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A REVISION OF FOSSIL TURTLES FROM THE KIEV CLAYS (UKRAINE, MIDDLE EOCENE) WITH COMMENTS ON THE HISTORY OF THE COLLECTION OF FOSSIL VERTEBRATES OF A.S. ROGOVICH

E.A. Zvonok¹ and I.G. Danilov^{2*}

¹Taras Shevchenko National University of Luhansk, Oboronnaya Str. 2, 91000 Luhansk, Ukraine;
e-mail: evgenij-zvonok@yandex.ru

²Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: igordanilov72@gmail.com, turtle@zin.ru

ABSTRACT

The paper revises material of fossil turtles from the Kiev clays (Vyshgorod and Tripolye localities, Kiev Province, Ukraine; Kiev Formation, upper Lutetian – lower Bartonian, middle Eocene) from the 19th century collection of fossil vertebrates of the Russian naturalist A.S. Rogovich. In the course of more than a century this collection was divided into parts several times and stored in different institutions of Moscow, Saint Petersburg, and Kiev. The turtle material from Rogovich's collection includes a partial skeleton and isolated shell fragments from Vyshgorod locality referred here to a pancheloniid sea turtle *Argillochelys antiqua* (König, 1825), a species formerly known only from the Paleogene of Western Europe, partial dentaries from Vyshgorod locality, belonging to "*Dollochelys*" *rogovichi* Averianov, 2002, a pancheloniid with unclear generic attribution, and sculptured shell fragments of Pan-Cheloniidae indet. from Tripolye locality, erroneously assigned to a crocodile by Rogovich. The material of *A. antiqua* unites some specimens previously described as *Puppigerus* sp. and *Dollochelys rogovichi*, as well as newly revealed specimens. According to our interpretation, parts of the skeleton of *A. antiqua* from Vyshgorod locality were stored in different institutions for a long time, sharing the fate of the whole Rogovich's collection of fossil vertebrates. The attribution of the Vyshgorod material to *A. antiqua* is supported by phylogenetic analysis of pancheloniids. This analysis also demonstrates an *Argillochelys* clade (*A. antiqua* + *A. cuneiceps* [Owen, 1849]), and removes "*A. africana*" Tong et Hirayama, 2008 from this clade. Analysis of the geographic and stratigraphic distribution of the genus *Argillochelys* shows that it is restricted to the ?Thanetian – Priabonian of the Peri-Tethyan area (Western and Eastern Europe and Kazakhstan) and possibly also to eastern North America. In addition, our study shows that sculptured pancheloniids of unknown affinities are quite common in the middle Eocene of Eastern Europe and Central Asia.

Key words: Kiev clays, middle Eocene, Pan-Cheloniidae, A.S. Rogovich, sea turtles, Ukraine

РЕВИЗИЯ ИСКОПАЕМЫХ ЧЕРЕПАХ ИЗ КИЕВСКИХ ГЛИН (УКРАИНА, СРЕДНИЙ ЭОЦЕН) С КОММЕНТАРИЯМИ ПО ИСТОРИИ КОЛЛЕКЦИИ ИСКОПАЕМЫХ ПОЗВОНОЧНЫХ А.С. РОГОВИЧА

Е.А. Звонок¹ и И.Г. Данилов^{2*}

¹Луганский национальный университет имени Тараса Шевченко, ул. Оборонная 2, 91000 Луганск, Украина;
e-mail: evgenij-zvonok@yandex.ru

²Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия;
e-mail: igordanilov72@gmail.com, turtle@zin.ru

РЕЗЮМЕ

В статье ревизуется материал по ископаемым черепахам из киевских глин (местонахождения Вышгород и Триполье, Киевская область, Украина; киевская свита, верхний лютет – нижний бартон, средний эоцен) из

*Corresponding author / Автор-корреспондент

коллекции ископаемых позвоночных русского естествоиспытателя А.С. Роговича. На протяжении более века эта коллекция несколько раз делилась на части и хранилась в различных учреждениях Москвы, Санкт-Петербурга и Киева. Материал по черепахам из коллекции Роговича включает неполный скелет и изолированные фрагменты панциря из местонахождения Вышгород, которые относятся к панхелониидной морской черепахе *Argillochelys antiqua* (König, 1825), виду, ранее известному только из палеогена Западной Европы, неполные зубные кости из местонахождения Вышгород, принадлежащие "*Dollochelys*" *rogovichi* Averianov, 2002, панхелонииду неясной родовой принадлежности, и скульптурированные фрагменты панциря Pan-Cheloniidae indet. из местонахождения Триполье, ошибочно отнесенные Роговичем к крокодилу. Материал по *A. antiqua* включает некоторые экземпляры, ранее описанные как *Puppigerus* sp. и *Dollochelys rogovichi*, а также вновь выявленные экземпляры. Согласно нашей интерпретации, части скелета *A. antiqua* из Вышгорода длительное время хранились в различных учреждениях, разделяя судьбу всей коллекции ископаемых позвоночных Роговича. Отнесение материала из Вышгорода к *A. antiqua* подтверждается филогенетическим анализом панхелониид. Этот анализ также демонстрирует кладу *Argillochelys* (*A. antiqua* + *A. cuneiceps* [Owen, 1849]) и удаляет "*A. africana* Tong et Hirayama, 2008 из этой клады. Анализ географического и стратиграфического распространения рода *Argillochelys* показывает, что оно ограничено ?танетом-приабомом Пери-Тетиса (Западная и Восточная Европа и Казахстан) и, возможно, также востоком Северной Америки. Кроме того, наше исследование показывает, что скульптурированные панхелонииды неясной принадлежности довольно обычны в среднем эоцене Восточной Европы и Центральной Азии.

Ключевые слова: киевские глины, средний эоцен, Pan-Cheloniidae, А.С. Рогович, морские черепахи, Украина

INTRODUCTION

Rich collection of fossil vertebrates was collected in the vicinities of Kiev (Ukraine) by Russian naturalist Afanasii Semenovitch Rogovich (Afanassi Semjonowitsch Rogowitsch; 1813–1878) in the 19th century (see Russian Biographical Dictionary 1913). A brief history of this collection is given in the "Comments on the history..." section. This paper presents results of the revision of turtle materials from the Rogovich's collection, which come from the so called blue Kiev clays (or marls) of the middle Eocene age in the vicinities of Kiev (Vyshgorod and Tripolye localities, see below). Some of these materials were described by Rogovich (1871, 1875a) as remains of fishes and mammals (see Averianov 2002). "Several fragments of the turtle shell" were reported in another paper of Rogovich (1875c: 2), but never described. In addition, Rogovich (1875b, c) mentioned material attributed by him to a crocodile, *Crocodylus spenceri* Buckland, 1836. As it is shown in our paper, this material belongs to turtles as well.

New mentionings of turtle material from the Eocene of Ukraine appeared more than 70 years after Rogovich's publications as: "an Eocene turtle from the limits of Ukraine <...>, probably, marine" (Khosatzky 1949: 223); "a small sea turtle, found in Kiev marl" (Khosatzky 1951: 24); "remains of sea turtles" from "the Eocene deposits of Northern Ukraine"

(Pidoplichko 1961: 90); "specimen of an Eocene sea turtle" (Tarashchuk 1971: 56); "Cheloniidae" (Dubrovo and Kapelist 1979: 10). Finally, Chkhikvadze (1983) described shell fragments and phalanges from Vyshgorod locality as a cheloniid *Puppigerus* sp. Even later, Averianov (2002) referred this and another material (dentary, cranial and shell remains) from the same locality to the new cheloniid species *Dollochelys rogovichi* Averianov, 2002. Very soon, Hirayama (2006: 4) suggested considering *D. rogovichi* "as a nomen dubium because it does not possess any diagnostic features of a taxonomic level below the superfamily Chelonioidea".

Recently we revealed previously undescribed sea turtle (pancheloniid; hereinafter all higher names follow Joyce et al. [2004]) material from the Kiev clays, including partial skeleton from Vyshgorod locality, and shell fragments from Tripolye locality from the Rogovich's collection. Additional preparation of the material described by Chkhikvadze (1983) allowed identifying new bones of the skeleton and reinterpreting some of the previously described elements. Part of the material referred to *Dollochelys rogovichi*, and the newly revealed partial skeleton from Vyshgorod locality appear to belong to *Argillochelys antiqua* (König, 1825), a pancheloniid species formerly known only from the Paleogene of Western Europe (Moody 1997; de Lapparent de Broin 2001). According to our interpretation, part of the *A. anti-*

qua material from Vyshgorod locality represents one turtle skeleton, which parts were stored in different institutions for many decades following the fate of the whole Rogovich's collection (see Comments on the history...). *Dollochelys rogovichi* is considered to be a valid pancheloniid species with unclear generic attribution (Pan-Cheloniidae incertae sedis). The material from Tripolye locality was referred to a crocodile by Rogovich, but here determined as Pan-Cheloniidae indet.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CC-MGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; IRSNB, Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium; IZU, I.I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kiev, Ukraine; MCZ, Museum of Comparative Zoology, Cambridge, USA; NHM, Natural History Museum, London, Great Britain; NMNHU-P, Department of Paleozoology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev, Ukraine; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; ZIN PH, Paleoherpetological collection in the same institute. See text for other institutional abbreviations.

COMMENTS ON THE HISTORY OF THE COLLECTION OF FOSSIL VERTEBRATES OF A.S. ROGOVICH

Rogovich's collection of fossil vertebrates united specimens collected by Rogovich himself and specimens sent to him by other collectors from the territory of the southwest Russian Empire (now Ukraine; Rogovich 1875a). Study of this collection resulted in the publication of two big papers devoted to fossil fishes (Rogovich 1860, 1871), and three smaller ones (Rogovich 1875a–c), which include descriptions of fossil mammals and a bird and mentionings of a crocodile and a turtle. Some of the original labels of Rogovich's collection are shown in Fig. 1A, C, F, G. Part of the specimens in the Rogovich's collection of fossil vertebrates comes from the blue Kiev clays (or marls) of the middle Eocene age, which were exposed in the former quarry of Eisman's brickworks near Vyshgorod (see Geology...).

Probably, after Rogovich's death his collection was divided into several parts and transferred to different institutions of Moscow, Saint Petersburg, and

Kiev (Fig. 2). In Moscow, Rogovich's collection first appeared in the Geological Room (Cabinet) of the Imperial Moscow University (GR; Pavlova 1910; mammals), later A.P. and M.V. Pavlovs Geological-Paleontological Museum, primarily within the Moscow Geological Prospecting Institute (MGRI; 1930–1987), and now within the Vernadsky State Geological Museum (SGM; for detailed history of SGM see Bessudnova 2006). In the unknown period, one turtle specimen from Rogovich's collection (ZIN PH 8/36) was transferred from MGRI to ZIN, as is documented by a label written by L.I. Khosatzky, which is accompanying the specimen (Fig. 1E). Some fishes from the Rogovich's collection are stored in SGM (Nessov 1992), although Bannikov (2010) noted that their storage is unknown. In 2017, one of us (IGD) during a visit to SGM managed to find two peripheral plates of a pancheloniid sea turtle in one box with Rogovich's material of fishes and mollusks from the Zaitsev's brickworks of Kiev (these specimens are not included in the description). The presence of Rogovich's mammals in SGM needs verification.

In Saint Petersburg, Rogovich's collection first appeared in the Paleontological-Stratigraphical Museum of the Saint Petersburg Imperial University (Anonymous 1897; PSM; now Saint Petersburg State University; Fig. 1A, B). In 1971, parts of the Rogovich's collections (all, besides shark teeth) were transferred from PSM to the Department of Vertebrate Zoology of the same university (fishes) and to ZIN (fishes, turtles and birds; Averianov et al. 1990; Nessov 1992). The bird material referred to "*Scolopax* Cuv." by Rogovich (1875c) was described by Averianov et al. (1990) as a new genus and species *Kievornis rogovitshi* Averianov et al., 1990. Later, he also described the turtle material as a new species *Dollochelys rogovichi* Averianov, 2002 (Averianov 2002). Recently, we also found one mammal specimen (part of the vertebra with a label "*Zeuglodon Paulsoni*") in ZIN. Vertebrae of this species were mentioned by Rogovich (1875a) from the sandstones of the Eocene formation near Chigirin.

In Kiev, fishes from the Rogovich's collection are stored in the Institute of Geological Sciences of the National Academy of Sciences of Ukraine (IGS; E.V. Popov pers. comm. 2017). Tarashchuk (1971: 56) clearly mentioned "specimen of an Eocene sea turtle" stored in IGS, which was later transferred to the Institute of Zoology of the Academy of Sciences of the Ukrainian SSR (currently IZU) and

На селси карале. Глина, 204.
 Офр. около Киева. 1872 г.
 А.Рогов

A

Городиш. Кав. С. П. Университети
 Coccidius
 Киев

B

Anthracotherium alsaticum
 Cuv.
 Cuvier, Oss. foss. IV. 500. tab.
 fig. 5. — Monn, Letn. geog.
 II. 1227. Taf. XLVI. fig. 4. 4a.
 Мислен. Кошт, висот. Кошт,
 јесец и Кина наведена на
 Киев. Глина 204. (Офр. 204)
 около Киева на Кур. Глина
 Е. см. 1872 г. 3 октубр.
 А.Рогов

C

Морская
 черепаха
 Зоцет
 Окрест. Киева
 из музея
 Рогова

D

? *Chelonia* sp.
 Киев
 Зоцет
 Кош. МТРИ.

E

Coccidius spenceri.
 из Киев. Голуб. Кар. Глина
 около Мраповца. 1874 г.
 18 октубр. Присл. Монтре-
 Горна
 А.Рогов

F

Коста Кротова из музея
 Киев. Глина около Мун-
 гора. 1876 г. 26 Зван.
 А.Рогов

G

Chelonia?
 Синяя глина
 Триполье
 А. Рогович

H

Это гермахи Гина
Syllomus (*Syllomyine*,
Cheloniidae)
 30.10.92
 Л. Керол

I

described by Chkhikvadze (1983) as *Puppigerus* sp. This specimen was assigned to *Dollochelys rogovichi* by Averianov (2002). Now it is stored in NMNHU-P. Unfortunately, we did not see the label of NMNHU-P specimen and its attribution to Rogovich's collection is based on indirect evidence (see Discussion).

GEOLOGY AND AGE OF THE LOCALITIES

Vyshgorod locality was situated in the former quarry of the Eisman's brickworks near Vyshgorod (Vyshhorod) City; now Vyshgorod District, Kiev Province, Ukraine; 50°35'N, 30°29'E; marly-clayey member of the Kiev Formation; upper Lutetian – lower Bartonian, NP16 (Fig. 3; Rogovich 1875c; Ryabokon' 2002).

Tripolye locality is located near Tripolye (Trypillia) village; now Obukhov (Obukhiv) District, Kiev Province, Ukraine; 50°07' N, 30°46' E; geology and age are the same as in Vyshgorod locality (Fig. 3).

The stratotype of the Kiev Formation is located 2 km E from Tripolye and 65 km SSE from Vyshgorod near Khalepye Village, Obukhov District, Kiev Province, Ukraine (Fig. 3).

In addition to turtles, the fauna of tetrapods known from the Kiev marls includes a possible procellariiform bird *Kievornis rogovitshi* Averianov et al., 1990 from Vyshgorod locality and a cetacean *Basilotritus uheni* Gol'din et Zvonok, 2013 from Kureniovka locality (12 km S from Vyshgorod) (Averianov et al. 1990; Gol'din and Zvonok 2013). Records of the crocodile remains (Rogovich 1875b, c; Averianov et al. 1990) are at least partially based on erroneously determined turtle material (see below).

MATERIAL AND METHODS

In addition to the material described in this paper (Figs. 4–12), the following taxa of panchelonioids

were used for comparison and/or phylogenetic analysis: *Allopleuron qazaqstanense* Karl et al., 2012, as described by Zvonok et al. (2015); *Argillochelys antiqua* (König, 1825) (= *Chelone subcristata* Owen, 1841), as described by Owen and Bell (1849) and Lydekker (1889), and photographs of IRSNB 1653, NHM 49465 (holotype), NHM 32386 and NHM 38952; *A. athersuchi* Moody, 1980, as described by Moody (1980); *A. cuneiceps* (Owen, 1849), as described by Owen and Bell (1849) and photographs of NHM 41636 (holotype) and NHM 38949; *Argillochelys* sp. a and b, as described by Lydekker (1889) and photographs of NHM 1447 and NHM 8681; *Argillochelys* sp. from the middle Eocene Ikovo locality, Ukraine, as described by Zvonok et al. (2013b) and personal observations of ZIN PH 5/145; *“Argillochelys” africana* Tong et Hirayama, 2008, as described by Tong and Hirayama (2008); *Ashleychelys palmeri* Weems et Sanders, 2014, as described by Weems and Sanders (2014); *Caretta caretta* (Linnaeus, 1758), based on Zangerl (1958: figs. 17, 18) and Cadena and Parham (2015: ch. 116); *Carolinochelys wilsoni* Hay, 1923, as described by Weems and Sanders (2014); *Catapleura repanda* (Cope, 1868) (= *Toxochelys atlantica* Zangerl, 1953; *Dollochelys casieri* Zangerl, 1971; = *Dollochelys coatesi* Weems, 1988; for other synonyms see Hirayama [2006]), as described by Zangerl (1953, 1971), Weems (1988), and Hirayama (2006); *Chelonia mydas* (Linnaeus, 1758), based on personal observation of four skulls (ZIN 230/0 and ZIN unnumbered), and Cadena and Parham (2015: ch. 116); *Ctenochelys stenoporus* (Hay, 1905), as described by Zangerl (1953) and Matzke (2007); *Ctenochelys acris* Zangerl, 1953, as described by Zangerl (1953) and Gentry (2017); *Eochelone brabantica* Dollo, 1903, as described by Casier (1968) and characters reported by Lapparent de Broin et al. (2014); *Eosphargis breinerei* Nielsen, 1959, as described by Nielsen (1963); *Eretmochelys imbricata* (Linnaeus, 1766), based on Zangerl (1958: figs. 17, 18) and Cadena and Parham

Fig. 1. Labels of turtle specimens from Vyshgorod (A–E) and Tripolye (F–I) localities: A, B – labels accompanied dentary specimens of *Dollochelys rogovichi*: A – original label written by A.S. Rogovich: “From blue brick clay, Eocene Formation near Kiev. 1872. A. Rogovich”; B – label of the Geological Room of the Saint Petersburg University (= PSM): “*Crocodylus*. Locality: Kiev”; C – original label written by A.S. Rogovich and accompanied ZIN PH 7/36: “*Anthracotheurium alsaticum* Cuv. Cuvier, Oss. Foss. IV. 500. tab. Fig. 5. – Bronn, Leth. Geog. II. 1227. Taf. <unclear> VI. Fig. 4.4a. Parietal, temporal, incisor and canine were found in blue Kiev clay (formation of brown coal) near Kiev at the Eisman's brickworks. October 3, 1874. A. Rogovich”; D – label written by L.I. Khosatzky: “Sea turtle. Eocene. Vicinity of Kiev”, with a postscript written by L.A. Nessov: “Is not it Rogovich's material?”; E – label written by L.I. Khosatzky: “? *Chelonia*. Kiev. Eocene. Collection of MGRI”; F, G – original labels written by A.S. Rogovich: F – “*Crocodylus spenceri*. From Kiev blue brick clay near Tripolye. October 18, 1874. Sent by Montregor. A. Rogovich”; G – “Bones of a crocodile from the blue brick clay near Tripolye. June 26, 1876. A. Rogovich”; H – inscription written by L.I. Khosatzky on the box cover: “*Chelonia*? Blue clay. Tripolye. A. Rogovich”; I – note written by L.A. Nessov: “This is a turtle of the *Syllomus* type (Syllomiinae, Cheloniidae). 30.10.92. L. Nessov”. See text for discussion.

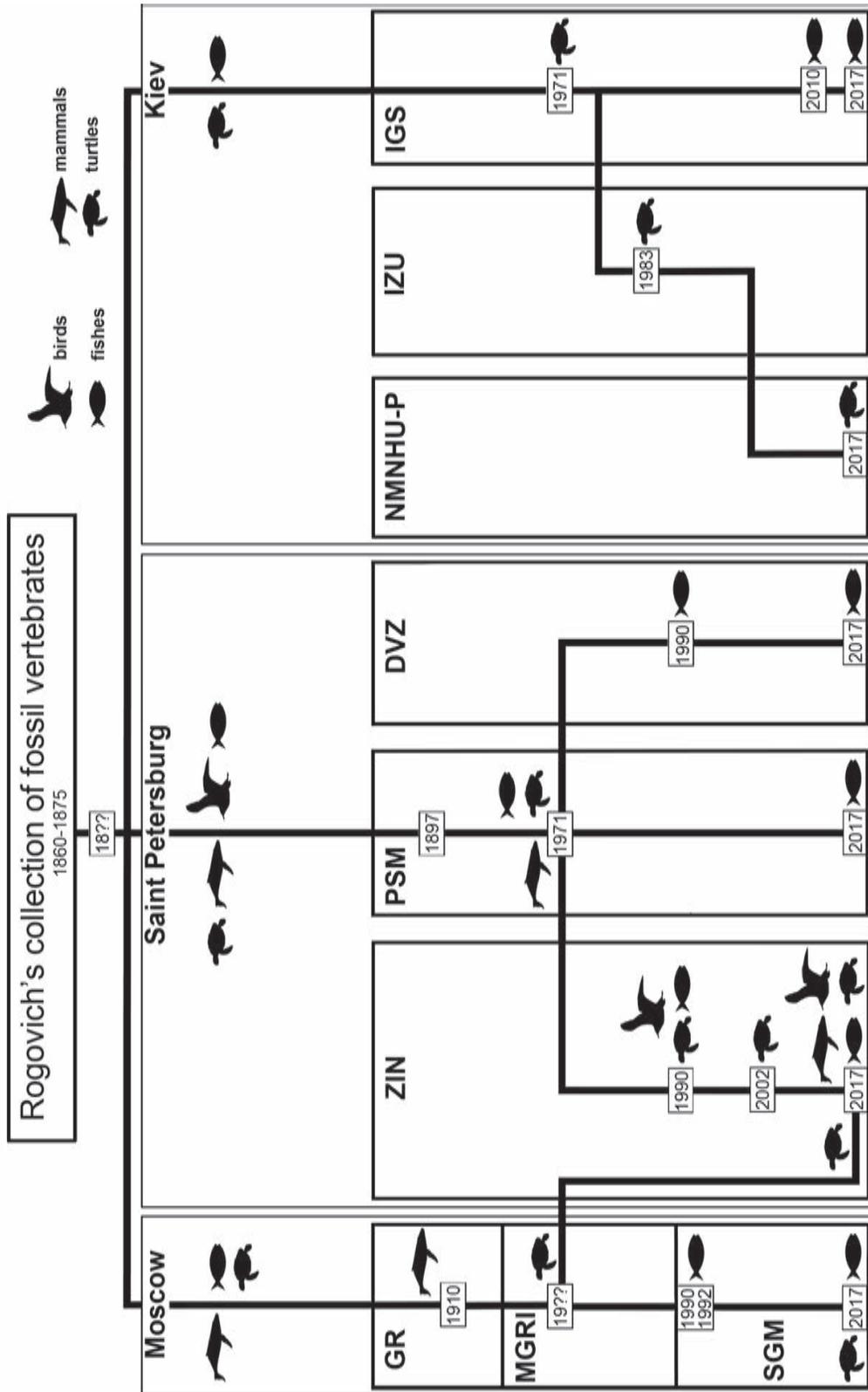


Fig. 2. A chart showing history of the Rogovich's collection of fossil vertebrates. Years mark time of the Rogovich's publications (1860–1875), division or transference of the material (18??, 19??, 1971) or its mentionings in the literature (Anonymous 1897; Pavlova 1910; Tarashchuk 1971; Chkhikvadze 1983; Averianov et al. 1990; Nessov 1992; Averianov 2002; Bannikov 2010; and this paper [2017]). See text for explanations and abbreviations.

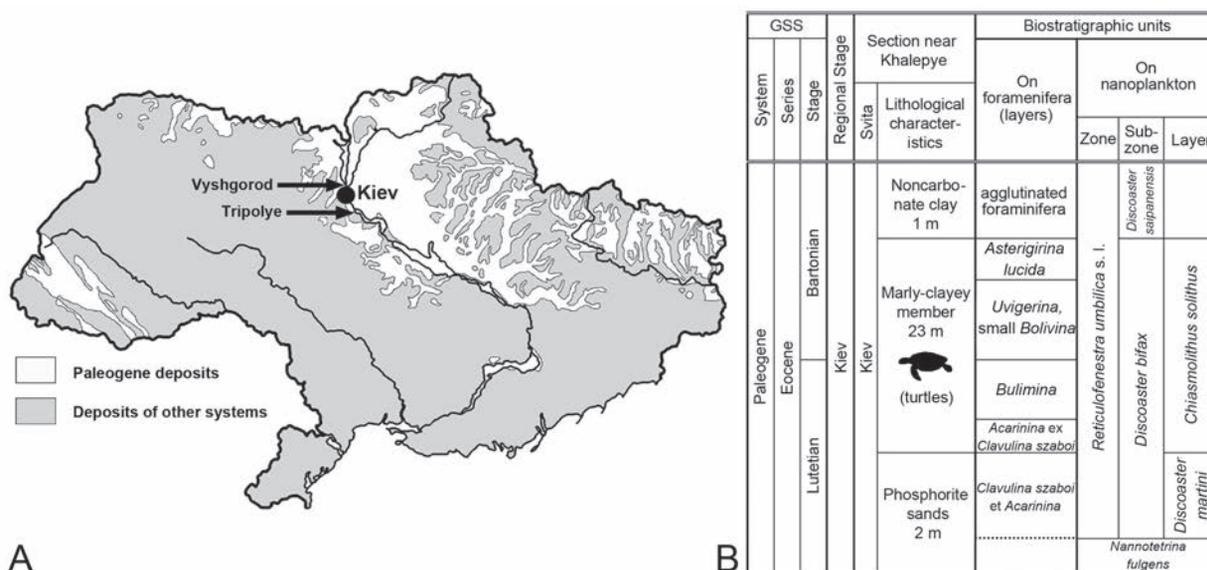


Fig. 3. Geographic position of Vyshgorod and Tripolye localities (A; map of the Ukrainian SSR after Nalivkin and Sokolov 1983, with changes) and stratigraphic section of the stratotype of the Kiev Formation near Khalepye Village, Obukhov District, Kiev Province, Ukraine (B; after Ryabokon' 2002, with changes).

(2015: ch. 116); *Erquelinnesia gosseleti* Dollo, 1886, as described by Zangerl (1971); *Euclastes acutirostris* Jalil et al., 2009, as described by Jalil et al. (2009); *E. platyops* Cope, 1867, as described by Hay (1908); *E. wielandi* (Hay, 1908) (= *Osteopygis roundsi* Weems, 1988; = *Osteopygoides priscus* Karl et al., 1998; for other synonyms see Parham and Pyenson 2010), as described by Hay (1908), Weems (1988) and Karl et al. (1998); *Lepidochelys kempii* (Garman, 1880), based on Zangerl (1958: figs. 17, 18) and Cadena and Parham (2015: ch. 116); *Lepidochelys olivacea* (Eschscholtz, 1829), based on Zangerl and Turnbull (1955: fig. 96), Wyneken (2001: fig. 37b) and Cadena and Parham (2015: ch. 116); *Mexichelys coahuilaensis* (Brinkman et al., 2009), as described by Brinkman et al. (2009); *Natator depressus* (Garman, 1880), as described by Zangerl et al. (1988); *Osonachelus decorata* Lapparent de Broin et al., 2014, as described by Lapparent de Broin et al. (2014); *Pacifichelys hutchisoni* (Lynch et Parham, 2003), as described by Lynch and Parham (2003); *Pacifichelys urbinai* Parham et Pyenson, 2010, as described by Parham and Pyenson (2010); *Procolpochelys charlestonensis* Weems et Sanders, 2014, as described by Weems and Brown (2017); *Procolpochelys grandaeva* (Leidy, 1851), as described by Weems and Brown (2017); *Puppigerus camperi* (Gray, 1831) (for synonyms see

Moody [1974]), as described by Moody (1974) and Tong et al. (2012); *Tasbacka aldabergeni* Nesso, 1987, as described by Nesso (1987) and personal observations of the type material (CCMGE 1/12175); *Tasbacka ouledabdounensis* Tong et Hirayama, 2002, as described by Tong and Hirayama (2002); *Tasbacka ruhoffi* (Weems, 1988), as described by Weems (1988); *Toxochelys latiremis* Cope, 1873, as described by Zangerl (1953) and Matzke (2008); *Trachyaspid lardyi* Meyer, 1843 (= *Syllomus aegyptiacus* Lydekker, 1889), as described by Hasegawa et al. (2005) and Villa and Raineri (2015).

Anatomical terminology in this paper used from Gaffney (1979; for cranial bones) and Romer (1956; for postcranial bones).

We included data on *Argillochelys antiqua* from Vyshgorod, *A. antiqua* from Western Europe and "*Argillochelys*" *africana* in a recently published character matrix of Weems and Brown (2017), which represents a modified variant of character matrix of Parham and Pyenson (2010). Three new characters (36–38) were added to the character matrix to distinguish species of *Argillochelys* and "*Argillochelys*" *africana* (see Appendix 1 for details about these new characters and Appendix 2 for characters coded for *A. antiqua* from Vyshgorod and *A. antiqua* from Western Europe and "*Argillochelys*" *africana*).

In addition, the codings of some characters were changed for six taxa (see Appendix 3). The ordering of characters 1–35 follows Weems and Brown (2017), the characters 36–38 were left unordered. A phylogenetic analysis was performed using TNT 1.5 (Goloboff and Catalano 2016) using traditional search with 1000 replicates and 10 trees saved per replicate followed by TBR of the trees in memory. The tree statistics and distribution of characters were obtained using WinClada 1.00.08 (Nixon 2002). The search resulted in ten most parsimonious trees of 96 steps (consistency index [CI] = 0.45; retention index [RI] = 0.66). The strict consensus of these trees (Fig. 13) differs from the tree of Weems and Brown (2017) in some details (see Discussion).

SYSTEMATICS

Testudines Batsch, 1788

Cryptodira Cope, 1868

Pan-Cheloniodea Joyce, Parham et Gauthier, 2004

Pan-Cheloniidae Joyce, Parham et Gauthier, 2004

***Argillochelys* Lydekker, 1889**

Type species. *Chelone cuneiceps* Owen, 1849.

Emended diagnosis. (1) Orbits directed laterally and slightly anteriorly. (2) Frontals contributing to the orbital margins. (3) The secondary palate reaches between half and two thirds the distance between the anterior margin of the skull and the fossa temporalis inferior. (4) Labial ridge of the upper jaw is vertical and sharp. (5) Vomer hexagonal in outline and in a wide contact with the palatines on the secondary palate. (6) Pterygoids broad anteriorly and with posterolaterally oriented external processes. (7) Length of the mandibular symphysis about one third the length of the mandibular ramus. (8) Triturating surface of the lower jaw with labial, lingual, and symphyseal ridges. (9) Plastron with wide axillo-inguinal distance (plastral bridge). See Discussion for details about characters.

Included species. *Argillochelys antiqua* (König, 1825), *A. athersuchi* Moody, 1980, and *Argillochelys cuneiceps* (Owen, 1849).

Distribution. See Discussion.

Remarks. Attribution of *Argillochelys africana* Tong et Hirayama, 2008 from the early Eocene (Ypresian) of Morocco (Tong and Hirayama 2008) to the

genus *Argillochelys* was questioned by some authors (Jalil et al. 2009; Danilov et al. 2010; Lapparent de Broin et al. 2014), who considered it “*A. africana*”. In this paper, we confidently remove this species from *Argillochelys* based on results of the phylogenetic analysis (see Discussion).

Argillochelys athersuchi was included in the genus *Eochelone* by Lapparent de Broin (2001; Lapparent de Broin et al. 2014), but without justification. Incompleteness of the material of this species along with a brief description does not allow its inclusion in the phylogenetic analysis. For this reason, its attribution to the genus *Argillochelys* should be considered as somewhat conditional.

***Argillochelys antiqua* (König, 1825)**

(Figs. 4–9, 12)

Chelone antiqua: König 1825: taf. 18, fig. 238.

Chelone convexa: Owen 1841: 575.

Chelone subcristata: Owen 1841: 576.

Hypsodon kioviensis [partim]: Rogovich, 1871: pl. 10, figs. 47, 48, 51.

Anthracotherium alsaticum [partim]: Rogovich 1875a: 36; 1875b: 46.

Several fragments of the turtle shell [?]: Rogovich 1875c: 2.
Argillochelys antiqua: Lydekker 1889: 41, fig. 10; Kuhn 1964: 157 (see for other references and synonyms).

Argillochelys subcristata: Lydekker 1889: 47; Kuhn 1964: 158 (see for other references and synonyms).

Argillochelys convexa: Lydekker 1889: 48; Kuhn 1964: 157 (see for other references and synonyms); Moody 1980: 165 (nomen vanum).

Argillochelys cuneiceps [partim]: Lydekker 1889: fig. 11 (see Discussion).

Cheloniidae [indet.]: Dubrovo and Kapelist 1979: 10.

Argillochelys antiqua = *A. subcristata* = *A. convexa*: Moody 1980: 165.

Puppigerus sp.: Chkhikvadze 1983: 30, figs 11, 13; 1990: 5; 1999: 259.

“*Puppigerus*” sp.: Nesson 1987: 82.

Dollichelys rogovichi [partim]: Averianov 2002: 147, figs. 8a–g, 1, 9, 10.

Holotype. NHM 49465, partial skull.

Previously referred material. See Lydekker (1889), Moody (1980, 1997), and Discussion.

Newly referred material. Partial skeleton, probably, of one individual consisting of the following specimens: NMNHU-P without number (formerly IZU; hereinafter NMNHU-P), nuchal, right peripheral 1, carapace fragment, including neurals 3, 4, and a small fragment of neural 5, right and left costals 3

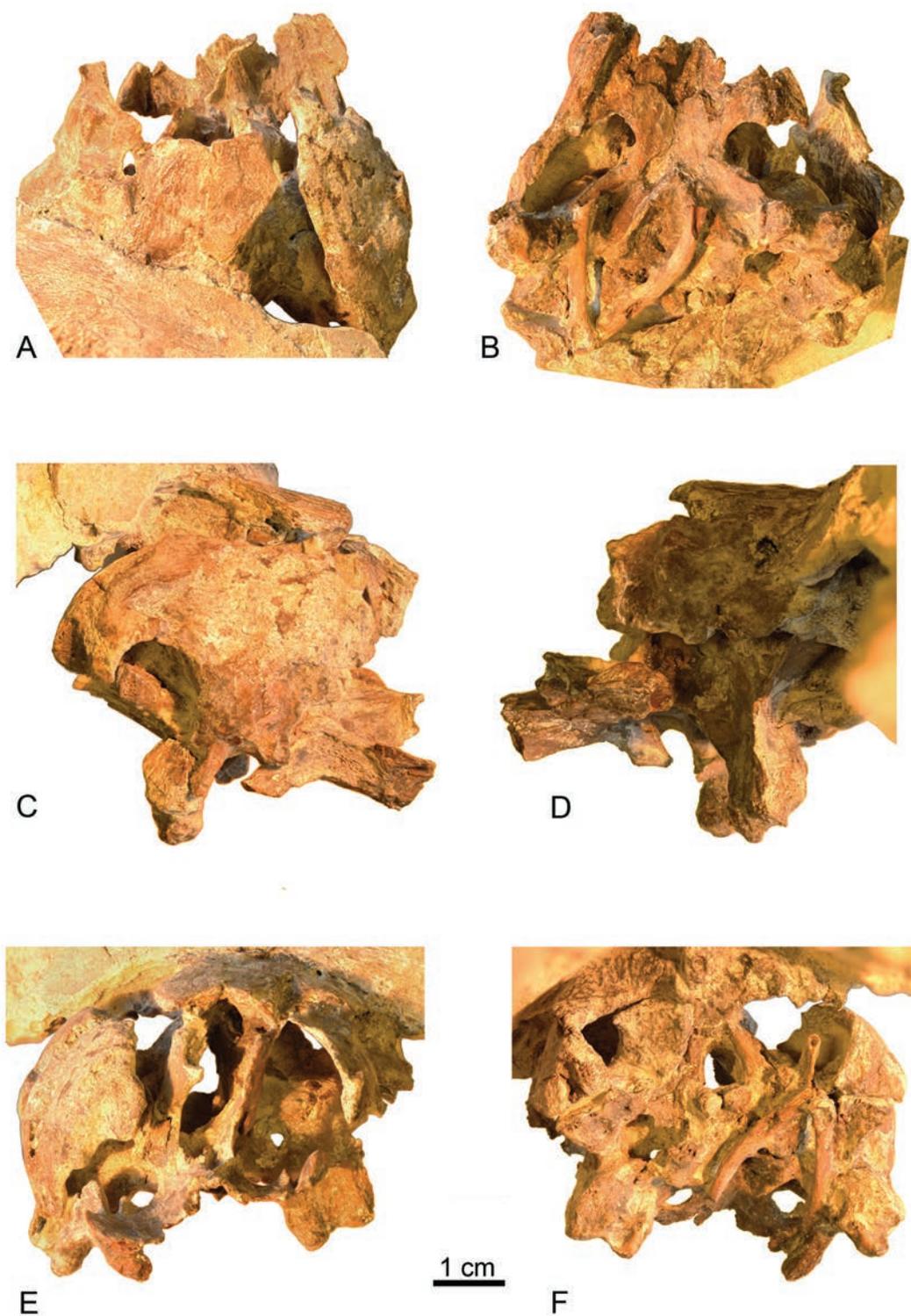
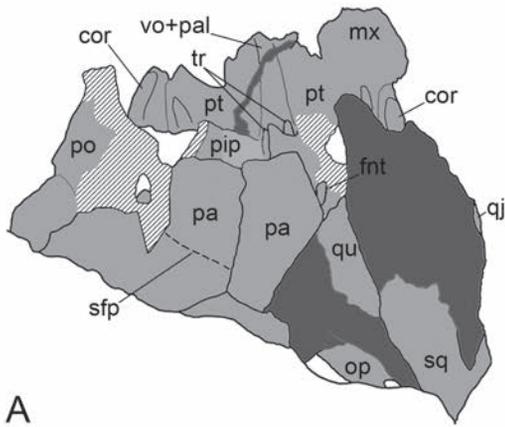
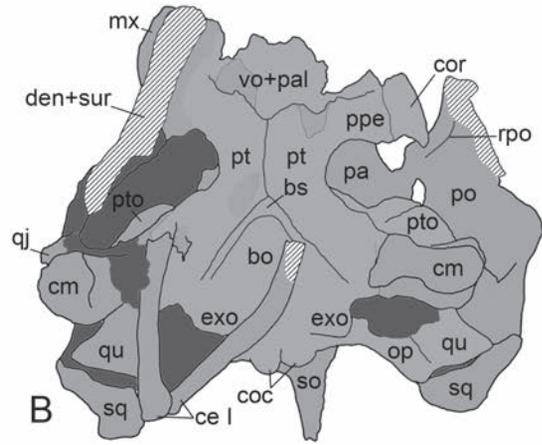


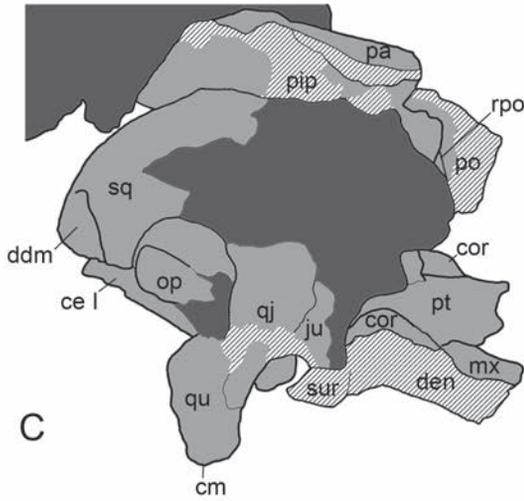
Fig. 4. *Argillochelys antiqua* from Vyshgorod locality, ZIN PH 8/36, posterior part of the skull with anterior margin of the carapace, photos: A – dorsal view; B – ventral view; C – right lateral view; D – left lateral view; E – anterior view; F – posterior view. See Fig. 5 for explanatory drawings.



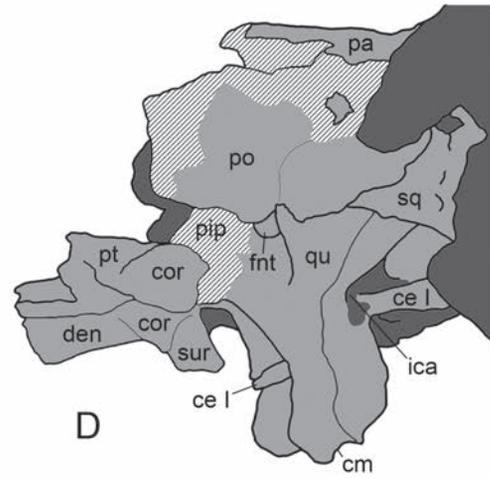
A



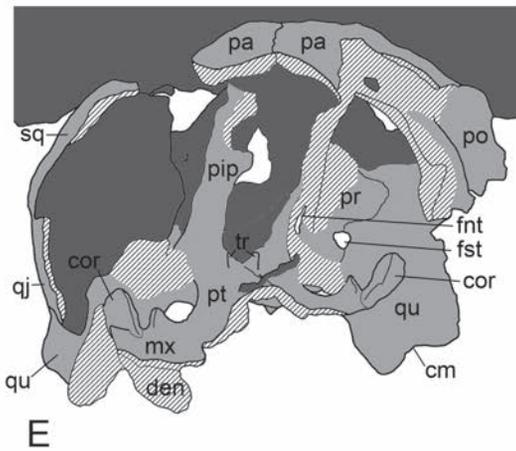
B



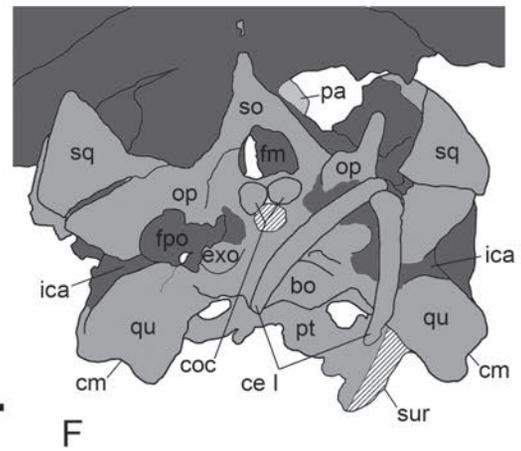
C



D



E



F

and 4, fragment of right hyoplastron, cervical vertebra V, metatarsal I, four phalanges; ZIN PH 2/36, premaxillae with anterior portions of both maxillae; ZIN PH 3/36 + 4/36, dentary symphysis (primarily was in two pieces; see Averianov 2002); ZIN PH 5/36, anterior part of the right ceratobranchiale I; ZIN PH 8/36, part of the skeleton, including the posterior part of the skull and lower jaw, and remains of the carapace, including ribheads and bases of neurals (neural arches) in matrix (gray-blue marl with pyrite), and imprints of the nuchal (with a thin layer of bone in the left part), three neurals and three pairs of costals, as well as a part of the internal surface of the right postorbital; ZIN PH 9/36, anterior portion of the right jugal; ZIN PH 10/36, right surangular; and ZIN PH 11/36, anterior part of the left ceratobranchiale I. ZIN PH 7/36, an isolated medial part of the right costal 4(?) from another individual.

Locality, horizon, and age for the newly referred material. Vyshgorod locality, Kiev Province, Ukraine; marly-clayey member of the Kiev Formation; upper Lutetian – lower Bartonian, middle Eocene (see Geology and age of the localities for details).

Distribution. ?Thanetian, Belgium; Ypresian, England; Lutetian – Bartonian, Ukraine; ?Eocene, Netherlands (see Discussion for details).

Emended diagnosis. (1) Frontoparietal scale with a posterior extension. (2) External pterygoid processes relatively large. (3) Lower jaw symphysis subtriangular. See Discussion for details about characters.

Description. Skull bones of ZIN PH 8/36 are variously deformed, displaced and damaged. Part of their surface is covered with a crust of pyrite or marl with hard particles, or with other displaced bones.

Scale sulci of the skull are represented by sulcus between the frontoparietal and parietal scales on the left parietal bone of ZIN PH 8/36 (Figs 4A, 5A) and between the jugal and maxilla scales on the right jugal bone of ZIN PH 9/36 (Figs. 6G, 7G). The posteromedial portion of the frontoparietal scale is extended posteriorly. The sulcus between the jugal and maxilla scales goes from the orbital margin to about the lower part of the contact between the jugal and quadratojugal bones.

Both parietals in articulation are partially preserved in ZIN PH 8/36 (Figs. 4, 5). All margins of their dorsal plates, except part of the medial margin, are damaged. The upper temporal emargination does not reach the level of the foramen stapedio-temporale. Both descending processes of the parietals are almost completely preserved. Ventrally, they contact the pterygoids and prootics, and form dorsal margins of the large foramina nervi trigemini, and posteroventrally, they contact the supraoccipital.

The jugals are represented by most part of the right jugal of ZIN PH 9/36 (Figs. 6G, 7G) and by fragment of its posterior part in ZIN PH 8/36 (Figs. 4C, 5C). The internal surface of the jugal has a thickening (ridge) parallel to the orbital margin. The preserved contacts of the jugal include contact with the quadratojugal and part of the contact with the postorbital. The jugal forms posteroventral margin of the orbit and anterior margin of the lower temporal (cheek) emargination.

Only right quadratojugal without dorsal part is preserved in ZIN PH 8/36 (Figs. 4A–C, E, 5A–C, E). It contacts the quadrate ventrally and the jugal anteriorly, whereas other contacts are not preserved. The quadratojugal forms the anterior rim of the semi-circular cavum tympani.

Fig. 5. *Argillochelys antiqua* from Vyshgorod locality, ZIN PH 8/36, posterior part of the skull, explanatory drawings: A – dorsal view (anterior margin of the carapace is not shown); B – ventral view (anterior margin of the carapace is not shown); C – right lateral view; D – left lateral view; E – anterior view; F – posterior view. Bones are filled with light-grey. Matrix is filled with dark-grey. Sutures are stippled. Breakages are hatched. See Fig. 4 for photos. *Abbreviations:* aam – area articularis mandibularis; Ab – abdominal scale; asg – “anchor-shaped” groove on the palatal surface of the premaxillae; bo – basioccipital; bs – basisphenoid; cai – canalis alveolaris inferior; cdm – canalis dentofaciale majus; Ce – cervical scale; ce I – ceratobranchiale I; cm – condylus mandibularis; co – costal; coc – condylus occipitalis; cor – coronoid; cr – skull; ddm – depression for the m. depressor mandibulae, den – dentary; exo – exoccipital; fcv – facet for cervical vertebra VIII; fdm – foramen dentofaciale majus; fm – foramen magnum; fnt – foramen nervi trigemini; fpm – foramina on the dorsal process of the premaxilla; fpo – fenestra postotica; fst – foramen stapedioteporale; hk – hyoplastral keel; ica – incisura columellae auris; ico – imprint of costal; ine – imprint of neural; inu – imprint of nuchal; ju – jugal; lar – labial ridge; lir – lingual ridge; mx – maxilla; ne – neural; nk – neural keel; op – opisthotic; pa – parietal; pal – palatine; Pe – pectoral scale; pip – processus inferior parietalis; Pl – pleural scale; pm – premaxilla; po – postorbital; ppe – processus pterygoideus externus; pr – prootic; pt – pterygoid; pto – processus trochlearis oticum; qj – quadratojugal; qu – quadrate; rpo – ridge on the internal surface of the postorbital; scm – sulcus cartilaginis meckelii; sfp – sulcus between frontoparietal and parietal scales; sir – symphyseal ridge; sjm – sulcus between jugal and maxilla scales; so – supraoccipital; sq – squamosal; sur – surangular; sv – sutural surface for contact with the vomer; tr – trabeculum; Ve – vertebral scale; vo – vomer.

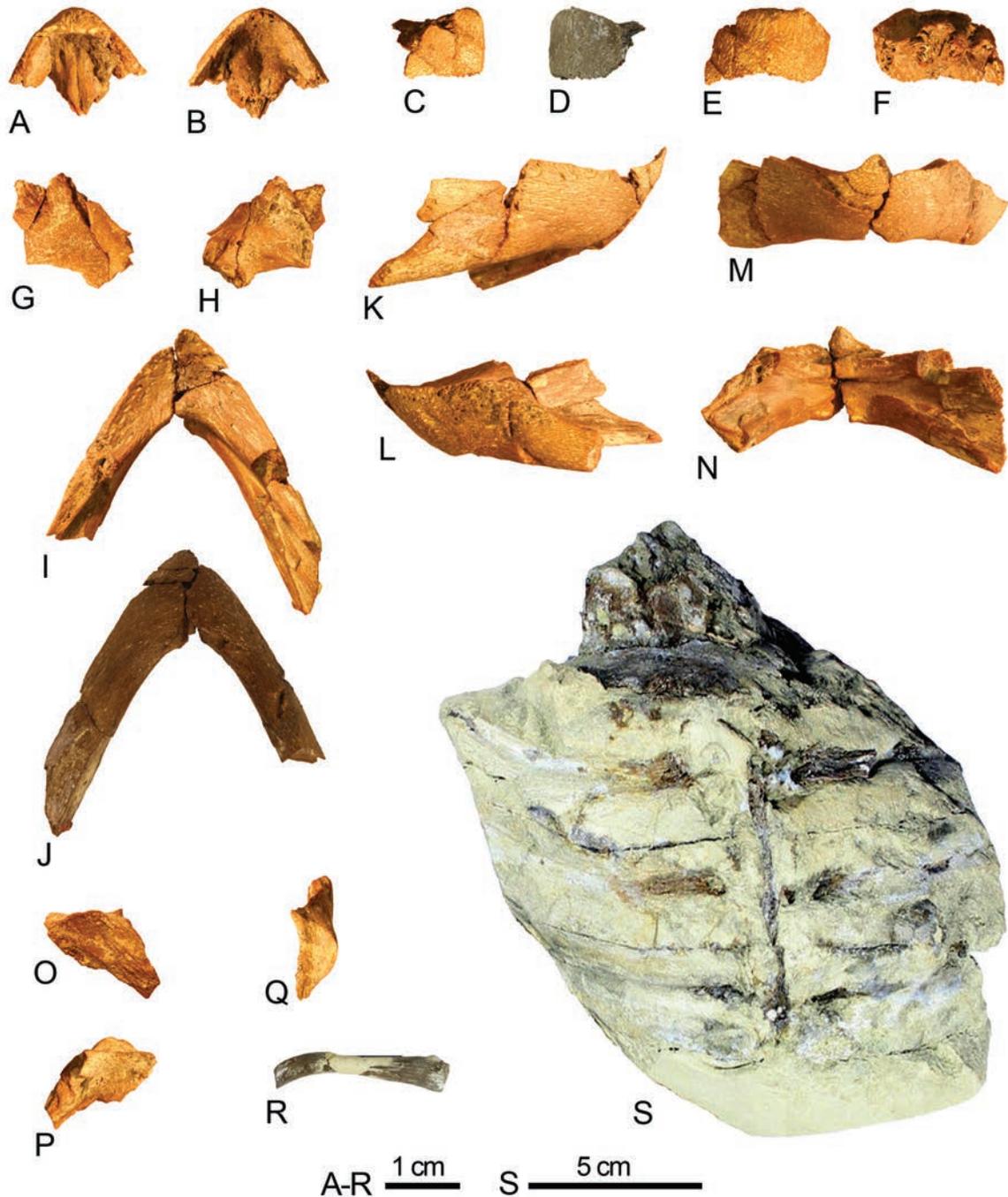


Fig. 6. *Argillochelys antiqua* from Vyshgorod locality, photos: A–F – ZIN PH 2/36, premaxillae with anterior portions of both maxillae: A – dorsal view; B – ventral view; C – right lateral view; D – left lateral view; E – anterior view; F – posterior view; G, H – ZIN PH 9/36, right jugal: G – lateral (external) view; H – medial (internal) view; I–N – ZIN PH 3/36 + 4/36, dentary symphysis: I – dorsal view; J – ventral view; K – right lateral view; L – left lateral view; M – anterior view; N – posterior view; O–Q – ZIN PH 10/36, right surangular: O – lateral view; P – medial view; Q – dorsal view; R – ZIN PH 5/36, anterior part of the right ceratobranchiale I; S – ZIN PH 8/36, part of the skeleton, including posterior part of the skull and lower jaw, and remains of the carapace (before preparation). See Fig. 7 for explanatory drawings.

Both squamosals are preserved in ZIN PH 8/36 (Figs. 4, 5), although the right one is damaged anteriorly, whereas the dorsal part of the left one is covered by a fragment of the ?left postorbital. The depression for the *m. depressor mandibulae* is deep, semilunate in shape, and oriented posterolaterally. The left squamosal preserves contact with the postoticum posteromedially, and both squamosals have contact with the quadrate ventrally; other contacts are not preserved. The squamosal forms the posterior border of the *cavum tympani* and the lateral border of the upper temporal emargination.

Anterior and probably posterior parts of the left postorbital are partially preserved in ZIN PH 8/36 (Figs. 4A–E, 5A–E). Internally, the postorbital bears a ridge (thickening) which is parallel to the orbital margin. Contacts of the postorbital and sulci on its surface are not visible.

Both premaxillae are preserved in articulation with each other and with anterior fragments of the maxillae (ZIN PH 2/36; Figs. 6A–F, 7A–F). The premaxillae are not fused and not involved in the formation of the foramina praepalatinum. The labial ridges of the premaxillae are sharp, vertical and does not form hook or notch. On the palatal surface of each premaxilla, posteriorly, there is a swelling, which must be continued on the maxilla. Between these swellings and anterior to them, there are depressions, forming an “anchor-shaped” groove, which accepts anterior parts of labial and lingual ridges of the dentaries. On the dorsal surface of each premaxilla, anteriorly, there is a high transverse process (as high as the labial ridge), which forms the lower margin of the external narial opening. There is a pair of foramina on the top of this process, and one foramen, probably connected with them, posterior to the process. Besides contacts with the maxillae, only contact surface for the vomer is visible posteriorly.

The maxillae are represented by small fragments in articulation with the premaxillae in ZIN PH 2/36 (Figs. 6A–F, 7A–F) and by the posterior part of the right maxilla in ZIN PH 8/36 (Figs. 4A–C, E, 5A–C, E), which is covered by a fragment of the dentary ventrally. No contacts of the maxillae, other than with the premaxillae, are observable.

The area of the vomer and palatines is preserved in ZIN PH 8/36 (Figs. 4A, B, 5A, B). This area is concave ventrally, suggesting presence of a wide choana. Posteriorly, this area contacts the pterygoids.

Both quadrates are preserved in ZIN PH 8/36, although the right one is strongly displaced from its natural position (Figs. 4, 5). The quadrates form lateral borders of a large, anterodorsally oriented foramina stapedio-temporale. The incisurae columellae auris, visible from posteriorly, are not closed. Both processus trochlearis oticum are well visible in ventral aspect. Both condylus mandibularis are divided into two facets. Both quadrates preserve contacts with the squamosals dorsally and with the pterygoids anteromedially, the right quadrate preserves contact with the quadratojugal anterolaterally, and the left quadrate, with the prootic anteromedially.

Both pterygoids are preserved in ZIN PH 8/36, although the posterior part of the right pterygoid is covered with the right ceratobranchiale I ventrally (Figs. 4, 5). Width of the pterygoid waist is 120% of the length of the interpterygoid contact. The external pterygoid process is large and directed posteriorly and slightly laterally. The foramen palatinum posterius is absent. The carotid foramina (foramen anterius canalis carotici palatinum and foramen posterius canalis carotici interni) are not preserved. The sagittal ventral ridge on the ventral surface of the pterygoid is not developed. The following contacts of the pterygoids are present: with the vomer-palatine area anteriorly, with the basisphenoid and basioccipital posteromedially, and with the quadrates posterolaterally.

The basisphenoid is preserved in ZIN PH 8/36 (Figs. 4A, B, E, 5A, B, E). In the ventral surface it has a V-shaped crest. The rod-like rostrum basisphenoidale, closely set trabeculae and the low dorsum sellae are visible in dorsal view, whereas the foramina anterius canalis carotici interni are not preserved. The basisphenoid contacts the pterygoids anterolaterally and the basioccipital posteriorly.

The supraoccipital is almost completely preserved in ZIN PH 8/36, but its dorsal part is covered with a pyrite cover (Figs. 4B, F, 5B, F). It forms the dorsal margin of the foramen magnum. The crista supraoccipitalis is partially visible. The only observable contact of the supraoccipital is that with the left exoccipital ventrally.

Both exoccipitals are preserved in ZIN PH 8/36, although the right one is partially covered with the displaced right opisthotic and matrix (Figs. 4B, F, 5B, F). The contacts of the exoccipitals are visible with the supraoccipital dorsally and with the left opisthotic dorsolaterally. The exoccipitals form

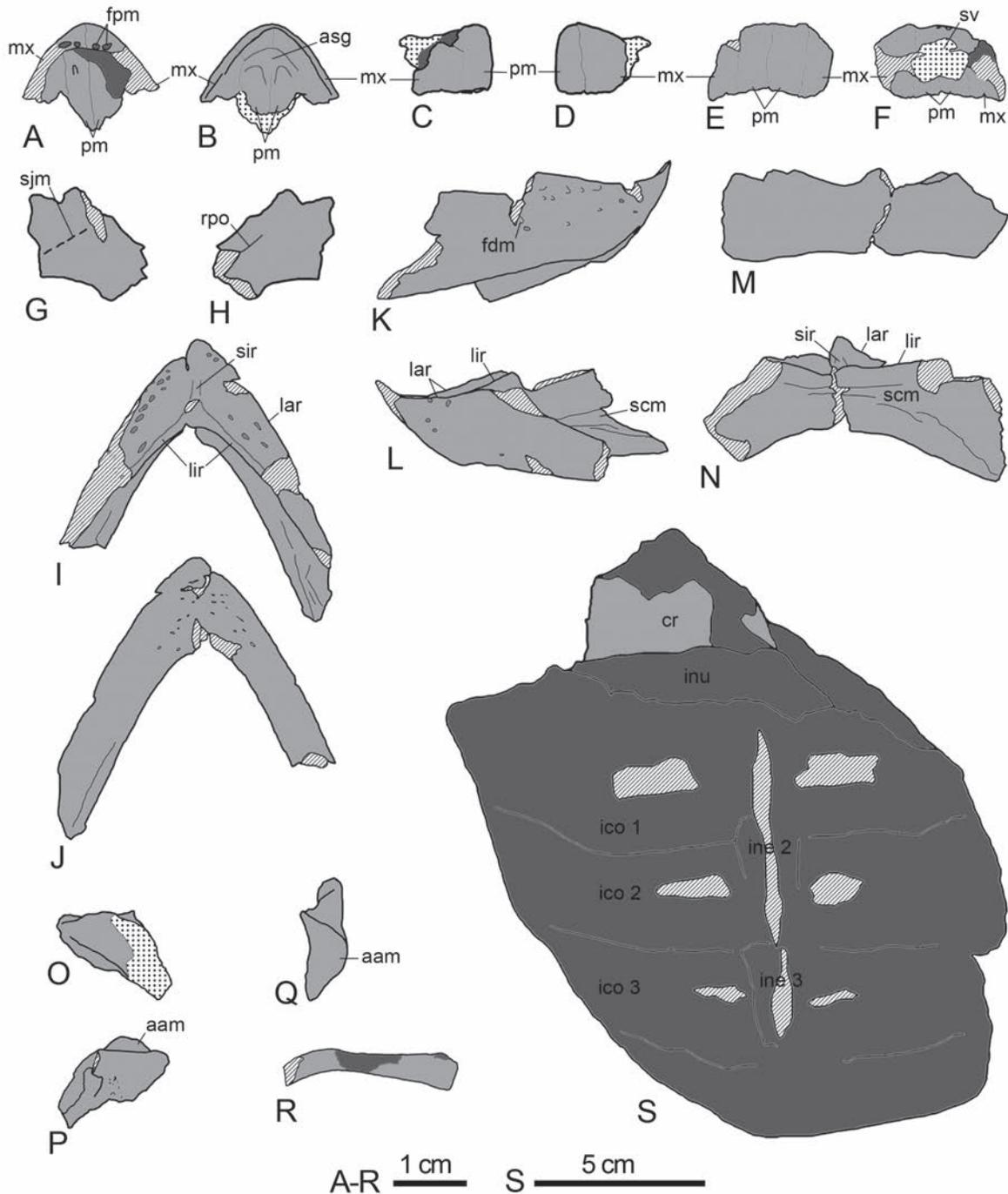


Fig. 7. *Argillochelys antiqua* from Vyshgorod locality, explanatory drawings: A–F – ZIN PH 2/36, premaxillae with anterior portions of both maxillae: A – dorsal view; B – ventral view; C – right lateral view; D – left lateral view; E – anterior view; F – posterior view; G, H – ZIN PH 9/36, right jugal: G – lateral (external) view; H – medial (internal) view; I–N – ZIN PH 3/36 + 4/36, dentary symphysis: I – dorsal view; J – ventral view; K – right lateral view; L – left lateral view; M – anterior view; N – posterior view; O–Q – ZIN PH 10/36, right surangular: O – lateral view; P – medial view; Q – dorsal view; R – ZIN PH 5/36, anterior part of the right ceratobranchiale I; S – ZIN PH 8/36, part of the skeleton, including posterior part of the skull and lower jaw, and remains of the carapace (before preparation). See Fig. 6 for photos and Fig. 5 for designations and abbreviations.

dorsolateral parts of the condylus occipitalis, lateral margins of the foramen magnum and medial margins of the fenestrae postotica.

The basioccipital is preserved in ZIN PH 8/36, but partially covered with the left ceratobranchiale I ventrally and missing ventral part of the condylus occipitalis (Figs. 4B, F, 5B, F). The ventral surface of the basioccipital forms a semi-oval depression, limited anteriorly and anterolaterally by a ridge at the posterior border of the basisphenoid and posteromedial borders of the pterygoids. There are no ridges in the depression. The contacts of the basioccipital are visible with the basisphenoid anteriorly and with the pterygoids anterolaterally.

Only the left prootic is preserved in ZIN PH 8/36 (Figs. 4E, 5E). It contacts the quadrate laterally and forms the lateral border of the foramen stapediotemporale and posterior border of the foramen nervi trigemini.

Both opisthotics are present in ZIN PH 8/36, and the right one is displaced from its normal position (Figs. 4A–C, F, 5A–C, F). The processus paroccipitalis, preserved in the right opisthotic only, is lancet-shaped. The contacts of the opisthotic with the quadrate, squamosal and exoccipital are visible on the left side of the skull.

The dentary is represented by the symphysis primarily described as two pieces (ZIN PH 3/36 and ZIN PH 4/36; Averianov 2002; Figs. 6I–N, 7I–N) and by the posterior part of the right dentary of ZIN PH 8/36 (Figs. 4B–E, 5B–E). The posterior part of the left dentary is missing. The labial ridge is high and forms a hook at the anterior edge of the symphysis. The symphyseal and lingual ridges are present, but low. The triturating surface between them is concave. The length of the symphysis is about one third the length of the dentary. The sulcus cartilagineus meckelii is deep in the area of the symphysis and lies in the horizontal plane. The foramen dentofaciale majus is preserved on the right side and situated far posterior from the symphysis. The dentaries bear a lot of nutritive foramina, especially large on the triturating surface. The contacts of the dentary with the coronoid posterodorsally and with the surangular posterolaterally are visible in ZIN PH 8/36.

Both coronoids are preserved in ZIN PH 8/36 (Figs. 4A–E, 5A–E). The coronoid process is low. The bone forms the anterior border of the fossa meckelii. There are contacts of the coronoid with the dentary anteriorly and with the surangular posterolaterally.

The surangular is represented by most part of the right bone in ZIN PH 10/36 (Figs. 6O–Q, 7O–Q) and by its anterior part in ZIN PH 8/36 (Figs. 4B–D, F, 5B–D, F). The surangular forms the lateral border of the fossa meckelii and the lateral part of the area articularis mandibularis. According to the sutural ventrolateral surface of the surangular, it contacted with the dentary and did not wedge into it in lateral aspect. In addition, the surangular had contact with the coronoid, whereas other contacts are not preserved.

Both ceratobranchiale I are preserved and represented by isolated anterior parts (ZIN PH 5/36 and ZIN PH 11/36; Figs. 6R, 7R) and posterior parts in matrix in ZIN PH 8/36 (Figs. 4B–D, F, 5B–D, F). ZIN PH 5/36 is partially reconstructed with gypsum. Middle parts of both bones are absent. As reconstructed, the bones were long and curved.

The right stapes is preserved within the otic capsule of ZIN PH 8/36. It is a small stick-like bone.

The nuchal of NMNHU-P is missing most of its right half, parts of the posterior and left borders (Figs. 8E, F, 9E, F). Part of the internal bone layer of the nuchal is preserved in ZIN PH 8/36 (Figs. 6S, 7S). As reconstructed, the nuchal was wide and short with a concave anterior border. Internally, the nuchal bears concavity for contact with cervical vertebra VIII. There were no postnuchal fontanelles.

NMNHU-P preserves neural 3 (missing left anterolateral part), neural 4 and anterior fragment of neural 5 in articulation with costals (Figs. 8G, 9G). ZIN PH 8/36 preserves neural spines of trunk vertebrae I–III and imprints of neurals 2 and 3 (Figs. 6S, 7S). According to available neurals and imprints, neurals 2–5 were hexagonal short-sided anteriorly, whereas neural 1 most probably was tetragonal. The anterior half of neural 3 has a low medial keel, whereas the posterior half and other available neurals are flat.

NMNHU-P preserves almost complete right costals 3 and 4 and medial parts of left costals 3 and 4 in articulation with neurals (Figs. 8G, 9G). ZIN PH 8/36 preserves ribheads and imprints of the ventral surface of right and left costals 1–3 (Figs. 6S, 7S). The free ribs of costals 3 and 4 are long, making up about one fourth of the costal widths.

The morphology of the isolated right costal 4 (ZIN PH 7/36; Figs. 8O, 9O) corresponds to those of NMNHU-P, from which it differs by larger size.

Peripheral 1 of NMNHU-P is long and narrow (Figs. 8H, 9H). Its free edge is rounded near nuchal

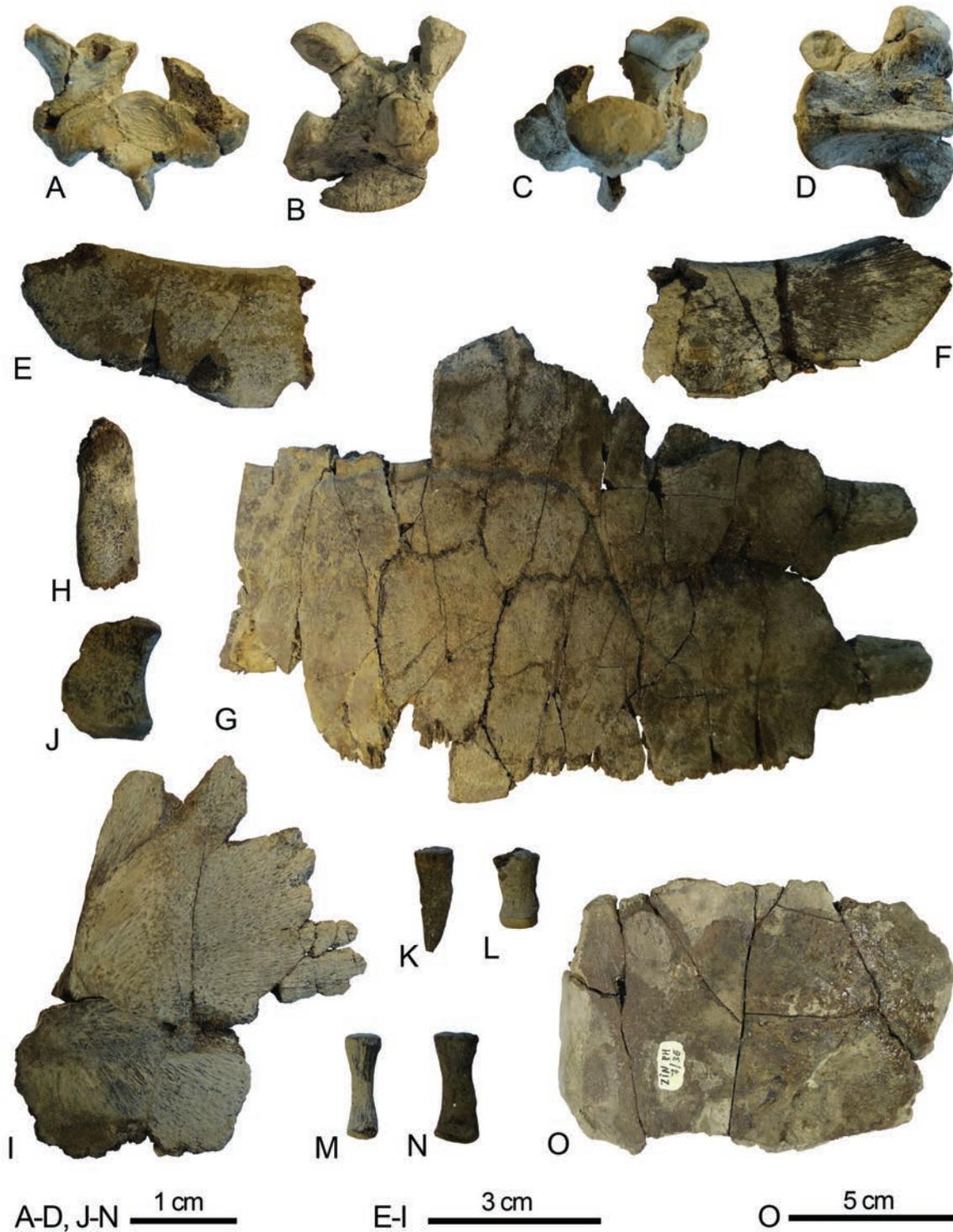


Fig. 8. *Argillochelys antiqua* from Vyshgorod locality, photos: A–N – NMNHU-P: A–D – cervical vertebra V: A – anterior view; B – right lateral view; C – posterior view; D – ventral view; E, F – nuchal: E – dorsal view; F – ventral view; G – carapace fragment in dorsal view; H – peripheral 1 in dorsal view; I – fragment of right hyoplastron in ventral view; J – metatarsal I; K – ungual phalange; L–N – non-ungual phalanges; O – ZIN PH 7/36, right costal 4 in dorsal view. See Fig. 9 for explanatory drawings.

(anterior) border, which forms an angle of about 45° to the posterior border of the plate.

The preserved sulci of the carapace of NMNHU-P (Figs. 8E–G, 9E–G) are represented by part of the sulcus between the cervical and vertebral 1 on the nuchal, the sulci between vertebrae 2 and 3 and left pleural 2, as well as right pleurals 2 and 3. Vertebral 3 was about as long as wide.

NMNHU-P includes the medial part of the right hyoplastron (Figs. 8I, 9I), previously erroneously interpreted as hypoplastron (Chkhikvadze 1983: fig. 13; Averianov 2002: fig. 9): the anterior breakage of the hyoplastron was considered to be a notch for the xiphoplastron, whereas the pectoral-abdominal sulcus was united with an anteroposteriorly directed keel. The medial border of the hyoplastron preserves a pair of long medial processes and a large postero-medial emargination of the central fontanelle. The central area of the ventral surface of the hyoplastron bears a thickening with an anteroposteriorly directed keel. The pectoral-abdominal sulcus is located just posterior to the ridge and parallel to the posterior border of the plate.

Cervical vertebra V of NMNHU-P is procoelous, missing part of the left neural arch and the spine process (Figs. 8A–D, 9A–D). The anterior articular facet of the centrum is rounded in the cross-section, whereas the posterior one is oval-shaped, due to slight dorsoventral flattening. The ventral (hypapophysial) keel is well developed. The prezygapophysial articular surface forms an angle of about 30° to the horizontal plane, whereas the postzygapophysial articular surface, about 40°. In general, this vertebra is similar to cervical vertebra V of *Argillochelys cuneiceps* (see Moody 1974, pl. 6).

Of the limb bones, NMNHU-P preserves a semi-lunar metatarsal I (Figs. 8J, 9J), one ungual and three non-ungual phalanges (Figs. 8K–N, 9K–N).

Remarks. According to our interpretation, the partial skeleton of *Argillochelys antiqua* from Vyshgorod locality described above, probably, was first mentioned by Rogovich (1875c) as a part of the turtle shell. Later parts of this skeleton were stored in different institutions of Moscow (MGRI), Saint Petersburg (PSM and ZIN), and Kiev (IGS, IZU, and NMNHU-P), sharing the fate of the whole Rogovich's collection of fossil vertebrates (see Comments on the history...; Fig. 2). It is unclear, what part of this material was mentioned by Khosatzky (1949, 1951) and Pidoplichko (1961) as sea turtle

(see Introduction for citations). Tarashchuk (1971: 56) clearly mentioned “specimen of an Eocene sea turtle” stored in IGS, which was later transferred to IZU and described by Chkhikvadze (1983) as *Puppigerus* sp. and now is stored in NMNHU-P. Averianov (2002) examined part of the material stored in ZIN (transferred from PSM) and assigned it, along with IZU (NMNHU-P) material, to *Dollochelys rogovichi* Averianov, 2002. Our study includes additional material from ZIN (transferred from MGRI). Another specimen (ZIN PH 7/36; transferred from PSM), referred to *D. rogovichi* by Averianov (2002) and to *A. antiqua* here, is labeled as a mammal *Anthracotherium alsaticum* (Fig. 1C) either due to misinterpretation by Rogovich (1875a, b) or due to a mistake with the label. The “fish” material of Rogovich (1871) assigned to *Dollochelys rogovichi* by Averianov (2002) needs additional study and only tentatively referred here to *A. antiqua*.

Pan-Cheloniidae incertae sedis

“*Dollochelys*” *rogovichi* Averianov, 2002 (Figs. 10A–G, 11A–G)

Dollochelys rogovichi: Averianov 2002: 147, fig. 8h–k; Hirayama 2006: 4 (nomen dubium); Chkhikvadze 2010: 99.

Holotype. ZIN PH 1/36, right fragmented dentary of an adult individual.

Material. Holotype and ZIN PH 6/36, left fragmented dentary (possibly from the same individual as the holotype).

Locality, horizon, and age. Vyshgorod locality, Kiev Province, Ukraine; marly-clayey member of the Kiev Formation; upper Lutetian – lower Bartonian, middle Eocene (see Geology and age of the localities for details).

Description. ZIN PH 1/36 and ZIN PH 6/36 have a similar size and morphology and possibly belong to one individual. Both specimens demonstrate high labial ridges, wide and dorsomedially oriented triturating surfaces, and rudimentary lingual ridges located in the middle of the triturating surfaces. The triturating surface between them is not concave. The area of the symphyseal ridge is missing. The sulcus cartilagineus meckelii is getting shallower towards the symphysis. The canalis dentofacialis major and canalis alveolaris inferior are visible on the posterior broken surface of ZIN PH 1/36.

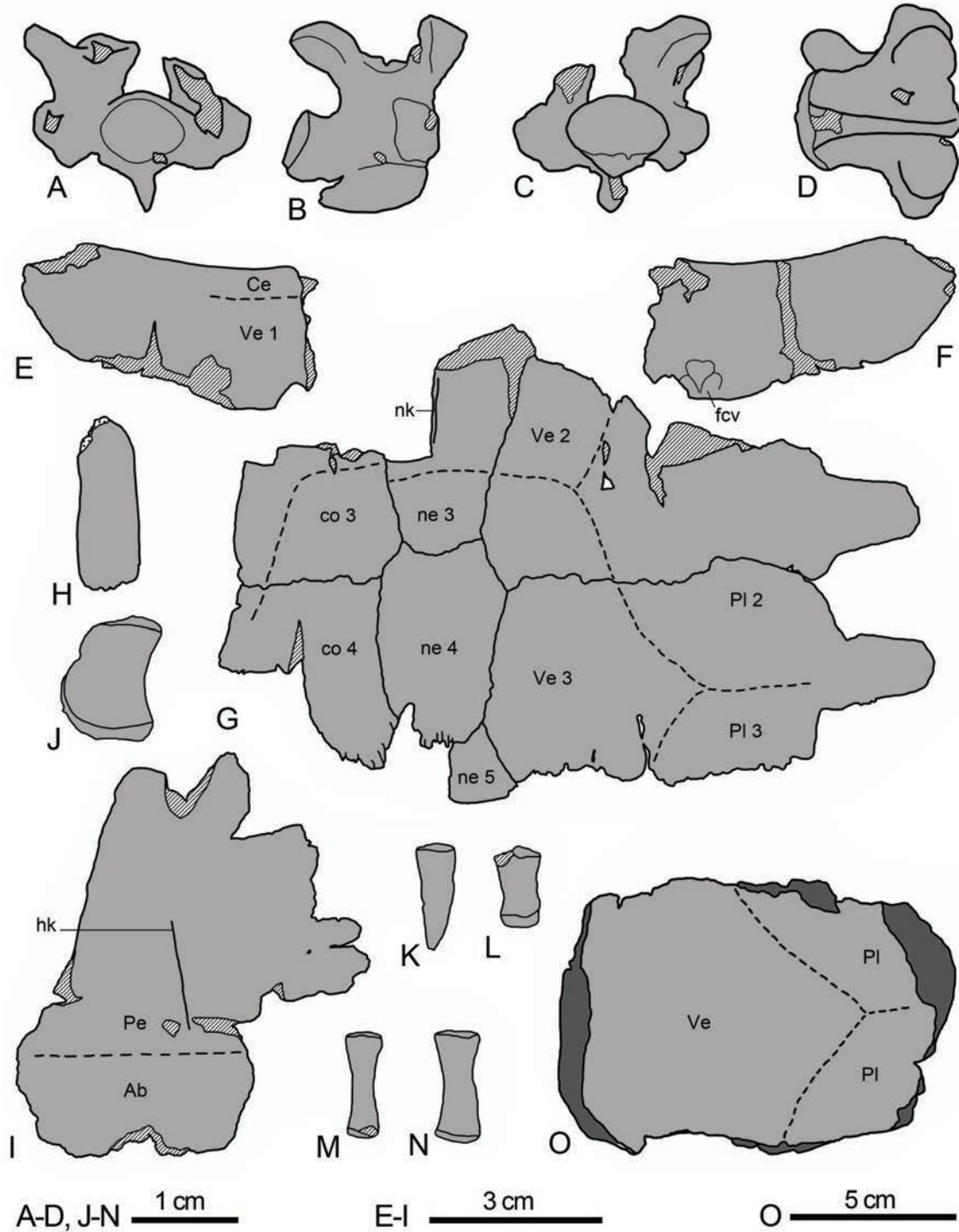


Fig. 9. *Argillochelys antiqua* from Vyshgorod locality, explanatory drawings: A–N – NMNHU-P: A–D – cervical vertebra V: A – anterior view; B – right lateral view; C – posterior view; D – ventral view; E, F – nuchal: E – dorsal view; F – ventral view; G – carapace fragment in dorsal view; H – peripheral 1 in dorsal view; I – fragment of right hyoplastron in ventral view; J – metatarsal I; K – unguial phalange; L–N – non-ungual phalanges; O – ZIN PH 7/36, right costal 4 in dorsal view. See Fig. 8 for photos and Fig. 5 for designations and abbreviations.

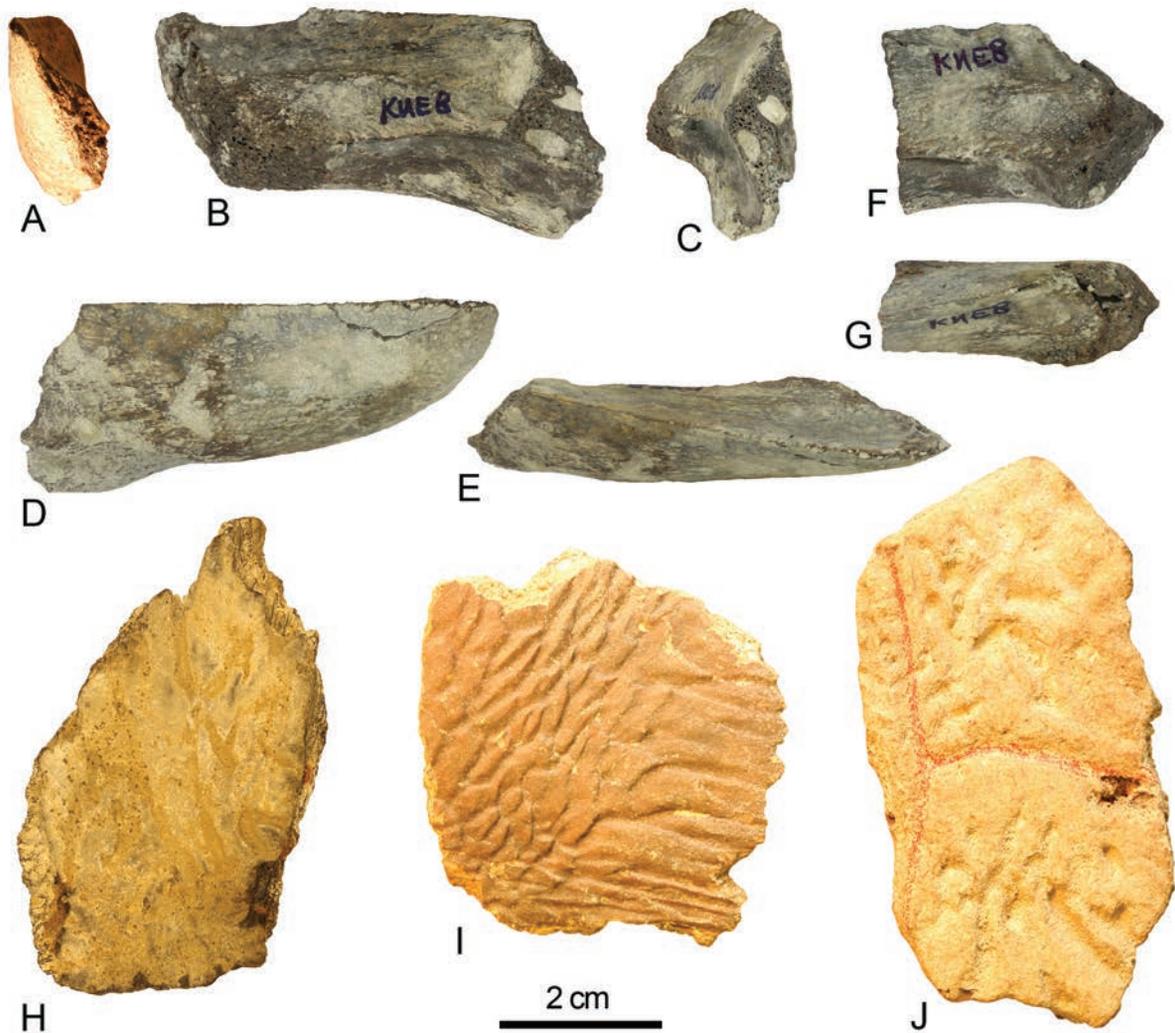


Fig. 10. *Dollochelys rogovichi* from Vyshgorod locality (A–F) and Pan-Cheloniidae indet. from Tripolye locality (H–J), photos: A–E – ZIN PH 1/36 (holotype of *D. rogovichi*), right fragmented dentary: A – anterior view; B – medial view; C – posterior view; D – lateral view; E – dorsal view; F, G – ZIN PH 6/36, left fragmented dentary: F – medial view; G – dorsal view; H – ZIN 1/239, partial neural in dorsal view; I – ZIN PH 3/239, partial costal; J – ZIN PH 2/239, medial part of the left costal. See Fig. 11 for explanatory drawings.

Remarks. Averianov (2002) attributed to *Dollochelys rogovichi* all turtle material known from Vyshgorod locality. Herein most part of this material is referred to *Argillochelys antiqua*. Contrary to Hirayama (2006) who considered *Dollochelys rogovichi* to be a nomen dubium (Cheloniodea indet.), here *D. rogovichi* is considered a valid pancheloniid taxon with unclear generic attribution – “*D.*” *rogovichi* (see Discussion). It is worth mentioning that the material of *Dollochelys rogovichi* is accompanied by the label

of the Geological Room (Cabinet) of the Saint Petersburg University (= PSM) “*Crocodylus*” (Fig. 1B), which is, probably, due to a mistake with the label. Other “crocodile” material of Rogovich (1875a–c) is referred here to Pan-Cheloniidae indet.

Pan-Cheloniidae indet.
(Figs. 10H–J, 11H–J)

Crocodylus spenceri: Rogovich 1875b: 46; 1875c: 2.

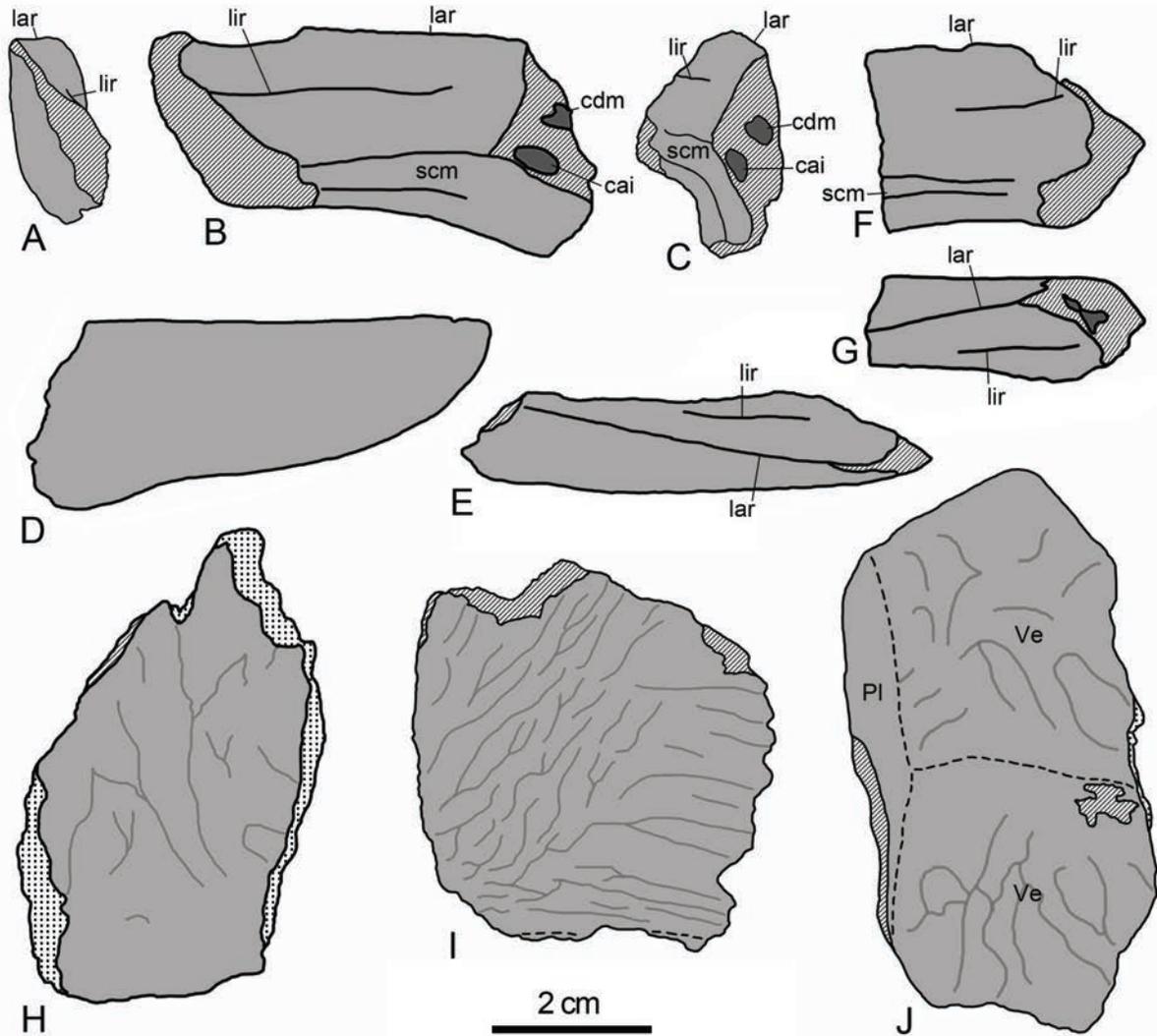


Fig. 11. *Dollochelys rogovichi* from Vyshgorod locality (A–F) and Pan-Cheloniidae indet. from Tripolye locality (H–J), explanatory drawings: A–E – ZIN PH 1/36 (holotype of *D. rogovichi*), right fragmented dentary: A – anterior view; B – medial view; C – posterior view; D – lateral view; E – dorsal view; F, G – ZIN PH 6/36, left fragmented dentary: F – medial view; G – dorsal view; H – ZIN 1/239, partial neural in dorsal view; I – ZIN PH 3/239, partial costal; J – ZIN PH 2/239, medial part of the left costal. See Fig. 10 for photos and Fig. 5 for designations and abbreviations.

Material. ZIN PH 1/239, partial neural; ZIN PH 2/239, medial part of the left costal; ZIN PH 3/239, costal fragment; ZIN PH 4–12/239, shell fragments.

Locality, horizon, and age. Tripolye locality, Kiev Province, Ukraine; marly-clayey member of the Kiev Formation; upper Lutetian – lower Bartonian, middle Eocene (see Geology and age of the localities for details).

Description. All specimens from Tripolye locality bear shell sculpturing consisting of the net of large

ridges and grooves. Some of the grooves begin with nutritive foramina. The sculpturing covers all external surface of the plates.

The partial neural (ZIN PH 1/239; Figs. 10H, 11H) is longer than wide, hexagonal short-sided anteriorly as reconstructed, without a midline keel and intervertebral sulcus. The estimated width of ZIN PH 1/239 is about 4 cm.

The medial part of the left costal (ZIN PH 2/239; Figs. 10J, 11J) has an estimated length of about

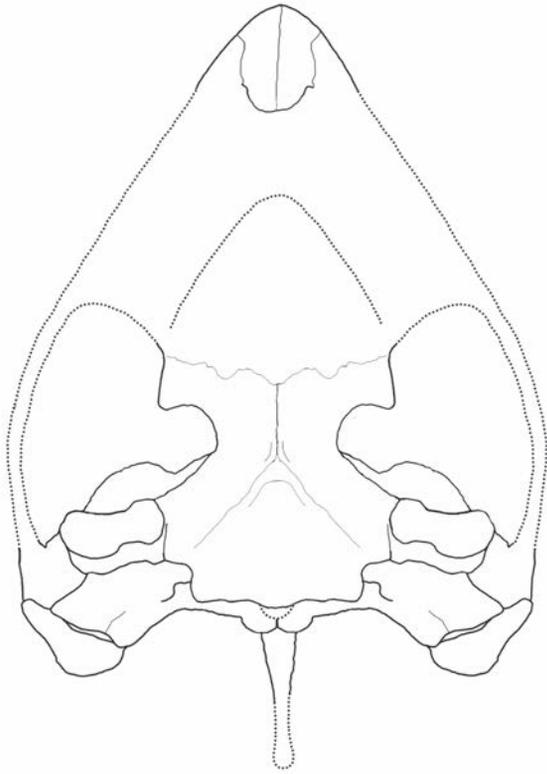


Fig. 12. *Argillochelys antiqua* from Vyshgorod locality, reconstruction of the ventral view of the skull based on ZIN PH 2/36 and 8/36 (left part of ZIN PH 8/36 is reflected to the right).

10 cm. The medial border of the plate is divided into short anteromedial and posteromedial sides and a long medial (central) side, suggesting contact with three consequent neurals. There are intervertebral and vertebral-pleural sulci on the external surface of the plate. The lateral border of the vertebrals is almost parallel and close to the medial border of the plate, suggesting relatively narrow and rectangular vertebrals.

The costal fragment (ZIN PH 3/239; Figs. 10I, 11I) demonstrates a well-developed sculpturing.

Remarks. According to labels (Fig. 1F, G), these specimens were attributed to *Crocodylus spenceri* by Rogovich (1875a–c). Of crocodile remains, Rogovich (1875c: 2) listed “maxilla, scapula, humerus, digital joint and scales.” The available specimens of the turtle shell may correspond to “maxilla” and “scales” (osteoderms), which are mistaken with the crocodile, probably, due to similarity of the surface sculpturing. L.I. Khosatzky determined this material

as “Chelonia?” (turtles in general or the genus of the cheloniid sea turtle; Fig. 1H), whereas L.A. Nessov noted that “This is a turtle of the *Syllomus* type (*Syllomiinae*, *Cheloniidae*)” (Fig. 1I). See Discussion for comparison.

DISCUSSION

Systematic position of turtles from the Kiev Formation. Turtle specimens from Vyshgorod locality belong to two turtle taxa (*Argillochelys antiqua* and “*Dollochelys*” *rogovichi*) which differ in morphology of the dentaries.

Material of *Argillochelys antiqua* includes part of the material previously referred to *Dollochelys rogovichi* by Averianov (2002; NMNHU-P, ZIN PH 2–5/36 and 7/36), as well as the newly referred specimens (ZIN PH 8–11/36). Specimens ZIN PH 2–5/36 and 8–11/36 appear to belong to one individual from the Rogovich’s collection, which was divided into several parts (specimens) and stored in different institutions for a long time (see Comments on the history...). NMNHU-P is considered to belong to the same individual based on similar preservation, size and because it compliments ZIN PH 2–5/36 and 8–11/36 material. ZIN PH 7/36 represents an isolated costal 4 which, probably, belongs to a larger individual of the same species.

ZIN PH 2–5/36 and 8–11/36 are referred to Pan-Cheloniidae based on the presence of a ventral V-shaped crest on the basisphenoid, a synapomorphy of this group also known in a dermochelyoid *Bouliachelys suteri* Kear et Lee, 2006 (Hirayama 1998; Kear and Lee 2006; Bardet et al. 2013).

ZIN PH 2–5/36 and 8–11/36 are referred to the genus *Argillochelys* based on vertical and sharp labial ridge of the upper jaw, wide anterior parts of the pterygoids, which have posterolaterally oriented external pterygoid processes, and the presence of the labial, symphyseal and lingual ridges on the lower jaw (see diagnosis of the genus).

ZIN PH 2–5/36 and 8–11/36 are referred to *Argillochelys antiqua* based on the following characters: 1) the frontoparietal scale of ZIN PH 8/36 is posteromedially elongated, similar to the holotype of *A. antiqua* (NHM 49465), and different from the holotype of *A. cuneiceps* (NHM 41636), in which the frontoparietal scale is emarginated posteriorly; 2) the external pterygoid processes of ZIN PH 8/36 are relatively large similar to *A. antiqua* (NHM 49465),

and different from *A. cuneiceps* (NHM 41636), in which these processes are smaller; 3) the symphysis of the dentaries of ZIN PH 3/36 and ZIN PH 4/36 is elongated, almost triangular (subtriangular) in shape similar to *A. antiqua* (NHM 38952, NHM 49465, and IRSNB 1653), and different from a more rounded symphysis of *A. cuneiceps* (NHM 38949). ZIN PH 8/36 differs from *A. antiqua*, *A. athersuchi* and *A. cuneiceps* in wider waist of pterygoids, but we consider this character to be subjected to intraspecific variation based on observation of specimens of *Chelonia mydas* in ZIN.

As was noted above, NMNHU-P most probably belongs to the same individual as ZIN PH 2–5/36 and 8–11/36. For this reason, NMNHU-P is also referred to *Argillochelys antiqua*. An additional character of this specimen known among Eocene pancheloniids only in *Argillochelys* is the presence of small keels (carinations) on the neurals (Lydekker 1889; Moody 1980; Zvonok et al. 2013b).

ZIN PH 7/36 (costal 4) is referred to *Argillochelys antiqua* based on similar morphology with the corresponding element of NMNHU-P and because there are no other pancheloniids with such a morphology known in the Kiev Formation.

Material of “*Dollochelys*” *rogovichi* includes only two specimens (ZIN PH 1/36 and 6/36), which most probably belong to one individual. “*Dollochelys*” *rogovichi* differs from *Argillochelys antiqua* by dorsomedially faced (steeply inclined inward or medioventrally inclined) triturating surfaces of the dentaries, weak lingual ridges and shallow (wedged) sulcus cartilaginis meckelii at the symphysis. Such differences suggest that “*Dollochelys*” *rogovichi* represents a distinct turtle taxon in the assemblage of the Kiev Formation, contrary to Hirayama (2006), who considered it a nomen dubium (*Chelonioidea* indet.). The attribution of “*D.*” *rogovichi* to Pan-Chelonioidea is supported by marine character of the assemblage and large size. Among Paleogene panchelonioids, “*D.*” *rogovichi* is similar in morphology only to some pancheloniids, like *Eochelone brabantica*, *Osonachelus decorata* and *Catapleura repanda*, in dorsomedially faced triturating surfaces of the dentaries. “*Dollochelys*” *rogovichi* differs from *E. brabantica* and *O. decorata* by presence of weak lingual ridges on the triturating surfaces and from *C. repanda* by flat (not concave) triturating surface. Thus, we consider “*D.*” *rogovichi* to be a distinct pancheloniid taxon with unclear generic attribution.

Turtle specimens from Tripolye locality are referred to Pan-Cheloniidae based on marine character of the assemblage, large size, presence of pronounced scale sulci on the shell bones and elongated and non-keeled neurals. The latter three characters are absent in the Paleogene dermochelyid *Eosphargis breineri* Nielsen, 1959 (Nielsen 1963). The pancheloniid from Tripolye differs from most other Paleogene pancheloniids in the presence of a well-developed surface sculpturing of the shell bones. Among Paleogene cheloniids with a well-developed surface sculpturing, the pancheloniid from Tripolye differs from *Ashleychelys palmeri* by narrower vertebrals and from *Osonachelus decorata* by distribution of the sculpturing in the area of pleurals. It cannot be ruled out that the pancheloniid from Tripolye may be associated with “*Dollochelys*” *rogovichi*. The pancheloniid from Tripolye is similar in surface sculpturing to the pancheloniid material reported as *Chelonioidea* indet. (*Dermochelyidae*?) from the unknown locality of middle Eocene in Lugansk Province, Ukraine (Averianov 2002: 144, fig. 7). According to personal communication of the collector of this material (N.I. Udovichenko), it comes from the Lutetian Buchak(?) Formation of Bakhmutovka locality, which was known to produce “*Chelonioidea*? indet with sculptured surface” (Averianov 2002: 144). “Shell fragments of *Chelonioidea*? indet. with sculptured surface” have also been reported from the Buchak(?) Formation of Krasno-rechenskoe locality in the same province (Averianov 2002: 144). The sculptured shell plates of Syllomiinae were reported from the middle Eocene Dzheroi 2 locality in Uzbekistan (see Averianov 2002, 2005). Shell material of sculptured *Cheloniidae* indet. (*Pan-Cheloniidae* indet. here) was reported from the middle Eocene of the Shorym Formation of Kazakhstan (Zvonok et al. 2011). Finally, a neural plate with surface sculpturing assigned to *Argillochelys* sp. was described from the middle Eocene of Ikovo locality in Lugansk Province, Ukraine (Zvonok et al. 2013b). These data demonstrate that sculptured pancheloniids of unknown affinities are quite common in the middle Eocene of Eastern Europe and Central Asia.

Phylogenetic analysis. The strict consensus tree resulted from our phylogenetic analysis (Fig. 13) differs from the tree of Weems and Brown (2017) in the following details: 1) *Erquelinnesia gosseleti*, *Tasbacka*, *Euclastes*, *Pacificchelys* and “*Argillochelys*” *africana* form a clade one step above Lophochelyiinae (in the analysis of Weems and Brown [2017] *Tasbacka* and

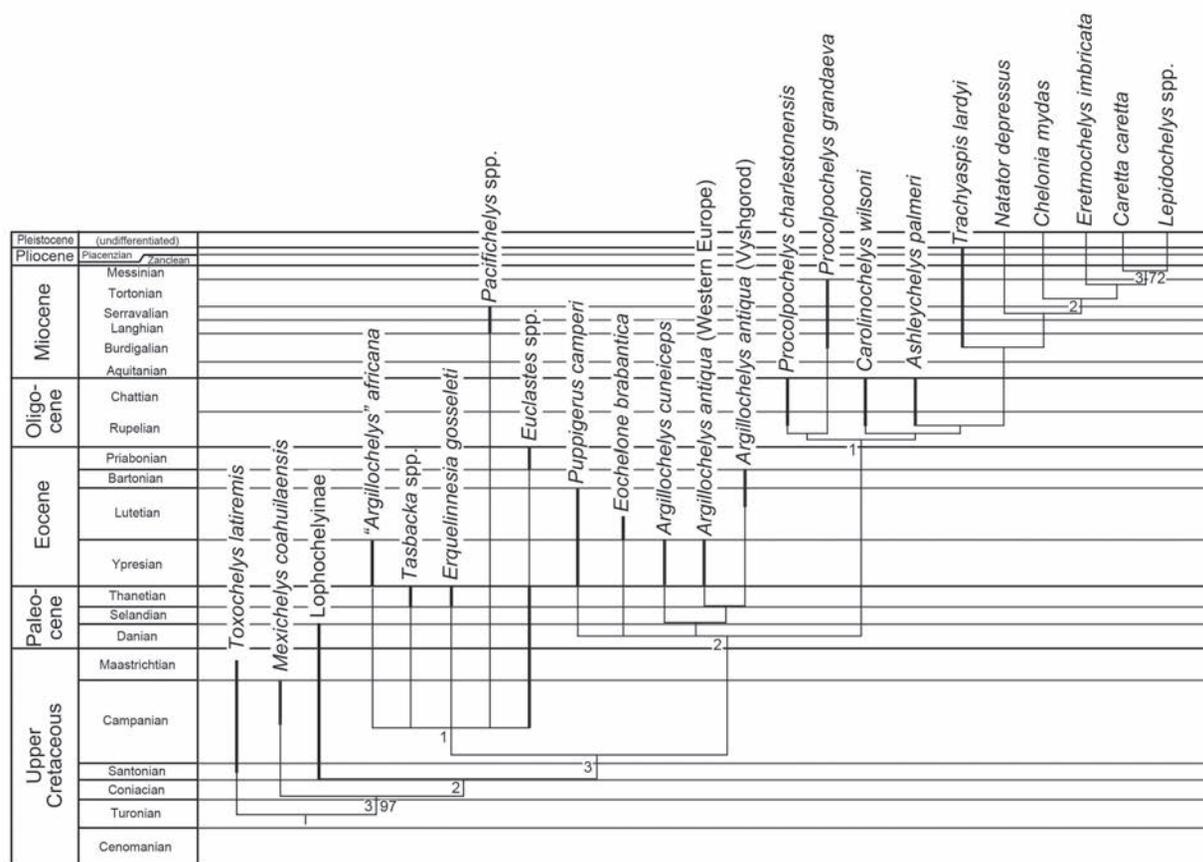


Fig. 13. Phylogeny of pancheloniid sea turtles showing position of *Argillochelys antiqua* from Vyshgorod and *A. antiqua* from Western Europe. This is a strict consensus tree retrieved by our phylogenetic analysis. Bremer and bootstrap support values are provided to the left and right of each clade where applicable. This figure is based on fig. 11 of Weems and Brown (2017) with the following modifications: the stratigraphic range of *Erquelinnesia gosseleti* (Dollo, 1886) is corrected from the Ypresian to the Thanetian (which corresponds to lower Landenian age; Zangerl 1971; Geyter et al. 2006); the stratigraphic range of *Puppigerus camperi* is corrected from the Ypresian–Priabonian to the Ypresian–Lutetian according to Weems and Brown (2017: table 2); the stratigraphic range of *A. antiqua* from Western Europe is given according to Moody (1997).

E. gosseleti + *Pacificchelys* clade form subsequent steps above Lophochelyinae, whereas *Euclastes* was recovered in eight possible positions, one of which was below *Tasbacka*; “*A.*” *africana* was not included in the analysis of Weems and Brown [2017]); 2) *Eocheilone brabantica* and *Puppigerus camperi* form a polytomy with *Argillochelys* clade and all more advanced pancheloniids (in the analysis of Weems and Brown [2017] *E. brabantica* forms a clade with *A. cuneiceps*, whereas *P. camperi* forms a clade with more advanced pancheloniids, except *Ashleychelys palmeri* + *Procolpochelys* clade); 3) *Procolpochelys* clade is sister to *Carolinchelys wilsoni* and all more advanced pancheloniids including *A. palmeri*, which is one step above *C. wilsoni* (in the analysis of Weems and

Brown [2017] *Ashleychelys palmeri* + *Procolpochelys* clade is sister to *A. cuneiceps*, *E. brabantica*, *P. camperi*, *C. wilsoni* and all more advanced pancheloniids). The important result of our analysis pertains to the *Argillochelys* clade, which includes *A. cuneiceps* and *A. antiqua*, which in turn includes *A. antiqua* from Vyshgorod and *A. antiqua* from Western Europe. The *Argillochelys* clade is supported by one unambiguous synapomorphy – character 6 state 2 (ridge along length of symphysis; this state is missing in Parham and Pyenson [2010] due to a typographic mistake; see Lapparent de Broin et al. [2014]). “*Argillochelys*” *africana* occupies position in a different clade. Thus, our phylogenetic analysis, on the one hand, supports attribution of part of the material from the Kiev clays

to *Argillochelys antiqua*, and, on the other hand, removes “A.” *africana* from *Argillochelys*.

Discussion of the diagnostic characters of the genus *Argillochelys*. The diagnosis of the genus *Argillochelys* was primarily suggested by Lydekker (1889) and later was modified by Moody (1980) and Tong and Hirayama (2008). In this paper we further modify the diagnosis of the genus *Argillochelys* and discuss characters used in the diagnosis and excluded from it below.

Characters that are included in the diagnosis:

1) Orbits directed laterally and slightly anteriorly. According to Lydekker (1889: 40), the orbits of *Argillochelys* “directed slightly upward”. Moody (1980: 165) wrote that the “orbits directed outwards and slightly forward”. Lapparent de Broin et al. (2014, Appendix A: 8) indicated “more laterally facing” orbits for *A. cuneiceps*. Our observation of photographs of *A. antiqua* and *A. cuneiceps* shows that their orbits directed laterally and slightly anteriorly, i.e. corresponds to Moody’s (1980) observation.

2) Frontals contributing to the orbital margins. This character is included in the diagnosis to distinguish typical *Argillochelys* from “*Argillochelys africana*, as well as from *Euclastes acutirostris* and *E. platyops* among Paleogene pancheloniids having the frontals well retracted from the orbital margins (Hay 1908; Tong and Hirayama 2008; Jalil et al. 2009).

3) The secondary palate reaches between half and two thirds the distance between the anterior margin of the skull and the fossa temporalis inferior. Tong and Hirayama (2008: 624) formulated this character as “secondary palate moderately developed”, whereas Lapparent de Broin et al. (2014, Appendix A: 5) noted that in *Argillochelys* spp. “the secondary palate reaches between half and two thirds the snout length.” We accept the latter formulation but replace the snout with the distance between the anterior margin of the skull and the fossa temporalis inferior, because the snout is usually understood as the pre-orbital part of the skull (see Gaffney 1979: fig. 120; Danilov et al. 2010: 26).

4) Labial ridge of the upper jaw is vertical and sharp. Lydekker (1889: 40) mentioned “palate with low alveolar walls” in the diagnosis of *Argillochelys*. Lapparent de Broin et al. (2014, Appendix A: 7) scored “a vertical and acute skull [tomial] border” for *Argillochelys cuneiceps*. We observed the same condition in *A. antiqua* (ZIN PH 2/36). We prefer to use the term labial ridge instead of tomial ridge following

Gaffney (1979: 89) to avoid further confusion (see Szczygielski et al. [2017] who applied the term tomial ridge to the lingual ridge).

5) Vomer hexagonal in outline and widely contacting the palatines in the secondary palate. Previous authors (Moody 1980; Tong and Hirayama 2008) mentioned the hexagonal shape of the vomer of *Argillochelys*. We added wide vomer-palatine contact to the diagnosis to distinguish *Argillochelys* spp. from *Eochelone brabantica*, in which this contact is narrow (short; Lapparent de Broin et al. 2014).

6) Pterygoids broad anteriorly and with posterolaterally oriented external processes. Lydekker (1889) and Moody (1980) included anteriorly broad pterygoids in the diagnosis of *Argillochelys*. Tong and Hirayama (2008) excluded this character from the diagnosis of the genus, because pterygoids are narrow anteriorly in “*Argillochelys africana*. We returned this character back to the diagnosis of *Argillochelys*, because “*Argillochelys africana* is removed from this genus. In addition, we complemented this character with the orientation of the external pterygoid processes to distinguish *Argillochelys* spp. from *Eochelone brabantica*. In the latter species, these processes have a lateral orientation (Casier 1968: pl. IIIC).

7) Length of the mandibular symphysis about one third the length of the mandibular ramus. The data about the length of the mandibular symphysis in *Argillochelys* is somewhat contradictory. Lydekker (1889: 40) noted that the “mandibular symphysis of moderate length” and that the “length of postsymphysial portion in some cases less than twice that of the symphysis”. Moody (1980: 165) wrote that the “mandibular symphysis short and less than one third the length of the mandibular ramus”. Finally, according to Tong and Hirayama (2008: 624), “mandibular symphysis about one third the length of the mandibular ramus,” which we here follow.

8) Triturating surface of the lower jaw with labial, lingual and symphyseal ridges. Previous authors mentioned ridged triturating (as oral; Lydekker 1889; as masticatory; Moody 1980) surface of the lower jaw in *Argillochelys*. Tong and Hirayama (2008: 624) modified this character as “sharp symphyseal ridge which is enlarged posteriorly, ended by a triangular swelling” due to inclusion of “*Argillochelys africana* in this genus. The presence of all three ridges on the lower triturating surface is characteristic only of *Argillochelys* among Paleogene pancheloniids.

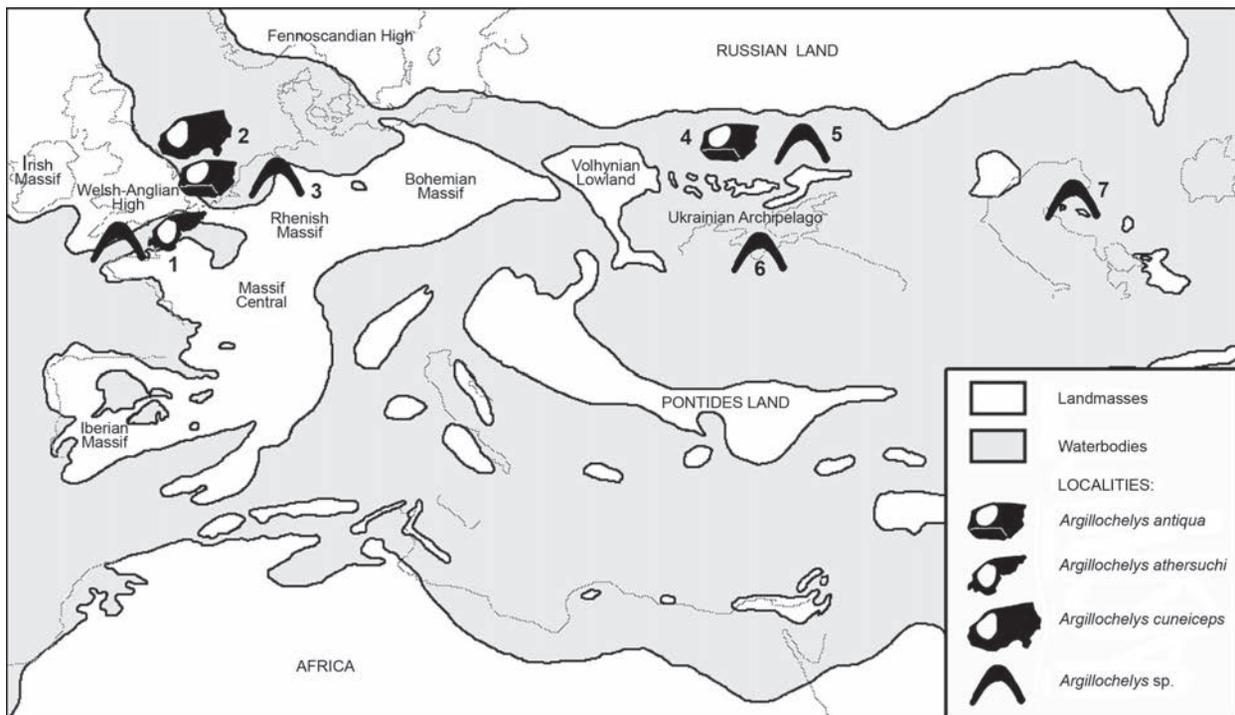


Fig. 14. Paleogeographic map of the Peri-Tethyan area during the late Lutetian (after Meulenkarp et al. 2000 with modifications) showing distribution of the genus *Argillochelys* during the late Paleocene – Eocene: 1 – Hampshire Basin, England, Ypresian – Bartonian; 2 – Harwich and Sheppey, England, Ypresian; 3 – Erquelinnes, Belgium, Thanetian; 4 – Vyshgorod, Ukraine, Lutetian – Bartonian; 5 – Ikovo, Ukraine, Lutetian; 6 – Ak-Kaya, Russia, Bartonian; 7 – Karakeshi and Monata, Bartonian and Adaev Formation, Priabonian, Kazakhstan. Data on geographic and stratigraphic distribution are taken from Moody (1997), Zvonok et al. (2011, 2013a, b) and this paper. See text for discussion.

9) Plastron with wide axillo-inguinal distance (plastral bridge). Moody (1980) indicated “plastron with large index 65–85” for *Argillochelys*. According to Zangerl (1953: table 4), the plastral index (axillo-inguinal distance \times 100/half width of plastron) is 86 and 98 for *A. subcristata* and *A. convexa* (now *A. antiqua*; Moody 1980) as illustrated by Owen and Bell (1849), respectively. We changed the wording of character because Moody (1974) used two different plastral indices: that of Zangerl (1953) and his own (plastral index B: axillo-inguinal width/length from hyo-hyosuture to xiphi tip). This character allows differentiating *Argillochelys* from pancheloniids with narrow axillo-inguinal distance.

Characters that are not included in the diagnosis.

The following characters were excluded from the diagnosis of *Argillochelys*: skull roof and shell surface with a well-developed ornamentation (Lydekker 1889; Moody 1980); short and wide skull (Lydekker 1889); short and blunt snout (Moody 1980); wide interorbital bar (Lydekker 1889; Moody 1980); out-

ward and slightly upward direction of the external nares (Lydekker 1889; Moody 1980); jugals and quadratojugals larger than in *Puppigerus* (Moody 1980); premaxillae and vomer shorter than in *Puppigerus* (Moody 1980); upper triturating surface with lingual ridges (Lydekker 1889; Moody 1980; Tong and Hirayama 2008); secondary palate with a medial groove (Lydekker 1889; Moody 1980; Tong and Hirayama 2008); large internal narial opening (Moody 1980); temporal fossae (fossae temporalis inferior) as wide as long (Lydekker 1889); presence of the basioccipital ridges (Moody 1980); carapace more elongate than those of *Puppigerus* (Moody 1980); keeled neurals (Lydekker 1889; Moody 1980); costo-peripheral fontanelles small or absent (Moody 1980); xiphiplastra united extensively in the midline (Lydekker 1889); forelimb and girdle elements slenderer than in *Puppigerus* (Moody 1980).

Most of these characters are in need of additional comparisons to other pancheloniids. The well-developed ornamentation of skull roof and shell

surface, the lingual ridges on the upper triturating surface and the keeled neurals are variable within the genus *Argillochelys* (Lydekker 1889: 42, 47, 48; Moody 1980: 165). In addition, some *Argillochelys* have a pointed snout (Lydekker 1889: fig. 10). The length of the premaxillae and the vomer and size of the internal narial opening are correlated with the development of the secondary palate. The presence/absence of the medial groove of the secondary palate is subjected to intraspecific variation in some pancheloniids (Tong et al. 2012). The basioccipital ridges are not always present in *Argillochelys* (ZIN PH 8/36). The degree of the development of the costo-peripheral fontanelles is a highly variable character in the ontogeny of pancheloniids (Moody 1974: fig. 15). The contact between the xiphiplastra is also subjected to variation as noted by Lydekker (1889: 40): "...the xiphiplastrals unite extensively in the middle line, while in one case the plastron is much less ossified than in the existing genus."

Discussion of the diagnostic characters of *Argillochelys antiqua*. The only existing diagnosis of *A. antiqua* was given by Lydekker (1889), although characters of this species were also discussed by Moody (1980). Below we discuss characters we used in the emended diagnosis of this species.

1) Frontoparietal scale with a posterior extension. The description of the scalation of the skull roof of *A. antiqua* by Lydekker (1889) is somewhat confusing, but the frontoparietal scale with a posterior extension is clearly visible on the published drawing (ibid.: fig. 10). In *A. cuneiceps*, the frontoparietal has no posterior extension and is emarginated posteriorly. In *A. athersuchi*, the scalation of the skull roof has never been described (Moody 1980). The posterior extension of the frontoparietal is also present in such Paleogene pancheloniids as "*Allopleuron qazaqstanense*, *Ashleychelys palmeri*, *Carolinochelys wilsoni*, "*Chelonia gwinneri*, *Eochelone brabantica*, and *Glarichelys knorri* (Wegner 1918; Zangerl 1958; Casier 1968; Weems and Sanders 2014; Zvonok et al. 2015).

2) External pterygoid processes relatively large. Moody (1980: 165) mentioned that "ectopterygoid processes <...> very large in *A. antiqua*." In *A. cuneiceps* (NHM 41636), these processes are smaller, whereas in *A. athersuchi* they are not preserved (Moody 1980).

3) Lower jaw symphysis subtriangular. Lydekker (1889: 41) described the lower jaw (mandible) of *A.*

antiqua as "comparatively narrow." Moody (1980) pointed out that the ventral surface of the mandibular symphysis is longer in *A. antiqua* and shorter in *A. cuneiceps*. According to our observations, the lower jaw symphysis is subtriangular in *A. antiqua* and semicircular in *A. cuneiceps* (NHM 38949). In *A. athersuchi*, the lower jaw is unknown (Moody 1980).

One more character suggested as diagnostic for *A. antiqua* by Moody (1980) is less pronounced lingual ridges on the palate in comparison with *A. cuneiceps*. We do not include this character in the diagnosis of the species because we find it difficult to reproduce.

A potentially diagnostic character of *A. antiqua* may be absence of the sagittal ventral ridge on pterygoids as observed in ZIN PH 8/36. Although this character was used in the phylogenetic analysis of pancheloniids (Lapparent de Broin et al. 2014), we consider it as subjected to intraspecific variation based on our examination of *Chelonia mydas* specimens (ZIN).

The skull NHM 37213 assigned to *Argillochelys cuneiceps* by Lydekker (1889: fig. 11) likely belongs to *A. antiqua*, given slight posterior extension of the frontoparietal scale, large external pterygoid processes, and a pointed snout, which better corresponds to the subtriangular symphysis of the lower jaw. Lapparent de Broin et al. (2014, Appendix A: 17) also question the attribution of this skull to *A. cuneiceps* based on presence of three parietal scales similar to *A. antiqua* (NHM 32386) and different from the holotype of *A. cuneiceps* (NHM 41636).

Moody (1980, 1997) mentioned *Argillochelys* and *A. antiqua* from the Thanetian of Belgium, probably having in mind IRSNB 1653, which was assigned to *Argillochelys* by Dollo (1907) and to "a cheloniid turtle" by Zangerl (1971: 4). We agree with the assignment of IRSNB 1653 to *Argillochelys* based on presence of the labial, lingual and symphyseal ridges on the triturating surface of the lower jaw. However, IRSNB 1653 differs from the holotype of *A. antiqua* (NHM 49456) in the shape of the frontoparietal scale which is posteriorly emarginated, and in the shape of the space between the rami of the dentaries, which is V-shaped, rather than U-shaped. For this reason, the assignment of IRSNB 1653 to *A. antiqua* remains unclear.

One more possible record of *A. antiqua* was mentioned from the Eocene of Netherlands without any details (Moody 1997; Lapparent de Broin 2001).

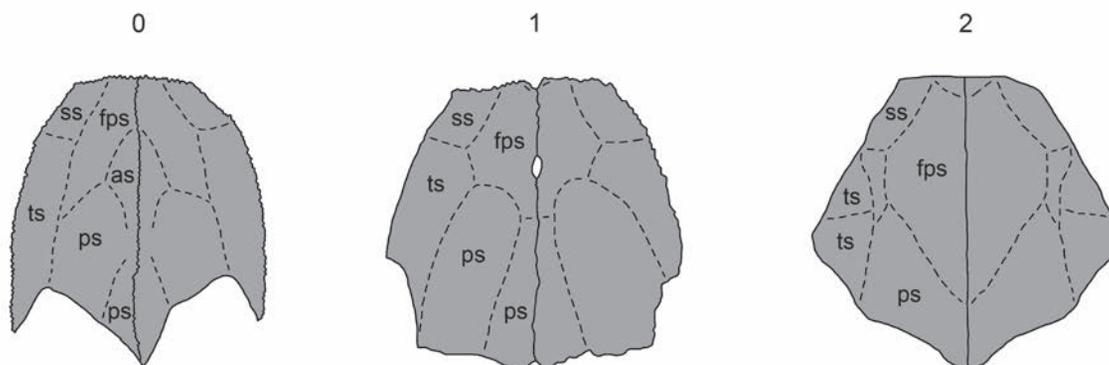


Fig. 15. Scalation pattern of parietal bones in pancheloniid turtles, illustrating states of character 36 (see Appendix 1): 0 – based on *Tasbacka ouledabdounensis* (AMNH 30033, holotype; Tong and Hirayama 2002: fig. 2A); 1 – based on *Tasbacka aldabergeni* (CCMGE 1/12175, holotype; Nessov 1987: fig. 1a); 2 – based on *Carolinochelys wilsoni* (MCZ 1005-A, holotype; Weems and Sanders 2014: fig. 3A). *Abbreviations:* as – additional scale; fps – frontoparietal scale; ps – parietal scale; ss – supraocular scale; ts – temporal scale.

Geographic and stratigraphic distribution of the genus *Argillochelys*.

Previous records of the genus *Argillochelys* were summarized by Moody (1980, 1997). These records were restricted in their distribution to the Thanetian – Bartonian of Western Europe, which corresponds to the north-eastern part of Atlantic area (Fig. 14). More recent findings of this genus (as *Argillochelys* sp.) were described from the Lutetian of Ukraine (Ikovo locality) and reported from the Bartonian of Russia (Ak-Kaya locality) and Bartonian – Priabonian of Kazakhstan (Mangyshlak; Zvonok et al. 2011, 2013a, b), which correspond to the Peri-Tethyan area (Fig. 14). The material of *A. antiqua* from the Lutetian – Bartonian of Ukraine described in this paper also comes from the Peri-Tethyan area. This finding seriously expands the geographic and stratigraphic distribution of this species previously confidently known only from the Ypresian of England and questionably from the Thanetian of Belgium and Eocene of Netherlands (see above). On the other hand, the presence of *A. antiqua* in the Lutetian-Bartonian of Ukraine is expected, because during most part of the Eocene sea area of this territory (part of the Tethys Ocean) had a direct connection with the North Sea Basin (Akhmetiev 2010). One more possible record of *Argillochelys* is a mandible fragment with the labial and lingual ridges on the triturating surface from the Ypresian of North America (Nanjemoy Formation), determined as *?Dollochelys* sp. by Weems (1999: pl. 5.2H1-2).

Thus, all known records of *Argillochelys* are restricted to the ?Thanetian – Priabonian of the Tethyan and the Northern Atlantic areas. Such a distribution does not necessary mean endemism of *Argillochelys* and may be explained by the fact that the Thanetian – Priabonian pancheloniid fossils determinable to the genus level with few exceptions are only known from the Northern Atlantic and Tethyan space. The only pancheloniid determined to the genus level beyond this region is *Eochelone monstigris* Grant-Mackie et al. 2011 from the Priabonian of New Zealand (Grant-Mackie et al. 2011), but its generic attribution was questioned by Lapparent de Broin et al. (2014: Appendix A2.1).

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Appendix 1. Details about new characters added to matrix of Weems and Brown (2017). Note that Weems and Brown (2017) used “–” instead of “?” in scorings

Character 36: Frontoparietal scale (Fig. 15; new character, but discussed in Lapparent de Broin et al., 2014: Appendix A5): 0, partially or completely divided posteriorly by additional medial scale; 1, not divided or divided into two parts along midline, without a strong posterior extension; 2, not divided or divided into two parts along midline, with a strong posterior extension.

Scorings: Outgroup, –; *Toxochelys latiremis*, –; *Mexichelys coahuilaensis*, –; Lophochelyinae, –; *Eochelone brabantica*, 2; *Erquelinnesia gosseleti*, 0; *Puppigerus camperi*, 1; *Tasbacka*, 0/1; *Euclastes*, 0; *Carolinochelys wilsoni*, 2; *Procolpochelys charlestonensis*, –; *P. grandaeva*, –; *Ashleychelys palmeri*, 2; *Pacificchelys*, –; *Chelonia mydas*, 1; *Natator depressus*, 1; *Trachyaspsis lardyi*, 2; *Eretmochelys imbricata*, 1; *Caretta caretta*, 1; *Lepidochelys*, 1; *Argillochelys cuneiceps*, 1; *A. antiqua* (Vyshgorod), 2; *A. antiqua* (Western Europe), 2; “A.” *africana*, 0.

Character 37. Frontal contribution to orbit (for history of this character see Joyce 2007: character 10): 0, present; 1, absent, prefrontal contacts postorbital. We changed numeration of states in comparison to Joyce (2007) to make the presence of the frontal contribution a primitive state for pancheloniids.

Scorings: Outgroup, 0; *Toxochelys latiremis*, 0; *Mexichelys coahuilaensis*, 0; Lophochelyinae, 0; *Eochelone brabantica*, 0; *Erquelinnesia gosseleti*, 0; *Puppigerus camperi*, 0; *Tasbacka*, 0; *Euclastes*, 0/1; *Carolinochelys wilsoni*, 0; *Procolpochelys charlestonensis*, 0; *P. grandaeva*, 0; *Ashleychelys palmeri*, 0; *Pacificchelys*, 0; *Chelonia mydas*, 0; *Natator depressus*, 0; *Trachyaspsis lardyi*, 0; *Eretmochelys imbricata*, 0; *Caretta caretta*, 1; *Lepidochelys*, 0; *Argillochelys cuneiceps*, 0; *A. antiqua* (Vyshgorod), –; *A. antiqua* (Western Europe), 0; “A.” *africana*, 1.

Character 38. Thick neurals with median keel (Hirayama 1998): 0, absent; 1, present.

Scorings: Outgroup, 0; *Toxochelys latiremis*, 0; *Mexichelys coahuilaensis*, 0; Lophochelyinae, 1; *Eochelone brabantica*, 0; *Erquelinnesia gosseleti*, 0; *Puppigerus camperi*, 0; *Tasbacka*, 0; *Euclastes*, –; *Carolinochelys wilsoni*, 0; *Procolpochelys charlestonensis*, 0; *P. grandaeva*, 0; *Ashleychelys palmeri*, 1; *Pacificchelys*, –; *Chelonia mydas*, 1; *Natator depressus*, 0; *Trachyaspsis lardyi*, 1; *Eretmochelys imbricata*, 0; *Caretta caretta*, 1; *Lepidochelys*, 0/1; *Argillochelys cuneiceps*, 0; *A. antiqua* (Vyshgorod), 1; *A. antiqua* (Western Europe), 1; “A.” *africana*, –.

Appendix 2. Characters coded for *Argillochelys antiqua* from Vyshgorod, *A. antiqua* from Western Europe, and “A.” *africana* and added to the matrix of Weems and Brown (2017)

Argillochelys antiqua from Vyshgorod
--10-200--0-00101-----1---0-2-1
Argillochelys antiqua from Western Europe
1-1--2----0----1-----1-1-000-201
“*Argillochelys*” *africana*
1110-01-10-1011-1-----01-

Appendix 3. List of changes in codings of some characters for six taxa in the matrix of Weems and Brown (2017)

The codings of ten characters were changed for *Tasbacka* based on data of *T. aldabergeni*, *T. ruhoffi* and *T. ouledabdounensis* (the latter taxon was not used by Weems and Brown [2017]): character 4 (contact of vomer and premaxilla) was changed from 1 to 0/1 as the contact is broad (1) in *T. ouledabdounensis*; character 7 (tomial ridge) was changed from 0 to 1 following Lapparent de Broin et al. (2014) and personal observations of *T. aldabergeni* material; character 9 (shape of the anterior portion of the vomer in ventral view) was changed from 0 to 1, because the vomer narrows anteriorly in *T. aldabergeni* and *T. ouledabdounensis*; character 19 (metischial process) was changed from – to 0; character 23 (centrum of seventh cervical vertebra) was changed from 1 to 0; character 24 (articulations of first and second digits) was changed from 0 to –; character 26 (coracoid length in relation to humerus) was changed from 0 to –; character 27 (seventh to eighth centrum articulation of the cervical vertebra) from 1 to 0; character

29 (rib-free peripherals) from 0 to 1: character 30 (post-nuchal fontanelles) from 0/1 to 0 (characters 19, 23, 24, 26, 27, 29, 30 were changed based on data of *T. aldabergeni*).

The coding of one character (6, dentary) was changed for Lophochelyinae from 0 to 1, based on the presence of the lingual ridge in *Ctenochelys* spp. (Gentry 2017).

The codings of two characters were changed for *Euclastes*: character 7 (tomial ridge) from 0 to 1, because *Euclastes* is characterized by low tomial ridge (Lynch and Parham 2003; Jalil et al. 2009); character 12 (direction of orbits) from 1 to 0, because *Euclastes* is characterized by dorsolaterally facing orbits (Jalil et al. 2009; Parham and Pyenson 2010).

The coding of one character (11, processus pterygoideus externus) was changed for *Puppi-*

gerus camperi from 1 to 0/1, because the size of the processus pterygoideus externus is variable in this species (Moody 1974: fig. 6; Tong et al. 2012: fig. 1C, D).

The coding of one character (14, mid-ventral ridge on pterygoids) was changed for *Eochelone brabantica* from 1 to 0 based on data from Lapparent de Broin et al. (2014: Appendix A: 8) that in this species “the basisphenoid <...> is anteromedially crested and its anterior point penetrates only a little between the pterygoids, which are elevated at its contact in one specimen, but this elevation does not extend anteriorly.”

The coding of one character (16, dorsum sellae) was changed for *Chelonia mydas* from 1 to 0/1 based on observation of a series of skulls of this species in ZIN.