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A new Trachyaspis-like pan-cheloniid turtle from the Bartonian of Kazakhstan

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ABSTRACT

The article describes a fossil pan-cheloniid Protrachyaspis shorymensis gen. et sp. nov. from the Karakeshi, Kert, Kuyulus, and Monata localities of the Shorym Formation (Bartonian, middle Eocene), as well as unknown localities of the Mangyshlak Peninsula, Kazakhstan. In addition, the shell bones of small pan-cheloniids from the Kuyulus and Tuzbair localities of the Shorym Formation with some traits of *P. shorymensis* are described, which probably represent remains of juvenile specimens of this species. The new taxon is characterized by a number of features rarely found in pan-cheloniids, including serrated dentaries, distally displaced lateral process of the humerus, and deeply sculptured external carapace surface. These features indicate a likely herbivorous diet and pelagic lifestyle of the new pan-cheloniid. According to the results of the cladistic analysis, P. shorymensis is sister to the Neogene species Trachyaspis lardyi Meyer, 1843, from which it differs in the absence of ridges on the carapace in adult individuals, the configuration of the scutes on the parietal bone, and the structure of the plastron. The stratigraphic gap between the appearance of *P. shorymensis* and its sister *T. lardyi* suggests a long ghost lineage of members of this clade throughout the Bartonian – Aquitanian (ca. 20.7 million years) preceding the appearance of T. lardyi. In most trees, the P. shorymensis + T. lardyi clade is located within the Chelonini clade, which, taking into account the middle Eocene age of P. shorymensis, indicates the early divergence of crown cheloniids, previously established based on molecular data. The new taxon is similar to the fragmentary remains of pan-cheloniids with a sculptured external surface of the shell, previously described from four localities of the upper part of the Buchak and lower part of Kiev formations in the south of European Russia and Ukraine, which makes it possible to determine these materials as cf. Protrachyaspis sp., and probably extends the appearance of the P. shorymensis + T. lardyi clade back to the middle Lutetian.

Key words: Bartonian, Cheloniidae, Kazakhstan, *Protrachyaspis shorymensis*, sea turtles, Shorym Formation, *Trachyaspis lardyi*

Новая Trachyaspis-подобная пан-хелониидная черепаха из бартона Казахстана

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РЕЗЮМЕ

В статье описан ископаемый пан-хелониид Protrachyaspis shorymensis gen. et sp. nov. из местонахождений Каракеши, Керт, Куюлус и Моната шорымской свиты (бартон, средний эоцен), а также неизвестных местонахождений п-ова Мангышлак, Казахстан. Помимо этого описаны кости панциря мелких пан-хелониид из местонахождений Куюлус и Тузбаир шорымской свиты с некоторыми признаками P. shorymensis, которые, вероятно, представляют собой остатки ювенильных особей этого вида. Новый таксон характеризуется рядом редко встречающихся у пан-хелониид черт, включая зазубренные зубные кости, дистально смещенный латеральный отросток плечевой кости и глубоко скульптированную наружную поверхность карапакса. Эти черты указывают на вероятную растительноядную диету и пелагический образ жизни нового пан-хелониида. По результатам кладистического анализа P. shorymensis является сестринским по отношению к неогеновому Trachyaspis lardyi Meyer, 1843, от которого отличается отсутствием килей карапакса у взрослых особей, конфигурацией щитков на теменной кости и строением пластрона. Стратиграфический разрыв между временем появления P. shorymensis и сестринского ему T. lardui предполагает продолжительную призрачную линию представителей этой клады на протяжении бартона – аквитана (около 20.7 млн лет), предшествующую появлению *T. lardyi*. На большей части деревьев клада *P. shorymensis* + *T. lardyi* находится внутри клады Chelonini, что с учетом среднеэоценового возраста *P. shorymensis* свидетельствует в пользу ранней дивергенции кроновых хелониид, установленной ранее по молекулярным данным. С новым таксоном сходны фрагментарные остатки пан-хелониид со скульптированной наружной поверхностью панциря, ранее описанные из четырех местонахождений верхней части бучакской и нижней части киевской свиты юга Европейской России и Украины, что позволяет определить эти материалы как cf. Protrachyaspis sp. и, вероятно, удревняет время появления клады *P. shorymensis* + *T. lardyi* до среднего лютета.

Ключевые слова: бартонский ярус, Cheloniidae, Казахстан, *Protrachyaspis shorymensis*, морские черепахи, шорымская свита, *Trachyaspis lardyi*

INTRODUCTION

Marine sedimentary rocks of the Paleogene and Neogene are exposed over large areas of the desertified land surface of the Mangyshlak Peninsula (Mangystau Province, Kazakhstan). Numerous remains of fossil turtles were collected in the Paleogene deposits of the Shorym, Adaev and Kuyulus formations and probably also in the Miocene section of this region (Fig. 1). These remains were collected from the surface of outcrops (Fig. 2). All of them, except those too fragmentary to identify, are defined as sea turtles (superfamily Chelonioidea Oppel, 1811; clade Pan-Chelonioidea Joyce et al., 2004; see Danilov et al. 2017; Joyce et al. 2021).

The vast majority of these materials (more than 100 remains of pan-cheloniids of three species and two remains of dermochelyids) come from ten localities (Bayurbas, Burlyu, Karakeshi, Kert, Kuyulus, Monata, Sandy, Tuzbair, Uzunbas, and Usak) of the Shorym Formation, dated as the middle-upper Bartonian (*Globigerina turkmenica* Zone, nanoplankton of Zone NP 17 was identified in the upper part of the formation; Zhelezko 1995). Turtles were collected in localities of the Shorym Formation by driver Telebay (family name unknown) in 1980 (Uzunbas locality, "Fish Formation", which corresponds to the Shorym Formation, see below), A.V. Panteleev in 2000-2001 (all localities of the Shorym Formation), N.I. Udovichenko in 2001, 2005 and 2013 (Kuyulus and Usak localities), V. Eliseev (collection year and locality unknown), A.V. Bratishko in 2013 (Kuvulus locality), and A. Nasyrov in 2015 (unknown locality). The unknown localities probably belong to the Shorym Formation judging by the type of rock, preservation, and turtle systematics. 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 (Pelagornithidae, Sulidae, Presbyornithidae, Anatidae), of which only the ?suliform Mangystania humilicristata Zvonok et al., 2016 has been described (Averianov 1997; Panteleev 2002, 2008; Snetkov 2011; Zvonok et al. 2016).

From the locality of the 12th Raz'ezd (12th Crossing) of the Adaev Formation, dated as the Priabonian (NP 18 – NP 21; Zhelezko and Kozlov 1999), come part of the skeleton and a separate bone of a cheloniid, collected by A.V. Panteleev in 2000.

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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 Geological map of Central Asia and adjacent areas (2008).

Other tetrapods of this formation are represented by sea snakes *Palaeophis nessovi* (Averianov 1997; Snetkov 2011).

From the Ungoza locality of the Kuyulus Formation, dated as the Rupelian (Zhelezko and Kozlov 1999), two fragments of cheloniid bones were collected by A.V. Panteleev in 2000–2001. Other tetrapods of this formation are represented by two undescribed taxa of birds (Panteleev 2002). According to the label, part of the cheloniid skeleton found by L.S. Glikman in 1962 comes from the Miocene scree on the surface of the Oligocene Burlyu locality.



Fig. 2. Remains of the holotype of *Protrachyaspis shorymensis* before the collection, as an example of the location of sea turtle remains on the weathering surface of the Shorym Formation (photograph by A.V. Panteleev, 2000).

Some preliminary results of the study of fossil turtles of the Mangyshlak Peninsula were presented earlier in a short communication (Zvonok et al. 2011), where three sea turtles (Cheloniidae s. l.) - Argillochelys sp., Cheloniidae indet. similar to Euclastes/ Pacifichelys, and Cheloniidae indet. represented by a humerus of the "advanced" type, and Geoemydidae indet. were reported from the Shorym Formation; Argillochelus sp. from the Adaev Formation; and Testudines indet. from the Kuyulus Formation. The mentioned Cheloniidae indet. represented by the humerus of the "advanced" type belongs to the new taxon described herein. Material of Geoemydidae indet. actually belongs to sea turtles. A sea turtle skeleton from the Lutetian of an unknown locality in Kazakhstan was described as a new species Allopleuron gazaqstanense by Karl et al., 2012 (Karl et al., 2012), which, according to the personal communication of M. Uhen (2013), comes from the Shorym Formation of the Karagala locality (see Danilov et al. 2017). Zvonok et al. (2015) described additional material of this species referred to as "*Allopleuron*" *qazaq-stanense* from the Shorym Formation of the Kuyulus locality.

Given the large amount of data on fossil sea turtles from Mangyshlak, we divided the publication of the results of our study into separate articles. This article is devoted to the description of *Protrachyaspis shorymensis* gen. et sp. nov., a new taxon of pan-cheloniids with a deeply sculptured carapace and limbs adapted to a pelagic lifestyle. The remains of this species come from the Karakeshi, Kert, Kuyulus and Monata localities of the Shorym Formation, as well as from unknown localities of the Mangyshlak Peninsula, and the remains of juvenile specimens of pan-cheloniids cf. *P. shorymensis* from the Kuyulus and Tuzbair localities of the Shorym Formation.

Institutional abbreviations. MRLHM, Mangystau Regional Local History Museum, Aktau, Kazakhstan; NHMUK, Natural History Museum, London, Great Britain; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; ZIN PH, Paleoherpetological collection in the same institute. The term 'Collection' immediately preceding an institutional catalogue number (e.g., collection ZIN PH 145) indicates that multiple specimens are accessioned under that number.

Geological settings of the Shorym Formation

The rocks of the Shorym Formation were first studied by Andrusov (1915), who named them the "Fish Formation" and concluded about their Bartonian age. The term "Shorym Formation" was first proposed by Liverovskaya (1960) to replace the term "Fish Formation". The Shorym Formation consists mostly of brownish thin-layered marls with intercalations of bluish-gray clayey tuffites and calcareous clays (Zhelezko and Kozlov 1999). Its thickness varies from 20 cm to 34 m with an average of 6-10 m (Liverovskava 1960). The turtle remains are found in different parts of the Shorym Formation. The Shorym Formation contains an assemblage of planktonic foraminifera of the Subbotina turkmenica Zone; nanoplankton of the Discoaster saipanensis Zone was identified in the upper part of the formation (Zhelezko 1995). The Shorym Formation corresponds to the Kuma Formation of the Crimean-Caucasian Region, from where (the Gorniy Luch locality) a skeleton of a juvenile sea turtle *Eochelone* sp. was recently described (Zvonok et al. 2019). The Amankizilit Formation (thickness 4-23 m) underlies the Shorym Formation and consists of the littoral facies of greenish polymictic sands with intercalations of marls, bentonite clays, and conglomerates; light gray marls, calcareous sandstones and chalk-like sandy limestones are common at a distance of the Karatau Ridge. The assemblages of the foraminifera zones identified in the Amankizilit Formation include the Acarinina bullbrooki Zone in the lower part of the formation, the Acarinina rotundimarginata Zone in the main middle part of the formation, and the Hantkenina "alabamensis" Zone in the upper part of the formation (Zhelezko and Kozlov 1999). The rocks of the Adaev Formation (thickness 30-45 m) unconformably overlie the Shorym Formation and consist of chalk-like marls. Nanoplankton zones NP 18, NP 19 and NP 20 are identified in the Adaev Formation; the assemblage of the coccolithophores of the Oligocene Zone NP 21 was identified in the upper part of the formation in the intercalation beds (Zhelezko and Kozlov



Fig. 3. Summary section of the Amankizilit, Shorym, and Adaev formations. Adapted from Liverovskaya (1960: fig. 3) with modifications.

1999). For a summary of the stratigraphic section of the Amankizilit, Shorym and Adaev formations, see Fig. 3. Taken together, these biostratigraphic data allow us to refer the Shorym Formation to the Bartonian stage, probably excluding its lower part (Zhelezko and Kozlov 1999: table 1; for data on the biozones, see Popov et al. 2018; Speijer et al. 2020).

Material and Methods

Materials and data used for comparison. For comparison with *Protrachyaspis shorymensis*, we used literature data on the following pan-cheloniid taxa known from the Eocene deposits:

- "Allopleuron" qazaqstanense Karl et al., 2012 from the Lutetian of an unknown locality in Kazakhstan (Karl et al. 2012; see Introduction) and material attributed to this species from the Bartonian Shorym Formation of the Kuyulus locality (Kazakhstan; Zvonok et al. 2015);

- Argillochelys antiqua (König, 1825) from the Ypresian of the London Clay Formation (England; Owen and Bell 1849; Lydekker 1889), as well as the upper Lutetian-lower Bartonian of the Kiev Formation of the Vyshgorod locality (Ukraine; Zvonok and Danilov 2017);

- *A. athersuchi* Moody, 1980 from the Bartonian of the Barton Clay Formation of Barton Cliff locality (England; Moody 1980);

- *A. cuneiceps* (Owen, 1849) from the Ypresian of the London Clay Formation (England; Owen and Bell 1849; Lydekker 1889);

 Argillochelys sp. from the Bartonian of the Ak-Kaya 1 locality (Russia; Zvonok and Danilov 2019, 2023);

- "Dollochelys" rogovichi Averianov, 2002 from the upper Lutetian – lower Bartonian of the Kiev Formation of the Vyshgorod locality (Ukraine; Zvonok and Danilov 2017);

- *Eochelone brabantica* Dollo, 1903 from the lower Lutetian of the Brussels Formation (Belgium; Casier 1968; de Lapparent de Broin et al. 2018);

- *E. monstigris* Grant-Mackie et al., 2011 from the Priabonian of the Ruatangata Sandstone Formation of the Whangarei locality (New Zealand; Grant-Mackie et al. 2011);

- *E. voltregana* de Lapparent de Broin et al., 2018 from the Priabonian of the Vic-Manlleu marls Formation (Spain; de Lapparent de Broin et al. 2018);

- *Eochelone* sp. from the Bartonian of the Kuma Formation of the Gorniy Luch locality (Russia; Zvonok et al. 2019);

- Osonachelus decorata de Lapparent de Broin et al., 2014 from the Priabonian of the Vic-Manlleu marls Formation (Spain; de Lapparent de Broin et al. 2014);

- Puppigerus camperi (Gray, 1831) from the Ypresian of the London Clay Formation, as well as the Lutetian of the Bracklesham Group (England; Owen and Bell 1849; Lydekker 1889; Moody et al. 2015); Ypresian of the Ouled Abdoun Basin (Morocco; Tong et al. 2012); Ypresian of the Nanjemoy Formation (USA; Weems 1999, 2014); lower Lutetian of the Brussels Formation (Belgium; Moody 1974); lower Lutetian of the Ikovo locality (Russia, formerly Ukraine; Zvonok et al. 2013); Lutetian–Bartonian boundary of the Dzheroi 2 locality (Uzbekistan; Averianov 2005);

Pan-Cheloniidae indet. with sculptured carapace from the Lutetian of the upper part of the Buchak – lower part of the Kiev Formation of the Bakhmutovka, Bulgakovka, and Krasnorechenskoye localities (Russia; Zvonok and Danilov 2023); as well as the Tripolye locality (Ukraine; Zvonok and Danilov 2017);

- Pan-Cheloniidae indet. (= Cheloniinae gen. et sp. indet.) from the upper Ypresian of the lower part of the Alay Formation of the Andarak 2 locality (Kyrgyzstan; Danilov and Averianov 1997).

In addition, comparison was made with the following Oligocene and Neogene pan-cheloniids with deep sculpturing on the external surface of the shell:

- Ashleychelys palmeri Weems et Sanders, 2014 from the upper Rupelian of the upper Ashley Formation and the upper Chattian of the Chandler Bridge Formation (USA; Weems and Sanders 2014);

- Bryochelys waterkeynii Van Beneden, 1871 from the Rupelian Boom Clay Formation (NP 23– 24; Speijer et al. 2020) of the Niel, Rupelmonde, Stendorp and Terhagen localities (Belgium; Smets 1887, 1888);

- *Trachyaspis lardyi* Meyer, 1873 from numerous Neogene localities in Egypt, France, Italy, Switzerland, USA, and Japan (Berry and Lynn 1936; Berry 1937; Weems 1974, 1980; Hasegawa et al. 2005; Villa and Raineri 2015).

Anatomical terminology used in this paper is from Zangerl et al. (1988; for scutes), Krahl et al. (2020; for humerus) and Romer (1956; for other postcranials).

Character-taxon matrix. As a basis for our phylogenetic analysis, the matrix of Evers et al. (2019) was used, which is derived from the matrix of Evers and Benson (2018). Characters of Protrachyaspis shorymensis gen. et sp. nov. and the following species of Cenozoic pan-cheloniids were added to the matrix: Ash*leychelys palmeri* (after: Weems and Sanders 2014); Carolinochelys wilsoni Hay, 1923 (after: Weems and Sanders 2014; Weems and Brown 2016); Itilochelus rasstrigin Danilov et al., 2010 (after: Danilov et al. 2010; personal observations on the type material); Osonachelus decorata (after: de Lapparent de Broin et al. 2014); Pacifichelys spp. (after: Lynch and Parham 2003; Parham and Pyenson 2010); Procolpochelys grandaeva (Leidy, 1851) (after: Zangerl and Turnbull 1955; Weems 2014; Weems and Sanders 2014); Tasbacka aldabergeni Nessov, 1987 (after: Nessov 1987; personal observations on the type material); and Trachyaspis lardyi (after: Berry 1937; Weems 1974, 1980; Hasegawa et al. 2005; Villa and Raineri 2015). Argillochelys cuneiceps was removed from the matrix, because specimen NHMUK R38955, the most complete of the two specimens on which the original taxon coding by Evers and Benson (2018) was based, is not classified as Argillochelys (see Zvonok and Danilov 2023). The taxon "*Oligochelone rupeliensis*" is not a valid species (de Lapparent de Broin 2001; Weems and Sanders 2014) and, for this reason, was also removed from the matrix. In addition, the following corrections were made to the matrix:

- *Caretta caretta* (Linnaeus, 1758): **character 213** (Costals, position of costo-peripheral fontanelles and exposure of dorsal rib ends) is changed from 1 (fontanelles and exposed rib ends present and retained in adults between all costals and along the anterior margin of the first costal) to 0 (limited to parts of the carapace) based on Zangerl (1958: Abb. 21); **character 214** (Costal, fontanelle along anterior margin of costal 1) is inapplicable and changed from 1 to -;

- Chelonia mydas (Linnaeus, 1758): character
177 (Dentary, lingual (tomial) ridge) is changed from 1 (weak or absent) to 0 (prominent) based on personal observations of collection ZIN; character
213 (see above) was changed from 1 to 0 based on Zangerl (1958: Abb. 23); character 214 (see above) is inapplicable and changed from 1 to -;

- *Lepidochelys kempii* (Garman, 1880): **character 213** (see above) is changed from 1 to 0 based on Zangerl (1958: Abb. 20); **character 214** (see above) is inapplicable and changed from 1 to -;

- L. olivacea (Eschscholtz, 1829): character 12 (Frontal, frontal contribution to orbit) is changed from 0 (absent, contact between prefrontal and postorbital) to 1 (present) based on Zangerl et al. (1988: tab. 1); character 213 (see above) is changed from 1 to 0 based on Zangerl (1958: Abb. 20); character 214 (see above) is inapplicable and changed from 1 to -;

- Natator depressus (Garman, 1880): character 12 (see above) is changed from 1 to 0 based on Zangerl et al. (1988: tab. 1); character 213 (see above) is changed from 1 to 0 based on Zangerl et al. (1988: fig. 14); character 214 (see above) is inapplicable and changed from 1 to -; character 328 (Ischium, lateral process of ischium or metischial process) is changed from 0 (absent) to 1 (present) based on Zangerl et al. (1988: fig. 23a, b); character 353 (Femur, intertrochanteric ridge) is changed from 1 (ridge is high and obliterates intertrochanteric notch, and the proximal surface of the trochanters and their connecting ridge forms a continuous surface) to 0 (ridge is low and concave, creating a notch between the major and minor trochanter) based on Zangerl et al. (1988);

- Eochelone brabantica: character 101 (Pterygoid, processus pterygoideus externus) is changed from 2 (forming a pointed triangular process that projects laterally into the subtemporal fenestra) to 1 (forming a large lateral wing that projects as a free process into the subtemporal fenestra) based on Casier (1968: pl. I, fig. B, pl. III, fig. C); character 222 (Suprapygals, number of suprapygals) is changed from 1 (two) to 2 (more than two) based on de Lapparent de Broin et al. (2018); character 237 (Plastron, posterior plastral fontanelle between the xiphiplastra and/or the hypoplastra) is changed from 0 (absent in adult stage) to 1 (retained in adult stage) based on Evers et al. (2019: fig. S1.26C; de Lapparent de Broin et al. 2018: figs. 9a2, c2); character 262 (Xiphiplastra, posteriorly in contact with one another, often sutured along the midline and forming a plastral lobe) is changed from 0 (present) to 1 (absent) based on de Lapparent de Broin et al. (2018: figs. 9a2, c2);

- Puppigerus camperi: character 92 (Pterygoid, pterygoid-basioccipital contact) is changed from 0 (absent) to 0&1 (absent or present) based on personal observations of specimens in collection ZIN PH 145; character 101 (see above) is changed from 2 (see above) to 0 (forming an extensive process that contacts the maxilla anterolaterally at the posteromedial end of the triturating surface, is anteriorly sutured to the anterior palate, and has a posterior projection into the subtemporal fenestra) based on Moody (1974: fig. 6); character 140 (Parabasisphenoid, rostrum basisphenoidale) is changed from 2 (singular median, rod-like, thick and rounded process) to 1 (flat base, but with trabeculae in contact with one another medially forming a short rod at the anterior end of the parabasisphenoid) based on personal observation of specimens in the collection ZIN PH 145; character 176 (Dentary, symphyseal ridge) is changed from 1 (present) to 0 (absent) based on personal observation of specimens in the collection ZIN PH 145; character 222 (see above) is changed from 1 (see above) to 1&2 (two or more than two) based on de Lapparent de Broin et al. (2018).

Parsimony analysis. The parsimony analysis was carried out using TNT version 1.6 (Goloboff et al. 2008). We used the same algorithm of the parsimony analysis as Evers et al. (2019). The molecular backbone constraint was adopted from Pereira et al. (2017). *Proganochelys quenstedtii* Baur, 1887 was selected as an outgroup. All fossil taxa were designated as floaters. All characters were equally weighted and treated as unordered. We employed the new technology search algorithm with default settings

and enabled tree drifting and parsimony ratchet. The initial level of driven search was set to 30, and the number of times the minimum tree length should be obtained was set to 30. The most parsimonious trees (MPTs) of this initial analysis were subjected to tree bisection and reconnection (TBR).

SYSTEMATICS

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)

Cheloniidae Cope, 1867 (Joyce et al. 2021)

Protrachyaspis shorymensis gen. et sp. nov.

(Figs 4-8)

Cheloniidae indet. (in part): Zvonok et al. 2011: 21.

Etymology. The genus name is from the Greek $\pi \rho o$ (*pro*), meaning "before", and *Trachyaspis*, the name of the turtle, which is sister to the new genus. The species name is after the Shorym Formation.

Holotype. ZIN PH 28/177, part of postcranial skeleton (Kert), including fragments of one cervical vertebra 8, one dorsal vertebra, sacral vertebra (?)1, anterior caudal vertebra, right humerus and anterodistal fragment of left humerus, right ilium and femur, eleven autopodial bones, neurals (?)5 and 6–8, right costals 5–8 and left costals 6–8, eleven fragments of peripherals, right hyoplastron and hypoplastron, two fragments of hyo- or hypoplastron and right xiphiplastron.

Referred material. ZIN PH 14/177, right parietal (Monata); ZIN PH 15/177, two parietals (Monata); ZIN PH 35/177, symphysis of dentaries (Monata); ZIN PH 73/177, part of cervical vertebra 2 or 3, fragment of posterior peripheral plate, fragment of right hyoplastron, two fragments of hyo- or hypoplastron and right xiphiplastron (Kuvulus); ZIN PH 29-31/177, left humeri (Kuyulus); ZIN PH 80/177, right humerus (Monata); collection ZIN PH 177, five autopodial bones and fragments of left peripheral (?)1 and left or right peripheral (?)3 (Monata); ZIN PH 19/177, incomplete carapace, including nuchal, neurals 1–4, right costals 1–5 and 7 and left costals 1–7 (Kuvulus); ZIN PH 22/177, block of carapace bones, including neurals 2-5, right costals 2-5 and left costals 2-4 (Monata); ZIN PH 23/177, neural 2 or 4, left costals 1–3 and lateral part of right hypoplastron of one individual (Kuyulus); ZIN PH 26/177, part of neural plate (?)1 (Monata); ZIN PH 82/177, suprapygal 1 and right costal 6 (Kuyulus); collection ZIN PH 177, left costal 3 or 5 (unknown locality of Mangyshlak, collector A. Nasyrov); ZIN PH 24/177, medial fragment of left costal 3 or 5 (Karakeshi); ZIN PH 25/177, lateral part of odd costal (unknown locality of Mangyshlak, collector Eliseev); ZIN PH 27/177, (?) right peripheral 3 (Monata).

Specimens ZIN PH 15/177, ZIN PH 19/177, ZIN PH 73/177, and ZIN PH 82/177 from the Kuyulus locality likely belong to the same individual, as they are consistent in their state of preservation and size and contain no duplicate elements.

Locality, horizon, and age. Karakeshi, Kert, Kuyulus and Monata localities of Shorym Formation, Bartonian, Eocene, Paleogene, and unknown localities, probably, from the same Shorym Formation, Mangyshlak Peninsula, Kazakhstan (see Introduction for other details).

Diagnosis. Protrachyaspis shorymensis can be differentiated from other pan-cheloniids by the following combination of characters: (1) large size (about 110 cm of carapacial length); (2) concave edge of the parietal bone in contact with the postorbital; (3) frontoparietal scute notched from behind; (4) single parietal scute; (5) presence of the symphyseal and lingual ridges of the dentary; (6) presence of serrations on the ridges of the dentary; (7) lateral process located close to the middle part of the humerus and (8) the deltopectoral crest forms a slightly distally curved anterior protrusion; (9) high major trochanter of the femur, connected to the small trochanter by a crest with a notch; (10) presence of deep sculpturing in the pattern of network of grooves on the entire external surface of the carapace; (11) absence of keels on the external surface of the shell in adult individuals; (12) very long anterior medial process of the hypplastron; (13) narrow xiphiplastron. Characters 3, 4, 11-13 differentiate P. shorymensis from its sister taxon Trachyaspis lardyi.

Description and comparisons

Parietal bones (Fig. 4A–C). The right parietal bone (ZIN PH 14/177) and two parietal bones in the articulation (ZIN PH 15/177) belong to individuals of approximately the same size. In ZIN PH 14/177, the ventral part of the processus inferior parietalis and the anteromedial part of the dorsal surface are not preserved; in ZIN PH 15/177, the anterior parts

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Fig. 4. Cranial bones and vertebrae of *Protrachyaspis shorymensis*, Shorym Formation: A–C – right parietal ZIN PH 14/177, Monata locality, photographs in ventral (A) and dorsal (B) views, and drawing in dorsal (C) view; D–J – dentary ZIN PH 35/177, Monata locality, photograph in dorsal (D) view, drawing in dorsal (E) view, photographs in ventral (F) and anterior (G) views, anterior view of the anterodorsal part, showing serration of the labial ridge (H), posterior (I) and left lateral (J) views; K–M – photographs of cervical vertebra 2 or 3 ZIN PH 73/177, Kuyulus locality, in anterior (K), left lateral (L) and posterior (M) views; N–P – photographs of cervical vertebra 8 ZIN PH 28/177, Kert locality, in anterior (N), left lateral (O) and posterior (P) views; Q – photograph of posterior dorsal vertebra ZIN PH 28/177 in dorsal view; R–S – sacral vertebra (?)1 ZIN PH 28/177 in dorsal view, photograph (R) and drawing (S); T–U – photograph of anterior caudal vertebra ZIN PH 28/177 in dorsal (T) and ventral (U) views.

Abbreviations: aas – anterior articular surface of centrum; asn – anterior articular surface for contact with neural arch; asr – articular surface for rib; cc – central cusp; ecp – edge in contact with postorbital; fps – frontoparietal scute; lar – labial ridge; lir – lingual ridge; na – base of neural arch; pas – posterior articular surface of centrum; pip – processus inferior parietalis; poz – base of postzygapophysis; prz – base of prezygapophysis; ps – parietal scute; psn – posterior articular surface for contact with neural arch; scm – sulcus cartilagini meckelii; sos – supraocular scute; sp – spinous process; syr – symphyseal ridge; tp – base of transverse process; ts – temporal scute; vk – ventral keel.

and medial edges are damaged, large ventral parts of the processus inferior parietalis are broken off. On the external surface of all parietal bones, there is sculpturing in the shape of a network of grooves. The sulci of the cranial scutes are better preserved in ZIN PH 14/177. The anteromedial part of the articulated parietals was occupied by the frontoparietal scute, notched from behind, whereas their posteromedial part was occupied by a single large parietal scute; the anterolateral part of each bone was covered by the supraorbital scute, and the posterolateral part of each bone by the temporal scute. A small area of the sulcus is preserved at the anterior edge of the bone, but whether it is the lateral edge of the frontal or frontoparietal scute is unclear due to damage of the bone. Among pan-cheloniids, a posteriorly notched frontoparietal scute was previously known only in Argillochelys cuneiceps and one specimen of Argillochelys sp. (ZIN PH 32/153) from the Ak-Kaya 1 locality (Owen and Bell 1849: tab. XV, fig. 4; Zvonok and Danilov 2019: fig. 2d). One of the specimens of Trachyaspis lardyi, depicted in Hasegawa et al. (2005: pl. 14B), also has a notch in the posterior part of the frontoparietal scute, but it is smaller and located in the posterior part of the posterior projection of the frontoparietal scute; this area is also complicated by fragmentation of the scutes, which indicates the atypical nature of this configuration. A single parietal scute is known in *A. cuneiceps* (Owen and Bell 1849: tab. XV, fig. 4) and Osonachelus decorata (de Lapparent de Broin et al. 2014: fig. 3B), although we are not sure of the homology of the posterior parietal scute of O. decorata with the parietal scute of A. cuneiceps. In ZIN PH 14/177, there are contacts for the counterpart parietal medially, the frontal anteriorly, the postorbital laterally and the squamosal posterolaterally. The edge of the parietal bone in contact with the postorbital, is slightly concave, as in O. decorata and T. lardyi and in contrast to A. cuneiceps and Eochelone brabantica, in which the corresponding contact is convex (Owen and Bell 1849: tab. XV, fig. 4; Casier 1968: fig. 1B; Weems 1980: fig. 3D-C; Hasegawa et al. 2005: figs. 5, 18–19; de Lapparent de Broin et al. 2014: fig. 3B). A concave posterior margin of the parietal bone formed part of the upper temporal emargination, with the medial part of the margin protruding back much more than the lateral part.

Dentaries (Fig. 4D–J). The dentaries (ZIN PH 35/177) have a broken-off posterodorsal part of the right ramus and damaged labial and lingual ridges of

the left side. The symphysis is short (11 mm), making up 26% of the dentaries' length along the midline (43 mm). The triturating surface along the inner edges bears high, sharp lingual ridges, which, however, are not visible in lateral view. The lingual ridges have no medial contact with each other, but end abruptly at the symphysis. The triturating surface also bears a weak symphyseal ridge, which ends in the anterior terminal part with a central cusp. In the presence of both symphyseal and lingual ridges, the dentaries differ from those of "Dollochelys" rogovichi, Eochelone brabantica, Eochelone sp. from the Gorniy Luch locality, Osonachelus decorata, and Puppigerus camperi, and are similar to those of "Allopleuron" qazaqstanense (ZIN PH 8/177), Argillochelys an*tiqua*, Argillochelys sp. from the Ak-Kaya 1 locality and Trachyaspis lardyi. However, in "A". gazagstanense ZIN PH 8/177 the lingual ridges gradually decrease in height in the anterior direction, in A. antiqua and Argillochelys sp. from the Ak-Kava 1 locality the lingual ridges contact the posterior edge of the symphyseal ridge, and in T. lardyi the lingual and symphyseal ridges are visible behind the labial ones in lateral view (Weems 1980: fig. 3B; Hasegawa et al. 2005: pl. 4A3, C2; Zvonok and Danilov 2017: fig. 7I; Zvonok and Danilov 2019). The labial ridges are well developed and finely serrated, as in extant Chelonia mydas (personal observation of two skulls of collection ZIN). Trachyaspis lardyi has much larger denticles (Weems 1980: fig. 3B; Hasegawa et al. 2005: pl. 4A3, C2), although given the small size of ZIN PH 35/177, the difference may be due to age variability. The anterior edge of the bone is rounded anteriorly in dorsal and ventral views. In lateral view, most of the dorsal edge of the bone is straight, only in the anterior part of the symphysis it bends slightly dorsally with a central "tooth" in the terminal anterior part. The sulcus cartilaginis meckelii is narrow and deep. The lower shelf of the dentary below the sulcus cartilaginis meckelii is slightly pushed back in dorsal view. The foramina dentofaciale majus and alveolare inferius are not visible.

Cervical vertebrae (Fig. 4K–P). The ventral part of cervical vertebra 2 or 3 (ZIN PH 73/177) and the ventral part of cervical vertebra 8 (ZIN PH 28/177; holotype) are preserved. Cervical vertebra 2 or 3 (ZIN PH 73/177) is deformed and asymmetric, and represented by the centrum and lower parts of the neural arches. The anterior articular surface is convex, the posterior one is concave. Before the

deformation, both articular surfaces were probably close to circular in shape. The ventral keel is high and forms a widening in the posterior part, adjacent to the posterior articular surface ventrally. The bases of the transverse processes are located in the posterior part of the vertebra, divided into dorsal and ventral parts by a suture between the centrum and the neural arches. Cervical vertebra 8 (ZIN PH 28/177) is represented by the centrum and bases of the neural arches, the right ventrolateral fragment is gouged out, the anterior articular surface is damaged. The centrum is extremely short (12 mm). The anterior articular surface is concave and probably close to circular in shape. The posterior articular surface is convex and slightly compressed dorsoventrally (height -17 mm, width -25 mm), lower than the anterior one. The anterior articular surface of cervical vertebra 8 (ZIN PH 28/177) is higher than that of *Trachyaspis* lardyi (Berry and Lynn 1936; Weems 1974: table 4). In pan-cheloniids, high articular surfaces between cervical vertebrae 7 and 8 are also known in Osonachelus decorata (de Lapparent de Broin et al. 2014: fig. 6A3). The bottom of the neural canal is concave. The bases of the neural arches are thin. The ventral keel is not preserved, although there is a narrowing ventrally to the posterior articular surface.

Dorsal vertebrae (Fig. 4Q). The centrum of the posterior dorsal vertebra (ZIN PH 28/177) is deformed due to dorsoventral compression. The anterior surfaces for contact with the neural arch are extended, whereas the posterior ones are short. There is no ventral keel.

Sacral vertebrae (Fig. 4R, S). Sacral vertebra (?)1 (ZIN PH 28/177) is deformed due to dorsoventral compression. The bases of the prezygapophyses are widely spaced, while the bases of the postzygapophyses are located close to each other. The spinous process is low and divided. The articular surfaces for unfused sacral ribs are large. The bases of the neural arch are extended in the anteroposterior direction.

Caudal vertebrae (Fig. 4T, U). The anterior caudal vertebra (ZIN PH 28/177) is represented by the centrum deformed due to dorsoventral compression with parts of the transverse processes and neural arches. The centrum is relatively long; its anterior articular surface is concave, and the posterior one is convex. The bases of the transverse processes (better preserved on the right side) and the neural arch are extended in the anteroposterior direction. The ventral keel is absent.

Ilium (Fig. 5A). The right ilium (ZIN PH 28/177; holotype) is deformed due to mediolateral compression; the medial edge of the posterior iliac process is damaged. The bend between the anterior and dorsal surfaces of the bone is sharp, knee-like. The part of the acetabulum formed by the ilium is large.

Humerus (Fig. 5B-L). The right humerus and anterodistal fragment of the left humerus of a large individual (ZIN PH 28/177; holotype), and isolated left ones (ZIN PH 29/177, ZIN PH 30/177, ZIN PH 31/177), and the right one (ZIN PH 80/177) of smaller individuals are preserved. In the right humerus ZIN PH 28/177, parts of the head, medial and lateral processes, as well as the entire anterodistal part were broken off; in ZIN PH 29/177, the ventral surface of the proximal part of the bone and a small section of the posterior edge in the middle part of the bone are damaged; in ZIN PH 31/177 the ventral surface is worn away and a small section of the anterior edge in the middle part of the bone is missing; ZIN PH 80/177 is heavily worn. The head of the humerus is flattened dorsoventrally, unlike Ashleychelys palmeri, Eochelone brabantica, Osonachelus decorata, Trachyaspis lardyi and Pan-Cheloniidae indet. from the Andarak 2 locality (Danilov and Averianov 1997: fig. 3b; Hasegawa et al. 2005: pl. 4D3; Grant-Mackie et al. 2011: fig. 3E; de Lapparent de Broin et al. 2014: fig. 10D; Weems and Sanders 2014: fig. S2D). This may be partly the result of deformation, although the flattening is expressed approximately equally in all specimens. The dorsal part of the head is slightly elongated posterodistally, as in A. palmeri and T. lardyi (Weems 1974: pl. 3, fig. 2; Hasegawa et al. 2005: pl. 4D1; Weems and Sanders 2014: fig. S2C). The medial process (preserved in ZIN PH 29/177, ZIN PH 30/177, ZIN PH 31/177) becomes longer as the bone size increases, forming a sequential row. Between the head and the medial process on the ventral side of ZIN PH 30/177, in which this area is well preserved, there is a depression clearly defined on the distal side. The lateral process is located close to the middle part of the bone, as in *T. lardyi* (Weems 1974: pl. 3, fig. 1; Hasegawa et al. 2005: pl. 4D2), and is connected by a narrow ridge to the head at the anterior edge of the bone. A weak, gradually smoothing ridge also extends from the lateral process towards the medial process. Together, the lateral process and these ridges border a large depression for the attachment of the m. coracobrachialis brevis proximal to the lateral process. The deltopectoral crest is located close to the middle part of the bone and is not connected with the lateral process. In dorsal and ventral views, the deltopectoral crest forms a tubercle pushed forward in the smaller specimens (ZIN PH 29/177 and ZIN PH 30/177), whereas in the larger specimen (ZIN PH 31/177), it forms a slightly distally curved anterior projection, as in *T. lardui* (Weems 1974: pl. 3, figs 1, 2). The diaphysis is wide in the anteroposterior direction, strongly compressed dorsoventrally, smooth when viewed from the front and back, and narrower in the larger specimens (ZIN PH 28/177 and ZIN PH 31/177), but wider than in Eochelone *monstigris*. The depression for attachment of the mm. latissimus dorsi et teres major is large, oval, located in the medial part of the bone. A small ridge leads into it from the anterior edge of the bone slightly distal to the head, which then extends to the anterior part of the bone distal to the deltopectoral crest. This ridge probably bordered the attachment area of the mm. deltoideus scapularis et deltoideus clavicularis (Krahl et al. 2020: fig. 1). In ZIN PH 29/177, ZIN PH 30/177, ZIN PH 31/177, and on the anterodistal fragment of the left humerus (collection ZIN PH 177), the ectepicondylar notch is preserved, but does not close into a canal. In ZIN PH 29/177 and ZIN PH 30/177, the ulnar and radial condyles are not differentiated; in the larger ZIN PH 31/177, there is a notch between these condyles, although they do not project ventrally.

Femur (Fig. 5M, N). The right femur (ZIN PH 28/177; holotype) is deformed due to mediolateral compression, the head is broken off, and the distal part of the bone is damaged. The femur is approximately half the length of the humerus. The major trochanter is tall, as in *Trachyaspis lardyi* (Weems 1974: pl. 2, fig. 7; Hasegawa et al. 2005: pl. 4E1, 2). The mi-

nor trochanter forms the anterior projection, and both trochanters are connected by a ridge with a notch, as in *Ashleychelys palmeri*, *Osonachelus decorata*, and *T. lardyi* (Weems 1974: pl. 2, fig. 7; Hasegawa et al. 2005: pl. 4E1, 2; de Lapparent de Broin et al. 2014: fig. 10F3; Weems and Sanders 2014: fig. S1H, J). The area of the ridge between the head and the major trochanter is damaged. The diaphysis is significantly wider than in *A. palmeri* (Weems and Sanders 2014: fig. S1H, J). The distal part of the bone is strongly expanded.

Autopodial bones (Fig. 50-T). ZIN PH 28/177 (holotype) preserves distal metatarsals 3 and 4 in articulation, an indeterminate mesopodial bone, metatarsal 1, one phalanx, as well as six fragments of long autopodial bones. One specimen in collection ZIN PH 177 preserves an indeterminate mesopodial bone, a phalanx without a proximal part, and three fragments of long metapodial bones or phalanges. The distal metatarsal 4 (ZIN PH 28/177) is round in dorsal and ventral views, and concave on the ventral and dorsal sides. It has a notch that articulates with a small subtriangular, round-cornered distal metatarsal 3. The indeterminate mesopodial bone (ZIN PH 28/177) is round and has a thickening on one side, which bears a notch. The indeterminate mesopodial bone (collection ZIN PH 177) has a pentagonal shape, slightly convex on the dorsal side and concave on the ventral side. Metatarsal 1, strongly flattened due to deformation, has a crescent shape with thickenings at the distal and ventral ends. The preserved part of the phalanx (collection ZIN PH 177) is large, strongly elongated, and dorsoventrally compressed. The preserved distal epiphysis is convex and has a dorsoventrally thin projection at its anterior margin. The phalanx (ZIN PH 28/177) is much shorter,

Abbreviations: ac – acetabulum; dcb – depression for attachment of m. coracobrachialis brevis; dhm – depression between head and medial process; dld – depression for attachment mm. latissimus dorsi et teres major; dpc – deltopectoral crest; dt3 – distal tarsal 3; dt4 – distal tarsal 4; een – ectepicondylar notch; fh – base of femoral head; hh – humeral head; ip – iliac process; itr – intertrochanteric ridge; lp – lateral process; mat – major trochanter; mit – minor trochanter; mp – medial process; pam – projection at anterior margin of distal part of phalanx; rc – radial condyle; rld – ridge crossing depression for attachment of mm. latissimus dorsi et teres major; rlh – ridge extending from lateral process to head; rlm – ridge extending from lateral process to medial process; uc – ulnar condyle.

Fig. 5. Girdle and limb bones of *Protrachyaspis shorymensis*, photographs, Shorym Formation: A – right ilium ZIN PH 28/177, Kert locality, in anterior view; B–E – right humerus ZIN PH 28/177 in dorsal (B), ventral (C), anterior (D) and posterior (E) views; F – anterodistal fragment of left humerus ZIN PH 28/177 in dorsal view; G – left humerus ZIN PH 29/177, Kuyulus locality, in dorsal view; H–K – left humerus ZIN PH 30/177, Kuyulus locality, in dorsal (H), ventral (I), anterior (J) and posterior (K) views; L – left humerus ZIN PH 31/177, Kuyulus locality, in dorsal view; M–N – right femur ZIN PH 28/177 in ventral (M) and dorsal (N) views; O – distal tarsal 3 and 4 ZIN PH 28/177 in dorsal or ventral view; P – indeterminate mesopodial bone, ZIN PH 28/177, dorsal or ventral view; Q – indeterminate mesopodial bone of collection ZIN PH 177, Monata locality, in dorsal or ventral view; T – phalanx ZIN PH 28/177 in ventral view.



hourglass-shaped, dorsoventrally compressed, both epiphyses are convex. Fragments of the remaining long bones of the metapodial or phalanges (ZIN PH 28/177 and unnumbered from collection ZIN PH 177) are dorsoventrally flattened, at least partly as a result of deformation. Two fragments of long bones of autopodial bones (ZIN PH 28/177) and three fragments of bones from collection ZIN PH 177 have concave epiphyses, while four fragments of bones (ZIN PH 28/177) have convex epiphyses.

Sculpturing of the shell (Fig. 6C, E–J). In ZIN PH 28/177 (large, obviously adult individual, holotype), islands of sculpturing in the shape of a network of grooves are visible on non-eroded areas of the external surface of the carapace. On neural (?)1 (ZIN PH 26/177; large individual), the sculpturing appears as sharp ridges, as in a fragment of the costal of Pan-Cheloniidae indet. (ZIN PH 3/239) from the Tripolye locality of the Kiev Formation (Zvonok and Danilov 2017: fig. 10I). On the peripheral (ZIN PH 27/177; large individual), the grooves are narrowed, and on one of the large peripherals from collection ZIN PH 177, the grooves are weakly expressed. In subadult (medium-sized) specimens ZIN PH 19/177, ZIN PH 22/177, ZIN PH 23/177, ZIN PH 24/177, ZIN PH 25/177, ZIN PH 73/177, ZIN PH 82/177 and an unnumbered specimen from collection ZIN PH 177, grooves are deep and densely set in the posterior part of the nuchal, on the neurals and in the larger medial part of the costals. Closer to the edge of the carapacial disc, in the anterior part of the nuchal, on suprapygal 1, in the smaller lateral part of the costals and on the peripherals, the network of grooves gradually becomes sparser and smaller. In large ZIN PH 28/177 and medium-sized ZIN PH 73/177, the plastral elements are not sculptured. Sculpturing of the external surface of the carapace in the form of a network of deep grooves is also known in Ashleychelys palmeri, Osonachelus decorata, Trachyaspis lardyi and Pan-Cheloniidae indet. from the upper part of the Buchak Formation - lower part of the Kiev Formation. At the same time, the sculpturing of the carapace of the new species is less dense and spreads over the entire external surface of the carapace, in contrast to *O. decorata*. It seems that deep and dense sculpturing of the external surface is present in adult *Bryochelys waterkeynii*. Less deep sculpturing of the carapacial plates in the shape of a network of grooves is present in *Carolinochelys wilsoni* (Weems and Sanders 2014).

Keels of the shell (Figs 6H, 7). Adult (large) specimens ZIN PH 28/177 (holotype) and ZIN PH 26/177 have no longitudinal ridges on the external surface of the shell, whereas subadult (medium-sized) specimens ZIN PH 19/177, ZIN PH 22/177, and ZIN PH 23/177 bear weak medial keels in the posterior part of neurals 2 and 4 and in the anterior part of neural 3. In suprapygal 1 (ZIN PH 82/177), the medial keel is very tall. The nuchal, neural 1 (ZIN PH 19/177), and plastral elements (ZIN PH 82/177) lack keels. In contrast to *Trachyaspis lardyi*, there is no ridge in the posterior part of the nuchal (Weems 1974: text-fig. 4; Hasegawa et al. 2005: figs 18-19). A longitudinal keel on the neurals, as in subadults of the new species, is known in Argillochelys antiqua, Ashleychelys palmeri, and most individuals of T. lardyi. The medial keel is depicted in A. antiqua on the dorsal surface of suprapygal 1 (Owen and Bell 1849: tab. VIII). There is no keel on the costals, unlike many specimens of *T. lardyi* (Weems 1974: tab. 2).

Scute sulci of the shell (Figs 6F, 7, 8H). The sulci of the horny scutes of the shell are not preserved in the holotype and other adult specimens, with the possible exception of neural (?)1 (ZIN PH 26/177), in which a small right lateral portion of the intervertebral sulcus is likely preserved in the area of the fracture. The cervical scute on the subadult nuchal (ZIN PH 19/177) occupied more than a third of the width of the plate and narrowed slightly in the posterior direction. Of the marginal scutes, the outlines of the medial part of large marginal scute 1 are visible in ZIN PH 19/177. Vertebral scute 1 of this specimen

Abbreviations: co5-8 - costals 5-8; ?ivs - (?)intervertebral sulcus; k - keel; ne6-8 - neurals 6-8; pe - peripherals.

Fig. 6. Carapacial bones of *Protrachyaspis shorymensis*, Shorym Formation: A – photograph of nuchal ZIN PH 19/177, Kuyulus locality, in ventral view; B – photograph of neural (?)5 ZIN PH 28/177, Kert locality, in dorsal view; C, D – part of carapace ZIN PH 28/177 in dorsal view, photograph (C) and drawing (D); E – photograph of part of carapace ZIN PH 19/177 in dorsal view; F – photograph of the anterior or posterior part of neural (?)1 ZIN PH 26/177, Monata locality, in dorsal view; G – photograph of neural 2 or 4 ZIN PH 23/177, Kuyulus locality, in dorsal view; H – photograph of right costal (?)6 ZIN PH 82/177, Kuyulus locality, in dorsal view; I – photograph of suprapygal 1 ZIN PH 82/177, Kuyulus locality, in dorsal view; J, K – photographs of the (?)right peripheral 3 ZIN PH 27/177, Monata locality, in dorsal (J) and anterior (K) views; L – photograph of posterior peripheral ZIN PH 73/177, Kuyulus locality, in dorsal or ventral view.



is wider than the nuchal plate. Vertebral scutes 1-4 (subadult ZIN PH 19/177, ZIN PH 22/177, ZIN PH 23/177, ZIN PH 24/177 and an unnumbered specimen from collection ZIN PH 177) are narrow and form a weak lateral protrusion at the level of contact of the pleural scutes, but are not subrectangular as in costals from the Tripolye (ZIN PH 2/239) and Bulgakovka (ZIN PH 1/259) localities (Zvonok and Danilov 2017: fig. 10J; Zvonok and Danilov 2023: fig. 10K). The sulcus between vertebral scutes 1–4 and the adjacent pleural scutes is sinuous, as seen in ZIN PH 19/177, ZIN PH 22/177 and ZIN PH 23/177. The sulcus between vertebral scutes 1 and 2 in ZIN PH 19/177 curves anteriorly on the surface of the neural; the sulcus between vertebral scutes 2 and 3 curves anteriorly in ZIN PH 19/177 and is straight in the smaller ZIN PH 22/177. The curved shape of the intervertebral sulcus is clearly visible on a fragment of the costal plate (ZIN PH 2/239) from the Tripolye locality of the Kiev Formation (Zvonok and Danilov 2017: fig. 10J). On the hypoplastron (ZIN PH 73/177), a wave-like curved sulcus is visible between the abdominal and femoral scutes.

Nuchal (Figs 6A, E, Fig. 7). The nuchals are represented by the nuchal of a subadult individual (ZIN PH 19/177). It has damaged lateral and posterior borders. The nuchal has a slightly concave anterior border. The lateral border forms an anterolateral protrusion for contact with peripheral plate 1. Behind the protrusion, the lateral border of the nuchal is straight, forming margin of the large costo-peripheral fontanelle, as in *Osonachelus decorata* (Lapparent de Broin et al. 2014: figs 7A1, A2, 8A1, A2). There are no postnuchal fontanelles. On the inner surface of the nuchal, the area of the facet or pedestal for cervical vertebra 8 is damaged.

Neurals (Figs 6B–G, 7). The neurals are represented by neural (?)5, the posterior part of neural 6, neural 7 and neural 8 without the left posterolateral part (ZIN PH 28/177; holotype); neurals 1–4 (ZIN PH 19/177), neurals 2–4 and the anterior part of neural 5 (ZIN PH 22/177), neural 2 or 4 (ZIN PH 23/177), and the anterior or posterior part of neural plate (?)1 of a large individual (ZIN PH 26/177). In ZIN PH 19/177, the anterior and posterior parts of neural 2, the lateral parts of neural 3, the anterior, right lateral and posterior borders of neural 4 are damaged. Neural 1 (ZIN PH 19/177) probably had the shape of an elongated oval. The anterior or posterior part of neural (?)1 (ZIN PH 26/177) is roughly

rectangular in shape. Neural 2 (ZIN PH 22/177), neural 2 or 4 (ZIN PH 23/177), neurals 3 (ZIN PH 19/177 and ZIN PH 22/177), and neural 4 (ZIN PH 22/177) are hexagonal, with short sides anteriorly; neural 4 (ZIN PH 19 /177) was probably of the same shape. In the preserved small anterior part of neural 5 (ZIN PH 22/177), the border for contact with left costal 4 is oriented anterolaterally, and the border for contact with the right costal 4 is oriented anteriorly. Neurals (?)5, 7 and 8 (ZIN PH 28/177) are narrow and flat, as in Pan-Cheloniidae indet. from the Bakhmutovka (ZIN PH 2/20) and Tripolye (ZIN PH 1/239) localities (Zvonok and Danilov 2017: fig. 10H; Zvonok and Danilov 2023: fig. 10F). Of these, neural 7 is hexagonal in shape, and neurals (?)5 and 8 are likely too, considering the damage. The shape of other neural fragments is unclear. Unlike Bryochelys waterkeynii, there are no neurals completely surrounded by costals in the carapace (Smets 1888).

Suprapygals (Figs 6H, 7). Suprapygal 1 of a subadult individual (ZIN PH 82/177) has its left side and front border damaged. The posterior border has a sutural surface, whereas the lateral border is free. There is a longitudinal elevation on the internal surface for contact with vertebrae.

Costals (Figs 6C–D, I, 7). The costals are represented by right costals 5-8 and left costals 6-8, as well as one medial and two lateral parts of an unidentified costal (ZIN PH 28/177; holotype); right costals 1-5 and 7 and left costals 1-7 (ZIN PH 19/177), and right costal (?)6 (ZIN PH 82/177), probably from the same individual; right costals 2-4, an anteromedial fragment of costal 5, left costal 2 and medial fragments of costals 3 and 4 (ZIN PH 22/177); left costals 1-3 (ZIN PH 23/177); left costal 3 or 5 (collection ZIN PH 177); a medial fragment of left costal 3 or 5 with a damaged medial edge (ZIN PH 24/177); and the lateral part of an odd costal with a broken free rib (ZIN PH 25/177). In ZIN PH 28/177, the medial part of right costals 5 and 6 and the lateral part of right costals 7 and 8, and left costals 6–8 are damaged; in the costals of ZIN PH 19/177 all free ribs are broken off, the posterior edge of right costal 5, the anterior and medial edges of right costal 7, the medial and posterior edges of left costals 5 and 6, the anterior and medial edges of left costal 7 are damaged; right costal (?)6 ZIN PH 82/177 has damaged medial and posterior edges; in the costal plates of ZIN PH 22/177 all free ribs are broken off, on the dorsal surface of left costals 2-4 in A new *Trachyaspis*-like pan-cheloniid turtle



Fig. 7. Reconstruction of the carapace of subadult *Protrachyaspis shorymensis* based on ZIN PH 19/177, Kuyulus locality, with an additional drawing based on ZIN PH 82/177, Kuyulus locality, and ZIN PH 22/177, Monata locality, in dorsal view. Elements preserved in ZIN PH 19/177 are filled with gray. *Abbreviations*: ce – cervical scute; co1–co7 – costals 1–7; k – keel; ne1–ne4 – neurals 1–4; nu – nuchal; ma1 – marginal scute 1; pl1–

Abbreviations: ce – cervical scute; co1–co7 – costals 1–7; k – keel; ne1–ne4 – neurals 1–4; nu – nuchal; ma1 – marginal scute 1; pl1– pl4 – pleural scutes 1–4; su1 – suprapygal 1; ve1–ve4 – vertebral scutes 1–4.

the area of pleural scute 2 the bone is damaged, but the damaged surface is smoothed, apparently due to regeneration. In all the costals with preserved lateral borders, these borders are free. They are convex in costals 1-6 (ZIN PH 28/177, ZIN PH 19/177, ZIN PH 22/177, ZIN PH 23/177 and an unnumbered specimen from collection ZIN PH 177) and rather straight in costals 7 and 8 (ZIN PH 28/177, ZIN PH 19/177). Right costal plates 5-7 (ZIN PH 28/177) have long free ribs, whereas the remaining costals with preserved lateral borders have only the bases of free ribs. The free ribs are located close to the middle part of the plate in costals 1–5 (ZIN PH 28/177, ZIN PH 19/177, ZIN PH 22/177, ZIN PH 23/177 and an unnumbered specimen from collection ZIN PH 177), close to the posterior border of the plate in costal 6, and adjacent to the posterior border in costals 7 and 8 (ZIN PH 28/177, ZIN PH 19/177). The heads of the ribs are preserved in left costal 8 (ZIN PH 28/177), right costal 3, left costals 1 and 7 (ZIN PH 19/177), and left costal 3 or 5 (ZIN PH 24/177); they are massive with a short neck.

Peripherals (Fig. 6C, D, J–L). The peripherals are represented by eleven fragments of at least six left or right peripherals of ZIN PH 28/177 (two of them are bridge peripherals, others can be posterior or dorsoventrally compressed bridge peripherals); (?) right peripheral 3 (ZIN PH 27/177); fragments of left peripheral (?)1 and left or right peripheral (?)3 (collection ZIN PH 177); a fragment of the left or right posterior peripheral (ZIN PH 73/177). Peripherals of ZIN PH 28/177 are dorsoventrally deformed due to compression; the peripheral of ZIN PH 27/177 has its ventral and posterior parts broken off; in peripherals (?)1 and (?)3 of collection ZIN PH 177 all borders, except for part of the lateral one, are broken off; peripherals 8-11 of ZIN PH 73/177 are represented only by the lateral part. The fragments of the peripherals of ZIN PH 28/177 are very narrow relative to the carapace; they are probably all broken off in the medial part; fragments of bridge peripherals are high dorsoventrally and rounded laterally in cross-section; fragments of other peripherals are low dorsoventrally and acute laterally in cross-section. In peripheral 3 (ZIN PH 27/177) the lateral border is rounded in dorsal view, the dorsal surface is wide mediolaterally, and its medial margin is serrated, indicating contact with the adjacent costal. Fragments of peripherals (?)1 and (?)3 (collection ZIN PH 177) have wide dorsal surfaces, although their medial border is broken off and whether they were in contact with the costals is unclear. Peripheral (?)1 is low dorsoventrally, perhaps partly due to deformation, and the lateral border is rounded in dorsal view. In lateral view, the lateral border is slightly curved dorsally. The dorsal surface is almost smooth. Peripheral (?)3 is high dorsoventrally with its lateral edge rounded in cross-section. The dorsal surface is slightly concave. A fragment of the posterior peripheral (ZIN PH 73/177) is low dorsoventrally, its lateral edge is sharp in cross-section. The anteroposterior groove between the dorsal and ventral parts is visible.

Hyoplastra (Fig. 8A, D, E). The hyoplastra are represented by the right hypplastron (ZIN PH 28/177; holotype) and a fragment of the right hyoplastron (ZIN PH 73/177). The hypplastron (ZIN PH 28/177) has all its processes broken off, except the anteromedial ones; the hyoplastron (ZIN PH 73/177) is represented only by the anterior medial process (without the anterior end) and the adjacent part of the hyoplastron. The hyoplastron of the adult individual (ZIN PH 28/177) is clearly significantly narrower than the hyoplastra (ZIN PH 37/177 and collection ZIN PH 177) of cf. P. shorymensis. A single anterior medial process is very long. In ZIN PH 28/177, judging by the ridges on the dorsal side, a cluster of three small processes adjoin posteriorly the anterior medial process. Among Cenozoic pan-cheloniids, such a long anterior medial process of the hypplastron is known only in Osonachelus decorata (de Lapparent de Broin et al. 2014: fig. 9). The hyo-hypoplastral suture is short and strongly interdigitated. The axillary notch is deep. In ZIN PH 28/177 (holotype), the plastral index is about 130 or slightly less.

Fig. 8. Plastral bones of *Protrachyaspis shorymensis*, Shorym Formation: A – photograph of the right hyo- and hypoplastron in articulation ZIN PH 28/177, Kert locality, in ventral view; B – photograph of the right xiphiplastron ZIN PH 73/177 in ventral view; C – photograph of the anterior part of the right xiphiplastron ZIN PH 28/177 in ventral view; D – reconstruction of the plastron of ZIN PH 28/177 in ventral view; E – photograph of an anteromedial fragment of the right hypoplastron ZIN PH 73/177, Kuyulus locality, in ventral view; F–H – lateral part of the left hypoplastron ZIN PH 23/177, Kuyulus locality, photographs in dorsal (F) and ventral (G) views, drawing of ventral (H) view; I – photograph of a fragment of the hyo- or hypoplastron ZIN PH 73/177 in dorsal or ventral view. *Abbreviations*: ab – abdominal scute; amp – anterior medial process; an – axillary notch; fe – femoral scute; hyo – hypoplastron; hyp – hypoplastron; in – inguinal notch; map – medial anterior process; plp – posterior lateral process; s – stiffener; xi – xiphiplastron.





Fig. 9. Shell bones of cf. *Protrachyaspis shorymensis*, Shorym Formation: A – photograph of the left part of the nuchal ZIN PH 42/177, Tuzbair locality, in dorsal view; B – photograph of the left part of nuchal ZIN PH 38/177, Kuyulus locality, in dorsal view; C – photograph of left hyoplastron 37/177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron of collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron di collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron di collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron di collection ZIN PH 177, Kuyulus locality, in ventral view; D, E – left hyoplastron di collection ZIN PH 177, Kuyulus locality, in ventral view; D, E

Abbreviations: ab - abdominal scute; ale - anterolateral protrusion for contact with peripheral 1; <math>amp - anterior medial process; an - axillary notch; im - inframarginal scutes; k - keel; ma1 - marginal scute 1; pe - pectoral scute; ve1 - vertebral scute 1.

Hypoplastra (Fig. 8A, D, F–H). The hypoplastra are represented by the right hypoplastron (ZIN PH 28/177; holotype) and the lateral part of the right hypoplastron (ZIN PH 23/177). In ZIN PH 28/177, all processes, except two posteromedial ones, and the entire posterolateral part are broken off, whereas ZIN PH 23/177 partially preserves the posterior lateral process. In ZIN PH 28/177, the preserved posteromedial processes form a cluster medially to the xiphiplastral notch. The base of one wide process lateral to the xiphiplastral notch is also preserved. Part of the xiphiplastral notch is visible only from the dorsal side, and a flattened epiphysis, probably of a pelvic bone, is wedged into it. In ZIN PH 23/177, only one large lateral process is preserved. The dorsal side of this process bears a stiffener that continues towards the center of the plate. The second stiffener, probably lying at the base of the process lateral to the xiphiplastral notch, extends from the center to the posteromedial border. The posterolateral border of the hypoplastron slopes strongly posteriorly from the deepest part of the inguinal notch. The hyo-hypoplastral suture is short and strongly interdigitated.

Hyo- or hypoplastra (Fig. 8I). There are two fragments of the hyo- or hypoplastron (ZIN PH 28/177; holotype) and two other fragments of the hyo- or hypoplastron (ZIN PH 73/177). In ZIN PH 28/177, one fragment is represented by the anterolateral part of the hypoplastron or the posterolateral part of the hypoplastron with most of one large lateral process and the adjacent base of the other; the second fragment is a small medial or lateral part of the left hyo- or hypoplastron or the posterolateral part of the right hypoplastron with a small process. In ZIN PH 73/177, each fragment consists of two processes with an adjacent portion of the middle part of the left or right hyo- or hypoplastron. The first fragment has small processes, whereas the second one has very long, thin processes.

Xiphiplastra (Fig. 8B–D). The xiphiplastra are represented by the anterior part of the right xiphiplastron (ZIN PH 28/177; holotype) and the right xiphiplastron (ZIN PH 73/177). ZIN PH 28/177 has a broken medial process, whereas in ZIN PH 73/177, the lateral part of the anterior process and a small posterior part of the plate are broken off. In ZIN PH 28/177, the preserved part was not in contact with the counterpart xiphiplastron, and there was a large xiphiplastral fontanelle, in contrast to Argillochelys antiqua, in which the xiphiplastra were widely in contact (Owen and Bell 1849: tab. VIIIA). The medial anterior xiphiplastral process is long. ZIN PH 73/177 is narrow mediolaterally, elongated, straight, and was not in contact with the counterpart xiphiplastron in the preserved part; there was a large xiphiplastral fontanelle. The medial anterior xiphiplastral process is short. The narrow xiphiplastron distinguishes the new species from Trachyaspis lardyi, which has a wide xiphiplastron (Berry and Lynn 1936: plate IV, fig. 2; Berry 1937: fig. 2F; Weems 1974: pl. 2, fig. 5).

cf. Protrachyaspis shorymensis

(Fig. 9)

Referred material. ZIN PH 38/177, left part of the nuchal (Kuyulus); ZIN PH 42/177, left part of

the nuchal (Tuzbair); ZIN PH 37/177, left hyoplastron (Kuyulus); collection ZIN PH 177, left hyoplastron and the medial part of the left hyoplastron (Kuyulus). Probably, specimens ZIN PH 37/177 and ZIN PH 38/177 belong to a single individual, since they come from the same locality and correspond to each other in size and state of preservation.

Locality, horizon and age. Kuyulus and Tuzbair localities of Shorym Formation, Bartonian, Eocene, Paleogene, Mangyshlak Peninsula, Kazakhstan.

Description and comparisons

Sculpturing of the shell (Fig. 9B–D). On the external surface of the shell bones of ZIN PH 37/177, ZIN PH 38/177, ZIN PH 42/177, and an unnumbered specimen from collection ZIN PH 177, there are densely set small ridges, known in juvenile pan-chelonioids (de Lapparent de Broin et al. 2014).

Keels of the shell (Fig. 9E). The longitudinal keel is present on the hyoplastra. It is better developed in the smallest unnumbered specimen.

Scute sulci of the shell (Fig. 9A, B, E). Of the marginal scutes, the outlines of the medial part of large marginal scute 1 are visible on the nuchals. Vertebral scute 1 is wider than the nuchal plate. The pectoral-abdominal sulcus is visible at the level of the anterior edge of the lateral fontanelle of the hyoplastra. In addition, the sulcus between the pectoral and inframarginal scutes is present in one unnumbered specimen from collection ZIN PH 177.

Nuchal (Fig. 9A, B). The nuchals are represented by the left parts of the nuchal plates of a small individual (ZIN PH 38/177) and an even smaller individual (ZIN PH 42/177). The anterior border of the nuchal probably is slightly concave in ZIN PH 38/177 and deeply concave in ZIN PH 42/177. The lateral border forms an anterolateral protrusion for contact with peripheral plate 1, as in *P. shorymensis* ZIN PH 19/177. The protrusion is longer in the smaller specimen (ZIN PH 42/177). Behind this protrusion, the lateral border of the nuchal is straight in ZIN PH 38/177 and constricted by the vertebral-marginal sulcus in ZIN PH 42/177.

Hyoplastra (Fig. 9C–E). The hyoplastra are represented by two left hyoplastra (ZIN PH 37/177 and an unnumbered specimen of collection ZIN PH 177) and the medial part of the left hyoplastron (collection ZIN PH 177). The posterolateral part of the hyoplastron (ZIN PH 37/177) is broken off; the hyoplastron (collection ZIN PH 177) and the medial part of the

hyoplastron (collection ZIN PH 177) have damaged processes. The hypplastra are significantly wider than the hyoplastron of an adult individual (ZIN PH 28/177) of P. shorymensis. The axillary notch is deep. ZIN PH 37/177 has eight medial processes. ZIN PH 37/177 and the medial part of the hyppastron from collection ZIN PH 177 have a bundle of three anterior medial processes, and in the smallest hypplastron (collection ZIN PH 177), a bundle of two anterior medial processes extends in the anteromedial direction. There are eight lateral processes in ZIN PH 37/177 and ten in the smallest specimen from collection ZIN PH 177. The hyo-hypoplastral suture is short. In the smallest unnumbered specimen from collection ZIN PH 177, the plastral index is about 96.

DISCUSSION

Intraspecific variability of *Protrachyaspis* shorymensis. The material of the new species comprises the remains of individuals of different ontogenetic ages, which allows for the identification of some variants of intraspecific variability. As the humerus grows, its medial process lengthens, and the humeral diaphysis becomes narrower. At lengths between 85 mm (ZIN PH 29/177) and 103 mm (ZIN PH 31/177), the deltopectoral crest is transformed from a tubercle into a slightly curved distal anterior projection, and a notch appears between the ulnar and radial condyles. In some areas, the sculpturing changes from a network of grooves into a network of ridges. The medial keels on the neurals disappear when the carapace size is between 47 cm (reconstructed from ZIN PH 23/177) and 110 cm (reconstructed from ZIN PH 28/177, holotype). It is possible that the neurals become narrower, and the anterior costo-peripheral fontanelles close up in adults.

The nuchals and hyoplastra referred here to cf. *Protrachyaspis shorymensis* most likely belong to juvenile individuals because they contain traits of *P. shorymensis*, differ from homologous elements of other pan-cheloniids from the Shorym Formation, and have a small size. In *P. shorymensis*, the sculpturing on the surface of the carapace in the shape of a network of grooves appears when the carapace length is between 18 cm (reconstructed from ZIN PH 38/177) and 36 cm (reconstructed from ZIN PH 22/177); the anterolateral projections of the nuchal are shortened, the hyoplastron becomes narrower as

it grows, and the anterior medial process becomes longer in proportion to the size of the hyoplastron.

Comparison of *Protrachyaspis shorymensis* **with morphologically and geologically close pancheloniids**. Another pan-cheloniid, previously described from the Shorym Formation, is a large individual ZIN PH 1–12/177 + MRLHM n/n from the Kuyulus locality, referred to "*Allopleuron*" qazaq*stanense*. The new species can be distinguished from this specimen by the posteriorly notched frontoparietal scute; serrated ridges of the dentary; the lateral process located close to the middle part of the humerus; the deltopectoral crest forming a distally curved anterior projection; and the sculptured external surface of the shell.

The new species can be compared with Argillochelys cuneiceps by the parietal bones, which are known in both species and characterized by the presence of the posteriorly notched frontoparietal scute and a single parietal scute. In addition, both species seem to share the presence of a developed lingual ridge on the upper triturating surface. The new species differs from A. cuneiceps in the concave edge of the parietal bone in contact with the postorbital (Owen and Bell 1849: tab. XV), and from the specimen of A. antiqua from the upper Lutetian-Bartonian of the Vyshgorod locality (Ukraine) by the posteriorly notched frontoparietal scute, serrated ridges of the dentary, medially interrupted lingual ridges and the presence of sculpture on the external surface of the carapace (Zvonok and Danilov 2017). The same characters distinguish the new species from Argillochelys sp. from the Bartonian of the Ak-Kaya 1 locality (Russia), except that one of the parietal specimens of Argillochelys sp. (ZIN PH 32/153) has the posteriorly notched frontoparietal scute. In addition, the new species differs from Argillochelys sp. from the Ak-Kaya 1 locality by morphology of the humerus and femur (Zvonok and Danilov 2019).

The new species differs from *Ashleychelys palmeri* in the posteriorly notched frontoparietal scute, distally displaced lateral process of the humerus and the deltopectoral crest forming a curved distally anterior projection, as well as a higher major trochanter of the femur (Weems and Sanders 2014).

The new species shares with Osonachelus decorata a single parietal scute and shell morphology (de Lapparent de Broin et al. 2014). Protrachyaspis shorymensis differs from O. decorata in the presence of the symphyseal and lingual ridges of the dentary, and the presence of serrations on these ridges, the close position of the lateral process to the middle part of the humerus, the deltopectoral crest forming a slightly distally curved anterior protrusion and in the presence of deep sculpturing in the pattern of a network of grooves on the entire external surface of the carapace.

The new species shares with its sister taxon *Trachyaspis lardyi* the morphology of the dentary and propodium, and deep sculpturing of the carapace. The characters distinguishing *P. shorymensis* from *T. lardyi* are listed in the Diagnosis.

Comparison of the new species with *Bryochelys* waterkeynii, which likely has deep sculpturing on the external surface of the shell in adult individuals, is difficult, since the latter was described from disarticulated and only partially depicted remains (Smets 1887, 1888). However, in *B. waterkeynii*, unlike the new species, the major trochanter of the femur is weakly protruded (Smets 1887: fig. V), and the posterior neurals become irregular, reduced and rounded, and some are completely surrounded by the costals (Smets 1888: p. 210).

The new species does not differ from the very fragmentary specimens of Pan-Cheloniidae indet., recently described from the Bakhmutovka, Bulgakovka, Krasnorechenskoe and Tripolye localities of the upper part of the Buchak – lower part of the Kiev formations (Zvonok and Danilov 2017, 2023). The new species shares with these materials the presence of deep sculpturing over the entire external surface of the carapace and narrow neurals in large individuals. The vertebral scutes of Pan-Cheloniidae indet. are narrower than those of *P. shorymensis*. The shape of the vertebral scutes is known only in the medium-sized (subadult) individuals of P. shorymensis (and they are already quite narrow; Fig. 7) and in the large (adult) individuals of Pan-Cheloniidae indet. (ZIN PH 2/239 from the Tripolye locality and ZIN PH 1/259 from the Bulgakovka locality (Zvonok and Danilov 2017: fig. 10J; Zvonok and Danilov 2023: fig. 10K)). Pan-cheloniids have a tendency towards narrowing of the vertebral scutes with ontogenetic growth (see diagnosis of Carolinochelys wilsoni in Weems and Sanders 2014); therefore, we interpret this difference in the shape of vertebral scutes as a variant of age variability. The sinuous shape of the intervertebral sulcus described in *P. shorymensis* is also visible on the costal fragment of Pan-Cheloniidae indet. ZIN PH 2/239 from the Tripolye locality (Zvonok and Danilov 2017: fig. 10J). Thus, pan-cheloniids from the deposits of the upper part of the Buchak – lower part of the Kiev formations belong to the same genus or are close to it and are defined here as cf. *Protrachyaspis* sp. These records expand the geographical and stratigraphic distribution of *Protrachyaspis*-like pan-cheloniids.

The proximal part of a humerus of Pan-Cheloniidae indet. (= Cheloniinae gen. et sp. indet.; ZIN PH 3/3) was described from the upper Ypresian lower part of the Alay Formation at the Andarak 2 locality (Kyrgyzstan; Danilov and Averianov 1997). This is the earliest known Cenozoic pan-cheloniid humerus with a distally displaced lateral process. However, the degree of displacement of the deltopectoral crest in this specimen more closely resembles that of *Eochelone brabantica* (Grant-Mackie et al. 2011: fig. 3F) than *P. shorymensis*.

The results of the comparison are also given in Table 1.

Results of parsimony analysis. The initial stage of parsimony analysis resulted in 105 MPTs with a length of 1777 steps. An additional TBR branch-swapping resulted in 3456 MPTs. The results of this analysis yielded a strict consensus tree (Fig. 10B), in which the size and composition of the Pan-Cheloniidae clade (excluding newly coded taxa) differ from those of Evers et al. (2019: fig. 18A). In

particular, the clade *Cabindachelys landanensis* Myers et al., 2018 + *Ctenochelys* sp. + *Peritresius martini* Gentry et al., 2018, as well as the taxa *Allopleuron hofmanni* (Gray, 1831) and *Nichollsemys baieri* Brinkman et al., 2006 were not included in the Pan-Cheloniidae clade. The clade *C. landanensis* + *Ctenochelys* sp. + *P. martini* was found at the base of the crown group Chelonioidea. *Allopleuron hofmanni* and *N. baieri* were placed in the clade Dermochelyidae.

At its base, the Pan-Cheloniidae clade (in our case, the crown group and the total group coincide) forms a polytomy, which includes: Chelonia mydas, Natator depressus, Erquelinnesia gosseleti (Dollo, 1886), Osonachelus decorata, clades Procolpochelys charlestonensis Weems et Sanders, 2014 + P. grandaeva, Carolinochelys wilsoni + Pacifichelys spp., Eochelone brabantica + Itilochelys rasstrigin + Tasbacka aldabergeni + Puppigerus camperi, Ashleychelys palmeri + Eretmochelys imbricate + Caret $ta \ caretta + Lepidochelys \ kempii + L. \ olivacea, and$ Trachyaspis lardyi + Protrachyaspis shorymensis. Synapomorphies of the pan-cheloniid clade are: posterodorsal margin of the temporal fossa roofed by an overhanging process of the skull roof present (ch. 17, state 1); frontal margin relatively narrow, with lateral bulge of postorbital on dorsal margin of orbit

Table 1. Comparison of Protrachyaspis shorymensis with morphologically and geologically close pan-cheloniids.

Characters / Taxa	Protrachyaspis shorymensis	"Allopleuron" qazaqstanense	Ashleychelys palmeri	Eochelone voltregana	Osonachelus decorata	Puppigerus camperi	Trachyaspis lardyi
Concave edge of the parietal bone in contact with the postorbital	+	?	+	?	+	-	+
Posteriorly notched frontoparietal scute	+	-	-	?	?	_	_
Labial, lingual and symphyseal ridges of the dentary	+	+	?	?	-	-	+
Serrated ridges of the dentary (in the case of <i>P. camperi</i> the ridges are absent)	+	-	?	?	-	_	+
Deltopectoral crest with a slightly distally curved anterior protrusion	+	-	-	-	-	-	+
Lateral process located close to the middle part of the humerus	+	_	-	-	_	_	+
High major trochanter of the femur	+	?	_	?	_	_	+
Major trochanter of the femur connected to the small trochanter by a crest with a notch	+	?	+	?	+	?	+
Carapace with deep sculpturing	+	_	+	_	+	_	+
Long anterior medial process of the hyoplastron	+	?	_	?	+	_	_

Notes: + present; - absent.



(ch. 45, state 1); foramen palatinum posterius absent (ch. 95, state 2). Synapomorphies of the *T. lardyi* + *P. shorymensis* clade are: sculpturing of dorsal surface (carapace) and ventral surface (plastron) of shell present, development of vermiculations, striations, or pitting (ch. 192, state 1); lateral process of humerus located at middle of humeral shaft (ch. 332, state 3); prominent anterior projection of lateral process of humerus present (ch. 333, state 1). Bremer support for this clade is 2. The position of *P. shorymensis* as the sister taxon of *T. lardyi* suggests a long ghost lineage throughout the Bartonian–Aquitanian (about 20.7 million years) preceding the appearance of the latter (Fig. 10).

In the 50% majority rule consensus tree (Fig. 10A), 87% of the trees include the clade P. shorymensis + T. lardyi, which is sister to N. depressus within the Chelonini clade (sensu Naro-Maciel et al. 2008). A synapomorphy of the clade P. shorymensis + T. lardyi + N. depressus is the presence of a posterior notch of the pygal (ch. 226, state 0). However, the posterior notch of the pygal, as seen in the N. depressus specimen depicted in Zangerl et al. (1988: fig. 14), is weak, whereas in P. shorymensis the pygal is unknown. On the other hand, the estimated time of separation between N. depressus and the clade P. shorymensis + T. lardyi is no later than the middle Lutetian (ca. 45 mya), considering cf. Protrachyaspis sp. from the upper Buchak – lower Kiev formations. Although somewhat older than the average, this timeframe does not contradict the time of divergence of N. depressus from Ch. mydas, which likely occurred before this. According to the results of molecular studies, N. depressus diverged from *Ch. mydas* 14.08 – 60.05 mya (95% highest posterior densities (HPD); median – about 34 mva; Naro-Maciel et al. 2008) or 21.92 – 52.51 mya (95% HPD; median – 36.43 mya; Duchene et al. 2012). Phylogenetic analyzes by Hirayama (1994) and Parham and Pyenson (2010) placed *T. lardyi* as the sister taxon to *N. depressus*, which is partly consistent with our results. Considering that the serrations on the dentary ridges are present in the clade *P. shorymensis* + *T. lardyi* and in a more basal *Ch. mydas*, this may support the proposal of Parham and Pyenson (2010) that *N. depressus* evolved from a shearing-specialized ancestor.

Synapomorphies of the clade Chelonini, including the clade *P. shorymensis* + *T. lardyi*, in the resulting trees are as follows: triturating surface of maxilla with labial, lingual, and accessory ridge(s) (ch. 59, state 2), processus trochlearis oticum of quadrate is present, very reduced (ch. 80, state 1), symphyseal ridge of dentary is present (ch. 176, state 1), surangular with anteromedial process forming a vertical lamina that projects anteriorly into the fossa meckelii is absent (ch. 180, state 0), position of costo-peripheral fontanelles and exposure of dorsal rib ends limited to parts of the carapace (ch. 213, state 0). In addition, the time of separation of the clades Chelonini and Carettini according to molecular data occurred about 35.59-91.38 mya (95% HPD; median - about 63 mya; Naro-Maciel et al. 2008) or 50.00-67.44 mya (95% HPD; median - 55.68 mya; Duchene et al. 2012), which is in agreement with the time of the first appearance of Protrachyaspis-like pan-cheloniids (ca. 45 mya) within this clade. The position of Protrachyaspis-like pan-cheloniids within the clade Chelonini in the 50% majority rule consensus tree (Fig. 10A) is the first evidence of such an early (no later than the Lutetian) diversification of crown cheloniids.

Lifestyle of *Protrachyaspis shorymensis*. The symphysis of the dentaries of *Protrachyaspis shorymensis* (ZIN PH 35/177) simultaneously has labial, symphyseal and lingual ridges, of which the labial

Fig. 10. Chronograms of Pan-Chelonioidea evolution: A - 50% majority rule consensus tree; B - strict consensus tree. Numbers below the clades in Fig. 10A indicate the percentage of trees supporting that clade; clades present in all trees are not labeled. Numbers to the right of the geochronological scale represent millions of years ago.

The data on the stratigraphical distribution of pan-cheloniids is given according to the following sources: Ashleychelys palmeri, Osonachelus decorata, Puppigerus camperi, Trachyaspis lardyi (see Material and Methods section); Allopleuron hofmanni, Archelon ischyros, Calcarichelys gemma, Chelosphargis advena, Ctenochelys spp., Desmatochelys lowi, D. padillai, Protostega gigas, Rhinochelys pulchriceps and Toxochelys spp. (Danilov et al. 2022); Cabindachelys landanensis, Eochelone brabantica, Erquelinnesia gosseleti, Tasbacka aldabergeni (Zvonok and Danilov 2023); Carolinochelys wilsoni, Pacifichelys spp. and Procolpochelys spp. (Weems and Brown 2017: tab. 2); Bouliachelys suteri (Kear and Lee 2006); Corsochelys haliniches (Zangerl 1960); Eosphargis breineri (Nielsen 1959); Itilochelys rasstrigin (Danilov et al. 2010); Nichollsemys baieri (Brinkman et al. 2006); Notochelone costata (Kear 2003); Ocepechelon bouyai (Bardet et al. 2013); Peritresius martini (Gentry et al. 2018); Rhinochelys nammourensis (Tong et al. 2006) and Santanachelys gaffneyi (Hirayama 1998).

ridges are finely serrated. The morphology of the triturating surface of the dentaries (ZIN PH 35/177) differs from that of Trachyaspis lardyi only in the less pronounced serrations on the labial ridge and less developed symphyseal and lingual ridges, with no visible serrations on them. However, given the small size of ZIN PH 35/177 (45 mm), this may well be due to age variability and the serrations in this individual may not have fully developed. The combination of sharp labial, symphyseal and lingual ridges of the dentary and serration on the ridges of the triturating surfaces is observed in the herbivorous cheloniid Che*lonia mydas* and is generally characteristic of turtles with a herbivorous diet (Parham and Pyenson 2010; Figgener et al. 2019; Foth et al. 2017). Therefore, a herbivorous diet can be assumed for P. shorymensis.

Protrachyaspis shorymensis is distinguished by limbs more adapted to a pelagic lifestyle than those of other Paleogene pan-cheloniids. In particular, the humerus, with a wide diaphysis, an anteriorly extended deltopectoral crest, and a distally displaced lateral process, resembles the humeri of dermochelyids (Karl and Tichy 2007: fig. 2). The femora, with highly protruded trochanters connected by a crest to the notch, appear more specialized than those of other Paleogene pan-cheloniids, including *Osonachelus decorata* (de Lapparent de Broin et al. 2014: fig. 10F).

Paleogeographic distribution of the new genus and species. Protrachyaspis shorymensis is known only from the type Shorym Formation, located within a relatively confined area along the 44°N latitude on the Mangyshlak Peninsula (Fig. 1). The Shorym Formation formed around an island that occupied the current location of the Karatau Ridge; this island was located in the central part of eastern Tethys, far from the continental landmass (Fig. 10; Liverovskava 1960; Zhelezko and Kozlov 1999). Considering the specialized pelagic lifestyle of the new species (see the previous section), its range was unlikely to be restricted to a small body of water and could be cosmopolitan. This assumption is supported by the report of cf. Syllomus sp. from the Bartonian Dolime Ouarry locality of the northwest Atlantic, although this material is undescribed and its taxonomic attribution needs to be confirmed (Ivany et al. 1990). The beaches on which P. shorymensis laid eggs could have been located on the shores of eastern Tethys, since the collection from the Shorym Formation contains bones of small (juvenile) individuals. In addition, the remains of sea turtles, referred to cf. Protrachyaspis



Fig. 11. The distribution of *Protrachyaspis*-like pan-cheloniids on the paleogeographical map of the Tethys and adjacent areas in the late Lutetian–Bartonian: 1 – *Protrachyaspis shorymensis*, Karakeshi, Kert, Kuyulus, Monata and Tuzbair localities, Shorym Formation, Bartonian; 2 – cf. *Protrachyaspis* sp., Bakhmutovka, Bulgakovka, Krasnorechenskoe and Tripolye localities, the upper part of the Buchak – lower part of Kiev formations, late Lutetian. The map is modified from Kazmin and Natapov (1998).

sp., are also known from slightly older upper Lutetian deposits of the upper part of the Buchak – lower part of the Kiev formations on the northern periphery of eastern Tethys (Zvonok and Danilov 2023; Fig. 11).

CONCLUSIONS

Protrachyaspis shorymensis gen. et sp. nov. described in this paper, along with Osonachelus decorata, is the second Eocene pan-cheloniid with a deeply sculptured carapace and limbs highly adapted to a pelagic lifestyle. After the Cretaceous–Paleogene bottleneck, *P. shorymensis* is an early pan-cheloniid highly specialized to a pelagic lifestyle that changes our understanding of the systematic and ecological diversity of pan-cheloniids in the middle Eocene, and provides probable evidence in support of the early A new Trachyaspis-like pan-cheloniid turtle

Paleogene diversification of crown cheloniids based on molecular data. *Protrachyaspis shorymensis* is the sister taxon to the Neogene *Trachyaspis lardyi*, which suggests a long ghost lineage throughout the Bartonian-Aquitanian (about 20.7 million years) preceding the appearance of the latter. The description of the new species has also made possible the clarification of the systematic affiliation of pan-cheloniid materials from four localities in the upper part of the Buchak – lower part of Kiev formations (upper Lutetian) in Eastern Europe, which may also belong to this genus.

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