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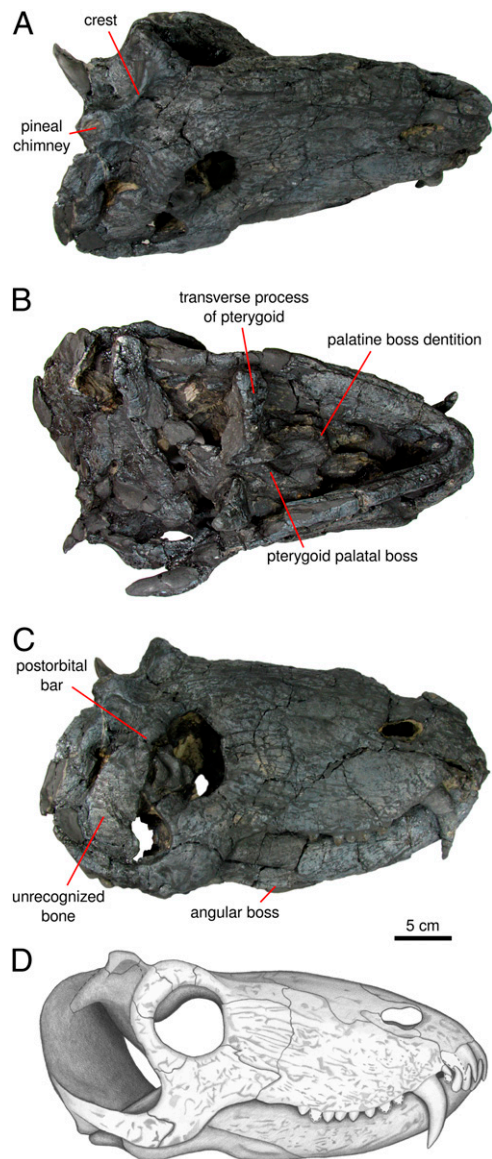
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Fig. 1. *P. biccai* from the Middle Permian of Brazil. Photographs of the cranium UFRGS PV386P (holotype) in (*A*) dorsal, (*B*) ventral, and (*C*) lateral view. Reconstruction (*D*) of holotype in lateral view.

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.
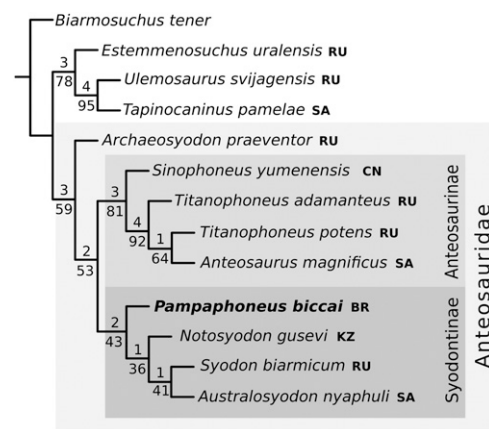

Fig. 2. Strict consensus of anteosaurid relationships, after pruning of *Microsyodon* (see *SI Text* for the four most parsimonious trees including all taxa). BR, Brazil; CN, China; KZ, Kazakhstan; RU, Russia, SA, South Africa. Decay index and symmetric resampling values (above and below, respectively) are provided as measures of support before each node. Decay index calculated from 422 trees. Resampling calculated from 3,000 replicates.
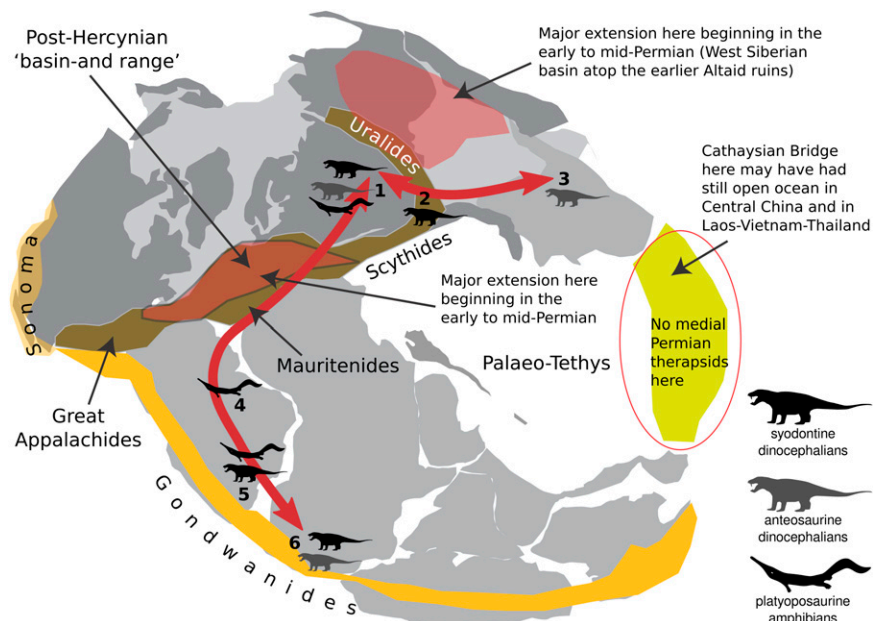
Fig. 3. Reconstruction of Pangaea B showing anteosaurid dinocephalians and platyoposaurid temnospondyles during the Middle Permian. Probable dispersal routes are indicated by red arrows. 1, Russian Platform; 2, southern fore-Urals, Kazakhstan; 3, Ordos Basin, China; 4, Parnaíba Basin, Brazil; 5, Paraná 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
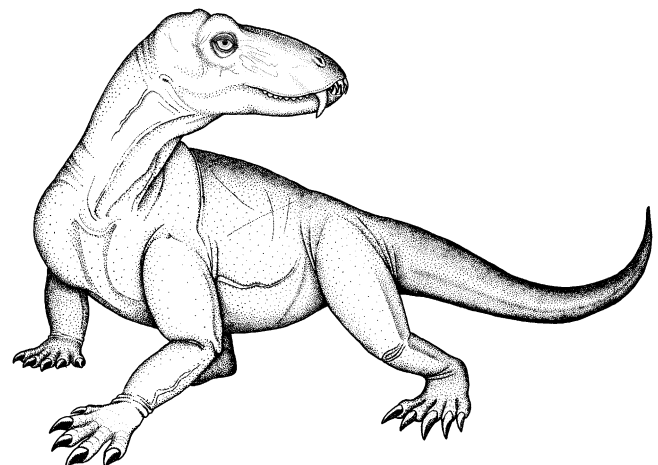

Fig. 4. Life reconstruction of the dinocephalian *P. biccai* from the Middle Permian of Brazil.

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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Supporting Information

Cisneros et al. 10.1073/pnas.1115975109

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Cladistic Analysis. To explore the phylogenetic affinities of *Pampaphoneus biccai* gen. et sp. nov., we added this taxon to a modified version of the recent data matrix for Anteosaurid dinocephalians presented in ref. 1. The taxon was included in the second block of data presented by the aforementioned author. This dataset only includes dental characters of the holotype of "*Stenocybus*," which is considered a juvenile specimen of *Sinophoneus yumenensis*. In addition to the taxon, the herbivorous dinocephalian *Ulemosaurus svijagensis* from Russia was included in the data matrix. The analysis was run on TNT (2), all characters having equal weights, using the implicit search algorithm (an exact solution is warranted) under collapsing rule 1 (collapsing branches if supported ambiguously), which produces more conservative phylogenetic hypotheses. Throughout the text, character numbers used by ref. 1 are indicated by a letter "K" in brackets. Some characters were proposed by previous authors; for more references, see ref. 1.

Specimens Examined. Institutional abbreviations: BP, Bernard Price Institute for Paleontological Research, University of the Witwatersrand, Johannesburg, South Africa; NM, National Museum, Bloemfontein, South Africa; PIN, Paleontological Institute, Moscow, Russia; SAM, Iziko South African Museum, Cape Town, South Africa.

Biarmosuchus tener: PIN 1758/2.

Anteosaurus magnificus: SAM PK-11296, BP/1/1369, NM QR3074.

Archaeosyodon praeventor: PIN 1758/3 (holotype), 1758/93, 1758/95, 1758/118, 1758/193, 1758/293, 1758/294, 1758/295, 1758/297, 1758/309, 1758/311, 1758/315, 1758/328.

Australosyodon nyaphuli: NM QR3152 (holotype).

Estemmenosuchus mirabilis: PIN 1758/6.

Microsyodon orlovi: PIN 4310/2 (holotype).

Notosyodon gusevi: PIN 2505/1 (holotype).

Syodon biarmicum efremovi: PIN 157/2, PIN 157/677.

Tapinocaninus pamelae: NM QR2987 (holotype), NM QR2986, NM QR2985, and SAM (ROZ) K95.

Titanophoneus potens: PIN 157/1 (lectotype), PIN 4662/1, PIN 4662/2.

Ulemosaurus svijagensis: PIN 2207/2 (lectotype) and PIN 2207/1.

Character List. New characters are indicated by an asterisk. A plus sign indicates that the character was treated as ordered (additive).

0. Number of upper postcanine teeth: [0] 10 or fewer; [1] more than 10. *
1. Postcanine morphology: [0] blade-like; [1] robust, bulbous at the base of the crown; [2] phylliform, laterally compressed, and leaf-shaped. [K1]
2. Postcanine basal-apical length × meso-distal length: [0] basal-apical length larger; [1] nearly equivalent. *
3. Posteriorly directed maxillary postcanine cusps: [0] present; [1] absent. *
4. Sectorial edge of postcanines: [0] directed anteroposteriorly; [1] angled anterolingually and posterolabially. [K2]
5. Posteriormost upper postcanines canted posterolaterally: [0] absent; [1] present. [K3]
6. Canine curvature: [0] straight or slightly recurved (<40°); [1] strongly recurved (>70°). [K4]
7. Incisors with lingual heels: [0] absent; [1] weak; [2] strong (heel width 30% or more larger than the base of the tooth apex). [K5] +
8. Location of external naris: [0] terminal; [1] nonterminal. [K6]
9. Alveolar margin of premaxilla: [0] subhorizontal; [1] canted upward. [K7]
10. Premaxilla forming broad, triangular plate palatally that separates anterior edge of vomers from incisor tooth row: [0] absent; [1] present. [K9]
11. Vomers with "scroll-like" raised edges: [0] absent; [1] present. [K10]
12. Morphology of the dentigerous region of the palate: [0] elongate triangular region; [1] distinct reniform boss. [K11] (In *Ulemosaurus* and *Tapinocaninus*, the score is based in the presence of a reniform boss, although there are no teeth in that structure.)
13. Dentition on palatine: [0] multiple tooth rows; [1] single tooth row. [K12]
14. Palatine bosses: [0] well-separated; [1] close or interconnected (but suture still visible). *
15. Dentition on palatal ramus of pterygoid: [0] numerous teeth; [1] reduced to 1 or non-tooth. [K13]
16. Dentition on transverse process of pterygoid: [0] extensive; [1] absent or reduced to a few teeth at the medial edges of the processes. [K14]
17. Posterior shelf on transverse process of pterygoid: [0] absent; [1] present. [K15]
18. Transverse process of pterygoid: [0] not expanded distally in palatal view; [1] palmate, massively expanded distally. [K16]
19. Quadrate rami of pterygoid intimately appressed, bifurcating the anterior margin of the basisphenoid: [0] absent; [1] present. [K17]
20. Dorsal margin of maxilla: [0] gently rounded, with no overhang on lacrimal; [1] acute, with no overhang on lacrimal; [2] with dorsoposterior process partly overhanging upper margin of lacrimal.
21. Dorsal margin of snout: [0] gradually sloping toward tip; [1] markedly concave, sloping upward acutely postnaris. [K20]
22. Snout proportions: [0] short, broad, 35% of total skull length; [1] long, narrow, >25% of total skull length. [K21]
23. Ridge extending along external surface of jugal-lacrimal suture: [0] absent; [1] present. [K22]
24. Location of fronto-nasal suture: [0] far anterior to orbits; [1] at anterior edge of orbits behind the anterior edge of the orbit. [K23]
25. Ornamentation consisting of anteroposterior ridges and sulci on the surface of lacrimal and maxilla: [0] weak or absent; [1] well-developed. *
26. Interorbital crest on midline of frontals: [0] absent; [1] present. [K24]
27. Crest lateral to the pineal foramen extending to the postorbital bar: [0] absent; [1] low; [2] well-developed (Fig. 1*A*). + *
28. Frontal contribution to anterior border of pineal boss: [0] absent; [1] present. [K25]
29. Frontal forms anterior margin area of jaw adductor musculature attachment: [0] no; [1] frontal forms only medial anterior border of adductor area; [2] frontal forms majority of the adductor area, excepting only the orbital rim, made of the postorbital. [K26] +
30. Shelf on posterior margin of orbit: [0] absent; [1] present. *
31. Ventral margin of posterior portion of zygoma on jugal: [0] straight; [1] convex; [2] convex and bearing a lateral bony process. *
32. Jaw adductor musculature attachment on pineal boss: [0] absent; [1] present. [K27]

33. Shape of postorbital bar: [0] not or gently curved; [1] strong anteroventral curvature, temporal fenestra undercuts orbit. [K28]
34. Postorbital bar: [0] transversally narrow; [1] transversally moderately expanded; [2] transversally prominently expanded. [K29]
35. Pachyostosis of the skull: [0] absent; [1] present but restricted to orbital and temporal rims; [2] entire surface of the skull pachyostosed. [K30] +
36. Shape of the symphysial region of mandible: [0] anterior edge gradually sloping upward; [1] anterior edge massive, nearly vertical. [K31]
37. Marked "step" down after the last incisor on dentary: [0] absent; [1] present, canine on an elevated platform relative to all postcanines. [K32]
38. Angular ornamentation: [0] absent; [1] boss; [2] prominent crest. [K34]
39. Angular boss morphology: [0] bar; [1] lenticular or diamond-shaped. *
40. Position of jaw articulation: [0] at back of skull; [1] rotated forward. [K35]

Character Modifications.

7. Incisors with lingual heels [K5]: State [1] "yes," was divided in two new states: [1] weak; [2] strong (heel width 30% or more larger than the base of the tooth apex).
20. Dorsal margin of maxilla [K19]: State [0] "gently rounded, with no overhang on lacrimal," was divided in two new states: [0] gently rounded, with no overhang on lacrimal; [1] acute, with no overhang on lacrimal. The new state [1] was coded present for *Tapinocephalus* and *Ulemosaurus.* The old state [1] "with dorso-posterior process partly overhanging upper margin of lacrimal" is now state [2].
38. Angular ornamentation [K34]: Wording changed, and one state was added: [2] prominent crest.

Excluded Characters.
Three characters were excluded from the data matrix by ref. 1, following their original numbers:

8. Alveolar margin of the precanine region: [0] straight; [1] concave.
18. Ventral margin of maxilla: [0] subhorizontal; [1] highly convex.
33. Dentary proportions in the region posterior to the canine and anterior to the coronoid process: [0] dorsoventrally narrow, constricted at region of postcanine tooth row; [1] tall, of constant height.

These characters were excluded because it was difficult to establish a boundary between the character states in certain taxa included in this study; in addition, character [K33] could not be coded for some taxa in which the relevant area of the skull is not sufficiently preserved (e.g., *Australosyodon*).

Rescored Character States.
The scoring of some characters was modified from ref. 1 for some taxa, following first-hand examination and interpretation of the relevant specimens.

1. Postcanine morphology [K1]: [0] blade-like; [1] robust, bulbous at the base of the crown; [2] phylliform, laterally compressed, and leaf-shaped. Rescored from [1] to [0] in *Australosyodon*.
4. Sectorial edge of postcanines [K2]: [0] directed anteroposteriorly; [1] angled anterolingually and posterolabially. Rescored from [1] to [0] in *Australosyodon*. Rescored from [?] to [0] in *Archaeosyodon* (coded from left side of PIN 1758/293 and PIN 1758/297).
10. Premaxilla forming broad, triangular plate palatally that separates anterior edge of vomers from incisor tooth row [K9]: [0] absent; [1] present. Rescored from [1] to [?] in *Australosyodon*, as the relevant area is not well-preserved.
26. Interorbital crest on midline of frontals [K24]: [0] absent; [1] present. The state [?] was rescored as [-] not applicable.
35. Shape of the symphysial region of mandible [K31]: [0] anterior edge gradually sloping upward; [1] anterior edge massive, nearly vertical. Modified from [0] to [1] in *Australosyodon* after observation of the holotype.
36. Marked "step" down after the last incisor on dentary [K32]: [0] absent; [1] present, canine on an elevated platform relative to all postcanines. Rescored from [0] to [1] in *Biarmosuchus tener* (PIN 1758/2).

1. Kammerer CF (2011) Systematics of the Anteosauria (Therapsida: Dinocephalia). *J Syst Palaeontology* 9:261–304.

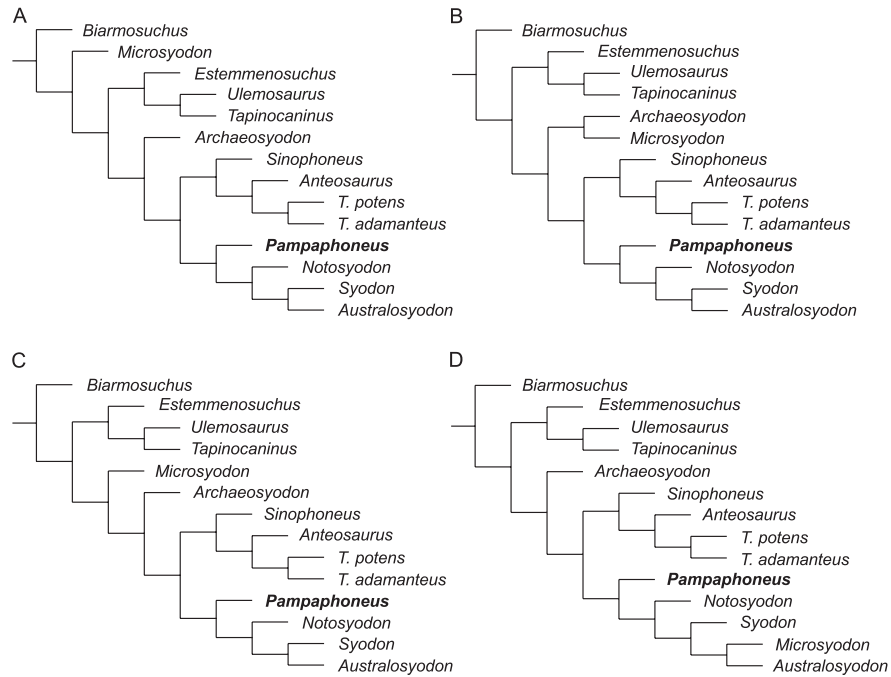2. Goloboff PA, Farris JS, Nixon K (2008) TNT: Tree Analysis Using New Technology (Willi Hennig Society Edition), Version 1.1. http://www.zmuc.dk/public/phylogeny/TNT.

Fig. S1. The four most parsimonious trees recovered in the phylogenetic analysis.

Table S1. Taxon/character matrix used in this analysis

| | | | + + | + |
| | + | 1111111111 | 2222222222 | 33333333334 |
Taxon	0123456789	0123456789	0123456789	01234567890
Biarmosuchus tener	0000000000	0000000000	0010000000	100000010–0
Estemmenosuchus uralensis	1201000000	0010000100	?000100000	020012000–1
Ulemosaurus svijagensis	0201A?02?0	001?01110?	100020000?	000022102?1
Tapinocaninus pamelae	0?01000210	0011011100	1000100000	010022002–1
Archaeosyodon praeventor	1101001101	0110000001	0001010200	100100000–0
Sinophoneus yumenensis	0100?00111	1?11011011	2001111200	1?010111??0
Anteosaurus magnificus	01A1110111	1111011011	210111–100	11011211101
Titanophoneus adamanteus	?10?110111	1111011011	2101111200	11011211111
Titanophoneus potens	0100110111	1111011011	21011???00	1?011211111
Pampaphoneus biccai	0111001111	?11110000?	2001111210	1111?10110?
Notosyodon gusevi	??????????	??????????	???????11	101101????0
Syodon biarmicum	0111101111	1111111001	2011111112	111101010–0
Australosyodon nyaphuli	10A0000111	?111101001	0011111112	1?1100110–0
Microsyodon orlovi	1000001???	??????????	0?????????	???????????

Ordered characters are indicated by a plus sign. Question marks represent missing information. Hyphens indicate inapplicable characters. A = 0,1.