Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea

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The medial Permian (∼270–260 Ma: Guadalupian) was a time of important tetrapod faunal changes, in particular reflecting a turnover from pelycosaurian- to therapsid-grade synapsids. Until now, most knowledge on tetrapod distribution during the medial Permian has come from fossils found in the South African Karoo and the Russian Platform, whereas other areas of Pangaea are still poorly known. We present evidence for the presence of a terrestrial carnivorous vertebrate from the Middle Permian of South America based on a complete skull. *Pampaphoneus biccai* gen. et sp. nov. was a dinocephalian "mammal-like reptile" member of the Anteosauridae, an early therapsid predator clade known only from the Middle Permian of Russia, Kazakhstan, China, and South Africa. The genus is characterized, among other features, by postorbital bosses, short, bulbous postcanines, and strongly recurved canines. Phylogenetic analysis indicates that the Brazilian dinocephalian occupies a middle position within the Anteosauridae, reinforcing the model of a global distribution for therapsids as early as the Guadalupian. The close phylogenetic relationship of the Brazilian species to dinocephalians from South Africa and the Russian Platform suggests a closer faunistic relationship between South America and eastern Europe than previously thought, lending support to a Pangaea B-type continental reconstruction.

Gondwana | Therapsida | Paleozoic | paleogeography | migration

Knowledge of the global distribution of medial Permian terrestrial faunas is limited by the paucity of rocks deposited in terrestrial environments at that time, known mainly from the Karoo Basin of southern Africa (1, 2) and the Russian Platform (3, 4). Recent additions to these classic localities are the Chinese Xidagou Formation (Gansu Province) (5) and the Ruhuhu Formation in Tanzania (6). The medial Permian witnessed a critical faunal turnover in the mammalian stem lineage, during which pelycosaur-grade synapsids were almost completely replaced by the more derived therapsids. This greatly modified the trophic web of the terrestrial vertebrates (7). Among the main actors in this ecological change were the dinocephalian therapsids, represented by both medium size-to-large carnivores and large herbivores (8, 9). Anteosaurids were the carnivore lineage within Dinocephalia, including the South African *Anteosaurus magnificus* and the Russian *Titanophoneus potens*, which were the largest (∼6 m long) terrestrial predators of the Permian. This group is well-represented in both South African and Russian strata, and has recently been found in north China as well (5).

The Rio do Rasto Formation of the Paraná Basin in southern Brazil is the only South American Permian stratigraphic unit known to preserve terrestrial fossil faunas (10, 11) that indicate a close link with the Permian Karoo faunas (2, 12–15). Although this formation was originally considered late Permian, based on the record of the dicynodont *Endothiodon* and the alleged presence of the parareptile *Pareiasaurus*, new fossil evidence (16, 17) indicates a medial Permian (Guadalupian) age for at least part of this stratigraphic unit. Some of these new fossils enabled the recognition of dinocephalians from South America (16), although the remains were too fragmentary to further explore their affinities with confidence. Here we present a diagnosable dinocephalian species from the Permian of South America, based on a complete and well-preserved cranium. This fossil is a member of the carnivorous clade Anteosauridae, and provides evidence for Pangaea-wide distribution of carnivorous dinocephalians during the Guadalupian.

Results

Systematic Paleontology. Synapsida Osborn, 1903; Therapsida Broom, 1905; Dinocephalia Seeley, 1894; Anteosauridae Boonstra, 1954; Syodontinae Ivakhnenko, 1994; *Pampaphoneus biccai* gen. et sp. nov.

Etymology. The generic name is derived from the *pampas*, the flatlands characteristic of southern South America, where the taxon was found, and the Greek *phoneus*, meaning "killer," a reference to predatory habits. The specific epithet is an homage to José Bicca, landowner of the farm where the fossil was found.

Holotype. UFRGS (Universidade Federal do Rio Grande do Sul) PV386P, an almost complete skull and lower jaw (Fig. 1).

Locality and Horizon. Collected on the farm Boqueirão (S 30 00′ 08′′; W 54 05′ 09′′), Catuçaba District, São Gabriel Municipality, Rio Grande do Sul State, Brazil. The exposure refers to the Morro Pelado Member of the Rio do Rasto Formation, of Guadalupian age (17).

Diagnosis. The taxon is a medium-sized anteosaurid with a moderately pachyostosed skull that can be distinguished from other anteosaurids by a premaxilla that bears only four teeth, a squamosal jugal process that surpasses the anteriormost margin of the temporal fenestra, and the presence of a shallow, elliptical, angular boss. *P. biccai* can further be distinguished from all anteosaurids except *Syodon biarmicum* by the presence of at least eight short, bulbous postcanines bearing fore and aft serrations. It can be distinguished from *S. biarmicum* by its larger size, more robust snout, thickened postorbital that forms an orbital boss, and well-developed crests that extend from the pineal boss to the orbital rim.

Description and Comparisons. For the sake of brevity, the description is restricted to characteristics of phylogenetic significance. A comprehensive description is in progress and will be provided elsewhere. *P. biccai* is a medium-sized anteosaurid; its

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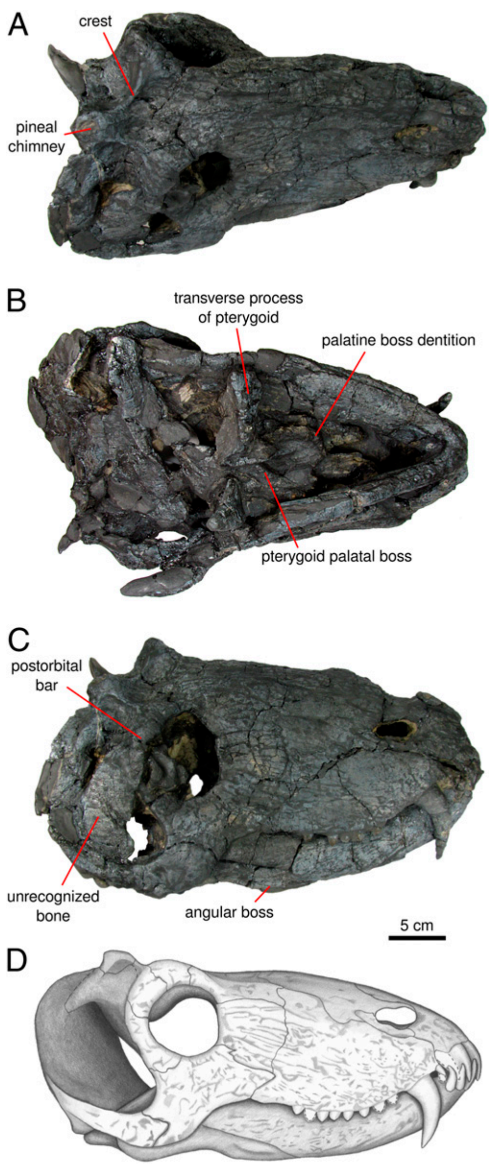

Fig. 1. *P. biccai* from the Middle Permian of Brazil. Photographs of the cranium UFRGS PV386P (holotype) in (*A*) dorsal, (*B*) ventral, and (*C*) lateral view. Reconstruction (*D*) of holotype in lateral view.

cranium measures ∼320 mm, a skull size that is shorter than all anteosaurines and larger than all syodontines but similar to that of the basal anteosaurid *Archaeosyodon praeventor* from Russia. The roof of the cranium is slightly pachyostosed and the snout features ornamentation in the form of longitudinal ridges that radiate from the orbital rim to the lacrimal and the maxilla. The premaxillary alveolar margin is raised in a typical anteosaurid fashion, and features four incisors that intermesh with those of the mandible, the small fourth incisor apparently being laterally covered by the maxilla. The canine is long (∼70 mm) and strongly recurved (72°), as in *A. praeventor* and *S. biarmicum* from Russia. The postcanines are very low and robust, similar to those of *S. biarmicum*, and bear fine serrations. The right maxilla features eight postcanines, and the left maxilla features nine. The skull roof of *P. biccai* has a well-developed medial crest and supraorbital bosses that are remarkably similar to those present in subadult *Titanophoneus potens* (Paleontological Institute, Russian Academy of Sciences, Moscow, 157/1) from Russia. The temporal fenestrae are large as in all syodontines, extending anteroventrally well below the orbits and dorsally above the orbits, contacting the pineal chimney. The anterodorsal border of the temporal fenestra is limited by a high ridge that connects the pineal chimney with the orbit, similar to that present in *T. potens*. In the palate, numerous teeth are present on the palatine and pterygoid bosses and transverse processes of the pterygoids. The palatine bosses are prominent, being connected along the midline as in the Russian *S. biarmicum* and *Australosyodon nyaphuli* from South Africa. The lower dentition is not as well-preserved as the upper, making it difficult to determine the number of incisors and postcanines. The lower canine is shorter than the upper and occludes mesio-lingually to the latter, fitting into a fossa. Lower postcanines are morphologically similar to the upper ones.

Phylogenetic Relationships. A cladistic analysis was performed to address the affinities of *P. biccai*. The taxon was included in the data matrix for Anteosauridae recently published (18), nine new characters were added to the list, and some character modifications were done, based on personal observation of holotypes and referred specimens (*SI Text*). The analysis was run under TNT (19) using the implicit search algorithm (an exact solution is guaranteed) and collapsing rule 1 (branches with ambiguous support are collapsed).

Only four most parsimonious trees were found (Fig. 2 and Fig. S1), with 84 steps. These trees only differ in the placement of *Microsyodon*, a taxon that is known only on the basis of a single maxilla. In all four trees, the analysis identifies *P. biccai* as the basalmost syodontine, a clade formed by *Notosyodon gusevi* from Kazakhstan, *S. biarmicum* from Russia, and *A. nyaphuli* from South Africa. Nonambiguous synapomorphies supporting this relationship are as follows: [2:1] postcanine basal-apical length × meso-distal length nearly equivalent; [14:1] palatine bosses close or interconnected (but suture still visible); [27:1] frontal contribution to the pineal chimney; and [32:1] jaw adductor musculature attachment on pineal chimney. The Syodontinae are a radiation of medium-sized carnivore dinocephalians with light skulls, in contrast to the Anteosaurinae, which comprise huge carnivorous dinocephalians with heavily constructed, pachyostotic skulls. The Brazilian taxon, which fits between the size ranges of these clades and combines morphological characteristics of both groups, occupies a basal position within the Syodontinae.

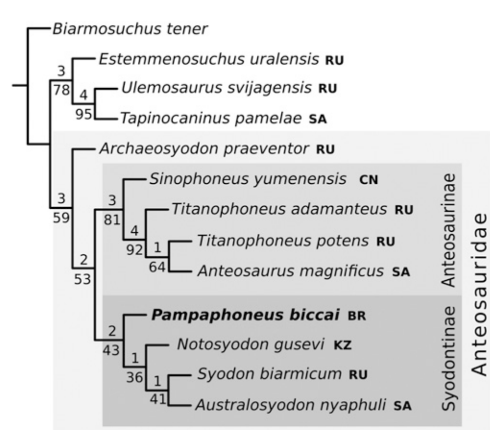

Fig. 2. Strict consensus of anteosaurid relationships, after pruning of *Microsyodon* (see *SI Text* for the four most parsimonious trees including all taxa). BR, Brazil; CN, China; KZ, Kazakhstan; RU, Russia, SA, South Africa. Decay index and symmetric resampling values (above and below, respectively) are provided as measures of support before each node. Decay index calculated from 422 trees. Resampling calculated from 3,000 replicates.

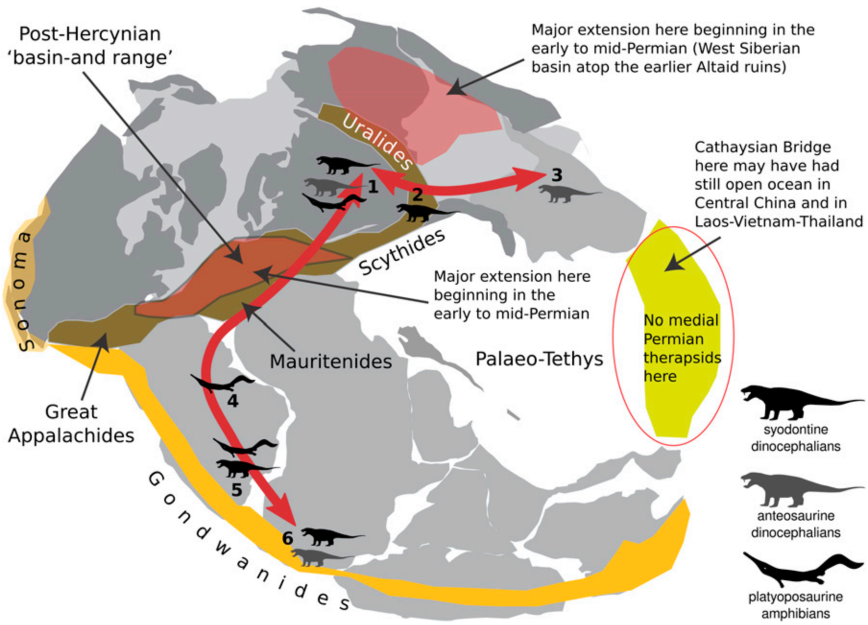

Fig. 3. Reconstruction of Pangaea B showing anteosaurid dinocephalians and platyoposaurid temnospondyles during the Middle Permian. Probable dispersal routes are indicated by red arrows. 1, Russian Platform; 2, southern fore-Urals, Kazakhstan; 3, Ordos Basin, China; 4, Parnaíba Basin, Brazil; 5, Paraná Basin, Brazil; 6, Karoo Basin, South Africa. The map is considerably modified from ref. 48 after new geological data.

Discussion

Trans-Pangaean Tetrapods During the Medial Permian. Our study corroborates a previous analysis (18) in placing the Russian *A. praeventor* as the most primitive anteosaurid and the Chinese *Sinophoneus yumenensis* as the basalmost anteosaurine. This evidence, in addition to the basal placement of *Pampaphoneus* among the syodontines, indicates that the Anteosauridae, from its earliest stages of evolution, already had a trans-Pangaean distribution, as the two anteosaurid subclades comprise species from both Laurasia and Gondwana. The Anteosaurinae has members from Russia, China, and South Africa, whereas the Syodontinae has representatives from Russia, Kazakhstan, South Africa, and, now, Brazil (Fig. 3). This cosmopolitan distribution is also reflected in other groups, such as the herbivorous dinocephalians, with forms such as the Russian *Ulemosaurus* being closely related to the South African *Tapinocaninus* (20). Other medial Permian basal therapsids with trans-Pangaean representation are the Biarmosuchia, known from Russia and South Africa (5, 21, 22), and the paraphyletic basal anomodonts, with species from Russia (23), China (24), South Africa (25), and Brazil (26).

Apart from therapsids, other Guadalupian tetrapod groups also have trans-Pangaean representatives. Varanopid synapsids originated in the Carboniferous of North America, and are recorded in Russia and South Africa in the medial Permian (27, 28). Nycteroleterids, a group of small parareptiles, are known from the medial Permian of Russia (3) and South Africa (29), and from North America (30) in a horizon that could be either early or medial Permian (31, 32).

Further evidence in support of faunistic proximity between these Pangaean subcontinents is provided by the distribution of platyoposaurine archegosaurids, a group of long-snouted, gharial-like amphibians. Three species are known in Brazil: *Bageherpeton longignathus*, *Australerpeton cosgriffi*, and *Prionosuchus plummeri* (33, 34). The first two are from the Rio do Rasto Formation, in the states of Rio Grande do Sul and Paraná, respectively, whereas the latter is found in the Pedra de Fogo Formation (?Cisuralian/Guadalupian) (35, 36), in the Parnaíba Basin of northern Brazil. Apart from Brazil, platyoposaurines are known only from the Ocher Assemblage of Russia of medial Permian age (4, 37, 38), where they are represented by *Platyoposaurus* spp. and *Bashkirosaurus cherdyncevi* (33).

Pangaea B as a Scenario for Faunal Dispersal. The global distribution of dinocephalians and other continental tetrapods in the medial Permian implies the existence of a barrier-free connection between Laurasia and Gondwana that allowed their migration across Pangaea. Two probable paths of dispersal around the Paleo-Tethyan Ocean need consideration: eastern Pangaea via the Cathaysian bridge (39) and western Pangaea around the central Pangaean mountains.

The Cathaysian continental fragments comprise small landmasses that include north China, Korea, south China, and Indochina (39, 40). These fragments were an archipelago that eventually formed a bridge and played an important role in therapsid dispersal during late Permian and early Triassic times (39). The Middle Permian Xidagou Formation, in the Ordos

Fig. 4. Life reconstruction of the dinocephalian *P. biccai* from the Middle Permian of Brazil.

Basin of northern China, has produced a fauna that shows strong similarities to that from Russian deposits of the same age and indicates a link between this part of Cathaysia and Laurasia during the medial Permian (5, 41, 42). This faunal link is supported by firm geological connections (43). The presence of Oman paleofloras that share elements from Cathaysia, Gondwana, and Laurasia (44) could be interpreted as evidence for a connection between Gondwana (through the Arabian Peninsula) and Cathaysia during the medial Permian. However, there is no direct evidence that the Cathaysian bridge was complete at this time (39). Although these fragments, consisting of island arcs and continental platforms, could have allowed the dispersal of flora, still existent marine barriers would have made it very difficult, if not impossible, for both terrestrial and freshwater tetrapods to cross Cathaysia to reach South Africa from eastern Europe in the medial Permian (39).

A more feasible migration route was via western Pangaea. Currently, two models of Pangaean reconstructions are debated: Pangaea A, which is similar to the classical Pangaea reconstructions, and Pangaea B, where South America is juxtaposed against the Appalachians until sometime in the early Triassic. In a Pangaea A reconstruction (39), the distance between the Russian Craton and southern Brazil was considerable, and the Appalachian/Mauritanian mountain ranges were important barriers. By contrast, in a Pangaea B configuration (Fig. 3), Brazil was not only closer to eastern Europe but the only mountain barrier along the way was the European Hercynides. Recent studies (39, 45, 46) indicate that right-lateral strike-slip motion during and after the Hercynian orogeny was much more significant than hitherto imagined, much more so in any case than initially proposed (47).

This right-lateral motion extended all of the way from the English Channel/Tornquist-Teisseyre Lineament in the north and northeast, to northwest Africa in the south and southwest (39, 46). The shear was distributed by a complex array of structures ranging from extensional basins and local structures of shortening to through-going strike-slip faults forming a very broad transtensional keirogen (a strike-slip system) (39, 47). Therefore, already in the early Permian the European Hercynides were much extended and large portions of them had subsided close to sea level in places such as the north German (or Lower Saxony) Basin (39). In the remaining areas, large rift basins had replaced the former mountains in which the Rotliegendes sedimentary rocks had been laid down. In eastern Europe, these basins had subsided sufficiently to allow, in Zechstein time, a marine communication between the Paleo-Tethys and the Panthalassa in eastern Greenland and western Norway (39).

In the medial Permian it is possible that tetrapods migrated from Russia to Brazil and beyond to South Africa via eastern Europe and western Africa across the broad post-Hercynian keirogen and behind the Appalachian/Mauritanian orogenic belt (see the major red arrow in Fig. 3) because, in eastern Europe, the Hercynides no longer created a geographical barrier to their migration. This hypothesis could be tested by searching for tetrapod fossils or tetrapod ichnofossils in the poorly fossiliferous medial Permian deposits of eastern Europe, such as part of the Carapelit Formation in Romania or the Çakraz Formation in northwestern Turkey.

Conclusions

The dinocephalian *P. biccai* (Fig. 4) is a terrestrial carnivore from the Permian of South America, contributing to an ecologically more balanced picture of continental vertebrate communities during the late Paleozoic in western Gondwana. The anteosaurid provides further support for an early cosmopolitan distribution of tetrapods, and especially basal therapsid groups, already in the Guadalupian. Comparison of the tetrapod content of the Brazilian Middle Permian with that of other known Pangaean faunas suggests a greater contribution from eastern Europe to the shaping of the terrestrial faunas in western Gondwana than previously recognized. A western Pangaean route for tetrapod dispersal, in a Pangaea B scenario, is here favored against migration through the Cathaysian bridge. Tetrapods could have used the low Hercynides as a corridor for migration from eastern Europe to Brazil and, from there, to South Africa.

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