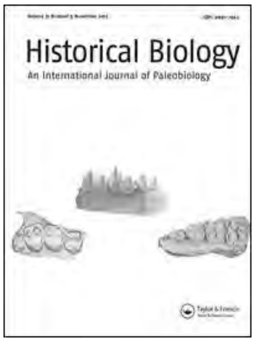

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ARTICLE

First sirenian remains from the Palaeogene of Crimea

Alexander O. Averianov[a] and Evgeny Zvonok[b]

[a]Department of Theriology, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; [b]Luhansk State Pedagogical University, Luhansk, Ukraine

ABSTRACT

Fragmentary remains, including two anterior premolars, axis fragment, a phalanx, and rib fragments from the Middle Eocene (late Bartonian) Ak-Kaya locality represent the first sirenian fossils from the Paleogene of Crimea. The lower p3 shows some similarity with p3 in the dugongid *Eotheroides* sp. from the Eocene of North America. The axis is similar in proportions to the axis of the stem sirenian *Sobrarbesiren* from the Middle Eocene of Spain. The manual(?) phalanx suggests a semiaquatic adaptation of the Crimean sirenian. These remains are identified as Sirenia indet. with possible affinities with the Dugongidae.

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KEYWORDS
Sea cows; Sirenia; Eocene; Crimea

Introduction

The Paleogene locality Ak-Kaya (N 45° 10′, E 34° 63′), situated in the Belogorsk District of Crimea (Figure 1), was discovered by paleoichthyologist N.I. Udovichenko in the late 1980s. This locality and the nearby locality Prolom (N 45° 03′, E 34° 36′) of apparently the same age produced a diverse fauna of Eocene vertebrates including chondrichthyan and osteichthyan fishes, sea snakes *Palaeophis* spp., marine and freshwater turtles, birds, and cetaceans (2002; Nesov 1992; Averianov 1997; Bratishko and Udovichenko 2007; Snetkov and Bannikov 2010; Panteleev 2011; Zvonok 2011, 2016; Zvonok and Snetkov 2012; Zvonok et al. 2013; Dernov and Udovichenko 2014; Zvonok and Danilov 2019).

In this paper, we report on the first finding of sea cows (Sirenia) at the Ak-Kaya locality. Eocene sirenians are poorly known in the Eastern Europe. A.S. Rogovich (1875, p. 37) reported on teeth and vertebrae of 'a cetacean animal' *Halicore maximovitschii* [nomen nudum] found in the 'upper green sandstone of the Cretaceous Formation' outcropping near Kanev, Ukraine. The generic name *Halicore* is a junior synonym of the Recent sea cow *Dugong* (Husar 1978). The bones reported by Rogovich belong to an Eocene cetacean (Averianov 2000). A possible sirenian tooth fragment was described from the upper(?) Eocene deposits at the Srednyaya Akhtuba locality in Volgograd Region, Russia (Averianov and Yarkov 2006). Isolated vertebrae and rib fragments of a sirenian are known from the early Oligocene Borysthenic Formation near Pokrov, Ukraine (Gol'din et al. 2019). Two poorly known sirenian taxa, *Sirenavus hungaricus* and *Anisosiren pannonica*, were described from the Middle Eocene (Lutetian) of Hungary (Kretzoi 1941; Kordos 1979, 1981, 1983, 2002). The fragmentary remains of Sirenia indet. were described from the upper Eocene (Priabonian) of Romania (Fuchs 1988).

The fossiliferous bed of the Ak-Kaya locality contains the calcareous nannoplankton taxa *Reticulofenestra umbilica*, *Cribrocentrum reticulatum*, and *Dictyococcites bisectus*, which are characteristic for the Bartonian (V.A. Musatov, personal communication). The lack of Lutetian (*Nannotetrina* spp.), lower Bartonian (*Rhabdosphaera gladius* and *Chiasmolithus solitus*), or Priabonian (*Isthmolithus recurvus* and *Chiasmolithus oamaruensis*) taxa allow dating of the locality to the upper part of the zone CP14b (upper part of NP17 zone), which corresponds to the upper Bartonian (V.A. Musatov, personal communication).

Institutional abbreviations

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Systematic palaeontology

Mammalia Linnaeus, 1758
Sirenia Illiger, 1811
Sirenia incertae sedis
Figures 2–6

Specimens. ZIN 106018, anterior premolar. ZIN 106017, right p3. ZIN 106019, right axis neural hemiarch. ZIN 106020, unidentified phalanx. ZIN 106021 and 106022, rib fragments.

Locality and age. Ak-Kaya (N 45° 10′, E 34° 63′), Belogorsk District, Crimea. Middle Eocene (upper Bartonian).

Description. ZIN 106018 is a single-rooted anterior premolar, possibly the first or second, of the upper or lower jaw (Figure 2). The crown is elongated mesiodistally, about 1.4 times longer than transversely wide. The mesial half of the crown is transversely wider than the distal half. The crown is dominated by a large cusp situated at the mesiolabial corner of the crown. A much smaller mesiolingual cusp is adjacent to the latter cusp. There are three ridges that extend lingually, distolingually, and distally from the main cusp and are separated by deep grooves. There are one large and one small cusp on the lingual ridge, three large cusps on the distolingual ridge, and five very small cusps on the distal ridge. The distal ridge terminates in a distinct cusp at the distolabial corner of the crown. The crown is deeper on the labial and distal sides compared with the lingual and mesial sides.

The p3 (ZIN 106017) is a single-rooted tooth represented by separate crown and root with the contact area missing (Figure 3). The crown is roughly oval in occlusal view. It has a slightly convex lingual side, strongly convex distolabial side, and a concave mesiolabial side. The crown is dominated by a large cone-like main cusp (protoconid) with a series of smaller cingular cusps around the

CONTACT Alexander O. Averianov dzharakuduk@mail.ru Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg, 199034, Russia

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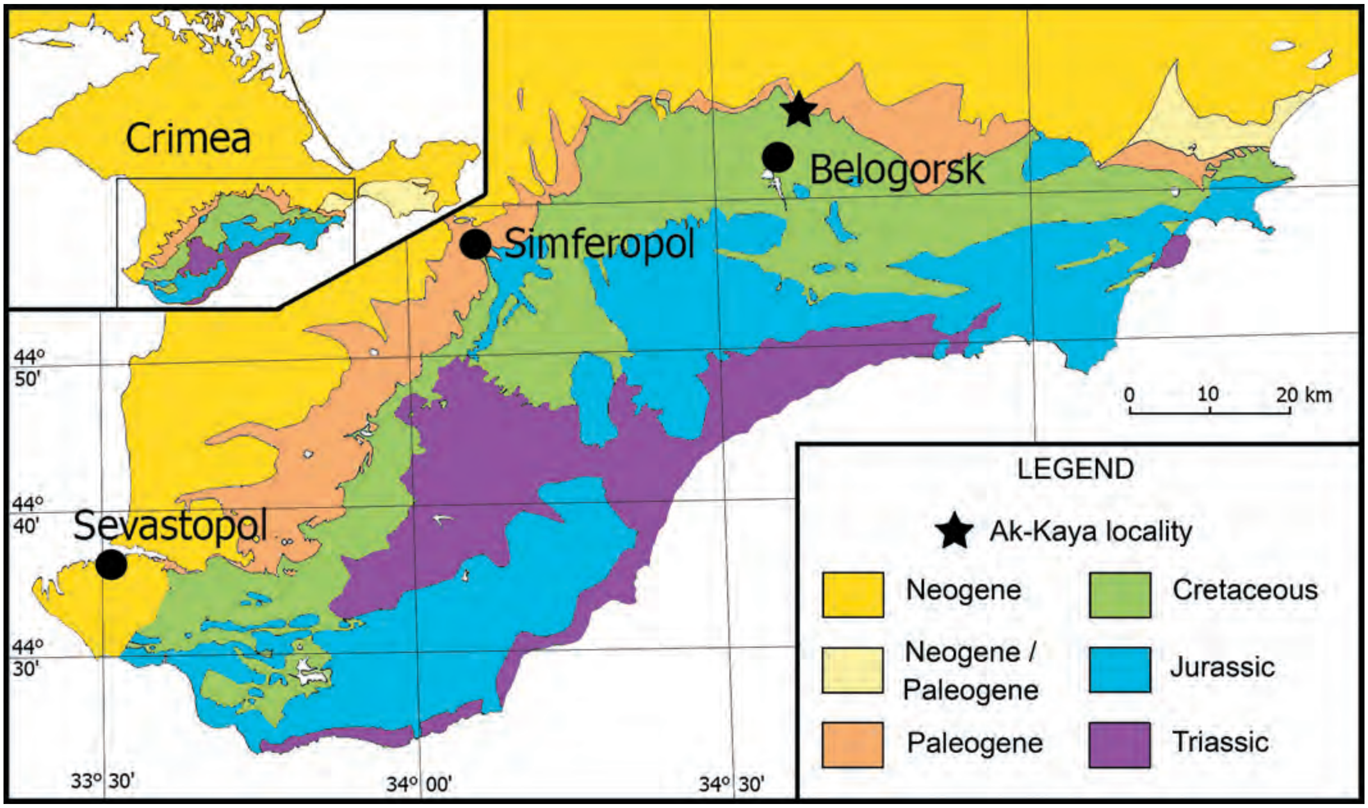

Figure 1. Position of the Ak-Kaya locality (asterisk) on the geological map of Crimea.

mesial, lingual, and distal margins of the crown. The protoconid is convex mesially, flat lingually, and concave labially and distally. There is a large wear facet on the apex of the protoconid, of semilunar form reflecting the curvature of the protoconid sides. It is concave mesially and convex distally. The wear facet faces mesially and slopes along the mesiolabial edge of the protoconid. The largest cingular cusp is at the mesiolingual corner of the crown and can be considered as the paraconid. It is heavily worn. The second-largest cusp is a slender hook-like cusp at the distolingual corner of the crown which can be considered as the metaconid. Between the paraconid and the metaconid there is a high lingual cingulid bearing five cusps of unequal size. The largest is the most distal cusp. The first and fourth cusps counting from the mesial end are smaller and of similar size. The second and third cusps are very small. The metaconid and lingual cingular cusps are unworn (the distalmost cusp on the lingual cingulid is broken). On the mesial cingulid there are three cusps decreasing in size labially. The lingual cusp is lower than the paraconid but has a wider base. All mesial cusps are heavily worn. There is no cingulid on the labial or distal sides of the crown. The crown is of uneven height. It is higher on the labial side compared with the lingual side. The root is convex on one side and has a voluminous deep groove along the opposite side (Figure 3(g, h)).

ZIN 106019 is a right neural hemiarch of the axis (epistropheus; Figure 4). The neural arch was not fused with the centrum. There are two oval sutural surfaces of similar size at the ventral end of the neural arch that meet ventrally at an angle of ~45°. The anterolateral surface represents the contact area with the epiphysis of the axial prezygapophysis. The medial side is the contact area with the axis centrum. Dorsally, the neural hemiarch was completely fused with the collateral neural hemiarch, part of which is preserved. The neural hemiarch is straight in anterior or posterior view and deflects medially only in its dorsal quarter. The anterolateral margin, forming the margin of the neural canal, is concave. On the ventral third of the medial side, there is a depression bordered anteriorly and posteriorly by vertical ridges. On the posterolateral side, there is a postzygapophysis with the oval postzygapophyseal facet facing posteroventrolaterally. The posterolateral margin of the neural hemiarch is concave between the postzygapophysis and the incompletely preserved diapophysis (transverse process). The concave margin ventral to the diapophysis is a medial margin of the transverse foramen. The narrowest point of the neural hemiarch in lateral view is just ventral to the postzygapophysis. Dorsal to the postzygapophysis the neural hemiarch is about twice as wide and slightly widens towards the dorsal end. In lateral view, the neural arch is directed anterodorsally.

ZIN 106020 is a short phalanx, which is only 1.4 times longer than its maximum transverse width (Figure 5). The phalanx is flattened dorsoventrally, with convex dorsal and concave ventral surfaces. The proximal articulation surface is concave and semilunar in proximal view, convex dorsally and concave ventrally. The distal articulation surface is distinctly narrower and convex in dorsoventral section. It is slightly depressed in the middle. One side of the phalanx (lateral?) extends more proximally compared with the other side.

There are two similarly curved rib fragments (Figure 6). There are no parts of proximal articulations or costal grooves preserved. The cross-section is oval. One fragment (ZIN 106021) is thicker, with the anteroposterior diameter 1.3 times greater than the mediolateral width. In the other specimen, this ratio is about 1.8. The bone structure is pachyosteosclerotic (Domning and Buffrénil 1991).

Measurements (in mm): ZIN 106018, anterior premolar, crown length 8.7; crown width 5.4. ZIN 106017, p3, crown length 7.7; crown width 7.0. ZIN 106020, phalanx, length 24.5; proximal width 17.5; proximal dorsoventral diameter 11.4; distal width 17.4; distal anteroposterior diameter 7.5. The largest diameters of the rib fragments are 16.2 and 14.2.

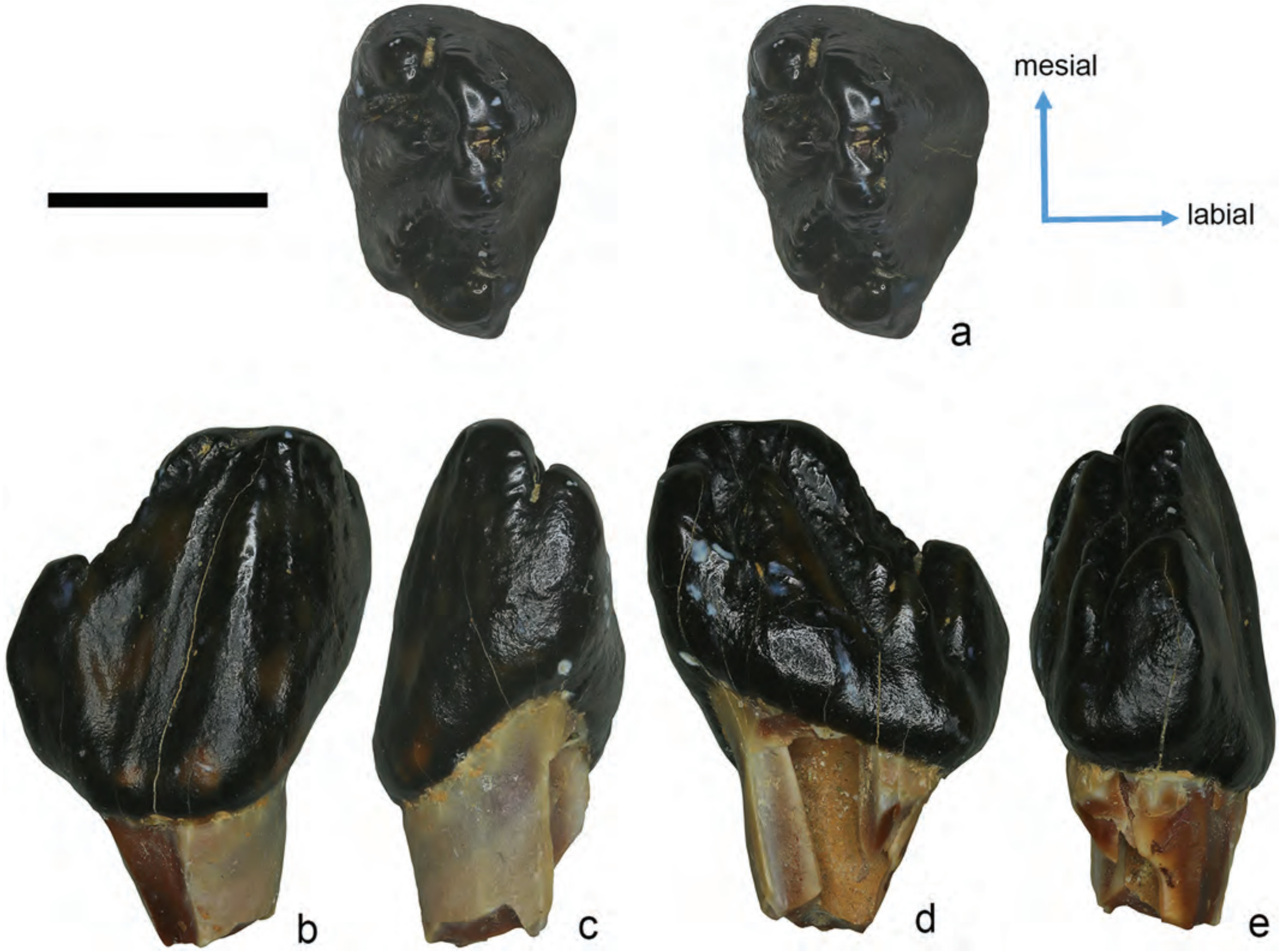

Figure 2. Sirenia indet., ZIN 106018, anterior premolar, in occlusal (a, stereopair), labial (b), mesial (c), lingual (d), and distal (e) views. Ak-Kaya locality, Crimea; Middle Eocene (Bartonian). Scale bar equals 5 mm.

Comparisons and discussion

Three groups of sirenians are known from the Eocene: fully quadrupedal Prorastomidae (Savage et al. 1994; Domning 2001; Hautier et al. 2012), quadrupedal semiaquatic Protosirenidae (Domning et al. 1982; Domning and Gingerich 1994; Gingerich et al. 1994, 1995; Zalmout et al. 2003) and completely aquatic Dugongidae (Hautier et al. 2012). In the Prorastomidae, the anterior premolars and phalanges are not known or described. Judging from the alveoli, in *Prorastomus sirenoides* from the Early-Middle Eocene of Jamaica, p1 was a large double-rooted tooth followed by smaller single-rooted p2 and p3 (Savage et al. 1994). In another prorastomid, *Pezosiren portelli* from the Middle Eocene of Jamaica, p1 was plesiomorphically unenlarged (Domning 2001). Attribution of the late Bartonian Crimean sirenian to the Prorastomidae is unlikely because all prorastomids are Lutetian in age (Benoit et al. 2013: Figure 5).

ZIN 106017 is most similar to p3 of the specimen USNM 214596 from the Eocene of North Carolina, USA (Domning et al. 1982: figs. 20B, 22B, 23C, D) and personal observation, identified originally as *Protosiren* sp. This specimen is now thought to represent a species of the dugongid *Eotheroides* (Domning, personal communication). Both teeth have a large cone-like protoconid, much smaller paraconid and metaconid, and a mesial cingulid with large cusps. ZIN 106017 differs from the p3 of USNM 214596 in having a smaller trigonid angle, cuspidate lingual cingulid between the paraconid and metaconid, and three instead of two cusps on the mesial cingulid.

The p3 of the dugongid *Halitherium taulannense* from the late Eocene (Priabonian) of France (Sagne 2001: fig. C) differs from the Crimean specimen by having high paraconid and metaconid which are only slightly lower than the protoconid, no lingual cingulid between paraconid and metaconid, and distinct distal cingulid.

The anterior border of the axis neural spine of ZIN 106,019 is inclined anteriorly to block the dorsal movement of the atlas, as in stem sirenians and *Dugong*, while in manatees (*Trichechus*) it is vertical (Sukhanov and Manzij 1986). A similar anterior inclination of the axis neural arch is found in the protosirenid *Protosiren fraasi*, the dugongid *Eosiren libyca*, and *Sobrarbesiren cardieli* (Sickenberg 1934: fig. 13, pl. 5, Figure 4; Díaz-Berenguer et al. 2018: Figure 6(d)). ZIN 106019 is further similar to *S. cardieli* and *P. fraasi* in having the neural arch restricted in lateral width ventral to the postzygapophysis, while in other stem sirenians the difference in width ventral and dorsal to the postzygapophysis is not so prominent.

The phalanx ZIN 106020 is relatively shorter and more flattened compared with the middle phalanx of the third or fourth manual digit of the Miocene dugongid *Metaxytherium medium* (Abel 1904: figs. 10–12). Both phalanges are similar in having a skewed proximal articulation surface, with the ventral margin more proximal compared with

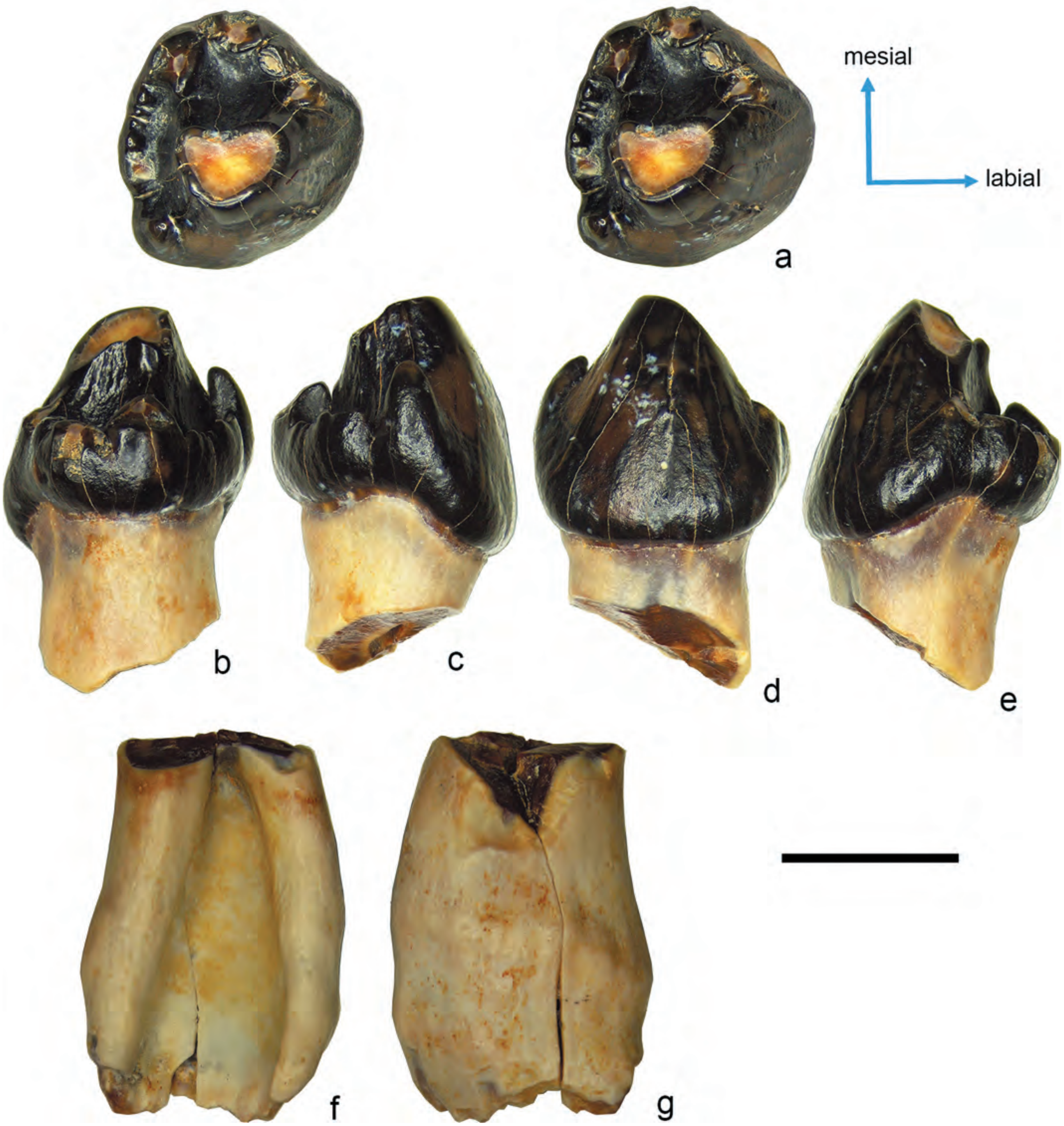

Figure 3. Sirenia indet., ZIN 106017, right p3, in occlusal (a, stereopair), lingual (b), distal (c), labial (d), mesial (e) views and root in two views (f and g). Ak-Kaya locality, Crimea; Middle Eocene (Bartonian). Scale bar equals 5 mm.

the dorsal margin. However, in contrast with manual phalanges of *Metaxytherium* and other dugongids, ZIN 106020 has well-developed functional articulated surfaces suggesting that the manus was capable of moving on land.

The determination of fragmentary sirenian remains from the Middle Eocene of Crimea is difficult because the anterior premolars are rarely preserved and poorly known in Eocene stem sirenians. The p3 shows some similarity with p3 of a dugongid *Eotheroides* sp. from the Eocene of North Carolina. The axis is more similar to that of the stem sirenian *Sobrarbesiren* from the Middle Eocene of Spain. The manual(?) phalanx ZIN 106020 suggests a semiaquatic adaptation of the Crimean sirenian. Currently, the Crimean Eocene sirenian cannot be determined beyond Sirenia indet., although its affinities with the Dugongidae are likely.

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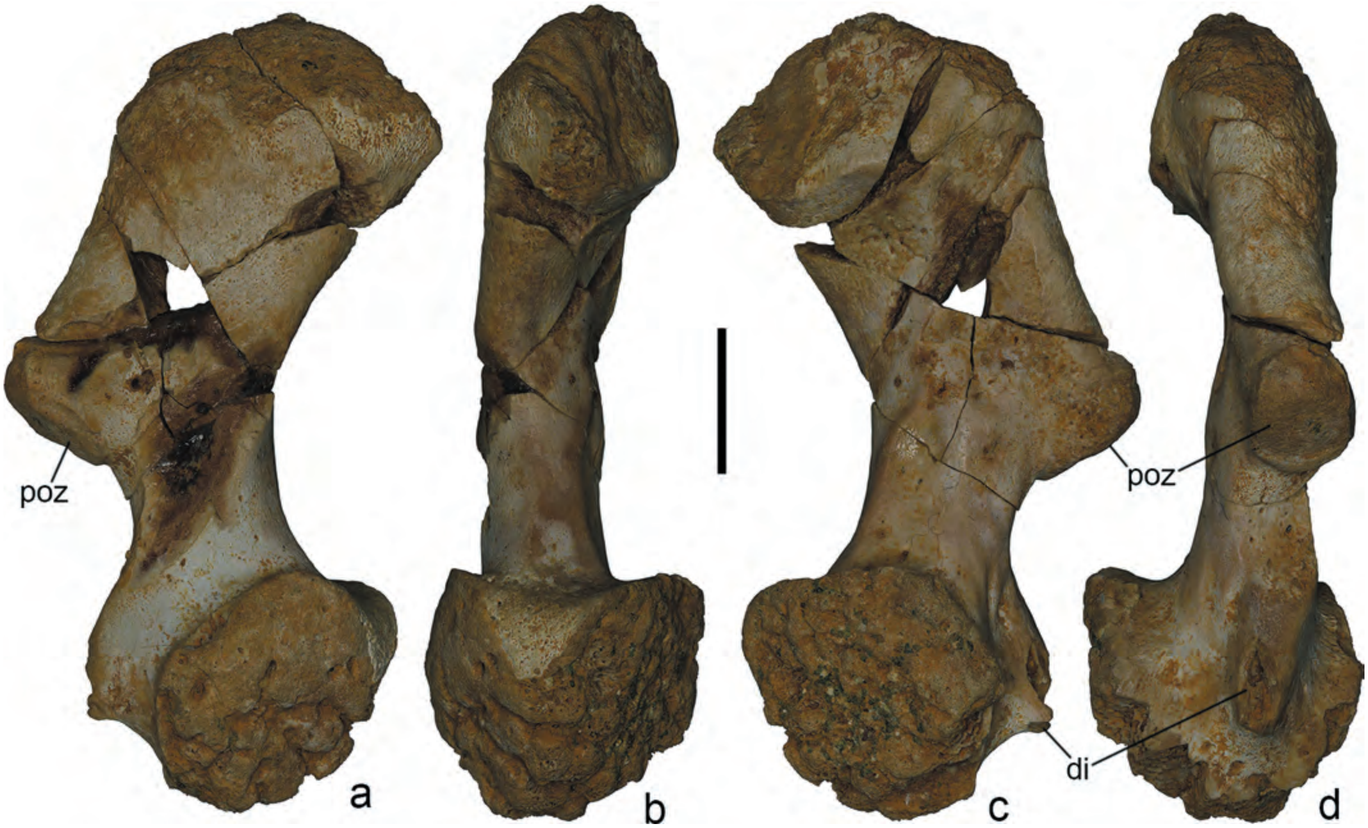

Figure 4. Sirenia indet., ZIN 106019, right neural hemiarch of the axis, in anterolateral (a), anteromedial (b), medial (c), and posterolateral (d) views. Abbreviations: di, diapophysis; poz, postzygapophysis. Ak-Kaya locality, Crimea; Middle Eocene (Bartonian). Scale bar equals 10 mm.

Figure 5. Sirenia indet., ZIN 106020, unidentified phalanx, in proximal (a), distal (b), dorsal (c), lateral (?) (d), ventral (e), and medial (?) (f) views. Ak-Kaya locality, Crimea; Middle Eocene (Bartonian). Scale bar equals 10 mm.

Figure 6. Sirenia indet., ZIN 106021 (a-c) and ZIN 106,022 (d-f), rib fragments, in dorsal (a, d), side (b, e), and ventral (c, f) views. Ak-Kaya locality, Crimea; Middle Eocene (Bartonian). Scale bar equals 10 mm.

biozone of calcareous nannofossils by sample of rock from the Ak-Kaya locality. We also grateful to D.P. Domning for reviewing of the paper and useful suggestions.

Disclosure statement

No potential conflict of interest was reported by the authors.

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ORCID

Alexander O. Averianov http://orcid.org/0000-0001-5948-0799

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