TO THE REVISION OF THE MIDDLE PERMIAN BOLOSAURIDS (TETRAPODA, BOLOSAURIDA) OF EASTERN EUROPE

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Abstract. A re-examination of the holotype of Permotriturus herrei Tatarinov, 1968 (Tetrapoda, Bolosaurida) supplemented by a new specimen from the type locality Isheevo, Republic of Tatarstan, European Russia, supports the validity of the genus Belebey Ivakhnenko, 1973. The differences between the genera Belebey and Permotriturus were established in the relationships of elements forming the suborbital portion of the skull roof, features of tooth implantation, as well as in the pattern of vasculature of the jaw bones. In spite the specialized condition of the dental system of P. herrei and its upper-most (terminal Urzhumian) stratigraphic position in comparison with other bolosaurid species, the morphology of its cheek region exhibits more similarity with that of the lower Permian bolosaurids of North America other than members of the genus Belebey. The absence of clear diagnostic criteria allows no possibility for subdivision of the order Bolosaurida on taxa of the family rank based on its middle Permian representatives.

Keywords: *Bolosaurida, Permotriturus, dental system, Isheevo, middle Permian, Urzhumian, Eastern Europe*

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INTRODUCTION

The family Bolosauridae (order Bolosaurida) is one of the earliest groups of amniotes that transitioned to obligate herbivory. The oldest bolosaurids are described from the Lower Permian of the USA and Germany (Cope, 1878; Reisz et al., 2002; Berman et al., 2000, 2021), while the Middle Permian stage of the family's evolution is reconstructed from materials originating from European Russia and China (Ivakhnenko, 1973; Ivakhnenko, Tverdokhlebova, 1987; Müller et al., 2008; Bulanov et al., 2022).

Despite their wide territorial distribution, bolosaur findings are few and consist mainly of isolated jaws, based on which, in particular, all species belonging to the Middle Permian genus Belebey were originally established: B. vegrandis Ivachnenko, 1973; B. maximi Ivachnenko et Tverdochlebova, 1987; B. chengi Müller et al., 2008; B. shumovi Bulanov et al., 2022 (Ivakhnenko, 1973; Ivakhnenko, Tverdokhlebova, 1987; Li, Cheng, 1995; Müller et al., 2008; Bulanov et al., 2022). The lack of morphological data resulted in the inclusion of a number of problematic taxa in the group at different stages of its study, the systematic position of which has now been revised or still needs clarification.

Thus, Davletkulia gigantea Ivachnenko, 1990, described from a single tooth, was excluded from the order, as its holotype demonstrates obvious affiliation with herbivorous dinocephalians of the superfamily Tapinocephaloidea (Reisz et al., 2002; Bulanov, 2024), as well as a form initially identified as the East European representative of the genus Bolosaurus – B. traati Tatarinov, 1974, which according to the results of a revision was reassigned to the order Diadectomorpha (Diadectidae) within the genus Stephanospondylus (Ivakhnenko, 2008; Bulanov, 2023). Relatively recently, the species Belebey augustodunensis Falconnet, 2012, described from a fragment of a jaw bone from the Artinskian deposits of France, was excluded from Bolosaurida, as the find was identified as belonging to sphenacomorph pelycosaurs (Spindler et al., 2020).

In the context of the revision of Eastern European bolosaurs, another problematic specimen discovered during excavations at the reference locality of the Isheevo faunal complex Isheevo (Republic of Tatarstan; Urzhumian stage) is significant. It is a jaw fragment (spec. PIN, No. 157/500; Fig. 1), described under the name Permotriturus herrei and originally interpreted as the maxillary bone of the oldest (Late Paleozoic) representative of tailed amphibians (Tatarinov, 1968).

The probable affiliation of specimen PIN, No. 157/500 to Bolosaurida was first indicated by M.F. Ivakhnenko (1990), which was reflected in the subsequent placement of the genus Permotriturus within this group (Ivakhnenko et al., 1997), without argumentation, however, for this decision due to the reference format of the publication. The diagnosis of the genus Permotriturus as a taxon of the family Bolosauridae was first given by the same author in the latest comprehensive compilation on the Permo-Triassic tetrapods of Eastern Europe (Ivakhnenko, 2008), which allows for a substantive discussion of the taxonomic status of the form from Isheevo. The correctness of attributing P. herrei to bolosaurids does not raise doubts, since the holotype demonstrates a number of features of jaw dentition organization (see below), which collectively distinctly distinguish bolosaurids among the known diversity of Paleozoic amniotes (Watson, 1954; Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2002, 2007; Snyder et al., 2020).

The present work aims to re-examine the holotype of Permotriturus herrei in order to compare it with species of the genus Belebey and clarify the taxonomic status of this form. The need for such a revision was pointed out by J. Falconnet (Falconnet, 2012), who emphasized the similarity of the specimen from Isheevo with the type specimens of Belebey species and suggested the probability of junior synonymy of the genus Belebey Ivachnenko, 1974 in relation to Permotriturus Tatarinov, 1968.

As additional material in the present study, a fragment of the maxillary bone (specimen KFU, No. B 823/54; Fig. 2) was used, which was discovered during excavations at the Isheevo locality in 2000 and had not been previously studied. It undoubtedly belongs to P. herrei, but, like the holotype, has not preserved the crowns of the teeth. Despite its fragmentary nature, this specimen carries important diagnostic information about the genus Permotriturus, and also allows verification of some morphological characteristics of the P. herrei holotype as taxonomically significant (i.e., not related to variability).

Since the teeth of both specimens from Isheevo have not preserved their coronary part, the morphology of which, along with the nature of their differentiation and distribution in dental rows, is important for diagnosing Bolosaurida taxa, additional emphasis in the work is placed on studying the jaw bones themselves, namely, their relationship with the surrounding cranial structures, features of tooth implantation, and intracostal vascularization. To solve these tasks, computed tomography was used, which complemented the characterization of bolosaurids in the indicated morphological aspects.

Tomographic scanning of the holotypes of Permotriturus herrei, Belebey vegrandis, B. maximi, and B. shumovi was carried out using a Neoscan 80 nanotomograph at the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS), where materials on these species are stored. The maxillary bone of P. herrei was scanned in the X-ray computed tomography laboratory of the Institute of Geology and Oil and Gas Technologies (IGiNGT) of Kazan Federal University (KFU) using a General Electric V|tome|x-S240 micro- and nanofocal X-ray system. The three-dimensional reconstructions and virtual sections presented in the work were obtained using Avizo V2019.1 and CTVox V1.5 software.

MORPHOLOGICAL DESCRIPTION

Dentary of Permotriturus herrei Tatarinov, 1968 (holotype PIN, No. 157/500)

As previously noted (Ivakhnenko et al., 1997; Ivakhnenko, 2001, 2008), the holotype of P. herrei (specimen PIN, No. 157/500) is not a maxilla, but a fragment of the left dentale, with a length of 34.6 mm. The bone contains eight alveoli, the anterior of which is damaged. For convenience of further description, the numbering of alveoli in the holotype of P. herrei begins from the very first (damaged) alveolus (Fig. 1), although it did not correspond to the first dental position of the jaw, as indicated by the absence of a symphyseal contact area on the specimen, fewer teeth compared to those in the dentale of bolosaurids where this element is completely preserved (Belebey vegrandis: specimens SGU, Nos. 104B/2020, 2021; B. maximi: holotype SGU, No. 104B/2027; B. chengi: specimen IVPP V 12007; Bolosaurus grandis: holotype OMNM 52311), as well as the elongated-oval shape of the cross-sections of all alveoli represented on the specimen, since the anterior mandibular teeth of bolosaurids have circular cross-sections (Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2002; Müller et al., 2008).

All teeth in the jaw are broken off at the level of the alveolar margin, but their root parts, deeply embedded in the supporting bone and firmly fused to it, are visible in all alveoli both through the open pulp cavity and on CT scans (Fig. 1, *a* , *d* , *f*). The size of the alveoli gradually increases in accordance with the expansion of the bone in the caudal direction, starting from the first alveolus to the sixth inclusive, which, judging by its size, contained the largest tooth of the jaw. The penultimate – seventh tooth was somewhat smaller than the sixth, and the eighth was smaller than the seventh, and approximately corresponded in size to the tooth in the third position. At the end of the tooth row in the holotype of P. herrei, there was no miniature (postbuccal) tooth, which often completes the tooth rows in Middle Permian bolosaurids and is characterized by a simplified crown structure (Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2002; Müller et al., 2008; Bulanov et al., 2022).

Vacant alveoli, like resorption traces, are absent on the jaw, i.e., at the moment preceding burial, all teeth of the dental row part presented in the specimen were functioning structures and had changed shortly before that (Snyder et al., 2020), which is also confirmed by the absence of replacement crowns inside the alveoli. Cross-sections of teeth at the alveolar margin level are elongated-oval in shape, with smooth, parallel or slightly diverging in the anterolabial direction sides (Fig. 1, *f*). The labial parapet is absent. The bases of the teeth are noticeably shifted from the outer edge of the dentale and placed diagonally in the jaw, due to the rotation of their lingual side in the caudal direction relative to the labial one. The angle of tooth rotation to the transverse section of the jaw (measured along the anterolingual wall of their root part at the alveolar margin level) changes from 30° in the anterior preserved teeth to 35° in the posterior ones; the ratio of length to width of sections in the most elongated last five teeth at the same level varies from 2.4 (fourth position from the end) to 2 (the last tooth of the jaw).

The dental bone is massive. The end of the dental row is limited posteriorly by a pronounced bone elevation, which formed part of the base of the hypertrophically developed coronoid process in bolosaurids (Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2002, 2007). The medial side of the dentale is very high and smooth, except for thin, straight, and parallel-oriented vascular grooves covering it, directed anterodorsally. The lateral and medial descending plates that framed Meckel's cartilage are broken off at the level of the dental shelf base in the specimen, but it can be stated that the cartilage groove, wide in the posterior part of the bone, sharply narrowed in the presymphyseal section to a slit-like state. In this part of the groove in specimen PIN, No. 157/500, there is a pair of foramina that allowed large vessels and, probably, accompanying nerves to pass in the direction of the symphysis. Throughout the rest of Meckel's groove, relatively narrow but extended vascular canals branch into the dentale at regular intervals. Inside the jaw, they follow in an anterodorsal direction to the bases of teeth (located significantly anterior to the point of entry into the bone), where they disappear into a network of lacunae separating the trabeculae of alveolar bone tissue (Fig. 1, *d*).

The lateral side of the dentale, especially in the area of the posterior end of the tooth row, is perforated with numerous vascular foramina. CT sections in the horizontal plane (Fig. 1, *h*) demonstrate a sharp structural boundary between the tooth implantation zone, formed by poorly vascularized walls of the alveoli and alveolar bone fixing the tooth roots, and the intensely vascularized zone located laterally, formed by a network of large anastomosing canals and lacunae. The vascular canals of the vascularized zone open with numerous foramina on the lateral surface of the dentale, which is partly due to its damage (Fig. 1, *b* , *c*), but they do not originate in the groove of Meckel's cartilage; instead, they follow inside the bone ascending from the lower edge of its broken lateral wall toward the alveolar margin.

The floor of the alveoli of teeth in the posterior part of the tooth row lies near the surface of the Meckelian groove, while the end of the anterior alveoli is located significantly above its vault (Fig. 1, *d*). The character of tooth implantation in the dentale of Permotriturus, except for the details discussed below, corresponds to that of Early and Middle Permian bolosaurids (Snyder et al., 2020; Bulanov et al., 2022): wide tooth roots are firmly fused to the walls of alveoli by means of trabeculae of the alveolar spongy matrix. In some places, partial overlapping of implantation zones of adjacent teeth is observed, with the implantation zone of the anteriorly positioned tooth always being captured by that of the posteriorly located tooth (Fig. 1, *f*). The latter indicates a sequential order of jaw teeth replacement, which is an important diagnostic characteristic of Bolosaurida (Snyder et al., 2020).

One of the consequences of implantation zone overlap is that the interalveolar septa formed by the jaw bone taper out in the dorsal direction without reaching the alveolar margin (Fig. 1, *d*, *e*). In cross-section, the lateral walls of most tooth roots are smooth on the outer side and slightly wavy on the inner side; however, in some cases, this unevenness is inherited by the outer side of the teeth, giving their bases a slightly folded character (Fig. 1, *f*, *i*). Toward the crown, this unevenness levels out, and in cross-sections at the level of the alveolar margin, it is not detected.

An interesting feature of the buccal teeth attachment in the P. herrei holotype is that the root portion of the teeth sinks into the alveoli only slightly beyond the middle of their depth (Fig. 1, *d* , *i*, *j*): the ratio of alveolar height to root height for all positions, except for the damaged first and last alveoli, varies in the range of 1.6–1.8. The labial and lingual walls of the tooth demonstrate the greatest depth of immersion, while the edge of the expanded lateral sides is slightly curved upward and thus located closer to the alveolar margin.

The consequence of the weak penetration of tooth roots into the alveoli in P. herrei is an increased volume of alveolar bone tissue developed within them and the predominantly elongated-vertical organization of the trabeculae forming it. The latter is especially well-expressed around the periphery of the lateral (expanded) sides of the tooth; in the basal part of the alveoli, the trabeculae are oriented less orderly but still maintain a mostly vertical direction. Directly at the base of the pulp cavity, the thickness of the trabeculae and the distance between them increases. As CT sections demonstrate, large basal trabeculae of alveolar tissue fix the tooth wall not only from its outer side but also, at the base, from the pulp cavity side (Fig. 1, *j*).

The maxillary bone of Permotriturus herrei Tatarinov, 1968 (specimen KFU, № B 823/54)

The second specimen of P. herrei from Isheevo is a jaw fragment 28 mm long, preserving the last seven alveoli of the dental row, of which the three anterior ones are severely damaged and represented only by medial walls (Fig. 2, *a*, *f*). Further numbering of the alveoli starts from the first, almost completely destroyed alveolus, where, nevertheless, the presence of a small part of the dentine wall of the root is recorded (Fig. 2, *f*).

Despite its fragmentary nature, this specimen cannot be interpreted as a dentale, as it lacks a meckelian groove depression, plates framing it, as well as a vertical projection behind the tooth row that forms the base of the coronoid process and is present in the holotype. The absence of these structures in specimen KFU, No. B 823/54 is not a consequence of the specimen being worn smooth, since the posterior edge of the bone is visually undamaged, which is confirmed by the continuity of vascular canals passing under its surface (Fig. 2, *i*). Furthermore, the specimen bears a well-defined contact area on one of its sides (Fig. 2, *b* , *c* , *j*), which, based on its termination near the alveolar margin, cannot be interpreted as the articulation surface of the angulare (if specimen KFU, No. B 823/54 is interpreted as a left dentale); a similar area is absent in the corresponding position on the holotype. The absence of symphyseal structures and the elongated shape of the cross-sections of the teeth also do not allow interpretation of specimen KFU, No. B 823/54 as the anterior section of the dentale of the right side of the skull. Thus, specimen KFU, No. B 823/54 can be confidently identified as the posterior part of the left maxillare, as evidenced by the subtriangular shape of the bone cross-sections, the ventromedial inclination of its inner side, the keel-shaped caudal termination, and the presence of a small notch on the medial side (Fig. 2, *d*, *j*), associated with the participation of the maxillare in constructing the anterolateral wall of the adductor cavity (by analogy with B. vegrandis: specimens SGU, Nos. 104B/2020 and 2021). The contact facet on the medial side of the bone, adjoining the indicated notch anteriorly and bearing smoothed oblique ridges, can thus be confidently identified as the articulation surface of the ectopterygoideum (Fig. 2, *d*), which in bolosaurids bounds the adductor fossa anteromedially (Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2007).

As in the holotype, all teeth of specimen KFU, No. B 823/54 are broken at the level of the alveolar margin. The completely preserved alveoli do not contain replacement teeth inside; resorption openings lingual to the tooth row are also absent.

The last alveolus undoubtedly closed the dental row, which follows from the smooth, undisturbed contour of the posterior end of the maxilla and is confirmed by the absence of alveolar structures behind the indicated tooth in virtual sections (Fig. 2, *e*, *h*, *i*). The relatively large size of the last alveolus indicates that, as in the holotype, the tooth placed in it was a functioning structure.

In horizontal section at the level of the alveolar margin, the posterolabial wall of the root portion of the teeth has a concave profile, which is most pronounced in the tooth that was located in the third alveolus (Fig. 2, *f*). In the preserved part of the dental row, the rotation of teeth relative to the transverse section of the jaw, measured along the posterolabial side, varies in a wide range - from 15° in the indicated position to 45° in the last one. At the same time, the ratio of length to width of the tooth bases at the level of the alveolar margin changes from 3.13 to 2.2 respectively, which indicates a stronger labiolingual elongation of the maxillary teeth compared to their antagonists in the dentale (holotype). In horizontal sections at the same level, specimen KFU, No. B 823/54 demonstrates a wide overlap of the implantation zone of the third tooth by that of the fourth, and of the fourth by the implantation zone of the fifth (Fig. 2, *f*).

In lateral projection, the bone is low. Besides the flange for ectopterygoideum articulation on the medial side, it bears a large and complexly structured contact surface in its posterolateral part, which contrasts with what is observed in Belebey vegrandis (specimens SGU, Nos. 104B/2020 and 2021), B. shumovi (holotype PIN, No. 4312/4) and, judging by published images, B. chengi (Müller et al., 2008, fig. 1a, b), in which the contact areas of the posterior section of maxillare, however, are not described in detail. The indicated surface in Permotriturus is divided into a posterior half, oriented vertically and covered with sharp, anteroventrally directed ridges (fig. 2, *b* , *c* ; *lfp*), and a slightly dorsally-laterally rotated and smoother anterior part, the upper edge of which forms a longitudinal ledge extending along the upper edge of the maxilla (ibid. *; lfa*). On the specimen, these parts are separated by a wide, anteroventrally directed vascular groove that enters the bone through a large foramen.

As in the holotype, specimen KFU, No. B 823/54 is characterized by very shallow immersion of buccal teeth roots into the alveoli, increased volume of alveolar matrix, and predominantly vertical orientation of the trabeculae forming it (fig. 2, *e*, *k*). Unlike the dentale, in the maxillare, manifestations of intensive vascularization are observed not only lateral to the implantation zone, but also, to a lesser extent, medially from it (fig. 2, *h*). In the lateral zone, intraosseous canals connecting the network of large lacunae are inclined anteroventrally, i.e., oriented at an angle to the alveolar margin, as is also observed in the holotype.

DISCUSSION

Problem of taxonomic identification of Permotriturus herrei

The reconstructed skull length of the specimens to which PIN, no. 157/500 and KFU, no. B 823/54 belonged was approximately 89 and 82 mm respectively, which follows from comparing the length of the dental rows presented on them with the corresponding sections of dental rows in Belebey vegrandis skulls from the Krymsky locality (specimens SGU, nos. 104B/2020 and 2021). Thus, both Permotriturus specimens are noticeably larger than Belebey vegrandis, B. maximi, and B. chengi specimens from the type localities (as well as all B. vegrandis specimens from the Krymsky locality) and are close in size to the holotype of B. shumovi (PIN specimen, no. 4312/4; reconstructed skull length 98 mm: Bulanov et al., 2022).

The features of implantation of jaw teeth established based on CT methods, the nature of their differentiation and diagonal rotation in the jaws, as well as the massiveness of the dentary bone and the presence of a dorsally directed prominence on its posterior edge, indicating the presence of a pronounced coronoid process, fully confirm the correctness of assigning Permotriturus herrei to the order Bolosaurida (Ivakhnenko et al., 1997; Ivakhnenko, 2001, 2008). The overlapping of dental implantation zones observed in places in the posterior-anterior direction in specimens PIN, no. 157/500 and KFU, no. B 823/54 indicates the sequential nature of tooth replacement, which is also a feature of the group under consideration (Snyder et al., 2020).

As mentioned above, the pronounced elongation of the bases of the posterior buccal teeth in the Isheevo form, similar to that of Belebey spp., raises the question of the probable junior synonymy of the type species of the genus Belebey – B. vegrandis Ivachnenko, 1973 – in relation to the previously established Permotriturus herrei Tatarinov, 1968 (Falconnet, 2012). Its solution is largely complicated by the fragmentary nature of P. herrei specimens, which does not allow the use of a number of taxonomically significant criteria when comparing this species with other bolosaurids, such as tooth shape, their number in the jaws, the presence of diastemas in the anterior part of the dental row, the angle of inclination of the incisors, the number of incisor-like teeth, etc.

Analysis of previously proposed diagnostic criteria for the genus Permotriturus

Ivakhnenko (2008) defined P. herrei as a species of a monotypic genus within the family Belebeyidae Ivachnenko, 2001 (elevating the rank of Eastern European forms to the family level, equivalent to Bolosauridae) based on the following diagnosis: "The dentary is very massive, the crowns of the buccal teeth, judging by the preserved bases, are very sharply flattened transversely. The massiveness and strong expansion of the upper edge of the dentary suggests the presence of the same crushing-grinding teeth as in Davletkulia, but with much more strongly compressed bases, which allows the form to be preserved as a separate genus."

Analyzing this diagnosis, it should be noted that the massiveness of the dentale cannot serve as a criterion for distinguishing P. herrei from species of the genus Belebey, as it is characteristic of all bolosaurids, including Early Permian ones, due to the intra-alveolar development of large replacement teeth of the buccal series (Snyder et al., 2020), which increases the height of the dental shelf by reducing the volume of the Meckelian cartilage cavity (Reisz et al., 2002). The available data also confidently excludes the genus Davletkulia (described based on a single tooth) from Bolosaurida (Reisz et al., 2002; Falconnet, 2012; Bulanov, 2024), and therefore the reconstruction of the shape and functional principles of Permotriturus teeth by analogy with this taxon is not relevant.

The flattening (narrowness) of tooth bases in Permotriturus herrei indicated in the diagnosis, however, requires separate consideration. All described species of the genus Belebey are characterized by an obvious elongation of the posterior buccal teeth across the bearing bones (with the labial side shifted forward relative to the lingual side). A review of the dental system of B. vegrandis specimens from the Krymsky locality (specimens SGU, No. 104B/2020-2022, 2029) allows us to conclude that the maxillary buccal teeth in this form are significantly wider than their antagonists in the lower jaw, which can be confidently stated for B. chengi as well based on published images (Müller et al., 2008, fig. 1c, f). The number and shape (degree of labiolingual elongation) of the jaw teeth, their rotation angle in the jaws, and the distance between them are subject to significant ontogenetic transformation. Thus, a correct comparison of species within the group according to these parameters requires comparing homologous jaw bones in specimens of similar size.

Regarding the holotype of Permotriturus herrei, such a comparison is impossible, however, because the dentary bones of Belebey vegrandis and B. maximi belong to individuals of significantly smaller size (most likely juvenile), and the structure of the dentale of the large bolosaurid representative B. shumovi is not yet known (Bulanov et al., 2022). Comparison of the maxillare of

Permotriturus herrei (specimen KFU, No. B 823/54) with the almost equal-sized holotype of Belebey shumovi (maxillare, specimen PIN, No. 4312/4) demonstrates a similar elongation of the largest teeth of the buccal series, which occupied the third and fourth positions from the end of the alveoli. Thus, in the first of these taxa, for these positions, the ratio of the length of the tooth bases to their width (at the level of the alveolar edge) is 3.13, and for the second - 3.04. At the same time, specimens from Isheevo demonstrate that, similar to B. vegrandis and B. chengi, the maxillary buccal teeth of Permotriturus were elongated across the bearing bone more than their mandibular antagonists; thus, it can be fairly confidently assumed that this feature was characteristic of all Bolosaurida; this requires consideration when comparing species within the group using jaw material.

Current diagnostics of the genus Permotriturus

Features of dental implantation. From the above, it follows that the taxonomic separation of the genera Belebey and Permotriturus based on the previously proposed diagnosis (Ivakhnenko, 2008) does not seem possible. Nevertheless, data obtained from computed tomography indicate an obvious difference between Permotriturus herrei and Belebey spp. in the manner of jaw teeth attachment, which consists in a significantly weaker immersion of their root portion into the alveoli and, consequently, an increased volume of alveolar bone tissue filling the periodontal area (fig. 1, 2). This condition is observed in both specimens from Isheevo, which is why it can be considered as normative for Permotriturus and serve as a diagnostic criterion for the genus. As shown above, the tooth roots in the holotype of P. herrei and specimen KFU, № B 823/54 are immersed in the bearing bone slightly deeper than the middle of the alveolar height (fig. 1, *e*, *i*, *j*), while in the other studied Eastern European bolosaurids, the tooth roots end near their bottom (fig. 3). The sample of Belebey vegrandis skulls from the Krymsky locality, belonging to different ontogenetic stages (skull length from 35 to 60 mm), does not demonstrate obvious variability in this character and is characterized by the same depth of jaw teeth immersion that is observed in the jaw bones of B. vegrandis and B. maximi from the type localities. A lesser depth of tooth immersion, comparable to that of Permotriturus herrei, is recorded in the dental bone of Belebey chengi (specimen IVPP V 12007: Snyder at al., 2020, fig. 3E), as well as in some areas of the holotype of B. shumovi (fig. 3, *a*), however, in both cases this is explained by the presence of almost fully formed replacement teeth inside the alveoli, the development of which, as shown earlier (Bulanov et al., 2022), is accompanied by resorption of the distal part of functional teeth roots, as well as the surrounding alveolar matrix.

The misalignment between the height of the alveoli and the height of the root part of the teeth observed in Permotriturus is atypical for primitive amniotes with a thecodont dental system, including bolosaurids (Fig. 3). This feature of P. herrei may indicate the absence of a need for stronger fixation of the most specialized teeth of the marginal complex in the jaws, which currently lacks a satisfactory explanation. Given this, the assumption that Permotriturus might have had a somewhat different tooth form (and consequently a slightly different functioning principle from other Middle Permian bolosaurids) remains relevant, although it cannot currently be confirmed by factual material. At the same time, it can be assumed that the "standard" depth of alveoli with relatively weak immersion of teeth in Permotriturus, regardless of probable causes, was maintained by the dental renovation pattern realized in bolosaurids, according to which replacement teeth completed their formation in their basal part (Snyder et al., 2020).

Intramandibular vascularization . Another distinctive feature of the genus Permotriturus, demonstrated by CT data, is the intensive vascularization of the jaw bones lateral to the dental implantation zone, i.e., the presence of a dense network of canals and lacunae oriented toward the alveolar margin (with their pronounced inclination in the rostral direction). The lateral area of increased vascularization is noted in both the dentale and maxillare of P. herrei (Fig. 1, *f*, *h*), however, tomography results do not demonstrate its presence within the jaw bones of other Eastern European bolosaurids, including the type specimens of Belebey vegrandis, B. maximi, and B. shumovi (Fig. 3), which formally allows this feature to be included in the diagnosis of the genus Permotriturus. The significant difference in the vascularization pattern of the jaw bones of P. herrei compared to other

Eastern European bolosaurids, despite similarities in the general structural plan, currently lacks morphofunctional argumentation and requires further consideration.

Organization of the suborbital region of the dermatocranium. The most obvious indicator of the taxonomic independence of the genus Permotriturus appears to be the presence of a large contact area on the lateral side of the maxillare, indicating a number of fundamental differences in the organization of the suborbital part of the skull compared to that of species of the genus Belebey for which the structure of this bone is known (B. vegrandis, B. shumovi, and B. chengi).

The morphology of this region in B. vegrandis was previously examined (Ivakhnenko, Tverdokhlebova, 1987; Reisz et al., 2007) based on materials from the Krymsky locality, and is clarified here based on specimen SGU, 104B/2021 from the same collection, which shows minimal damage and displacement of the bones forming the lower wall of the orbit (Fig. 4).

The suborbital section of the maxillary bone of B. vegrandis is a high plate, narrow in plan, contacting the jugale and lacrimale (Fig. 4, *a*); in addition, the anterior end of the quadratojugal bone is maximally approached to the posterior edge of the maxilla, although the contact of these elements cannot be reliably established on either side of the skull.

Anterior to the temporal opening, the jugal bone extends medial to the maxillare almost to the anterior edge of the orbit, where it articulates with the suborbital process of the lacrimale, framing it from below and partly medially. This contact completely isolates the maxillare from the orbit both medially - due to the fairly wide junction of the lacrimale and jugale - and dorsally, since in lateral projection the edges of these bones are raised above the maxilla (Fig. 4, *a*). The consequence of the medial adjacency of the lacrimale and jugale to the maxillary bone in B. vegrandis is the absence of a contact area in the posterolateral position, which appears to be an important distinction of this form from Permotriturus herrei, for which the presence of such an area requires a separate interpretation.

Based on the reconstructions of the suborbital section of the skull roof provided by D. Watson for Bolosaurus striatus (Watson, 1954, pp. 307-309, fig. 1-3), the posterolateral contact area of the maxillary bone of Permotriturus, or more precisely - its posterior half covered with sharp ridges and oriented vertically (fig. 2, fig. 2, *b* , *c* , *j*: *lfp*), is interpreted here as the attachment site for the jugale. In Bolosaurus, as in Belebey, the jugal bone almost reaches the anterior margin of the orbit, however, it overlaps the suborbital section of the maxilla from above and, with high probability, partially overlaps it laterally. This is supported by the very insignificant height of the suborbital section of the maxillare and the remote position of this element from the orbital margin in lateral projection (fig. 4, *b*), which, based on the overall height of the bone, is also assumed for Permotriturus (fig. 4, *c*).

The smoother and more obliquely oriented anterior half of the posterolateral contact area of the P. herrei holotype (fig. 2, *b* , *c* : *lfa*), thus, can be interpreted as the articulation site for the lacrimal bone, which, unlike in Belebey vegrandis, broadly joined with the jugal above the maxillare, rather than medial to it (fig. 4, *c*).

According to the provided interpretation, the anterior end of the posterolateral contact area of the maxillare should roughly correspond to the position of the anterior orbital wall (Fig. 4, *c*); consequently, five or six posterior alveoli, represented on the specimen KFU, No. B 823/54 and containing the largest and most specialized teeth of the upper jaw, were located in the suborbital part of the maxilla, which is not characteristic for Belebey species. In Permotriturus, the maxillary tooth row extended to the very end of the maxilla, i.e., it reached the level of the mid-length of the orbit, since at this level the maxillary bone ends in all bolosaurids known from complete skull remains, with the exception of Eudibamus cursoris, in which the maxilla almost reached the level of the posterior orbital wall (Berman et al., 2021). The significant posterior extension of the maxillary tooth row under the orbit, presumed for Permotriturus, is reconstructed for Early Permian forms – Bolosaurus striatus (Watson, 1954) and Eudibamus cursoris (Berman et al., 2021, Fig. 4), but is not observed in specimens of Belebey vegrandis from the Krymsky locality (Ivakhnenko, Tverdokhlebova, 1987) due to the fragmentary nature of the material and cannot be confirmed for any of the Belebey specimens from the type localities. It is worth noting separately that the shape of the posterolateral contact area of the maxillare in Permotriturus herrei indicates the absence of articulation between this bone and the quadratojugale.

Current diagnosis of the genus Permotriturus

From the above, it follows that P. herrei combines features of deeply specialized dental system, consisting in strong labiolingual elongation of the buccal series teeth similar to that observed in Belebey spp., with the structure of the maxillary-jugal region found in more primitive – Early Permian – bolosaurids (dorsolateral junction of the jugale and lacrimale relative to the suborbital section of the maxillary bone and, consequently, the lesser height of its facial surface). At the same time, Permotriturus is characterized by unique features of dental implantation within the group, namely – weak submersion (partial reduction) of the roots of the jaw teeth, as well as the presence of lateral and medial zones of jaw vascularization, which together confirm the taxonomic independence of the genus Permotriturus and, consequently, the validity of the genus Belebey.

Question of the taxonomic definition of the order Bolosaurida

The differences listed above make it unlikely that Permotriturus and Belebey belong to the same family; however, in our opinion, the previously proposed separation of the Middle Permian forms into a separate family Belebeyidae (Ivakhnenko, 2001) needs additional justification.

The diagnosis of Belebeyidae was provided by Ivakhnenko (2008, p. 90): "The maxillary bone is long, more than half the length of the skull. The tooth crowns are low, flattened, with well-defined wide horizontal heels. The palatine bone covers almost half of the posterior part of the bony choana, forming a well-defined secondary palate."

The length of the maxillary bone of Belebey vegrandis is correctly reflected in the diagnosis and previously published reconstructions (Ivakhnenko, Tverdokhlebova, 1987, fig. 1; Reisz et al., 2007, fig. 9) based on material from the Krymsky locality (specimen SGU, Nos. 104B/2020, 2021); however, as indicated, for most bolosaurids known from complete cranial material, the maxillare ends in a similar position – approximately at the level of the middle of the orbit length, while in the Early

Permian genus Eudibamus it extends significantly further back (Watson, 1954; Ivakhnenko, Tverdokhlebova, 1984; Reisz et al., 2007; Berman et al., 2021). The fundamental differences may be related to the extent of the maxillary tooth row, which either reaches or does not reach the posterior end of the maxilla; however, it cannot be excluded that this condition varies during ontogeny due to the addition of new tooth positions.

The strong expansion of the posterior teeth of the buccal series in Middle Permian bolosaurids (the presence of a pronounced heel and, consequently, lower tooth height relative to width) is not unique, as it is characteristic, in particular, of the posterior mandibular teeth of Bolosaurus grandis (Snyder et al., 2020, fig. 1d) and, based on the general pattern, should be more pronounced in the maxillary teeth of this species (the maxillary bones of B. grandis have not yet been described).

The presence of a secondary palate among bolosaurids is reliably established only for specimens of Belebey vegrandis from the Krymsky locality (Ivakhnenko, Tverdokhlebova, 1987), while data on the structure of the palatal complex in other representatives of the order are either incomplete (B. striatus) or absent, which does not allow the use of this criterion for the division of taxa of any rank within the group.

Potential definitions for the family-level separation of Early and Middle Permian Bolosaurida in the future may be differences in the shape and size of the temporal fenestra and the corresponding disproportion of its framing elements (jugale and quadratojugale), however, the structure of this section of the dermatocranium in Bolosaurus is reconstructed conditionally (Watson, 1954) and needs clarification.

An additional problematic circumstance of the taxonomic differentiation of the order Bolosaurida is that all Belebey species in the type localities are represented by isolated jaw material. As a result, the criteria for distinguishing family-level taxa (both previously proposed and potentially possible) cannot be traced beyond the sample of B. vegrandis specimens from Krymsky. At the same time, the attribution of materials from this locality to B. vegrandis, accepted a priori after their first publication (Ivakhnenko, Tverdokhlebova, 1987), requires revision due to the subsequent description of other species within the genus Belebey – B. maximi Ivachnenko, 1990; B. chengi Müller et al., 2008 and B. shumovi Bulanov et al., 2022.

From the above, it follows that the establishment of family-level taxa within the order Bolosaurida based on its Middle Permian forms appears premature due to the absence of correct diagnostic criteria, which is primarily related to the incompleteness of data on already described Early Permian forms. Moreover, the mosaic combination of primitive and evolutionarily advanced cranial characteristics in the genus Permotriturus does not allow to definitively determine its family affiliation even with further confirmation of the valid status of the family Belebeyidae. In the event that new data will allow positioning the genera Belebey and Permotriturus within one family-level taxon, the type genus of the latter should be Permotriturus, since the family Permotrituridae Tatarinov, 1968 was proposed earlier than Belebeyidae Ivachnenko, 2001.

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CONFLICT OF INTERESTS

The author declares no conflict of interest.

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Figure Captions

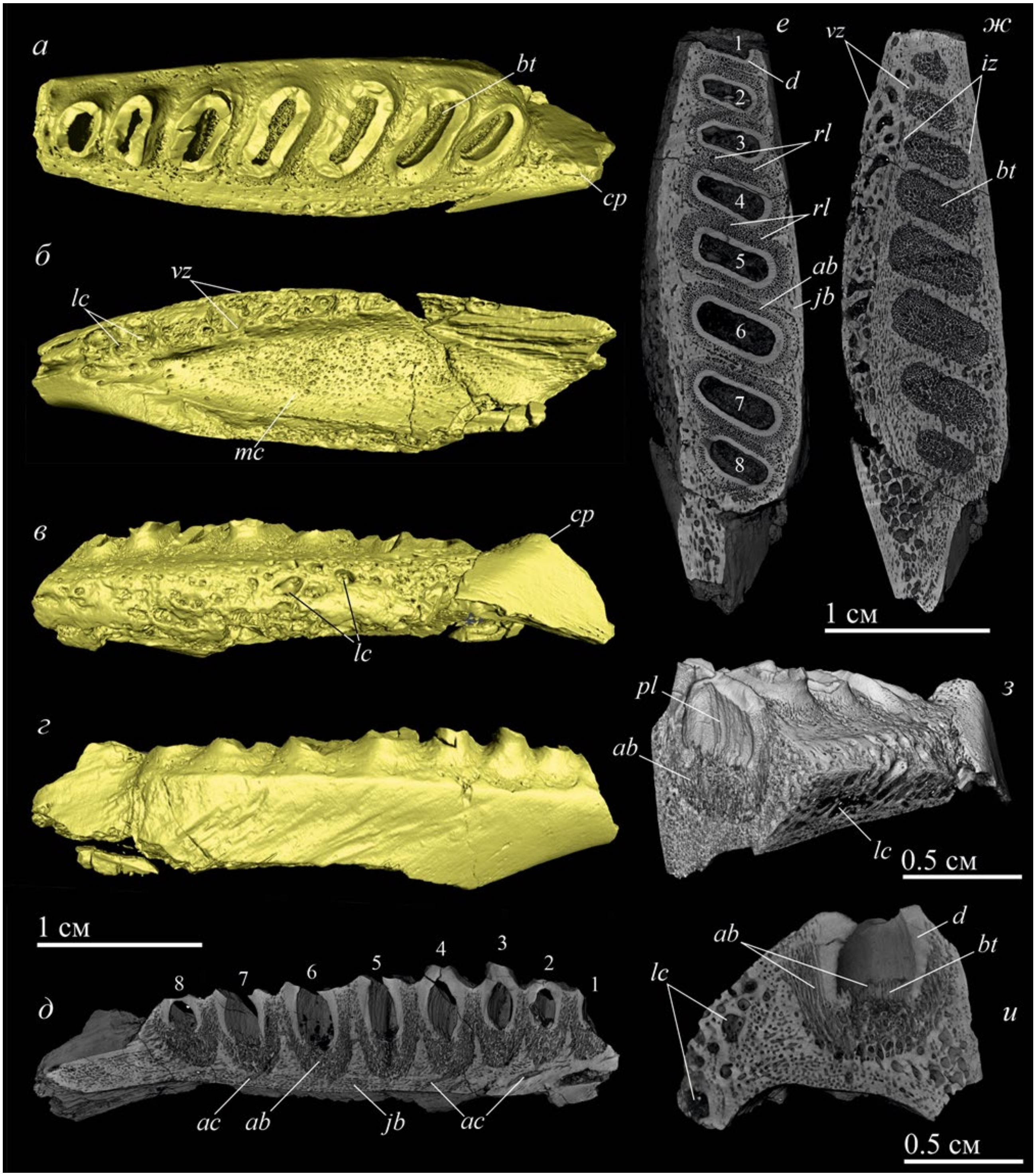
Fig. 1. Permotriturus herrei Tatarinov, holotype PIN, No. 157/500, left dentale: *a–d* – CT reconstruction from above, below, laterally and medially, respectively; *e* – longitudinal vertical section of the CT model (virtual) at the level of the middle width of the teeth; *f, g* – horizontal virtual sections slightly below the alveolar margin and below the end of the root part of the teeth, respectively; *h* – virtual sections (vertical along the longitudinal axis of the sixth alveolus from the end and inclined through the lateral zone of vascularization); *i* – vertical transverse virtual section through the fifth alveolus from the end; Russia, Republic of Tatarstan, Isheevo locality; Middle Permian, Urzhumian stage. Designations: *ab* – alveolar bone tissue, *ac* – basal alveolar vessels, *bt* – basal trabeculae of alveolar bone tissue, *cp* – coronoid process, *d* – dentine wall of tooth root, *iz* – zone of tooth implantation, *jb* – jaw bone tissue, *lc* – intramural lacunae, *mc* – Meckelian cartilage groove, *pl* – folding of the inner surface of the dentine wall of the root, *rl* – boundary of overlapping implantation zones of adjacent teeth, *vz* – zone of intensive vascularization.

Fig. 2. Permotriturus herrei, spec. KFU, No. B 823/54, left maxillare: *a–d* , *and* – CT-reconstruction ventrally, laterally, dorsally, medially and caudally, respectively; *e* – longitudinal vertical section of

the CT model (virtual) at the level of the middle width of the teeth; *f, g* – horizontal virtual sections at the level of the alveolar margin and basal part of the tooth roots, respectively; *h, j* – virtual cross-sections through the alveolus of the last and penultimate maxillary teeth; Russia, Republic of Tatarstan, Isheevo locality; Middle Permian, Urzhumian stage. Designations: *flEct* – attachment site of ectopterygoideum; *lfa* and *flp* – anterior and posterior parts of the lateral contact surface, respectively; *pl* – folding of the wall of the root part of the tooth in its basal part; others as in Fig. 1. Numbers indicate tooth positions, starting from the first preserved alveolus.

Fig. 3. Implantation depth of buccal teeth in Middle Permian bolosaurids of Eastern Europe (vertical CT sections along the longitudinal axis of the crown): *a* – penultimate (tenth) maxillary tooth of the holotype of Belebey shumovi (spec. PIN, No. 4312/4); *b* – maxillary tooth from the middle part of the buccal series of the holotype of B. vegrandis (spec. PIN, No. 164/50); *c* – mandibular tooth from the middle part of the buccal series of the holotype of B. maximi (spec. SGU, No. 104B/2027). Designations: *d* – dentine, *ab* – alveolar bone tissue, *jb* – jaw bone tissue, *rf* – resorption foramen associated with the immersion of the replacement tooth primordium inside the alveolus, *rpt* – intra-alveolar forming crown of the replacement tooth.

Fig. 4. Reconstruction of the relationship between skull roof elements in the suborbital region of various representatives of Bolosaurida: *a* – Belebey vegrandis (based on spec. SGU, No. 104B/2021), *b* – Bolosaurus striatus (after: Watson, 1954, with modifications), *c* – Permotriturus herrei (based on holotype PIN, No. 157/500). Designations: *J* – jugale, *L* – lacrimale, *Mx* – maxillare, *Qj* – quadratojugale.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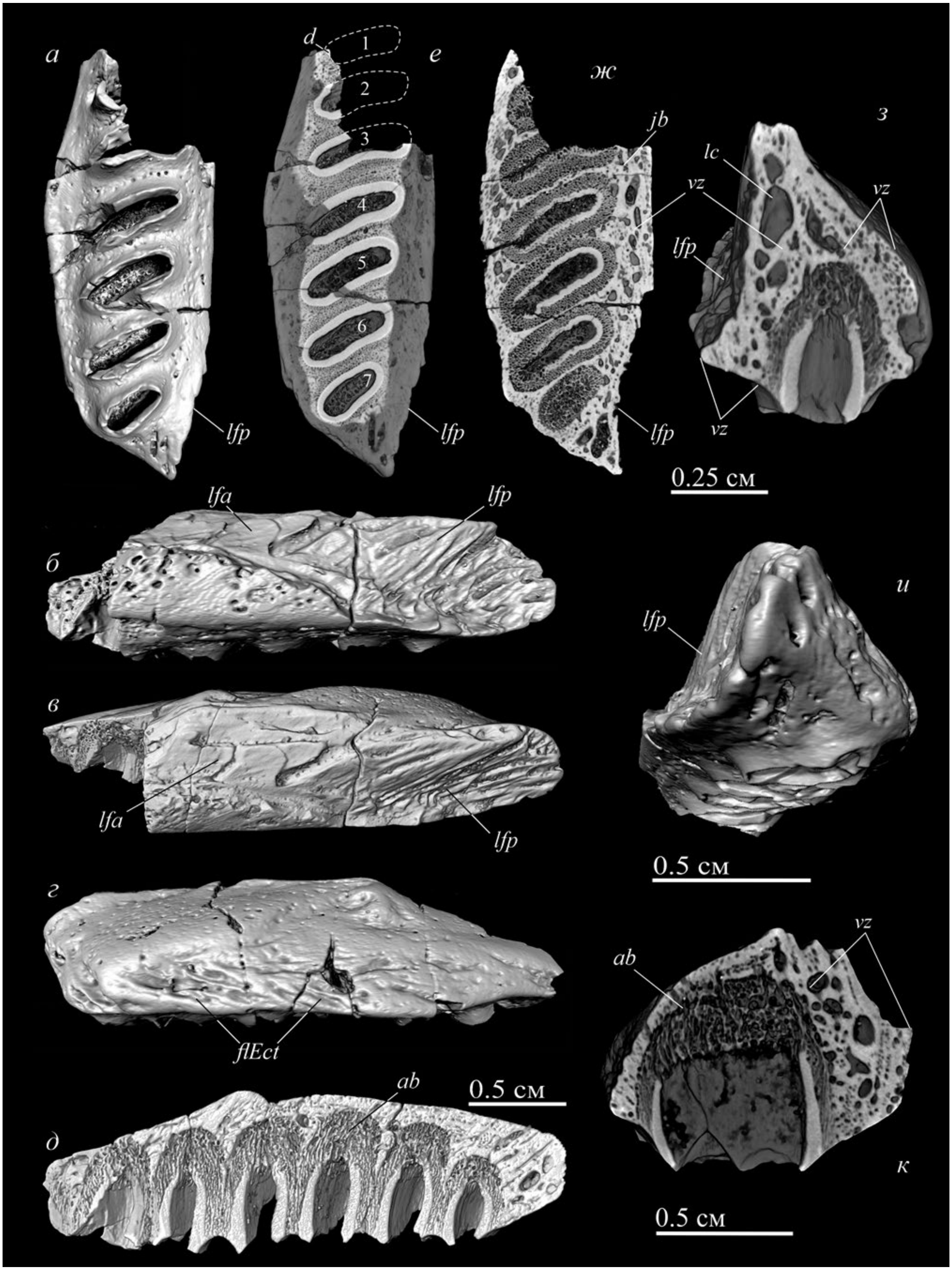
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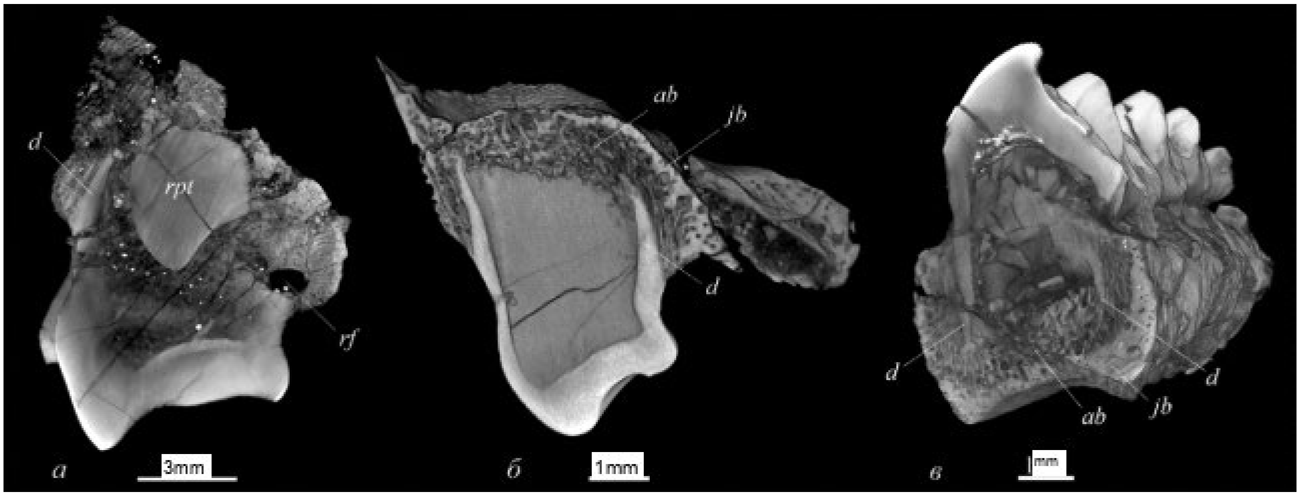
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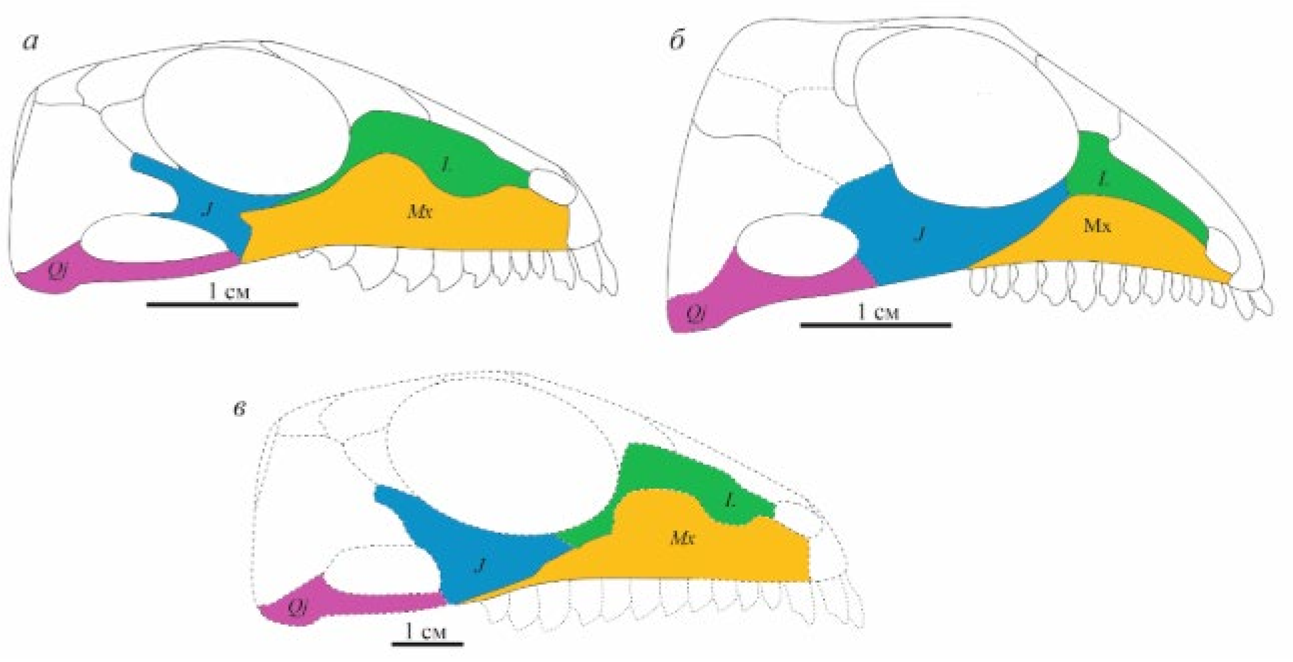
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Fig. 4