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ITILOCHELYS RASSTRIGIN GEN. ET SP. NOV, A NEW HARD-SHELLED SEA TURTLE (CHELONIIDAE *SENSU LATO*) FROM THE LOWER PALEOCENE OF VOLGOGRAD PROVINCE, RUSSIA

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ABSTRACT

Itilochelys rasstrigin, gen. et sp. nov., a new hard-shelled sea turtle (Cheloniidae *sensu lato*), is established based on a partial skull, two lower jaws, a humeral bone and cervical vertebrae I–III from the Lower Paleocene of Volgograd Province, Russia. *Itilochelys rasstrigin* differs from other cheloniids s.l. by the following combination of characters: (1) long skull; (2) short snout; (3) deep cheek emargination; (4) frontal contributing to orbital margin; (5) prefrontal/postorbital contact absent; (6) long anteroventral process of postorbital; (7) extensive secondary palate; (8) moderate vomer length on triturating surface; (9) deep and narrow midline groove on triturating surface through vomer length; (10) swellings lateral to midline groove present; (11) long lower jaw symphysis; (12) concave lower triturating surface; (13) blunt and shallow symphyseal ridge ending in a triangular elevation; (14) lingual ridges on the lower jaw absent. The new taxon increases diversity of stem-cheloniids and represents the most complete finding of these turtles in Russia.

Key words: Cheloniidae, Paleocene, Russia, Testudines, Volgograd Province

ITILOCHELYS RASSTRIGIN GEN. ET SP. NOV, НОВАЯ ТВЕРДОПАНЦИРНАЯ МОРСКАЯ ЧЕРЕПАХА (CHELONIIDAE *SENSU LATO*) ИЗ НИЖНЕГО ПАЛЕОЦЕНА ВОЛГОГРАДСКОЙ ОБЛАСТИ, РОССИЯ

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РЕЗЮМЕ

Itilochelys rasstrigin gen. et sp. nov., новая твердопанцирная морская черепаха (Cheloniidae *sensu lato*), установлена на основе неполного черепа, двух нижних челюстей, плечевой кости и I–III шейных позвонков из нижнего палеоцена Волгоградской области, Россия. *Itilochelys rasstrigin* отличается от других хелониид следующей комбинацией признаков: (1) длинный череп; (2) короткое рыло; (3) глубокая нижняя височная вырезка; (4) участие лобных костей в формировании краев глазниц; (5) контакт предлобной/заглазничной костей отсутствует; (6) длинный антеровентральный отросток заглазничной кости; (7) хорошо развитое вторичное костное нёбо; (8) сошник умеренной длины на альвеолярной поверхности; (9) глубокий и узкий средин-

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ный желоб на альвеолярной поверхности вдоль всей длины сошника; (10) вздутия по бокам от срединного желоба имеются; (11) длинный нижнечелюстной симфиз; (12) вогнутая альвеолярная поверхность нижней челюсти; (13) тупой и низкий симфизный гребень, оканчивающийся треугольным возвышением; (14) лингвальные гребни нижней челюсти отсутствуют. Новый таксон увеличивает разнообразие стволовых хелониид и представляет наиболее полную находку этих черепах в России.

Ключевые слова: Cheloniidae, палеоцен, Россия, Testudines, Волгоградская область

INTRODUCTION

Cretaceous and Paleogene turtles of European Russia are poorly known. They are represented by remains of various sea turtles (Chelonioidea), soft shell turtles (Trionychidae; beginning with Paleocene) and undetermined turtle material (Averianov and Yarkov 2000, 2004; Averianov 2002). Most of these remains come from several Late Cretaceous and Paleocene localities in Volgograd Province (Averianov and Yarkov 2000, 2004). Usually these materials are very fragmentary and allow only family level determinations. In this paper we describe more complete turtle specimens, including a partial skull and other remains of a hard-shelled sea turtle (Cheloniidae *sensu lato*), from the lower Paleocene (Danian) deposits of Rasstrigin locality (= Rasstrigin 2), Dubovka District, Volgograd Province, Russia (Fig. 1). This material is attributed to a new genus and species – *Itilochelys rasstrigin* gen. et sp. nov. We follow a phylogenetic taxonomy and use Cheloniidae *sensu lato* for the stem-based definition of Cheloniidae and Cheloniidae *sensu stricto* for the crown-group name (Lynch and Parham 2003; Joyce et al. 2004). Stem-cheloniids include mostly Cretaceous and Paleogene forms with primitive morphology (see Parham and Fastovsky 1997). There are only two stem-cheloniids previously reported from Russia. Both of them come from the late Paleocene of Volgograd Province and are based on very fragmentary remains: *Euclastes* sp. from Karpovka (= Bereslavka 2a) locality and cf. *Tasbacka* sp. from Malaya Ivanovka locality (Nessov and Yarkov 1989; Averianov and Yarkov 2000; Averianov 2002; Lynch and Parham 2003). Thus, *Itilochelys rasstrigin* not only increases diversity of stem-cheloniids, but also represents the most complete finding of these turtles in Russia.

Institutional abbbreviations. BMNH, Natural History Museum, London, Great Britain; CCMGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

MATERIAL

In addition to the materials described in this paper, the following taxa of stem-cheloniids were used for comparison: "*Argillochelys*" *africana* Tong and Hirayama, 2008, as described by Tong and Hirayama (2008), we consider this taxon as separate from typical *Argillochelys* Lydekker, 1889, due to many differences from the latter and until its relationships is shown by phylogenetic analysis (see Discussion); *Argillochelys cuneiceps* (Owen, 1849) (type species of *Argillochelys*), as described by Owen and Bell (1849) and personal observations (IGD) of BMNH 41636, the holotype, based on photos offered by Ren Hirayama; *Eochelone brabantica* Dollo, 1903 (type species of *Eochelone* Dollo, 1903), as described by Casier (1968); *Euclastes hutchisoni* Lynch and Parham, 2003 (one of the better-known species of *Euclastes* Cope, 1867; Lynch and Parham 2003), as described by Lynch and Parham (2003); *Puppigerus camperi* Gray, 1831 (type species of *Puppigerus* Cope, 1871), as described by Moody (1974); *Tasbacka aldabergeni* Nessov, 1987 (type species of *Tasbacka* Nessov, 1987), as described by Nessov (1987) and personal observations of CCMGE 1/12175, the holotype, by IGD.

SYSTEMATICS

Testudines Batsch, 1788

Cryptodira Cope, 1868

Chelonioidea Baur, 1893

Cheloniidae Bonaparte, 1832 *sensu lato*

***Itilochelys rasstrigin* gen. et sp. nov.**
(Figs. 2–11)

Etymology. The genus name is after *Itil'*, the medieval Arabian/Persian name of Volga River; and χέλυς, the Greek word for turtle. The species name is after Rasstrigin locality.

Holotype. ZIN PH 1/118, partial skull with a disarticulated lower jaw and I–III cervical vertebrae.

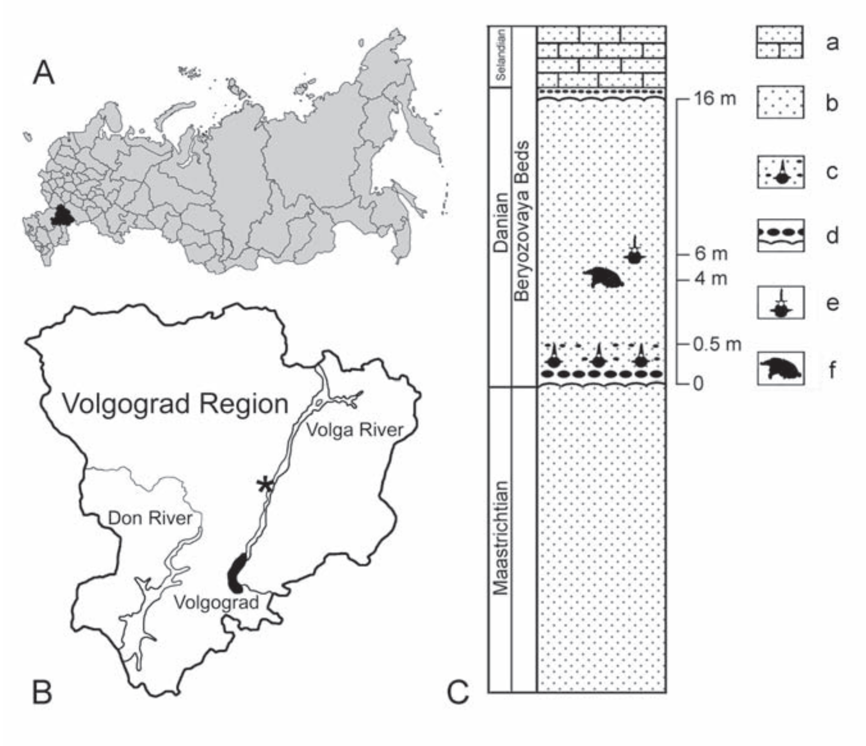


Fig. 1. Locality and geology data of Rasstrigin locality: A – map of Russia with Volgograd Province filled with black; B – map of Volgograd Province with Rasstrigin khutor shown by asterisk; C – schematic stratigraphic section in the Krutoi ravine, Rasstrigin 2 locality: a – sandstone; b – sand; c – remains of mosasaurs in the layer with dispersed phosphorites; d – phosphorites on the weathered horizon; e – crocodile vertebra; f – turtle remains.

Referred material. ZIN PH 2/118, dentary; ZIN PH 3/118, right humerus. All material was collected by the one of us (AAY) in 1990.

Locality, horizon, and age. Rasstrigin 2 locality, middle of Krutoi ravine, 1 km North-West of Rasstrigin khutor, about 80 km North-North-West of Volgograd, Dubovka District, Volgograd Province, Russia; the upper fossiliferous level, lower Paleocene, Danian (Averianov and Yarkov 2004).

Diagnosis. Can be differentiated from other cheloniids s.l. by the following combination of characters: (1) long skull; (2) short snout; (3) deep cheek emargination; (4) frontal contributing to orbital margin; (5) prefrontal/postorbital contact absent; (6) long and narrow anteroventral process of postorbital; (7) extensive secondary palate; (8) moderate vomer length on triturating surface; (9) deep and narrow midline groove on triturating surface through vomer length; (10) swellings lateral to midline groove present; (11) long lower jaw symphysis; (12) concave lower triturating surface; (13) blunt and shallow symphyseal ridge ending in a triangular elevation; (14) lingual ridges on the lower jaw absent.

Description and comparisons. The skull has a roughly triangular outline in dorsal view, with a narrow snout. The ratio of its width (at the jugals) to estimated length (from tip of the snout to the occipital condyle) is about 0.84. Thus, the skull is relatively longer than in *Argillochelys cuneiceps* (the same ratio is about 0.93) and *Euclastes hutchisoni* (1.05), but shorter than in *Puppigerus camperi* (0.60), *Eochelone brabantica* and *Tasbacka aldabergeni* (both – 0.78). The skull is high, as in living cheloniids, and thus different from the much lower skull of *Euclastes* spp. The orbits are large and laterally directed as in most cheloniids, except some *Euclastes* (see Lynch and Parham, 2003). The snout (preorbital part of the skull) is relatively short making up about 20% of the skull length, similar to *Argillochelys cuneiceps*, but shorter than in other cheloniids s.l. used for comparison. The apertura narium externa is oval-shaped and directed anterodorsally. The skull is well roofed, with a shallow temporal emargination. The cheek emargination, as reconstructed, is rather deep, similar to "*Argillochelys*" *africana*.

In palatal view, the secondary palate is extensive; its maximal length makes up about 60% of the skull length, similar to *Puppigerus camperi* and *Tasbacka aldabergeni*, unlike *Argillochelys cuneiceps* and *Euclastes hutchisoni*, which have less developed (moder-

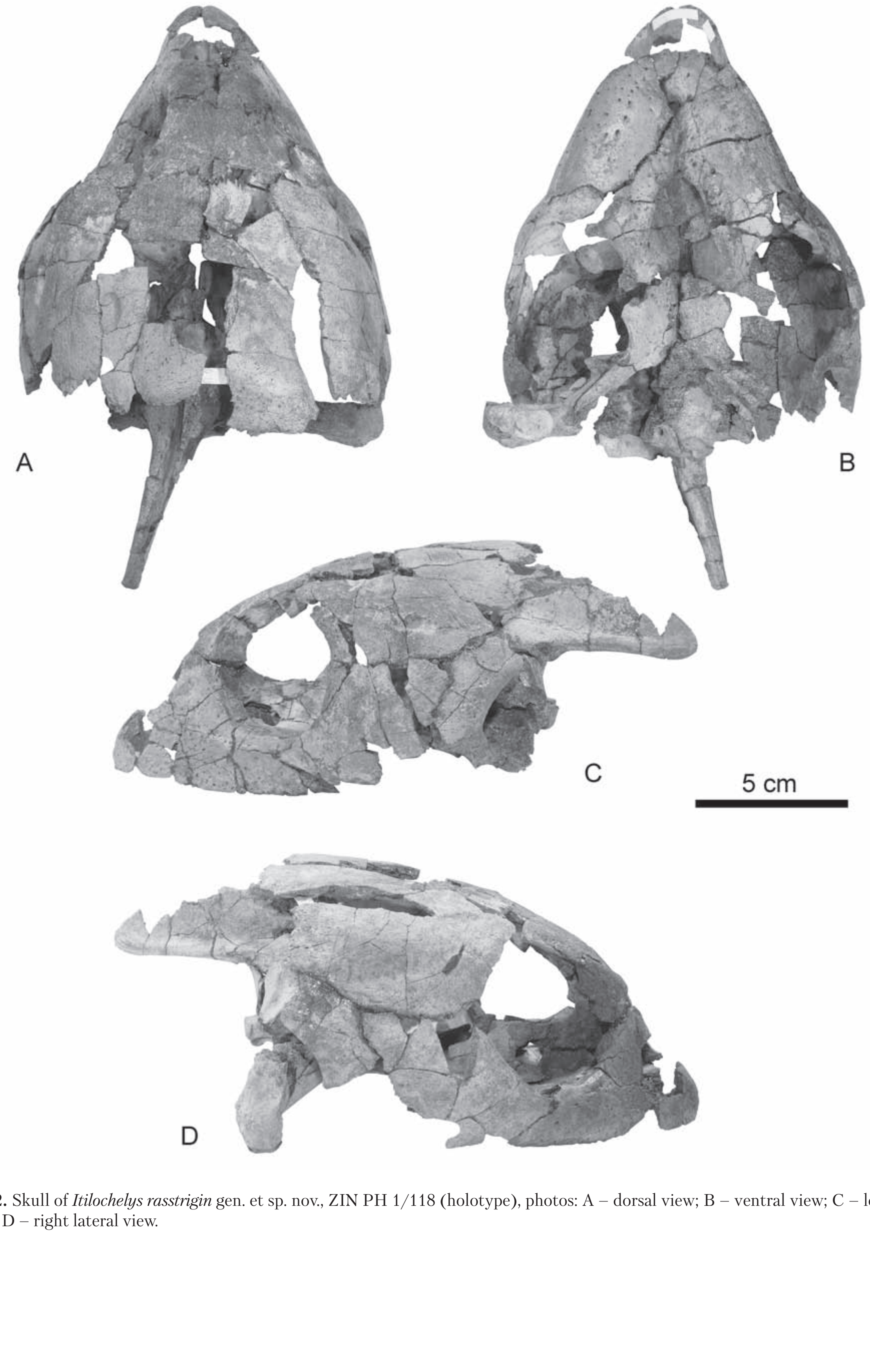


Fig. 2. Skull of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), photos: A – dorsal view; B – ventral view; C – left lateral view; D – right lateral view.

ate) secondary palate (45–50% of the skull length), and *Eochelone brabantica*, in which the secondary palate is absent.

Only parts of scale sulci are visible, but nevertheless allow discerning supraorbital, temporal, parietal, jugal and maxilla scales. The scale pattern of the middle part of the skull roof (i.e. presence and number of frontal, frontoparietal and additional scales) is not clear.

The snout area of the skull, although somewhat damaged, shows that the nasal is clearly absent. Both prefrontals are well visible, although their contacts with the maxillae are cracked on both sides. The prefrontal is an anteroposteriorly elongated element as seen from above, forming the upper rim of the apertura narium externa and anterior portion of the upper margin of the orbit. The midline prefrontal/prefrontal contact makes up about one third of the total prefrontal length, as also observed in *Tasbacka aldabergeni*. The same contact is slightly longer in *Argillochelys cuneiceps*, *Eochelone brabantica* and *Euclastes hutchisoni* and much longer in *Puppigerus camperi*, making up about half of the total prefrontal length. The prefrontal contacts the frontal posteromedially and does not reach the postorbital posteriorly, thus not separating the frontal from the orbital margin. This is similar to the condition in many cheloniids s.l., but unlike the condition in "*Argillochelys*" *africana* and *Euclastes* spp.

In the fossa orbitalis, the descending process of the prefrontal contacts the palatine and the vomer posteromedially and the maxilla laterally, although sutures between these bones are not always clear.

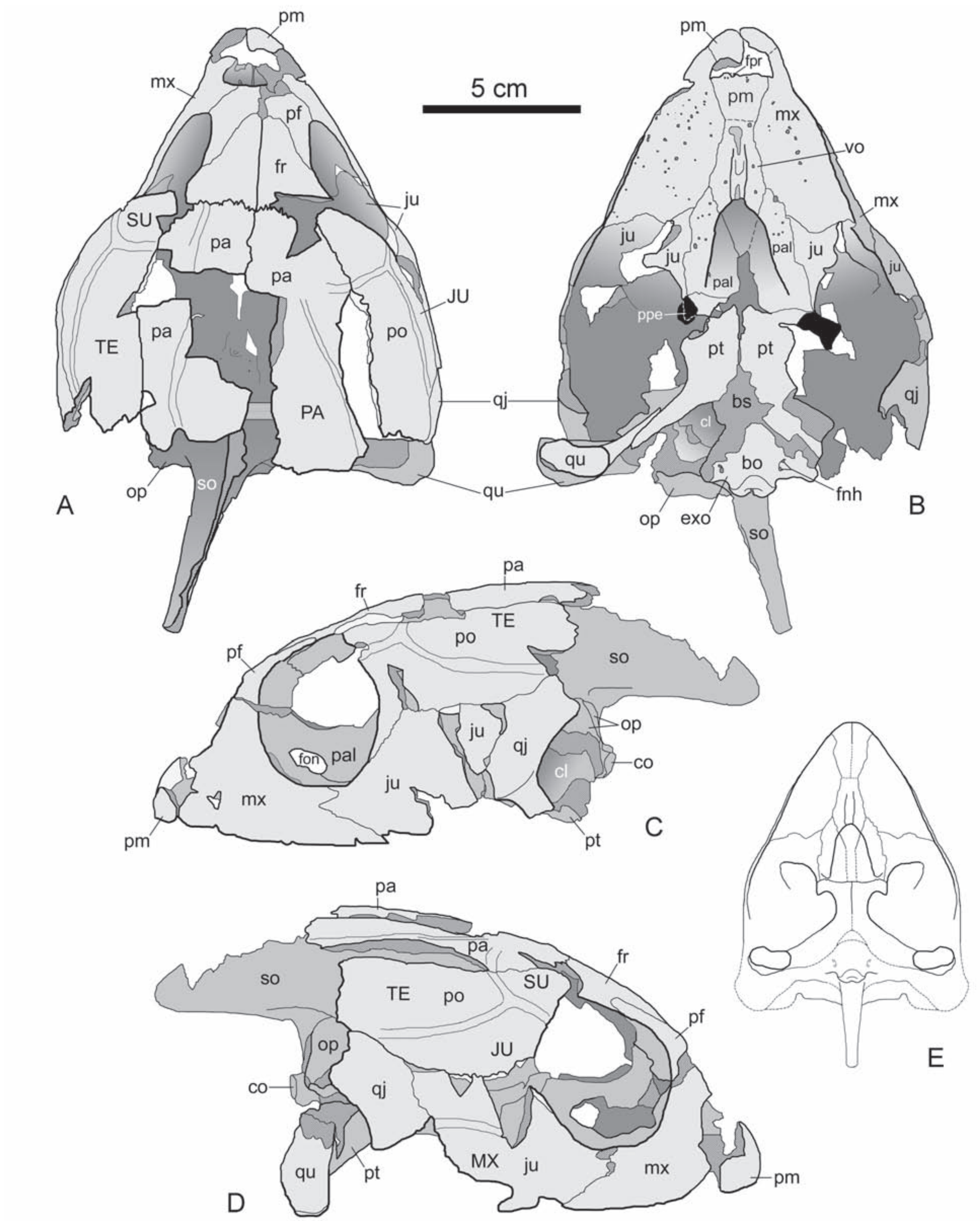
The left frontal is complete, whereas the right one lacks its most posterior portion. The two frontals form a triangle as seen from above. The frontal contacts the prefrontal by a strongly anteriorly convex suture, the parietal posteriorly by a straight transverse suture and the postorbital posterolaterally by a short suture. The frontal makes a short contribution to the orbital margin preventing the prefrontal/postorbital contact.

The parietals are not complete, their dorsal plates are not connected with the the inferior parietal processes. The parietal is the largest element of the skull roof, forming the medial portion of the temporal emargination. It contacts the frontal anteriorly and the postorbital laterally by a very long suture. There is a small notch at the posterior border of the parietal, at point where the parietal is crossed with the sulcus between parietal and temporal scales. Posterolaterally, the parietal has a short sutural surface for contact with the squamosal, which is not preserved in the described specimen. The processus inferior parietalis has contacts (from front to back) with the pterygoid, prootic and supraoccipital. The foramen nervi trigemini is well visible on the left side of the braincase. It is a large oval-shaped opening bordered by the processus inferior parietalis anterodorsally, prootic posteriorly and pterygoid ventrally. The processus inferior parietalis has short anterior extension to the lateral braincase wall similar to other Cheloniidae *sensu lato*.

Both postorbitals are preserved and complete. The right postorbital is missing its anteroventral process, whereas the left one has a little damage at the posterior and medial borders. The postorbital is a large and anteroposteriorly elongated flat bone, forming the posterodorsal portion of the orbital margin. Its proportions are similar to those of "*Argillochelys*" *africana*, *Eochelone brabantica*, and *Tasbacka aldabergeni*, but different from those of *Puppigerus camperi*, which has a much wider postorbital. The postorbital contacts the frontal anteriorly at the orbital margin, the jugal anteroventrally, the quadratojugal posteroventrally and the parietal medially. Anteriorly, the postorbital forms a long and narrow anteroventral

Fig. 3. Skull of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), drawings: A – dorsal view; B – ventral view; C – left lateral view; D – right lateral view; E – reconstruction of the ventral view of the skull (without scale). Bones are filled with light-grey (foreground) and dark-grey (background). Matrix is filled with black. Breakages are hatched.

Abbreviations: ang – angular; art – articular; bo – basioccipital; bs – basisphenoid; btb – basis tuberculi basalis; cl – cavum labyrinthicum; co – condylus occipitalis; cor – coronoid; den – dentary; ds – dorsum sellae; exo – exoccipital; facci – foramen anterius canalis carotici interni; fcl – foramen caroticum laterale; fdm – foramen dentofaciale majus; fim – foramen intermandibularis medius; fm – fossa meckelii; fna – foramen nervi abducentis; fnh – foramen nervi hypoglossi; fnt – foramen nervi trigemini; fnv – foramen nervi vidiani; fon – foramen orbito-nasale; fpr – foramen praepalatinum; fr – frontal; foramen stapedio-temporalis; JU – jugal scale; ju – jugal; MX – maxilla scale; mx – maxilla; op – opisthotic; pa – parietal; PA – parietal scale; pal – palatine; pcl – processus clinoideus; pf – prefrontal; pm – premaxilla; po – postorbital; ppe – processus pterygoideus externus; pr – prootic; pra – prearticular; pt – pterygoid; qj – quadratojugal; qu – quadrate; rb – rostrum basisphenoidale; sc – sulcus cavernosus; scm – sulcus cartilaginis meckelii; so – supraoccipital; st – sella turcica; SU – supraorbital scale; sur – surangular; TE – temporal scale; vo – vomer.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process, which considerably increases contribution of the postorbital to the orbital margin. This process is much less developed in *Argillochelys cuneiceps* and *Tasbacka aldabergeni* and absent in other cheloniids used for comparison. Posteriorly, the postorbital has a wide sutural surface for contact with the squamosal. The postorbital does not reach the temporal emargination, as in all cheloniids. There is a low, sharp and transversally directed ridge (transverse ridge) on the ventral surface of the postorbital, behind the orbit. It continues as a ridge on the jugal and extends medially on the postorbital. It may have reached the parietal as well, but this area is damaged in the described specimen. A similar ridge is reported, among compared cheloniids, for "*Argillochelys*" *africana*, *Tasbacka aldabergeni* and *Euclastes hutchisoni*.

Both jugals, although damaged, allow reconstructing their shape. In lateral view, the jugal forms the posteroventral rim of the orbit and the anterior half of the cheek emargination. It contacts the maxilla anteriorly below the orbit, the postorbital dorsally, and the quadratojugal posteriorly. The posterior part of the jugal's free border is notched, forming the anterior border of the cheek emargination. This notch is absent in other cheloniids used for comparison. In ventral view, the jugal makes a small contribution to the posterior end of the triturating surface. The internal surface of the jugal bears a strong ridge posteroventral to the orbit, which is the continuation of the postorbital ridge (see above). Another blunt and low ridge extends from the point much lower than the point where the jugal-postorbital ridge meets the jugal/postorbital suture to the cheek emargination. This condition is similar to *Tasbacka aldabergeni* and different from "*Argillochelys*" *africana*, where this low ridge begins at the mentioned point.

Incomplete quadratojugals are preserved on both sides of the skull and represented only by their upper parts. The quadratojugal is a sheet of bone anterodorsal to the quadrate. It forms the posterior portion of the cheek margin and the anterior rim of the cavum tympani. It contacts the jugal anteriorly and the postorbital dorsally. Other contacts of the quadratojugal (with the squamosal and quadrate) are not preserved.

The squamosals are not preserved, although their contacts with the parietal and postorbital are clear.

Both premaxillae are damaged and represented by fragments. Their contacts with the maxillae are preserved only partially, whereas the area of their contacts with the vomer is damaged. The suture between the premaxillae is visible only anteriorly and seems to be obliterated posteriorly. The dorsal surface of the premaxilla bears a pair of anteroposteriorly directed grooves. In ventral view, the premaxilla is wider anteriorly than posteriorly and nearly as long as the palatal portion of the vomer.

Both maxillae are preserved, although their anterior margins are damaged. In lateral view, the maxilla contributes to the anterior and lower rim of the orbit and contacts the premaxilla anteriorly, the jugal posteriorly and the prefrontal anterodorsally. In dorsal view, the maxilla forms the lateral portion of the orbital floor, and contacts the palatine medially, the jugal posteriorly and the prefrontal anteromedially. The foramen orbito-nasale is preserved on the left side of the skull, but almost completely damaged on the right side. It is formed by the maxilla laterally and the palatine medially and posteriorly. It is unclear if the prefrontal contributes to its anterior margin or not. In ventral view, the maxilla forms most of the triturating surface and its labial ridge. The secondary palate (maximal length) is extensive, about 60% of the skull length, which is similar to those of *Puppigerus camperi* and *Tasbacka aldabergeni*. The anterior margin of the apertura narium interna is at about two thirds of the total length of the triturating surface, which is similar to the condition in "*Argillochelys*" *africana* and *Euclastes hutchisoni*, but different from those in other cheloniids used for comparison. The apertura narium interna itself is relatively narrow and long in ventral view. The triturating surface is smoothly curved with a distinct midline groove (see vomer) and a pair of blunt swellings. The swellings are well preserved and mainly formed by the maxilla. They are anteroposteriorly elongated, start posterior to the maxilla/premaxilla suture and reach maxilla/jugal suture posteriorly. On the triturating surface, the maxilla contacts the premaxilla anteriorly, the vomer medially, the palatine posteromedially and the jugal posteriorly.

The vomer is almost complete. It is an anteroposteriorly elongate element, which can be divided into two parts: a horizontal ventral sheet and a dorsal sheet that are connected by a vertical vomerine pillar. The ventral sheet forms the central portion of the triturating surface and the anteriodorsal rim of the apertura narium interna. It is hexagonal, longer than wide and makes up about 1/2 of the midline length of the secondary palate. Similar proportions of the vomer

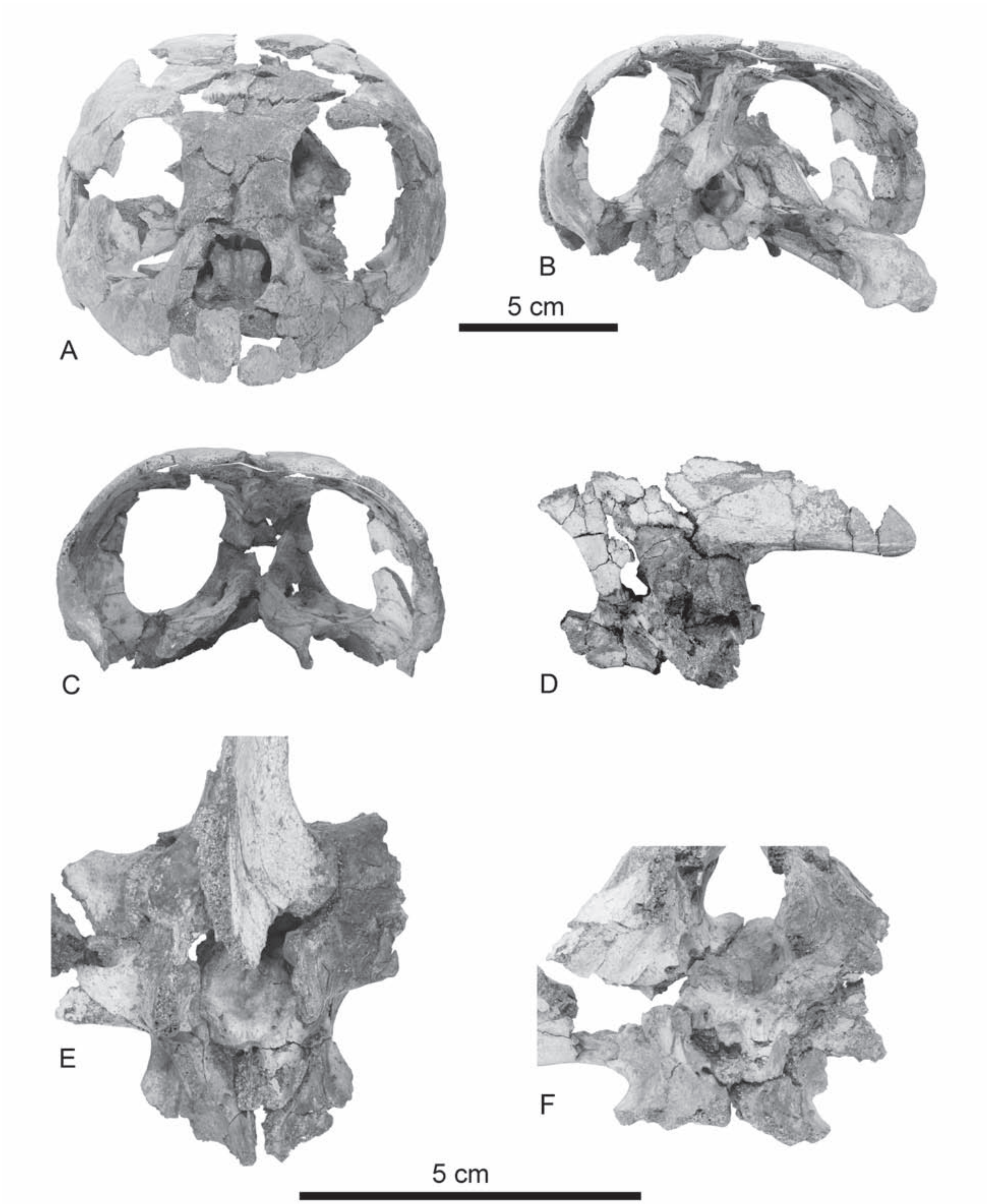

Fig. 4. Skull of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), photos: A – anterior view; B – posterior view; C – posterior view (braincase removed); D – braincase in left lateral view; E – braincase in dorsal view; F – braincase in anterior view.

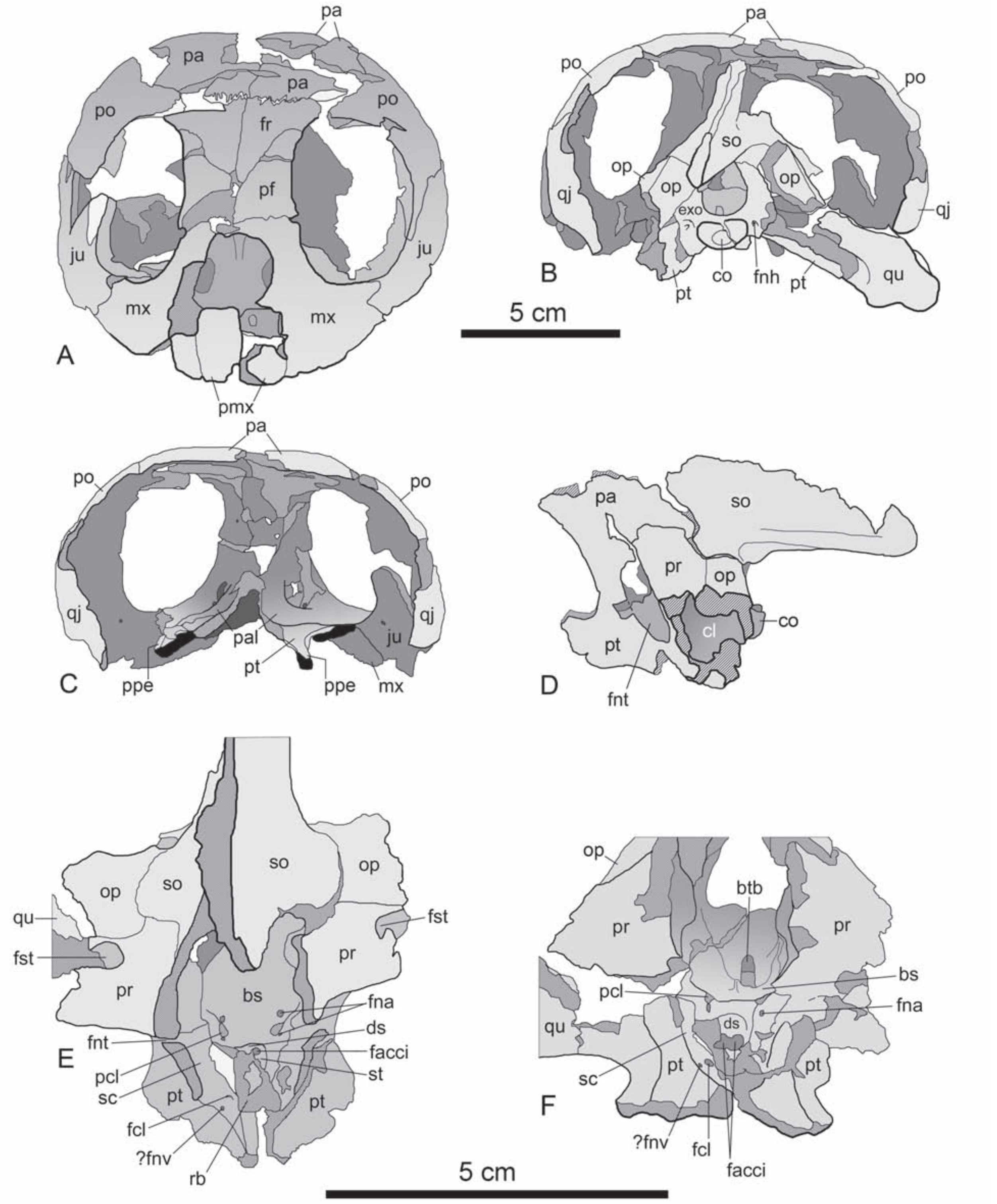

Fig. 5. Skull of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), drawings: A – anterior view; B – posterior view; C – posterior view (braincase removed); D – braincase in left lateral view; E – braincase in dorsal view; F – braincase in anterior view. See Fig. 2 for designations and abbreviations.

Fig. 6. Lower jaws of *Itilochelys rasstrigin* gen. et sp. nov., photos: A–F – ZIN PH 1/118 (holotype): A – dorsal view; B – right lateral view; C – ventral view; D – anterior view; E – left posterolateral view; F – posterior view (left posterior fragment removed); G–K – ZIN PH 2/118: G – dorsal view; H – right lateral view; I – ventral view; J – anterior view; K – posterior view.

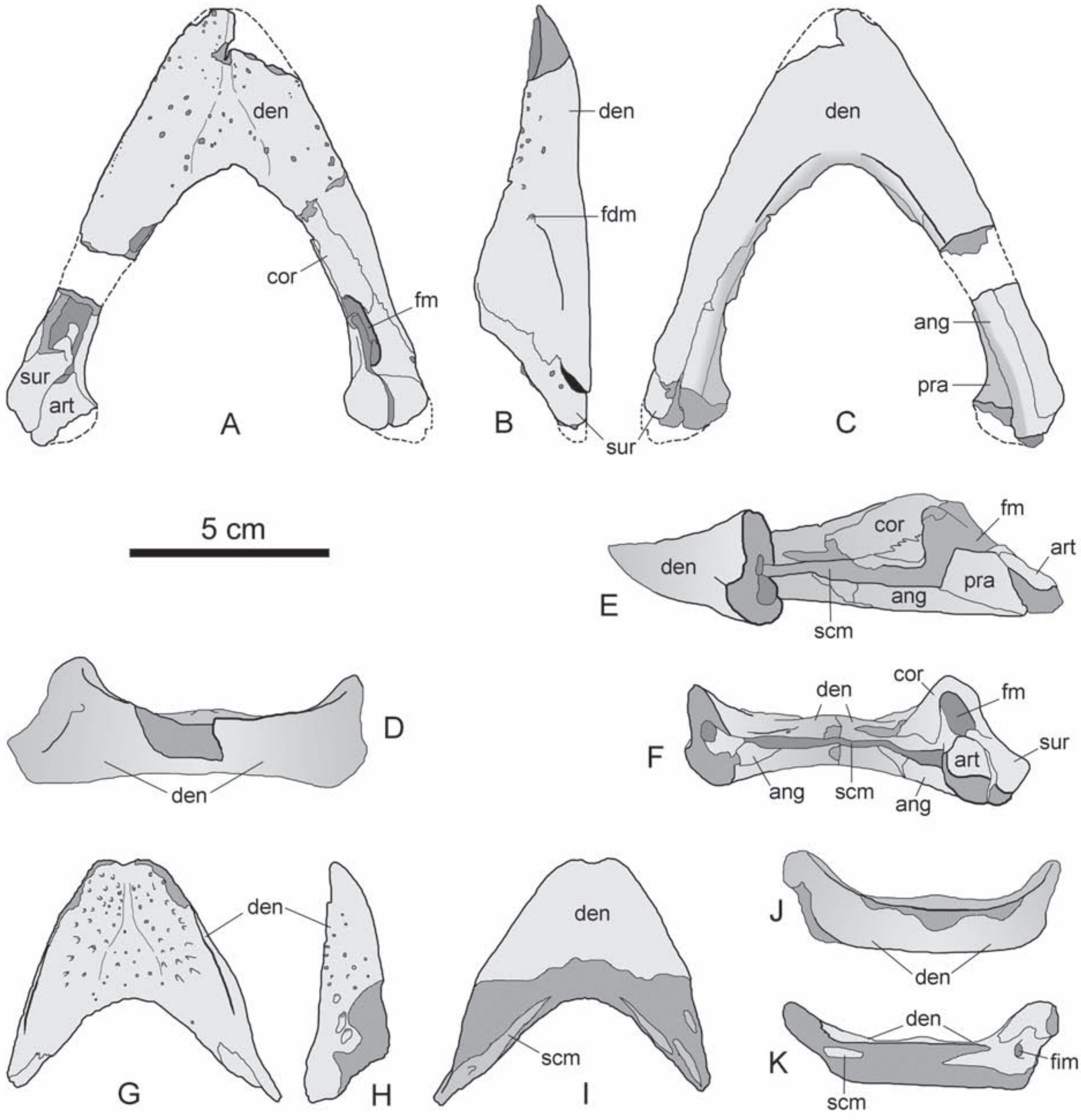

Fig. 7. Lower jaws of *Itilochelys rasstrigin* gen. et sp. nov., drawings: A–F – ZIN PH 1/118 (holotype): A – dorsal view; B – right lateral view; C – ventral view; D – anterior view; E – left posterolateral view; F – posterior view (left posterior fragment removed); G–K – ZIN PH 2/118: G – dorsal view; H – right lateral view; I – ventral view; J – anterior view; K – posterior view. See Fig. 2 for designations and abbreviations.

Fig. 8. Right humerus of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 3/118, photos: A – dorsal view; B – lateral view; C – ventral view; D – medial view.

are only known only in "*Argillochelys*" *africana*. The ventral surface of the vomer bears a groove to receive the symphysial ridge of the lower jaw. Similar groove is present, among compared forms, in species of *Argillochelys*. The vomerine pillar extends nearly to the posterior end of the ventral sheet of the vomer. The dorsal sheet is longer than the ventral one, forming the roof of the narial passage. The vomer contacts the maxilla anterolaterally, the palatine posterolaterally for both the dorsal and ventral sheets. The vomer/premaxilla and the vomer/pterygoid contacts are poorly preserved.

The palatines are almost complete. The palatine forms the posteromedial portion of the triturating surface and the lateral margin of the apertura narium interna. It contributes to the medial and posterior rim of the large foramen orbito-nasale and contacts the maxilla anterolaterally, the prefrontal anteriorly, the vomer medially, the pterygoid posteriorly and the jugal posterolaterally. The palatine does not reach the lower temporal emargination, being excluded from it by the pterygoid/jugal contact as in other cheloniids sensu lato. On the dorsal surface, the palatine forms most of the orbital floor. There is no midline palatine contact on the ventral surface. The presence or absence of such a contact on the dorsal surface is not clear.

Both pterygoids are damaged and not complete. Due to the disarticulation and deformation of the braincase, the position of the pterygoids in the preserved skull (Fig. 1B, 2B) is furthermore unnatural. The presumably correct position and shape of the pterygoids is shown on the reconstruction (Fig. 2E). The pterygoid is an elongate element, with a slightly concave ventral surface. Posteriorly, the pterygoid curves laterally, forming an anteromedially/posterolaterally directed groove between the condylus mandibularis of the quadrate and the basisphenoid. The processus externus pterygoidei is preserved on both sides, but covered with matrix from below. As reconstructed (Fig. 2E), it is well developed and directed posteriorly. The foramen palatinum posterius is absent, as in other cheloniids. The foramen posterior canalis carotici interni is not preserved. The pterygoid contacts the palatine and the jugal

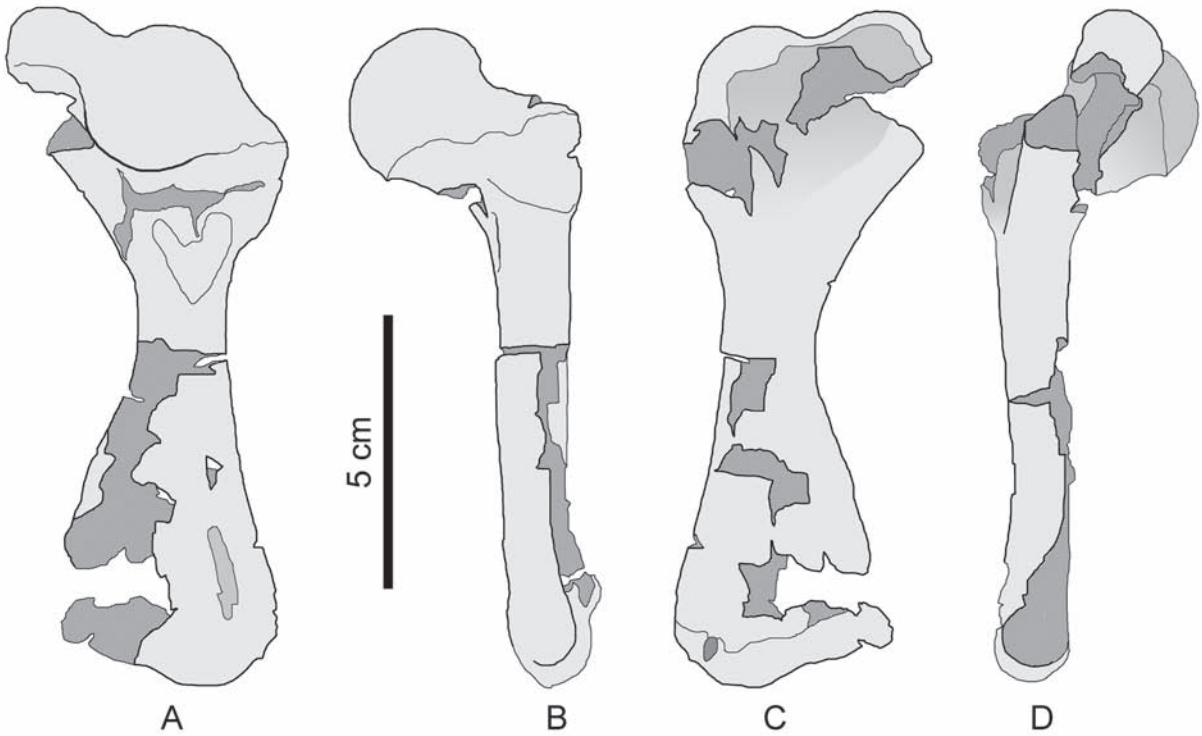

Fig. 9. Right humerus of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 3/118, drawings: A – dorsal view; B – lateral view; C – ventral view; D – medial view.

anterolaterally, the basisphenoid posteromedially, and basioccipital posteromedially behind the basisphenoid, the exoccipital posteriorly and the quadrate posterolaterally. Anteriorly, the contact with the vomer is not preserved. The pterygoid has a long contact at the midline with its counterpart, between the vomer and basisphenoid.

The basisphenoid is damaged externally (ventrally) and its outlines are not clear. It seems to have had contacts with the surrounding bones (pterygoids anteriorly and basioccipital posteriorly) that are usual for cheloniids. On the left side of the external surface along the basisphenoid/pterygoid suture, there is a high crest, corresponding to the V-shaped crest typical of Cheloniidae *sensu lato*. On the dorsal side of basisphenoid, the rostrum basisphenoidale is short as in other stem-cheloniids. The dorsum sellae is rather high, but does not conceal the posterior portion of the sella turcica, like in other cheloniids. Both processes clinoides are broken off. The foramina nervi abducentis are well visible. The sellae turcica is damaged, although the foramina anterius canalis carotici interni are discernable and appear to be larger than the more anteriorly placed foramina caroticum laterale. The basis tuberculi basalis is present on the suture between the basisphenoid and the basioccipital.

The basioccipital is little damaged and indistinguishably fused with the exoccipitals. The condylus occipitalis and the tuberculum basioccipitale are preserved. The basioccipital has a concave ventral surface. The condylus occipitalis is a triangular condyle formed by the basioccipital and the exoccipitals. The basioccipital contacts the basisphenoid anteriorly, the pterygoid laterally and the exoccipital posterolaterally.

Both exoccipitals are preserved, but damaged. They contribute to the medial rim of the fenestra postotica and form most of the foramen magnum and part of the condylus occipitalis. The foramen jugulare posterius seems to be completely confluent with the fenestra postotica. Two small foramina nervi hypoglossi, of similar size, are present on the exoccipital, ventrolateral to the condylus occipitalis. The exoccipital contacts the basioccipital ventrally (although

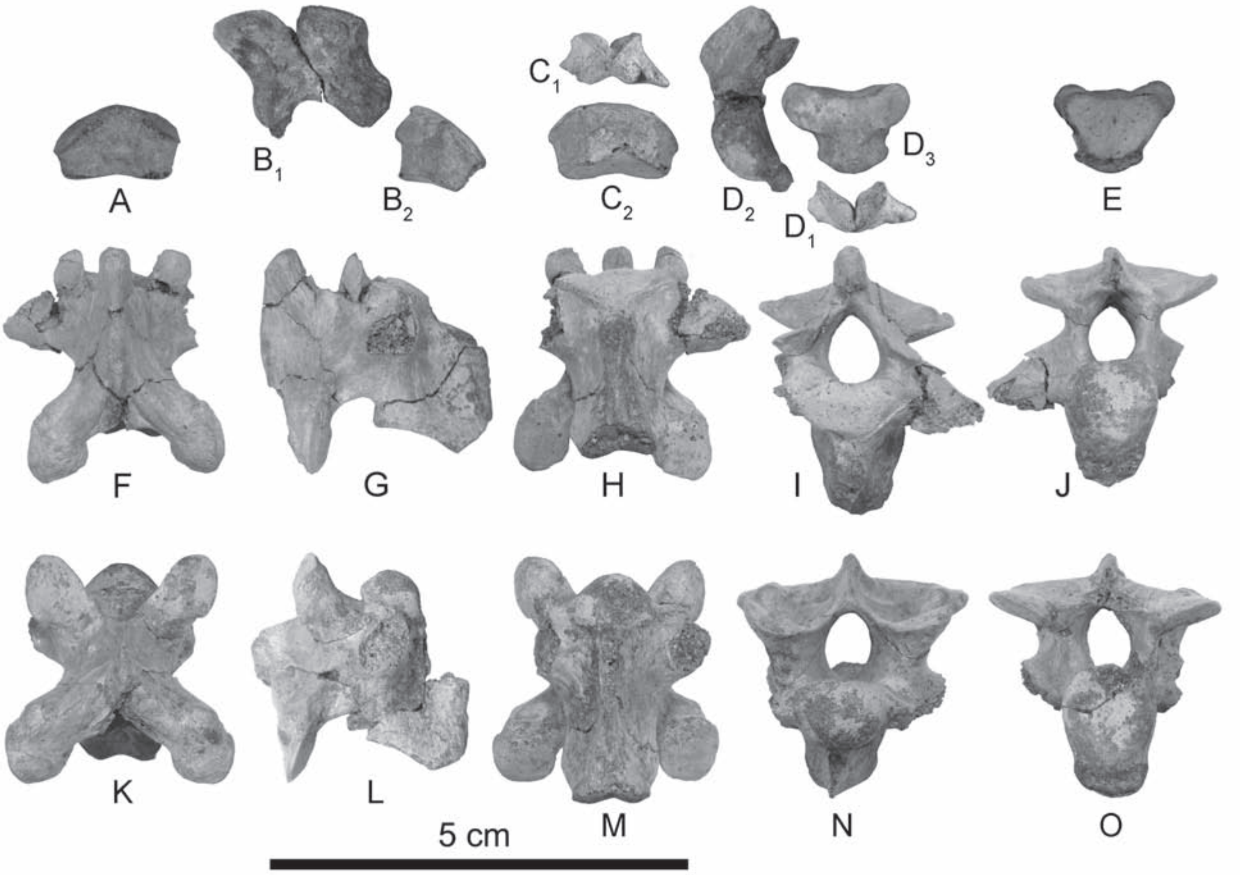

Fig. 10. Cervical vertebrae of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), photos: A–E – first cervical: A – centrum in dorsal view; B – right neural arch (B_1) and centrum (B_2) in right lateral view; C – intercentrum (C_1) and centrum (C_2) in ventral view; D – intercentrum (D_1), right neural arch (D_2) and centrum (D_3) in anterior view; E – centrum in posterior view; F–J – second cervical: F – dorsal view; G – right lateral view; H – ventral view; I – anterior view; J – posterior view; K–O – third cervical: K – dorsal view; L – right lateral view; M – ventral view; N – anterior view; O – posterior view.

this suture is obliterated), the supraoccipital dorsally, and the opisthotic laterally.

The supraoccipital is not complete, its anterior part and the upper margin of the crista supraoccipitalis are broken. The crista supraoccipitalis forms a strong, vertical blade that extends beyond the posterior margin of the skull roof. The supraoccipital contacts the prootic anterolaterally, the opisthotic laterally, the exoccipital ventrally and the parietal anterodorsally.

Only part of the right quadrate, represented by the condylus mandibularis, is preserved. The condylus mandibularis has a slightly concave and transversely elongate facet. Among contact of the quadrate only quadrate/pterygoid contact is observable.

The prootic is preserved on both sides but damaged. Anteriorly, it forms the posterolateral margin of the foramen nervi trigemini and laterally contributes to the foramen stapedio-temporale. The prootic contacts the parietal dorsally, the supraoccipital posterodorsally, the pterygoid anteroventrally and the opisthotic posteriorly. The prootic/quadrate contact is not preserved.

Both opisthotics are preserved, but damaged being represented only by their medial portions. The opisthotic contacts the prootic anteriorly, the supraoccipital dorsomedially and the exoccipital medially. The contacts of the opisthotic with the quadrate (laterally) and the squamosal (dorsolaterally) are not preserved.

The lower jaw is almost complete in ZIN PH 1/118, missing only part of its left ramus. ZIN PH 2/118 is represented only by the dentaries.

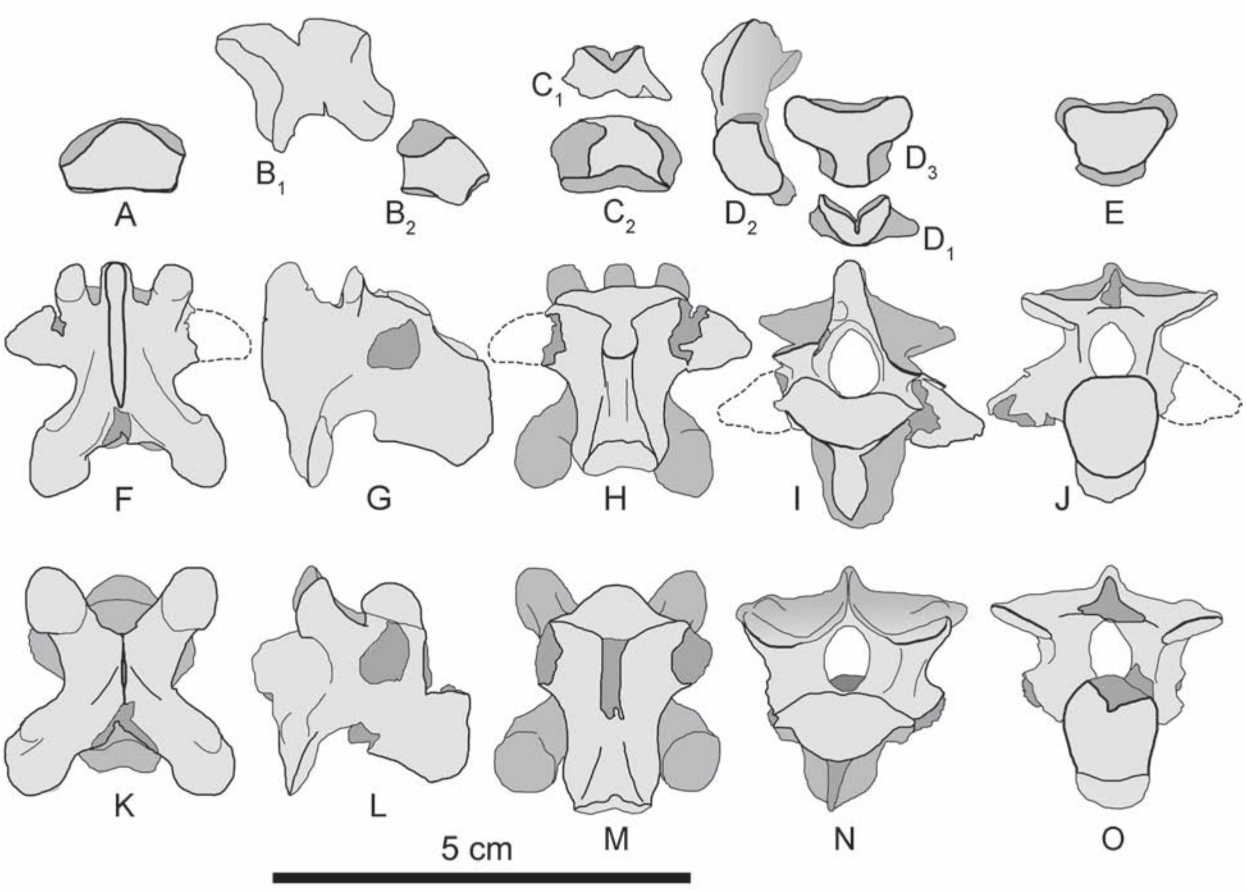

Fig. 11. Cervical vertebrae of *Itilochelys rasstrigin* gen. et sp. nov., ZIN PH 1/118 (holotype), drawings: A–E – first cervical: A – centrum in dorsal view; B – right neural arch (B_1) and centrum (B_2) in right lateral view; C – intercentrum (C_1) and centrum (C_2) in ventral view; D – intercentrum (D_1), right neural arch (D_2) and centrum (D_3) in anterior view; E – centrum in posterior view; F–J – second cervical: F – dorsal view; G – right lateral view; H – ventral view; I – anterior view; J – posterior view; K–O – third cervical: K – dorsal view; L – right lateral view; M – ventral view; N – anterior view; O – posterior view.

The dentaries form the rather flat and wide anterior portion of the lower jaw. The symphysis is relatively long, but does not extend to the level of the foramen dentofaciale majus (similar to "*Argillochelys*" *africana*, *Euclastes hutchisoni* and *Tasbacka aldabergeni*). There is an anteroposteriorly directed blunt and low symphysial ridge on the triturating surface. This ridge is narrow anteriorly and ends posteriorly in a triangular elevation of the same height. Other cheloniids used for comparison are different in that the symphysial ridge is sharp and high (*Argillochelys* spp.), or absent (most other forms). A very low or absent symphysial ridge is reported for *Puppigerus camperi* (Moody 1974; Tong and Hirayama 2008). Lingual ridges, present in *Argillochelys cuneiceps*, are absent. The triturating surface is concave between the symphysial ridge and the labial ridge similar to *Argillochelys* spp. The foramen dentofaciale majus is preserved on both sides of ZIN PH 1/118, whereas not preserved in ZIN PH 2/118; the line connecting these foramina is behind the symphysis. The foramen alveolare inferius is not preserved.

The complete right coronoid is preserved. The coronoid forms the medial part of the coronoid process, which is low as in other cheloniids.

Both angulars are preserved, but their anterior ends are broken. The angular is a long sheet of bone that sits along the ventomedial border of the posterior half of the lower jaw. The angular contacts the dentary anteromedially, the prearticular dorsally, the articular posteriorly and the surangular ventrolaterally.

The surangular is complete in the right ramus of the mandible and only partially preserved in the left ramus. The surangular forms much of the lateral wall of the fossa Meckelii, which is large, as in other cheloniids. The posterior part of the surangular forms the lateral part of the area articularis mandibularis as in other cheloniids. The surangular contacts the dentary anterolaterally, the coronoid anteriorly, the prearticular medially and the angular ventromedially.

Both articulars are preserved, although a little damaged posteriorly. The dorsal portion of the articular forms the medial part of the area articularis mandibularis. The articular contacts the surangular laterally, the prearticular medially and the angular ventrally.

Both prearticulars are preserved, but their anterior ends are broken. This is a large flat bone forming most of the medial wall of the fossa Meckelii. The prearticular contacts the articular posterolaterally and the angular ventrally. Its contact with the coronoid is not preserved, although there is a sutural surface for this contact on the coronoid.

ZIN PH 1/118 includes three cervical vertebrae (I – III) from the same individual as the skull. Originally these vertebrae were in articulation with the skull, but later separated during the preparation. The first cervical is only represented by the intercentrum, centrum and right neural arch, whereas the second and the third cervicals are complete. The second and the third cervicals are opisthocoelous with single anterior and posterior articular facets. The hypapophysial keels are well developed and the zygapophysial surfaces are rather horizontal. Thus, in these characters *Itilochelys rasstrigin* is similar to *Puppigerus camperi* and different from *Argillochelys cuneiceps* (see Moody 1974).

A single isolated right humeral bone (ZIN PH 3/118) is referred to *Itilochelys rasstrigin*. This specimen possesses a relatively narrow and cylindrical shaft when viewed in dorsal and ventral aspect. The shaft is almost straight in lateral view and the distal articular surface of the humerus is reduced. The medial process is elongated proximally, but unlike living cheloniids (Cheloniidae *sensu stricto*), the proximal extent of the medial process is subequal to the head in ventral view. The lateral process of ZIN PH 3/118 also differs from those of modern cheloniids in its more proximal position, adjacent to the intertubercular fossa. Therefore, *Itilochelys rasstrigin* is a typical stem-cheloniid in its humeral morphology.

DISCUSSION

Itilochelys rasstrigin clearly belongs to Cheloniidae *sensu lato* because of the following cranial characters: parietal/squamosal contact present, upper triturating surface involving palatines, apertura narium interna entirely formed by vomer and palatines, excluding maxillae, ventral surface of basisphenoid with V-shaped crest emarginated from posterior (Hirayama 1998).

The attribution of *Itilochelys rasstrigin* to the stem of Cheloniidae is supported by its humeral morphology, which is intermediate between the plesiomorphic non-pelagic condition and the derived condition of Cheloniidae *sensu stricto* (see Description and comparisons). Among stem-cheloniids, *Itilochelys rasstrigin* demonstrates a unique combination of characters, which diagnose it as a new genus and species (see Diagnosis). The only autapomorphic characters of *Itilochelys rasstrigin*, not found in other Cheloniidae *sensu lato*, is the long anteroventral process of the postorbital. *Itilochelys rasstrigin* demonstrates many similarities with *Argillochelys* (*sensu* Tong and Hirayama 2008): short snout, deep cheek emargination, presence of a deep midline groove on the triturating surface and swellings lateral to this groove, concave lower triturating surface and presence of the symphysial ridge (see Table 1). Within *Argillochelys*, *Itilochelys rasstrigin* especially resembles "*Argillochelys*" *africana* in midline length of the secondary palate at about 2/3 of its maximal length, moderate vomer length on the triturating surface, long lower jaw symphysis and absence of lingual ridges of the lower jaw. On the other hand, "*Argillochelys*" *africana* is very different from the typical *Argillochelys* in the characters listed as its similarities with *Itilochelys rasstrigin* and in the frontal not contributing to the orbital margin (Tong and Hirayama 2008). Interestingly, monophyly of *Argillochelys* (*sensu* Tong and Hirayama 2008) has never been demonstrated by phylogenetic analysis. For this reason, we question the generic atribution of "*Argillochelys*" *africana* pending further study of this species. In our study we also refrain from inclusion of *Itilochelys rasstrigin* into phylogenetic analysis, pending additional material and data (especially those of the shell and unknown non-shell postcrania) on this species. Modern studies have shown that the diversity of stem-cheloniids is higher than formerly considered and that their generic attribution is not

Table 1. Comparisons between some stem-cheloniids.

Characters	*"Argillochelys" africana*	*Argillochelys cuneiceps*	*Eochelone brabantica*	*Euclastes hutchisoni*	*Itilochelys rasstrigin*	*Puppigerus camperi*	*Tasbacka aldabergeni*
Skull shape	Skull wide with short snout	Skull wide with short snout	Skull long with long snout	Skull very wide with long snout	Skull long with short snout	Skull very long with very long snout	Skull long with long snout
Cheek emargination	Deep	Deep	Deep	?	Deep	Shallow	Shallow
Frontal contributing to orbital margin	No	Yes	Yes	No	Yes	Yes	Yes
Anteroventral process of postorbital	Absent	Short	Absent	?	Long and nar-row	Absent	Short
Secondary palate (maximal length)	Moderate	Moderate	–	Moderate	Extensive	Extensive	Extensive
Secondary palate (midline length)	About 2/3 of maximal length	About 1/2 of maximal length	–	About 2/3 of maximal length	About 2/3 of maximal length	About 5/6 of maxi-mal length	About 5/6 of maximal length
Vomer length on triturating surface	Moderate	Short	–	Long	Moderate	Long	Long
Midline groove on triturating surface through vomer length	Deep	Deep	–	Absent	Deep	Shallow or absent	Absent
Swellings lateral to mid-line groove on triturating surface	Present	Present	–	Absent	Present	Absent	Absent
Lower jaw symphysis	Long	Short	Short	Long	Long	Very long	Long
Lower triturating surface	Concave	Concave	–	Flat	Concave	Flat	Flat
Symphysial ridge ending in a triangular elevation	Present, as high as labial ridge	Present, as high as labial ridge	Absent	Absent	Present, very low	Present, very low or absent	Absent
Lingual ridges on the lower jaw	Absent	Present	Absent	Absent	Absent	Absent	Absent

always apparent (Tong and Hirayama 2002; Hirayama and Tong 2003; Hirayama 2006; Brinkman et al. 2006; 2009; Tong and Hirayama 2008). Our study adds a new genus and species to this diversity.

As was mentioned above (see Introduction), of the few stem-cheloniids known in Russia most come from the late Paleocene of Volgograd Province (Nessov and Yarkov 1989; Averianov and Yarkov 2000; Averianov 2002; Lynch and Parham 2003). Together with the new finding, these data emphasize the significance of the Volgograd Province of Russia as a field area to find new materials of stem-cheloniids, that are important for the understanding of the early evolution of hard-shelled sea turtles.

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