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A NEW SPECIES OF SOFT-SHELLED TURTLE (TRIONYCHIDAE) FROM THE MIDDLE EOCENE OF UKRAINE

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ABSTRACT

Trionyx ikoviensis sp. nov., a new species of soft-shelled turtles (Trionychidae: Trionychinae), is established based on a partial but well preserved skull, isolated shell bones and cervical vertebrae VII and VIII from the Middle Eocene (Early Lutetian) Ikovo locality in the Luhansk Province of Ukraine. *Trionyx ikoviensis* cannot be assigned to any modern group within Trionychinae, but demonstrates most similarities with Trionychini (sensu Meylan 1987). Among fossil forms, *T. ikoviensis* is most similar to species of the genus *Rafetoides* and/or to some species of *Trionyx* sensu lato (sensu Lapparent de Broin 2001) from Europe with middle-sized carapace and long and wide jaws and snout, especially to *Trionyx michauxi* from the Lower Eocene of France. Although the taxonomic status and phylogenetic position of both *Rafetoides* and *Trionyx* sensu lato (sensu Lapparent de Broin 2001) need additional study, the latter assignment seems to be better corroborated. *Trionyx ikoviensis* is the easternmost representative of *Trionyx* sensu lato (sensu Lapparent de Broin 2001). *Trionyx ikoviensis* furthermore represents the first discovery of a trionychid skull in the Cenozoic deposits of the Ukraine in particular and the best discovery of this kind from the Cenozoic of the former USSR in general.

Key words: Middle Eocene, systematics, Trionychidae, turtles, Ukraine

НОВЫЙ ВИД ТРЕХКОГОТНОЙ ЧЕРЕПАХИ (TRIONYCHIDAE) ИЗ СРЕДНЕГО ЭОЦЕНА УКРАИНЫ

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РЕЗЮМЕ

Trionyx ikoviensis sp. nov., новый вид трехкоготных черепах (Trionychidae: Trionychinae), установлен на основе неполного, но хорошо сохранившегося черепа, изолированных костей панциря и VII и VIII шейных позвонков из среднего эоцена (ранний лютет) местонахождения Иково в Луганской области Украины. *Trionyx ikoviensis* не может быть отнесен ни к одной современной группе среди Trionychinae, хотя и демонстрирует наибольшее сходство с Trionychini (sensu Meylan 1987). Среди ископаемых форм *T. ikoviensis* наиболее похож на виды рода *Rafetoides* и/или некоторые виды *Trionyx* sensu lato (sensu Lapparent de Broin 2001) из Европы с карапаксом средних размеров и длинными и широкими челюстями и мордой, особенно с *Trionyx michauxi* из нижнего

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эоцена Франции. Хотя таксономический статус и филогенетическое положение *Rafetoides* и *Trionyx* sensu lato требуют дополнительного изучения, отнесение *T. ikoviensis* в состав *Trionyx* sensu lato (sensu Lapparent de Broin 2001) кажется лучше обоснованным. *Trionyx ikoviensis* – наиболее восточный представитель этой группы трионихид. Кроме того, *Trionyx ikoviensis* представляет первую находку черепа трионихида в кайнозойских отложениях Украины и лучшую подобную находку для кайнозоя бывшего СССР в целом.

Ключевые слова: средний эоцен, систематика, Trionychidae, черепахи, Украина

INTRODUCTION

Paleogene turtles from Eastern Europe (herein defined as the European portion of the former USSR) are poorly studied. Most of the Paleogene turtle material known from this territory are very fragmentary and belong to sea turtles (Chelonioidea Oppel, 1811; see Averianov 2002; Danilov et al. 2010). Fragmentary material of other turtle groups (trionychids and several undetermined forms) comes from the Paleocene of the Volgograd Province of Russia (Averianov and Yarkov 2000, 2004). Recently, a new locality of Paleogene vertebrates, including a relatively rich assemblage of turtles, was discovered in the Ukraine (Fig. 1; Zvonok et al. 2010; in press). This locality, called Ikovo (= Osinovo; 49°52′82′′N, 39°7′30′′E), is located near Osinovo Village, Novopskov District, Luhansk Province and its age is considered to be early Lutetian, Middle Eocene (see Udovichenko 2009). Zvonok et al. (2010) reported the presence of Trionychidae indet. and *Argillochelys* sp. (Cheloniidae Oppel, 1811 sensu lato) from this locality. Later, Zvonok et al. (in press) described the remains of Cheloniidae (*Argillochelys* sp., *Puppigerus nessovi* Averianov, 2005 and Cheloniidae indet.) and reported the presence of remains of Testudinoidea indet. Thus, the assemblage of Ikovo contains at least four turtle taxa. Other vertebrates from the Ikovo assemblage include fishes, a crocodile, and birds (Udovichenko 2009; Zvonok and Skutschas 2011; Mayr and Zvonok 2011).

This paper is devoted to the description of the trionychid material from this locality. The material is referred to a new species – *Trionyx ikoviensis*. This material is remarkable in that it includes, besides other elements, a partial, but well preserved skull, which makes a detailed description possible, although only few other species of fossil trionychids are known from cranial material. *Trionyx ikoviensis* represents the first discovery of a trionychid skull in the Cenozoic deposits of the Ukraine in particular and the best discovery of this kind from the Cenozoic of the former USSR in general (see Kordikova 1994a, b).

Fig. 1. Map showing the Ikovo locality.

The anatomical terms follow Gaffney (1979) for the skull, Zangerl (1969) for the shell, and Meylan (1987) for non-shell postcrania.

Institutional abbreviations. MNHN, Muséum national d'Histoire naturelle, Paris, France; ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

SYSTEMATICS

Trionychidae Gray, 1825

Trionychinae Gray, 1825

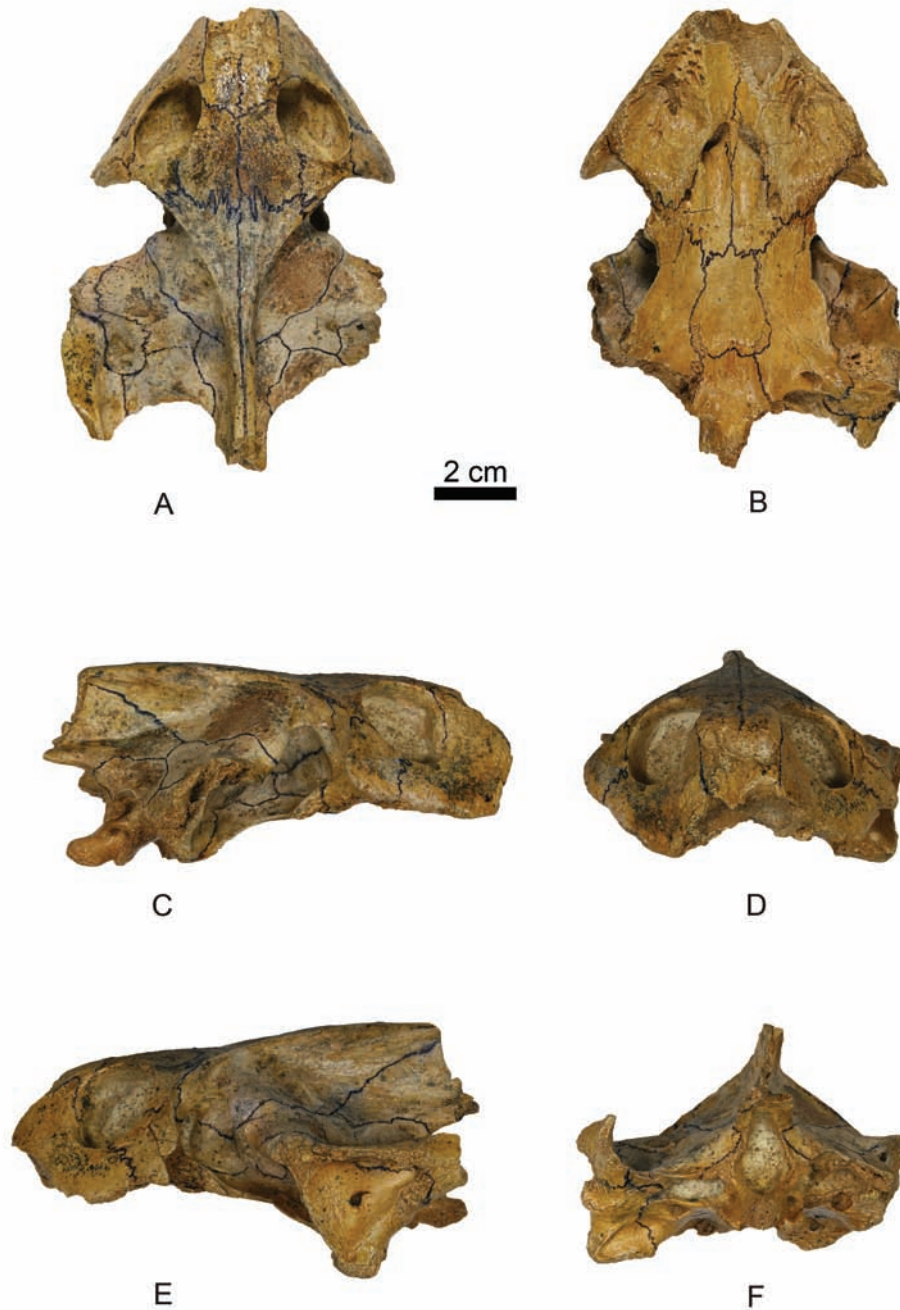***Trionyx* Geoffroy, 1809 sensu lato
(sensu Lapparent de Broin 2001)**

***Trionyx ikoviensis* sp. nov.**
(Figs 2–4)

Etymology. The species is named after the Ikovo locality.

Holotype. ZIN PH 37/145, a partial skull.

Locality and age. Ikovo, Luhansk Province, Ukraine; early Lutetian, Middle Eocene (see [Udovichenko 2009] for description of the locality).

Fig. 2. Skull of *Trionyx ikoviensis* sp. nov., ZIN PH 37/145 (holotype), photos: A – dorsal view; B – ventral view; C – right lateral view; D – anterior view; E – left lateral view; F – posterior view.

Referred material. ZIN PH 38–41/145, neurals; ZIN PH 42/145, right costal 1; ZIN PH 43/145, left middle costal; ZIN PH 44/145, lateral fragment of a middle costal; ZIN PH 45/145, left posterior costal; ZIN PH 46/145, fragment of the left last costal; ZIN PH 47/145, right hyoplastron; ZIN PH 48/145, cervical VII; ZIN PH 49/145, cervical VIII; other isolated bones and their fragments in the same collec-
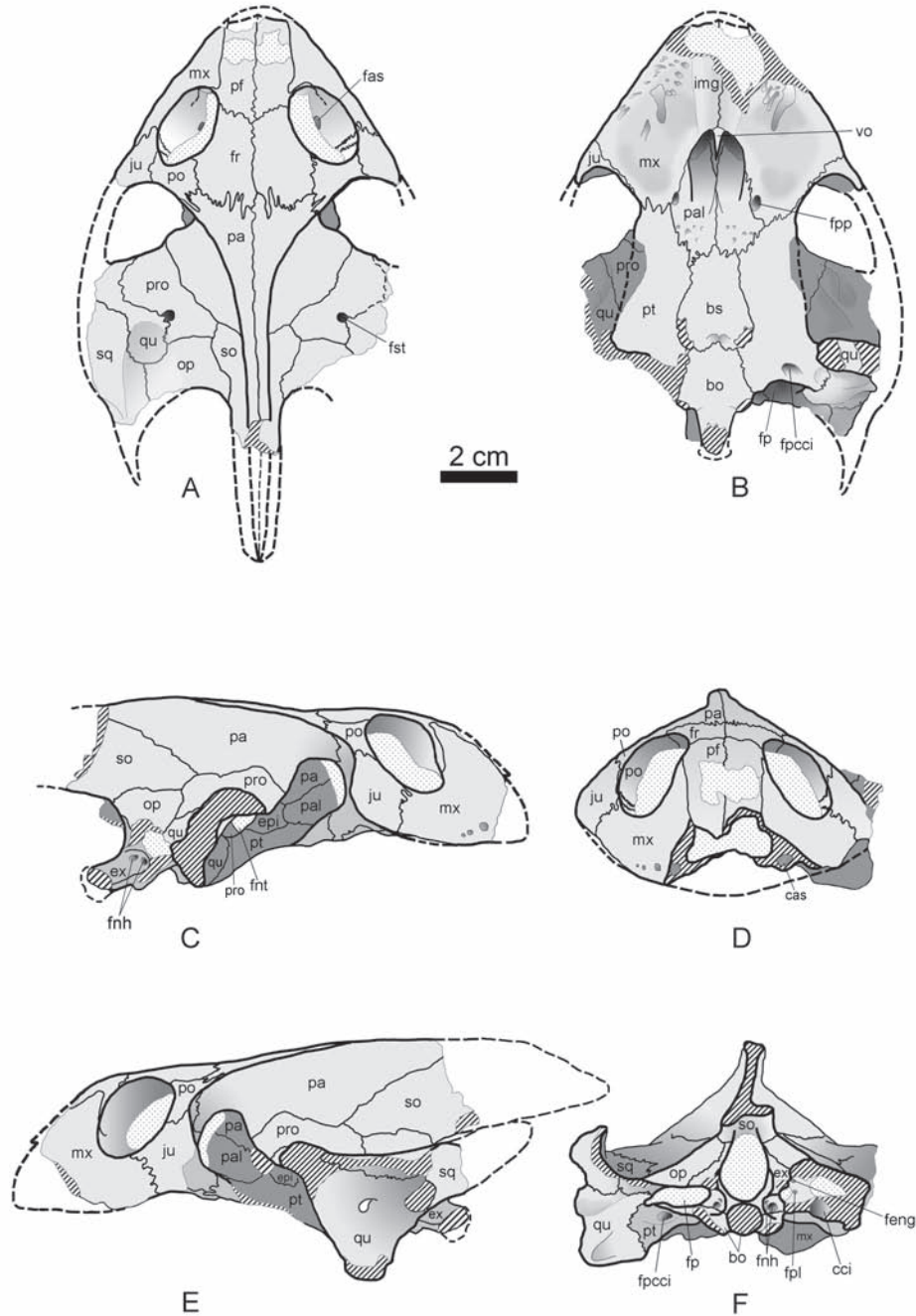
Fig. 3. Skull of *Trionyx ikoviensis* sp. nov., ZIN PH 37/145 (holotype), drawings: A – dorsal view; B – ventral view; C – right lateral view; D – anterior view; E – left lateral view; F – posterior view. Bones are filled with light grey (foreground) and dark grey (background). Matrix is stippled. Breakages are hatched.

Abbreviations: bo – basioccipital; bs – basisphenoid; cas – canalis alveolare superior; cci – canalis caroticus internus; epi – epiptery-goid; ex – exoccipital; fas – foramen alveolare superius; feng – foramen externum nervi glossopharyngei; fnh – foramen nervi hypoglossi; fnt – foramen nervi trigemini; fp – fenestra postotica; fpl – fenestra perilymphatica; fpcci – foramen posterius canalis carotici interni; fpp – foramen palatinum posterior; fr – frontal; img – intermaxillary groove; mx – maxilla; fst – foramen stapedio-temporale; ju – jugal; op – opisthotic; pa – parietal; pal – palatine; pf – prefrontal; po – postorbital; pro – prootic; pt – pterygoid; qu – quadrate; so – supraoc-cipital; sq – squamosal; vo – vomer.

tion (ZIN PH 145). All material was collected by one of us (EAZ) in 2009–2011.

Diagnosis. A trionychine which is most similar to modern members of Trionychini Gray, 1825 (sensu Meylan 1987) in that the parietal makes up nearly one-quarter of the processus trochlearis oticum; to species of the genus *Rafetoides* Karl, 1998 and/or to some species of *Trionyx* sensu lato (sensu Lapparent de Broin 2001) from Europe with middle-sized carapace and long and wide jaws and snout, especially to *Trionyx michauxi* Broin, 1977 from the Lower Eocene of France, in that the snout is relatively short and the maxillae form expanded triturating surfaces. It can be differentiated from Trionychini (except *Rafetus* Gray, 1864) by the dorsal margin of the apertura narium externa which is not strongly emarginated, and from *Rafetus* (and Apalonina Meylan, 1987) by the smaller intermaxillary foramen and by the vomer which does not divide the maxillae. It can be differentiated from *Rafetoides* by the presence of a hyoplastral shoulder. It can be differentiated from *Trionyx michauxi* by the skull roof narrower at the anterior border of the parietals, dorsal plate of the parietals more strongly narrowed posteriorly, slightly narrower triturating surfaces, shallower postorbital part of the maxilla, lower skull in lateral view, anteriorly widened intermaxillary groove, wider palatines and palatine grooves, basisphenoid more widened anteriorly.

Description. *Skull* (Figs 2, 3). The partial skull is missing the most rostral part of the snout, both jugal arches, the lateral part of the right otic capsule, and the supraoccipital crest. The estimated condylobasal length of the skull is 12 cm; its estimated width at the level of the quadrates is 9.6 cm. Thus, the estimated width/length ratio is 0.8. The face of the skull is relatively wide and short. The lateral borders of the snout are straight (not convex) in dorsal view. The eyes face dorsolaterally and slightly anteriorly. The ratio of the interorbital distance to the length of the orbit is about 0.75.

Both prefrontals are clearly visible, although they are slightly damaged dorsally, and the left one is missing its most anterior margin. The dorsal plate of the prefrontal conforms to that of the other members of the Trionychidae in that it contacts the frontal posteriorly and the maxilla laterally, forms the anterodorsal part of the margin of the orbit between the frontal and maxilla, and forms the dorsal edge of the apertura narium externa. The descending process of the prefrontal is visible along the anterior margin of the orbit, but its contacts with other bones other than the maxilla are not observable. The anterior margin of the prefrontal (i.e. the dorsal edge of the apertura narium externa) is weakly emarginated laterally as in many trionychids (Meylan 1987).

Both frontals are complete. The frontal contacts the prefrontal anteriorly, the parietal posteriorly, and the postorbital posterolaterally and forms greater part of the dorsal border of the orbit between the prefrontal and postorbital. The suture between the frontal and prefrontal is slightly oblique and the prefrontal therefore projects slightly between the frontals. The suture between the frontal and parietal is perpendicular to the midline and strongly interdigitated. The ventral surface of the frontals is not visible and its condition (fused or unfused; see Joyce and Lyson 2011) cannot be established.

Both parietals are almost complete, except for their most posterior portions. The dorsal plate of the parietal contacts the frontal anteriorly and the postorbital and jugal anterolaterally. The parietal does not contribute to the orbital margin or walls. The ventral plate of the parietal contacts the palatine and epipterygoid anteriorly and the prootic and supraoccipital posteriorly. Between the epipterygoid and prootic contacts, the parietal forms the dorsal border of the trigeminal foramen. The contribution of the ventral plate of the parietal to the formation of the processus trochlearis oticum is about one-fourth of the total width.

The squamosal is preserved on the left side of the skull. Its lateral edge is damaged and the posterior part is broken off. Ventrally and anteromedially, the squamosal contacts the quadrate and posteromedially the opisthotic. Dorsally, the squamosal bears an oblique ridge in its posterior part.

Both postorbitals are complete. The postorbital contacts the frontal anteromedially, the parietal posteromedially and the jugal laterally. Thus, the postorbital completely separates the parietal from the jugal on the external surface of the skull and forms most of the postorbital bar, which is about 1/4 of the orbit diameter. The ventral contact between the parietal and jugal is clearly visible within the fossa temporalis. Within the fossa orbitalis, the postorbital is expanded to form the majority of the posterior wall of this fossa. The anteroventral process of the postorbital approaches the maxilla, but is separated from it by the narrow strip of the jugal.

Both jugals are represented only by their anterior portions. On the external surface of the skull, the jugal contacts the maxilla anteriorly and the postorbital anterodorsally, makes a small contribution to the orbital margin and separates the maxilla from the postorbital. Within the fossa orbitalis, the jugal forms a narrow strip separating the maxilla from the postorbital. Dorsomedially, the jugal contacts the parietal, and posteromedially, the pterygoid. It is not clear if the jugal has contact with the palatine.

The quadratojugals and premaxillae are not preserved.

Both maxillae are missing their anterior portions and are damaged along the labial ridges. On the external surface, the maxilla contacts the prefrontal anterodorsally and the jugal posterior and forms the anteroventral margin of the orbit. Three nutrient foramina are visible along the ventral margin of the right maxilla. Dorsally, within the orbital fossa, the maxilla is penetrated by the foramen alveolare superius, which leads into the canalis alveolaris superior, which in return is visible along a break in the anterior view of the skull. On the ventral surface of the skull, the maxillae have a long contact (only part of which preserved) with each other along the midline, contact the vomer posteromedially, the palatines and pterygoids posterior and the jugals posterolaterally. Together with the vomer and palatines they form the internal narial openings. In addition, the maxilla and palatine border the small foramen palatinum posterius. The maxillae form expanded triturating surfaces. These surfaces are concave and each bears two elongated and obliquely oriented pits, one in the middle part and another at the posterior border of the maxilla. Between these triturating surfaces the maxillae form a rather deep and wide intermaxillary groove, which clearly widens anteriorly and is separated from the triturating surfaces by sharp ridges. The intermaxillary foramen, although not preserved, was probably relatively small, because there is not enough space for a large foramen due to the long contact between the maxillae.

Only a small part of the vomer is visible, just posterior to the intermaxillary suture between the internal narial openings. Posteriorly, the vomer is wedged slightly between the palatines. Other contacts of the vomer are not observable.

The palatines are complete and clearly visible in ventral view. The palatine contacts the vomer anteriorly, the maxilla anterolaterally, the pterygoid posterolaterally and the basisphenoid posteriorly. The palatines participate in the formation of the internal narial openings and together with the maxillae border the foramina palatinum posterius (see above). In lateral view, the palatine participates in the formation of the lateral wall of the braincase and contacts the parietal dorsally, the epipterygoid posteriorly and the pterygoid ventrally.

Both pterygoids are almost complete, except that their lateral margins are damaged and the right pterygoid is missing its posterolateral portion. The pterygoid forms the posterolateral surface of the palate, meets the maxilla anteriorly, the palatine anteromedially, the jugal anterolaterally, the basisphenoid medially, the basioccipital posteromedially, and the quadrate posterolaterally. It is not clear if the pterygoid contacts the exoccipital, because this region is damaged. Dorsally, the pterygoid also contacts the epipterygoid and forms part of the anteroventral margin of the foramen nervi trigemini between the epipterygoid anteriorly and the quadrate posteriorly. The pterygoid does not participate in the formation of the triturating surface. The anterior part of the processus pterygoideus externus is visible on the right side only. The foramen posterius canalis carotici interni is situated completely within the pterygoid, below the lateral crest of the basioccipital tubercle.

The epipterygoid is better preserved on the right side. It contacts the parietal anterodorsally, the palatine anteriorly, the pterygoid ventrally and forms most of the anterior border of the foramen nervi trigemini. The epipterygoid is separated from the quadrate by the pterygoid.

The basisphenoid is trapezoidal, wider posteriorly than anteriorly. It contacts the palatines anteriorly, the pterygoids laterally and the basioccipital posteriorly.

The supraoccipital is represented by its anterior portion. Most of the supraoccipital crest is not preserved. In dorsal view, the supraoccipital contacts the parietal anteriorly, the prootic anterolaterally and the opisthotic posterolaterally. In occipital view, the supraoccipital contacts the opistothic laterally and the exoccipitals ventrally, and forms the dorsal margin of the foramen magnum.

The exoccipital contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally; a contact with the pterygoid is possible, but not clear. The exoccipital forms the ventrolateral border of the foramen magnum and the medial
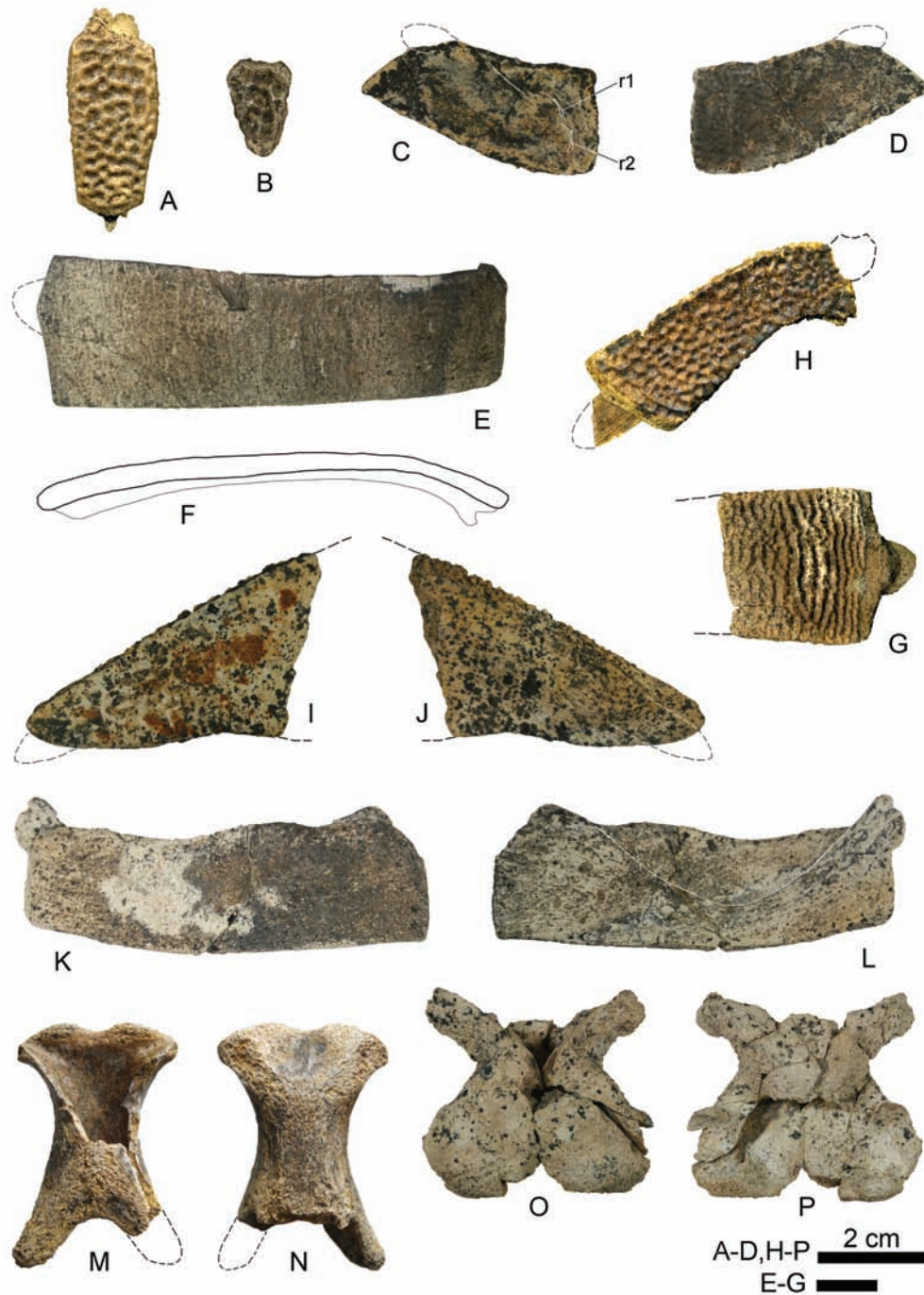
Fig. 4. Shell elements (A–L) and cervicals (M–P) of *Trionyx ikoviensis* sp. nov.: A – neural 4 to 6, ZIN PH 38/145, in dorsal view; B – last neural, ZIN PH 39/145, in dorsal view; C, D – right costal 1, ZIN PH 42/145, in ventral (C) and dorsal (D) views; E, F – left middle costal, ZIN PH 43/145, in dorsal (E) and posterior (F) views; G – lateral fragment of a middle costal, ZIN PH 44/145, in dorsal view; H – left posterior costal, ZIN PH 45/145, in dorsal view; I, J – lateral fragment of the left last costal, ZIN PH 46/145, in dorsal (I) and ventral (J) views; K, L – right hyoplastron, ZIN PH 47/145, in ventral (K) and dorsal (L) views; M, N – cervical VII, ZIN PH 48/145, in dorsal (M) and ventral (N) views; O, P – cervical VIII, ZIN PH 49/145, in dorsal (O) and ventral (P) views. A–E, G–P – photos; F – drawing.

Abbreviations: r1, r2 – rib heads of rib 1 and 2.

border of the foramen jugulare posterius. It is not clear if the foramen jugulare posterius was separated from the fenestra postotica or not, because of the broken dorsal surface of the pterygoid in this region. On the other hand, it is clear that there was no descending process of the opisthotic which subdivides the foramen jugulare posterius in some trionychines. There are two foramina nervi hypoglossi in each exoccipital.

The basioccipital forms the ventral half of the occipital condyle and contacts the exoccipital dorsally, the basisphenoid anteriorly and the pterygoid laterally. As is generally the case in trionychids, the basioccipital has a crest that extends laterally from the basioccipital tubercle, flooring a concavity into which opens the foramen nervi hypoglossi and foramen jugulare posterius.

Both prootics are preserved. Dorsally, the prootic is almost equally wide anteriorly and posteriorly. It contacts the parietal anteromedially, the supraoccipital posteromedially, the opisthotic posteriorly, and the quadrate laterally. The canalis stapedio-temporalis exits in the prootic at its border with the quadrate. No groove is present leading from this foramen across the prootic or parietal. Anteriorly, the prootic forms the greater part of the processus trochlearis oticum, and ventrally forms the dorsal border of the foramen nervi trigemini.

Both opisthotics are damaged posteriorly. In dorsal view, the opisthotic contacts the prootic anteriorly, the quadrate and squamosal laterally, and the supraoccipital medially. In occipital view, the opisthotic contacts the quadrate and squamosal laterally and the supraoccipital and exoccipital medially and forms the dorsal margin of the fenestra postotica. Clearly, the opisthotic did not contact the dorsal arch of the pterygoid, as is characteristic of Cyclanorbinae Hummel, 1929 (Meylan 1987). The cavum acustico-jugulare is clearly visible on the right side of the skull, where the margins of the fenestra postotica are damaged. The cavum acustico jugulare contains the processus interfenestralis, which is penetrated by two small openings: the foramen externum nervi glossopharyngei in the upper part and the fenestra perilymphatica in the lower part.

The left quadrate is almost complete, whereas the right one is only partially preserved. The tympanic cavity is almost the shape of an equilateral triangle. It is closed posteriorly and the incisura columellae auris is therefore closed. There is no ridge stretching from the incisura columellae auris posteriorly as in some trionychids. The quadrate contacts the squamosal dorsally, the prootic and opisthotic dorsomedially, and the pterygoid ventromedially. Posteriorly, the quadrate bears two oblique ridges (upper and lower), between which the Eustachian tube passed. Below the lower ridge, the quadrate has a depression (probably, for m. dilatator tubae Eustachii), which also extends to the adjacent part of the pterygoid.

Shell (Fig. 4A–L). Shell material is represented by isolated plates and their fragments.

The neurals are represented by four isolated elements. The biggest neural (ZIN PH 38/145; Fig. 4A) is narrow and asymmetrically pentagonal with short antero- or posterolateral side. Most probably this neural was at the point of reversal or adjacent to it, i.e. neural 4 to 6. Taking into account that anterior neurals are usually longer than posterior ones, this may be neural 4. The next neural (ZIN PH 39/145; Fig. 4B) is small, hexagonal and short-sided anteriorly. It is most probably the last neural in the series. Two other neurals (ZIN PH 40/145, 41/145) are small and tetragonal (isometric) and belong to juvenile individuals.

The costals are represented by costal 1, a middle costal, a posterior costal, a fragment of the last costal, and a lateral fragment of a large costal.

Costal 1 (ZIN PH 42/145; Fig. 4C, D) is complete, but missing its free rib. The length of the specimen along its posterior border is about 47 mm. The medial border is almost straight and lacks a subdivision into two parts, indicating that there was no preneural. The anterior border is slightly concave and bears a suture, suggesting the absence of suprascapular fontanelles. The free rib protruded at the anterior part of the lateral border, which is rounded and faces anterolaterally. The posterior border of costal 1 is convex and directed posterolaterally. The internal surface of costal 1 bears ribheads of the thoracic ribs 1 and 2.

The left middle costal (ZIN PH 43/145; Fig. 4E, F) is complete, but the free rib is broken off. The length of the plate along the anterior border is about 150 mm. The plate is wider laterally than medially and with almost straight anterior and posterior borders. The medial border is divided into short anterior and long posterior parts, which contacted the corresponding neurals (probably, hexagonal short-sided posteriorly). The free rib protruded at the anterior part of the lateral border of the plate. Where this rib projects, the lateral border of the costal plate is convex.

The lateral fragment of a middle costal (ZIN PH 44/145; Fig. 4G) also belongs to a large individual (the length of the lateral border is 48 mm). This specimen is important because it has a complete free rib, which only slightly protrudes beyond the middle of the free margin of the plate in its middle part. As in the case with ZIN PH 43/145, the free margin grows over the beginning of the free rib, forming a projection.

The left posterior costal (probably, costal 7; ZIN PH 45/145; Fig. 4H) belongs to a small individual. The length of the plate along the anterior margin is about 50 mm. The plate is slightly wider laterally than medially. Its anterior margin is convex and directed anterolaterally, whereas the posterior margin is concave and directed posteromedially, suggesting a relatively wide costal 8. The medial margin is divided into two parts: the anterior one for contact with the corresponding neural and the posterior one for contact with the counterpart costal. The lateral margin is convex and directed posterolaterally. The long free rib protrudes from the middle of the lateral margin.

The lateral fragment of the left last costal (probably, costal 8; ZIN PH 46/145; Fig. 4I, J) is from a large individual. Its anterior margin is straight, whereas the posterior margin is laterally convex laterally and medially concave. A depression for articulations with the ilium is absent.

The right hyoplastron (ZIN PH 47/145; Fig. 4K, L) is about 80 mm in width along the posterior border. It contacted the hypoplastron along an unfused transverse suture. The hyoplastral callosity is somewhat rectangular in shape and does not fully extend laterally to the bridge. A lateral fontanelle was thus present. The hyoplastral callosity is slightly longer medially than laterally; its anterior border is convex at the middle part forming a shoulder just lateral to the articulation site of the entoplastron. Medial processes are only slightly protrude anteromedially. The lateral processes are double. Anteromedially a fontanel likely existed between the hyoplastra and the entoplastron. Internally, the anterior hyoplastral lappet is distinct from the main body of the hyoplastron. The external surface of the plate is almost smooth, probably due to weathering. In its outline this hyoplastron is very similar to the hyoplastron attributed to *Trionyx michauxi* (Broin 1977, pl. X, fig. 19), but can be distinguished from the latter by an almost straight posterior border (in *T. michauxi* this border is strongly angled).

All the above described shell specimens display the distinct sculpturing characteristic of trionychids. In some specimens (ZIN PH 38/145, 39/145, 43/145) this sculpturing consists of thin, connected ridges forming a honeycomb pattern, whereas in ZIN PH 44/145, the ridges are parallel to the lateral border of the plate; in ZIN PH 42/145 and 47/145, the sculpturing is less pronounced, probably due to the weathering.

Cervicals. Cervical VII (ZIN PH 48/145; Fig. 4M, N) is missing the anterior part of the neural arch, the right postzygapophysis, and the posteriormost part of the centrum The estimated width of the cervical at the level of postzygapophyses is 30 mm. The cervical is longer than wide in dorsal aspect. The anterior articulation surface is doubled and convex, as is usual in trionychids. The posterior articulation surface is not preserved. A strong dorsal process that is known in posterior cervicals of some trionychids (Meylan 1987) is absent in this specimen.

Cervical VIII (ZIN PH 49/145; Fig. 4O, P) is known from a slightly bigger individual than ZIN PH 48/145. Its width at the level of prezygapophyses is 41 mm. The cervical is wider than long in dorsal aspect. The anterior and posterior articulation surfaces of the centrum are damaged. A small posterior keel on the ventral surface of the centrum is absent in this specimen.

DISCUSSION

The isolated specimens described above are referred to a single species, because they closely correspond to each other morphologically and there is no indication for the presence of more than one trionychid taxon at the locality, for instance through the presence of different types of sculpturing of shell elements.

Trionyx ikoviensis clearly belongs to Trionychidae because of the following synapomorphies (sensu Meylan 1987): in the skull the quadratojugal does not contact the postorbital and the jugal contacts the parietal; in the shell the shape of the plates, the absence of scute sulci and typical trionychid sculpturing; in the non-shell postcrania cervical VIII has no ventral process.

Trionyx ikoviensis is referred to Trionychinae based on the following synapomorphies (sensu Meylan 1987): the dorsal edge of the apertura narium externa is weakly emarginated; the reversal of neural

orientation is probably present; depressions for the articulation of ilia are absent from last costal; the bridge is short. In addition, it lacks the cyclanorbine synapomorphies (sensu Meylan 1987): the foramen palatinum posterius is not formed within the palatine; the foramen jugulare posterius is not isolated from the fenestra postotica by dorsal arch of the pterygoid; the hyo- and hypoplastra are not fused.

Trionyx ikoviensis cannot be attributed to the clade Plastomenidae Hay, 1902, which is considered as a stem representatives of Cyclanorbinae (see Joyce and Lyson 2011), because of absence of the following synapomorphies: the contribution of the parietal to the orbit wall, the foramen jugulare posterius is separated from the fenestra postotica, and the maxillae form the extensive, infolded secondary palate.

Within Trionychinae, *Trionyx ikoviensis* cannot be assigned to the tribe Chitrini Gray, 1870 (sensu Meylan 1987), because the foramen posterius canalis carotici interni does not lie within a ridge extending laterally from the basioccipital tubercle, the epipterygoid contacts the palatine and does not contact the prootic anterior to the foramen nervi trigemini and the absence of the small posterior keel on the ventral surface of the centrum. However, given that the Chitrini clade is not supported by phylogenetic analysis of molecular data (Engstrom et al. 2004), it is appropriate to compare the new species with two subtribes of the Chitrini: Chitrina Gray, 1870 and Amydina Loveridge, 1942. Chitrina unites two genera (*Chitra* Gray, 1844 and *Pelochelys* Gray, 1864) and is supported by both morphological and molecular data (Meylan 1987; as Chitraina, Engstrom et al. 2004). *Trionyx ikoviensis* cannot be assigned to Chitrina because the jugal is not in contact with the parietal on the skull surface, the dorsal emargination of the apertura narium externa is present, and the vomer does not divide the maxillae and reach the intermaxillary foramen. Similarly, *T. ikoviensis* cannot be assigned to Amydina (with a single genus *Amyda* Geoffroy, 1809), because the basisphenoid is not medially constricted.

Trionyx ikoviensis cannot be assigned to the tribe Aspideretini Meylan, 1987, because the basisphenoid is not medially constricted, and the quadrate is not excluded from the foramen nervi trigemini by a contact of the pterygoid and prootic posterior to this structure. The Aspideretini clade, including genera "*Aspideretes*" Hay, 1904 and *Nilssonia* Gray, 1872, is supported by the study of Engstrom et al. (2004).

Trionyx ikoviensis cannot be assigned to the tribe Pelodiscini Meylan, 1987, because the descending process of the opisthotic is absent and the pterygoid does not contact the foramen nervi trigemini between the epipterygoid and the parietal. Given that the Pelodiscini clade is not supported by study of Engstrom et al. (2004), it is appropriate to compare the new species with three genera of Pelodiscini: *Pelodiscus* Gray, 1844, *Dogania* Gray, 1844 and *Palea* Meylan, 1987. *Trionyx ikoviensis* cannot be assigned to *Pelodiscus* because the foramen palatinum posterius is not surrounded by the palatine. *Trionyx ikoviensis* cannot be assigned to *Dogania* and *Palea*, because the postorbital bar is not less than one-fifth of the orbit diameter. In addition, it cannot be assigned to *Dogania*, because the basisphenoid is not constricted and the maxillae do not contact the frontals along the anterior margin of the orbits; it cannot be assigned to *Palea*, because the jugal does not contact the parietal on the skull surface and the epipterygoid does not contact the prootic anterior to the foramen nervi trigemini.

Trionyx ikoviensis is similar to the tribe Trionychini (sensu Meylan 1987) in that the parietal makes up nearly one-quarter of the processus trochlearis oticum (see below), but different from all members of the tribe except *Rafetus* Gray, 1864 in that the dorsal margin of the apertura narium externa is not strongly emarginated. Given that the Trionychini clade is not supported by phylogenetic analysis of molecular data (Engstrom et al. 2004), it is appropriate to compare *T. ikoviensis* with two subtribes of Trionychini: Trionychina Gray, 1825 (with a single genus *Trionyx* Geoffroy, 1809) and Apalonina Meylan, 1987 (with genera *Rafetus* and *Apalone* Rafinesque, 1832). According to study of Engstrom et al. (2004), Apalonina is monophyletic, whereas *Trionyx* is united with the clade Chitraina in the clade Gigantaestuarochelys Engstrom et al., 2004. *Trionyx ikoviensis* cannot be assigned to *Trionyx* (sensu Meylan 1987) because the epipterygoid is not fused to the pterygoid. Similarly, *T. ikoviensis* cannot be assigned to Apalonina, because the intermaxillary foramen likely was small and the vomer does not divide the maxillae.

Among fossil forms of Trionychinae, *Trionyx ikoviensis* is most similar to some trionychine taxa from Europe, such as members of the genus *Rafetoides* (Karl 1998) and/or representatives of a group of middle-sized forms of carapace with long and wide jaws and snout of *Trionyx* sensu lato (sensu Lapparent de Broin 2001).

The genus *Rafetoides* was established by Karl (1998) based on *Trionyx henrici* Owen, 1849, a shell taxon from the Lower Eocene of England (London Clay; Owen and Bell 1849). *Trionyx silvestris* Walker et Moody, 1974, a skull taxon from the Lower Eocene of England (Blackheath beds; Walker and Moody 1974), was considered to be a junior synonym of *T. henrici*. The second species of *Rafetoides*, *R. austriacus* (Peters, 1858) (= *T. messelianus* Reinach, 1900; for other synonyms, see Karl 1998; Karl and Müller 2008) is typical for the Eocene – Early Oligocene of Europe. Its skull morphology is also known (Karl 1998, Abb. 8). *Rafetoides* was placed in the monotypic subtribe Rafetoidina Karl, 1998 of Trionychini, although methods of the phylogenetic analysis were not clearly presented (Karl 1998, 1999). *Trionyx ikoviensis* demonstrates the following characters of Rafetoidina and *Rafetoides* (sensu Karl 1998): probably well developed costals 8, intermaxillary foramen is less than 1/3 of the primary palate length, preneural and permanent suprascapular (postnuchal) fontanelles are absent, presence of two lateral processes of hyoplastron (processus cardinis masculi anterior). Moreover, *T. ikoviensis* shares with *Rafetoides* weak emargination of the apertura narium externa, contrary to Karl (1998), who reported that *Rafetoides* has strong emargination of the apertura narium externa. However, the state of other important characters of *Rafetoides* (entoplastron with acute angle; anterior process of epiplastron shorter than posterior one; small xiphiplastra) is unknown in *T. ikoviensis*. In addition, *T. ikoviensis* differs from species of *Rafetoides* in the presence of a hypoplastral shoulder. *Trionyx ikoviensis* differs furthermore from *R. henrici* (= *T. silvestris*; Walker and Moody 1974, pl. 118, text-fig. 1) in having a wider intermaxillary groove, wider basisphenoid and cavum tympani that is not elongated. *Trionyx ikoviensis* differs from *R. austriacus* (Karl 1998, Abb. 8) in the frontals, which are relatively longer and with greater contribution to the orbital margin. Because *T. ikoviensis* is different from both species of *Rafetoides* and does not demonstrate some important characters of this genus, we refrain from attributing it to *Rafetoides* and Rafetoidina. Moreover, we think that the synonymy of *Trionyx henrici* with *T. silvestris* as well as a long list of synonyms of *Rafetoides austriacus* suggested by Karl (1998; Karl and Müller 2008) need additional corroboration. Finally, the phylogenetic position of *Rafetoides* should be studied using computer-assisted cladistic analysis.

According to Lapparent de Broin (2001), "*Trionyx* s. l. [sensu lato] in Europe only" is a lineage of Trionychinae leading to *Trionyx* sensu stricto (sensu Meylan 1987), i.e. corresponds to a stem (total) clade, including *Trionyx* sensu stricto. *Trionyx* sensu lato (sensu Lapparent de Broin 2001) is diagnosed by the type of carapace and principal skull characters of *Trionyx* sensu stricto (Broin 1977; Lapparent de Broin pers. comm. 2011; only some skull characters are mentioned below): the intermaxillary foramen is larger than the choanae, the distance between the intermaxillary foramen and the choanae is more than the foramen length; the intermaxillary groove has the parallel lateral borders (anterior to the choanes), which are slightly converging anteriorly and diverging posteriorly. Apart from *Trionyx* sensu stricto (a crown clade), *Trionyx* sensu lato (sensu Lapparent de Broin 2001) contains two stem-groups (Lapparent de Broin 2001): the first one includes "a small form of carapace (and rather short lower jaw symphysis)" from the Paleocene – Lower Eocene of Belgium and France; and the second one includes "middle-sized forms of carapace" from the Paleocene – Miocene interval of Europe. The second group is divided into three subgroups: the first one with mid-short lower jaw symphysis (Thanetian, Cernay-Mont Berru, earliest Eocene of Belgium and France); the second one with long and wide jaws and snout (see below); the third one with long and narrow jaws as in *Trionyx triunguis* (Forsskål, 1775) (Messel, Germany; Monte Bolca and Monteviale, Italy; Miocene faluns d'Anjou, France).

The above mentioned skull characters of *Trionyx* sensu lato (sensu Lapparent de Broin 2001) are either unknown or demonstrate different states in *Trionyx ikoviensis*. The size of the intermaxillary foramen is unknown, whereas the borders of the intermaxillary groove are not parallel but clearly diverging anteriorly. On the other hand, *T. ikoviensis* demonstrates similarity to the members of the second subgroup of *Trionyx* sensu lato (sensu Lapparent de Broin 2001), such as *Trionyx michauxi* Broin, 1977 from the Lower Eocene of France, *T. silvestris* (see above), and *T. styriacus* Peters, 1855 from the Miocene of Austria and France in that the snout is relatively short (shorter than in members of the third subgroup) and the maxillae form expanded triturating surfaces.

Within the second subgroup *Trionyx ikoviensis* is most similar to *T. michauxi* (based on cast of the holotype and photographs from Broin 1977, fig. 72, pl. XI) in the shape of the snout, which is relatively

short and with straight lateral borders in dorsal view and in the degree of expansion and shape of the triturating surfaces. *Trionyx ikoviensis* can be differentiated from *T. michauxi* by the following characters: the skull roof at the anterior border of the parietals is narrower; the dorsal plate of the parietals is more strongly narrowed posteriorly; the triturating surfaces are slightly narrower; the postorbital part of the maxilla is shallower; the skull is lower in lateral view; the intermaxillary groove is widened anteriorly (in *T. michauxi* this groove has almost parallel borders); the palatines and palatine grooves are wider; the basisphenoid is wider anteriorly. In addition to similarities of the skull morphology, *Trionyx ikoviensis* shares with *T. michauxi* the presence of a hyoplastral shoulder. However, the hyoplastra of these species are different in shape, having an almost straight posterior border in *T. ikoviensis* and an angled posterior border in *T. michauxi*. Other potential differences in the shell morphology between these species are not clear due to a lack of material.

The differences of *Trionyx ikoviensis* from *T. silvestris* (as *Rafetoides henrici*) were given above.

Trionyx ikoviensis can be differentiated from *Trionyx styriacus* (Broin 1977, figs 28–30, 73, pl. XIII, fig. 2) by the following characters: the snout is relatively shorter; its lateral borders are straight in dorsal view (in *T. styriacus* the lateral borders of the snout are convex); the orbits are larger; the postorbital bar is wider; the prootic is not narrowed posteriorly; the cavum tympani is not elongated; the triturating surfaces are less expanded; the intermaxillary groove is widened anteriorly (in *T. styriacus* this groove has almost parallel borders).

To summarize, it is clear that *Trionyx ikoviensis* cannot be assigned to any modern group within Trionychinae, although it is most similar to Trionychini (sensu Meylan 1987). Among fossil forms, *T. ikoviensis* is most similar to species of the genus *Rafetoides* and/or to some species of *Trionyx* sensu lato (sensu Lapparent de Broin 2001) from Europe with middle-sized carapace and long and wide jaws and snout, especially to *Trionyx michauxi* from the Lower Eocene of France. Although the taxonomic status and phylogenetic position of both *Rafetoides* and *Trionyx* sensu lato (sensu Lapparent de Broin 2001) need additional study, the latter assignment seems to be better corroborated. *Trionyx ikoviensis* is the easternmost representative of *Trionyx* sensu lato (sensu Lapparent de Broin 2001). In this study

we refrain from the inclusion of the new taxon into phylogenetic analysis, because the material is not clearly associated and complete. New findings of associated material on this group of fossil trionychids are needed to clarify its phylogenetic position.

The turtle assemblage of Ikovo includes cheloniids (*Argillochelys* sp., *Puppigerus nessovi* and Cheloniidae indet.), a trionychid (*Trionyx ikoviensis*) and a testudinoid (Testudinoidea indet.) (Zvonok et al. 2010; in press).

The comparison of the Ikovo assemblage of turtles with contemporary assemblages of Eurasia demonstrates its greatest similarity with the assemblages of London Clay (Lower Eocene, Ypresian), Bracklesham Beds (Lower – Middle Eocene) and Barton Cliff (Middle Eocene, Bartonian) of Great Britain (Benton and Spencer 1995). All these assemblages include cheloniid genera *Argillochelys* Lydekker, 1889 and *Puppigerus* Cope, 1871 and trionychids. In addition, the London Clay assemblage contains representatives of testudinoids, which are also present in the Ikovo assemblage, and a number of other turtle taxa (absent from the Ikovo): a pelomedusid, two different genera of cheloniids, a dermochelyid, a carettochelyid and two indeterminate turtle taxa (Benton and Spencer 1995). This fact suggests that we may expect discoveries of new turtle taxa from the Ikovo.

Puppigerus nessovi is the only common turtle element between the Ikovo assemblage and the Dzheroi 2 assemblage of Uzbekistan (Averianov 2005), although other undescribed turtle taxa (a cheloniid and testudinoids) have been reported from the Dzheroi 2 (see Averianov 2005). Nevertheless, the Ikovo turtle assemblage is unique in that it represents a connection between Early – Middle Eocene turtle assemblages of Western Europe and Asia.

Together these data emphasize the significance of the Ikovo locality as a prospective field area for finding new material, including skull specimens, of Middle Eocene turtles of Eastern Europe, that are important for understanding of the interconnection between the turtle faunas of Western Europe and Asia at that time.

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