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# Dental Occlusion in a 260-Million-Year-Old Therapsid with Saber Canines from the Permian of Brazil

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Anomodonts, a group of herbivorous therapsid “mammal-like reptiles,” were the most abundant tetrapods of the Permian. We present a basal anomodont from South America, a new taxon that has transversally expanded palatal teeth and long saber canines. The function of the saber teeth is unknown, but probable uses include deterring attack from predators and intraspecific display or combat. The complex palatal teeth were used to process high-fiber food and represent early evidence of dental occlusion in a therapsid. This discovery provides new insight into the evolution of heterogeneous dentition in therapsids and broadens our understanding of ecological interactions at the end of the Paleozoic.

Critical modifications in terrestrial communities occurred during the Permian period as an increasing variety of herbivorous tetrapods and their predators evolved. This process resulted in the establishment of a modern trophic pyramid by the end of the period (1). A key faunal element in this ecological transformation was the appearance of therapsid “mammal-like reptiles” during the Middle Permian (2–4) and the development of heterodont dentition and diverse feeding adaptations within this group, which facilitated their exploitation of different ecological niches (1, 2).

By far the most successful Permo-Triassic therapsid lineage in terms of individual abundance was the herbivorous Anomodontia (~130 species (5)), which includes the paraphyletic basal anomodonts and the more derived monophyletic dicynodonts (5). Basal anomodonts comprise only 11 species and are known from Middle-Late Permian rocks of China, Russia, and South

Africa (6). Dicynodonts, the most speciose clade within Anomodontia, are known from every continent (6) and have a distinctive keratinous beak that replaced marginal dentition and, together with modification of the occlusal musculature, facilitated proplinal jaw masticatory movements (7). This adaptation was probably the key to their successful exploitation of herbivory. Here we report an early basal anomodont from the Permian of South America, *Tiarajudens eccentricus* gen. et spec. nov. (8) (Fig. 1), a taxon with dentition that is markedly different from all other anomodont and therapsid dental patterns.

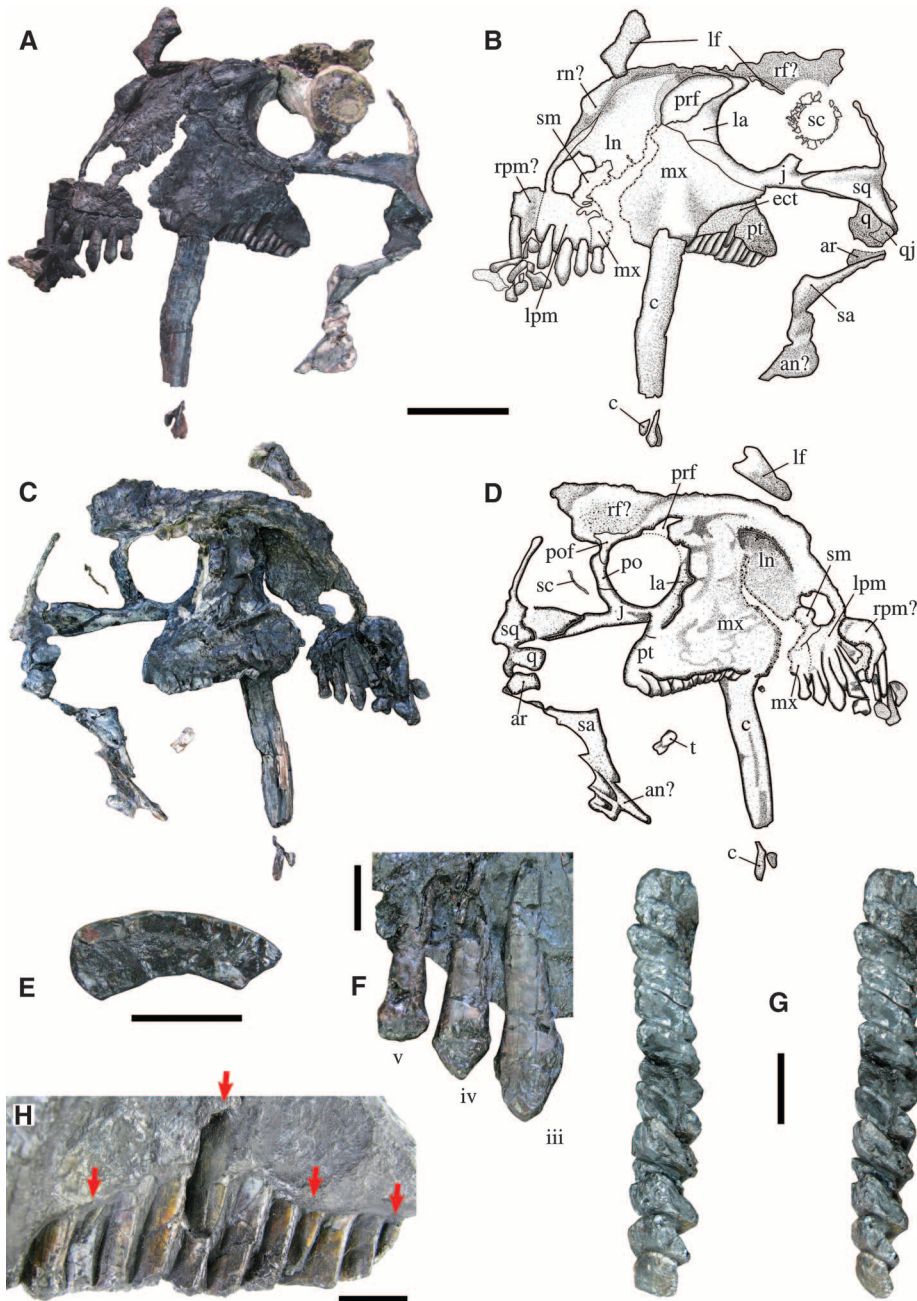
The skull of *Tiarajudens* (~225 mm long) is large for a basal anomodont, with a preorbital length only slightly shorter than the postorbital length (~45% of cranial length). Most anomodonts have shorter snouts, but these proportions are comparable to those of the South African *Anomocephalus* (9) and the Chinese *Biseridens* (6). *Tiarajudens* has five prominent leaf-shaped upper incisoriform teeth (Fig. 1F) with coarse serrations on their crowns. The last tooth in the maxillary row, below the anterior margin of the orbit, is a large canine measuring ~120 mm in length despite post-fossilization damage to the tip. This laterally compressed fang is reniform in basal cross section (Fig. 1E) and features enamel.

Thirteen large, transversally expanded palatal teeth (Fig. 1G) are present on the pterygoid and ectopterygoid, medial to the canine. The crown blades are oblique, arranged in echelon, and the palatal tooth row is straight, oriented 20° in relation to the lateral margin of the jugal. Unworn teeth are tall and chisel-like (Fig. 2A) and old, worn teeth display wide occlusal surfaces (Fig. 2, B and C), subdivided into two uneven wear platforms; a labial wear facet separated by a step from a larger, ventrally convex lingual facet. Palatal teeth have long roots, partially exposed in lateral view (Fig. 1H), and distinct alveoli, indicating thecodont implantation.

The presence of a shortened snout and elevated zygoma (Fig. 1) identify *Tiarajudens* as an anomodont (6), but it is the only one yet described to possess large canines. The flattened cross section of these teeth contrasts with the much shorter and thicker tusks of dicynodonts, which are circular in basal cross section and lack enamel (10–12). The leaf-shaped and serrated upper incisoriform teeth resemble those of the plant-eating Russian basal anomodonts *Ulemica* and *Suminia* (13, 14), and are also characteristic of other herbivorous groups such as pareiasaurs, ornithischian and prosauropod dinosaurs, and extant iguanid lizards (1, 13).

*Tiarajudens* is also unusual in having large, transversally expanded palatal teeth. Palatal teeth are absent in all basal anomodonts except *Biseridens*, in which they are small, rounded, and bulbous (6). The presence of teeth in the ectopterygoid is a feature unknown in any other therapsid but is characteristic of pelycosaur-grade synapsids such as *Edaphosaurus* (15). In occlusal aspect, the palatal teeth of *Tiarajudens* resemble the maxillary molariforms of the Early Permian *Diadectes* (16), except that they have the codont implantation, evinced by long roots and distinct alveoli. The dentary is not preserved, but wear facets on the palatal teeth suggest that they occluded against mandibular teeth, resembling a mechanism present in *Edaphosaurus* (15), where a cluster of homodont palatal teeth are opposed to a matching set of lower teeth on the coronoid, anterior coronoid, and prearticular bones (15, 16). The presence of replacement teeth (Figs. 1H and 2A) and their positioning and

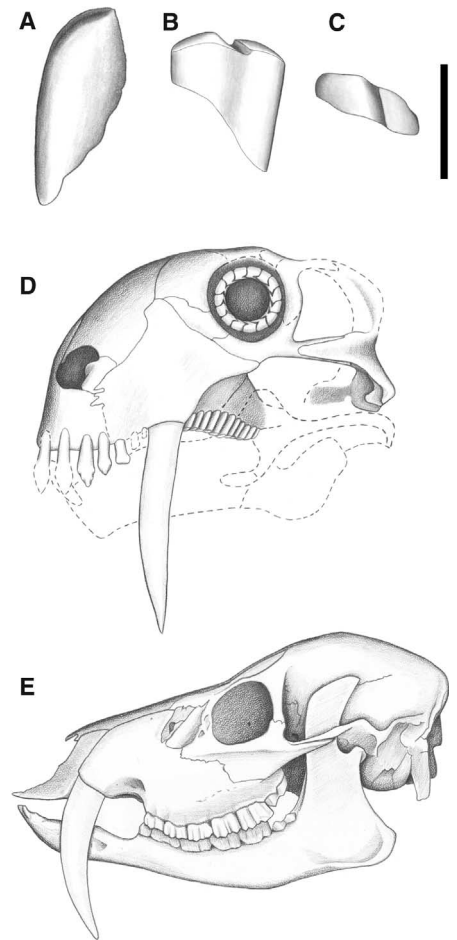
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**Fig. 1.** Cranium and dentition of *T. eccentricus* from the Permian of Brazil (UFRGS PV393P, holotype). (A) Photograph and (B) drawing of the skull in lateral view. (C) Photograph and (D) drawing of the skull in medial view (parasagittal section). (E) Saber canine in basal cross section; anterior is to the left. (F) Incisiforms in lingual view (iii to v indicate tooth positions). (G) Palatal molariforms in occlusal view (stereophotograph). (H) Lateral view of palatal teeth, showing a posterior-to-anterior replacement sequence; replacement teeth are indicated by arrows. Scale bars, 50 mm for (A) to (D) and 10 mm for (E) to (H). Abbreviations: an, angular; ar, articular; c, canine; ect, ectopterygoid; j, jugal; la, lacrimal; lf, left frontal; ln, left nasal; lpm, left premaxilar; mx, maxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; rf, right frontal; rn, right nasal; rpm, right premaxilar; sa, surangular; sc, scleral ossicles; sm, septomaxilla; sq, squamosal; t, teeth.

stages of eruption are consistent with a posterior-to-anterior alternating pattern of substitution. This evidence indicates that *Tiarajudens* was a sophisticated heterodont herbivore capable of processing high-fiber food through a set of palatal molariform teeth.

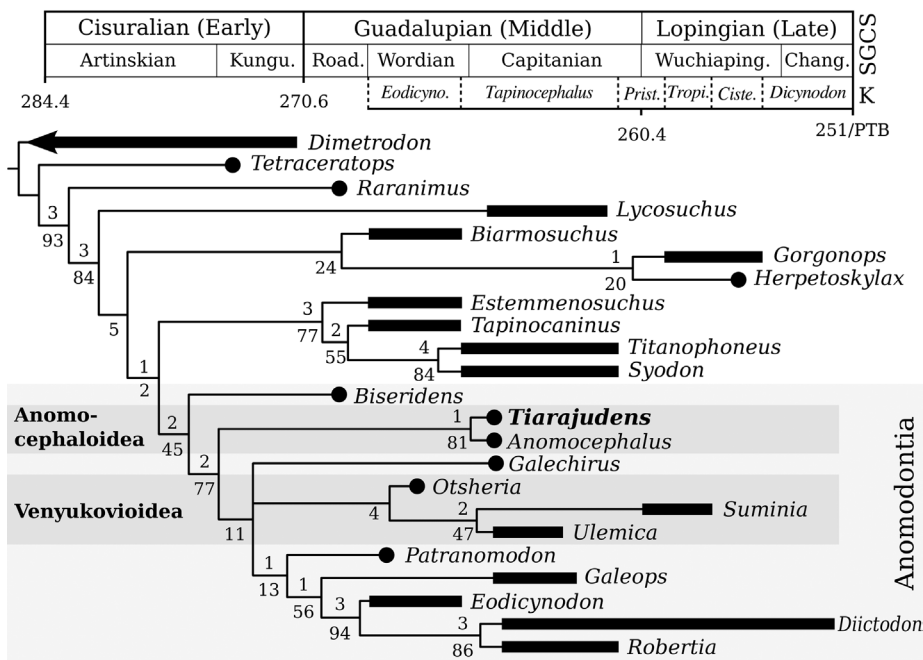
Large saber canines are unexpected in a herbivore. All Permian tetrapods with saber teeth [biarmosuchians, anteosaurid dinocephalians, and gorgonopsians (2, 17, 14)] are mid- to top-level predators. The canines of *Tiarajudens* are as long as those of the largest gorgonopsian *Inostrancevia*



**Fig. 2.** (A) Replacement palatal tooth in posterior view (last tooth in the row, apex to the top). (B and C) Reconstruction of fourth palatal tooth, (B) posterior, slightly medial view, (C) occlusal view. (D) and (E) Comparative figures showing a skull reconstruction of *T. eccentricus* (D) and the skull of the extant saber-toothed water deer *Hydropotes* sp. (E). Scale bar, 10 mm for (A) to (C). (D) and (E) are not to scale.

from Russia (14), but relative to skull size the canines of *Tiarajudens* are larger (1:0.26 for *Inostrancevia* and 1:0.57 in *Tiarajudens*). However the saber teeth of *Tiarajudens* lack the serrations characteristic of the canines of Permian carnivorous therapsids (2, 14). Despite their great length, the canines were not fragile. These could have served to manage food items before processing, to deter attacks from predators (18), or for intraspecific display and combat (18, 19), as seen in extant antlerless water deer (*Hydropotes* sp.; Fig. 2E) and musk deer (*Moschus* sp.) from Asia (20, 21). The latter could have been an alternative to the head-butting combat employed by coexisting Permian dinocephalians (22) and extant ruminants. The earliest saber-toothed herbivores hitherto known were Late Paleocene (57 million years ago) uintatheres and the pantodont *Titanoides* (23). The presence of saber teeth in

**Fig. 3.** Stratigraphically calibrated phylogeny of Permian basal anomodonts (5) and other therapsids. Circles represent taxa known from a single locality. Values represented above the branches are decay values; values below are from symmetric resampling. The temporal range of *Dimetrodon* extends to the earliest Permian (Asselian). Abbreviations: *Ciste.*, *Cistecephalus*; Chang., Changhsingian; *Eodicyno.*, *Eodicynodon*; K, Karoo Assemblage Zone; Kungu., Kungurian; *Prist.*, *Pristerothrips*; PTB, Permo-Triassic Boundary; Road., Roadian; SGCS, Standard Global Chronostratigraphic Scale (27); *Tropi.*, *Tropidostoma*; Wuchiaping., Wuchiapingian. Ages are in million years ago.



*Tiarajudens* extends this specialization in terrestrial herbivores back to the Paleozoic, some 260 million years ago.

The majority rule consensus tree of a phylogenetic analysis of early anomodonts (Fig. 3) (24) shows *Biseridens* to be the most basal anomodont, followed by a new Gondwanan monophyletic clade, Anomocephaloidea (8), comprising *Tiarajudens* and *Anomocephalus* (see supporting online material). This is followed by a polytomy including the South African *Galechirus*, the Russian monophyletic group Venyukovioidea (25) (comprising *Otsheria*, *Suminia* and *Ulemica*), and a monophyletic Chainosauria, which incorporates the South African basal anomodonts *Patranomodon* and *Galeops* and dicynodonts. The basal position of the Brazilian taxon implies that its saber teeth predate the tusks of dicynodonts and do not represent homologies.

The new clade Anomocephaloidea represents a previously unrecognized Gondwanan radiation of large, relatively robust basal anomodonts and contrasts with the Russian Venyukovioidea, formed by small, gracile taxa, including one arboreal form (26). The extensive morphological experimentation observed in *T. eccentricus* and other basal anomodonts played a major role in the evolution of dicynodonts, the most successful Permo-Triassic tetrapod lineage.

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