



Paranthodon

Iain Reid* *et al.*

Abstract

Paranthodon (*/pəˈrænθədɒn/*) is a [genus](#) of [extinct stegosaurian](#) dinosaur that lived in [South Africa](#) during the [Early Cretaceous](#), between 139 and 131 [million years ago](#). Discovered in 1845, it was one of the first stegosaurians found. Its only remains, a partial skull and isolated teeth, were found in the [Kirkwood Formation](#). British paleontologist [Richard Owen](#) initially identified the fragments as those of the [pareiasaur Anthodon](#). After remaining untouched for years in the [British Museum of Natural History](#), the partial skull was identified by South African paleontologist [Robert Broom](#) as belonging to a different genus; he named the specimen [Palaeoscincus africanus](#). Several years later, Hungarian paleontologist [Franz Nopcsa](#), unaware of Broom's new name, similarly concluded that it represented a new [taxon](#), and named it [Paranthodon owenii](#). Since Nopcsa's species name was assigned after Broom's, and Broom did not assign a new genus, both names are now [synonyms](#) of the current binomial, [Paranthodon africanus](#). The genus name combines the [Ancient Greek](#) [para](#) (near) with the genus name [Anthodon](#), to represent the initial referral of the remains.

In identifying the remains as those of [Palaeoscincus](#), Broom initially classified [Paranthodon](#) as an [ankylosaurian](#), a statement backed by the research of [Coombs](#) in the 1970s. However, in 1929, [Nopcsa](#) identified the taxon as a [stegosaurid](#), with which most modern studies agree. In 1981, the genus was reviewed with modern taxonomy, and found to be a valid genus of stegosaurid. However, a 2018 review of [Paranthodon](#) could only identify one distinguishing feature, and while that study still referred it to [Stegosauria](#) based on similarity and multiple phylogenetic analyses, no diagnostic features of the group could be identified in [Paranthodon](#).

History of discovery

In 1845, amateur geologists [William Guybon Atherstone](#) and [Andrew Geddes Bain](#) discovered several fossils near [Dassieklip](#), [Cape Province](#), in the [Bushmans River Valley](#).^{[1][2]} This was the first dinosaur find in all of the Southern Hemisphere and Africa.^[3] In 1849 and 1853, Bain sent some of the fossils to [Richard Owen](#) for identification. Among them was an upper jaw Bain referred to as the "Cape [Iguanodon](#)", so the site was named "Iguanodonhoek". Atherstone published a short paper about the discovery in 1857,^[1] but lamented in 1871 that it had thus far received no attention in London.^{[2][4]} Only in 1876 were a series of specimens from the collection named by Owen as [Anthodon serrarius](#), basing the generic name on the resemblance of the teeth to a flower.^[5] The partial [holotype](#) skull BMNH 47337, the left jaw BMNH 47338, the [matrix](#) BMNH 47338 including bone fragments and impressions of the [anterior](#) skull, and the [vertebrae](#) BMNH 47337a were all assigned to [Anthodon](#).^[6] In 1882, [Othniel Charles Marsh](#)

assigned [Anthodon](#) to [Stegosauridae](#) based on BMNH 47338, and in 1890, [Richard Lydekker](#) found that although [Anthodon](#) was a [pareiasaur](#), its teeth were similar to those of the [Stegosauridae](#).^[6] Lydekker in 1890 also corrected a mistake of Owen, who had incorrectly summarized all the material as coming from a single locality, whereas there was separate material from two clearly distinct localities.^[2]

In 1909, [Robert Broom](#) visited the collection of the [British Museum of Natural History](#). He concluded that Owen had mixed the partial distorted skull, teeth, and a [mandible](#) of a [pareiasaur](#) and a partial upper jaw of a dinosaur, BMNH 47338, which were actually from two different species.^{[5][7]} Broom kept the name [Anthodon](#) for

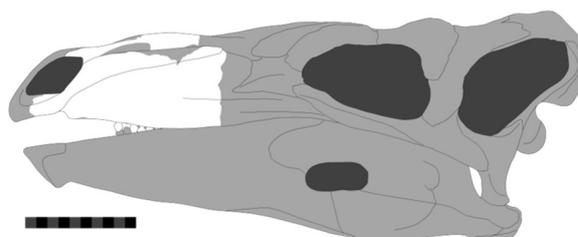


Figure 1 | Reconstruction of the skull of [Paranthodon](#); grey material is unknown. Scale bar = 10cm.

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the pareiasaur, but identified the other fossil as a member of the genus *Palaeoscincus*, naming the new species *Paleoscincus africanus* in 1912. He found that the anatomy of the teeth were quite different, even though they resembled each other, as well as those of *Stegosaurus*.^{[2][7]} In 1929, Franz Nopcsa, unaware of Broom's previous publication, provided a second novel name as *D.M.S. Watson* believed that the jaw should be differentiated from *Anthodon*.^{[2][8]} Nopcsa named the species *Paranthodon Owenii*, with the generic name derived from the Latin *para*, meaning "similar", "near", or "beside", and *Anthodon*, and specific name honoring Owen.^{[8][9][10]} Per to present conventions, the specific name was later emended to *owenii*.^[6] Both names were brought into the current nomenclature by Walter P. Coombs in his 1971 dissertation as the new combination *Paranthodon africanus*, as the name *Paranthodon* was the first new generic name for the fossils and *africanus* was the first new specific name.^{[2][11]} This makes *Paranthodon africanus* the proper name for the taxon previously known as *Palaeoscincus africanus* and *Paranthodon owenii*.^{[2][6]}

Material

The holotype of *Paranthodon*, BMNH 47338, was found in a layer of the [Kirkwood Formation](#) that has been dated between the [Berriasian](#) and early [Valanginian](#) ages. It consists of the back of the snout, containing the [maxilla](#) with [teeth](#), the posterior caudodorsal ramus of the [premaxilla](#), part of the [nasals](#), and some isolated teeth probably from the lower jaw. One additional specimen was assigned to it based on the [dentition](#), BMNH (now NHMUK) R4992, including

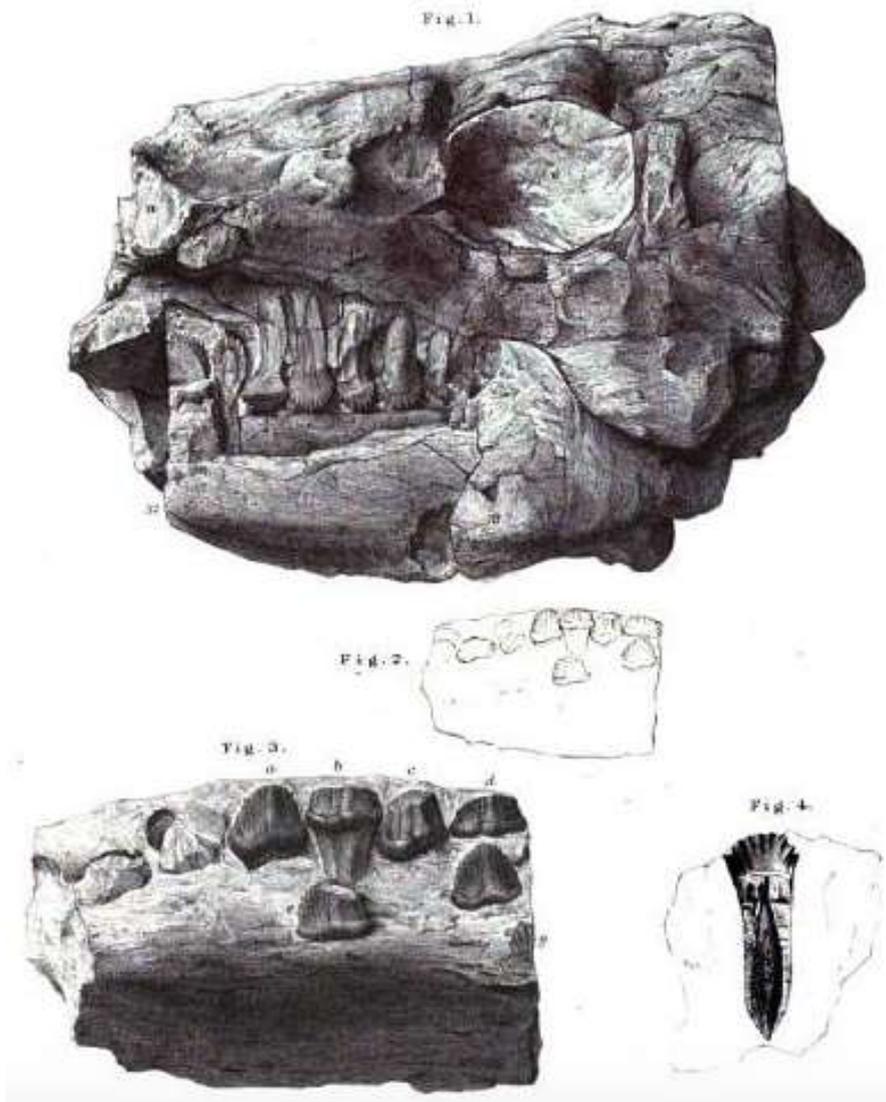


Figure 2 | Holotype of *Anthodon serrarius*; the taxon *Paranthodon* was originally assigned. C.L. Griesbach, public domain

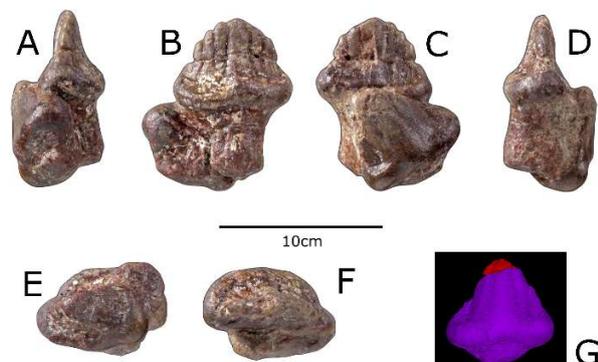


Figure 3 | Previously referred tooth (NHMUK R4992) in multiple views.

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only isolated teeth sharing the same morphology as those from the holotype.^[6] Some bones that were unidentified by the review of Galton & Coombs (1981) were described as a fragment of a vertebra in 2018 by Raven & Maidment.^[12] However, the teeth do not bear any autapomorphies of *Paranthodon* and were referred to an indeterminate stegosaurid in 2008.^[13] The teeth were identified in 2018 as also lacking any distinct stegosaurian features, and were thus designated as indeterminate *Thyreophora*.^[12]

The *Mugher Mudstone Formation* of Ethiopia was screened in the 1990s by the *University of California Museum of Paleontology*, and in it were discovered multiple dinosaur teeth, pertaining to many groups of taxa. The locality has been described as "the largest and most complete record of dinosaur fossils from a Late Jurassic African locality outside of *Tendaguru*" by Lee Hall.^[14] Two of the partial teeth discovered were referred to *Paranthodon* by Hall and Mark Goodwin in 2011. However, the reasons for the referral to *Paranthodon* were not discussed.^[14]

Description

Paranthodon was a small relative of larger stegosaurids such as *Stegosaurus*. *Thomas R. Holtz Jr.* estimated that the animal was 5.0 m (16.4 ft) long and weighed between 454 and 907 kg (1,001 and 2,000 lb).^{[9][15]} The snout is elongated, though not extremely so, and convex on top. The back of the premaxilla is long and broad, and the external nares are large. The teeth have a prominent primary ridge. The fossilized nasal and maxillary bones are relatively complete, and an incomplete premaxilla is also preserved. The partial snout resembles *Stegosaurus* in its large posterior premaxillary process and the extension of the palate. However, *Stegosaurus* was the only stegosaurid known from adequate cranial material to compare with *Paranthodon* during the 1981 review of the taxon, and even though their resemblance is great, tooth morphology is very distinguishing among the stegosaurians. For example, cranial material is known from *Stegosaurus*, *Paranthodon*, *Kentrosaurus*, and *Tuojiangosaurus*, and the tooth morphology differs in all of them.^{[6][12]}

The premaxilla of *Paranthodon* is incomplete, but the anterior process is sinuous and curves ventrally. This is similar to in *Miragaia*, *Huayangosaurus*, the ankylosaur *Silvisaurus*, and *Heterodontosaurus*, but unlike in *Chungkingosaurus*, *Stegosaurus*, *Edmontonia* and *Lesothosaurus*. The premaxilla also lacks any teeth, like in every

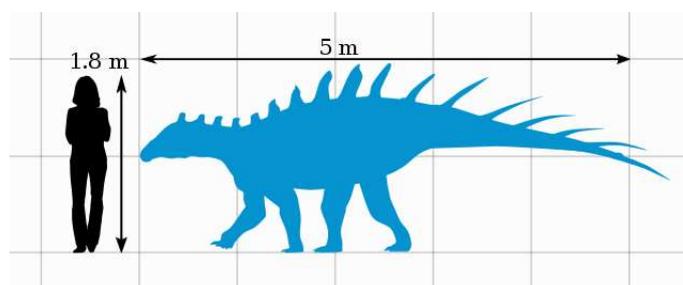


Figure 4 | Size comparison between *Paranthodon* and a human. *PaleoGeekSquared, CC-BY-SA 3.0*

stegosaur except *Huayangosaurus* where the premaxilla is preserved. Like in *Huayangosaurus* but not *Stegosaurus* or *Hesperosaurus*, the nasal fenestra faces anterolaterally, being visible from the front and sides. The naris is longer than wide like in other stegosaurs, and also has a smooth internal surface, so it was most likely a simple passage.^[12] The maxilla is roughly triangular, as in most other thyreophorans. The tooth row is horizontal in lateral view, and in ventral view it is sinuous. *Stegosaurus* and *Huayangosaurus* possess a straight tooth row in ventral view, although *Scelidosaurus* and *Jiangjunosaurus* do not.^[12] The maxilla of *Paranthodon* preserves the tooth row, and shows that there is little to no overhang. This differs from ankylosaurians, where there is a large amount of overhang of the maxilla.^[16] Like in *Stegosaurus* and *Silvisaurus* there is a diastema

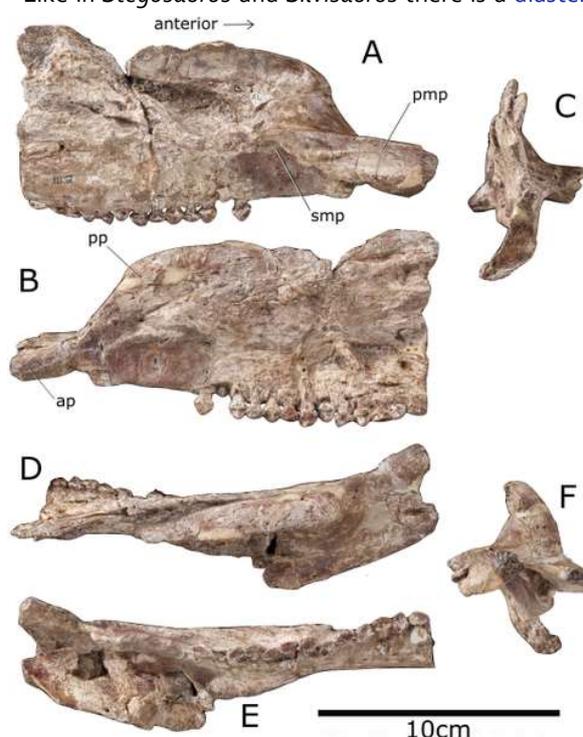


Figure 5 | Holotype maxilla and premaxilla in multiple view. *Thomas Raven & Susannah Maidment, CC-BY 4.0*

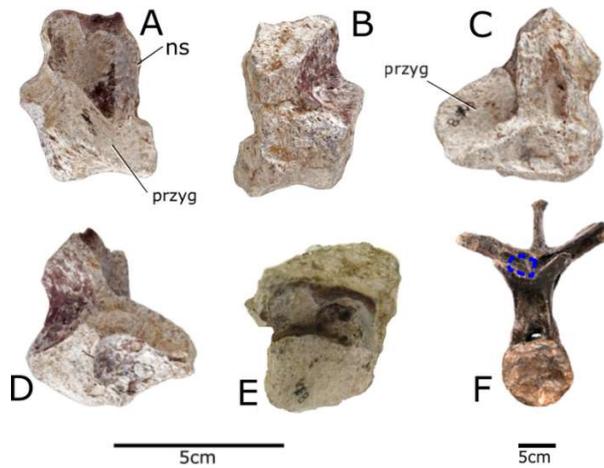


Figure 6 | Known vertebra fragments; compared to a complete *Stegosaurus* dorsal.

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(gap in the tooth row) on the maxilla in front of the tooth row. The posterior maxilla is incomplete so there is no information known about the jugal or lacrimal contact.^[12] *Paranthodon* has an elongate, dorsally convex nasal, like in most other stegosaurs. There are thickened ridges along the sides of the nasals. The preserved portion of the nasal does not contact the premaxilla or maxilla.^[12]

13 teeth are preserved in *Paranthodon*, but as they extend to the back of the maxilla there were possibly more in life. The teeth are symmetrical as in stegosaurs except *Chungkingosaurus*. Along the base of the tooth crown there is a swelling (cingulum), which is seen in all other stegosaurs from teeth are known, except *Huayangosaurus*.^[12] The teeth have a middle ridge, with five fewer prominent ridges on either side. This is similar to the size ridges seen on *Kentrosaurus*.^[16] Like all stegosaurians, the denticles on the teeth are rounded at the tips, in contrast to ankylosaurians. Also, like *Huayangosaurus*, but unlike *Kentrosaurus* and *Stegosaurus*, *Paranthodon* possesses a prominent buccal margination (a ridge beside the tooth row). *Paranthodon* teeth preserve wear, but wear is absent on most teeth, similar to *Huayangosaurus*, meaning it is likely that *Paranthodon* lacked occlusion between teeth.^[17]

As only two fragments of a vertebra are known, little anatomical details can be observed. The right transverse process and prezygapophysis are preserved. The vertebra is possibly a middle dorsal, based on the angle of the transverse process and the orientation of the prezygapophysis. Similar to *Stegosaurus* and *Chungkingosaurus* mid-dorsals, the

transverse process is angled about 60° dorsally. Unlike in all other stegosaurs except *Stegosaurus*, the prezygapophysis faces dorsally.^[12]

Classification

Currently, *Paranthodon* is classified as a stegosaur related to *Stegosaurus*, *Tuojiangosaurus*, and *Loricatosaurus*. Initially, when Broom assigned the name *Palaeoscincus africanus* to the *Paranthodon* fossils, he classified them as an ankylosaurian. This classification was later changed by Nopcsa, who found that *Paranthodon* best resembled a stegosaurid (before the group was truly defined^[18]). Coombs (1978) did not follow Nopcsa's classification, keeping *Paranthodon* as an ankylosaurian, like Broom, although he only classified it as Ankylosauria *incertae sedis*.^[19] A subsequent review by Galton and Coombs in 1981 instead confirmed Nopcsa's interpretation, redescribing *Paranthodon* as a stegosaurid from the Late Cretaceous.^{[6][16]} *Paranthodon* was distinguished from other stegosaurs by a long, wide, posterior process of the premaxilla, teeth in the maxilla with a very large cingulum, and large ridges on the tooth crowns.^[10] Not all of these features were considered valid in a 2008 review of Stegosauria, with the only autapomorphy found being the possession of a partial second bony palate on the maxilla.^[13]

Multiple phylogenetic analyses have placed *Paranthodon* in Stegosauria, and often in Stegosauridae. A 2010 analysis including nearly all species of stegosaurians found that *Paranthodon* was outside Stegosauridae,

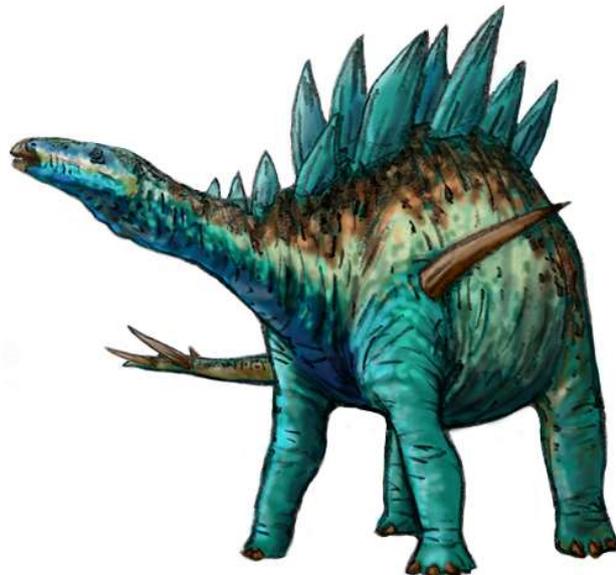


Figure 7 | Hypothetical restoration based on related stegosaurians.
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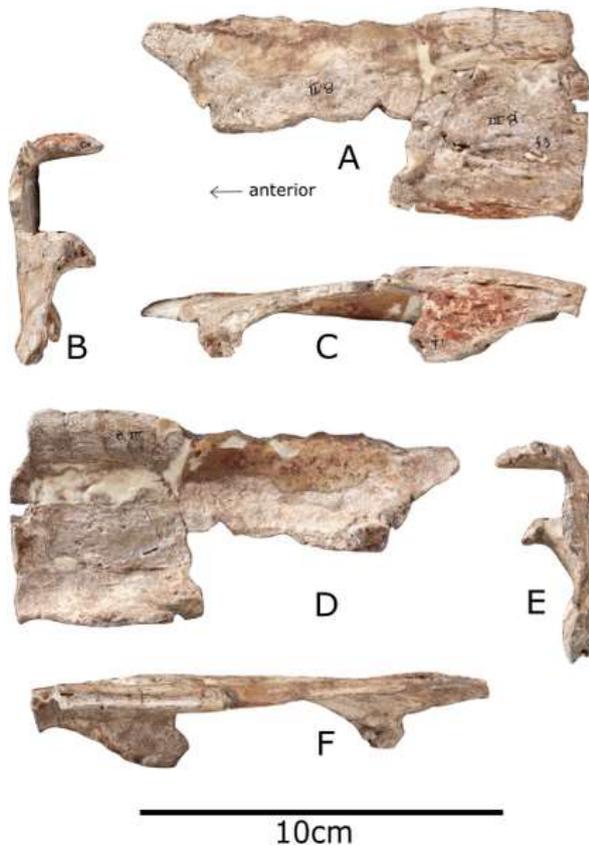


Figure 8 | Holotype nasal in multiple views.
 Thomas Raven & Susannah Maidment, CC-BY 4.0

and in a polytomy with *Tuojiangosaurus*, *Huayangosaurus*, *Chungkingosaurus*, *Jiangjunosaurus*, and *Gigantspinosaurus*. However, when the latter two genera were removed, *Paranthodon* grouped with *Tuojiangosaurus* just outside Stegosauridae, and *Huayangosaurus* grouped with *Chungkingosaurus* in Huayangosauridae.^[20] An elaboration upon this analysis was published in 2017 by Susannah Maidment and Thomas Raven, which achieved much greater resolution of the relationships inside Stegosauria. Nearly all described stegosaur taxa were included, and *Paranthodon* grouped with *Tuojiangosaurus*, *Huayangosaurus* and *Chungkingosaurus* as the most basal true stegosaurians. However, the position of *Alcovasaurus* was uncertain, and further work could yield different results, with the phylogeny vulnerable to changes in taxon sampling. Below is the single most parsimonious tree recovered from analysis of a combined dataset of discrete and continuous characters in that study.^[21]

Other analyses have found *Paranthodon* closely related to *Tuojiangosaurus*, *Loricatosaurus*, and *Kentrosaurus* within *Stegosaurinae*.^{[13][22]} Even though phylogenetic analyses recognize *Paranthodon* as a stegosaurid, the type material actually bears no *synapomorphies* of Stegosauria. However, the material is very likely representative of the group, with phylogenetic analyses performed in separate studies by separate authors having resolved it as a stegosaurian.^{[20][12]}

Paleoecology

As a stegosaur, *Paranthodon* would have been a slow-moving, mid-level quadrupedal browser that defended itself using a tail with spines on it.^[23]

The Kirkwood Formation is in South Africa, and many fossils of different species and genera have been discovered in it, with *Paranthodon* being the first uncovered.^[24] The formation is of a Late Jurassic to Early Cretaceous age, with the oldest deposits from the Tithonian, about 145.5 million years ago, and the youngest rocks being from the Valanginian, about 130 million years ago.^{[9][10][25]} The specific vertebrate-bearing portion of the formation is approximately level with the upper region of the Sundays River Formation, which has been dated to 139 to 131 mya based on microfossils.^[26] A large variety of different animal groups have been found in the formation, including dinosaurs, at least two different sphenodontian lizards, multiple teleost fishes, a few crocodylians, some frog specimens, and also turtles. However, a large amount of the material of the Kirkwood formation only includes isolated teeth or partial and fragmentary pieces of bone. Dinosaurs of the formation include a basal tetanuran, the primitive ornithomimosaurian *Nqwebasaurus*, the sauropod *Algoasaurus*, a potential titanosaur, many ornithischians, *Paranthodon*, a genus of iguanodontian, and a "hypsilophodontid" (the family Hypsilophodontidae is



Figure 9 | The Kirkwood Formation, the location of the fossil discovery



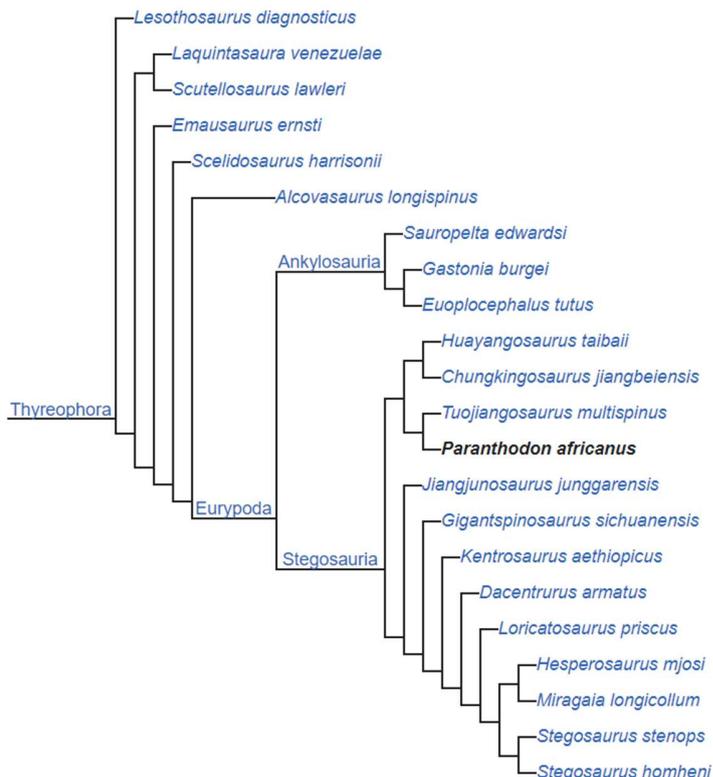
no longer considered to be a natural grouping^[27].^{[24][28]} Multiple additional sauropod taxa have been discovered in the Kirkwood deposits, including a basal **eusauropod**, a **brachiosaurid**, a **dicraeosaurid** and a derived **diplodocid**.^[26]

If the referral of teeth from Ethiopia to *Paranthodon* is correct, then the taxons geographic range is extended significantly. The Mughler locality is approximately 151 million years old, about 14 million older than has previously been suggested for *Paranthodon*, as well as across both southern and eastern Africa. The fauna in the Mughler locality differ from elsewhere of the same time and place in Africa. While the Tendaguru has abundant stegosaurs, sauropods, **ornithopods** and **theropods**, the Mughler Mudstone preserves the stegosaur *Paranthodon*, a hypsilophodontid ornithopod, a probably sauropod, and theropods referred to **Allosauridae** and **Dromaeosauridae**.^[14]

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