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First evidence of a bolosaurid parareptile in France (latest Carboniferous-earliest Permian of the Autun basin) and the spatiotemporal distribution of the Bolosauridae

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Key-words. – Carboniferous, Permian, Parareptilia, Anatomy, Taxonomy, Phylogeny, Biodiversity, Biogeography.

Abstract. **–** A new species of Bolosauridae, *Belebey augustodunensis*, is described from fragmentary cranial material collected in the late Gzhelian-Asselian beds of the Autun basin, central France. *Be. augustodunensis* is one of the oldest bolosaurids and represents the first occurrence of the family in France. The dentition of this species is unique within Bolosauridae in exhibiting a progressive shift from a mesio– to a disto-lingual orientation of the tooth apex and lingual facet. Other features show that *Be. augustodunensis* belongs to the genus *Belebey*, although it lacks several specializations known in other species of the genus. A review of the valid bolosaurid taxa increases their stratigraphic and geographic distribution, in addition to the description of *Be. augustodunensis*. The distributions and diversification of Bolosauridae are briefly discussed.

Première découverte d'un parareptile bolosauridé en France (Carbonifère terminal-Permien initial) et la distribution spatiotemporelle des Bolosauridae

Mots-clés. – Carbonifère, Permien, Parareptilia, Anatomy, Taxonomie, Phylogénie, Biodiversité, Biogéographie.

Résumé. – Une nouvelle espèce de Bolosauridae, *Belebey augustodunensis*, est décrite d'après du matériel crânien fragmentaire collecté dans les couches du Gzhélien supérieur-Assélien du bassin d'Autun, en France. *Be. augustodunensis* est l'un des plus ancien bolosauridés connus et représente la première occurrence de la famille en France. La denture de cette espèce est unique au sein des Bolosauridae car l'apex des dents et leur facette linguale passe progressivement d'une orientation mésio– à distolinguale. D'autres traits montrent que *Be. augustodunensis* appartient au genre *Belebey*, bien qu'il lui manque plusieurs des spécialisations connues chez les autres espèces du genre. Une revue des taxons bolosauridés valides accroît leur distribution stratigraphique et géographique, en plus de la description de *Be. augustodunensis* présentée ici. Les distributions et la diversification des Bolosauridae sont brièvement discutées.

INTRODUCTION

Bolosauridae are small, lizard-like parareptiles characterized by a complex dentition specialized for plant-eating [Berman *et al.*, 2000]. Although known for more than 120 years [Cope, 1878], they were considered as one of the most enigmatic amniote clades until recently. They were previously known from cranial and fragmentary postcranial material [e.g., Cope, 1878; Case, 1907; Broom, 1913; Watson, 1954; Tatarinov, 1968; Ivakhnenko, 1973; Ivakhnenko and Tverdokhlebova, 1987; Ivakhnenko, 1990; Li and Cheng, 1995], but the discovery of a nearly complete, articulated bolosaurid skeleton provided new insights into their anatomy, locomotion, and relationships, leading to their placement in Parareptilia [Berman *et al.*, 2000; Reisz *et al.*, 2007; Müller *et al.*, 2008].

Six species included in three genera are recognized today according to Müller *et al.* [2008], namely *Bolosaurus striatus* COPE, 1878 and *Bolosaurus grandis* REISZ, BARKAS & SCOTT, 2002 from the uppermost Carboniferous to Lower Permian of the United States [Watson, 1954; Reisz *et al.*, 2002; Lucas, Berman *et al.* 2005]; *Belebey vegrandis* IVAKHNENKO, 1973 and *Belebey maximi* TVERDOKHLEBOVA, 1987 [in Ivakhnenko and Tverdokhlebova, 1987] from the Middle Permian of Russia; *Belebey chengi* MÜLLER, LI & REISZ, 2008 from the Middle Permian of China; *Eudibamus cursoris* BERMAN, REISZ, SCOTT, HENRICI, SUMIDA & MARTENS, 2000 from the Lower Permian of Germany. Four additional, enigmatic species, *Bolosaurus major* BROOM, 1913 from the Lower Permian of the United States [Broom, 1913] and *Gnorhimosuchus satpaevi* EFREMOV, 1951, *Permotriturus herrei* TATARINOV, 1968, and *Timanosaurus ivachnenkoi* GUBIN, 1993 from the Middle Permian of Russia [Ivakhnenko, 1990; Ivakhnenko *et al.*, 1997], were previously mentioned but did not appear in recent literature on bolosaurids. Additional material was also described from the uppermost Carboniferous of the United States but could not be assigned confidently to one of the previously known species [Harris *et al.*, 2004]. The bolosaurid assignment of the Lower Permian *Bolosaurus traati* TATARINOV, 1974 and of the Middle Permian *Davletkulia gigantea* IVAKHNENKO, 1990 of Russia proved

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to be ill-founded [Modesto and Rybczynski, 2000; Reisz *et al.*, 2002]. Despite a wide stratigraphical and geographical distribution, bolosaurids remain very rare.

The first evidence for the presence of bolosaurids in France is brought by the description of an overlooked specimen, MNHN.F.AUT 891, housed in the Muséum National d'Histoire Naturelle, in Paris. MNHN.F.AUT 891 was first mentioned by Thévenin [1910] who referred it to the sphenacodont *Haptodus baylei*. The absence of description or illustrations, which would have allowed further discussion, was lamented by Romer and Price [1940] in their redescription of *H. baylei*. MNHN.F.AUT 891 was even not mentioned in the latter revision of the genus *Haptodus* by Currie [1979] and Laurin [1993], both of whom ignored the work of Thévenin [1910]. When it was found by the present author in fall 2007, MNHN.F.AUT 891 was still labeled as *Haptodus baylei*. Comparison with the holotype of *H. baylei* (MNHN 1886-83-3A and B), however, did not support this assignment. Its dentition suggested instead that MNHN.F.AUT 891 belongs to a new kind of bolosaurid. This specimen is thus described here as the first French member of the Bolosauridae, with a discussion on bolosaurid phylogenetic relationships. The stratigraphic and geographic distribution of Bolosauridae is also discussed, with respect to their relationships.

Remark

The terminology used in the description of the dentition follows the conventions proposed by Smith and Dodson [2003].

Institutional abbreviations

AMNH–American Museum of Natural History, New York City, New York, United States; CM–Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States; IVPP–Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCZ–Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States; MNG–Museum der Natur Gotha, Gotha, Thuringia, Germany; MNHN–Muséum National d'Histoire Naturelle, Paris, France; NMMNH–New Mexico Museum of Natural History, Albuquerque, New Mexico, United States; OMNH–Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, United States; PIN–Palaeontological Institute, Russian Academy of Science, Moscow, Russia; SGU–Saratov Geological University, Saratov, Russia; TMM–Texas Memorial Museum, Austin, Texas, United States; UCMP–University of California Museum of Paleontology, Berkeley, California, United States.

SYSTEMATIC PALEONTOLOGY

Parareptilia Olson, 1947
Ankyramorpha deBraga & Reisz, 1996
Bolosauridae Cope, 1878
Belebeyinae Ivakhnenko, 2001
Belebey Ivakhnenko, 1973
Belebey augustodunensis sp. nov.
(figs 1-3, tabl. I)

Holotype. – MNHN.F.AUT 891 (formerly R 142), pro parte, cranial remains of a single individual comprising a left tooth-bearing maxilla and an indeterminate triradiate bone. A right humerus may possibly belong to the same individual (see below).

Etymology. – Species name from the Latin for "from Augustodunum", former name of the town of Autun, which gave its name to the geological basin where MNHN.F.AUT 891 was found.

Type locality. – Exact provenance unknown, Autunois, Saône-et-Loire, Burgundy, France.

Type horizon and age. – Bituminous beds of the 'Autunian' series, Autun basin. There was unfortunately no indication of the geographical or stratigraphical provenance on the label found with MNHN.F.AUT 891 or in the registration catalogue when it was originally numbered R-142. However, the preservation state of the specimen, as well as its embedding matrix, are very similar than those of the holotype of *Haptodus baylei* (MNHN 1884-26-3A and B), therefore suggesting MNHN.F.AUT 891 was collected from the same Millery Formation. Notwithstanding these uncertainties, MNHN.F.AUT 891 can be relatively well dated, thanks to the abundant macro- and microflora produced by the whole 'Autunian' series (Moloy to Millery formations) [e.g., Châteauneuf *et al.*, 1992; Broutin *et al.*, 1999]. A similar Autunian flora have indeed been identified in other Peri-Tethyan basins, notably in the Donets basin [Izart, Briand *et al.,* 1998; Broutin in Izart, Vaslet *et al.*, 1998; Stchegolev in Izart, Vaslet *et al.*, 1998] in which the presence of marine interbedding allowed the stratigraphic correlation of the Autunian with the late Gzhelian (= Orenburgian Russian stage) to Asselian interval on the basis of fusulinids and conodonts [Izart, Briand *et al.*, 1998; Izart, Vaslet *et al.*, 1998]. In the Donets basin, the underlying Stephanian 'C' is correlated to the early Gzhelian (= Gzhelian sensu stricto Russian stage), but the Stephanian 'C'/Autunian boundary remains uncertain as long as the Autunian can be defined by either the First Appearance Datum (FAD) or the acme of meso-xerophytic flora [Izart, Vaslet *et al.*, 1998]. In addition, the absence of younger flora precludes the identification of the upper Autunian boundary in the overlying early Sakmarian strata [Izart, Briand *et al.*, 1998; Izart, Vaslet *et al.*, 1998 – contra Broutin *et al.*, 1999].

Diagnosis. – Distinguished from all other bolosaurids by showing a unique steady shift from a mesio- to a disto-lingual orientation of the apex and lingual facets on its maxillary cheek teeth. Bears also a unique combination of plesiomorphies and apomorphies with respect to previously known species of *Belebey*: nearly straight posterodorsal margin of the maxilla and cutting edges on maxillary posterior teeth, but shows no transverse expansion of the cheek teeth or sharp lingual recurvature of the apex.

Remark. – The erection of a new species is warranted by the identification of the diagnostic characters given above. The erection of a new genus, however, is not deemed necessary considering the closer affinities of this new species with *Belebey* than with *Bolosaurus* (see Discussion) and the fact that the genus name *Belebey* may turn out to be synonymous with the senior name *Permotriturus* (see Discussion).

Description

Cranium

The maxilla, exposed in lateral aspect, is a long bone that is about 6 mm high and 3 cm long, but missing its anterior end (fig. 1). It consists of a tooth row overlain by a dorsal lamina, with both dorsal and ventral margins being subparallel. Posterior to the level of the tooth row, the

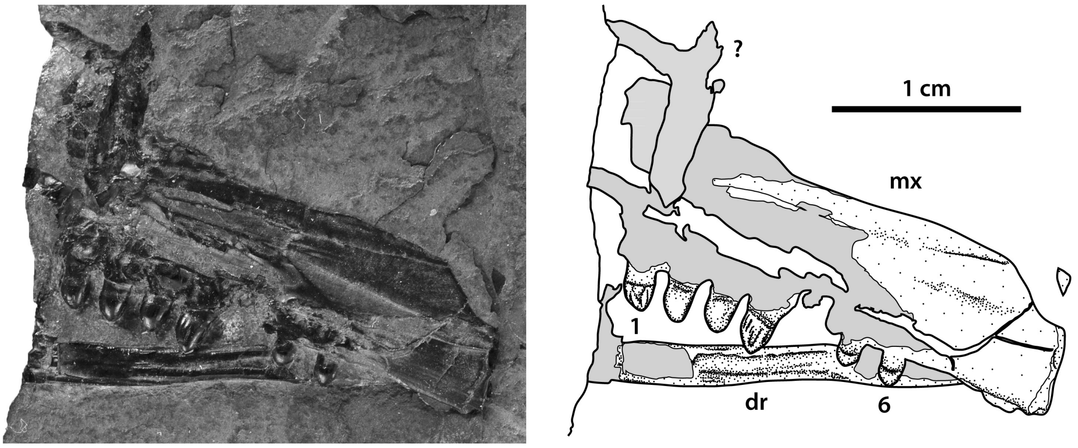

FIG. 1. – *Belebey augustodunensis*, sp. nov. (holotype MNHN.F.AUT 891) from the late Gzhelian-Asselian of the Autun basin. Abbreviations: 1, 6, first and sixth preserved teeth; dr, dorsalrib; mx, maxilla; ?, unidentified cranial element. Grayed-out areas are broken.

FIG. 1. – Belebey augustodunensis*, sp. nov., (holotype MNHN.F.AUT 891), du Gzhélien supérieur-Assélien du bassin d'Autun. Abréviations:* 1, 6, *première et sixième dents préservées* ; dr, *côte dorsale* ; mx*, maxillaire ; ?, élément crânien non-identifié. Les surfaces grisées sont cassées.*

dorsal margin of the maxilla slopes posteroventrally before becoming vertical. There is a faint alveolar shelf, formed by the lateral expansion of the maxilla dorsal to the two distalmost teeth. Its actual extent is unknown because the surface is broken anteriorly. The lateral surface of the maxilla is smooth where preserved, with no evidence of the foramina for blood vessels present in *Be. vegrandis* [Reisz *et al.*, 2007].

The triradiate bone overlying the anterior part of the maxilla resembles a diapsid jugal or postorbital (question mark on fig. 1). This bone consists of a main straight branch from which arises a slender, straight, but slanted process near one of its extremities. In this, it is very similar to a diapsid jugal, with a long suborbital and a short zygomatic horizontal process, and a more slender, posteriorly slanted postorbital process. Although the jugal and the postorbital are very different in shape in bolosaurids and there is no apparently no bone matching such a shape in *Bo. striatus* [Watson, 1954], *Be. vegrandis* [Reisz *et al.*, 2007] and *Be. chengi* [Müller *et al.*, 2008].

Dentition

Six teeth are preserved on the maxilla and there is a gap for an additional one, before the two last ones, where the maxilla is broken. For convenience, the preserved teeth will be numbered mesiodistally from 1 to 6 (fig. 1). The presence of eleven, ten, and ten or nine teeth on the maxilla in *Bo. striatus* [Watson, 1954], *Be. chengi* [Müller *et al.*, 2008], and *Be. vegrandis* [Reisz *et al.*, 2007], respectively, suggests the maxilla is only lacking its anterior third. The maxillary teeth are well preserved in labial view (fig. 2) and, although their mesial surfaces are still partly embedded in matrix, they display a typical bolosaurid shape. They consist of a bulbous crown terminating in a pointed and slightly lingually recurved apex. The cusps display a mesiodistal edge separating its lingual and labial surfaces. The dentition varies in size (tabl. I) and shape along the row. Teeth 1-4 are quite larger than teeth 5-6. On teeth 1-2, the lingual facet is still embedded in the matrix, but a general mesiolingual orientation of the apex is visible (see fig. 2 for tooth 3). Tooth 4, which is slightly displaced labially from its original position by the underlying dorsal rib, is the largest.

The facets of teeth 1-4 are weakly developed, but they show a slight concavity lingually delimited by a blunt edge. Their labial surface is covered by low, wide parallel ridges running longitudinally, from the apex to a level close to the base for teeth 1-3, or up to the base in the case of tooth 4. These ridges are wide and high on teeth 1 and 4, while they are narrow and densely packed together on teeth 2 and 3. Teeth 5-6 are quite different. They have lower and stouter crowns with no evidence of ridging on their surface, and bear sharp rather than blunt edges bordering more concave lingual facets. The lingual facets and the apex also show a distolingual rather than a mesiolingual orientation, a change more pronounced on the last tooth. The lingual facet and the apex therefore shift from a mesiolingual to a distolingual direction – a feature so far unknown in all other bolosaurids. There is no trace of ridging on the surface of teeth 5-6.

TABL. I. – Tooth measurements (in mm) of *Belebey. augustodunensis*, sp. nov. (holotype MNHN.F.AUT 891) from the late Gzhelian-Asselian of the Autun basin.

TABL. I. – *Mesures dentaires (en mm) de* Belebey augustodunensis*, sp. nov. (holotype MNHN.F.AUT 891) du Gzhélien supérieur-Assélien du bassin d'Autun.*

	Length	Width
Mesial		
Tooth 1	1.42	2.42
Tooth 2	1.52	2.16
Tooth 3	1.60	2.34
Tooth 4	1.86	2.37
Tooth 5	1.52	1.47
Tooth 6	1.48	1.55
Distal		

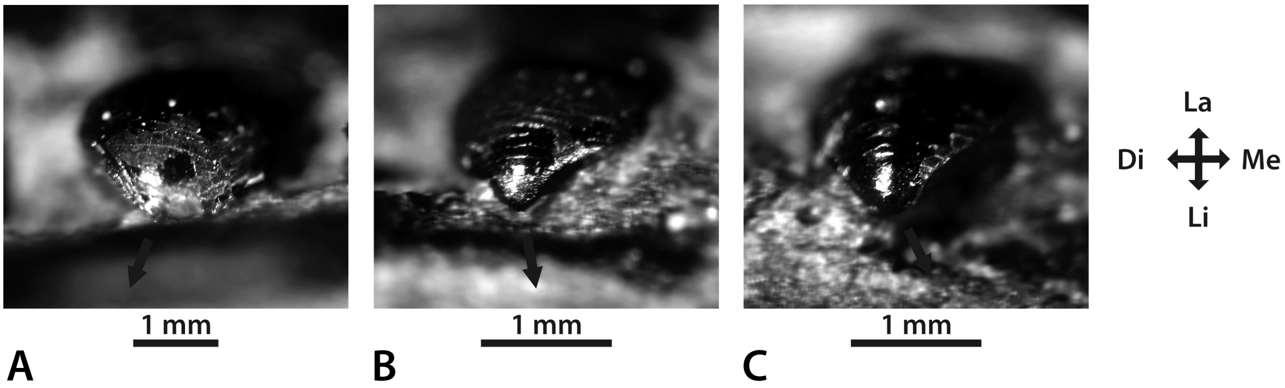

FIG. 2. – *Belebey augustodunensis*, sp. nov. (holotype MNHN.F.AUT 891) from the late Gzhelian-Asselian of the Autun basin. Maxillary cheek teeth 3 (A), 5 (B), and 6 (C), in apical view. Abbreviations: La, labial; Me, mesial; Li, lingual; Di, distal.

FIG. 2. – Belebey augustodunensis*, sp. nov., (holotype MNHN.F.AUT 891), du Gzhélien supérieur-Assélien du bassin d'Autun. Dents maxillaires 3 (*A*), 5 (*B*) et 6 (*C*) de la joue, en vue apicale. Abréviations:* La*, labial;* Me*, mésial;* Li*, lingual;* Di*, distal.*

Postcranium

The slab MNHN.F.AUT 891 includes many disarticulated postcranial remains (but see Discussion), such as two-headed ribs from the cervical and dorsal series, varying greatly in length and slightly dilated at the end. Directly associated to the maxilla is the proximal half of a dorsal rib, a slender, rod-like bone with 'lipped', subparallel margins and widening proximally (fig. 1). This element was originally mistaken for the slender quadratojugal seen in *Bo. striatus* [Watson, 1954] and *Be. vegrandis* [Reisz *et al.*, 2007]. Following the suggestion of S. Modesto (pers. com.), however, this element was re-identified as a partial dorsal rib of which the crushing resulted in this 'lip' – shown by other ribs preserved on the slab. A few limb and possibly girdle elements are also preserved on MNHN.F.AUT 891, although they are little informative given their poor condition and ossification. One of the few identifiable elements is a right humerus (fig. 3), a slender bone measuring about 16.5 mm in length, 7.6 mm in proximal width, and at least 5.3 mm in distal width. This humerus underwent indeed dorsoventral compression, which resulted in the flattening of the proximal head and in the breaking of the distal one. The former has a roughly triangular outline, with a convex proximal margin, and shows a short but distinct deltopectoral crest.

Discussion

Cranium/postcranium association

Although the cranial material preserved on MNHN.F.AUT 891 has undoubtedly bolosaurid affinities, its association with the postcranium preserved on the same slab is more questionable. The few ribs known in bolosaurids such as *Eudibamus* are short rod-like bones, even shorter than the skull [Berman *et al.*, 2000: Fig. 1]. The ribs preserved in MNHN.F.AUT 891 are hence much larger than expected, proportionally to the cranial remains. Furthermore, these ribs match in size, shape, and preservation those of the holotype of *Haptodus baylei* (MNHN 1886-83-3A and B), which belongs from the same facies – and comes presumably from the same formation. As a matter of fact, as the postcranium of MNHN.F.AUT 891 exhibits no bolosaurid or parareptilian synapomorphy, it is therefore difficult to refer them to *Belebey augustodunensis* save the right humerus mentioned above. This humerus is indeed much smaller and slender than that of *Haptodus baylei*, but similar in shape, relative size, and proportions than that of the close *Eudibamus* [Berman *et al.*, 2000]. It is thus tentatively referred to the same individual as the cranium preserved on MNHN.F.AUT 891, here described as *Belebey augustodunensis*. On the other hand, the remainder of the postcranium is assigned to an indeterminate amniote.

Phylogenetic position

The taxonomy of Bolosauridae has been treated in several recent papers, including the description of new species and the revision of earlier ones [Berman *et al.*, 2000; Reisz *et al.*, 2002, 2007; Müller *et al.*, 2008]. These data allowed an investigation of the phylogenetic position of Bolosauridae within Amniota [Berman *et al.*, 2000; Reisz *et al.*, 2007] resulting in a phylogenetic position close to Procolophonia within Parareptilia. More recently, Müller *et al.* [2008] attempted for the first time to understand Bolosauridae intrarelationships, including the six currently recognized species in their phylogenetic analysis. They also considered several non-bolosaurid parareptilian taxa such as Mesosauridae, Millerettidae, Owenettidae, and the lanthanosuchoid *Acleistorhinus* DALY, 1969. The first two taxa were used as outgroup. Their analysis resulted in a monophyletic Bolosauridae with *Eudibamus* as the sister group of the *Bolosaurus* + *Belebey* clade, and both genera as monophyletic even if the relationships of the three species of *Belebey* remained indeterminate. The phylogenetic position of the new species described here, *Be. augustodunensis*, is tested by using a modified version of the data matrix of Müller *et al.* [2008]. Two characters (#12, 14) were changed from Müller *et al.* [2008], seven were added, of which two (#1, 7) were taken from previous works [deBraga and Reisz, 1996; Laurin and Reisz, 1995] and four (#6, 8, 9, 20) are new (see Appendices 1 and 2).

The analysis was performed using the exact algorithm of TNT 1.1 [Goloboff *et al.*, 2008], with all characters left equally weighted and unordered and polymorphism treated as uncertain. Branches with a maximal length of zero were collapsed using Collapsing Rule 3. The analysis generated three equally parsimonious trees of which the strict consensus (Length=37; RI=0.851; CI=0.811) shows most of the clades found by Müller *et al.* [2008]. The only difference so far lies in the position of *Acleistorhinus*, which is here closest to Bolosauridae than to Owenettidae. Their relationships were previously left unresolved by Müller *et al.* [2008]. Yet, the clade B [*Acleistorhinus* + Bolosauridae] and the clade E [*Bolosaurus*] are the weakest, both having a Bremer support of only 1 and a low bootstrap value (even for the latter). In contrast, clade C [Bolosauridae] is the best supported, with a Bremer support of 4 and a bootstrap value of 95. This clade is defined by the presence of (#5) a slender, rod-like quadratojugal, (#16) bulbous mid and distal cheek teeth, (#19) "intermediate" mesial teeth on the maxilla or the dentary, and (#20) cheek teeth with heel and talon. Synapomorphic characters for which *Be. augustodunensis* is scored are detailed below.

The presence of a lower temporal fenestra, enclosed by the squamosal, jugal, and quadratojugal, or more rarely the postorbital and supratemporal, is not uncommon in parareptiles [e.g., Gow, 1972; deBraga and Reisz, 1996; Cisneros *et al.*, 2004; Müller and Tsuji, 2007]. In bolosaurids, the temporal fenestra is bordered ventrally by an unusually (#5) slender quadratojugal with a rod-like shape, having its dorsal and ventral margins nearly parallel [Berman *et al.*, 2000; Carroll and Gaskill, 1971; Reisz *et al.*, 2007]. In other parareptiles, the contribution of the quadratojugal to the lower arcade is much shorter and heavier than in bolosaurids correlatively to the size and shape of the fenestra [e.g., Gow, 1972; deBraga and Reisz, 1996; Müller and Tsuji, 2007].

The dentition of bolosaurids, including *Be. augustodunensis*, is also quite distinctive, with their mesial and distal cheek teeth having (#16) a bulbous crown. This shape, besides, was already emphasized by Cope [1878] when erecting the genus *Bolosaurus*. The bulbousness varies quite a lot between teeth, depending mostly on their position in the row. The dentary teeth of *Bolosaurus grandis*, for instance, are increasingly stockier distally, except for the last distal tooth [Reisz *et al.*, 2002]. In contrast, the non-bolosaurid taxa considered in the present analysis possess simple, conical crowns, which show no broadening at the base [Gow, 1972; deBraga and Reisz, 1996; Reisz and Scott, 2002; Modesto, 2006]. The first three synapomorphies have already been considered by Müller *et al.* [2008], but, surprisingly, they did not mention the last one. The mandible and dentition of bolosaurids is indeed placed so that there is dental occlusion, resulting in the wearing of cheek maxillary and dentary teeth. Because the dentary tooth rows are slightly shifted medially to the maxillary ones, the teeth are respectively worn labially and lingually and thus acquire a heel-and-talon morphology [Reisz *et al.*, 2007]. A similar occlusion pattern is known in some anomodont and dinocephalian therapsids [e.g., Reisz, 2006; Ivakhnenko, 2008a], but not in other parareptiles. Only procolophonids, close to '*Owenetta*' *kitchingorum*, feature dental occlusion and the correlative tooth wearing, but in this case the cheek tooth rows are lined up so that the wear occurred mostly apically [Gow, 1977]. The less inclusive clade D, comprising *Bolosaurus* and *Belebey*, is supported by four unambiguous synapomorphies. The members of clade D share indeed (#6) the presence of a lateral boss formed by the prefrontal and nasal, (#14[4]) the presence of two premaxillary teeth, which (#15) are distinctly larger than the closest maxillary teeth, and (#22) the presence of low longitudinal ridges on distal cheek teeth. These ridges were identified originally by Cope [1878], a condition reflected by the name of the type species of *Bolosaurus*, *Bo. striatus*. The ridges extend vertically from the apex to a level close to the base of the crown, but they are known to vary in development and extension depending on taxa and

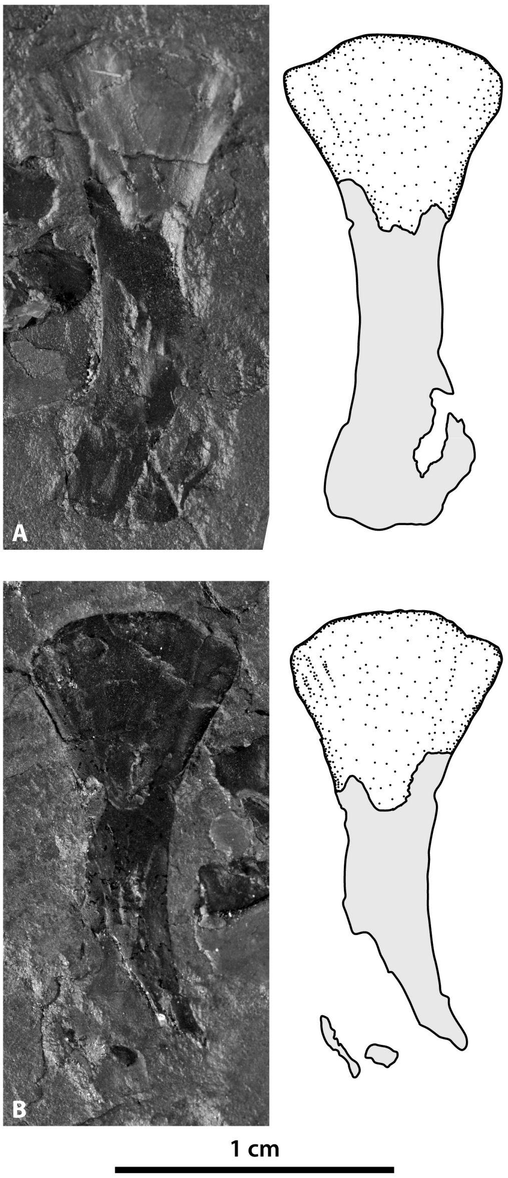

FIG. 3. – *Belebey augustodunensis*, sp. nov. (holotype MNHN.F.AUT 891) from the late Gzhelian-Asselian of the Autun basin. Part (A) and counterpart (B) of the right humerus in proximal dorsal view. Grayed-out areas are broken.

FIG. 3. – Belebey augustodunensis, *sp. nov., (holotype MNHN.F.AUT 891), du Gzhélien supérieur-Assélien du bassin d'Autun. Partie (*A*) et contrepartie (*B*) de l'humérus droit en vue proximale dorsale. Les surfaces grisées sont cassées.*

tooth position [Reisz *et al.*, 2002; Reisz, 2006; this paper]. The monophyly of *Belebey* is supported by two unambiguous synapomorphies: (#4) a straight posterodorsal margin of the maxilla and (#21) cutting ridges on distal teeth. In these forms, indeed, the maxilla height remains nearly the same until it terminates quite abruptly posterior to the level of the last teeth (#4) [Reisz *et al.*, 2007; Müller *et al.*, 2008; this paper]. In contrast, the dorsal lamina of the maxilla of *Bolosaurus striatus*, mesosaurids, millerettids, owenettids, and *Acleistorhinus* decreases steadily in height posteriorly much before the end of the tooth row [Gow, 1972; deBraga and Reisz, 1996; Reisz and Scott, 2002; Modesto, 2006]. Also, the type of occlusion becomes more complicated in *Belebey*, because it leads to the formation of cutting ridges on the mesiodistal margins of the distal cheek crowns (#21) whereas *Eudibamus* and *Bolosaurus* spp. both retain a simple kind of dental occlusion that produces no such ridges [Ivakhnenko and Tverdokhlebova, 1987; Reisz *et al.*, 2002; Müller *et al.*, 2008; this paper]. Because of the phylogenetic position of *Be. augustodunensis*, the clade G [*Be. vegrandis*, *Be. maximi*, *Be. chengi*] is now defined by only two unambiguous synapomorphies, (#23) the transverse expansion and (#24) the sharp recurvature of the main cusp of distal cheek teeth.

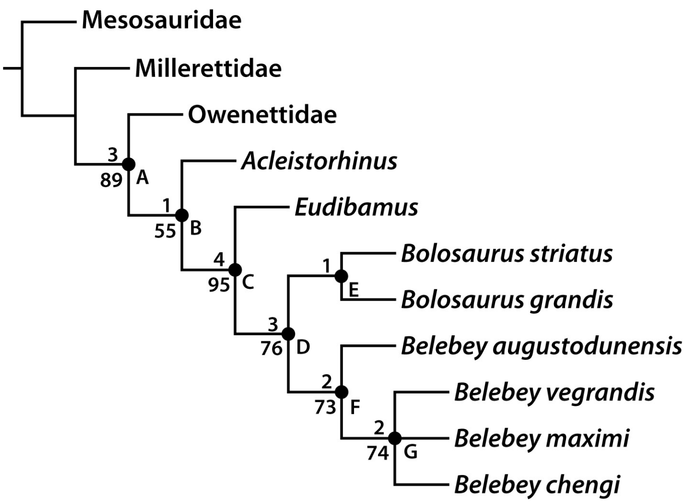

FIG. 4. – Strict consensus of the three most parsimonious trees obtained by running a modified and augmented version of Müller *et al.* [2008]'s dataset with TNT 1.1 [Goloboff *et al.,* 2008] and edited with WinClada 1.00.08 [Nixon, 2002]. Bremer support (above) and bootstrap value (below) are given for each node, except for clade E, which has a bootstrap support lower than 50. Lettered clades are characterized by the following synapomorphies, a star indicating when the transformation is homoplastic.
Clade A (Ankyramorpha): 7, 13, 27; AccTran 26; DelTran 1. Clade B: 8, 11; AccTran 12. Clade C (Bolosauridae): 5, 16, 19, 20; AccTran 9, 18; DelTran 12, 26. Clade D: 6, 14(4), 15, 21; AccTran 10, 17; DelTran 9. Clade E (Bolosaurinae, *Bolosaurus*): 25; DelTran 10*, 17(0)*, 18*. Clade F (Belebeyinae, *Belebey*): 4, 21; AccTran 2*, 3, 18(0)*. Clade G: 23, 24; DelTran 3. Owenettidae: 14; DelTran 26*. *Acleistorhinus*: 2*, 14(2); AccTran 26(0)*. *Eudibamus*: DelTran 18*. *Belebey vegrandis*: DelTran 2*, 10*, 17*. *Belebey chengi*: 11(0)*; AccTran 11(0)*, 17(0)*.

FIG. 4. – *Consensus strict des trois arbres équiparcimonieux obtenu en lançant une version modifiée et augmentée du jeu de données de Müller* et al. *[2008] avec TNT 1.1 [Goloboff* et al., *2008] et édité avec WinClada 1.00.08 [Nixon, 2002]. Les indices de Bremer (au-dessus) et valeurs de bootstrap (au-dessous) sont donnés pour chaque nœud, sauf pour le clade E qui a une valeur de bootstrap inférieur à 50. Les clades lettrés sont caractérisés par les synapomorphies suivantes, une astérisque indicant une transformation homoplastique.*

INVENTORY OF BOLOSAURID MATERIAL

Bolosaurid remains are easily recognized when they include tooth material, thanks to their dietary specialization. Although these animals are rare and still poorly known, bolosaurid were thus identified from a number of distant localities of latest Carboniferous to Middle Permian age. It is therefore very interesting to investigate the evolution of their biodiversity and biogeography through time. An inventory of the published bolosaurid material is given below in this purpose. Specimens are sorted by taxon and are associated with information on their respective age and locality, and comments on their identification as needed. The maximal stratigraphic range of bolosaurids is given according to the correlation between regional stratigraphical units with the international stratigraphical scale (fig. 5).

Concerning the geological information given below, the particularities of the Russian stratigraphy have to be kept in mind and not be confused with the usual international concepts. Contrary to the customary use, the Russian 'gorizont' and 'svita' should indeed not be treated as the international 'horizon' and 'formation', respectively. Gorizonts are regional stratigraphical units, which are largely defined on their paleontological content, regardless of lithostratigraphy. Svitas, in contrast, are lithostratigraphical units, but rely also partly on paleontological data. Gorizonts may include several svitas, parts of svitas, or deposits with different facies and from various geographical areas as long as their paleontological content indicates they are clearly contemporaneous. The conventions used here regarding Russian stratigraphy and English transliterations of Russian terms follow the recommendations of Benton [2000]. Recently, however, an intensive reworking of the Russian regional stratigraphy led to the redefinition of widely used gorizonts as stages and to their correlation with the standard chronostratigraphy [Menning *et al.*, 2006; Ogg *et al.*, 2008].

Bolosaurus striatus COPE, 1878

Lectotype. – AMNH FR 4320, posterior part of a skull and mandible in articulation, several vertebrae, ribs, and gastralia.

Referred material. – AMNH FR 4321, skull and mandible; AMNH FR 4322, partial dentary and four articulated vertebrae; AMNH FR 4324, anterior part of a skull and mandible in articulation and maxillary and dentary fragments; AMNH FR 4326, maxillary and dentary fragments, five articulated vertebrae; AMNH FR 4327, skull and mandible in articulation; AMNH FR 4462, anterior part of a skull and mandible in articulation; MCZ 1436, anterior part of a right dentary, dentary fragment, and posterior part of a left dentary; MCZ 1910, right premaxilla and maxilla; MCZ 2087, maxilla, dentary, and other jaw bones, manus, ilium, partial femora, tibia, fibula, and ungual phalanges; MCZ 2088, partial left mandibular ramus and twelve articulated vertebrae; MCZ 2089, fragment of left dentary; MCZ 2090, maxillary fragment and partial mandible; MCZ 8002, dentary; CM 47873, left maxillary fragment; UCMP 45921, left dentary fragment; TMM 45561-9, partial mandible; TMM 45561-16, mandible.

Type locality. – Mount Barry locality, Wichita County, Texas, United States (lectotype AMNH FR 4320, 4321, 4322, 4324, 4326, 4327, 4462).

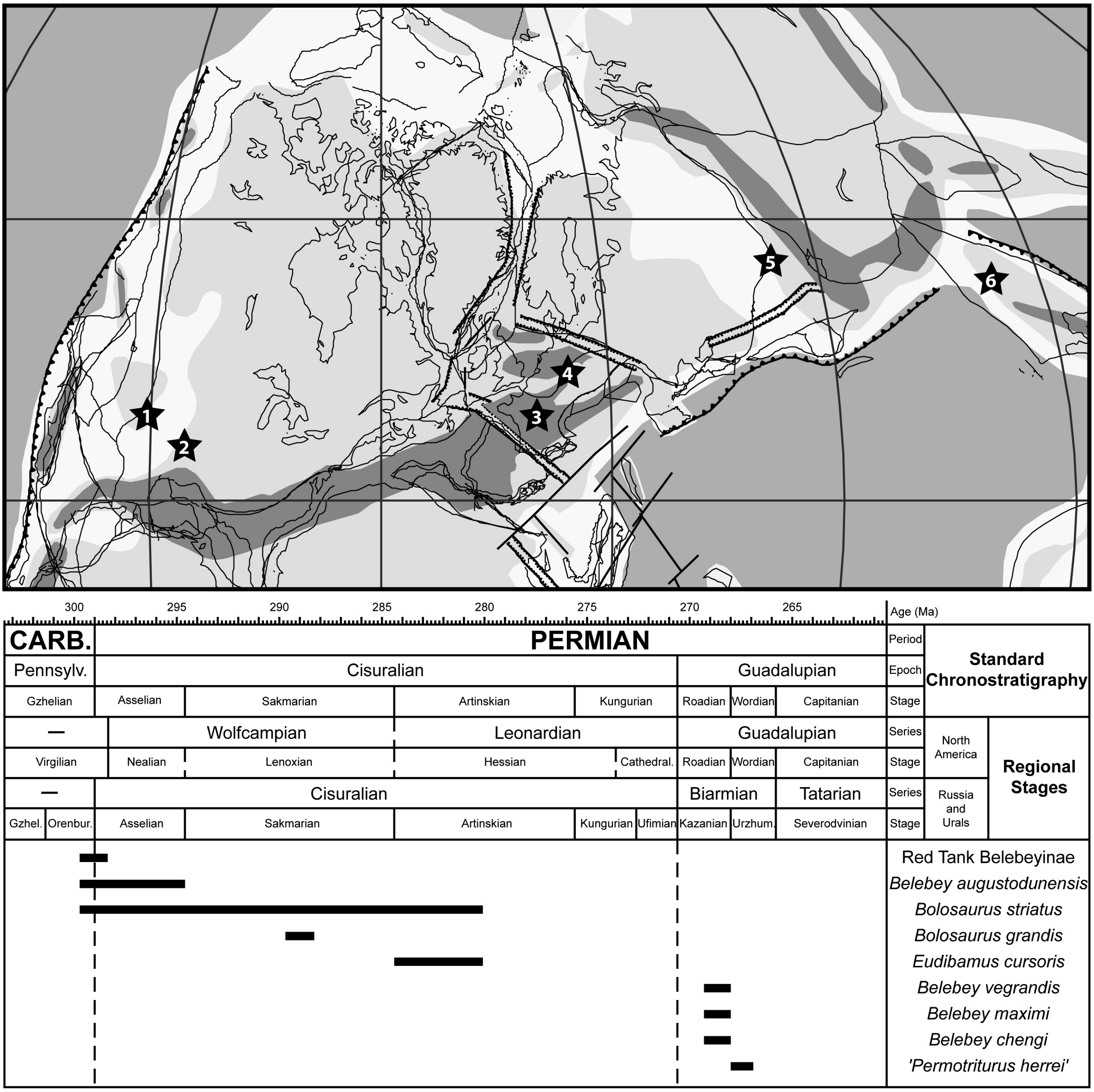

FIG. 5. – Geographic and maximal stratigraphic distribution of Bolosauridae. *Top*: global paleogeographic reconstruction during the Sakmarian-Kungurian interval (Early Permian) modified after Golonka [2000, Fig. 17] with bolosaurid localities. **1**, *Bolosaurus striatus*: El Cobre Formation, Rio Arriba County, New Mexico; Red Tank Belebeyinae: Red Tanks Member, Bursum Formation, Valencia County, New Mexico. **2**, *Bolosaurus striatus*: Archer City Formation, Wichita County, Texas; Archer City, Petrolia, and Nocona formations, Archer County, Texas. *Bolosaurus grandis*: unnamed formation, Comanche County, Oklahoma. **3**, *Belebey augustodunensis*: ?Millery Formation, Saône-et-Loire, Burgundy, France. **4**, *Eudibamus cursoris*: Tambach Formation, Gotha District, Thuringia, Germany. **5**, *Belebey vegrandis*: Belebeiskaya Svita, Belebeevskii District, Bashkortostan, Russia; Aleksandrovskaya District, Orenburg Oblast, Russia. *Belebey maximi*: Matveevskii District, Orenburg Oblast, Russia. *'Permotriturus herrei'*: Urzhumskaia Svita, Apastovskii District, Tatarstan, Russia. **6**, *Belebey chengi*: Xidagou Formation, Jiuquan, Gansu Province, China. *Bottom*: stratigraphic distribution of Bolosauridae (see Discussion for more details). Time and stratigraphic scale created with TS-Creator [Ogg and Lugowski, 2009] with regional and international chronostratigraphic and geochronologic correlations slightly modified after Menning *et al.* [2006] and Ogg *et al.* [2008] regarding the removal of the Bursumian regional stage of North America.

FIG. 5. – *Distribution géographique et stratigraphique maximales des Bolosauridae.* Haut*: reconstitution paléogéographique globale pendant l'intervalle Sakmarien-Kungurien (Permien inférieur) modifié d'après Golonka [2000, Fig. 17] avec les localités à bolosauridés.* Bas*: distribution stratigraphique des Bolosauridae (voir Discussion pour plus de détails). Echelle temporelle et stratigraphique créée avec TS-Creator [Ogg and Lugowski, 2009] avec corrélations chronostratigraphiques et géochronologiques régionales et internationales légèrement modifiées d'après Menning* et al. *[2006] and Ogg* et al. *[2008] concernant la suppression de l'étage régional du Bursumien en Amérique du Nord.*

Additional localities. – Godwin Creek locality, Archer County, Texas (MCZ 1436); Geraldine Bonebed locality, Archer County, Texas (MCZ 1910, 2089); Briar Creek Bonebed locality, Boone Ranch, Archer County, Texas (MCZ 2087, 2088, 2090); TMM locality 45561, Archer City Bonebed, near Archer City, Archer County, Texas (TMM 45561-9, 45561-16); Anderson quarry locality, Rio Arriba County, New Mexico (CM 47873 and UCMP 45921).

Type horizon and age. – Petrolia Formation, Wichita Group (lectotype AMNH FR 4320, 4321, 4322, 4324, 4326, 4327, 4462; MCZ 1436), upper Wolfcampian to lower Leonardian, the boundary being located in the lowermost part of this formation [Lucas, 2006].

Additional horizons and ages. – Archer City Formation, Bowie Group (TMM 45561-9, 45561-16), Wolfcampian age indicated by fusulinids and ammonoids [Lucas, 2006]; Nocona Formation, Wichita Group (MCZ 1910, 2087-2090), Wolfcampian age indicated by fusulinids and ammonoids [Lucas, 2006]; upper El Cobre Formation (CM 47873 and UCMP 45921), a part encompassing the Virgilian-Wolfcampian boundary according to the tetrapod, macrofloral, and microfloral record [see Lucas, Harris *et al.*, 2005 for discussion].

Comments. – The original description of *Bolosaurus striatus* by Cope [1878] was based on several specimens including good cranial material collected from the same locality and horizon. This description relied mainly on AMNH FR 4320 according to Case [1907], which he designated as lectotype, but also on AMNH FR 4321 and possibly other specimens from the type locality and horizon. The Mount Barry material, the best known to date, was repeatedly used in subsequent anatomical descriptions of *Bo. striatus* [Case, 1907, 1911; Broom, 1913; Watson, 1954; Carroll and Gaskill, 1971]. Additional isolated remains collected in Texas [Case, 1907, 1911; Watson, 1954; Reisz *et al.*, 2002; Lucas, Berman *et al.*, 2005] and New Mexico [Berman, 1993; Lucas, Berman *et al.*, 2005] have been referred to *Bo. striatus* on the dentition.

Bolosaurus major BROOM, 1913

Holotype. – AMNH FR 4461, skull and mandible.

Type locality. – Mount Barry locality, Wichita County, Texas, United States.

Type horizon and age. – Petrolia Formation, Wichita Group (see *Bo. striatus*).

Comments. – Broom [1913] compared AMNH FR 4461 to other Mount Barry and Godwin Creek *Bo. striatus*. This specimen appeared to be larger and to have a larger dentition and higher crowns, and therefore to be sufficiently different according to Broom [1913] to warrant the erection of a new species. He named it *Bolosaurus major*, after its large size. The holotype has never been restudied. The diagnosis provided by Broom [1913] seems rather doubtful, given intraspecific variations have never been investigated in bolosaurids. Apart of size and proportions, there is nothing in the original description distinguishing *Bo. major* from *Bo. striatus*, suggesting they may be synonymous.

Gnorhimosuchus satpaevi EFREMOV, 1951

Holotype. – PIN 622/1, dorsal vertebra.

Type locality. – Ters-Akkan locality, Esil'skii District, Akmola Oblys, Kazakhstan.

Type horizon and age. – Kiiminskaya Svita, Inta Assemblage, correlated to the Ufimian on its tetrapod fauna [Golubev, 2000].

Comments. – Efremov [1951] considered *Gnorhimosuchus* as a seymouriamorph, but Ivakhnenko *et al.* [1997] transferred it (with hesitation) to Bolosauridae. So far, vertebrae bear unfortunately no useful information for bolosaurid taxonomy. *Gnorhimosuchus* was recently compared to *Stephanospondylus* by Ivakhnenko [2008b] on the absence of the intervertebral articulations seen in other diadectids. Considering *Stephanospondylus* as a bolosaurid, *Gnorhimosuchus* is thus supposed to be one as well. However, bolosaurid taxonomy is currently based exclusively on cranial anatomical features. The absence of intervertebral articulation in *Gnorhimosuchus* is of no help regarding its affinities. Given the swollen appearance of the neural arch and the low neural spine [Efremov, 1951, Fig. 1], *Gnorhimosuchus satpaevi* is either a parareptile or a captorhinid of indeterminate position.

Permotriturus herrei TATARINOV, 1968

Holotype. – PIN 157/500, partial left dentary with teeth crowns broken at the base.

Type locality. – Isheevo locality, Apastovskii District, Tatarstan, Russia.

Type horizon and age. – Urzhumskaia Svita, correlated to the Urzhumian according to the tetrapod Isheevo Subassemblage [Ivakhnenko *et al.*, 1997; Golubev, 2000] and the ostracod assemblage typical of the *Paleodarwinula fragiliformis* Biozone [Gorsky *et al.*, 2003].

Comments. – Originally, *Permotriturus* was considered by Tatarinov [1968] as the first Permian caudate and the oldest ever found, hence the genus name. He even placed *Permotriturus* in its own family, Permotrituridae TATARINOV, 1968. Later on, the systematic position of *Permotriturus* was rejected by Hecht (cited by Estes [1981]) who suggested it might rather be a chondrichthyan. In contrast, Ivakhnenko [1990] claimed there is evidence for considering *Permotriturus* as a bolosaurid close to *Belebey*, but gave no explanation. Ivakhnenko [2008b] confirmed the bolosaurid affinities of *Permotriturus* and provided a short diagnosis without discussing its taxonomic status and position. It is thus necessary here to bring a few comments regarding *Permotriturus*. Originally mistaken for a left maxilla by Tatarinov [1968], the holotype was since identified as a left dentary by Ivakhnenko *et al.* [1997]. Again no justification was provided. Still, the comparison with *Bo. grandis* [Reisz *et al.*, 2002, Fig. 1] and *Be. vegrandis* [Reisz *et al.*, 2007, Fig. 4-5] show the holotype of *Permotriturus* is indeed best interpreted as a bolosaurid left dentary. The following comparisons are based on the illustrations published previously in Tatarinov [1968, Fig. A-B] and Ivakhnenko *et al.* [1997, Pl. 54, Fig. 5]. *Permotriturus* presents a wide sutural surface with the prearticular, extending far anteriorly. Posterior to the last tooth, the so-called pterygoid process of Tatarinov [1968] represents the medial base of the coronoid process of the dentary. This is a small eminence that is seemingly broken so that its real dorsal extent cannot be determined. The tooth row bears eight teeth, of which only the base of each crown is preserved. The most mesial teeth are slightly oval in cross section, but the distal teeth increase in size and are expanded labiolingually, correlatively to the mediolateral swelling of the dentary. Also, this expansion is not perpendicular to the long axis of the dentary but is slightly slanted so that the labial and lingual surfaces of the teeth are respectively shifted mesialward and distalward. The synapomorphic features listed here are strong evidence for the bolosaurid assignment of *Permotriturus*. Further, its *Belebey*-like dentition supports Ivakhnenko's [1990] statement. Except for *Be. chengi*, which has a short prearticular, I was unable to distinguish *Permotriturus* from either *Be. vegrandis* or *Be. maximi* based on the available descriptions and illustrations [Ivakhnenko, 1990; Ivakhnenko and Tverdokhlebova, 1987; Ivakhnenko *et al.*, 1997; Reisz *et al.*, 2007; Müller *et al.*, 2008]. If *P. herrei* proves indeed to be indistinguishable from *Be. vegrandis*, the genus *Permotriturus* and the family Permotrituridae should thus be treated as senior synonyms of *Belebey* and Belebeyinae, respectively.

Belebey vegrandis IVAKHNENKO, 1973

Holotype. – PIN 104/50, partial left maxilla and palatine.

Referred material. – PIN 104/51 and PIN 104/52, partial upper jaws; PIN 104/55 and PIN 104/56, several teeth; SGU 104/B-2020, complete skull and mandible in articulation; SGU 104/B-2021, complete skull and mandible in articulation; SGU 104/B-2022, posterior part of a skull.

Type locality. – Belebei locality, Belebeevskii District, Bashkortostan, Russia (holotype PIN 104/50, 104/51, 104/52, 104/55, 104/56).

Additional localities. – Krymskii locality, Aleksandrovskaya District, Orenburg Oblast, Russia (SGU 104/B-2020, 104/B-2021, 104/B-2022).

Type horizon and age. – Belebeiskaya Svita (holotype PIN 104/50, 104/51, 104/52, 104/55, 104/56; SGU 104/B-2020, 104/B-2021, 104/B-2022), correlated to the Late Kazanian by the tetrapod Ocher Subassemblage [Ivakhnenko *et al.*, 1997; Golubev, 2000], the ostracod *Paleodarwinula fainae* and palynological *Lueckisporites virkkiae* biozones, as well as the foraminiferan, bivalve, and brachiopod associations [Gorsky *et al.*, 2003].

Comments. – The material originally (PIN 104/50, 104/51, 104/52, 104/55, 104/56) ascribed to *Be. vegrandis* by Ivakhnenko [1973] was collected near Belebei. It was supplemented later by several well preserved skulls (SGU 104/B-2020, 104/B-2021, 104/B-2022) which served as the base for the skull reconstructions provided by Ivakhnenko and Tverdokhlebova [1987] and later by Reisz *et al.* [2007] with a few modifications. Tverdokhlebov *et al.* [2005] designated SGU 104/B-2022 as the lectotype of *Be. vegrandis* without apparent reason, as PIN 104/50 was explicitly identified as the holotype of the species by Ivakhnenko [1973]. In Ivakhnenko *et al.* [1997], the holotype is misprinted PIN 164/50 on page 22 (but is correct page 110).

Bolosaurus traati TATARINOV, 1974

Holotype. – PIN 3318/1, partial maxilla.

Type locality. – Mylva locality, banks of the Mylva River, Ust'-Kulomskii District, Komi Republic, Russia.

Type horizon and age. – Unknown geological formation of Sakmarian age [Ivakhnenko *et al.*, 1997].

Comments. – Despite the earlier description of *Be. vegrandis*, Tatarinov [1974] was the first to mention the presence of bolosaurids in Russia with the description of *Bolosaurus traati*. The Sakmarian (Asselian according to Tatarinov [1974]) age of the deposits in which its holotype PIN 3318/1 was found is consistent with its generic identification as it is roughly contemporaneous with its American counterparts. While Ivakhnenko [1990] and Ivakhnenko *et al.* [1997] followed Tatarinov [1974], subsequent reviewers questioned the validity and taxonomic position of *Bo. traati*. Modesto and Rybczynski [2000] could not differentiate *Bo. traati* from *Be. vegrandis* or *Be. maximi* so they considered it as a bolosaurid of uncertain relationship. Later, Reisz [in Reisz *et al.*, 2002] disclaimed the bolosaurid assignment of the Mylva maxilla because he was unable to identify any bolosaurid synapomorphies on it. There is indeed no evidence for placing *Bo. traati* in Bolosauridae, save the presence of wear facet indicating dental occlusion [Ivakhnenko *et al.*, 1997, Pl. 54, Fig. 6], a feature which is not unique to the members of this family. Though its taxonomic position needs to be clarified, the dentition of *Bo. traati* is distinct from that of the contemporaneous Permian amniotes known so far. Contra Modesto and Rybczynski [2000], it is therefore considered as a valid species but it should be allocated in another genus than *Bolosaurus*.

Belebey maximi TVERDOKHLEBOVA, 1987
in Ivakhnenko & Tverdokhlebova, 1987

Holotype. – SGU 104/B-2027, partial mandible.

Type locality. – Sarai-Gir locality, Matveevskii District, Orenburg Oblast, Russia.

Type horizon and age. – Belebeiskaya Svita, correlated to the Late Kazanian by the tetrapod Ocher Subassemblage [Ivakhnenko *et al.*, 1997; Golubev, 2000], the ostracod *Paleodarwinula fainae* and palynological *Lueckisporites virkkiae* biozones, as well as the foraminiferan, bivalve, and brachiopod associations [Gorsky *et al.*, 2003].

Comments. – *Be. maximi*, suspected to be a junior synonym of *Be. vegrandis* by Modesto and Rybczynski [2000], is valid according to Müller *et al.* [2008] who coded it in a unique combination of character states.

Davletkulia gigantea IVAKHNENKO, 1990

Holotype. – PIN 4311/1, upper (?) left tooth crown.

Type locality. – Yaman-Yushatyr' locality, Tyul'ganskii District, Orenburg Oblast, Russia.

Type horizon and age. – Belebeiskaya Svita, correlated to the Late Kazanian by the tetrapod Ocher Subassemblage [Ivakhnenko *et al.*, 1997; Golubev, 2000], the ostracod *Paleodarwinula fainae* and palynological *Lueckisporites virkkiae* biozones, as well as the foraminiferan, bivalve, and brachiopod associations [Gorsky *et al.*, 2003].

Comments. – *Davletkulia gigantea* was described as the third bolosaurid from the Ocher Subassemblage of the Belebeiskaya Svita by Ivakhnenko [1990]. Its holotype consists of an isolated, heavily worn out tooth crown which is also unusual in being much larger than any other bolosaurid tooth known so far – hence the specific name. Ivakhnenko [1990] estimated a skull length of about 30 cm, compared to about 5 cm only for *Belebey vegrandis*. According to Reisz *et al.* [2002], however, there is no trace in *Davletkulia* of the typical striations seen in bolosaurids and the heavy wear prevents any detailed observation of the occlusal surface which would confirm its taxonomic position. These observations led Reisz *et al.* [2002] to consider *Davletkulia* as dubious but without justification. It should still be noted that Ivakhnenko [1990] mentioned the presence of swollen striations on the surface of the crown, which may represent the usual bolosaurid condition. It is also interesting that Reisz *et al.* [2002] compared the heavy wearing seen in *Davletkulia* to that seen in herbivorous dinocephalians. The very large size of the holotype would be indeed more consistent if *Davletkulia* proved to be a herbivorous dinocephalian rather a giant bolosaurid. Ivakhnenko [2008b] did not discuss the affinities of this form. The identification of *Davletkulia gigantea*, though considered here as a possible bolosaurid, needs thus a direct reexamination of its holotype in order to confirm the presence of striations and their shape, and to compare it to dinocephalian dentitions to resolve its taxonomic position.

Timanosaurus ivachnenkoi Gubin, 1993

Holotype. – PIN 4416/22, dorsal vertebra.

Referred material. – PIN 4416/28, a vertebra.

Type locality. – Ust'-Koin locality, Knyazhpogostskii District, Komi Republic, Russia.

Type horizon and age. – Unnamed horizon, Golyusherma Subassemblage, correlated to the Early Kazanian on its tetrapod fauna [Ivakhnenko *et al.*, 1997; Golubev, 2000].

Comments. – *Timanosaurus* was described as a new diadectid by comparison with *Stephanospondylus* and *Gnorhimosuchus* by Gubin [1993]. Later, Ivakhnenko *et al.* [1997] moved tentatively *Timanosaurus* to Bolosauridae. The remarks given for *Gnorhimosuchus* apply also here: *Timanosaurus* bears no diadectid synapomorphy and the swollen appearance of the neural arch and the low neural spine [Gubin, 1993, Fig. 4] are not unlike those of parareptiles and captorhinids.

Eudibamus cursoris Berman, Reisz, Scott, Henrici, Sumida & Martens, 2000

Holotype. – MNG 8852, nearly complete articulated skeleton.

Type locality. – Bromacker quarry, near Tambach-Dietharz, Thuringia, Germany.

Type horizon and age. – Tambach sandstone, Tambach Formation, Upper Rotliegend Group, correlated to the lower Artinskian [Menning *et al.*, 2006].

Comments. – MNG 8852 is the most complete bolosaurid specimen known to date. In their description, Berman *et al.* [2000] focused mainly on the locomotor specializations of its appendicular skeleton, suggesting *Eudibamus* was a facultative bipedal runner, but neglected the remainder of its anatomy, which still awaits a full description.

Bolosaurus grandis Reisz, Barkas & Scott, 2002

Holotype. – OMNH 52311, left dentary.

Referred material. – OMNH 15104, left maxillary fragment; OMNH 56818, partial right dentary.

Type locality. – OMNH locality V51, Dolese Brothers quarry, Richards Spur, Comanche County, Oklahoma, United States (holotype OMNH 52311, 15104, 56818).

Type horizon and age. – Fissure-fill deposits (holotype OMNH 52311, 15104, 56818) in the Early Ordovician Kindblade Formation, Arbuckle Group, which is in turn circumscribed by the Leonardian upper Garber Formation, Sumner Group. These deposits have been tentatively correlated to the Leonardian Arroyo Formation of Texas on the basis of their respective vertebrate assemblages [Reisz *et al.*, 2002]. Lastly, however, a newly elaborated method allowed a much more accurate datation of the Dolese Brother quarry cave deposits. U-Pb radiometric datation provided therefore an age of 289±0.68 Ma for sectioned speleothems [Woodhead *et al.*, 2010], an age corresponding to the middle Sakmarian stage [Ogg *et al.*, 2008].

Red Tank Belebeyinae

Material. – NMMNH P-33416, cheek tooth crown and root; NMMNH P-33417, incisiform tooth crown; NMMNH P-33418, cheek tooth crown; NMMNH P-33419, cheek tooth crown; NMMNH P-33420, partial cheek tooth crown.

Locality. – NMMNH locality 3423, near Red Tank, Valencia County, New Mexico; United States.

Horizon and age. – Red Tanks Member, Bursum Formation, dated as latest Virgilian on palynology, fusulinids, and conodonts [Orchard *et al.*, 2004; Utting *et al.*, 2004; Wahlman and Kues, 2004].

Comments. – The Red Tank cheek teeth are typically bolosaurid, according to Harris *et al.* [2004], in having a bulbous, ridged crown with distinct heel and talon. These cheek teeth present a unique combination of bolosaurid apomorphies and plesiomorphies suggesting it belongs to a new taxon [Harris *et al.*, 2004], informally referred below as the 'Red Tank Belebeyinae' for practical reasons. The Red Tank bolosaurid resembles *Belebey* more than *Bolosaurus* in the transverse expansion of the crowns and the presence of a ridge on the heel margin, but distinguishes itself in this ridge having a blunt rather than a cutting edge and in retaining a blunt, upright apex [Harris *et al.*, 2004]. A single incisiform tooth collected from Red Tank (NMMNH P-33417) was referred to Bolosauridae by Harris *et al.* [2004], but they noted its morphology would also agree with identification as diadectid.

Belebey chengi Müller, Li & Reisz, 2008

Holotype. – IVPP IG CAGS V 331, right maxilla.

Referred material. – IVPP V 12007, right dentary; IVPP V 15906, left maxilla and lacrimal; IVPP V 15907, partial right dentary; four unnumbered mandibular remains.

Type locality. – Dashankou locality, near Yumen, Gansu Province, China.

Type horizon and age. – Xidagou Formation. According to Battail [2000] and Rubidge [2005], the Xidagou tetrapod assemblage is comparable to the *Eodicynodon* Assemblage Zone of South Africa and to the Late Kazanian Ocher Assemblage of Russia. The affinities of the Xidagou assemblage are even stronger with the latter following Li [2001]. More recently, Liu *et al.* [2009] suggested an older early Roadian age for the Dashankou fauna based on the association of endemic primitive therapsids with a typically Early Permian dissorophoid-bolosaurid assemblage. The same could be said of the Ocher Assemblage, however [Ivakhnenko *et al.*, 1997; Golubev, 2000]. Consequently, there is currently no evidence for the precedence of the Dashankou fauna, which is considered as Late Kazanian following the opinions of previous authors.

IMPLICATIONS FOR BOLOSAURID STRATIGRAPHIC RANGE, DIVERSITY, AND BIOGEOGRAPHY

Seven bolosaurid species are considered as valid: *Bolosaurus striatus, Belebey vegrandis, Belebey maximi, Eudibamus cursoris, Bolosaurus grandis, Belebey chengi,* and *Belebey augustodunensis*. Two other species, *Bolosaurus major* and *Permotriturus herrei*, are most likely synonymous with one or another of the species above. There is also at least one new, unnamed species of belebeyine from the Red Tank locality. Four putative bolosaurids are excluded from the family: *Bolosaurus traati* is a tetrapod of uncertain relationship, *Davletkulia gigantea* is probably a dinocephalian, *Gnorhimosuchus satpaevi* and *Timanosaurus ivachnenkoi* are either captorhinids or parareptiles but cannot be assigned to Bolosauridae in particular [Modesto and Rybczynski, 2000; Reisz *et al.*, 2002; this paper]. Bolosauridae range from an age close to the Gzhelian-Asselian boundary (Red Tank Belebeyinae, Anderson quarry *Bo. striatus*, and *Be. augustodunensis*) to the early part of the Wordian (*'Permotriturus herrei'*). Unfortunately, the respective studies of Harris *et al.* [2004] and Lucas, Berman *et al.* [2005] on the Red Tank Belebeyinae and the Anderson quarry *Bo. striatus* have been overlooked in the recent papers dealing with the early evolution of parareptiles [e.g., Reisz *et al.*, 2007; Müller *et al.*, 2008; Modesto *et al.*, 2009; Tsuji *et al.*, 2010]. Yet, this material has great implications on the age of the origination, pattern and timing of diversification, and biogeography of parareptiles. These bolosaurids, and possibly also *Be. augustodunensis*, are thus the oldest parareptiles known to date and they show that belebeyines were already present as soon as bolosaurids appeared in the fossil record. This suggests a rapid initial diversification of bolosaurids near the Carboniferous-Permian boundary. Still, the diversity of bolosaurids is hard to assess before the Middle Permian because of the poor resolution of the stratigraphic correlation of continental deposits with their marine counterparts, and also because of the difficulty to correlate regional stages to standard chronostratigraphy (i.e., the Wolfcampian-Leonardian boundary position). In comparison, the stratigraphic resolution is far better for Middle Permian bolosaurids, at least regarding *Be. vegrandis*, *Be. maximi*, and *'Permotriturus herrei'* for which microflora, foraminiferans, ostracods, and bivalves bring crucial information for continental and marine stratigraphical correlations. The associated tetrapod assemblage can then be used for correlating localities lacking the biostratigraphic markers listed before, such as in the case of the Dashankou locality, with the standard chronostratigraphy. These are the reasons why the maximal stratigraphic ranges are considered here (fig. 5), despite the fact that most bolosaurids are known from a single specimen, or at least from a single locality and horizon. So far, a maximal diversity of bolosaurids would have been attained at the time of the Carboniferous-Permian boundary and during the Roadian, each with three taxa. The evolution of bolosaurids has already been discussed in terms of age, relationships and biogeography by Müller *et al.* [2008]. They noted the sister taxon of all other bolosaurids, *Eudibamus*, is younger than *Bo. striatus*, an unexpected pattern reminiscent of that documented for captorhinids. Müller *et al.* [2008] also suggested parareptiles originated in Europe, and that one branch (*Bolosaurus*) had spread to North America whereas another one (*Belebey*) reached Russia and China. It must be remembered that the Russian platform and Gansu province were close to each other during the Middle Permian (fig. 5). In other words, bolosaurids would have spread from central to western and eastern Laurasia during the Permian. The present review and the description of *Be. augustodunensis* indicate the evolution of bolosaurid follows a more complicated pattern than that suggested by Müller *et al.* [2008], one that is not easy to decipher. *Eudibamus* and *Bolosaurus* are indeed restricted to Europe and North America, respectively, but Belebeyinae are now known in the same areas of Laurasia, in addition to its eastern part, and were present at the same time (Red Tank Belebeyinae) or even earlier (*Be. augustodunensis*) than these two taxa. Bolosaurids had a Laurasian distribution, present in western and central Laurasia before establishing in eastern Laurasia in the Middle Permian. Otherwise, the genera *Bolosaurus* and *Belebey* are the only clades consistent with stratigraphy and biogeography. Fortunately, recent discoveries of early parareptiles [Modesto and Reisz, 2008; Modesto *et al.*, 2009; Tsuji *et al.*, 2010] may help to elucidate their evolution and that of early amniotes in bringing new information relative to their phylogenetic relationships, their pattern of diversification, and their geographical distributions.

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Appendix 1

List of the phylogenetic characters used in the present analysis. The original reference and character number is given for each character taken from a previous work.

Character (#14) was originally defined as a binary character by Müller *et al.* [2008, #8], separating taxa with three or more or only two premaxillary teeth. The premaxillary tooth count has, however, a much wider range of variation considering the taxa used in this analysis, i.e. two in *Bolosaurus striatus* [Watson, 1954] and *Belebey vegrandis* [Reisz *et al.*, 2007], three in *Eudibamus* [Berman *et al.*, 2000] and *Milleretta* [Gow, 1972; Thommasen and Carroll, 1981], four in *Acleistorhinus* [deBraga and Reisz, 1996], five in '*Owenetta*' *kitchingorum* [Reisz and Scott, 2002], and 14–15 to 20 and more in mesosaurids [Modesto, 1999; Modesto, 2006], that is much more than in others. The character (#14) is therefore redefined as a multistate character as follows: 10 or more [state 0], 5 [1], 4 [2], 3 [3], or 2 [4] premaxillary teeth.

In the dataset of Müller *et al.* [2008], a tall coronoid process on the mandible for which several bones contribute is coded as present in *Bolosaurus* and *Belebey* (save *Be. maximi* for which the condition is unknown) but not in *Eudibamus,* which is supposed to have none, or at most a small one. This is most likely a mistake, as Berman *et al.* [2000], Reisz *et al.* [2007], and Müller and Tsuji [2007] considered *Eudibamus* as having the first condition. The scoring of this character (#12) was thus changed accordingly.

dBR = deBraga and Reisz [1996]; LR = Laurin and Reisz [1995]; MLR = Müller *et al.* [2008].

1. Premaxillary dorsal process: broad, narial opening faces predominantly laterally (0); narrow, narial opening faces anteriorly (1). [dBR, #1]
2. Contact between maxilla and quadratojugal: absent (0); present (1). [MLR, # 10]
3. Lacrimo-maxillary suture: anterodorsal margin of maxilla irregular or straight (0); anterodorsal margin concave (1). [MLR, # 14]
4. Maxilla posterodorsal margin: slopes posteroventrally (0); straight (1). [MLR, # 15]
5. Quadratojugal shape: sheet-like (0); rod-like (1). [MLR, # 20]
6. Lateral boss formed by prefrontal and nasal: absent (0) or present (1). New
7. Posterior extension of orbit: absent (0); present (1). [LR, #37]
8. Temporal fenestra in adult: absent (0); present (1). New
9. Parietal table: gently domed, on the skull roof (0); strongly curved ventrally just posterior to the pineal foramen, contributing to the occipital table in addition to the skull roof (1). New
10. Anterior extent of prearticular on dentary: terminating prior to the anterior third of the tooth-bearing portion (0); reaching well into the anterior third (1). [MLR, # 4]
11. Dentary in dorsal view: sigmoidal (0); straight (1). [MLR, # 16]
12. Coronoid process: absent or small (0); tall, multipartite (1). [MLR, # 17]
13. Surangular: extends beyond coronoid eminence (0); does not extend beyond eminence (1). [MLR, # 18]
14. Number of premaxillary teeth: 10 or more (0); 5 (1); 4 (2); 3 (3); 72 (4). [Modified from MLR, #8]
15. Premaxillary teeth, size: smaller than or almost equal to mesial maxillary teeth (0); larger (1). [MLR, # 9]
16. Tooth shape of middle and distal teeth in the upper and lower jaw: slender (0); bulbous (1). [MLR, # 1]
17. Mesial teeth in the upper and lower jaw: not procumbent (0); procumbent (1). [MLR, # 2]
18. Incisiform mesial tooth on maxilla: present (0); absent (1). [MLR, # 6]
19. "Intermediate" mesial teeth 3 and 4 (on maxilla/dentary): absent (0); present (1). [MLR, # 7]
20. Cheek teeth: conical (0); distinct heel and talon with lingual wear facet (1). New
21. Cutting ridges on distal teeth: absent (0); present (1). [MLR, # 12]
22. Distinct striations on tooth crowns: absent (0); present (1). [MLR, # 13]
23. Transverse expansion of distal cheek teeth: absent (0); present (1). [MLR, # 3]
24. Main cusp of distal cheek teeth: pointing straight upwards (0); sharply recurved (1). [MLR, # 5]
25. Distal most tooth on dentary: equal or slightly smaller than preceding teeth (0); very small and peg-like (1). [MLR, # 11]
26. Teeth on pterygoid transverse flange: present (0); absent (1). [MLR, # 19]
27. Number of sacral vertebrae: 2 (0); 3 (1). [MLR, # 21]

Appendix 2

Character state data matrix consisting of 27 characters coded for 10 taxa, with Mesosauridae chosen here as outgroup taxon. The following characters are taken from Müller *et al.* [2008] unless specified otherwise. Changes and additions made to their data matrix were scored according to: Modesto [2006] for Mesosauridae; Gow [1972] for Millerettidae; Reisz and Scott [2002] for '*Owenetta*' *kitchingorum*; deBraga and Reisz [1996] for *Acleistorhinus*; Berman *et al.* [2000] for *Eudibamus*; Watson [1954], Carroll and Gaskill [1971], and Reisz *et al.* [2002] for *Bolosaurus striatus*; Reisz *et al.* [2002] for *Bo. grandis*; Reisz *et al.* [2007] for *Belebey vegrandis*; Ivakhnenko and Tverdokhlebova [1987] for *Be. maximi*; Müller *et al.* [2008] for *Be. chengi*; personal observations for *Be. augustodunensis* (holotype MNHN.F.AUT 891).

Character number		1	11111	11112	22222	22
(A=0/1)	12345	67890	12345	67890	12345	67
Mesosauridae	00000	00000	??000	00000	00000	00
Millerettidae	?0000	00A00	00030	00000	00000	00
Owenettidae	10000	11000	00110	00000	00000	11
Acleistorhinus	11000	01100	1?120	00000	0000?	0?
Eudibamus	10?01	011?0	11?30	10111	0000?	11
Bo. striatus	10001	11111	11141	11111	01001	??
Bo. grandis	?????	????1	11???	111?1	01001	??
Be. augustodunensis	???1?	?????	?????	1???1	1100?	??
Be. vegrandis	11111	11111	11141	11011	11110	11
Be. maximi	?????	?????	?????	1???1	1111?	??
Be. chengi	??11?	????0	01???	10011	11110	??

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