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A New Plesiosaur of the Family Aristonectidae from the Early Cretaceous of the Center of the Russian Platform

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Abstract—A new plesiosaur, *Abyssosaurus nataliae* gen. et sp. nov. from the Upper Hauterivian Substage (Lower Cretaceous) of Chuvashia, is described based on a postcranial skeleton. The new taxon is assigned to the family Aristonectidae where it presumably occupies an intermediate position between Late Jurassic *Tatenectes* and *Kimmerosaurus* and Late Cretaceous *Aristonectes* and *Kaiwhekea*. This is the first reliable record of this family in Russia.

Keywords: Aristonectidae, plesiosaurs, postcranial skeleton, new taxa, Early Cretaceous, Chuvashia, Russia.

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INTRODUCTION

To date, three valid species of Plesiosauria have been recorded in Russia (Arkhangelsky and Sennikov, 2008). A new plesiosaur was found in 1992 on the Menya River near the village of Mishukovo of the Poretskii District of Chuvashia by the paleontologist V.V. Mitta (Mitta and Starodubtseva, 2000). He collected 20 cervical vertebrae and transferred to the Museum of Moscow City Station of Nature Explorers. In 1998, an expedition of the Chuvash Natural Historical Society "Terra incognita" found and collected additional fragments of the plesiosaur skeleton in the same locality. Teeth and cranial bones have not been found. Subsequently, Mitta placed at our disposal the vertebrae collected by him. The distinctive structure of plesiosaurian cervical vertebrae suggests that they belong to the poorly understood family Cimoliasauridae (Berezin, 2010).

In the mid-19th century, the American researcher J. Leidy described *Cimoliasaurus magnus* Leidy, 1851 from the Upper Cretaceous green sand of New Jersey. Later, many representatives of this genus and related forms from different continents were described and assigned to a separate family, the Cimoliasauridae (Delair, 1959); at the end of the 20th century, it was considered to be a composite taxon. At the beginning of the 21st century, new plesiosaur specimens, including cervical vertebrae similar to that of *Cimoliasaurus*, were found and assigned to the family Cimoliasauridae; available skulls allowed the recognition of distinctive cranial characters of this group (O'Keefe, 2001). Based on new material and redescription of North American *Cimoliasaurus laramiensis* Knight, 1900, O'Keefe and Street (2009) revised the systematics of the group and proposed that *Cimoliasaurus magnus* Leidy, 1851 belongs to the group of conservative Elasmosauridae, while all other Cimoliasauridae (O'Keefe, 2001) were referred to a new family, Aristonectidae, related to Polycotylidae. At present, opinions differ as to the systematics of Plesiosauria. Some researchers believe that young *Aristonectes* is a typical Elasmosauridae (Gasparini et al., 2003), while others propose that the Polycotylidae belong to a phylogenetic branch of Pliosauroidea and should be placed close to Leptocleididae (Smith, 2007; Smith and Dyke, 2008; Druckenmiller and Russell, 2008).

I use the family name Aristonectidae, although the taxonomy of this group remains an open question. The Aristonectidae occur in both Northern and Southern hemispheres (Fig. 1). The Northern Hemisphere has only yielded Late Jurassic plesiosaurs: *Tatenectes laramiensis* (Knight, 1900) from the Oxfordian of North America and *Kimmerosaurus langhami* Brown, 1981 from the Kimmeridgian of England. Aristonectidae from the Southern Hemisphere include only Upper Cretaceous taxa: *Aristonectes parvidens* Cabrera, 1941 from the Maastrichtian of Argentina and the Antarctic Region and *Kaiwhekea katiki Cruickshank et Fordyce, 2002* from the Maastrichtian of New Zealand (O'Keefe and Wahl, 2003). *Cimoliasaurus magnus* from North America, *C. maccoyi* Etheridge, 1904 from the Albian of Australia, *Scanisaurus nazarowi* Bogolubov, 1911 from Russia and Sweden and many other forms are considered to be nomen dubium. In the present study, the evolutionary scheme proposed by O'Keefe (2001) and developed by O'Keefe and Street (2009) is accepted.

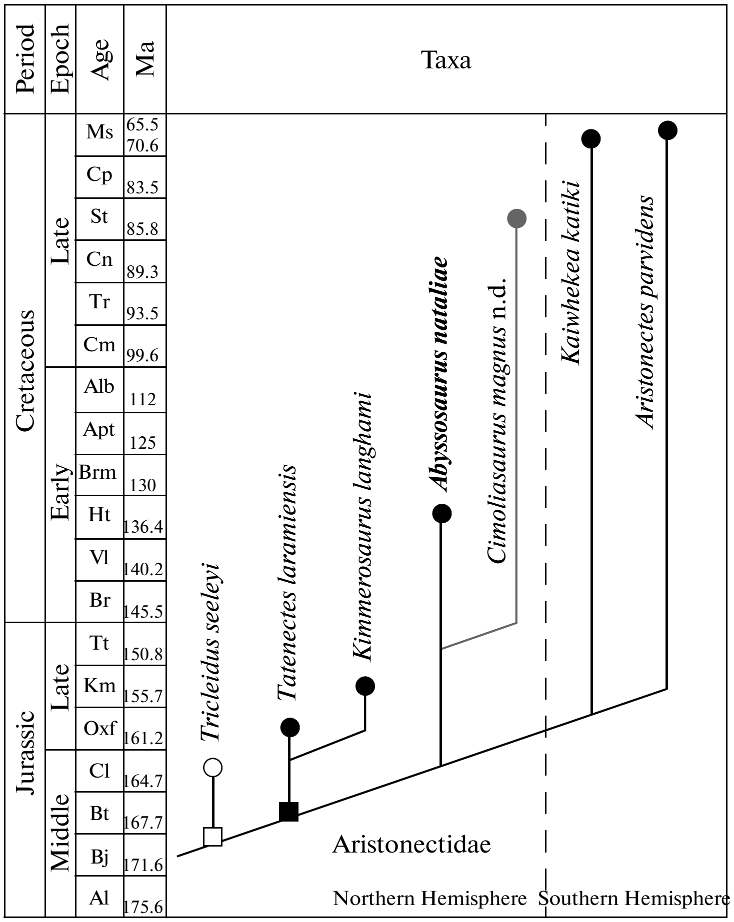


Fig. 1. Stratigraphic and phylogenetic position of *Abyssosaurus nataliae* gen. et sp. nov. in family Aristonectidae.

SYSTEMATIC PALEONTOLOGY

Order Sauropterygia

Suborder Plesiosauria

Superfamily Cryptocleidoidea

Family Aristonectidae O'Keefe et Street, 2009

Diagnosis (the new diagnosis includes only postcranial characters of adult plesiosaurs). Number of cervical vertebrae more than 32, possibly 51. Cervical vertebrae wider than long, with large widely spaced foramina. Vertebrae varying widely in shape even in one individual, ranging from binocular-shaped with dorsoventral compression at medial line to rounded trapeziform with dorsolateral compression and ovate articular surfaces. Neural arches and canals small relative to vertebral centra. In cervical vertebrae, neural spines usually at most as high as centrum; ribs short. Pectoral girdle showing tendencies towards division of scapular symphyses at midline and anterior displacement of dorsal ramus. In early forms, symphyses of ventral rami of scapulae coming in contact at greater individual age and along only part of midline and dorsal rami curving only slightly posteriorly. In late forms, symphyses of ventral rami of scapulae lacking contact at midline and probably widely spaced; dorsal rami displaced anteriorly. Axial skeleton, pectoral and pelvic girdles widened. Middle parts of abdominal ribs massive. Forelimbs much larger than hind limbs. Propodial bones elongated, with thickened diaphyses and expanded distal epiphyses; articular surfaces for epipodial equal in length. Forelimbs with supplementary bones in epipodial series. Anterior part of fin of all limbs having perichondral bone.

Genus *Abyssosaurus* Berezin, gen. nov.

Etymology. From the Greek *abyssos* (bottomless) and the Latin *saurus* (lizard).

Type species. *Abyssosaurus nataliae* sp. nov.

Diagnosis. Large plesiosaur about 7 m long. Neck half of animal length. Apparently, number of cervical vertebrae, 51 (44 +); pectoral, 3; dorsal, 21; sacral, 3; and caudal, about 20 (5 +). Centra of cervical vertebrae ovate trapeziform, without compression in medial part, wider than long and as long as high. Articular surfaces slightly concave, with distinct sharp edges. Neural arch and canal small relative to diameter of centrum. Pre- and postzygapophyses of cervical vertebrae fused and articulated with neighboring vertebrae like spigot joint. Cervical ribs short, dorsoventrally compressed, with rounded ends. Dorsal vertebrae rapidly decreasing in size towards sacral region. Neural arches of dorsal vertebrae high, cerebrospinal canal wide, pre- and postzygapophyses also fused, transverse processes in high position. Interclavicle thickened and fused with clavicles, which turned in vertical plane, resembling ribs in shape. Scapulae widely spaced, without contact at midline. Dorsal ramus of scapula extended anteriorly, with ventrally curved anterior margin. Coracoid wide, probably without incisure in medial margin. Pubis wider than long. Central parts of gastralia thick and wide. Propodial bones massive, extended; articular surfaces for epipodial bones equal in length. Forelimbs much larger than hind limbs, having supplementary and perichondral bones.

Species composition. Type species.

Comparison. The number of vertebrae in the cervical region of Aristonectidae is only known in Late Jurassic *Kimmerosaurus* (=*Colymbosaurus* Seeley, 1874); (42) and Late Cretaceous *Kaiwhekea* (43). In *Tatenectes* and *Aristonectes*, the number of vertebrae is not known. Thus, *Abyssosaurus* has the longest neck known in Aristonectidae (presumably of 51 vertebrae). The shape and proportions of the cervical vertebrae are similar to that of large vertebrae of *Cimoliasaurus*, which are rounded trapeziform in section, with an even lower edge (Leidy, 1864, pls. V, VI); they differ from the vertebrae of *Tatenectes, Kimmerosaurus, Kaiwhekea,* and *Aristonectes*, which are binocular in shape. The pectoral girdle resembles in structure that of specimen UW, no. 15943, the neotype of *Tatenectes laramiensis* (O'Keefe and Wahl, 2003). The wide middle part of gastralia is similar to that of *Tatenectes* (Street and O'Keefe, 2010), but more massive. In the last two characters, *Abyssosaurus* approaches *Tatenectes* and differs from other Cryptocleidoidea.

***Abyssosaurus nataliae* Berezin, sp. nov.**

Plate 11, figs. 1–15; Plate 12, figs. 1–10

Etymology. The species is named in honor of Nataliya Berezina, research worker, my associate and wife.

Holotype. MChEIO (Museum of Chuvash Natural Historical Society), no. PM/1, bones of postcranial skeleton; Russia, Chuvashia, Menya River, left tributary of the Sura River, 55°02′43.6″ N, 46°09′46.2″ E; Lower Cretaceous, Upper Hauterivian Substage, *Speetoniceras versicolor* Zone.

Description (Figs. 2, *3*). The axial skeleton is represented by vertebrae of all regions and pectoral ribs. In the cervical region, 44 vertebrae of presumable 51 are preserved; seven vertebrae (between C15 and C23) are absent. In the centra of the cervical vertebrae, the length (D) is approximately equal to the height (H) and considerably smaller than the width (W), with the mean ratio D : H : W = 100 : 97 : 125. The centra of the cervical vertebrae are trapezoid; the articular surfaces are ovate trapeziform or ovate, with an even lower margin. The height-to-length ratio of the cervical vertebrae is almost constant, whereas the width-to-length ratio increases (Table 1).

The well-preserved atlas and axis are fused, but distinguishable on the dorsal and lateral sides (Pl. 11, fig. 1; Fig. 2, *1a–1d*). The articular fossa for the occipital condyle is spherical, 28 mm in internal diameter; the lower margin projects anteriorly. On the ventral surface of the atlas, there is a large conical tubercle of the hypapophysis, which is connected to the medial crest of the axis, so that the vertebrae do not differ from each other. The lateral and posterior articular surfaces of the axis are concave. Ribs are absent.

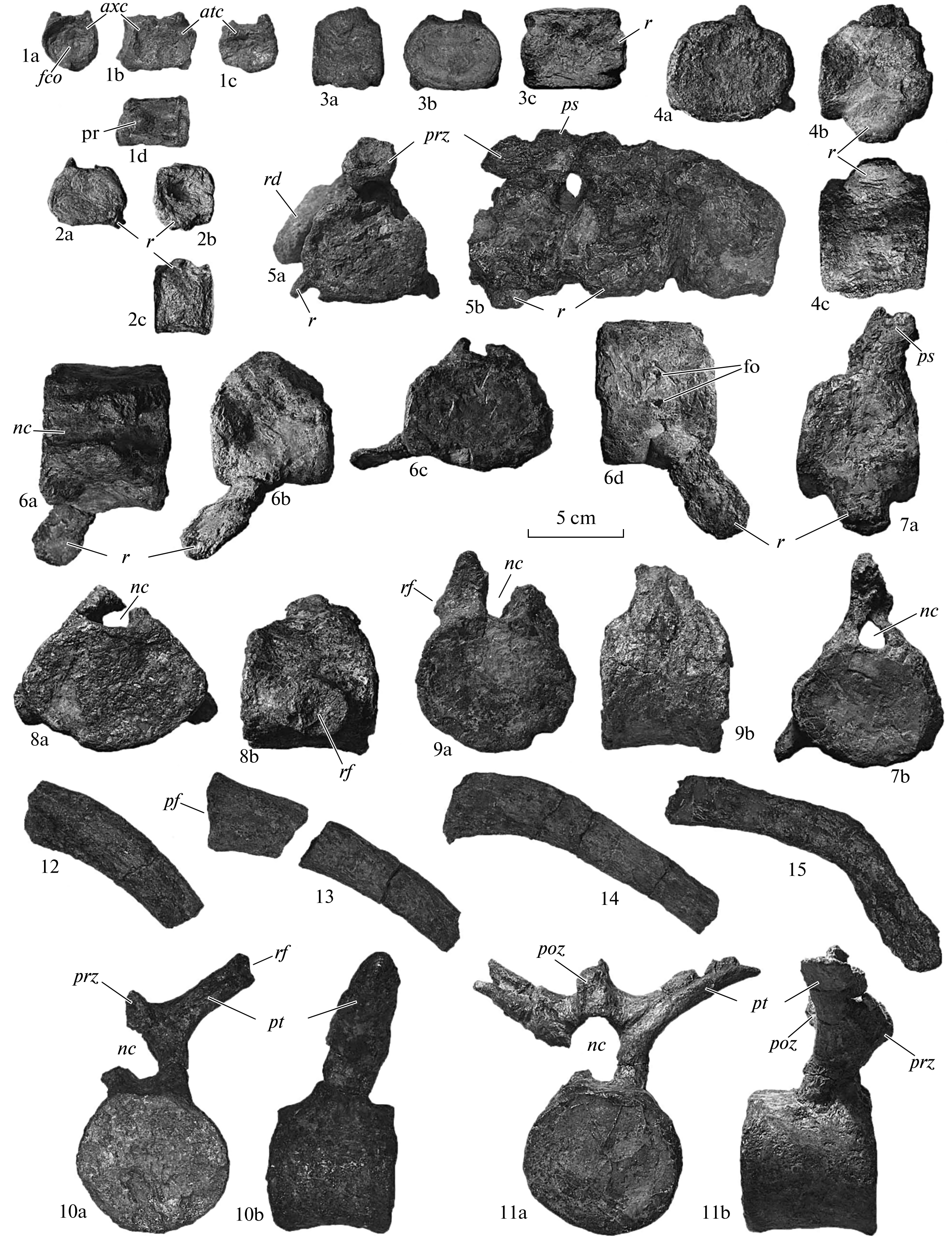
The cervical vertebrae have slightly concave articular surfaces with thickenings along the perimeter and in the center, with sharply differentiated margins (Pl. 11, figs. 2–8, Fig. 2, *2a, 2b*). The lateral surface of the vertebral centra has a fossa in the upper part; the ventral surface has a medial eminence between two longitudinal fossae with large foramina. The neurapophyses are narrow, deviate vertically upwards, fused with the corpora without distinct sutures. The cerebrospinal canal is narrow relative to the diameter of the vertebral corpus, widened anteriorly and posteriorly and narrowed in the middle. The middle cervical vertebra C24 is particularly well preserved (Fig. 2, *2a, 2b*). The neural spine is broken off; however, it is evident that it was up to 38 mm long and 10 mm thick at the base; the neural arches are 24 mm high. The prezygapophyses are fused in the shape of a deep groove, which is 30 mm long and 18 mm in diameter. A small foramen is preserved at the base of the prezygapophyses. The postzygapophyses are fused to form a single rounded rod 18 mm in diameter. The articulated pre-

→

Explanation of Plate 11

Figs. 1–15. *Abyssosaurus nataliae* gen. et sp. nov.; holotype MChEIO, no. PM/1: (1–11) vertebrae: (1) atlas–axis: (1a) anterior, (1b) lateral, (1c) posterior, and (1d) ventral views; (2) C7: (2a) anterior, (2b) lateral, and (2c) ventral views; (3) C13: (3a) lateral, (3b) anterior, and (3c) ventral views; (4) C24–C26: (4a) anterior and (4b) lateral views; (5) C29: (5a) anterior, (5b) lateral, and (5c) ventral views; (6) C37: (6a) dorsal, (6b) lateral, (6c) anterior, and (6d) ventral views; (7) C41: (7a) lateral and (7b) posterior views; (8) C51: (8a) anterior and (8b) lateral views; (9) P3: (9a) anterior and (9b) lateral views; (10) D4: (10a) anterior and (10b) lateral views; (11) D11: (11a) posterior and (11b) lateral views; (12–15) pectoral ribs. Designations: (*atc*) corpus of atlas, (*axc*) corpus of axis, (*fco*) fossa for occipital condyle, (*fo*) foramen of canal, (*hpr*) hypapophysis, (*nc*) neural canal, (*pf*) facet for transverse process, (*poz*) postzygapophysis, (*prz*) prezygapophysis, (*ps*) neural spine, (*pt*) transverse process, (*r*) cervical rib, (*rd*) pectoral rib, and (*rf*) facet for rib.

Plate 11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and postzygapophyses of neighboring vertebrae formed a strong, but weakly mobile articulation, like a spigot joint. Cervical ribs are fused with the vertebral corpora without sutures, with an ossification at the base. However, ribs of the anterior cervical vertebrae are underdeveloped and short (Pl. 11, figs. 2–4). Cervical ribs are located in the lower part of the lateral surface of corpora, compressed dorsoventrally, and displaced slightly posteriorly, curving downwards at an angle of 135°–150°, with a longitudinal fossa at the end. The measurements of cervical ribs L : Wd (L is total length and Wd is distal expansion, in mm) C7 = 13 : 15, C13 = 15 : 18, C23 = 25 : ?, C37 = 58 : 31. In vertebra C37, the rib is flattened, narrows from the base to the middle, but expands and becomes rounded at the end (Pl. 11, fig. 6). At the end of the neck, the ribs curve posteriorly and ventrally, with pointed ends. The corpora of the pectoral vertebrae are rounded cordate in P1 and rounded in P2 and P3. The transverse processes approach the neural arches and connected to them (Pl. 11, fig. 9).

The dorsal region includes 21 vertebrae. D4 and D11 are preserved better than others (Pl. 11, figs. 10, 11; Fig. 2, *3*). The centra are circular, the articular surfaces are slightly concave, with distinct margins. Vertebrae D3–D11 are equal in size, succeeding vertebrae are considerably smaller. The neural arches are high. The transverse processes are 70–75 mm long, deviate dorsally at an angle of 135° at the height about 30 mm. In D4, the neurapophyses with transverse processes are inclined slightly posteriorly. In D11, the neurapophyses are displaced towards the anterior edge of the centrum and the transverse processes are inclined posteriorly. The processes of the pre- and postzygapophyses are probably fused, as in cervical vertebrae. Pectoral ribs are slightly curved, their articular facets are flat or concave (Pl. 11, figs. 12–15) and, along with high transverse processes, form a wide thorax.

Three disrupted sacral vertebrae and five caudal vertebrae are preserved. The reconstructed tail is approximately 1 m long. The caudal vertebrae are short, hexahedral. Relatively low neurapophyses are located at the middle of the centra. The cerebrospinal canal is circular. The ribs are circular in section at the

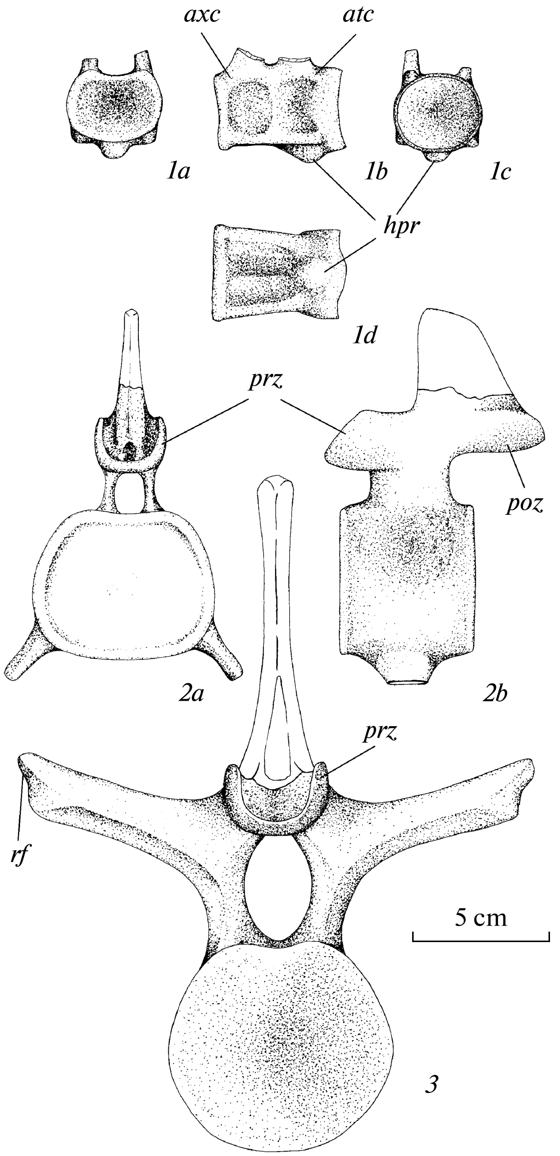
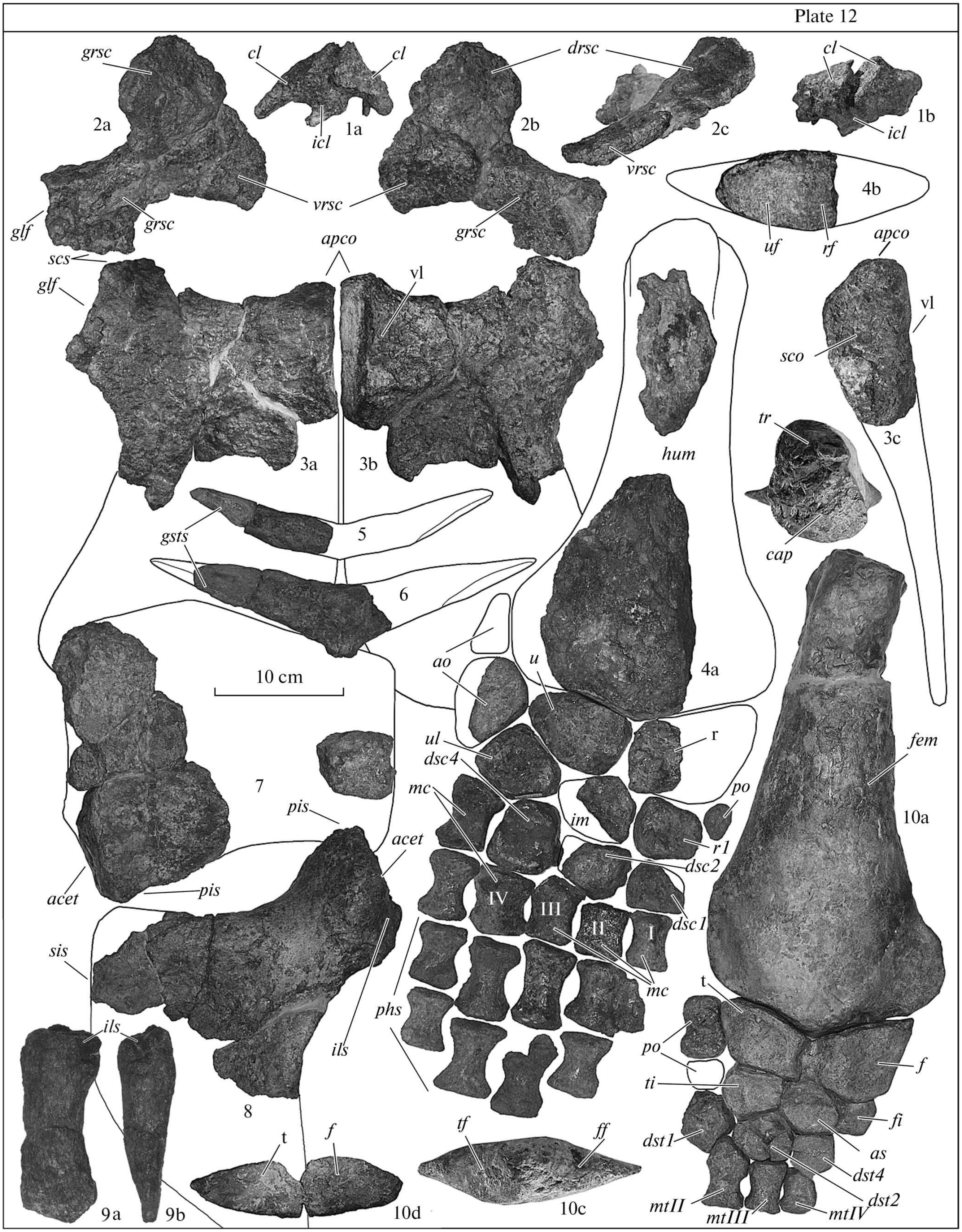


Fig. 2. *Abyssosaurus nataliae* gen. et sp. nov., holotype MChEIO, no. PM/1: (1) atlas–axis: (*1a*) posterior, (*1b*) lateral, (*1c*) anterior, and (1d) ventral views; (*2*) C24: (*2a*) anterior and (*2b*) lateral views; (*3*) D4, anterior view. Designations: (*atc*) corpus of atlas, (*axc*) corpus of axis, (*hpr*) hypapophysis, (*poz*) postzygapophysis, (*prz*) prezygapophysis, and (*rf*) facet for rib.

Explanation of Plate 12

Figs. 1–10. *Abyssosaurus nataliae* gen. et sp. nov.; holotype MChEIO, no. PM/1: (1) complex of clavicles and interclavicle: (1a) dorsal and (1b) anterior views; (2) left scapula: (2a) dorsal, (2b) ventral, and (2c) anterior views; (3) left coracoid: (3a) dorsal and (3b) ventral views, (3c) symphyseal surface; (4) right forelimb: (4a) dorsal view and (4b) epipodial facets; (5, 6) central gastralia; (7) left pubis; (8) right ischium; (9) right ilium: (9a) lateral and (9b) anterior views; (10) left hind limb: (10a) dorsal view, (10b) head of proximal epiphysis of femur, (10c) epipodial facets, and (10d) internal surfaces of epipodial bones. Designations: (*acet*) acetabulum, (*ao*) supplementary bone, (*apco*) apical projection of coracoid, (*as*) talus, (*cap*) head of femur, (*cl*) clavicle, (*drsc*) dorsal ramus, (*dsc1–4*) distal carpals 1–4, (*dst1–4*) distal tarsals 1–4, (*f*) fibula, (*fem*) femur, (*ff*) facet for fibulare, (*fi*) fibulare, (*glf*) glenoid facet, (*grsc*) glenoid ramus, (*gsts*) articular facet for gastralia, (*hum*) humerus, (*icl*) interclavicle, (*ils*) ilioischiadic symphysis, (*im*) intermedium, (*mcI–V*) metacarpals 1–5, (*mtI–V*) metatarsals 1–5, (*phs*) phalanges of digits, (*pis*) ischiopubic symphysis, (*po*) perichondral ossification, (*r*) radius, (*rl*) radiale, (*sco*) symphysis of coracoid, (*scs*) scapulocoracoid symphysis, (*sis*) symphysis of ischium, (*t*) tibia, (*tf*) facet of tibiale, (*ti*) tibiale, (*tr*) trochanter, (*u*) ulna, (*ul*) ulnare, (*vl*) ventral fossa of coracoid, and (*vrsc*) ventral ramus of scapula.

Plate 12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9b
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mtIV

Table 1. Measurements of vertebrae in all regions of the axial skeleton

Vertebral no.	L	H	W	LA	LN	VLI	Vertebral no.	L	H	W	LA	LN	VLI
C1	24	26	35	–	13	78.6	C46	67.5	66	93	43	43	84.9
C2	21	31*	32*	–	18	79.2	C47	63	69	91	43	35	78.8
C3	27	–	37	16	–	90.7	C48	66.5	67	90	38	–	84.7
C4	31.5	26	38	18.5	–	98.4	C49	62	62	93	35	44	80
C5	32	30	41	19	20	90.1	C50	66	66	–	–	broken off	
C6	32	30	–	19	20	92.8	C51	68	67.5	99	32	45	81.7
C7	33	31	42	20	22	90.4	P1	67	69	95	28	–	81.7
C8	34	33	43	20	22	89.5	P2	64	69	89	43	–	81
C9	35	35	45	19	24	87.5	P3	64	69	85	39	–	83.1
C10	35	35	47	20	25	85.4	D1	66	73	86	–	–	83.5
C11	37	36.5	49	–	–	86.5	D2	71.5	77	91	–	37	85.1
C12	38	37.5	52	–	21	84.9	D3	70	82	88	–	–	82.4
C13	39	38	52.5	21	21	86.2	D4	74	82	82	–	39	90.2
C14	39.5	37	53	20	22	87.8	D5	75	85	88	41	–	86.7
C15	41	41	54	21.5	21	86.3	D6	75	76.5	83	–	–	94
C23	49.5	49.5*	65*	27	–	86.5	D7	75	75*	84	–	–	94.3
C24	50	52.3*	67.2	30	28	84.5	D8	76	78.5*	86	–	–	95.9
C25	51	–	70	34	–	–	D9	75	–	–	41	–	95.2
C26	51.5	53*	71*	34.5	–	83.1	D10	–	79*	85.5	33.5	–	–
C27	52	50	63	–	–	92.0	D11	71.5	77.5	85	36.5	–	88
C28	55	54*	62*	31	–	94.8	D12	70	–	80	–	broken off	
C29	58	52	69	31	31	95.9	D13	67	78	87	36	–	87
C30	52	52	72	30	–	83.9	D14	68	72	78	–	–	95.1
C31	53	53	73	33	35.5	84.1	D15	64	–	762*	–	broken off	
C32	55	52	70.5	32	–	89.8	D16	62	69*	76*	–	–	85.5
C33	57	53*	75	34	–	89	D17	66	70*	75*	–	–	91
C34	57.5	55	72.5	32	36	90.2	D18	63	65*	68	34	–	94.7
C35	58.5	56	76	37	40	88.6	D19	60.5	69*	72.3*	–	–	85.6
C36	61	60	75	–	39	90.4	D20	–	–	broken off			
C37	63	60.5	77.5	26	43	91.3	D21	61	–	broken off			
C38	?(54)	?(83)	?(56)	distorted			S1	60	64	78	27	28	84.5
C39	63	63	78	38	45	89.4	S2	51	63*	73	–	–	76.7
C40	63	64	83	38	56	85.7	S3	45	57*	71	19.5	–	70.3
C41	65	64	83.5	35	48	88.1	Ca1	49	56.5*	71	–	–	78.1
C42	69	66	83.5	43	47	92.3	Ca2	–	–	broken off			
C43	66	67	87.5	39	47	85.4	Ca9	41.5	49	49	–	–	84.6
C44	65	64	89	41	47	85	Ca10	36	40	41	–	–	88.8
C45	65	71	85	46	37	83.3	Ca11	33	41	43	–	–	78.5

Designations: all measurements are in mm: (L) length of the ventral surface, (H) height and (W) width of the posterior (* anterior) articular surface, (LA) length of articulation between the rib and vertebra, (LN) length of the neural arch base, (VLI) ratio of the length to corpus diameter of vertebra = 100 (L/(H+W) 0.5).

base. Articular facets for intervertebral ribs are small, triangular.

The limb skeleton is represented by a series of bones of the pectoral and pelvic girdles and bones of the fore- and hind limbs. The interclavicle and two winglike clavicles are fused into a single complex with hardly discernible sutures (Pl. 12, fig. 1; Fig. 3, *1a, 1b*). In the anterior part, the interclavicle is thick and wide; the dorsal side has a longitudinal groove and the ventral side has a large carinate projection. In the posterior part, the interclavicle narrows laterally, forming a projection with a ventrally sharpened edge. The clavicles are similar to ribs, turned vertically and diverge posteriorly at a right angle. The anterior edges of clavicles are uneven, slightly expanded and rounded, closely approach each other, but do not adjoin to form a narrow fissure; the upper edges are raised above the interclavicle (Pl. 12, fig. 1b; Fig. 3, *1a*). The distance between the posterior ends of clavicle wings is about 110 mm; the wings of clavicles are 87 mm long, the anterior part is 52 mm wide, and the posterior articular ends are 35 mm wide. The total medial length of the clavicle–interclavicle complex is 73 mm and its thickness, including the lower projection, is about 73 mm.

The left scapula composed of three rami is preserved (Pl. 12, fig. 2; Fig. 3, *1a, 1b*). The glenoid ramus is short and thick, triangular in section. Its dorsal and ventral side converge internally and, along with the abdominal ramus, form the sharp internal edge. Externally, there is a 38-mm-wide area providing passage for the increased scapulo-humeralis anterior muscle. On the ventral side, at the transition to the scapular blade, this area becomes smooth. The glenoid fossa and articular surface for the coracoid are triangular; their edges form a tuberculate projecting border for attachment of muscles. The dorsal and ventral rami are positioned in almost the same plane. The dorsal ramus is rectangular, without posterior inclination; its anterior margin extends anteriorly and curves ventrally. Thus, the origin of muscles inserted in the humerus is reinforced and displaced anteriorly, so that the humerus is provided with a greater anterior stroke and increased angle of rotation (a feature of divers). Short ventral rami do not form a symphyseal connection at the midline nor come in contact with the coracoid. They are positioned at a distance about 100 mm from each other. The thickened anterior edge was probably continued by cartilaginous tissue.

The coracoid is partially preserved (Pl. 12, fig. 3; Fig. 3, *1a, 1b*), including the anterior part of the left part and symphyseal and glenoid parts of the right part. In projection, the left and right parts of the coracoid diverge dorsally at an angle of 155°, and its glenoid parts curve ventrally at an angle of 15°. A small depression is located on the ventral side before the smoothly ventrally thickened symphyseal edge. The articular facets for the scapulae and glenoid fossa are triangular, their margins are tuberculate and extended. The apical projection of the coracoid is thickened and

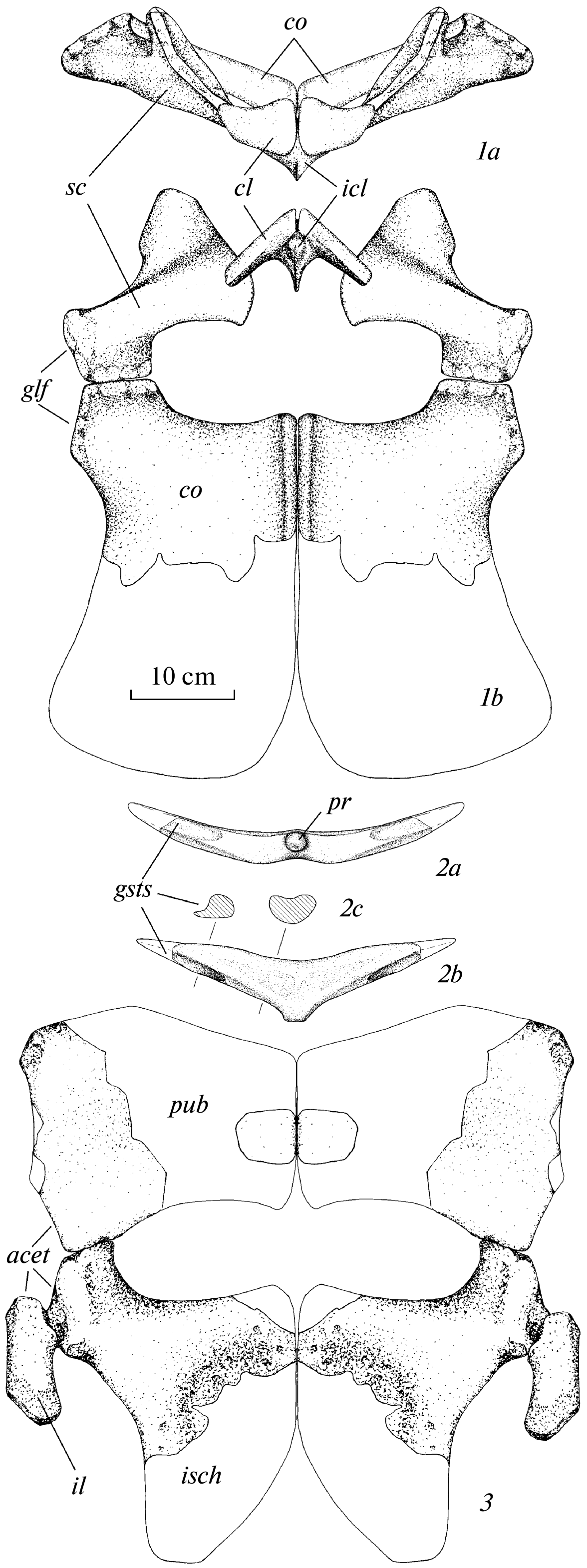

Fig. 3. *Abyssosaurus nataliae* gen. et sp. nov.; holotype MChEIO, no. PM/1: (1) pectoral girdle: (*1a*) anterior and (1b) ventral views; (*2*) central part of gastralium: (*2a*) posterior and (*2b*) dorsal views, (*2c*) cross section; (*3*) pelvic girdle, dorsal view. Designations: (*acet*) acetabulum, (*cl*) clavicle, (*co*) coracoid, (*glf*) glenoid facet, (*gsts*) articular surface of an abdominal rib, (*icl*) interclavicle, (*il*) ilium, (*isch*) ischium, (*pr*) cusp, (*pub*) pubis, and (*sc*) scapula.

Table 2. Measurements of bones of the pectoral and pelvic girdles

Left scapula	mm
L × W – of scapula	185 × 152* + 2
C – along anterior edge	10–15
C – of scapula at joint of three rami	37
L × W – of glenoid ramus	90 × 54
L × W – of dorsal ramus	85 × 92*+2
L × W – of ventral ramus	77 × 67
L × C – of articular surface for coracoid	55 × 52
L × C – of glenoid surface	60 × 48
L × W – of anteriorly curved area of dorsal ramus	47 × 82
Angle between glenoid and articular surfaces	120×
L × W – of scapulocoracoid foramen	96 × 125
Left part of the coracoid	
L × W – of coracoid on ventral side	200* × 225
W – coracoid on dorsal side	205
L × C – of glenoid part of coracoid	107 × 41
L × C – of glenoid surface	65 × 45
L × C – of articular surface for scapula	42 × 40
L × W – of symphyseal articulation of coracoid	115* × 62
Angle between glenoid and articular surfaces	130×
Left pubis	
L – along external edge	210
L × C – of trochanteric surface	80 × 52
L × C – of articular surface for ilium	40 × 45
Right ischium	
W – greatest, perpendicular to symphyses	235
L – in the middle part of trochanteric ramus	91
L × C – of trochanteric surface	62 × 45
L × C – of articular surface for ilium	37 × 35
Left ilium	
L – maximum	155
W × C – of proximal end	62 × 40
W × C – in the middle part	46 × 36
W × C – of distal end	60 × 13

Designations: (L) length, (W) width, (C) thickness, and (*) incomplete.

Table 3. Measurements of fore and hind limb bones

Propodial bones	Humerus	Femur
L – of propodium	–	378
L – of propodium before distal expansion	–	260
W × C – in the middle of L	–	105 × 80
Circle in the middle of L	–	30
W × C – of proximal end	–	66 × 97
W × C – of articular surface of trochanter	–	60 × 41
W × C – articular surface of capitulum	–	75 × 66
W × C – of distal end	? × 60.5	190 × 50
W × $C_{mid.}$ – articular facets for radius, tibia	? × 60	80 × 45
W × $C_{mid.}$ – articular facets for ulna, fibula	? × 50.2	80 × 38

Podial bones

	u	ra	ul	dsc 1	dsc 2	dsc 4	ao	po
L	57	46	60	40	45	56	57	30
W	85	52	68	46	–	51	45*	22
C	25–50	20–45	23–32	16–40	45	38–42	25	10–18
	t	f	ti	fi	as	dst 2	dst 4	po
L	46.5	58	42	30	49	41	35	51
W	75.5	81	48	20–25	48	48	36	30–37
C	20–44	34–40	25–38	20–22	23–38	24–32	17–28	14–20

Designations: (L) length, (W) width, (C) thickness, (*) incomplete, in mm.; (u) ulna, (ra) radiale, (ul) ulnare, (as) astragalus, (t) tibia, (f) fibula, (ti) tibiale, (fi) fibulare, (dsc) distal carpal, (dst) distal tarsal, (ao) supplementary ossification, and (po) perichondral ossification.

slightly projects. The medial incisure of the coracoid was probably absent.

The pelvic girdle is represented by fragments of the left pubis, right ischium, left and right ilia (Pl. 12, figs. 7–9; Fig. 3, *3*). The pubis is slightly wider than long, the angle between the acetabulum and articular surface for the ischium is sharp and thickened. On the ventral side of the anterolateral corner of the pubis, there is a massive rounded thickening for attachment of protractors of the femur. The entire pelvic girdle is approximately as long as wide. The pubic–ischiadic fenestra is short and wide. The ilium is massive, thickened, almost vertical in lateral view.

The central parts of composite gastralia are strongly thickened, widened, and heavy due to the increased density of bony tissue (Pl. 12, figs. 5, 6; Fig. 3, *2*). They are inclined dorsally, making the trunk wide and strengthening and increasing the weight of the abdominal region, as a keel. Posteriorly, the last gastralium has a tubercle in the middle region.

The bones preserved in the left forelimb, right and left hind limbs differ in preservation (Pl. 12, figs. 4, 10). The forelimb is much larger and more massive than the hind limb. Epipodial bones are wide. The epipodial series had one or two supplementary bones, probably, there were two. A small perichondral bone (or two bones) is present between the radius and radiale. The left femur is well preserved (Pl. 12, fig. 10). Its diaphysis is massive, gradually widened, becoming thinner at the extended distal end. The bone is twice as long as its maximum width. The diaphysis is widely ellipsoidal in section at the distal end, rounded square in the middle, and high rounded rectangular at the proximal end. The capitulum and trochanter are outlined laterally by superficial grooves, but are not separated. The trochanter is turned slightly posteriorly and the capitulum is directed anteriorly. On the ventral side, the articular head is outlined by a groove. The articular facets for epipodial bones are well preserved, two facets equal in length for the tibia and fibula are seen. They are elongated concave areas positioned at an angle of 135° to each other. Some podial bones of the left hind fin are retained in natural positions (Pl. 12, figs. 10a, 10d). The edges of articular facets are distinct, slightly elevated. Epipodial bones are wide. On the ventral side, they tightly adjoin each other; on the dorsal side, the tibia and fibula are separated by a fissure, which expands proximally. The tibia is wide and thick, has an articular surface with a perichondral bone in the anterior part. The dorsal and ventral surfaces of the fibula converge posteriorly, forming a sharp edge. Towards the distal end, the fibula becomes narrower, its facets for mesopodial bones are positioned at an angle of 140°. Posterior to the epipodial series, additional bones are absent. Of three mesopodial bones, the fibulare is the smallest, and the tibiale and intermedium are approximately equal in size. The first distal tarsal and first metatarsal are displaced anteriorly.

Remarks. The cervical vertebrae of *Abyssosaurus nataliae* are similar to that of the Cryptocleidoidea, which have shorter corpora and high neural arches. However, in the Cryptoclididae, the cervical vertebrae are usually longer and, in the Policotylidae, they are shorter, with more concave articular facets. The proportions of the cervical vertebrae of *A. nataliae* are the same as in other known Aristonectidae, the length is equal to the height and much less than the width (Persson, 1962, 1963; O'Keefe, 2001). In *A. nataliae*, the vertebral length gradually increases along the entire neck and VLI is at most 100% (Table 1). In the middle part of the neck, VLI only slightly differs from that of anterior and posterior vertebrae of the neck, as in young plesiosaurs. The structure of pre- and postzygapophyses of the vertebrae of *A. nataliae* differs from that of other Jurassic and Cretaceous plesiosaurs. The same strong attachment is only recorded in the elasmosaurid *Mauisaurus haasti* Hector, 1874 from the Upper Cretaceous of New Zealand (Hiller et al., 2005). Probably, this structure was formed convergently in different plesiosaur groups.

The structure of the clavicle–interclavicle complex of *A. nataliae* resembles that of the Early Jurassic plesiosaur *Occitanosaurus tournemirensis* Sciau, Crochet et Mattei, 1990. In *Occitanosaurus*, the wings of clavicles are also fused with a thickened interclavicle, but the clavicles extend horizontally, forming anteriorly a medial incisure (Bardet et al., 1999). As the wings of clavicles of *Occitanosaurus* are positioned dorsally and their posterior margins extend posteriorly as ribs, the clavicle–interclavicle complex looks like that of *A. nataliae*.

Forelimb bones of *A. nataliae* are larger than in hind limbs, as in many Elasmosauridae and Cryptocleidoidea. However, the presence of supplementary epipodial bones distinguish *A. nataliae* from many Elasmosauridae and draw it closer to the Cryptocleidoidea. The presence of a perichondral bone between the radius and radiale of *A. nataliae*, just as in *Cryptoclidus* (Caldwell, 2002) and *Opallionectes* (Kear, 2005), is evidence that the new genus is close to the Cryptoclididae.

The pectoral girdle of *A. nataliae* differs from that of the majority of known Cryptoclididae in the anteriorly rather than posteriorly displaced and extended dorsal ramus of the scapula and in the widely spaced ventral ramus (Fig. 3, *1a, 1b*). A similar convergent anterior displacement of the dorsal ramus is observed in *Pliosaurus macromerus* Phillips, 1871, although it is achieved by the anterior curvature of the dorsal ramus into the plane of the ventral ramus rather than by the lengthening of the dorsal ramus. This structure increases the stroke span of the forefin, which provided rapid immersion, emergence, and turning (Tarlo, 1958). In the family Aristonectidae, an unusual structure of the scapulae, such as in *A. nataliae*, is known in the neotype (UW, no. 15943) of *Tatenectes laramiensis* Knight, 1900. The unusual structure of the pectoral girdle of this plesiosaur is reflected in the generic name *Tatenectes*, from the Greek *diver*. As O'Keefe and Wahl (2003) remarked, the dorsal ramus of the scapula in this specimen is unusual, it is inclined mostly anteriorly rather than posteriorly and dorsally, as in the majority of plesiosaurs. The ventral ramus is also very unusual; it is well developed, but does not extend onto the midline and, hence, the structure of the pectoral girdle of *Tatenectes* is intermediate between early plesiosaurs (*Plesiosaurus*), which lack a connection at the midline, and later taxa (*Cryptoclidus, Tricleidus*, and all Elasmosauridae). This scapular structure has not been recorded in other plesiosaurs. These characters are possibly typical of juveniles; although O'Keefe and Wahl (2003) initially indicated that the distal region of the humerus is completely formed and the neural arches are fused with the vertebrae, suggesting that this was an adult animal. However, subsequently, as other individuals of this species with a different structure of the pectoral girdle were examined, O'Keefe and Street (2009) changed their mind and determined the neotype (UW, no. 15943) as a young individual (O'Keefe and Street, 2009). It is probable that, in *Tatenectes*, the scapulae were drawn close to the midline at late ontogenetic stages, since, even in mature individuals, the scapulae came in contact along only a part of the symphyseal extent, in contrast to that of *Cryptoclidus* and *Tricleidus*. *A. nataliae* and *T. laramiensis* are also similar in the structure of gastralia. In *T. laramiensis*, the central part of gastralia is thicker than in other known plesiosaurs (Street and O'Keefe, 2010). However, in *A. nataliae*, they look even more massive than in *T. laramiensis*. In this connection, it should be noted that *Tatenectes* is a small Middle Jurassic plesiosaur with a relatively short neck, the earliest representative of the Aristonectidae (Fig. 1).

It should be noted that the holotype of *A. nataliae* belonged to an adult with the neurapophyses and cervical ribs fused with the vertebral centra, completely formed symphyses and joints, podial and propodial limb bones. A distinctive structural feature of *A. nataliae* is the preservation of juvenile characters in adults, i.e., the cervical vertebrae are short and only slightly differentiated into regions, the cervical ribs are poorly developed and short, with rounded ends, the scapulae also look shortened and underdeveloped, with the anteriorly extended dorsal rami and widely spaced ventral rami, without symphyseal connection at the midline, the coracoid is relatively wide, the thorax is wide, with thickened gastralia, and the propodial bones are massive and elongated. The strong connections at the neurapophyses make the long neck less flexible. The highly positioned transverse processes of the pectoral vertebrae and the thickened gastralia expand the thorax and allow an increase in muscular tissue. These features of the new plesiosaur confirm that it led a deepwater mode of life.

The narrow nondifferentiated teeth of Aristonectidae formed a "trap" of a sort for small food objects, such as squids and crustaceans. At the same time, the skull of some species are high, with increased orbits. This suggests that they hunted at certain depth, with restricted illumination, catching prey (soft-body organisms) by a "net" formed by its mouth. Adaptation for deepwater hunting could have been accompanied by neoteny. It is probable that the morphology of the family Aristonectidae resulted from the preservation of juvenile characters. A vivid example is provided by *Kaiwhekea katiki*, which is characterized by a high, relatively large skull with short and high jugals, widened and anteriorly directed orbits located close to the anterior region of the skull, and jaws with many small and closely positioned teeth (Cruickshank and Fordyce, 2002). This cranial structure corresponds to the appearance of young plesiosaurs.

A. nataliae is probably intermediate between the lineage of Late Jurassic *Tatenectes* and *Kimmerosaurus*, which are similar in structure and distribution in the Northern Hemisphere, and the independent lineage of Late Cretaceous *Aristonectes* and *Kaiwhekea* from the Southern Hemisphere (Fig. 1). *A. nataliae* is more similar in vertebral structure to *Cimoliasaurus magnus* from North America; therefore, it is premature to refer *Cimoliasaurus magnus* to Elasmosauridae (O'Keefe and Street, 2009). Opinions differ as to the taxonomic position and relationships of *Cimoliasaurus magnus*, primarily because of incomplete preservation of the specimen. However, as was repeatedly marked in the literature, each new record changes and supplements the phylogeny of plesiosaurs; this is particularly true of the poorly understood family Aristonectidae.

Material. Holotype.

REFERENCES

Arkhangelsky, M.S. and Sennikov, A.G., The Subclass Synaptosauria, in *Iskopaemye pozvonochnye Rossii i sopredel'nykh stran. Iskopaemye reptilii i ptitsy. Chast' 1,* (Fossil Vertebrates of Russia and Adjacent Countries: Fossil Reptiles and Birds: Part 1), Ivakhnenko, M.F. and Kurochkin, E.N., Eds., Moscow: GEOS, 2008, pp. 229–243.

Bardet, N., Godefroit, P., and Sciau, J., A New Elasmosaurid Plesiosaur from the Lower Jurassic of Southern France, *Palaeontology*, 1999, vol. 42, part 5, pp. 927–952.

Berezin, A.Yu., A New Cimoliasauridae Plesiosaur from the Early Cretaceous (Hauterivian) of Chuvashia of the Central Russian Platform, in *Materialy Pyatogo Vserossiiskogo soveshchaniya "Melovaya sistema Rossii i blizhnego zarubezh'ya: problemy stratigrafii i paleogeografii," 23–28 avgusta 2010 g.* (Materials of the 5th All-Russia Conference on the Cretaceous System of Russia and Adjacent Countries: Problems of Stratigraphy and Paleogeography, August 23–28, 2010), Baraboshkin, E.Yu., and Blagoveshchenskii, I.V., Eds., Ulyanovsk: UlGU, 2010, pp. 84–87.

Caldwell, M.W., From Fins to Limbs to Fins: Limb Evolution in Fossil Marine Reptiles, *Am. J. Med. Gen.*, 2002, vol. 112, pp. 236–249.

Cruickshank, A.R.I. and Fordyce, R.E., A New Marine Reptile (Sauropterygia) from New Zealand: Further Evidence for a Late Cretaceous Austral Radiation of Cryptoclidid Plesiosaurs, *Palaeontology*, 2002, vol. 45, no. 3, pp. 557–575.

Delair, J.B., The Mesozoic Reptiles of Dorset, *Proc. Dorset Natur. Hist. Archaeol. Soc.*, 1959, vol. 30, pp. 52–90.

Druckenmiller, P.S. and Russel, A.P., *A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of Leptocleidus Andrews*, 1922, *Zootaxa*, 2008, vol. 1863, pp. 1–120.

Gasparini, Z., Salgado, L., and Casadio, S., Maastrichtian Plesiosaurs from Northern Patagonia, *Cret. Res.*, 2003, vol. 24, pp. 277–303.

Hiller, N., Mannering, A.A., Jones, C.M., and Cruickshank, A.R.I., The Nature of *Mauisaurus haasti* Hector, 1874 (Reptilia: Plesiosauria), *J. Vertebr. Paleontol.*, 2005, vol. 25, no. 3, pp. 588–601.

Kear, B.P., A New Elasmosaurid Plesiosaur from the Lower Cretaceous of Queensland, Australia, *J. Vertebr. Paleontol.*, 2005, vol. 25, no. 4, pp. 792–805.

Leidy, J., Cretaceous Reptiles of the United States, *Smithson. Contrib. Knowl.,* 1864, vol. 192, pp. 1–135.

Mitta, V.V. and Starodubtseva, I.A., V.A. Shchirovskii and the Study of the Mesozoic of the Alatyr-Kurmysh Region (Middle Volga Region), *Vernadsky Mus. Novit.*, 2000, no. 5, pp. 1–20.

O'Keefe, F.R., A Cladistic Analysis and Taxonomic Revision of the Plesiosauria (Reptilia: Sauropterygia), *Acta Zool. Fenn.*, 2001, vol. 213, pp. 1–63.

O'Keefe, F.R. and Street, H.P., Osteology of the Cryptocleidoid Plesiosaur *Tatenectes laramiensis*, with Comments on the Taxonomic Status of the Cimoliasauridae, *J. Vertebr. Paleontol.*, 2009, vol. 29, no. 1, pp. 48–57.

O'Keefe, F.R. and Wahl, W., Jr., Preliminary Report on the Osteology and Relationships of a New Aberrant Cryptocleidoid Plesiosaur from the Sundance Formation, Wyoming, *Paludicola*, 2003, vol. 4, no. 2, pp. 48–68.

Persson, P.O., Notes on Some Reptile Finds from the Mesozoic of Scania, *Geol. Foer. Stockholm Ferh.*, 1962, vol. 84, pp. 144–150.

Persson, P.O., A Revision of the Classification of the Plesiosauria with a Synopsis of the Stratigraphical and Geographical Distribution of the Group, *Lunds Univ. Årsskrift, NF Avd.*, 1963, vol. 2, no. 59, pp. 1–60.

Smith, A.S., Anatomy and Systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria), *Doct. Thes., School of Biol. Environm. Sci.*, Dublin: Nat. Univ. Ireland, Univ. College Dublin, 2007, pp. 1–22.

Smith, A.S. and Dyke, G.J., The Skull of the Giant Predatory Pliosaur *Rhomaleosaurus cramptoni*: Implications for Plesiosaur Phylogenetics, *Naturwissenschaften*, 2008, vol. 95, pp. 975–980.

Street. H.P. and O'Keefe, F.R., Evidence of Pachyostosis in the Cryptocleidoid Plesiosaur *Tatenectes laramiensis* from the Sundance Formation of Wyoming, *J. Vertebr. Paleontol.*, 2010, vol. 30, no. 4, pp. 1279–1282.

Tarlo, L.B., The Scapula of *Pliosaurus macromerus* Phillips, *Palaeontology*, 1958, vol. 1, pp. 193–199.