

New Data on the Morphology and Systematic Position of the Sea Turtle *Allopleuron qazaqstanense* Karl et al. from the Middle Eocene of Kazakhstan

E. A. Zvonok^a, N. I. Udovichenko^b, and A. V. Bratishko^b

^aDidorenko Lugansk State University of the Internal Affairs, ul. Didorenko 4, Lugansk, 91493 Ukraine

e-mail: evgenij-zvonok@yandex.ru

^bTaras Shevchenko Lugansk National University, Oboronnaya ul. 2, Lugansk, 91011 Ukraine

Received April 16, 2014

Abstract—A new specimen of the sea turtle *Allopleuron qazaqstanense* Karl et al., 2012 is described. The material includes skeletal elements previously unknown for this taxon and comes from the Shorym Formation of the Kuyulus locality (Kazakhstan, Mangystau Region; Bartonian, Paleogene). Comparative analysis involving other cheloniid taxa has shown that *A. qazaqstanense* should not be assigned to the genus *Allopleuron*; it is rather closer to Eocene *Eochelone brabantica* and some Oligocene cheloniids. The similarity of *Allopleuron qazaqstanense* to Late Cretaceous *Allopleuron hofmanni* results from convergence caused by similar adaptations to the pelagic lifestyle.

Keywords: *Allopleuron*, Cheloniidae, turtles, Bartonian, Paleogene, Kazakhstan

DOI: 10.1134/S0031030115020124

INTRODUCTION

Sea turtles of the superfamily Chelonioidea Agassiz, 1857 appeared for the first time in the fossil record in the Aptian Stage of the Cretaceous System (Hirayama, 1998). During the Late Cretaceous and Cenozoic, members of this superfamily played an important role among marine vertebrates.

One of the most diverse fossil faunas of sea turtles comes from the Shorym Formation of Mangyshlak (Kazakhstan, Mangystau Region; NP 17, Bartonian Stage: Zhelezko and Kozlov, 1999); it includes four morphotypes of these animals (Zvonok et al., 2011). On a weathered surface of this formation of the Kuyulus locality (43°51'43.81" N, 51°37'6.68" E), new bone remains of a large sea turtle distinguished from the previously described morphotypes have been found. These bones belong to one individual, since they were found close to each other, while the concentration of vertebrate remains in these beds is rather low, correspond to each other in size, two elements are connected by sutures, and duplicated bones are absent. The absence of some skeletal elements and selective character of damages apparently results from attack of a predator hunting the living turtle or consuming its corpse. The presence of semicircular incisions up to 8 mm long in the maxilla and parietal (Pl. 9, figs. 5, 14, 15) is evidence that the predator was large and had conical teeth (crocodile or whale). Judging from fresh breaks, some damages were formed after the appearance of bones on the day surface. Some bones were distorted in the burial.

This individual is generally similar to the specimen described by Karl et al. (2012) as the holotype of *Allopleuron qazaqstanense* Karl et al., 2012. The study of these remains has provided new data on the morphology and systematic position of this species and improves its stratigraphical and geographical ranges.

The material under study is stored in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN; Paleoherpertological Collection: ZIN PH) and Mangystau Regional Historical Museum, Aktau, Kazakhstan (MPHNM). In addition, we used comparative material from the Natural History Museum, London, Great Britain (NHM) and Royal Belgian Institute of Natural Sciences, Brussels (IRSNB). The bones stored in the Mangystau Regional Historical Museum were measured with a ruler in field conditions; therefore, their measurements are approximate.

In the present study, the osteological terminology follows Gaffney (1979; for cranial bones) and Matzke (2007; for postcranial bones).

RESULTS AND DISCUSSION

Morphology of the Turtle from the Middle Eocene of Kazakhstan

Turtle remains include 1 prefrontal, 1 parietal, 2 squamosal, 1 premaxilla, 1 maxilla, 1 quadrate, 2 dentaries, 1 prearticular, 1 articular, 3 cervical vertebrae, 1 neural and 4 peripheral plates, 1 scapula, and 1 humerus.

Skull. The nasal bones are absent, judging from the absence of contact with the prefrontal bone.

Prefrontal (Pl. 9, fig. 1-4). The right prefrontal (specimen ZIN PH, no. 1/177) is preserved; the lower part of the descending process is broken off. The medial margin is 41.9 mm long; the distance from the orbit to medial margin is 22.2 mm. The bone is massive; its medial margin is up to 13.4 mm thick. In dorsal view, the prefrontal is almost pentagonal; grooves of horn scutes are not observed. The anterior margin is almost straight, lacks a projection; the anterolateral margin is almost straight; the lateral margin is arcuately concave; the posterior margin is positioned almost perpendicular to the medial margin and lacks contact with the postorbital. In lateral view, the descending process of the prefrontal passes posteriorly into a high parasagittal crest. In ventral view, the descending process is positioned obliquely relative to the sagittal skull plane. The bone adjoined the maxilla anterolaterally and the frontal posteriorly; contact with the vomer is not preserved. It formed the upper part of the external naris, the anterodorsal orbital rim, the upper part of the fissura ethmoidalis margin, and the upper margin of the orbitonasal foramen.

Parietal (Pl. 9, fig. 5). Most of the right parietal (specimen ZIN PH, no. 2/177) is preserved, except for the lateral and caudal parts; its ventral surface is damaged. The medial margin of this fragment is 58.8 mm long. Only the sutural surfaces for contact with the right frontal and left parietal are preserved. The dorsal surface of the bone has grooves for contact of the frontoparietal, supraorbital, temporal, and parietal horn scutes. A sulcus between the frontoparietal and frontal scutes is absent. Lateral and caudal to the frontoparietal scute, additional scutes between the frontoparietal and parietal scutes are absent.

Squamosal (Pl. 9, fig. 6, 7). Both bones (specimens ZIN PH, nos. 3/177, 4/177) are preserved. The left and right squamosals are 45.3 and 44.7 mm high, respectively. Only the contact surface of the left squamosal with the quadratojugal is preserved. Other contact surfaces are damaged. The anterior margin of the bone formed the posterior part of the cavum tympani; the posterior margin of the bone formed lateral margin of the temporal fossa. The depression for attachment of the depressor mandibulae is deep, crescent in shape, well visible in lateral view.

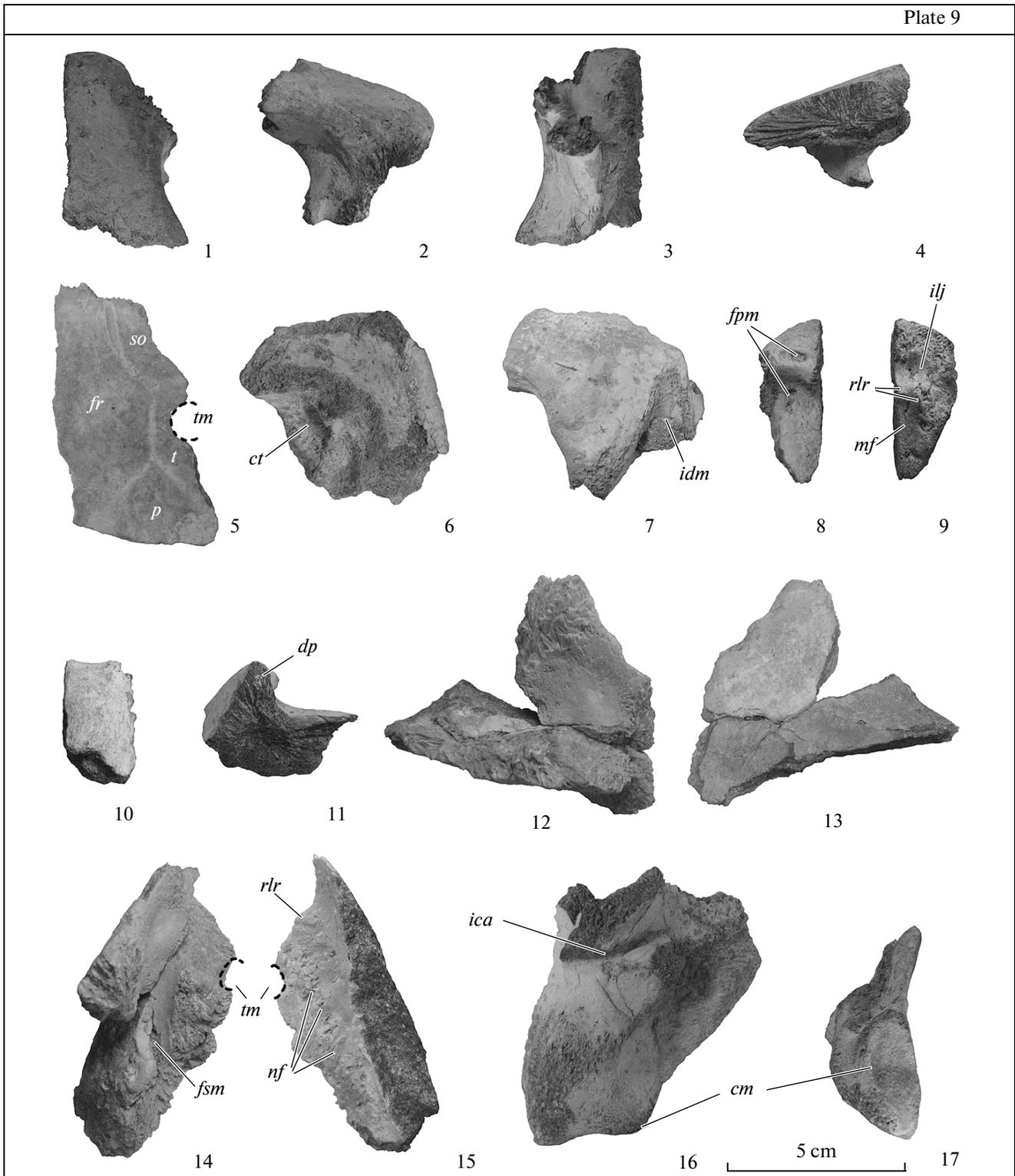
Premaxilla (Pl. 9, figs. 8-11). The left premaxilla with a broken off labial ridge (specimen ZIN PH, no. 5/177) is preserved. The bone is 40.6 mm long, 15.8 mm wide, and up to 17.4 mm thick at the posterior margin. The premaxilla is moderately long, subtriangular in ventral view. The anterior part of the palatal surface has a groove for the anterior margin of the lower jaw, which is bordered mediocaudally by a ventrally directed process (rudimentary lingual ridge). The medial groove is also present. The dorsal bone part

has a high process bordering from below the external naris. The labial ridge is broken off, but its massive base suggests that it was high. In dorsal view of the bone surface, two large foramina connected by a canal are observed; one is at the apex of the process considered, the other is just behind this process. The bone widely adjoined the maxilla laterocaudally and narrowly adjoined the vomer posteriorly, slightly wedging in the anterior part of the vomer; it was not fused with the right premaxilla; it formed the lower margin of the external naris and anterior part of the labial ridge.

Maxilla (Pl. 9, figs. 12-15). The anterior part of the left maxilla (specimen ZIN PH, no. 6/177) is preserved; almost the entire labial ridge and a part of the orbital floor are broken off. The fragment is 73.0 mm long; contact with the vomer is 23.9 mm long and contact with the palatine is more than 19.7 mm long. The greatest bone width at the level of the vomer and palatine is 29.2 and 24.4 mm, respectively. In ventral view, the anterior part of the palatine process shows a ventrally directed process (rudimentary lingual ridge) of the premaxilla. The palatine process does not participate in the formation of the apertura narium interna; thus, the maxilla does not contribute to the formation of this aperture. The foramina of blood vessels supplying the rhamphotheca are scattered throughout the palatine surface. In dorsal view, the palatine process formed the anterolateral part of the orbital floor, the lateral part of the orbitonasal foramen, caudal to which there is the supramaxillary foramen. The alveolar process lacks grooves on the external surface. In lateral view, preserved fragment of the labial ridge is moderately high, sharp. The prefrontal process is high. The bone adjoined the premaxilla anteromedially, the prefrontal dorsally, the vomer medially, and the palatine caudally and formed the lateral border of the internal naris, most of the labial ridge of the upper jaw, the anteroventral orbital rim, and the lateral part of the orbital floor; other contacts and margins are not preserved.

Quadrates (Pl. 9, figs. 16, 17). The lower part of the left quadrate (specimen ZIN PH, no. 7/177) is preserved. The fragment is 60.7 mm high and 64.3 mm wide, the mandibular condyle is 27.1 mm wide. The anterior bone surface is wide, slightly concave. In anterior and posterior views, the lateral margin of the articular process is convex. In ventral view, the mandibular condyle is bean-shaped. The incisura columellae auris is open, positioned laterally. The quadrate adjoined the pterygoid anteromedially, other contacts are not preserved.

Dentary (Pl. 10, figs. 1-6). Both dentaries are preserved in articulation (specimen ZIN PH, no. 8/177). The posterior margins of both bones and anterior margin of the left bone are slightly damaged. The total length of dentaries from the anterior margin to the middle point of the line between their posterior ends is 104.8 mm; the symphysis is 46.8 mm long and



147.1 mm wide at the level of the posterior bone end. In dorsal view, the symphysis of dentaries is semioval; the anterior margin is rounded and the posterior symphyseal margin is arched. The symphysis terminates far from reaching the level of the foramen dentofaciale majus. The labial ridges are high. The symphyseal

ridge is rudimentary. The lingual ridges are rounded, high posteriorly, lowering gradually anteriorly and disappearing near the symphysis. The surface between the labial and lingual ridges lacks depressions and has many nutrient foramina. In anterior and posterior views, the anterior part of the labial ridge is raised and

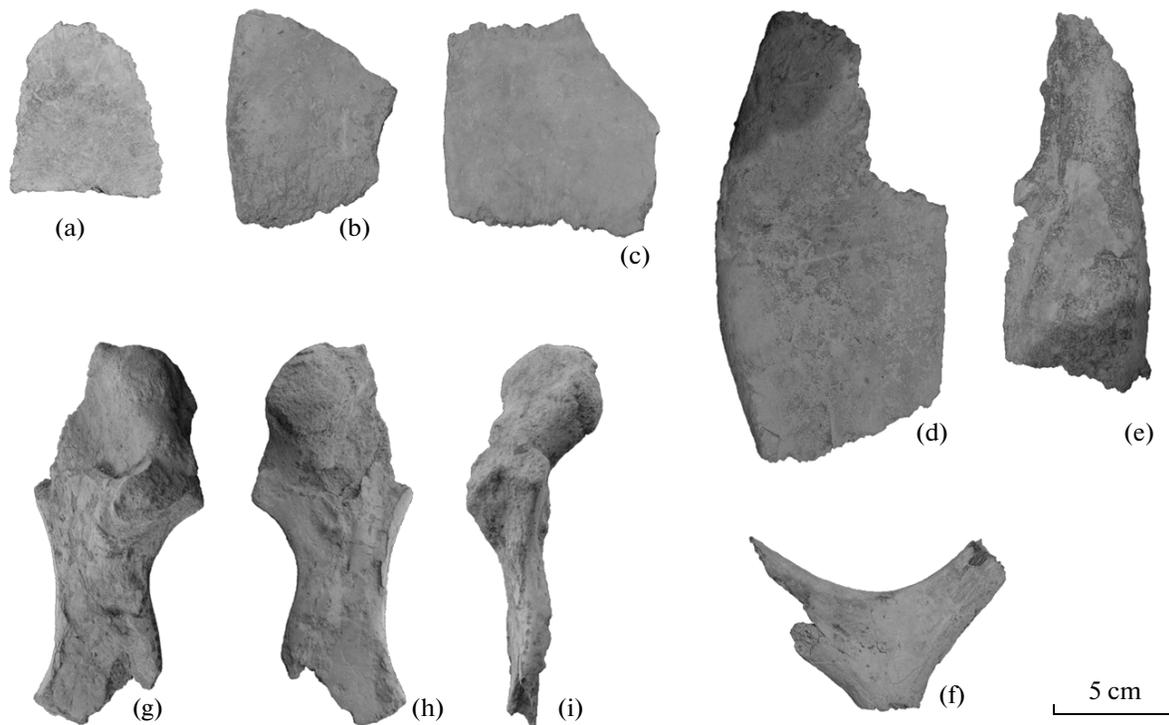


Fig. 1. “*Allopleuron*” *qazaqstanense* (specimen without number), housed in the Mangystau Regional Historical Museum: (a) neural plate I–VI, dorsal view; (b) peripheral plate A, dorsal view; (c) peripheral plate B, dorsal view; (d) peripheral plate C, dorsal view; (e) left peripheral plate IV, lateral view; (f) scapula, dorsal or ventral view; (g–i) left humerus: (g) ventral, (h) dorsal, and (i) anterior views.

slightly pointed at the apex. The upper and lower shelves formed by the sulcus cartilaginis meckelii are approximately equal. The foramen alveolare inferius is positioned slightly more rostrally than the foramen dentofaciale majus. In lateral view, caudal to the symphysis, the dentary rami increase in thickness posteriorly. The foramen dentofaciale majus is located close to the posterior bone margin in the anterior part of a small depression for attachment of the adductor mandibulae externus muscle. Contacts with the coronoid and angular bones are preserved; the areas of contact with other bones are broken off.

Prearticular (Pl. 10, figs. 7, 8). The distal part of the right prearticular is preserved; this element is mediolaterally flat and adjoins laterally the articular bone (specimen ZIN PH, no. 9/177).

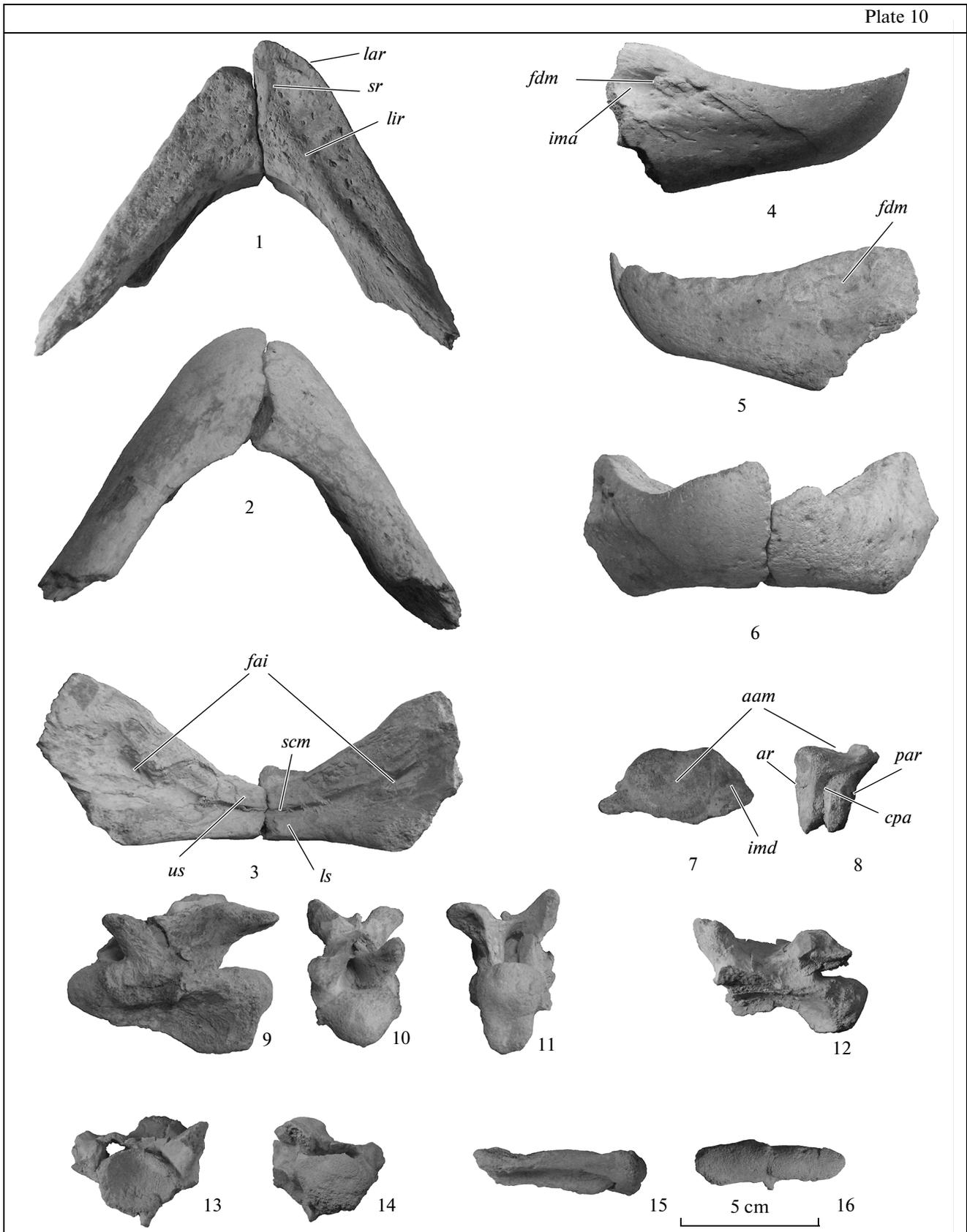
Articular (Pl. 10, figs. 7, 8). The right articular bone is preserved in natural articulation with the distal part of the prearticular; it is 45.8 mm long (specimen ZIN PH, no. 9/177). The dorsal part of the articular bone formed the middle part of the area articularis mandibularis and facet for attachment of the depressor mandibulae muscle. The articular bone came in contact with the prearticular medially, the angular ventrally, and the surangular laterally.

Carapace. Neural plates (Fig. 1a). The anterior part of neural plate I or posterior part of neural plate I–VI (specimen MPHNM, without no.) is preserved; it is semioval in shape, about 64 mm wide. The external surface is flat, without a keel.

Peripheral plates (Figs. 1b–1e). Four peripheral plates are preserved; left plate IV and three of uncer-

Explanation of Plate 9

Figs. 1–17. “*Allopleuron*” *qazaqstanense* Karl et al., 2012; Kazakhstan, Mangystau Region, Kuyulus locality; Eocene, Bartonian, Shorym Formation: (1–4) specimen ZIN PH, no. 1/177, right prefrontal: (1) dorsal, (2) lateral, (3) ventral, and (4) medial views; (5) specimen ZIN PH, no. 2/177, right parietal, dorsal view; (6, 7) specimen ZIN PH, no. 3/177, left squamosal: (6) medial and (7) lateral views; (8–11) specimen ZIN PH, no. 5/177, left premaxilla: (8) dorsal, (9) ventral, (10) anterior, and (11) lateral views; (12–15) specimen ZIN PH, no. 6/177, left maxilla: (12) medial, (13) lateral, (14) dorsal, and (15) ventral views; (16, 17) specimen ZIN PH, no. 7/177, left quadrate: (16) posterior and (17) ventral views. Designations: (*cm*) condylus mandibularis; (*ct*) cavum tympani; (*dp*) dorsal process of premaxilla; (*fpm*) foramina in dorsal surface of premaxilla; (*fsm*) supramaxillary foramen; (*ica*) incisura columellae auris; (*ilj*) depression for anterior margin of lower jaw; (*idm*) depression for depressor mandibulae; (*nf*) nutrient foramina; (*mf*) medial groove; (*rlr*) rudimentary lingual ridge; (*tm*) traces of bites of large vertebrate.



tain positions (specimen MPHNM, without no.). In plate A (which lateral margin is about 84 mm long), the lateral margin is longer than the medial margin, slightly convex. In plate B (lateral margin is about 72 mm long), the medial margin is longer than the lateral margin, which is almost straight. In plate C (lateral margin is about 180 mm long), the lateral margin is strongly convex; the medial margin is straight, shorter than the lateral margin; the dorsal surface has grooves between horn scutes. Left IV peripheral plate (lateral margin about 145 mm long) considerably increases in thickness posteriorly; a musk duct groove is seen at the medial edge. The position of the plate is determined based on the comparison with *Tasbacka aldabergeni*, peripheral plates IV of which sometimes have grooves of the musk duct (Nessov, 1987).

Nonshell postcranial skeleton. Cervical vertebrae. Cervical vertebra IV (Pl. 10, figs. 9–11; specimen ZIN PH, no. 10/177) is strongly distorted; the right prezygapophysis and transverse processes are broken. The centrum is 74.2 mm long, biconvex, longitudinally extended. The anterior condyle of the centrum is circular in section and the posterior condyle is oval, vertically extended. The ventral keel is well developed. The element is determined as cervical vertebra IV based on the fact that cervical vertebra IV of cheloniids is usually biconvex (Williams, 1950).

Cervical vertebra V (Pl. 10, figs. 12–14; specimen ZIN PH, no. 11/177) is strongly distorted; the right prezygapophysis, right postzygapophysis, transverse processes, and ventral carina are broken off. The centrum is 53.9 mm long. The anterior and posterior articular facets of the centrum are circular in section. The centrum is procelous, longitudinally extended. Judging from the thickness of the preserved base, the ventral keel was high. The element is determined as vertebra V because the vertebra is procelous (in cheloniids, this is characteristic of cervical vertebrae V–VIII), with circular articular facets of the centrum (in *Puppigerus camperi* and *Tasbacka aldabergeni*, this is cervical vertebra V) (Moody, 1974, pl. 4; Nessov, 1987, pl. VII).

Cervical vertebra VII (Pl. 10, figs. 15, 16; specimen ZIN PH, no. 12/177) is only represented by the posterior part of the vertebral centrum, which is 61.6 mm

long. The posterior articular facet is flattened strongly dorsoventrally, divided by a groove into two parts. The ratio of height (10.6 mm) to width (51.6 mm) is about 1 : 5. The ventral carina is moderately developed. This element is determined as vertebra VII based on the fact that the posterior articular facet of the centrum is flattened strongly dorsoventrally, as in *Argillochelys cuneiceps*, *Puppigerus camperi*, and *Tasbacka aldabergeni* (Moody, 1974, pls. 4, 6; Nessov, 1987, pl. VII).

Scapula (Fig. 1f). Only a central scapula fragment (specimen MPHNM, without no.) is preserved; it is about 100 mm long. The angle between the acromion and scapular process is wide; however, it is impossible to measure them because these elements are incomplete.

Humerus (Figs. 1g–1i). In the left humerus (specimen MPHNM, without no.), the medial process and distal epiphysis are broken off. The bone is about 150 mm long and the minimum width of the shaft is about 32 mm. The shaft is wide, almost straight. The lateral process is short, located slightly distal to the humeral head. At the level of the lateral process, the dorsal bone surface has a small oval crateriform structure for attachment of joint tendon of the latissimus dorsi and teres major muscles.

Comparison with other cheloniid taxa. The sea turtle remains described above are referred to Cheloniidae sensu Hirayama, 1998 based on the fact that the maxilla does not participate in the formation of the apertura narium interna and has deep grooves of horn scutes on the surface of the parietal and plates of the shell (Hirayama, 1998).

The individual described here is referred to "*Allopleuron*" *qazaqstanense* based on the following characters: elements with a keel are absent; the humerus has a short lateral process; the alveolar surface of dentaries is simple, without vertical differentiation, their symphysis is short, without depressions (Karl et al., 2012). Note that rudimentary symphyseal and lingual ridges of specimen ZIN PH, no. 8/177 are probably treated as vertical differentiation of the alveolar surface of dentaries; however, at least the rudimentary symphyseal ridge is seen on the lower jaw of "*A.*" *qazaqstanense* (photographs of the holotype provided by Karl).

Explanation of Plate 10

Figs. 1–16. "*Allopleuron*" *qazaqstanense* Karl et al., 2012; Kazakhstan, Mangystau Region, Kuyulus locality; Bartonian, Shorym Formation: (1–6) specimen ZIN PH, no. 8/177, symphysis of dentaries: (1) dorsal, (2) ventral, (3) posterior, (4) right lateral, (5) left lateral, and (6) anterior views; (7, 8) specimen ZIN PH, no. 9/177, right prearticular and articular bones: (7) dorsal and (8) anterior views; (9–11) specimen ZIN PH, no. 10/177, cervical vertebra IV: (9) left lateral, (10) anterior, and (11) posterior views; (12–14) specimen ZIN PH, no. 11/177, cervical vertebra V or VI: (12) lateral, (13) anterior, and (14) posterior views; (15, 16) specimen ZIN PH, no. 12/177, cervical vertebra VI or VII: (15) left lateral and (16) posterior views. Designations: (*ar*) articular; (*aam*) area articularis mandibularis; (*epa*) contact of prearticular and articular bones; (*fai*) foramen alveolare inferius; (*fdm*) foramen dentofaciale majus; (*ima*) depression for musculus adductor mandibulae externus; (*imd*) area for attachment of musculus depressor mandibulae; (*lar*) labial ridge; (*lir*) lingual ridge; (*ls*) lower shelf of lower jaw symphysis; (*par*) prearticular; (*scm*) sulcus cartilaginis meckelii; (*sr*) symphyseal ridge; (*us*) upper shelf of lower jaw symphysis.

At the same time, the holotype of “*Allopleuron*” *qazaqstanense* and the individual described above considerably differ from *A. hofmanni* (Gray, 1831), the type species of *Allopleuron*, so that it should not be assigned to this genus, the systematic position of which within the superfamily Cheloniodea is debatable (Danilov, 2005). In particular, in contrast to *A. hofmanni* from the Upper Cretaceous of Western Europe, the cavum tympani of the species from Kazakhstan is partially formed of the anterior rather than ventral part of the squamosal and high lingual ridges of dentaries and keels of the neural plates are absent (Zangerl, 1980; Hirayama, 1994; Karl, 2007; Karl et al., 2012). In addition, in contrast to *Allopleuron*, the species from Kazakhstan has distinct grooves corresponding to horn scutes on bones of the skull roof and carapace (Hirayama, 1994). Taking into account the above features, it seems expedient to compare the taxon from Kazakhstan with other Paleogene cheloniids to gain a better understanding of its taxonomic position.

In a preliminary study, Zvonok et al. (2011) reported that localities of the Shorym Formation yielded at least two taxa of Cheloniidae sensu lato. These are *Argillochelys* Lydekker, 1889 and *Euclastes* Cope, 1867/*Pacificchelys* Parham et Pyenson, 2010 represented by cranial bones. In addition, sea turtles with well-pronounced surface ornamentation of the carapace and humeri of the “advanced” type, which could have belonged to separate taxa, were mentioned (Zvonok et al., 2011). The specimen described differs from *Pacificchelys*/*Euclastes* in the short symphysis of the lower jaw with a high labial ridge. It differs from the taxa with ornamented plates of the carapace in the absence of ornamentation and the thinner plates and from the taxa with advanced humeri in the more proximally located and less projecting lateral process. Comparison with *Argillochelys* is provided below.

The following Paleocene and Eocene taxa with the extended alveolar surfaces are tentatively assigned to Paleocene–Eocene durophagous cheloniids: “*Argillochelys*” *africana* Tong et Hirayama, 2008, *Erquelinnesia* spp., *Euclastes* spp., *Glossochelys planimentum* (Owen, 1842), *Itlochelys rasstrigin* Danilov et al., 2011, *Puppigerus* spp., and *Tasbacka* spp. (see also Parham and Pyenson, 2010). “*A.*” *qazaqstanense* differs from “*Argillochelys*” *africana*, *Erquelinnesia* spp., *Euclastes* spp., and, probably, *Glossochelys planimentum* and *Tasbacka ouledabdounensis* Tong et Hirayama, 2002 in the absence of an additional scute between the frontoparietal and parietal scutes; it differs from *Puppigerus* spp. and *Tasbacka aldabergeni* Nessonov, 1987 in the straight rather than concave contacts between the frontoparietal and parietal scutes (Owen and Bell, 1849; Fig. 2). The premaxilla differs in the triangular shape from that of *Euclastes wielandi* (Hay, 1908) and cf. *Glossochelys* sp. and in the smaller

length from *Erquelinnesia* spp., *Euclastes acutirostris* Jalil et al., 2009, *E. platyops* Cope, 1867, *Puppigerus* spp., and *Tasbacka* spp. (Hay, 1908; Zangerl, 1971; Moody, 1974; Nessonov, 1987; Karl et al., 1998; Tong and Hirayama, 2002; Hirayama, Tong, 2003; de la Fuente et al., 2009; Jalil et al., 2009; Zvonok, 2011, 2013). In addition, the premaxillae of “*A.*” *qazaqstanense* are separate in contrast to that of *Erquelinnesia* spp. (Zangerl, 1971; de la Fuente et al., 2009). The maxilla differs in the presence of a high labial ridge from that of *Erquelinnesia* spp., *Euclastes* spp., and *T. ouledabdounensis* (Tong and Hirayama, 2002; Parham and Pyenson, 2010). The alveolar process of the maxilla lacks grooves on the external surface, unlike that of cf. *Glossochelys* sp. (Zvonok, 2011). “*A.*” *qazaqstanense* differs from taxa of this group in the shorter symphysis of the dentary, the presence of high labial ridges of dentaries, the wider and straight shaft of the humerus, the more medially located and small depression for attachment of joint tendon of the latissimus dorsi and teres major muscles (Figs. 3, 4).

“*Allopleuron*” *qazaqstanense* differs from *Argillochelys* spp. in the arrangement of scutes on the parietal (Fig. 2), the rudimentary condition of lingual ridges of the maxillae and dentaries, and symphyseal ridge of the dentaries (Fig. 3), the flat surface of neural plates (Lydekker, 1889). At the same time, “*A.*” *qazaqstanense* is similar to *Argillochelys* spp. in the presence of ridges (although reduced) on the alveolar surfaces, short symphysis of the lower jaw, and wide facial region of the skull (Fig. 5).

“*A.*” *qazaqstanense* and *Eocheleone brabantica* Dollo, 1903 are similar in the arrangement of horn scutes on the parietal (Fig. 2), high dorsal processes of the premaxillae and prefrontal processes of the maxillae, providing a high position of the external naris (Fig. 5), high labial ridge, and short symphysis of dentaries (Fig. 3), wide and almost straight shaft of the humerus (Fig. 4), absence of keel and well-developed ornamentation of carapace (Casier, 1968; Gaffney, 1979; Weems and Sanders, 2014). Informative comparison of the individual described here with *Eocheleone monstigris* Grant-Mackie et al., 2011 is impossible; in particular, only two cervical vertebrae and humeral shaft are known in both forms (Grant-Mackie et al., 2011). “*A.*” *qazaqstanense* differs from *E. brabantica* in the more massive lower jaw and the longer symphysis, the presence of rudimentary symphyseal and lingual ridges of the dentary (Fig. 3), and the shallower depression for attachment of joint tendon of the latissimus dorsi and teres major muscles (Fig. 4).

“*Allopleuron*” *qazaqstanense* is similar to *Catalepleura repanda* (Cope, 1868) in the lower jaw structure (Fig. 3) and flat neural plates. However, the lower jaw of *C. repanda* has a projecting shelf below the sulcus

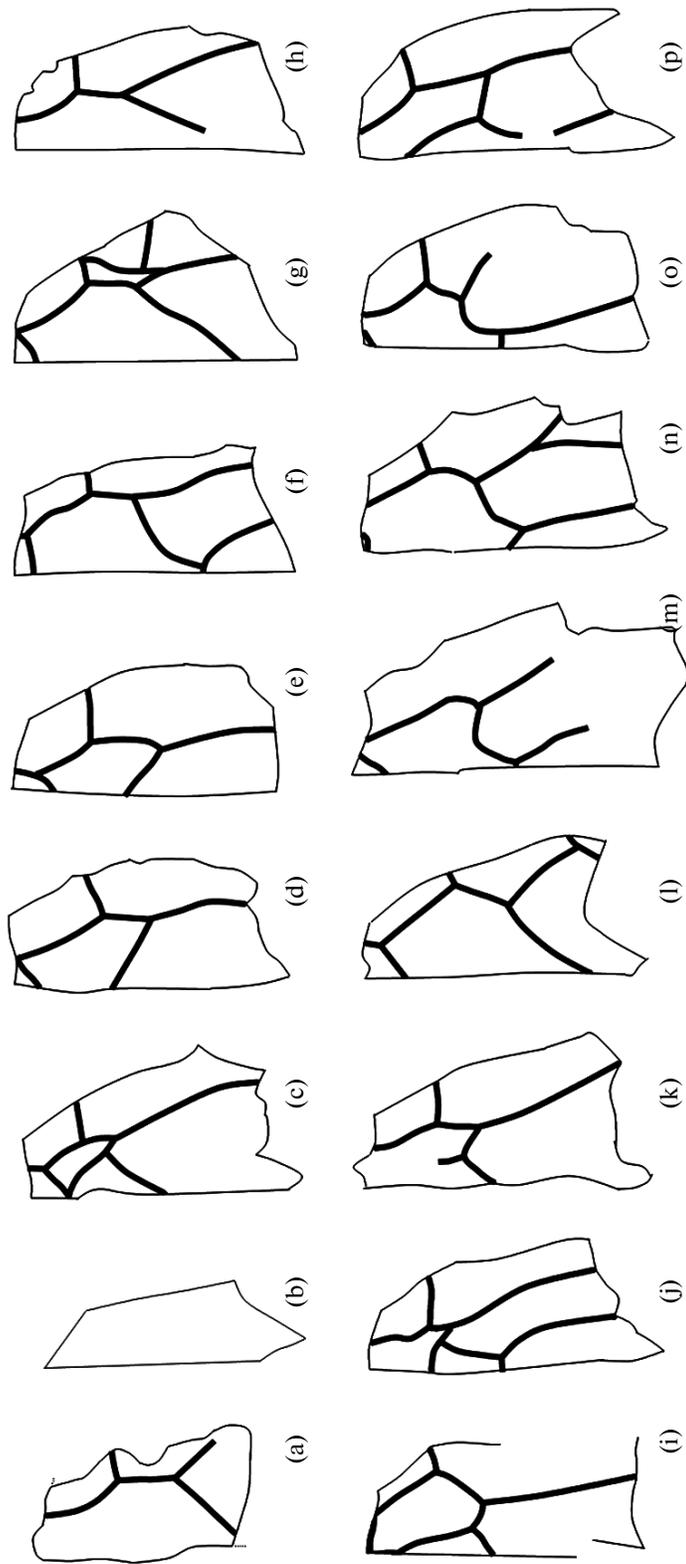


Fig. 2. Right parietals of Paleogene cheloniids and *Allopleuron*, dorsal view: (a) “*Allopleuron*” *qazaqstanense*, specimen ZIN PH, no. 2/177; (b) *Allopleuron hofmanni* (Hirayama, 1994, text-fig. 2); (c) “*Argillocheilus*” *africana* (Tong and Hirayama, 2008, text-fig. 2); (d) *Argillocheilus antiqua*, specimen IRSNB, no. 1653, photograph provided by Hirayama; (e) *Argillocheilus cuneiceps*, specimen NHM, no. 4.1636, photograph provided by Hirayama; (f) *Ashleycheilus palmeri* (Weems and Sanders, 2014, text-fig. 11); (g) *Carolinocheilus wilsoni* (Weems and Sanders, 2014, text-fig. 2); (h) *Eochelone brabantica* (Casier, 1968, text-fig. 1); (i) *Erquelimnesia gosseletii* (Zangerl, 1971, text-fig. 5); (j) *Euclastes acutirostris* (Jalil et al., 2009, text-fig. 3); (k) *Euclastes wielandi* (Hirayama, 1994, text-fig. 2); (l) *Glari-cheilus knorri* (Karl, 2007, text-fig. 9); (m) *Puppigerus camperi* (Moody, 1974, pl. 3); (n) *Puppigerus nessovi*, specimen ZIN PH, no. 53/145; (o) *Tasbacka altdabergeni* (Nessov, 1987, text-fig. 1); (p) *Tasbacka outledabdounensis* (Tong and Hirayama, 2002, text-fig. 2). Not to scale.

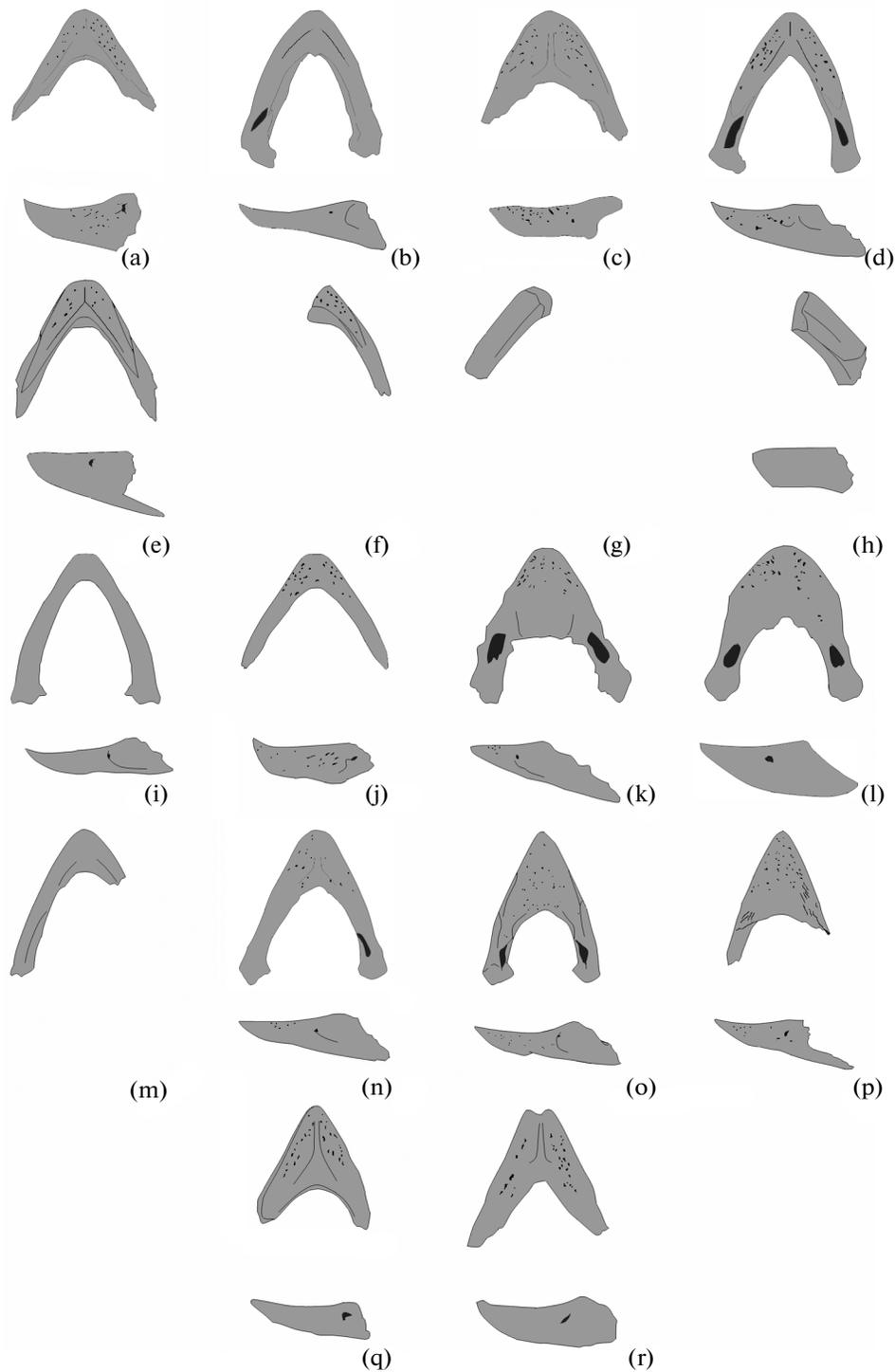


Fig. 3. Lower jaws of Paleogene cheloniids and *Allopleuron hofmanni*; upper row is dorsal view and lower row is left lateral view: (a) “*Allopleuron qazaqstanense*, specimen ZIN PH, no. 8/177; (b) *Allopleuron hofmanni* (dorsal view after Karl, 2007, pl. 7; lateral view after Hirayama, 1994, text-fig. 5); (c) “*Argillochelys africana* (Tong and Hirayama, 2008, text-fig. 4); (d) *Argillochelys antiqua*, specimen IRSNB, no. 1653, based on the photograph provided by Hirayama; (e) *Argillochelys* sp., specimen ZIN PH, no. 5/145; (f) *Catapleura repanda* (Zangerl, 1971, pl. 2); (g) *Catapleura* sp. (Weems, 1999, pl. 5.2); (h) Chelonioidea indet. (= *Dolichochelys rogovichi*: Averianov, 2002, text-fig. 8); (i) *Eocheilone brabantica* (dorsal view after Casier, 1968, pl. 2; lateral view after Hirayama, 1994, text-fig. 5); (j) *Eocheilone* sp., specimen ZIN PH, no. 51/145; (k) *Erquelinnesia gosseleti* (Zangerl, 1971, pl. 6); (l) *Euclastes wielandi* (Hirayama and Tong, 2003, text-fig. 1); (m) *Glarichelys knorri* (Karl, 2007, pl. 7); (n) *Itilochelys rasstrigin* (Danilov et al., 2010, text-fig. 6); (o) *Puppigerus camperi* (Moody, 1974, text-fig. 9); (p) *Puppigerus nessovi*, specimen ZIN PH, no. 9/145; (q) *Tasbacka aldabergeni* (Nessov, 1987, text-fig. 3); (r) *Tasbacka ouledabdounensis* (Tong and Hirayama, 2002, text-fig. 3). Not to scale.

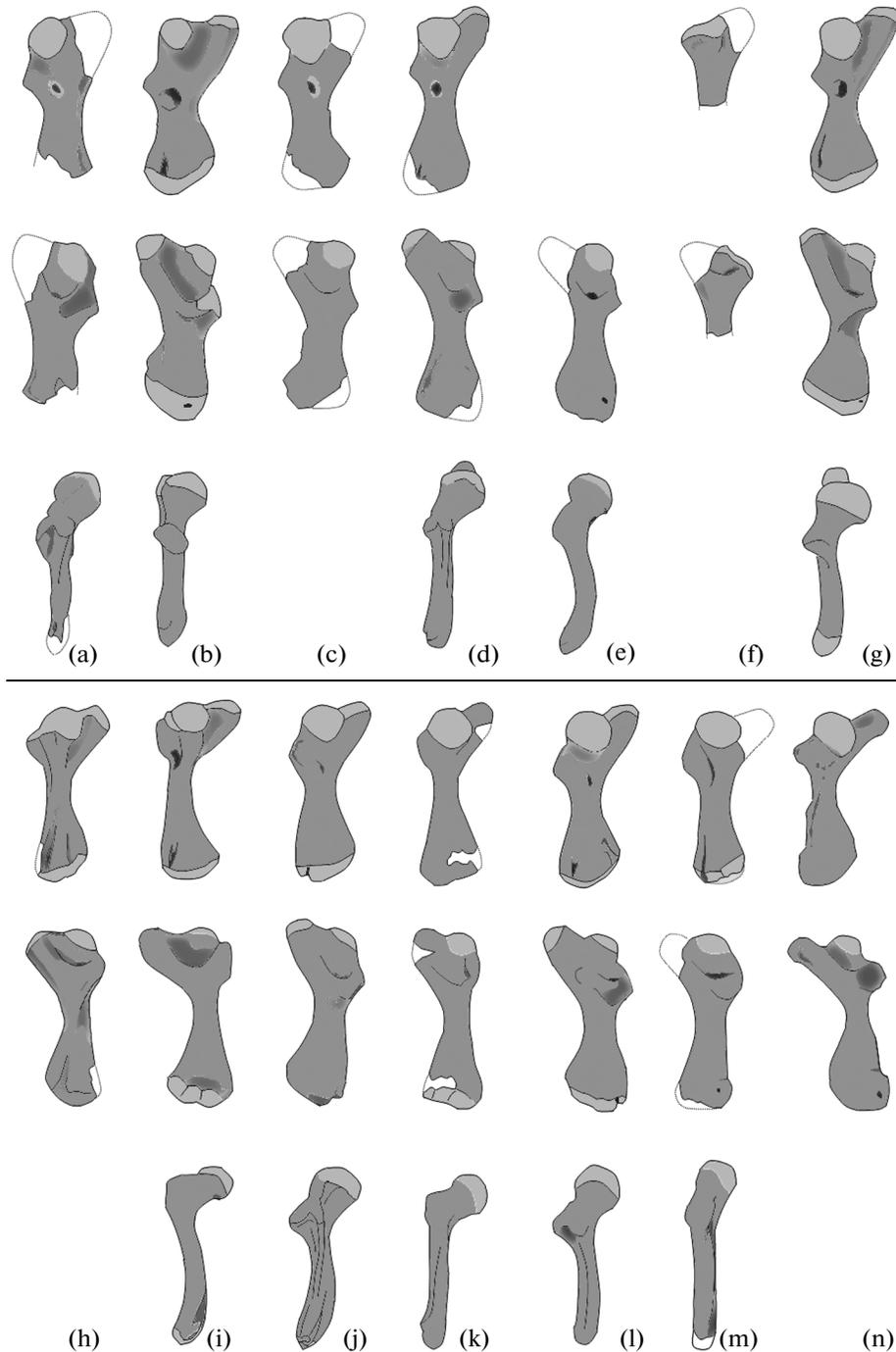


Fig. 4. Left humeri of Paleogene cheloniids and *Allopleuron hofmanni*; upper row is dorsal view, middle row is ventral view, and lower row is anterior view: (a) “*Allopleuron*” *qazaqstanense*, specimen MPHNM, without no.; (b) *Allopleuron hofmanni* (Hirayama, 1994, text-fig. 6); (c) “*Allopleuron*” *lipsiensis* (Karl, 2007, pl. 11); (d) *Ashleychelys palmeri* (Weems and Sanders, 2014, text-fig. S1); (e) *Carolinochelys wilsoni* (Weems and Sanders, 2014, text-fig. 8); (f) *Catapleura repanda* (Zangerl, 1971, pl. 2); (g) *Eochelone brabantica* (Hirayama, 1994, text-fig. 6); (h) *Erquelinnesia gosseleti* (Zangerl, 1971, pl. 8); (i) *Euclastes wielandi* (Hirayama, 1994, text-fig. 6); (j) *Glarichelys knorri* (Karl, 2007, pl. 6, fig. 10); (k) *Itiochelys rasstrigin* (Danilov et al., 2010, text-fig. 8); (l) *Procolpochelys charlestonensis* (Weems and Sanders, 2014, text-fig. S4); (m) *Puppigerus nessovi* (Averianov, 2005, pl. 7); (n) *Tasbacka aldabergeni* (Nessov, 1987, text-fig. 24); not to scale.

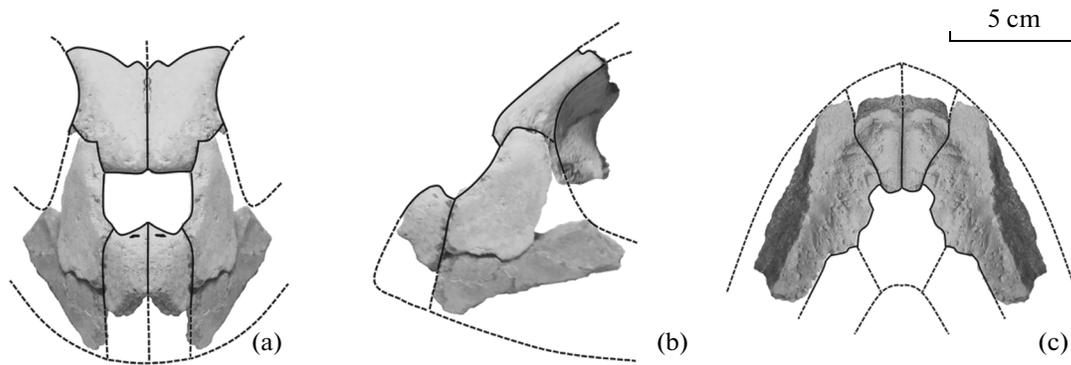


Fig. 5. Reconstruction of the facial skull region of “*Allopleuron*” *qazaqstanense*: (a) anterodorsal view; (b) left lateral view; (c) ventral view.

cartilaginis meckelii (Zangerl, 1971). The humerus of “*A.*” *qazaqstanense* is wider and its lateral process is positioned more distally (Fig. 4). Specimen ZIN PH, no. 8/177 is somewhat similar to the individual determined by Weems (1999) as ?*Dollochelys* sp. (= ?*Catapleura* sp.), although the latter has a better developed lingual ridge (as in *Argillochelys* spp.) (Fig. 3).

In the species diagnosis, “*Allopleuron*” *qazaqstanense* differs from “*Allopleuron*” *lipsiensis* Karl, 2007 only in the relative length of free ribs (Karl, 2007; Karl et al., 2012). These species are similar in wide, almost straight humeral diaphysis (Fig. 4), absence of keel of neural plates, and deep sculpture of the carapace (Karl, 2007; Karl et al., 2012). Taking into account the fact that “*A.*” *qazaqstanense* does not belong to the genus *Allopleuron* (see below), there is no reason to refer to this genus the closely related species “*A.*” *lipsiensis*.

“*Allopleuron*” *qazaqstanense* differs from *Carolinochelys wilsoni* Hay, 1923 in the absence of a groove between the frontal and frontoparietal scutes on parietals and additional scutes located lateral to the frontoparietal (Fig. 2), the wider straight humeral shaft (Fig. 4), and the poorly pronounced ornamentation of the carapace (Weems and Sanders, 2014).

“*Allopleuron*” *qazaqstanense* differs from *Ashleychelys palmeri* Weems et Sanders, 2014 in the absence of a groove between the frontal and frontoparietal scutes on the parietals (Fig. 2), the cavum tympani partly formed by the anterior margin of the squamosal, the presence of a groove on the palatal surface of the premaxillae, the flat neural plates, and in the poorly pronounced ornamentation of the carapace (Weems and Sanders, 2014).

“*Allopleuron*” *qazaqstanense* differs from *Glarichelys knorri* (Gray, 1831) in the absence of a groove between the frontal and frontoparietal scutes on the parietals (Fig. 2), the shorter prefrontals, and in the flat neural plates (Karl, 2007). At the same time, these species are similar in the humeral structure (Fig. 4).

“*Allopleuron*” *qazaqstanense* differs from *Procolpochelys charlestonensis* Weems et Sanders, 2014 in the posterior margin of the prefrontal positioned almost perpendicular to the medial edge (Weems and Sanders, 2014). These species are similar in wide, almost straight humeral shaft (Fig. 4), absence of keel of neural plates, and well-pronounced ornamentation of the carapace (Weems and Sanders, 2014).

Specimen ZIN PH, no. 1/177 differs from *Rupelchelys breittkreutzii* Karl et Tichy, 1999 in the posterior margin of the prefrontal positioned almost perpendicular to the medial edge (Karl and Tichy, 1999). The holotype of “*A.*” *qazaqstanense* is also distinguished by the structure of the anterior part of the carapace (Karl and Tichy, 1999; Karl et al., 2012).

“*Allopleuron*” *qazaqstanense* differs from *Bryochelys waterkeynii* (van Beneden, 1871) in the poorly developed ornamentation of the carapace (Smets, 1888). These species are similar in the presence of depression on the palatal surface of the premaxillae (Smets, 1888).

Specimen ZIN PH, no. 8/177 has certain features in common with *Chelonioidea* indet. (= *Dollochelys rogovichi*) and differs from it in the curved edge of labial ridges of the lower jaw; however, a closer comparison is impossible because the material is fragmentary (Averianov, 2002, text-fig. 3).

Remarks. The large size, strongly fontanelized carapace, and wide straight flattened humeral diaphysis apparently independently developed in Late Cretaceous *Allopleuron hofmanni* and Eocene “*A.*” *qazaqstanense* in connection with similar mode of life. Such complex morphological changes in the evolution of sea turtles repeatedly occurred in connection with transition from littoral to pelagic habitats (Zangerl, 1980; Nessonov, 1987). At the same time, the shape of grooves formed by horn scutes on the parietal; structural features of the alveolar surfaces, neural plates, and humerus; the absence of well-developed ornamentation of the carapace of “*A.*” *qazaqstanense* sug-

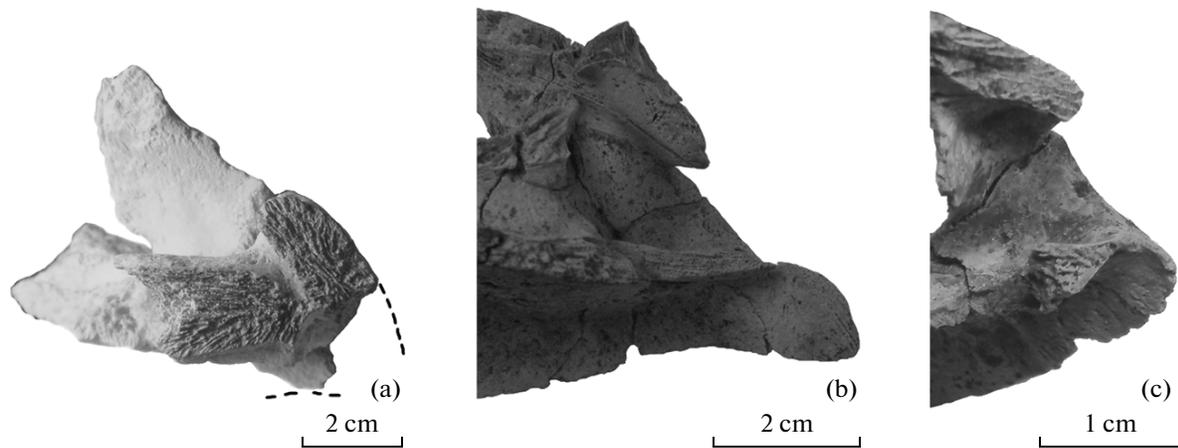


Fig. 6. Premaxilla and adjacent bones of some Eocene cheloniids, medial view: (a) “*Allopleuron*” *qazaqstanense*, specimen ZIN PH, no. 5/177 (Kazakhstan, Kuyulus; Bartonian Stage); (b) *Puppigerus nessovi*, unregistered specimen (Ukraine, Ikovo; Lutetian Stage); (c) cf. *Glossochelys* sp., specimen ZIN PH, no. 50/145 (Ukraine, Ikovo; Lutetian Stage).

gest affinity of this taxon to Eocene *E. brabantica*; a similar structure of the last three elements is also observed in Oligocene cheloniids, such as “*A.*” *lipsiensis* and *P. charlestonensis*; somewhat weaker similarity is observed in *Argillochelys* spp. and *Glarichelys knorri* (see above).

The jaw apparatus structure of “*A.*” *qazaqstanense* provides evidence of its diet. The lower jaw of specimen ZIN PH, no. 8/177 is similar to that of living *Caretta Rafinesque*, 1814 (loggerheads), although the lower jaw rami are positioned at a wider angle. A significant part of the diet of *Caretta* is mollusks, crabs, and soft benthic organisms (Jones et al., 2012). A similar diet was probably characteristic of “*A.*” *qazaqstanense*. Paleocene–Eocene durophagous cheloniids which are included in comparison (see above; Fig. 3) had a longer alveolar surface of the lower jaw without a high labial ridge. This lower jaw type is adapted for crushing testaceous organisms by alveolar skull surfaces. Some of these species, for example, *Puppigerus nessovi*, had very thin bones of the facial skull region; in others, for example, cf. *Glossochelys* sp., these bones were moderately thick (Fig. 6), suggesting that they fed on relatively fragile skeletal organisms. In “*A.*” *qazaqstanense*, high labial ridges of the lower jaw are likely adapted for cutting rather than crushing the protective cover of prey. Very thick bones of the facial skull region capable of withstanding a great load (Fig. 6) suggest that the diet of these turtles included animals with a rather strong external skeleton.

As the authors of species reported (Karl et al., 2012), the holotype of “*A.*” *qazaqstanense* was found in the Lutetian beds of an unknown locality. The individual described by us was found in the Shorym Formation of the Kuyulus locality of Kazakhstan. The holotype probably also comes from this formation,

since Lutetian beds, which are productive with reference to higher vertebrates, have not been recorded in Kazakhstan.

Our comparative analysis has shown that “*A.*” *qazaqstanense* should not be referred to the genus *Allopleuron*. However, the description of a new genus or assignment of this species to a previously described genus necessitates redescription of the holotype or description of new, more complete specimens. It is also beyond reason to assign other Paleogene cheloniids, such as “*A.*” *lipsiensis* and “*A.*” *insularis*, to the genus *Allopleuron* (see above; Hirayama, 1997). Thus, *Allopleuron* is a monotypic Upper Cretaceous genus.

Cheloniids from the latter half of the Eocene are still very poorly understood and mostly represented by fragmentary specimens (Moody, 1980, 1997; Grant-Mackie et al., 2011). The assemblage of sea turtles from the Shorym Formation is probably the richest in number and diversity of sea turtles of this stratigraphic interval. “*Allopleuron*” *qazaqstanense* shows a higher level of adaptation to the pelagic mode of life than the majority of Paleogene cheloniids. This is an additional confirmation of the complex character of evolution of cheloniids, with many parallelisms (see also Zangerl, 1980; Nessov, 1987; Hirayama, 1994; Parham and Pyenson, 2010).

ACKNOWLEDGMENTS

We are grateful to I.G. Danilov (ZIN) for valuable remarks concerning the text, H.-V. Karl (Goettingen University, Goettingen, Germany) for providing us with photographs of the holotype of *Allopleuron qazaqstanense*, R. Hirayama (Waseda University, Tokyo, Japan) for photographs of *Argillochelys* spp., E.V. Syr-

omyatnikova (ZIN) for help with finding publications, and to Yu. Bunyatov for assistance during field works.

REFERENCES

- Averianov, A.O., Review of Mesozoic and Cenozoic sea turtles from the former USSR, *Russ. J. Herpetol.*, 2002, vol. 9, no. 2, pp. 137–154.
- Averianov, A.O., A new sea turtle (Testudines, Cheloniidae) from the Middle Eocene of Uzbekistan, *Paleontol. J.*, 2005, vol. 39, no. 6, pp. 646–651.
- Casier, E., Le squelette céphalique de *Eochelone* brabantica L. Dollo, du Bruxellien (Lutétien inférieur) de Belgique, et sa comparaison avec celui de *Chelone mydas* Linné, *Bull. Inst. R. Sci. Natur. Belg.*, 1968, no. 44, pp. 1–22.
- Danilov, I.G., Die fossilen Schildkröten Europas, in *Handbuch der Reptilien und Amphibien Europas*, vol. 3/IIIB: *Schildkröten (Testudines) II*; herausgegeben von U. Fritz, Wiebelsheim: AULA-Verlag, 2005, pp. 329–448.
- Danilov, I.G., Averianov, A.O., and Yarkov, A.A., *Itiochelys rasstrigin* gen. et sp. nov., a new hard-shelled sea turtle (Cheloniidae sensu lato) from the Lower Paleocene of Volgograd Province, Russia, *Proc. Zool. Inst. Russ. Acad. Sci.*, 2010, vol. 314, no. 1, pp. 24–41.
- Fuente, M.S. de la, Fernandez, M.S., Parra A., et al. *Euclastes meridionalis* (de la Fuente and Casadio) (Testudines: Pancheloniidae) from Danian levels of the Jaguel Formation at Cerro Azul, Northern Patagonia, Argentina, *Neues Jahrb. Geol. Paläontol. Abh.*, 2009, vol. 253, pp. 327–339.
- Gaffney, E.S., Comparative cranial morphology of recent and fossil turtles, *Bull. Am. Mus. Natur. Hist.*, 1979, vol. 164, pp. 65–376.
- Grant-Mackie, J.A., Hill, J., and Gill, B.J., Two Eocene chelonioid turtles from Northland, New Zealand, *New Zeal. J. Geol. Geophys.*, 2011, no. 54, pp. 181–194.
- Hay, O.P., Fossil turtles of North America, *Carnegie Inst. Wash. Publ.*, 1908, no. 75, pp. 1–568.
- Hirayama, R., Phylogenetic systematics of chelonioid sea turtles, *Isl. Arc.*, 1994, no. 3, pp. 270–284.
- Hirayama, R., Distribution and diversity of Cretaceous chelonioids, in *Ancient Marine Reptiles*, Callaway, J.M. and Nicholls, E.L., Eds., San Diego: Acad. Press, 1997, pp. 225–241.
- Hirayama, R., Oldest known sea turtle, *Nature*, 1998, no. 392, pp. 705–708.
- Hirayama, R. and Tong, H., *Osteopygis* (Testudines: Cheloniidae) from the Lower Tertiary of the Ouled Abdoun Phosphate Basin, Morocco, *Palaeontology*, 2003, vol. 46, pp. 845–856.
- Jalil, N.-E., Lapparent de Broin, F., de Bardet, N., et al., *Euclastes acutirostris*, a new species of littoral turtle (Cryptodira, Cheloniidae) from the Palaeocene phosphates of Morocco (Oulad Abdoun Basin, Danian–Thanetian), *C. R. Palevol.*, 2009, vol. 8, pp. 447–459.
- Jones, M.E.H., Werneburg, I., Curtis, N., et al., The head and neck anatomy of sea turtles (Cryptodira: Cheloniidae) and skull shape in Testudines, *PLoS ONE*, 2012, no. 7 (11). DOI: 10.1371/journal.pone.0047852.
- Karl, H.-V., The fossil reptiles (Reptilia: Chelonii, Crocodylia) from the marine Early Oligocene of the Weissenloster Basin (Central Germany: Saxonia), *Stud. Geol. Salmanticensia*, 2007, no. 43, pp. 25–66.
- Karl, H.-V., Groning, E., and Brauckmann, C., New materials of the giant sea turtle *Allopleuron* (Testudines: Cheloniidae) from the marine Late Cretaceous of central Europe and the Palaeogene of Kazakhstan, *Stud. Geol. Salmanticensia*, 2012, vol. esp., no. 9, pp. 153–173.
- Karl, H.-V. and Tichy, G., Zur Taxonomie eines neuen Tribus von Seeschildkröten aus dem Oligozän von Deutschland (Testudines: Cheloniidae), *Joannea Geol. Paläontol.*, 1999, vol. 1, pp. 61–77.
- Karl, H.-V., Tichy, G., and Ruschak, H., *Osteopygoides priscus* n. gen. n. sp. und die Taxonomie und Evolution der Osteopygidae (Testudines: Cheloniidae), *Mitt. Geol. Paläontol. Landesmus. Joanneum*, 1998, vol. 56, pp. 329–350.
- Lydekker, R., *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History): Part III. The Order Chelonia*, London: Brit. Mus. Natur. Hist., 1889.
- Matzke, A.T., An almost complete juvenile specimen of the cheloniid turtle *Ctenochelys stenoporus* (Hay, 1905) from the Upper Cretaceous Niobrara Formation of Kansas, USA, *Palaeontology*, 2007, vol. 50, pp. 669–691.
- Moody, R.T.J., The taxonomy and morphology of *Puppigerus camperi* (Gray), an Eocene sea turtle from northern Europe, *Bull. Brit. Mus. Natur. Hist. Geol.*, 1974, vol. 25, pp. 153–186.
- Moody, R., Notes on some European Palaeogene turtles, *Tert. Res.*, 1980, no. 2, pp. 161–168.
- Moody, R.T.J., The paleogeography of marine and coastal turtles of the North Atlantic and Trans-Saharan regions, in *Ancient Marine Reptiles*, Callaway, J.M. and Nicholls, E.L., Eds., San Diego: Acad. Press, 1997, pp. 259–278.
- Nessov, L.A., On sea turtles from the Paleogene of southern Kazakhstan and phylogenetic relationships of Toxochelyidae and Cheloniidae, *Paleontol. Zh.*, 1987, no. 4, pp. 76–87.
- Owen, R. and Bell, A., Reptilia of the Tertiary beds: Part 1. Chelonia, in *Monography of the Fossil Reptilia of the London Clay*, London: Palaeontogr. Soc., 1849, pp. 1–76.
- Parham, J. and Pyenson, N., New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous, *J. Paleontol.*, 2010, vol. 84, no. 2, pp. 231–247.
- Smets, G., Les chelonees Rupeliennes, *Ann. Soc. Sci. Brux.*, 1888, no. 12, pp. 193–214.
- Tong, H. and Hirayama, R., A new species of *Tasbacka* (Testudines: Cryptodira: Cheloniidae) from the Paleocene of the Ouled Abdoun phosphate basin, Morocco, *Neues Jahrb. Geol. Paläontol. Mh.*, 2002, vol. 5, pp. 277–294.
- Tong, H. and Hirayama, R., A new species of *Argillochelys* (Testudines: Cryptodira: Cheloniidae) from the Ouled Abdoun phosphate basin, Morocco, *Bull. Soc. Géol. Fr.*, 2008, vol. 179, no. 6, pp. 623–630.
- Weems, R.E., Reptile remains from the Fisher/Sullivan site, *Vir. Div. Miner. Res. Publ.*, 1999, no. 152, pp. 101–121.
- Weems, R.E. and Sanders, A.E., Oligocene pancheloniid sea turtles from the vicinity of Charleston, South Carolina, U.S.A., *J. Vertebr. Paleontol.*, 2014, vol. 34, no. 1, pp. 80–99.

- Williams, E.E., Variation and selection in the cervical central articulations of living turtles, *Bull. Am. Mus. Natur. Hist.*, 1950, no. 94, pp. 505–562.
- Zangerl, R., Two toxochelyid sea turtles from the Landenian sands of Erquelinnes (Hainaut) of Belgium, *Mém. Inst. R. Sci. Natur. Belg.*, 1971, no. 169, pp. 1–32.
- Zangerl, R., Patterns of phylogenetic differentiation in the toxochelyid and cheloniid sea turtles, *Am. Zool.*, 1980, vol. 20, pp. 585–596.
- Zhelezko, V.I. and Kozlov, V.A., Elasmobranchs and Paleogene biostratigraphy of the Trans-Ural Region and Central Asia, *Mater. Stratigr. Paleontol. Ural.*, 1999, vol. 3, pp. 1–323.
- Zvonok, E., New data on localities and a taxonomic diversity of Eocene crocodiles and turtles of Ukraine, *Paleontol. Zbirn. Lviv*, 2011, no. 43, pp. 107–120.
- Zvonok, E.A., Skull structure of *Puppigerus nessovi* Averianov, 2005 (Reptilia, Testudines, Cheloniidae sensu lato) from the Middle Eocene beds of Ukraine, *Geol. Zh.*, 2013, no. 1, pp. 57–67.
- Zvonok, E.A., Danilov, I.G., Syromyatnikova, E.V., et al., Preliminary results of the study of turtles from the Paleogene of Mangyshlak (Kazakhstan), in *Sovremennaya paleontologiya: klassicheskie i noveishie metody. Tezisy dokladov VIII Vserossiiskoi nauchnoi shkoly molodykh uchenykh–paleontologov* (Reports of the VIII All-Russia Scientific School of Young Scientists Paleontologists on Recent Paleontology: Classical and Modern Methods), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 2011, pp. 20–21.

Translated by G. Rautian