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A fossil leatherback sea turtle from the Bartonian of Kazakhstan

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ABSTRACT

The article describes fossil material of a leatherback sea turtle Dermochelyidae indet. from the Bayurbas and Sandy localities of the Shorym Formation (Bartonian, Middle Eocene) of the Mangyshlak Peninsula, Kazakhstan. The material is represented by cranial remains of one individual (Bayurbas) and an epithecal plate of the shell (Sandy). Dermochelyidae indet. from the Shorym Formation differ from all known dermochelyids in the morphology of the skull roof and the dentary. Based on the morphology of the epithecal plate, it is most similar to the representatives of the genera *Cosmochelys* Andrews, 1919 and *Egyptemys* Wood et al., 1996, whose skulls are unknown. The described cranial remains partially fill a large temporal gap (about 13.9 Ma) in our knowledge of the skull morphology of dermochelyids, between the oldest Ypresian species and the Rupelian *Cardiochelys rupeliensis* (Van Beneden, 1883). In addition, these are the first cranial remains of dermochelyids described from northern Eurasia (territory of the former Soviet Union).

Key words: Bartonian, Dermochelyidae, Kazakhstan, sea turtles, Shorym Formation

Ископаемая кожистая морская черепаха из бартона Казахстана

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РЕЗЮМЕ

В статье описывается ископаемый материал по кожистой морской черепахе Dermochelyidae indet. из местонахождений Баюрбас и Санды шорымской свиты (бартон, средний эоцен) полуострова Мангышлак, Казахстан. Материал представлен черепными остатками одной особи (Баюрбас) и эпитекальной пластинкой панциря (Санды). Dermochelyidae indet. из шорымской свиты отличаются от всех известных дермохелиид морфологией крыши черепа и зубной кости. По морфологии эпитекальной пластинки они наиболее сходны с представителями родов *Cosmochelys* Andrews, 1919 и *Egyptemys* Wood et al., 1996, череп которых неизвестен. Описанные черепные остатки частично заполняют большой временной пробел (около 13.9 млн лет) в наших знаниях о морфологии черепа дермохелиид между древнейшими

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ипрскими видами и рюпельскими *Cardiochelys rupeliensis* (Van Beneden, 1883). Кроме того, это – первые черепные остатки дермохелиид, описанные из Северной Евразии (территория бывшего Советского Союза).

Ключевые слова: бартон, Dermochelyidae, Казахстан, морские черепахи, шорымская свита

INTRODUCTION

Paleogene dermochelyids of Russia have been reported from the following localities: Tschelyuskinets (Upper Lutetian – Priabonian; Luhansk People's Republic), Ak-Kaya 1, Bakhchisarai 2 and Prolom (all Bartonian; Crimea), and Zarechnyi (= Sassau; Rupelian; Kaliningrad Province; for review, see Zvonok and Danilov 2023). The material of these dermochelyids was represented by cervical vertebra 8 (Ak-Kaya 1) and epithecal plates (other localities).

In 2000–2001, one of us (A.V.P.) collected remains of fossil tetrapods in the rocks of the middle–upper Bartonian Shorym Formation of the Mangyshlak Peninsula, Kazakhstan (for details, see Zvonok et al. 2024). Among these remains, there is abundant material of sea turtles (superfamily Chelonioidea Oppel, 1811; clade Pan-Chelonioidea Joyce et al., 2004), including cranial remains of one individual from the Bayurbas locality and an epithecal plate from the Sandy locality, referred to a leatherback sea turtle Dermochelyidae indet. (Fig. 1) and described in this article. Other turtles so far described or reported from the Shorym Formation are represented by the following pan-cheloniids: *Protrachyaspis shorymensis* Zvonok et al., 2024; a specimen referred to "*Allopleuron*" *qazaqstanense* Karl et al., 2011; *Argillochelys* sp., which may belong to the same taxon as *"A." qazaqstanense*; and Cheloniidae indet. similar to *Euclastes/Pacifichelys* (Zvonok et al. 2011, 2015; Zvonok et al. 2024). In addition to turtles, tetrapods of the Shorym Formation are represented by sea snakes *Palaeophis nessovi* Averianov, 1997 and *Palaeophis* sp., undescribed crocodiles and cetaceans, and several taxa of birds, of which only the ?suliform *Mangystania humilicristata* Zvonok et al., 2016 has been described (Averianov 1997; Panteleev 2002; Snetkov 2011; Zvonok et al. 2016).

Institutional abbreviations. FSAC DAK, Ad-Dakhla collection from Faculty of Sciences Aïn Chock, Casablanca, Morocco; IRSNB, Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium; LACM, Los Angeles County Museum, Los Angeles, USA; MLP, Museo de La Plata, La Plata, Argentina; NHMUK, Natural History Museum, London, UK; ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

MATERIAL AND METHODS

Material and data used for comparison. For comparison with the skull bones described below, we used data on cranial material of the following dermochelyids: *Cardiochelys rupeliensis* (Van Beneden, 1883) from the Rupelian Boom Formation of several localities, Belgium (Smith 1989; Köhler 1996); extant *Dermochelys coriacea* (Vandelli, 1761) (Evers and Benson 2019); *Eosphargis breineri* Nielsen, 1959 from the Ypresian Mo Clay Formation of the Knude Klint locality, Denmark (Nielsen 1959); *Eosphargis gigas* (Owen, 1880): holotype NHMUK R31 from the Ypresian London Clay Formation of the Isle of Sheppey locality, UK, and referred specimen IRSNB 1736 from the Ypresian of the Quenast locality, Belgium (Owen 1880; Nielsen 1959; Smith 1989; Köhler 1996); *Psephophorus* sp. LACM 1348/4094 from the Serravalian Monterey Formation of the Point Fermin locality, USA (Smith 1989; Köhler 1996); *Psephophorus*(?) *oregonensis* Packard, 1940 from the Burdigalian Astoria Formation of the Spencer Creek locality, USA (Smith 1989; Köhler 1996); *Pseudosphargis ingens* (Koenen, 1891) from the Chattian Doberg Formation of the Doberg locality, Germany (Karl 2014); "*Thalassochelys*" *testei* Bergounioux, 1956 from the Ypresian Gafsa Phosphates Formation of Metlaoui, Tunisia (Bergounioux 1956; Moody and Buffetaut 1981; Köhler 1996).

For comparison with the epithecal plate described below, we used data on epithecal plates of the following dermochelyids: *Arabemys crassiscutata* Tong et al., 1999 from the Thanetian or Ypresian Aruma Formation of the Linah locality, Saudi Arabia (Tong et al. 1999); *Cardiochelys rupeliensis* from the Rupelian Boom Formation of several localities, Belgium (Köhler 1996; Wood et al. 1996); *Cosmochelys dolloi*

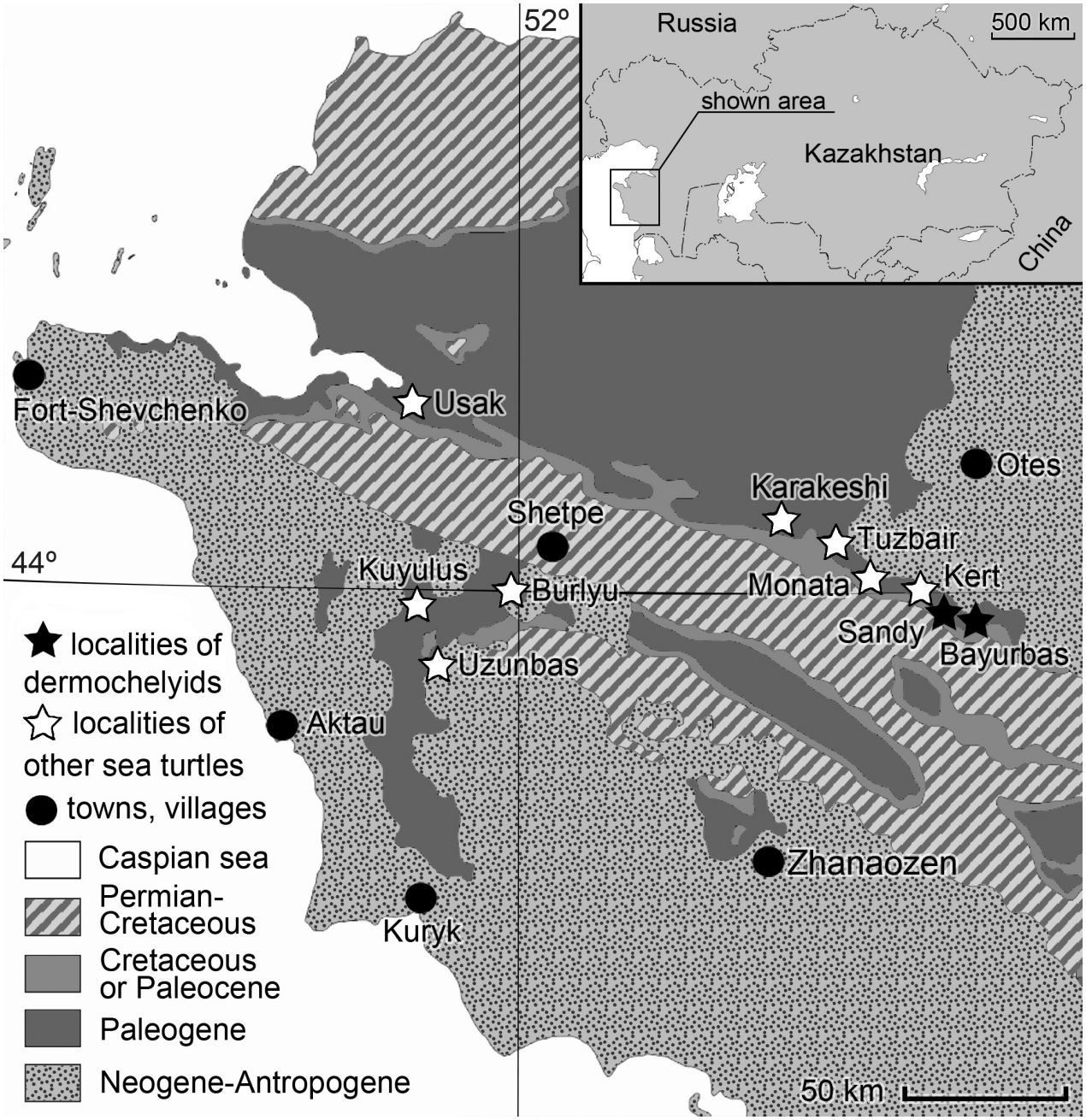

Fig. 1. The localities of fossil sea turtles of the Shorym Formation on the geological map of the Mangyshlak Peninsula. The map is redrawn from Zvonok et al. (2024).

Andrews, 1919 from the Bartonian Ameki Formation of the Port Harcourt locality, Nigeria (Andrews 1919; Tong et al. 1999); *Cosmochelys* sp. from the Bartonian of the Ak-Kaya 1 locality (Zvonok et al. 2013; Zvonok and Danilov 2019, 2023); extant *Dermochelys coriacea* (Delfino et al. 2013); *Egyptemys eocaenus* (Andrews, 1901) from the Priabonian Qasr el-Sagha Formation of the Fayum Depression, Egypt (Wood et al. 1996); cf. *Egyptemys* sp. from the Priabonian Samlat Formation of the Ad-Dakhla locality, Morocco (Zouhri et al. 2017); *Natemys peruvianus* Wood et al., 1996 from the Chattian Pisco Formation of the

Rio Ica locality, Peru (Wood et al. 1996); "*Psephophorus*" *terrypratchetti* Köhler, 1995 from the upper Lutetian–Bartonian Waihao Greensand Formation of the Waihao Downs locality, New Zealand (Köhler 1996); *Psephophorus* sp. from the upper Ypresian–upper Lutetian Bracklesham Group of an unknown locality, UK (Köhler 1996); *Pseudosphargis ingens* from the Chattian Doberg Formation of the Doberg locality, Germany (Karl 2014); *Psephophorus calvertensis* Palmer, 1909 from the Burdigalian–Langhian Calvert Formation of the Chesapeake Bay locality, USA (Köhler 1996); *Psephophorus polygonus* Meyer, 1847 (Delfino et al. 2013); dermochelyids referred to *Psephophorus terrypratchetti* and cf. *Psephophorus* sp. from the Bartonian La Meseta Formation of several localities, Antarctica (de la Fuente et al. 1995; Albright et al. 2003); dermochelyids referred to cf. *Egyptemys* sp., *Natemys* spp., and cf. *Psephophorus* sp. from the Oligocene Ashley and Chandler Bridge formations of several localities, USA (Fallon and Boessenecker 2020); Dermochelyidae indet. from the Lutetian–Priabonian of the Tschelyuskinets locality, Russia, Bartonian of the Bakhchisarai 2 and Prolom localities, Russia, Priabonian Yazoo Formation of Alabama, USA, and the Priabonian Clinchfield Formation of the Hardie Mine locality, USA (Müller 1847; Wood et al. 1996; Parmley et al. 2006; Zvonok and Danilov 2023).

Anatomical terminology for skull bones used in this paper is from Gaffney (1979).

SYSTEMATICS

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

Chelonioidea Baur, 1893 (Joyce et al. 2021)

Dermochelyidae Lydekker, 1889

Dermochelyidae indet.

(Figs 2–3)

Material. ZIN PH 57/177, a part of the skull represented by isolated left frontal, postorbital, and maxilla, a right quadrate, a fragment of the right dentary of one individual, and an indeterminate skull bone fragment (Bayurbas); ZIN PH 58/177, an isolated epithecal plate (Sandy).

Locality, horizon, and age. Bayurbas and Sandy localities, Mangyshlak Peninsula, Kazakhstan; Shorym Formation, Bartonian, Eocene, Paleogene.

Description and comparisons. All the skull bones of ZIN PH 57/177 match each other in size, color, and more or less developed surface sculpturing on the skull roof in the form of a network of grooves, which suggests that they belong to the same individual.

The left frontal (Fig. 2A–E) is completely preserved. It is pentagonal in shape, and wedges deeply between the prefrontals, as in other dermochelyids. The crista cranii on the ventral surface of the frontal is very shallow, and the sulcus olfactorius is a low trough. The frontal has sutural surfaces for contact with the second frontal medially, the prefrontal anterolaterally, the postorbital laterally, and the parietal posteriorly. It did not contribute to the orbit, like all other dermochelyids, except "*Thalassochelys*" *testei*. There are no cranial scute sulci on the frontal.

The left postorbital (Fig. 2F–J) has its anterodorsal part broken off. The bone is elongated, with almost straight and parallel dorsal and ventral borders contacting the parietal and jugal, respectively; the anteroventral border contributes to the orbit, and the posterior and posteroventral borders contacts the squamosal. The ventral border is jagged in the anterior part, where there is a thickening. In *Dermochelys coriacea*, in contrast to ZIN PH 57/177, the ventral border of the postorbital bone is concave in lateral view. In *Pseudosphargis ingens*, in contrast to ZIN PH 57/177, the free posterior border of the postorbital bone is present, as figured by Karl (2014: figs 88b, 91). There are no cranial scute sulci on the postorbital.

The left maxilla (Fig. 2K–U) is incomplete, missing the posterior part of the palatine process and a small posteriormost fragment of the alveolar process. The maxilla contacts the premaxilla anteriorly, the palatine medially, and the jugal posteriorly, and forms the lateral margin of the external nasal opening, the posteroventrolateral part of the fossa nasalis, as well as the anterior and ventral margins of the orbit and the lateral part of the floor of the fossa orbitalis. The labial ridge is vertical and high, reaching its maximum height approximately in the middle part of the bone, and tapering in both anterior and posterior directions. The labial ridge has a notch in its anterior part; in front of this notch, at the suture with the premaxilla, is the posterior part of a cusp that continues onto the premaxilla. This notch is absent in the Miocene *Psephophorus* sp. LACM 1348/4094 and *Psephophorus*(?) *oregonensis*. The labial ridge is

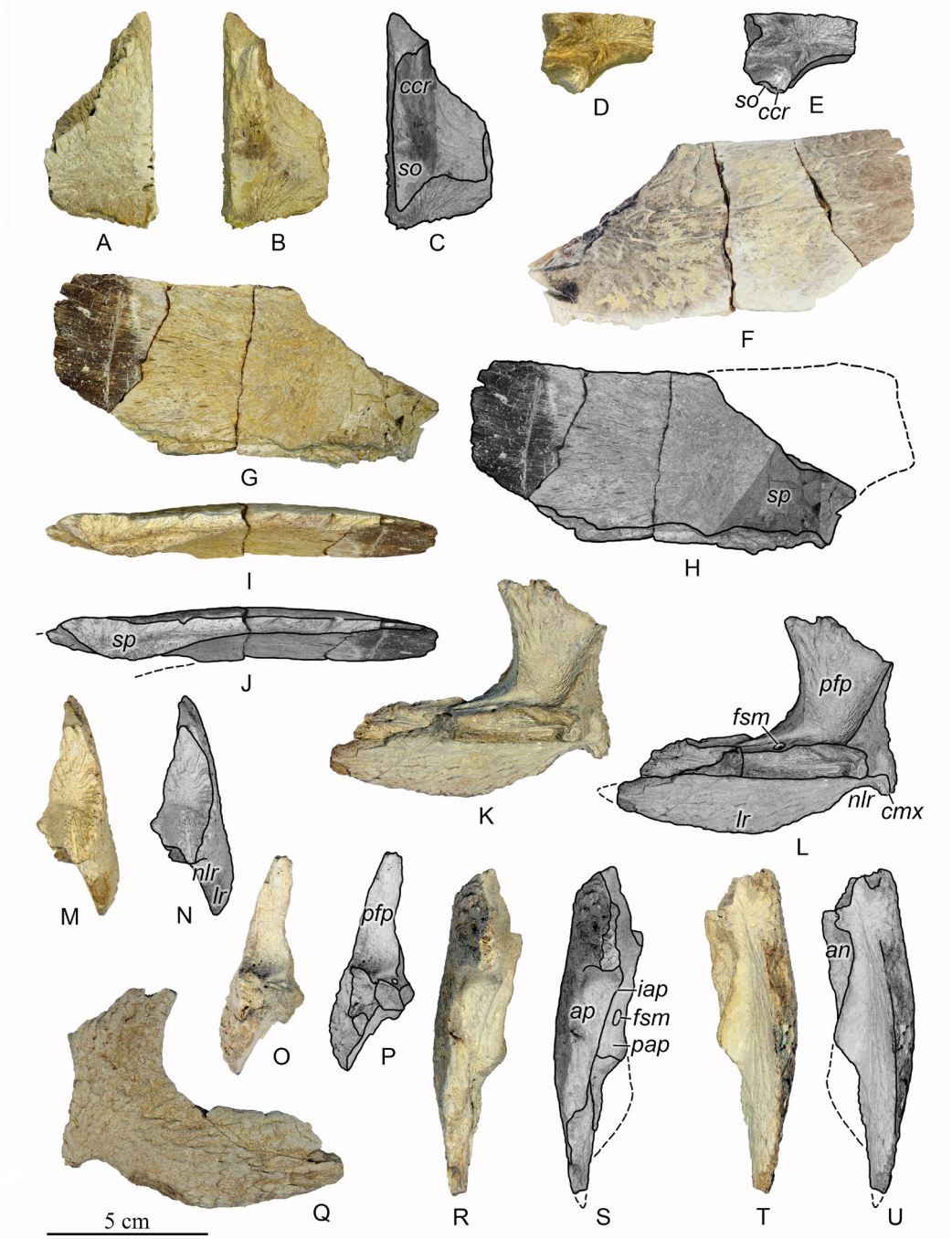

Fig. 2. Skull bones of Dermochelyidae indet. ZIN PH 57/177, Bayurbas locality, Mangyshlak Peninsula, Kazakhstan; Shorym Formation, Bartonian: A–E – left frontal: A – photograph in external view, B, C – photograph (B) and drawing (C) in ventral view, D, E – photograph (D) and drawing (E) in frontal view; F–J – left postorbital: F – external view, G, H – photograph (G) and drawing (H) in internal view, I, J – photograph (I) and drawing (J) in ventral view; K–U – left maxilla: K, L – photograph (K) and drawing (L) in medial view, M, N – photograph (M) and drawing (N) in anterior view, O, P – photograph (O) and drawing (P) in posterior view, Q – photograph in lateral view, R, S – photograph (R) and drawing (S) in dorsal view, T, U – photograph (T) and drawing (U) in ventral view.
Abbreviations: an – arcuate notch on palatine process, ap – alveolar process, ccr – crista cranii, cmx – cusp of the maxilla, fsm – foramen supramaxillare, iap – inflection between alveolar and palatine processes, lr – labial ridge, nlr – notch of labial ridge, pap – palatine process, pfp – prefrontal process, so – sulcus olfactorius, sp – swelling on postorbital.

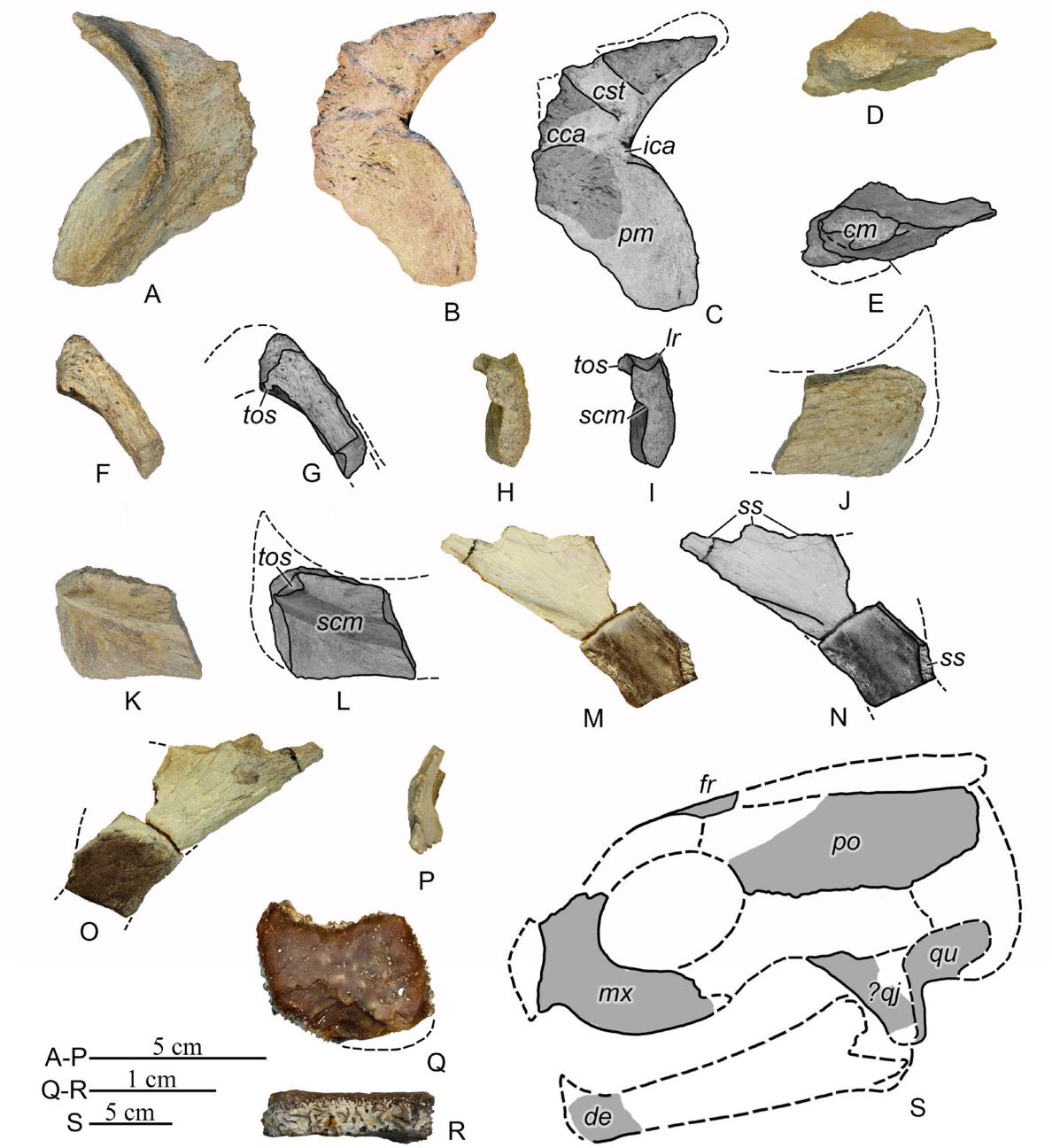

Fig. 3. Skull bones (A-P, S; ZIN PH 57/177), epithecal plate (Q, R; ZIN PH 58/177) and reconstruction of the skull (S) of Dermochelyidae indet., Bayurbas (ZIN PH 57/177) and Sandy (ZIN PH 58/177) localities, Mangyshlak Peninsula, Kazakhstan; Shorym Formation, Bartonian: A–E – right quadrate: A – photograph in anterior view, B, C – photograph (B) and drawing (C) in posterior view, D, E – photograph (D) and drawing (E) in ventral view; F–L – fragment of the right dentary: F, G – photograph (F) and drawing (G) in dorsal view, H, I – photograph (H) and drawing (I) in posterior view, J – photograph in lateral view, K, L – photograph (K) and drawing (L) in posterior view; M–P – indeterminate skull bone fragment: M, N – photograph (M) and drawing (N) in internal view, O – photograph in external view, P – photograph in (?) anterodorsal view; Q, R – epithecal plate: Q – external view, R – side view; S – reconstruction of the skull in left lateral view, based on ZIN PH 57/177; preserved elements are highlighted in gray.
Abbreviations: cca – canalis cavernosus, cm – condylus mandibularis, cst – canalis stapedio-temporalis, de – dentary, fr – frontal, ica – incisura columellae auris, lr – labial ridge, mx – maxilla, pm – processus mandibularis, po – postorbital, qj – quadratojugal, qu – quadrate, scm – sulcus cartilagini meckelii, ss – sutural surface, tos – tubercle overhanging sulcus cartilaginis meckelii.

sharp, except at the edges of the notch, where it becomes blunt. The prefrontal process is high in lateral view, and is not sloped posteromedially as much as in *Eosphargis* spp. The palatine process is narrow; in ventral view in the anteroventral part, it has an extensive arcuate notch for the palatine, which almost reaches the labial ridge and then widens gradually in the posterior direction. In *Cardiochelys rupeliensis*, *Psephophorus* spp., and *Dermochelys coriacea*, the palatine process also almost wedges out in the anterior part, whereas in *Eosphargis* spp., on the contrary, the palatine process is wider in the anterior part. The ventral surface of the palatine process is oriented horizontally and is not ventrally slanted, in contrast to *Eosphargis breineri* and *Eosphargis gigas* IRSNB 1736. The dorsal surface of the palatine process is recessed relative to the alveolar process and is separated from it by a scarp-like bend (the inflection between the alveolar and palatine processes). On the dorsal surface of the palatine process, posteromedial to the base of the prefrontal process, there is the foramen supramaxillare.

The right quadrate (Fig. 3A–E) is incomplete, missing the processus epipterygoideus and possibly some areas where it contacted the squamosal and prootic, and is deformed mostly due to anteroposterior compression. The processus mandibularis is tall and has a small condylus mandibularis. The incisura columellae auris is widely open. On the medial surface (partially displaced posteriorly due to deformation), there are parts of the canalis stapedio-temporalis and canalis cavernosus dorsally and the sutural surface for the pterygoid ventrally. The area of contact with the prootic is situated dorsolaterally to the canalis stapedio-temporalis. Anterodorsolaterally, there is an arcuate strip indicating the area for contact with the quadratojugal. The areas of contact with the prootic ventromedially from the canalis stapedio-temporalis and with the squamosal posterodorsolaterally are poorly discernible due to breakage or deformation. The quadrate also contributes to the formation of the cavum tympani.

The fragment of the right dentary (Fig. 3F–L) represents the anterior part of the ramus with the damaged labial ridge. The triturating surface is narrow and concave between the low labial ridge and medial margin, unlike other dermochelyids. As in *Eosphargis gigas* IRSNB 1736 and *Dermochelys coriacea*, there is a tubercle posterolateral to the posterior edge of the symphysis, overhanging the sulcus cartilaginis meckelii. The ventral edge of the dentary is sharpened.

The indeterminate skull bone fragment (Fig. 3M–P) is narrow, thin and slightly convex externally, with two (longer and shorter) sutural surfaces preserved on opposite sides of the specimen and one free or very tightly sutured border; the remaining borders are broken off. The longer sutural surface of the fragment is sharp and partially overlapping, whereas the shorter one is thick and jagged. This morphology is reminiscent of some areas of the jugal, quadratojugal, squamosal and lower jaw elements of *Dermochelys coriacea*. However, the fragment differs from the squamosal of this species by having a bend between the suture and the free border and by its sutural surfaces not corresponding to the posterior sutures of the postorbital; and from bones of its lower jaw, by not overlapping the shorter sutural surface. On the other hand, the fragment may be the right quadratojugal, although in other dermochelyids the exposure of the quadratojugal on the external surface of the skull is small (Fig. 3S; Smith 1989). It also cannot be ruled out that this fragment is an unusual posterior protrusion of the left jugal, which was separated from the anterior part of the bone by a bend.

The epithecal plate (ZIN PH 58/177; Fig. 3Q, R) has part of its border broken off and the external surface partially damaged. It is 4 mm thick and has a maximum diameter of 16 mm. In external view, the plate has a comma-like shape. The external surface is not swollen in the middle part of the plate, unlike *Arabemys crassiscutata*, and has a sculpture in the form of tubercles, similar to *Arabemys crassiscutata*, *Cosmochelys dolloi*, some specimens of *Cosmochelys* sp. from the Ak-Kaya locality 1, two plates of cf. *Psephophorus* sp. MLP 95-1-10-12/13 from the IAA 1/90 locality, Antarctica, cf. *Egyptemys* sp. FSAC DAK-135 from the Ad-Dakhla locality, Morocco, Dermochelyidae indet. from the Bakhchisarai 2 and Prolom localities, and probably *Egyptemys eocaenus*, judging from the description by Wood et al. (1996). The inner surface of the plate is slightly concave.

DISCUSSION

The skull bones of ZIN PH 57/177 belong to Dermochelyidae based on the following characters: the cranial scute sulci on dermal roofing elements are absent (Hirayama 1998); frontal contribution to orbit is absent, a contact between prefrontal and postorbital

is present (Evers and Benson 2019: ch. 12); crista cranii on ventral surface of frontals very shallow, sulcus olfactorius developed as a low trough (Evers and Benson 2019: ch. 15); the cusps developed on the labial ridge in conjunction of the premaxilla with maxilla are present (Evers and Benson 2019: ch. 54). Among dermochelyids, ZIN PH 57/177 differs from "*Thalassochelys*" *testei* by the absence of the frontal contribution to the orbit, and from *Eosphargis* spp. by a narrower palatine process of the maxilla with a deep notch for the palatine, by a taller prefrontal process of the maxilla in lateral view and a less slanted posteromedially prefrontal process in dorsal and anterior views. In addition, ZIN PH 57/177 differs from *Eosphargis breineri* and *Eosphargis gigas* IRSNB 1736 by the horizontal orientation of the ventral surface of the palatine process of the maxilla. Judging from the description by Smith (1989: 124), *Eosphargis gigas* IRSNB 1736, *Cardiochelys rupeliensis*, and *Dermochelys coriacea* have narrow simple triturating surfaces on the dentary, in contrast to ZIN PH 57/177, which has a concave triturating surface. In *Pseudosphargis ingens*, a free posterior border of the postorbital bone was present, as figured and described by Karl (2014); however, the holotype of this species is now unavailable (Köhler 1996: 113) and these data may be erroneous. *Psephophorus* sp. LACM 1348/4094 and *Psephophorus*(?) *oregonensis* have no notch on the maxilla (Köhler 1996). *Dermochelys coriacea* has a concave ventral margin of the postorbital in lateral view. Unusual is an indeterminate fragment of ZIN PH 57/177, which represents the jugal or quadratojugal and differs from other known dermochelyids.

The epithecal plate ZIN PH 58/177 belongs to Dermochelyidae because a mosaic of small bone ossicles (epithecal plates) is characteristic of Cenozoic dermochelyids, with the exception of *Eosphargis* spp. (Wood et al. 1996; Danilov et al. 2017). The external surface of the epithecal plate ZIN PH 58/177 is not swollen in the middle and therefore cannot belong to *Arabemys crassiscutata*. In addition to the latter species, a tuberculated sculpture on the external surface is also known in *Cosmochelys* spp. and probably in *Egyptemys eocaenus*, as well as in a number of other dermochelyid materials of the Bartonian and Priabonian ages. The sculpture on the external surface of the epithecal plates is also known in *Cardiochelys rupeliensis* and *Psephophorus polygonus*, but it has the appearance of radial ridges (Tong et al. 1999). At the same time, the sculpture of the epithecal mosaic in the geographically and stratigraphically close *Cosmochelys* sp. from the Ak-Kaya 1 locality probably shows ontogenetic variability ranging from weakly rugose in the smallest specimens through well-tuberculated in medium-sized specimens to almost flat in the largest specimens (Zvonok and Danilov 2023). ZIN PH 58/177 is comparable to the medium-sized specimens of *Cosmochelys* sp. from the Ak-Kaya 1 locality and has the same well-tuberculated sculpture of the external surface. Thus, we can only point out the similarity of ZIN PH 58/177 to *Cosmochelys* spp. and *Egyptemys eocaenus*, especially to the medium-sized specimens of *Cosmochelys* sp. from the Ak-Kaya 1 locality, but we cannot confidently attribute it to either genus.

Prior to this work, cranial materials of dermochelyids have not been known in the Lutetian–Priabonian interval, which spans about 13.9 Ma. It can be assumed that the skull fragment ZIN PH 57/177 belongs to the same species as the epithecal plate ZIN PH 58/177, which was found in another nearby location and comes from the same Shorym Formation (Fig. 1). This epithecal plate shows characteristics of *Cosmochelys* spp. and probably also *Egyptemys eocaenus*. Thus, the association of ZIN PH 57/177 and ZIN PH 58/177 is defined as Dermochelyidae indet., likely representing the genus *Cosmochelys* or *Egyptemys*.

CONCLUSIONS

Dermochelyidae indet. from the Shorym Formation of Mangyshlak includes the first cranial remains of dermochelyids from Northern Eurasia (the territory of the former Soviet Union). In addition, the materials from the Bayurbas and Sandy localities are the first described dermochelyids in the Lutetian–Priabonian interval from which skull bones are known. These remains clearly differ from the known Ypresian dermochelyids and, based on the available materials, show fewer differences from the stratigraphically subsequent Rupelian *Cardiochelys rupeliensis*. At the same time, the new material differs from all known dermochelyids in the presence of a concave triturating surface of the dentary and the morphology of the ventral part of the skull roof. The only available epithecal plate of Dermochelyidae indet. from the Shorym Formation corresponds morphologically to *Cosmochelys* and possibly also to *Egyptemys* suggesting that the described cranial material may be associated with one of these genera.

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