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Paleogene turtles of Eastern Europe: new findings and a revision

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ABSTRACT

The article provides an overview of all known 39 localities of the Paleogene turtles of Eastern Europe. Numerous remains of turtles are described for the first time from 19 localities, of which six are new, and 13 are the localities from which materials were only mentioned previously. Among them are Pan-Trionychidae indet., Pan-Cheloniidae indet., Dermochelyidae indet. and Pan-Testudines indet., as well as pan-cheloniids *Argillochelys* sp. from the Ypresian Novoivanovka and the Ypresian or Lutetian Gruzinov localities. Several indeterminate specimens from Eocene localities show similarity to pan-cheloniids *Argillochelys cuneiceps* (Owen, 1849) and *Puppigerus camperi* (Gray, 1831) or *Tasbacka aldabergeni* Nessov, 1987, and dermochelyids *Natemys peruvianus* Wood et al., 1996 or "*Psephophorus*" *rupeliensis* van Beneden, 1883. One specimen of costal 1 of Pan-Testudines indet. from the Lutetian Krasnorechenskoe locality resembles that of pleurodires *Eocenochelus* spp. and *Neochelys* spp. In addition, new materials of turtles are described from five previously known localities. Among them, new and additionally restored specimens from the Bartonian Ak-Kaya 1 locality of the pan-cheloniid *Argillochelys* sp., and the dermochelyid *Cosmochelys* sp., which expand data on their morphology and intraspecific variability. The specimens of pan-cheloniids with deep and dense sculpturing of the external shell surface from the Bakhmutovka, Bulgakovka, Krasnorechenskoe and Tripolye localities clearly belong to a new species, not described due to fragmentary material. It is supposed that *Anhuichelys*-like pan-testudinoids migrated from Asia in Eastern Europe in the Danian age, and were preserved as relict *Dithyrosternon valdense* Pictet et Humbert, 1855 until the Priabonian age.

Key words: *Argillochelys*, Dermochelyidae, Eastern Europe, Paleogene, Pan-Cheloniidae, Pan-Trionychidae, turtles

Палеогеновые черепахи Восточной Европы: новые находки и ревизия

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РЕЗЮМЕ

В статье представлен обзор всех известных 39 местонахождений палеогеновых черепах Восточной Европы. Впервые описаны многочисленные остатки черепах из 19 местонахождений, из них шесть местонахождений новые и 13 местонахождений, из которых материалы ранее только упоминались.

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Среди них Pan-Trionychidae indet., Pan-Cheloniidae indet., Dermochelyidae indet. и Pan-Testudines indet., а также панхелонииды *Argillochelys* sp. из ипра местонахождения Новоивановка и ипра или лютета местонахождения Грузиново. Несколько неопределенных экземпляров из эоценовых местонахождений обнаруживают сходство с панхелониидами *Argillochelys cuneiceps* (Owen, 1849) и *Puppigerus camperi* (Gray, 1831) или *Tasbacka aldabergeni* Nessov, 1987 и дермохелиидами *Natemys peruvianus* Wood et al., 1996 или "*Psephophorus*" *rupeliensis* van Beneden, 1883. Один экземпляр костальной пластинки 1 Pan-Testudines indet. из лютета местонахождения Краснореченское сходен с таковым плевродир *Eocenochelus* spp. и *Neochelys* spp. Кроме того, новые материалы по черепахам описаны из пяти ранее известных местонахождений. Среди них новые и дополнительно восстановленные экземпляры из бартонского местонахождения Ак-Кая 1 по панхелонииду *Argillochelys* sp. и дермохелииду *Cosmochelys* sp., которые расширяют данные об их морфологии и внутривидовой изменчивости. Экземпляры панхелониид с глубокой и тесно посаженной орнаментацией наружной поверхности панциря из местонахождений Бахмутовка, Булгаковка, Краснореченское и Триполье явно принадлежат к новому виду, не описанному из-за фрагментарности материала. Сделано предположение, что *Anhuichelys*-подобные пантестудиноиды мигрировали из Азии в Восточную Европу в датском веке и сохранились как реликтовые *Dithyrosternon valdense* Pictet et Humbert, 1855 до приабона.

Ключевые слова: *Argillochelys*, Dermochelyidae, Восточная Европа, палеоген, Pan-Cheloniidae, Pan-Trionychidae, черепахи

INTRODUCTION

The study of Paleogene turtles of Eastern Europe (within the boundaries of the European part of the USSR; see Material and Methods) began in the 1870s with papers of the Russian naturalist A.S. Rogovich (1871, 1875a, b, c) describing turtle remains, partially erroneously identified as belonging to fishes, crocodiles and mammals, from the middle Eocene Kiev clays (vicinities of Kiev, Ukraine; see Zvonok and Danilov [2017] for a detailed description of this material and history of the Rogovich's collection of fossil vertebrates). Up to the 1980s, in addition to the Rogovich's material, which was later considered as belonging to sea turtles (Chelonioidea; Khosatzky 1949, 1950; for other references see Zvonok and Danilov 2017), there were only a few mentions of other turtle findings from the Paleogene of Eastern Europe, all from Russia (Crimea, Stavropol and Krasnodar territories, and Middle Povolzhye) and all belonging to sea turtles (Khosatzky 1950, 1975; Chkhikvadze 1977; Alekperov 1978).

In the 1980s–2000s, new data on Paleogene turtles from Kiev Province of Ukraine, Luhansk People's Republic (at that time Province of the USSR or Ukraine), Crimea, as well as Krasnodar Territory, and Volgograd Province of Russia were published (Chkhikvadze 1983, 1987, 1990, 1999; Nessov 1987, 1992; Nessov and Yarkov 1989; Averianov and Yarkov 2000, 2004; Averianov 2002). The cited publications contained not only mentions, but also illustrations and descriptions of fragmentary remains of sea turtles and representatives of other turtle groups, including Trionychidae and undetermined turtles. In total, for the territory under consideration, Chkhikvadze (1983) listed data on three Paleogene localities of sea turtles, one of which (Vyshgorod) was considered by him as Paleogene, and two others (Abadzekhskaya and Otradnaya), as Neogene, whereas Averianov (2002) considered 11 Paleogene localities of sea turtles.

During the 2010s and 2020, new Paleogene turtle material was described from all the mentioned regions, as well as from Cherkassy Province of Ukraine and Rostov Province of Russia (Danilov et al. 2010, 2011; Zvonok 2011, 2013, 2014; Zvonok et al. 2013a, 2013b, 2019; Zvonok and Danilov 2017, 2018, 2019, 2020). Unlike previous, this material is represented not only by isolated bones and their fragments, but also by more complete specimens, including partial skulls and skeletons. Taxonomically, it was attributed to cheloniid and dermochelyid sea turtles, trionychids, basal testudinoids, geoemydids, testudinids, as well as basal turtles or basal cryptodires.

In spite of this progress, some of the previously mentioned and new materials remain undescribed, unfigured or described very briefly (see Material and Methods). Considering this, the main objective of the current paper is a presentation of the results of study of the taxonomic composition, osteology, stratigraphic and paleobiogeographic distribution of Paleogene turtles of Eastern Europe with a detailed description of the previously undescribed or poorly described materials and an expanded datalist on their localities.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; IKBFU, Immanuel Kant Baltic Federal University (formerly, Albertus-Universität Königsberg), Kaliningrad, Russia; IPG, Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi, Georgia; IRSNB, Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK; NMNHU-P, Department of Paleozoology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev, Ukraine; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; ZIN PH, Paleoherpetological collection of the same institute.

MATERIAL AND METHODS

The following material was used for comparison: the sichuanchelyid *Laurasichersis relicta* Perez-Garcia, 2020 from the upper Thanetian (Sables de Bracheux Formation) of the Mont de Berru locality, France (Perez-Garcia 2020); Cryptodira incertae sedis sp. 2 from the Maastrichtian Bereslavka 1 locality (Averianov and Yarkov 2004); the podocnemidids: *Eocenochelus eremberti* (Broin, 1977) from the Lutetian (Milioles limestone) of the Saint-Germain-en-Laye locality, France (Broin 1977; Perez-Garcia et al. 2017); *Eocenochelus farresi* Perez-Garcia et al., 2017 from the Priabonian (Sant Marti Xic Formation) of the Can Beulovi locality, Spain (Perez-Garcia et al. 2017); *Eocenochelus lacombianus* Perez-Garcia et al., 2017 from the Ypresian (Upper Sandstone-Marly Formation) of the Soulane locality, France (Perez-Garcia et al. 2017); *Neochelys laurenti* (Tong, 1998) from the Ypresian (Clays of Saint-Papoul) of the Saint-Papoul locality, France (Perez-Garcia and de Lapparent de Broin 2015); *Neochelys liriae* Perez-Garcia et de Lapparent de Broin, 2013 from the Ypresian (Gres d'Assignan Formation) of the Soleillades locality, France (Perez-Garcia end de Lapparent de Broin 2013); the trionychids: *Lissemys punctata* (Lacepede, 1788), extant (pers. obs. of coll. ZIN); *Pelodiscus sinensis* (Wiegmann, 1835), extant (pers. obs. of coll. ZIN); "*Trionyx*" *ikoviensis* Danilov et al., 2011 from the Lutetian of the Ikovo locality, Russia (Danilov et al. 2011); "*Trionyx*" *silvestris* Walker et Moody, 1974 from the Ypresian (Blackheath Beds) of the Abbey Wood locality, UK (Walker and Moody 1974; Georgalis and Joyce 2017); *Trionyx triunguis* (Forskål, 1775), extant (pers. obs. of coll. ZIN); the cheloniids: "*Allopleuron*" *qazaqstanense* Karl et al., 2012 from the Bartonian (Shorym Formation) of the Kuyulus locality (Zvonok et al. 2015); *Argillochelys antiqua* (König, 1825) from the Ypresian (London Clay Formation) of the Isle of Sheppey locality, UK and the upper Lutetian–Bartonian (Kiev Formation) of the Vyshgorod locality, Ukraine (Owen and Bell 1849; Lydekker 1889; Moody 1980; Zvonok and Danilov 2017; de Lapparent de Broin et al. 2018); *Argillochelys athersuchi* Moody, 1980 from the Bartonian (Barton Clay Formation) of the Barton Cliff locality, UK (Moody, 1980); *Argillochelys cuneiceps* (Owen, 1849) from the Ypresian (London Clay Formation) of the Isle of Sheppey locality, UK (Owen and Bell 1849; 3D model of the holotype NHMUK 41636 observed in www.MorphoSource.org); *Argillochelys* sp. (referred to *A. antiqua* by Dollo [1907] and to cheloniid by Zangerl [1971]) from the Thanetian (Hannut Formation) of the Erquelinnes locality, Belgium (photographs of IRSNB 1653 from R. Hirayama); *Argillochelys* sp. from the Bartonian of Ak-Kaya 1 locality, Russia (Zvonok and Danilov 2019); *Argillochelys* sp. from the Lutetian of Ikovo locality, Russia (Zvonok et al. 2013b); *Ashleychelys palmeri* Weems et Sanders, 2014 from the upper Rupelian (upper part of the Ashley Formation) and the upper Chattian (Chandler Bridge Formation) of several localities (East bank of the Limehouse Branch type locality), USA (Weems and Sanders 2014); *Bryochelys waterkeynii* Smets, 1887 from the Rupelian (Boom Formation) of several localities, Belgium (Smets 1887, 1888); *Carolinochelys wilsoni* Hay, 1923 from the upper Rupelian (upper part of the Ashley Formation) and the upper Chattian (Chandler Bridge Formation) of several localities (Ingleside type locality), USA (Weems and Sanders 2014); "*Chelone*" *convexa* Owen, 1842 (probable synonym of *Argillochelys cuneiceps*) from the Ypresian (London Clay Formation) of the Isle of Sheppey locality, UK (Owen and Bell 1849); "*Dollochelys*" *casieri* Zangerl, 1971 (= *Catapleura repanda* (Cope, 1868) *sensu* Hirayama, 2006) from the Thanetian (Hannut Formation) of Erquelinnes locality, Belgium (Zangerl 1971); *Eochelone brabantica* Dollo, 1903 from the lower Lutetian (Brussel Formation) of several localities (Saint Remy-Geest type locality), Belgium (Casier 1968; Evers et al. 2019:

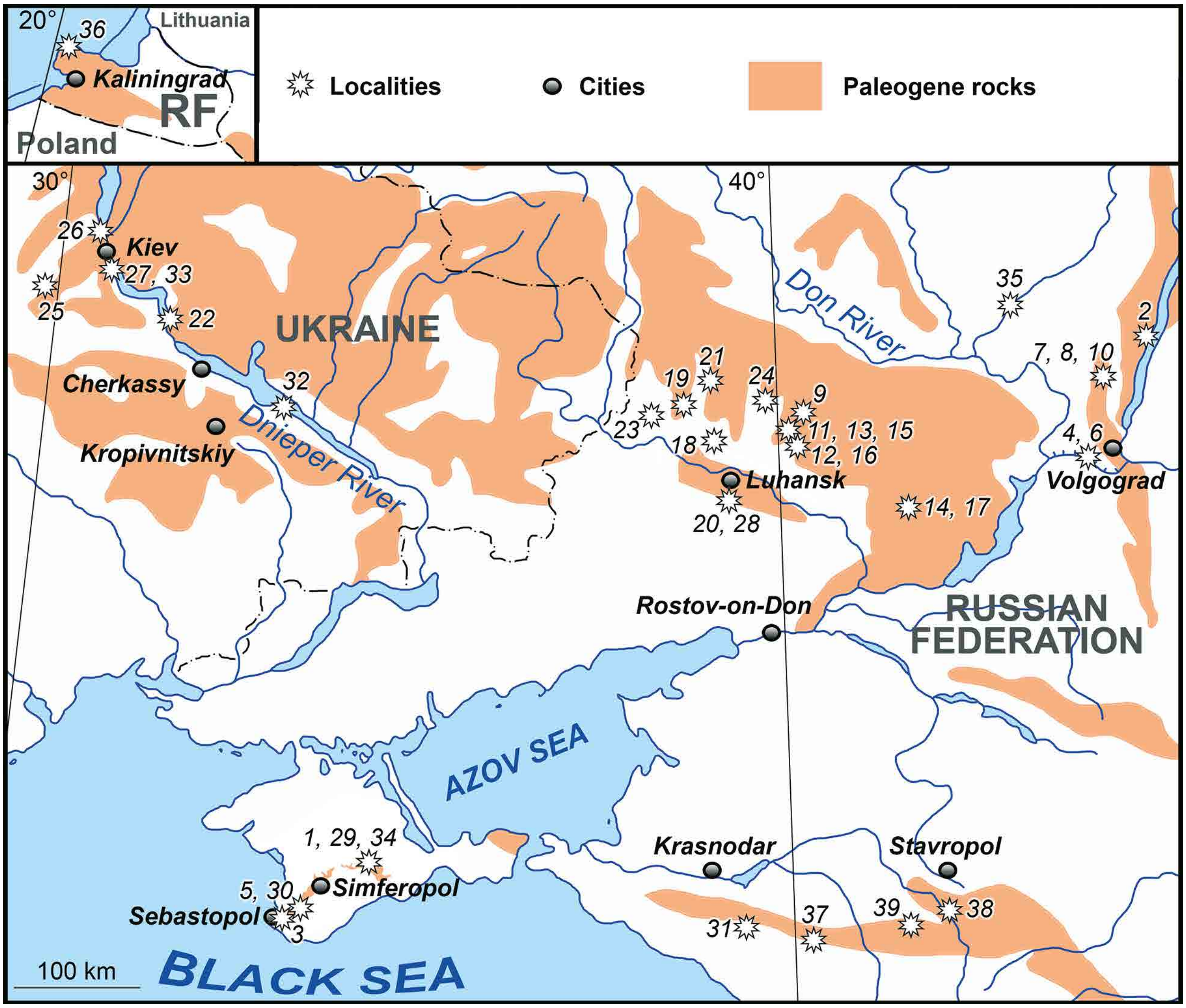

Fig. 1. The localities of Paleogene turtles of Eastern Europe. Danian: 1 – Ak-Kaya 2, 2 – Rasstrigin 2, 3 – Sakharnaya Golovka; Selandian: 4 – Bereslavka 2a; Thanetian: 5 – Bakhchisarai 1, 6 – Bereslavka 2b, 7 – Loznoe 1, 8 – Malaya Ivanovka; Ypresian: 9 – Kudinovka, 10 – Loznoe 2, 11 – Malchevsko-Polnenskaya, 12 – Novoivanovka; Ypresian – Lutetian: 13 – Grekovo, 14 – Gruzinov, 15 – Malchevskaya, 16 – Verkhnetalovka, 17 – Voznesenskiy; Lutetian: 18 – Bakhmutovka, 19 – Bulgakovka, 20 – Georgievka, 21 – Ikovo, 22 – Kostyanetskiy Yar, 23 – Krasnorechenskoe, 24 – Krinichnoe, 25 – Sosnovka; Lutetian–Bartonian: 26 – Vyshgorod, 27 – Tripolye; Lutetian–Priabonian: 28 – Tschelyuskinets; Bartonian: 29 – Ak-Kaya 1, 30 – Bakhchisarai 2, 31 – Gorniy Luch, 32 – Nagornoe, 33 – Pirogovo, 34 – Prolom; Priabonian: 35 – Otradnoe; Rupelian: 36 – Zarechnyi; Rupelian–Chattian: 37 – Abadzekhskaya; Paleogene or Neogene: 38 – Belomechetskaya; 39 – Otradnaya. For further details see Appendix 1. The map is redrawn from Nalivkin (1983).

fig. S1.26C); *Eochelone voltregana* de Lapparent de Broin et al., 2018 from the Priabonian (Vic-Manlleu marls Formation) of several localities, Spain (de Lapparent de Broin et al. 2018); *Eochelone* sp. from the Bartonian (Kuma Formation) of the Gorniy Luch locality, Russia (Zvonok et al. 2019); *Erquelinnesia gosseleti* (Dollo, 1886) from the Thanetian (Hannut Formation) of the Erquelinnes locality, Belgium (Zangerl 1971); *Euclastes roundsi* (Weems, 1988) from the Thanetian (Aquia Formation) of the Liverpool Point and Pamunkey River bluffs localities (Weems 1988); *Euclastes wielandi* (Hay, 1908) from several Maastrichtian–Thanetian formations and localities of Angola, Chile, Morocco and USA (Ullmann and Carr 2021); *Glossochelys planimentum* (Owen, 1842) (probable synonym of *Erquelinnesia gosseleti*) from the Ypresian (Harwich Formation) of the Harwich locality, UK (Owen and Bell 1849); *Glyptochelone suyckerbuycki* (Ubaghs, 1879) from the upper Maastrichtian (Maastricht Formation) of the Valkenburg aan de Geul locality, Netherlands (de Lapparent de Broin et al. 2018: fig. 11h, i); *Lepidochelys olivacea* (Eschscholtz, 1829), extant (pers. obs. of coll. ZIN); *Natator depressus* (Garman, 1880), extant (Zangerl et al. 1988); *Osonachelus decorata* de Lapparent de Broin et al., 2014 from the Priabonian (Vic-Manlleu marls Formation) of the Santa Cecilia de Voltrega and Munter localities, Spain (de Lapparent de Broin et al. 2014); *Peritresius ornatus* (Leidy, 1856) from the several Campanian–Maastrichtian formations and localities of USA (Gentry et al. 2018); *Puppigerus camperi* (Gray, 1831) from the Ypresian (London Clay Formation) and Lutetian (Bracklesham Group) of several localities, UK (Owen and Bell 1849; Lydekker 1889; Chapman et al. 2015), the lower Lutetian (Brussel Formation) of the Maransart and Vieux-Genappe localities, Belgium (Moody 1974), the Ypresian (Nanjemoy Formation) of the Bluffs near Popes Creek locality, USA (Weems 1999), the Lutetian of the Ikovo locality, Russia (Zvonok et al. 2013b), the Lutetian–Bartonian boundary of the Dzheroi 2 locality, Uzbekistan (Averianov 2005); *Tasbacka aldabergeni* Nessov, 1987 from the upper Thanetian or lower Ypresian of the Zhylga 1 locality, Kazakhstan (Nessov 1987; pers. obs. of coll. CCMGE 12175); *Tasbacka ouledabdounensis* Tong et Hirayama, 2002 from the Danian (Ouled Abdoun Phosphate Basin) of Ouled Abdoun Basin Recette 4 (Tong and Hirayama 2002); *Tasbacka ruhoffi* from the Thanetian (Aquia Formation) of the Indian Head Road near Piscataway Creek locality, USA (Weems 1988, 2014); *Trachyaspis lardyi* Meyer, 1843 from several Burdigalian–Piacenzian formations and localities of Egypt, Italy, Japan, France, Switzerland, and USA (Weems 1974; Hasegawa et al. 2007; Villa and Raineri 2015); the dermochelyids: cf. *Egyptemys* sp. from the Priabonian (Samlat Formation) of the Ad-Dakhla locality, Morocco (Zouhri et al. 2017: fig. 6i, j); *Natemys peruvianus* Wood et al., 1996 from the Chattian (Pisco Formation) of the West Bank of Rio Ica locality, Peru (Wood et al. 1996); "*Psephophorus*" *rupeliensis* van Beneden, 1883 from the Rupelian (Boom Formation) of several localities of Belgium (Wood et al. 1996); the testudinoid *Dithyrosternon valdense* Pictet et Humbert, 1855 from the Priabonian of the Mauremont locality, Switzerland (Pictet et al. 1855–1857); the geoemydids: *Cuvierichelys iberica* (Bergounioux, 1958) from the Rupelian (Calcaries de Tàrrega Formation) of the El Talladell locality, Spain (Hervet 2003); *Cuvierichelys parisiensis* (Gray, 1831) from several Bartonian–Rupelian formations and localities of Belgium, France and UK (Hervet 2003; Perez-Garcia et al. 2016b); *Geoclemys hamiltonii* (Gray, 1831), extant (McDowell 1964); the testudinid *Pelorochelon soriana* Perez-Garcia et al., 2016 from the Bartonian (Mazateron Formation) of the Mazateron locality, Spain (Perez-Garcia et al. 2016a).

Our paper contains data on 39 localities of Paleogene turtles of Eastern Europe (Fig. 1) presented in geochronological order (see Table 1 and Appendix 1 for the list of localities of Paleogene turtles of Eastern Europe including information about the geographical coordinates, stratigraphic units and geological age, materials, literature and fieldworks of collectors). A detailed description is given only for the material that has not been described previously, or has been additionally prepared, or if its attribution is changed. The material from six localities (Bulgakovka, Grekovo, Gruzinov, Loznoe 2, Nagornoe, and Verkhnetalovka) is mentioned and described here for the first time. The material from 13 localities (Bakhchisarai 1, Bereslavka 2b, Georgievka, Krasnorechenskoe, Krinichnoe, Malaya Ivanovka, Malchevskaya, Malchevsko-Polnenskaya, Novoivanovka, Otradnaya, Otradnoe, Tschelyuskinets, and Voznesenskiy) was previously mentioned without description (Averianov 2002; Averianov and Yarkov 2004; Zvonok and Danilov 2018; Benitskiy and Zvonok 2020; Nesterov and Zvonok 2020), and is described here for the first time. In addition, this paper describes new material from five previously known localities (Ak-Kaya 1, Bakhchisarai 2, Bakhmutovka, Loznoe 1, and Prolom), of which the material from Bakhmutovka and Loznoe 1 (as Loznoe) was mentioned by Zvonok and Danilov (2018). Due to the large amount, data on new material from the Bereslavka 2a and Ikovo localities will be published elsewhere.

Averianov (2002) listed four "Unknown localities" of sea turtles from the Paleogene of Eastern Europe: "34. Unknown locality, Lugansk Region, Ukraine", "41. Unknown locality in the Crimea, Ukraine", "42. Unknown locality in Ukraine", "49. Unknown locality in Middle Povolzhye, Russia". Two of these localities (34 and 42) appear to correspond to the Bakhmutovka (34) and probably to Vyshgorod and Tripolye (42) localities (see sections on the

Table 1. Turtle taxa known from the Paleogene localities of Eastern Europe. Sign "*" designates mention only. Abbreviations: Bar – Bartonian, Cha – Chattian, Dan – Danian, Lut – Lutetian, Mio – Miocene, Neo – Neogene, Oli – Oligocene, Pc – Paleocene, Pg – Paleogene, Pri – Priabonian, Rup – Rupelian, Sel – Selandian, Tha – Thanetian, Ypr – Ypresian. For references see Appendix 1.

No	Locality	Age	Pan-Trionychidae	Pan-Cheloniidae	Dermochelyidae	Pan-Testudinoidea	Pan-Testudines	Number of records (taxa)
1	Ak-Kaya 2	Dan	indet.	–	–	–	–	1
2	Rasstrigin 2	Dan	–	*Itilochelys rasstrigin*	–	–	–	1
3	Sakharnaya Golovka	Dan	–	indet.	–	–	–	1
4	Bereslavka 2a	Sel	indet.	*Euclastes wielandi*	–	indet. 1 and 2	Pan-Testudines tax. nov	5
5	Bakhchisarai 1	Tha	-	indet.	–	–	–	1
6	Bereslavka 2b	Tha	indet.	indet.	–	–	–	2
7	Loznoe 1	Tha	indet.	indet.	–	–	indet.	3
8	Malaya Ivanovka	Tha	–	cf. *Tasbacka* sp.	–	–	indet.	2
9	Kudinovka	Pc-Ypr	–	*Tasbacka aldabergeni*	–	–	–	1
10	Loznoe 2	Ypr	–	–	–	–	indet.	1
11	Malchevsko-Polnenskaya	Ypr	indet.	indet.	–	–	indet.	2–3
12	Novoivanovka	Ypr	–	*Argillochelys* sp., *Puppigerus camperi / Tasbacka aldabergeni*, indet.	–	–	–	2–3
13	Grekovo	Ypr-Lut	–	-	–	–	indet.	1
14	Gruzinov	Ypr-Lut	–	*Argillochelys* sp., indet.	–	–	-	1–2
15	Malchevskaya	Ypr-Lut	–	–	–	–	indet.	1
16	Verkhnetalovka	Ypr-Lut	indet.	–	–	–	–	1
17	Voznesenskiy	Ypr-Lut	–	indet.	–	–	indet.	1–2
18	Bakhmutovka	Lut	–	indet.	–	–	–	1
19	Bulgakovka	Lut	–	indet.	–	–	–	1
20	Georgievka	Lut	–	–	–	–	indet.	1
21	Ikovo	Lut	Plastomenidae indet., *"Trionyx" ikoviensis*	*Argillochelys* sp., *Eochelone* sp., *Puppigerus camperi*	–	Pan-Geoemydidae gen. et sp. nov., Pan-Testudinidae indet.	–	7
22	Kostyanetskiy Yar	Lut	–	indet.	–	–	–	1
23	Krasnorechenskoe	Lut	–	indet.	–	–	indet.	2
24	Krinichnoe	Lut	–	indet.	–	–	–	1
25	Sosnovka	Lut	–	indet.	–	–	–	1
26	Tripolye	Lut-Bar	–	indet.	–	–	–	1
27	Vyshgorod	Lut-Bar	–	*Argillochelys antiqua*, *"Dollochelys" rogovichi*	–	–	–	2
28	Tschelyuskinets	Lut-Pri	–	indet.	indet.	–	–	2
29	Ak-Kaya 1	Bar	indet.	*Argillochelys* sp.	*Cosmochelys* sp.	–	indet.	3–4
30	Bakhchisarai 2	Bar	–	indet.	indet.	–	indet.	3
31	Gorniy Luch	Bar	–	*Eochelone* sp.	–	–	–	1
32	Nagornoe	Bar	–	indet.	–	–	–	1
33	Pirogovo*	Bar	–	indet.		–	–	1
34	Prolom	Bar	indet.	indet.	indet.	–	–	3
35	Otradnoe	Pri	–	indet.	–	–	–	1
36	Zarechnyi	Rup	indet.	-	indet.	–	–	2
37	Abadzekhskaya*	Rup-Cha	–	indet.	–	–	–	1
38	Belomechetskaya	Oli-Mio	–	–	–	–	indet.	1
39	Otradnaya	Pg-Neo	–	indet.	–	–	–	1
Number of localities			10 (26%)	31 (79%)	5 (13%)	2 (5%)	13 (33%)	
Number of records (taxa)			11	35–37	5	4	13	68–70

corresponding localities below). Of two other localities, 41 was based on a mention by Khosatzky (1950: 24) that "there was information about a specimen of a sea turtle, nowadays, perhaps, lost, from the Eocene of Crimea", whereas 49 was based on another mention by Khosatzky (1975: 440), reproduced by Chkhikvadze (1983: 29), of "indeterminate forms of the family Cheloniidae" from the Paleogene of Middle Povolzhye. Both of these mentions have no references to any material. For this reason, these localities are excluded from further consideration.

The term "Eastern Europe" in this paper means European part of the post-Soviet realm with the southern border on the watershed of the Greater Caucasus. In fact, the material of Paleogene turtles on this territory comes only from the European Russia and Ukraine.

All higher-rank names of turtles follow phylogenetic nomenclature (Joyce et al. 2004, 2021). Anatomical terminology follows Gaffney (1979; for cranial bones) and Romer (1956; for postcranial bones). Most shell specimens of Pan-Trionychidae described below demonstrate a typical trionychid sculpturing in the form of pits and ridges, which corresponds to type A (see Danilov et al. 2014): a pattern of thin, connected ridges forming a honeycomb or netlike pattern.

SYSTEMATICS

Pan-Testudines Joyce et al., 2004 (Joyce et al. 2020a)

Testudines Batsch, 1788 (Joyce et al. 2020b).

Pan-Cryptodira Joyce et al., 2004 (Joyce et al. 2020c)

Cryptodira Cope, 1868b (Joyce et al. 2020d)

Pan-Trionychidae Joyce et al., 2004 (2021)

Pan-Trionychidae indet. from the Bereslavka 2b locality

(Fig. 2A, B)

Trionychidae indet.: Averianov and Yarkov 2004: 42

Trionychidae subfam. indet. 24: Danilov et al. 2017: 124

Material. A neural fragment (ZIN PH 1/276).

Description. ZIN PH 1/276 represents the anterior or posterior part of a neural, which is rounded at the preserved border. Externally, the specimen has a typical trionychid sculpturing. The base of the neural arch is preserved on the internal surface of the specimen.

Remarks. Collection ZIN PH contains two neural fragments, including ZIN PH 1/276, from the Bereslavka 2 locality without specification – Bereslavka 2a or Bereslavka 2b. Because ZIN PH 1/276 is similar to the costals of Pan-Cheloniidae indet. from the Bereslavka 2b locality in a finer preservation of the bone tissue, it is supposed here that ZIN PH 1/276 comes from the Bereslavka 2b locality.

Pan-Trionychidae indet. from the Loznoe locality

(Fig. 2C, D)

Trionychidae indet.: Zvonok and Danilov 2018: 95

Material. Two indeterminate shell fragments (ZIN PH 1/253 and ZIN PH 2/253).

Description. Both shell fragments have a typical trionychid sculpturing. ZIN PH 1/253 (Fig. 2C) bears scratches (bite marks) from sharp teeth on its external surface.

Pan-Trionychidae indet. from the Malchevsko-Polnenskaya locality

(Fig. 2E)

Trionychidae indet.: Benitskiy and Zvonok 2020: 101

Material. Four indeterminate shell fragments (ZIN PH 1–4/254).

Description. All shell fragments have a typical trionychid sculpturing. ZIN PH 1/254 (Fig. 2E) bears bite marks on its external surface: the scratches from sharp teeth and a strip of the cortex of the plate is cut off.

Pan-Trionychidae indet. from the Verkhnetalovka locality

(Fig. 2F–H)

Material. A costal fragment (ZIN PH 1/275) and an indeterminate shell fragment (ZIN PH 2/275).

Description. Both shell fragments are heavily worn, with broken-off or indistinct borders. ZIN PH 1/275 (Fig. 2F, G) is the medial part of a costal of a very large individual. Externally, it has a typical trionychid sculpturing and a deep pit caused by an invertebrate borer (trace of boring) near its medial border, whereas internally, there is a breakage from the rib head. The sculpturing of ZIN PH 2/275 (Fig. 2H)

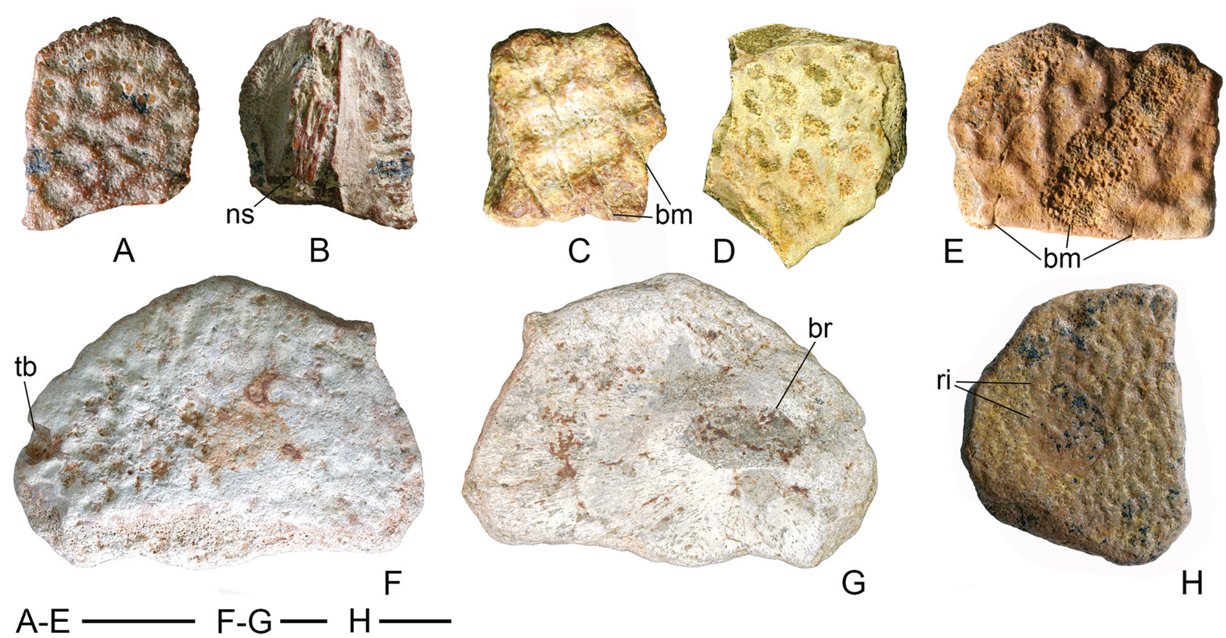

Fig. 2. Pan-Trionychidae indet. from Bereslavka 2b (A, B) and Loznoe (C, D) localities, both Thanetian, Malchevsko-Polnenskaya locality, Ypresian (E), and Verkhnetalovka locality, Ypresian or Lutetian (remains probably redeposited from the Cretaceous) (F–H): A, B – anterior or posterior part of neural ZIN PH 1/276 in dorsal (A) and ventral (B) views; C, D – fragments of shell plates in external view (C – ZIN PH 1/253, D – ZIN PH 2/253); E – fragment of shell plate ZIN PH 1/254 in external view; F–G – costal plate ZIN PH 1/275 in dorsal (F) and ventral (G) views; H – fragment of shell plate ZIN PH 2/275 in external view. *Abbreviations:* bm – bite mark, br – base of rib head, ns – neural spine, ri – rounded impression, tb – trace of boring. Scale bar: 1 cm.

is denser than in ZIN PH 1/275, with connected ridges and pits forming a ripple-like pattern. In addition, externally, there are two large and shallow, overlapping, rounded impressions clearly of biogenic nature.

Pan-Chelonioidea Joyce et al., 2004 (Joyce et al. 2021)

Chelonioidea Baur, 1893 (Joyce et al. 2021)

Pan-Cheloniidae Joyce et al., 2004 (Joyce et al. 2021)

***Argillochelys* Lydekker, 1889**

***Argillochelys* sp. from the Novoivanovka locality**

(Fig. 3A–E)

Argillochelys sp.: Zvonok and Danilov 2018: 95, fig. 1K; Benitskiy and Zvonok 2020: 101

Material. A dentary symphysis (ZIN PH 1/247).

Description. The dentary symphysis with a damaged anterior part (Fig. 3A–E) belongs to a large individual. The symphysis is short, not reaching the level of the foramen dentofaciale majus. The labial and lingual ridges are high and sharp; the area of the symphyseal ridge is broken off. The labial ridge is almost straight (slightly concave) in lateral view; without a high hook anteriorly. The lingual ridges do not reach the level of the labial ridges in height. The posterior edge of the triturating surface has an arcuate shape in dorsal view. Posteriorly and slightly ventrally to the foramen dentofaciale majus there is a shallow depression for the attachment of the m. adductor mandibulae externus. In the posteroventrolateral part of the dentary branch, there is a long process for contact with the angular and surangular. On the medial side of the bone, there are the Meckel's groove, the foramen alveolare inferius, as well as the sutural surfaces for the coronoid, surangular and angular.

Remarks. The specimen is referred to *Argillochelys* based on the presence of high lingual ridges on the dentary, and a short symphysis, not reaching the level of the foramen dentofaciale majus, like in other specimens of *Argillochelys* spp. It differs from *Argillochelys antiqua* from the Vyshgorod locality, Ukraine, by the absence of the high hook of the labial ridge anteriorly; from *Argillochelys* sp. from the Hainaut

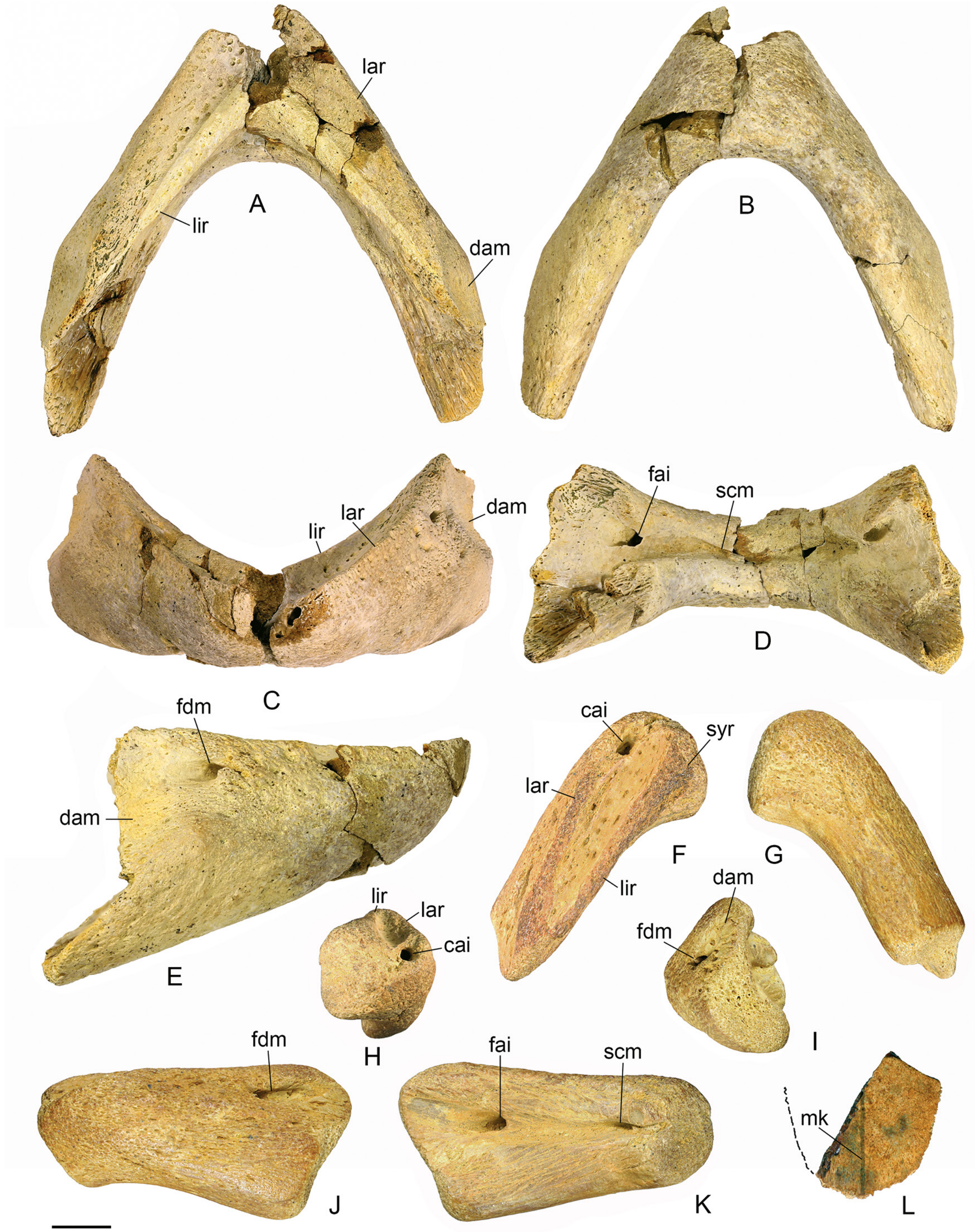

Fig. 3. *Argillochelys* sp. from Novoivanovka locality, Ypresian (A–E), and Gruzinov locality, Ypresian or Lutetian (F–L): A–E – symphysis of dentaries 1/247 in dorsal (A), ventral (B), anterior (C), posterior (D) and right lateral (E) views; F–K – left dentary ZIN PH 1/256 in dorsal (F), ventral (G), anterior (H), posterior (I), lateral (J) and medial (K) views; L – posterior part of neural ZIN PH 8/256 in dorsal view. The median keel on neural ZIN PH 8/256 is highlighted. *Abbreviations:* cai – canalis alveolare inferius, dam – depression for attachment of m. adductor mandibulae externus, fai – foramen alveolare inferius, fdm – foramen dentofaciale majus, lar – labial ridge, lir – lingual ridge, mk – median keel, scm – sulcus cartilaginis meckelii, syr – symphyseal ridge. Scale bar: 1 cm.

locality, Belgium, by an arcuate shape (in contrast to a V-shape) of the posterior edge of the triturating surface in dorsal view.

Argillochelys sp. from the Gruzinov locality

(Fig. 3F–K)

Material. The left branch of the dentary of *Argillochelys* sp. (ZIN PH 1/256) and the posterior part of a neural (ZIN PH 8/256).

Description. The left branch of the dentary (ZIN PH 1/256; Fig. 3F–K) is lacking its most anterior and posterior parts, the bone is worn. The bases of the high labial, lingual and symphyseal ridges are preserved. The canalis alveolaris inferius is exposed anteriorly. On the lateral surface, at the posterior edge, there is a foramen dentofaciale majus. Posteriorly and slightly ventrally to the foramen dentofaciale majus, there is a shallow depression for the attachment of the m. adductor mandibulae externus. On the medial surface, in the posterior part of the deep sulcus cartilaginis meckelii, there is the foramen alveolare inferius.

The posterior part of the neural (ZIN PH 8/256; Fig. 3L) belongs to a medium-sized individual. The preserved dorsal surface is not ornamented. There is a weak median keel on the dorsal surface, like in *Argillochelys* sp. from the Ikovo locality. The posterior margin is convex and the neural is getting wider in the anterior direction.

Remarks. ZIN PH 1/256 is referred to *Argillochelys* based on the presence of lingual ridges on the dentary (see Zvonok and Danilov 2017). ZIN PH 8/256 is referred to *Argillochelys* based on the presence of the median keel on the neural (see Zvonok et al. 2013b).

Argillochelys sp. from the Ak-Kaya 1 locality

(Figs 4, 5)

New material. A posteromedial fragment of a maxilla (ZIN PH 69/153), two vomers (ZIN PH 70/153 and ZIN PH 71/153), a basioccipital (ZIN PH 73/154), a basisphenoid (ZIN PH 72/153), a fragment of a coronoid (ZIN PH 74/155), the distal part of a left ulna (ZIN PH 75/153), three radii fragments (ZIN PH 76–78/153), three manual phalanges (ZIN PH 79–81/153), a left femur (ZIN PH 61/153), metatarsal 5 (ZIN PH 82/153) and a phalanx of a manus or pes (ZIN PH 83/153). The femur (ZIN PH 61/153), described by Zvonok and Danilov (2019), was represented by the proximal part of the bone. Herein, this femur is redescribed based on the proximal and an additional distal part of the same specimen.

Description. The posteromedial fragment of the right maxilla (ZIN PH 69/153; Fig. 4A, B) belongs to a large individual. The triturating surface bears numerous nutritive foramina and a sharp lingual ridge along its medial margin (suture for the palatine).

Two vomers are represented by ventral parts of the bones, belonging to large individuals. ZIN PH 70/153 (Fig. 4C–F) is more complete, whereas ZIN PH 71/153 (Fig. 4G, H) preserves only the right anterolateral sutural surface. ZIN PH 70/153 has a hexagonal shape in ventral view with a relatively narrow anterior border for contact with premaxillae, slightly shorter anterolateral borders for contact with the maxillae, even shorter posterolateral borders for contact with the palatines, and a wide posterior border forming a margin of the secondary palate. As reconstructed, ZIN PH 71/153 was slightly narrower and longer than ZIN PH 70/153. The ventral surface of both vomers is deeply concave and bears nutritive foramina. In the anterior part of the ventral surface of ZIN PH 70/153, there is a very narrow midline sulcus, which is absent in ZIN PH 71/153. In posterior view, a pair of foramina is visible at the base of the vomerine pillar, like in other pan-cheloniids, and an additional foramen is located close to the ventrolateral corner on the left side. In anterior view, there are two pairs of foramina on the sutural surface for the premaxillae.

The basioccipital (ZIN PH 73/154; Fig. 4I–K) belongs to a moderate-sized individual. Its left anterolateral part is broken off. The dorsal surface of the bone is concave, bearing a weak crista dorsalis basioccipitalis in the central part and the basis tuberculi basalis anteriorly. The preserved base of the tuberculum basioccipitale is rounded and not expanded laterally. The posterior part of the basioccipital formed the ventral part of the condylus occipitalis. There is a concavity between the condylus occipitalis and the posterior edge of the tuberculum basioccipitalis. The basioccipital bears smooth sutural surfaces for the basisphenoid anteriorly and the exoccipitals posterodorsally.

The basisphenoid (ZIN PH 72/153; Fig. 4L–P) belongs to a large individual. Its anterior and left parts are broken off. In dorsal view, the main body of the basisphenoid was hexagonal-shaped with anterolateral borders for contact with the prootics, and the

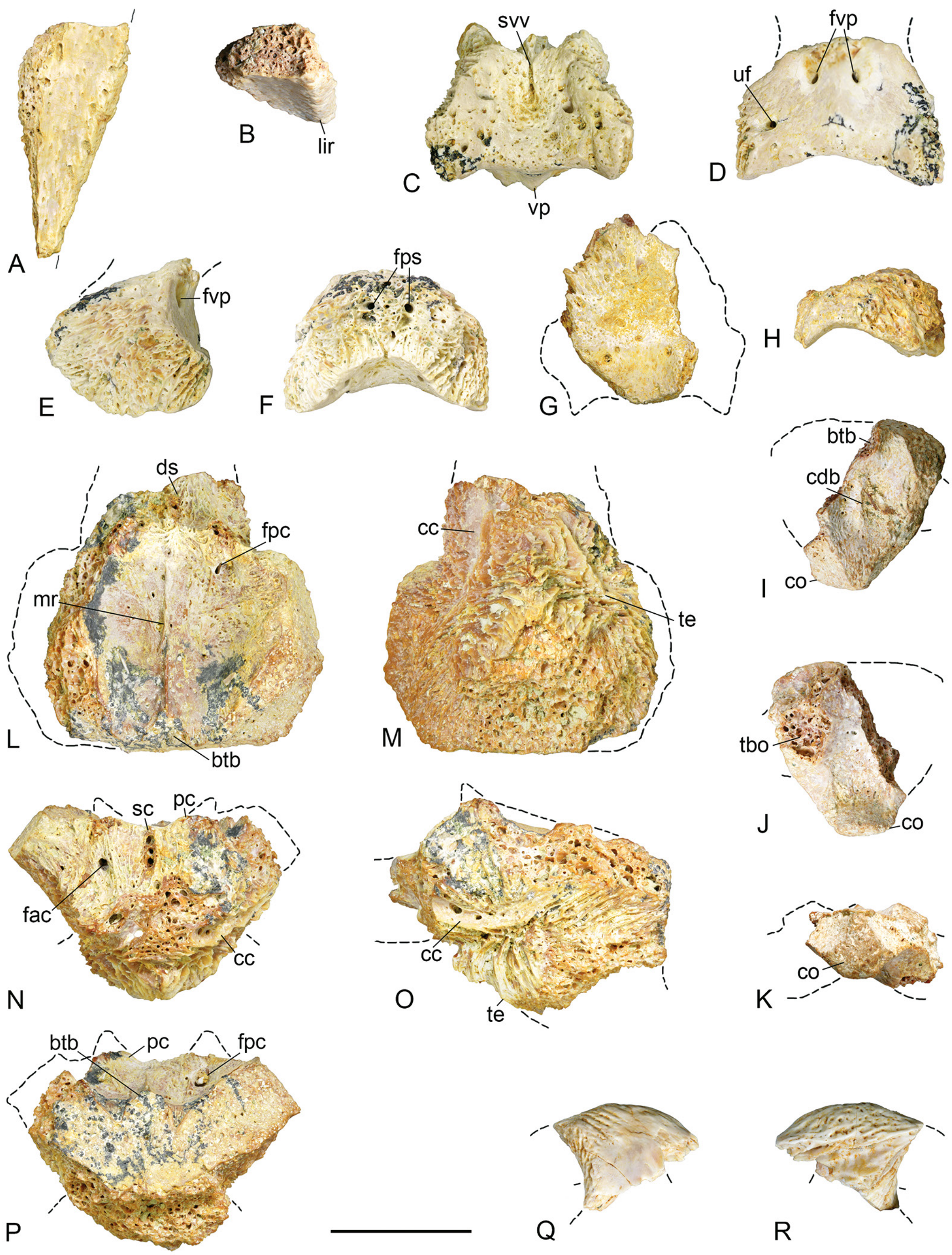

Fig. 4. Cranial bones of *Argillochelys* sp. from Ak-Kaya 1 locality, Bartonian: A, B – medial part of right maxilla ZIN PH 69/153 in ventral (A) and anterior (B) views; C–H – ventral parts of vomer: C–F – ZIN PH 70/153 in ventral (C), posterior (D), left lateral (E), and anterior (F) views; G, H – ZIN PH 71/153 in ventral (G) and posterior (H) views; I–K – basioccipital ZIN PH 73/153 in dorsal (I), ventral (J), and posterior (K) views; L–P – basisphenoid ZIN PH 72/153 in dorsal (L), ventral (M), anterior (N), left lateral (O), and posterior (P) views; Q, R – left coronoid ZIN PH 74/153 in medial (Q) and lateral (R) views. *Abbreviations:* btb – basis tuberculi basalis, cc – canalis carotici interni, cdb – crista dorsalis basioccipitalis, co – condylus occipitalis, ds – dorsum sellae, fac – foramen anterior canalis nervi abducentis, fpc – foramen posterior canalis nervi abducentis, fps – foramina on posterior surface of vomer, fvp – foramina on vomerine pillar, lir – lingual ridge, mr – medial ridge, pc – processus clinoideus, sc – sagittal crest on dorsum sellae, svv – sulcus on ventral surface of vomer, tbo – tuberculum basioccipitale, te – triangular elevation, uf – unnamed foramen, vp – vomerine pillar. Scale bar: 1 cm.

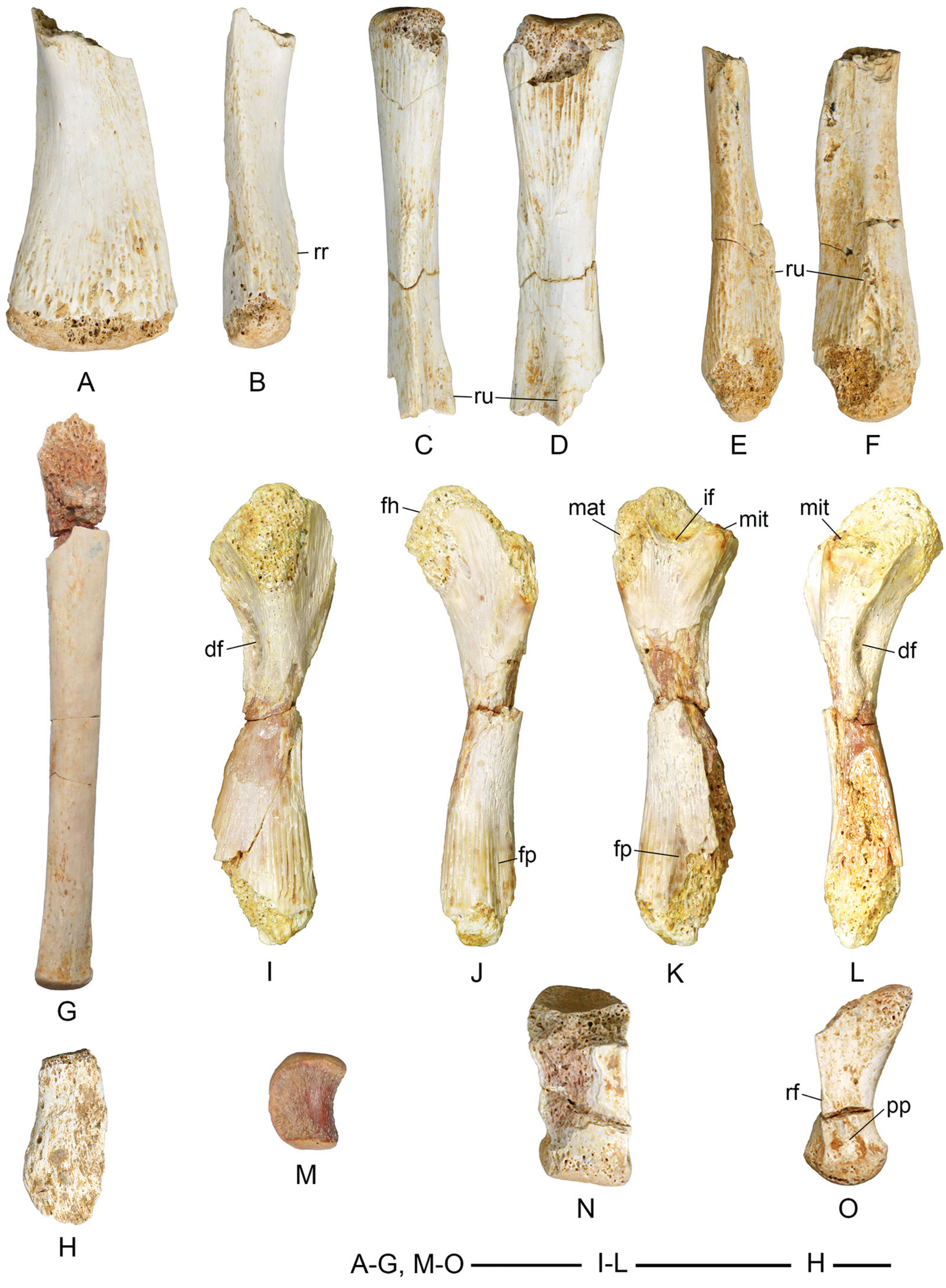

Fig. 5. Limb bones of *Argillochelys* sp. from Ak-Kaya 1 locality, Bartonian: A, B – distal part of left ulna ZIN PH 75/153 in ventral (A) and anterior (B) views; C, D – proximal part of right radius ZIN PH 76/153 in posterior (C) and dorsal (D) views; E, F – distal part of right ulna ZIN PH 77/153 in posterior (E) and dorsal (F) views; G – phalanx 2 of digit 4 of manus ZIN PH 81/153 in ventral view; H – phalanx 2 of digit 5 of manus ZIN PH 79/153 in dorsal or ventral view; I–L – left femur ZIN PH 61/153 in dorsal (I), posterior (J), ventral (K) and anterior (L) views; M – metatarsal 5 ZIN PH 82/153 in dorsal or ventral view; N, O – phalanx 1 of digit 1 of manus or pes ZIN PH 83/153 in dorsal (N) and lateral or medial (O) views. *Abbreviations:* df – depression on dorsal surface of femur, fh – femoral head, fp – fossa poplitea, if – intertrochanteric fossa, mat – major trochanter, mit – minor trochanter, pp – pit on distal part of phalanx, rf – ridge on diaphysis of phalanx, rr – rugosity for attachment to radius, ru – rugosity for attachment of ulna. Scale bar: 1 cm.

posterior border for contact with the basioccipital. The dorsal surface of the main body is concave. There is a midline ridge running posteriorly from the dorsum sellae to the basis tuberculi basalis. The foramen posterius canalis nervi abducentis is visible on the right side near the anterior border of the main body. The dorsum sellae does not overhang the sella turcica. There is a sagittal ridge running from the dorsum sellae anteriorly to the sella turcica, which is not preserved. The clinoid processes are broken off. In anterior view, there are the foramen anterius canalis nervi abducentis (visible on the right side), and openings of the internal carotid canals (sulci). The ventral side of the basisphenoid is represented by the sutural surface for the pterygoids and is broken off posteriorly. The central part of the ventral side bears a large triangular elevation, bordered laterally by sulci of the canalis caroticus internus (better visible on the right side).

The fragment of the left coronoid (ZIN PH 74/155; Fig. 4Q, R), belonging to a moderate-sized individual, is represented by its dorsal part, forming a process slightly overhanging the dentary.

The distal part of the left ulna (ZIN PH 75/153; Fig. 5A, B) belongs to a moderate-sized individual. The bone is flattened dorsoventrally, and with sharp anterior and posterior margins. The rugosity for the attachment of the radius is located on the ventral side of the ulna close to its distal epiphysis, like in other pan-cheloniids (Hirayama 1998).

The fragments of the radii are represented by the proximal part of the right radius (ZIN PH 76/153; Fig. 5C, D), and the distal parts of the right (ZIN PH 77/153; Fig. 5E, F) and left radii (ZIN PH 78/153; not figured) of medium-sized individuals. The posterior margin of ZIN PH 76/153 is sharp and slightly convex in the middle portion. ZIN PH 76/153 and ZIN PH 77/153 have rugosity for the attachment of the ulna dorsally close to the distal epiphyses, like in all pan-cheloniids (Hirayama 1998).

Phalanx 2 of digit 4 of a manus (ZIN PH 81/153, Fig. 5G) belongs to a moderate sized individual; the anterior part is broken off. The phalanx is strongly elongate, narrows distally. It is circular in cross-section in the middle part and slightly flattened dorsoventrally in the distal part. ZIN PH 81/153 does not differ in its overall shape from the same phalanx of *Lepidochelys olivacea*.

Two phalanges 2 of digit 5 of a manus (ZIN PH 79/153; Fig. 5H and ZIN PH 80/153; not figured); their distal tips are broken off. The phalanges are strongly flattened dorsoventrally, which is typical for pan-cheloniids, with a convex anterior margin.

The left femur (ZIN PH 61/153; Fig. 5I–L) belongs to a small individual. The femoral head, both trochanters, part of the diaphysis, and distal epiphysis are damaged. The intertrochanteric fossa is extensive. The intertrochanteric ridge is absent. The ridge between the femoral head and the trochanter minor is present. An elongate depression is located distally from this ridge on the diaphysis. The diaphysis is thin, slightly curved, and roundish in cross-section. On the ventral side of the bone, there is a proximodistally directed depression (fossa poplitea).

Metatarsal 5 (ZIN PH 82/153; Fig. 5M) belongs to a small individual. It has roughly semilunate shape with concave anterior and convex posterior edges. ZIN PH 82/153 does not differ in its overall shape from the same phalanx of *Lepidochelys olivacea*.

Phalanx 1 of digit 1 of a manus or pes (ZIN PH 83/153; Fig. 5N–O) belongs to a moderate sized individual; its proximoventral part and lateral or medial side is damaged. The proximal epiphysis is concave. The distal epiphysis is convex, sloped mediolaterally and slightly rotated in relation to the proximal epiphysis. There are large pits in the medial and lateral surfaces of the distal epiphysis, and sharp ridges along the lateral and medial sides of the phalanx.

Remarks. The pan-cheloniid skull material from the Ak-Kaya 1 locality described above is referred to *Argillochelys* sp. based on the following characters: the presence of the lingual ridge on the maxilla, hexagonal and ventrally concave ventral part of the vomer, similar shape of the basisphenoid, basioccipital and coronoid. The pan-cheloniid non-shell postcranial material from the Ak-Kaya 1 locality is referred to the same taxon as there are no other pan-cheloniid taxa known from this locality (see Zvonok and Danilov 2019).

The vomers of *Argillochelys* sp. from the Ak-Kaya 1 locality has moderate anterolateral borders and short posterolateral margins, a condition intermediate between the type species of *Argillochelys* – *A. cuneiceps*, and the type species of *Eochelone* Dollo, 1903 – *Eochelone brabantica*. The same condition is observable in *Argillochelys athersuchi* and an undescribed pan-cheloniid specimen from the lower Bartonian (Auversian) of Beauchamp, France (MNHN; Danilov, pers. obs., 2007). The basisphenoid of *Argillochelys* sp. from the Ak-Kaya 1 locality is very similar to an undescribed pan-cheloniid specimen

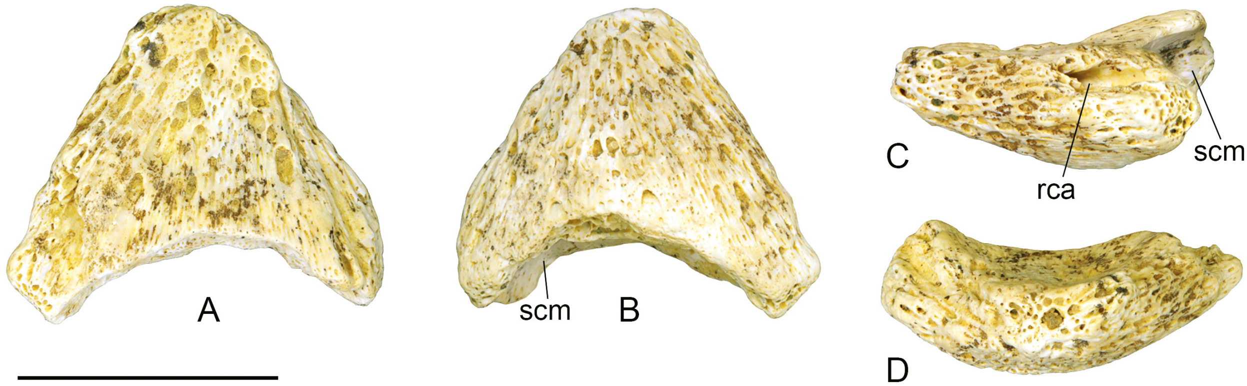

Fig. 6. Symphysis of dentaries of *Puppigerus camperi* or *Tasbacka aldabergeni* ZIN PH 2/247 from Novoivanovka locality, Ypresian, in dorsal (A), ventral (B), left lateral (C) and anterior (D) views. *Abbreviations:* rca – ramification of canalis alveolare inferius and canal leading to foramen dentofaciale majus, scm – sulcus cartilaginis meckelii. Scale bar: 1 cm.

from the lower Bartonian (Auversian) of Beauchamp, France (MNHN; Danilov, pers. obs., 2007).

The shape of the diaphysis of the femur and the presence of the elongate depression distally to the ridge between the femoral head and the trochanter minor of *Argillochelys* sp. from the Ak-Kaya 1 locality make it similar to those of *Erquelinnesia gosseleti* and *Tasbacka aldabergeni* (Zangerl 1971: pl. IX, fig. 1c, d; pers. obs. of coll. CCMGE 12175).

The sharp ridges along the lateral and medial sides of phalanx ZIN PH 82/153 are absent on the phalanges of extant *Lepidochelys olivacea*, but present on some undescribed phalanges of *Tasbacka aldabergeni*. The Pan-Trionychidae, which are also present in the locality, unlike ZIN PH 82/153, have phalanges with a swollen ventral part of the proximal epiphysis (pers. obs. of *Lissemys punctata*, *Pelodiscus sinensis,* and *Trionyx triunguis*).

Zvonok and Danilov (2019) have described the vertebra of *Argillochelys* sp. ZIN PH 57/153 as cervical 8. Additional comparison with material of *Tasbacka aldabergeni* (collection CCMGE 12175), containing dorsoventrally flattened caudal vertebrae with a weak ventral keel, allowed reassignment of ZIN PH 57/153 as an anterior caudal vertebra, which is also confirmed by the position of the transverse processes in the middle part of the centrum.

Puppigerus **Cope, 1870 or** ***Tasbacka*** **Nessov, 1987**

Puppigerus camperi **(Gray, 1831) or** ***Tasbacka aldabergeni*** **Nessov, 1987**

Puppigerus camperi **or** ***Tasbacka aldabergeni*** **from the Novoivanovka locality**

(Fig. 6)

Puppigerus sp.: Benitskiy and Zvonok 2020: 101

Material. A dentary symphysis (ZIN PH 2/247).

Description. Dentary symphysis ZIN PH 2/247 belongs to a juvenile individual. It is heavily worn and subtriangular in shape. The triturating surface is extensive, lacking ridges. The posterior edge of the symphysis is arcuate. The sulcus cartilaginis meckelii is deep at the symphysis level. The split of the canalis alveolaris inferior and a canal leading to the foramen dentofaciale majus is exposed slightly anterior to the level of the posterior edge of the symphysis. Thus, the foramen dentofaciale majus was located at or slightly posteriorly to the level of the posterior edge of the symphysis.

Remarks. The dentary symphysis is referred to *Puppigerus camperi* or *Tasbacka aldabergeni* based on the subtriangular shape, extensive triturating surface without ridges and arcuate concave posterior edge of the symphysis, as well as the same geological age (Ypresian).

Pan-Cheloniidae indet.

Pan-Cheloniidae indet. from the Bereslavka 2b locality

(Fig. 7A–C)

Cheloniidae indet.: Averianov and Yarkov 2004: 42

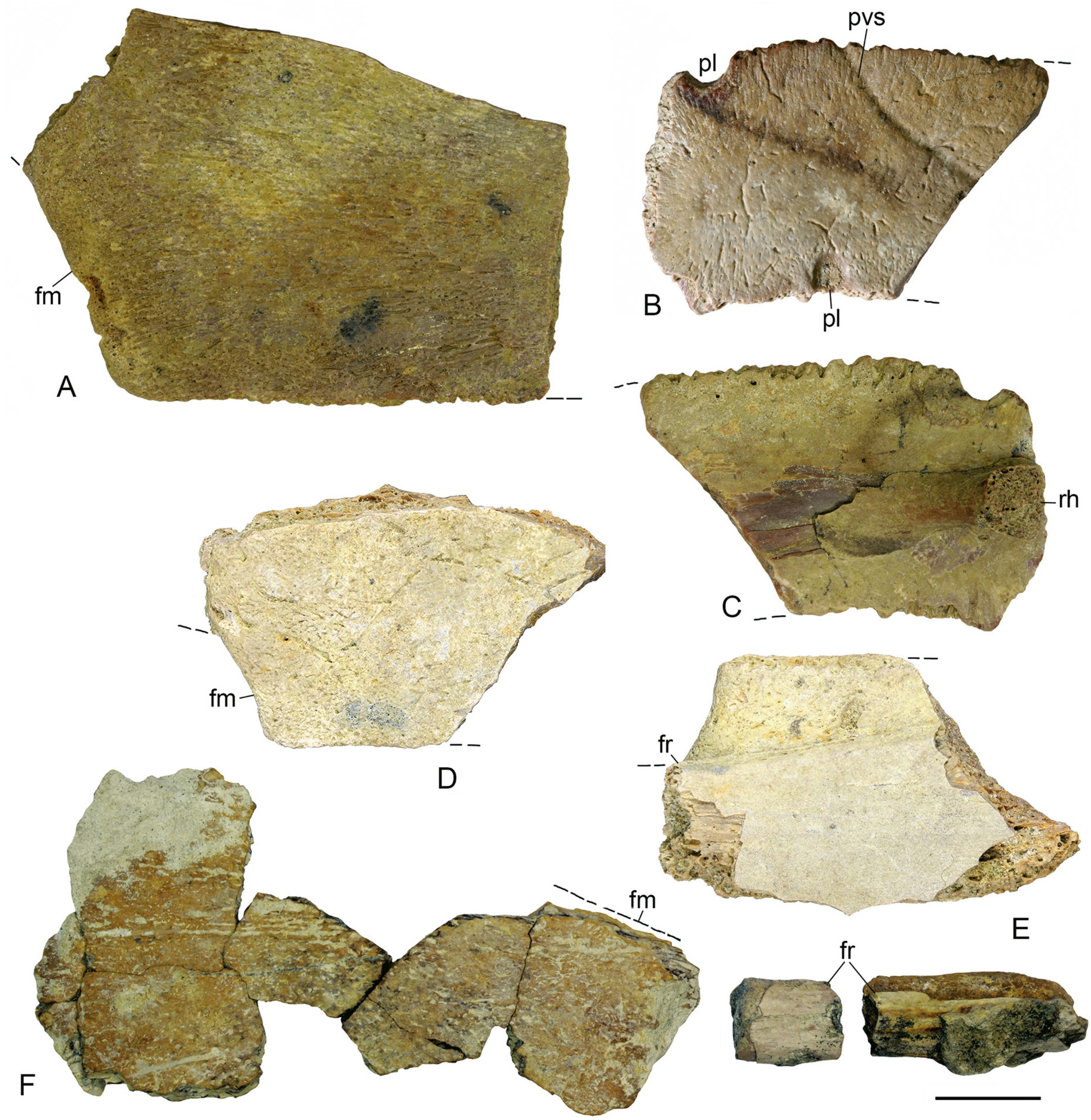

Fig. 7. Pan-Cheloniidae indet. from Bereslavka 2b (A–C), Loznoe (D, E) and Bakhchisarai 1 (F) localities, all Thanetian: A – lateral costal fragment ZIN PH 2/276 in dorsal view; B, C – medial part of costal 4 or 6 ZIN PH 3/276 in dorsal (B) and ventral (C) views; D, E – lateral costal fragment ZIN PH 3/253 in dorsal (D) and ventral (E) views; F – fragments of costal ZIN PH 1/251 in dorsal view. *Abbreviations:* fm – free margin, fr – free rib, pl – parasitic lesion, pvs – pleural-vertebral sulcus, rh – rib head. Scale bar: 1 cm.

Material. Eight fragments of small and medium-sized costals of several individuals (ZIN PH 2–9/276).

Description. A series of costals containing three medial, four middle and one lateral fragments. The external surface of all specimens is smooth. The lateral costal fragment (ZIN PH 2/276; Fig. 7A) belongs to a large individual. It has free anterolateral or posterolateral margin typical for pan-cheloniids. The best preserved is the medial half of right costal 4 or 6 (ZIN PH 3/276; Fig. 7B, C). The anterior border of the plate is slightly convex, whereas the posterior one is slightly concave. In the medial part of the anterior border, there is a rounded perforation obviously caused by an epibiont or parasite. The medial border is divided into longer anteromedial and shorter posteromedial parts. Externally, there is a part of the pleural-vertebral sulcus directed posterolaterally from the anterior border, and a deep round pit with a central boss caused by an epibiont or parasite. The rib head is large.

Remarks. The large size, smooth external surface of the carapace and the presence of the costoperipheral fontanelles allow attribution of the material to Pan-Cheloniidae indet.

Pan-Cheloniidae indet. from the Loznoe 1 locality

(Fig. 7D, E)

Material. A lateral costal fragment (ZIN PH 3/253).

Description. ZIN PH 3/253 represents the antero- or posterolateral part of a large individual (Fig. 7D, E). Its external surface is smooth, with small nutrient foramina and narrow grooves. The lateral border of the plate is rounded, indicating the presence of a costoperipheral fontanelle. The base of the free rib is very wide and dorsoventrally flattened.

Remarks. The large size, smooth external surface of the carapace and the presence of the costoperipheral fontanelles allow attribution of the material to Pan-Cheloniidae indet.

Pan-Cheloniidae indet. from the Bakhchisarai 1 locality

(Fig. 7F).

"Bones of [sea] turtles": Nessov 1987: 77; Chkhikvadze 1990: 5

Chelonioidea indet.: Averianov 2002: 139, 142; Danilov et al. 2017: 193

Material. Five fragments of a large costal (ZIN PH 1/251).

Description. The fragments of the costal are partially embedded in pieces of the limestone (Fig. 7F). Their external surface is smooth. Two fragments of a long free rib are round in cross-section.

Remarks. The large size, smooth external surface of the carapace and the presence of the costoperipheral fontanelles allow attribution of the material to Pan-Cheloniidae indet.

Pan-Cheloniidae indet. from the Malchevsko-Polnenskaya locality

(Figs 8, 9A–G)

Cheloniidae indet.: Benitskiy and Zvonok 2020: 100

Material. A supraoccipital (ZIN PH 6/254), a right squamosal (ZIN PH 5/254), the neural arch of cervical vertebra 8 (ZIN PH 7/254), the diaphysis of a right ulna (ZIN PH 8/254), two metacarpals 2 or 3 or 4 (ZIN PH 9/254 and ZIN PH 10/254), phalanx 2 of digit 4 of a manus (ZIN PH 11/254), metatarsal 1(?) (ZIN PH 12/254), a left tibia (ZIN PH 13/254), three neurals (ZIN PH 14–16/254), a medial costal fragment (ZIN PH 17/254), and three peripherals (ZIN PH 18–20/254).

Description. The supraoccipital (ZIN PH 6/254; Fig. 8A–D) belongs to a large individual. The crista supraoccipitalis and the left part of the bone are broken off. The base of the crista supraoccipitalis is very narrow in its lower part. There are sutural surfaces for the parietals dorsally, prootic and opisthotic laterally, and the exoccipital posterolaterally. Internally, on the right side, there are the canalis semicircularis anterius anteriorly, the canalis semicircularis posterius posteriorly, and the foramen aquaducti vestibuli in the medial wall of the cavum labyrinthicum.

The right squamosal (ZIN PH 5/254; Fig. 8E–G) is lacking areas along the posterior margin and suture for the quadrate bone. The margin forming the posterior part of the cavum tympani is slightly concave in lateral view. The preserved lateral surface of the squamosal is smooth. The depression for the lateral part of the m. depressor mandibulae (Jones et al. 2012) is deep and fissure-like; it is situated on the posteroventral surface of the squamosal, almost horizontal and barely visible in lateral view.

The neural arch of cervical 8 (ZIN PH 7/254; Fig. 8H–J) is missing most of its ventral part and prezygapophyses. The postzygapophyses are oriented posteroventrolaterally. The neural spine bears a thickening for articulation with the nuchal. On the ventral surface of this thickening, there is a rounded depression.

The diaphysis of the right ulna (ZIN PH 8/254; Fig. 8K) is curved in the middle part.

The first specimen of metacarpal 2 or 3 or 4 (ZIN PH 9/254; Fig. 8L) has partially worn epiphyses. The proximal epiphysis is slightly concave, whereas the distal one is slightly convex. The diaphysis is

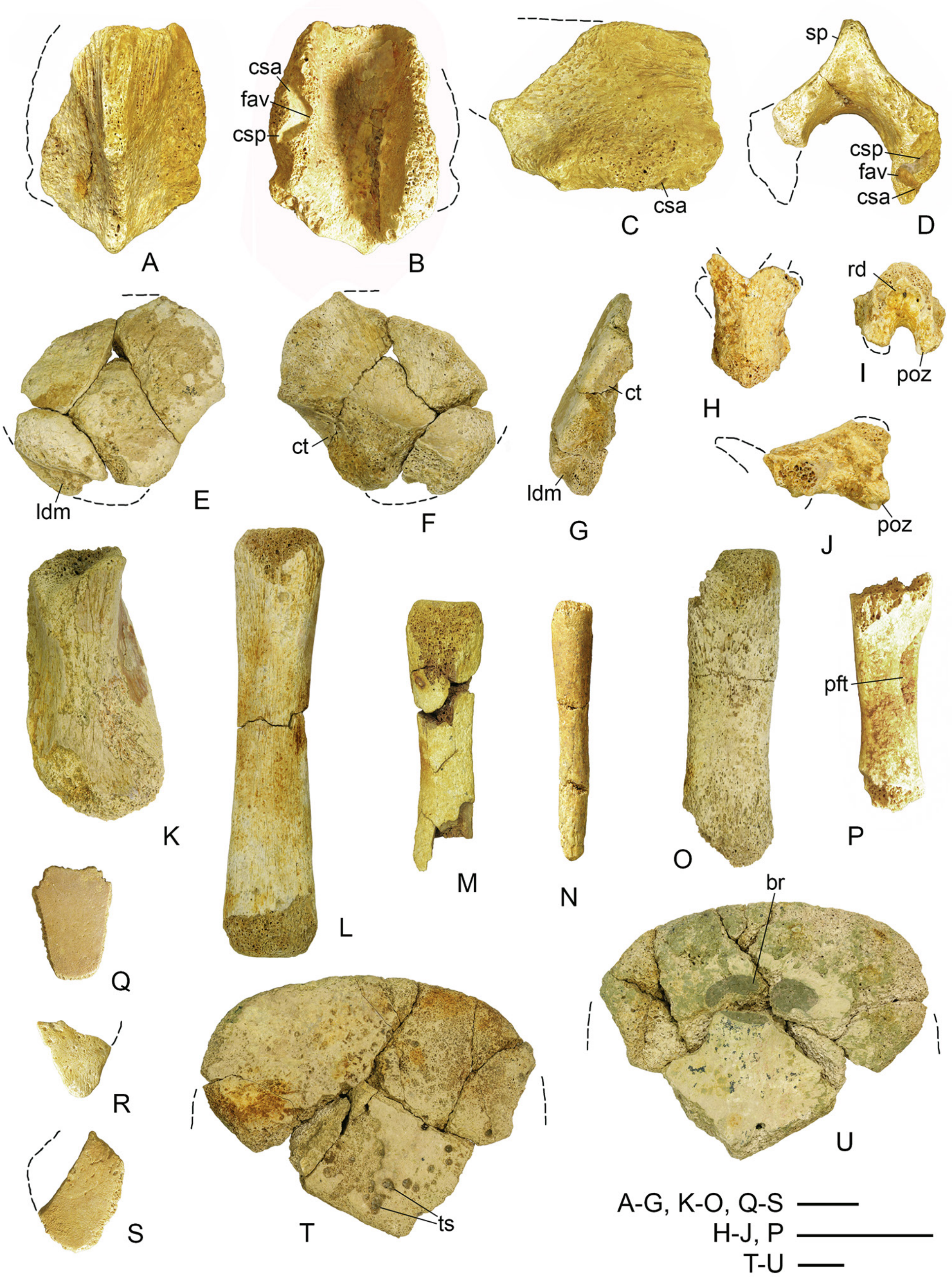

Fig. 8. Non-shell bones, neurals and costal of Pan-Cheloniidae indet. from Malchevsko-Polnenskaya locality, Ypresian: A–D – supraoccipital ZIN PH 6/254 in dorsal (A), ventral (B), right lateral (C) and posterior (D) views; E–G – right squamosal ZIN PH 5/254 in lateral (E), medial (F) and anterior (G) views; H–J – neural arch of cervical vertebra 8 ZIN PH 7/254 in dorsal (H), posterior (I) and left lateral (J) views; K – diaphysis of right ulna ZIN PH 8/254 in ventral view; L–M – metacarpals 2 or 3 or 4 in ventral view (L – ZIN PH 9/254, M – ZIN PH 10/254); N – phalanx 2 of digit 4 of manus ZIN PH 11/254 in dorsal or ventral view; O – metatarsal 1(?) ZIN PH 12/254 in ventral view; P – left tibia ZIN PH 13/254 in ventral view; Q–S – neurals in dorsal view (Q – ZIN PH 14/254, R – ZIN PH 15/254, S – ZIN PH 16/254); T–U – costal ZIN PH 17/254 in dorsal (T) and ventral (U) views. *Abbreviations:* br – base of rib head, csa – canalis semicircularis anterius, csp – canalis semicircularis posterius, ct – cavum tympani, fav – foramen aquaducti vestibuli, ldm – depression for attachment of m. depressor mandibulae pars lateralis, pas – posterior articular surface, pft – pit for insertion of tendons of mm. flexor tibialis internus and pubio-tibialis, poz – postzygapophysis, rd – rounded depression, sp – supraoccipital process, ts – traces of possible nutrition of scavengers. Scale bar: 1 cm.

subtriangular-shaped in cross-section. The second specimen of metacarpal 2 or 3 or 4 (ZIN PH 10/254; Fig. 8M) is lacking its distal part. The proximal epiphysis is slightly concave. The diaphysis has a teardrop shape (flattened) in cross-section.

Phalanx 2 of digit 4 of a manus (ZIN PH 11/254; Fig. 8N) is strongly elongated and tapering distally, similar to the corresponding element of other pan-cheloniids (Mulder 2003: pls. 45–47).

Metatarsal 1(?) (ZIN PH 12/254; Fig. 8O) has a damaged proximal epiphysis and lacking a distal one. The bone is flattened dorsoventrally like in other pan-cheloniids. The diaphysis is almost equally wide proximally and distally, and with a sharp ridge along the posterior margin. The proximal epiphysis is slightly concave.

The left tibia (ZIN PH 13/254; Fig. 8P) belongs to a small individual. Its epiphyses are broken off. In the proximal part, the diaphysis bears an elongated pit for insertion of the tendons of the mm. flexor tibialis internus and pubio-tibialis characteristic for early Cenozoic pan-cheloniids and *Natator depressus* (Zangerl 1980; Zangerl et al. 1988).

The three neurals (ZIN PH 14–16/254; Fig. 8Q–S) belong to small individuals. Their external surface is smooth. ZIN PH 14/254 (Fig. 8Q) is hexagonal short-sided anteriorly. ZIN PH 15/254 (Fig. 8R) is represented by a pointed posterior fragment. ZIN PH 16/254 (Fig. 8S) is lacking the left anterolateral part; the plate is pointed posteriorly and with a relatively long anterolateral border.

The medial costal fragment (ZIN PH 17/254; Fig. 8T, U) has a smooth external surface and bears numerous rounded fossae and a large irregular depression likely caused by invertebrate scavengers. All borders of the plate are worn. Internally, there is the base of the rib head.

Of the peripheral specimens, ZIN PH 18/254 (Fig. 9A–C) belongs to a medium-sized individual and represents left peripheral 5 or 6. The areas of the dorsal plate and small anterior and posterior parts of the specimen are broken off. The external surface is smooth. The peripheral is angular in cross-section. The dorsal plate is much wider than the ventral one and bears a medial notch for insertion of the free rib of the costal. ZIN PH 19/254 (Fig. 9D, E) belongs to a smaller individual than ZIN PH 18/254 and represents a posterior peripheral (9–11). Its posterior and part of the medial borders are broken off. The external surface bears a net of grooves and the intermarginal sulcus. The dorsal plate is wider than the ventral one. There is no pit for the rib insertion on the medial border. ZIN PH 20/254 (Fig. 9F, G) belongs to a small individual and represents a posterior peripheral. All borders of the plate, except a small part of the lateral border, are broken off. The plate is wedge-shaped in cross-section. The external surface is smooth. The pit for the rib insertion is situated in the middle part of the plate.

Remarks. The supraoccipital (ZIN PH 6/254) is referred to Pan-Cheloniidae based on its large size and differences from Pan-Trionychidae also present in the locality, in which the crista supraoccipitalis usually is very wide in the lower part.

The depression for the lateral part of the m. depressor mandibulae occupies most of the lateral surface of the squamosal posteriorly to the cavum tympani in *Erquelinnesia gosseleti*, *Puppigerus camperi,* and *Tasbacka aldabergeni* and the posterior part of this area in "*Allopleuron*" *qazaqstanense* from the Kuyulus locality, *Argillochelys antiqua* from the Vyshgorod locality, *Argillochelys* sp. from the Ak-Kaya 1 locality and *Eochelone brabantica*. The smooth lateral surface of the squamosal and ventrally situated and horizontally oriented depression for the lateral part of the m. depressor mandibulae, like ZIN PH 5/254, is observable among Eocene pan-cheloniids only in *Argillochelys cuneiceps.*

The neural arch of cervical vertebra 8 (ZIN PH 7/254) has a thickening for articulation with the nuchal, like in other pan-cheloniids (Zangerl and Turnbull 1955: pl. 4). The morphology of the preserved part of the ulna (ZIN PH 8/254) does not differ from those of *Lepidochelys olivacea*. The metacarpals (ZIN PH 9/254 and 10/254) are referred to Pan-Cheloniidae indet. based on the large size and flattening. The posterior peripheral (ZIN PH 20/254) is similar to Pan-Cheloniidae indet. ZIN PH 7/256 from the Gruzinov locality by sculpturing. The morphology of other shell specimens from the Malchevsko-Polnenskaya locality corresponds to pan-cheloniids.

Pan-Cheloniidae indet. from the Novoivanovka locality

(Fig. 9H)

Material. The anterior part of a neural (ZIN PH 3/247).

Description. The anterior part of the neural (ZIN PH 3/247; Fig. 9H) demonstrates short anterolateral

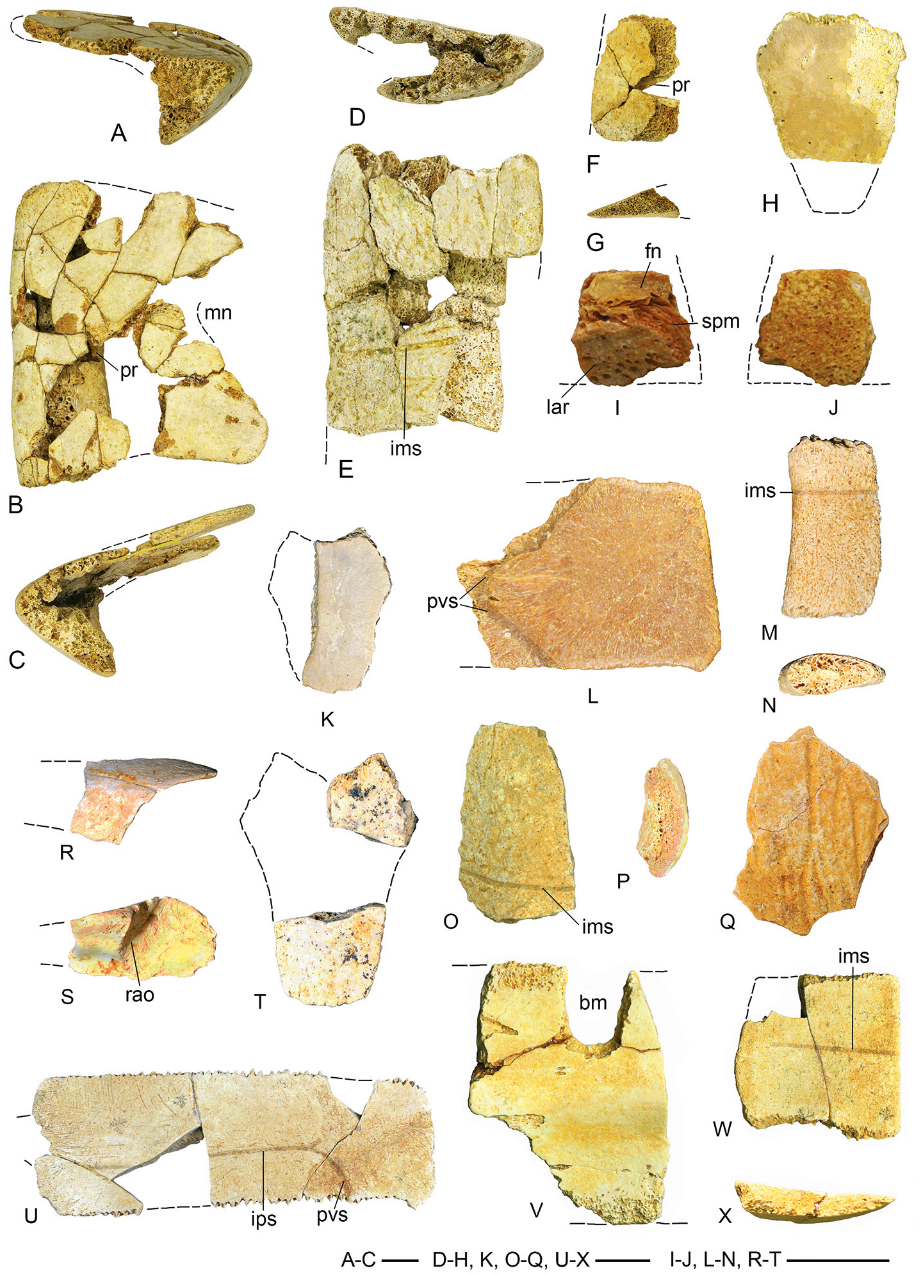

Fig. 9. Pan-Cheloniidae indet. from Malchevsko-Polnenskaya (A–G) and Novoivanovka (H) localities, both Ypresian, and Gruzinov (I–Q) and Voznesenskiy (R–X) localities, both Ypresian or Lutetian: A–C – left peripheral 5 or 6 ZIN PH 18/254 in posterior (A), dorsal (B), and posterior (C) views; D, E – posterior peripheral (9–11) ZIN PH 19/254 in anterior or posterior (D) and dorsal (E) views; F, G – posterior peripheral ZIN PH 20/254 in dorsal (F) and anterior or posterior (G) views; H – neural ZIN PH 3/247 in dorsal view; I–J – anterior part of maxilla ZIN PH 9/256 in medial (I) and lateral (J) views; K – neural ZIN PH 3/256 in dorsal view; L – medial part of left even costal ZIN PH 5/256 in dorsal view; M, N – peripheral 2 ZIN PH 6/256 in dorsal (M) and posterior (N) views; O, P – fragment of peripheral 4 or 5 ZIN PH 7/256 in external (O) and anterior or posterior (P) views; Q – fragment of unknown shell plate ZIN PH 10/254 in external view; R, S – right postorbital ZIN PH 1/266 in lateral (R) and internal (S) views; T – neural ZIN PH 10/266 in dorsal view; U – left even costal ZIN PH 2/266 in dorsal view; V – fragment of costal ZIN PH 7/266 in ventral view; W, X – right peripheral 11(?) ZIN PH 9/266 in dorsal (W) and posterior (X) views. *Abbreviations:* bm – bioerosion mark, fn – wall of fossa nasalis, ims – intermarginal sulcus, ips – interpleural sulcus, lar – labial ridge, mn – medial notch for costal, pr – pit for rib insertion, pvs – pleural-vertebral sulcus, rao – ridge along orbital rim, spm – suture for premaxilla. Scale bar: 1 cm.

and long posterolateral borders, indicating that the plate was hexagonal, short-sided anteriorly. The external surface of the specimen is smooth and slightly convex.

Remarks. The neural with a short anterolateral border, and smooth and slightly convex external surface of it, may correspond either to *Argillochelys* sp. or *Puppigerus camperi* / *Tasbacka aldabergeni*, known from the same locality; thus, we referred ZIN PH 3/247 to Pan-Cheloniidae indet.

Pan-Cheloniidae indet. from the Gruzinov locality
(Fig. 9I–Q)

Material. The anterior part of a left maxilla (ZIN PH 9/256), two fragmentary neurals (ZIN PH 2/256 and ZIN PH 3/256), two medial parts of left even costals (ZIN PH 4/256 and ZIN PH 5/256), peripheral 2 (ZIN PH 6/256), a fragment of peripheral 4 or 5 (ZIN PH 7/256) and a fragment of an unknown shell plate (ZIN PH 10/256).

Description. The anterior part of the left maxilla (ZIN PH 9/256; Fig. 9I–J) belongs to a small individual; the anteriormost margin of the labial ridge and the dorsal part of the fragment are damaged. The labial ridge is high and sharp; it bears numerous nutrient foramina on the medial surface. Anteriorly and dorsally the labial ridge of the maxilla terminates by the suture for the premaxilla. Dorsally to this suture, partially preserved is the lateral wall of the fossa nasalis.

Neural ZIN PH 2/256 is lacking both lateral parts, whereas neural ZIN PH 3/256 (Fig. 9K) is lacking the left part only. Both plates are flat, with concave anterior borders. ZIN PH 3/256 demonstrates short anterolateral and long posterolateral borders.

The medial parts of the left even costals (ZIN PH 4/256 and ZIN PH 5/256) have long anteromedial and short posteromedial borders for contact with the corresponding neurals. In the smaller specimen (ZIN PH 5/256; Fig. 9L), the vertebral scute was wide and with deep scute sulci.

Peripheral 2 (ZIN PH 6/256; Fig. 9M, N) belongs to a juvenile individual. It is drop-shaped in cross-section and with a slightly concave lateral border. The medial margin is free, which indicates a developed costoperipheral fontanelle 1. The intermarginal sulcus lies in the anterior part of the plate.

The fragment of peripheral 4 or 5 (ZIN PH 7/256; Fig. 9O, P) is high and rounded laterally in cross-section. Externally, the plate has the intermarginal sulcus and sculpturing of a net of grooves like in several species of pan-cheloniids.

The fragment of an unknown flat shell plate (ZIN PH 10/256; Fig. 9Q) has all margins damaged. The external surface of this fragment is sculptured by a net of grooves.

Remarks. The presence of the costoperipheral fontanelles and sculpturing of the shell in the form of the net of grooves allow attribution of these materials to Pan-Cheloniidae indet. (see de Lapparent de Broin et al. 2014; Evers et al. 2019). The rest of the material is referred to pan-cheloniids conditionally, as there are no other determinable turtle groups in the Gruzinov locality.

Pan-Cheloniidae indet. from the Voznesenskiy locality
(Fig. 9R–X)

Cheloniidae indet.: Zvonok and Danilov 2018: 96

Material. The anterior part of a right postorbital (ZIN PH 1/266), a neural (ZIN PH 10/266), six costals (ZIN PH 2–7/266) and two peripherals (ZIN PH 8/266 and 9/266).

Description. The anterior part of the right postorbital (ZIN PH 1/266; Fig. 9R, S) suggests that the bone was extended anteroposteriorly and formed the posterodorsal rim of the orbit. Internally, there is a sharp ridge stretching along the orbit.

The neural (ZIN PH 10/266; Fig. 9T) is represented by posterior and right anterolateral fragments. The plate is convex, with a smooth external surface. As reconstructed, it was hexagonal, short-sided anteriorly.

Of the costals, ZIN PH 2/266 (Fig. 9U) is a left even costal lacking the free rib and two fragments along the anterior and posterior borders. The plate has long anteromedial and short posteromedial borders for contact with the corresponding neurals, and a free lateral border indicating the presence of the costoperipheral fontanelle. There are interpleural and pleural-vertebral sulci on the external surface of the plate. ZIN PH 3/266 is the middle part of right costal 1. ZIN PH 4/266 is the proximal part of a right even costal of a large individual. It has a short posteromedial border. ZIN PH 5/266 is the proximal part of a costal of a medium-sized individual. ZIN PH 6/266 is right odd costal 5(?). ZIN PH 7/266 (Fig. 9V) is a middle fragment of an indeterminate costal plate with a bioerosion mark on the anterior or posterior border in the shape of a deep notch with rough edges. All the costal specimens have a smooth external surface.

Of the peripherals, ZIN PH 8/266 is a fragment of peripheral 6 or 7 of a small individual. In cross-section, the plate is sharpened laterally. ZIN PH 9/266 (Fig. 9W, X) is right posterior peripheral 11(?). The plate is almost quadrangular in dorsal view, flattened dorsoventrally, with straight anterior and lateral borders, convex medial border and concave posterior border. The intermarginal sulcus is visible on the external surface of the plate.

Remarks. A sharp ridge stretching along the orbital margin observable on the internal surface of postorbital ZIN PH 1/266 is known in several pan-cheloniids (Danilov et al. 2010). The free lateral border of costal ZIN PH 2/266, indicating the presence of the costoperipheral fontanelle, is also characteristic of pan-cheloniids (Evers et al. 2019). The morphology of other specimens corresponds to pan-cheloniids as well.

Pan-Cheloniidae indet. from the Bakhmutovka locality

(Fig. 10A–P)

Chelonioidea indet.: Averianov 2002: 139

Chelonioidea? indet.: Averianov 2002: 144, fig. 7

Chelonioidea indet.: Danilov et al. 2017: 193

Cheloniids: Zvonok and Danilov 2018: 93

New material. The fragmented skeleton (ZIN PH 2/20) belongs to a large individual, including one sacral vertebra or caudal vertebra 1, one middle caudal vertebra, and 66 shell fragments among which are identifiable: the anterior part of neural 5(?), posteromedial part of costal 8, three isolated rib heads, two distal parts of costals, six fragments of free ribs, five lateral fragments of peripherals, and two fragments of unidentified plates (probably costal and plastral elements).

Description. The first vertebral fragment is represented by the right dorsolateral part of a sacral vertebra or caudal vertebra 1 (Fig. 10A, B). The neural spine was double, like in caudal vertebra 1 of *Lepidochelys olivacea,* but its dorsal parts are broken off. The dorsal part of the articular surface for a sacral rib or an unfused transverse process is visible in lateral view.

The second vertebral fragment is represented by the left lateral part of a middle caudal vertebra (Fig. 10C–E). The posterior articular surface of the centrum is worn; the transverse process is broken off. The anterior articular surface of the centrum is concave, almost round. The posterior articular surface of the centrum is convex. The bottom of the neural canal bears a pit near the posterior articular surface, like that known in *Lepidochelys olivacea.* Only the bases of the prezygapophysis and postzygapophysis are preserved.

The external surface of all shell bones, except for one fragment (see below), bears sculpturing of a net of grooves. The anterior part of neural 5(?) (Fig. 10F), judging by the preserved part, was anteroposteriorly long and strongly concave anteriorly. Left costal 8 (Fig. 10G, H) has the posteromedially directed base of ribhead 10 situated close to the posterior margin of the plate. The isolated rib head 10 (Fig. 10I), belonging to the same costal, is narrow and elongate. Two other isolated rib heads are very large (the anteroposterior length of the larger of them is 31 mm; Fig. 10J). Two distal parts of the costals (Fig. 10K) consist of the base of the free rib and a small overlapping portion of the dorsal surface. The fragments of the free ribs (Fig. 10L) are round in cross section, up to 19 mm in diameter. The lateral fragments of the peripherals (Fig. 10M, N) sharpen laterally in cross-section. One fragment of an unidentified shell plate (Fig. 10O), probably costal, has a deep scute sulcus.

The fragment with a smooth external surface (Fig. 10P) probably represents an element of the plastron, as it has weak longitudinal uplifts, like those transiting into digitations of plastral elements.

Remarks. This material was identified as Chelonioidea indet. or Chelonioidea? indet. by Averianov (2002). Zvonok and Danilov (2018) changed the attribution to cheloniids, but without an argumentation, which can be formulated here as follows: narrow neurals with a concave anterior margin and well-developed scute sulci of the carapace are characteristic of Pan-Cheloniidae, but not of the Cenozoic Dermochelyidae (Hirayama 1998).

Pan-Cheloniidae indet. from the Bulgakovka locality

(Fig. 10Q)

Material. A costal fragment (ZIN PH 1/259).

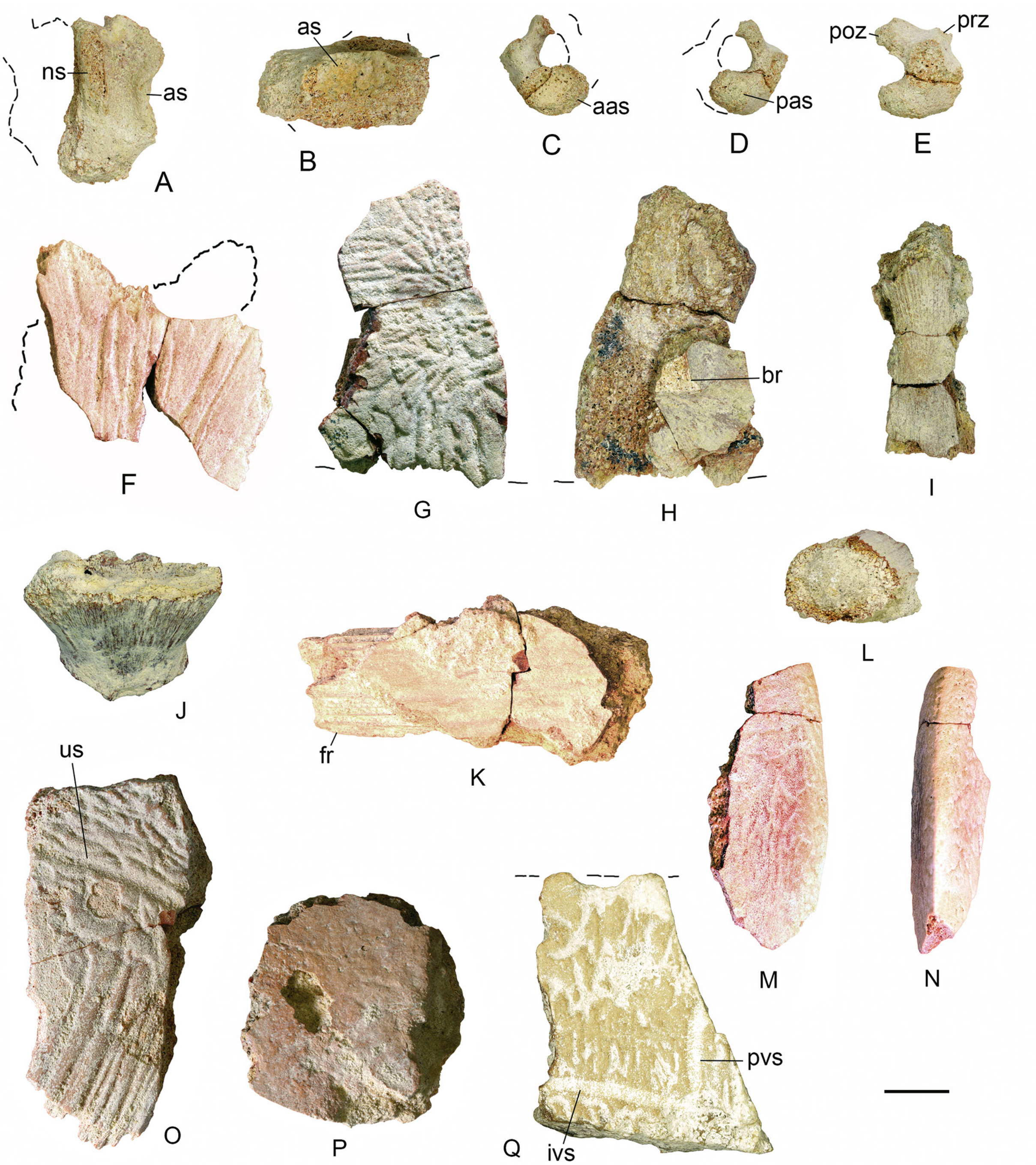

Fig. 10. Pan-Cheloniidae indet. from Bakhmutovka (ZIN PH 2/20; A–P) and Bulgakovka (ZIN PH 1/259; Q) localities, both Lutetian: A, B – sacral or caudal 1 vertebra in dorsal (A) and right lateral (B) views; C–E – caudal vertebra in anterior (C), posterior (D), right lateral (E) views; F – neural in dorsal view; G, H – posterior fragment of left costal 8 in dorsal (G) and ventral (H) views; I – head of rib 10(?) in ventral view; J – rib head in ventral view; K – distal part of costal in dorsal view; L – fragment of free rib in cross-section; M, N – lateral fragment of peripheral in ventral(?) (M) view and lateral (N) views; O – fragment of shell plate in external view; P – fragment of hyo- or hypoplastron(?) in ventral view; Q – fragment of uneven costal in dorsal view. *Abbreviations:* aas – anterior articulation surface, as – articulation surface for sacral rib or transverse process, br – base of rib head, fr – free rib, ivs – intervertebral sulcus, ns – neural spine, pas – posterior articulation surface, poz – postzygapophysis, prz – prezygapophysis, pvs – pleural-vertebral sulcus, us – unknown sulcus. Scale bar: 1 cm.

Description. The costal fragment represents the antero- or posteromedial part of an even costal. The plate is thick and with sculpturing of a net of grooves on the external surface. The interpleural and pleural-vertebral sulci converge at an angle close to 90°, like in specimen ZIN PH 2/239 from the Tripolye locality, *Osonachelus decorata* and *Trachyaspis lardyi*.

Remarks. The presence of sculpturing of a network of grooves, narrow vertebral scutes and the same or close stratigraphic interval make it possible that ZIN PH 1/259 belongs to the same pan-cheloniid taxon as those from the Bakhmutovka, Krasnorechenskoe, Tripolye, and Otradnoe localities (see Discussion).

Pan-Cheloniidae indet. from the Kostyanetskiy Yar locality

(Fig. 11)

Cheloniidae gen. et sp. indet. 2: Zvonok 2011: 114, pl. I, figs 6, 7

Cheloniidae gen. indet. 4: Danilov et al. 2017: 188

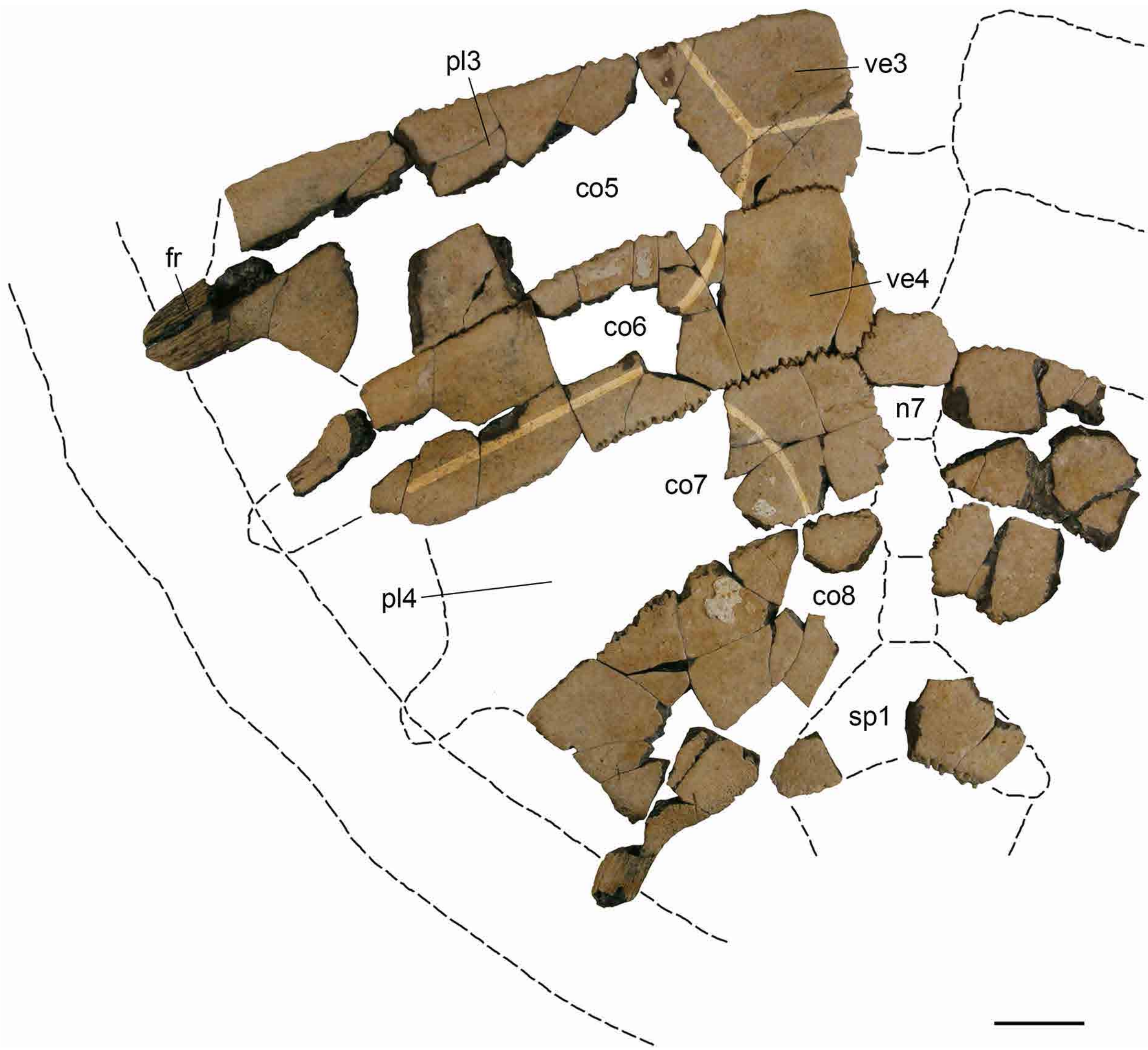

Fig. 11. Part of carapace of Pan-Cheloniidae indet. ZIN PH 1–6/150 from Kostyanetskiy Yar locality, Lutetian, in dorsal view. *Abbreviations:* co5–co8 – costals 5–8, fr – free rib, n7 – neural 7, pl3–pl4 – pleural scutes 3–4, sp1 – suprapygal 1, ve3–ve4 – vertebral scutes 3–4. Scale bar: 1 cm.

Material. A part of the carapace (ZIN PH 1–6/150).

Description. The part of the carapace ZIN PH 1–6/150 includes the anterior part of neural 7, most part of left costals 5, 6 and 8, medial fragments of left costal 7 and right costals 7 and 8, and two fragments of suprapygal 1. The external surface of the plates is smooth. Neurals 5 and 6 were hexagonal with short anterolateral margins judging by the shape of the adjacent medial margins of costals 5 and 6. The anteriorly preserved neural 7 had the same shape. Neural 8 was hexagonal with roughly equal antero- and posterolateral margins judging by the shape of the adjacent medial margins of costals 7 and 8. The preserved costals are wide mediolaterally but their lateral margins form costoperipheral fontanelles; the free ribs are short. Suprapygal 1 was short anteroposteriorly and wide mediolaterally, boomerang-shaped. Posterior to it, there is an extended space for elongated suprapygal 2 or two suprapygals. Outlines of vertebral scutes 3 and 4, and pleural scutes 3 and 4 are partially visible. Vertebral scute 4 is moderately extended laterally.

Remarks. The presence of costoperipheral fontanelles allows attribution of these materials to Pan-Cheloniidae indet. The high degree of ossification of the carapace in juvenile age is similar to *Puppigerus camperi*, but the carapace was wider, like in *Eochelone brabantica*.

Pan-Cheloniidae indet. from the Krasnorechenskoe locality

(Fig. 12A)

Chelonioidea indet.: Averianov 2002: 139; Danilov et al. 2017: 193

“Shell fragments of Chelonioidea? indet. with sculptured surface”: Averianov 2002: 144

Cheloniids: Zvonok and Danilov 2018: 93

Material. Four shell fragments including a part of a free rib of a costal plate and three unidentified fragments of shell plates (ZIN PH 1–4/261).

Description. The part of the free rib of a costal plate (ZIN PH 4/261; not figured) belongs to a large specimen. It is rounded in cross-section like in ZIN PH 2/20 from the Bakhmutovka locality.

Three unidentified shell fragments (ZIN PH 1–3/261) have sculpturing of a net of grooves on the external surface. One fragment (ZIN PH 1/261; Fig. 12A) is large, crossed by a scute sulcus.

Remarks. The material is assigned to Pan-Cheloniidae indet. based on the presence of the scute sulcus and similarity to the pan-cheloniid material from the Bakhmutovka, Bulgakovka and Tripolye localities in sculpturing and the presence of a cross-sectionally rounded free rib of the costal plate.

Pan-Cheloniidae indet. from the Krinichnoe locality

(Fig. 12B–D)

Cheloniidae indet.: Zvonok and Danilov 2018: 95

Material. Right peripheral 1 (ZIN PH 1/262) and a fragment of a posterior peripheral or pygal (ZIN PH 2/262).

Description. Right peripheral 1 (ZIN PH 1/262; Fig. 12B) has a smooth dorsal surface and a damaged ventral one. The plate is narrow at the suture with the nuchal and wide at the suture with peripheral 2. The medial part of the anterior margin participated in the formation of the nuchal emargination. The posterior margin has a suture for costal 1, indicating the absence of a costoperipheral fontanelle there. On the dorsal surface, there are two sulci between carapacial scutes. The first sulcus runs from the posterior end of the nuchal suture to the anterior margin of peripheral 1, similar to the sulcus between the cervical and marginal 1 scutes of *Trachyaspis lardyi* (Hasegawa et al. 2005: pl. 2). The second sulcus runs from the posterior end of the suture for peripheral 2 to the anterior margin of peripheral 1, being a true intermarginal sulcus.

The fragment of a posterior peripheral or pygal (ZIN PH 2/262; Fig. 12C, D) is acute-angled in cross-section. Its surfaces are smooth, the dorsal one is convex, whereas the ventral one is almost flat. There is a deep intermarginal sulcus on the dorsal surface.

Remarks. ZIN PH 1/262 is referred to Pan-Cheloniidae indet. because peripheral 1 has a short suture for the nuchal indicating that the nuchal was short anteroposteriorly like in other pan-cheloniids and because the cervical scute probably slightly overlapped peripheral 1, like in pan-cheloniid *Trachyaspis lardyi*. ZIN PH 2/262 is referred to Pan-Cheloniidae indet. as there are no other determinable turtle taxa in the Krinichnoe locality.

Pan-Cheloniidae indet. from the Tschelyuskinets locality

(Fig. 12E–S)

Cheloniidae indet.; Nesterov and Zvonok 2020: 155

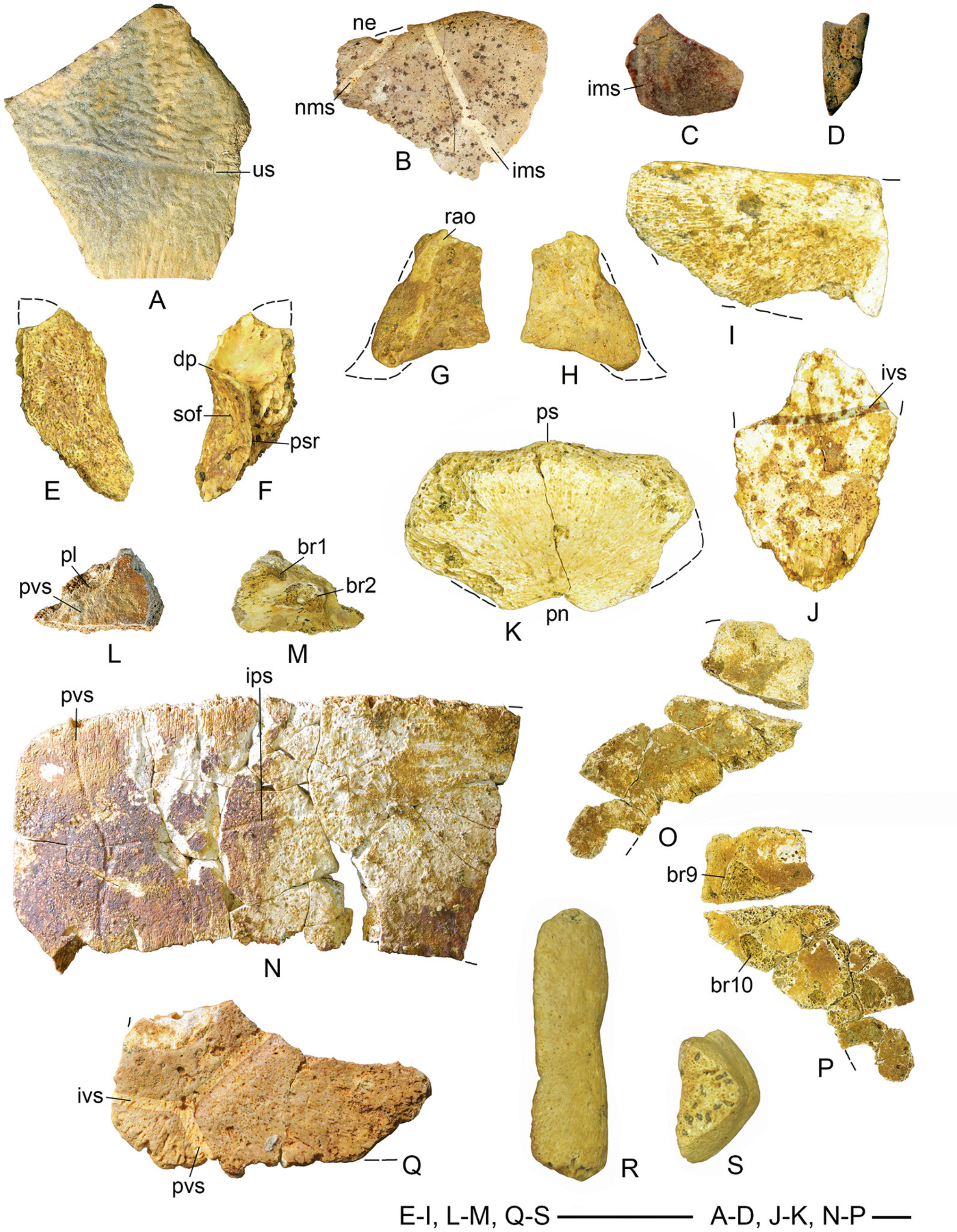

Fig. 12. Pan-Cheloniidae indet. from Krasnorechenskoe (A) and Krinichnoe (B–D) localities, both Lutetian, and Tschelyuskinets (E–S) locality, Lutetian–Priabonian: A – fragment of shell plate ZIN PH 1/261 in external view; B – right peripheral 1 ZIN PH 1/262 in dorsal view; C, D – fragment of posterior peripheral or pygal ZIN PH 2/262 in dorsal view (C) and cross-section (D); E, F – right prefrontal ZIN PH 1/263 in dorsal (E) and ventral (F) views; G, H – right jugal ZIN PH 2/263 in medial (G) and lateral (F) views; I – left part of nuchal ZIN PH 3/263 in dorsal view; J – neural ZIN PH 4/263 in dorsal view; K – pygal ZIN PH 5/263 in ventral view; L, M – medial fragment of costal 1 ZIN PH 6/263 in dorsal (L) and ventral (M) views; N – medial part of right costal 4 ZIN PH 7/263 in dorsal view; O, P – left costal 8 ZIN PH 8/263 in ventral (O) and dorsal (P) views; Q – uneven right costal ZIN PH 9/263 in dorsal view; R, S – peripheral 4 or 5 ZIN PH 10/263 in dorsal or ventral (R) and posterior (S) views. *Abbreviations:* br1, 2, 9, 10 – base of rib heads 1, 2, 9, 10, dp – descending process, ims – intermarginal sulcus, ips – interpleural sulcus, ivs – intervertebral sulcus, ne – nuchal emargination, nms – nuchal-marginal (?) sulcus, pl – parasitic lesion, pn – pygal notch, pvs – pleural-vertebral sulcus, sof – supraorbital foramen, ps – projection for contact with suprapygal, psr – parasagittal ridge, rao – ridge along orbit, us – unknown sulcus. Scale bar: 1 cm.

Material. A right prefrontal (ZIN PH 1/263), left jugal (ZIN PH 2/263), left part of a nuchal (ZIN PH 3/263), neural (ZIN PH 4/263), pygal (ZIN PH 5/263), four costals (ZIN PH 6–9/263), two partial posterior peripherals (ZIN PH 10/263 and 11/263) and peripheral 4 or 5 (ZIN PH 12/263).

Description. The right prefrontal (ZIN PH 1/263; Fig. 12E, F) has a slightly damaged anterior part and the ventral edge of a descending process. The bone is elongated, the posteromedial suture for contact with the frontal is long. There are also sutures for contact with the maxilla, contralateral prefrontal, and postorbital. On the internal surface of the bone, there are a sharp parasagittal ridge, which runs from the descending process posteriorly, and the supraorbital foramen.

The left jugal (ZIN PH 2/263; Fig. 12G, H) is worn with a broken-off medial process. It is short anteroposteriorly. A blunt ridge runs along the orbit on the internal surface of the bone.

The left part of the nuchal (ZIN PH 3/263; Fig. 12I) has damaged lateral and posterior borders. The bone extends laterally. Its anterior margin is almost straight.

The neural (ZIN PH 4/263; Fig. 12J) has a damaged anterior part and a pointed posterior border. The plate is crossed by the intervertebral sulcus.

The pygal (ZIN PH 5/263; Fig. 12K) belongs to a small individual. Its lateral margins are damaged, whereas the anterior margin forms a projection for contact with the suprapygal anteriorly, and a notch posteriorly.

The external surface of all costals has no sculpturing. In a small medial fragment of right costal 1 of a medium-sized individual (ZIN PH 6/263; Fig. 12L, M), all margins are broken off. On the dorsal surface, there are a partially preserved pleural-vertebral sulcus and a large notch with a steep edge, which may be a trace of parasitic lesion. The internal surface bears bases of two rib heads (1 and 2) – rib head 1 is smaller and situated more laterally than rib head 2. The medial half of right costal 4 (ZIN PH 7/263; Fig.12N) is from a medium-sized individual. It preserves a short posteromedial margin for contact with the anterolateral margin of a corresponding neural. Vertebral scute 3 is narrow, almost not projecting laterally. The fragmented left costal 8 (ZIN PH 8/263; Fig. 12O, P) belongs to a medium-sized individual. On its internal surface, there are bases of two rib heads (9 and 10). The uneven right costal (ZIN PH 9/263; Fig. 12Q) has a damaged anterior border and a worn internal surface. In the medial part, it bears intervertebral and pleural-vertebral sulci. Vertebral scutes expand laterally.

All peripherals belong to small individuals. Peripheral 4 or 5 (ZIN PH 10/263; Fig. 12R, S) is complete, longer than wide. Its lateral border is slightly emarginated in the middle part, whereas the posterior half of the medial border has a pit for the free rib of the costal. The dorsomedial margin is free indicating the presence of a costoperipheral fontanelle. ZIN PH 10/263 and ZIN PH 11/263 (not figured) are preserved only partially, flattened, with a sharp lateral border, indicating that they are posterior peripherals.

Remarks. The ridge stretching along the orbital margin observable on the internal surface of the postorbital ZIN PH 2/263 is known in several pan-cheloniids (Danilov et al. 2010). The presence of costoperipheral fontanelles in ZIN PH 5/263 and ZIN PH 12/263 is also characteristic of pan-cheloniids (Evers et al. 2019). The morphology of other elements also corresponds to pan-cheloniids.

Pan-Cheloniidae indet. from the Bakhchisarai 2 locality

(Fig. 13A, B)

New material. The proximal part of a left femur (ZIN PH 10/151).

Description. The proximal part of the left femur belongs to a juvenile individual. The proximal fragment of the femoral head, the proximal part of the minor trochanter and the whole major trochanter are broken off. The femoral head is pitted, indicating that it was not completely ossified. There is an elongate depression distally from the area between the bases of the femoral head and the minor trochanter, like in *Argillochelys* sp. ZIN PH 61/153 from the Ak-Kaya 1 locality (fig. 5I, L; Zvonok and Danilov 2019: fig. 3ee) and *Tasbacka aldabergeni*.

Remarks. ZIN PH 10/151 is referred to Pan-Cheloniidae indet. based on the similarity to *Argillochelys* sp. from the Ak-Kaya 1 locality and *Tasbacka aldabergeni*, and the presence of other remains of pan-cheloniids in the Bakhchisarai 2 locality (Zvonok and Danilov 2019).

Pan-Cheloniidae indet. from the Nagornoe locality

(Fig. 13C, D)

Material. A left frontal (ZIN PH 1/264).

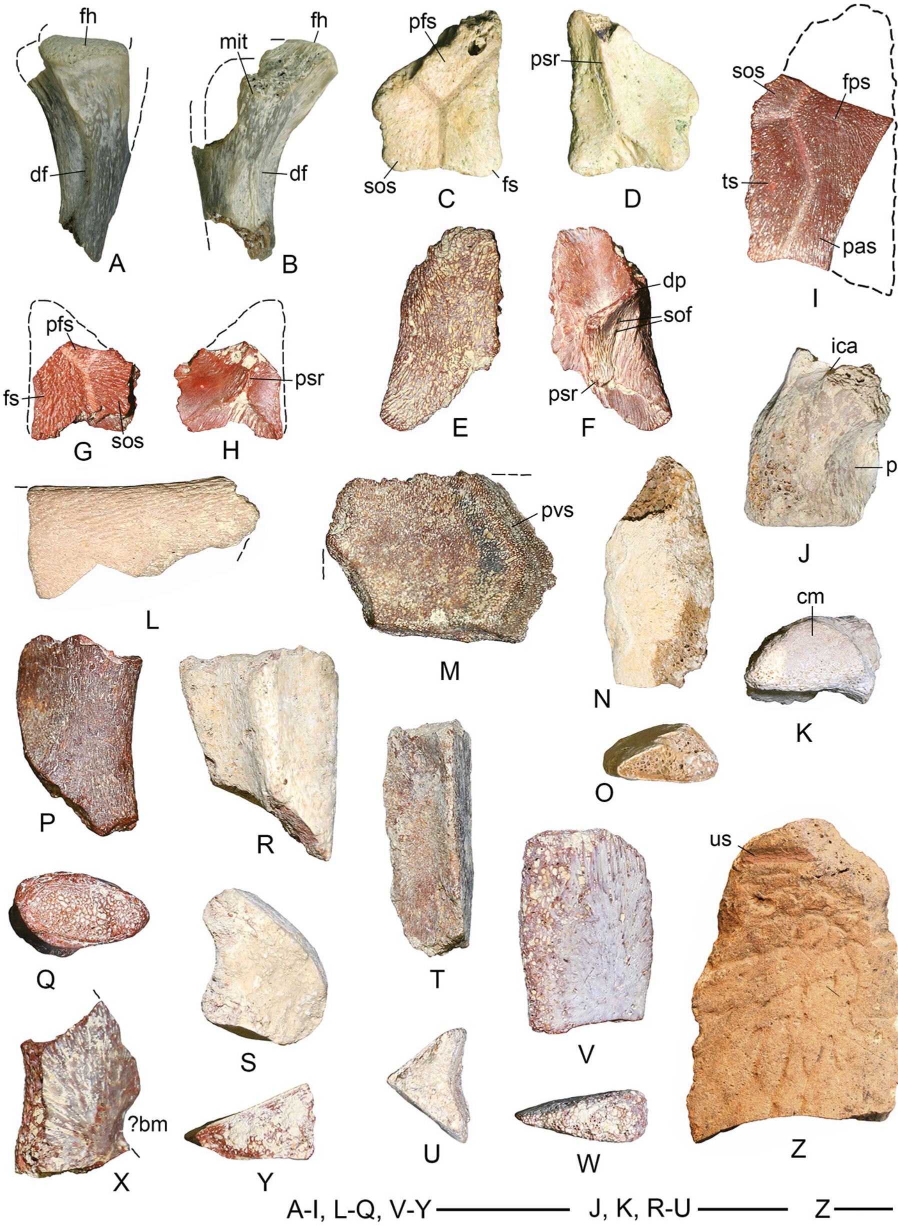

Fig. 13. Pan-Cheloniidae indet. from Bakhchisarai 2 (A, B), Nagornoe (C, D) and Prolom (E–W) localities, all Bartonian, and Otradnoe (Z) locality, Priabonian: A, B – proximal part of left femur ZIN PH 10/151 in dorsal (A) and anterior (B) views; C, D – left frontal ZIN PH 1/264 in dorsal (C) and ventral (D) views; E, F – left prefrontal ZIN PH 9/18 in dorsal (E) and ventral (F) views; G, H – right frontal ZIN PH 10/18 in dorsal (G) and ventral (H) views; I – left parietal ZIN PH 11/18 in dorsal view; J, K – ventral part of left quadrate ZIN PH 12/18 in posterior (J) and ventral (K) views; L – right part of nuchal ZIN PH 13/18 in dorsal view; M – fragment of costal ZIN PH 17/18 in dorsal view; N, O – right peripheral 1 ZIN PH 18/18 in dorsal (N) posterior (O) views; P, Q – right peripheral 2 ZIN PH 19/18 in dorsal (P) and anterior (Q) views; R, S – left peripheral 3 ZIN PH 20/18 in dorsal (R) and anterior (S) views; T, U – peripheral 5–6 ZIN PH 22/18 in dorsal (T) and posterior (U) views; V, W – posterior peripheral ZIN PH 23/18 in dorsal or ventral (V) and anterior or posterior (W) views; X, Y – posterior peripheral or pygal ZIN PH 24/18 in dorsal or ventral view (X) and cross-section (Y); Z – fragment of shell plate ZIN PH 1/265 in external view. *Abbreviations:* bm – bite mark, cm – condylus mandibularis, df – depression distal from femoral head and minor trochanter, dp – descending process, fh – femoral head, fps – frontoparietal scute, fs – frontal scute, ica – incisura columellae auris, mit – minor trochanter, pas – parietal scute, pfs – prefrontal scute, pm – processus mandibularis, psr – parasagittal ridge, pvs – pleural-vertebral sulcus, sof – supraocular foramen, sos – supraoccipital scute, ts – temporal scute, us – unknown sulcus. Scale bar: 1 cm.

Description. The left frontal formed a small part of the orbital margin; it has sutural surfaces for the prefrontal anterolaterally, the right frontal medially, the parietal posteriorly, and the postorbital posterolaterally. On the dorsal surface, there are sulci separating the anteriorly narrowed frontal scute, the posterior part of the prefrontal scute and the anterior part of the supraorbital scute. On the ventral surface of the frontal, there is a parasagittal ridge.

Remarks. ZIN PH 1/264 is referred to Pan-Cheloniidae indet. based on similarity with pan-cheloniids *Argillochelys* sp. from the Ak-Kaya 1 locality and *Eochelone* sp. from the Gorniy Luch locality.

Pan-Cheloniidae indet. from the Prolom locality
(Fig. 13E–Y)

“Bones of [sea] turtles”: Nessov 1987: 77; Chkhikvadze 1990: 5

“Remains of <...> sea turtles”: Nessov 1992: 38

Cheloniidae indet.: Averianov 2002: 145; Danilov et al. 2017: 190; Zvonok and Danilov 2019: 68, fig. 4g–i

New material. A left prefrontal (ZIN PH 9/18), a right frontal (ZIN PH 10/18), a left parietal (ZIN PH 11/18), the ventral part of a left quadrate (ZIN PH 12/18), the right part of a nuchal (ZIN PH 13/18), four costals (ZIN PH 14–17/18), six peripherals (ZIN PH 18–23/18) and a posterior peripheral or pygal (ZIN PH 25/18).

Description. The left prefrontal (ZIN PH 9/18; Fig. 13E, F) is complete with a slightly damaged descending process. The prefrontal is longer than wide. It contacted the right prefrontal medially and the left frontal posteromedially. In ventral view, there are a sharp parasagittal ridge running from the base of the descending process posteriorly and a pair of supraorbital foramina. It is unclear, whether the bone was in contact with the postorbital.

The right frontal (ZIN PH 10/18; Fig. 13G, H) has its medial, anterior and anterolateral borders damaged. There are sutures for the parietal posteriorly and the postorbital, posterolaterally. On the dorsal surface, there are sulci of the prefrontal, frontal, and supraorbital scutes. On the ventral surface, there is a parasagittal ridge.

The left parietal (ZIN PH 11/18; Fig. 13I) has broken-off anterior and medial parts. The lateral margin of the parietal preserves the suture for the squamosal and the posterior part of the suture for the postorbital. On the dorsal surface, the sulci of the frontoparietal, parietal, and temporal scutes are preserved. The frontoparietal scute is fused with the parietal one.

The ventral part of the left quadrate (ZIN PH 12/18; Fig. 13J, K) has a moderately high and laterally curved processus mandibularis. The condylus mandibularis is semicircular. The incisura columellae auris is open posteriorly.

The right part of the nuchal (ZIN PH 13/18; Fig. 13L) has a damaged posterior edge. The plate is extended laterally and with a straight anterior border.

The costals are represented by much of the left costal (ZIN PH 14/18) and three medial costal fragments (ZIN PH 15–17/18). The left costal is medially embedded in a limestone block. It has a short posteromedial side for contact with the neural. One costal fragment (ZIN PH 17/18; Fig. 13M) bears deep pleural-vertebral sulci.

The peripherals are represented by peripheral 1 of a juvenile individual (ZIN PH 18/18), a fragment of peripheral 2 (ZIN PH 19/18), the anterior part of peripheral 3 of a medium-sized individual (ZIN PH 20/18), a fragment of peripheral 3 of a juvenile individual (ZIN PH 21/18), complete peripheral 5 or 6 (ZIN PH 22/18), a fragment of peripheral 5 or 6 (ZIN PH 23/18), and posterior peripherals (ZIN PH 24/18). All the peripherals have a free medial margin. Peripheral 1 of a juvenile individual (ZIN PH 18/18; Fig. 13N, O) is subtriangular with rounded edges in cross-section. The anterior part of its lateral border is slightly convex in dorsal view. The fragment of peripheral 2 (ZIN PH 19/18; Fig. 13P, Q) is oval in cross section, its lateral border is slightly concave. The anterior part of peripheral 3 of a medium-sized individual (ZIN PH 20/18; Fig. 13R, S) is comma-like in cross-section. Its ventral surface is slightly concave in the anterior part. The fragment of peripheral 3 of a juvenile individual (ZIN PH 21/18; not depicted) is comma-like in cross-section. The complete peripheral 5 or 6 (ZIN PH 22/18; Fig. 13T, U) has an acute lateral border in cross section and widely spaced dorsal and ventral medial margins. The posterior peripheral (ZIN PH 23/18; Fig. 13V, W) is dorsoventrally flattened and with lateral borders, acute in cross section.

The posterior peripheral or pygal (ZIN PH 24/18; Fig. 13X, Y) is dorsoventrally flattened and with an outer margin, acute in cross section. It has a rounded notch in the lateral part, which may represent a bite mark.

Remarks. The peripherals from the Prolom locality are referred to Pan-Cheloniidae indet. based on a free medial margin of the peripherals indicating the presence of costoperipheral fontanelles (Evers et al. 2019). The morphology of other elements also corresponds to pan-cheloniids.

Pan-Cheloniidae indet. from the Otradnoe locality

(Fig. 13Z)

Cheloniidae indet.: Zvonok and Danilov 2018: 95

Material. A shell plate fragment (ZIN PH 1/265).

Description. The shell plate fragment of a large individual has lost its margins. The external surface is slightly convex; the internal surface is slightly concave. The plate has a distinct sculpturing of the external surface, which is dense close to the sulcus and becomes more scattered farther away from it. A short part of the sulcus between scutes on the external surface is preserved.

Remarks. The shell plate fragment from the Otradnoe locality has sculpturing typical for Pan-Cheloniidae (de Lapparent de Broin et al. 2014).

Pan-Cheloniidae indet. from the Otradnaya locality

(Fig. 14)

"?*Chelonia* sp.": Chkhikvadze 1977: 226

"Nearly complete carapace of Cheloniidae gen. et sp. indet.": Chkhikvadze 1983: 39; Chkhikvadze 1990: 5

Possibly "Eochely[i]nae – relatively small sea turtles of *Puppigerus* type": Chkhikvadze 1987: 85

Cheloniidae indet.: Averianov 2002: 139, 145; Danilov et al. 2017: 190

Material. A partial shell of a juvenile individual of Pan-Cheloniidae indet. on a piece of chalk (IP n/n).

Description. The specimen is visible from the ventral side. The carapacial bones are represented by neurals 2–9, suprapygal 2, pygal, right and left costals 2–8, and right and left peripherals 4–11. Neural 2, suprapygal 2, right costal 2 and left costals 2 and 3, and both peripherals 4 are slightly displaced relative to the rest of the carapace elements, which are in a natural position.

All the neurals have broken-off neural arches. Neural 2 is elongated and rectangular. The shape of neural 3 is unclear due to damage. Neurals 4–7 are hexagonal with short anterolateral sides. Neurals 8–9 are small, rounded in shape.

Suprapygal 2 has the anterior part damaged; the plate was triangular in shape, narrowing posteriorly, and had a point contact with the pygal.

The pygal has a small anterior protrusion for contact with suprapygal 2 and a posterior notch.

Left costal 3 is broken; right costal 3 and left costals 4 and 5 are damaged; the rest of the costals seem intact. Right costal 2 is partially covered by an indeterminate bone, whereas right and left costals 4 and 5 are partially covered by elements of the plastron. Free ribs are about half the length of the costals. The tips of free ribs of the non-displaced costals are oriented in relation to the peripherals as follows: right costal 4 – the posterior part of peripheral 6; right costals 5–7 – contacts between right peripherals 7–10, respectively; and left costals 4–6 – contacts between left peripherals 6–9, respectively; left costal 7 – the anterior part of peripheral 10; both costals 8 – the anterior part of peripherals 11.

In left peripheral 4, only the posterior part is visible; in right peripheral 4, the lateral part is slightly damaged; in both peripherals 5, the medial borders are slightly damaged; the rest of the peripherals are not significantly damaged. Small incisions are visible on the lateral borders of peripherals 5. The intermarginal sulci are visible on the ventral surface of left peripherals 9 and 10.

Of the plastral elements, some lateral digitations of the hyo- and hypoplastra and their areas near the hyo-hypoplastral contact are preserved. The lateral and central fontanelles were deep, judging by the preserved posteromedial border of the right hyoplastron, the anteromedial border of the right hypoplastron, and the anterolateral border of the left hypoplastron. The hyo-hypoplastral suture is serrated.

There are four indeterminate elements of the shell. One of them, placed between right costals 2 and 3, is an elongated element, which may represent the free rib of costal 1 or the posterior part of the entoplastron. Two damaged indeterminate bones are situated posterolaterally to the left side of the carapace. In addition, posterior to the free rib of right costal 6, there is an annular element, which may represent cross section of a limb bone.

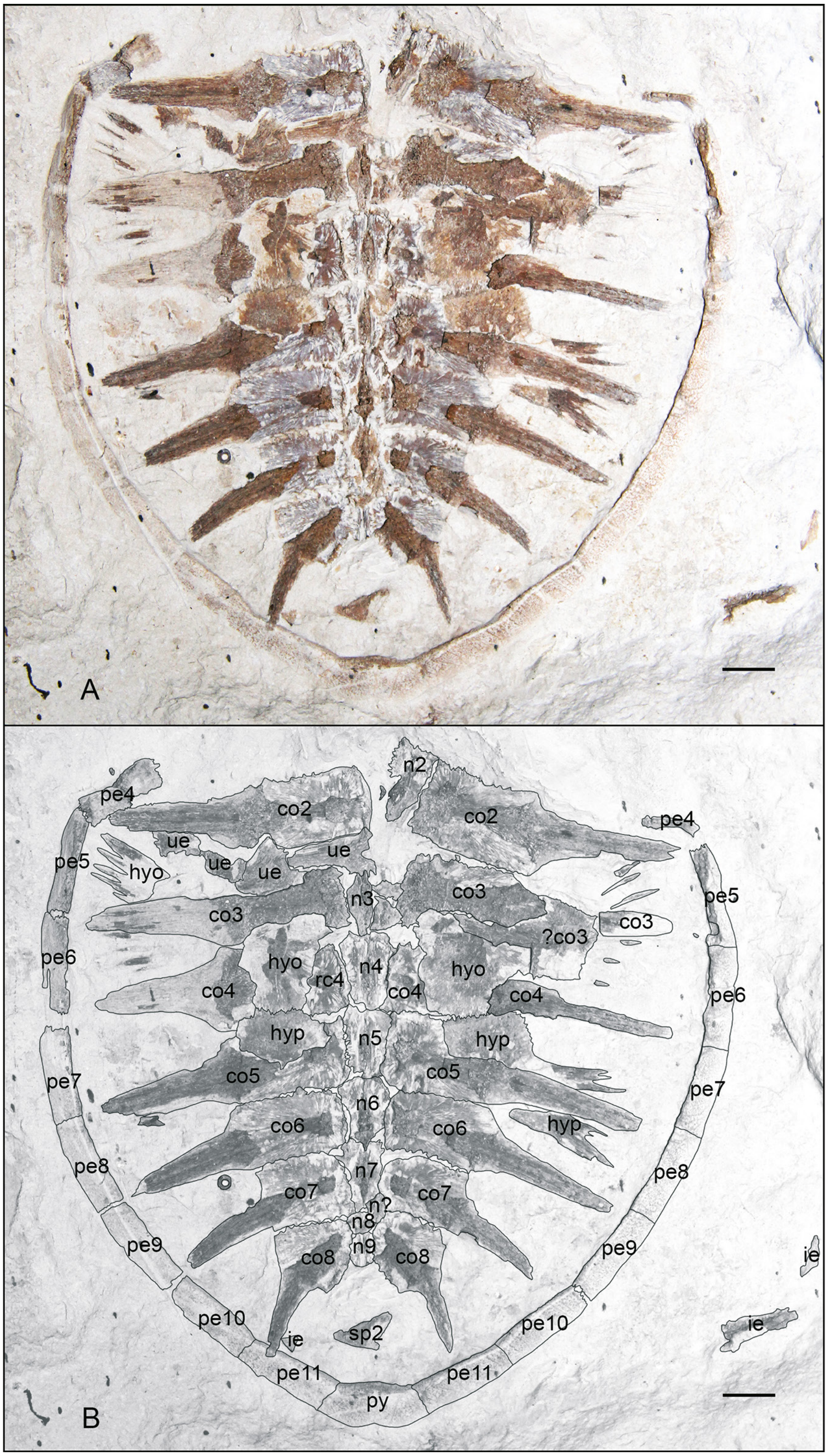

Fig. 14. Shell of Pan-Cheloniidae indet. IP n/n from Otradnaya locality, Eocene(?), in ventral view: A – photograph; B – interpretative drawing. *Abbreviations:* co2–co8 – costals 2–8, hyo – hyoplastron, hyp – hypoplastron, ie – indeterminate element, n2–n9 – neurals 2–9, pe4–pe11 – peripherals 4–11, py – pygal, sp2 – suprapygal 2. Scale bar: 1 cm.

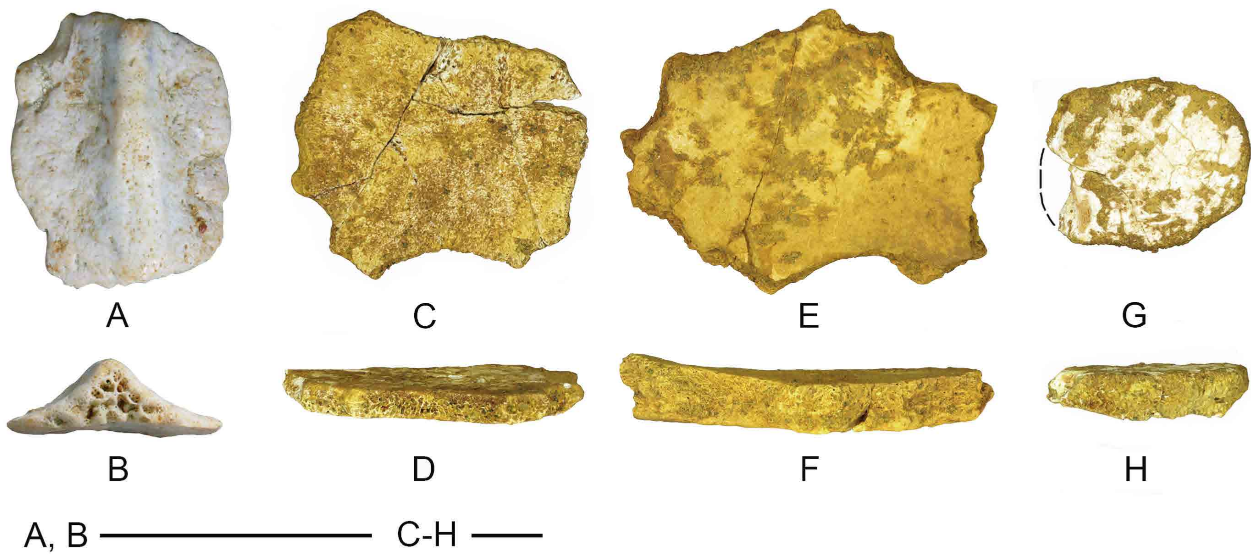

Fig. 15. Epithecal plates of *Cosmochelys* sp. from Ak-Kaya 1 locality, Bartonian (A, B) and Dermochelyidae indet. from Tshelyuskinets locality, Lutetian–Priabonian (C–H): A, B – ZIN PH 81/153 in external (A) and anterior or posterior (B) views; C, D – ZIN PH 13/263 in external (C) and side (D) views; E, F – ZIN PH 15/263 in external (E) and side (F) views; G, H – ZIN PH 14/263 in external (G) and side (H) views. Scale bar: 1 cm.

Remarks. The specimen from the Otradnaya locality belongs to Pan-Cheloniidae indet. because of the presence of costoperipheral fontanelles and the digitations of the hyo- and hypoplastra (Evers et al. 2019).

Dermochelyidae Lydekker, 1889

Cosmochelys sp. from the Ak-Kaya 1 locality

(Fig. 15A, B)

Material. An epithecal plate (ZIN PH 81/153).

Description. ZIN PH 81/153 belongs to a small individual. Its dorsal surface is weakly rugose and bears a median ridge, triangular in cross-section.

Remarks. ZIN PH 81/153 corresponds in its overall shape to a previously described slightly thicker epithecal plate of *Cosmochelys* sp. ZIN PH 63/153 belongs to a juvenile specimen (Zvonok and Danilov 2019). It differs from this specimen by a weakly rugose external surface.

The relief of the epithecal mosaic of *Cosmochelys* sp. from the Ak-Kaya 1 locality probably shows ontogenetic variability from weakly rugose in the smallest specimen (ZIN PH 81/153) through well tuberculated in medium-sized specimens to almost flat in the largest specimens (see Zvonok et al. 2013; Zvonok and Danilov 2019).

Dermochelyidae indet. from the Tschelyuskinets locality

(Fig. 15C–H)

Dermochelyidae indet.: Nesterov and Zvonok 2020: 155

Material. Three epithecal plates (ZIN PH 13–15/263).

Description. Two larger plates (ZIN PH 13/263; Fig. 15C–D and ZIN PH 14/263; Fig. 15E–F) are polygonal, with cutouts for small rounded plates. ZIN PH 14/263 has a “sunflower” pattern. A smaller plate (ZIN PH 15/263; Fig. 15G–H) is close to oval in shape. The sculpturing of the external surface of the plates consists of poorly developed tubercles.

Remarks. The epithecal plates are characteristic elements for Cenozoic Dermochelyidae. The sunflower pattern of ZIN PH 14/263 is diagnostic for Oligocene ridgeless dermochelyids *Natemys peruvianus* and “*Psephophorus*” *rupeliensis* (Wood et al. 1996: figs 10, 12). A similar epithecal plate with a smooth external surface and the sunflower shape is present in cf. *Egyptemys* sp. from the Ad-Dakhla locality (Zouhri et al. 2017: fig. 6i, j).

Pan-Testudines indet.

Pan-Testudines indet. from the Loznoe 1 locality

(Fig. 16A–K)

Testudines indet.: Averianov and Yarkov 2004: 48, fig. 7; Zvonok and Danilov 2018: 95.

Testudines subord. indet. 13: Danilov et al. 2017: 340.

New material. A neural (ZIN PH 5/253), an anterior fragment of costal 5 (ZIN PH 4/253), a fragment of the posterior peripheral (ZIN PH 6/253), and a fragment of the left hypoplastron (ZIN PH 7/253); in addition, there are 20 indeterminate shell fragments.

Description. The neural (ZIN PH 5/253; Fig. 16A–C) lacks the left posterolateral or right anterolateral and posterior or anterior parts; all borders are worn. The plate is slightly convex dorsally in transverse cross-section, with a smooth external surface. The plate as preserved is hexagonal with unequal anterolateral and posterolateral sides, wider than long. No scute sulci are preserved on the external surface. A lenticular bioerosion mark is visible on the external surface. On the internal surface, there is a breakage of the neural spine, which narrows posteriorly or anteriorly.

The anterior fragment of right costal 5 (ZIN PH 4/253; Fig. 16D–F) is represented by the anterolateral part of the plate. Its external surface is smooth, whereas the internal surface bears the posterior part of the rounded inguinal buttress fossa surrounded by a wall elevated above the surface of the plate. The internal surface of the buttress fossa is smooth, suggesting loose (not sutural) attachment of the inguinal buttress. In posterior view, the plate becomes thicker laterally. The anteromedial border of the fragment bears rounded emarginations – probably penetrating tooth marks or parasitic lesions. In addition, two closely placed rounded bioerosion marks are present near the posterior border of the plate, in the lateral half of the fragment.

The fragment of the posterior peripheral (ZIN PH 6/253; Fig. 16G, H) is missing the anterior or posterior and medial parts, whereas its lateral border is damaged, probably by a bite. The external surface of the plate is smooth. The scute sulci are absent. In cross-section, the plate tapers laterally. The lateral border is convex, indicating serration of the posterior carapace margin.

The fragment of the left hyoplastron (ZIN PH 7/253; Fig. 16I–K) is represented by its anteromedial part, which has partially preserved anterior and medial margins. The external surface is flat and bears a net of striae. The medial border has a deep pit for a process of the entoplastron, thin anteriorly and becoming thicker posteriorly. The anterior border is rounded externally and has two fused processes, a smaller medial and a larger lateral, which entered into the posterior border of the epiplastron.

Remarks. Neural ZIN PH 5/253 is similar in shape, smooth external surface and large size to the posterior neurals of Paleocene pan-cheloniids, like *Erquelinnesia gosseleti*. However, because in the Paleocene localities of Eastern Europe, there is also another yet undescribed large turtle (Zvonok and Danilov 2018), herein ZIN PH 5/253 is referred to Pan-Testudines indet.

The fragment of costal 5 ZIN PH 4/253 is similar to Testudinoidea indet. 1 from the Bereslavka 2a locality in the rounded inguinal buttress fossa with a smooth internal surface (Zvonok and Danilov 2018: fig. 1J). However, because the attribution of Testudinoidea indet. 1 from the Bereslavka 2a locality needs additional justification, herein ZIN PH 4/253 is referred to Pan-Testudines indet.

The serrated posterior peripherals, like ZIN PH 7/253, are known among Paleocene European turtles in pan-cheloniids (*Erquelinnesia gosseleti*; Zangerl, 1971: pl. VIIa), but are also present in other groups of turtles. For this reason, this specimen is referred to Pan-Testudines indet.

Hyoplastron ZIN PH 8/253 is referred to Pan-Testudines indet, because it has a deep pit for the process of the entoplastron reminiscent of some stem turtles, including Paleocene European *Laurasichersis relicta*.

Pan-Testudines indet. from the Malaya Ivanovka locality

(Fig. 16L–N)

Material. A costal fragment (ZIN PH 1/252).

Description. The costal fragment is a lateral part of an odd costal (without an interpleural sulcus). The external surface is smooth. The lateral border is sutured and has a slight protrusion of the distal rib. The anterior or posterior broken edge of the bone is

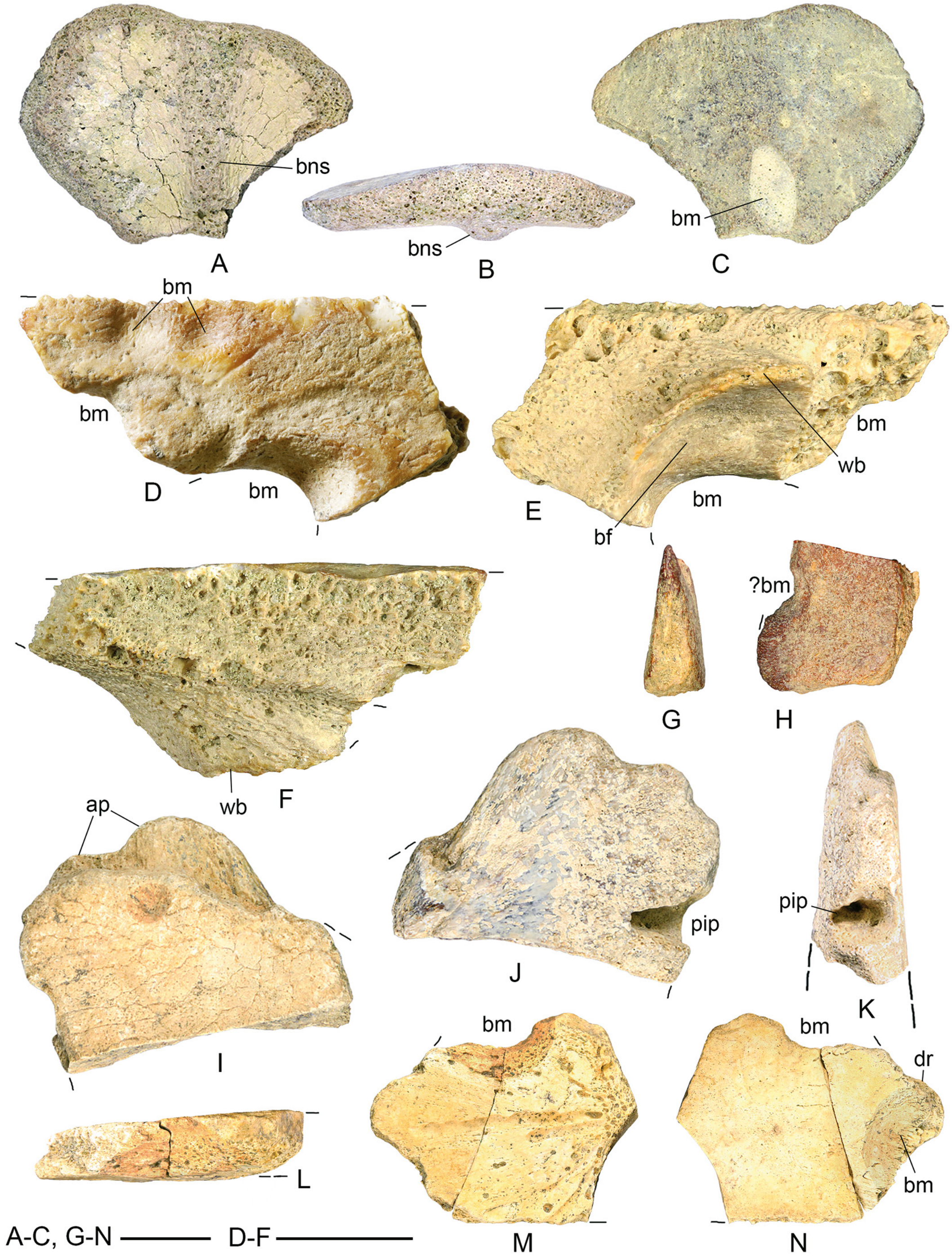

Fig. 16. Testudines indet. from Loznoe 1 (A–C) and Malaya Ivanovka (D) localities, both Thanetian: A–C – neural ZIN PH 5/253 in ventral (A), anterior or posterior (B) and dorsal (C) views; D–F – anterior fragment of right costal 5 ZIN PH 4/253 in dorsal (D), ventral (E) and anterior (F) views; G, H – posterior peripheral ZIN PH 6/253 in anterior or posterior (G) and dorsal (H) views; I–K – anterior part of left hyoplastron ZIN PH 7/253 in dorsal (I), ventral (J) and medial (K) views; L–N – lateral part of costal ZIN PH 1/252 in anterior or posterior (L), ventral (M) and dorsal (N) views. *Abbreviations:* ap – anterior hyoplastral process, bm – bioerosion mark, bf – buttress fossa, bns – base of neural spine, dr – distal rib, pip – pit for insertion of process of the entoplastron, wb – wall of buttress fossa. Scale bar: 1 cm.

emarginated by a bioerosion mark – a round hole penetrating the costal. On the dorsal surface close to the distal rib, there is a bioerosion mark in the shape of a rounded indentation. The internal surface has no rib elevation.

Remarks. ZIN PH 1/252 is referred to Pan-Testudines indet., as it cannot be attributed to Pan-Cheloniidae due to the absence of a characteristic elongate distal rib. Even in Paleocene pan-cheloniids that have lost or almost lost costoperipheral fontanelles (*Tasbacka aldabergeni*), the distal rib is more elongate than in ZIN PH 1/252.

Pan-Testudines indet. from the Loznoe 2 locality
(Fig. 17A)

Material. A fragment of an unidentified shell plate (ZIN PH 1/289).

Description. The fragment of an unidentified shell plate is thin dorsoventrally and flat externally. Only the parts of two margins convergent at an obtuse angle are preserved, suggesting that it can be the right anterolateral part of a neural.

Remarks. ZIN PH 1/289 is referred to Pan-Testudines indet., as it has no diagnostic features of any turtle group.

Pan-Testudines indet. from the Malchevsko-Polnenskaya locality
(Fig. 17B–G)

Material. An anterior caudal vertebra (ZIN PH 21/254), a partial femur (ZIN PH 22/254).

Description. The anterior caudal vertebra (ZIN PH 21/254; Fig. 17B–E) is lacking the dorsal part of the neural arch and postzygapophyses. The ventral surface is heavily worn. The anterior and posterior articulation surfaces of the centrum are moderately compressed dorsoventrally. The anterior articulation surface of the centrum is concave, oriented anteroventrally; the posterior one is convex, oriented posteriorly. The tips of the transverse processes are broken off but they were oriented rather posterolaterally. The prezygapophyses are situated at the level of the middle height of the neural canal; their tips are broken off as well.

The partial left femur (ZIN PH 22/254; Fig. 17F, G) belongs to a small individual. Its epiphyses are broken off, and only a small distal part of the femoral head is preserved. The diaphysis is strongly curved.

Remarks. The dorsoventrally compressed centrum of the anterior caudal vertebra is known in pan-cheloniids *Tasbacka aldabergeni* and pan-trionychids *Lissemys punctata* and *Trionyx triunguis*.

The strongly curved diaphysis of the femur is peculiar to many freshwater turtles, including pan-trionychids, and different from pan-cheloniids, which have a straighter diaphysis (see Evers et al. 2019: fig. S1.31). Thus, Pan-Testudines indet. from Malchevsko-Polnenskaya may correspond to the pan-trionychid taxon known from the same locality or represent a distinct taxon.

Pan-Testudines indet. from the Grekovo locality
(Fig. 17H, I)

Material. A medial fragment of a costal (ZIN PH 1/255).

Description. The medial fragment of a costal is worn; spongy tissue is exposed over the whole dorsal surface of the costal. One side of the costal, anterior or posterior, is slightly concave. The opposite side is preserved only medialmost; its slope narrowing the plate medially. The preserved base of the rib head is wide. The rib elevation is slightly developed. The canal of unknown, probably biogenic, origin penetrates the plate near the base of the rib head.

Remarks. ZIN PH 1/255 is referred to Pan-Testudines indet., as it has no diagnostic features of any turtle group.

Pan-Testudines indet. from the Malchevskaya locality
(Fig. 17J)

Testudines indet.: Zvonok and Danilov 2018: 95

Material. A costal fragment (ZIN PH 1/257).

Description. The costal fragment is represented by the anterior or posterior part of the middle portion of the costal of unknown position. Its dorsal surface is smooth. Ventrally, the plate has a weak rib elevation.

Remarks. ZIN PH 1/257 is referred to Pan-Testudines indet., as it has no diagnostic features of any turtle group.

Pan-Testudines indet. from the Voznesenskiy locality
(Fig. 17K–M)

Testudines indet.: Zvonok and Danilov 2018: 96

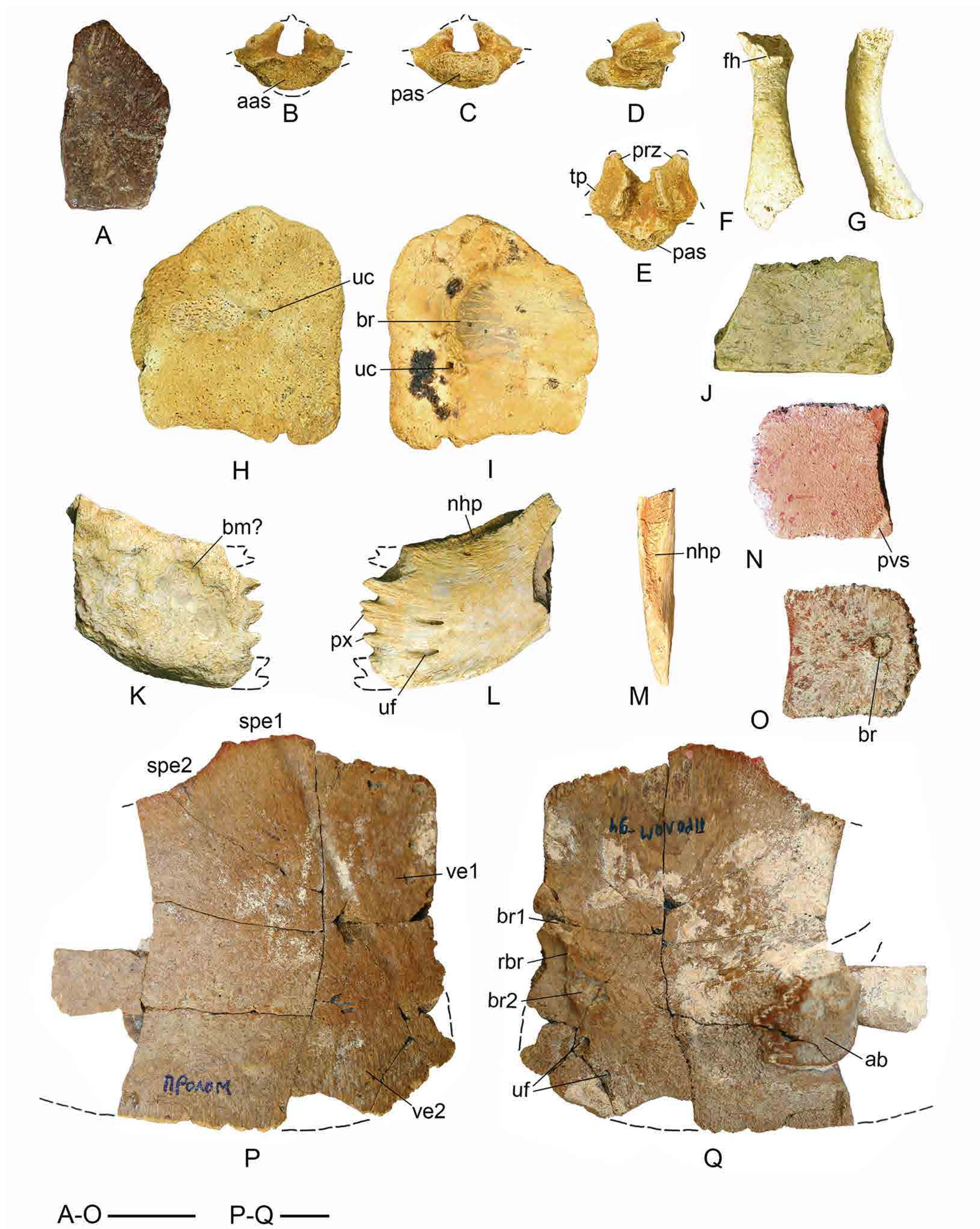

Fig. 17. Testudines indet. from Loznoe 2 (A) and Malchevsko-Polnenskaya (B–G) localities, both Ypresian, Grekovo (H, I), Malchevskaya (J) and Voznesenskiy (K–M) localities, all Ypresian or Lutetian, Georgievka (N, O) and Krasnorechenskoe (P, Q) localities, Lutetian: A – fragment of unknown shell plate ZIN PH 1/289 in external view; B–E – caudal vertebra ZIN PH 21/254 in anterior (B), posterior (C), right lateral (D) and dorsal (E) views; F, G – left femur ZIN PH 22/254 in dorsal (F) and anterior (G) views; H, I – medial part of costal ZIN PH 1/255 in dorsal (H) and ventral (I) views; J – anterior or posterior fragment of costal ZIN PH 1/257 in dorsal view; K–M – posterior part of right xiphiplastron ZIN PH 11/266 in ventral (K), dorsal (L) and anterior (M) views; N, O – medial part of even costal ZIN PH 1/260 in dorsal (N) and ventral (O) views; P, Q – left costal 1 ZIN PH 5/261 in dorsal (P) and ventral (Q) views. *Abbreviations:* aas – anterior articular surface, ab – axillary buttress, bm – bite mark, br – base of rib head, br1, br2 – base of rib heads 1 and 2, fh – femoral head, nhp – notch for hypoplastron, pas – posterior articular surface, pb – plastral buttress, prz – prezygapophysis, pvs – pleural-vertebral sulcus, px – process of xiphiplastron, rbr – ridge between bases of rib heads, spe1, spe2 – suture for peripherals 1 and 2, tp – transverse process, uc – unknown canal, uf – unknown foramen, ve1, ve2 – vertebral scutes 1 and 2. Scale bar: 1 cm.

Material. A posterior fragment of the right xiphiplastron (ZIN PH 11/266).

Description. The posterior fragment of the right xiphiplastron (ZIN PH 11/266) with several broken-off anterior and posterior medial processes. The anteromedial border is concave and has an extended suture for contact with the hypoplastron. The medial border bears four preserved processes. The posterior border is convex. The ventral surface has numerous overlapping damages including three roundish depressions, probably bite marks. On the dorsal surface, there are three medially directed foramina located in the medial part of the fragment.

Remarks. ZIN PH 11/266 is reminiscent of the pan-cheloniid *Eochelone brabantica*, but is much shorter anteroposteriorly and has more prominent digitations. In general shape, it is also similar to pan-trionychids (Brinkman et al. 2017: fig. 4).

Pan-Testudines indet. from the Georgievka locality

(Fig. 17N, O)

Testudines indet.: Zvonok and Danilov 2018: 95

Material. A medial fragment of a right even costal (ZIN PH 1/260).

Description. The costal fragment is represented by the medial part of the plate. The dorsal surface is smooth. Small parts of pleural-vertebral sulci are preserved. The plate has the posterolateral margin for contact with the anterolateral margin of a neural. The base of the rib head is narrow. The rib elevation is present.

Remarks. ZIN PH 1/260 is referred to Pan-Testudines indet., as it has no diagnostic features of any turtle group.

Pan-Testudines indet. from the Krasnorechenskoe locality

(Fig. 17P, Q)

Geoemydidae indet.; Zvonok and Danilov 2018: 93, fig. 1A

Material. Left costal 1 with a part of an axillary buttress (ZIN PH 5/261).

Description. Left costal 1 lacks the lateral part and rib heads; a small part of the adjacent hyoplastral buttress is preserved in articulation. It belongs to a large turtle: the maximal anteroposterior length of costal 1 is 77 mm; the length of whole carapace is estimated as about 50 cm. The plate is relatively thin, its thickness at the anterior margin is about 4 mm. The external surface is smooth, slightly abraded. The sulcus between the vertebral 1 and pleural 1 scutes is deep, whereas the sulci between vertebrals 1 and 2, and vertebral 2 and pleural 1 are poorly visible. The lateral sulcus of the vertebral 1 scute crosses border for contact with peripheral 1, indicating that the vertebral 1 scute was wider than the nuchal plate. The lateral border of the vertebral 1 scute is almost straight, as it turned out after additional restoration, but not lyre-shaped (Zvonok and Danilov 2018). The preserved lateral border of the vertebral 2 scute is slightly convex laterally. The suture for peripheral 1 is straight and shorter than the suture for peripheral 2. The suture for peripheral 2 is concave. The lateral extension of the plate is unclear due to damage. The medial margin of costal 1 is slightly concave; the posteromedial margin for the anterolateral side of neural 2 is present; the posterior margin is convex. The preserved base of rib head 1 partially overlapped neural 1 from the ventral side. The base of rib head 2 has the same size as the base of rib head 1, is situated posterolaterally and connected to the base of rib head 1 by a short sharp ridge. There are two foramina posterior to them. The area of the suture for axillary buttress is thickened. The suture for axillary buttress is rounded and sharply narrows in the anterolateral direction in ventral view like in *Eocenochelus* spp. and *Neochelys* spp. The axillary buttress seems to be loosely connected with costal 1.

Remarks. At the beginning of this study, ZIN PH 5/261 was represented by two fragments stored in two different boxes: the first with the material from the Krasnorechenskoe locality and the second with the material from the Prolom locality. On the surface of the second fragment, there are inscriptions “Prolom” and “Prolom-94”. The second fragment was briefly described and figured by Zvonok and Danilov (2018: 93, fig. 1A). Later, both fragments appeared to fit to each other. Herein, they are referred to the Krasnorechenskoe locality for the following reasons: 1) hollows on the bone surface of both fragments contain light colored quartz sand characteristic of the Krasnorechenskoe locality; 2) the preservation of both fragments corresponds to the material from the Krasnorechenskoe locality and different from more fragile and usually reddish remains from the Prolom locality.

Among Middle Eocene European turtles, the robust suture for the axillary buttress on costal 1, like in ZIN PH 5/261, is known in Pan-Geoemydidae and Pan-Podocnemididae. Of them, the vertebral 1 scute is wider than the nuchal plate, like in ZIN PH 5/261, in pan-geoemydids *Cuvierichelys* spp. and pan-podocnemidids *Eocenochelus* spp. and *Neochelys* spp. The rounded axillary buttress attachment, like in ZIN PH 5/261, is observable in pan-podocnemidids *Eocenochelus* spp. and *Neochelys* spp., whereas in *Cuvierichelys* spp. it is developed like a narrow high ridge (Perez-Garcia and de Lapparent de Broin 2013: fig. 2c, d; Perez-Garcia and de Lapparent de Broin 2015: figs 5b1, b2, 7b1, b2; Perez-Garcia et al. 2016b: fig. 2B, D, G; Perez-Garcia et al. 2017: fig. 4(1, 2)). The possible pan-podocnemidid attribution of ZIN PH 5/261 is also supported by its large size (*Cuvierichelys* spp. are smaller) and stratigraphic position, as the first pan-geoemydids with a wide vertebral 1 scute in Europe appear in the Bartonian (Hervet 2003; Perez-Garcia et al. 2016b). However, ZIN PH 5/261 has no synapomorphies that allow its unequivocal attribution to Pleurodira or taxa inside this clade.

Pan-Testudines indet. from the Ak-Kaya 1 locality

(Fig. 18A–E)

Material. Two fragments, probably from a single caudal vertebra (ZIN PH 83/153 and 84/153).

Description. Two fragments of caudal vertebra: ZIN PH 83/153 is the left part of the neural arch with the transverse process and prezygapophysis with broken-off distal tips; ZIN PH 84/153 is the right part of the neural arch with the bases of the transverse process and neural spine. The prezygapophysis is thin. The transverse process is connected by a sharp ridge with the prezygapophysis. Another sharp ridge runs along the ventral surface of the transverse process. The articulation surfaces of the neural arch for contact with the centrum are smooth anteriorly and ridged posteriorly.

Remarks. The same arrangement of ridges on the anterior part of the neural arch of anterior caudal vertebrae, like in ZIN PH 83/153 and 84/153, is observable in a juvenile trionychid *Pelodiscus sinensis*.

Pan-Testudines indet. from the Belomechetskaya locality

(Fig. 18F)

Cheloniidae?: Alekperov 1978: 184, fig. 52b, g

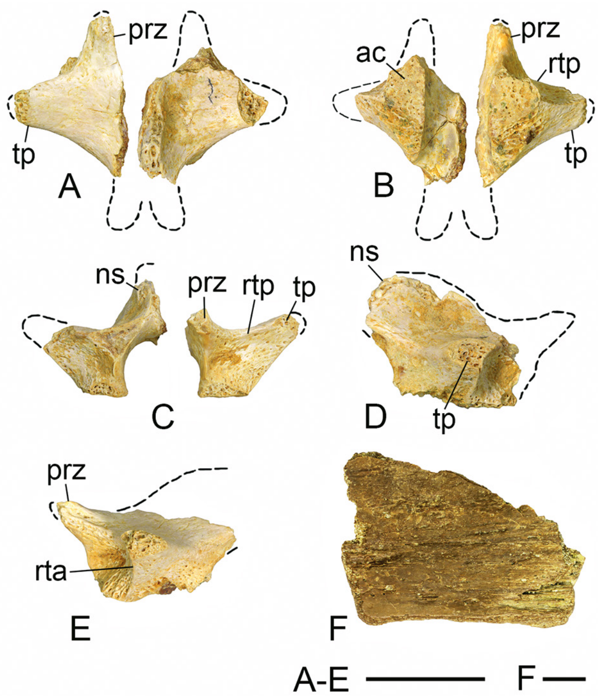

Fig. 18. Testudines indet. from Ak-Kaya 1 (A–E) locality, Bartonian, and Belomechetskaya (F) locality, Oligocene or Miocene: A–E – dorsal fragments of caudal vertebra of presumably one specimen ZIN PH 83/153 + ZIN PH 84/153 in dorsal (A), ventral (B), anterior (C), right lateral (D) and left lateral (E) views; F – fragment of shell plate ZIN PH 2/139 in ventral view. *Abbreviations:* ac – articulation surface for centrum, ns – neural spine, prz – prezygapophysis, rta – ridge between transverse process and articulation surface for centrum, rtp – ridge between transverse process and prezygapophysis, tp – transverse process. Scale bar: 1 cm.

Chelonioidea indet.: Averianov 2002: 139, 146; Danilov et al. 2017: 193

Material. A shell fragment (ZIN PH 2/139).

Description. The shell fragment is about 6 cm in length. All its borders, except for the sutural one, are broken off. The external surface of the specimen is completely worn to spongiosa, whereas its internal surface is smooth with longitudinal(?) striae. The fragment changes its thickness, being the thinnest at one corner and the thickest at the opposite one.

Remarks. The attribution of the shell fragment to Cheloniidae? (Alekperov 1978) or Chelonioidea indet. (Averianov 2002; Danilov et al. 2017) was probably based on its large size and occurrence in the marine deposits. In fact, the poor preservation of the specimen does not allow a more precise attribution than Pan-Testudines indet.

DISCUSSION

Taxonomic diversity and paleobiogeography of Paleogene turtles of Eastern Europe. Paleogene turtles of Eastern Europe are represented by Pan-Trionychidae, Pan-Cheloniidae, Dermochelyidae, Pan-Testudinoidea, and Pan-Testudines.

The remains of pan-trionychids are present in ten of 39 localities (26%) of the Danian (1; Ak-Kaya 2), Selandian (1; Bereslavka 2a), Thanetian (2; Bereslavka 2b, Loznoe), Ypresian (1; Malchevsko-Polnenskaya), Ypresian–Lutetian (1; Verkhnetalovka), Lutetian (1; Ikovo), Bartonian (2; Ak-Kaya 1, Prolom) and Rupelian (1; Zarechnyi) ages (see Table 1). Most of them (nine of eleven records; 82%) are represented by fragmentary remains, determined as Pan-Trionychidae indet. The fragmentary nature of the pan-trionychid material from the Paleocene localities of Eastern Europe (Averianov and Yarkov 2000, 2004; Danilov et al. 2017; Zvonok and Danilov 2018, 2019) does not allow clarifying if they are more closely related to Western European or Asian forms and if pan-trionychids dispersed to Europe from Asia or North America (see Georgalis and Joyce 2017).

"*Trionyx" ikoviensis*, known only from the Ikovo locality, is the only pan-trionychid species described from the Paleogene of Eastern Europe (Danilov et al. 2011). The phylogenetic position of "*Trionyx*" *ikoviensis* is unknown, although it is very similar to Western European "*Trionyx*" *messelianus* Reinach, 1900 from the Lutetian of Germany (Geiseltal and Messel) and "*Trionyx*" *silvestris* from the Ypresian of the United Kingdom (Abbey Wood) and France (Mancy) (Danilov et al. 2011; Georgalis and Joyce 2017). Thus, the existence of a common biogeographical range for these pan-trionychids at approximately the generic level in the Lutetian is evident (Fig. 19), but at the species level, they were probably endemic either to Western ("*T.*" *messelianus* and *"T." silvestris*) or Eastern (*"T." ikoviensis*) Europe. Plastomenidae indet. from Ikovo clearly represents a new pan-trionychid taxon, and, if correctly identified, the first true plastomenid outside North America (Zvonok and Danilov 2018).

The remains of pan-cheloniids are present in 31 of 39 localities (79%) of the Danian (2; Rasstrigin 2; Sakharnaya Golovka), Danian–Ypresian (1; Kudinovka), Selandian (1; Bereslavka 2a), Thanetian (4; Bakhchisarai 1, Bereslavka 2b, Loznoe 1, Malaya Ivanovka), Ypresian (2; Malchevsko-Polnenskaya, Novoivanovka), Ypresian–Lutetian (2; Gruzinov, Voznesenskiy), Lutetian (7; Bakhmutovka, Bulgakovka, Ikovo, Kostyanetskiy Yar, Krasnorechenskoe, Krinichnoe, Sosnovka), Lutetian–Bartonian (2; Tripolye, Vyshgorod), Lutetian–Priabonian (1; Tschelyuskinets), Bartonian (6; Ak-Kaya 1, Bakhchisarai 2, Gorniy Luch, Nagornoe, Pirogovo, Prolom), Priabonian (1; Otradnoe), Rupelian–Chattian (1; Abadzekhskaya), and Paleogene–Neogene (1; Otradnaya) ages (see Table 1). Twenty one of 37 (57%) records are represented by Pan-Cheloniidae indet., two of which (Novoivanovka and Gruzinov) may correspond to other pan-cheloniid taxa known from the same localities. The high frequency of occurrence of pan-cheloniids is not surprising as all these localities are of marine origin. The Paleogene pan-cheloniids of the region are represented by at least nine different generic or species level taxa: *Argillochelys antiqua*, *Argillochelys* sp., "*Dollochelys*" *rogovichi* Averianov, 2002, *Eochelone* sp., *Euclastes wielandi*, *Itilochelys rasstrigin* Danilov et al., 2010, *Puppigerus camperi*, *Tasbacka aldabergeni*, and a sculptured pan-cheloniid taxon (see below). Some specimens of pan-cheloniids can be determined more precisely than Pan-Cheloniidae indet.: the dentary symphysis ZIN PH 2/247 from the Novoivanovka locality belongs to *Tasbacka aldabergeni* or *Puppigerus camperi*; the squamosal ZIN PH 5/254 from the Malchevsko-Polnenskaya locality is similar to *Argillochelys cuneiceps* (see Systematics). In addition, Averianov (2002) mentioned cf. *Tasbacka* sp. from the Thanetian of Malaya Ivanovka, but this material is not specified.

Unlike most species of Recent pan-cheloniids, which have a wide geographic distribution, almost cosmopolitan, or within a large sea basin (see Rhodin et al. 2021), most Paleogene cheloniids demonstrate more restricted ranges, which is likely due to the geographical incompleteness of their fossil records (see Fig. 19).

Argillochelys spp. is known from the Ypresian–Priabonian of the northeastern periphery of the Tethys (Ak-Kaya 1, Gruzinov, Ikovo, Novoivanovka and Vyshgorod localities in Eastern Europe; and Shorym and Adaev formations of Kazakhstan), as well as from the Thanetian–Bartonian of the North Sea (Hannut Formation, Belgium; London Clay, Bracklesham Group, Barton Beds, United Kingdom) (Lydekker 1889; Moody 1980; Zvonok et al. 2011; Zvonok and Danilov 2018; this study).

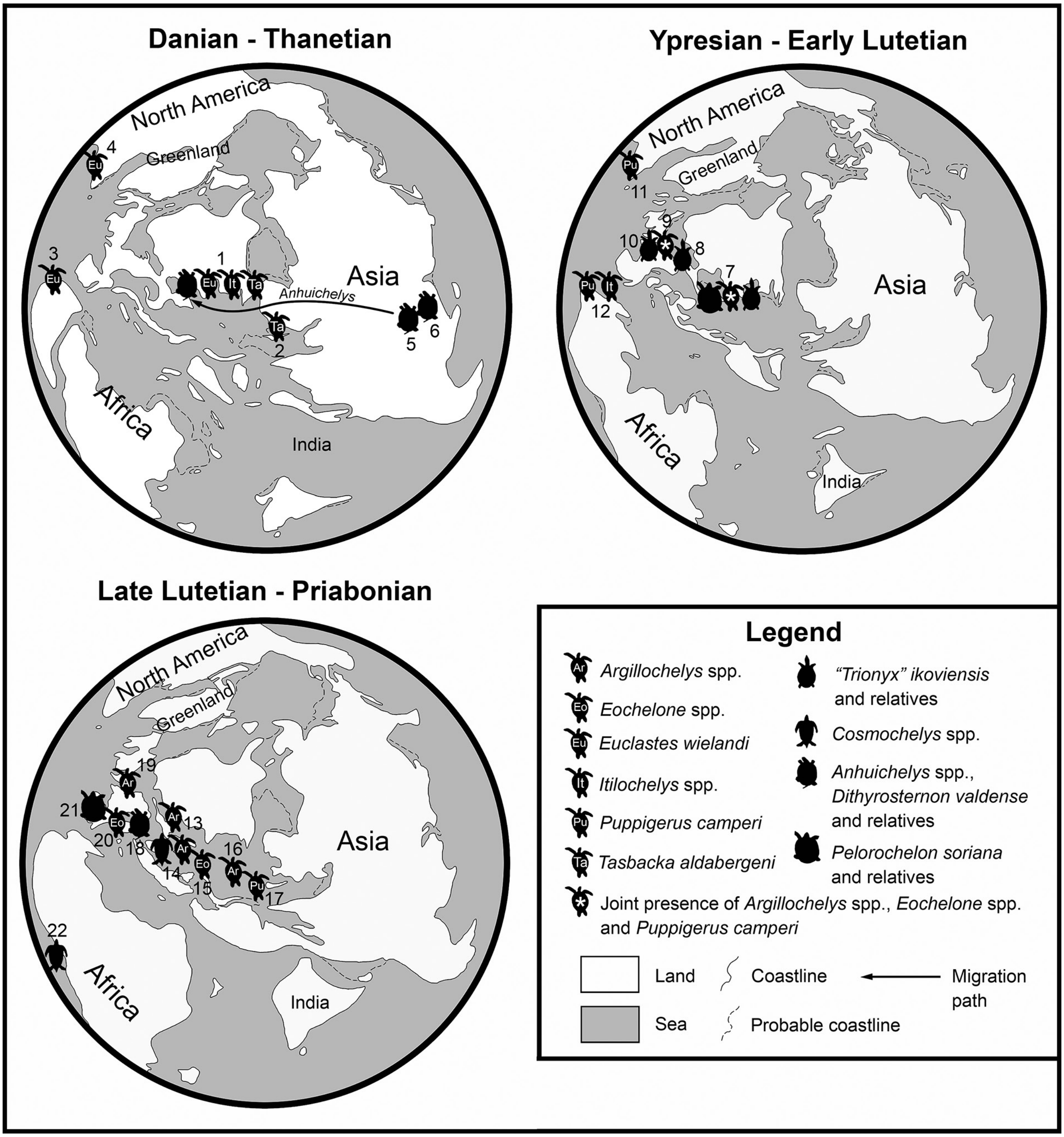

Fig. 19. Some Paleogene localities showing distribution of turtle taxa from Eastern Europe and their presumable relatives: 1 – Bereslavka 2a locality, Russia, Selandian; Kudinovka locality, Russia, Paleocene–Ypresian; 2 – Zhylga 1 locality, Kazakhstan, Thanetian–Ypresian; 3 – Ouled Abdoun phosphates, Morocco, Danian; 4 – Brightseat Formation, USA, Danian; 5 – Zhaigang locality, China, Paleocene; 6 – Wanghudun and Doumu Formations, China, Danian–Selandian; 7 – Ikovo locality, Russia, Lutetian; Novoivanovka locality, Russia, Ypresian; Gruzinov locality, Russia, Ypresian–Lutetian; 8 – Messel and Geiseltal localities, Germany, Lutetian; 9 – London Clay, Bracklesham Group, UK, Ypresian–Lutetian; Sables de Bruxelles, Sables de Wemmel, Belgium, Lutetian; 10 – Abbey Wood, United Kingdom, Ypresian; Mancy, France, Ypresian; 11 – Nanjemoy Formation, USA, Ypresian; 12 – Ouled Abdoun phosphates, Morocco, Ypresian; 13 – Vyshgorod locality, Ukraine, Lutetian–Bartonian; 14 – Ak-Kaya 1 locality, Russia, Bartonian; 15 – Gorniy Luch locality, Russia, Bartonian; 16 – Shorym and Adaev formations, Kazakhstan, Bartonian–Priabonian; 17 – Dzheroi 2 locality, Uzbekistan, Lutetian–Bartonian; 18 – Mauremont locality, Switzerland, Priabonian; 19 – Barton Beds, UK, Bartonian; 20 – Vic-Manlleu marls Formation, Spain, Priabonian; 21 – Mazateron locality, Spain, Bartonian; 22 – Port Harcourt, Nigeria, Bartonian.

"*Dollochelys*" *rogovichi* is known only from the Lutetian–Bartonian of the northeastern periphery of the Tethys (Vyshgorod), although it cannot be excluded that this taxon is congeneric with some other Paleogene turtles, especially *Eochelone* (see Appendix 1: Vyshgorod).

Eochelone spp. are known from the Lutetian–Bartonian of the northeastern periphery of the Tethys (Ikovo and Gorniy Luch) as well as from the Lutetian of North Sea (Brussel Formation, Belgium) and Priabonian of the western Tethys (Vic-Manlleu marls Formation, Spain) (Casier 1968; Lapparent de Broin et al. 2018; Zvonok et al. 2019; this study).

Euclastes wielandi is known from the Selandian of the northeastern periphery of the Tethys (Bereslavka 2a) as well from the Maastrichtian–Selandian of the coastal zones of the northwestern Atlantic (Brightseat, Hornerstown, and Vincentown formations, USA), and the vicinity of the Gibraltar Strait between the Atlantic and the Tethys (Ouled Abdoun phosphates, Morocco) (Hirayama and Tong 2003; Weems 2014; Zvonok and Danilov 2018).

Itilochelys rasstrigin is known only from the Danian of the northeastern periphery of the Tethys (Rasstrigin 2), whereas its presumable close relative *Itilochelys* (orig. *Argillochelys*) *africana* (Tong et Hirayama, 2008) comes from the Ypresian of the vicinity of the Gibraltar Strait between the Atlantic and the Tethys (Ouled Abdoun phosphates, Morocco) (Tong and Hirayama 2008; Danilov et al. 2010).

Puppigerus camperi also had a wide geographical distribution, being known from the Ypresian–Lutetian of the northeastern periphery of the Tethys (Ikovo) as well as from the Ypresian of northwestern Atlantic (Nanjemoy Formation, USA), the Ypresian of the vicinity of the Gibraltar Strait between the Atlantic and the Tethys (Ouled Abdoun phosphates, Morocco), the Ypresian–Lutetian of the North Sea (London Clay, Bracklesham Group, United Kingdom; Sables de Bruxelles, Sables de Wemmel, Belgium), and the Lutetian or Bartonian of the eastern periphery of the Tethys (Dzheroi 2, Uzbekistan) (Lydekker 1889; Moody 1974; Weems 1999; Averianov 2005; Tong et al. 2012; this study).

Tasbacka aldabergeni is known from the Paleocene or Ypresian of the northeastern periphery of the Tethys (Kudinovka) as well as from its more eastern part (Zhylga 1, Kazakhstan) (Nessov 1987; Zvonok et al. 2023). Other species of *Tasbacka* come from the Danian of the vicinity of the Gibraltar Strait between the Atlantic and the Tethys (Ouled Abdoun phosphates, Morocco; *T. ouledabdounensis*), Thanetian of northwestern Atlantic (Aquia Formation, USA; *T. ruhoffi*) and probably Ypresian of the North Sea (Fur Formation, Denmark; *T. danica* Karl et Madsen, 2012) (Weems 1988, 2014; Tong and Hirayama 2002; Karl and Madsen 2012).

The remains of the deeply sculptured pan-cheloniids are known from the Lutetian (Bakhmutovka, Bulgakovka, Krasnorechenskoe) and the Lutetian–Bartonian (Tripolye) of Eastern Europe (see "Comments on the sculptured pan-cheloniids from the Paleogene of Eastern Europe" below).

The remains of dermochelyids are present in five of 39 localities (13%) of the Lutetian–Priabonian (1; Tschelyuskinets), Bartonian (3; Ak-Kaya 1, Bakhchisarai 2, Prolom) and Rupelian (1; Zarechnyi) ages (see Table 1). Most of these records are represented by Dermochelyidae indet. (Bakhchisarai 2, Prolom, Tschelyuskinets, Zarechnyi), and only one is determined to the generic level (*Cosmochelys* sp. from Ak-Kaya 1). The Cenozoic dermochelyids were highly specialized pelagic turtles and probably cosmopolitan, like Recent *Dermochelys coriacea* (Vandelli, 1761). The "sunflower" epithecal pattern of Dermochelyidae indet. from Tschelyuskinets is diagnostic for Oligocene ridgeless dermochelyids *Natemys peruvianus* (Peru) and "*Psephophorus*" *rupeliensis* (Belgium) (Wood et al. 1996). *Cosmochelys* sp. from the Bartonian Ak-Kaya 1 locality is similar to *Cosmochelys dolloi* Andrews, 1920 from the Bartonian Port Harcourt locality of Nigeria (Andrews 1919) (Fig. 19).

The remains of pan-testudinoids are present in two of 39 localities (5%) of the Selandian (1; Bereslavka 2a) and Lutetian (1; Ikovo) ages (see Table 1). There are two different pan-testudinoids (Pan-Testudinoidea indet. 1 and 2) in the Bereslavka 2a locality, and Pan-Geoemydidae gen. et sp. nov. and Pan-Testudinidae indet. in the Ikovo locality.

Pan-Testudinoidea indet. 1 from the Selandian Bereslavka 2a locality is similar in morphology to some basal testudinoids, whereas Pan-Testudinoidea indet. 2 from the Bereslavka 2a locality is similar to problematic pan-testudinoids *Anhuichelys* spp., which are numerous in the Paleocene of Asia (see Tong et al. 2016; Zvonok and Danilov 2018). On the other hand, *Anhuichelys* spp. is similar to a problematic pan-testudinoid *Dithyrosternon valdense* from the Priabonian of Switzerland in the presence of two hinges in the plastron, overall shape of the plastron, position of the pleuro-marginal sulci on the peripherals, and probably a low posterior pair of the marginals restricted to the pygal (Pictet et al. 1855–1857). It can be supposed that these *Anhuichelys*-like turtles migrated from Asia to Europe via the land bridge over the Turgai Strait during the Danian and *Dithyrosternon valdense* is the Priabonian relic of this lineage (Fig. 19; Kuzmin and Zvonok 2021).

Pan-Geoemydidae gen. et sp. nov. from the Ikovo locality demonstrates a combination of morphological characters known only in some pan-geoemydids, like *Geoclemys hamiltonii*: participation of the jugal in the rim of the upper temporal emargination, and wide and not-ridged triturating surface of the upper jaw with participation of the palatine (see Zvonok and Danilov 2018). It is also similar to "*Ocadia*" *kehreri* Staesche, 1928 from the Lutetian Messel locality, Germany, in its laterally extended and rounded shape of the skull with a notched external surface of the maxilla (Gassner et al. 2001: fig 2a).

Pan-Testudinidae indet. from the Lutetian Ikovo locality is very similar in its shape and scute sulci of the epiplastron to *Pelorochelon soriana* from the Bartonian Mazateron locality of Spain (Perez-Garcia et al. 2016a; Zvonok and Danilov 2020). The fact that *Pelorochelon*-like turtles existed in Eastern Europe earlier may indicate the direction of migration of *Pelorochelon* Perez-Garcia et al., 2016 from Eastern to Western Europe or the disjunction of their geographic range.

The remains of other Pan-Testudines are present in 13 of 39 localities (33%) of the Selandian (1; Bereslavka 2a), Thanetian (2; Loznoe 1, Malaya Ivanovka), Ypresian (2; Loznoe 2, Malchevsko-Polnenskaya), Ypresian–Lutetian (3; Greskovo, Malchevskaya, Voznesenskiy), Lutetian (2; Georgievka, Krasnorechenskoe), Bartonian (2; Ak-Kaya 1, Bakhchisarai 2), and Oligocene–Miocene (1; Belomechetskaya) ages (see Table 1). Eleven of 13 records (85%) are represented by Pan-Testudines indet., three of which (Ak-Kaya 1, Malchevsko-Polnenskaya, Voznesenskiy) may correspond to other turtles known from the same localities. Pan-Testudines tax. nov. from the Bereslavka 2a locality demonstrates similarities with some basal turtles, like *Laurasichersis relicta* from the Paleocene of France, as well as with Cryptodira incertae sedis sp. 2 from the Maastrichtian Bereslavka 1 locality (Averianov and Yarkov 2004). Pan-Testudines indet. ZIN PH 5/261 from the Krasnorechenskoe locality can belong to Pan-Geoemydidae, but more likely to Pan-Podocnemididae (see Systematics).

Comments on the sculptured pan-cheloniids from the Paleogene of Eastern Europe

In the Paleogene of Eastern Europe, the remains of the sculptured pan-cheloniids are known from the Ypresian (Malchevsko-Polnenskaya), Ypresian–Lutetian (Gruzinov), Lutetian (Bakhmutovka, Bulgakovka, Krasnorechenskoe), Lutetian–Bartonian (Tripolye), and Priabonian (Otradnoe) ages.

The deep and dense sculpturing of the same type is peculiar for pan-cheloniids from the Bakhmutovka, Bulgakovka, Krasnorechenskoe and Tripolye localities. Among fossil pan-cheloniids, the sculpturing of the shell surface is also known in the Campanian–Maastrichtian *Peritresius ornatus*, the Maastrichtian *Glyptochelone suyckerbuycki*, the Priabonian *Osonachelus decorata*, the Oligocene *Ashleychelys palmeri*, *Bryochelys waterkeynii* and *Carolinochelys wilsoni*, and the Neogene *Trachyaspis lardyi*. The sculptured pan-cheloniids from the Paleogene of Eastern Europe can be differentiated from *Glyptochelone suyckerbuycki* and *Peritresius ornatus* by the sculpturing of the neurals composed of grooves, rather than of ridges and tubercles radiating from the centers of the plates; from *Osonachelus decorata* by the sculpturing present on both vertebral and pleural areas of the costals, as well as the peripherals, rather than only the vertebral areas of the costals; from *Ashleychelys palmeri* by the absence of a medial carina on the neurals and by narrow vertebral scutes; from *Trachyaspis lardyi* by the absence of carinae on the neurals and costals. On the other hand, the sculptured pan-cheloniids from the Paleogene of Eastern Europe share narrow vertebral scutes with *Osonachelus decorata* and *Trachyaspis lardyi*. Thus, the sculptured pan-cheloniids of the Paleogene of Eastern Europe probably represent a new taxon, whose description will be possible after accumulation of a more complete material. A similar sculptured pan-cheloniid material was reported from the Bartonian Shorym Formation of Western Kazakhstan (Zvonok et al. 2011).

The pan-cheloniid shell plates from the Ypresian Malchevsko-Polnenskaya (ZIN PH 19/254), the Ypresian–Lutetian Gruzinov (ZIN PH 7/256 and ZIN PH 10/256) and the Priabonian Otradnoe (ZIN PH 1/265) have a different sculpturing with less densely spaced and shallower grooves, and can belong to other pan-cheloniid taxa. In the cases of the Malchevsko-Polnenskaya and Gruzinov localities, there is a possibility that they belong to *Argillochelys* sp., which is present (Gruzinov) or probably present (Malchevsko-Polnenskaya) in these localities. Another previously described Eocene pan-cheloniids from this region – *Eochelone* sp., *Puppigerus camperi* and *Tasbacka aldabergeni* – are smooth-shelled (Nessov 1987; Moody 1974; de Lapparent de Broin et al. 2018).

Comments on the composition of the genera *Argillochelys* and *Puppigerus*

Argillochelys. After revisions and discussions, two species of the genus *Argillochelys* are considered valid: *Argillochelys antiqua* and *Argillochelys cuneiceps* (Moody 1980; de Lapparent de Broin et al. 2018; Zvonok and Danilov 2019). *Argillochelys athersuchi* has a controversial generic attribution being assigned either to *Argillochelys* or to *Eochelone* (Moody 1980; de Lapparent de Broin et al. 2014, 2018). Comparisons and phylogenetic studies show that another species, *"Argillochelys" africana*, does not belong to this genus and should be attributed to the genus *Itilochelys* Danilov et al. 2010 (Danilov et al. 2010; Scavezzoni and Fischer 2018; Ullmann and Carr 2021).

The type species of *Argillochelys* is *Argillochelys cuneiceps*, based on the skull from the London Clay of England (Lydekker 1889). A likely synonym for *Argillochelys cuneiceps* is "*Chelone*" *convexa* (de Lapparent de Broin et al. 2018).

Argillochelys antiqua from the London Clay is known from a number of specimens, including skulls, but there is no recent description of them. A well-preserved specimen NHM 38955 (*Argillochelys antiqua* of Lydekker 1889) is clearly a juvenile *Puppigerus camperi* (as used in Neenan et al. 2017). De Lapparent de Broin et al. (2018) noted the following differences in the ventral part of the skull between *Argillochelys antiqua* and *Argillochelys cuneiceps* based on their study, which included an unpublished partial skull from Sheppey: *Argillochelys cuneiceps* has "a longer union of the vomer with the palatine, a relative wider vomer at midlength, and the more separated and acutely protruding pterygoid processes", another differences are "whole external shape, the orbit size, the interorbital space and the characteristic pattern of scutes..." (de Lapparent de Broin et al. 2018, Supplement: pp. 6–7).

Argillochelys athersuchi from the Bartonian Barton Beds of England, based on an incomplete skull (Moody 1980), referred by de Lapparent de Broin et al. (2018) to the genus *Eochelone* on the basis that it "presents the roof shape, scute pattern and secondary palate characteristic of the skull of the genus, shared with the type species *E. brabantica*" (de Lapparent de Broin et al. 2018: p. 260).

The cranial remains of pan-cheloniids from the Ak-Kaya 1 locality, referred to *Argillochelys* sp., contain a vomer and a fragment of the maxillary bone, similar to those of the above-mentioned specimen of *Argillochelys athersuchi* from the Bartonian of Western Europe. At the same time, the remains of *Argillochelys* sp. from the Ak-Kaya 1 locality contain a dentary with the lingual and symphyseal ridges. These ridges are definitely absent in *Eochelone brabantica* (Casier 1968). Consequently, if the material from the Ak-Kaya 1 locality is a species identical or close to the Bartonian pan-cheloniids of Western Europe, then they are more likely to belong to *Eochelone*-like *Argillochelys* than to *Argillochelys*-like *Eochelone*. In addition, the differences between *Argillochelys antiqua* and *Argillochelys athersuchi* are unclear, at least according to the description in the literature: in both species, in contrast to *Argillochelys cuneiceps*, there are a narrow interorbital space, three scutes behind the frontoparietal scute, and a shorter suture between the palatine and vomer. Thus, this species of *Argillochelys* needs a redescription of the collections from the type localities.

Puppigerus. The species *Puppigerus nessovi* Averianov, 2005 was described from the middle Eocene Dzheroi 2 locality of Uzbekistan based on the dentary fragment (holotype) and isolated bones of the skeleton (Averianov 2005). This species was distinguished from *Puppigerus camperi* (type species of *Puppigerus*) by the longer mandibular symphysis located close to the level of the foramen dentofaciale majus, the preservation of the costoperipheral fontanelles in adults, and by the presence of a longitudinal horn sulcus on the pygal plate. *Puppigerus* from Ikovo (Eastern Europe) was for some time attributed to *Puppigerus nessovi* (Danilov et al. 2011; Zvonok 2013; Zvonok et al. 2013; Danilov et al. 2017), although Tong et al. (2012) placed *Puppigerus nessovi* in the synonymy of *Puppigerus camperi*. Based on the study of skull ZIN PH 53/145 from Ikovo, Zvonok (2013) added to the diagnosis of *Puppigerus nessovi* one more character: a greater width of the prefrontal and frontal bones.

Our personal observation of a series of the dentaries from Ikovo (collection ZIN PH 145) showed that the position of the foramen dentofaciale majus in relation to the posterior margin of the symphysis varies depending on the bone size, and is subject to intraspecific variability. The possibility of the presence of the costoperipheral fontanelles in adult specimens was indicated in the diagnosis of the genus *Puppigerus*, and the longitudinal horn sulcus on the pygal plate is present in some specimens of *Puppigerus camperi* (Moody 1974: fig. 14A). Moreover, the width of the prefrontal bones and the related orientation of the orbits also vary within *Puppigerus camperi* (Owen and Bell 1849; Moody 1974: pl. 3; Tong et al. 2012: fig. 1A–B). Thus, none of the diagnostic characters of *Puppigerus nessovi* allows distinguishing it from *Puppigerus camperi*, and the former should be considered a junior synonym of the latter (pro Tong et al. 2012).

Another species previously referred to *Puppigerus*, *Puppigerus* (orig. *Chelone*) *crassicostatus* (Owen, 1849), is considered herein to be conspecific with *Glossochelys* (orig. *Chelone*) *planimentum*, which in turn is a probable synonym of *Erquelinnesia* (orig. *Pachyrhynchus*) *gosseleti* (Dollo, 1886). *Chelone crassicostata* was founded on the carapace (holotype) and additional cranial and postcranial specimens from the Harwich cliffs (not Isle of Sheppey, contra Moody 1968), England (Owen and Bell 1849: tabs XI–XIIIB). Cope (1870) was first to refer this species to the genus *Puppigerus*. Lydekker (1889) confirmed assignment of the cranial and postcranial specimens to the same species (*Lytoloma crassicostatum*), because one of the referred specimens (NHMUK R 918) demonstrated both cranial and postcranial characters, and placed *Erquelinnesia gosseleti* in the synonymy of *Lytoloma crassicostatum*. Hay (1908), on the contrary, transferred the species *crassicostata* to *Erquelinnesia gosseleti*. Moody (1968) referred *Chelone crassicostata* to his new genus *Eochelys* Moody, 1968, with the type species *Chelone longiceps* Owen, 1842. He excluded *crassicostata* from the genus *Erquelinnesia* Dollo, 1887 with reference to then unpublished work of Zangerl that "the type of *Erquelinnesia gosseleti* to be toxochelyid, while the type shell of the species *crassicostata* is cheloniid" (Moody 1968: 130). However, Zangerl (1971: 27) stated that "the carapace (type specimen) of *Chelone crassicostata* <...> should be difficult to distinguish from the smaller shells of *Erquelinnesia gosseleti*", and it "shows no features that identify it as either toxochelyid or cheloniid". The skull material of *Chelone crassicostata* was tentatively referred to the genus *Glossochelys* Seeley, 1871 until a restudy of the material is done, with a comparison with *Erquelinnesia* and *Euclastes* Cope, 1867 (Zangerl 1971). Later, Moody (1974) considered *Eochelys longiceps* to be conspecific with *Puppigerus* (orig. *Emys*) *camperi* (Gray, 1831), *Eochelys* as a junior synonym of *Puppigerus*, and *Puppigerus crassicostatus* as the second species of this genus. Thus, this species appeared in the genus *Puppigerus* for the second time. Even later, Moody (1980) referred *Chelone crassicostata* (in part, including skull NHMUK 37205 but not the type specimen) and *Erquelinnesia gosseleti* to *Erquelinnesia planimenta*. More recently, some authors (Tong et al. 2012; Zvonok 2013) accepted the taxonomic status of *Puppigerus crassicostatus* after Moody (1974, 1980), whereas other authors (Parham and Pyenson 2010; Lapparent de Broin et al. 2018) synonymized this species with *Glossochelys planimentum* following Zangerl (1971). In the current article, we follow Zangerl (1971) based primarily on morphological similarity of *Chelone crassicostata*, *Erquelinnesia gosseleti* and *Glossochelys planimentum*. Most notable trait of *Chelone crassicostata*, which distinguishes it from *Puppigerus*, is an extremely developed secondary palate, which is even more extensive than in *Euclastes roundsi* and *Tasbacka ouledabdounensis*, and close to *Erquelinnesia* in its degree of development. The synonymy of *Chelone crassicostata* and *Glossochelys planimentum* is supported by the provenance of the holotype of *Chelone crassicostata* coming from the same locality (Harwich cliffs) as the holotype of *Glossochelys planimentum* (Owen and Bell 1849). All specimens assigned to these taxa, but not originating from the type locality, need additional comparison. In particular, the specimen of *Eochelys crassicostata* described by Moody (1968) does not differ from *Puppigerus camperi* and may belong to this species. Specimens NHMUK 38955 and NHMUK 37213a, referred by Moody (1974: table 4) to *Puppigerus crassicostatus*, have the choanae situated more anteriorly than in the specimens referred to *Puppigerus camperi*. This contrasts sharply to the state of the skull of *Chelone crassicostata* from the type locality with choanae situated far posteriorly (Lydekker 1889). The specimens of *Puppigerus* from Ikovo do not differ from *Puppigerus camperi*, whereas the skulls of the Ypresian *Puppigerus* from Walton on the Naze (England; Chapman et al. 2015) and

Ouled Abdoun phosphate basin (Morocco; Tong et al. 2012) differ from the typical skulls of *Puppigerus camperi* and require additional study (see Zvonok et al. 2023). Thus, the only valid species of *Puppigerus* is *Puppigerus camperi* (= *Puppigerus nessovi*), whereas *Puppigerus crassicostatus* should be placed in the synonymy of *Glossochelys planimentum*.

CONCLUSIONS

The results of this study significantly expand our knowledge of the localities, systematic composition, morphology, stratigraphic and geographic distribution, and probable direction of migration of Paleogene turtles of Eastern Europe.

We summarized data on 39 localities of Paleogene turtles of Eastern Europe including information about the geographical coordinates, stratigraphic units and geological age, materials, literature and fieldworks of collectors.

The results of the study of all previously mentioned and new materials of Paleogene turtles of Eastern Europe are presented in a systematic order, except for the materials from Selandian Bereslavka 2a and the Lutetian Ikovo localities, which, due to their large volume, require separate studies. Materials of turtles from 19 Paleogene localities are described for the first time, including 13, which have previously been only mentioned in the literature (see details in the Material and Methods section). Most of the materials from new localities are not identified more accurately than Pan-Trionychidae, Pan-Cheloniidae, Dermochelyidae, or Testudines, except for the pan-cheloniids *Argillochelys* sp. from the Ypresian Novoivanovka and Ypresian or Lutetian Gruzinov localities, new data on which expand the geographical distribution of the genus *Argillochelys*. Some materials from new localities cannot be identified to the genus or species level, but contain features that make them similar to certain taxa: a pan-cheloniid squamosal from the Ypresian Malchevsko-Polnenskaya locality shows similarities with the isochronous *Argillochelys cuneiceps* from England; one of the pan-cheloniid dentaries from the Ypresian Novoivanovka locality may belong to *Puppigerus camperi* or *Tasbacka aldabergeni*; the epithecal plates of Dermochelyidae indet. from the Tschelyuskinets locality are similar to the Oligocene *Natemys peruvianus* and "*Psephophorus*" *rupeliensis*; and costal plate 5 of Testudines indet. from the Thanetian Loznoe 1 locality does not differ from yet undescribed turtles tentatively referred to Pan-Testudinoidea from a geographically close Selandian Bereslavka 2a locality. Of interest is also costal plate 1 of Pan-Testudines indet. from the Lutetian Krasnorechenskoe locality, which shows similarities with the pan-podocnemidids *Eocenochelus* spp. and *Neochelys* spp. If the affiliation to these genera is confirmed, then this is the first find of side-necked turtles in Eastern Europe. There are also other unusual specimens in the described materials.

In addition, material from five previously known localities was described. New anatomical elements of *Argillochelys* sp. from the Bartonian Ak-Kaya 1 locality confirm its assignment to the genus *Argillochelys* and shows a similarity to the isochronous *Argillochelys athersuchi* from England. The epithecal plate of a juvenile *Cosmochelys* sp. expands the range of intraspecific variability of this taxon from the Ak-Kaya 1 locality.

The wide stratigraphic distribution of sculptured pan-cheloniids in the Eocene of Eastern Europe is unexpected, given the new described specimens. Such specimens have been described from two Ypresian, three Lutetian, one Lutetian or Bartonian, and one Priabonian localities of Eastern Europe. The specimens of pan-cheloniids with deep and dense sculpturing of shell plates from the Bakhmutovka, Bulgakovka, Krasnorechenskoe and Tripolye localities clearly belong to a new species, which is not described here due to the fragmentarity of the remains, but is clearly distinct from another deeply sculptured pan-cheloniid from the Eocene of Europe, *Osonachelus decorata*.

Based on the stratigraphical-geographical sequence of events, we hypothesized that *Anhuichelys*-like pan-testudinoids migrated from Asia in Eastern Europe in the Danian age, and preserved as relict *Dithyrosternon valdense* until the Priabonian age. Pan-Trionychidae indet. from the Lutetian Ikovo locality is similar to endemic North American plastomenids, but its affinity needs confirmation. Other continental Paleogene turtles of Eastern Europe have clear similarity only with turtles of Western Europe. The geographic range of Paleogene marine turtles presented in Eastern Europe sometimes is wider than presented in the fossil record, but does not give a notion of their true range and directions of migration due to the weak influence of geographical barriers on marine forms.

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Appendix 1. The list of localities of Paleogene turtles of Eastern Europe

Danian

1. Ak-Kaya 2, Belogorsk District, Crimea, Russia.

Geographical coordinates. 45°06'N, 34°37'E.

Horizon and age. Belokamensk regiostage, Danian (Zvonok and Danilov 2019).

Material and references. A fragment of the shell plate of Pan-Trionychidae indet. (as Trionychidae indet.; Zvonok and Danilov 2019: 70, fig. 4z).

Collector. N.I. Udovichenko

2. Rasstrigin 2, Dubovka District, Volgograd Province, Russia.

Geographical coordinates. 49°32'N, 44°59'E.

Horizon and age. Beryozovaya beds, the upper fossiliferous level, Danian (Danilov et al. 2010).

Material and references. A partial skull with a disarticulated lower jaw and cervical vertebrae 1–3 (holotype), dentary and humerus of the pan-cheloniid *Itilochelys rasstrigin* Danilov et al., 2010 (Danilov et al. 2010: 25, figs 2–11; 2017: 180, pl. XIX, figs 3–18; pl. XX, figs 1–19).

Collector. Yarkov A.A., 1990.

Remarks. Danilov et al. (2010) noted the similarity of *Itilochelys rasstrigin* with *"Argillochelys" africana* Tong et Hirayama, 2002 from the Paleocene of Morocco (Tong and Hirayama 2008). The phylogenetic analysis of pan-chelonioids by Scavezzoni and Fischer (2018) found both taxa to be in basal polytomy of pan-cheloniids, whereas modification of the same analysis by Ullmann and Carr (2021) resulted in their placement in one clade, which corresponds to the genus *Itilochelys* Danilov et al., 2010 with two species *Itilochelys rasstrigin* and *Itilochelys africana*.

3. Sakharnaya Golovka, Sebastopol District, Crimea, Russia.

Geographical coordinates. 44°35'N, 33°37'E.

Horizon and age. Limestone of Belokamensk beds, Danian (Zvonok 2014).

Material and references. Five plate fragments probably belonging to a single individual of Pan-Cheloniidae indet. (as Cheloniidae indet; Zvonok 2014: 83; Zvonok and Danilov 2019: 68, fig. 4cc).

Collector. Yu.O. Zhukov, 2013.

Selandian

4. Bereslavka 2a (= Karpovka), Gorodishche District, Volgograd Province, Russia.

Geographical coordinates. 48°37'N, 44°06'E.

Horizon and age. Green-gray quartz-glauconite sands with phosphorites of the Syzran Formation, Selandian (Averianov and Yarkov 2004).

Material and references. Fragmented right maxilla and premaxilla and some shell fragments of the pan-cheloniid *Euclastes wielandi* (Hay, 1908) (as "shell fragments of sea turtles (cheloniids)"; Efimov and Yarkov 1993: 88; as Osteopyginae gen. et sp. indet.; Averianov and Yarkov 2000: 164, figs 3a–e, 4; as Osteopyginae indet.; Averianov 2002: 142; as "Karpovka *Euclastes*"; Lynch and Parham 2003: 35; as Cheloniidae gen. indet. 1; Danilov et al. 2017: 187; *Euclastes wielandi*: Zvonok and Danilov 2018: 95, fig. 1H, I); nine shell fragments, including four pieces of costals of Pan-Trionychidae indet. (as Trionychidae indet.; Averianov and Yarkov 2000: 164, fig. 3f; as Trionychidae subfam. indet. 23; Danilov et al. 2017: 124); a carapace fragment of Pan-Testudinoidea indet. 1 (probably as Cheloniidae indet.; Averianov and Yarkov 2004: 42; as Testudinoidea indet. 1; Zvonok and Danilov 2018: 95, fig. 1J); costal 6(?) of Pan-Testudinoidea indet. 2 (as Testudinata indet.: genus and species indet. 1; Averianov and Yarkov 2000: 165, fig. 3g–i; as Testudines subord. indet. 11; Danilov et al. 2017: 340; as Testudinoidea indet. 2; Zvonok and Danilov 2018: 95); a neural and numerous shell fragments of Pan-Testudines tax. nov. (as Testudinata indet.: genus and species indet. 2; Averianov and Yarkov 2000: 166, fig. 3j, k; as Testudines subord. indet. 12; Danilov et al. 2017: 340; as a basal turtle or basal cryptodire; Zvonok and Danilov 2018: 95).

Collectors. E.V. Popov, 2001; A.A. Yarkov, 1980s–2010s.

Remarks. Averianov and Yarkov (2000) described the first turtle material from Bereslavka 2a (as Karpovka), including cranial and shell fragments of Osteopyginae gen. et sp. indet., shell fragments of Trionychidae indet., Testudinata indet.: genus and species indet. 1 and 2. Lynch and Parham (2003) referred this material to as "Karpovka *Euclastes*". Averianov and Yarkov (2004) mentioned additional material of Cheloniidae indet. and Trionychidae indet. from there. Danilov et al. (2017) referred "Karpovka *Euclastes*" to Cheloniidae gen. indet. 5 following the restriction of the genus *Euclastes* Cope, 1870 by Parham and Pyenson (2010), Trionychidae indet. to Trionychidae subfam. indet. 23, and Testudinata indet.: genus and species indet. 1 and 2 to Testudines subord. indet. 11 and 12, respectively. Zvonok and Danilov (2018) reported new turtle material from Bereslavka 2a and changed systematic attribution of some taxa. Cheloniidae gen. indet. 1 (= Osteopyginae gen. et sp. indet.; = "Karpovka *Euclastes*") was assigned to *Euclastes wielandi*, based on weakly elongated palatal elements and a rounded anterior tip of the skull (see Hirayama and Tong 2003; Jalil et al. 2009). Cheloniidae indet., mentioned by Averianov and Yarkov (2004), was reinterpreted as Testudinoidea indet. 1, based on similarities with some basal testudinoids in the presence of a smooth buttress fossa on costal 5, suggesting a loose plastron-carapace connection. Testudinata indet.: genus and species indet. 1 was referred to as Testudinoidea indet. 2 based on a wedge-like shape of the costal and the absence of the rib thickening on its internal surface (both characters are present in problematic testudinoids *Anhuichelys* spp. from the Paleocene of Asia; Tong et al. 2016). Testudinata indet.: genus et species indet. 2, primarily represented by a thick neural with a folded external surface (Averianov and Yarkov 2000), was referred to basal turtles or basal cryptodires based on new shell fragments with deep and undulating scute sulci, similar to Cryptodira incertae sedis sp. 2, represented by fused epiplastra and entoplastron from the Maastrichtian of the Bereslavka 1 locality (Averianov and Yarkov 2004). Herein, the attribution of all these taxa is converted to phylogenetic nomenclature (see Joyce et al. 2004, 2021). The previously published and new material from Bereslavka 2a will be revised in a separate paper.

Thanetian

5. Bakhchisarai 1, Bakhchisarai District, Crimea, Russia.

Geographical coordinates. 44°43'N, 33°52'E.

Horizon and age. Thanetian (Averianov 2002).

Material and references. Five fragments of a large costal of Pan-Cheloniidae indet. (as “bones of [sea] turtles”; Nessov 1987: 77; Chkhikvadze 1990: 5; as Chelonioidea indet.; Averianov 2002: 139, 142; Danilov et al. 2017: 193). See Systematics section for description.

Collector. N.I. Udovichenko.

Remarks. To distinguish the Thanetian locality Bakhchisarai (Averianov 2002) from the eponymous Bartonian locality (formerly considered the lower Priabonian; Zvonok 2011) here we use for them the names Bakhchisarai 1 and Bakhchisarai 2, respectively.

6. Bereslavka 2b, Gorodishche District, Volgograd Province, Russia.

Geographical coordinates. 48°37'N, 44°06'E.

Horizon and age. Quartz sand of the Kamyshin Formation, Thanetian (Averianov and Yarkov 2004).

Material and references. Costals of Pan-Cheloniidae indet. (as “few very fragmented costals of a large, but thin-plated Cheloniidae indet. with massive rib heads”; Averianov and Yarkov 2004: 42); a neural of Pan-Trionychidae indet. (as “one fragmented neural of Trionychidae indet.”; Averianov and Yarkov 2004: 42; as Trionychidae subfam. indet. 24; Danilov et al. 2017: 124). See Systematics section for description.

Collector. A.A. Yarkov, 1990.

7. Loznoe 1, Dubovka District, Volgograd Province, Russia.

Geographical coordinates. 49°19'N, 44°25'E.

Horizon and age. Quartz sand of Kamyshin Formation, Thanetian (Averianov and Yarkov 2004).

Material and references. Shell fragments and a phalanx of Pan-Testudines indet. (as Testudines indet.; Averianov and Yarkov 2004: 48, fig. 7; Zvonok and Danilov 2018: 95; as Testudines subord. indet. 13; Danilov et al. 2017: 340); two shell fragments of Pan-Trionychidae indet. (as “shell fragment of Trionychidae indet.”; Zvonok and Danilov 2018: 95); a costal fragment of Pan-Cheloniidae indet. See Systematics section for description.

Collectors. A.V. Panteleev, 2003, 2005; A.A. Yarkov.

8. Malaya Ivanovka, Dubovka District, Volgograd Province, Russia.

Geographical coordinates. 49°21'N, 44°31'E.

Horizon and age. Yellowish sands with gravel, Thanetian (Averianov 2002).

Material and references. Not specified material of the pan-cheloniid cf. *Tasbacka* sp. (Averianov 2002: 139, 142; Danilov et al. 2010: 25; Danilov et al. 2017: 182; as “sea turtles, similar with *Tasbacka aldabergeni* Ness., but twice larger”; Nessov and Yarkov 1989: 80); a costal fragment of Pan-Testudines indet. See Systematics section for description.

Collectors. A.A. Yarkov, 1989, 1990; A.V. Panteleev, 2003, 2005.

Ypresian

9. Kudinovka, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 49°12'N, 40°31'E.

Horizon and age. Brownish sand with pebbles and phosphorite nodules, Ypresian (remains of vertebrates in phosphorite nodules can be redeposited from the Paleocene; Zvonok and Danilov 2023).

Material and references. The phosphorite nodules containing a shell with a number of anatomically closely spaced bones, three bone agglomerates, three poorly preserved costals of indeterminate position, and seven indeterminate flat bones of *Tasbacka aldabergeni* Nessov, 1987 (Zvonok and Danilov 2023; as Cheloniidae indet.; Benitskiy and Zvonok 2020: 100).

Collectors. K.S. Benitskiy, 2018–2019; E.A. Zvonok, 2019.

10. Loznoe 2, Dubovka District, Volgograd Province, Russia.

Geographical coordinates. 49°19'N, 44°25'E.

Horizon and age. Horizon unknown, quartz sand with white cement remains in the hollows of fossils; Ypresian, according to pers. comm. of A.A. Yarkov.

Material and references. A shell fragment of Testudines indet. See Systematics section for description.

Collectors. S.N. Monikov.

11. Malchevsko-Polnenskaya, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 49°00'N, 40°14'E.

Horizon and age. Yellow-brownish sand with pebbles, Ypresian (Benitskiy and Zvonok 2020).

Material and references. Two skull bones, seven carapacial bones, cervical vertebra 8, and six limb bones of Pan-Cheloniidae indet. (as Cheloniidae indet.; Benitskiy and Zvonok 2020: 100); four shell fragments of Pan-Trionychidae indet. (as Trionychidae indet.; Benitskiy and Zvonok 2020: 101); a caudal vertebra and a partial femur of Pan-Testudines indet. See Systematics section for description.

Collectors. K.S. Benitskiy, E.A. Zvonok, 2020, 2021.

12. Novoivanovka, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 48°50'N, 40°23'E.

Horizon and age. Light yellow sand with gravel, Ypresian (Benitskiy and Zvonok 2020).

Material and references. Dentary symphysis of the pan-cheloniid *Argillochelys* sp. (Zvonok and Danilov 2018: 95, fig. 1K; Benitskiy and Zvonok 2020: 101); dentary symphysis of the pan-cheloniid *Puppigerus camperi* (Gray, 1831) or *Tasbacka aldabergeni* (Benitskiy and Zvonok 2020: 101); a neural of Pan-Cheloniidae indet. See Systematics section for description.

Collectors. K.S. Benitskiy, 2015, 2019; E.A. Zvonok, 2018.

Remarks. Initially, the age of the Novoivanovka locality was indicated as the ?Lutetian (Zvonok and Danilov 2018), but later changed to the Ypresian (Benitskiy and Zvonok 2020).

Ypresian–Lutetian

13. Grekovo, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 48°54'N, 40°12'E.

Horizon and age. Quartz sand, Ypresian–Lutetian.

Material and references. A costal fragment of Pan-Testudines indet. See Systematics section for description.

Collector. K.S. Benitskiy.

Remarks. The quartz sand of the Grekovo locality likely belongs to the Kanev or Buchak horizons of this area (Ypresian – lower Lutetian; Akhmedov et al. 2011).

14. Gruzinov, Morozovsk District, Rostov Province, Russia.

Geographical coordinates. 48°23'N, 41°45'E.

Horizon and age. Quartz sand, Ypresian–Lutetian.

Material and references. Left dentary branch of the pan-cheloniid *Argillochelys* sp., fragment of the maxilla and seven shell bones of Pan-Cheloniidae indet. See Systematics section for description.

Collectors. A.V. Panteleev, E.V. Popov.

Remarks. The quartz sand of Gruzinov locality likely belongs to the Kanev or Buchak horizons of this area (Ypresian – lower Lutetian; Akhmedov et al. 2011).

15. Malchevskaya, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 49°03'N, 40°22'E.

Horizon and age. Quartz sand, Ypresian–Lutetian.

Material and references. Costal fragment of Pan-Testudines indet. (as Testudines indet.; Zvonok and Danilov 2018: 95). See Systematics section for description.

Collectors. A.V. Panteleev, E.V. Popov, 2003.

Remarks. The age of the Malchevskaya locality was originally indicated as the ?Lutetian (Zvonok and Danilov 2018). According to the state geological map of the Russian Federation (Akhmedov et al. 2011), the deposits of the Kanev and Buchak formations (Ypresian and lower Lutetian) contain the beds of quartz sand in the area of the Malchevskaya locality. For this reason, we conventionally determined the geological stage of this locality as the Ypresian – lower Lutetian.

16. Verkhnetalovka, Millerovo District, Rostov Province, Russia.

Geographical coordinates. 48°49'N, 40°21'E.

Horizon and age. Quartz sand with pebbles, Ypresian–Lutetian.

Material and references. Two shell fragments of Pan-Trionychidae indet. See Systematics section for description.

Collector. K.S. Benitskiy, 2018.

Remarks. The shell fragments of Pan-Trionychidae indet. from the Verkhnetalovka locality have the same degree of preservation as vertebrae of Mosasauridae indet. from this locality (E.A. Zvonok, pers. obs.), and could be redeposited from the Upper Cretaceous deposits.

Remarks. According to the state geological map of the Russian Federation (Akhmedov et al. 2011), the deposits of the Kanev and Buchak formations (Ypresian and lower Lutetian) contain the beds of quartz sand in the area of the Verkhnetalovka locality. For this reason, we conventionally determined the geological stage of this locality as the Ypresian – lower Lutetian.

17. Voznesenskiy, Morozovsk District, Rostov Province, Russia.

Geographical coordinates. 48°22'N, 41°56'E.

Horizon and age. Quartz sand, Ypresian–Lutetian.

Material and references. A fragment of postorbital and nine carapacial bones of Pan-Cheloniidae indet. (as Cheloniidae indet.; Zvonok and Danilov 2018: 96); a fragment of the xiphiplastron of Pan-Testudines indet. (as Testudines indet.; Zvonok and Danilov 2018: 96). See Systematics section for description.

Collector. A.V. Panteleev, 2000, 2003, 2005; E.V. Popov, 2004.

Remarks. Initially, the age of the Voznesenskiy locality was indicated as the ?Lutetian (Zvonok and Danilov 2018). According to the state geological map of the Russian Federation (Akhmedov et al. 2011), the deposits of the Kanev and Buchak formations (Ypresian and lower Lutetian) contain the beds of quartz sand in the area of the Voznesenskiy locality. For this reason, we conventionally determined the geological stage of this locality as the Ypresian – lower Lutetian.

Lutetian

18. Bakhmutovka, Novoaidar District, Luhansk People's Republic, Russia.

Geographical coordinates. 48°52'N, 39°01'E.

Horizon and age. Yellowish sand with sandstone nodules of the (?) Buchak Formation 10–20 cm below the Phosphate member of the Kiev Formation, Lutetian (Averianov 2002; see Zvonok and Danilov 2018).

Material and references. A sacral vertebra or caudal vertebra 1, a middle caudal vertebra, and 66 shell fragments of a single large individual of Pan-Cheloniidae indet. (as Chelonioidea indet. or Chelonioidea? indet.; Averianov 2002: 139, 144, fig. 7; Chelonioidea indet.; Danilov et al. 2017: 193; as cheloniids; Zvonok and Danilov 2018: 93). See Systematics section for description.

Collector. N.I. Udovichenko, 1988, 1990.

Remarks. The specimen reported as Chelonioidea indet. (Dermochelyidae?; ZIN PH 1/20) from the "Unknown locality" of the middle Eocene of the Luhansk Province (No. 34; Averianov 2002: 144, fig. 7) in fact comes from the Bakhmutovka locality (see Zvonok and Danilov 2017). This specimen is included in a large phosphorite nodule, which indicates its origin from the Phosphate member of the Kiev Formation. A new specimen, described in this paper, comes from sand of an unclear formation, either the uppermost Buchak Formation or the lowermost Kiev Formation.

19. Bulgakovka, Starobel'sk District, Luhansk People's Republic, Russia.

Geographical coordinates. 49°11'N, 38°32'E.

Horizon and age. The bed on the border between Buchak and Kiev Formations, Lutetian (pers. comm. of N.I. Udovichenko).

Material and references. A costal fragment of Pan-Cheloniidae indet. See Systematics section for description.

Collector. N.I. Udovichenko.

20. Georgievka, Lutugino District, Luhansk People's Republic, Russia.

Geographical coordinates. 48°26'N, 39°19'E.

Horizon and age. Glauconitic sand, the lower part of the Kiev Formation, Lutetian.

Material and references. A costal fragment of Pan-Testudines indet. (as Testudines indet.; Zvonok and Danilov 2018: 95). See Systematics section for description.

Collector. N.I. Udovichenko.

21. Ikovo, Novopskov District, Luhansk People's Republic, Russia.

Geographical coordinates. 49°31'N, 39°03'E.

Horizon and age. Quartz sand, sandstone, clay, and conglomerates of the Buchak Formation, Lutetian (Udovichenko 2009).

Material and references. A partial skull and postcranial remains of the pan-trionychid "*Trionyx*" *ikoviensis* Danilov et al., 2011 (Danilov et al. 2017:

116, pl. XIII, figs 4–9; Georgalis and Joyce 2017: 142; Zvonok and Danilov 2018: 93; as Trionychidae; Zvonok et al. 2010: 15; Udovichenko and Zvonok 2011: 129; as *Trionyx ikoviensis*; Danilov et al. 2011: 400, figs 2–4); a partial skull of Plastomenidae indet. (as "a partial skull of the second trionychid assigned to the clade Plastomenidae", "Trionychidae indet. (Plastomenidae)"; Zvonok and Danilov 2018: 93, 94, fig. 1B); numerous shell bones of Pan-Trionychidae indet. (as "numerous shell bones of trionychids"; Zvonok and Danilov 2018: 93); isolated bones of the pan-cheloniid *Argillochelys* sp. (Zvonok et al. 2010: 15; Zvonok et al. 2013b: 610, fig. 1k–v; Udovichenko and Zvonok 2011: 129; Danilov et al. 2011: 400, 410; Zvonok and Danilov 2018: 93; as *Argillochelys* sp. indet. 1: Danilov et al. 2017: 181); skulls and isolated bones of the pan-cheloniid *Puppigerus camperi* (for taxonomic attribution see Discussion; as *Puppigerus nessovi* Averianov, 2005: Danilov et al. 2011: 400, 410; Danilov et al. 2017: 184; Zvonok 2013: 59, fig. 1; Zvonok et al. 2013b: 608, fig. 1a–j; Zvonok et al. 2015: fig. 6 "b"; as *Puppigerus* Cope, 1870; Zvonok and Gorobets 2012: 23; Zvonok and Danilov 2018: 93); a symphysis of the dentaries of the pan-cheloniid *Eochelone* sp. (Zvonok 2011: 112, pl. II, fig. 1; Danilov et al. 2017: 185; Zvonok and Danilov 2018: 93); isolated skeletal elements of Pan-Cheloniidae indet. (as Cheloniidae gen. indet.; Zvonok et al. 2013: 611, fig. 2); a facial skull region, maxilla, fragments of peripherals 2 and 3, and xiphiplastron of Pan-Geoemydidae gen. et sp. nov. (as cf. *Glossochelys* sp.; Zvonok 2011: 109, fig. 2, pl. I, fig. 1; Zvonok et al. 2015: fig. 6c; as Cheloniidae gen. indet. 3; Danilov et al. 2017: 188; as Testudinoidea indet. [partim]; Danilov et al. 2011: 400; Zvonok 2011: 108; Zvonok et al. 2013: 607; Zvonok and Danilov 2018: 93; as Geoemydidae gen. et sp. nov.; Zvonok and Danilov 2018: 93, fig. 1C–E); a premaxilla and shell fragments of Pan-Testudinidae indet. (as Testudinidae; Zvonok and Danilov 2018: 93, fig. 1F, G; 2020: 241, fig. A–J; as Testudinoidea indet. [partim]; Danilov et al. 2011: 400; Zvonok 2011: 108; Zvonok et al. 2013: 607; Zvonok and Danilov 2018: 93).

Collectors. N.I. Udovichenko, 2004; E.A. Zvonok, 2010–2013.

Remarks. Zvonok et al. (2010) reported the presence of Trionychidae indet. and *Argillochelys* sp. from the Ikovo locality. Danilov et al. (2011) described all then known trionychid material from this locality, including a partial skull and postcranial remains, as a new species "*Trionyx*" *ikoviensis*, and mentioned there the presence of *Puppigerus nessovi* and Testudinoidea indet. Zvonok (2011) described *Eochelone* sp., based on a symphysis of the dentaries, and cf. *Glossochelys* sp., based on a facial skull region. Zvonok and Gorobets (2012) listed all then available specimens of *Puppigerus* from Ikovo, including two skulls, and noted their similarity with *Puppigerus camperi.* Zvonok et al. (2013) described cranial and postcranial remains of *Argillochelys* sp., *Puppigerus nessovi* and Cheloniidae indet. from the Ikovo locality. Zvonok (2013) described one of the skulls of *Puppigerus* from Ikovo (as *P. nessovi*). Danilov et al. (2017) mentioned from Ikovo "*Trionyx*" *ikoviensis*, *Argillochelys* sp. indet. 1, *Eochelone* sp. indet., *Puppigerus nessovi*, and Cheloniidae gen. indet. 3 (= cf. *Glossochelys* sp.). Zvonok and Danilov (2018) added to the list of turtle taxa from Ikovo Trionychidae indet. (Plastomenidae), based on a partial skull, reinterpreted cf. *Glossochelys* sp. as Geoemydidae gen. et sp. nov., with a putative attribution of additional skull and shell material to the latter taxon, and reported the presence of Testudinidae indet. there, based on shell material. The Testudinidae indet. material was briefly described by Zvonok and Danilov (2020). Herein, the attribution of all these taxa is converted to phylogenetic nomenclature (see Joyce et al. 2004, 2021). The numerous isolated skeletal elements of Pan-Trionychidae indet. and Pan-Cheloniidae indet. from the Ikovo locality most probably belong to other pan-trionychid and pan-cheloniid taxa known from this locality (Zvonok et al. 2013; Zvonok and Danilov 2018). For this reason, they are not considered as distinct taxa (see Table 1). The previously published and new material from this locality will be revised in separate papers.

22. Kostyanetskiy Yar (= Kostyanets Ravine), Kanev District, Cherkassy Province, Ukraine.

Geographical coordinates. 49°47'N, 31°31'E.

Horizon and age. Quartz sand of the Buchak Formation, Lutetian (Zosimovich and Shevchenko 2015).

Material and references. A part of carapace of a single individual of Pan-Cheloniidae indet. (as Cheloniidae gen. et sp. indet. 2; Zvonok 2011: 114, pl. I, figs 6, 7; as Cheloniidae gen. indet. 4: Danilov et al. 2017: 188). See Systematics section for description.

Collector. N.I. Udovichenko, 2002.

Remarks. Previously, the same material was mentioned "as fragments of five costals and a neural" (Zvonok 2011: 114; Danilov et al. 2017: 188).

23. Krasnorechenskoe, Kremennaya District, Luhansk People's Republic, Russia.

Geographical coordinates. 49°12'N, 38°10'E.

Horizon and age. Light colored sand of the (?) Buchak Formation directly under the Phosphate member of the Kiev Formation, and the Phosphate member of the Kiev Formation, Lutetian (emended from Averianov 2002).

Material and references. Four shell fragments of Pan-Cheloniidae indet. (as Chelonioidea indet., "shell fragments of Chelonioidea? indet. with sculptured surface"; Averianov 2002: 139, 144; as Chelonioidea indet.; Danilov et al. 2017: 193; as cheloniids; Zvonok and Danilov 2018: 93); fragment of left costal 1 with a part of the axillary buttress of Pan-Testudines indet. (as Geoemydidae indet.; Zvonok and Danilov 2018: 93, fig. 1A). See Systematics section for description.

Collector. N.I. Udovichenko, 1989.

Remarks. Originally, the horizon and age of the locality was indicated as "light colored sand of Buchak(?) Formation, below phosphate horizon at the bottom of Kiev Formation <...> Lutetian-Bartonian" (Averianov 2002: 144; see Zvonok and Danilov 2018). There are four specimens with the corresponding label, but one of them is overgrown with phosphorites, suggesting that it comes from the Phosphate member of the Kiev Formation. Thus, one specimen definitely comes from the Phosphate member of the Kiev Formation, whereas the other three come from sand with an unclear belonging to the formation, either the uppermost Buchak or lowermost Kiev.

24. Krinichnoe, Melovoe District, Luhansk People's Republic, Russia.

Geographical coordinates. 49°19'N, 40°04'E.

Horizon and age. Quartz sand with phosphate nodules, Lutetian (A.A. Berezovskiy, pers. comm., age determination based on bivalves).

Material and references. Two isolated peripherals of Pan-Cheloniidae indet. (as Cheloniidae indet.; Zvonok and Danilov 2018: 95). See Systematics section for description.

Collector. E.A. Zvonok, 2013.

25. Sosnovka, Fastov District, Kiev Province, Ukraine.

Geographical coordinates. 50°12'N, 29°51'E.

Horizon and age. Black sand of the Yaroshovka Beds, Lutetian (Zosimovich and Shevchenko 2015).

Material and references. Four shell fragments of Pan-Cheloniidae indet. (as Cheloniidae gen. et sp. indet. 1; Zvonok 2011: 113, pl. I, figs 2–5; as Cheloniidae gen. indet. 5; Danilov et al. 2017: 188).

Collector. E.A. Zvonok, 2011.

Lutetian–Bartonian

26. Tripolye, Obukhov District, Kiev Province, Ukraine.

Geographical coordinates. 50°07'N, 30°46'E.

Horizon and age. The Phosphate or Marly-clayey member (the lower or middle part) of the Kiev Formation; Lutetian – lower Bartonian (Zvonok and Danilov 2017).

Material and references. Twelve shell fragments of Pan-Cheloniidae indet. (Zvonok and Danilov 2017: 504, figs 10H–J, 11H–J; as *Crocodylus spenceri* (Buckland, 1836): Rogovich 1875b: 46; Rogovich 1875c: 2).

Collector. A.S. Rogovich, 19th century (see Zvonok and Danilov 2017).

Remarks. Although the label indicates that the turtle remains from the Trypolye locality come from the blue brick clay, three shell fragments of 12 are covered with phosphorites, suggesting that these remains rather come from the Lutetian Phosphate member of the Kiev Formation, like the remains from the Bakhmutovka, Bulgakovka, and Krasnorechenskoe localities (Zosimovich and Shevchenko 2015). See also remarks on the Vyshgorod locality below.

27. Vyshgorod, Kiev City, Ukraine.

Geographical coordinates. 50°24'N, 30°31'E.

Horizon and age. The Marly-clayey member (the middle part) of the Kiev Formation; upper Lutetian – lower Bartonian (Averianov 2002; Zvonok and Danilov 2017).

Material and references. A partial skeleton, probably of one individual, and an isolated medial part of right costal 4(?) from another individual of the pan-cheloniid *Argillochelys antiqua* (König, 1825) (Danilov et al. 2017: 191, pl. XX, figs 30–32; as *Hypsodon kioviensis* Rogovich, 1871 [partim]: Rogovich 1871: pl. 10, figs 47, 48, 51; as *Anthracotherium alsaticum* Cuvier, 1822 [partim]: Rogovich 1875a: 36; Rogovich 1875b: 46; as "several fragments of the turtle shell" [?]: Rogovich 1875c: 2; as Cheloniidae [indet.]: Dubrovo and Kapelist 1979: 10; as *Puppigerus* sp.: Chkhikvadze 1983: 30, figs 11, 13; Chkhikvadze 1990: 5; Chkhikvadze 1999: 259; as "*Puppigerus*" sp.: Nessov 1987: 82; as *Dollochelys* *rogovichi* Averianov, 2002 [partim]: Averianov 2002: 147, figs 8a–g, l, 9, 10); two dentaries, probably of one individual of the pan-cheloniid "*Dollochelys*" *rogovichi* Averianov, 2002 (Zvonok and Danilov 2017: 501, figs 10A–G, 11A–G; as *Dollochelys rogovichi*; Averianov 2002: 147, fig. 8h–k; Hirayama 2006: 4 (nomen dubium); Chkhikvadze 2010: 99).

Collector. A.S. Rogovich, 19th century (see Zvonok and Danilov 2017).

Remarks. The "Unknown locality in Ukraine" of the Eocene listed by Averianov (2002: 146) and based on a mention of "remains of sea turtles" by Khosatzky (1975: 440) may represent a collective reference to the Vyshgorod and Tripolye localities, whose material was available to L.I. Khosatzky. The same material was mentioned earlier by Khosatzky (1949, 1950) and Pidoplichko (1961) (see Zvonok and Danilov 2017).

Zvonok and Danilov (2017) noted that "*Dollochelys*" *rogovichi* is similar in morphology to some pan-cheloniids, like *Eochelone brabantica* Dollo, 1903, *Osonachelus decorata* de Lapparent de Broin et al., 2014 and "*Dollochelys*" *casieri* Zangerl, 1971, in dorsomedially faced triturating surfaces of the dentaries. They also noted that "*Dollochelys*" *rogovichi* differs from *Eochelone brabantica* and *Osonachelus decorata* by the presence of weak lingual ridges on the triturating surfaces of the dentaries, and from "*Dollochelys*" *casieri* by flat (not concave) triturating surfaces of the dentaries. Based on these differences, "*Dollochelys*" *rogovichi* was considered a distinct pan-cheloniid taxon with unclear generic attribution. However, the examination of more detailed images of the dentary of *Eochelone brabantica* holotype (photo from P. Holroyd) showed the presence of a rudimentary lingual ridge (a ledge on the alveolar surface). A similar scarcely discernible ledge is observed in *Eochelone* sp. from the Ikovo locality (ZIN PH 51/145).

"*Dollochelys*" *casieri* was described by Zangerl (1971) based on a single specimen IRSNB 1631 having a short mandibular symphysis with a dorsomedially faced triturating surface. This specimen was reassigned to *Catapleura repanda* (Cope, 1868) by Hirayama (2006). Ullmann and Carr (2021) revealed identity of *Catapleura repanda* with *Euclastes wielandi*, and reassigned IRSNB 1631 to the latter species. Since the short mandibular symphysis with a dorsomedially faced triturating surface of IRSNB 1631 bears no resemblance to that of *Euclastes wielandi* (Zangerl 1971: pl. IIa), we use for it the primary determination of "*Dollochelys*" *casieri* adjusted by the fact that the genus *Dollochelys* Zangerl, 1971 is invalid according to Hirayama (2006).

Lutetian–Priabonian

28. Tschelyuskinets, Lutugino District, Luhansk People's Republic, Russia.

Geographical coordinates. 48°26'N, 39°11'E.

Horizon and age. Complex layer with clay, sand, gravel and phosphorites, upper Lutetian–Priabonian (Nesterov and Zvonok 2020).

Material and references. Two cranial and ten carapacial bones of Pan-Cheloniidae indet. (as Cheloniidae indet.; Nesterov and Zvonok 2020: 155); and epithecal plates of Dermochelyidae indet. (Nesterov and Zvonok 2020: 155). See Systematics section for description.

Collector. L.V. Nesterov, 2018–2020; E.A. Zvonok, 2020.

Bartonian

29. Ak-Kaya 1, Belogorsk District, Crimea, Russia.

Geographical coordinates. 45°06'N, 34°38'E.

Horizon and age. Calcareous glauconitic phosphate beds, CP14b (upper NP17), Bartonian (Zvonok and Danilov 2019).

Material and references. The previously described material: 227 bones of the pan-cheloniid *Argillochelys* sp. (Zvonok and Danilov 2019: 65, fig. 2; Zvonok et al. 2013: 199; as *Argillochelys* sp. indet. 3; Danilov et al. 2017: 181; as Cheloniidae indet.; Zvonok 2011: 72; Zvonok et al. 2013: 199; as Cheloniidae gen. indet. 6; Danilov et al. 2017: 188); two fragments of the same cervical 8, and 172 epithecal plates of the dermochelyid *Cosmochelys* sp. (Zvonok and Danilov 2019: 68, fig. 4j–s; as Dermochelyidae indet.; Zvonok et al. 2013: 200, fig. 1; as Dermochelyidae gen. indet. 2; Danilov et al. 2017: 191); two bones of Pan-Trionychidae indet. (as Trionychidae indet.; Zvonok and Danilov 2013: 199; Zvonok and Danilov 2019: 70, fig. 4v–x; as Trionychoidea indet.; Zvonok 2011: 72). The new material includes six cranial and nine limb bones of *Argillochelys* sp., an epithecal plate of *Cosmochelys* sp. and two fragments of caudal vertebrae of Testudines indet. Femur ZIN PH 61/153 of *Argillochelys* sp., described by Zvonok and Danilov (2019), is additionally restored and redescribed. See Systematics section for description.

Collectors. N.I. Udovichenko, 1988, 1993, 2003; E.A. Zvonok, 2010–2012.

30. Bakhchisarai 2, Bakhchisarai District, Crimea, Russia.

Geographical coordinates. 44°46'N, 33°50'E.

Horizon and age. Marls, CP14b (upper NP17), Bartonian (Zvonok and Danilov 2019).

Material and references. The previously described material includes cervical 8, peripheral 4(?), two fragments of peripherals, and the epiplastron of Pan-Cheloniidae indet. (as Cheloniidae indet.; Zvonok and Danilov 2019: 68, fig. 4a–f); three epithecal plates of Dermochelyidae indet. (Zvonok and Danilov 2019: 70, fig. 4t); the middle part of the left branch of the dentary of Pan-Testudines indet. (as Testudines indet.; Zvonok and Danilov 2019: 70, fig. 4aa, bb). A new material includes the proximal part of the left femur of Pan-Cheloniidae indet. See Systematics section for description.

Collector. N.I. Udovichenko, 2002; A.F. Bannikov, 2009.

Remarks. The correct numbers of specimens ZIN PH 4-6/151 of Dermochelyidae indet. indicated from the Bakhchisarai 2 locality (as Bakhchisarai; Zvonok and Danilov 2019: 70, fig. 4t) are ZIN PH 6/151, 8/151, and 9/151, respectively.

31. Gorniy Luch, Apsheronsk District, Krasnodar Territory, Russia.

Geographical coordinates. 44°19'N, 39°48'E.

Horizon and age. The upper part of the Kuma Horizon, upper Bartonian (Zvonok et al. 2019).

Material and references. A partially disarticulated skeleton of the pan-cheloniid *Eochelone* sp. (Zvonok et al. 2019: 531, figs 2–4, 5a, c, f, h–j, 6, 7; as Cheloniidae indet.; Zvonok and Danilov 2018: 95).

Collector. A.F. Bannikov, 2001.

32. Nagornoe, Svetlovodsk District, Kirovograd Province, Ukraine.

Geographical coordinates. 49°05'N, 33°08'E.

Horizon and age. Yellowish-green aleuritic sand or sandy aleurite, (?) upper part of the Kiev Formation, Bartonian (Goldin et al. 2014).

Material and references. A frontal of Pan-Cheloniidae indet. See Systematics section for description.

Collector. N.I. Udovichenko, 2010.

33. Pirogovo, Kiev City, Ukraine.

Geographical coordinates. 50°13'N, 30°38'E.

Horizon and age. Phosphate beds, the upper part of the Kiev Formation, Bartonian (Averianov 2002).

Material and references. Bones of Pan-Cheloniidae indet. (as "bones of small-sized sea turtles"; Nessov 1987: 76; Chkhikvadze 1990: 5; as "shell fragment of sea(?) turtle"; Udovichenko and Nessov 1987: 171; as Chelonioidea indet.; Averianov 2002: 139, 144; Danilov et al. 2017: 193).

Collector. N.I. Udovichenko, 1971–1972.

Remarks. This material most probably belongs to Pan-Cheloniidae, because another group of Cenozoic Chelonioidea, Dermochelyidae, has a very distinct morphology.

34. Prolom (= Belogorsk), Belogorsk District, Crimea, Russia.

Geographical coordinates. 45°05'N, 34°39'E.

Horizon and age. Calcareous glauconitic phosphate beds; Bartonian.

Material and references. Four shell fragments of Pan-Cheloniidae indet. (as "bones of [sea] turtles"; Nessov 1987: 77; Chkhikvadze 1990: 5; as "remains of <...> sea turtles"; Nessov 1992: 38; as Cheloniidae indet.; Averianov 2002: 145; Danilov et al. 2017: 190; Zvonok and Danilov 2019: 68, fig. 4g–i); two epithecal plates of Dermochelyidae indet. (Zvonok and Danilov 2019: 70, fig. 4u); two fragments of unidentified plates of Pan-Trionychidae indet. (as Trionychidae indet.; Zvonok and Danilov 2019: 70, fig. 4y). In addition to the previously described material (Zvonok and Danilov 2019), there are four cranial and twelve carapacial bones of Pan-Cheloniidae indet. from this locality in collection ZIN PH 18. See Systematics section for description.

Collector. N.I. Udovichenko, late 1980s – early 1990s.

Remarks. Initially, the age of the bone-bearing beds of the Prolom locality was indicated as the Bartonian – ?Priabonian (see Averianov 2002). Later, Bratishko and Udovichenko (2007) determined the age of this locality as the Lutetian (in Zvonok and Danilov 2019 erroneously referred to as the Bartonian). We believe that the bed of the Prolom locality, bearing tetrapod remains, has the same Bartonian age as the geographically close Ak-Kaya 1 locality. Both assemblages have almost no differences in the composition of fishes (Bratishko and Udovichenko 2007) and no differences in dominant tetrapods (palaeophiids, pan-cheloniids and dermochelyids; Zvonok and Snetkov 2012; Zvonok and Danilov 2019).

Priabonian

35. Otradnoe, Mikhaylovka District, Volgograd Province, Russia.

Geographical coordinates. 50°01'N, 43°09'E.

Horizon and age. Phosphate horizon, Priabonian (according to A.A. Yarkov).

Material and references. A shell plate fragment of Pan-Cheloniidae indet. with a sculptured external surface (as Cheloniidae indet.; Zvonok and Danilov 2018: 95). See Systematics section for description.

Collector. A.A. Yarkov.

Rupelian

36. Zarechnyi (= Sassau), Svetlogorsk (= Rauschen), Kaliningrad Province, Russia.

Geographical coordinates. 54°56'N, 20°11'E.

Horizon and age. Amber quarry (Bernsteingrube), Rupelian (see Danilov et al. 2017).

Material and references. ?IKBFU n/n, shell fragments (epithecal plates) of Dermochelyidae indet. (as *Psephophorus*; Koken 1892: 43; as *Psephophorus* sp.; Dames 1894: 199; as Dermochelyidae gen. indet. 3; Danilov et al. 2017: 191); ?IKBFU n/n, shell fragments of Pan-Trionychidae (as *Pseudotrionyx* Dollo 1886; Koken 1892: 43; as *Trionyx* sp.; Dames 1894: 199; as Trionychidae subfam indet. 28; Danilov et al. 2017; as pan-trionychid; Georgalis and Joyce 2017: 123).

Collector. Dr. Sommerfeld, 1872 (see Dames 1894).

Remarks. The material from Sassau was only briefly described and never figured (Koken 1892; Dames 1894). For this reason, the pan-trionychid material from Sassau is considered to be of dubious status (Georgalis and Joyce 2017).

Rupelian–Chattian

37. Abadzekhskaya, Maykop District, Krasnodar Territory, Russia.

Geographical coordinates. 44°23'N, 40°13'E.

Horizon and age. Gray clays of the Khadum Formation, Rupelian – lower Chattian (emended after Averianov 2002).

Material and references. Remains of Pan-Cheloniidae indet. (as "sea turtle"; Chkhikvadze 1983: 30; Chkhikvadze 1999: 259; as possibly "Eochely[i]nae – relatively small sea turtles of *Puppigerus* type"; Chkhikvadze 1987: 85; as "remains <...> of a sea turtle"; Chkhikvadze 1990: 5; Chkhikvadze 1999: 259; Nessov 1992: 39; as Cheloniidae indet.; Averianov 2002: 139, 145; Danilov et al. 2017: 190).

Collector. A.A. Svichenskaya, 1972.

Remarks. Initially, the age of this locality was indicated as the Eocene? or Early Oligocene (Averianov 2002). Popov et al. (2019) referred the beds of the Khadum Formation to the Rupelian – lower Chattian (upper NP 21 – NP 24 or 25).

Paleogene or Neogene

38. Belomechetskaya, Kochubeev District, Stavropol Territory, Russia.

Geographical coordinates. 44°29'N, 41°56'E (approximately).

Horizon and age. Deposits with marine mollusks *Pectunculus*(?), below the level with the Middle Miocene (MN 6) *Platybelodon* mammal fauna; Oligocene? or Miocene (Averianov 2002).

Material and references. A shell plate fragment of Pan-Testudines indet. (as "fragment of costal or plastron of Cheloniidae?"; Alekperov 1978: 184, fig. 52b, g; as Chelonioidea indet.; Averianov 2002: 139, 146; Danilov et al. 2017: 193). See Systematics section for description.

Collector. N.K. Vereschagin, 1950.

39. Otradnaya, Otradnaya District, Krasnodar Territory, Russia.

Geographical coordinates. 44°21'N, 41°28'E (approximately).

Horizon and age. Chalk, ?Neogene (Aslanova et al. 1979) or ?Eocene (Averianov 2002).

Material and references. A partial shell of a juvenile individual of Pan-Cheloniidae indet. on a piece of chalk (as "?*Chelonia* sp."; Chkhikvadze 1977: 226; as "nearly complete carapace of Cheloniidae gen. et sp. indet."; Chkhikvadze 1983: 39; Chkhikvadze 1990: 5); as possibly "Eochely[i]nae – relatively small sea turtles of *Puppigerus* type"; Chkhikvadze 1987: 85; as Cheloniidae indet.; Averianov 2002: 139, 145; Danilov et al. 2017: 190). See Systematics section for description.

Collector. Unknown.