A NEW SPECIES OF CLEVOSAURUS (LEPIDOSAURIA: RHYNCHOCEPHALIA) FROM THE UPPER TRIASSIC OF RIO GRANDE DO SUL, BRAZIL

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Abstract: Well-preserved cranial remains of a small sphenodontian lepidosaur from the Upper Triassic Caturrita Formation of Rio Grande do Sul, Brazil, are the first record of the genus Clevosaurus Swinton, 1939 from South America. They represent a new species, Clevosaurus brasiliensis, which is distinguished by a very short antorbital region of the skull (corresponding to about 20 per cent of skull length) and the presence of teeth in addition to two longitudinal rows on the pterygoid. C. brasiliensis most closely resembles C. bairdi from the Lower Jurassic of Nova Scotia (Canada) and C. mcgilli from the Lower Jurassic of Yunnan (China). The discovery of Clevosaurus in the Upper Triassic of southern Brazil provides a significant range extension of this widely distributed sphenodontian genus. Along with other recent finds, it also suggests that there may have been less biotic provincialism among terrestrial vertebrates during the Late Triassic than has previously been assumed.

Key words: Sphenodontia, Clevosaurus, Brazil, Triassic, Caturrita Formation, palaeobiogeography.

FIELDWORK undertaken in 2000 and 2002 by personnel from the Instituto de Geologia of the Universidade Federal de Rio Grande do Sul (UFRGS) in strata of the Caturrita Formation exposed near Faxinal do Soturno, Rio Grande do Sul (Brazil), led to the discovery of skeletal remains representing a diverse assemblage of early Late Triassic tetrapods. The assemblage includes several taxa of small derived cynodonts (Bonaparte et al. 2001, 2003), a basal saurischian dinosaur (Bonaparte et al. 1999), as yet unidentified small archosaurian reptiles, a procolophonid parareptile (Cisneros and Schultz 2003) and a sphenodontian lepidosaur, which forms the subject of this paper (see also Ferigolo 2000).

Sphenodontians were once considered primitive diapsid reptiles. With the advent of modern phylogenetic analyses, they are recognized as the sister-group of Squamata, the two groups together constituting the Lepidosauria. Diagnostic cranial features of Sphenodontia include absence of the lacrimal, typically acrodont tooth implantation and addition of teeth at the back of the jaw (Evans 1988; Reynoso 1996). The fossil record of sphenodontians extends back to the early Late Triassic, and the group had already attained a wide geographical distribution at that time. Today represented only by the genus Sphenodon, which is restricted to a few small islands off the coast of New Zealand, they were diverse and widely distributed across Pangaea during the early Mesozoic (Fraser 1982, 1986, 1988, 1993; Fraser and Benton 1989; Whiteside 1986; Sues et al. 1994; Wu 1994; Sues and Reisz 1995; Ferigolo 2000; Evans et al. 2001). Recent discovery of Late Cretaceous sphenodontians (Apesteguía and Novas 2003; Martinelli and Forasiepi 2004) in Patagonia show they survived in South America until the end of the Mesozoic.

GEOLOGICAL SETTING

The fossiliferous beds are exposed in a quarry for road metal, which is located 2 km north-east of the city of Faxinal do Soturno in the state of Rio Grande do Sul in southern Brazil. The massive, fine-grained sandstone beds that have yielded fossils of the sphenodontian and associated tetrapods were deposited in a low-energy fluvial environment and correspond to the medial section of the Caturrita Formation (Andreis et al. 1980; Rubert and Schultz 2004). This unit overlies the Santa María Formation, which has yielded a very diverse tetrapod assemblage including traversodontid and chiniquodontid cynodonts, dicynodonts, rhynchosaurids, and numerous archosaurian taxa including basal saurischians (Barberena et al. 1985).

Rubert and Schultz (2004) recently proposed an 'Ictidosaur Association Zone' for the fossiliferous beds of the
Caturrita Formation as a new faunal horizon for the Upper Triassic of southern Brazil. The vertebrate assemblage can be correlated with the Lower Coloradian faunal stage (Bonaparte 1973; Rubert and Schultz 2004), which is thought to correspond to the early Norian of the European standard succession.

**Institutional abbreviations.** PV, Fossil Vertebrate Collection, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; PVT, Instituto de Geologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

**Abbreviations on text-figures.** AN, angular; BPT, basipterygoid process; D, dentary; DMX, maxillary dentine; EPT, ectopterygoid; EPTT, extra pterygoid teeth; FR, frontal; J, jugal; MX, maxilla; N, nasal; P, parietal; PFR, postfrontal; PL, palatine; PMX, premaxilla; PO, postorbital; PRF, prefrontal; PT, pterygoid; Q, quadrate; RP, retroarticular process; SA, surangular; SD, secondary dentine; SM, score marks; SQ, squamosal; ST, supra-temporal; VPT, ventral process of pterygoid.

### SYSTEMATIC PALAEONTOLOGY

**LEPIDOSAURIA** Haeckel, 1866  
**RHYNCHOCEPHALIA** Günther, 1867  
**SPHENODONTIA** Williston, 1925

**Family CLEVOSAURIDAE fam. nov.**

**Definition.** Clevosauridae comprises the last common ancestor of *Brachyrhinodon*, *Polysphenodon* and *Clevosaurus* and all of its descendants. It is the formal taxonomic equivalent of the informal grouping ‘clevosaurs’ recognized in the phylogenetic analyses by Wu (1994) and Reynoso (1996).

**Diagnosis** (modified from Reynoso 1996). Length of antorbital region one-quarter or less of total skull length. Length of lower temporal fenestra more than one-quarter of skull length. Anterior (premaxillary) process of maxilla small or absent. [Maxilla excluded from posterior margin of external naris in *Clevosaurus*; condition uncertain in *Brachyrhinodon* (Fraser and Benton 1989).]

**Genus CLEVOSAURUS** Swinton, 1939  

**Type species.** *Clevosaurus hudsoni* Swinton, 1939.

**Clevosaurus brasiliensis** sp. nov.  

**Text-figures 1–4**

**Derivation of name.** From the Latinized version of Brazil and Latin -ensis, a suffix denoting a place or location.

**Holotype.** PV0748T, a complete, slightly dorsoventrally crushed skull of an adult individual, with mandible in articulation (Text-figs 1A–B, 2).

**Referred specimens.** PV0613T, incomplete, obliquely dorsoventrally and laterally crushed skull and mandible of a juvenile specimen (Text-figs 1C, 3), with attached anterior cervical vertebrae. An incomplete skull (PV2852) illustrated by Ferigolo (2000, figs 4–6) is probably also referable to *C. brasiliensis*, but we were unable to examine this specimen.

**Horizon and locality.** Massive, fine-grained sandstones of the Caturrita Formation (Andreis et al. 1980), from a site 2 km north-west of the city of Faxinal do Soturno, Rio Grande do Sul, Brazil. The Caturrita Formation corresponds to the lower Coloradian faunal stage *sensu* Bonaparte (1973), which is considered late Carnian – early Norian in age. Kischlat and Lucas (2003) also dated the Caturrita Formation as late Carnian based on its tetrapods. This date awaits confirmation by other lines of stratigraphic evidence.

**TEXT-FIG. 1.** *Clevosaurus brasiliensis* sp. nov., PV0748T (holotype). A, left lateral, and B, right lateral views of the skull. C, referred specimen PV0613T, left lateral view of the skull. For definitions, see text. Scale bars represent 5 mm.
**Diagnosis.** *Clevosaurus brasiliensis* can be distinguished from other species referred to *Clevosaurus* by the following combination of character-states: antorbital region very short, comprising about 20 per cent of skull length; pterygoid with two longitudinal rows of teeth and three or four additional teeth positioned posterolateral to the lateral longitudinal tooth row. Adult maxilla with two flanged teeth, followed by one or two smaller, subconical teeth.

**Description.** This preliminary account is based only on the holotype and the referred specimen PV0613T. Additional skeletal material has been collected but has not yet been available to us for preparation and study. As the cranial structure of *Clevosaurus* has already been documented in considerable detail (Fraser 1988; Sues *et al*. 1994; Wu 1994) we restrict ourselves to presenting information pertinent to the identification of the new sphenodontian material from Brazil.

Based on the extensive development of the secondary dentine ‘lips’ on the labial surfaces of the maxillae and dentaries, with obliteration of the anterior teeth (Fraser 1988), the holotype skull (PV0748T) represents an adult individual. The length along the mid-line on the ventral surface of this skull is 23 mm, and the length measured from the rostral tip of the snout to the centre of the occipital embayment formed by the parietals is 17 mm.

The maxillary dentition of PV0748T has two large flanged teeth, which are followed by one more or less conical tooth on the left maxilla and by two conical teeth on the right. In PV0613T, a large, conical anterior tooth is followed by several small teeth and, in turn, by two large ones. The latter teeth are succeeded by three very small teeth. The dentary tooth row is not exposed in the holotype. The denition of the dentary in PV0613T resembles that of the maxilla. The secondary dentine ‘lip’ of each dentary in PV0613T bears distinct, triangular score marks that were produced by contact with the two large maxillary teeth when the jaws were closed. These features demonstrate that there was no propalinal jaw motion in *C. brasiliensis*, as inferred in *C. hudsoni* (Fraser 1988). Each premaxilla in the adult specimen PV0748T only has a single tusk-like ‘incisor’ tooth, as in *Clevosaurus bairdi* (Sues *et al*. 1994).

The snout is very short, with the antorbital length comprising only about 20 per cent of the length of the skull, as measured from the rostral tip of the snout to the parietal embayment. The intertemporal region of the skull roof is wider transversely than the interorbital region (PV0748T: 4.5 mm vs. 3 mm).

The prefrontal is large, and the lacrimal is absent as in other sphenodontians. It forms the anterodorsal margin of the orbit and extends posterodorsally towards the floor of the orbit. The long posteroventral process of the prefrontal covers the anterolateral edge of the frontal. The foramen for the nasolacrimal duct is situated on the suture between the prefrontal and the maxilla.

The frontal is transversely concave and forms only a rather small portion of the orbital margin. If correctly identified the frontoparietal suture has an unusual anterior position.

The postfrontal has a broad medial contact with the parietal and makes up a considerable portion of the posterior margin of the orbit as well as the anteromedial border of the supratemporal fenestra.

The narrow anterior process of the jugal extends anteromedial to the maxilla on the ventral margin of the orbit, contacting the descending process of the prefrontal anteriorly. The jugal is broadly contacted medially by the ectopterygoid. The long posterior process of the jugal may have formed a complete infra-
temporal bar, as reconstructed by Fraser (1988) for *Clevosaurus hudsoni*, but the process is incompletely preserved in the two specimens examined by us.

The intertemporal region of the parietales is distinctly concave transversely, rather than flat as in *C. hudsoni*, and slightly constricted at mid-length. The extensive posterolateral process of the parietal contacts the supratemporal posterolaterally.

The supratemporal is elongate posterolaterally and narrow. It contacts the squamosal along its anterolateral and posterior margins, and appears to be even larger than in other known species of *Clevosaurus*.

In PV0613T, the ventral process of the squamosal extends only half-way down that of the quadrate-quadratojugal in lateral view.

The structure of the palate in *C. brasiliensis* closely resembles that in other species of *Clevosaurus*. The most conspicuous difference is the presence of a cluster of teeth lateral to the posterior end of the more lateral of the two pterygoid tooth rows. The suborbital fenestra is bounded by the palate and ectopterygoid. The ectopterygoid has an extensive lateral contact with the jugal and maxilla. The pterygoid extends laterally above the ectopterygoid and bears a well-developed ventral process near the interpterygoid vacuity (Text-fig. 3).

The basipterygoid joint is formed between a subcircular recess in the pterygoid and the condyle-like distal end of the long basipterygoid process of the parabasisphenoid. The base of the rostrum of the parabasisphenoid (cultriform process) is situated well posterior to the level of the basipterygoid joint.

**DISCUSSION**

The sphenodontian material from the Caturrita Formation of Rio Grande do Sul is referable to *Clevosaurus* Swinton, 1939 based on the exclusion of the maxilla from the margin of the external naris by the long posterior process of the premaxilla (Fraser 1988; Sues et al. 1994; Wu 1994). It also shares with other species of *Clevosaurus* the enclosure of the suborbital fenestra only by the ectopterygoid and palatine and the presence of a distinct supratemporal [which is absent in *Gephyrosaurus* (Evans 1980) and in other sphenodontians]. Comparing its character-states with the character-taxon matrix for *Clevosaurus* and other sphenodontians by Wu (1994), as modified by Sues et al. (1994), *Clevosaurus brasiliensis* is most closely related to *C. bairdi* Sues et al., 1994 from the Lower Jurassic McCoy Brook Formation of Nova Scotia (Canada) and *C. megilli* Wu, 1994 from the Lower Jurassic lower Lufeng Formation of Yunnan (China). It also closely resembles *Clevosaurus* sp. from the Lower Jurassic of southern Africa, which is virtually indistinguishable from *C. bairdi* (Sues and Reisz 1995). *C. brasiliensis* differs from these forms primarily in the presence of a cluster of teeth on the pterygoid in addition to the two longitudinal tooth rows and by a proportionately shorter antorbital region of the skull. It is further distinguished from *C. megilli* by the absence of the distinct hourglass-shaped constriction of the intertemporal region of the skull roof and in the shape of the suborbital fenestra, which is L-shaped in the Chinese form (Wu, 1994).

The discovery of *Clevosaurus brasiliensis* provides a significant range extension for this widely distributed sphenodontian genus during the early Mesozoic. This is consistent with the distribution of other Late Triassic and Early Jurassic terrestrial tetrapods (Sues and Reisz 1995; Lucas 1998). *Clevosaurus* was first described from Late Triassic fissure-fillings in south-west England (Swinton 1939; Robinson 1973; Fraser 1988). Subsequently, representatives of this genus have been reported from the Lower Jurassic of Nova Scotia (Canada; Sues et al. 1994), Yunnan (China; Wu 1994) and southern Africa (Sues and Reisz 1995). *C. brasiliensis* also adds another Northern Hemisphere faunal element to the Late Triassic tetrapod assemblages from Brazil. Langer and Schultz (2000) and Lucas (2002) reported several other tetrapod taxa that are shared between Triassic tetrapod assemblages from South America and the Northern Hemisphere. Cisneros and Schultz (2003) described a new procolophonid parareptile, *Soturnia calidodon*, from the Caturrita Formation, which represents the first record of Leptopleuroninae sensu Modesto et al. (2002) from the Southern Hemisphere. Most recently, Kischlat and Lucas (2003) reported the occurrence of an indeterminate phytosaur from the Caturrita Formation of Rio Grande do Sul. Phytosaurs are very common in Late Triassic tetrapod assemblages in Europe, India and North America, but we are not convinced that the fragmentary material reported by
Kischlat and Lucas is correctly assigned to this group. The presence of *Clevosaurus* and a leptopleuronine procolophonid in the Caturrita Formation suggests that there may have been less biotic provincialism during the Late Triassic than has traditionally been assumed.

Recent discoveries in the Lower Cretaceous of South Africa (Ross *et al.* 1999) and Upper Cretaceous of Argentina have extended the fossil record of sphenodontians from Gondwana into the Cretaceous Period. Exceptionally complete skulls and jaws of the eilenodontine sphenodontian *Priosphodon avelasi* (Apesteguía and Novas 2003) have been recovered from the Cenomanian–Turonian Candeleros Formation of northern Patagonia. Furthermore, fragmentary lower jaws of non-eilenodontine sphenodontians have been recorded from the Campanian–Maastrichtian Allen and Los Alamitos formations of northern Patagonia (Martinelli and Forasiepi 2004). Clearly, sphenodontians formed a significant component of at least some Cretaceous terrestrial assemblages in the Southern Hemisphere.

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REFERENCES


