuding areas of the floodplains and concentrating fossil remains and pedogenic nodules. The coarser-grained facies represent high energy intervals some of which are associated with the channel systems where in places large tree trunks and clasts have been incorporated (Fig. 3).

6.2. Implications for correlations with other units regionally and worldwide

In this study we have adopted Hosking's (1981) informal Tashinga Formation and provide local stratigraphic context for the new phytosaur-bearing sites. We note two distinct facies associations that, due to the lack of formal lithostratigraphic descriptions, are hard to define as either the 'Fine Red Marly Sandstone' or 'Pebbly Arkose' subunits proper. It is most likely that the fossil localities, because of their paleo-pedogenic alteration and the presence of pedogenic nodules, are in the 'Ta facies' of the Tashinga Formation (Hosking, 1981). This would indicate that these sites belong to the 'Fine Red Marly Sandstone', but more detailed field descriptions and relationships are needed to confirm this assessment. However, we can state confidently that the sites lie within the upper part of the Tashinga Formation, below the Forest Formation (=Forest Sandstone).

In the Mid-Zambezi Basin, the Tashinga Formation, and in particular the 'Pebbly Arkose' subunit, has been regarded as Late Triassic in age. This is based on the abundant fossil wood it contains, but in the absence of other key index fossils or radiometric dates it could only be correlated

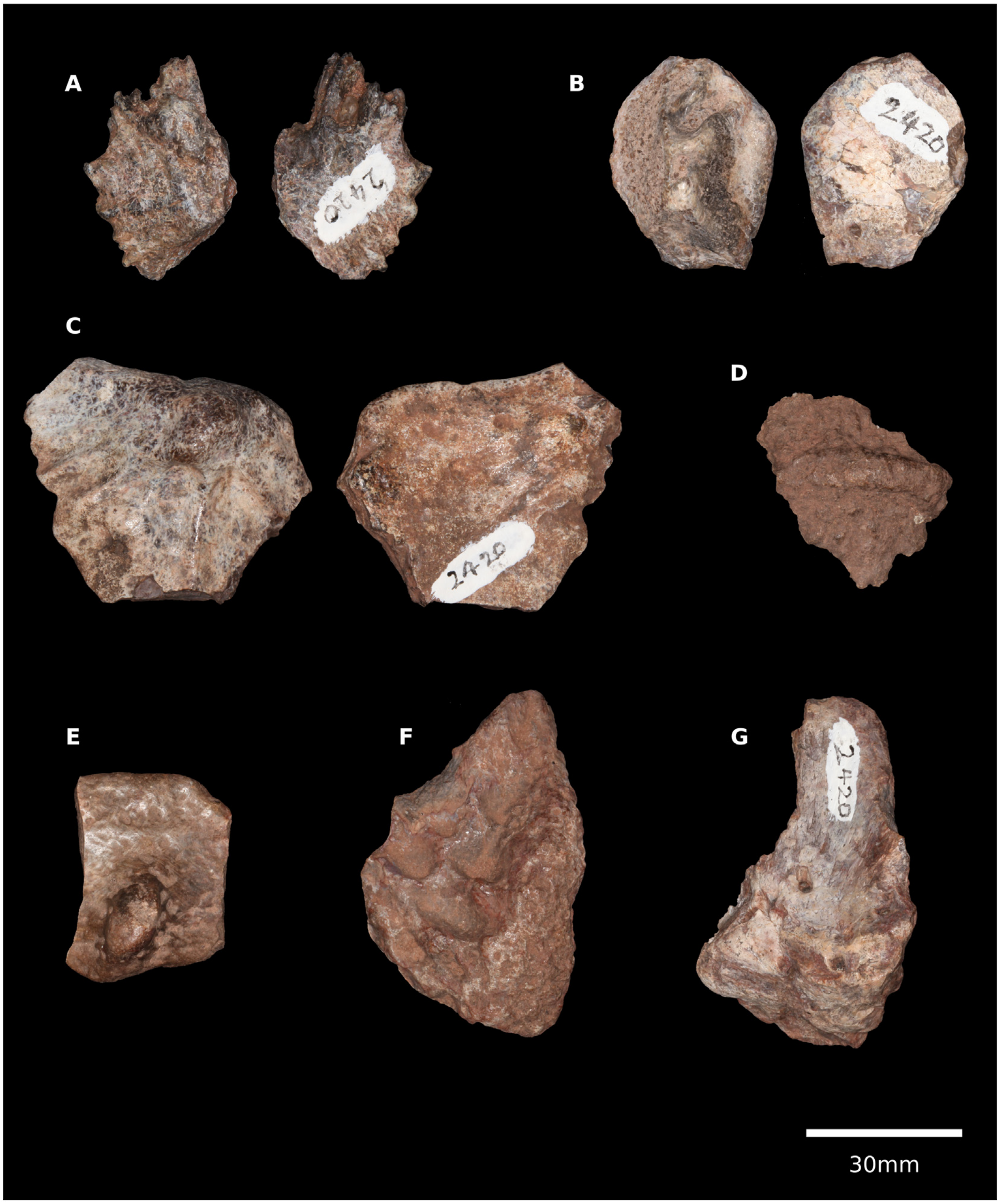


Fig. 9. Isolated osteoderms of a taxonomically indeterminate phytosaur from the Tashinga Formation of 'Steve's Phytosaur Site', probably representing multiple individuals (NHMZ 2420). A, NHMZ 2420.1 in external (left) and internal (right) views; B, NHMZ 2420.2 in external (left) and internal (right) views; C, NHMZ 2420.3 in external (left) and internal (right) views; D, NHMZ 2420.4 in external view; E, NHMZ 2420.5 in external view; F NHMZ 2420.6 in external view; G, NHMZ 2420.7 in external view.

tentatively with units in neighboring basins (e.g., Cabora Bassa Basin) and the main Karoo Basin (Thompson, 1975; Watkeys, 1979; Cooper, 1980; Johnson et al., 1996; Bordy and Catuneanu, 2002a, 2002b). An uppermost constraining age for fossils from the 'Upper Karoo Group' of the Mid-Zambezi Basin is supplied by the radiometrically dated Batoka Basalts (~182 Ma; Early Jurassic, Toarcian; Duncan et al., 1997). Material of the early sauropod *Vulcanodon karibiensis* was originally reported from sandstone interbeds within the Batoka Basalts but is now believed to be from within the older Forest Formation (?Sinemurian–Pliensbachian; Viglietti et al., 2018). The lower parts of the Forest Formation record the co-occurrence of *Megapnosaurus* (formerly *Syntarsus*/*Coelophysis*) and *Massospondylus* in the Mana Pools Basin (Raath et al., 1970; Bond, 1973). These taxa co-occur in the upper Elliot Formation and lower parts of the Clarens Formation, thus providing a preliminary means to correlate the Forest Formation to the main Karoo Basin, suggesting a similar Rhaetian–Early Jurassic age (Knoll, 2005; Sciscio et al., 2017). These biostratigraphical constraints provide a minimum age for the underlying uppermost Tashinga Formation as Late Triassic (~Rhaetian).

The newly described phytosaur material described herein provides new biostratigraphic evidence confirming the Late Triassic age of the upper part of the Tashinga Formation in the Mid-Zambezi Basin. Given the restriction of phytosaurs to Late Triassic sediments worldwide (Stocker and Butler, 2013), and the maximum depositional age of 209.2 ± 4.5 Ma obtained stratigraphically below 'The Dentist' locality, this new occurrence reinforces our biostratigraphic inferences. Given these new data, the Tashinga Formation can now be correlated more confidently with the Stormberg Group in the main Karoo Basin, despite the lack of overlapping fossil taxa. The upper part of the Tashinga

Formation appears to have been deposited contemporaneously with the Late Triassic (Norian–Rhaetian) lower Elliot Formation (Stormberg Group) of South Africa (Sciscio et al., 2017).

Previously, subunits within the Mid-Zambezi Basin, particularly the 'Pebbly Arkose', were loosely correlated with a much thicker unit in the neighboring Cabora Bassa Basin, termed the Pebbly Arkose Formation (Johnson et al., 1996; Catuneanu et al., 2005). The Western Cabora Bassa Basin's Pebbly Arkose Formation has produced rhynchosaur and *Dicroidium* fossils, both of which are considered to be Late Triassic (Carnian) index taxa (Raath et al., 1992). In general, rhynchosaurs are found associated with phytosaurs and metoposaurs in similarly-aged basins in India (Chatterjee, 1978), Brazil (Kischlat and Lucas, 2003) and Argentina (Bonaparte, 1966). However, the late Norian/early Rhaetian date for the Tashinga Formation 'Pebbly Arkose' subunit indicates that it was likely deposited after the global extinction of rhynchosaurs, which is thought to have occurred prior to the Norian (e.g., Lucas, 1998; Ezcurra et al., 2016). Thus, the 'Pebbly Arkose' facies was probably deposited at least partially diachronously in these neighboring basins, with the onset (and potentially termination) of deposition occurring much earlier in the Western Cabora Bassa Basin (see Oesterlen, 1998).

Our detrital zircon date and the new phytosaur material also assists in correlating the Tashinga Formation with the upper Chinle Formation in the southwestern United States. Recent U-Pb dates retrieved from the upper Chinle Formation have yielded ages between ~218–212 Ma for the most important fossil bearing units which include phytosaur remains (Parker, 2005; Irmis et al., 2011; Martz and Parker, 2017). Heuristic biostratigraphic correlations now link the Mid-Zambezi Basin's Tashinga Formation to other Late Triassic deposits in Laurasian continents (e.g., Buffetaut and Ingavat, 1982; Morales and Ash, 1993; Renesto and Lombardo, 1999; Zeigler et al., 2002; Heckert et al., 2005; Parker and Irmis, 2005; Brusatte et al., 2013).

6.3. Phytosaur geographic distribution

The phytosaur specimens described herein represent the first records of this clade in sub-Saharan mainland Africa. Although they are too poorly preserved to enable the erection of a new taxon, their provenance, which is far distant from that of other phytosaur occurrences, suggests that the discovery of more complete material would confirm its identification as a distinct species. These occurrences are significant as they extend the global distribution and paleolatitudinal range of this group to a previously unsampled area and augment the handful of Gondwanan records known for the clade (see reviews in Buffetaut, 1993; Brusatte et al., 2013; Stocker and Butler, 2013).

Previously, it was suggested that that absence of phytosaurs from southern Africa might be due to a latitudinal preference, as all known localities were situated in the paleotropics, at paleolatitudes between ~30°N and ~30°S (Shubin and Sues, 1991). However, the discovery of phytosaur material from the Baltic region, which was at a paleolatitude of approximately 45° N during the Late Triassic, undermined this hypothesis (Brusatte et al., 2013). The new Zimbabwean localities reported herein were at paleolatitudes of approximately 40°S at this time (Van Hinsbergen et al., 2015: Fig. 10), further demonstrating that they were not limited to the paleotropics. Moreover, more recent paleogeographic reconstructions place the phytosaur localities known from Brazil (Kischlat and Lucas, 2003) and India (e.g., Chatterjee, 1978) at similarly high southern paleolatitudes (Van Hinsbergen et al., 2015).

Although the vertebrate faunas of the Stormberg Group in the main Karoo Basin of South Africa and Lesotho have been sampled extensively, phytosaurs have never been identified in this region (see reviews in Knoll, 2004, 2005). These localities would have been situated at more southerly paleolatitudes than those in Zimbabwe, so it is possible that the Zimbabwean sites are close to a potential southern limit for the clade, even if their total latitudinal range is now greater than previously appreciated. Climate or local habitat conditions have been suggested as a limiting factor for phytosaurs, which would be congruent with their semi-aquatic habits and their coincident distribution with aquatic metoposaurid temnospondyls (Buffetaut, 1993; Brusatte et al., 2013). It has been noted that the majority of phytosaur occurrences worldwide coincide with environments that are seasonally wet, with tropical, humid summers (see Sellwood and Valdes, 2006) and it has been proposed that they were excluded from regions that experienced more arid climates (Brusatte et al., 2013). However, some phytosaur remains

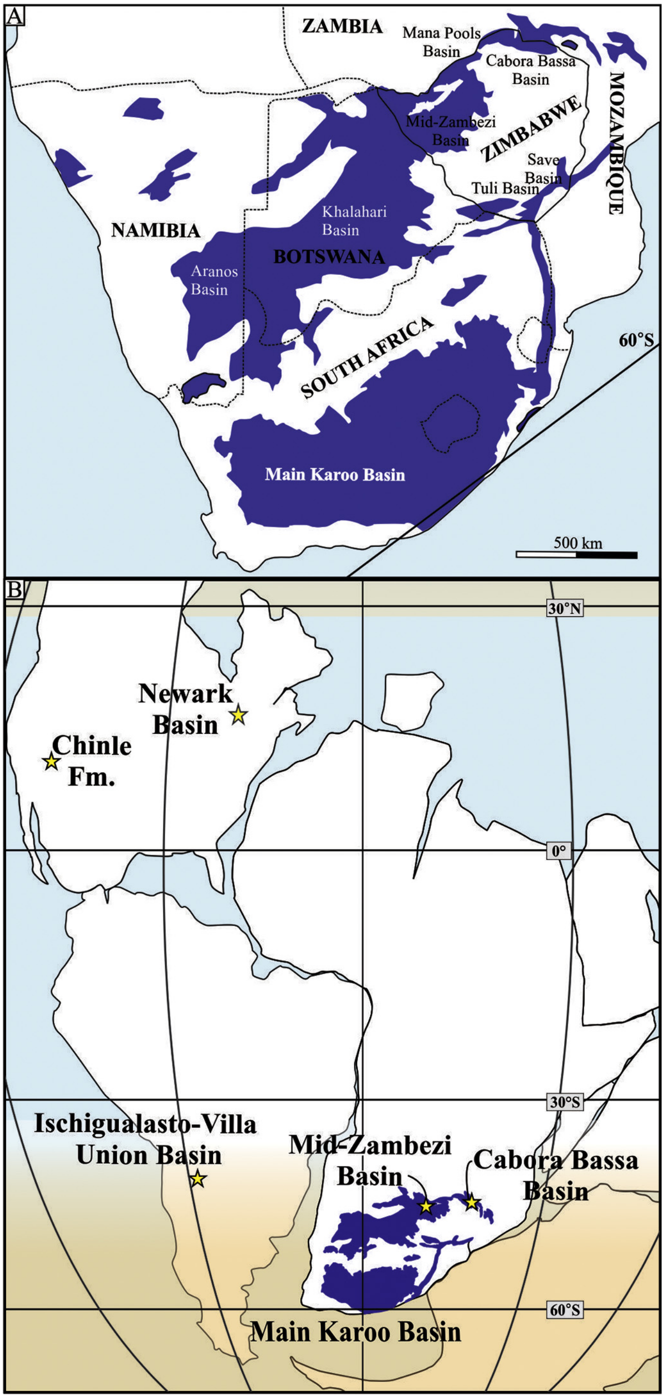


Fig. 10. A, reconstruction of the present-day distributions of the main Karoo Basin and Karoo-aged basins in southern Africa and their Late Triassic paleolatitudes. B, Late Triassic paleogeographic map, adapted from Kent et al. (2014), illustrating the position of the Karoo basins relative to other global basins in North America (i.e., Newark Basin and Chinle Formation, Colorado Plateau) and South America (Ischigualasto-Villa Unión Basin) at ~210 Ma (see Kent et al., 2014, 2017). Estimated broad zonal climatic belt of decreasing humidity-increasing aridity is indicated by orange-shaded zone that runs from ~30°S as taken from Kent et al. (2014, 2017).

from the upper Chinle Formation have been recovered from braided channels within arid paleoenvironments (Martz et al., 2014), so it is possible that at least some taxa might have been capable of living in much drier areas. General circulation models indicate that several climatic zones were present in southern Africa during the Late Triassic, although the resolution of these models makes it difficult to distinguish between localities that are only a few degrees of latitude apart (Sellwood and Valdes, 2006). Nevertheless, these models suggest that the Mid-Zambezi Basin was in an area that experienced either cool temperate or warm temperate humid climates (Sellwood and Valdes, 2006). The other fossil vertebrates co-occurring with phytosaurs in the Tashinga Formation, lungfish and metoposaurids (see below), as well as the presence of abundant fossil wood, also suggest that this region received high rainfall for at least part of the year.

It is noteworthy that to the north of the Zimbabwean localities, general circulation models predict desert-like conditions (Sellwood and Valdes, 2006), which might have acted as a barrier to phytosaur dispersal, suggesting that they either reached southern Africa before this extensive arid zone was in place or that temporary climatic ameliorations (or a series of more localized mesic areas) enabled them to cross this apparent obstacle. The only phytosaur locality in Brazil falls firmly within this central Gondwanan desert, partially undermining their association with wet environments, but as noted by Brusatte et al. (2013) this might reflect specific local climatic conditions. Areas immediately to the south of the narrow humid temperate belt that crossed southern Africa included a patchwork of humid and dry temperate environments (Sellwood and Valdes, 2006), some of which might have had conditions that would have been suitable for phytosaurs. In particular, lower Elliot Formation paleoenvironments are known to have been at least seasonally wet and to have supported permanent water courses (e.g., Smith et al., 1993; Bordy et al., 2004), so the absence of phytosaurs from the main Karoo Basin remains mysterious. Further research is needed to determine the full geographic and temporal ranges of phytosaurs in Gondwana (Chatterjee, 1978; Dutuit, 1978; Jalil, 1999; Kischlat and Lucas, 2003; Rayfield et al., 2009).

6.4. Late Triassic paleoecology of the Mid-Zambezi Basin

The Tashinga Formation yields a biota that is unique among those known from the Karoo-aged basins of southern Africa. The majority of Late Triassic/Early Jurassic ecosystems in the region, such as those recovered from the Karoo and Tuli basins, are dominated by terrestrial taxa, notably sauropodomorph dinosaurs, alongside early crocodylomorphs, ornithischian dinosaurs, tritylodontid synapsids and rare members of other clades, such as testudinates and theropod dinosaurs (e.g., Haughton, 1924; Bond, 1973; Kitching and Raath, 1984; Olsen and Galton, 1984; Knoll, 2004, 2005). Aquatic and semi-aquatic taxa, such as lungfish and temnospondyls, are either rare or totally absent in most of these localities (Kitching and Raath, 1984; Marsicano et al., 2014). By contrast, the new Tashinga Formation localities described herein have not yielded any sauropodomorph dinosaur specimens but are dominated numerically by phytosaur elements and lungfish toothplates, which co-occur with rarer metoposaurid temnospondyl material (see Supplementary Fig. S1). The only strictly terrestrial vertebrate remains yet recovered from the phytosaur-bearing localities are rare teeth of an indeterminate carnivorous archosaur (either a rauisuchian pseudosuchian or a theropod dinosaur). These new sites therefore represent the first example of a Late Triassic terrestrial-aquatic biome from the whole of southern Africa. However, other laterally equivalent facies within the Tashinga Formation do yield sauropodomorph material, demonstrating that this unit samples a range of contemporary environments that form parts of the same broader ecosystem.

Fossil wood is common in the Tashinga Formation, including the remains of locally abundant large trees with trunk diameters of up to 1 m, which have been referred tentatively to *Rexoxylon* or *Dadoxylon* (Marsh and Jackson, 1974). The co-occurrence of fossil forests with phytosaurs, lungfish and metoposaurs thus provides the first Gondwanan analogue for various North American Late Triassic biomes, notably that recovered from various members within the Chinle Formation of Arizona and adjacent areas (latest Carnian–early Rhaetian: Ramezani et al., 2011), which yields abundant material of aquatic and semi-aquatic taxa, as well as fossil forests, and that also lacks any indication of sauropodomorph dinosaurs (Irmis, 2005; Parker, 2005). However, the freshwater biota of the Tashinga Formation occurs at a much higher latitude than that of the Chinle Formation, as the latter inhabited an area that was 10–15°N of the paleoequator.

7. Conclusions

The first radioisotopic date for the Upper Karoo Group of the Mid-Zambezi Basin, of 209.2 ± 4.5 Ma (late Norian–early Rhaetian), allows a robust correlation between the upper part of the Tashinga Formation and the lower Elliot Formation (Stormberg Group) of South Africa's main Karoo Basin. This date is complemented by the discovery of the first phytosaur material from sub-Saharan mainland Africa in the upper part of the Tashinga Formation, which itself is indicative of a Late Triassic age for this unit in the Mid-Zambezi Basin.

The upper part of the Tashinga Formation represents a fluvio-lacustrine environment in a semi-arid setting prone to monsoon-like conditions. The paleoclimatic and paleofaunal assemblage represented by the Mid-Zambezi and Cabora Bassa basins appears to signify a southern Gondwanan analogue to Late Triassic Laurasian sites (e.g., Chinle Formation, southwestern USA). The phytosaur specimens also extend the geographic distribution of this clade in Gondwana and its paleolatitudinal range globally. More broadly, the Tashinga Formation can now be demonstrated to represent an important Late Triassic deposit that can be correlated with the upper Chinle Formation, the Newark Basin and other well-known Laurasian Late Triassic deposits. The fauna reported herein also represents the first freshwater-aquatic biome reported from the Late Triassic of southern Africa, adding substantially to our knowledge of the paleoenvironments present in the region.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gr.2019.12.008.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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