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New Data on Late Jurassic Ichthyosaurs of the Genus *Grendelius* from European Russia

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Abstract—Many ichthyosaur researchers consider the Late Jurassic genera *Grendelius* and *Brachypterygius* synonymous, but do not take into account species of the genus *Otschevia* (synonym of *Grendelius*) described from Russia, which is partly due to their brief initial descriptions. We provide a detailed description and photographs of the bones of *Grendelius pseudoscythicus* and *Grendelius zhuravlevi* holotypes and compare them with the other species of the genus; several new specimens belonging to the genus *Grendelius* from European Russia are also described. *Grendelius pseudoscythicus* and *G. zhuravlevi* differ from each other and from the other species of the genus in the morphology of some cranial bones (quadrate and stapes), pectoral girdle, and forelimbs, and they should be considered as valid species. Therefore, at least three species of the genus *Grendelius* were present in the Middle Russian Sea in the Middle Volgian. Some of the new specimens described in this paper differ from the known species, which suggests the presence of other species of the genus *Grendelius* in European Russia. Based on the available data, there is still insufficient evidence for synonymy between the genera *Brachypterygius* and *Grendelius*.

Keywords: *Brachypterygius*, *Grendelius*, *Otschevia*, Jurassic, Middle Volgian, Volga Region

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INTRODUCTION

One of the most controversial problems in the taxonomy of Late Jurassic ichthyosaurs is the case of phylogenetic relationships and the taxonomic status of several forms in which the intermedium wedges between the radius and ulna and contacts the humerus. Prior to the discussion of this problem, it seems necessary to outline its history. In 1976, McGowan described a new genus and species of ichthyosaur from the Upper Kimmeridge Clay (Upper Jurassic, Lower Volgian Substage) of Norfolk (East of England), *Grendelius mordax* McGowan, 1976, characterized by a proportionally small orbit, a robust rostrum, and large teeth. The holotype of *Grendelius mordax* and the only specimen of this species known at that time (CAMSM J 68516) is represented by an almost complete left part of the skull and a few isolated cranial and postcranial elements, some of which were not described or depicted by McGowan, since he did not consider them taxonomically informative (McGowan, 1976). Twenty years later, McGowan reported on a new specimen, BRSMG Ce 16696, which represented an almost complete skeleton from the Kimmeridge Clay of Dorset on the south coast of England (McGowan, 1997). In his brief communication on this specimen, he provided only a drawing of its forelimb, which was partially prepared by that time. McGowan preliminarily interpreted it as the right forelimb, exposed dorsally, which made an impression of its significant similarity to the forelimb of another ichthyosaur from the English Kimmeridge Clay, *Brachypterygius extremus* (Boulenger, 1904). This taxon also has a contact between the intermedium and humerus but was previously known exclusively from descriptions of forelimb bones (Delair, 1960, 1986). Based mainly on the presence of contact between the intermedium and humerus in specimen BRSMG Ce 16696 and *Brachypterygius extremus*, as well as on the similarity of the skull of BRSMG Ce 16696 with the skull of the holotype of *G. mordax* (CAMSM J 68516), McGowan proposed the genera *Brachypterygius* and *Grendelius* to be considered synonymous. However, he did not provide any detailed description and images of the specimen BRSMG Ce 16696 confirming this conclusion.

In 1998, two ichthyosaur taxa characterized by contact between the intermedium and humerus were described from the Volgian Stage of European Russia. The papers were published one after another in the second issue of the Paleontological Journal. In the first article, V.M. Efimov described a new genus and species, *Otschevia pseudoscythica*, from the Lower Volgian Substage of the Ulyanovsk Region (Efimov, 1998). In the second article, M.S. Arkhangelsky described a new species of the genus *Brachypterygius*, *B. zhuravlevi,* from the Middle Volgian Substage of the Saratov Region (Arkhangelsky, 1998). Both taxa are represented by incomplete skeletons, including skull fragments, vertebrae, elements of pectoral girdles, and forelimbs. However, Arkhangelsky believed that the cranial remains of the specimen that he studied included fragments of the lower jaws rather than fragments of the upper and lower jaws, which implied that they belonged to at least two individuals (this is not confirmed by new observations of the authors of this study and by the original numbering of the bones performed by K.I. Zhuravlev (no. 2847 on all elements), as well as by the fact that this specimen is mentioned in his work (Zhuravlev, 1943) as a single skeleton that was found in mine no. 1 in 1934). Therefore, only elements of the forelimb, in which the humerus bears a distal facet for the intermedium (which was considered a unique feature of *Brachypterygius* at that time), were chosen as the holotype of the new species (Arkhangelsky, 1998). In the article of Efimov, attention was focused on the distal contact of the intermedium with one distal carpal ("longipinnate" type), which many researchers of the 20th century considered a taxonomically important "high-rank" character (e.g., Huene, 1922; McGowan, 1972; Appleby, 1979). Therefore, he compared the new taxon only with other "longipinnate" ichthyosaurs ("*Leptopterygius*", *Temnodontosaurus*, *Stenopterygius*, *Platypterygius*, and *Plutoniosaurus*), even though he noted that "a similar feature of the intermedium was previously recorded (Huene, 1956) only for the genus *Brachypterygius* from the Kimmeridgian of Northern (sic!) England, which, however, belongs to latipinnate superfamily" (Efimov, 1998, p. 82; translation from the original Russian version, as the published English translation is imprecise). Efimov did not provide any description or comparison for the bones of the skull of the new taxon.

Two years later, Arkhangelsky (2000) described a new specimen of *B. zhuravlevi* based on an incomplete skeleton from the Middle Volgian of the Kashpir Shale Mine in the Samara Region. Based on the single distal facet of the intermedium, he assigned this species to Efimov's genus *Otschevia*. In 2001, Arkhangelsky described the third species within the genus *Otschevia*, *O. alekseevi*, based on a fairly complete skeleton from the Middle Volgian of the Ulyanovsk Region (Arkhangelsky, 2001). It is important to note that this article hypothesized that the genus *Caypullisaurus* Fernández, 1997 from the Tithonian of Argentina also has contact between the intermedium and humerus and was probably similar to the genus *Otschevia*. However, until recently, this assumption was not taken into account by other researchers.

In revisions published in the early 2000s, western researchers were rather categorical about the validity of many taxa from Russia. Maisch and Matzke (2000) supported the synonymy of *Brachypterygius* and *Grendelius* proposed by McGowan (1997); at the same time, they retained the type species of these taxa as valid. In addition, according to their opinion on the taxa described from Russia, the species *Otschevia zhuravlevi* and *O. pseudoscythica* are synonymous; based on "the presence of a middle facet for the intermedium on the humerus, the diagnostic autapomorphy of *Brachypterygius*" (Maisch and Matzke, 2000, pp. 87–88), they proposed a new combination *Brachypterygius pseudoscythius* (sic!). In another major review on ichthyosaurs, published three years later, McGowan and Motani (2003) proposed that all species described within the genera *Brachypterygius*, *Grendelius*, and *Otschevia* be considered synonyms of *Brachypterygus extremus*. They considered all the observed differences insufficient for species differentiation (including different configurations of mesopodial elements and different number of digits in the forelimb: six in *B. extremus* vs. five in all known specimens of *Grendelius* and *Otschevia,* for which fairly complete limbs were preserved). At the same time, *Otschevia alekseevi* was not considered in their study. The opinion advanced by McGowan and Motani (2003) was subsequently used in most publications on ichthyosaurs. Maisch (2010) was the only one who continued to consider *Brachypterygius extremus* and *B. mordax* as separate valid species and also considered the Russian species *B. pseudoscythicus* and *B. alekseevi* as valid but assigned all of them to the genus *Brachypterygius*.

In 2015, the authors of this work redescribed the holotype of *Otschevia alekseevi* and a referred specimen of *Otschevia zhuravlevi* (Zverkov et al., 2015). Based on a high similarity of cranial elements between *Otschevia alekseevi* and *Grendelius mordax,* it was suggested that the genera *Otschevia* and *Grendelius* are synonymous; however, taking into account the differences in the structure of the forelimbs of *Otschevia* spp. and *Brachypterygius extremus,* it was proposed to consider these taxa separately. It was also noted that the limb of the second specimen of *G. mordax* (BRSMG Ce 16696) was misinterpreted by McGowan (the upper and lower, as well as anterior and posterior sides, were misidentified) and that the structure of limb of this specimen in the new interpretation is more similar to that of *Otschevia* than *Brachypterygius*. These opinions (Zverkov et al., 2015) were not supported by other researchers and are currently used mainly in publications by Zverkov et al. (Zverkov and Efimov, 2019a; Zverkov and Prilepskaya, 2019b;

Zverkov and Grigoriev, 2020; Zverkov and Jacobs, 2021).

In 2018, during the revision of ichthyosaurs from the Kimmeridge Clay of England, Moon and Kirton (2018) attempted to assert the "conservative" opinion of McGowan and Motani (2003). All specimens from the Kimmeridge Clay of England, in which the humerus bears a facet for the intermedium, or the elements of the skull are more similar to *Grendelius mordax* than to *Ophthalmosaurus icenicus*, were attributed by these authors to *Brachypterygius extremus*. This led to the concept that most of the specimens from the Kimmeridge Clay of England were determined as *B. extremus* or unidentifiable ophthalmosaurids, excepting the holotype of *Nannopterygius enthekiodon* and three isolated humeri assigned to the dubious genus *Macropterygius* (see the comment in Zverkov and Jacobs, 2021). The *Brachypterygius* concept presented by Moon and Kirton (2018) is now accepted by many researchers (Campos et al., 2021; Cortés et al., 2021; Barrientos-Lara and Alvarado-Ortega, 2021; Fernández et al., 2021) and the consequences of the above-mentioned taxonomic controversies so far become increasingly significant. Thus, in 2021, Mexican researchers identified another genus and species of ichthyosaurs with contact between the intermedium and humerus, namely, *Parrassaurus yacahuitztli* (Barrientos-Lara and Alvarado-Ortega, 2021). At the same time, the existing controversies in the taxonomy of forms characterized by this feature were not discussed and most of the species from Russia were not taken into account during the comparison and phylogenetic analysis presented in that paper. This can be partly explained by the scarcity of published data on the type species of the genus *Otschevia*, *Otschevia pseudoscythica* Efimov, 1998, which are available only from a very brief original description (Efimov, 1998). This is also due to the incomplete description of *Otschevia zhuravlevi* (Arkhangelsky, 1998), as the descriptions of its skull, pectoral girdle, and axial skeleton have not yet been published. All of this motivated the preparation of the present paper, the purpose of which is to describe in detail the holotypes of "*Otschevia*" *pseudoscythica* and "*Brachypterygius*" *zhuravlevi* and to discuss their significance for understanding the taxonomy and species diversity of Late Jurassic ichthyosaurs with intermedium—humerus contact.

Institutional abbreviations: BRSMG, Bristol Museum and Art Gallery, Bristol, United Kingdom; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, United Kingdom; GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SGM, Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; SKM, Local Lore Museum of the city district of Syzran; SRM, Saratov Regional Museum of Local Lore, Saratov, Russia; UPM, Undory Palaeontological Museum, Undory, Ulyanovsk Region, Russia; YKM, Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov, Ulyanovsk, Russia.

SYSTEMATIC PALEONTOLOGY

Order Ichthyosauria De Blainville, 1835

Group without rank, Ophthalmosauria Motani, 1999

Family Platypterygiidae Bardet, 1995

***Grendelius pseudoscythicus* (Efimov, 1998)**

Plate 15

Otschevia pseudoscythica: Efimov, 1998, p. 83, Figs. 1–4; Motani, 1999a, p. 485; Pervushov, Arkhangelsky, and Ivanov, 1999, p. 26; Storrs, Arkhangel'skii, and Efimov, 2000, p. 202; Arkhangelsky, 2001, p. 69, text-fig. 4; 2008, p. 252, text-fig. 5.

Brachypterygius pseudoscythius [sic]: Maisch, Matzke, 2000, p. 79 (*pars*); Maisch, 2010, p. 167 (*pars*).

Brachypterygius extremus: McGowan and Motani, 2003, p. 117; Moon and Kirton, 2018, p. 86 [*pars*].

Grendelius pseudoscythicus: Zverkov, Arkhangelsky, and Stenshin, 2015, p. 561, fig. 18D.

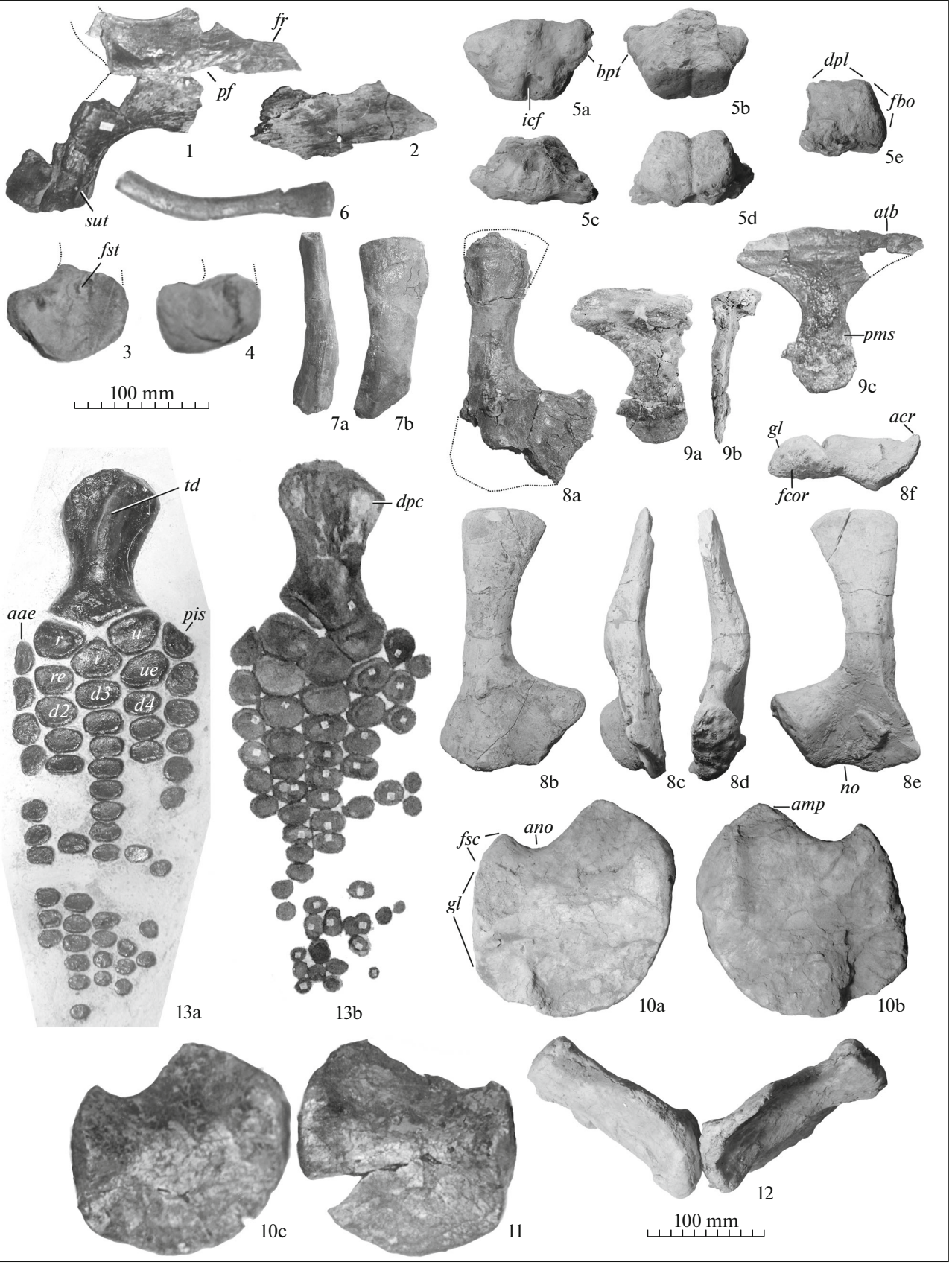
Holotype. Undory Paleontological Museum (Undory, Ulyanovsk Region, Russia), UPM, no. 3/100, incomplete skeleton, including fragments of the roof and occipital part of the skull, pectoral girdle, forelimbs, and incomplete vertebral column; Ulyanovsk Region, Ulyanovsk District, right bank of the Volga River, 8 km east of the village of Novaya Bedenga ("Detskiy sanatorium"); Upper Jurassic, Volgian Stage, Middle Substage, lower part of the *D. panderi* Zone; Efimov, 1998, text-figs. 1–4.

Diagnosis. The species is characterized by the following combination of features: quadrate with an anteroposteriorly expanded ventral part and without angular process; scapula with a strongly fan-shaped proximal part and a glenoid markedly protruding backwards from the main axis; notch on the proximal margin of the scapula; extensive anterolateral coracoid notch and moderately well-developed anteromedial process; humerus with slender diaphysis; narrow humeral facet for the intermedium; dorsally oval autopodial elements; absence of centralia distal to the intermedium.

Description. In addition to the description published in the work of Efimov (1998), there are the following new observations.

Skull. Judging from the available photograph, the parietals of the holotype had anteroposteriorly extended medial symphysis and strong, wide posterolateral processes for the supratemporal (Pl. 15, fig. 1). Although this cannot be unambiguously stated from the dorsal projection on the photograph, there are no obvious contradictions to the statement of Efimov (1998) that the sagittal crest was not developed. The parietal foramen is at the junction of the parietal and frontal and has a small size and a rhombic outline (Pl. 15, fig. 1).

Plate 15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Quadrates are characterized by anteroposteriorly wide ventral parts with posteroventrally facing condyles. Judging from the preserved part, the quadrate foramen was extensive: its anterior notch is deep, in contrast to *G. zhuravlevi* (see the description below). The anteromedial protrusion of the quadrate is not clearly defined; the ventral margin gradually curves, turning into the vertical anterior margin of the element (Pl. 15, figs. 3, 4). The bosses of the articular condyle are unevenly developed: the boss for the articular is better pronounced and shifted to the ventral position relative to the boss for the surangular (Pl. 15, fig. 4).

The basisphenoid has a structure typical for the representatives of the genus: pentagonal in ventral view and trapezoidal in lateral view (Pl. 15, fig. 5). In the anterior part, it reaches the greatest mediolateral width owing to laterally widely spaced basipterygoid processes. It narrows noticeably in the posterior part. Facet of the basipterygoid process for the pterygoid faces posterolaterally. The facet for the basioccipital has a pentagonal outline and is strongly shifted to the posterior plane, so that no additional free surface is formed between it and the ventral surface of the element. The dorsal surface of the element is occupied by an extensive dorsal plateau (Pl. 15, fig. 5b). The anterior surface of the basisphenoid is high and vertical, forming the dorsum sellae. In the center, it is pierced by a large rounded foramen for the internal carotid arteries. There are triangular depressions with an irregular surface (trabecular cartilage traces) ventrolaterally to both sides of this foramen (Pl. 15, fig. 5c). Facets for contact with the medial flange of the posterior pterygoid rami are shallow on the ventral side of the element (Pl. 15, fig. 5a). The posterior foramen for the internal carotid arteries is between the facets for the pterygoids and connected to the posterior margin of the element by a groove. It is located closer to the posterior margin of the element in the described species than in other species of the genus.

The hyoid is a long, curved rod-like element widening at one of the ends (Pl. 15, fig. 6).

Pectoral girdle. The scapula is characterized by a strongly fan-shaped proximal end, and a long dorsal ramus with a narrow diaphysis and a widened spatulate distal end (Pl. 15, figs. 7, 8). The axial part of the dorsal ramus of the scapula has a rounded cross-section in the middle and becomes wide and mediolaterally flat at the distal end. The acromial process is separated from the glenoid part of the scapula by a weakly pronounced notch (Pl. 15, figs. 8e, 8f). The posterior margin of the scapula, which forms the anterior part of the glenoid, is strongly widened and projects backwards from the main axis of the element (Pl. 15, figs. 8a, 8b). Coracoid and glenoid facets are poorly demarcated. The coracoid facet has a triangular shape and smoothly turns into the semicircular glenoid facet.

Coracoids are rounded in dorsal view. Anteromedial processes are small; however, they are better developed than those in the type species (NGZ pers. obs. on CAMSM J 68516, November 2018). Anterolateral notches are extensive. The lateral facet for the scapula and glenoid surface are poorly demarcated (Pl. 15, fig. 10). The medial symphysis is thickened and lenticular in outline and has no sharp protrusions. The angle between the articulated coracoids is 120° (Pl. 15, fig. 12).

The interclavicle is a wide, robust T-shaped element. Lateral rami of the anterior part are straight (Pl. 15, fig. 9). The posteromedial process is widened along its entire length, reaching its maximum width in the distal part (Pl. 15, fig. 9). The ventral knob is less pronounced than that in *G. alekseevi*.

Forelimb. Unfortunately, neither the preserved cast, nor the photographs (Pl. 15, fig. 13), nor the drawings in the original publication (and in the thesis of Efimov (1997)) make it possible to determine the exact shape of the proximal end of the humerus. It can only be stated that it was dorsoventrally wider than that of *G. zhuravlevi*. The distal facet of the humerus for the intermedium is very narrow and less pronounced than that in other species of the genus. The intermedium is in contact with five elements and distally bears one facet for the distal carpal three. There

Explanation of Plate 15

Figs. 1–13. *Grendelius pseudoscythicus* (Efimov, 1998) UPM EP-3/100, holotype; elements of the skull, pectoral girdle and forelimbs; Ulyanovsk Region, Ulyanovsk District, Volga River near the village of Novaya Beden'ga; Middle Volgian, *Dorsoplanites panderi* Zone: (1) parietals in articulation with the left frontal and right supratemporal, dorsal view; (2) partial ?pterygoid; (3) left quadrate posteromedially; (4) right quadrate anterolaterally; (5) parabasisphenoid (cast), (5a) ventral view, (5b) dorsal view, (5c) anterior view, (5d) posterior view, and lateral view (5e); (6) hyoid; (7) dorsal ramus of the left scapula (7a) anterior view and (7b) lateral view; (8) right scapula as currently preserved (8a) and its cast (8b–8f): (8a, 8b) dorsomedial view, (8c) anterior view, (8d) posterior view, (8e) lateroventral view and (8f) proximal view; (9) interclavicle, (9a) ventral view, (9b) lateral view, and (9c) ventral view (archive photograph); (10) right coracoid, (10a) ventral view and (10b) dorsal view of the cast, (10c) ventral view (archive photograph); (11) left coracoid, ventral view (archive photograph); (12) articulated coracoids (casts), anterior view; (13) left forelimb, (13a) dorsal view (cast) and (13b) ventral view (archive photograph). Abbreviations: (*aae*) anterior accessory epipodial element, (*amp*) anteromedial process, (*atb*) anterior transverse bar, (*bpt*) basipterygoid process, (*d2–d4*) distal carpals, (*dpc*) deltopectoral crest, (*dpl*) dorsal plateau, (*fbo*) facet for basioccipital, (*fcor*) facet for coracoid, (*fsc*) facet for scapula, (*fr*) frontal, (*fst*) facet for stapes, (*gl*) glenoid contribution, (*i*) intermedium, (*icf*) foramen for internal carotid arteries, (*no*) notch, (*pf*) parietal foramen, (*pis*) pisiform, (*pms*) posterior median stem, (*r*) radius, (*re*) radiale, (*sut*) supratemporal, (*td*) dorsal process, (*u*) ulna, (*ue*) ulnare. Scale bars are given separately for figs. 1–6 and figs. 7–13; figs. 1–4, 6, 9c, 10c, 11, 13b, photographs from V.M. Efimov's personal archive.

are no centralia in the limb. The epipodial and autopodial elements are characterized by a rounded outline and are loosely spaced in the limb (Pl. 15, fig. 13).

Dimensions. See Efimov (1998).

Comparison. See the corresponding section in the description of *G. zhuravlevi* below.

Remarks. Most of the bones of the holotype are either destroyed or severely damaged by pyrite decay. Archival photographs by V.M. Efimov and casts from some elements of the skeleton (the basisphenoid, coracoids, scapula, and forelimb) are preserved. One of the authors (N.G. Zverkov) had the opportunity to study the remains of the type material casts during his visit to the UPM in 2016. Unfortunately, after the change of the management of UPM in 2017, this specimen disappeared from the collections of the museum and, apparently, is currently deposited in the private collection of V.M. Efimov, former director of UPM.

In the type locality, the bank outcrops of the Volga River near the "Detskiy sanatorium" (3 km east of the village of Novaya Bedenga) expose the deposits of the Middle and Upper substages of the Volgian Stage. The modern knowledge of the stratigraphy of the Lower and Middle Volgian substages in this area (Rogov, 2013) suggest that the Lower Volgian deposits near the "Detskiy sanatorium" are below the water level. Therefore, the holotype of *Grendelius pseudoscythicus* (specimen UPM 3/100) comes from the lower part of the *Dorsoplanites panderi* Zone. The most basal beds exposed at low water in this locality are marls similar to those from the upper part of the first member of the Gorodischi section (personal observations by N.G. Zverkov and M.A. Rogov in 2015 and I.M. Stenshin in 2018–2020). Apparently, specimen UPM 3/100 comes from an interbed of gray clays (bed 1/3 according to Rogov (2013)), separating marl beds. Efimov attributed the bed with the skeleton to the Lower Volgian Substage, *Ilowaiskya pseudoscythica* Zone, based on lithology rather than ammonite data; therefore, his decision to fix the name of the ammonite Zone (*Ilowaiskia pseudoscythica*) in the name of the ichthyosaur species does not seem to be appropriate in the light of the above.

Distribution. The species is known only from the type locality. Upper Jurassic, Volgian Stage, Middle Substage, lower part of the *D. panderi* Zone; European Russia, Ulyanovsk Region, Ulyanovsk District.

Material. Holotype and casts from it.

Grendelius zhuravlevi (Arkhangelsky, 1998)

Plates 16–19

Brachypterygius zhuravlevi: Arkhangelsky, 1998, p. 90, text-fig. 4; Motani, 1999a, p. 485.

Otschevia zhuravlevi: Pervushov, Arkhangelsky, and Ivanov, 1999, p. 27, text-figs. 14, 15; Arkhangelsky, 2000, p. 79, text-figs. 1, 2; Arkhangelsky, 2008, p. 252, text-fig. 6.

Brachypterygius pseudoscythius [sic]: Maisch and Matzke, 2000, p. 79 (*pars*); Maisch, 2010, p. 167 (*pars*).

Brachypterygius extremus: McGowan and Motani, 2003, p. 117(pars.); Moon and Kirton, 2018, p. 86 (pars.).

Grendelius zhuravlevi: Zverkov, Arkhangelsky, and Stenshin, 2015, p. 572, figs 10–12, 18E.

Holotype. PIN 426/60-76; left humerus with epipodial and autopodial elements; Saratov Region, Krasnopartizansky District, Gorny village, Savel'evskii Shale Mine; Upper Jurassic, Volgian Stage, Middle Substage, *Dorsoplanites panderi* Zone; Arkhangelsky, 1998, p. 90, text-fig. 4.

Diagnosis. The species is characterized by the following unique characters and their combination: ventral part of the quadrate significantly shortened anteroposteriorly, so that the space between the posterior margin of the articular condyle and the stapedial facet is equal to or slightly greater than the diameter of the stapedial facet (autapomorphy); articular condyle of the quadrate directed posterolaterally and poorly visible in ventral view; lateral process of the stapes moderately thickened; proximal end of the humerus strongly elongated anteroposteriorly and flattened dorsoventrally; well-developed protruding tubercles for muscle attachment on the dorsal and ventral surfaces of the humerus at the ulnar facet edge; ulna trapezoidal in dorsal view and bearing a facet for the pisiform along its entire posterior margin; autopodial elements dorsoventrally thickened and polygonal, with distinct angles, and tightly packed in the limb; centralia distal to the intermedium in the forelimb absent.

Description. **Cranium and mandible.** The preserved remains of the upper jaw are from its middle part; it is represented by articulated fragments of the premaxillae, nasals, and maxillae (Pl. 16, figs. 2, 3). The maximum height of the premaxilla is 6 cm. The maxilla extends far anteriorly, albeit it is weakly pronounced in lateral view (Pl. 16, figs. 2, 3). The anterior margins of the nasals, visible in dorsal view, extend slightly further (by 4.5 cm on the left side and 1.8 cm on the right side) than the anterior margins of the maxillae (Pl. 16, figs. 2b, 3c).

Only a few fragments have been preserved from the skull roof; the most informative of these are articulated fragments of the frontal, parietal, prefrontal, posterior frontal, and nasal (Pl. 16, fig. 1). All these elements are tightly articulated, overlapping each other, and forming complex interdigitated sutures. Judging from the preserved fragments, the frontal was involved in the formation of the anterior margin of the supratemporal fenestra, thereby forming the lateral process. The postfrontal is slightly expanded in the anterior part and the prefrontal does not form the anterodorsal process.

The preserved right part of the supraoccipital is rather wide mediolaterally (Pl. 17, fig. 5). Traces of semicircular canals on its anterolateral margin are L-shaped (Pl. 17, fig. 5a).

Quadrates are characterized by ventral parts 88 mm wide, significantly narrowed in anteroposterior view (Pl. 17, figs. 5, 6). Apparently, the anterior margin of the quadrate foramen was shallow in the ventral part. The stapedial facet is extensive (36 mm in diameter) and deeply concave on the posteromedial side. It has a rounded outline and is located high, at the level of the upper margin of the ventral expansion of the quadrate. The anteroventral protrusion (angular protrusion) of the quadrate is well defined and separated from the condyle by a ventral notch (Pl. 17, figs. 6a, 6d, 7a). The condyle for articulation with the mandile has an oval outline and is directed posteromedially (Pl. 17, figs. 6, 7). Its height is 78 mm and width is 51 mm. Bosses for the articular and surangular are weakly demarcated by a shallow groove (Pl. 17, figs. 6d, 6e).

Only the basipterygoid process of the left side has been preserved from the parabasisphenoid. It protrudes less anterolaterally than basipterygoid processes in other species, and its long axis is oriented more vertically.

The opisthotic is massive, characterized by a shortened but posteriorly rather narrow paraoccipital process (Pl. 17, fig. 2b). A well-defined crest for attachment of the jaw muscles extends along it on the anterior side (Pl. 17, figs. 2a, 2c, 2f). The massive medial head of the element is divided into an extensive posteroventrally directed facet for the basioccipital and a smaller oval, ventrally directed facet for the stapes (Pl. 17, figs. 2b, 2e). Imprints of the semicircular canals of the inner ear on the medial side of the element are deeply immersed in the body of the opisthotic. The poor preservation of this area on both opisthotics does not make it possible to characterize the shape of the canals (Pl. 17, figs. 2d, 4b).

The stapes is characterized by a massive medial head and a strong lateral process for contact with the quadrate (Pl. 17, fig. 1). The mediolateral length of the element is 68 mm. The height of the medial head (45 mm) exceeds its width (37 mm); it has an oval outline (Pl. 17, fig. 1f). The medial head is divided into three facets: a large posterodistally directed facet for the basioccipital, a smaller anteromedially directed facet for the basisphenoid, and a dorsally directed facet for the opisthotic, having a semicircular outline (Pl. 17, fig. 1f). The facet for the opisthotic is divided by a deep canal for the facial nerve into two unequal areas (Pl. 17, fig. 1c). The distal part of the lateral process of the stapes curves anteroventrally and expands, thereby forming an oval facet for the quadrate (Pl. 17, fig. 1e). The hyoid process on the posterior side of the element is not developed (Pl. 17, figs. 1a, 13).

The preserved fragment of the mandible consists of articulated angular, surangular, prearticular, splenial, and dentary (Pl. 16, fig. 5). Its preserved length is 50 cm and height is 7 cm. The dentary has the maximum dorsoventral height of 56 mm, while its height in the broken anterior portion is 40 mm. The angular is externally overlapped by the dentary, not reaching the posterior margin of the mandibular symphysis (Pl. 16, fig. 5a). The splenial forms a significant part of the symphysis, extending forward for at least 25 cm (Pl. 16, fig. 5a), although its anterior margins have not been preserved together with the anterior part of the rostrum.

The preserved fragment of the surangular has a low and weakly pronounced paracoronoid process (Pl. 16, fig. 4), unlike that of the type species. The preglenoid process, located behind it, was apparently also less developed than that in the type species, although it is not completely preserved.

The articular is ovoid in medial view (Pl. 17, fig. 8b). Its dorsoventral height exceeds its anteroposterior length (68 × 65 mm). The lateral surface of the articular is flat, bearing a series of diagonal grooves and ridges; the medial surface is saddle-shaped (Pl. 17, fig. 8). The anterior surface of the bone (part of the glenoid fossa) is widened and inclined backwards and has teardrop-shaped outlines (Pl. 17, fig. 8c). The posterior margin of the element is round.

The dentition is similar to that in the type species and *G. pseudoscythicus* (Efimov, 1998; Moon and Kirton, 2018). The size and shape of the teeth varies in different parts of the jaws: in the middle part of the jaws, the teeth are rather large, up to 5 cm high apicobasally; crowns are conical and only slightly curved. The height of the largest fully preserved crown is 12 mm and its basal diameter is 10 mm (Fig. 1c); however, judging by the size of some fragments, there were larger crowns. Crowns are ornamented with numerous thin grooves that do not reach the apex, leaving it externally smooth (Fig. 1c); however, its magnified view shows that the surface of the crown apex is rough and covered with numerous small tubercles. At the base of the crown, a band of acellular cementum retains traces of plicidentine folds (Fig. 1a). The roots of the teeth have a subrectangular cross-section. Small teeth with low (5 mm high) unornamented crowns are preserved in the posterior part of the jaws; some of these crowns are strongly curved (Fig. 1e).

Vertebral column (Pl. 18). Twenty-six vertebral centra from all parts of the spinal column are preserved in PIN 426. With respect to their shape and the arrangement of rib facets, they do not significantly differ from other species of the genus *Grendelius* and from most Late Jurassic ophthalmosaurians. The only noticeable difference is the presence of laterally markedly projecting apophyses for rib articulation from the middle of the trunk region to the caudal region (Pl. 18, figs. 3a, 4a, 5a, 6a).

Pectoral girdle. The scapula is characterized by a strongly expanded proximal end and a narrow diaphysis (Pl. 19, fig. 8). The axial part of the dorsal ramus of the scapula is rod-shaped; it has a rounded cross-section in the proximal part, and flattens at the distal end (Pl. 19, fig. 8f). The well-developed acromial process

Plate 16

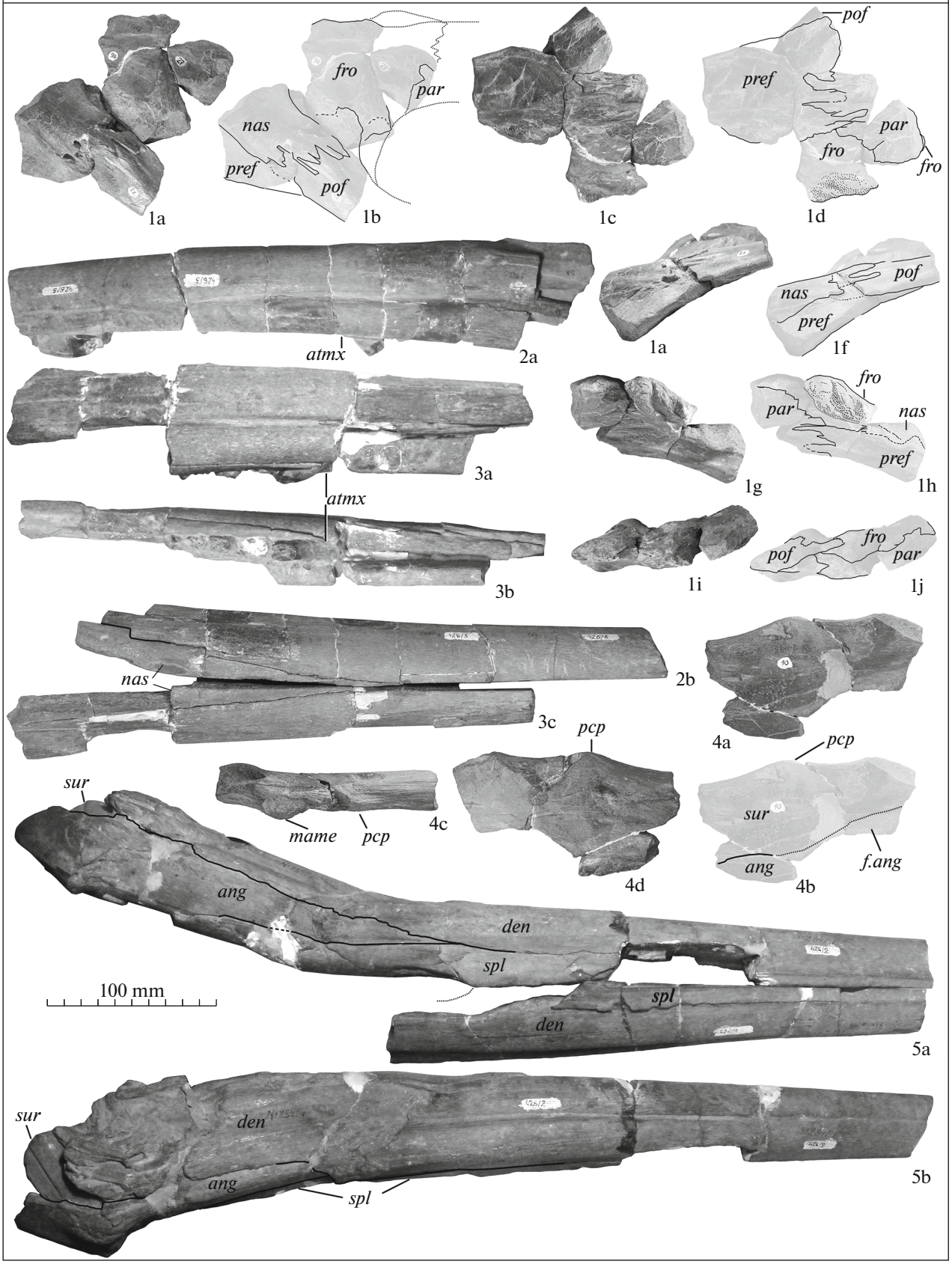
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Fig. 1. Teeth of *Grendelius zhuravlevi* PIN, no. 426: (a), (b) one of the biggest preserved tooth from the middle part of the jaw; (c) teeth with well-preserved tooth crowns; (d), (e) small teeth from the posterior parts of the jaws. Scale bar, 1 cm.

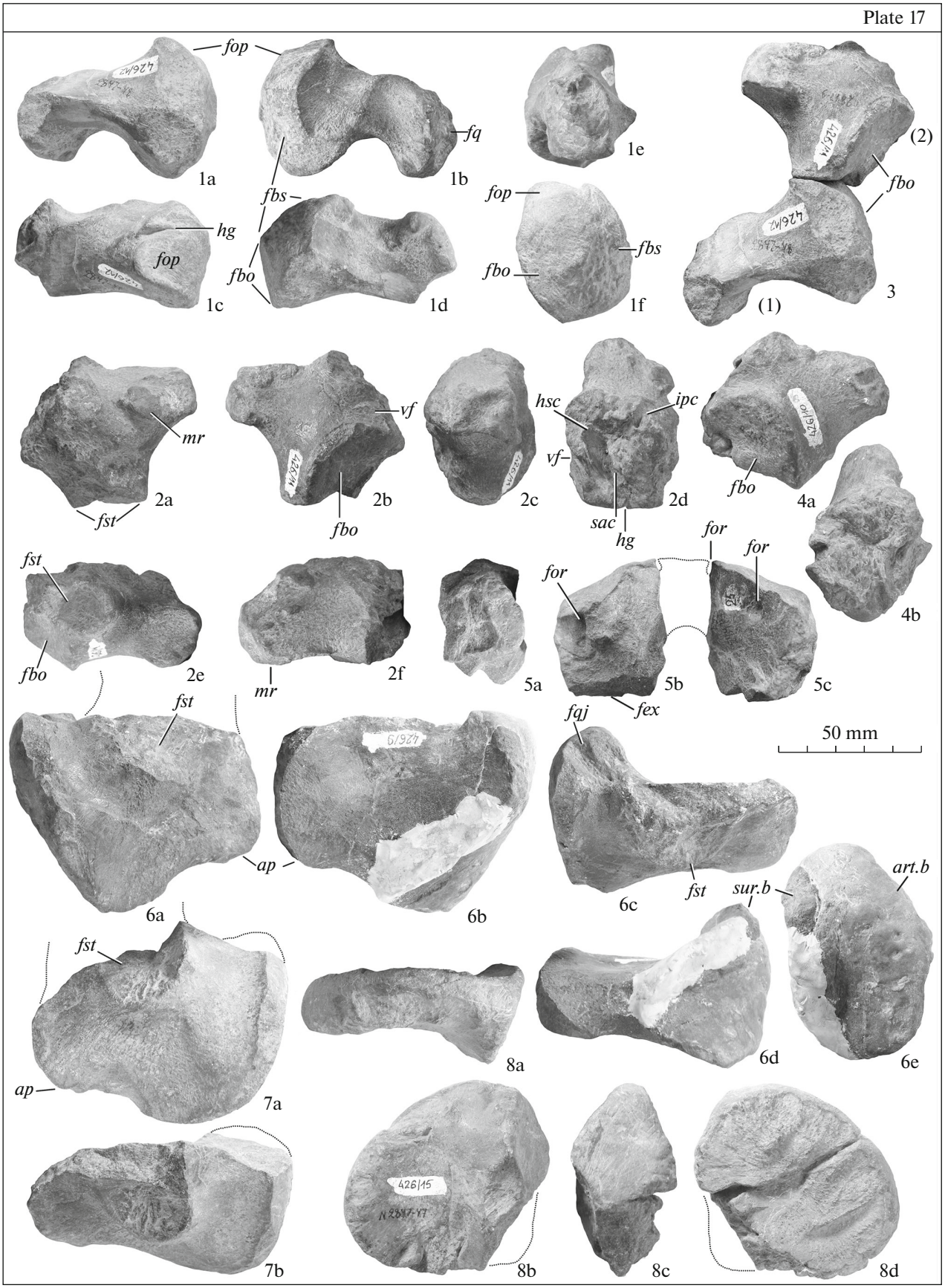
curves ventrally. It is separated from the glenoid portion of the scapula by an extensive notch of complete ossification (Pl. 19, figs. 8a, 8d, 8e). The posterior margin of the scapula, which bears facets for the coracoid and glenoid in its proximal part, is strongly widened and bent backwards from the main axis of the element (Pl. 19, figs. 8a, 8e). Coracoid and glenoid facets are of equal size. The coracoid facet is triangular in shape and turns into an extensive oval-shaped glenoid facet (Pl. 19, figs. 8c, 8d).

Several coracoid fragments are preserved, allowing the following observations: the medial articular surface is dorsoventrally wide and has a lenticular outline (Pl. 19, fig. 6b). Its dorsal and ventral margins are convex, the ventral margin being more convex and evenly curving without sharp projections. The anteroposterior length of the medial symphysis is 133 mm and dorsoventral thickness is 70 mm. The lateral surface is dorsoventrally thickened, but not as strongly as the medial one. Glenoid and scapular facets are poorly demarcated from each other. The scapular facet is smaller than the glenoid contribution. The anterior notch is relatively extensive and shallow (Pl. 19, fig. 7).

Explanation of Plate 16

Figs. 1–5. *Grendelius zhuravlevi* (Arkhangelsky, 1998), PIN, no. 426/1–4, 27; elements of the skull and mandible; Saratov Region, Krasnopartisansky District, Gorny village, Savel'evskii Shale Mine; Middle Volgian, *Dorsoplanites panderi* Zone: (1) fragment of the frontal part of the skull roof: (1a), (1b) dorsal view, (1c), (d) ventral view, (1e), (f) lateral view, (1g), (h) medial view and (1i), (j) posterior view; (2) fragment of the premaxilla in articulation with the maxilla and nasal of the left side: (2a) lateral view, (2b) dorsal view; (3) fragment of the premaxilla in articulation with the maxilla and nasal of the right side: (3a) lateral view, (3b) ventral view, (3c) dorsal view; (4) fragment of the posterior part of the left surangular: (4a), (4b) lateral view, (4c) dorsal view, (4d) medial view; (5) incomplete mandible: (5a) ventral view, (5b) lateral view. Abbreviations: (*ang*) angular, (*atmx*) anterior termination of the maxilla, (*f.ang*) facet for the angular, (*fro*) frontal, (*den*) dentary, (*mame*) process for the muscle (*M. adductor mandibulae externus*) attachment, (*nas*) nasal, (*par*) parietal, (*pcp*) paracoronoid process, (*pof*) postfrontal, (*pref*) prefrontal, (*spl*) splenial, (*sur*) surangular.

Plate 17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Forelimb. The humerus has a peculiar shape with an anteroposteriorly strongly elongated and dorsoventrally flattened proximal end and a dorsoventrally thickened distal end (Pl. 19, fig. 1). The dorsal process is plate-like and well developed, anterodistally extending from the posterior margin of the proximal end for a third of the proximodistal length of the bone (Pl. 19, fig. 1a). The deltopectoral crest is poorly developed; however, it is more pronounced in the holotype than in the referred specimen SRM Hb 30192 (Pl. 19, fig. 1b; Zverkov et al., 2015). The ventral surface of the bone is slightly concave. The humeral torsion is significantly pronounced: the long axes of the proximal and distal ends are at an angle of 70° in the holotype and 50° in SRM Hb 30192. The posterior margin of the humerus is distinctly dorsoventrally flattened along its entire length; however, it does not form a posterior keel (Pl. 19, fig. 1f). The proximal end of the humerus is strongly elongated anteroposteriorly and has a nearly lanceolate outline with a slightly concave, almost straight ventral edge and a convex anterodorsal edge (Pl. 19, fig. 1f). The diaphysis is rather narrow in dorsal view and has irregularly oval outlines with rounded anterior and posterior margins. The distal end is dorsoventrally thickened and bears three facets (Pl. 19, fig. 1g). Radial and ulnar facets have semicircular outlines; the facet for the intermedium, located between them, has parallelogram-like outlines. The facet for the intermedium is wider in specimen SRM Hb 30192 than in the holotype; the angle between the facets for the radius and ulna is 103° in the holotype and 130° in SRM Hb 30192. Tubercles for muscle attachment rise above the facet for the ulna on the dorsal and ventral sides (Pl. 19, figs. 1a, 1b, 1e).

The epipodium is formed by three elements: the radius, intermedium, and ulna. Only the radius is preserved in the holotype. It has irregularly pentagonal outlines; it contacted with the preaxial accessory element anterodistally, with the radiale distally, and with the intermedium along the posterior margin. The facet for the preaxial accessory element is separated from the humeral facet by a free surface without the formation of the cortical bone (Pl. 19, Fig. 1a). The elements of the epipodium are strongly expanded proximally in representatives of this species; their proximal surfaces are rugose and slightly convex. Elements of the autopodium have an irregularly hexagonal or rectangular shape in dorsal view, with clearly separated, distinct edges and well-defined angles between them, which indicates a tight arrangement of the elements in the limb in life. The dorsoventral thickness of the autopodial elements exceeds their proximodistal length in the middle part of the forelimb; elements of marginal digits are more dorsoventrally flattened (Pl. 19, figs. 2–5). Some elements of the autopodium bear small notches on the dorsal and ventral edges (Pl. 19, fig. 2).

The femur is characterized by a strongly developed ventral process (Pl. 19, figs. 9a, 9c). The dorsal process is located closer to the anterior margin of the bone; it is narrower and more pointed than the ventral process (Pl. 19, figs. 9a, 9b). The proximal end of the femur is irregularly triangular in outline (Pl. 19, fig. 9a). A more detailed description of the femur is given in previous publications of the authors for specimen SRM Hb 30192, in which it is completely preserved (Arkhangelsky, 2000; Zverkov et al., 2015).

Dimensions. See Arkhangelsky (1998, 2000) and Zverkov et al. (2015). The dimensions of the vertebral centra are given in Table 1.

Comparison. The species *G. zhuravlevi* and *G. pseudoscythicus* are most similar to each other in the shape and size of the pectoral girdle elements and humeri: the proximal end of the scapula in these species is widely fan-shaped (weakly expanded in *G. alekseevi,* but unknown for the type species); unlike *G. alekseevi*, *G. zhuravlevi* and *G. pseudoscythicus* have a notch at the proximal end of the scapula between the acromial process and coracoid facet; the anteromedial process of the coracoid is weak in these species and their anterior notch is extensive, as in the type species (narrow in *G. alekseevi*; Fig. 2). In *G. zhuravlevi* and *G. pseudoscythicus,* the diaphysis of the humerus is well defined and slender and its posterior margin does not form a keel, in contrast to the type species (specimen BRSMG Ce 16696) and *G. alekseevi*. The limbs of these species also have no centralia distally to the intermedium, which forms an extensive flat facet for the third distal carpal (while there are developed cen-

Explanation of Plate 17

Figs. 1–8. *Grendelius zhuravlevi* (Arkhangelsky, 1998) PIN, no. 426/8-13,15,25; occipital elements of the skull, and the articular; Saratov Region, Krasnopartisansky District, Gorny village, Savel'evskii Shale Mine; Middle Volgian, *Dorsoplanites panderi* Zone: (1) left stapes in (1a) posterior, (1b) anterior, (1c) dorsal, (1d) ventral, (1e) lateral, and (1f) medial views; (2) left opisthotic in (2a) posterior, (2b) anterior, (2c) lateral, (2d) medial, (2e) ventral, and (2f) dorsal views; (3) articulated stapes and opisthotic, posterior view; (4) right opisthotic in (4a) posterior and (4b) medial view; (5) supraoccipital (left portion) in (5a) anterolateral view, showing the impression of semicircular canals, (5b) posteriorly and (5c) anteriorly; (6) partial left quadrate in (6a) posteromedial, (6b) anterolateral, (6c) dorsal, (6d) ventral, and (6e) posteroventral views; (7) right quadrate in (7a) posteromedial, and (7b) dorsal views; (8) left articular in (8a) dorsal, (8b) medial, (8c) anterior, and (8d) lateral views. Abbreviations: (*ap*) anteroventral angular protrusion, (*art.b*) articular boss, (*fbo*) facet for basioccipital, (*fbs*) facet for basisphenoid, (*fq*) facet for quadrate, (*fst*) facet for stapes, (*fop*) facet for opisthotic, (*for*) foramen, (*hg*) groove for transmission of hyomandibular branch of facial (CN VII) or glossopharyngeal (CN XI) nerve, (*hsc*) impression of horizontal semicircular canal, (*ipc*) impression of posterior vertical semicircular canal, (*mr*) ridge for muscle attachment, (*sac*) impression of sacculus, (*sur.b*) surangular boss, (*vf*) vagus foramen border.

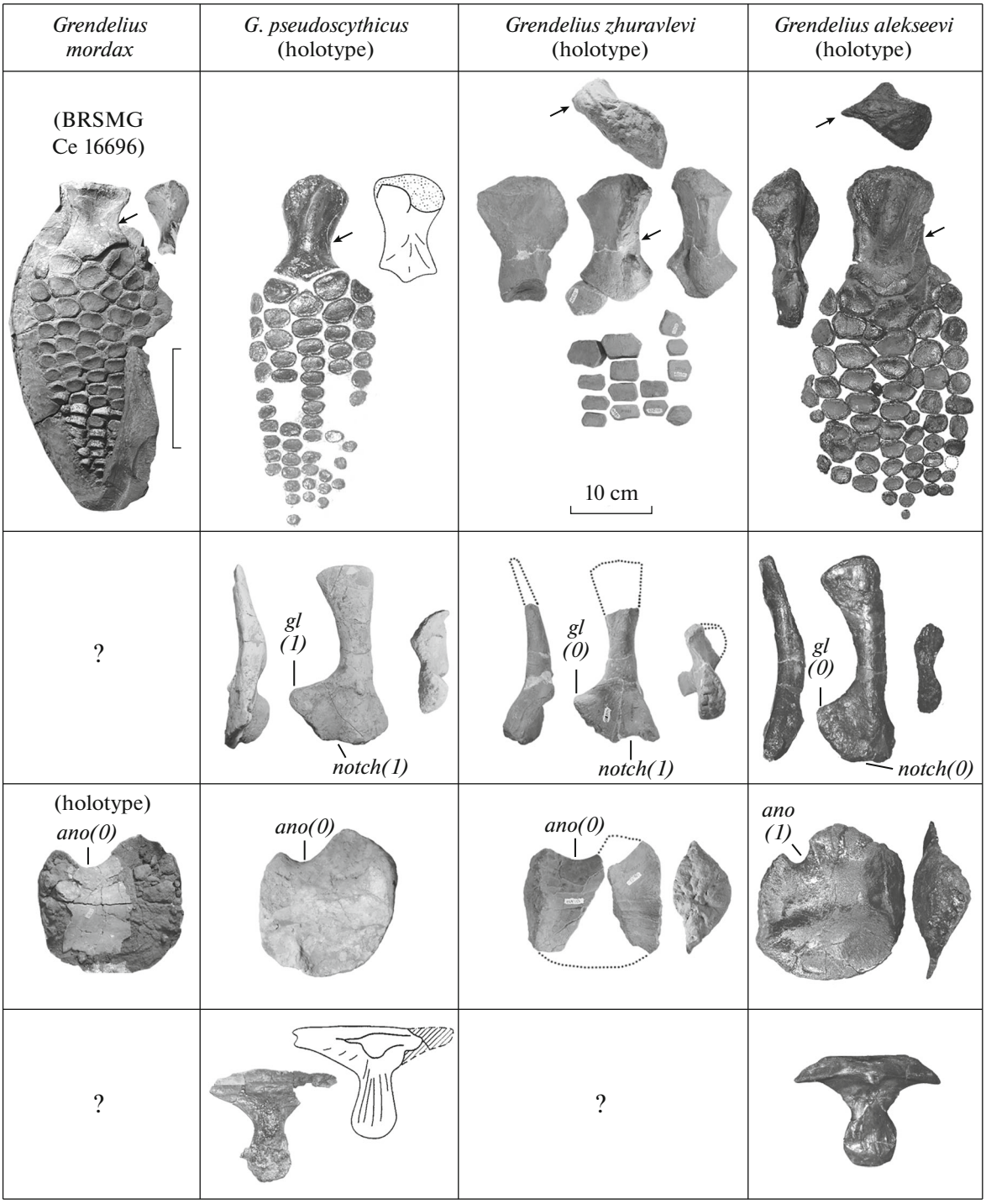


Fig. 2. Comparison of forelimbs and elements of the pectoral girdle of the *Grendelius* species. From left to right in columns: *Grendelius mordax* (forelimb of BRSMG Ce 16696 and coracoid of the holotype CAMSM J 68516), *G. pseudoscythicus* (holotype), *G. zhuravlevi* (holotype), and *G. alekseevi* (holotype). Top to bottom in rows: forelimb, scapula, coracoid, and interclavicle. Illustrations for *G. pseudoscythicus* after Efimov (1998). Designations: arrows indicate the posterior margin of the humerus; *gl(0)*, moderate glenoid contribution of the scapula, *gl(1)*, extensive glenoid contribution; *notch(0)*, not developed, *notch(1)*, present; *ano(0)*, anterior notch of the coracid extensive, *ano(1)*, narrow. Scale bar, 10 cm.

tralia in the type species and *G. alekseevi,* Figs. 2, 3). *Grendelius zhuravlevi* differs from all other species of the genus in the shape of its quadrates, the ventral part of which is strongly shortened anteroposteriorly and has a posterolaterally directed articular condyle, poorly visible in ventral view (in other species of the genus, the ventral part of the quadrate is wider and the articular surface is positioned more ventrally, thereby

Table 1. Measurement of the vertebral centra of *Grendelius zhuravlevi* (Arkhangelsky, 1998) PIN 426/16-43

Centrum position	Catalogue No current (historical)	Length	Height of the articular surface (maximum)	Width of the articular surface (maximum with apophyses)
Anterior presacral	426/26 (11)	28	65 (68)	66 (74)
	426/38 (12)	29	67 (71)	68 (74)
	426/23 (14)	29.5		0.5 = 33 (35)
	426/18 (15)	29.5	65 (67)	0.5 = 35 (38)
	426/24 (13)	31.5	NA	0.5 = 35 (38)
	426/17 (16)	32	71 (75)	72 (79)
	426/39 (17)	34	73 (75)	72.5 (81)
Posterior presacral	426/16 (18)	34	75 (79)	73 (81.5)
	426/31 (19)	37	78 (81)	76 (86)
	426/40 (20)	37	80 (83)	78 (89.5)
	426/21 (21)	37	80 (84)	81 (94)
	426/37 (22)	37	80 (84)	82.5 (94)
	426/19 (23)	36	81 (83)	88 (99)
	426/43 (–)	37.5	NA	NA
	426/30 (–)	38	82 (85)	87 (94)
	426/25 (28)	38	83 (86)	87 (94)
Caudal	426/36 (29)	36	80 (83)	0.5 = 43 (46)
	426/20 (30)	34.5	80 (85)	85.5 (87.5)
	426/34 (?26)	35	NA	0.5 = 42 (–)
	426/35 (26)	35	NA	NA
	426/32 (31)	35	81 (85)	85.5
	426/22 (25)	35	NA	80
	426/28 (35)	33	NA	NA
	426/27 (33)	32	78 (83)	80 (84)
	426/33 (32)	31.5	79 (81.5)	78 (84)
	426/41 (34)	31	77 (81.5)	78 (83)
	426/17 (37)	28	67	75 (79)
	426/29 (36)	27	625 (66.5)	71.5 (76)

forming a deeper notch of the quadrate foramen, Fig. 4). The stapes of *G. zhuravlevi* differs from those of *G. pseudoscythicus* and *G. alekseevi* in a moderately wide lateral process (Fig. 4). The species *G. pseudoscythicus* and *G. alekseevi* differ from the type species in a reduced additional posterior area under the basioccipital facet of the basisphenoid (Fig. 4), as well as in the absence of deep facets with an irregular surface for the posteromedial rami of the pterygoids on the ventral surface of the basisphenoid; however, the basisphenoid of *G. zhuravlevi* is too poorly preserved for comparison (Fig. 4). Unlike the other species of the genus, *Grendelius zhuravlevi* is characterized by a significantly anteroposteriorly elongated, dorsoventrally flattened proximal end of the humerus and a pronounced torsion between the proximal and distal humeral ends (humeral proximal end is more massive and dorsoventrally thickened in all other species, Fig. 2). Judging from specimen SRM Hb 30192, the ulna of *G. zhuravlevi* is trapezoidal in dorsal outline (pentagonal in other species of the genus), which is determined by the extended posterior facet for the pisiform, while it faces posterodistally and has a smaller size in other species. Autopodial elements of *G. zhuravlevi* are dorsoventrally thickened and tightly packed; they have polygonal outlines with clearly demarcated articular surfaces (oval-round and more loosely spaced elements in the autopodium of all other species of the genus).

Occurrence. Upper Jurassic, Volgian Stage, Middle Substage, *Dorsoplanites panderi* Zone; European part of Russia, Samara and Saratov regions.

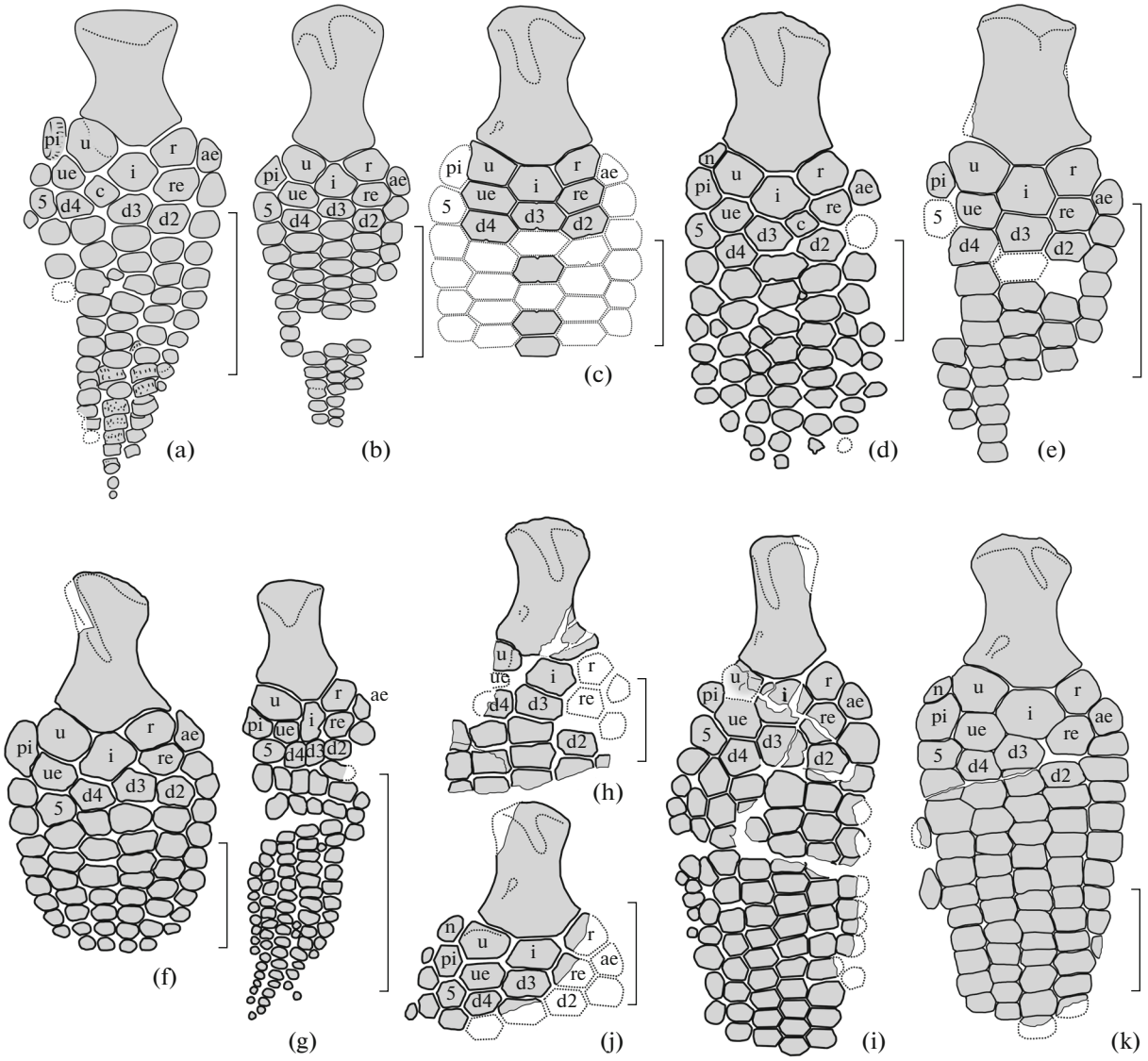


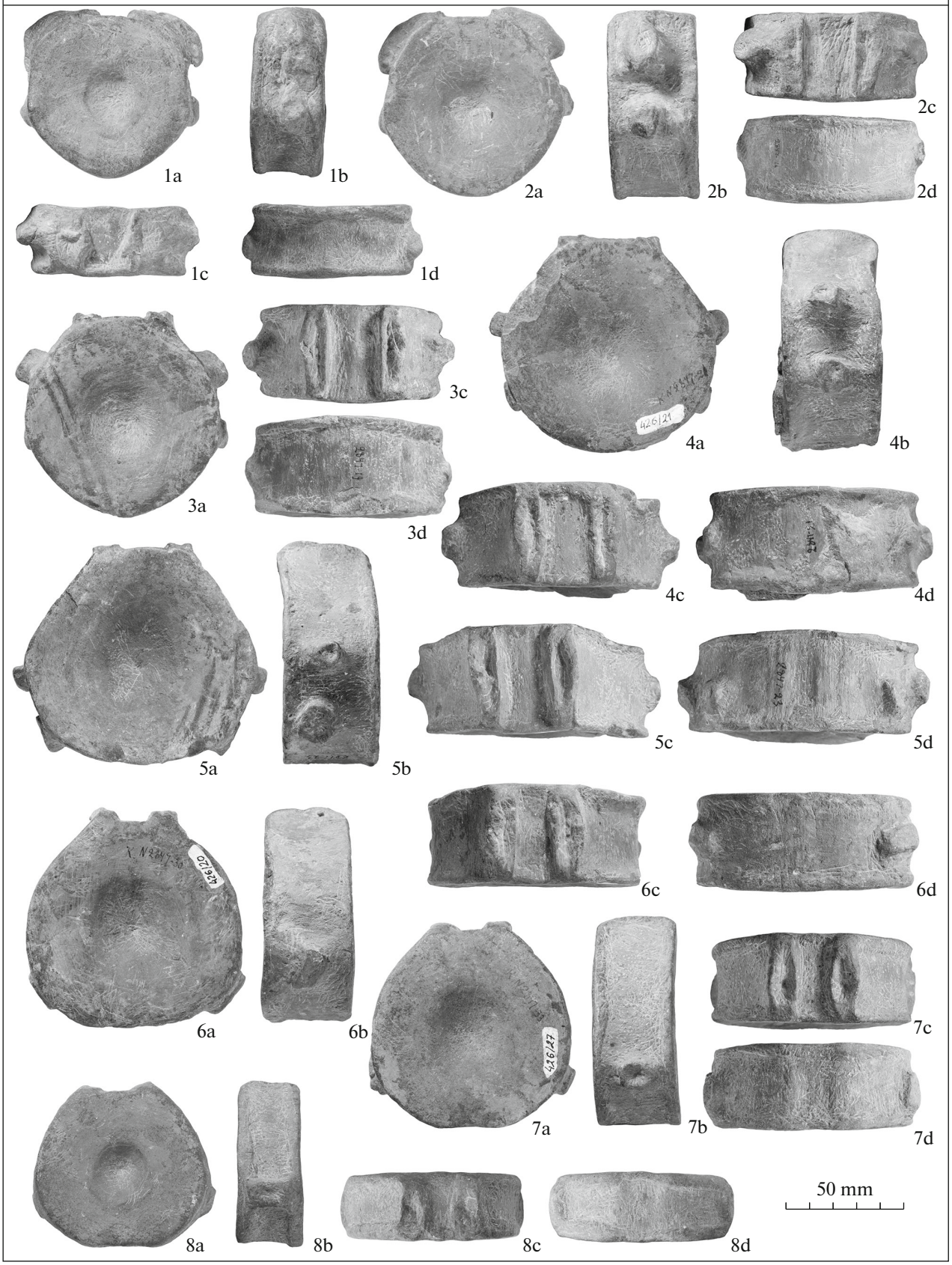
Fig. 3. Comparison of forelimbs of Late Jurassic platypterygiids with intermedium contacting humerus: *Grendelius mordax* BRSMG Ce 16696 (a); *G. pseudoscythicus* (b); *G. zhuravlevi* (c); *G. alekseevi* (d); *Grendelius* cf. *zhuravlevi* UPM 2887/1-37 (e); *Brachypterygius extremus* (f); *Aegirosaurus leptospondyus* (g); *Caypullisaurus bonapartei*, holotype (h), (i), and paratype (j); undescribed specimen that was on display at UPM up to 2017 (k); (a) and (i) are mirrored for consistency. Designations: ae, anterior accessory epipodial element; c, centrale; d2–d4, distal carpals; i, intermedium; n, postaxial neomorphic element; pi, pisiform; r, radius; re, radiale; u, ulna; ue, ulnare; (5), metacarpal 5. (a)–(c), (g) modified from Zverkov et al., 2015, (d), (f), (h)–(j) from Zverkov and Grigoriev, 2020, (e), (k) illustrated for the first time. Scale bar, 10 cm.

M a t e r i a l. Holotype (PIN 426/60-76, incomplete forelimb), as well as parts of the skeleton of the same specimen from the PIN 426 collection, which were not included by Arkhangelsky (1998) in the holotype; Saratov Region, Krasnopartizansky District, Gorny village, Savel'evskii Shale Mine; Volgian Stage, Middle Substage, *Dorsoplanites panderi* Zone. Specimen SRM Hb 30192 also belongs to this species; it represents a skeleton mounted on the wall of the museum, including mandibular fragments, an incomplete vertebral column, rib fragments, humerus, epipodial and autopodial elements, and left femur;

E x p l a n a t i o n o f P l a t e 18

Figs. 1–8. *Grendelius zhuravlevi* (Arkhangelsky, 1998) PIN, no. 426/60-76; vertebral centra; Saratov Region, Krasnopartisansky District, Gorny village, Savel'evskii Shale Mine; Middle Volgian, *Dorsoplanites panderi* Zone: (1), (2) anterior dorsal vertebral centra; (3), (5) posterior dorsal vertebral centra; (6)–(8) caudal preflexural centra. Letter designations in all figures: (a) intervertebral articular surface, (b) lateral view, (c) dorsal view, (d) ventral view.

Plate 18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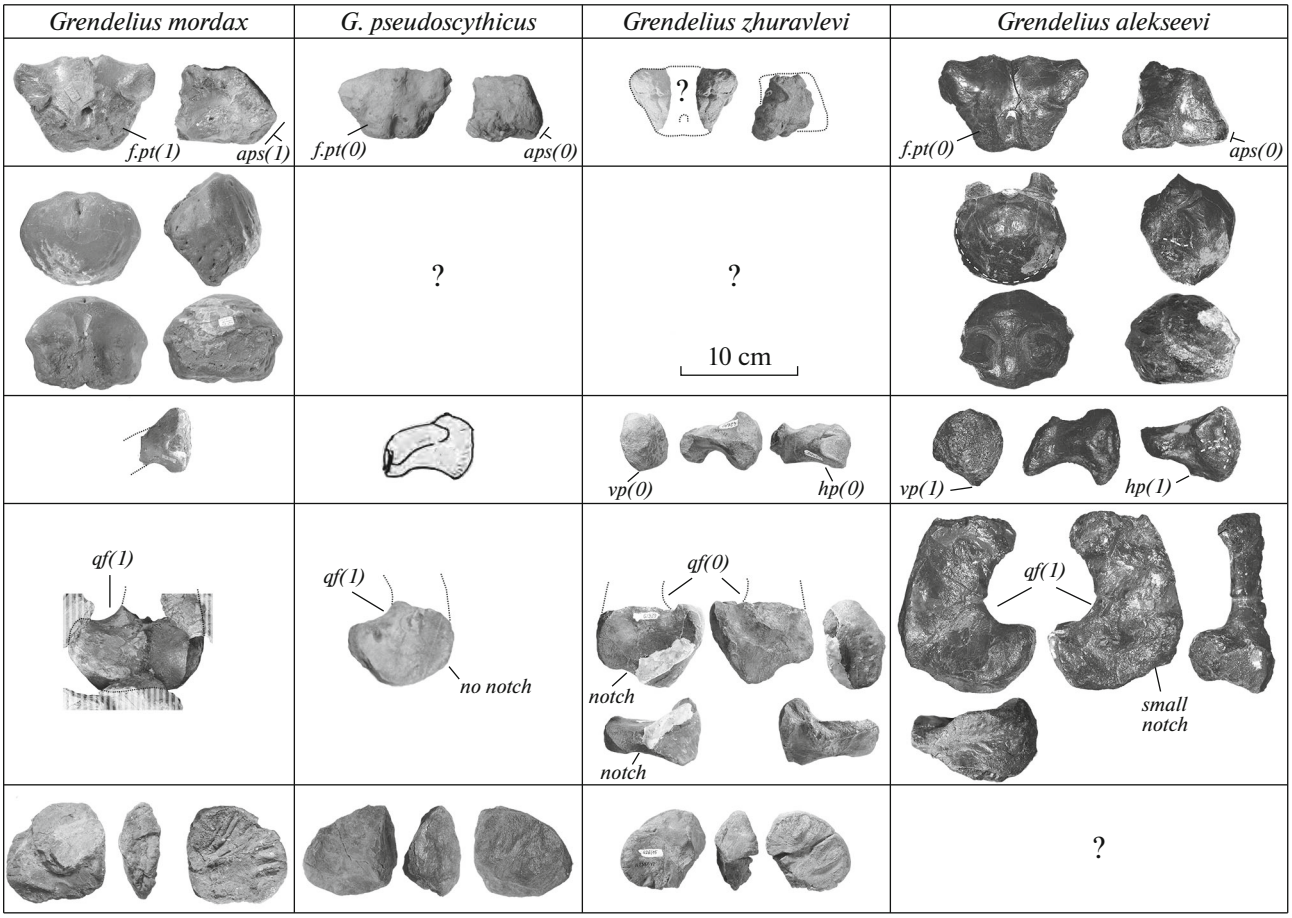


Fig. 4. Comparison of the selected elements of the skull and mandible of the species of *Grendelius.* From left to right in columns: *Grendelius mordax*, *G. pseudoscythicus*, *G. zhuravlevi*, and *G. alekseevi*. Top to bottom in rows: basisphenoid, basioccipital, stapes, quadrate, articular. Illustration of the stapes of *G. pseudoscythicus* is from Efimov (1998). Designations: *aps(0)*, additional posterior surface absent or poorly developed, *aps(1)*, well developed; *f.pt(0)*, pterygoid facets poorly pronounced, *f.pt(1)*, deep and well demarcated; hp(0), hyoid process absent, *hp(1)*, well pronounced; *qf(0)*, anterior margin of the quadrate foramen deeply concave, *qf(1)*, slightly concave; *vp(0)*, ventral process not developed, *vp(1)*, well developed. Scale bar, 10 cm.

Samara Region, Syzransky District, Kashpir mines (Mine no. 3); Volgian Stage, Middle Substage, lower part of the *Dorsoplanites panderi* Zone. SRM Hb 30192 was described in detail and depicted by the authors in previous papers (Arkhangelsky, 2000; Zverkov et al., 2015).

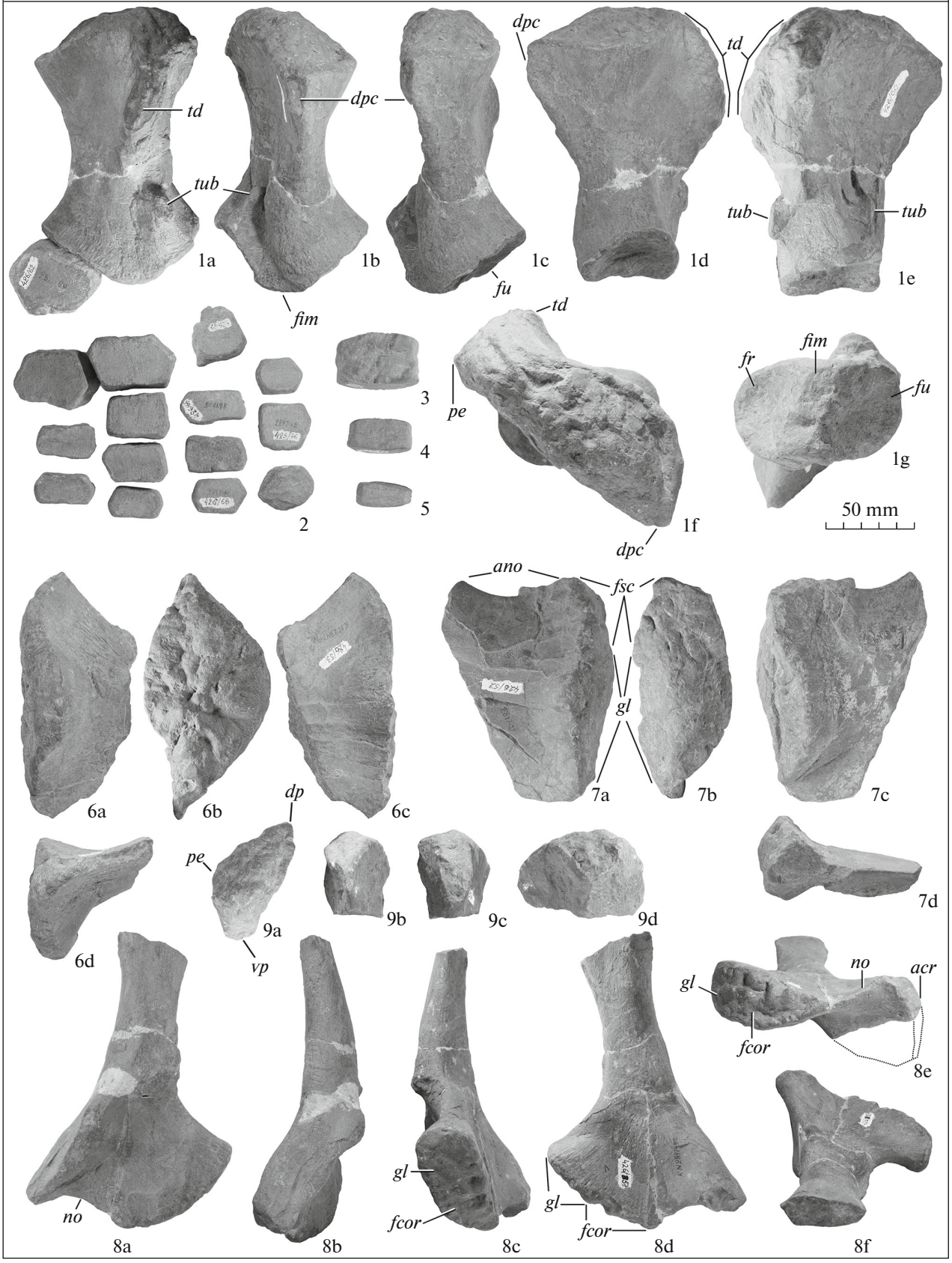
***Grendelius* sp. indet.**

The structure of the skull roof is still very poorly studied in some Late Jurassic ophthalmosaurians, including representatives of the genus *Grendelius,* which makes it difficult to confidently assign specimen SKM-KP 12889 P-633, originating from the

Explanation of Plate 19

Figs. 1–9. *Grendelius zhuravlevi* (Arkhangelsky, 1998) PIN, no. 426/60-76, holotype; left humerus with associated epipodial and autopodial elements, fragments of the pectoral girdle; Saratov Region, Krasnopartisansky District, Gorny village, Savel'evskii Shale Mine; Middle Volgian, *Dorsoplanites panderi* Zone: (1) left humerus: (1a) dorsal view (in articulation with the radius), (1b) ventral view, (1c, 1d) anterior view in different angles, (1e) posterior view, (1f) proximal end, (1g) distal end; (2–5) autopodial elements, dorsal view (2), and their articular surfaces, (3)–(5); (6) medial fragment of the left coracoid, ventral view (6a), medial view (6b), dorsal view (6c), and anterior view (6d). (7) lateral fragment of the right coracoid, dorsal view (7a), lateral view (7b), ventral view (7c), and anterior view (7d); (8) left scapula, lateroventral view (8a), anterior view (8b), posterior view (8c), dorsomedial view (8d), proximal view (8e), and distal view (8f); (9) proximal part of the left femur, proximal view (9a), dorsal view (9b), ventral view (9c), and posterior view (9d). Abbreviations: (*acr*) acromial process, (*ano*) anterior notch, (*dp*) dorsal process, (*dpc*) deltopectoral crest, (*fcor*) facet for coracoid, (*fim*) facet for intermedium, (*fr*) facet for radius, (*fsc*) facet for scapula, (*fu*) facet for ulna, (*gl*) glenoid contribution, (*no*) notch, (*pe*) posterior margin, (*td*) dorsal process, (*tub*) tubercle for muscle attachment.

Plate 19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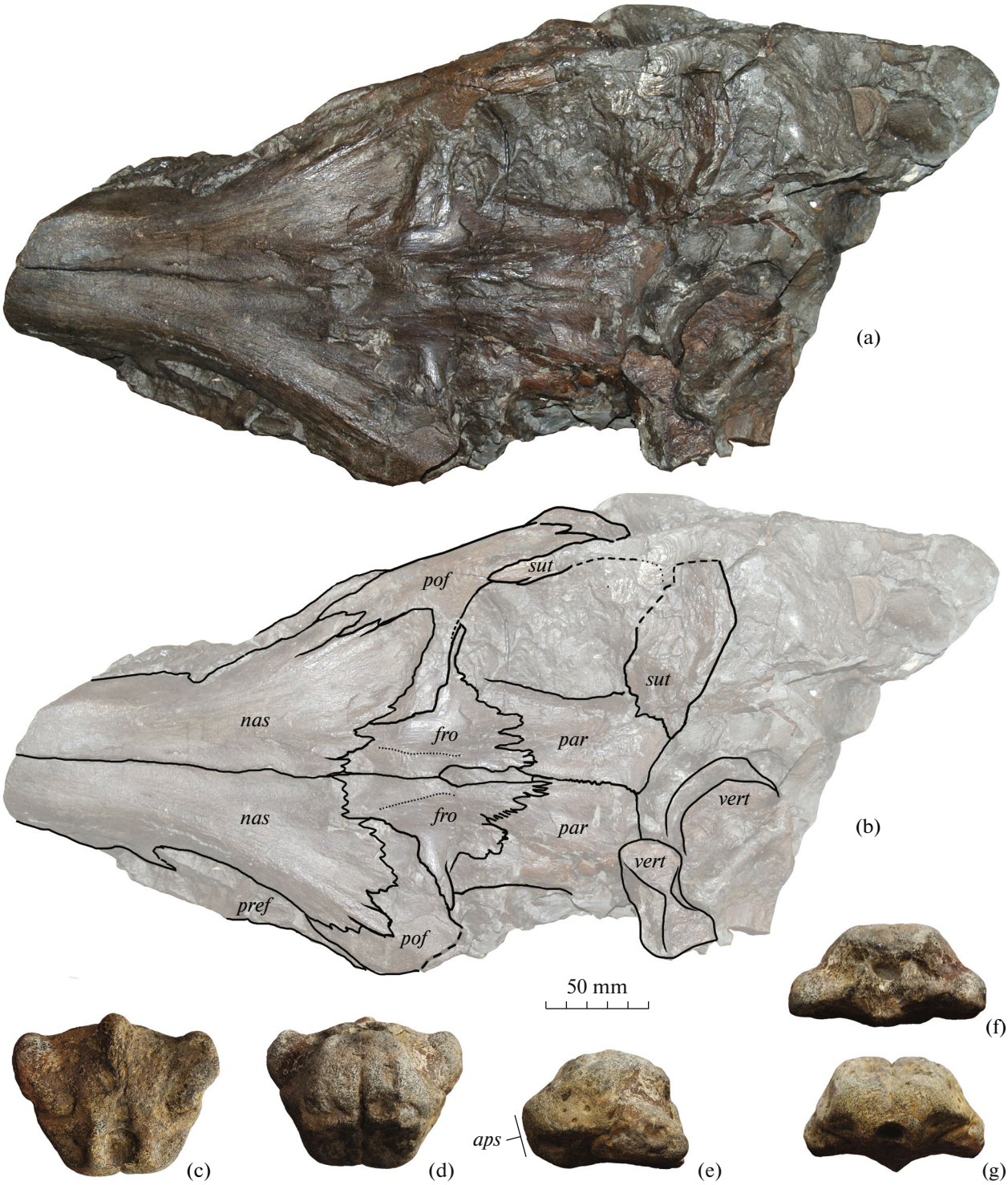

Fig. 5. Skull roof of SKM-KP 12889 P-633 from the Middle Volgian *D. panderi* Ammonite Zone of Kashpir locality (Samara region) and isolated parabasisphenoid UPM 2845 from the Middle Volgian *D. panderi* Ammonite Zone of Gorodischi locality (Ulyanovsk region). (a, b) Skull roof of SKM-KP 12889 P-633, dorsal view; (c–g) parabasisphenoid UPM 2845, ventral view (c), dorsal view (d), right lateral view (e), anterior view (f), and posterior view (g). Abbreviations: *aps*, additional posterior surface of basisphenoid; *fro*, frontal; *nas*, nasal; *par*, parietal; *pof*, postfrontal; *pref*, prefrontal; *vert*, vertebra.

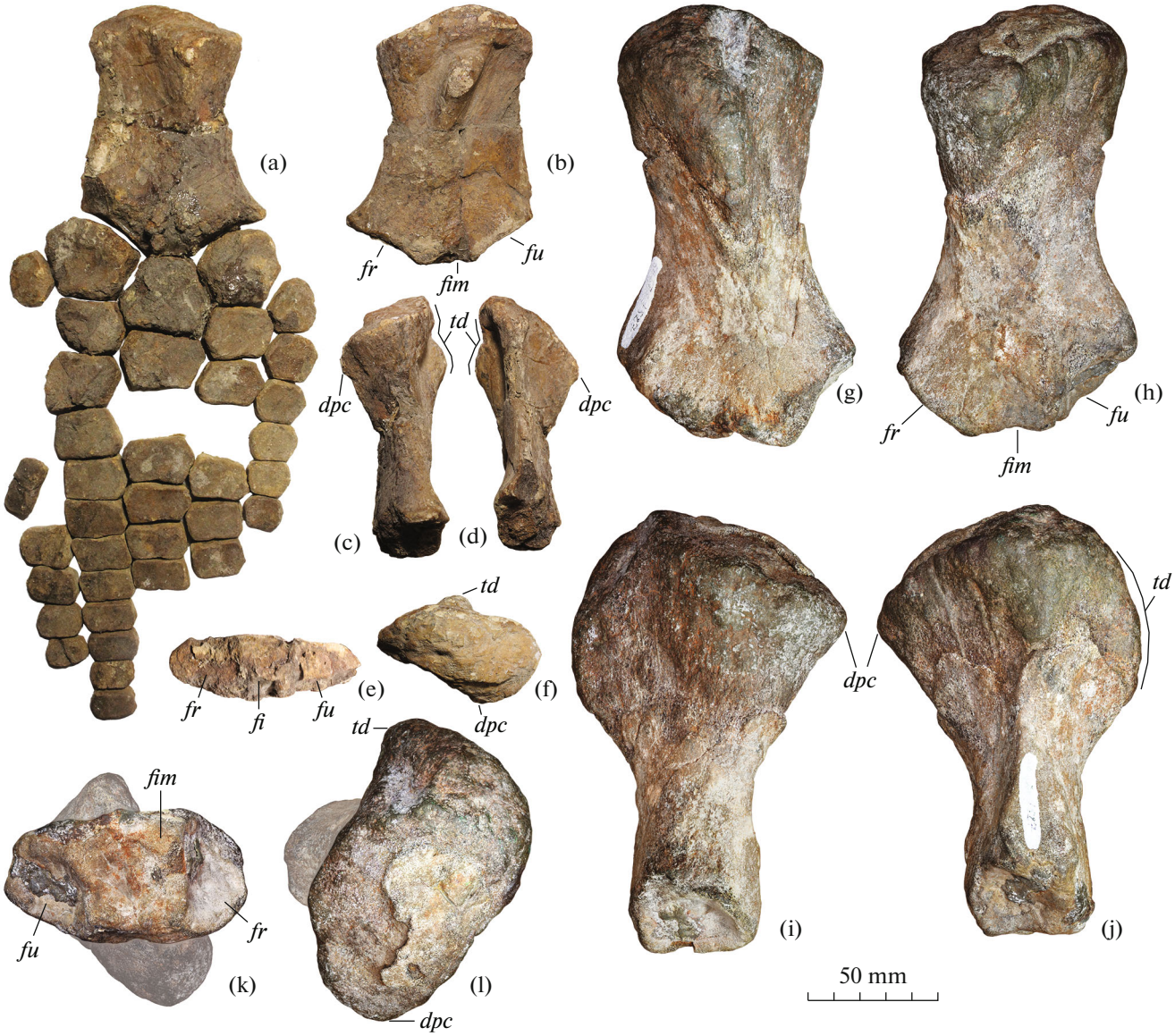

Fig. 6. Articulated left forelimb UPM 2887/1-37 and isolated right humerus YKM 50577/527 from the Middle Volgian *D. panderi* Ammonite Zone of Gorodischi locality (Ulyanovsk Region). (a)–(f) forelimb UPM 2887/1-37, dorsal view, and humerus, dorsal view (b), anterior view (c), posterior view (d), distal view (e), and proximal view (f); (g)–(l) right humerus YKM 50577/527, dorsal view (g), ventral view (h), anterior view (i), posterior view (j), distal view (k), and proximal view (l). Abbreviations: *dpc*, deltopectoral crest; *fim*, facet for intermedium; *fr*, facet for radius; *fu*, facet for ulna; *td*, dorsal process.

Middle Volgian (*D. panderi* Zone) of Kashpir (Samara Region) to this genus, let alone to any of the known species. However, a similar structure of the preserved fragment of the frontal part of *G. zhuravlevi* (Pl. 16, fig. 1) suggests that specimen SKM-KP 12889 P-633 is more likely to belong to the genus *Grendelius*. This is currently the only taxon from the Middle Volgian of the Volga Region in which the frontal forms an extended lateral process that limits the anterior margin of the supratemporal fenestra and excludes contact between the parietal and postfrontal (Figs. 5a, 5b). This structure of the skull roof is typical of many Cretaceous platypterygiids (e.g., Fischer et al., 2011; Kear, 2005). In addition to these traits, specimen SKM-KP 12889 P-633 demonstrates a number of other structural features of the skull roof (Figs. 5a, 5b). Its parietals are characterized by short, wide posterolateral processes; their medial symphysis is extended and strong, while the posterior notch is not developed. The sagittal crest of the parietal is not clearly defined. The anteromedial process of the supratemporal is short and narrow. The parietal foramen is slit-like and elongated, located between the frontals with a minor contribution of the parietals in its posterior part. The post-

frontal plate-like widens in the anterior part (under the posterior process of the nasal), while its posterior part is mediolaterally narrow and short and has an oval cross-section. The posterior parts of the nasals form extensive digitating contacts with the postfrontals and, to a lesser extent, with the frontals. Foramina between the nasals are not developed. Prefrontals are poorly visible from above; they do not form anteromedial extensions, in contrast to some other ophthalmosaurians, including *Caypullisaurus* (Fernández, 2007).

The parabasisphenoid UPM 2845 from the Middle Volgian (*D. panderi* Zone) of Gorodischi (Figs. 6c–6g) has a shape typical for representatives of the genus *Grendelius*; however, it combines features of the type species (the presence of an extensive additional surface under the facet for the basioccipital) and species from the Volga Region (less deep and sharply demarcated pterygoid facets than those of the type species), except *G. zhuravlevi*, for which this element is insufficiently well known. For this reason, specimen UPM 2845 cannot be confidently assigned to any of the known *Grendelius* species and is identified here in open nomenclature.

The collection of UPM contains a nearly complete small forelimb, originating from the Middle Volgian (*D. panderi* Zone) of Gorodischi (specimen UPM 2887/1-37), which apparently belongs to a young individual. The preserved proximodistal length of the limb is 26 cm, and length of the humerus is 9.3 cm. This limb is most similar in its structure to the limbs of *G. zhuravlevi*, judging from its tightly packed polygonal and dorsoventrally thickened autopodial elements (Fig. 6a). As in *G. zhuravlevi*, the proximal and distal margins of some phalanges bear small notches in the middle part. It differs from other known specimens of *G. zhuravlevi* in a wider diaphysis (Figs. 6a, 6b) and a dorsoventrally much less flattened and anteroposteriorly less elongated proximal end of the humerus (Fig. 6f), as well as in the absence of tubercles for muscle attachment above the ulnar facet. However, some of these differences may be ontogenetic, given the significantly smaller size of UPM 2887/1-37. Also, in contrast to the ulna of *G. zhuravlevi* (specimen SRM Hb 30192), the pisiform facet in specimen UPM 2887/1-37 is directed posterodistally, rather than posteriorly, and leaves a small free surface at the posterior margin of the ulna (Fig. 6a), thereby giving it a pentagonal rather than trapezoidal shape. This may be associated with individual variation. Taking into account the existing differences, we consider this specimen in open nomenclature as *Grendelius* sp. juv. cf. *G. zhuravlevi*.

A rather large humerus YKM 50577/527 (the proximodistal length is 15.8 cm) from the Middle Volgian (*D. panderi* Zone) of Gorodischi is also of interest. This humerus is characterized by an elongated, slender diaphysis, as in *G. pseudoscythicus* and *G. zhuravlevi* (cf. Figs. 2 and 6g), which distinguishes it from *G. mordax* and *G. alekseevi*. The proximal end of YKM 50577/527 is rather massive and significantly differs in shape from those of *G. zhuravlevi* and *G. alekseevi* and most similar to the proximal end of the humerus of SGM 1566 from the Moscow region (Zverkov et al., 2015, text-fig. 15E). The wide distal facet of this humerus for the intermedium (3.6 cm wide, while the facets of the radius and ulna barely exceed 4 cm; Figs. 6g, 6k) is similar to that of *Caypullisaurus bonapartei* and an undescribed specimen from the Middle Volgian of Gorodischi (Figs. 3h–3k), which was on display at UPM until 2017 (however, it disappeared from the museum after the dismissal of its former director). Along with the above-mentioned skeleton, the humerus of YKM 50577/527 may belong to a new, yet undescribed species of the genus *Grendelius,* or another genus with intermedium–humeral contact, such as *Caypullisaurus*.

DISCUSSION

The forelimbs of the holotype of *Grendelius mordax* (CAMSM J 68516) are not preserved, which makes its direct comparison with the holotype of *B. extremus* impossible. An additional specimen assigned to *G. mordax* (BRSMG Ce 16696; McGowan, 1997) makes it possible to perform this comparison. However, it is important to note that the attribution of this specimen to the species *G. mordax,* rather than to any other species of *Grendelius*, is not so unambiguous: it is based on the general proportions of the skull and pattern of bone articulation in the region of the external nares (Moon and Kirton, 2018); at the same time, neither the skull roof nor the elements of the occiput and basicranium are known for BRSMG Ce 16696, which makes it difficult to carry out a more detailed comparison. Specimen BRSMG Ce 16696 is currently referred to *G. mordax* in all papers (including this one); however, taking into account the presence of three distinct species of *Grendelius* in the Middle Volgian of the Volga Region, it cannot be ruled out that several species of this genus also lived in Western Europe in the Late Jurassic and that BRSMG Ce 16696 may actually represent some other species than the type species.

The mesopodium of the forelimb of BRSMG Ce 16696 has a peculiar configuration that makes difficult an unambiguous interpretation of its elements. It is most difficult to interpret the region between the ulna, intermedium and distal carpals. To date, three different interpretations have been proposed for the elements of this region (McGowan, 1997; Zverkov et al., 2015; Moon and Kirton, 2018); however, analysis of all known limbs of representatives of *Grendelius* and other forms with a similar forelimb structure (Fig. 3) allows to suggest a new interpretation that explains some of the existing contradictions. We assume that the limb of BRSMG Ce 16696 has neomorphic ossification at the posterodistal margin of the intermedium. According

to Shubin and Alberch's hypothesis of limb development (Shubin and Alberch, 1986), reptiles have centralia derivating from the intermedium. Therefore, it is most likely that the element located distal to the intermedium in BRSMG Ce 16696 is homologous to centrale, although it is neomorphic. In the holotype of *Grendelius alekseevi*, both forelimbs also have neomorphic ossifications, which, however, are at the anterodistal margin of the intermedium (Zverkov et al., 2015).

An important point that is often not taken into account in recent publications is the interpretation of epipodial elements in the limbs of *Caypullisaurus bonapartei* from the Tithonian of Argentina. Initially, the three epipodial elements of this taxon were interpreted as an ulna, radius and a preaxial accessory element (Fernández, 1997; Motani, 1999b). However, Arkhangelsky (2001) proposed an alternative interpretation, according to which the middle element in the epipodium of *C. bonapartei* is an intermedium. This interpretation is considered as the only possible in recent works by Zverkov et al. (Zverkov and Efimov, 2019; Zverkov and Grigoriev, 2020); however, it is not taken into account by other researchers, which leads to disagreements in coding for phylogenetic analyzes and their results, respectively. It is interesting to note that the forelimb of *C. bonapartei* (Figs. 3h–3j) is very similar in its structure to that of an undescribed specimen from the Middle Volgian of Gorodischi (Fig. 3k), in which the middle element of the epipodium is undoubtedly the intermedium, although it is larger than the radius and ulna. This additionally confirms Arkhangelsky's interpretation (2001).

Among the Late Jurassic forms characterized by the contact between the intermedium and humerus, *Brachypterygius extremus* is most similar to *Aegirosaurus leptospondylus* from the Tithonian of Solnhofen (Germany) in the structure of the forelimb, differing from it only in a strongly elongated anterodistal margin of the humerus and, possibly, in shorter digits (Figs. 3f, 3g). This is also confirmed by the results of some phylogenetic analyzes, according to which these genera form a clade at the base of Platypterygiidae (Zverkov and Jacobs, 2021). At the same time, the type species of these two genera differ in size and some details in the structure of the forelimb, which makes it possible to consider them as separate species. During the differentiation of *Aegirosaurus*, Bardet and Fernandez (2000) actually compared this taxon with the chimeric *Brachypterygius extremus* + *Grendelius mordax* taxon, as the genus *Brachypterygius* was understood at that time (McGowan, 1997), rather than comparing it with the type material of *Brachypterygius extremus*; therefore, the differences between the two genera were obvious to them. Indeed, *Aegirosaurus* and *Grendelius* significantly differ in the structure of their skull; however, the synonymy between *Brachypterygius extremus* and *Grendelius mordax* has as much, if not less, evidence than the assumption about the synonymy between *Aegirosaurus* and *Brachypterygius*, which are characterized by the presence of six digits in the forelimbs (five in *Grendelius* spp.) and tightly spaced phalanges (rounded in all *Grendelius* species except *G. zhuravlevi*). In addition, the forelimbs of *Parrassaurus yacahuitztli* described from the Tithonian of Mexico (Barrientos-Lara and Alvarado-Ortega, 2021) have similar structure to those of *B. extremus*. This taxon also has a rostrum that is longer and thinner than that of *Grendelius mordax* and similar to that of *Aegirosaurus leptospondylus*. Barrientos-Lara and Alvarado-Ortega carried out a phylogenetic analysis in which *Brachypterygius extremus* and *Grendelius mordax* were considered as synonyms and coded as the same operational taxonomic unit. The results of their analysis show that *P. yacahuitztli* forms a clade with *A. leptospondylus* at the base of platypterygiids, similarly to the results of the analysis by Zverkov and Jacobs (2021) for the *A. leptospondylus* and *B. extremus* clade, which, however, was not discussed by Mexican researchers (Barrientos-Lara and Alvarado-Ortega, 2021). Another problem with the differentiation of *P. yacahuitztli* as a separate taxon is the determination of the very status of *B. extremus*. The limb of *P. yacahuitztli* according to its reconstruction (Barrientos-Lara and Alvarado-Ortega, 2021; fig. 7A) differs little from the holotypic limb of *B. extremus*; therefore, for the validity of *P. yacahuitztli*, the authors should have recognized *B. extremus* as a *nomen dubium*, or to study more thoroughly the forelimbs of these forms and to identify differences between them. However, in any scenario, these taxa (*B. extremus*, *A. leptospondylus*, and *P. yacahuitztli*) are apparently closely related and represent a separate evolutionary lineage of platypterygiids with a "latipinnate" hexadactyl limb and a long and slender rostrum. Possibly, further studies will find it to be more reasonable to consider them as one genus. Along with *A. leptospondylus*, *Parrassaurus yacahuitztli* currently requires revision, since the characters taken as diagnostic features for *P. yacahuitztli* (Barrientos-Lara and Alvarado-Ortega, 2021) have been recorded for the skeletal regions, which are insufficiently studied in representatives of the genera *Brachypterygius, Aegirosaurus, Grendelius*, and *Caypullisaurus*, which makes it difficult to assess the status of this taxon.

CONCLUSIONS

All three species from European Russia, described within the genus *Otschevia*, are valid species of the genus *Grendelius*. They differ from each other and from the type species, *G. mordax*, in the structure of the occipital and basicranial elements, pectoral girdles, and limbs. The taxonomic approach that interprets all or some of these species as part of the separate genus, *Otschevia*, rather than part of *Grendelius*, cannot be completely ruled out; however, in our opinion, there is so far insufficient evidence to confirm this

assumption. Based on the available materials, the synonymy of the type species of the genera *Brachypterygius* and *Grendelius* cannot be confirmed due to differences in the structure of their limbs (the number of digits, shape of the distal end of the humerus, and configuration of the mesopodial elements); at the same time, the synonymy of the genera *Grendelius* and *Otschevia* can be justified by a strong similarity in the structure of the skull roof , its occipital region and basicranium (Zverkov et al., 2015). The concept that most of the large Late Jurassic ichthyosaurs from the northern hemisphere with a clearly defined contact between the intermedium and humerus are assigned to the genus *Brachypterygius* (Moon and Kirton, 2018) seems inconsistent, since it does not take into account the Late Jurassic genera *Caypullisaurus*, *Aegirosaurus*, and ?*Parrassaurus*, which are also characterized by this condition. The taxonomic significance of the derived state of this character seems to be overestimated by other authors. This state either independently evolved several times in the evolution of platypterygiids (according to the results of all phylogenetic analyzes published to date) or it characterizes a rather large suprageneric clade, which so far cannot be recovered by phylogenetic analyses due to the insufficient number of other revealed apomorphies. Along with *A. leptospondylus*, *Parrassaurus yacahuitztli* needs to be revised. It is possible that these taxa are actually more closely related to each other and to *B. extremus* than is believed; however, confident conclusions on this issue require additional data directly on *B. extremus*, which is still reliably known only from the forelimb.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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