

New Data on Skull Morphology of *Psittacosaurus sibiricus* (Dinosauria: Ceratopsia) Using Micro-Computed Tomography

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Abstract—The morphology of the skull and endocranium of juvenile and adult specimens of the basal ceratopsian dinosaur *P. sibiricus* from the Lower Cretaceous Ilek formation (Kemerovo oblast-Kuzbass, Western Siberia, Russia) is described using micro-computed tomography scans and three-dimensional modelling. The diagnostic cranial characters of *P. sibiricus* include premaxilla-rostral canal present, maxillary fossa and maxillary protuberance absent, ten maxillary teeth in adults, maxillary-lacrimal contact, postorbital horn composed of the postorbital and the jugal present, large ventrolaterally projecting pyramidal jugal horns, deeply bifurcating jugal posterior process, external mandibular fenestra absent, dentary flange lacks the anterior corner but has a prominent posterior angle extending on the angular, and angular tuber projecting laterally at the posterior end of the ventral flange.

Keywords: Dinosaurs, Ceratopsia, *Psittacosaurus*, morphology, ontogeny, micro-computed tomography

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INTRODUCTION

The ceratopsian dinosaur *Psittacosaurus* is known from numerous remains in the Lower Cretaceous deposits of Eastern Asia. Most records come from the localities in Mongolia and China (Osborn, 1923; Sereno and Chao, 1988; Sereno et al., 1988, 2010; Zhou et al., 2006). The fragmentary remains of psittacosaurus are known from the Lower Cretaceous of Japan (Manabe and Hasegawa, 1991). Psittacosaurus often dominate the terrestrial vertebrate assemblages which led to recognition of the “*Psittacosaurus* biochron” (Lucas, 2006), the chronostratigraphic time interval which covers the time period from the Barremian to the Albanian.

Historically psittacosaurus have been divided into two genera and 17 species. Half of the species was rejected in a recent revision of the genus by Sereno (2010) because of vague diagnostic characters and fragmentarity and juvenile nature of some type specimens. The species of *Psittacosaurus* are distinguished by size, shape of the skull and lower jaw, teeth construction, development of the skull bones outgrowths,

and also by the contacts between certain skull elements.

The fragmentary remains of psittacosaurus in the Lower Cretaceous Ilek Formation at Shestakovo 1 locality in Kemerovo oblast-Kuzbass, West Siberia, have been known since the middle of the XX century (Rozhdestvensky, 1955a, 1955b, 1960). However, only in 1995 the locality Shestakovo 3 with more complete skeletons and numerous isolated bones and bone accumulations of psittacosaurus was discovered. One of these skeletons became the holotype of *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000 (Leshchinskii et al., 2000).

In 2014, Kuzbass State Museum of Local Lore and Borissiak Paleontological Institute of the Russian Academy of Sciences carried out large-scale excavations at Shestakovo 3 locality. An accumulation of 12 articulated skeletons has been found and excavated (Lopatin et al., 2015). Later, two more partially articulated skeletons have been found at Shestakovo 1 and 3 localities (Podlesnov et al., 2018). This article is devoted to the description of skull morphology of the



Fig. 1. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Skulls KOKM 22985/5 (a) and KOKM 22985/2 (b) in lateral view. Scale bars, 20 mm.

two specimens of *P. sibiricus* collected in 2014 at Shestakovo 3 locality, juvenile KOKM 22985/5 and adult KOKM 22985/2, based on micro-computed tomography. The craniovertebral joint morphology of the adult skull KOKM 22985/2 and other specimens of *P. sibiricus* was described in detail by Podlesnov (2018).

MATERIALS AND METHODS

The two studied skulls, KOKM 22985/5 and KOKM 22985/2 (Fig. 1), were collected in 2014 at Shestakovo 3 locality in the monolith 3 of the accumulation of 12 psittacosaur skeletons of different individual age (Lopatin et al., 2015). The transportation of the skeletons before burial was not significant because of their completeness and good preservation of the bones. The skull length of the seven relatively complete skulls of *P. sibiricus* from Shestakovo 3 locality housed in the KOKM collection ranges from 58 to over 260 mm. Some fragments of the jugal and frontal bones belong to even larger individuals. KOKM 22985/5 is the smallest specimen in this sample. KOKM 22985/2 with the skull length of 220 mm is an adult specimen but not the largest.

The skulls KOKM 22985/5 and KOKM 22985/2 were scanned in the Center of Petroleum Science and Technology, Skolkovo Institute of Science and Technology, Moscow, on a micro-computed tomography system General Electric Phoenix v|tome|x L240/180

(Table 1) with a circular cone-beam projection using nanofocus X-Ray tube. The segmentation and virtual reconstruction of the skull bones was done using Avizo 9.1 (FEI Visualization Sciences Group, Hillsboro, OR, USA). The isosurface module of Avizo 9.1 was used for the reconstructions of the complete skulls, which were subsequently outlined in Adobe Photoshop 19.1.6.

Anatomical abbreviations. **A**, angular; **aas**, angular articular surface; **ad**, apical denticle; **aras**, articular articular surface; **al**, alveolus; **alp**, anterolateral process; **amp**, anteromedial process; **ap**, anterior process; **Ar**, articular; **asc**, anterior semicircular canal; **asca**, ampulla of anterior semicircular canal **at**, angular tuber; **avpp**, anteroventral process of premaxilla, **bcc**, bottom of cerebral cavity; **Bo**, basioccipital; **bptf**, fossa for basiptyergoid process of basisphenoid; **bsas**, basisphenoid articular surface; **Bs/Ps** basisphenoid/parasphenoid; **bpt**, basiptyergoid process; **bsr**, basisphenoid recess; **bt**, basal tuber; **boas**, basioccipital articular surface; **cav Mc**, cavity for Meckelian cartilage; **cbl**, cerebellum; **cd**, cochlear duct; **cfo**, carotid foramen; **Cor**, coronoid; **coras**, coronoid articular surface; **cqas**, articular surface for quadrate condyles (glenoid fossa); **ci**, cingulum; **cr**, **cr**, crista cranii; **cri**, crista interfenestralis; **cr pr**, crista prootica; **cr sg**, crista sagittalis; **co**, occipital condyle; **cop**, coronoid process; **dbd**, distal basal denticle; **De**, dentary; **deas**, dentary articular surface; **df**, dentary flange; **dmas**, attachment surface for the

Table 1. Scanning protocols of the studied skulls of *Psittacosaurus sibiricus*

Specimen	Voltage, kV	Current, μ A	Voxel size, μ m	Number of images in the stack
KOKM 22985/5	100	250	31	1458
KOKM 22985/2	120	300	145	2024

depressor mandibulae; **dph**, dorsal postorbital horn; **dp**, dorsal process; **Ec**, ectopterygoid; **ecas**, ectopterygoid articular surface; **en**, external naris; **eoas**, exoccipital-opisthotic articular surface; **Ex/Op**, exoccipital-opisthotic; **F**, frontal; **fas**, frontal articular surface; **fc**, fossa for the cerebrum (telencephalon); **fl**, lacrimal foramen; **fob**, fossa for the olfactory bulb; **fo**, fenestra ovalis or fenestra vestibuli; **fos lig co**, fossa ligamentum condyles occipitalis; **fom**, foramen magnum; **foi**, fossula intertubercularis; **fpl**, footplate of stapes; **fs**, fossa supraoccipitalis; **ftof**, fossa for the tractus olphactorius; **g Mc**, groove for Meckelian cartilage; **gpalp**, groove for palpebral; **ic**, internal carotid; **imf**, internal mandibular fenestra; **J**, jugal; **jas**, jugal articular surface; **jh**, jugal horn; **jpec**, jugal process of ectopterygoid; **L**, lacrimal; **lab**, bony labyrinth of inner ear; **las**, lacrimal articular surface; **lc**, lacrimal canal; **lco**, lateral condyle; **ledp**, lateral expansion of the dorsal process; **lp**, lateral process; **lsc**, lateral semicircular canal; **lsca**, ampulla of lateral semicircular canal; **Lt**, laterosphenoid; **ltas**, laterosphenoid articular surface; **lth**, head of laterosphenoid; **mco**, medial condyle; **mdb**, mesial basal denticle; **mdpe**, mediodorsal process of ectopterygoid; **mecr**, medial crest of rostral; **mecs**, medial crest of surangular; **mf**, metotic foramen; **mob**, medulla oblongata; **mp**, medial process; **mpp**, medial plate of pterygoid; **mpl**, medial plate of prementary; **mr**, maxillary ramus of pterygoid; **ms**, maxillary symphysis; **mst**, metotic strut; **mtrar**, middle triangular area of rostral; **Mx**, maxilla; **mxas**, maxillary articular surface; **mxf**, maxillary foramen; **mxpp**, maxillary plate of palatine; **mxr**, maxillary recession; **N**, nasal; **nas**, nasal articular surface; **npp**, nasal process of premaxilla; **npr**, nasal process of rostral; **nsu**, nasal sulci opening; **ovs**, occipital venous sinus; **P**, parietal; **pas**, parietal articular surface; **pcf**, processus cultriformes; **pct**, paracultriform trough; **Pd**, prementary; **pdas**, prementary articular surface; **Pf**, prefrontal; **pfas**, prefrontal articular surface; **Pl**, palatine; **Pm**, premaxilla; **pmlf**, premaxillary-lacrimal foramen; **plas**, palatine articular surface; **Plp**, palpebral; **plp**, palatine process of premaxilla (lamina palatina); **plpp**, posterolateral process of premaxilla, **plr**, palatal ramus of pterygoid; **pmas**, premaxillary articular surface; **pmf**, premaxillary fossa; **pmp**, posteromedial process of maxilla; **Po**, postorbital; **poas**, postorbital articular surface; **pojh**, postorbital-jugal horn; **polp**, postero-lateral process of frontal; **pop**, paraoccipital process; **por**, postorbital ramus of squamosum; **pp**, posterior process; **pppf**, posterior process of prefrontal; **pppr**, posterior process of prootic; **Pr**, prootic; **Pra**, prearticular; **praas**, prearticular articular surface; **pras**, prootic articular surface; **pri**, primary ridge; **proaas**, articular surface for proatlas; **psc**, posterior

semicircular canal; **pzca**, ampulla of posterior semicircular canal; **prsc**, premaxilla-rostral subvertical canal; **Pt**, pterygoid; **ptas**, pterygoid articular surface; **ptpp**, pterygoid plate of palatine; **ptre**, pterygoid ramus of ectopterygoid; **ptrq**, pterygoid ramus of quadrate; **ptv ch**, pterygoid-vomerine channel; **Q**, quadrate; **qas**, quadrate articular surface; **qh**, quadrate head; **Qj**, quadratojugal; **qjas**, quadratojugal articular surface; **qr**, quadrate ramus of pterygoid; **qs**, quadrate shaft; **R**, rostral; **ras**, rostral articular surface; **rcc**, roof of cerebral cavity; **rec**, ridge of ectopterygoid; **rp**, retroarticular process; **rt**, root of tooth; **rvp**, rostroventral process of nasal, **Sa**, surangular; **saas**, surangular articular surface; **sd**, secondary denticle; **sh**, shaft of stapes; **So**, supraoccipital; **soas**, supraoccipital articular surface; **somr**, supraoccipital medial ridge; **Spl**, splenial; **splas**, splenial articular surface; **sps**, sulcus parasphenoidal; **Sq**, squamosal; **sqas**, squamosal articular surface; **sri**, secondary ridge; **stu**, sella turcica (pituitary fossa); **sv**, sulcus vomeris; **ts**, triturating surface; **tpw**, transverse palatine wing; **utrr**, utricular recess (recess for cruss communis), **vcd** vena capitis dorsalis; **ve**, vestibule; **vers**, vestibular recess; **vf**, ventral fossa; **vmp**, ventromedial process of jugal; **Vo**, vomer; **voas**, vomeral articular surface; **vob**, vomerine bar; **vp**, ventral process of postorbitale; **vph**, ventral postorbital horn; **vr**, ventral ridge of articular; **wcc**, wall of cerebral cavity; **V**, trigeminal nerve canal; **V₁**, ophthalmic branch of the trigeminal nerve canal; **VII**, facial nerve canal; **X**, **XI**, vagus and accessorius cranial nerve canals; **XII_{ant}**, anterior hypoglossal nerve canal; **XII_{post}**, posterior hypoglossal nerve canal.

Institutional abbreviations. (AMNH), American Museum of Natural History, New York, USA. (IGM), Mongolian Institute for Geology, Ulaanbaatar, Mongolia; (IVPP), Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; (KOKM) Kuzbass State Museum of Local Lore, Kemerovo, Russia; (PM TGU) Paleontological Museum, Tomsk State University, Tomsk, Russia.

SYSTEMATIC PALEONTOLOGY

Order Ornithischia Seeley, 1888

Suborder Ceratopsia Marsh, 1890

Family Psittacosauridae Osborn, 1923

Genus *Psittacosaurus* Osborn, 1923

Psittacosaurus sibiricus Voronkevich et Averianov
in Leshchinskiy et al., 2000

Plate 6, 7

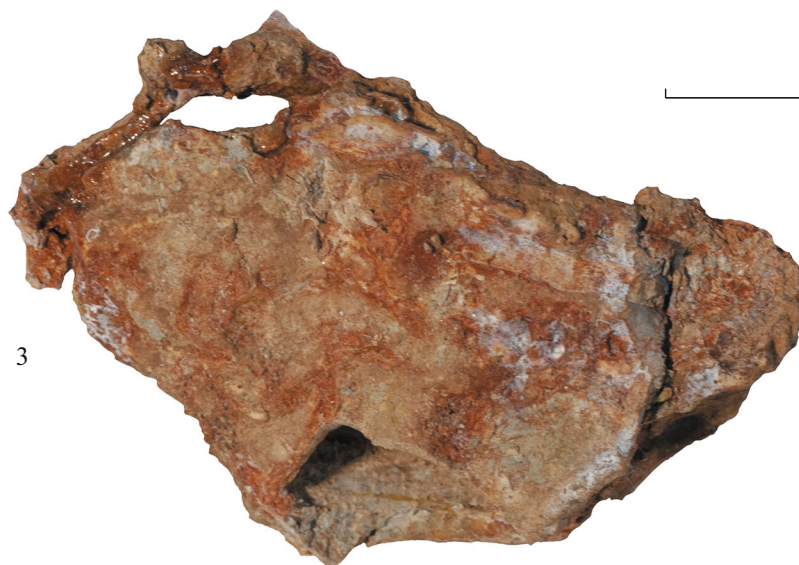
Psittacosaurus sp.: Rozhdestvensky, 1955a: p. 118; Rozhdestvensky, 1960: p. 165; Rozhdestvensky and Khozatsky, 1967: p. 84.

Explanation of Plate 6

Psittacosaurus sibiricus Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast-Kuzbass, Russia; Ilek Formation, Lower Cretaceous, no. 22985/2: skull with mandibles: (1) right lateral, (2) left lateral, (3) posterior, (4) anterior, (5) dorsal, (6) ventral view. Scale bar, 50 mm.

Plate 6





Explanation of Plate 7

Psittacosaurus sibiricus Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous, no. 22985/5: skull: (1) postero-lateral, (2) right lateral, (3) ventral view. Scale bar, 20 mm.

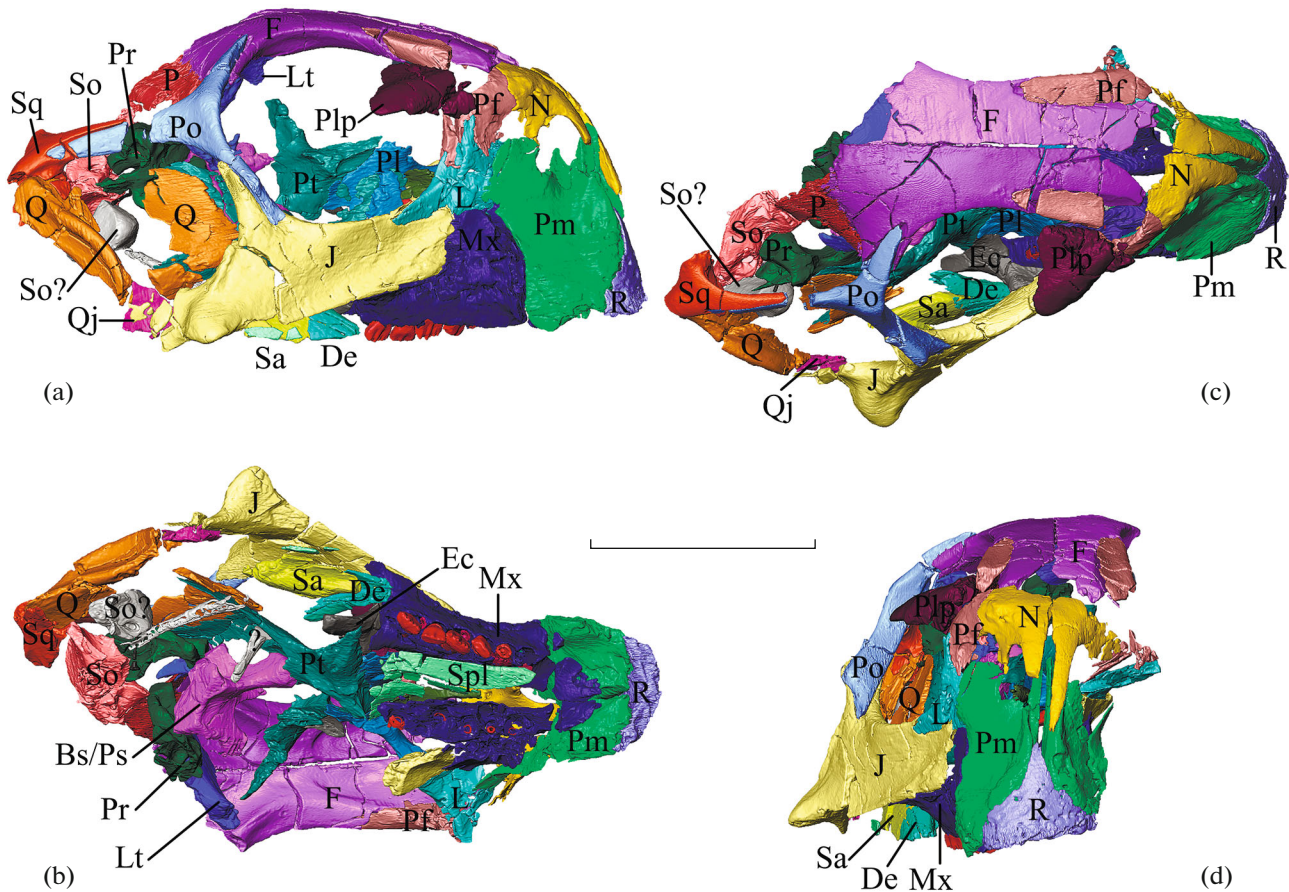


Fig. 2. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented skull KOKM 22985/5 in lateral (a), ventral (b), dorsal (c), and anterior (d) views. See text for abbreviations. Scale bar, 20 mm.

Psittacosaurus mongoliensis: Rozhdestvensky, 1973: p. 96; Rozhdestvensky, 1974: p. 122; Rozhdestvensky, 1977: p. 106; Nesov, 1995: p. 87; Alifanov et al., 1999: p. 492.

Psittacosaurus aff. *mongoliensis*: Voronkevich, 1998, p. 191, text-Figs. 2–4.

Psittacosaurus cf. *xinjiangensis*: Alifanov et al., 1999, p. 492.

Psittacosaurus sibiricus: Leshchinskiy et al., 2000: p. 364, text-Fig. 3; Averianov et al., 2006: p. 362, text-Figs. 2–23, 24D; Sereno, 2010: p. 34; Alifanov, 2012: p. 250; Podlesnov, 2018: text-Figs. 1–6; Skutschas et al., 2021: text-Figs. 2–8.

Holotype. PM TGU 16/4-20, an articulated almost complete adult skeleton including the skull.

Type locality and horizon. Shestakovo 3, Chebula rayon, Kemerovo oblast-Kuzbass, Russia; Ilek Formation, Lower Cretaceous (Aptian).

Studied specimens. KOKM 22985/5, a partially preserved and mostly articulated skull of a juvenile animal (Fig. 1a). The skull length is 58 mm. The right side is well preserved (Fig. 2a), whereas the left side is almost totally destroyed (Figs. 2c, 2d). The basioccipital and exoccipital/opisthotic are not preserved. Among the lower jaw bones, only the right splenial and small fragments of the right dentary and angular are preserved.

KOKM 22985/2, the skull articulated with the lower jaws of an adult animal (Fig. 1b). The skull length from the rostrum end to the squamosal is 220 mm; the transverse width between the ends of squamosal processes is 290 mm. The anterior part of the skull roof is destroyed (Figs. 3, 4b, 5), as well as the right squamosal and quadrate. The braincase is completely preserved (Figs. 4a, 6, 7). Both studied specimens come from the type locality.

DESCRIPTION

Dermal Skull Roof

Rostral. The rostral is well preserved in both specimens (Figs. 2, 3, 4b, 5–8). The rostral is an unpaired bone forming the anterior part of the rostrum and contacting the premaxillae posteriorly. The rostral is convex anteriorly and triangular in anterior/posterior view (Figs. 8a, 8b, 8f, 8g), with the dorsally pointed nasal process and a wide edentulous cutting edge shearing against a similar cutting edge on the pre-dentary. On the anterior surface, there are numerous vascular foramina along the cutting edge, and the rostral

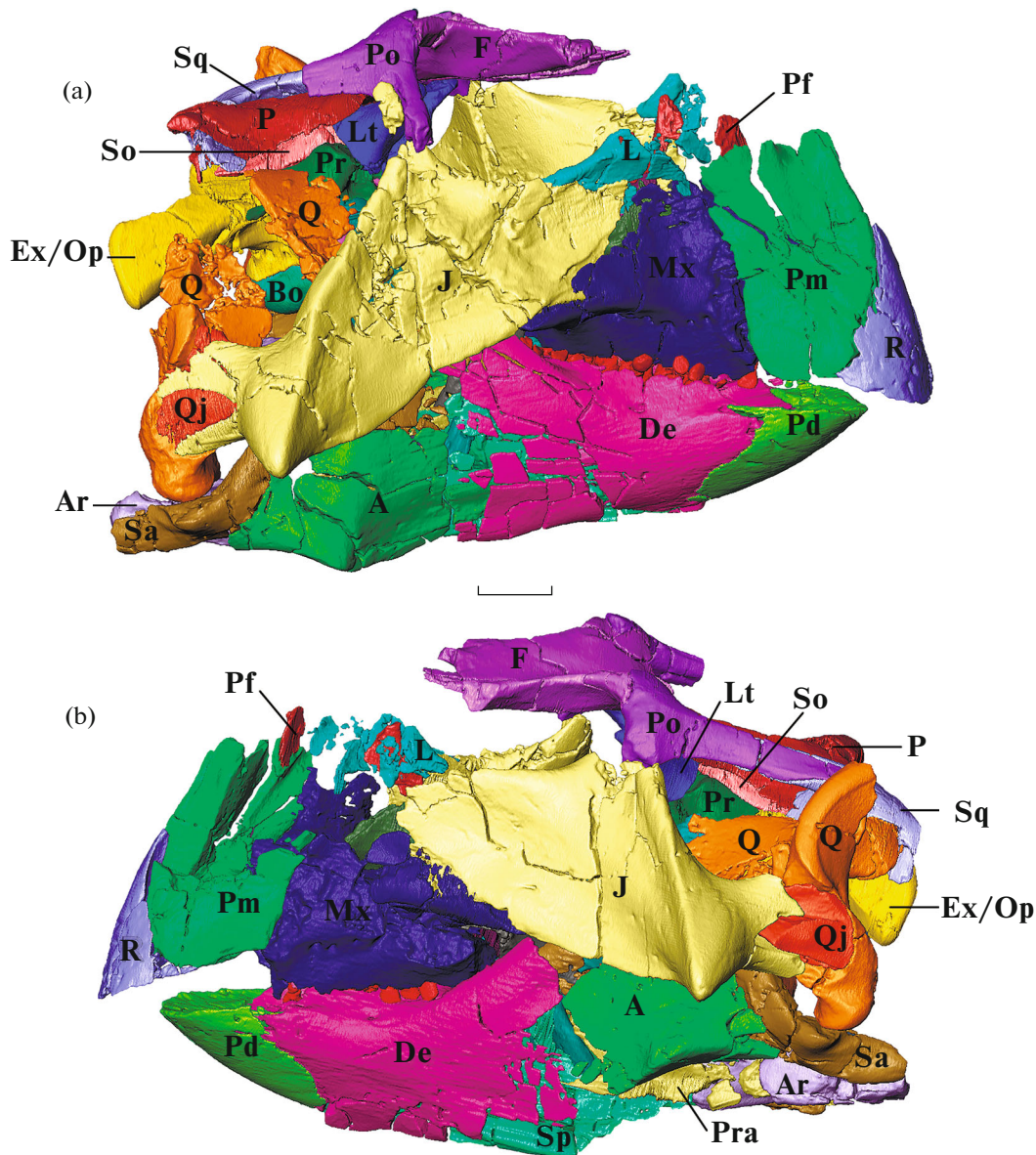


Fig. 3. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented skull KOKM 22985/2 in right lateral (a) and left lateral (b) views. See text for abbreviations. Scale bar, 20 mm.

was likely covered by the keratinous sheath at least partially. In lateral view, the rostral is also triangular, with straight cutting edge, convex anterior margin, and concave posterior margin (Figs. 8c, 8h). On the posterior side, there is a flat triangular area in the middle, which continues dorsally into the medial crest (Figs. 8b, 8g). The triangular area and the medial crest are flanked by the depressed areas that contact the premaxillae. The triangular area is forming the anterior wall of the nasal cavity in the skull. Ventrally, there is a free tritulating surface facing posteroventrally. There are some proportional differences between the juvenile (Figs. 8a–8e) and adult (Figs. 8f–8j) specimens. On the juvenile specimen, the rostral is wider

than high, with larger premaxillary facets and smaller tritulating surface. The nasal process is more clearly separated by concave margins of the bone and the medial crest is longer. The rostral is not coossified with the premaxillae. It is coossified in the holotype of *P. gobiensis* (Serenio et al., 2010).

Premaxilla. Both premaxillae are preserved in KOKM 22985/5, although the left bone is not complete (Fig. 2). In KOKM 22985/2, the left bone is incomplete and the right bone is damaged dorsally (Figs. 3, 4b, 5). The premaxilla is a large plate-like bone forming most of the lateral surface of the preorbital part of the skull (Fig. 9). The premaxilla contacts

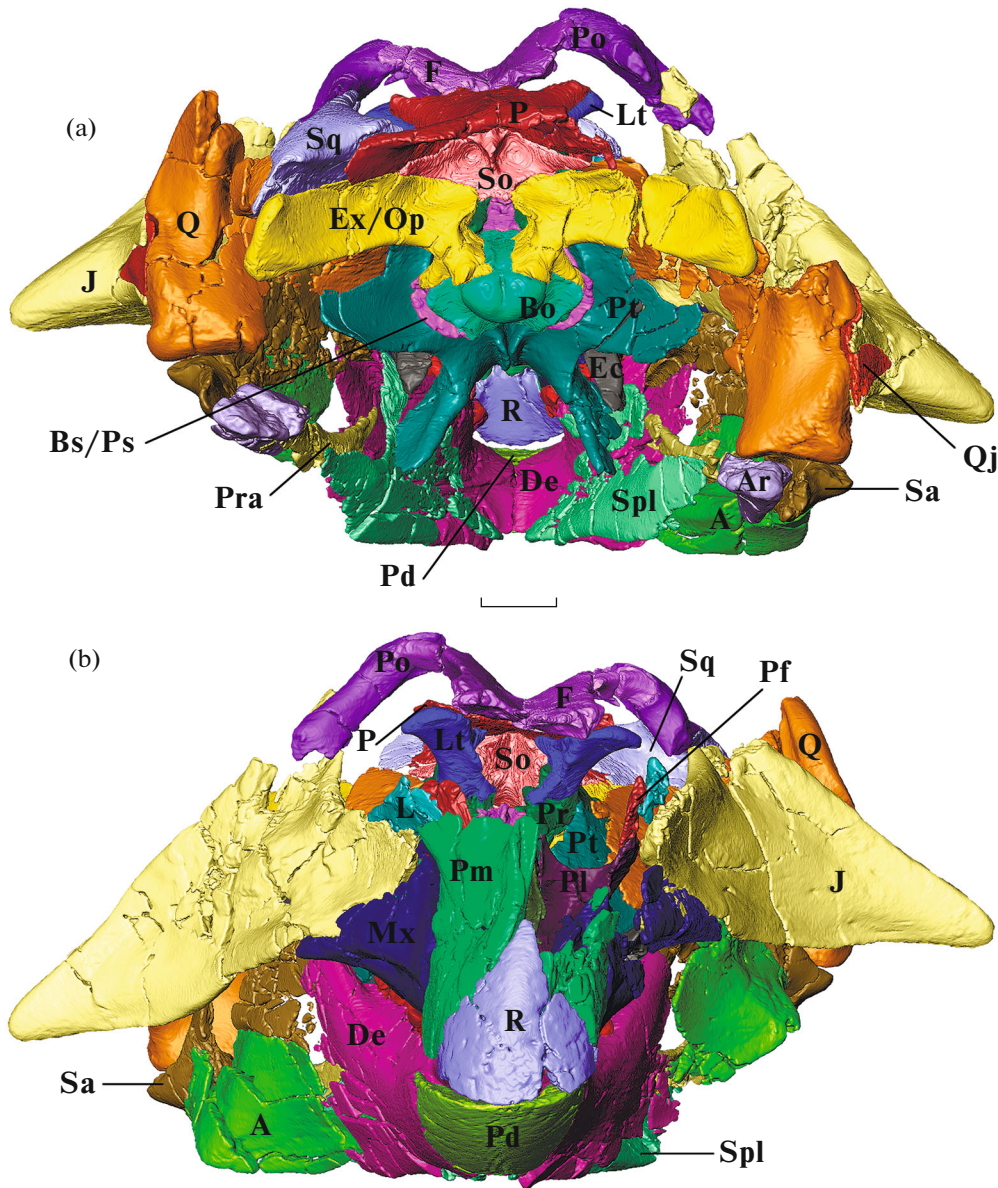


Fig. 4. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented skull KOKM 22985/2 in posterior (a) and anterior (b) views. See text for abbreviations. Scale bar, 20 mm.

the rostral anteriorly, nasal dorsally, prefrontal and lacrimal posterodorsally, and maxillary posteriorly. Contrary to the previous description of *P. sibiricus* (Averianov et al., 2006), the premaxilla does not contact the jugal. The premaxilla forms the ventral margin of the nasal opening. The ratio of the premaxilla length to the height is about 0.6 in both specimens. The bone is thick along the anterior margin, whereas its posterior part is a thin plate previously described as the posterolateral process (Averianov et al., 2006). There are two facets along the anterior margin set at an obtuse angle. The flat medial facet is for the opposite premaxilla. It is widest at its midheight and pointed ventrally.

In adult KOKM 22985/2, there is a vertical ridge in dorsal part of the premaxilla facet, which is absent in the juvenile KOKM 22985/5. The lateral facet along the anterior margin is for the rostral. It occupies the ventral half of the bone and is slightly convex. The rostral facet is pointed dorsally and expands laterally in the ventral part. Its dorsal part is on the medial side of the bone and ventral part extends on the lateral side. Within the rostral facet, there is a subvertical canal that continues onto the rostral. In the juvenile KOKM 22985/5, this canal is relatively smaller. Medial to the canal, the ventral side of the anterior premaxilla margin projects into a short sharp process with convex lateral and flat

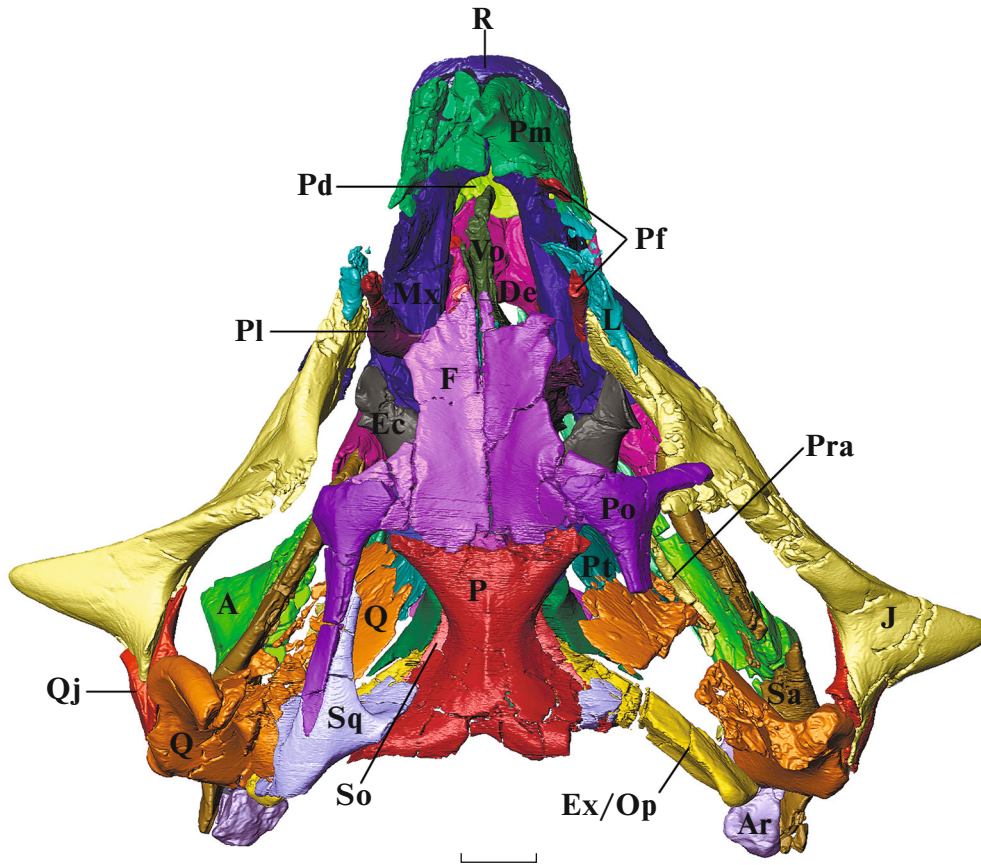


Fig. 5. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ileik Formation, Lower Cretaceous. Segmented skull KOKM 22985/2 in dorsal view. See text for abbreviations. Scale bar, 20 mm.

medial sides (anteroventral process or anteroventral tip). Dorsal to the rostral facet there is a deep vertical groove for the rostroventral process of the nasal, which is placed on a spine-like nasal process of the premaxilla (Figs. 9a, 9c, 9e, 9g, 9i, 9k) which probably homologous posterodorsal process in *Thescelosaurus neglectus* (Boyd, 2014: Figs. 5a, 5b). The elongate posterodorsal part of the premaxilla separates the maxilla from the nasal opening. Along the margin of the nasal opening, there is a lateral depression, more pronounced in the juvenile KOKM 22985/5 (Fig. 9a). There are three nutrient foramina on the lateral side of the premaxilla along its anterior margin in the juvenile KOKM 22985/5. In an adult KOKM 22985/2, this area is partially destroyed and nutrient foramina cannot be detected there. On the medial side, somewhat below the midheight of the bone, there is a shelf-like palatine process (lamina palatina) (Figs. 9b–9f, 9h–9l). The angle between the palatine process and the main body of the bone is about 45°. The palatine process is oriented obliquely relative to the dorsoventral axis of the bone, extending anteroventrally-dorsolaterally. Its anterior margin projects towards the sharp anteroventral process of the bone. The anterior part of the palatine process

contacts the opposite premaxilla, whereas its posterior parts contacts the maxilla (Figs. 9b, 9d, 9h, 9j).

Maxilla. The maxilla is preserved in both specimens (Figs. 2, 3). The maxilla is a stout bone with four processes (Fig. 10). The maxilla is vertically orientated in the skull. There are six teeth in the juvenile specimen KOKM 22985/5 (Fig. 10d). In the adult specimen KOKM 22985/2, there are ten tooth positions—nine teeth and one alveolus (Fig. 10j). Thus the maximum maxillary tooth count in *P. sibiricus* is ten instead of nine as previously thought (Averianov et al., 2006). The lateral surface of the maxilla is divided by a strong horizontal ridge into ventral part, bearing the teeth, and dorsally tapering dorsal process (Figs. 10a, 10g). The ridge is convex dorsally in KOKM 22985/5, whereas it is more horizontal in KOKM 22985/2. The angle between the ventral part and dorsal process is about 90°. In both specimens, there is a row of five nutrient foramina just ventral to the lateral ridge. In the juvenile specimen, these foramina perforate the maxillary and open on its medial side. In KOKM 22985/2, no nutrient foramina perforate the maxilla, in contrast with an adult specimen PM TGU 16/1-73, which has two posterior foramina perforating the bone (Averianov et al., 2006). There is no maxillary protu-

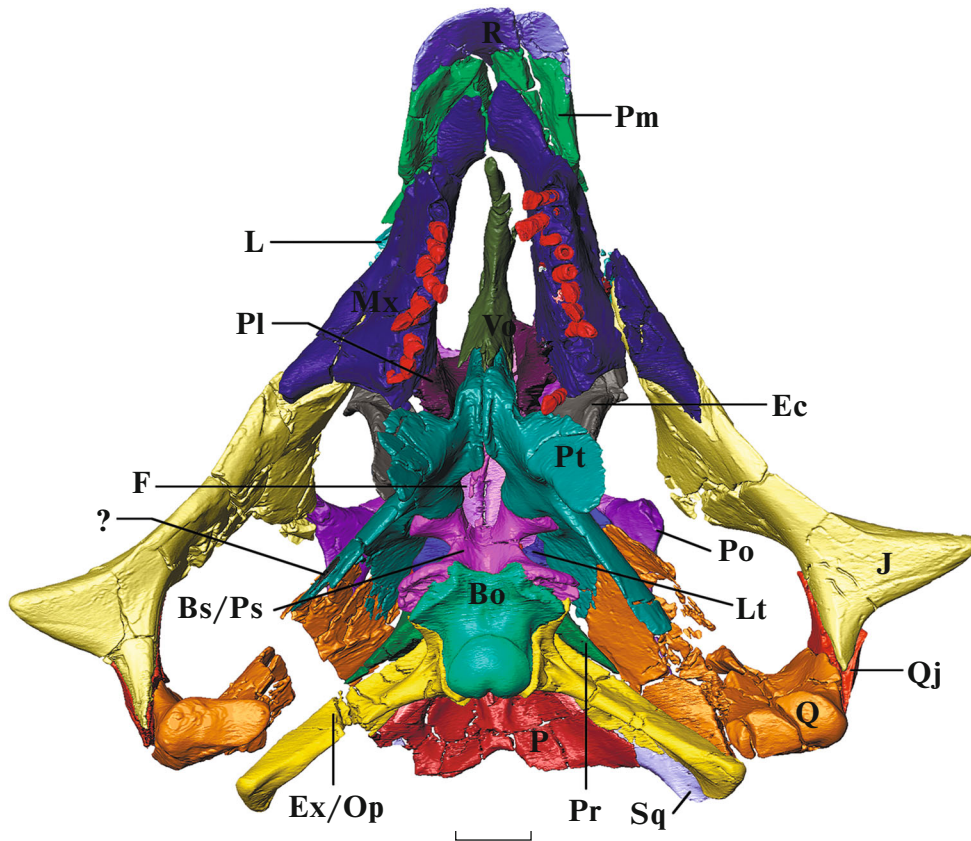


Fig. 6. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented skull KOKM 22985/2 without mandible in ventral view. See text for abbreviations. Scale bar, 20 mm.

berance on the lateral ridge. The ventral margin of the maxilla is straight. The anterior margin of the maxillary lateral surface is excavated by the premaxillary facet, which has a rough surface and is bordered posteriorly by a subvertical ridge. The premaxillary facet is more prominent in the adult KOKM 22985/2 compared with the juvenile KOKM 22985/5 (Figs. 10a, 10g). The premaxillary facet is of triangular shape in lateral view, with a prominent anterior process extending anteriorly and contacting the posterior end of the palatine process of the premaxillary (Fig. 10). The anterior margin of the maxilla is deeply incised just ventral to the anterior process. The anterior process is a thin plate, convex dorsally and tapering anteriorly (Fig. 10). The lateral ridge continues posteriorly into the posterior process, which is shorter than the anterior process and directed posterolaterally (Fig. 10). The posterior process is relatively larger in the adult KOKM 22985/2 compared with the juvenile KOKM 22985/5, which gives a triangular outline to the adult maxilla in ventral view (Figs. 10d, 10j). In ventral view, the maxilla has convex lateral and posterior margins and a straight medial margin. The tooth row is straight in ventral view (Figs. 10d, 10j). On the dorsal side of posterior process, there is a flat rough area contacting the jugal,

which is partially visible in lateral view (Figs. 10a, 10c, 10e, 10g, 10i, 10k). The jugal facet tapers anteriorly and extends as a narrow strip along the posterior margin of the dorsal process. On the medial side of maxilla, there is prominent ridge similar in size to that on the lateral side (Figs. 10b, 10h). This ridge is convex dorsally and continues anteriorly into the anterior process and posteriorly into the posteromedial process in the juvenile KOKM 22985/5 (Fig. 10b). In the adult KOKM 22985/2, this ridge is straight and obliquely oriented (Fig. 10h). Its anterior end terminates in a short process dorsal to the anterior process. The posterior part of this ridge is occupied by a rough palatine facet. The short posteromedial process contacts the palatine medially and the ectopterygoid posterolaterally (Figs. 10c, 10i). Ventral to the medial ridge, the medial surface of the bone is slightly concave. There is a row of six large replacement foramina on medial side just dorsal to the functional teeth in the juvenile KOKM 22985/5 (Fig. 10b). In the adult KOKM 22985/2, there are only two much smaller replacement foramina (Fig. 10h). Dorsally to the medial ridge, there is a thin dorsal process, which extends along the lateral margin of the bone. Its short dorsal margin contacts the lacrimal (Figs. 2a, 3b, 10b). In the previ-

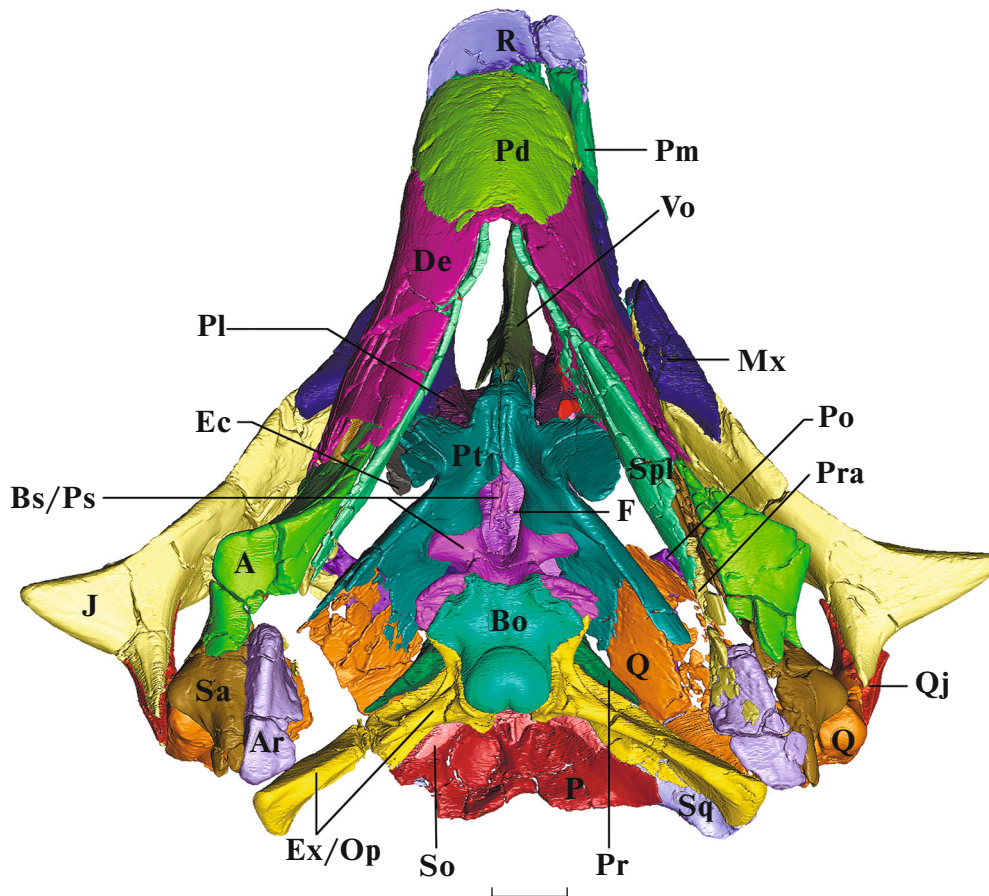


Fig. 7. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented skull KOKM 22985/2 with mandible in ventral view. See text for abbreviations. Scale bar, 20 mm.

ous description of *P. sibiricus*, based on less complete specimens, the maxillary-lacrimal contact was questioned (Averianov et al., 2006). The posterior part of the dorsal surface is occupied by a deep, anteriorly pointed recess for the ectopterygoid (Figs. 10c, 10i).

Nasal. The nasals miss its posterior margin contacting the frontals in the juvenile KOKM 22985/5 (Fig. 11) and are not preserved in the adult KOKM 22985/2. The nasal consists of the three processes: dorsal, rostroventral, and lateral. The rostroventral process is nearly vertical, trihedral, and rod-shaped. It fits into the groove on the anterior side of the premaxilla, dorsal to the rostral bone. The ventral margin of this process is nearly approaching the dorsal end of the rostral. The rostroventral process probably could have come into contact with the nasal process of rostral. The rostroventral processes of the opposite nasals are separated from each other by the premaxillae. The rostroventral process forms the anterior and dorsal margins of the nasal opening. In KOKM 22985/5, the length of the rostroventral process is about 9 mm. A plate-like lateral process forms the posterior margin of the nasal opening and overlapped dorsally by the pos-

terolateral part of the premaxilla (Figs. 2a, 2c). The dorsal process contacts the frontal posteriorly (the contact area is not preserved) and prefrontal posterolaterally, being overlapped by the prefrontal dorsally. On the ventral side of the dorsal process, there is a high longitudinal ridge flanked by convex depressions, as in *P. mongoliensis* (Sereno, 2010: text-Fig. 2.11B). The nasal is pierced by a short canal, which is parallel to this ridge and opens ventrally on its lateral slope. The opposite nasals contact by a short area confined to the dorsal process. The contact area of each nasal has a groove and a ridge, which fit in the corresponding ridge and groove of the opposite nasal.

Lacrimal. The lacrimal is incomplete in KOKM 2985/2. In KOKM 2985/5, both lacrimals are complete except some parts of the lacrimal canal walls (Fig. 2). The lacrimal is a thin plate-like triangular bone pierced by a large lacrimal canal (Fig. 12). Lacrimal forms the anteroventral margin of the orbit. The anterior margin of the lacrimal is overlapped laterally by the posterodorsal process of the premaxilla (Figs. 2a, 2d). The ventral margin is concave in lateral view and represents a sharp ridge fitting in the corre-

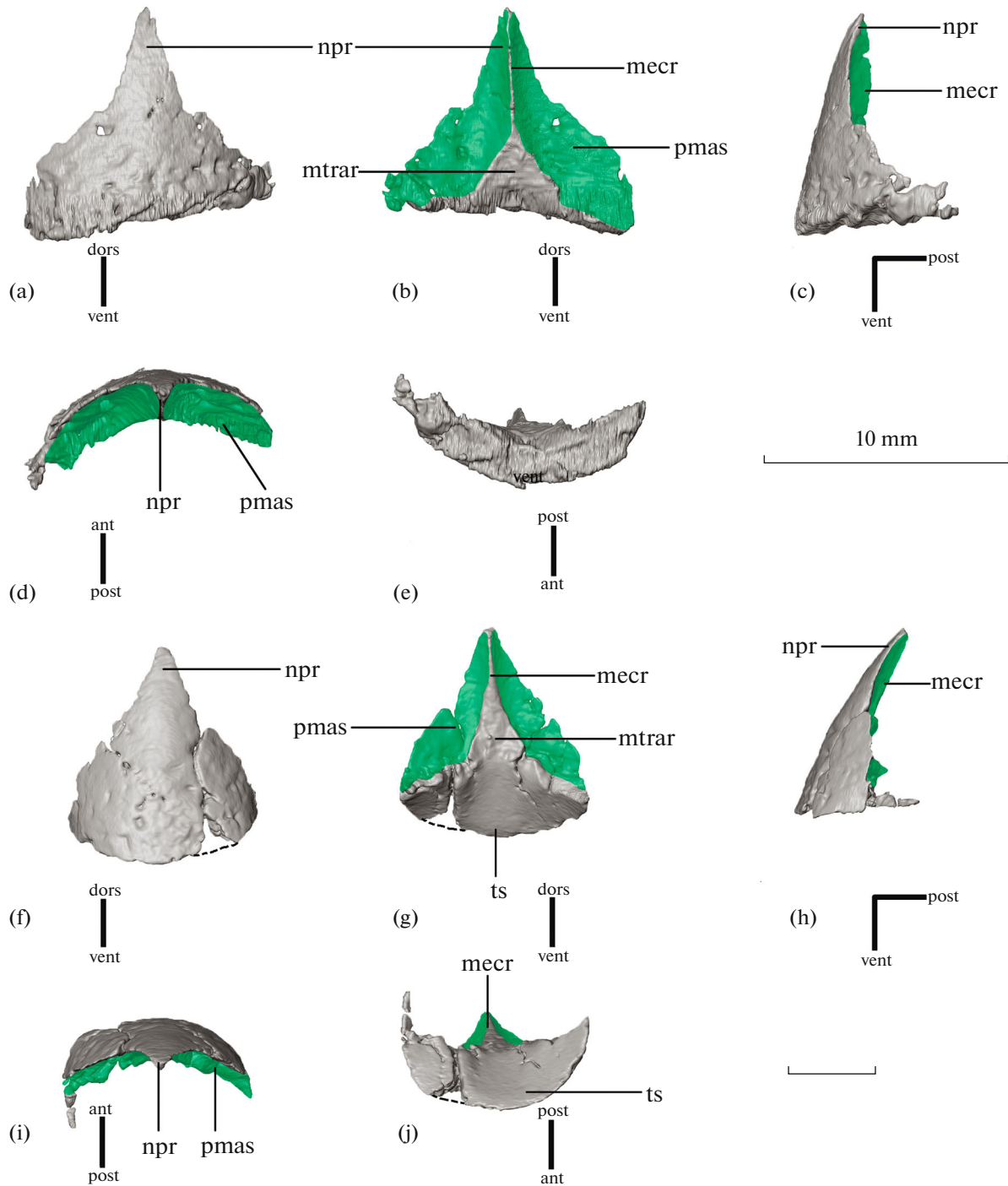


Fig. 8. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Rostral of KOKM 22985/5 (a–e) and KOKM 22985/2 (f–j). (a, f) anterior view; (b, g) posterior view; (c, h) left lateral view; (d, i) dorsal view; (e, j) ventral view. See text for abbreviations. Scale bar, 10 mm.

sponding groove on the jugal (Figs. 12a–12d). Its anterior part is overlapped by the maxilla laterally. The posterior margin of the lacrimal, participating in the orbit, is concave in lateral view (Figs. 12a–12d). Most of the medial side of the lacrimal is occupied by a flat facet for the prefrontal (Figs. 12c, 12d). Along its ven-

tral margin, there is a smaller facet for the jugal (Figs. 12c, 12d). The posterior margin of the lacrimal is thin dorsally and ventrally and expanded in the middle, where there is a large oval lacrimal foramen (Figs. 12e, 12f). The lacrimal canal expands anteriorly and occupies most of the lacrimal body. The lateral

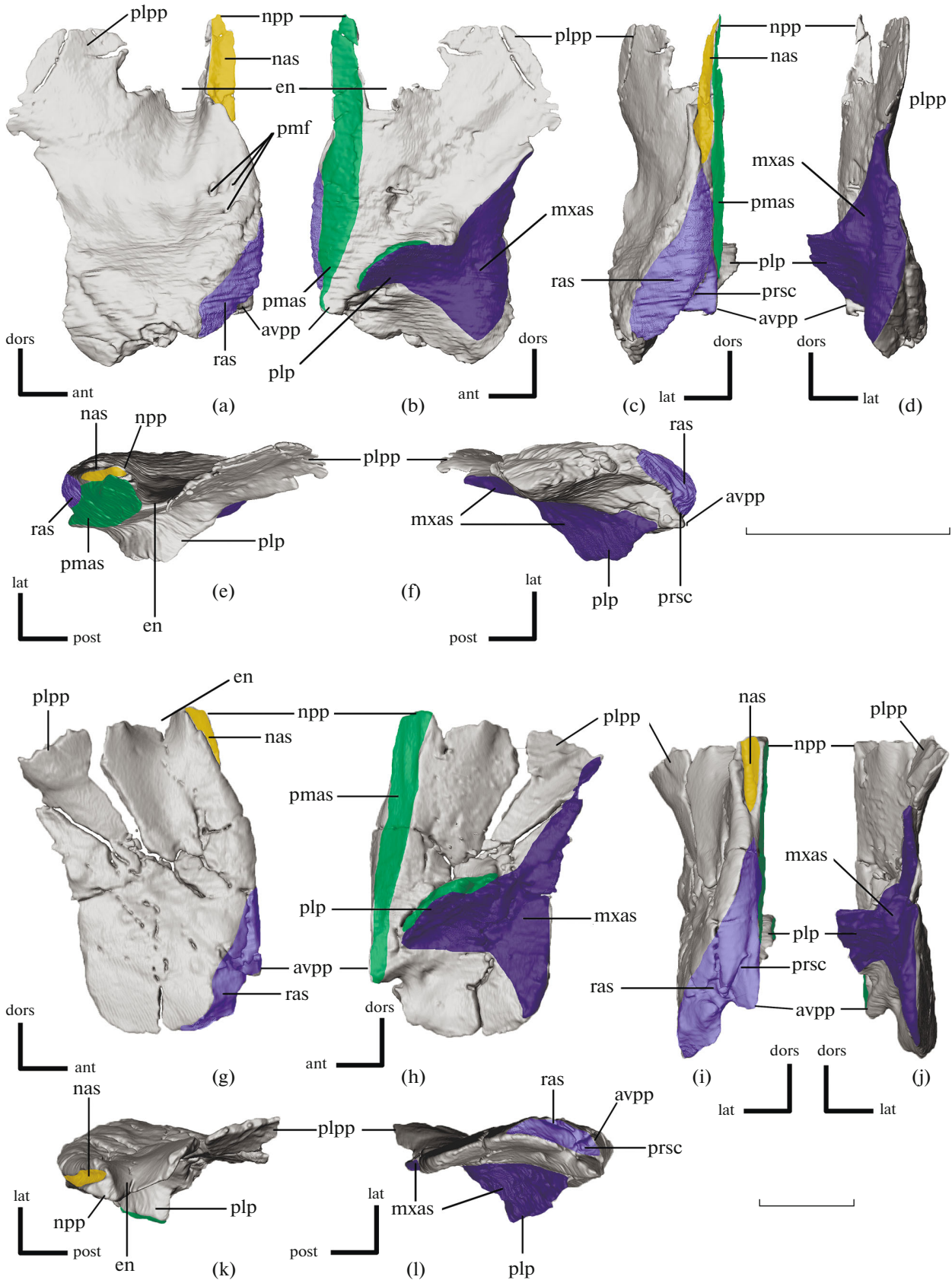


Fig. 9. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right premaxilla of KOKM 22985/5 (a–f) and KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i) anterior view; (d, j) posterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bar, 10 mm.

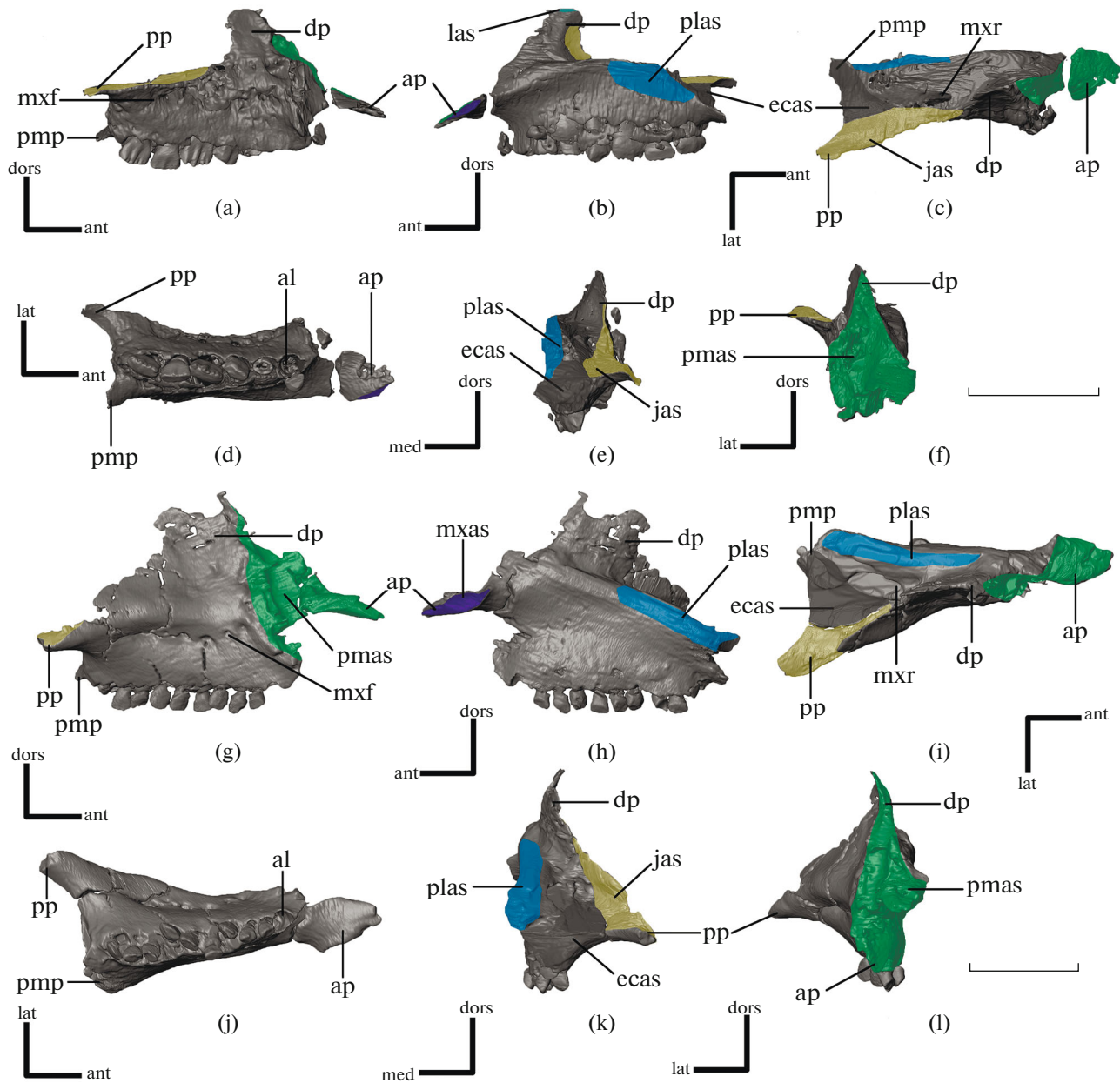


Fig. 10. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right maxilla of KOKM 22985/5 (a–f) and KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i) dorsal view; (d, j) ventral view; (e, k) posterior view; (f, l) anterior view. See text for abbreviations. Scale bars, 10 mm for (a–f) and 30 mm for (g–l).

wall of the lacrimal canal is incompletely preserved. In psittacosaurids, the lateral wall of the lacrimal canal is not ossified, leaving the premaxillary-lacrimal foramen there (Serenó, 2000, 2010), but in the holotype of *P. sibiricus* it was apparently fully ossified (Averianov et al., 2006).

Prefrontal. The prefrontals are partially preserved in KOKM 22985/5 (Figs. 2a, 2c, 2d). The prefrontal is a relatively small bone, exposed on dorsal and lateral sides of the skull and forming the anterodorsal margin

of the orbit. The bone consists of two parts oriented at a nearly right angle, the posterior process, directed and tapering posteriorly, and the anterior part, directed and tapering ventrally (Fig. 13). The posterior process is triangular in cross-section, with slightly concave dorsal surface and convex ventrolateral surface (Figs. 13a, 13e). The angle between the two surfaces is about 45°. On the ventrolateral surface, there is depression for reception of the palpebral horn, which is only partially preserved (Fig. 13a). The ventromedial surface, contacting the frontal, is flat ante-

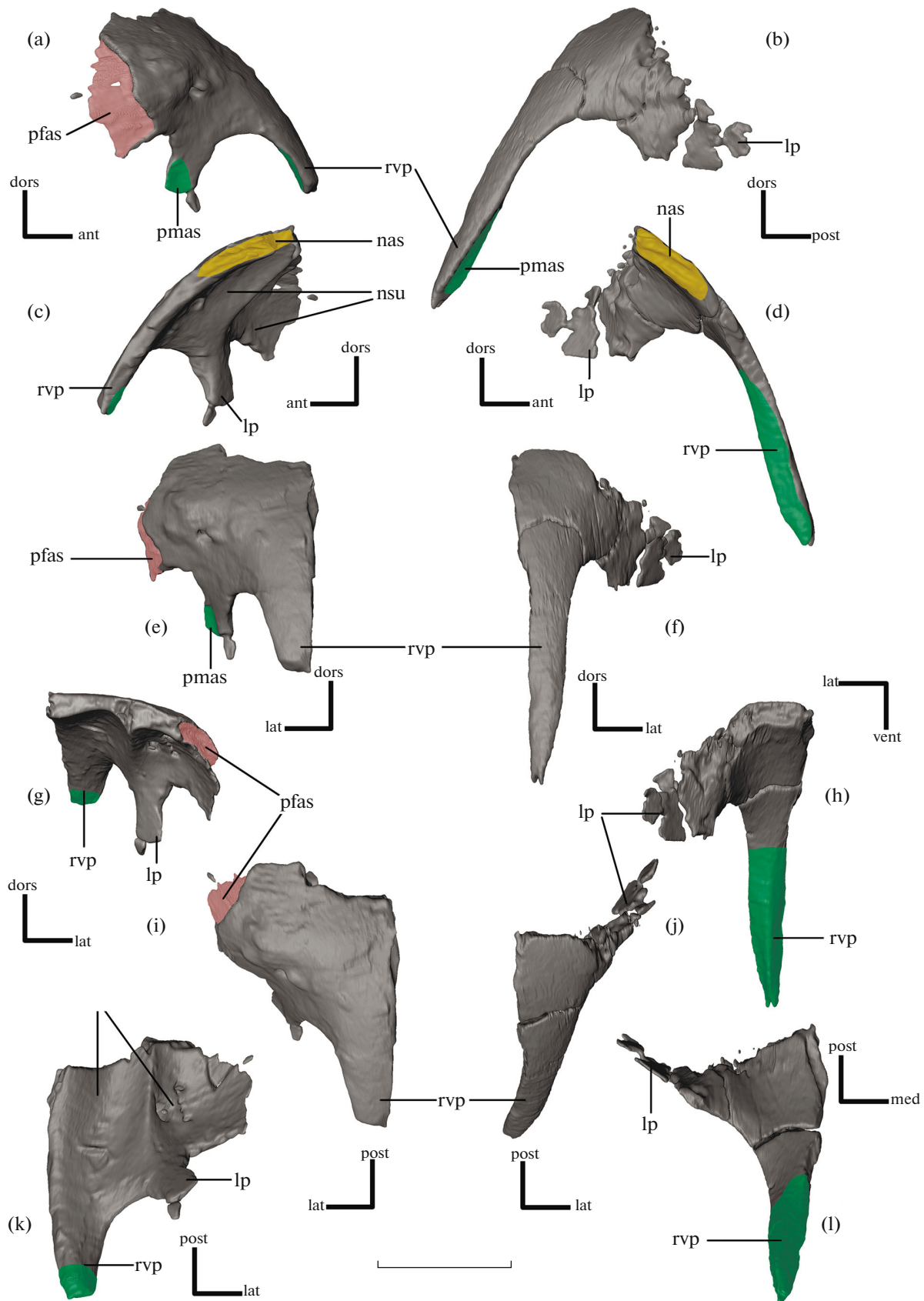


Fig. 11. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right (a, c, e, g, i, k) and left (b, d, f, h, j, l) nasals of KOKM 22985/5. (a, b) Lateral view; (c, d) medial view; (e, f) anterior view; (g, h) posterior view; (i, j) dorsal view; (k, l) ventral view. See text for abbreviations. Scale bar, 5 mm.

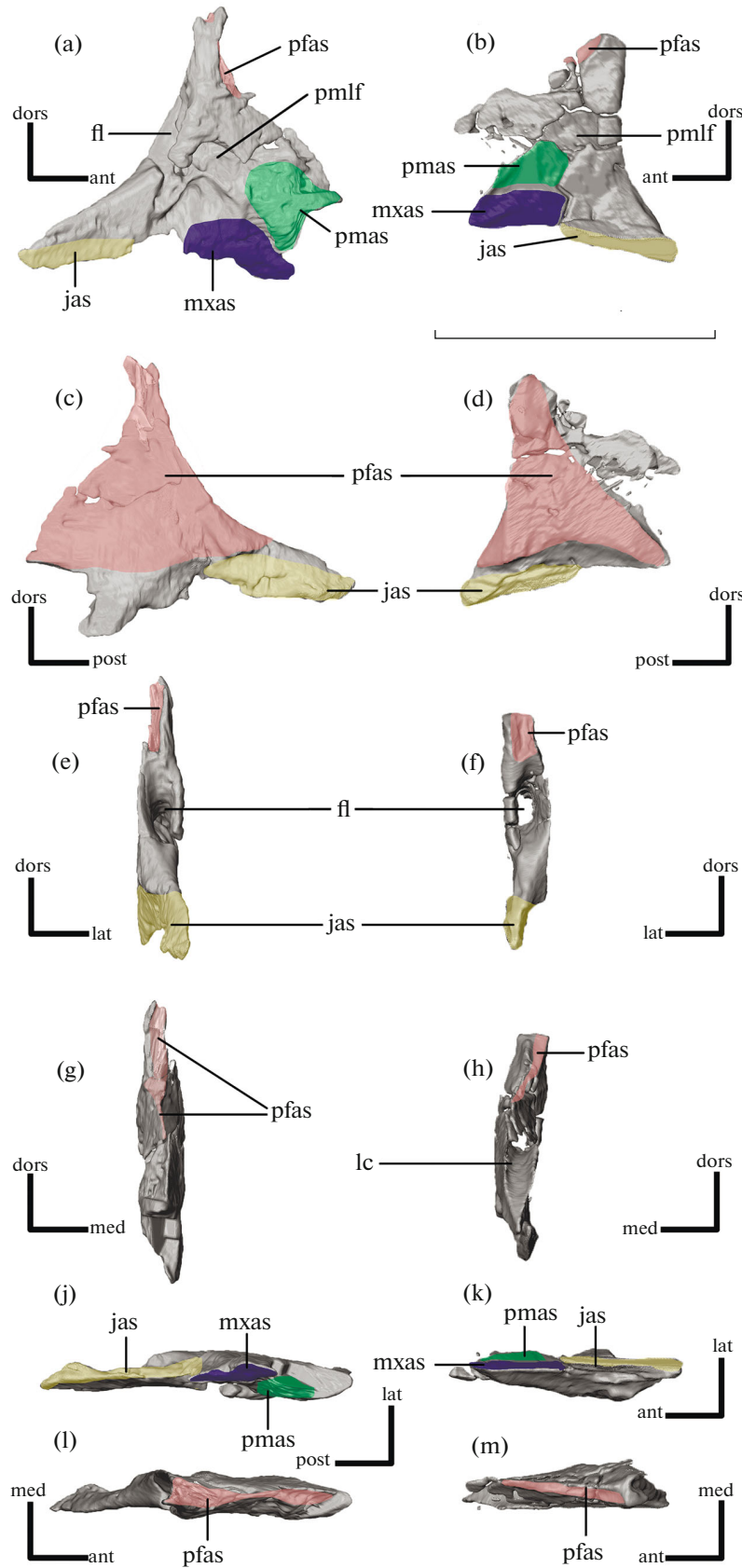


Fig. 12. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right (a, c, e, g, j, l) and left (b, d, f, h, k, m) lacrimal of KOKM 22985/5. (a, b) Lateral view; (c, d) medial view; (e, f) posterior view; (g, h) anterior view; (j, k) ventral view; (l, m) dorsal view. See text for abbreviations. Scale bar, 10 mm.

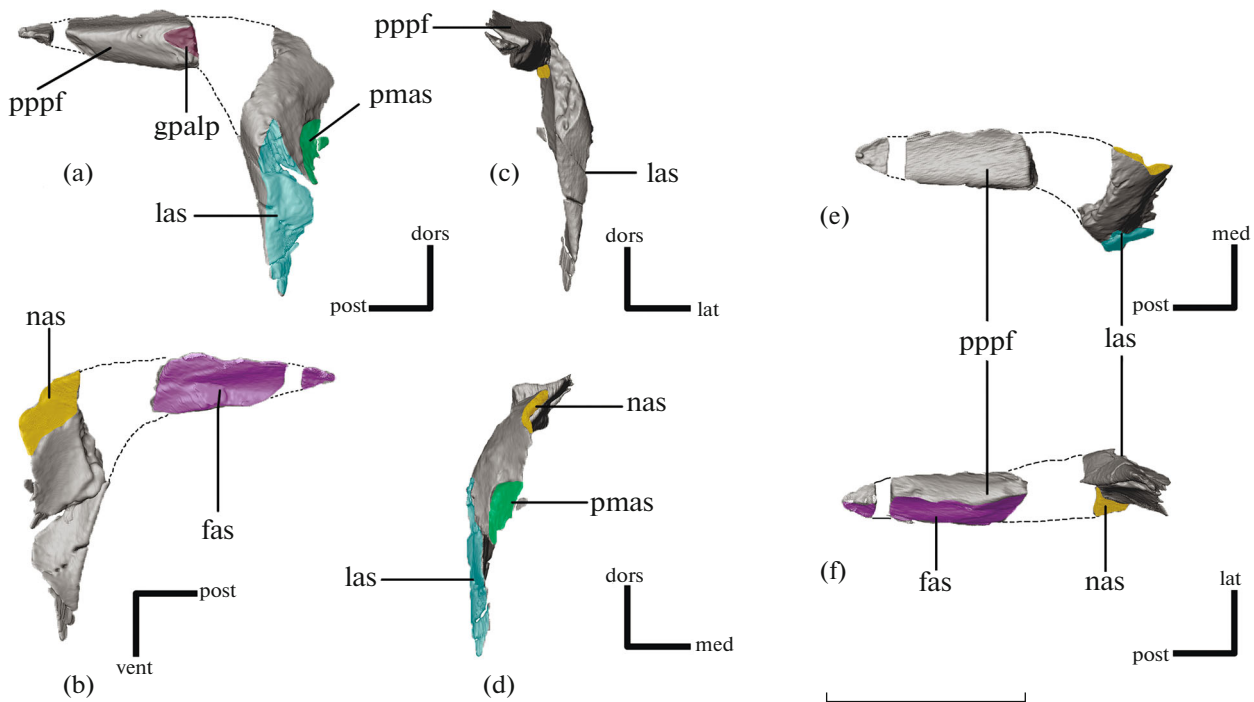


Fig. 13. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right prefrontal of KOKM 22985/5. (a) Lateral view; (b) medial view; (c) posterior view; (d) anterior view; (e) dorsal view; (f) ventral view. See text for abbreviations. Scale bar, 10 mm.

riorly and excavated by a wide groove posteriorly (Fig. 13b). The anterior part of the prefrontal is plate like, with a convex posteromedial side. Along the dorsal margin of this side, there is a depressed contact area with the nasal (Fig. 13b). The anterolateral side of the bone is slightly convex and has a large lacrimal facet on its ventral and lateral parts and a small premaxillary facet medially (Figs. 13a, 13d).

Postorbital. In KOKM 22985/5 only right postorbital is preserved, which is complete (Figs. 2a, 2c, 2d, 14a–14f). In KOKM 22085/2, both bones are fragmentary (Figs. 3–7, 14g–14r). The postorbital is a triradiate bone forming the posterior margin of the orbit, dorsal margin of the infratemporal fenestra, and anterolateral margin of the supratemporal fenestra (Figs. 2a, 2c, 5). In the juvenile specimen KOKM 22985/5, there is an obtuse angle between all the three postorbital processes (Figs. 14a, 14b). All processes are roughly similar in length. On the lateral side, at the confluence of ventral and medial processes, there is a slight eminence, the dorsal postorbital horn (Fig. 14a). The ventral process tapers ventrally in lateral view, but in anterior/posterior views has a consistent width (Figs. 14c, 14d). Its anterior surface is flat. The posterior surface is narrowed to a ridge dorsally and expanded ventrally, where it is excavated by a deep jugal facet (Fig. 14d). The ventral end of the ventral process fits into the socket on the jugal dorsal process (Fig. 2a). On the lateral side of the ventral process, close to its distal end present small growth

(Figs. 14a, 14c, 14d), which forms together with the corresponding structure on the jugal the postorbital-jugal horn. In the skull, the ventral process is oriented anteroventrally and somewhat laterally (Figs. 2a, 2c, 2d). The medial process tapers medially and has a triangular cross-section, with flat dorsal surface and a ridge on the ventral side. This ridge is confluent with the medial side of the ventral process. For most of its length, the medial process fits into the socket on the dorsal surface of the frontal (Figs. 2a, 2c). In the skull, the medial process is oriented anterodorsomedially. The posterior process is transversely thin and tapers posteriorly. For most of its length, it is adjacent by its medial side to the anterior process of the squamosal (Figs. 2a, 2c, 14b). The lateral side of the posterior process is flat, whereas on the medial side there is a longitudinal groove (Fig. 14b). In the skull, the posterior process is directed posteriorly and slightly laterally (Fig. 2c). The medial process on both postorbitals in KOKM 22985/2 is incomplete, but the size of the postorbital sulcus on the frontals clearly shows that medial process was proportionately as long as in KOKM 22985/5 (Fig. 5). On the medial side of the medial process, there is a small cup-like depression for the articulation with the latherosphenoid (Figs. 14b, 14c, 14f, 14g, 14i, 14l, 14n, 14o). The angle between the ventral and posterior processes is about 90°, as in other adult specimens of *P. sibiricus* (Averianov et al., 2006), in contrast with an obtuse angle in the juvenile specimen. The jugal facet occupies nearly all the

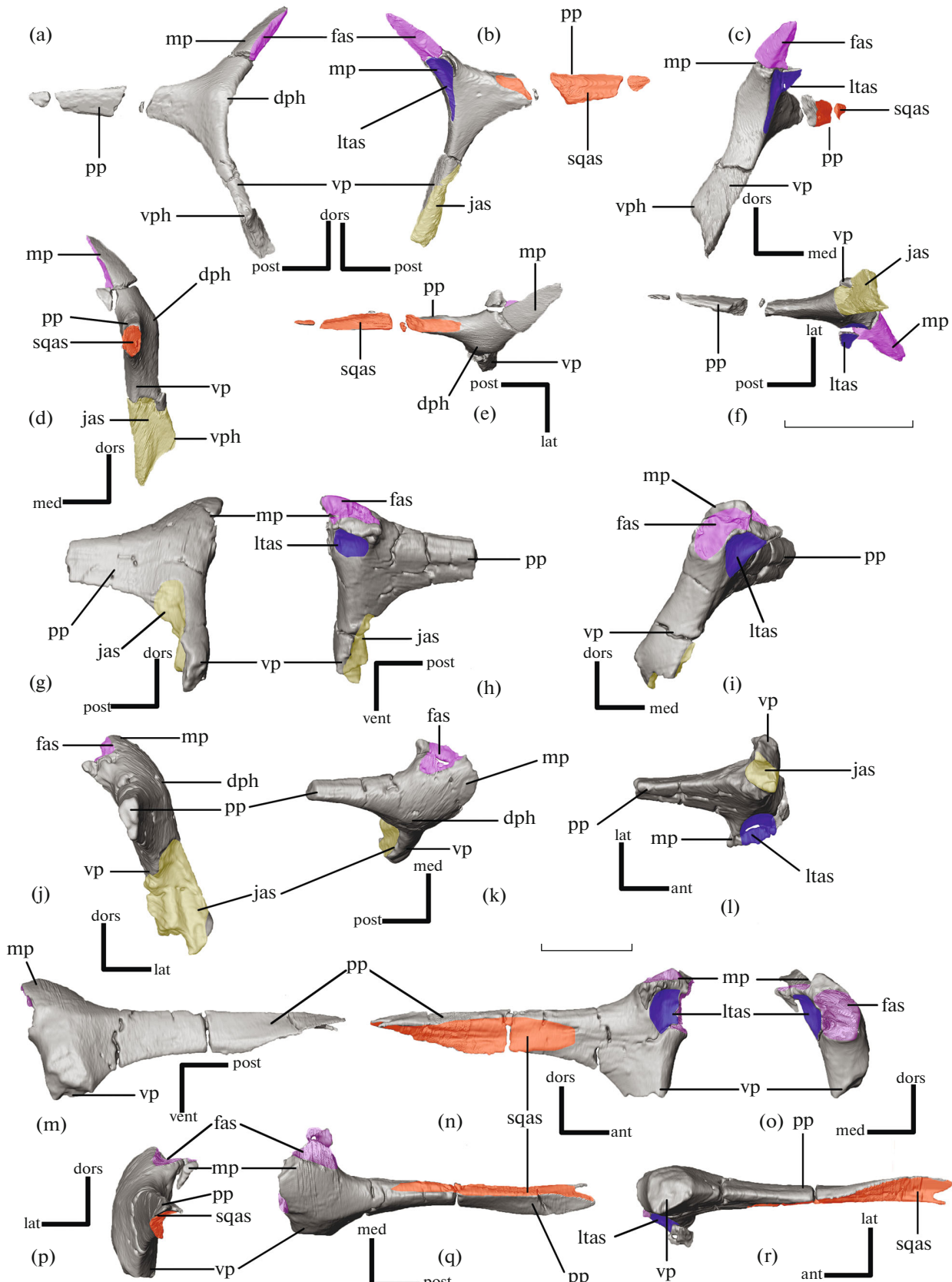


Fig. 14. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right postorbital of KOKM 22985/5 (a–f). Right (g–l) and left (m–r) postorbital of KOKM 22985/2. (a, g, m) Lateral view; (b, h, n) medial view; (c, i, o) anterior view; (d, j, p) posterior view; (e, k, q) dorsal view; (f, l, r) ventral view. See text for abbreviations. Scale bars, 10 mm for (a–f) and 20 mm for (g–r).

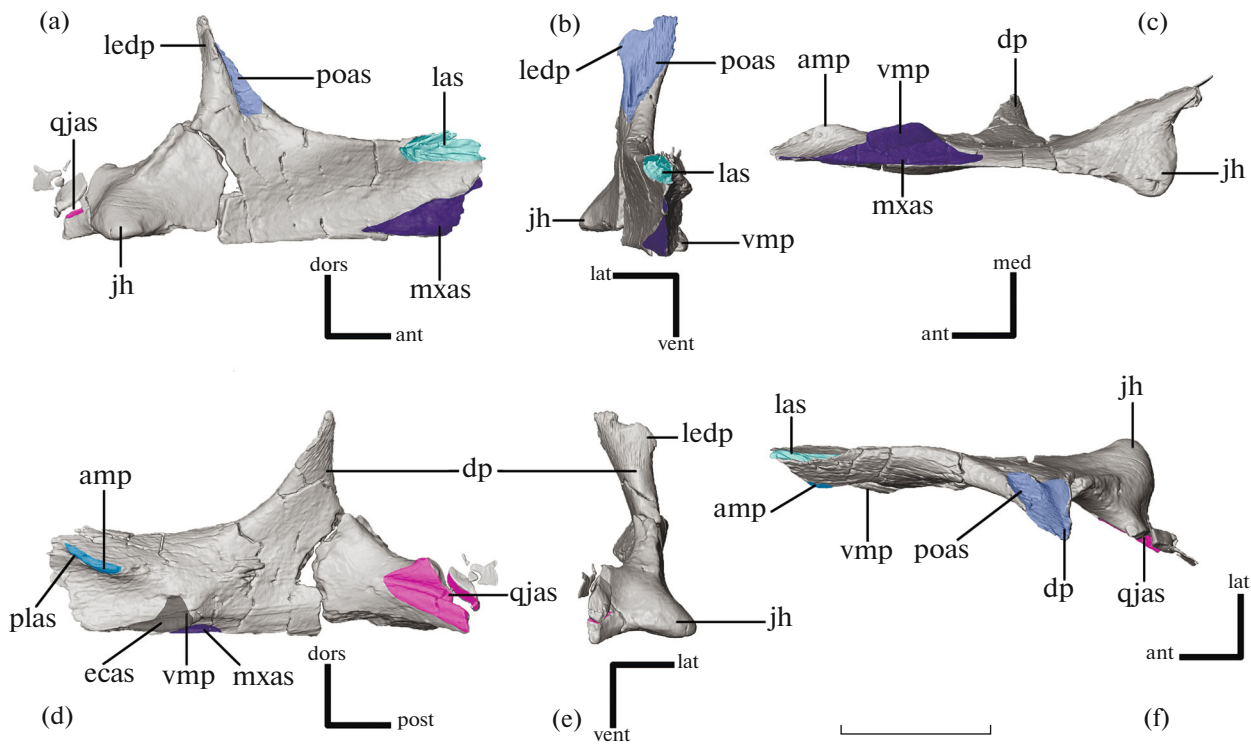


Fig. 15. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right jugal of KOKM 22985/5. (a) Lateral view; (b) anterior view; (c) ventral view; (d) medial view; (e) posterior view; (f) dorsal view. See text for abbreviations. Scale bar, 10 mm.

length of the ventral process (Fig. 14j), but only a half of its length in the juvenile specimen. The posterior process is somewhat wider transversely, with a flat dorsal surface and a smaller groove on the medial side compared with the juvenile specimen (Figs. 14n, 14q).

Jugal. The right jugal is complete in the juvenile KOKM 22985/5, and both jugals are complete in the adult KOKM 22985/2 (Figs. 2–5, 15, 16). This is a large bone forming the ventral margin of the orbit and the anteroventral margin of the infratemporal fenestra and having a large spine-like jugal horn projecting laterally. The length of the jugal is 30 mm in the juvenile KOKM 22985/5 and about 150 mm in the adult KOKM 22985/2. The shape of the bone is quite different in juvenile and adult specimens. In the juvenile specimen, the main body of the jugal is a thin vertical plate of rectangular shape (Fig. 15). Its lateral surface is slightly concave. The anteromedial corner of the jugal body lateral surface is occupied by a triangular maxillary facet with rough surface (Fig. 15a). The maxillary facet is also present on the ventral side of the jugal body as a triangular widening of the bone terminating into the ventromedial process (Fig. 15c). This process contacts also the lateral process of the ectopterygoid. On the anterodorsal corner of the jugal body, there is a deep groove for the lacrimal (Figs. 15a, 15b). The medial side of the jugal body is depressed between the ventromedial process and a ridge-like

anteromedial process (Fig. 15d). The ventromedial process connects with the dorsal surface of the maxillary posterior process ventrally and with the lateral process of the ectopterygoid. The jugal does not contact the premaxillary, contrary to the previous assumption (Averianov et al., 2006). The dorsal process is placed posterior to the bone midlength and directed posterodorsally and somewhat medially (Fig. 15). Its height is similar to that of the jugal body. The dorsal process is deeply excavated anteriorly by a groove for the postorbital. The dorsal process tapers dorsally in lateral/medial view, but slightly expands near dorsal end in anterior/posterior view (Figs. 15a, 15b, 15d, 15e). This lateral expansion of the dorsal process, together with the corresponding expansion of the ventral postorbital horn, form the postorbital-jugal horn (Figs. 15a, 15b, 15e). The dorsal margin of the jugal body is slightly concave anterior and posterior to the dorsal process. The posterior part of the jugal is about twice lower and deflected medially and slightly ventrally (Figs. 15a, 15c, 15d, 15f). It bears the jugal horn on lateral side and jugal prongs on medial side. The jugal horn is relatively small and has a blunt end. It has a flat ventral and convex dorsal surfaces. On the skull, the jugal horn is directed laterally and somewhat ventrally (Fig. 2). The jugal prongs are the two processes of similar size with a flat medial side, contacting the quadratojugal and separated by a slit receiving the

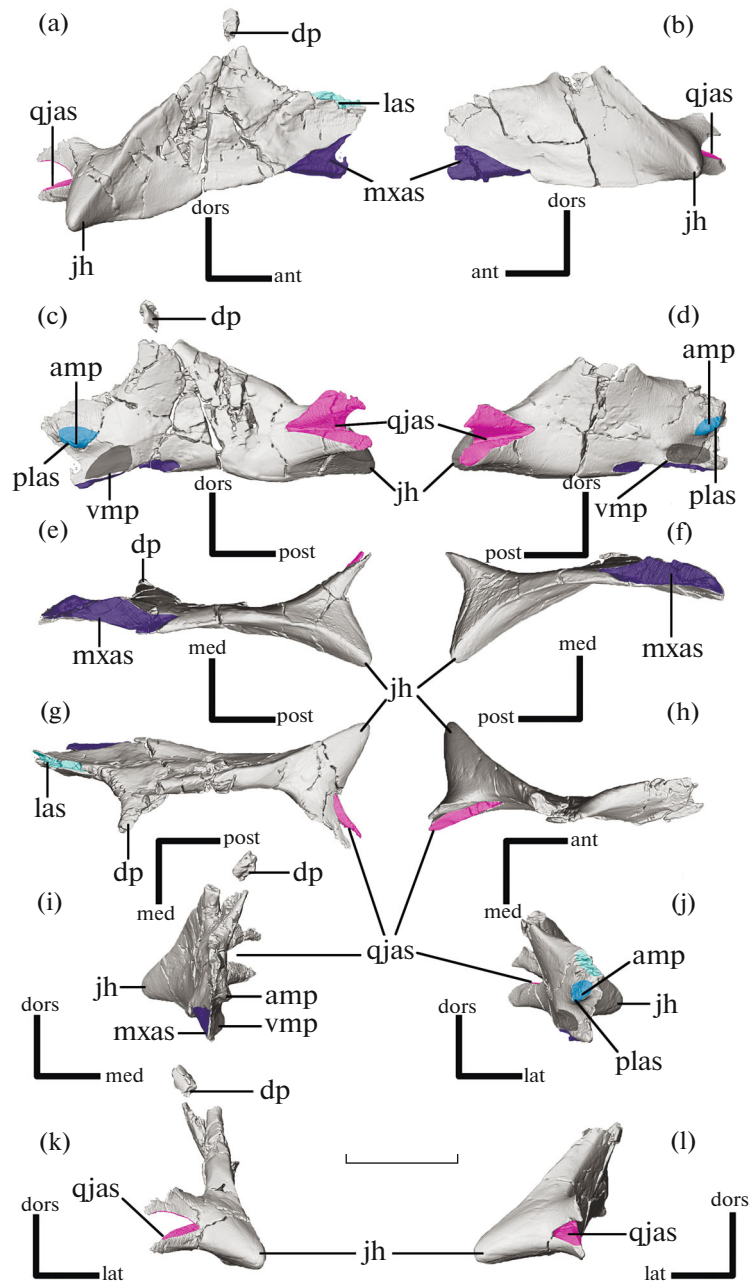


Fig. 16. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right (a, c, e, g, i, k) and left (b, d, f, h, j, l) jugal of KOKM 22985/2. (a, b) Lateral view; (c, d) medial view; (e, f) ventral view; (g, h) dorsal view; (i, j) anterior view; (k, l) posterior view. See text for abbreviations. Scale bar, 50 mm.

ridge on the quadratojugal (Fig. 15d). This slit extends anteriorly towards the posterior side of the jugal horn. On the adult bone, the jugal horn and prongs are much larger (Figs. 3–6, 16). The dorsal process is incomplete in both adult bones but it seems to be relatively smaller than in the juvenile specimen. The lateral surface of the jugal body is slightly concave, with a low horizontal ridge in the middle. The maxillary and lacrimal facets are smaller compared with the juvenile

bone (Figs. 16a, 16b). The postorbital facet is not as deep as on the juvenile bone. The jugal horn has a pointed end. It is triangular in cross section, with flat anterior, slightly concave ventral, and convex postero-dorsal sides. On the skull, it is directed laterally and somewhat ventrally, as in the juvenile specimen. The cleft between the jugal prongs is much wider than in the juvenile specimen.

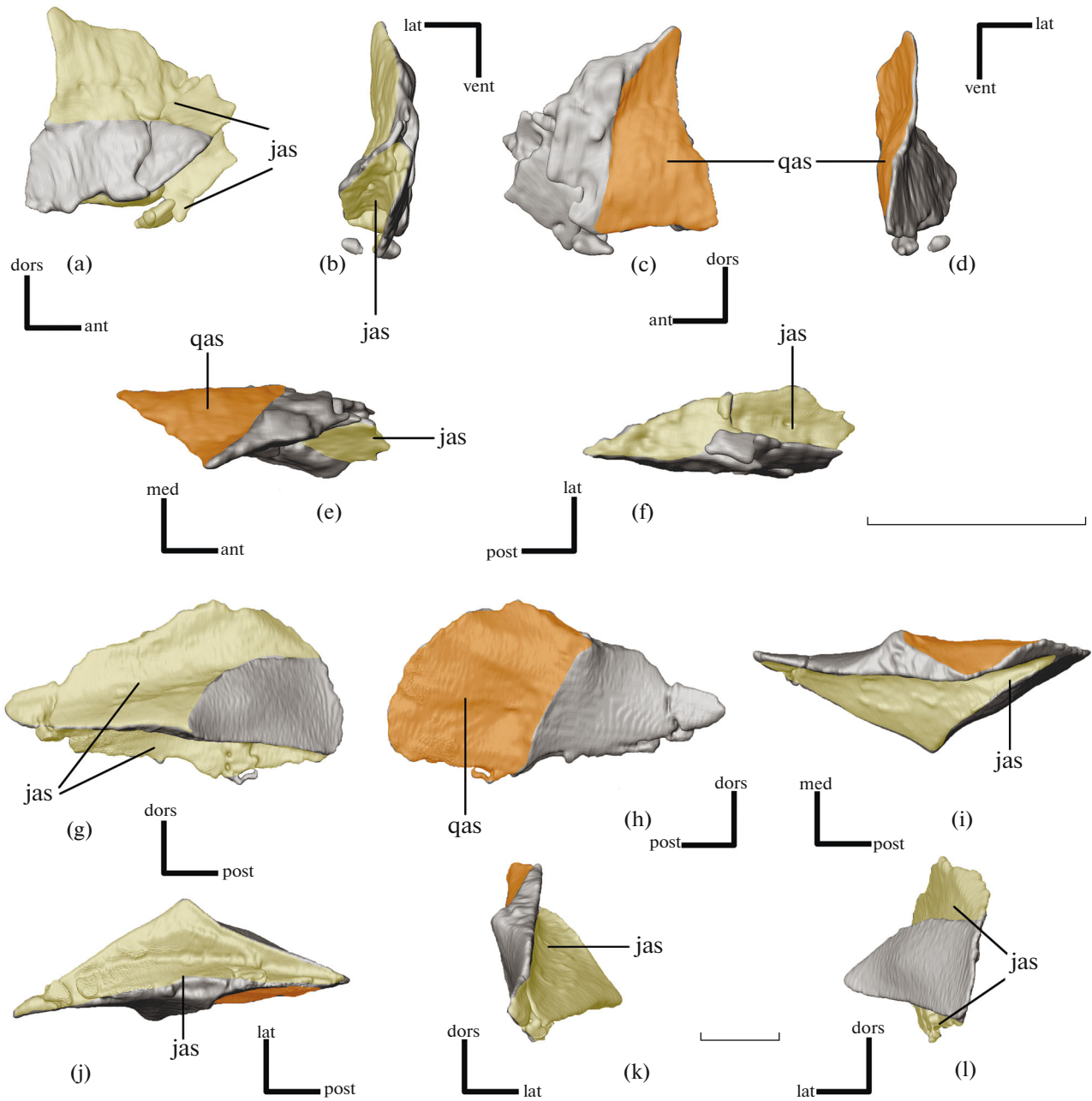
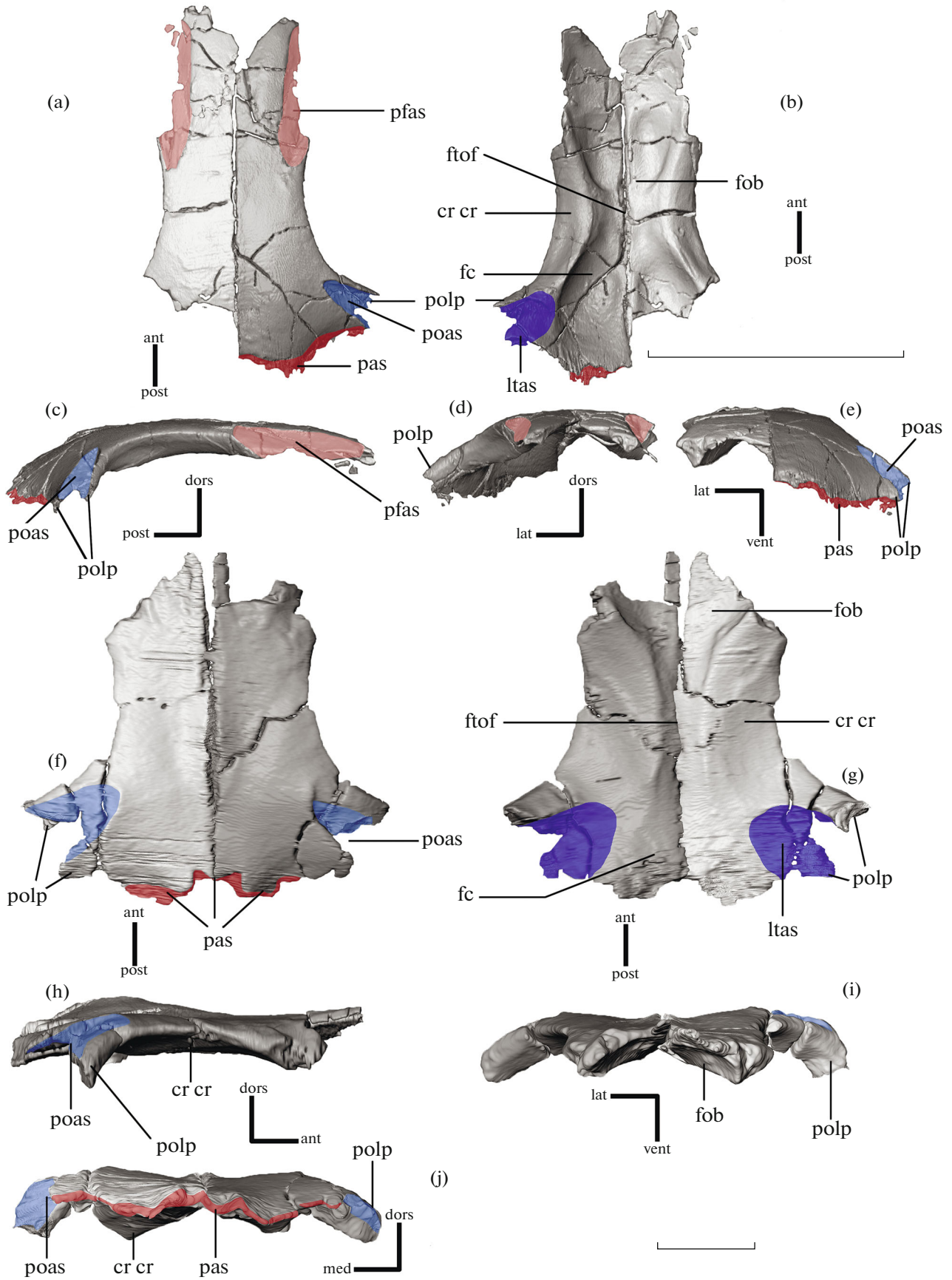


Fig. 17. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right quadratojugal of KOKM 22985/5 (a–f) and left quadratojugal of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, k) anterior view; (c, h) medial view; (d, l) posterior view; (e, i) dorsal view; (f, j) ventral view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 10 mm for (g–l).

Quadratojugal. In KOKM 22985/5, the right preserved quadratojugal is disarticulated and partially destroyed (Figs. 17a–17f). In KOKM 22985/2, both bones are almost complete, articulated with the jugal and quadrate (Figs. 2, 17g–17l). The quadratojugal

forms the posteroventral corner of the infratemporal fenestra. The bone is plate-like, with a strong horizontal ridge on the lateral side wedged between the jugal prongs (Fig. 17g). The flat exposed triangular area occupies the posterior half of this ridge. The dorsal

Fig. 18. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast–Kuzbass, Russia; Ilek Formation, Lower Cretaceous. Frontals of KOKM 22985/5 (a–e) and KOKM 22985/2 (f–j). (a, f) Dorsal view; (b, g) ventral view; (c, h) right lateral view; (d, i) anterior view; (e, j) posterior view. See text for abbreviations. Scale bars, 20 mm.



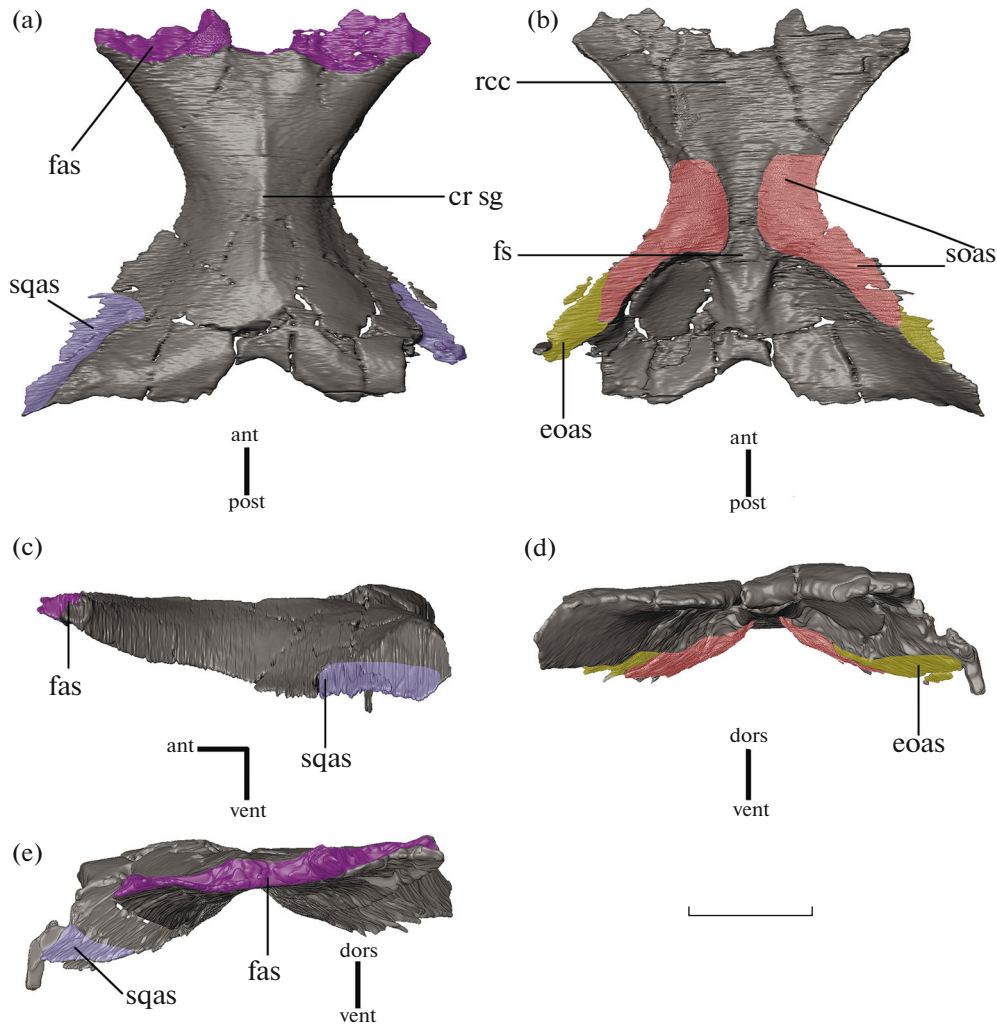


Fig. 19. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Parietal of KOKM 22985/2. (a) Dorsal view; (b) ventral view; (c) left lateral view; (d) posterior view; (e) anterior view. See text for abbreviations. Scale bar, 20 mm.

and ventral surfaces of the lateral ridge merge into a sharp crest in the anterior half of the ridge. These surfaces, as well as the rest of the bone, are covered by the jugal (Fig. 17g). The sharp and flat areas of the ridge meet at an obtuse angle (Figs. 17i, 17j). In contrast with *P. mongoliensis* and similarly with *P. meileyingensis*, the quadratojugal only partially covers the ventral part of the quadrate, which is visible in lateral view (Fig. 3b) (Serenio et al., 1988: text-Figs. 2A, 2D, 5). In the middle of the quadratojugal medial side, there is a subvertical ridge delimiting the anterior margin of a large quadrate facet (Figs. 17c, 17h).

Frontal. The frontals are paired bones occupying most of the skull roof (Figs. 2c, 5, 18). In an adult specimen of KOKM 22985/2, 3D models of the pressed in frontal were straightened to their natural anatomical position using the Transform Editor module of Avizo 9.1. The frontals contact the nasals anteriorly, prefrontals anterolaterally, postorbitals and lat-

erosphenoids posterolaterally, and parietals posteriorly. The anterior part of the frontals is missing in both specimens, and the left frontal of the juvenile specimen KOKM 22985/5 misses its posterolateral part (Figs. 2a, 5, 18a, 18b, 18f, 18g). Thus, the frontonasal articulation cannot be described. The frontal is a long bone expanded transversely posteriorly and, to a lesser extent, anteriorly (Figs. 18a, 18b, 18f, 18g). The medial margin, contacting the opposite frontal by a serrated suture, is straight. The free lateral margin, forming the dorsal margin of the orbit, is concave. The frontal overlaps anteriorly the medial process of the postorbital, excluding it from the dorsal orbital margin (Fig. 5). The frontal is convex dorsally, with the greatest convexity in the posterior part of the bone, opposite to the postorbital facet. The dorsal surface of frontal is smooth. The prefrontal facets are preserved only in KOKM 22985/5 (Figs. 18a, 18c). The prefrontal facet is a long groove extending along the anterolateral

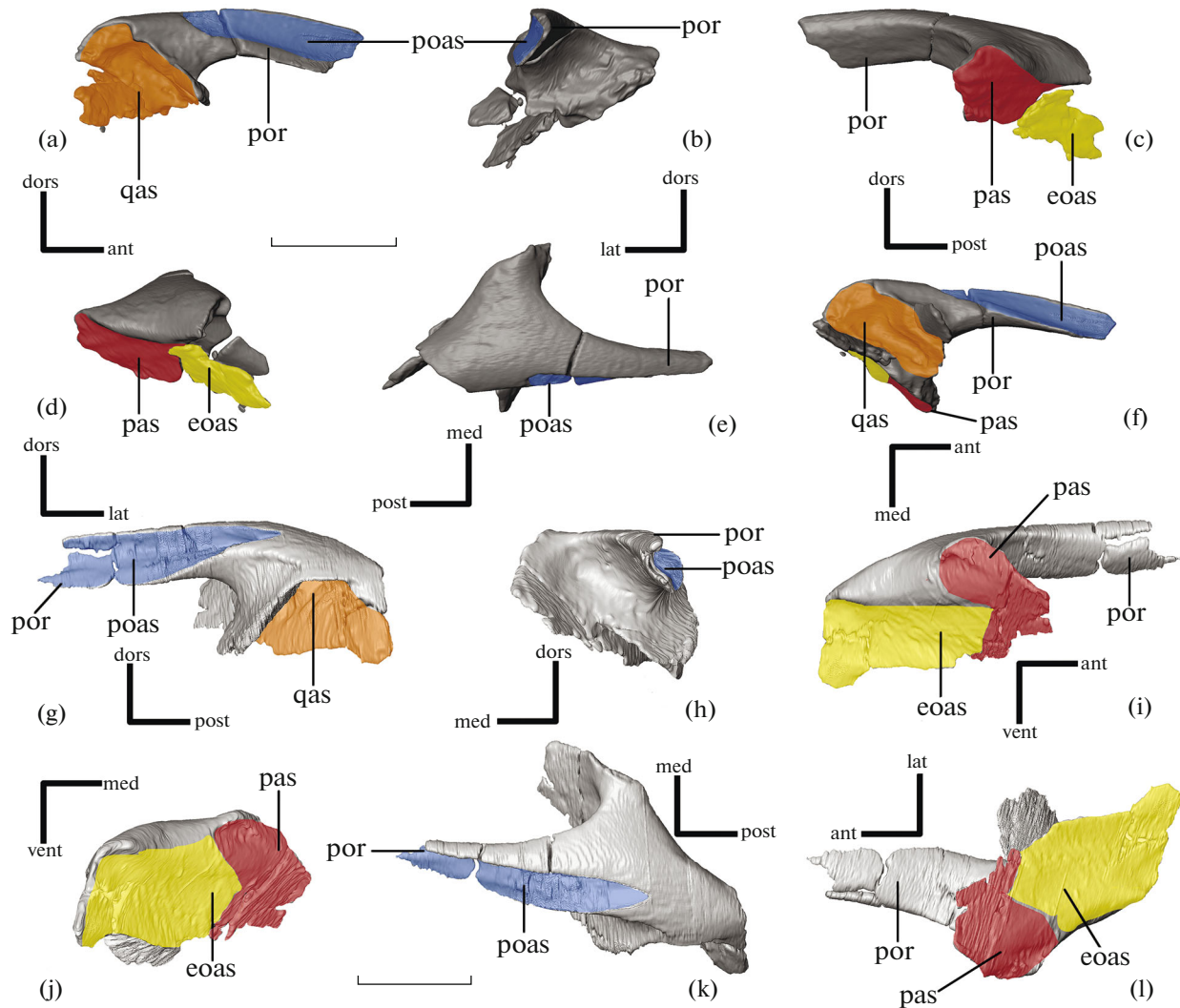


Fig. 20. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right squamosal of KOKM 22985/5 (a–f) and left squamosal of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) anterior view; (c, i) medial view; (d, j) posterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 20 mm for (g–l).

margin of the bone. In its widest part, the prefrontal facet occupies more than one third of the frontal width. The prefrontal facet terminates posteriorly by a pocket-like depression. On the dorsal surface of the posterolateral process, there is a deep groove for the medial process of the postorbital (Figs. 18a, 18f). The groove is pointed proximally and directed anteromedially. In the juvenile specimen KOKM 22985/5, the posterior margin of the frontal, contacting with the parietal by sutura squamata, forms an angle directed posterolaterally (Fig. 18a). In the adult specimen KOKM 22985/2, the frontoparietal suture is straight, but incised anteriorly at the midline (Fig. 18f). The groove for the postorbital is wider, compared with the juvenile specimen. The crista cranii are more pronounced and closer to the orbital margin in the juvenile specimen, compared with the adult specimen

(Figs. 18b, 18g). In the juvenile specimen, the ventral surface of frontals is lowered between the crista cranii and has distinct oval depressions for the olfactory bulbs anteriorly and cerebral hemisphere posteriorly (Fig. 18b). In the adult specimen, the lateral surface of the crista cranii is wider, and they approach closer to the midline, leaving less space for the olfactory tract (Fig. 18g). The ventral surface of the frontals between the crista cranii is shallower. Only posterior parts of the olfactory bulb impressions are preserved (Fig. 18g). The posterior part of the ventral surface is nearly flat, without distinct depressions of the cerebral hemispheres. In the juvenile specimen, at the posterior end of the crista cranii, there is a flat triangular area for contacting with the head of laterosphenoid (Fig. 18b). In the adult specimen, this area is distinctly larger and depressed (Fig. 18g). It is separated from the

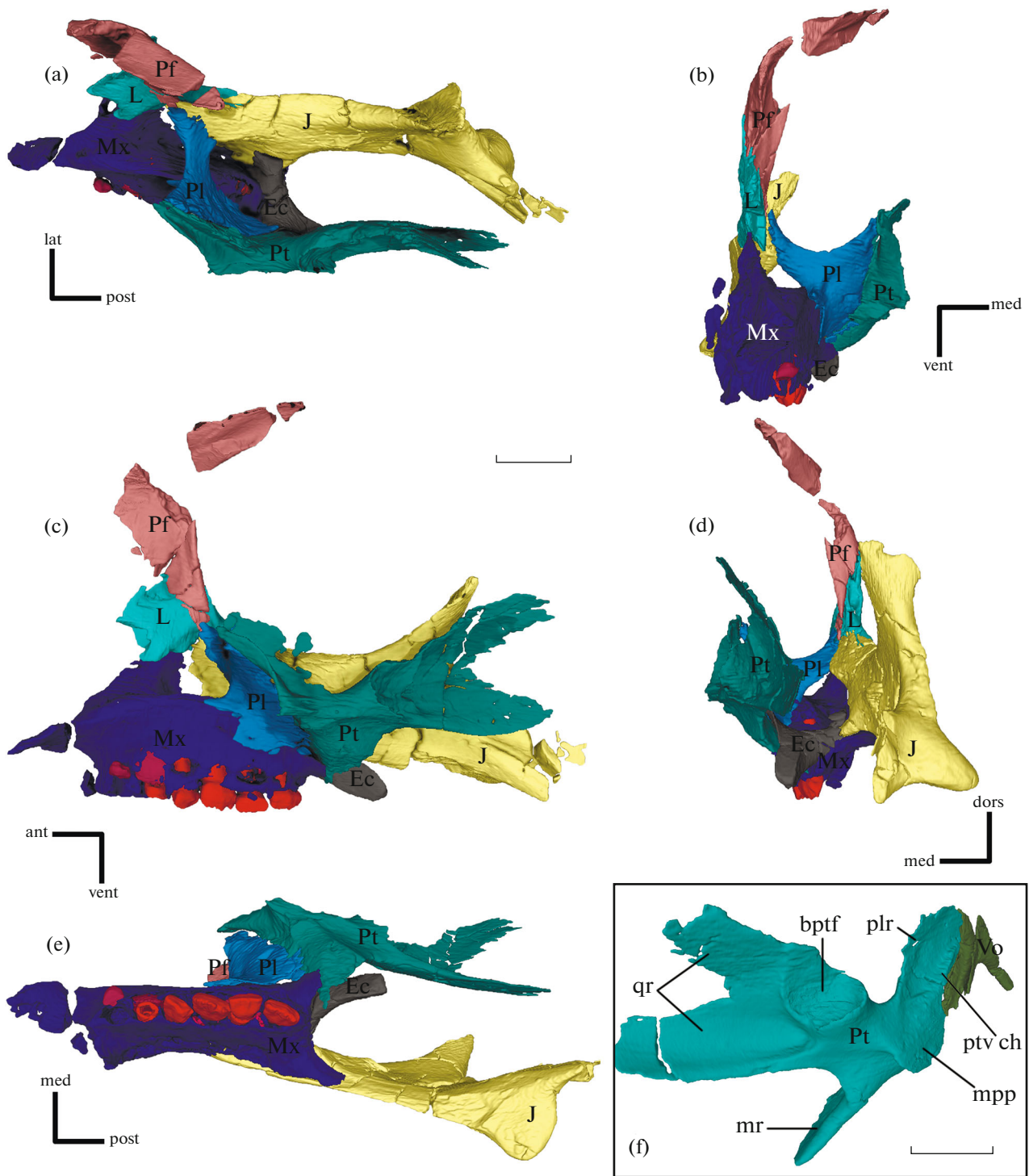


Fig. 21. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right palatal and adjacent bones of KOKM 22985/5 (a–e). (a) Dorsal view; (b) anterior view; (c) medial view; (d) posterior view; (e) ventral view. Articulated left vomer and pterygoid of KOKM 22985/2 in posteromedial view (f). See text for abbreviations. Scale bars, 5 mm for (a–e) and 20 mm for (f).

orbital cavity by a distinct transverse ridge. The frontals are paired in all known specimens of *P. sibiricus*, including the largest known skull KOKM 22985/8. The frontals are paired also in other species of *Psitta-*

cosaurus (Sereno et al., 1988; Napoli et al., 2019). Bul-lar et al. (2019) reconstructed fused frontals for adult, juvenile, and even hatchling specimens of *P. lujiatun-*
ensis. This contradicts the previous reconstruction of

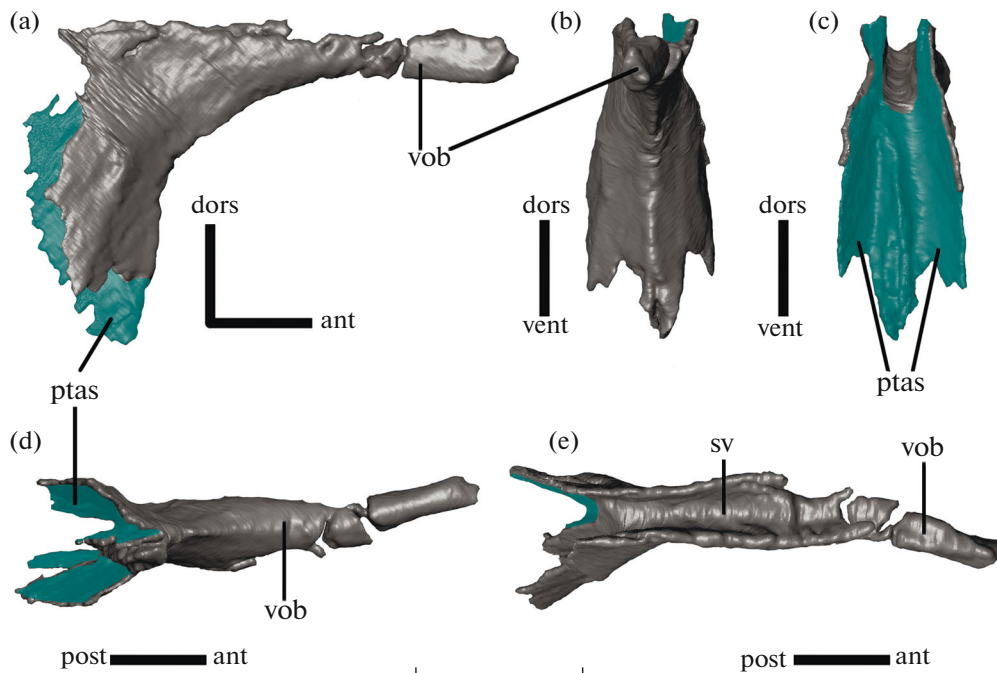


Fig. 22. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Vomer of KOKM 22985/2 in right lateral (a), anterior (b), posterior (c), ventral (d), and dorsal (e) views. See text for abbreviations. Scale bar, 20 mm.

this species with paired frontals (Zhou et al., 2006: text-Fig. 3B) and seems unlikely.

Parietal. In KOKM 22985/5 only a small piece of parietal is preserved, which is articulated with the right frontal (Figs. 2a, 2c). The parietal is fully preserved in the adult specimen KOKM 22985/2 (Figs. 5, 19). Because of strong curvature of the frontals, the parietal in the juvenile specimen should face posterodorsally (Fig. 2a) rather than dorsally, as in the adult specimen. In dorsal/ventral view, the parietal has an hour-glass shape, with a larger posterior part and a round incision in the middle of the posterior margin (Figs. 19a, 19b). On the dorsal side along the midline, there is a distinct sagittal crest (Fig. 19a). The frontal facets occupy the entire anterior margin of the dorsal side (Fig. 19a). The anterior margin of the parietal is broken in the middle, where an anterior projection should be wedging between the frontals, as in other psittacosaurids. The squamosal facet is a small strap in the posterior part of the lateral margin (Figs. 19a, 19c). On the ventral side, the anterior part of the parietal is depressed forming the cranial cavity (Fig. 19b). This cavity narrows in the middle of the parietal and terminates into a distinct oval supraoccipital fossa for the articulation with the round tuber on the dorsal surface of the supraoccipital (Fig. 19b). The supraoccipital facets also occupy a vast area along the lateral margins in the middle and posterior parts of the parietal (Fig. 19b). Posterior to these facets, there are narrow contacts of the parietal with the exoccipital/opisthotic. The posterior margin of the parietal forms a

parietal frill that overhangs the occiput. The parietal frill is relatively long, more than one third of the parietal length. Averianov et al. (2006) erroneously indicated that the parietal frill is horizontal in *P. sibiricus*. In the holotype of *P. sibiricus*, as well as in KOKM 22985/2 (Fig. 4a), the opposite parts of the parietal frill meet at the midline at an obtuse angle.

Squamosal. Only left squamosal is preserved in the juvenile skull KOKM 22985/5 (Figs. 2a–2c, 20a–20f). In the adult skull KOKM 22985/2, there is only a small piece of the right squamosal, whereas the left squamosal is nearly complete (Figs. 5, 20g–20l). The squamosal forms the posterolateral margin of the supratemporal fenestra and the posterodorsal corner of the infratemporal fenestra. The bone contacts the postorbital by the postorbital or anterior ramus, and the parietal, exoccipital/opisthotic, and quadrate by the medial or posterior ramus. The juvenile and adult squamosals do not differ significantly in shape. The postorbital ramus extends nearly to the anterior end of the supratemporal fenestra (Fig. 5). The postorbital ramus is higher than wide and widens posteriorly. Its medial surface is flat and lateral surface dorsal to the postorbital facet is slightly convex. Both surfaces meet at an acute angle forming a sharp rim of the supratemporal fenestra. The lateral surface of the postorbital ramus is deeply excavated by the facet for the posterior process of the postorbital (Figs. 20a, 20f, 20g, 20k). This facet extends on the lateral surface of posterior ramus and has a pointed posterior end. The postorbital facet deepens anteriorly, thus the postorbital ramus of

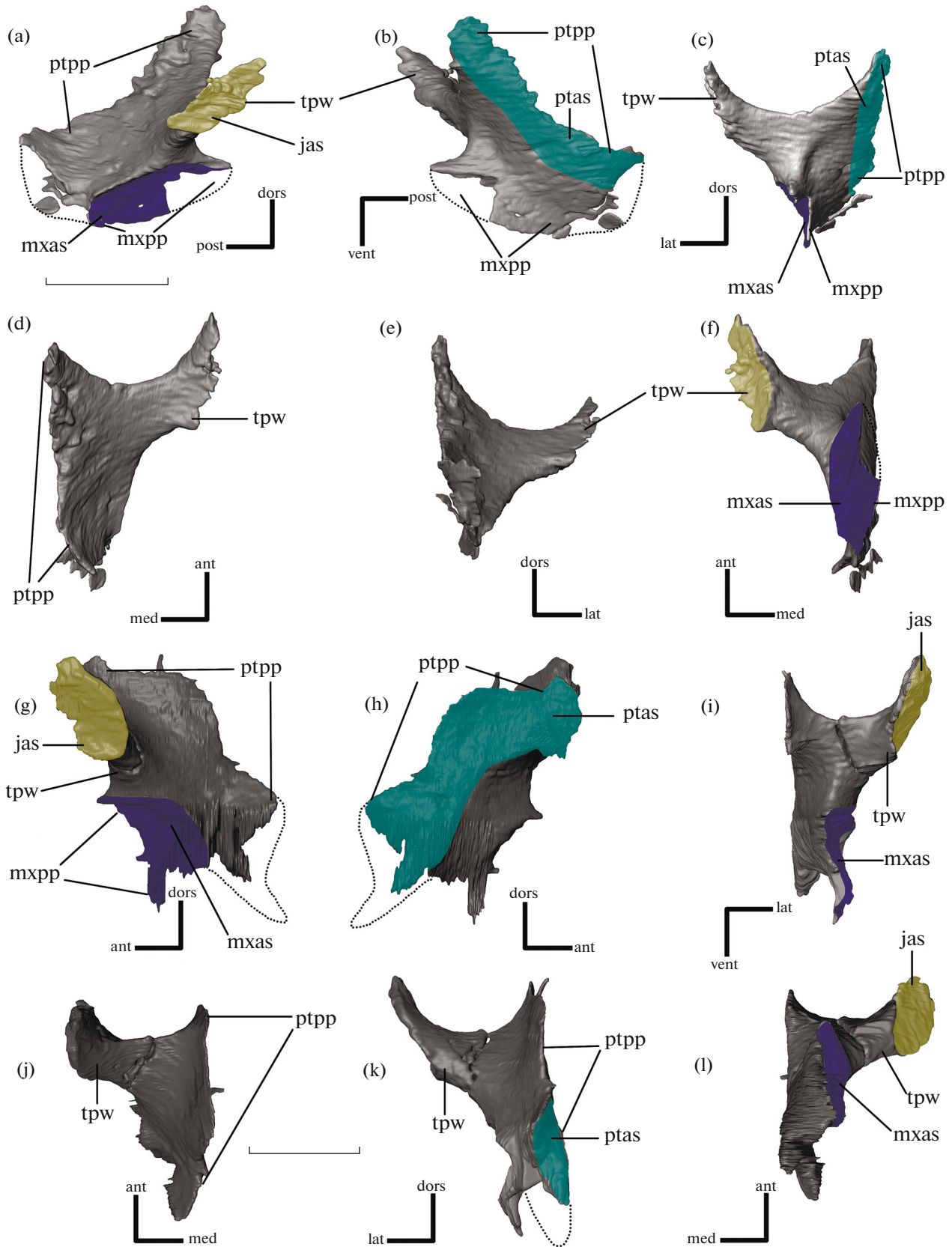


Fig. 23. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right palatine of KOKM 22985/5 (a–f) and left palatine of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i) anterior view; (d, j) dorsal view; (e, k) posterior view; (f, l) ventral view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 20 mm for (g–l).

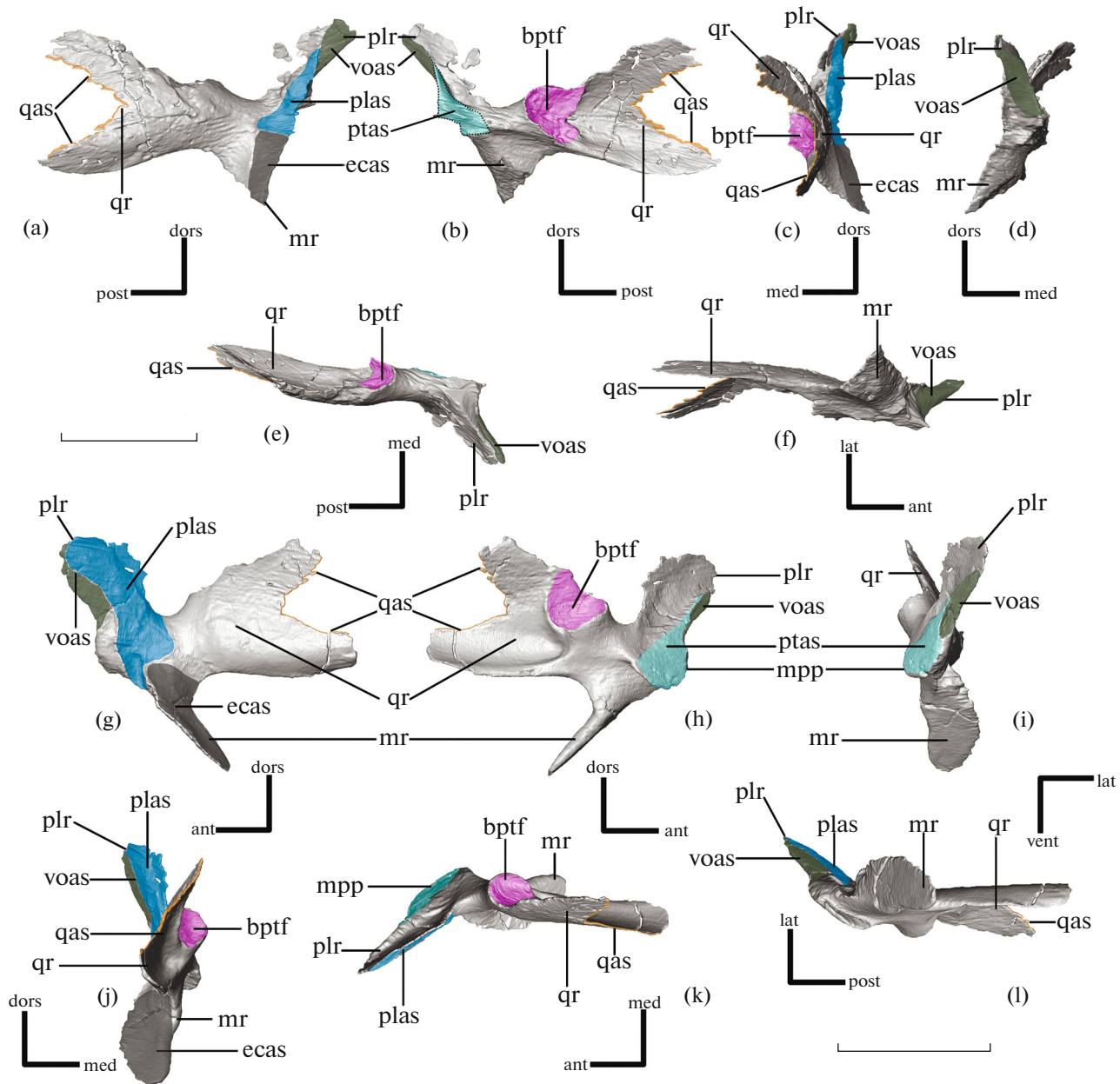


Fig. 24. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right pterygoid of KOKM 22985/5 (a–f) and left pterygoid of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, j) posterior view; (d, i) anterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bars, 10 mm for (a–f) and 50 mm for (g–l).

the squamosal becomes a thin plate anteriorly. The postorbital process of the squamosal does not extend to the anterior margin of the upper temporal fenestra. The shorter and higher medial ramus of the squamosal consists of two thin plates. A large medial plate is oriented at about 38° to the postorbital margin and contacts the parietal frill and the paroccipital process of the exoccipital/opisthotic by its flat medial surface (Figs. 20c, 20i, 20j, 20l). Just ventral to the postorbital

ramus, there is a lateral plate, which is oriented to the medial plate at about 21° . Both plates form walls of a large cavity housing the quadrate head (Figs. 20a, 20f, 20g). This cavity is open posteriorly and has a narrow groove at the bottom. Contrary to the previous description of *P. sibiricus* (Averianov et al., 2006), the medial ramus of the squamosal completely separates the quadrate head from the paroccipital process of the exoccipital/opisthotic.

Palatoquadrate Region

The juvenile specimen KOKM 22985/5 preserves most palatal bones from the right side (Fig. 2b). The vomer is mostly destroyed. In the adult specimen KOKM 22985/2, all palatal bones, including the vomer, are well preserved (Fig. 7). The palatal bones articulated with each other and with surrounding bones are shown in Fig. 21.

Vomer. The vomer is an unpaired bone situated along the skull midline, contacting the maxillae anteriorly and the pterygoids posteriorly and forming the medial margins of the choanae (Fig. 5). The vomer is fragmentary in KOKM 22985/5 and nearly complete in KOKM 22985/2 (Figs. 5, 22). The bone consists of a plate-like posterior vertical part (vomerine alae) and a rod-like horizontal vomerine bar (Osmólska, 1986). The angle between the two parts is $\sim 128^\circ$ in KOKM 22985/5 and $\sim 100^\circ$ in KOKM 22985/2. In the skull, the vomerine bar is directed anteroventrally and the posterior part is directed posteroventrally. The anterior end of the vomer in KOKM 22985/2 does not contact the maxillae apparently because of postmortem displacement. In adult specimens IVPP V1053 and V12617 of *P. lujiatunensis*, the anterior end of the vomer rests on the dorsal surface of the maxillae at their medial junction (Zhou et al., 2006: fig. 4; Dodson et al., 2010: text-Fig. 15.9B). The anterior end of the vomer in *P. sibiricus* likely had a similar position. On the dorsal surface of the vomerine bar, there is a large groove (sulcus vomeris; Fig. 22e) that continues posteriorly onto the pterygoids (the pterygoid-vomerine channel: Fig. 21f). The vomerine alae cover laterally the palatine rami of the pterygoids (Figs. 22c, 22d). On the bottom of the vomerine posterior part, there is a prominent ridge continuing posteriorly as a median process (Fig. 22c). This ridge fits into a groove formed by the ventral surfaces of the palatine rami of the opposite pterygoids.

Palatine. The palatine is well preserved in both specimens (Figs. 21, 23). The palatine forms antero-medial part of the orbital wall and contacts the pterygoid and maxilla medially and the jugal laterally. The palatine consists of two parts, a plate-like pterygoid plate and a dorsolaterally directed process termed the transverse palatine wing (Osmólska, 1986). The larger dorsoposterior part of the medial side of the pterygoid plate is occupied by a flat pterygoid facet contacting the palatine ramus of the pterygoid (Figs. 23b, 23h). The pterygoid facet is S-shaped in the adult specimen KOKM 22985/2 (Fig. 23h), whereas it is more narrow and strap-like in the juvenile specimen KOKM 22985/5 (Fig. 23b). The rest of the medial surface of the pterygoid plate is depressed relative to the pterygoid facet. At the anteroventral corner of the pterygoid plate, there is a vertical maxillary plate with a deeply excavated maxillary facet on its lateral surface (Figs. 23f, 23g). In the juvenile specimen, the maxillary plate is dorsoventrally shallower and anteroposteriorly longer

(Fig. 23a). The transverse palatine wing is oriented at an angle of $\sim 25^\circ$ to the pterygoid plate (Fig. 23). The anterior margin of the transverse palatine wing is concave, which makes the anterior margin of the palatine arcuate. The expanded distal end of the transverse palatine wing contacts the anteromedial process of the jugal just posterior to the jugal-lacrimal articulation (Figs. 23a, 23b). In the juvenile specimen KOKM 22985/5, the transverse palatine wing is relatively less expanded distally compared with the adult specimen (Figs. 23c, 23d).

Pterygoid. The pterygoid is a complex bone consisting of three parts, the quadrate or posterolateral ramus, the maxillary ramus, and the palatine ramus (Fig. 24). The quadrate ramus is the largest part of the pterygoid. Its base, adjacent to other parts of the pterygoid, has concave dorsal and ventral margins (Figs. 24a, 24b, 24g, 24h). The posterior part of the quadrate ramus is expanded vertically and convex laterally. On the medial side, there is a large cup-like facet for the basipterygoid process of the basisphenoid, which is adjacent to the dorsal margin of the quadrate ramus (Figs. 24b, 24h). The dorsal margin of the basipterygoid facet is concave. Ventral to the basipterygoid facet starts the ridge that continues posteriorly along the ventral border of the quadrate ramus. Dorsal to this ridge, there is a large concave depression. The medial surface of the quadrate ramus posterodorsal to the basipterygoid facet is flat. The deeply incised posterior margin of the quadrate ramus contacts the pterygoid ramus of the quadrate (Figs. 24a, 24b, 24g, 24h). The maxillary ramus is a thin plate directed ventrolaterally. In the juvenile specimen KOKM 22985/5, it is triangular and oriented at an angle of $\sim 131^\circ$ to the quadrate ramus (Figs. 24a–24d). In the adult KOKM 22985/2, it is kidney-shaped, with concave medial and convex lateral margins, and oriented nearly perpendicular to the quadrate ramus (Figs. 24g–24j). The maxillary ramus contacts the ectopterygoid by its dorsal surface (Figs. 2b, 5, 24c, 24d, 24e). The palatine ramus is larger than the maxillary ramus and oriented at an angle of $\sim 140^\circ$ to the latter in both specimens (Fig. 24). The palatine ramus is oval in medial/lateral view and constricted at the base. It is separated from the maxillary ramus by a deep vertical groove on the lateral surface, which extends and grows shallow on the lateral surface of the palatine ramus. The lateral surface of the palatine ramus is slightly convex. It contacts with the palatine and the posterior ala of the vomer (Figs. 21, 24a, 24c, 24g, 24j). In medial view, the palatine ramus has the shape of a figure eight separated by a diagonal ridge (Fig. 24h). The thickened ventral part of this figure is the medial plate of the pterygoid contacting the opposite pterygoid. The ventral margins of medial plates of the opposite pterygoids form a distinct ridge on the ventral side of pterygoids (Fig. 6). The medial plate is absent in the juvenile specimen KOKM 22985/5 possibly because of incomplete ossification. A narrow

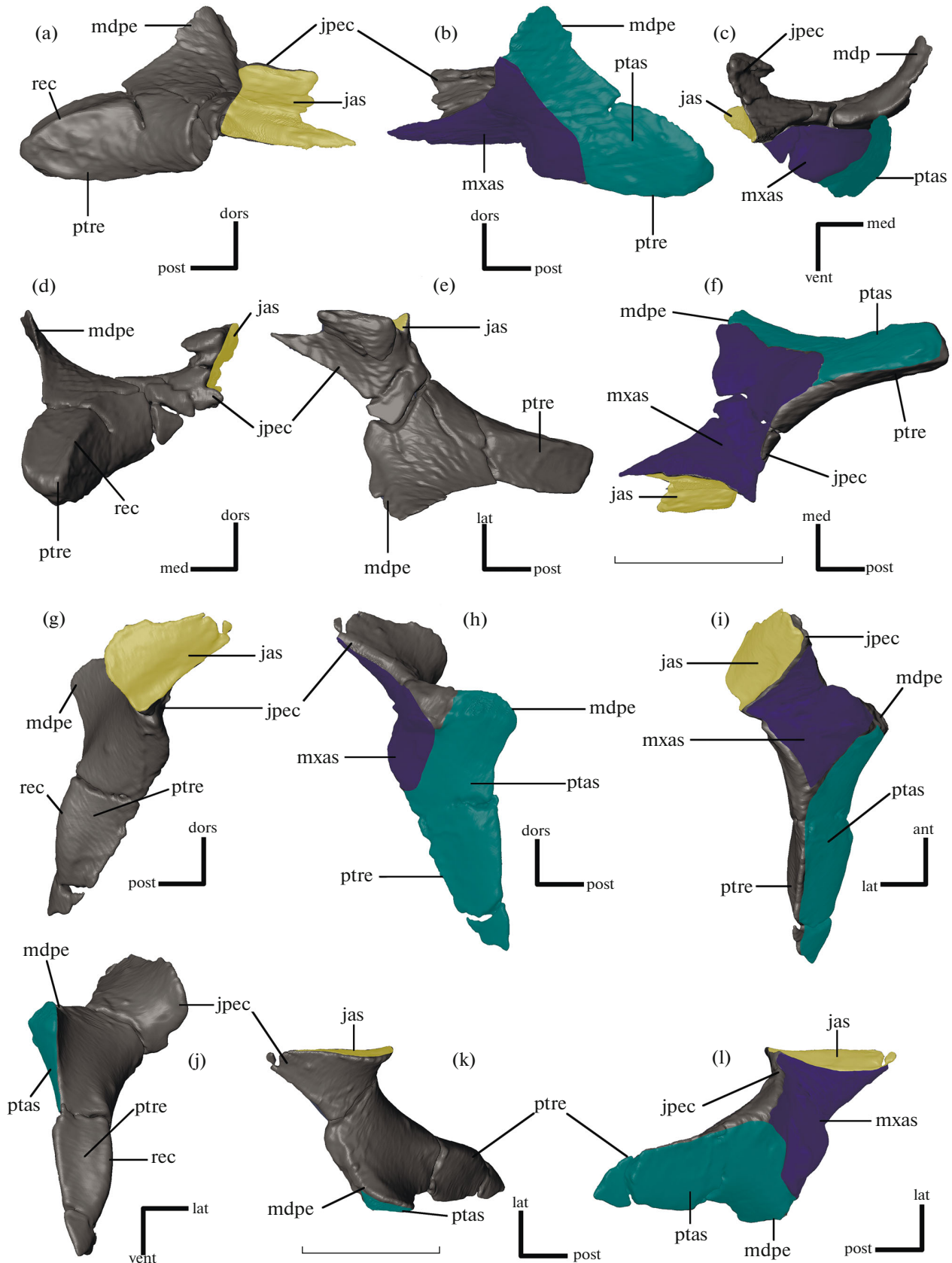


Fig. 25. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right ectopterygoid of KOKM 22985/5 (a–f) and KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i) anterior view; (d, j) posterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 20 mm for (g–l).

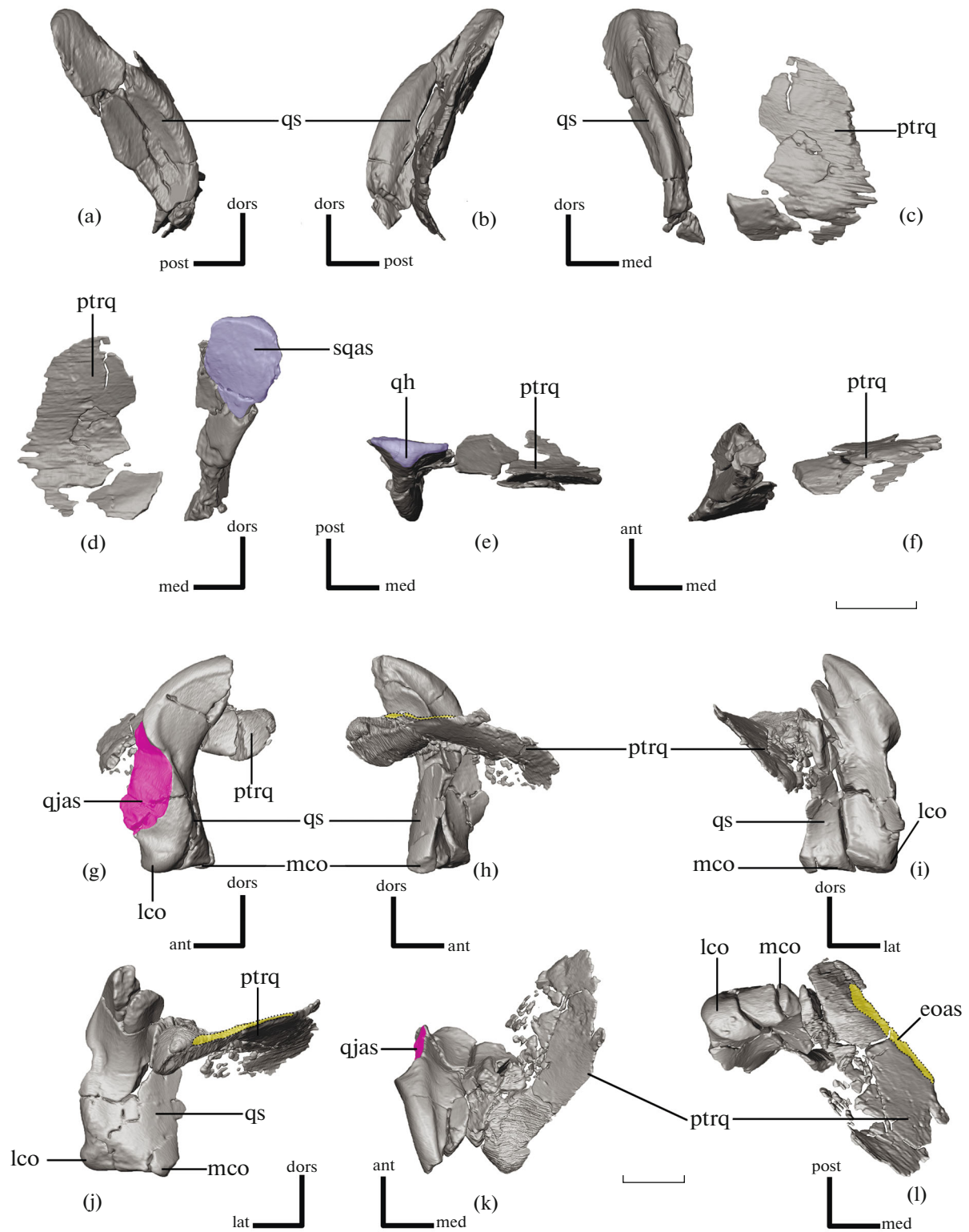


Fig. 26. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right quadrate of KOKM 22985/5 (a–f) and left quadrate of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i), anterior view; (d, j) posterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 20 mm for (g–l).

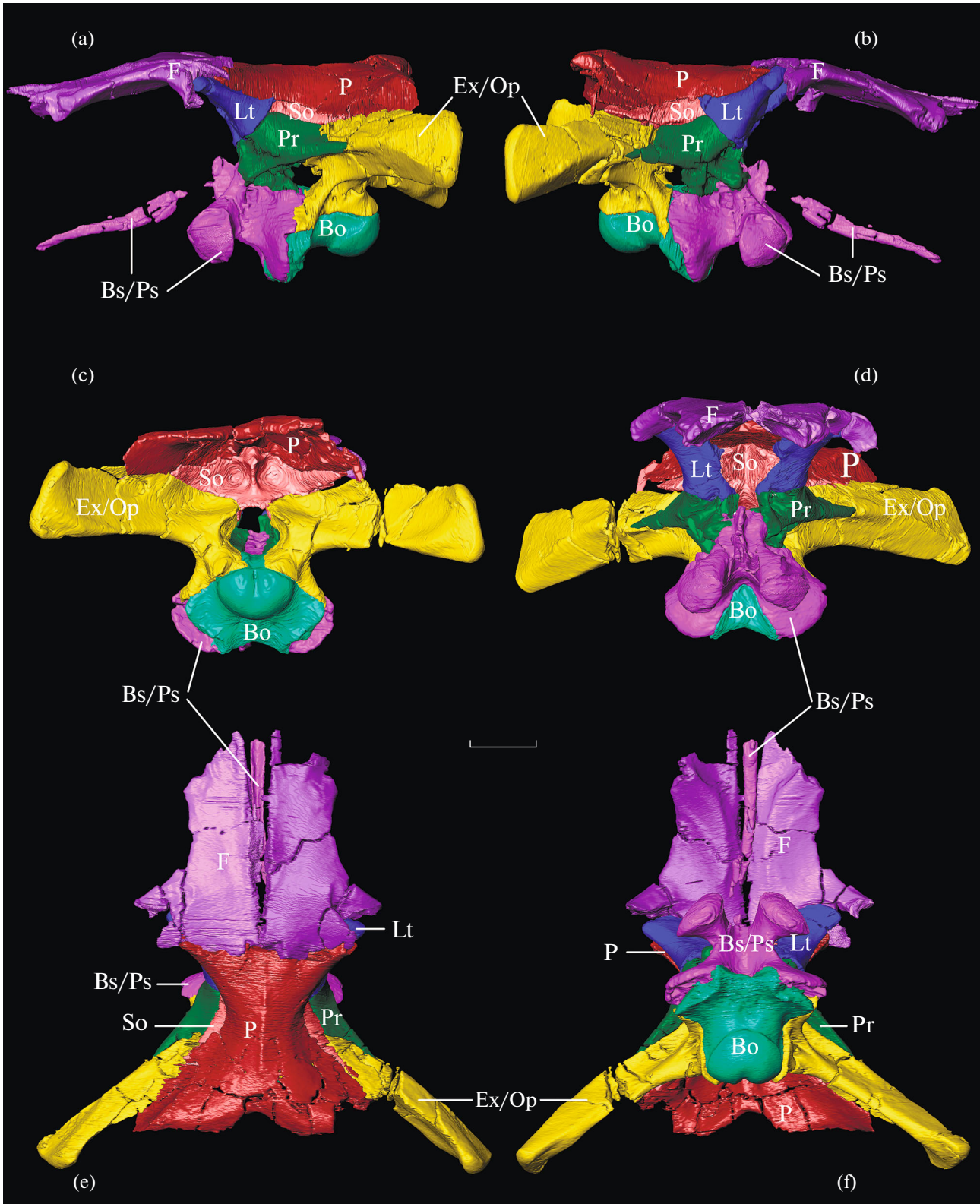


Fig. 27. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented braincase of KOKM 22985/2. (a) Left lateral view; (b) right lateral view; (c) posterior view; (d) anterior view; (e) dorsal view; (f) ventral view. See text for abbreviations. Scale bar, 20 mm.

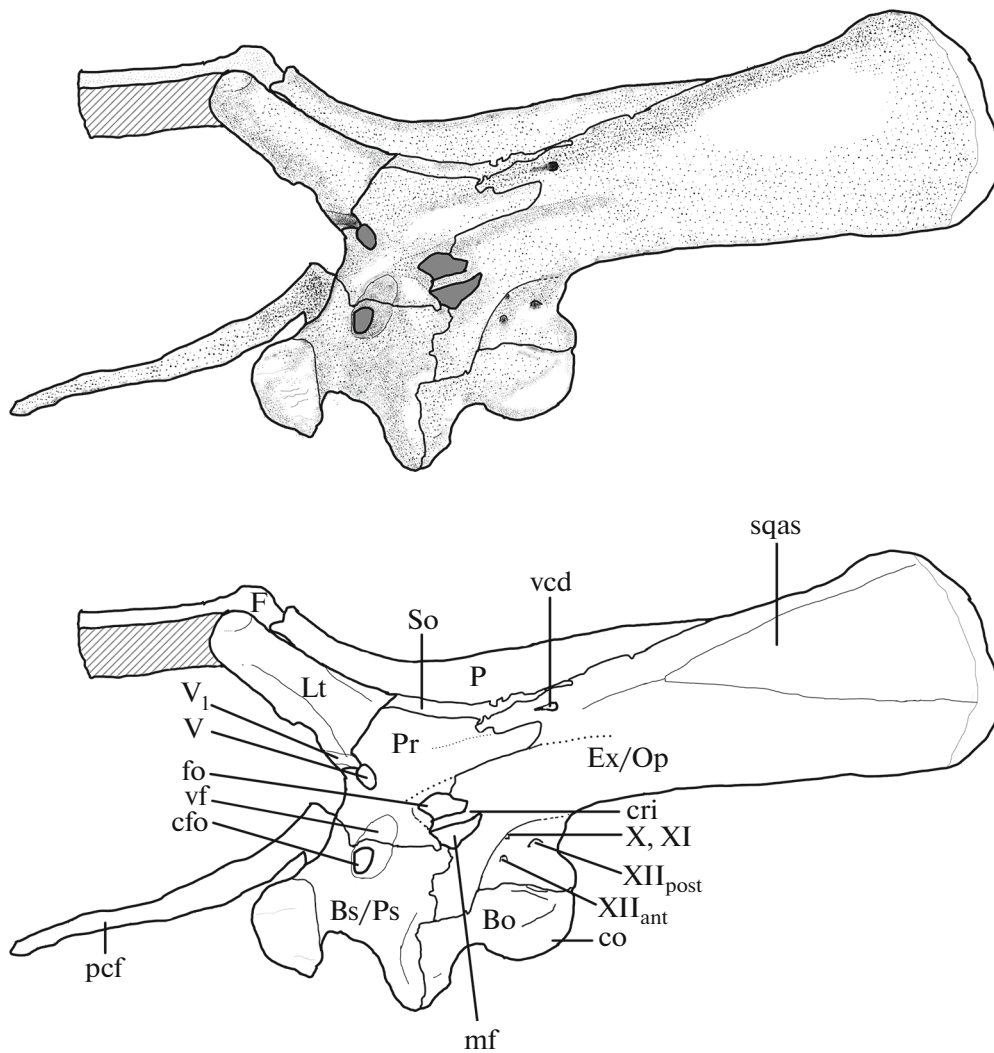


Fig. 28. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Reconstruction of braincase in left lateral view. See text for abbreviations.

bone strip ventral to the diagonal ridge and anterior to the medial plate forms the wall of a groove receiving the ridge between the vomerine alae and the median process of the vomer (Figs. 6, 24i). The depressed part dorsal to the median ridge is a thin plate with concave surface. These plates of the opposite pterygoids form a channel continuing anteriorly onto the vomer and having the diagonal ridges of the opposite pterygoids as a bottom.

Ectopterygoid. The ectopterygoid is well preserved in both specimens (Figs. 21a–21d, 25). The ectopterygoid is a small bone that extends between the pterygoid and the jugal posterior to the palatine. The bone consists of the long tapering distally pterygoid ramus with two short branches, the mediodorsal process and jugal process (Fig. 25). The pterygoid ramus is relatively shorter in the juvenile specimen KOKM 22985/5 (Figs. 25a–25f). The pterygoid ramus is triangular in cross section. The flat medial side contacts

the dorsal surface of the pterygoid mandibular ramus (Figs. 25b, 25h). A high longitudinal ridge on the opposite side divides it into slightly concave dorsolateral surface and a larger flat ventrolateral surface. The ridge is gently sloping, with the highest point in the middle. The mediodorsal process is a triangular extension at the middle of the dorsal margin of the bone (Fig. 25). It is bent laterally, with convex lateral and concave medial surfaces. Dorsal margin of the mediodorsal process represents a narrow facet contacting the pterygoid (Fig. 25j). Its medial side is occupied by a concave maxillary facet, which partially extends on the pterygoid ramus (Figs. 25f, 25i). The jugal process is twisted in relation to the pterygoid ramus. It is set at an angle of $\sim 140^\circ$ to the pterygoid ramus in medial/lateral view and slightly deflected laterally from the pterygoid ramus (Fig. 25), being parallel to the transverse palatine wing (Figs. 25a, 25d). The ventral surface of the jugal process contacts the posterior

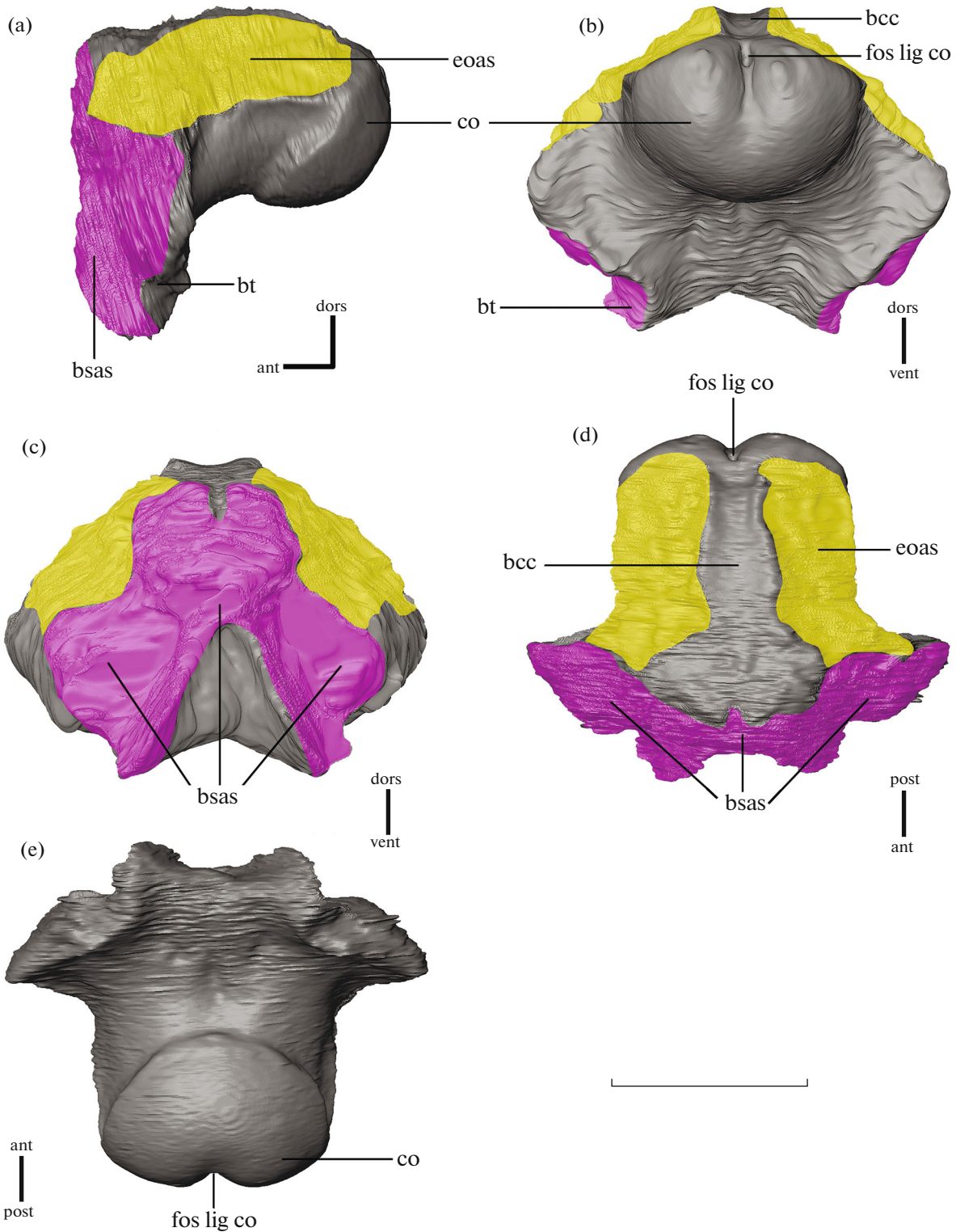


Fig. 29. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Basioccipital of KOKM 22985/2 in left lateral (a), posterior (b), anterior (c), dorsal (d), and ventral (e) views. See text for abbreviations. Scale bar, 20 mm.

part of the maxilla, including the posterior maxillary process. The distal end of the jugal process is greatly expanded and contacts the ventromedial process of

the jugal by its entire lateral surface (Figs. 25a, 25g, 25i). On the lateral surface, there is groove along its medial margin that widens ventrally. The specimens

PM TGU 16/0-18 and 16/1-79 of *P. sibiricus*, described as ectopterygoids in Averianov et al. (2006: text-Fig. 6K–6O), are actually squamosals.

Quadrate. Only partially preserved right quadrate is present in KOKM 22985/5 (Figs. 2a, C, 26a–26f). In KOKM 22985/2, both quadrates are present, but the right one is less complete (Figs. 4–6, 26g–26l). The quadrate consists of a vertical shaft, contacting the squamosal dorsally and quadratojugal laterally and forming the mandibular condyles ventrally, and anteriorly projecting pterygoid ramus contacting the exoccipital/opisthotic and pterygoid. The quadrate shaft is massive and transversely wide ventrally and tapers dorsally towards the quadrate head. The quadrate shaft is S-shaped in lateral/medial view, with the mandibular condyles slightly deflecting anteriorly and the dorsal part of the shaft strongly deflecting posteriorly (Figs. 26g, 26h). The dorsal part of the shaft also strongly deflects medially in anterior/posterior view (Figs. 26i, 26j). The mandibular condyles are saddle-shaped. The anterior surface of the quadrate shaft is deeply concave. Its posterior surface is convex in ventral part; in dorsal part, it has a strong longitudinal ridge in the middle (Fig. 26j). The lateral surface of the quadrate shaft is wide, with the widest point placed some distance dorsal to the mandibular condyle. On this surface, there is a large quadratojugal facet, which tapers dorsally and ventrally and occupies the entire middle part of the lateral surface (Fig. 26g). The quadratojugal facet is divided into two parts, a larger depressed ventral part with a sharp anterior margin, and a smaller dorsal part, which extends on the elevated and posteriorly bending dorsal part of the shaft. The border between the two parts is marked by a deep incision on the posterolateral margin of the quadrate shaft (Fig. 26j). The medial margin of the quadrate shaft is very thin. The quadrate head is preserved only in the juvenile specimen KOKM 22985/9 (Figs. 26a–26f). There, the medial side of the quadrate shaft contacting the squamosal is flat, and the quadrate head is triangular in dorsal view, with a straight medial margin and an angle on the lateral margin formed by the lateral ridge (Figs. 26d, 26e). The pterygoid ramus is a plate inserted at the dorsal part of the quadrate shaft. The contact area of the pterygoid ramus and the quadrate shaft is missing or poorly preserved in all specimens. The posterior part of the pterygoid ramus is thick, with a wide posterior surface. In the posterior part of the pterygoid ramus, on its lateral surface, there is an anteriorly pointed facet probably for the paroccipital process of the exoccipital/opisthotic. Distally, it transforms into a thin plate contacting the quadrate ramus of the pterygoid. The ventral margin of this plate is slightly deflected medially.

Braincase

The preserved braincase of KOKM 22985/5 includes the basisphenoid, both prootics, left latero-

sphenoid, and incomplete supraoccipital (Fig. 2b). The braincase of KOKM 22985/2 is almost completely preserved (Figs. 6, 7, 27). Its reconstruction is shown in Fig. 28.

Basioccipital. The basioccipital forms most of the occipital condyle and fuses with the basisphenoid anteriorly and exoccipital/opisthotic dorsally (Figs. 27–29). The anterior part of the basioccipital is a vertical plate expanded laterally in the middle and fused with the basisphenoid by its anterior surface. The anterior surface can be divided into four parts (Fig. 29a). A slightly elevated rounded dorsal part is attached to the basisphenoid and has a short vertical furrow in the middle of dorsal margin. Depressed triangular ventrolateral parts attach to the basisphenoid and form the basal tubera. There is a cleft between the basioccipital and basisphenoid components of the basal tubera (fossula intertubercularis). The fossula intertubercularis is also present in the adult specimen IVPP V12617 of *P. lujiatunensis* (Bullar et al., 2019: text-Fig. 20b), but absent in the juvenile specimens of this species. The free ventral surface has a triangular outline and is bordered by ridges converging towards the center of the anterior surface. The part of the basioccipital between the basal tubera is narrow anteroposteriorly and incised towards the midline (Figs. 29b, 29c, 29e). The posterior part of the basioccipital is the occipital condyle. In lateral view, it is about twice lower than the anterior part (Fig. 29a). When the anterior part of the basioccipital is vertically oriented, the occipital condyle is directed posterovertrally. The condyle is round, except for truncated dorsolateral parts contacting the exoccipital/opisthotic (Fig. 29b). The condyle has a deep vertical furrow in the middle of dorsal surface extending towards the center of the condyle (fossa ligamentum condyles occipitalis; Fig. 29b, 29d, 29e). The condylar surface is more exposed on the ventral surface compared with the dorsal surface (Figs. 29d, 29e). The dorsal margin of the basioccipital is dorsally convex in lateral view (Fig. 29a). On the dorsal surface of the basioccipital, there are dorsolaterally facing marginal facets for the exoccipital/opisthotic, separated by a narrow concave midline free surface forming the bottom of the neurocranial cavity (Fig. 29d). On the ventral surface of the basioccipital, between the basal tubera and the occipital condyle, there is a short midline groove flanked by small round depressions (Fig. 29e). In *P. amitabha*, there is small foramen in place of this groove that would have entered the posterior floor of the braincase (Napoli et al., 2019: text-Fig. 3a). This foramen appears to be present in *P. lujiatunensis* as well (Zhou et al., 2006: Figs. 2f, 3d). However, the computed tomography data of the KOKM 22985/2 do not show any channels in the zone of this depression. According to Bullar et al. (2019: text-Fig. 20D), the occipital condyle in an adult specimen of *P. lujiatunensis* consists entirely of the basioccipital, and the boundary between the basioccipital and the exoccipital/opist-

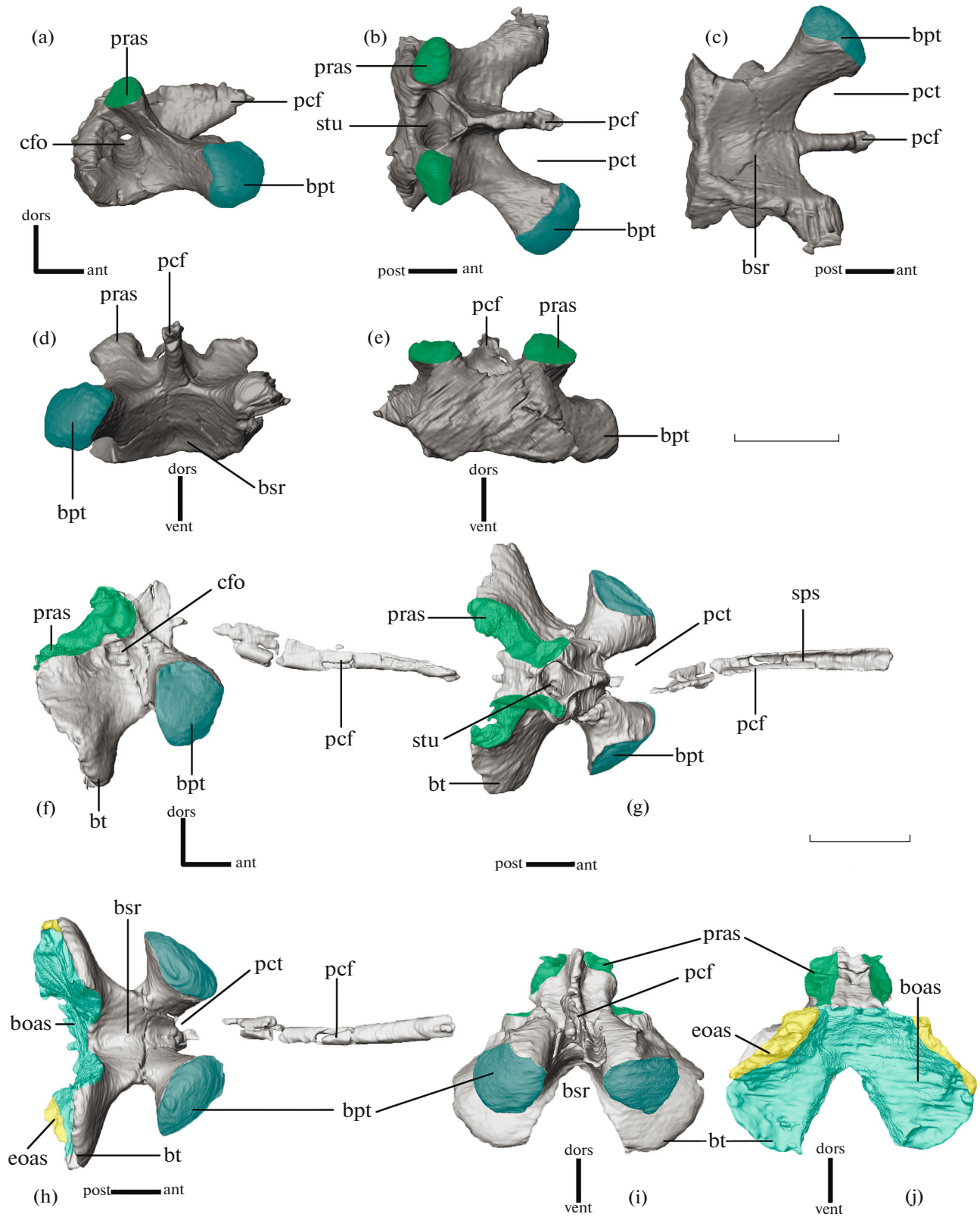


Fig. 30. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Basisphenoid of KOKM 22985/5 (a–e) and KOKM 22985/2 (f–j). (a, f) Right lateral view; (b, g) dorsal view; (c, h) ventral view; (d, i) anterior view; (e, j) posterior view. See text for abbreviations. Scale bars, 5 mm for (a–e) and 20 mm for (f–j).

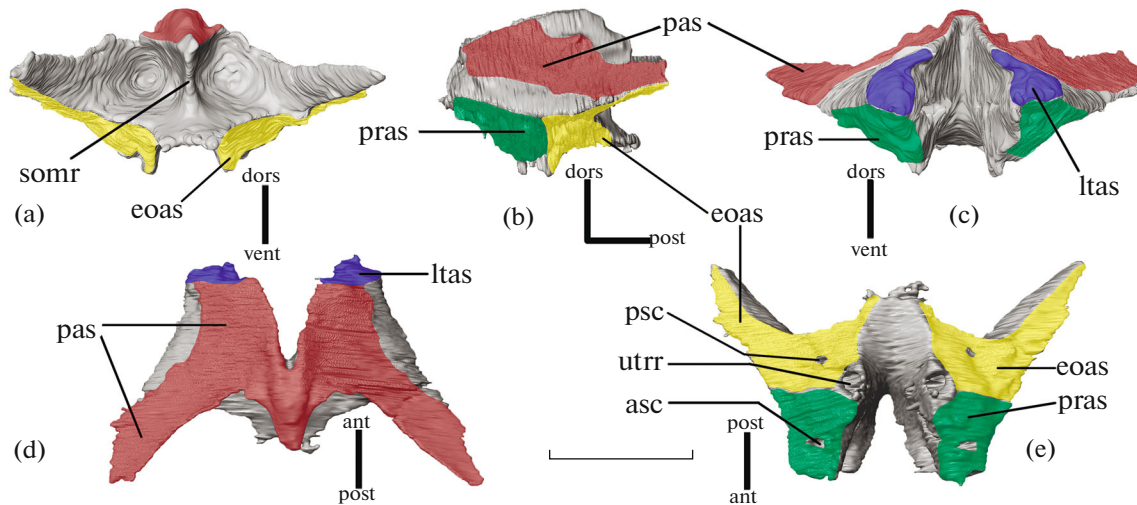


Fig. 31. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Supraoccipital of KOKM 22985/2 in posterior view (a), left lateral view (b), anterior view (c), dorsal view (d), ventral view (e). See text for abbreviations. Scale bar, 20 mm.

hotic lies more dorsally, compared with the condition in *P. sibiricus*. In this case, the basioccipital contributes to the base of the paroccipital processes in *P. lujiatunensis*, which we suppose highly unlikely. This reconstruction is considered here as an artifact due to incorrect segmentation.

Basisphenoid. In KOKM 22985/5, the basisphenoid is missing the posterior part (Figs. 2b, 30a–30e). In KOKM 22985/2, the basisphenoid is almost complete (Figs. 6, 7, 27a–27d, 27f, 28, 30f–30j). The cultriform process is incomplete in both specimens. The basisphenoid contacts the prootic dorsally, the exoccipital/opisthotic posterodorsally, and the basioccipital posteriorly. The basisphenoid is crestiform in dorsal/ventral view due to the strongly ventrally and laterally protruding basal tubera and basipterygoid processes (Fig. 30). The basisphenoid contacts the basioccipital by its entire posterior surface (Fig. 30j). This surface is Λ -shaped, with a incised central part and ventral projections forming the basisphenoid part of the basal tubera. The space between the basisphenoid tubera is a posterior opening of a deep groove (basisphenoid recess) that extends through the entire ventral surface of the basisphenoid and separates the basipterygoid processes anteriorly. This recess is triangular in cross section, with an angle between the basipterygoid processes of $\sim 100^\circ$ in KOKM 22985/5 and $\sim 56^\circ$ in KOKM 22985/2. In KOKM 22985/5, the basisphenoid recess is shallower than in KOKM 22985/2. The basisphenoid recess extends posteriorly onto the basioccipital. The basisphenoid recess of *P. sibiricus* differs markedly from that of an adult specimen of *P. xinjiangensis* in lack of a deep round pit between the basal tubera (Brinkman et al., 2001: text-Fig. 2D). This pit is absent in the juvenile type specimen of *P. xinjiangensis* (Sereno and Chao, 1988: text-

Fig. 4C). The ventrolateral margins of the basal tubera are rounded, and their anterior surface is slightly convex. The basipterygoid processes are slightly shorter than the basal tubera and expand significantly more distally. The oval surface articulating with the pterygoid is convex in KOKM 22985/5 and separated into two flat facets in KOKM 22985/2. On the dorsal surface of the basisphenoid, there is a deep triangular depression housing the pituitary gland, sella turcica or hypophyseal cavity (Figs. 30b, 30g). It is flanked laterally by the facets articulating with the prootics. In KOKM 22985/5, there are large oval anterior parts of the prootic facets that face dorsolaterally and similar in size with the sella turcica (Figs. 30a, 30b). In KOKM 22985/2, these anterior parts are smaller and face laterally, and the larger part of the prootic facet (not preserved in KOKM 22985/5) extends posteriorly along the dorsal margin of the basisphenoid (Figs. 30f, 30g), where it merges with the facet for the exoccipital/opisthotic. A similar difference in the construction of the prootic facet between the juvenile and adult specimens was found in *P. lujiatunensis* (Bullar et al., 2019). The sella turcica connects ventrally with the short carotid canals that open on the lateral sides of the basisphenoid in the carotid foramina. The carotid foramen is much larger in the juvenile KOKM 22985/5 compared with the adult KOKM 22985/2 (Figs. 30a, 30f). The lateral surface of the basisphenoid is concave between the basipterygoid process and basal tuber. The transversely narrow base of the cultriform process is in the middle of the anterior surface of the basisphenoid and occupies its entire depth. The sharp ridges forming the anterolateral margins of the sella turcica converge onto the dorsal margin of the cultriform process, where they delimit a small surface facing posterodorsally. This surface is relatively

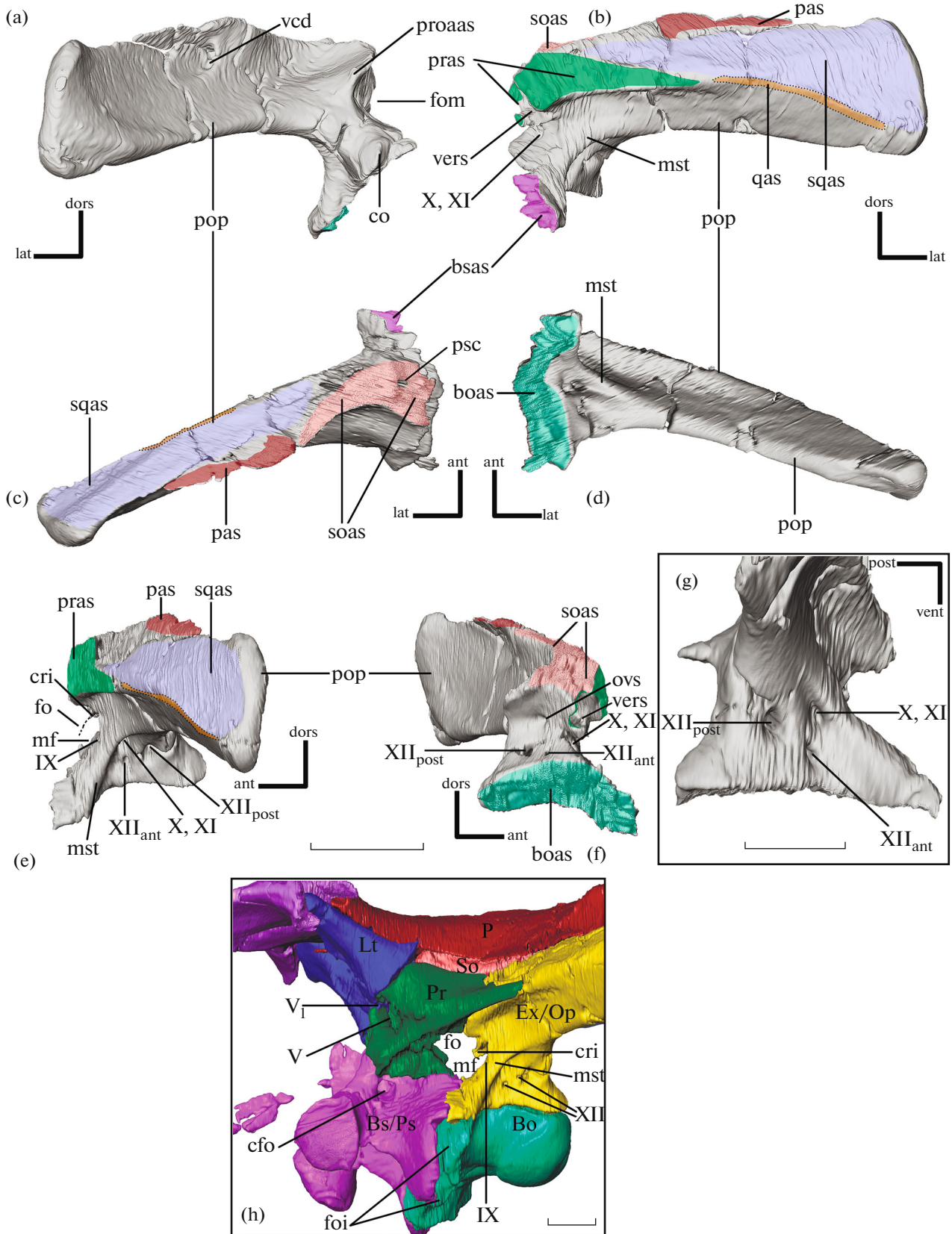


Fig. 32. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left exoccipital/opisthotic of KOKM 22985/2 (a–f), right exoccipital/opisthotic of KOKM 22985/2 (g), and segmented braincase of KOKM 22985/2 in left lateral view (h). (a) Posterior view; (b) anterior view; (c) dorsal view; (d) ventral view; (e) lateral view; (f) medial view; (g) enlarged ventrolateral view. See text for abbreviations. Scale bars, 20 mm for a–f, and 10 mm for g, h.

smaller and more vertical in the adult specimen (Figs. 30b, 30g). The depth of the cultriform process decreases anteriorly. Along the dorsal side of the cultriform process, there is a wide and deep groove (sulcus parasphenoidalis) that occupies almost the entire process, leaving thin bony walls and a bottom. This groove apparently occupies a significant part of the process. Its anterior end is not preserved in KOKM 22985/2, and KOKM 22985/5 preserves only posterior part of the cultriform process without the groove (Fig. 30). The basisphenoid of *P. major* differs significantly from that of *P. sibiricus* in having the basiptyergoid processes much longer and directed more anteriorly (Sereno, 2010: text-Fig. 2.4B).

Supraoccipital. Only fragments of the supraoccipital are preserved in KOKM 22985/5 (Figs. 2a–2c). In KOKM 22985/2, the supraoccipital is complete (Figs. 4a, 31). The supraoccipital is exposed on the occiput as a transversely elongated rhombus above the foramen magnum and between the exoccipital/opisthotic and the parietal (Figs. 10a, 27c). The supraoccipital forms the dorsal margin of the foramen magnum. In lateral view of the braincase, the supraoccipital is exposed as a narrow strip between the parietal, laterosphenoid, prootic, and exoccipital/opisthotic (Figs. 27a, 27b, 28). In dorsal/ventral view, the supraoccipital is W-shaped, with two anterior prongs separated by a deep triangular cleft, two narrower posterolateral prongs, and a midline posterior ridge (Figs. 31d, 31e). The entire dorsal surface of the supraoccipital is covered by the parietal (Fig. 31d). The ventral surface is divided between the anterior prootic facet and the posterior exoccipital/opisthotic facet (Fig. 31e). The prootic facets extends on the anterior surface of the supraoccipital and contacts dorsally with a small laterosphenoid facet (Fig. 31c). The supraoccipital medial crest on the posterior side is confined to its dorsal half and flanked by deep round depressions (Fig. 31a). A small free surface on the ventral side between the foramen magnum and the anterior prongs forms part of the cranial cavity roof (Fig. 31e). On the ventral surface, there are three openings (Fig. 31e): a large along the border of cranial cavity between the prootic and exoccipital/opisthotic facets (utricular recess), a smaller anterior within the prootic facet (for the anterior semicircular canal) and smallest posterior within the exoccipital/opisthotic (for the posterior semicircular canal). Bullar et al. (2019) described extreme reduction in size of the supraoccipital in juvenile and adult specimens of *P. lujiatunensis* compared with the hatchling specimen, admitting the fused and obscured sutures of this bone with surrounding bones in the adult specimen. According to this reconstruction, the semicircular canals do invade the supraoccipital in a hatchling individual but not in a juvenile and an adult individual, which is hardly possible. The relationships between canals and bones are established very early in the ontogeny and do not

change. We consider this reconstruction as an artifact of incorrect segmentation.

Exoccipital/opisthotic. Both exoccipital/opisthotics are destroyed in KOKM 22985/5, whereas in KOKM 22985/2 they are almost completely preserved (Figs. 27, 28, 32). The exoccipital/opisthotic is a transversely elongated bone exposed along the ventral margin of the occiput and forming its ventrolateral corners. The medial end of the exoccipital/opisthotic forms the lateral wall of the foramen magnum and contacts the supraoccipital dorsally and the basioccipital ventrally. The bone consists of the ventral peduncle contacting the basioccipital and the posterolaterally directed paroccipital process (Fig. 32). The peduncle is separated from the rest of the bone by a constriction in both anteroposterior and mediolateral planes (Fig. 32). On its posterior end, there is a small articulation surface of the occipital condyle (Fig. 32a). On its anterior end, there is a small articulation surface for the basisphenoid. The basioccipital facet occupies the entire ventral surface of the bone. It is Γ -shaped, with the anterior part directed anterolaterally (Fig. 32f). The peduncle forms the lateral wall of the posterior part of the endocranial cavity. It is pierced by three foramina containing the exits of the cranial nerves: anterodorsal foramen for X–XI nerves, anteroventral foramen for XII_{ant} nerves, and a large posterior foramen for XII_{post} nerve (Figs. 32e, 32g). On the medial side of the peduncle, dorsal to the foramina for cranial nerves, there is a pit apparently corresponding of the occipital venous sinus (Fig. 32f). On the lateral side of the peduncle, along its anterior margin, there is a crest (metotic strut; Figs. 32b, 32d), which continues on the ventral margin of the paroccipital process. The metotic strut borders posteriorly the metotic foramen (Fig. 32e). The metotic foramen was likely separated from the oval window (fenestra ovalis) by the crista interfenestralis, of which only a small fragment is preserved (Fig. 32e). A small groove on the posterior margin of the metotic foramen (Fig. 32e) is likely for the cranial nerve IX and vena capitis posterior. A crest-like eminence along the foramen magnum margin, close to the supraoccipital, is the proatlas facet (Fig. 32a; Podlesnov, 2018). The paroccipital process is convex dorsally in anterior/posterior view (Figs. 32a, 32b). Its posterior side is concave, with a large opening for the vena capitis dorsalis (Boyd, 2014; Bullar et al., 2019) or transverso-occipital vein (Kuzmin et al., 2020) in the middle, close to the dorsal margin (Fig. 32a). In *P. amitabha*, this foramen is associated with a large and deep oval depression posterior to it (Napoli et al., 2019: text-Fig. 5B). In *P. sibiricus*, the latter depression is much shallower. On the anterior side of the paroccipital process, there is a prominent longitudinal ridge separating the free ventral part of the process and its dorsal part occupied by the facets for the prootic and the squamosal (Fig. 32b). The ventral part of the process is strongly concave. The prootic facet is of triangular

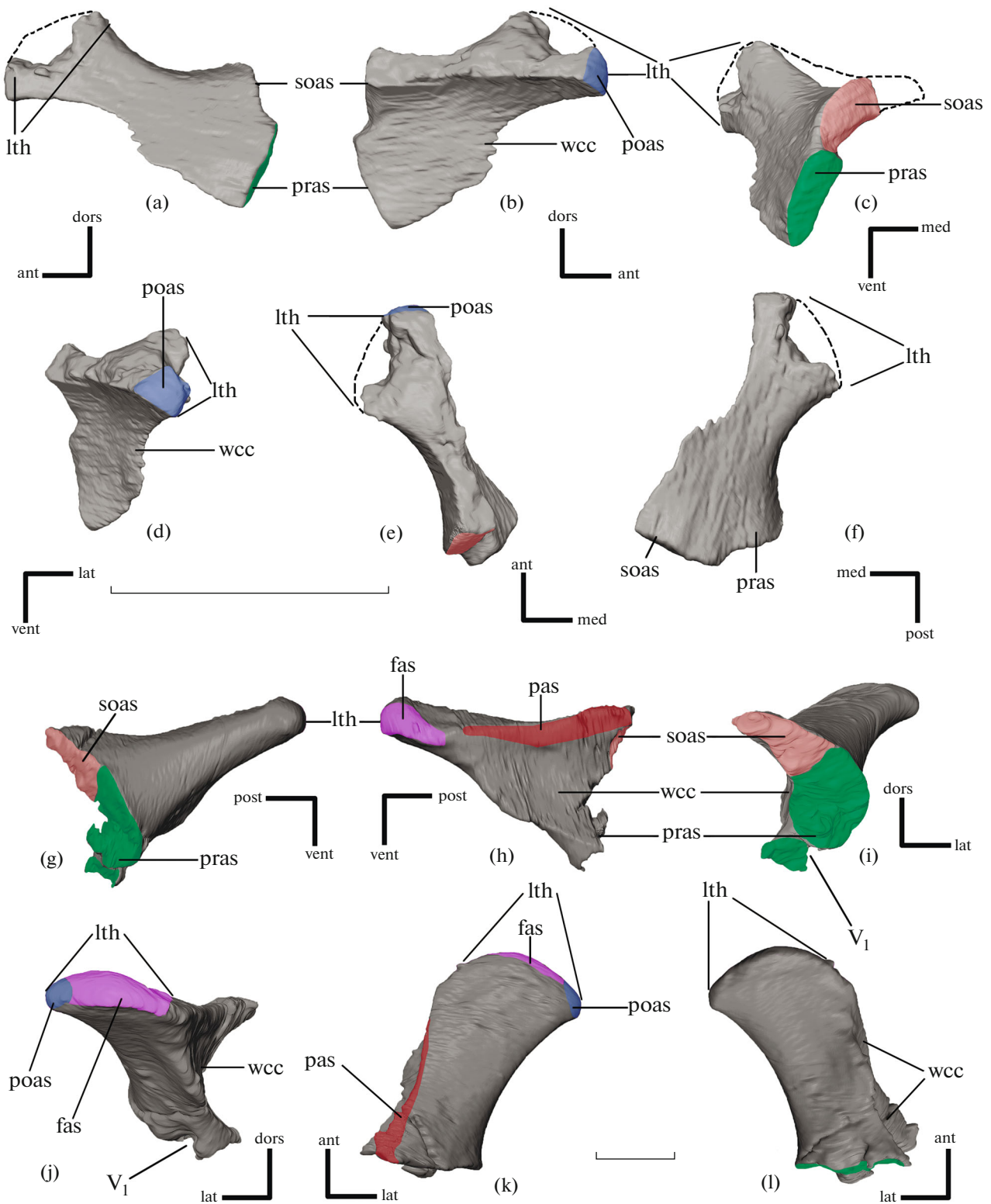


Fig. 33. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left laterosphenoid of KOKM 22985/5 (a–f) and right laterosphenoid of KOKM 22985/2 (g–l). (a, g) Lateral view; (b, h) medial view; (c, i) posterior view; (d, j) anterior view; (e, k) dorsal view; (f, l) ventral view. See text for abbreviations. Scale bars, 10 mm.

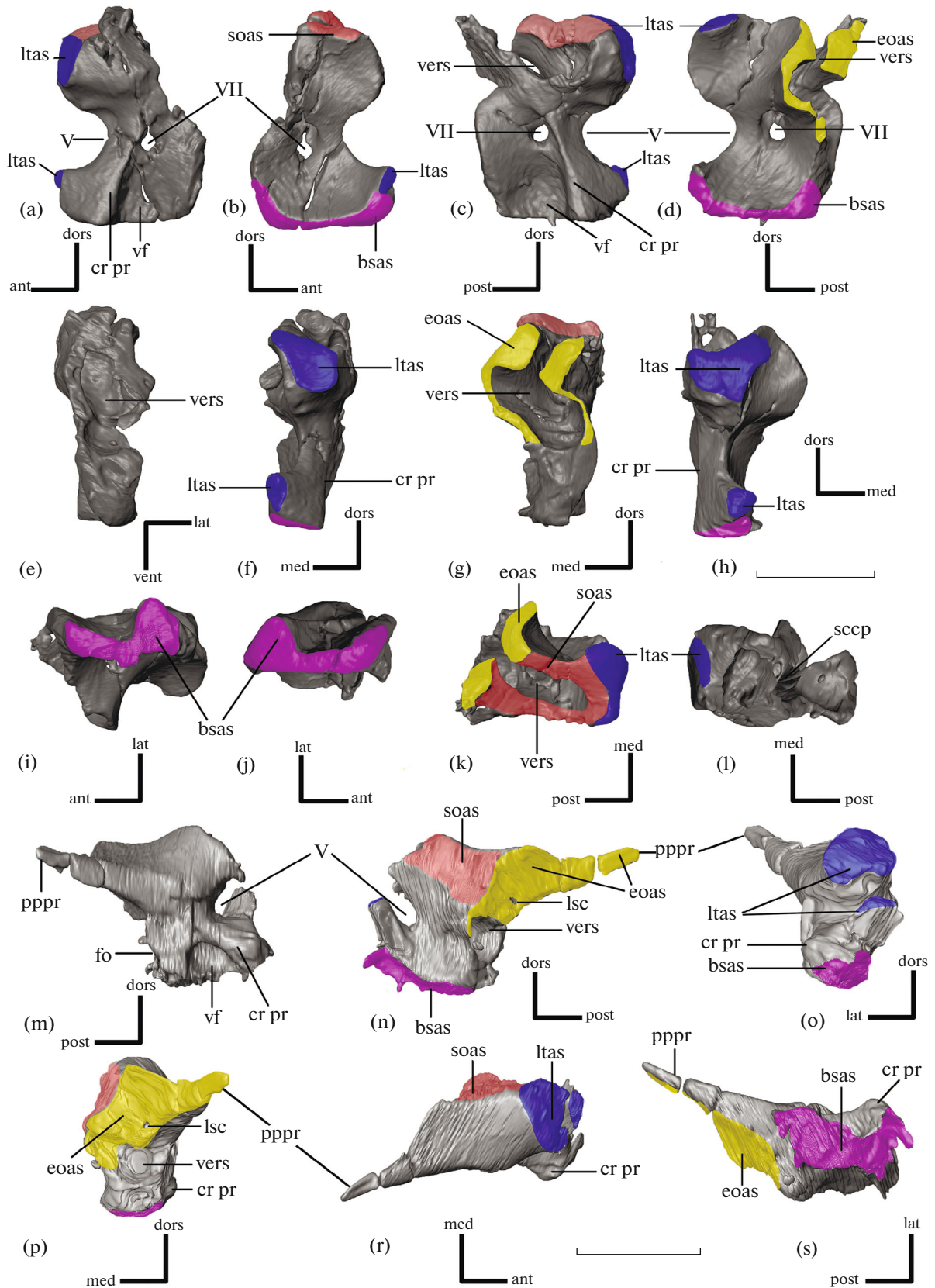


Fig. 34. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilel Formation, Lower Cretaceous. Left (a, b, e, f, j, l) and right (c, d, g, h, i, k) prootic of KOKM 22985/5 and right prootic of KOKM 22985/2 (m–r). (a, c, m) Lateral view; (b, d, n) medial view; (e, g, p) posterior view; (f, h, o) anterior view; (i, j, r) ventral view; (k, l, q) dorsal view. See text for abbreviations. Scale bars, 5 mm for a–l, and 20 mm for m–r.

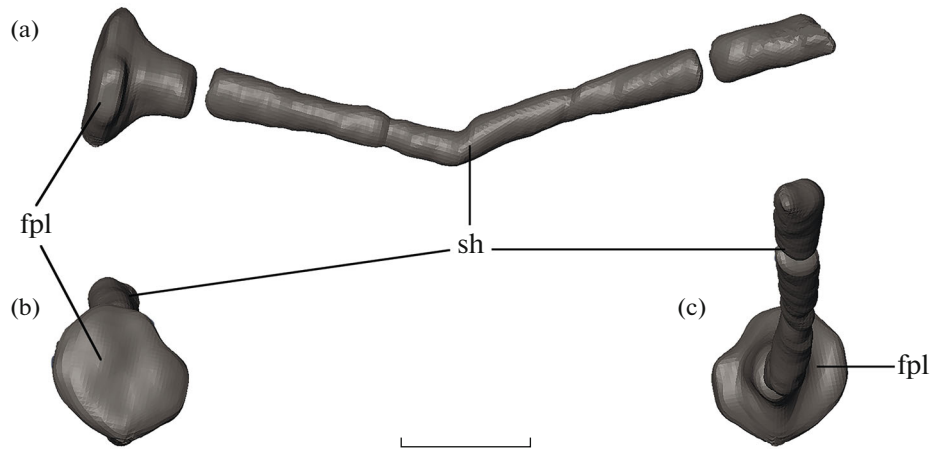


Fig. 35. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Stapes (uncertain side) of KOKM 22985/5 in frontal plane (a), from eardrum (b), and from inner ear (c). See text for abbreviations. Scale bar, 1 mm.

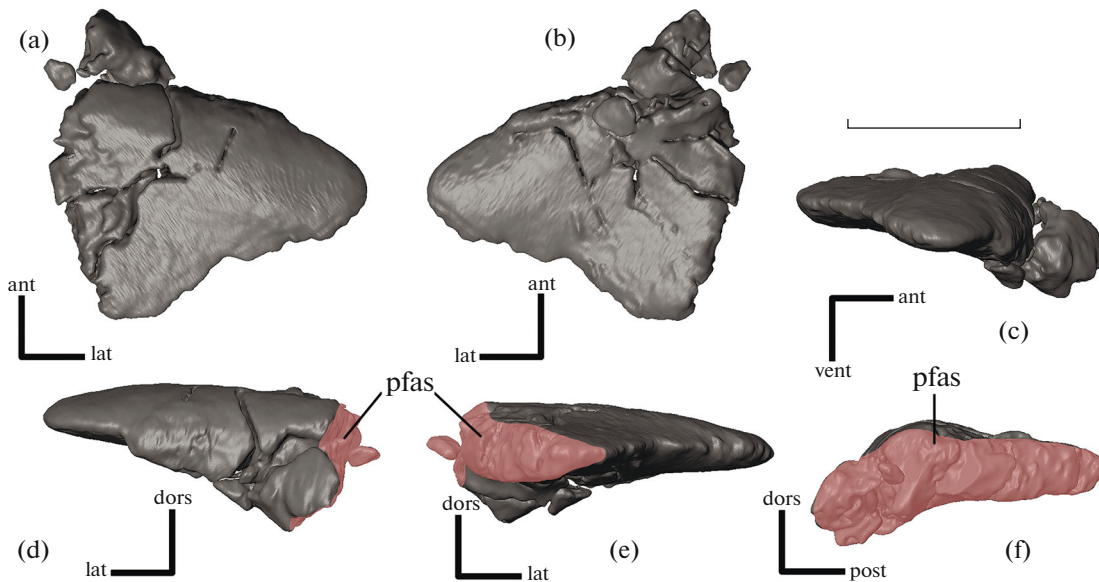


Fig. 36. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right palpebral of KOKM 22985/5 in dorsal (a), ventral (b), lateral (c), anterior (d), posterior (e), and medial (f) views. See text for abbreviations. Scale bar, 5 mm.

shape, pointed laterally, and occupies less than half of the paroccipital process length. The squamosal facet is much larger, extends for the entire paroccipital process, and points medially. Dorsal to the squamosal facet, there is a small strip of the parietal facet. On this side, there is also small facet for the supraoccipital (Fig. 32b). Below the squamosal facet, there was probably a narrow facet for the pterygoid ramus of the quadrate.

Laterosphenoid. Both laterosphenoids are preserved in KOKM 22985/2 (Figs. 33a–33f) and the left laterosphenoid is almost complete in KOKM 22985/5 (Figs. 27a, 27b, 27d, 28f, 28, 33g–33l). The latero-

sphenoid is a small bone forming the anterodorsal margin of the braincase and contacting the prootic and the supraoccipital posteriorly and the parietal, the postorbital and the frontal dorsally. The posterior end of the bone is expanded dorsoventrally and excavated by a large depression on medial side that result in a semicircular shape of the posterior articular surface, contacting the supraoccipital dorsally and the prootic ventrally (Figs. 33c, 33i). Along the ventral margin of the posterior part of the bone surface, there is an incision continuing anteriorly into a short groove. These are parts of the trigeminal foramen and canal transmitting the cranial nerve V (Figs. 33i, 33j). The ante-

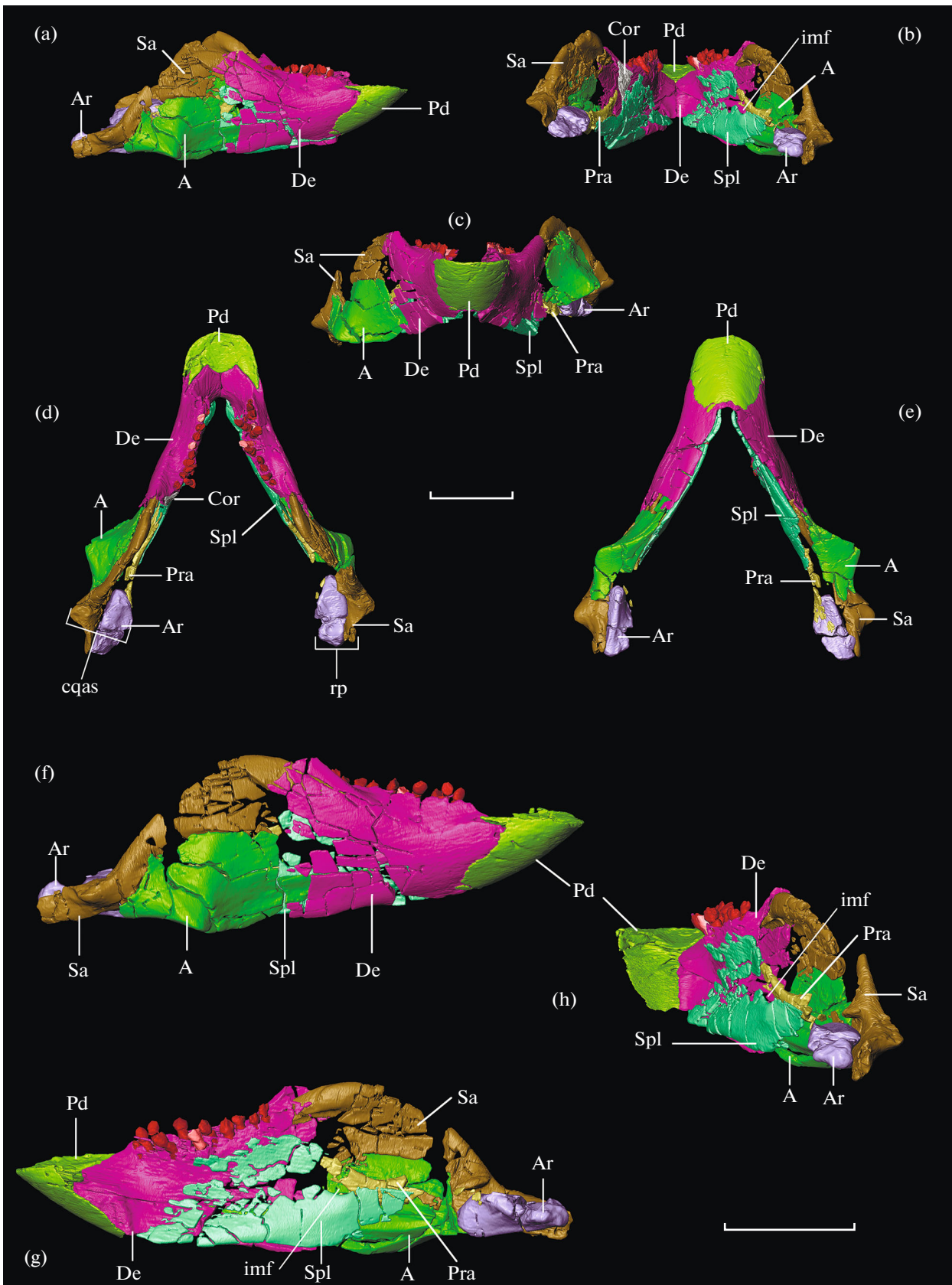


Fig. 37. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Segmented mandibles of KOKM 22985/2 in right lateral (a), posterior (b), anterior (c), dorsal (d), ventral (e) views. The right mandible of KOKM 22985/2 in lateral (f), medial (g), and posteromedial (h) views. See text for abbreviations. Scale bars, 50 mm.

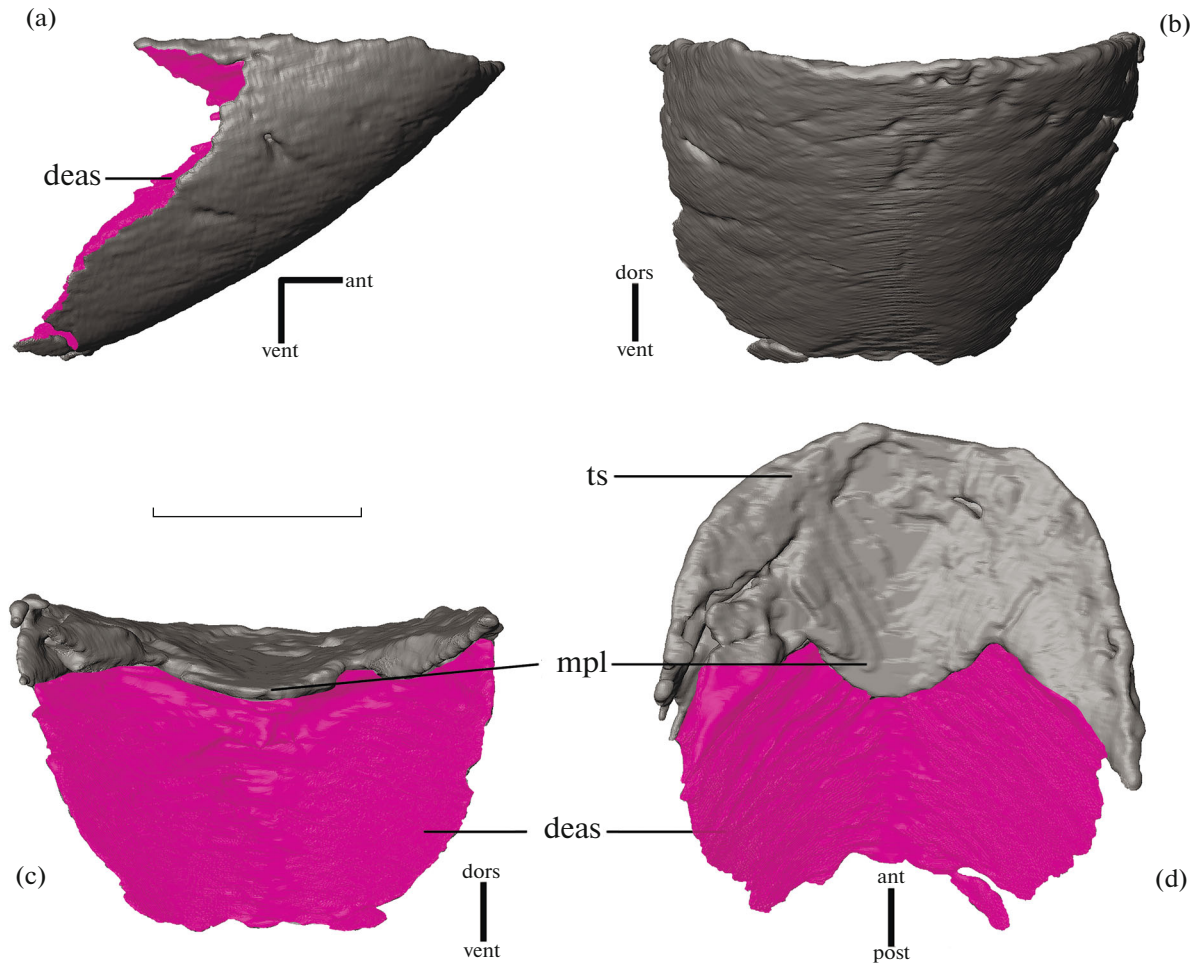


Fig. 38. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Predentary of KOKM 22985/2 in right lateral (a), anterior (b), posterior (c), and dorsal (d) views. See text for abbreviations. Scale bar, 20 mm.

rior end of the bone is the dorsoventrally flattened and mediolaterally expanded laterosphenoid head that contacts the frontal and the postorbital by its dorsal surface. The dorsal surface posterior to the frontal facet contacts the parietal (Fig. 33h).

Prootic. The prootics are partially preserved in KOKM 22985/5 and complete in KOKM 22985/2 (Figs. 27, 28, 34). The prootic forms the lateral wall of the braincase and contacts the exoccipital/opisthotic posteriorly, basisphenoid ventrally, laterosphenoid anteriorly, and the supraoccipital dorsally. This bone houses most of the inner ear. The prootic is a roughly rectangular bone with a prominent posterodorsal process that contacts the exoccipital/opisthotic by its entire medial surface. The convex dorsal surface of the bone has a sharp posterior margin that overlaps the exoccipital/opisthotic. Its medial margin contacts the supraoccipital, and the anterior margin contacts the laterosphenoid. There are thick contact areas for these bones on the medial and anterior sides of the prootic, respectively (Figs. 34n, 34o). The lateral side of the

bone is divided into a flat posterior part, which is confluent with the posterior process, and an anterior part, bearing a strong oblique ridge (crista prootica) flanked by trigeminal foramen dorsally and ventral fossa ventrally (Fig. 34m). The ventral fossa extends ventrally onto the basisphenoid. The prootic contacts the basisphenoid by its entire ventral surface. On the postero-medial surface of the bone, ventral to the exoccipital/opisthotic facet, there is a large hole for the semi-circular canal (Fig. 34n). In the juvenile prootic KOKM 22985/5 (Figs. 34a–34l), the crista prootica is more vertical, parallel to the posterior margin of the bone. The trigeminal foramen is relatively larger, with the laterosphenoid facet placed both dorsal and ventral to it. The ventral fossa is shallower. There is a distinct foramen presumably for the VII cranial nerve dorsal to the ventral fossa. This foramen is absent in the adult specimen KOKM 22985/2, where the VII cranial nerve likely exits through the trigeminal foramen. Almost the entire dorsal part of the juvenile prootic is occupied by a large cavity (vestibular recess)

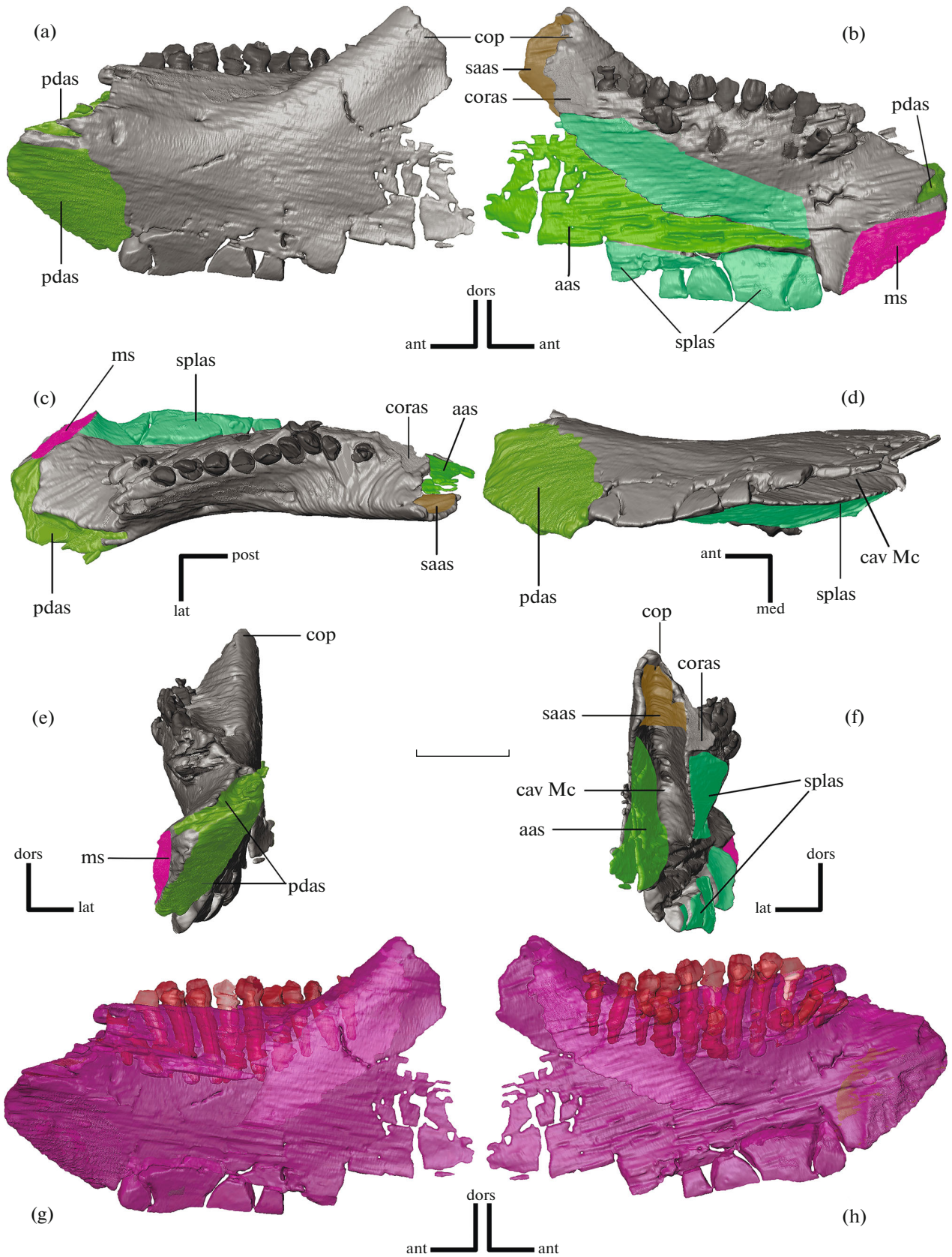


Fig. 39. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left dentary of KOKM 22985/2 in lateral (a), medial (b), dorsal (c), ventral (d), anterior (e), and posterior (f) views. The same dentary in translucent form in lateral (g) and medial (h) views. See text for abbreviations. Scale bar, 20 mm.

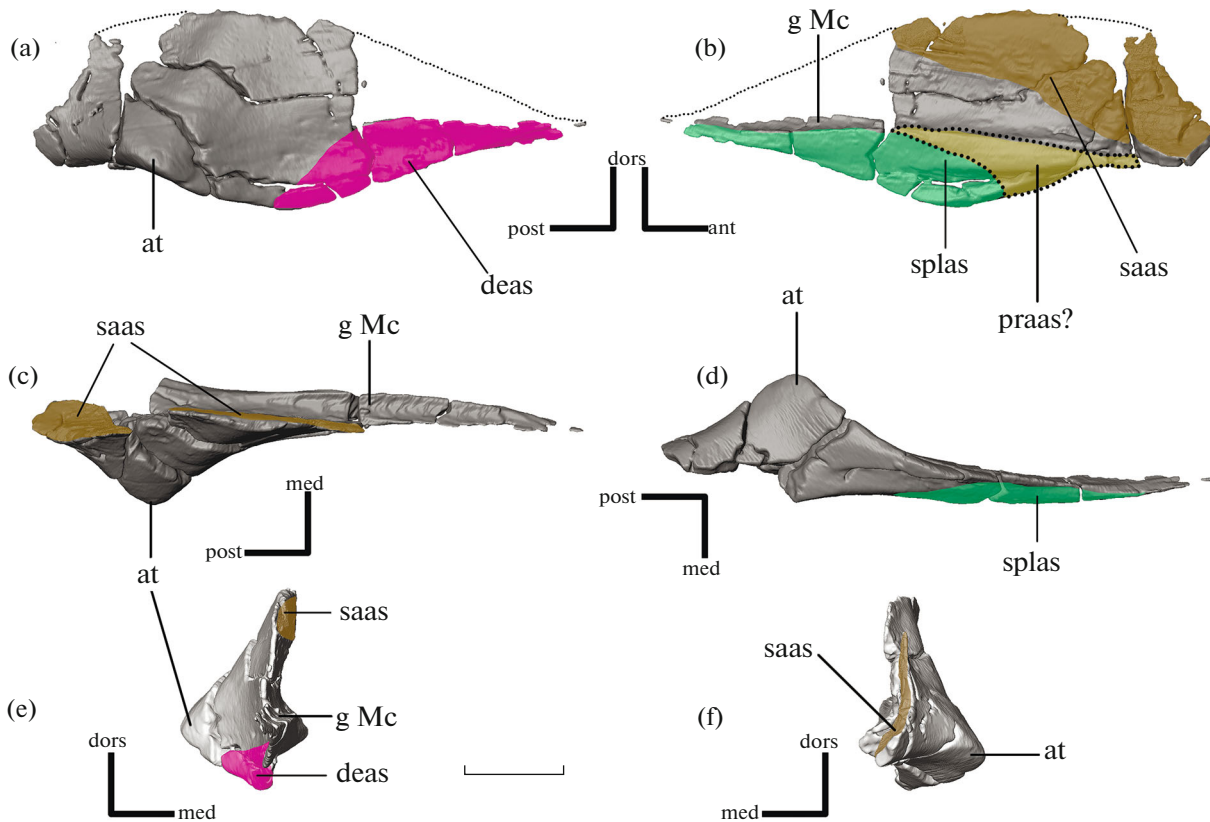


Fig. 40. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right angular of KOKM 22985/2 in lateral (a), medial (b), dorsal (c), ventral (d), anterior (e), and posterior (f) views. See text for abbreviations. Scale bar, 20 mm.

for vestibule of inner ear. The juvenile prootic lacks the posterior process, which is prominent in the adult specimen, which is probably due to poor preservation.

Stapes. One stapes is preserved in the juvenile specimen KOKM 2295/5 (Fig. 35). It is displaced from its original position and it is not clear whether it is right or left. The bone consists of a long and thin shaft and a round footplate that was inserted on the eardrum.

Accessory Dermal Elements

Palpebral. The palpebral is preserved only in KOKM 22985/5 (Fig. 36). The palpebral is an additional ossification above the orbit that was attached to the prefrontal. The palpebral is a triangular plate pointed laterally. Its entire medial surface is occupied by the prefrontal articulation facet. The palpebral is convex dorsally and concave ventrally.

Lower Jaw

In KOKM 22985/5 the lower jaw is not preserved except small pieces of the surangular and splenial (?) (Figs. 2a, 2b). In KOKM 22985/2, the lower jaw is almost completely preserved (Figs. 3, 4, 7, 37). The

dentaries are connected in the mandibular symphysis, which is attached to the predentary forming a beak with the rostral on the skull. There is one accessory ossification, the coronoid. Another accessory ossification, the intercoronoid, found in *P. mongoliensis* (Sereno, 2010: text-Fig. 2.14), is absent. The external mandibular fenestra is closed.

Predentary. The predentary consists of two thin parts connected at an acute angle along the cutting edge (Figs. 37, 38). The predentary covers about half of the dentary symphysis dorsally and almost completely ventrally, leaving only a small strip of the dentary symphysis exposed ventrally posterior to it. The predentary contacts the dentary by its entire internal surface, and the dentary is deeply wedged into a cleft between the predentary plates. The ventral part of the predentary is strongly convex anteriorly and egg-shaped in anterior/posterior view, with a convex dorsal cutting edge and a slightly narrower concave ventral margin (Fig. 38d). The dorsal part of the predentary forms the triturating surface. It is concave dorsally and has a round medial plate projecting posteriorly (Figs. 38c, 38d). The posterolateral process of the dorsal part fits in a groove on the dentary end extends posteriorly almost to the anterior end of the tooththrow (Figs. 38a, 38c, 38f). The predentary is fused with the

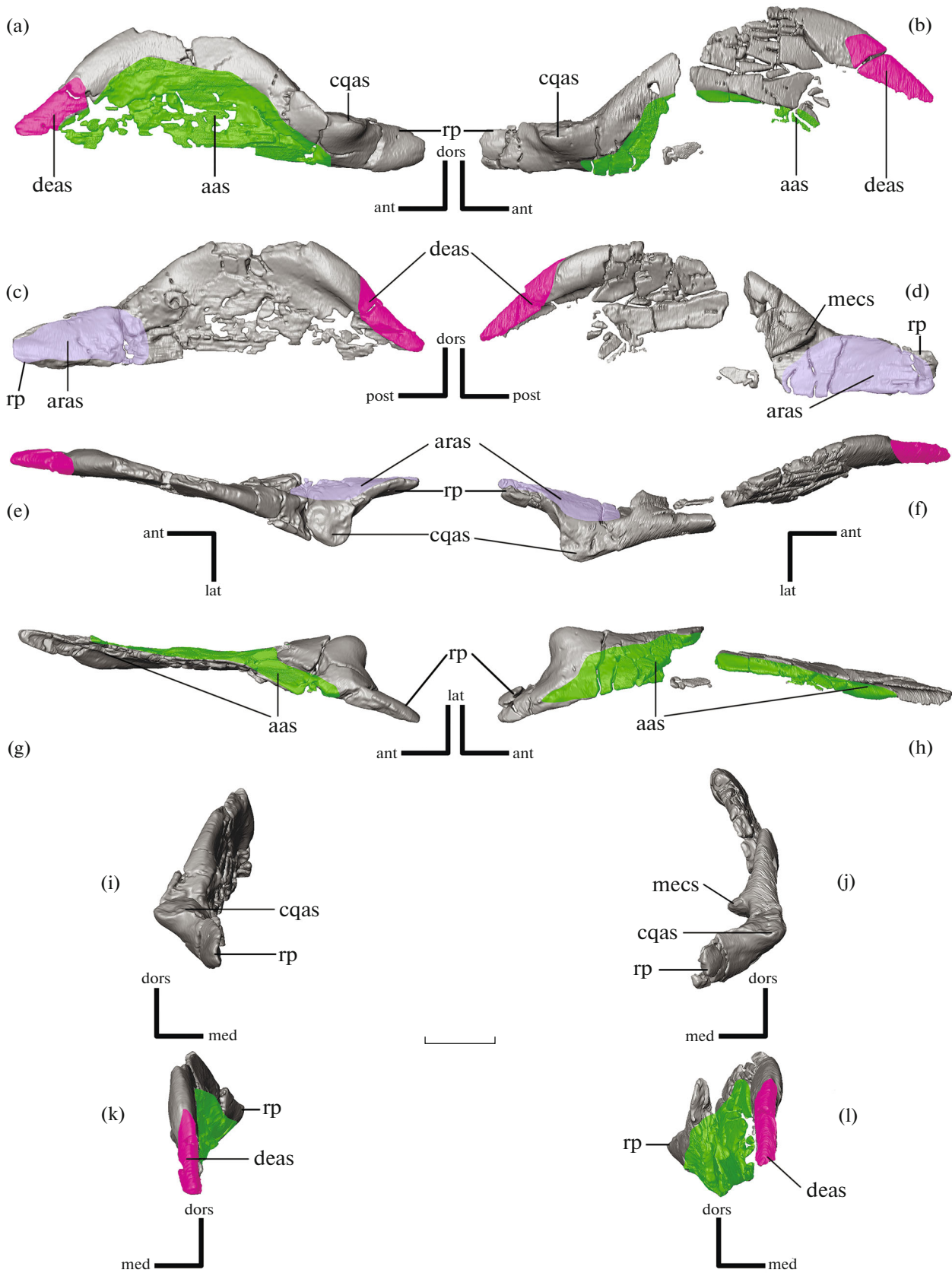


Fig. 41. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left (a, c, e, g, i, k) and right (b, d, f, h, j, l) surangular of KOKM 22985/2. (a, b) Lateral view; (c, d) medial view; (e, f) dorsal view; (g, h) ventral view; (i, j) posterior view; (k, l) anterior view. See text for abbreviations. Scale bar, 20 mm.

dentaries in the holotype of *P. gobiensis* (Serenio et al., 2010).

Dentary. The dentary is the largest bone of the lower jaw, extending for about half of its length (Figs. 37, 39). The anterior end of dentary deflects medially and forms a symphysis with the opposite dentary. In lateral/medial view, the dentary has a slightly concave dorsal dentigerous margin and the ventral margin concave in the middle. The anterior margin is pointed anteriorly. On its lateral side, there is large flat facet for the prementary ventrally and a groove for the posterolateral process of the prementary dorsally. A previous description of *P. sibiricus* (Averianov et al., 2006) stated that this groove is absent, which is apparently an artifact of inadequate preservation. The groove for the prementary posterolateral process does not reach the toothrow, in contrast with *P. amitabha*, where it extends posteriorly beyond the first tooth (Napoli et al., 2019: text-Fig. 7A). The dentary is convex labially; as a result, the toothrow and the ventral margin of the bone are placed medially to the lateral bone surface in the middle. The toothrow is slightly concave labially in dorsal view (Fig. 39c). There is a row of replacement foramina on the medial side, ventral to the toothrow. Some of these foramina house replacement teeth. There is a prominent coronoid process inclined at an angle of $\sim 39^\circ$ to the horizontal. It is placed lateral to the toothrow and starts in the middle of the latter. On the medial side, a narrow symphysis extends along the anteroventral margin of the bone. On the medial side, a large cavity occupies the entire coronoid process and extends anteriorly ventral to the toothrow. This cavity likely housed the Meckelian cartilage, except its dorsal part, occupied by the surangular. On the coronoid process, posterior to the toothrow, there is a small flat area contacting the coronoid. A large part of the medial bone surface, posterior to the symphysis and ventral to the toothrow, is covered by the splenial (Fig. 39b). A distinct groove in the posteroventral corner of the medial side, housing the anterior part of the angular, is preserved only on the right dentary. The dentaries are fused in the holotypes of *P. gobiensis* and *P. amitabha* (Serenio et al., 2010; Napoli et al., 2019: text-Fig. 7). Brinkman et al. (2001: text-Fig. 3B) described the dentary of *P. xinjiangensis* as completely lacking the ventral part. More likely, the ventral part of the dentary is broken off on this specimen. *P. sibiricus* lacks the anterior corner of the ventral flange.

Angular. The angular is exposed mostly on the lateral side of the lower jaw, ventral to the surangular and posterior to the dentary (Fig. 37). On the medial side of the lower jaw, a small strip of the angular is exposed posterior to the splenial and ventral to the prearticular. The angular forms parts of the ventral and lateral sides of a large adductor cavity. In lateral view, the angular has a teardrop shape pointed anteriorly (Fig. 40). The ventral margin is sinusoidal in lateral/medial view, with a convexity in the middle (Figs. 40a, 40b). On the

lateral side, close to the posterior end, there is a prominent angular tuber. Its highest point is on the ventral margin of the bone. A low ridge extends from the angular tuber anterodorsally. The lateral surface is concave anterior to this ridge. The anteroventral part of the lateral side was overlapped by the dentary (Fig. 40a). On the medial side, there is a prominent horizontal ridge along the ventral margin of the bone. In anterior part of this ridge, on its dorsal surface, there is a groove housing the Meckelian cartilage. The surangular attachment area is on the medial side of a thin dorsal plate (Fig. 40b). The medial side of the horizontal ridge contacts the splenial and probably with the prearticular. Ventral to the vertical ridge, on the medial side of the ventral convexity and anterior to the angular tuber, there is a short but deep groove.

Surangular. Both surangulars are incomplete. The surangular forms the dorsal margin of the posterior part of the lower jaw, contacting the dentary anteriorly, the angular ventrally, and the articular posteriorly, and contributes to the glenoid articular fossa (Fig. 37d). A larger anterior part of the surangular is a thin plate with a greatly convex dorsal margin, forming the coronoid process of the lower jaw, and a straight ventral margin. The dorsal margin of the anterior part is thickened anteriorly where it is separated from the rest of the bone by a groove (Figs. 41c, 41d). Anterior part of this thickened margin fits into a cavity within the coronoid process of the dentary (Fig. 41). All lateral side of the surangular, except its dorsal margin and posterior surface, is covered by the angular (Figs. 41a, 41b). The medial side of the anterior part of the surangular forms the lateral wall of the large adductor fossa. In dorsal view, the anterior part of the surangular is slightly concave laterally. The posterior part of the surangular is about a third of the length of the bone and consists of the glenoid articular fossa and a short posteromedially deflecting retroarticular process (Fig. 41). The quadrate articulation surface is flat and has rounded lateral and straight medial margins. It faces dorsally and slightly laterally. The retroarticular process has convex lateral and concave medial sides. The surangular contacts the articular by the medial side of the glenoid articular fossa and retroarticular process. The articular attachment area is limited anteriorly by a short but high oblique crest on the medial side, which is preserved only on the right surangular (Figs. 41d, 41j). This medial crest is obliquely oriented related to the bone long axis and overhangs a depressed area contacting the articular.

Splenial. The splenial is a thin plate-like bone on the medial side of the lower jaw, covering the dentary anteriorly and the angular posteriorly and contacting the prearticular posterodorsally and coronoid dorsally (Figs. 37, 42). The splenial and the prearticular form the margins of the internal mandibular fenestra. The bone is highest in the middle and tapers anteriorly and posteriorly (Figs. 42a–42d). The anterior pointed end is on the ventral margin of the bone, whereas the pos-

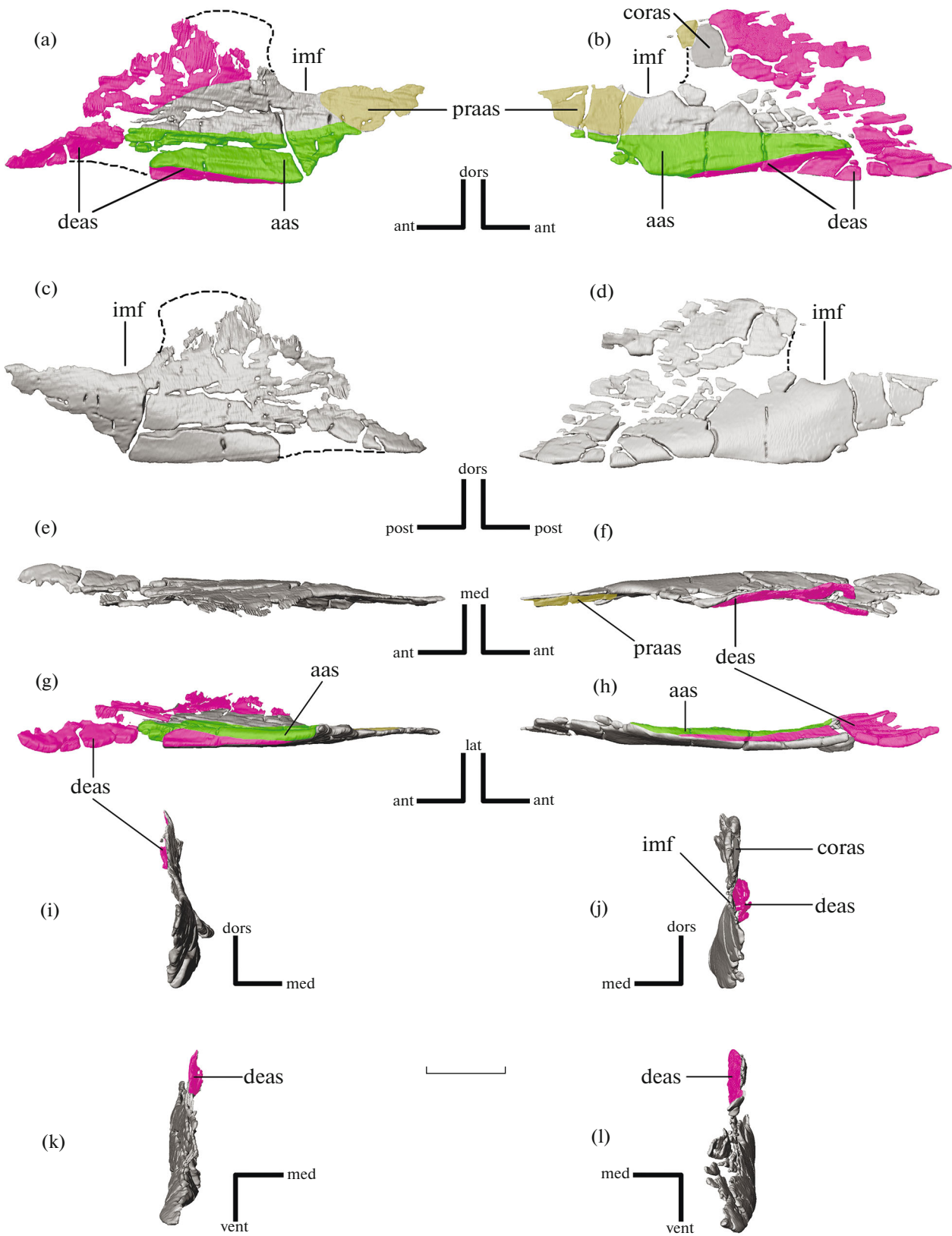


Fig. 42. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right (a, c, e, g, i, k) and left (b, d, f, h, j, l) splenial of KOKM 22985/2. (a, b) Lateral view; (c, d) medial view; (e, f) dorsal view; (g, h) ventral view; (i, j) posterior view; (k, l) anterior view. See text for abbreviations. Scale bar, 20 mm.

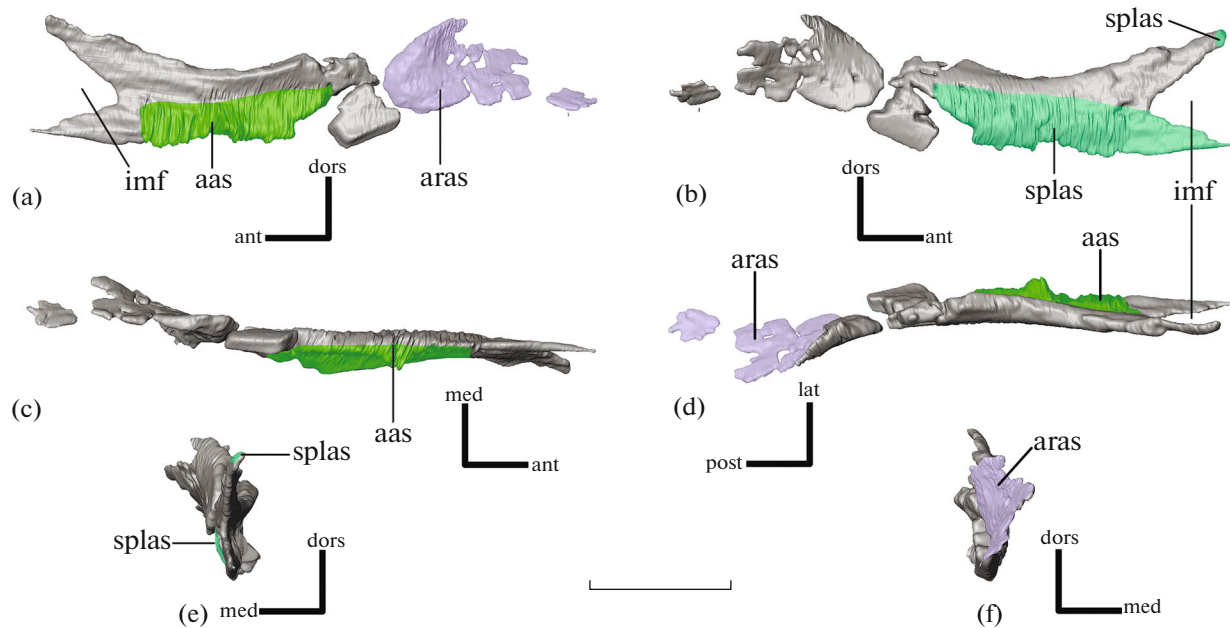


Fig. 43. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left prearticular of KOKM 22985/2 in lateral (a), medial (b), ventral (c), dorsal (d), anterior (e), and posterior (f) views. See text for abbreviations. Scale bar, 20 mm.

terior pointed end is offset somewhat dorsally from the ventral margin. The ventral margin of the bone is concave in the middle. The posterodorsal margin is deeply incised by the round internal mandibular fenestra. The bone is very thin except the thickened ridge along the ventral margin on the lateral side. This ridge separates the angular and the dentary facets (Figs. 42a, 42b). The dentary facet occupies anterodorsal and anteroventral parts of the lateral side (Figs. 42a, 42b). The triangular, anteriorly tapering angular facet is placed dorsally to the ridge on the lateral side. The prearticular facet occupies the lateral side of the posterior projection of the bone. On the dorsal margin of the lateral side, posterior to the dentary facet, there is a small coronoid facet. Some lateral bone surface is free and forms the medial wall of the adductor fossa.

Prearticular. The prearticular is more complete on the left side (Figs. 37, 43). It is a thin stripe-like bone extending on the medial side of the lower jaw between the internal mandibular fenestra and the articular and contacting the splenial and the angular ventrally. Its lateral side forms the medial wall of the adductor fossa. The anterior end, encompassing the posterior half of the internal mandibular fenestra, is bifurcated. The posterior margin of the internal mandibular fenestra is triangular, in contrast to its round anterior margin, formed by the splenial. In medial/lateral view, the prearticular is sinusoidal, with ventrally convex anterior part and dorsally convex posterior part (Figs. 43a, 43b). In dorsal/ventral view, the prearticular is slightly convex medially. The anteroventral part of the medial side, including the ventral prong of the anterior bifur-

cated end, is covered by the splenial (Fig. 43b). There is also a small piece of the splenial facet on the dorsal prong of the anterior bifurcated end. On the lateral side, there are facets for the angular anteroventrally and for the articular posteriorly (Fig. 43a).

Articular. The articular is a small bone forming parts of the glenoid articular fossa and the retroarticular process and contacting with the prearticular medially and the surangular laterally (Figs. 37, 44). The articular contribution to the retroarticular process is similar to that of the surangular, contra the previous description of *P. sibiricus* stating that the retroarticular process is formed mainly by the surangular (Averianov et al., 2006). According to Sereno et al. (1988: p. 373), the retroarticular process in *P. meileyingensis* is composed by the surangular and the angular, and the glenoid fossa is formed mostly by the articular. In *P. gobiensis*, the retroarticular process consists of the articular and is directed posteromedially (Sereno et al., 2010: text-Fig. 2d). The articular is longer than wide and triangular in cross-section, with a prominent longitudinal ridge ventrally. This ridge separates the prearticular and the surangular facets (Fig. 44d). On the dorsal surface of the anterior part of the bone, there is a slightly concave articular surface for the quadrate. On the dorsal surface of the retroarticular process, there is a round pit apparently for insertion of *m. depressor mandibulae* (Sereno, 2010). The retroarticular process is lower dorsoventrally than the anterior part of the bone (Figs. 44a, 44b).

Coronoid. The coronoid is a small roughly rhomboid thin plate attached by the dorsal part of its medial

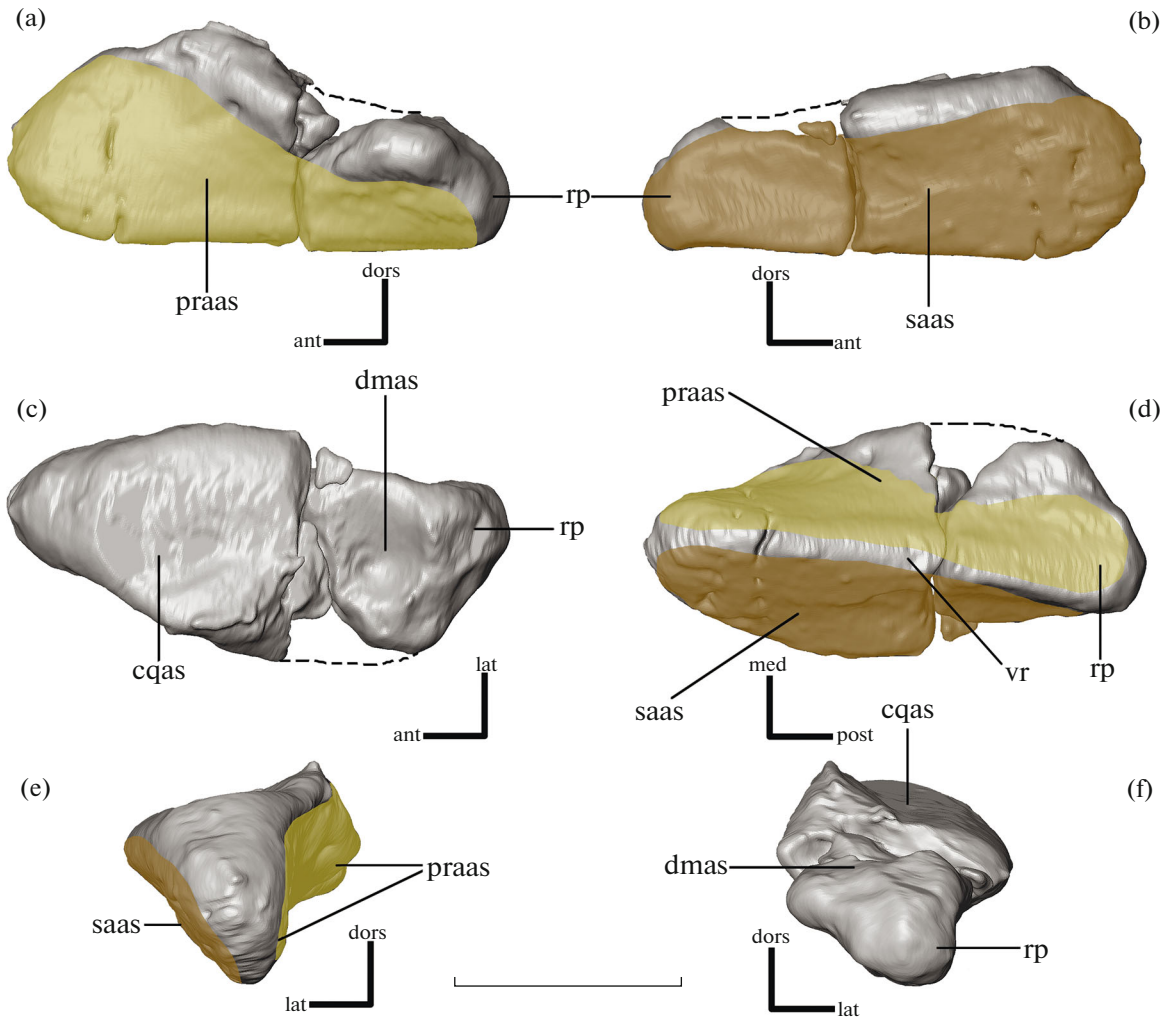


Fig. 44. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Right articular of KOKM 22985/2 in medial (a), lateral (b), dorsal (c), ventral (d), anterior (e), and posterior (f) views. See text for abbreviations. Scale bar, 20 mm.

side to the coronoid process of the dentary (Figs. 37, 45). The splenial overlaps the lateral side of the coronoid along its ventral margin. In anterior/posterior view, the coronoid is sinusoidal (Figs. 45b, 45c).

Dentition

The dentition is complete in KOKM 22985/2, whereas in KOKM 22985/5 only upper dentition is preserved. As in other psittacosaurids, there are no premaxillary teeth. In the maxilla, there are six (KOKM 22985/5) or ten (KOKM 22985/2) tooth positions. In the right maxilla of KOKM 22985/5, the functional teeth are present in the positions 2–6 (Fig. 46). The tooth 2 has no crown. The crown is worn in the teeth 3, 5 and unworn in the teeth 4, 6. The tooth 4 has the largest crown. There are three replacement teeth (positions 1, 2, and 5), placed in the replacement pits medial to the functional toothrow.

The replacement tooth 2 is much larger than the replacement tooth 1. It is similar in size with the largest functional tooth 4. The replacement tooth 5 was likely larger, but only the apex of the crown remained from it, apparently because it was not fully calcified. There are three roots of the previous functional teeth placed lateral to the functional toothrow between the positions 3–4, 4–5, and 5–6 (Fig. 46). In the left maxilla of KOKM 22985/2, there are replacement teeth in positions 4 and 6. Only apex of the replacement tooth 4 is preserved, possibly because of incomplete ossifications. In the right maxilla, there are no replacement teeth. In the left dentary of KOKM 22985/2, there are nine tooth positions, with the functional teeth present in the positions 2–9. The replacement teeth are present in the positions 1, 4, and between the functional teeth 6, 7. In the right dentary of KOKM 22985/2, there are eleven tooth positions,

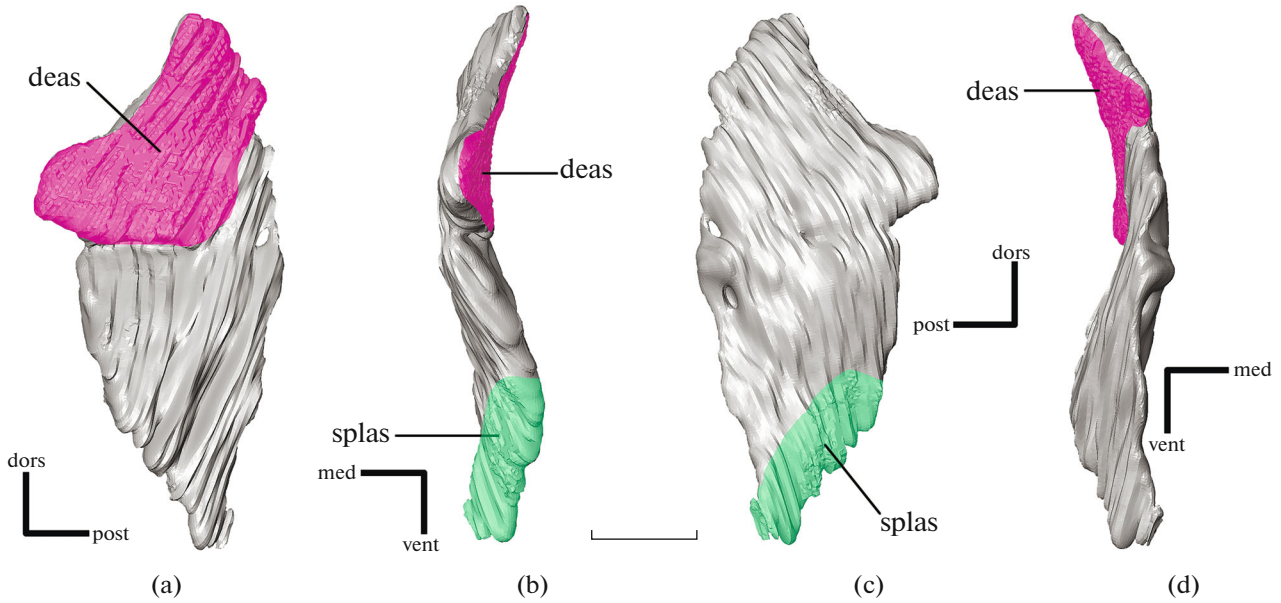
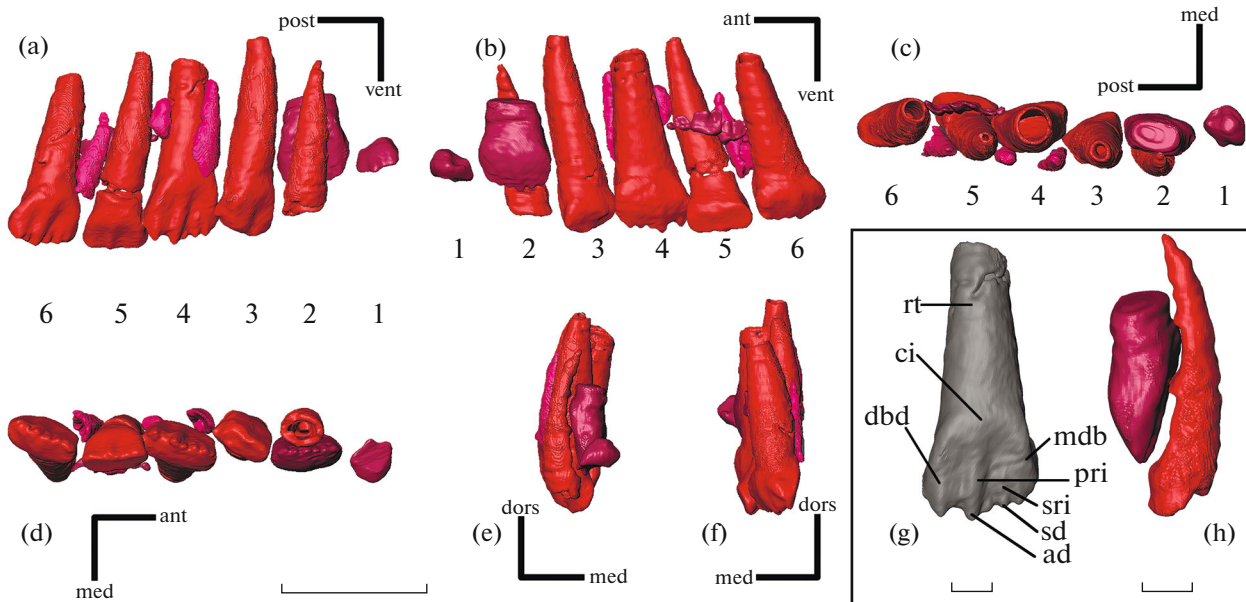


Fig. 45. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left coronoid of KOKM 22985/2 in lateral (a), anterior (b), medial (c), and posterior (d) views. See text for abbreviations. Scale bar, 5 mm.



Functional maxillary teeth
 Replacement maxillary teeth
 Remnants of mostly functional maxillary teeth

Fig. 46. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left maxillary dentition of KOKM 22985/5 in lateral (a), medial (b), dorsal (c), ventral (d), anterior (e), and posterior (f) views. (g) enlarged lateral view of fourth tooth. (h) functional and replacing teeth in the second position in posterior view. See text for abbreviations. Scale bars, 5 mm for (a–f) and 1 mm for g, h.

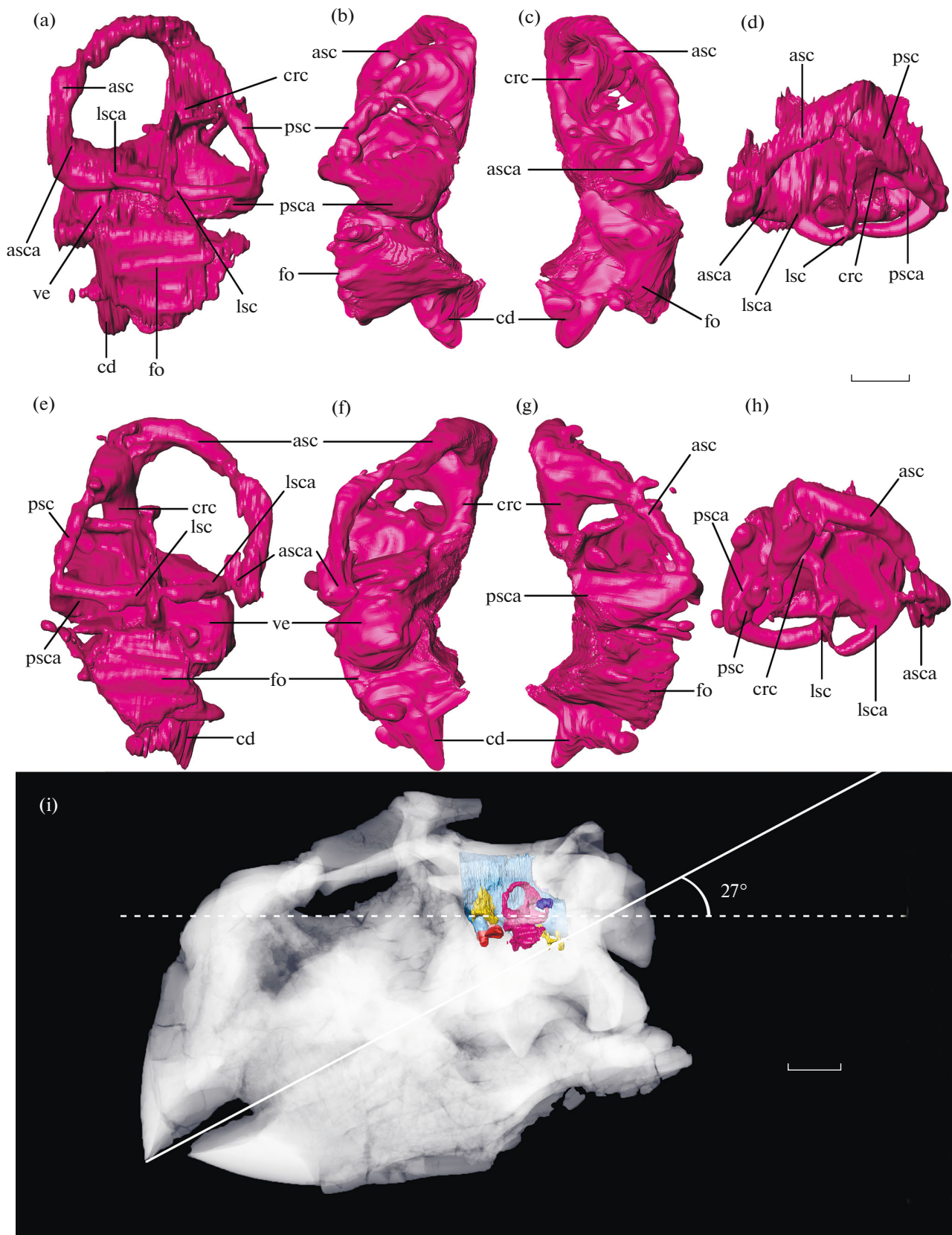


Fig. 48. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Left (a–d) and right (e–h) inner ear endocast of KOKM 22985/2. (a, e) Lateral view; (b, f) posterior view; (c, g) anterior view; (d, h) dorsal view. (i) position of the head when the lateral semicircular canal is parallel to the ground. See text for abbreviations. Scale bars, 5 mm for (a–h) and 20 mm for (i).

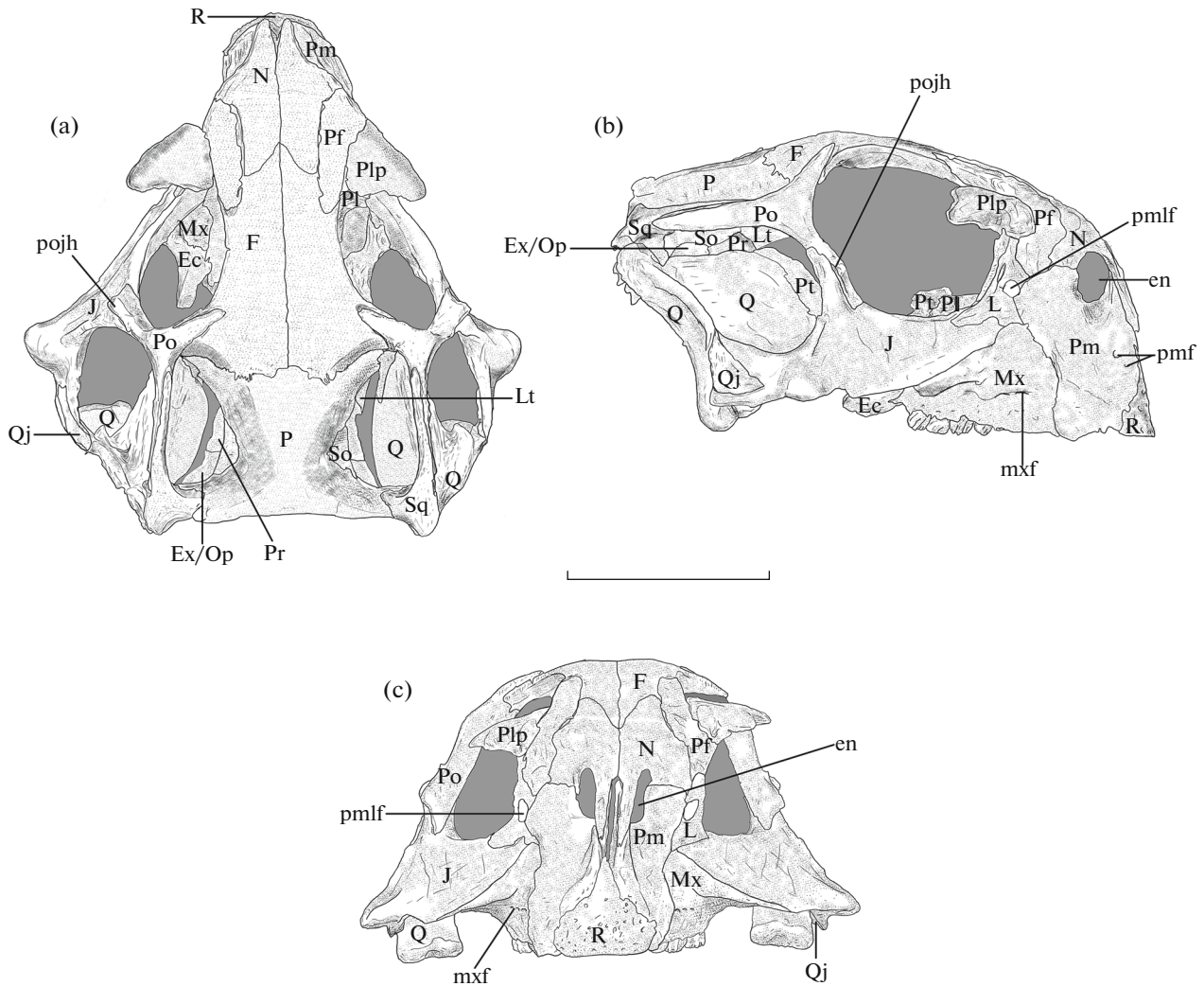


Fig. 49. *Psittacosaurus sibiricus* Voronkevich et Averianov, 2000. Shestakovo 3 locality, Kemerovo oblast (Kuzbass, Russia); Ilek Formation, Lower Cretaceous. Graphic reconstruction of the skull KOKM 22985/5 in dorsal (a), right lateral (b), and anterior (c) views. See text for abbreviations. Scale bar, 30 mm.

all occupied by the functional teeth. There are no replacement teeth in this dentary.

The wear facets develop on the lingual side of the maxillary teeth and the labial side of the dentary teeth. The teeth have a basal cingulum, the primary ridge with a large apical denticle, and smaller marginal denticles (Fig. 46g). The mesial and distal marginal denticles are formed by cingulum and are somewhat larger than the other marginal denticles. The intermediate margin denticles are usually connected with the secondary ridges, which are variously developed.

Endocast

The endocast was partially reconstructed for KOKM 22985/2 (Fig. 47). In this specimen, the orbitosphenoid is not preserved, apparently because of incomplete ossification, and the frontals and latero-

sphenoids are displaced (Fig. 4), which makes impossible the full reconstruction of the endocast.

The medulla oblongata is ovate in cross-section. Three caudal nerves originate from the medulla oblongata: X, XI, XII_{ant}, and XII_{post} (Fig. 47). A swelling dorsal to the cranial nerves likely corresponds to the occipital venous sinus (Figs. 47a, 47b). The metencephalon is distinctly higher than the medulla oblongata, apparently because of development of the venous sinus rather than the cerebellum. A high dorsal crest on the metencephalon can be considered as a part of the dorsal venous sinus (Figs. 47a–47c, 47e). This structure is often represented on the endocasts of many dinosaurs (Paulina-Carabajal et al., 2023). For example, similar structure on the endocast of *Tyrannosaurus rex* was termed the dural peak and interpreted as a structure housing the dural venous sinus (Witmer and Ridgely, 2009). According to an alternative inter-

pretation, this crest may represent the unossified anteroventral part of the supraoccipital (Oelrich, 1956; Zangerl, 1960; Hopson, 1979). The cranial nerve V originates from the anterior part of the metencephalon (Fig. 47). They are only approximately reconstructed because of the deformation of the braincase in this region. Nerves VII and VIII could not be detected in the endocast. The cerebellar flocculus as well as the nodulus are not apparent in the endocast. The endocast of the hypophysis is directed ventrally and somewhat posteriorly. It connects ventrally with the internal carotid arteries (Figs. 47a, 47b, 47d, 47f).

The inner ear endocast is completely reconstructed (Figs. 47, 48). The cochlear duct is relatively short, directed ventromedially. The semicircular canals are housed inside the prootic and the supraoccipital (anterior semicircular canal), the prootic and the exoccipital/opisthotic (lateral semicircular canal), and supraoccipital and the exoccipital/opisthotic (posterior semicircular canal). The bases of the semicircular canals are widened into ampullae. The anterior semicircular canal is the longest whereas the lateral semicircular canal is the shortest. The anterior and posterior semicircular canals are connected by the crus commune. The angle between the planes of the lateral semicircular canal and the palate is 27° (Fig. 48i). A similar angle (25°) was calculated for a juvenile individual of *P. lujiatunensis* (Bullar et al., 2019).

DISCUSSION

The tomographic study of the two specimens of *P. sibiricus*, one juvenile (KOKM 22985/5) and one adult (KOKM 22985/2), provides a wealth of new information on the cranial anatomy of this species. Reconstruction of these skulls is shown in Figs. 49 and 50. In this section, we review some cranial characters diagnostic for *P. sibiricus* and other *Psittacosaurus* species.

Premaxilla-rostral canal. A short canal is present between the premaxilla and the rostral (Fig. 9H). A similar canal is likely present in *P. meileyingensis* (Serenó et al., 1998: text-Fig. 2A), but not in other psittacosaur species (Averianov et al., 2006).

Premaxilla-jugal contact. The premaxilla does not contact the jugal in all *Psittacosaurus* species, except *P. sinensis* (Serenó, 2010: text-Fig. 2.8) and *P. gobiensis* (Serenó et al., 2010: text-Fig. 2a). This contact cannot be traced on the holotype of *P. sibiricus* because of obliterated sutures but presence of this contact was inferred by Averianov et al. (2006) from the isolated premaxillae. In both KOKM 22985/5 and KOKM 22985/2, there is an extensive lacrimal-maxilla contact, which separates the premaxilla and the jugal (Figs. 2a, 3a). Thus, *P. sibiricus* is similar with the majority of *Psittacosaurus* species in lacking of the premaxilla-jugal contact.

Maxillary protuberance. A protuberance on the lateral ridge of the maxilla is present in *P. mongoliensis*, *P. xinjiangensis*, *P. meileyingensis*, *P. mazongshanensis*, and *P. amitabha* (Serenó and Chao, 1988; Sereno et al., 1988: text-Figs. 2A, 5; Xu, 1997: text-Fig. 1A; Sereno et al., 2010: text-Fig. 2a; Napoli et al., 2019). This protuberance is absent in *P. sibiricus*, *P. sinensis*, *P. lujiatunensis*, and *P. major*.

Postorbital horn. The postorbital horn composed of the postorbital and the jugal is present in *P. sibiricus* and *P. sinensis*. In *P. sibiricus*, this horn is present even in the juvenile specimens (KOKM 22985/5). The postorbital horn composed entirely of the postorbital is an autapomorphy of *P. gobiensis* (Serenó, 2010: text-Figs. 2.2A, 2.2B). The postorbital horn is absent in *P. mongoliensis*, *P. neimongoliensis*, *P. lujiatunensis*, and *P. major* (Serenó, 2010).

Jugal posterior process bifurcation. The jugal with a deep cleft for the quadratojugal extending to the posterior surface of the jugal horn was cited as an autapomorphy in the diagnosis of *P. sibiricus* provided by Averianov et al. (2006). This character was excluded from the diagnosis of *P. sibiricus* by Sereno (2010: p. 34) because “the posterior cleft in the jugal is difficult to differentiate from several other species on available evidence”. However, now there is enough information to evaluate this character at least in some *Psittacosaurus* species. The jugal posterior process is simple tongue-shaped in *P. amitabha* (Napoli et al., 2019: text-Fig. 4). In *P. mongoliensis*, *P. neimongoliensis*, *P. meileyingensis*, *P. sinensis*, *P. gobiensis*, *P. lujiatunensis*, and *P. major*, the posterior process of the jugal is bifurcated only distally, and the quadratojugal does not approach the posterior side of the jugal horn (Serenó et al., 1988: text-Figs. 2C, 5; Russell and Zhao, 1996: text-Fig. 1B; Zhou et al., 2006: text-Figs. 2A, 2B, 3A; Sereno et al., 2007: text-Fig. 1A; Sereno, 2010: text-Figs. 2.2A, 2.8A). Only in *P. xinjiangensis* the quadratojugal approaches closely the posterior side of the jugal horn, as in *P. sibiricus* (Serenó and Chao, 1988: text-Figs. 3, 4D). However, in this species, the posterior process of the jugal is not split but covered laterally by the quadratojugal (Serenó and Chao, 1988: text-Fig. 4D). Thus, we consider the deeply bifurcated posterior process of the jugal as an autapomorphy of *P. sibiricus*.

Quadratojugal protuberance. In *P. sibiricus*, the lateral surface of the quadratojugal exposed between the prongs of the bifurcated jugal posterior process is flat (Fig. 3), as in most other psittacosaur species. In *P. meileyingensis*, *P. gobiensis*, and *P. lujiatunensis*, there is a variably developed protuberance in this place (Serenó et al., 1988: text-Figs. 2A, 2D; Sereno et al., 2010: text-Fig. 2a; Sereno, 2010).

Frontal posterolateral process. In *P. sibiricus*, the frontal overlaps anteriorly the medial process of the postorbital excluding it from the orbital margin (Fig. 5). The same condition is present in *P. mongo-*

liensis, *P. amitabha*, *P. gobiensis*, *P. lujiatunensis*, and *P. major* (Sereno et al., 1988: text-Fig. 6; Zhou et al., 2006: text-Fig. 3B; Sereno et al., 2007: text-Fig. 1A; Sereno et al., 2010: text-Fig. 2b; Napoli et al., 2019: text-Fig. 3B). In contrast, in *P. meileyingensis*, *P. neimongoliensis*, and *P. sinensis*, the postorbital overlaps the frontal and form the posterior part of the dorsal orbital margin (Sereno et al., 1988: text-Fig. 2C; Russell and Zhao, 1996: text-Fig. 1; Sereno, 2010: text-Fig. 2.9A). The latter character was considered as an autapomorphy of *P. neimongoliensis* (Sereno, 2010), which is not correct as it has a wider distribution.

Parietal frill. The parietal frill is straight horizontal in posterior view in *P. mongoliensis*, *P. sinensis*, *P. lujiatunensis*, and *P. major* (Osborn, 1923: text-Fig. 2D; Sereno, 1990: text-Fig. 15.7B; Zhou et al., 2006: text-Fig. 3C; You et al., 2008: text-Fig. 2C). It is arcuate in *P. meileyingensis* and *P. amitabha* (Sereno et al., 1988: text-Fig. 2B; Napoli et al., 2019: text-Fig. 5B). In *P. sibiricus* the opposite parts of the parietal frill meet at the midline at an obtuse angle, which is close to the arcuate condition.

Squamosal postorbital process. In *P. mongoliensis*, the squamosal postorbital process is long; it extends towards the anterior end of the upper temporal fenestra and is situated on the dorsal aspect of the postorbital (Sereno et al., 1988: text-Fig. 6). The latter character is included in the diagnosis of the genus *Psittacosaurus* (character 13 in Sereno, 2010). This condition is present also in *P. sinensis* and *P. gobiensis* (Sereno et al., 2010: text-Fig. 2b; Sereno, 2010: text-Fig. 2.9A). In *P. lujiatunensis* and *P. major*, the squamosal postorbital process is shorter, does not reach the anterior end of the upper temporal fenestra, but similarly situated on the dorsal side of the postorbital (Zhou et al., 2006: text-Fig. 3B; Sereno et al., 2007: text-Fig. 1B; You et al., 2008: text-Fig. 1A). In *P. sibiricus* (Fig. 5), *P. neimongoliensis* (Russell and Zhao, 1996: text-Fig. 1A), and *P. amitabha* (Napoli et al., 2019: text-Fig. 3B), the squamosal postorbital process is also short, but attached mostly to the medial side of the postorbital, so the latter bone is well exposed on the dorsal aspect of the upper temporal bar. In *P. xinjiangensis*, the squamosal postorbital process is attached to the medial side of the postorbital, but is long, reaching the anterior margin of the upper temporal fenestra (Sereno and Chao, 1988: text-Fig. 3). The character “squamosal with anterior ramus extending anteriorly to anterior end of supratemporal fossa” (character 14 in Averianov et al., 2006) should be removed from the diagnosis of *P. sibiricus*.

Quadrate-paroccipital process contact. In *P. sibiricus*, *P. mongoliensis*, and *P. lujiatunensis*, the medial ramus of the squamosal completely separates the quadrate head from the paroccipital process of the exoccipital/opisthotic (Sereno et al., 1988; Zhou et al., 2006). The quadrate head contacts the paroccipital process in *P. xinjiangensis*, *P. meileyingensis*,

and *P. sinensis* (Sereno and Chao, 1988; Sereno et al., 1988).

External mandibular fenestra. In *P. sibiricus*, the external mandibular fenestra is closed, as in *P. sinensis*, *P. neimongoliensis*, *P. major*, *P. gobiensis*, and *P. lujiatunensis* (Russell and Zhao, 1996; Sereno et al., 2007, 2010; Sereno, 2010). The external mandibular fenestra is present in *P. mongoliensis*, *P. meileyingensis*, and *P. ordosensis* (Sereno et al., 1988; Russell and Zhao, 1996).

Dentary flange. A dentary flange with anterior corner is present in *P. mongoliensis*, *P. neimongoliensis*, *P. meileyingensis*, *P. lujiatunensis* (Sereno et al., 1988: text-Figs. 2A, 5; Russell and Zhao, 1996: text-Fig. 1B; Zhou et al., 2006: text-Figs. 2A, 2B; Sereno, 2010). The dentary flange is hypertrophied in *P. major*, with the anterior corner being ~30% of the dentary depth and approximating closely the prementary (Sereno et al., 2007: text-Fig. 1A). In *P. sibiricus*, the ventral flange of the mandible has a different configuration. It has no anterior corner on the dentary but has a prominent posterior angle extending to the angular. *P. sibiricus* was diagnosed previously as having the ventral flange of mandible (character 19 in Averianov et al., 2006). This should be changed to dentary flange with anterior corner absent. The dentary flange is also absent in *P. sinensis*, *P. ordosensis*, and *P. gobiensis* (Russell and Zhao, 1996: text-Fig. 5; Sereno et al., 2010: Fig. 2a; Sereno, 2010: text-Fig. 2.8).

Angular tuber. Angular tuber projecting laterally at posterior end of the ventral flange of the mandible is an autapomorphy for *P. sibiricus* (Averianov et al., 2006; Sereno, 2010).

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AUTHOR CONTRIBUTIONS

Conceptualization: A.V. Podlesnov, A. O. Averianov. Investigation: A.V. Podlesnov, A.O. Averianov. Visualization: A.V. Podlesnov, A.A. Burukhin. Writing—original draft: A.V. Podlesnov, A.O. Averianov. Writing—review and editing: A.V. Podlesnov, A.O. Averianov, A.A. Burukhin, O.A. Feofanova, O.N. Vladimirova.

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ETHICS APPROVAL
AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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