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A new sphenodontian (Lepidosauria: Rhynchocephalia) from the Late Triassic of Argentina and the early origin of the herbivore opisthodontians

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Sphenodontians were a successful group of rhynchocephalian reptiles that dominated the fossil record of Lepidosauria during the Triassic and Jurassic. Although evidence of extinction is seen at the end of the Laurasian Early Cretaceous, they appeared to remain numerically abundant in South America until the end of the period. Most of the known Late Cretaceous record in South America is composed of opisthodontians, the herbivorous branch of Sphenodontia, whose oldest members were until recently reported to be from the Kimmeridgian–Tithonian (Late Jurassic). Here, we report a new sphenodontian, *Sphenotitan leyesi* gen. et sp. nov., collected from the Upper Triassic Quebrada del Barro Formation of northwestern Argentina. Phylogenetic analysis identifies *Sphenotitan* as a basal member of Opisthodontia, extending the known record of opisthodontians and the origin of herbivory in this group by 50 Myr.

1. Introduction

Lepidosaurian reptiles, comprising Squamata and Rhynchocephalia, constitute a large proportion of extant terrestrial vertebrate fauna. Squamates include more than 7000 extant species (lizards, snakes and amphisbaenas), whereas the only living rhynchocephalian is *Sphenodon punctatus* from New Zealand [1]. Contrary to the extant record, the fossil record demonstrates that the sphenodontians—the most successful group of rhynchocephalian reptiles—were the dominant lepidosaurians during the Triassic and Jurassic [1–7]. During the early Cretaceous, sphenodontians nearly became extinct in Laurasia, replaced by the diversifying squamates [8]. By contrast, South American sphenodontians remained abundant until at least the end of the Campanian, and it was only during the Palaeogene that squamates began to dominate small reptilian fauna [9]. Most Argentinean Upper Cretaceous sphenodontians are eilenodontine opisthodontians [9–11], a herbivorous branch of Sphenodontia characterized by lateromedially expanded dentary teeth and advanced propalinal jaw movements. The opisthodontians have been observed across several regions and periods, from the Upper Jurassic of North America [12–14], Europe [15] and South Africa [16], to the Upper Cretaceous of South America [9]. Until now, the oldest known opisthodontian was *Opisthias*, a widely distributed genus from the Kimmeridgian–Tithonian of North America, and Kimmeridgian and Berriasian of Europe [12–16]. Here, we report partial skeletons of a new opisthodontian from the Upper Triassic of South America, which extends the oldest record of this group by 50 Myr.

The specimens described here were collected from the Upper Triassic Quebrada del Barro Formation in northwestern Argentina (see electronic supplementary material, figure S1). This unit was originally dated as Norian [17], although that age was later questioned [18]. A recent stratigraphic

survey and the discovery of a new vertebrate association confirm the Norian age of the Quebrada del Barro Formation [19] (see electronic supplementary material).

2. Systematic palaeontology

Lepidosauria Haeckel, 1866 [20]

Rhynchocephalia Günther, 1867 [21]

Sphenodontia Williston, 1925 [22]

Opisthodontia Apesteguía and Novas, 2003 [9]

Sphenotitan leyesi gen. et sp. nov.

(a) Etymology

Spheno refers to Sphenodontia. *Titan*, meaning giant (Greek), refers to the large size of the new taxon (largest specimen of *Sphenotitan* reached more than 100 mm in skull length). The species name is dedicated to the Leyes family from the small town of Balde de Leyes, which is located close to the type locality.

(b) Holotype

PVSJ 886 (Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina) consists of a partially articulated posterior portion of the skull of an adult individual. The specimen preserves partial pterygoids, ectopterygoids, palatines, maxillae, right premaxilla, parietals, squamosals, quadrates, left jugal and postorbital, and the rear half of the lower jaws, from the level of posterior-most dentary teeth.

(c) Referred material

PVSJ 887, left dentary; PVSJ 888, both incomplete maxillae, anterior part of both lower jaws, both premaxillae; PVSJ 889, left maxilla; PVSJ 890, right quadrate; PVSJ 891, incomplete lower jaws; PVSJ 892, right palatine, pterygoid and ectopterygoid; PVSJ 893, right premaxilla and postorbital, left incomplete palatine and pterygoid; PVSJ 895, articulated sequence of three distal dorsal vertebrae, sacral vertebrae 1 and 2, and first caudal vertebra.

(d) Locality and horizon

Upper layers of the Quebrada del Barro Formation (Norian) of the Marayes–El Carrizal Basin, ‘Balde de Leyes’ fossil locality, San Juan Province, Argentina (see electronic supplementary material, figure S1). The specimens were found in fluvial sandstones, in association with basal sauropodomorph dinosaurs, tritheledontid cynodonts and ‘sphenosuchid’ pseudosuchians.

(e) Diagnosis

Sphenotitan differs from other sphenodontians in the following autapomorphies: large supratemporal fenestra—one-third of the skull length; posterodorsal process of the premaxilla, which ends posteriorly as a projection wedged between the anterolateral process of the nasal and the premaxillary process of the maxilla; palatine bearing a small cluster of 15 conical teeth lying medial to the main tooth row and posterior to the internal naris; four prominent rows of dozens of small teeth on the anterior palatal shelf of the pterygoids; large quadrate–quadratojugal foramen, consisting of more than one-third of the maximum length of the quadrate; straight orbital border of the maxilla; long posterior maxillary teeth, reaching 90% of the total dorsoventral height of the maxilla;

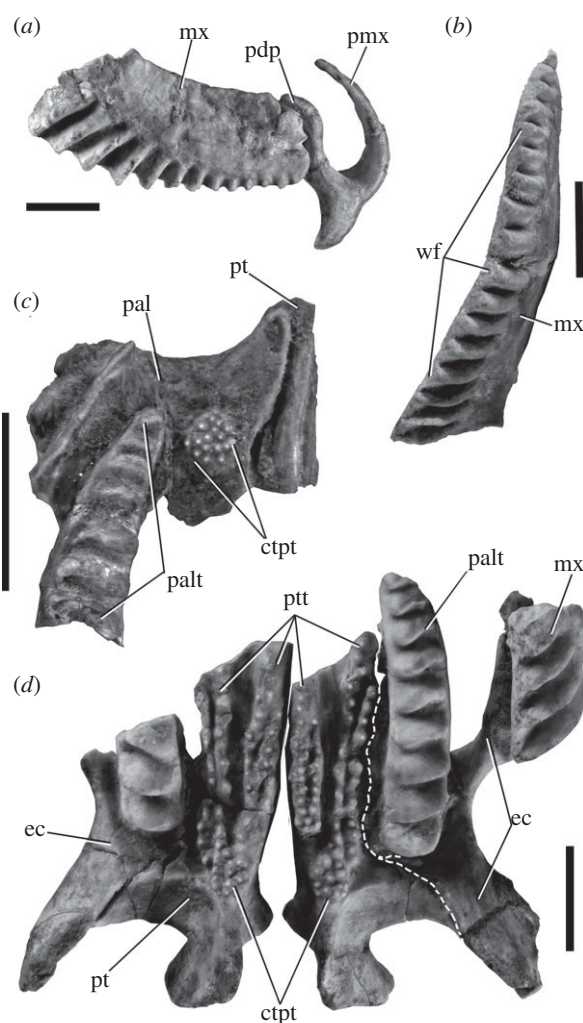


Figure 1. *Sphenotitan leyesi* gen. et sp. nov. (a) Right maxilla and premaxilla (PVSJ 886) in lateral view. (b) Left maxilla (PVSJ 889) in occlusal view. (c) Anterior palatal fragment (PVSJ 892) in palatal view. (d) Posterior palatal fragment (PVSJ 886) in palatal view. Scale bars equal 10 mm. White dashed lines indicate sutures. ctpt, cluster of pterygoid teeth; ec, ectopterygoid; mx, maxilla; pal, palatine; palt, palatine teeth; pdp, posterodorsal process of the premaxilla; pmx, premaxilla; pt, pterygoid; ptt, pterygoid teeth; wf, wear facet.

pronounced, stout, square-section and dorsally curved retro-articular process of the lower jaw; additional wide teeth with a transverse width : anteroposterior length ratio of five.

3. Description

The skull of *Sphenotitan* is lightly built, roughly triangular in dorsal view and characterized by the presence of large supratemporal fenestrae—making up over one-third of the skull length—separated by very narrow and fused parietals, and a short preorbital region (figures 1–4). Adult specimens of *Sphenotitan* reached more than 100 mm in skull length, larger than any previously known sphenodontian besides the eilenodontine *Kaikaifilusauros* [9].

The premaxillae of both small and large specimens of *Sphenotitan* form a beak comprising a single chisel-like cutting edge (figures 1a and 4c), similar to that of *Kaikaifilusauros* and very large specimens of *Clevosaurus* [23]. The posterodorsal process of the premaxilla is long, excluding the maxilla from the margin of the external naris (figures 1a and 4c) as seen

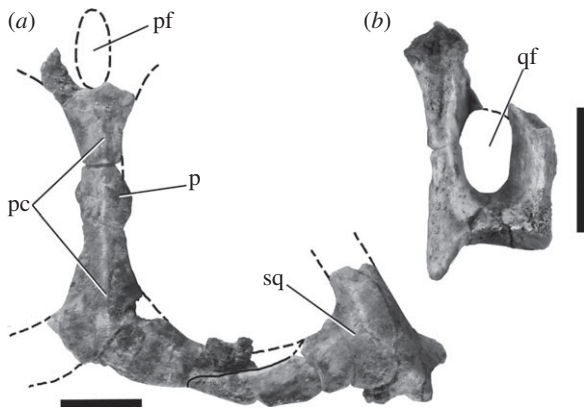


Figure 2. *Sphenotitan leyesi* gen. et sp. nov. (a) Fused parietals and right squamosal (PVSJ 886) in dorsal view. (b) Left quadrate (PVSJ 890) in posterior view. Scale bars equal 10 mm. p, parietal; pc, parietal crest; pf, parietal foramen; qf, quadrate foramen; sq, squamosal.

in *Clevosaurus*, *Godavarisaurus* [24], *Pamizinsaurus* [25] and *Kaikaifilusaurus*. However, this differs from all other sphenodontians in that the posterodorsal process of the premaxilla is curved and hook-like, and wedged between the anterolateral process of the nasal and the premaxillary process of the maxilla (figures 1a and 4c).

The maxilla is stout, with a short premaxillary process (figure 1a). Over half of the maxillary length forms the straight lower border of the orbit. The maxilla of a large individual of *Sphenotitan* has 17–18 long, closely packed teeth, anteriorly decreasing in size, with long anterolateral flanges (figure 1a,b). The maxillary teeth vary from 8.7 mm long and 2.2 mm wide for the posterior-most to 2.6 mm long and 1.6 mm wide for the anterior-most, which are the most worn (figure 1a,b). The ratio of the length of the longest tooth to the corresponding dorsoventral depth of the maxilla is 0.9, greater than in any other sphenodontian (which are generally less than 0.3).

The palatine widens anteriorly and bears a row of at least 13 large teeth on its lateral margin, located parallel to those of the maxilla (figures 1c,d and 4b). The palatal teeth are blade-like, lateromedially wide, posteriorly pointed, and with extended lateral and medial flanges. The size of teeth increases posteriorly in a manner similar to that of *Kaikaifilusaurus* (although in the latter, the row of teeth is straight while in the former it is markedly curved with lateral convexity). Anteromedially, the palatine also bears a small cluster of 15 conical teeth lying medial to the main tooth row and posterior to the internal naris (figures 1c and 4b)—a similar location to that of the isolated tooth present in *Clevosaurus* [23]. These small palatine teeth are closely packed in a subcircular area 2 mm wide (figures 1c and 4b). The pterygoids have broad anterior contact with each other and are excluded from the margin of the suborbital fenestra (figures 1d and 4b), as in most other derived sphenodontians (e.g. *Kaikaifilusaurus*, *Clevosaurus* and *Sphenodon*). The palatal shelf bears four prominent rows of dozens of small teeth (figures 1d and 4b). Each pterygoid has two anteroposteriorly oriented double rows of teeth that are roughly parallel to each other (figures 1d and 4b). The lateral double-row, which ends more posteriorly than the medial double-row, caudally ends in a small subcircular cluster of 12 very small teeth (figures 1d and 4b). The arrangement of two double rows of pterygoid teeth and the aforementioned cluster of palatine teeth are unique features among Rhynchocephalia.

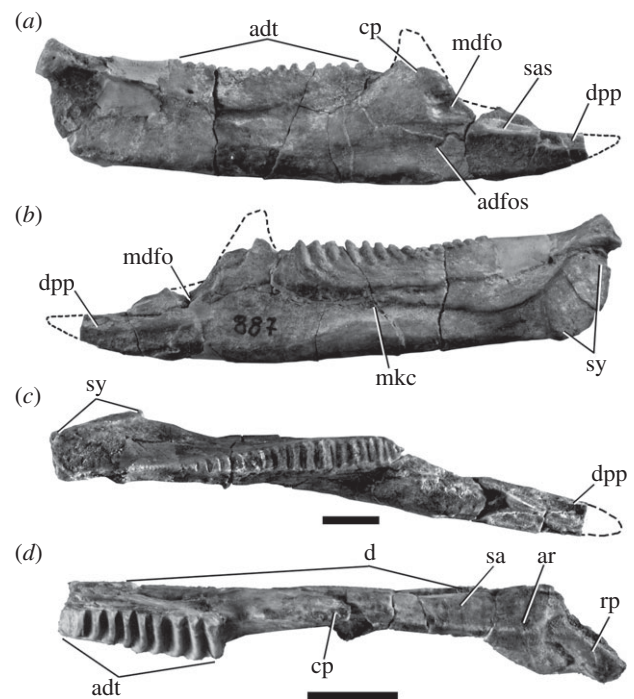


Figure 3. Lower jaw of *S. leyesi* gen. et sp. nov. Left dentary (PVSJ 887) in (a) lateral, (b) medial and (c) occlusal view. (d) Posterior portion of the right lower jaw (PVSJ 886) in occlusal view. Scale bar equals 10 mm. adfos, adductor fossa; adt, additional teeth; ar, articular; cp, coronoid process; d, dentary; dpp, dentary posterior process; mdfo, mandibular foramen; mfc, meckelian channel; rp, retroarticular process; sa, surangular; sas, surface for articulation with surangular; sy, symphysis.

The quadrate–quadratojugal foramen, located between the quadrate and the quadratojugal (figure 2b) as in *Sphenodon* and *Zapatadon* [26], is proportionally large—over one-third of the maximum length of the quadrate (figure 2b). The size of the foramen is larger than that of other rhynchocephalians (except for the dorsoventrally reduced quadrate of *Sphenodon* [27]).

The lower jaw is stout and deep (figures 3 and 4c,d), as in all opisthodontians (e.g. *Opisthias* [12], *Kaikaifilusaurus* [9,10] and *Toxolophosaurus* [13,28]). *Sphenotitan* also shares the anterior edentulous area of the dentary and the absence of dental regionalization with opisthodontians, lacking caniniform and hatchling teeth (figure 3a–c). Tooth implantation is acrodont without evidence of replacement. As in all eilenodontines (e.g. *Eilenodon*, *Toxolophosaurus* and *Kaikaifilusaurus*), in *Pelecymala* [3] and *Clevosaurus latidens* [29] the teeth of the dentary are transversally wide, uniform in shape, closely packed and increase in size progressively towards the posterior additional series (figures 3 and 4d). However, unlike eilenodontines, the teeth of *Sphenotitan* are prism-like, with straight labiolingual cutting edges parallel to each other. The teeth are extremely wide (labiolingual width : mesiodistal length ratio = 5), closely packed (5 teeth cm^{-1}) and lack lateral flanges (figures 3 and 4d). The lateral surfaces of the dentary teeth have vertical wear facets as a result of the shearing action of the maxillary dentition (figures 3a,c and 5), similar to that reported in *Pelecymala* and *C. latidens*. The continuous rasp-like surface formed by the row of teeth faces dorso-medially at an angle of 45° with respect to the horizontal at the posterior-most region, and decreases progressively toward the anterior end. The coronoid process is moderately high, triangular and anterodorsally pointed (figures 3a,b and 4c),

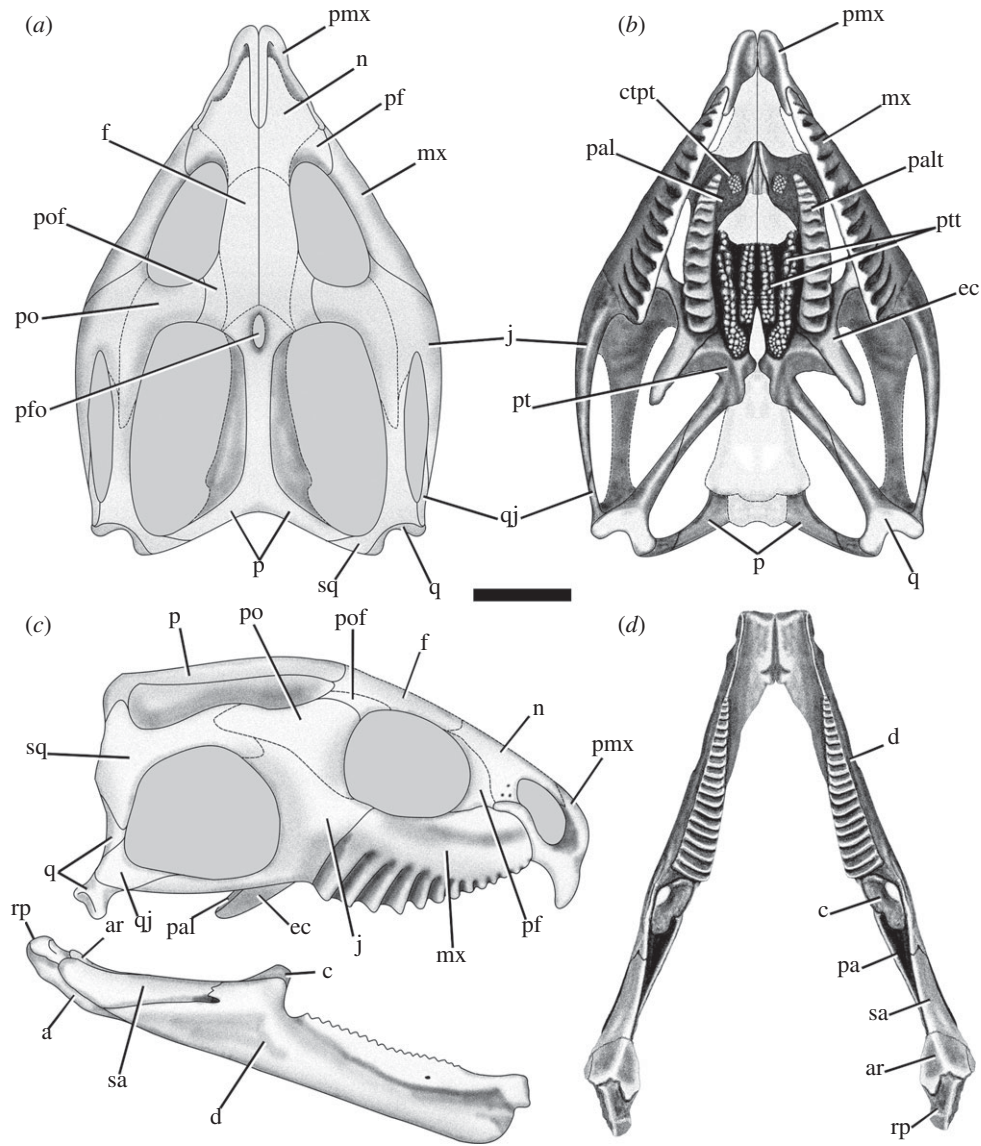


Figure 4. Reconstruction of the skull and lower jaw of a mid-range size individual of *S. leyesi* gen. et sp. nov. in (a) lateral, (b) ventral and (c) dorsal view. (d) Lower jaw in occlusal view. Scale bar equals 20 mm. Dark grey tone indicates cavities. Light grey tone indicates missing fragments. a, angular; ar, articular; c, coronoid; ctpt, cluster of pterygoid teeth; d, dentary; ec, ectopterygoid; f, frontal; j, jugal; mx, maxilla; n, nasal; p, parietal; pa, prearticular; pal, palatine; palt, palatine teeth; pf, prefrontal; pfo, parietal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pt, pterygoid; ptt, pterygoid teeth; q, quadrate; qj, quadratojugal; rp, retroarticular process; sa, surangular; sq, squamosal.

similar to that of *Kallimodon* and *Sapheosaurus* [2], but different from the low coronoid process of all opisthodontians. The glenoid cavity is markedly symmetrical with a central anteroposteriorly ridge (figures 3d and 4d) as in the eilenodontines *Eilenodon* and *Kaikaiifilusaurus* (although in the latter the glenoid is anteroposteriorly longer). The retroarticular process is pronounced as in basal sphenodontians, but in *Sphenotitan* it is dorsally curved and very stout, with uniformly roughly squared cross-sections along its entire length (figures 3d and 4c,d).

4. Phylogenetic analysis

The phylogenetic relationship of *S. leyesi* was analysed by adding it and the Triassic taxa *C. latidens* and *Pelecymala* to the data matrix of Apesteguía *et al.* [7] (see the electronic supplementary materials).

The strict consensus tree (see electronic supplementary material, figure S3) depicted *Sphenotitan* as the basal-most

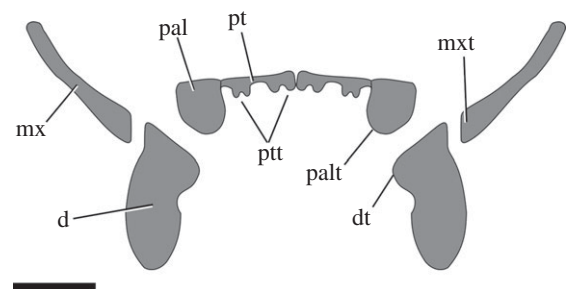


Figure 5. Schematic posterior view cross-section through the snout level of *S. leyesi* gen. et sp. nov. Scale bar equals 10 mm. d, dentary; dt, dentary teeth; mx, maxilla; mxt, maxillary teeth; pal, palatine; palt, palatine teeth; pt, pterygoid; ptt, pterygoid teeth.

opisthodontian sphenodontian related to the Upper Jurassic *Opisthias*, *Toxolophosaurus* and *Eilenodon*, and to the Upper Cretaceous *Kaikaiifilusaurus*. In this context, opisthodontians share five synapomorphies: a rounded and well-developed mandibular symphysis (Character 34.2), a well-developed

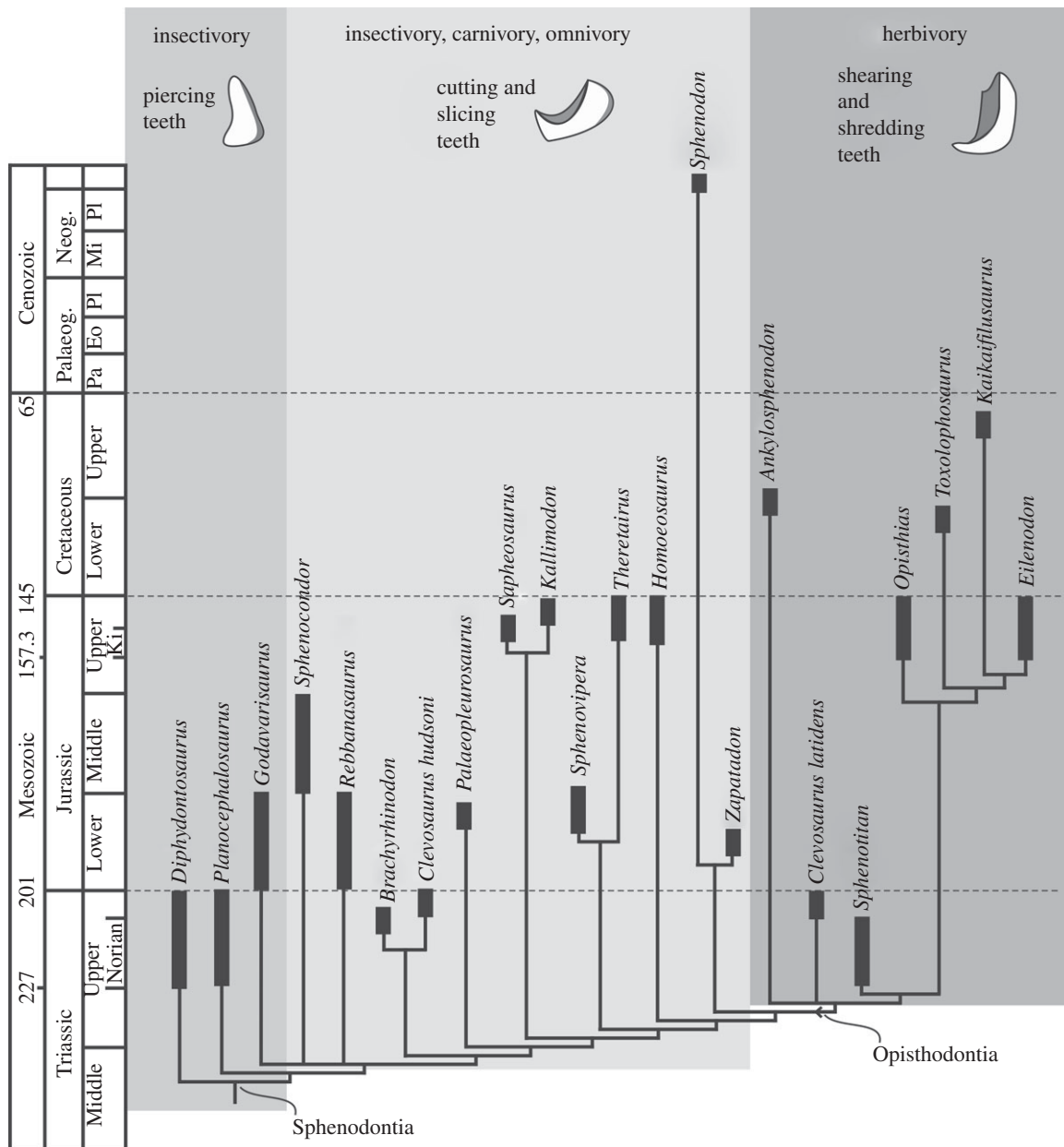


Figure 6. Calibrated reduced strict consensus tree summarizing the results obtained in the constrained searches. Calibrated phylogeny of sphenodontians, indicating different tooth morphotypes and dietary interpretations.

anterodorsally projecting mandibular spur (Character 37.1), dentary regionalization absent in juveniles and adults (Character 45.3), posteromedial flanges on posterior maxillary teeth present as extensive flanges (Character 51.2) and the presence of anteromedial flanges on mandibular teeth (Character 58.1). With the exception of *Sphenotitan*, all opisthodontians (*Opisthitas* and more derived Opisthodontia) share an unambiguous synapomorphy: the presence of dental ridges on additional mandibular teeth (Character 59.1). The presence of the plesiomorphic state in that character—the absence of dental ridges in additional mandibular teeth (Character 59.0)—supports the basal position of *Sphenotitan* within Opisthodontia.

This study classifies Opisthodontia as part of a polytomy (see electronic supplementary material, figure S3) that includes several derived crown-sphenodontian taxa (i.e. *Pelecymala*, *C. latidens*, *Ankylosphenodon*, *Kawasphenodon*, *Sphenodon*, *Cynosphenodon*, *Zapatodon*, *Homoeosaurus*, *Sphenovipera*, *Theretairus*, *Sapeosaurus* and *Kallimodon*). In order to evaluate the cause of this polytomy, pruned trees were compared to obtain a reduced consensus tree [30] (see electronic supplementary

material). The result shows three unstable taxa: *Pelecymala*, *Kawasphenodon* and *Cynosphenodon*. The instability of the three taxa is owing to missing data (unknown character states) and character conflict (some characters support alternative positions in different trees), as determined by iterative PCR [31]. Excluding the three unstable taxa from the consensus shows a completely resolved reduced strict consensus tree (figure 6). Owing to the close relation of *Ankylosphenodon* and *C. latidens* with basal opisthodontians in most parsimonious trees (see electronic supplementary material), the strict consensus shows these two taxa in a polytomy with *Sphenotitan* and more derived opisthodontians (figure 6). Therefore, according to the stem-based definition of Opisthodontia [9], the topology of the reduced strict consensus suggests *Ankylosphenodon* and *C. latidens* may be regarded as basal opisthodontians.

Until now, the oldest known opisthodontians were from the Late Jurassic (e.g. *Eilenodon* and *Opisthitas* from the Kimmeridgian–Tithonian Morrison Formation of Wyoming [12–14]; an opisthodontian mandible from the Kimmeridgian Alcobaça Formation of Portugal [16]). *Sphenotitan* is the earliest

record of this group, extending its origin back by at least 50 Myr to the Norian. This suggestion is also strengthened by the position of the Upper Triassic *C. latidens* in a polytomy with the basal opisthodontians (figure 6). Moreover, the relationships of opisthodontians and sphenodontines (the branch that includes *Sphenodon*), coupled with the Norian record of *Sphenotitan*, suggest a Triassic origin of the lineage leading to sphenodontines, as was previously suggested [27,28].

5. Discussion

Sphenodontians are characterized by substantial variation in body size, body shape, habit, skull structure and size, and size and shape of teeth [32]. From these different traits, the diversity of tooth shape and arrangement suggests that Sphenodontia pursued a wide range of feeding strategies [33]. Based on tooth dimensions (mesiodistal length versus labiolingual width), three main morphotypes have been defined, each of them suited for a different mechanism of food processing: (i) small columnar teeth for piercing, indicative of an insectivorous diet; (ii) large elongated teeth for cutting and slicing, indicative of insectivory and/or a carnivorous diet; (iii) large wide teeth for shearing and shredding, indicative of an herbivorous diet [32]. The dentary of *Sphenotitan* has a large number of wide and closely packed teeth, increasing the surface area in contact with food (figures 1*a,b* and 3). This arrangement is present in all opisthodontians, including *C. latidens* and *Pelecymala*, although in *Sphenotitan* the teeth are wider and more closely packed than in any other sphenodontian. *Clevosaurus latidens* (which has not previously been proposed as Opisthodontia) and *Pelecymala* are the only known wide-toothed sphenodontians located out of Opisthodontia, which suggests that this feature has evolved twice within Sphenodontia [32]. Although *Pelecymala* was found to be unstable in this analysis owing to a lack of information on several character states, in several MPTs of the reduced strict consensus it is located close to the opisthodontians (see electronic supplementary material, figure S4). On the other hand, *C. latidens* is depicted in a polytomy with Opisthodontia and *Ankylosphenodon* (figure 6), which suggests an affinity towards Opisthodontia according to its stem-based

definition [7]. Although the known material of *C. latidens* and *Pelecymala* is limited and more material is needed to definitively solve this problem, the result of the present analysis suggests that wide-toothed herbivorous sphenodontians evolved just once in the evolutionary story of Sphenodontia.

The shared landmarks of *C. latidens* with Opisthodontia are not surprising, because both are wide-toothed, but the distance from *Clevosaurus hudsoni* is notable (figure 6), especially considering the fact that both have been related to the same genus. These results suggest that critical review of these materials is needed in order to determine the validity of the assignment of *C. latidens* to the genus *Clevosaurus*, which exceeds the scope of this work.

The anteroposteriorly enlarged and symmetrical glenoid articular cavity (figures 3*d* and 4*d*), the continuous shear facets found on the ventromedial side of the maxillary tooth row (figures 1*b* and 5), and the lateral surface of the dentary tooth row (figure 3*a*) indicate that a propalinal component of jaw movement played a major role in intraoral food processing in *Sphenotitan*. This seems to have been produced by two principal modes: slicing occurring between the ventromedial side of the maxillary teeth and the labial face of the dentary tooth row, and shredding being done by the ventrolateral side of the palatine tooth row and the dorsolingual face of the dentary tooth row, coupled with conspicuous rows of pterygoid teeth (figure 5). This masticatory mechanism is similar to that proposed for the most derived opisthodontians, the eilenodontines (e.g. *Toxolophosaurus* [28] and *Eilenodon* [34]). *Sphenotitan* shows that the most relevant advanced herbivorous traits present in the younger eilenodontines (e.g. large adult size, dentary teeth much more wide than long and eupropalinity) were acquired at least 50 Myr earlier than previously documented, at the end of the Late Triassic.

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