

Remains of Sea Turtles from the Ikovo Locality (Lugansk Region, Ukraine; Middle Eocene)

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Received December 19, 2012

Abstract—Fragmentary remains of sea turtles (Cheloniidae sensu lato: *Argillochelys* sp., *Puppigerus nessovi* Averianov, 2005, and Cheloniidae gen. indet.) from the Ikovo locality (Lugansk Region, Ukraine; Lower Lutetian, Middle Eocene) are described. The genera *Argillochelys* and *Puppigerus* are recorded for the first time in Eastern Europe. The turtle assemblage from Ikovo is similar at the generic level to West European assemblages (Belgium, Great Britain) of approximately the same age (Lower–Middle Eocene). In the presence of *P. nessovi*, the Ikovo assemblage is similar to that from the Middle Eocene Dzheroi 2 locality (Uzbekistan).

Keywords: *Argillochelys*, *Puppigerus nessovi*, Cheloniidae, sea turtles, Eocene, Lutetian, Ukraine, Eastern Europe

DOI: 10.1134/S0031030113050134

INTRODUCTION

Paleogene turtles of Eastern Europe (within the former USSR) are very poorly understood. Most of the Paleogene materials known from this territory are extremely fragmentary and belong to sea turtles (superfamily Chelonioidea Opper, 1811: Chkhikvadze, 1983; Averianov, 2002). More complete materials of sea turtles (Cheloniidae Opper, 1811 sensu lato), including an almost complete skull and isolated bones of nonshell postcranial skeleton from the Lower Paleocene of the Volgograd Region (Russia) have recently been described as a new genus and species, *Itiochelys rasstrigin* Danilov et al., 2010 (Danilov et al., 2010). Fragmentary specimens of other turtle groups (Trionychidae and several undetermined forms) come from the Paleocene of the Volgograd Region (Averianov and Yarkov, 2000, 2004). Turtles are also known from several Eocene localities of Ukraine (Zvonok, 2011a, 2011b), including a particularly rich turtle assemblage from the Ikovo locality (=Osino; 49°31'42" N, 39°3'59.5" E; near the village of Osino, Novopskov District, Lugansk Region, Ukraine; Lower Lutetian, Middle Eocene; for dating, see Udovichenko, 2009). Preliminary results of the study of turtles from this locality (collected in 2004–2010; Zvonok et al., 2010; Udovichenko and Zvonok, 2011) have

shown the presence of soft-shelled taxa (Trionychidae indet.) and sea turtles (*Argillochelys* sp.). Soft-shelled turtles were subsequently described as *Trionyx ikoviensis* Danilov et al., 2011 (Danilov et al., 2011). In the same paper, the presence of the sea turtle *Puppigerus nessovi* Averianov, 2005 and testudinoids (Testudinoidea indet.) was recorded in this locality. Subsequently, two more sea turtles, *Eochelone* sp. (symphysis of the dentaries) and *Glossochelys* sp. (facial skull region) were described from this locality (Zvonok, 2011b). Finally, Zvonok and Gorobets (2012) mentioned in a brief report not yet described specimens of the genus *Puppigerus* from Ikovo, including two skulls. Thus, the turtle assemblage from Ikovo includes at least six taxa.

In the present study, the material of primitive sea turtles (stem group Cheloniidae) collected by E.A. Zvonok in 2009–2011 in Ikovo are described. It includes *Puppigerus nessovi* (species also known from the Middle Eocene of Uzbekistan: Averianov, 2005), *Argillochelys* sp., and other presently undetermined remains of sea turtles (Cheloniidae gen. indet.).

The Cheloniidae sensu lato comprises both basal and crown groups of Cheloniidae (Lapparent de Broin, 2001; Lynch and Parham, 2003). The basal group of Cheloniidae includes the taxa previously

assigned to Toxochelyidae Baur, 1895, Osteopyginae Zangerl, 1953, and “Eochelyinae” Moody, 1968. At present, Toxochelyidae and Eochelyinae are regarded as paraphyletic taxa, representing two successive primitive evolutionary levels (grades) of sea turtles (Nessov, 1986, 1987; Parham and Fastovsky, 1997). The nomen Osteopyginae is regarded as a senior synonym of Macrobaenidae Sukhanov, 1964, i.e., does not belong to sea turtles (Parham, 2005). The crown group of Cheloniidae (=Cheloniidae sensu stricto) is considered to include all living members of the family and a number of extinct taxa from the Miocene and Pliocene (Laparent de Broin, 2001).

The specimens mentioned in the study are housed in the following institutions: (BMNH) Natural History Museum, London, Great Britain; (IRSNB) Musée de l’Institut royal des sciences naturelles de Belgique, Brussels, Belgium; (CCMGE) Chernyshev’s Central Museum of Geological Exploration St. Petersburg, Russia; (ZIN PH) Zoological Institute of the Russian Academy of Sciences, paleoherpetological collection, St. Petersburg, Russia.

For comparison, the data on the following taxa of Cheloniidae sensu lato are examined: “*Argillochelys*” *africana* Tong et Hirayama, 2008 (Tong and Hirayama, 2008; Danilov et al., 2010); *Argillochelys cuneiceps* Owen, 1849 (type species of *Argillochelys* Lydekker, 1889; Owen and Bell, 1849; photographs of the holotype BMNH, no. 41636 and specimen BMNH, no. 38952, provided by R. Hirayama); *A. antiqua* (König, 1825) (= *Chelone subcristata* Owen, 1849; Owen and Bell, 1849; Lydekker, 1889); and *Argillochelys* sp. a and b (Lydekker, 1889; photographs of specimens BMNH, nos. R1447a and R8681, provided by R. Hirayama); *Itilochelys rasstrigin* Danilov et al., 2010; species of the genus *Puppigerus* Cope, 1871: *P. camperi* Gray, 1831 (type species; Moody, 1974; Tong et al., 2012); *P. nessovi* Averianov, 2005 (Averianov, 2005; our examination of the type series of collection ZIN PH, no. 46); *Tasbacka aldabergeni* Nessov, 1987 (our examination of the holotype CCMGE, no. 1/12175).

SYSTEMATIC PALEONTOLOGY

Order Testudines

Family Cheloniidae Opper, 1811 sensu lato

Genus *Puppigerus* Cope, 1871

Puppigerus nessovi Averianov, 2005

Puppigerus nessovi: Averianov, 2005, p. 73, text-fig. 1, pls. VII, VIII; Chkhikvadze, 2010a, p. 100; Danilov et al., 2011, p. 400.

Puppigerus: Zvonok and Gorobets, 2012, p. 23.

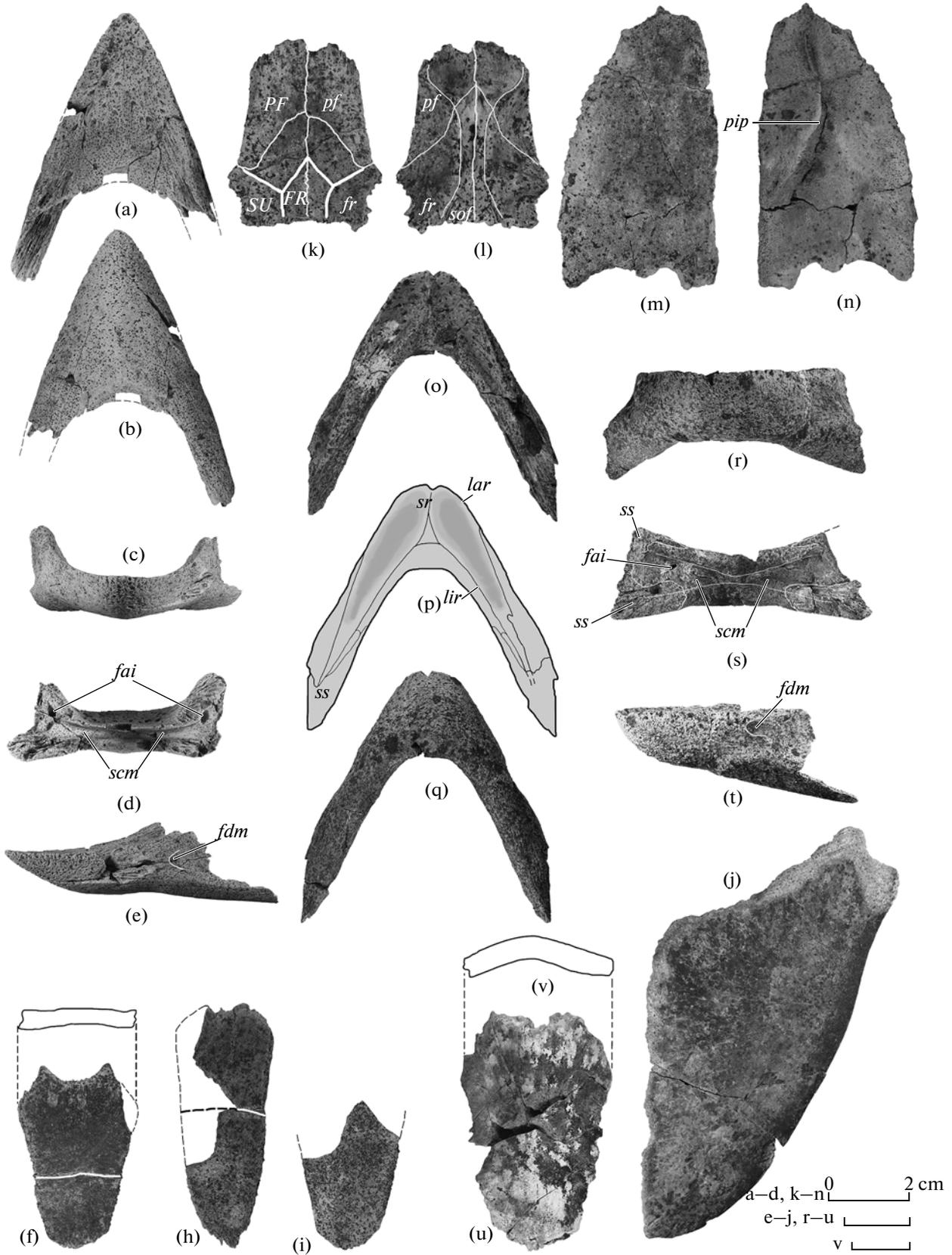
Puppigerus nessovi (junior synonym of *P. camperi*): Tong et al., 2012, p. 640.

Holotype. ZIN PH, no. 1/46, dentary fragment; Uzbekistan, central Kyzyl Kum, Navoi District, about 20 km north of the village of Muruntau, Dzheroi 2 locality; Middle Eocene, Lutetian–Bartonian, gray and yellow sand with phosphorites.

Description (Figs. 1a–1j). An almost complete symphysis of the dentaries (specimen ZIN PH, no. 9/145; Figs. 1a–1e); the posterior part of the right dentary is broken off. In dorsal view, the alveolar surface is triangular and pointed anteriorly; posteriorly, it is concave and passes farther than the line connecting the foramina dentofaciale majus. In the anterior part, the alveolar surface is almost flat, with many nutrient foramina; in the posterior part, it is concave without nutrient foramina. The symphyseal ridge is very poorly developed (hardly perceptible to the touch, but almost indiscernible by eye). Lingual ridges are absent. The lateral margins of the alveolar surface (labial ridges) are sharp, but raise above the alveolar surface only in its posterior part. The Meckel’s grooves are better visible in the posterior projection, because they are located almost entirely under an overhanging shelf of the alveolar surface, where they are fused. In addition, in posterior view, the foramina alveolaris inferior are seen, which are located slightly above the posterior part of the Meckel’s grooves. On the lateral side of the posterior part of the dentary, there is the foramen dentofaciale majus, which is followed by a semilunate depression. Medially and posteriorly, there are sutural surfaces for the coronoid and other mandibular bones.

Other dentaries (specimens ZIN PH, nos. 10–12/145) are smaller and similar in morphology to that described above, except for the fact that, in specimens ZIN PH, nos. 10/145 and 12/145, the alveolar surface

Fig. 1. *Puppigerus nessovi* (a–j) and *Argillochelys* sp. (k–v) from the Middle Eocene of the Ikovo locality (Ukraine): *Puppigerus nessovi*: (a–e) specimen ZIN PH, no. 9/145, dentary symphysis: (a) dorsal, (b) ventral, (c) lateral, (d) anterior, and (e) posterior views; (f, g) specimen ZIN PH, no. 13/145, neural plate III or V: (f) dorsal and (g) anterior views; (h) specimen ZIN PH, no. 15/145, odd neural plate fragment, dorsal view; (i) specimen ZIN PH, no. 14/145, even neural plate fragment, dorsal view; (j) specimen ZIN PH, no. 16/145, left xiphoplastron, ventral view. *Argillochelys* sp.: (k, l) specimen ZIN PH, no. 3/145, skull roof fragment, including the prefrontals and frontals: (k) dorsal and (l) ventral views; (m, n) specimen ZIN PH, no. 4/145, left parietal: (m) dorsal and (n) ventral views; (o–t) specimen ZIN PH, no. 5/145, dentary symphysis: (o) dorsal view, (p) the same, schematic drawing, (q) ventral, (r) anterior, (s) posterior, and (t) lateral views; (u, v) specimen ZIN PH, no. 8/145, neural plate II or IV: (u) dorsal and (v) anterior views. Designations: (*ch*) humeral head, (*fai*) foramen alveolare inferius, (*fas*) foramen alveolare superius, (*fdm*) foramen dentofaciale majus, (*fr*) frontal, (*FR*) frontal scute, (*fs*) foramen supramaxillare, (*it*) fossa intertubercularis, (*lar*) labial ridge, (*ld*) fossa for attachment of tendons of the latissimus dorsi and teres major muscles, (*lir*) lingual ridge, (*lp*) lateral process, (*mfi*) place for attachment of flexor tibialis internus muscle, (*mp*) medial process, (*mpt*) area for attachment of pubio-tibialis muscle, (*mx*) maxilla, (*orb*) orbit, (*pal*) palatine, (*pf*) prefrontal, (*PF*) prefrontal scute, (*pip*) processus inferior parietalis, (*pm*) premaxilla, (*scm*) Meckel’s sulcus, (*sof*) olfactory sulcus, (*sr*) symphyseal ridge, (*ss*) sutural surface, (*SU*) supraorbital scute, and (*vo*) vomer.



is shorter, does not reach the line connecting the foramina dentofaciale majus. In specimen ZIN PH, no. 11/145, the state of this character is uncertain, because it is strongly rounded.

The neural plates are represented by three specimens (ZIN PH, nos. 13–15/145; Figs. 1f–1i), all of which have a flat dorsal surface and lack a distinct sculpturing formed of fine grooves. Specimen ZIN PH, no. 13/145 is an almost complete hexagonal odd (III or V) neural plate, with short anterolateral sides; the intercentral sulcus crosses the plate in the posterior part. Specimen ZIN PH, no. 14/145 is a neural plate broken anteriorly, which was apparently identical in shape and size to the previous plate; it is an even plate (not crossed by the intercentral sulcus). Specimen ZIN PH, no. 15/145 is an odd neural plate broken off on the left side; it is very long, hexagonal, with short anterolateral sides; the intercentral sulcus crosses it in the middle.

Two xiphiplastra are distinguished by the size: large (specimen ZIN PH, no. 16/145) and small (specimen ZIN PH, no. 17/145). Other structural features are identical. The xiphiplastron (specimen ZIN PH, no. 16/145; Fig. 1j) is relatively wide (the ratio of the xiphiplastron width measured at the level of the lateral end of the hypo-xiphiplastron suture perpendicular to the medial margin of the xiphiplastron to the length of its medial margin is about 0.70). The anterior margin of the xiphiplastron, which corresponds to the suture with the hypoplastron, is directed anteromedially by its larger (medial) part and slightly concave; in the lateral part, it forms a spine, which enters respective incisure in the hypoplastron, and, then, an incisure for respective spine of the hypoplastron. The lateral margin of the hypoplastron is slightly anteriorly concave and, then, curves gently posteriorly to pass into the medial margin. Scale sulci and surface sculpturing of the xiphiplastron are absent.

M e a s u r e m e n t s in mm and ratios. Length of the alveolar surface of the dentaries along the midline: ca. 13 (specimen ZIN PH, no. 10/145); 18.5 (ZIN PH, no. 12/145); 32 (specimen ZIN PH, no. 11/145); 42 (specimen ZIN PH, no. 9/145); neural plates: length, 46; width-to-length ratio, 0.65; thickness in the middle of the lateral margin, 4.5 (specimen ZIN PH, no. 13/145); length, ca. 63; width-to-length ratio, 0.55; thickness in the middle of the lateral margin, 6.1 (specimen ZIN PH, no. 15/145); length of xiphiplastron along the midline: 39 (specimen ZIN PH, no. 17/145) and 104 (specimen ZIN PH, no. 16/145).

R e m a r k s. Among the specimens in question, only dentary symphyses are assigned with certainty to *Puppigerus nessovi*; of them, specimen ZIN PH, no. 9/145 corresponds to the diagnosis of this species (the alveolar surface is positioned close to the level of the foramen dentofaciale majus). Smaller symphyses have a shorter alveolar surface, suggesting variability of this character (see Discussion). The neural plates are tentatively referred to this species, based only on the

similarity to the plates of Cheloniidae sensu lato and differences from the neural element referred above to *Argillochelys* sp. in the flatness and the absence of well-pronounced surface sculpturing of fine grooves. The thickness of the neural plates approximately corresponds to that of the even neural plate of the same size of *Puppigerus nessovi* from the Middle Eocene of Uzbekistan (specimen ZIN PH, no. 9/46: 46.8 mm long and 5.9 mm thick in the middle of the lateral margin). The xiphiplastra studied are also similar in proportions to that of *Puppigerus*, while xiphiplastra of *Argillochelys* are narrower (see Owen and Bell, 1849, pl. VIII, fig. 1).

O c c u r r e n c e. Lower Lutetian of Ukraine, Lutetian–Bartonian of Uzbekistan.

M a t e r i a l. Specimens ZIN PH, nos. 9/145 and 10/145, two almost complete dentary symphyses; specimen ZIN PH, no. 11/145, a strongly rounded symphysis; and specimen ZIN PH, no. 12/145, right half of a symphysis; specimen ZIN PH, no. 13/145, neural plate III or V; specimen ZIN PH, no. 14/145, an even neural plate fragment; specimen ZIN PH, no. 15/145, an odd neural plate fragment; specimens ZIN PH, nos. 16/145 and 17/145, two left xiphiplastra; Ukraine, Lugansk Region, Ikovo locality; Middle Eocene, Lower Lutetian.

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***Argillochelys* sp.** The material of *Argillochelys* sp. (Figs. 1k–1v) includes the following elements: specimen ZIN PH, no. 3/145, a skull roof fragment, including both prefrontals and both frontals; specimen ZIN PH, no. 4/145, a left parietal; specimens ZIN PH, nos. 5/145 and 6/145, dentary symphyses; specimen ZIN PH, no. 7/145, a right dentary; specimen ZIN PH, no. 8/145, neural plate II or IV.

The skull roof fragment including both prefrontals and both frontals (specimen ZIN PH, no. 3/145; Figs. 1k, 1l) is 46 mm long along the midline (extent of the suture between the prefrontals and frontals). The prefrontals are elongated, slightly posteriorly widened. Anteriorly, they formed the upper border of the nares; anterolaterally, they came in short contact with the maxillae and, laterally, formed the anterior parts of the upper orbital border. The extent of contact of the prefrontals along the midline is about half of the maximum length. Posteromedially, the prefrontals adjoined the frontals and did not reach the postorbitals posteriorly. The descending processes of the prefrontals are broken off. In dorsal view, the frontals form a pentagonal pattern. Anteriorly, they adjoin the prefrontals, relatively strongly wedging in between them; anterolaterally, they form a short piece of the orbital border; posterolaterally, they adjoin the postorbitals; and posteriorly, they form a straight transverse suture with the parietals. From below, the frontals form the parasagittal ridges bordering the sulcus olfactorius. The dorsal surface of the fragment described has distinct sulci of

the following horny scutes: the anterior part of the frontal scute (apparently hexagonal) was located in the center of the skull roof in the posterior part of the frontals; lateral to the frontal scute, there were supraorbital scutes, which covered the posterolateral parts of the frontals and adjacent bones (parietals and postorbitals); anterior and lateral to the frontal scute, there were two prefrontal scutes, the anterior borders of which are indiscernible; the sulcus between the prefrontal and supraorbital scutes adjoins or crosses the posterior part of the prefrontal.

The parietal (specimen ZIN PH, no. 4/145; Figs. 1m, 1n) is long (65.5 mm long along the midline; the length to maximum width ratio is about 1.6), posteriorly widened (the posterior margin is approximately twice as wide as the anterior margin). Medially, it adjoined its counterpart; anteriorly, anterolaterally, and posterolaterally, it was bounded by the frontal, postorbital, and squamosal, respectively. Sutural surfaces for these bones are distinctly separated from each other. The anterior margin of the parietal (adjoining the frontal) is convex. The lateral margin (adjoining the postorbital and squamosal) is also convex and lacks a sharp bend at contact of the postorbital and squamosal. The posterior margin of the parietal has two small incisions. The lower surface of the parietal, has a descending process (processus inferior parietalis), ventral parts of which are broken off; lateral to this process, anterior one-third of the bone has a weak transverse ridge passing onto the postorbital. Scale sulci on the dorsal surface of the parietal are indiscernible.

The dentary symphysis (specimen ZIN PH, no. 5/145; Figs. 1o–1t) has a relatively short alveolar surface in the symphyseal region (21 mm long), which terminates far from reaching the line connecting the foramina dentofaciale majus; the symphyseal ridge is high and sharp; lingual ridges are present; the alveolar surface between the symphyseal, lingual, and labial ridges is concave. In lateral view, the posterior margin of the dentary (completely preserved on the left side) is rounded in the upper part (approximately at the level of the coronoid process) and forms a pointed, strongly posteriorly projecting process in the lower part. Posterior to the foramen dentofaciale majus, there is a superficial depression, below which the dentary is somewhat thickened and forms a longitudinal stiffening plate. On the medial side of the dentary, the Meckel's groove, foramen alveolare inferius, and sutural surfaces for the coronoid, surangular, angular, and, probably, prearticular are visible. Other mandibular fragments (specimens ZIN PH, nos. 6/145 and 7/145) are in general similar in morphology to specimen ZIN PH, no. 5/145.

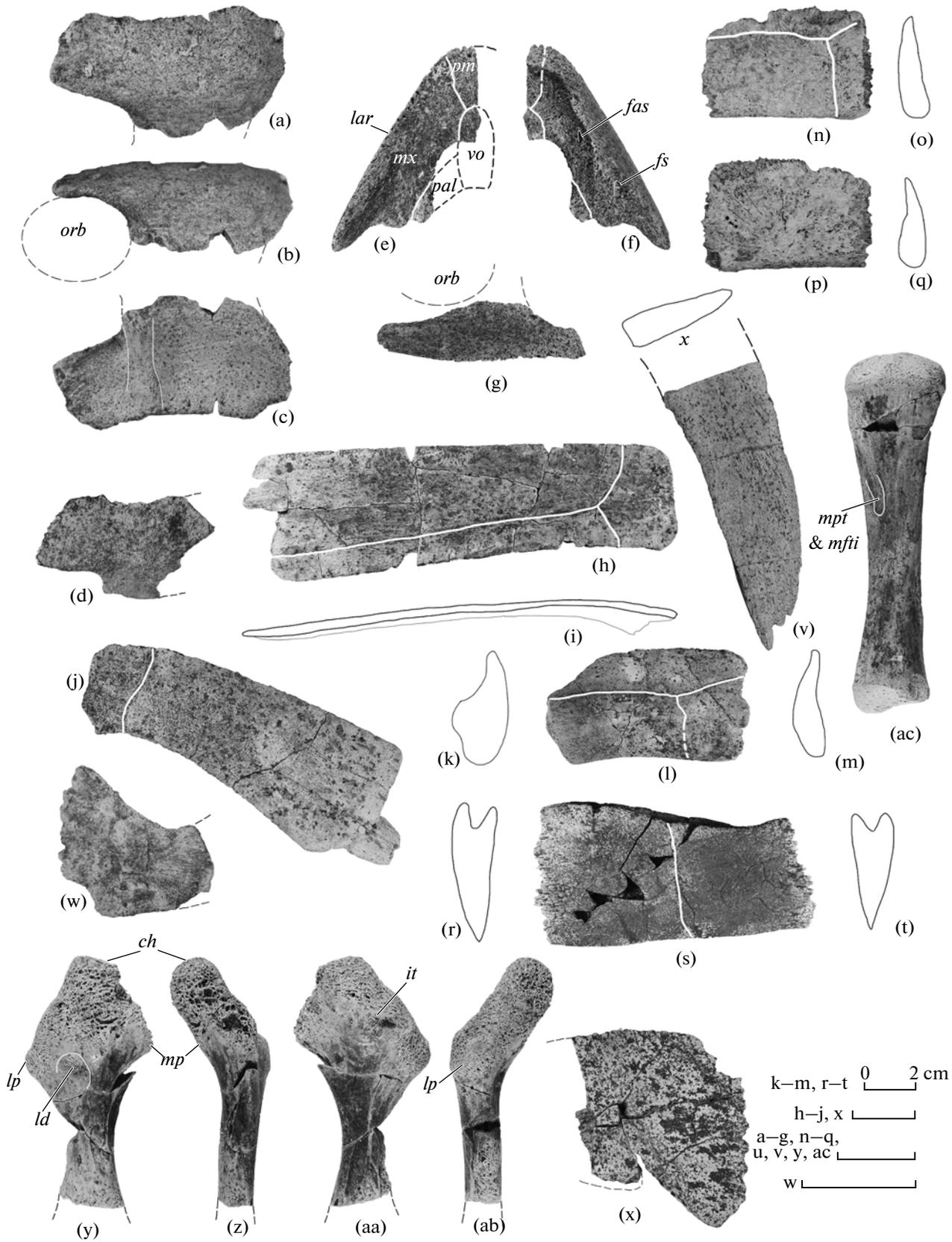
Neural plate II or IV (specimen ZIN PH, no. 8/145; Figs. 1u, 1v) is large (73.5 mm long), hexagonal, with short anterolateral sides, relatively long (the width-to-length ratio is about 0.70), convex in cross section. The dorsal surface of the plate is covered

with variously directed grooves (probably, for blood vessels); the plate is not crossed by a scale sulcus.

Among the specimens described, the dentary symphyses undoubtedly belong to the genus *Argillochelys*, since they are typical in morphology of this genus (a relatively short and concave alveolar surface, the presence of symphyseal and lingual ridges). Of *Argillochelys* species (forms), the specimens in question are most similar to *Argillochelys* spp. a and b (Lydekker, 1889), which differ from typical members of this genus in the shorter mandibular symphysis and the more strongly developed symphyseal and lingual ridges (Moody, 1980). The skull roof fragment is also similar to that of members of the genus *Argillochelys* (excluding "*A. africana*") in the proportions and contacts of the prefrontals and frontals, and position of scale sulci. However, there are differences from typical *Argillochelys* (*A. cuneiceps*) in the relatively longer connection of the prefrontals along the midline. The difference from "*A. africana*" is in the frontals not separated from the orbital border. The differences from members of the genus *Puppigerus* include the shorter connection between the prefrontals and maxillae, the wider prefrontals in the anterior part, and in the close positions of the posterior margin of the prefrontal and the sulcus between the prefrontal and supraorbital scutes. The parietal also corresponds in structure to members of the genus *Argillochelys*; the differences from *Puppigerus* include the relatively longer parietal, the wider posterior margin of this bone, and the absence of a sharp bend of the lateral margin of the parietal at contact between the postorbital and squamosal. The assignment of the neural plate to *Argillochelys* (instead of *Puppigerus*) is based on the convexity and presence of deep grooves on its external surface (in *Puppigerus*, the neural plates are flat and their surface sculpturing composed of grooves is weaker or absent).

Cheloniidae gen. indet. The material of Cheloniidae gen. indet. (Fig. 2) includes the following elements: specimens ZIN PH, nos. 18/145 and 19/145, two postorbitals; specimen ZIN PH, no. 20/145, fragmentary right half of upper jaw; specimen ZIN PH, no. 21/145, costal plate IV; specimen ZIN PH, no. 22/145, costal plate VII; specimens ZIN PH, nos. 23–27/145, fragments of five costal plates; specimen ZIN PH, no. 28/145, right peripheral plate II (?); specimen ZIN PH, no. 29/145, left peripheral plate II (?); specimen ZIN PH, no. 30/145, peripheral plate VI or VII; specimen ZIN PH, no. 31/145, posterior part of left epiplastron; specimen ZIN PH, no. 32/145, medial part of left hyoplastron; specimen ZIN PH, no. 33/145, medial part of right hyoplastron; specimen ZIN PH, no. 34/145, proximal part of left humerus; specimens ZIN PH, nos. 35/145 and 36/145, two right tibiae.

The postorbitals vary in size and preservation (Figs. 2a–2d): specimen ZIN PH, no. 18/145, relatively large postorbital with a broken off lateral margin;



specimen ZIN PH, no. 19/145, relatively small postorbital with a broken off posterior part. The anterior margin of the postorbital (adjoining the frontal) is relatively wide (relatively wider than respective margin of the frontal of *Argillochelys* sp. described above), oriented anteromedially; the anterolateral margin forms the posteroinferior orbital border; anteroventral process is absent; the lateral margin (partially preserved in specimen ZIN PH, no. 19/145) came in contact with the jugal; the medial margin of the postorbital (adjoining the parietal) is slightly concave; it is followed by a short posteromedial margin apparently for contact with the squamosal; the posterior margin (preserved in specimen ZIN PH, no. 18/145) is convex, adjoined the squamosal. The internal surface of the postorbital has a relatively high transverse ridge extending from the parietal downwards onto the jugal. Scale sulci on the dorsal surface of the parietal are indiscernible.

The fragment of the right part of the upper jaw (specimen ZIN PH, no. 20/145; Figs. 2e–2g) is a large part of the maxilla (with the broken off and rounded prefrontal process, orbital border, and the contact area for the jugal), premaxilla, and vomer and palatine fragments. The anterolateral border of the nares, which faced anterodorsally, is preserved anteriorly. The labial ridge is absent in the anteriormost part of the upper jaw; posteriorly, it becomes sharp and high. The alveolar surface is formed by the premaxilla, maxilla, vomer, and palatine. The prepalatal foramen between the premaxilla and vomer is absent. Between the vomer and palatine, the medial margin of the alveolar surface is cut, so that these bones do not come in contact. This incisure apparently appeared as a result of disruption (rounding) of the fragment. The part of the alveolar surface located medial to the labial ridge is rather flat; the vomer lacks a medial sulcus and bulge lateral to it. On the dorsal surface of the maxilla, there is the foramen alveolare superius in the anterior part and foramen supramaxillare in the posterior part.

Among the costal plates, there are two complete or almost complete bones (Figs. 2h–2j): costal plate IV (specimen ZIN PH, no. 21/145) and costal plate VII (specimen ZIN PH, no. 22/145). Specimen ZIN PH, no. 21/145 is large (147 mm wide along the anterior margin), its lateral margin is slightly wider than the medial margin, apparently lacks a sutural surface, suggesting that the costoperipheral fontanelles were pre-

served; the free rib is broken off, however, it is evident that it extended in the middle of the lateral margin; the anterior and posterior plate margins are almost straight. In anterior view, the plate is relatively thin (in the middle of the anterior margin, it is 3 mm thick, that is, approximately half as thick as the smaller odd plate of *Puppigerus nessovi*, specimen ZIN PH, no. 12/46), almost straight, and only slightly curved in the proximal part. The central scute (III) was relatively narrow and covered at most 20% of the plate width. The sulcus between the pleural scutes (II and III) is positioned closer to the posterior margin of the plate, even closer approaching it distally. Specimen ZIN PH, no. 22/145 is smaller (about 90 mm wide), curved posteriorly (the anterior margin is slightly convex and the posterior margin is distinctly concave), widened relatively strongly distally, as thin as specimen ZIN PH, no. 21/145. The lateral margin is smooth, lacks a sutural surface; its posterior half has a free rib. Central scute IV is narrow, covered about 15% of the plate width; its lateral sulcus is S-shaped. Surface sculpturing of costal plates (presence–absence of grooves) is uncertain. The carapace reconstructed based on the fragments described above was at least 400 mm long. In addition, the collection includes fragments of five more costal plates (specimens ZIN PH, nos. 23–27/145), four of which belonged to smaller individuals.

Specimen ZIN PH, no. 28/145 (Figs. 2k–2m) is apparently peripheral plate II. The plate is about 70 mm long along the free margin; the ratio of the maximum width to length is 0.69. The anterior and posterior sutural surfaces are probably preserved, although both are damaged. The free (lateral) margin is rounded in section. The medial margin has a partially preserved sutural surface (for contact with costal plate I) and lacks a fossa for a free rib. The internal plate surface is only partially preserved; close to the middle of its posterior part, there is a stiffening plate which becomes thicker towards the posterior plate margin. The pleuromarginal sulcus is positioned closer to the medial margin and the intermarginal sulcus is in the anterior half of the plate. The surface lacks distinct surface sculpturing.

Specimen ZIN PH, no. 29/145 (Figs. 2n–2q) is probably also peripheral plate II, but it is considerably smaller, 40.5 mm long along the free margin; the maximum width to length ratio is 0.68; anteriorly, it is

Fig. 2. Cheloniidae gen. indet. from the Middle Eocene of the Ikovo locality (Ukraine): (a–c) specimen ZIN PH, no. 18/145, left postorbital: (a) dorsal, (b) lateral, and (c) ventral views; (d) specimen ZIN PH, no. 119/145, left postorbital, dorsal view; (e–g) specimen ZIN PH, no. 20/145, fragment of right half of upper jaw: (e) ventral, (f) dorsal, and (g) lateral views; (h, i) specimen ZIN PH, no. 21/145, left costal plate IV: (h) dorsal and (i) posterior views; (j) specimen ZIN PH, no. 22/145, right costal plate VII, dorsal view; (k–m) specimen ZIN PH, no. 28/145, right peripheral plate II (?): (k) posterior, (l) dorsal, and (m) anterior views; (n–q) specimen ZIN PH, no. 29/145, left peripheral plate II (?): (n) dorsal, (o) posterior, (p) ventral, and (q) anterior views; (r–t) specimen ZIN PH, no. 30/145, peripheral plate VI or VII: (r) posterior, (s) dorsal, and (t) anterior views; (u, v) specimen ZIN PH, no. 31/145, posterior part of left epiplastron: (u) cross section and (v) ventral view; (w) specimen ZIN PH, no. 32/145, medial part of left hyoplastron, ventral view; (x) specimen ZIN PH, no. 33/145, medial part of right hypoplastron, ventral view; (y–ab) specimen ZIN PH, no. 34/145, proximal part of left humerus: (y) dorsal, (z) posterior, (aa) ventral, and (ab) anterior views; (ac) specimen ZIN PH, no. 36/145, right tibia, ventral view. For designations, see Fig. 1.

slightly narrower than posteriorly. The plate is teardrop-shaped, with a rounded free margin in cross section. The medial plate margin has a sutural surface, without a notch for a free rib. The internal surface lacks a stiffening plate. The sulcus between the marginal scutes is positioned near the posterior plate margin and the pleuromarginal sulcus extends along its medial margin. The plate surface lacks distinct surface sculpturing.

Peripheral plate VI or VII (specimen ZIN PH, no. 30/145; Figs. 2r–2t) is also large (105 mm long along the free margin), relatively long and narrow, widened somewhat posteriorly. Medially, the plate is split into the dorsal and ventral parts, with a relatively deep sulcus between them. In the anterior quarter of the plate, this sulcus contains a fossa for a free rib. The medial plate margins are smooth, without sutural surfaces, suggesting that the costoperipheral fontanelles were preserved. The plate is wedge-shaped in cross section, with a sharp free margin. The scale sulci between the marginal scutes cross the plate approximately in the middle; a trace of the pleuromarginal sulci is absent. In places, the dorsal and ventral plate surfaces have sculpturing of a net of fine superficial grooves.

The posterior part of the epiplastron (specimen ZIN PH, no. 31/145; Figs. 2u, 2v) is wide anteriorly and gradually narrows posteriorly. The epiplastron is wedge-shaped in cross section, pointed towards the lateral margin. The medial epiplastron margin forms a sutural surface for the hyoplastron.

The medial part of the left hyoplastron (specimen ZIN PH, no. 32/145; Fig. 2w) belonged to a small individual (the maximum plate length is 27 mm). Anteriorly, the medial margin has typical toothlike processes for articulation with the entoplastron and other hyoplastron; posteriorly, it formed the border of the central fontanelle of the plastron. In the region of the bridge, the hyoplastron is 14 mm long. The external plate surface shows traces of erosion.

The medial part of the right hypoplastron (specimen ZIN PH, no. 33/145; Fig. 2x) belonged to a larger individual (the maximum plate length is 71 mm). The medial hypoplastron margin formed anteriorly the border of the central fontanelle, posterior to which it was articulated with the other hypoplastron through toothlike processes. The posterior-most part of the medial hypoplastron margin apparently participated in the formation of the hypoxiphial fontanelle. The posteromedial lobe of the hypoplastron for articulation with the xiphial plastron is relatively long.

The humerus (specimen ZIN PH, no. 34/145; Figs. 2y–2ab) lacks the distal part; the surfaces of the proximal epiphysis (head and processes) are rounded; the reconstructed bone is 80–90 mm long. The preserved part of the diaphysis is straight and relatively narrow. The angle α is 150° ; the angle β is impossible to measure, because the humeral head is strongly rounded. The lateral process is displaced distally, its

shape remains uncertain because of poor preservation. At the level of the lateral process, the dorsal bone surface has a large oval fossa for the joint tendon of the latissimus dorsi and teres major muscles. The ventral side has an extensive intercondylar fossa, which contains a circular depression at the lateral process.

The tibiae differ somewhat in size (Fig. 2ac): specimen ZIN PH, no. 35/145 is 100.7 mm long and specimen ZIN PH, no. 36/145 is 91.8 mm long. On the assumption that the proportions of the tibiae in the sea turtles in question were the same as in other Cheloniidae sensu lato (see Zangerl, 1953), the carapace of turtles that possessed these tibiae was within 700–750 mm long. The proximal epiphysis of both specimens, closer to the ventromedial side, has a distinct circular concave area. The medial part of the distal epiphysis has a projection. On the ventromedial bone side, close to its middle, but closer to the proximal margin, there is an elongated fossa for attachment of the flexor tibialis internus and pubio-tibialis muscles.

The material described is determined as Cheloniidae gen. indet., because it is impossible to assign it with certainty to *Argillochelys*, *Puppigerus*, or other primitive Cheloniidae. This is caused not only by poor preservation of particular bones, but also by the fact that distinctions between genera of primitive Cheloniidae in the structure of some bones under study are either absent or unknown. The postorbitals differ from that of *Argillochelys* and *Puppigerus* in the relatively wider anterior margin (for connection with the frontals); in addition, the differences from *Argillochelys*, *Itiochelys*, and *Tasbacka* include the absence of the anteroventral process. The assignment of the upper jaw fragment to Cheloniidae is based on the participation of the vomer and palatine in the formation of the alveolar surface and the absence of a prepalatal foramen. The absence in this fragment of another distinctive feature (synapomorphy) of Cheloniidae, i.e., contact of the vomer with the palatine in the choanal border apparently results from destruction (it is strongly rounded). This fragment differs from *Argillochelys* in the absence of the medial sulcus on the vomer and bulge lateral to this sulcus; it differs from *Puppigerus* in the less extended and anteriorly narrower alveolar surface of the upper jaw. The humeral structure corresponds to the cheloniid level (Hirayama, 1992) and is similar to that described for *Puppigerus nessoivi* (Averianov, 2005, pl. VII, fig. 9), except for the fact that specimen ZIN PH, no. 34/145 belonged to a larger individual and its diaphysis more strongly narrows in the middle part. The humerus of *P. camperi* (Moody, 1974, pl. 5D) has a diaphysis narrowing to approximately the same extent as in specimen ZIN PH, no. 34/145. The humeral structure in species of the genus *Argillochelys* is not known. The tibiae described above are typical in structure for many Cheloniidae sensu lato (Zangerl, 1980, text-fig. 10; Zangerl et al., 1988, text-fig. 26).

DISCUSSION

The specimens described above expand our knowledge of the distribution of primitive sea turtles. In particular, the genus *Argillochelys* has previously been known from the Lower and Middle Eocene of Great Britain and the Lower Eocene of Morocco (Tong and Hirayama, 2008), although the assignment of the Moroccan species ("*A.*" *africana*) to this genus is questionable (Danilov et al., 2010). Certain undescribed materials have also been recorded in the same period in Belgium and Holland (Lapparent de Broin, 2001) and in the Middle–Upper Eocene of Kazakhstan (Mangyshlak: Zvonok et al., 2011).

Reliable members of the genus *Puppigerus* have previously been recorded in the Eocene of Great Britain and Belgium, Early Eocene of Morocco, and Middle Eocene of Uzbekistan (Moody, 1974; Averianov, 2005; Tong et al., 2012). A sea turtle from the Middle Eocene of Ukraine (Vyshgorod) which was initially identified as *Puppigerus* sp. (Chkhikvadze, 1983) was subsequently referred to a different sea turtle taxon, *Dollochelys rogovichi* Averianov, 2002 (Averianov, 2002). However, Hirayama (2006) takes the last for nomen dubium, because the material referred to this species is impossible to determine more closely than the superfamily Chelonioidae. The materials from the Kamchatka Peninsula (Russia), initially referred to as *Puppigerus* sp. (Chkhikvadze, 1984), are also presently identified as Chelonioidae indet. (Averianov, 2002). Thus, *Puppigerus* from Ikovo, like *Argillochelys*, is the first reliable record of this genus in Ukraine and Eastern Europe as a whole. It is presently referred to as *P. nessovi* based on one character, the relative length of the mandibular symphysis; thus, it certainly requires additional evidence, as well as the independence of this species described based on fragmentary material. The point of view that *P. nessovi* is a synonym of *P. camperi* (Tong et al., 2012) also requires additional data. Possibly, some specimens from the Dzheroi 2 locality (Uzbekistan; type locality of *P. nessovi*) belong to a different sea turtle taxon. In particular, the humerus from Dzheroi 2 is distinguished from that of *P. camperi* (and the humerus from Ikovo) by the less narrowing diaphysis. At the same time, the extent of diaphysis narrowing is regarded as an essential character determining the evolutionary level of sea turtles (Hirayama, 1992). In addition, two sea turtle taxa were initially reported from the Dzheroi 2 locality: Eochelyinae and cf. Syllomiinae (Nessov, 1988). Subsequently, Eochelyinae was described as *P. nessovi* and identification of Syllomiinae, which is represented by sculptured plate fragments, was regarded as doubtful (Averianov, 2005). We believe that the material of "Syllomiinae" requires additional studying.

Puppigerus nessovi from Ikovo shows size (age) variation, manifested in the length of the alveolar surface of the lower jaw; in smaller (younger) individuals, the alveolar surface is shorter than in larger forms

(adults) (see also Zvonok and Gorobets, 2012). We observed the same variability in *P. nessovi* from Dzheroi 2: in the smaller fragment of the dentary symphysis (specimen ZIN PH, no. 4/46), the alveolar surface is shorter than in the larger fragment (specimen ZIN PH, no. 1/46). The data on variability of this character in *P. camperi* have not been reported (Moody, 1974).

The material examined has shown the maximum individual size (the length of the skull and carapace) of sea turtles from Ikovo in comparison with the data on *Argillochelys cuneiceps* and *Puppigerus camperi* (the sign "*" designates reconstructed parameters and the number of specimens, which provided the measurements or estimates, are given in parentheses): skull length from below: *Argillochelys* sp. (specimen ZIN PH, no. 3/145), about 120* mm; *A. cuneiceps* (specimen BMNH, no. 41636), 91 mm; *P. nessovi* (specimen ZIN PH, no. 9/145), about 80* mm; *P. camperi* (specimen IRSNB, no. R.16), 92 mm; carapace length: *Argillochelys* sp. (specimen ZIN PH, no. 8/145), about 700* mm; *A. cuneiceps* (specimen BMNH, no. 38952), about 260* mm; *P. nessovi* (specimen ZIN PH, no. 16/145), 700–750* mm; *P. camperi* (specimen IRSNB, no. R.13), about 470* mm. The estimates of the same parameters in Cheloniidae gen. indet. from Ikovo do not exceed the above values. Thus, if the carapace specimens described above are identified correctly, *Argillochelys* sp. and *P. nessovi* were considerably larger than *A. cuneiceps* and *P. camperi*.

A comparison of the turtle assemblage from Ikovo with approximately contemporaneous to turtle assemblages from Eurasia shows that it is most similar to assemblages from Belgium and Great Britain (Lapparent de Broin, 2001). In Great Britain, these are assemblages from the London Clay (Ypresian), Barton Cliff (Bartonian), and Bracklesham Beds (Lower–Middle Eocene) (Benton and Spencer, 1995). The three assemblages include sea turtles of the genera *Argillochelys* and *Puppigerus* and soft-shelled turtles; and the first and second assemblages include the sea turtle genus *Eochelone*. In addition, the London Clay assemblage includes members of Testudinoidea, a group that was also recorded in Ikovo (see above). The fact that the above Great Britain assemblages include some other turtle groups [for example, London Clay has yielded at least one species of side-necked turtles (*Pelomedusoides incertae sedis*: Gaffney et al., 2006, pp. 109–110), two more genera of Cheloniidae, one species of Dermochelyidae, one species of Caretochelyidae, and two taxa of uncertain taxonomic position: Benton and Spencer, 1995] suggests that some new turtle taxa may be found in Ikovo.

The similarity to the Dzheroi 2 assemblage is presently based on one shared element (*Puppigerus nessovi*), although it is possible to expect some other shared groups (one more sea turtle taxon and certain Testudinoidea: Averianov, 2005).

According to the modern concept, *Argillochelys* was the only Paleogene turtle with the “cutting” jaw apparatus, that is, having well-developed ridges on the alveolar surfaces of jaws (Parham and Pyenson, 2010). A similar strongly specialized structure of the jaw apparatus is known among extant sea turtles, such as *Chelonia mydas* Linnaeus, 1758 and is correlated with the herbivorous diet (feeding on algae).

The diet of *Puppigerus* is not known (Moody, 1974). However, the long and flat alveolar jaw surfaces suggest that these turtles were durophagous, i.e., fed on certain firm (armored) invertebrates (Parham and Pyenson, 2010). The strongly elongated and narrowed jaws and weak downward curvature of the upper jaw tip (see Moody, 1974, text-fig. 4) suggest a peculiar specialization, for example, more selective and precise picking up (smaller) food objects.

ACKNOWLEDGMENTS

We are grateful to R. Hirayama (Waseda University, Tokyo, Japan) for providing us with photographs of specimens of the genus *Argillochelys* from the BMNH collection and for valuable advice.

This study was supported by the Program of the President of the Russian Federation for Support of Leading Scientific Schools (NSh-6560.2012.4).

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Translated by G. Rautian