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SHORT COMMUNICATION

A new bolosaurid parareptile, *Belebey chengi* sp. nov., from the Middle Permian of China and its paleogeographic significance

Johannes Müller · Jin-Ling Li · Robert R. Reisz

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Abstract A new bolosaurid parareptile, *Belebey chengi* sp. nov., is described from Dashankou, Gansu Province, China, a Middle Permian locality which is known mostly for its therapsid fauna. The material consists of well-preserved mandibular and anterior skull remains and currently represents the largest and latest surviving member of Bolosauridae. Phylogenetic analysis of bolosaurid interrelationships, the first analysis of any clade of Early Permian parareptiles, indicates that the new taxon groups consistently with the other (Russian) members of the genus *Belebey*, and forms the sister clade to the genus *Bolosaurus* from North America. The Early Permian *Eudibamus cursoris* from Germany falls into the basal most position within Bolosauridae. Our analysis also shows that the split between the main bolosaurid lineages must have occurred near or before the Permo-Carboniferous boundary and that the paleo-equatorial region of Laurasia probably served as the center of origination for these parareptiles. A similar pattern can be found in other clades of Paleozoic amniotes, suggesting that this may be the general trend in early amniote evolution.

Keywords Parareptilia · Bolosauridae · Middle Permian · China

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J. Müller (✉)
Humboldt-Universität zu Berlin, Museum für Naturkunde,
10099 Berlin, Germany
e-mail: johannes.mueller@museum.hu-berlin.de

J.-L. Li
Institute of Vertebrate Paleontology and Paleoanthropology,
Chinese Academy of Sciences,
P.O. Box 643, Beijing 100044, People's Republic of China

R. R. Reisz
Department of Biology, University of Toronto at Mississauga,
3359 Mississauga Rd. N.,
Mississauga, Ontario, Canada L5L 1C6

Introduction

Permian bolosaurids, until recently a highly enigmatic group, are now generally considered to be part of Parareptilia, one of the three major clades of basal Amniota (Berman et al. 2000; Reisz et al. 2007; Müller and Tsuji 2007). Three genera and five species are currently recognized, *Bolosaurus grandis* and *B. striatus* from the Lower Permian of Texas and Oklahoma (Watson 1954; Reisz et al. 2002), *Belebey vegrandis* and *B. maximi* from the Middle Permian of Russia (Ivakhnenko 1973; Ivakhnenko and Tverdochlebova 1987), and *Eudibamus cursoris* from the Lower Permian of Germany (Berman et al. 2000). The unique dentition of bolosaurids is highly heterodont, with anterior incisiform and posterior greatly expanded cheek teeth, indicating a feeding ecology very different from other contemporaneous amniotes of comparable size. Despite recent descriptions of more complete cranial and postcranial material (Berman et al. 2000; Reisz et al. 2007), bolosaurid dentition has so far remained the most widely used tool for taxonomic investigations because of its excellent preservation. However, while our knowledge of bolosaurid anatomy and phylogenetic affinities has increased recently, there is no understanding of the ingroup relationships, thus hampering interpretations of adaptive radiation of this stratigraphically and geographically widespread clade. Given the fact that bolosaurids are also the stratigraphically oldest known parareptiles, information on the history of their adaptive radiation might also be helpful for understanding the contentious issue of parareptilian biogeography in general (e.g., Modesto 2000; Reisz et al. 2007).

The new species of bolosaurid described here comes from the Chinese Dashankou locality, which is probably Middle Permian in age and has yielded a variety of tetrapods, including dissorophoid and chroniosuchid amphibians, synapsids, and reptiles (Cheng and Li 1997; Li and Cheng 1995, 1997, 1999). The material can be assigned to the genus *Belebey* on the basis of the shape of the transversely expanded posterior cheek teeth, the recurved tooth cusps, the presence of apical cutting ridges, and the maxilla being concave anterodorsally and straight posterodorsally. Parts of the material were briefly described by Li and Cheng (1995) without drawing any taxonomic or phylogenetic conclusions, but the authors correctly asserted that it most likely can be assigned to the genus *Belebey*. Even though the specimens consist mostly of dentigerous remains, the characteristic features of the dentition are sufficiently diagnostic to warrant the erection of a new species. On the basis of this description and a review of previously published taxa, we present for the first time an ingroup phylogeny of bolosaurids and discuss its biogeographic implications.

Systematic Paleontology

Bolosauridae Cope 1878
Belebey Ivakhnenko 1973
Belebey chengi sp. nov.

Etymology

Named in honor of Zheng-Wu Cheng who discovered the Dashankou locality and collected the specimens described in this study.

Material

Holotype: right maxilla [Institute of Vertebrate Paleontology and Paleoanthropology Beijing, China (IVPP) IG CAGS V 331]; paratype: right dentary (IVPP V 12007); referred specimens: left maxilla with attached lacrimal (IVPP V 15906); posterior part of a right dentary (IVPP V 15907); four uncatalogued mandibular remains.

Locality and horizon

Xidagou Formation, Dashankou locality near Yumen, Gansu Province, China, Middle Permian.

Diagnosis

Comparatively large-sized bolosaurid of the genus *Belebey* (maximum recorded length of maxilla, 45 mm, thus approximately one third larger than *B. vegrandis* and one fifth larger than *Bolosaurus grandis*) with the following autapomorphies: lack of procumbent teeth, posterior most tooth on the maxilla distinctively reduced, lack of anterolateral maxillary foramen, dentary sigmoidally curved.

Anatomical description

The maxilla (Fig. 1a–c, g–i) consists of an elongate and fairly tall bone with the anterior end slightly bent ventrally, indicating an originally downturned snout notably different from *B. vegrandis*, which possesses a straight rostrum (Reisz et al. 2007). Another difference from *B. vegrandis* is the apparent lack of anterolateral foramina on the maxilla; in fact, the surface appears to be very smooth without any trace of openings for nerves and blood vessels. The anterior portion of the maxilla is taller than the central area of the bone, resulting in an undulating dorsal margin similar to *B. vegrandis*. In addition, the shape of the suborbital process of the bone is very similar to the latter taxon in being tall and showing no significant decrease in height posteriorly. In medial view, the maxilla has a massive, almost swollen appearance due to the strongly expanded alveolar shelf. The anteromedial portion of the bone slopes strongly anterolaterally and probably forms the area of contact with the premaxilla. In ventral view, the anterior and posterior areas of the maxilla are much narrower than the remaining body of the bone, and the medial margin of the alveolar shelf shows its greatest expansion in the central third of the element, a condition that is also seen in *B. vegrandis*. Unfortunately, the lateral margin of the alveolar shelf is incomplete in the known material, which makes it difficult to establish the nature of the presumed contact with the palatine and ectopterygoid bones.

The maxilla carries ten teeth, which, with the exception of the posteriormost tooth, all possess a strongly constricted heel and apical striations but otherwise are notably variable in shape and size. In contrast to *B. vegrandis*, none of the teeth is procumbent but all point straight downward, and nearly all of them extend beyond the lateral margin of the alveolar shelf. The two mesial teeth differ from the rest in that they are slender and only moderately expanded, showing a mesolabial–distolingual orientation in occlusal view. These teeth are somewhat widely spaced, in contrast to the more distal teeth which are densely packed. A distinctively recurved cusp with labial and lingual cutting ridges can be found on the labial side of the two mesial teeth, with that of the first one being much longer than that of the second; the first tooth can therefore be interpreted as

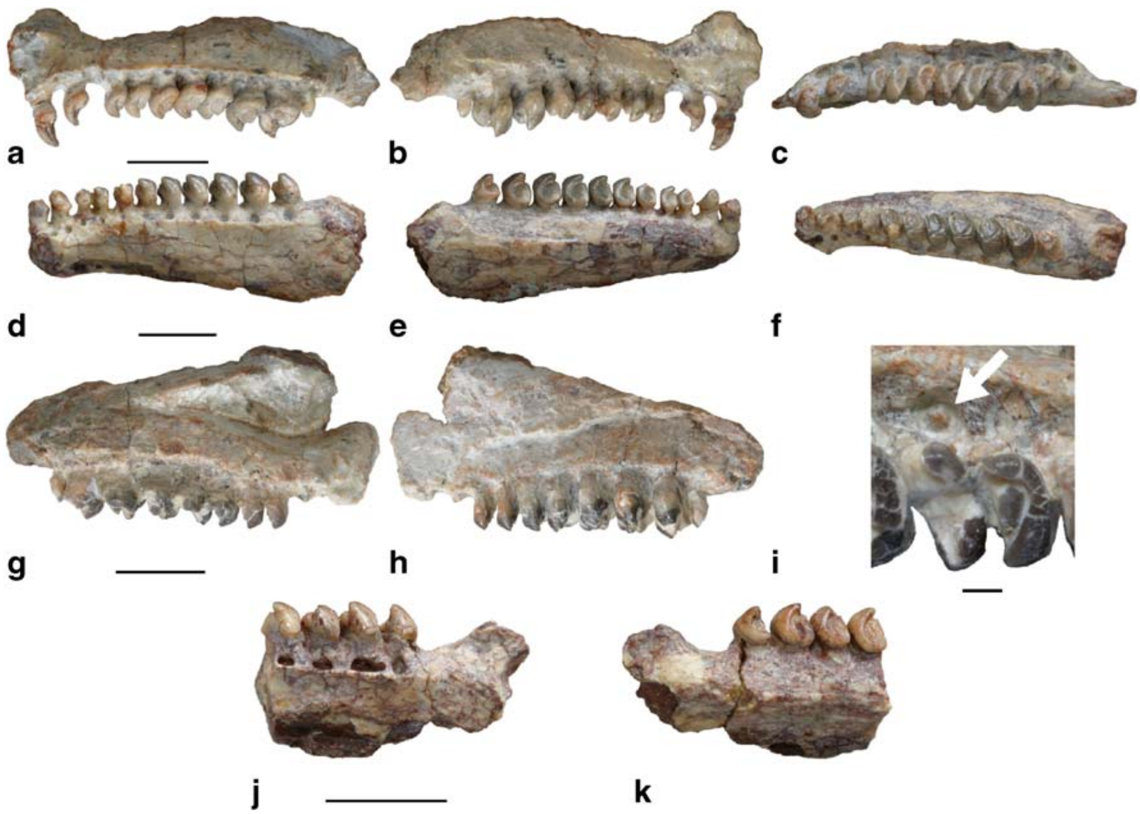

Fig. 1 *Belebey chengi* sp. nov., material described in this study. **a**–**c** Right maxilla (IVPP IG CAGS V 331) in medial, lateral, and occlusal views; **d**–**f** right dentary (IVPP V 12007) in medial, lateral, and occlusal views; **g**, **h** left maxilla (IVPP V 15906) with dorsally attached lacrimal in medial and lateral views; **i** same specimen, enlarged section of tooth row in occlusal view showing the small replacement tooth (*arrow*); **j**, **k** right dentary fragment (IVPP V 15907) in medial and lateral views. Scale bars equal 10 mm except for **i** (2 mm)

incisiform. Well-developed facets can be found on the distolingual side of the teeth with the labial edge being worn, indicating specialized occlusal movements that were typical for bolosaurids.

The distally following seven teeth are very different from the two mesial ones; though they share the distolingually situated facet and the recurved labial cusp, they all are strongly transversely expanded and successively increase in size distally, with the size of the first tooth of the series being comparable to that of the second mesial tooth. The last three teeth of the series are relatively massive. The orientation of the long axis of the expansion varies from roughly labial–lingual mesially to strongly mesolabial–distolingual posteriorly, whereas the occlusal surface always slopes apicolingually. In all seven teeth, the recurved cusp is lower than in the two anterior teeth. There is indication of extensive wear extending from the cusp into a lingual direction all along the mesial edge of each tooth, which makes the distolingually situated facet appear more like a ridge rather than a concavity. The distal most tooth of the maxillary series differs from all other teeth by being extremely small, slender, and almost conical in appearance, with only slight traces of irregular wear around the cusp, unseen in any other known bolosaurid. Another distinctive feature of *B. chengi* is the presence of well-developed resorption pits situated at the lingual base of each tooth, with one specimen showing even the emergence of a new tooth (Fig. 1i). Resorption pits similar to those found here have not been recorded in *B. vegrandis*, but seem to be at least partly present in the genus *Bolosaurus* (Reisz et al. 2002). It currently remains unclear if these taxic differences are due to preservation or different techniques of preparation or if they are indeed a real biological phenomenon.

There is only one specimen (IVPP V 15906) showing a triangular remnant of the lacrimal attached to the maxilla (Fig. 1g,h). Although incomplete, it shows that anteriorly, the lacrimal must have reached the posterior margin of the external naris, whereas posteriorly, it was forming part of the anteroventral margin of the orbit through a very thin posterior extension, thus excluding the maxilla from the orbital rim. On the medial side, a shallow excavation in the ventral part of the bone might be related to the naso-lacrimal duct.

The anatomy of the dentary (Fig. 1d–f,j,k) can be described on the basis of information derived from several specimens. It differs from that of *B. vegrandis* in that in lateral view, the bone does not slope anteroventrally, whereas in dorsal view, the bone appears sigmoidally recurved. At least two foramina can be detected in the anterior and central portions of the lateral side of the bone. More posteriorly, the dentary possesses a straight lateral ridge, which is not seen in other bolosaurid taxa. The posterior end of the bone presents a well-developed coronoid process; unfortunately, the distal part of the process is broken off, and its original height cannot be determined. The posteroventral margin of the process is concave. In medial view, the flattened symphyseal area of the dentary is strongly bent medially. The remaining medial side is rather smooth, with the posterior two thirds being of an almost polished appearance, indicating the original overlap by the prearticular. The ventral side of the dentary is strongly excavated for reception of the splenial, which originally must have extended almost up to the anterior third of the bone, thus obliterating the Meckelian groove ventrally.

The dentary carries 11 teeth, whereas an additional resorption pit at the posterior end of the alveolar shelf suggests that the maximum tooth count might have been 12. As seen in the maxilla and in contrast to other bolosaurids, none of the teeth are procumbent. A shared feature with *B. vegrandis* is that the mesial two teeth are taller than teeth 3 and 4. The tips of the two mesial teeth are unfortunately broken off, but what is preserved is a distolingually facing facet similar to that seen on the maxillary teeth. Starting with the third tooth, this facet is situated on the mesolabial side, thus forming a complementary occlusal surface for the maxillary teeth, which also results in a similar wear pattern. At the same time, the teeth become increasingly transversely expanded, though the distal teeth of the dentary are clearly not as massive as those on the maxilla. The most distal tooth of the series is smaller than the preceding teeth, but still of the same shape. Overall, the morphology of the distal teeth is very similar to that of *B. vegrandis*.

Phylogenetic analysis and discussion

The new taxon was entered in a phylogenetic analysis of bolosaurid ingroup relationships, which represents the first analysis of this kind for Bolosauridae. Twenty-one informative characters, mostly focusing on mandibular and dental features, and all six bolosaurid taxa were included, as well as four parareptilian outgroup taxa (Mesosauridae, Millerettidae, *Acleistorhinus*, and Owenettidae). Aside from personal observations, relevant information was taken from Gow (1972), deBraga and Reisz (1996), Reisz and Scott (2002), and Modesto (2006). See the Electronic Supplementary Material for character list and data matrix. Using the branch-and-bound search option in PAUP* (Swofford 2002), six equally parsimonious trees were obtained (TL, 27; CI, 0.7778; HI, 0.2222; RI, 0.8421; RC, 0.6550; Fig. 2) in which bolosaurids nest in an unresolved polytomy with *Acleistorhinus* and Owenettidae and with *Eudibamus* being the sister taxon of *Bolosaurus* and *Belebey*. The clade Bolosauridae is robust and unequivocally characterized by the presence of bulbous teeth (#1[1]), the presence of "intermediate" mesial teeth 3 and 4 (#7[1]), and a rod-like quadratojugal (#20[1]); *Bolosaurus/Belebey* share unequivocally a reduced number of premaxillary teeth (#8[1]), which are also smaller than the mesial maxillary teeth (#9[1]), the presence of distinct striations on the tooth crowns (#13[1]), and a tall coronoid process (#17[1]). Unequivocal apomorphies of *Belebey* are the transversely expanded posterior cheek teeth (#3[1]) with a recurved cusp (#5[1]), the presence of cutting ridges (#.12[1]), and an anterodorsally concave maxilla (#14[1]) with a straight posterdorsal margin (#15[1]). The relationships within the genus *Belebey* remain unresolved, partly because of the fragmentary nature of *Belebey maximi*. Bootstrap support, however, is fairly strong for the genus (Fig. 2). The members of *Bolosaurus* are unequivocally characterized by the presence of a peg-like posterior tooth on the dentary (#11[1]).

Our analysis indicates that *Eudibamus* from the Lower Permian (Sakmarian) of Germany is the basal most taxon among currently known bolosaurids, even though *Bolosau-*

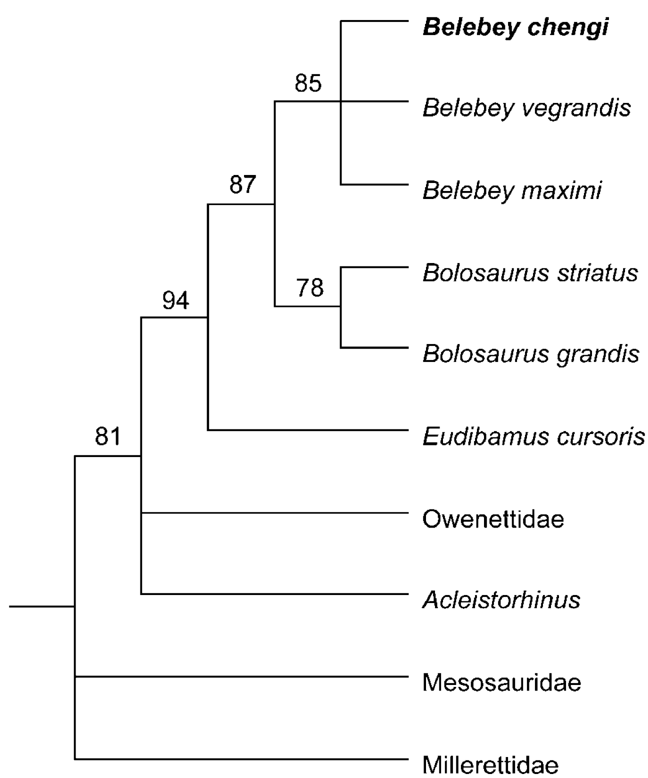

Fig. 2 Phylogenetic relationships among Bolosauridae. *Numbers* indicate bootstrap values

rus striatus from the Permian Red Beds (Artinskian) of North America is stratigraphically older. While this scenario implies that the early evolution of this group is still unknown, the situation reflects the one found in Captorhinidae in which the sister taxon, *Thuringothyris* from the same Lower Permian locality in Germany, is also stratigraphically younger than the oldest known captorhinid, *Concordia* from the Upper Carboniferous (Gzhelian) of Kansas (Müller and Reisz 2005, 2006; Müller et al. 2006). Thus, the split between the currently known bolosaurid genera must have taken place no later than the Permo-Carboniferous transition, with the basal most taxon being known from the paleo-equatorial region of central Laurasia (Europe), one lineage spreading into the paleo-equatorial regions of Western Laurasia (North America), and one lineage migrating into the eastern part of the supercontinent, reaching what is now northern China at latest in the Middle Permian. Further studies will be required to determine if the European part of Laurasia served as the center of origination for Bolosauridae as well as for other amniote clades, as suggested by the phylogeny. Our study emphasizes once again that the early evolution of Parareptilia remains poorly known, much less well known than those of the other two major clades of Paleozoic amniotes, Synapsida, and Eureptilia. It is clear that new fossils, particularly from the Upper Carboniferous and Lower Permian, will be required to resolve the history of this enigmatic clade.

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Appendix

Character list and data matrix for the phylogenetic analysis of bolosaurid ingroup relationships.

1. Tooth shape of middle and distal teeth in the upper and lower jaw: slender (0); bulbous (1).
2. Mesial teeth in the upper and lower jaw: not procumbent (0); procumbent (1).
3. Transverse expansion of distal cheek teeth: absent (0); present (1).
4. 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).
5. Main cusp of distal cheek teeth: pointing straight upwards (0); sharply recurved (1).
6. Incisiform mesial tooth on maxilla: present (0); absent (1).
7. “Intermediate” mesial teeth 3 and 4 (on maxilla/dentary): absent (0); present (1).
8. Number of premaxillary teeth: 3 or more (0); 2 (1).
9. Premaxillary teeth, size: smaller than or almost equal to mesial maxillary teeth (0); larger (1).
10. Contact between maxilla and quadratojugal: absent (0); present (1).
11. Distal most tooth on dentary: equal or slightly smaller than preceding teeth (0); very small and peg-like (1).
12. Cutting ridges on distal teeth: absent (0); present (1).
13. Distinct striations on tooth crowns: absent (0); present (1).
14. Lacrimo-maxillary suture: anterodorsal margin of maxilla irregular or straight (0); anterodorsal margin concave (1).
15. Maxilla posterodorsal margin: slopes posteroventrally (0); straight (1).
16. Dentary in dorsal view: sigmoidal (0); straight (1).
17. Coronoid process: absent or small (0); tall, multipartite (1).
18. Surangular: extends beyond coronoid eminence (0); does not extend beyond eminence (1).
19. Teeth on pterygoid transverse flange: present (0); absent (1)
20. Quadratojugal shape: sheet-like (0); rod-like (1)
21. Number of sacral vertebrae: 2 (0); 3 (1).

Mesosauridae	00000	00000	00000	??0000
Millerettidae	00000	00000	00000	000000
Owenettidae	00000	00000	00000	001101
Acleistorhinus	00000	00001	?0000	1?100?
Bolosaurus striatus	11010	11110	10100	111?1?
Bolosaurus grandis	11010	1????	101??	11????
Eudibamus cursoris	10000	11000	?00?0	10?111
Belebey vegrandis	11111	01111	01111	111111
Belebey maximi	1?1?1	?????	?11??	??????
Belebey chengi	10101	01???	01111	01????

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