Proceedings of the Zoological Institute RAS
Vol. 316, No. 4, 2012, pp. 392–400

УДК 568.115:551.781.4 (477.7)

NEW FINDINGS OF SNAKES OF THE GENUS *PALAEOPHIS* OWEN, 1841 (ACROCHORDOIDEA: PALAEOPHIIDAE) FROM THE MIDDLE EOCENE OF CRIMEA

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ABSTRACT

The vertebrae of aquatic snakes, referred to the three known species of the genus *Palaeophis* (*P. tamdy*, *P. nessovi* and *P.* cf. *toliapicus*), are described from the Middle Eocene (Lutetian) deposits of the Ak-Kaya locality of Crimea, Ukraine. These species demonstrate different degree of aquatic adaptations and lived in a restricted area in the eastern part of the Tethys Ocean during the Middle Eocene.

Key words: Acrochordoidea, aquatic snakes, Eocene, Lutetian, Palaeophiidae

НОВЫЕ НАХОДКИ ЗМЕЙ РОДА *PALAEOPHIS* OWEN, 1841 (ACROCHORDOIDEA: PALAEOPHIIDAE) ИЗ СРЕДНЕГО ЭОЦЕНА КРЫМА

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РЕЗЮМЕ

Из среднеэоценовых (лютетских) отложений Крыма (местонахождение Ак-Кая) описаны остатки водных змей, отнесенные к трем ранее известным видам рода *Palaeophis* (*P. tamdy*, *P. nessovi* и *P.* cf. *toliapicus*). Эти виды демонстрируют разную степень специализации к водному образу жизни и обитали в одной акватории в восточной части океана Тетис в среднем эоцене.

Ключевые слова: Acrochordoidea, водные змеи, эоцен, лютет, Palaeophiidae

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INTRODUCTION

The superfamily Acrochordoidea Bonaparte, 1831 traditionally includes the extant family Acrochordidae Bonaparte, 1831 and fossil Cretaceous-Paleogene families Nigerophiidae Rage, 1975 and Palaeophiidae Lydekker, 1888 (Averianov 1997; Snetkov 2011). The acrochordids, as well as nigerophiids and palaeophiids, are aquatic snakes, according to their vertebral morphology (Averianov 1997). The genus *Palaeophis* Owen, 1841, which is most abundant by number of species among the genera of the Acrochordoidea, includes 13 species and materials, unidentified to the species level from the Maastrichtian to the Priabonian (Rage et al. 2003; Bajpai and Head 2007; Snetkov and Bannikov 2010).

In Ukraine and Eastern Europe in general, remains of aquatic snakes are known from five vertebrate bearing localities (Figs 1, 2): Ak-Kaya, Bakhchisarai, Prolom (all in Crimea), Sbornaya (Luhansk Province), and Kiev (Kiev Province). The remains of the Acrochordoidea from the Bakhchisarai locality (Kuma Horizon, Bartonian, excluding its lowermost part) are represented by one vertebra of *Palaeophis nessovi* Averianov, 1997 (Snetkov and Bannikov 2010). The Prolom locality (Novopavlovsk Horizon, Lutetian – lowermost Bartonian) yields 13 vertebrae of *P. nessovi* described as *Palaeophis udovichenkoi* Averianov, 1997 (Averianov 1997; Bratishko and Udovichenko 2007; Snetkov and Bannikov 2010; Bratishko 2011). The remains of *Palaeophis* sp. from the Sbornaya locality (Belorechensk beds, Ypresian) and aquatic snakes from the Kiev locality (Kiev Horizon, upper Lutetian – Bartonian) are known from brief reports (Moroz and Savron 1975; Nessov 1995).

The presence of the vertebrae of aquatic snakes in the Ak-Kaya locality (45°6´N, 34°38´E; Belogorsk District, Crimea, Ukraine; Lutetian, middle Eocene) was first mentioned by Bratishko and Udovichenko (2007). Later, one vertebra of *Palaeophis* sp. was described from this locality (Snetkov and Bannikov 2010). In 2010, E.A. Zvonok made an exploratory excavation pit about 500 m to the east from the nummulite limestone quarry of Ak-Kaya and collected six vertebrae of *Palaeophis nessovi* (Zvonok, 2011). In 2011, E.A. Zvonok excavated the second pit from which numerous vertebrae of aquatic snakes and their fragments were collected. A description of this material is the main aim of our paper.

In addition to snakes, the vertebrate assemblage of the Ak-Kaya locality includes different bony and cartilaginous fishes, turtles Cheloniidae indet., Trionychidae indet., Dermochelyidae indet., unidentified birds of different sizes and mammals (Bratishko and Udovichenko 2007; Zvonok 2011; Zvonok et al. in press; E.A. Zvonok, unpublished data).

Modern acrochordids live in estuaries and rivers. They are able to crawl on land and to swim in the sea (Shine and Houston 1993). Different degrees of aquatic specialization may be a point of ecological and spatial divergence of Paleogene Acrochordoidea in the Eastern part of the Tethys, which made possible cohabitation of different species. The remains of all snakes discussed in this paper were found in marine sediments, but the remains of forms slightly adapted to marine life could be carried over by flows from estuaries and rivers. For this reason, we use the term "aquatic snakes" for these snakes.

Institutional abbreviation. ZIN PH and ZISP PC, Paleoherpetological and Paleontological collections respectively, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; PIN RAS – Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

MATERIAL AND METHODS

Because of the absence of natural or artificial outcroppings of bone-bearing layers in the Ak-Kaya locality, E.A. Zvonok excavated a pit (Fig. 1) near the pit made and described as "excavation pit no. 2" by Bratishko and Udovichenko (2007). The assemblage

Fig. 1. The excavation pit in the Ak-Kaya locality made in 2011.

Table 1. Measurements (mm) of the *Palaeophis* vertebrae from the Ak-Kaya locality. *Abbreviations*: a – anterior trunk vertebrae, m – middle trunk vertebrae, p – posterior trunk vertebrae. For other abbreviations see Material and methods.

Species	ZIN PH no.	CL	Co	Pr	Zy	Region of vertebral column
Palaeophis tamdy	18/153	?	3.4	?	?	?
	22/153	5.8	2.7	?	2.2	?
	20/153	9	3.6	?	3.1	?
	21/153	6.1	3	?	2.4	?
	23/153	?	3.7	?	3.5	?
Palaeophis nessovi	15/153	13.7	7.1	13.1	?	a
	26/153	?	10	19.6	?	m
	16/153	14	8.1	14.3	7.5	m
	28/153	?	?	?	8.5	m
	27/153	?	7.4	?	7.3	p
	17/153	13.6	7.2	?	6.9	p
	25/153	14.7	7.9	?	8.4	p
	24/153	13	?	?	?	p
Palaeophis cf. *toliapicus*	14/153	9.6	4.4	8.1	3.5	?

of cartilaginous fishes from the Ak-Kaya locality corresponds to those of the Lutetian part of the Novopavlovsk Horizon (Bratishko and Udovichenko 2007).

The new pit extends from the west to the east, being 8 m in length and 1.6–2.3 m in depth (Fig.1). The surface of the bottom of the pit is about 12 m^2. The remains of vertebrates were taken from layers of green-fulvous and rusty-fulvous clay sands intercalated with sublayers of clay. In the western part of the pit, bone-carrying layers are strongly gypseous. In the eastern part of the pit, the layers of green-fulvous sands are absent and the layers of rusty-fulvous sands are getting thinner until reaching a thickness of 1 cm. The highest concentration of vertebrate remains was found in the layers of green-fulvous and rusty-fulvous sands located in the central part of the pit where the layers are thicker. Almost all of the snake remains were obtained by screen-washing using sieves with a mesh diameter of 5 mm.

Measurements. The following measurements were made for the complete or nearly complete vertebrae (Table 1): CL – length of the centrum on the ventral side; Co – width of the cotyle; Pr – distance between the tips of the prezygapophyses; Zy – width of the zygosphene.

SYSTEMATICS

Order Serpentes Linnaeus, 1758

Suborder Alethinophidia Nopcsa, 1923

Superfamily Acrochordoidea Bonaparte, 1831

Family Palaeophiidae Lydekker, 1888

Subfamily Palaeophiinae Lydekker, 1888

Genus *Palaeophis* Owen, 1841

***Palaeophis tamdy* (Averianov, 1997)**
(Fig. 3A–E)

Holotype. ZISP PC 7/34, anterior trunk vertebra; Dzheroi 2 locality, Bukhara Viloyat, Uzbekistan; middle Eocene (Bartonian).

Previously referred material. ZISP PC 4/34, 6/34, 8–11/34, anterior trunk vertebrae; 3/34 and 5/34, posterior trunk vertebrae; all are paratypes from the type locality (see Averianov 1997).

Newly referred material. ZIN PH 18/153, 20–23/153, five trunk vertebrae; Ak-Kaya locality, 45°6′N, 34°38′E, Belogorsk District, Crimea, Ukraine; middle Eocene (Lutetian).

Fig. 2. Localities of *Palaeophis tamdy* and *P. nessovi* on the paleogeographical map (Eocene; after Meulenkamp et al. 2000): 1 – Bakhchisarai (Bartonian); 2 – Ak-Kaya (Lutetian); 3 – Prolom (Lutetian); 4 – Uzunbas (Upper Bartonian); 5 – Kujulus (Bartonian); 6 – Karagaly (Upper Bartonian); 7 – Monata (Priabonian); 8 – Ussak (Upper Bartonian, Priabonian); 9 – Kachar (Priabonian); 10 – Dzheroi 2 (Lutetian/Bartonian boundary). Age of 1 according to Snetkov and Bannikov (2010), 2 – current article, 3 – Bratishko and Udovichenko (2007), 4–7 – Snetkov (2011), 8 – Averianov (1997) and Snetkov and Bannikov (2010), 9 – Averianov (1997), 10 – Case et al. (1996) and Averianov (2005).

Description. The vertebrae are elongated. The axis of centrum is slightly oblique. The shape of the cotyle is close to circular. The shape of a cross section of the centrum of one of these vertebrae is closer to triangular than that of the other vertebrae and is less elongated than the others. The synapophyses are located low. On two vertebrae (ZIN PH 20/153 and ZIN PH 22/153) most likely occupying more posterior positions than the others in the vertebral column, the hypapophysis is poorly developed and turns into a well-developed haemal keel. On the three other vertebrae, the hypapophysis is well developed and the haemal keel (in this paper a keel which prolongs the hypapophysis anteriorly is called "haemal keel") is only slightly developed. The subcentral foramina are presented on three vertebrae. The subcentral ridges are slightly developed. The zygosphene is narrow and the dorsal surface is concave and only on one vertebra is it plate. The neural canal is subtriangular and wide with the width being similar to that of the cotyle. The neural spines are broken away. They were located in the posterior part of the vertebrae. The prezygapophyses, when completely preserved, are long and oblique, with the medial edges of their articular surfaces being located at the level of the dorsal margin of the centrum. The prezygapophyseal processes are absent. The interzygapophyseal ridge is well developed on three vertebrae (ZIN PH 18/153, ZIN PH 20-21/153) and less developed on the others. This is not related to the size of the hypapophysis and, therefore, with their position in the vertebral column. The pterapophyses are not preserved, but in the lateral view the posterior part of the neural arch rises clearly.

Remarks. In addition to the Lutetian of Ak-Kaya, the vertebrae of *Palaeophis tamdy* were described from the Lutetian-Bartonian boundary sediments of Uzbekistan (Dzheroi 2 locality) as *Nessovophis tamdy* considered as a nigerophiid (Averianov 1997; the age according to Case et al. [1996] and Averianov [2005]). Rage et al. (2003) referred *N. tamdy* to the genus *Palaeophis* on the basis of the comparatively reduced prezygapophyses, horizontal axis of the condyle and the presence of the hypapophysis in the middle trunk vertebrae and the haemal keel on posteriormost ones. These authors also noted that the pterapophyses of *P. tamdy* have the same size as those of *Palaeophis toliapicus* Owen, 1841 and *Palaeophis casei* Holman, 1982.

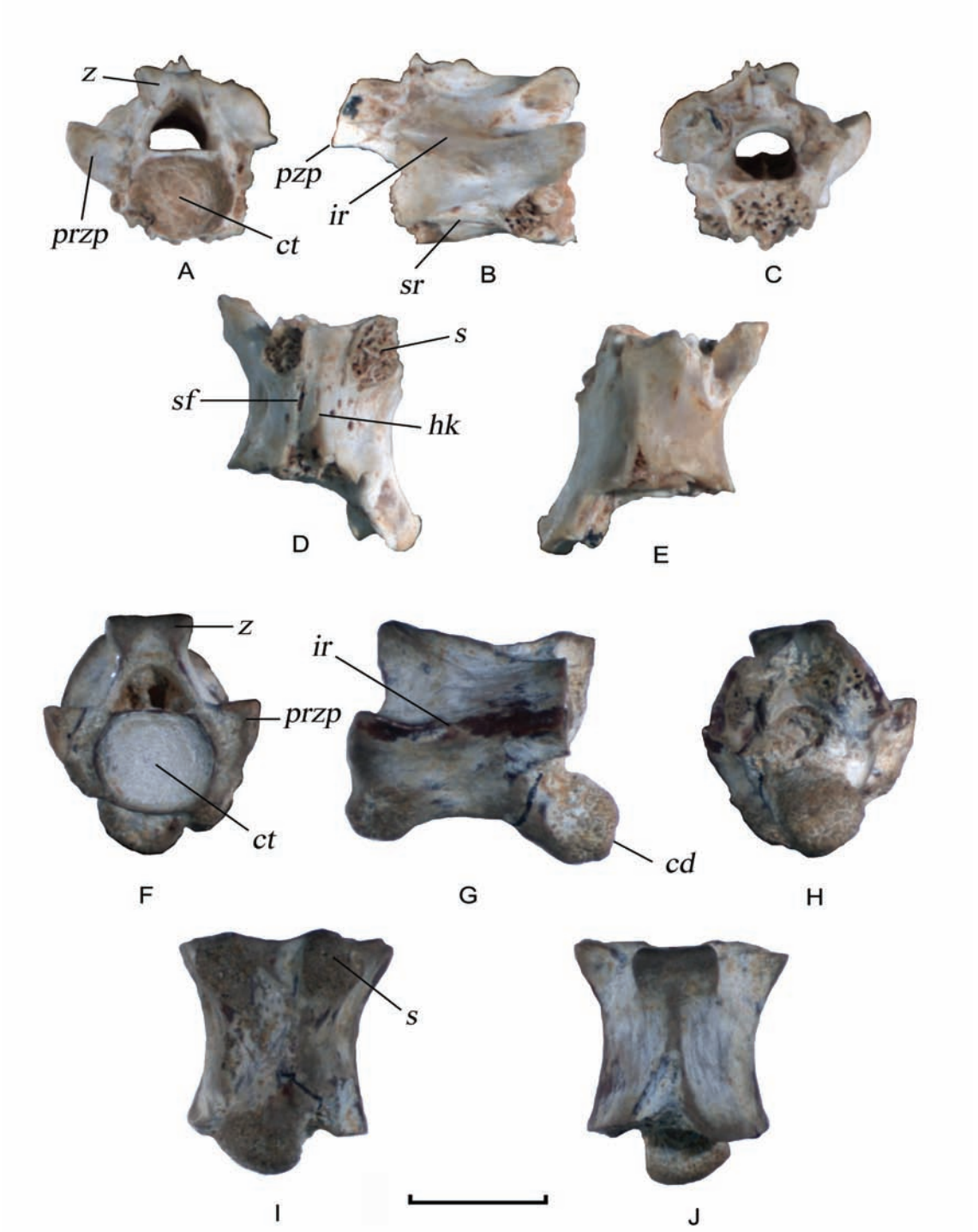

Fig. 3. Trunk vertebrae of *Palaeophis tamdy* and *P.* cf. *toliapicus* from the Ak-Kaya locality (Lutetian of Crimea): A–E – *P. tamdy* (ZIN PH 18/153): A – anterior view; B – lateral view; C – posterior view; D – ventral view; E – dorsal view; F–J – *P.* cf. *toliapicus* (ZIN PH 14/153): F – anterior view; G – lateral view; H – posterior view; I – ventral view; J – dorsal view. *Abbreviations*: *cd* – condyle; *ct* – cotyle; *hk* – haemal keel; *ir* – interzygapophyseal ridge; *pt* – pterapophysis, *przp* – prezygapophysis; *pzp* – postzygapophysis; *s* – synapophysis; *z* – zygosphene. Scale bar = 5 mm.

***Palaeophis nessovi* Averianov, 1997**
(Fig. 4)

Holotype. ZISP PC 1/36, middle trunk vertebra; Kachar locality, northern Kazakhstan; upper Eocene (Priabonian).

Previously referred material. ZIN PH 7/119, 58–59/119, 60–110/119, isolated and articulated trunk vertebrae; Kujulus locality, Western Kazakhstan, middle Eocene, Bartonian; ZIN PH 1–3/119, 23–57/119, isolated and articulated trunk vertebrae; Uzunbas locality, Western Kazakhstan, middle Eocene, Bartonian; ZIN PH 10–22/119, isolated and articulated trunk vertebrae; Karagaly locality, Western Kazakhstan, middle Eocene, Bartonian; ZIN PH 9/119, two articulated trunk vertebrae; Monata locality, Western Kazakhstan, upper Eocene, Priabonian; ZIN PH 8/119, anterior trunk vertebrae; Ussak locality, Western Kazakhstan, upper Eocene, Priabonian; PIN RAS 1/5361, posterior trunk vertebra; Bakhchisarai locality, Crimea, Ukraine, middle Eocene, Bartonian.

Newly referred material. ZIN PH 15–17/153, 24–28/153 and unnumbered specimens in the collection ZIN PH 153, total 51 trunk vertebrae; Ak-Kaya locality, 45°6´N, 34°38´E, Belogorsk District, Crimea, Ukraine; middle Eocene (Lutetian).

Description. The vertebrae are relatively short. The axis of the centrum is slightly oblique. The shape of the cotyle vary from oval to circular and on the dorsal margin of the cotyle there is usually a notch. The synapophyses are located rather low. On the ventral surface of the centrum in the posterior part there is a short hypapophysis. It is very shallow and looks like a haemal keel in most vertebrae. The subcentral foramina are usually asymmetric when subcentral ridges are present. The zygosphene is vaulted. The neural canal in the anterior view has a subtriangular shape and is significantly narrower than the cotyle. On the anterior trunk vertebrae, the neural canal is slightly wider than on the others. The neural spines are broken on all vertebrae. They occupied the entire length of the vertebrae. The prezygapophyses are slightly oblique in the dorsal view. The prezygapophyseal processes are absent. The interzygapophyseal ridge is present. The pterapophyses are well developed, however, on many vertebrae they are broken.

In the described material, some morphological variation occurs. On some vertebrae (for example ZIN PH 15/153), the hypapophyses are enlarged, the subcentral ridges are developed and the haemal keels are absent. According to these characteristics, these vertebrae belong to the anterior trunk region of the vertebral column. The vertebrae also differ in the degree of lateral compression and degree of development of the haemal keel with the more posterior vertebrae being more laterally compressed, the haemal keel being better developed and the hypapophysis being less developed. On some vertebrae the notch on the upper margin of the cotyle is absent. On one vertebra (ZIN PH 24/153), most likely a posterior trunk, the axis of centrum is obviously more oblique than on others. Some vertebrae (ZIN PH 25–28/153) are much larger than the others, but they do not significantly differ from them in morphology, so the difference in size is most probably caused by age-related variables.

Remarks. In addition to the Lutetian of Ak-Kaya, vertebrae of *Palaeophis nessovi* have been found in two Ukrainian and six Kazakhstan localities of the Lutetian-Priabonian age (Fig. 3). Vertebrae from the Prolom locality were described as a separate species *Palaeophis udovichenkoi* (Averianov 1997), which was later reconsidered as a junior synonym of *P. nessovi* (Snetkov and Bannikov 2010). The Prolom locality is situated only 5 km east of Ak-Kaya. The anterior, middle and posterior trunk vertebrae of *P. nessovi* are known from the Kazakhstan localities of Uzunbas and Karagaly (Snetkov 2011). They have the same morphology as the vertebrae from Ak-Kaya described here.

***Palaeophis* cf. *toliapicus* Owen, 1841**
(Fig. 3F–J)

Material. ZIN PH 14/153, trunk vertebra; Ak-Kaya locality, 45°6´N, 34°38´E, Belogorsk District, Crimea, Ukraine; middle Eocene (Lutetian).

Description. The vertebra is elongated. The condyle is deformed. The cotyle has a circular shape. The synapophyses are located rather low. The ventral surface of the centrum is eroded, thus the presence or form of the haemal keel, hypapophyses, subcentral foramina and subcentral ridges are unknown. The zygosphene is significantly narrower than the cotyle and its dorsal surface is flat. The cross section of the neural canal is subtriangular. It is slightly narrower than the cotyle. The neural spine is broken but, if present, would have been located in the posterior part of the vertebra. The prezygapophyses are smaller than that of *P. tamdy* and *P. nessovi*, with their articular surfaces

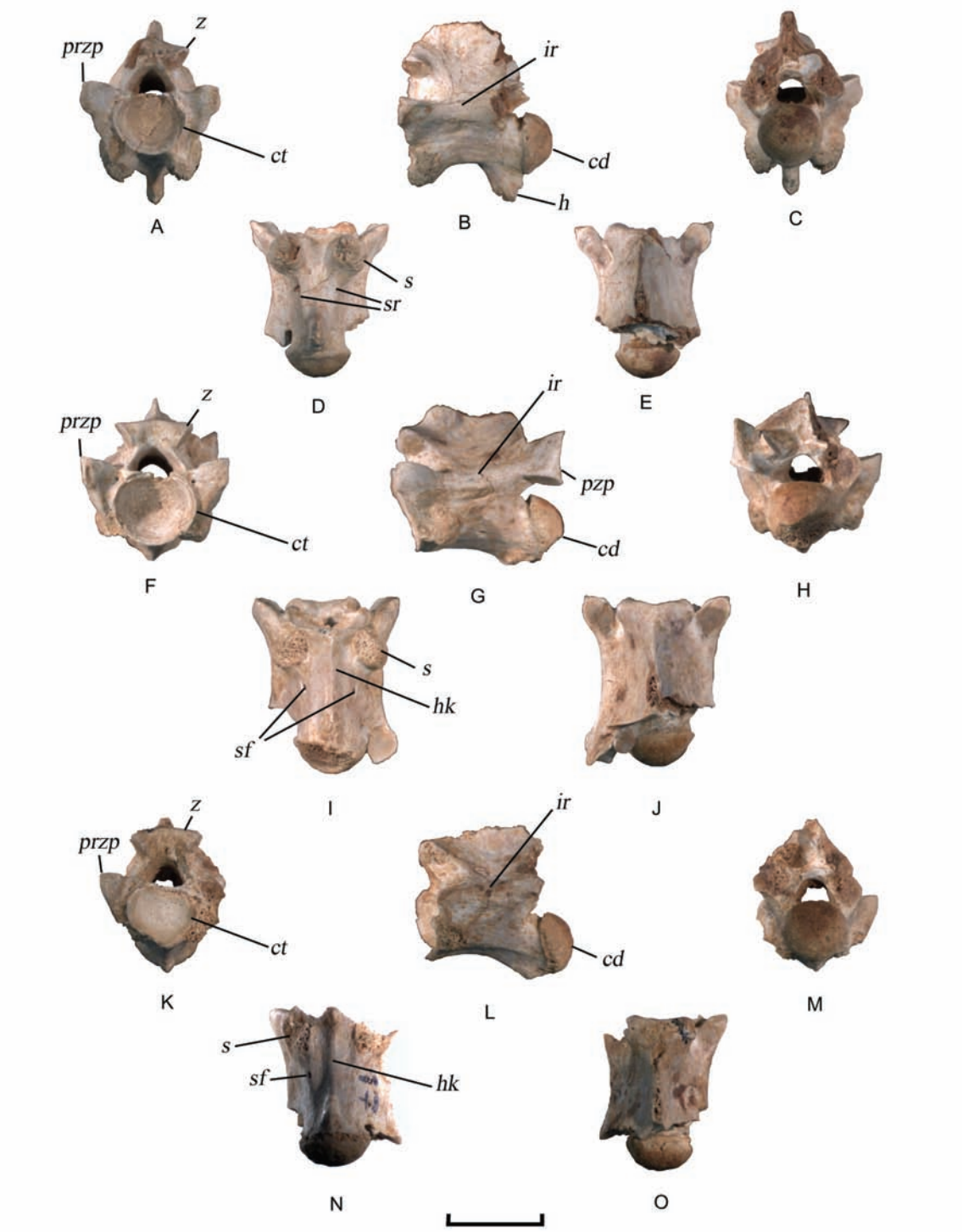

Fig. 4. Trunk vertebrae of *Palaeophis nessovi* from the Ak-Kaya locality (Lutetian of Crimea): A–E – anterior trunk vertebra (ZIN PH 15/153): A – anterior view; B – lateral view; C – posterior view; D – ventral view; E – dorsal view; F–J – middle trunk vertebra (ZIN PH 16/153): F – anterior view; G – lateral view; H – posterior view; I – ventral view; J – dorsal view; K–O – Posterior trunk vertebra (ZIN PH 17/153): K – anterior view; L – lateral view; M – posterior view; N – ventral view; O – dorsal view. *Abbreviations*: *h* – hypapophysis; *sf* – subcentral foramen; *sr* – subcentral ridges. Scale bar = 10 mm.

being horizontal and located at the level of the dorsal margin of the cotyle. The prezygapophyseal processes are absent. The interzygapophyseal ridge is weak. The posterior part of the neural arch is broken, but one pterapophysis appears to be entirely preserved.

Remarks. Such characteristics of the described vertebra as a small size and horizontal position of the prezygapophyses, the low position of the synapophyses and the strong lateral compression allow to consider it as an evolutionary advanced species of *Palaeophis*, according to Rage et al. (2003). It is most reminiscent of the vertebrae of *P. toliapicus* known from the Ypresian of Western Europe (Rage et al. 2003), but differs from them by a slightly lower position of the articular surfaces of the prezygapophyses. *Palaeophis toliapicus* has anterior hypapophysis on the anterior trunk vertebrae (Rage 1983). Due to the damaged ventral surface of the centrum, the position of the vertebra from the Ak-Kaya locality in the vertebral column was impossible to determine.

DISCUSSION

The assemblage of aquatic snakes of the Ak-Kaya locality includes both middle Eocene (*Palaeophis tamdy*) and middle-upper Eocene (*Palaeophis nessovi*) species of Acrochordoidea. The third form of aquatic snakes from the Ak-Kaya locality (*Palaeophis* cf. *toliapicus)* is similar to *Palaeophis toliapicus* from the lower Eocene of England. *Palaeophis nessovi* has well developed pterapophyses, comparatively short prezygapophyses and strongly laterally compressed posterior and anterior trunk vertebrae. These characters suggest that *P. nessovi* was well adapted to the aquatic mode of life (Rage et al. 2003). *Palaeophis tamdy* has large prezygapophyses and lacks pterapophyses, and can be considered as a less specialized form. *Palaeophis cf. toliapicus,* probably, was adapted to the aquatic mode of life even better than *P. nessovi* according to less developed prezygapophyses and stronger lateral compression of the vertebra.

The complex faunas of aquatic snakes of the Middle Eocene are known from the series of localities of the territory of the former USSR. In the locality Ussak (Bartonian-Priabonian of Western Kazakhstan), in addition to the vertebrae of *Palaeophis nessovi*, vertebrae determined as *Palaeophis* sp. were found (Averianov 1997). The latter form demonstrates moderate specialization to the aquatic life, as it has slightly developed pterapophyses but low positioned synapophyses and strong laterally compressed vertebrae. From the locality of Dzheroi 2 (Bartonian of Uzbekistan), in addition to vertebrae of *Palaeophis tamdy,* vertebrae described as *Pterosphenus muruntau* Averianov, 1997 are known (Averianov 1997). Rage et al. (2003) considered the latter species to be a nomen dubium, because of the bad preservation of the vertebrae. However, it is possible to make a conclusion that "*Pterosphenus muruntau*" was a snake strongly adapted to the aquatic life as far as it had reduced prezygapophyses and high vertebrae. *Palaeophis* cf. *toliapicus* from the Ak-Kaya locality also shows high degree of aquatic adaptations. The localities of Crimea, Western and Northern Kazakhstan and Uzbekistan from which remains of *P. tamdy*, *P. nessovi*, *P.* cf. *toliapicus*, *P.* sp. and "*Pterosphenus muruntau*" were collected, are situated on the territory which in the Eocene was covered by the Eastern part of Tethys (Fig. 2). Thus, in the middle Eocene there are slightly, medium and well adapted to the aquatic mode of life species of Acrochordoidea. However, all together these three species of snakes were found only in the Lutetian of the Ak-Kaya locality.

The bone bearing Middle Eocene deposits of Crimea in some places such as the Ak-Kaya and Prolom localities contain abundant remains of aquatic snakes, so there is an opportunity for their further collection and study.

ACKNOWLEDGMENTS

The authors are grateful to I.G. Danilov (Zoological Institute RAS) for partial financial support of the expedition, N.I. Udovichenko (Lugansk National T. Shevchenko University) for accurate information concerning the optimal placement of excavation pits, V.S. Dernov (Luhansk National T. Shevchenko University) for assistance during field work; W.V. McKenzie and E.A. Veikher for linguistic correction of the English version of the manuscript.

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Submitted July 23, 2012; accepted November 20, 2012.