

***Pterospheenus muruntau* – valid species of sea snakes (Squamata: Palaeophiidae) from the middle Eocene of Uzbekistan**

***Pterospheenus muruntau* – валидный вид морских змей (Squamata: Palaeophiidae) из среднего эоцена Узбекистана**

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Abstract. A palaeophiid sea snake *Pterospheenus muruntau* Averianov, 1997 was based on two trunk vertebrae and several vertebral fragments from the middle Eocene (Bartonian) coastal marine deposits of Dzheroi 2 locality in the Central Kyzylkum Desert, Uzbekistan. The species was considered a *nomen dubium* by Rage and coauthors in 2003 based on alleged poor preservation of the type specimens. However, the preservation of the holotype of *P. muruntau* is sufficient to discern a slightly laterally compressed vertebra and a low pterapophysis, the characters that distinguish this species from the other species of *Pterospheenus*. These characters are also clear in a new and better preserved vertebra of *P. muruntau* from the type locality. *Pterospheenus muruntau* should be considered a valid species of the genus *Pterospheenus*.

Резюме. Вид палеофиидных морских змей *Pterospheenus muruntau* Averianov, 1997 был основан на двух туловищных позвонках и нескольких фрагментах позвонков из среднеэоценовых (бартон) прибрежно-морских отложений местонахождения Джерой 2 в Центральных Кызылкумах, Узбекистан. Этот вид рассматривался как *nomen dubium* в публикации Rage с соавторами в 2003 г. на основании приписываемой плохой сохранности типовых экземпляров. Однако, сохранность голотипа *P. muruntau* достаточна, чтобы различить слабую латеральную сжатость позвонка и низкий птеропофиз – признаки, которые отличают этот вид от других видов рода *Pterospheenus*. Эти признаки также хорошо выражены у нового и лучше сохранившегося позвонка *P. muruntau* из типового местонахождения. *Pterospheenus muruntau* должен рассматриваться как валидный вид рода *Pterospheenus*.

Key words: Eocene, Uzbekistan, morphology, diagnostic characters, redescription, Squamata, Palaeophiidae

Ключевые слова: эоцен, Узбекистан, морфология, диагностические признаки, переописание, Squamata, Palaeophiidae

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Introduction

The quartz sands with phosphorites exposed in several quarries in the vicinity of Muruntau Village in the Central Kyzylkum Desert, Uzbekistan, produce a rich complex of nearshore and marine vertebrates, including various sharks, rays, teleost fishes, turtles, sea snakes, and birds (Nesov et al., 1987; Nesov, 1988, 1995; Averianov et al., 1991; Panteleev & Nesov, 1993; Case et al., 1996; Averianov, 1997, 2005; Malyshkina & Ward, 2016). The sea snakes are known from two localities, Dzheroi 1 and Dzheroi 2 (Nesov et al., 1987; Nesov, 1995; Averianov, 1997). Averianov (1997) described two taxa of sea snakes based on isolated trunk vertebrae from Dzheroi 2 locality: *Nessophis tamdy* Averianov, 1997 (Nigerophiidae) and *Pterosphenus muruntau* Averianov, 1997 (Palaeophiidae). The validity of the latter species was questioned by Rage et al. (2003), who considered it a *nomen dubium* mostly because of poor preservation of the two published specimens (holotype and paratype). Based on this opinion, Snetkov (2011) did not include *P. muruntau* in his phylogenetic analysis of the acrochordoidean snakes. Here I report on a new, more complete and better preserved, trunk vertebra of *P. muruntau*, the study of which made it possible to clarify the diagnosis of the species and to confirm its validity. I also provide better illustrations for the type specimens of *P. muruntau* and discuss the phylogenetic position of this species.

Material and methods

The study is based on seven specimens including the types, all kept at the Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia). Institutional abbreviations: ZIN PC, Paleontological collection, Zoological Institute, Russian Academy of Sciences; ZIN PH, Paleoherpological collection, same institution.

The photos are taken with a Canon EOS 760D camera supplied with a Canon Macro lens EF-S 60 mm. Focal stack images were montaged with Helicon Focus 7.6.4 software and edited in Adobe Photoshop.

Abbreviations used for measurements follow Averianov (1997): CL, length of vertebral centrum (from the ventral surface); Co, width of coty-

le; Pr, distance between the tips of prezygapophyses; Zy, width of zygosphene.

Systematic palaeontology

Order **Serpentes** Linnaeus, 1758

Suborder **Alethinophidia** Nopcsa, 1923

Family **Palaeophiidae** Lydekker, 1888

Genus ***Pterosphenus*** Lucas, 1899

Pterosphenus muruntau Averianov, 1997

(Figs 1–4)

Palaeophis [sp.]: Nesov, 1995: 8.

Palaeopheididae [indet.]: Nesov, 1995: 8.

Pterosphenus muruntau Averianov, 1997: 138, fig. 7.

Pterosphenus muruntau: Alifanov, 2012: 145.

Type material examined. Holotype. ZIN PC 1/34 (anterior trunk vertebra), **Uzbekistan, Navoiy Prov. (Navoiy Viloyati)**, Central Kyzylkum Desert, Dzheroi 2. Middle Eocene (Bartonian).

Paratype. ZIN PC 2/34 (middle trunk vertebra), same locality.

Other material examined. Uzbekistan, Navoiy Prov. (Navoiy Viloyati), Central Kyzylkum Desert: Dzheroi 2, ZIN PH 2/287 (neural arch anterior fragment), ZIN PH 3/287 (neural arch posterior fragment), ZIN PH 4/287 (anterior trunk vertebra), ZIN 5/287 (posterior trunk vertebra); Dzheroi 1, ZIN PH 1/287 (neural arch posterior fragment).

Referred specimens. In addition to the holotype and the paratype, Averianov (1997) referred to *P. muruntau* five unnumbered vertebral fragments, three from the type locality and two from Dzheroi 1 locality. In this work, only two of these specimens from the type locality are referred to *P. muruntau* that receive numbers ZIN PH 2/287 and ZIN PH 3/287. Only one specimen from Dzheroi 1 locality (ZIN PH 1/287) is referred here to *P. muruntau*. The more recently collected specimens are ZIN PH 4/287 and 5/287 from the type locality.

Specimens ZIN PH 1/287, 2/287 and 3/287 are fragmentary and were not used in the redescription, but ZIN PH 2/287 was included in the measurements (Table 1).

Comparison. The species is assigned to the genus *Pterosphenus* because of prezygapophyses markedly reduced, zygosphene convex dorsally, and anterior border of the neural spine originating

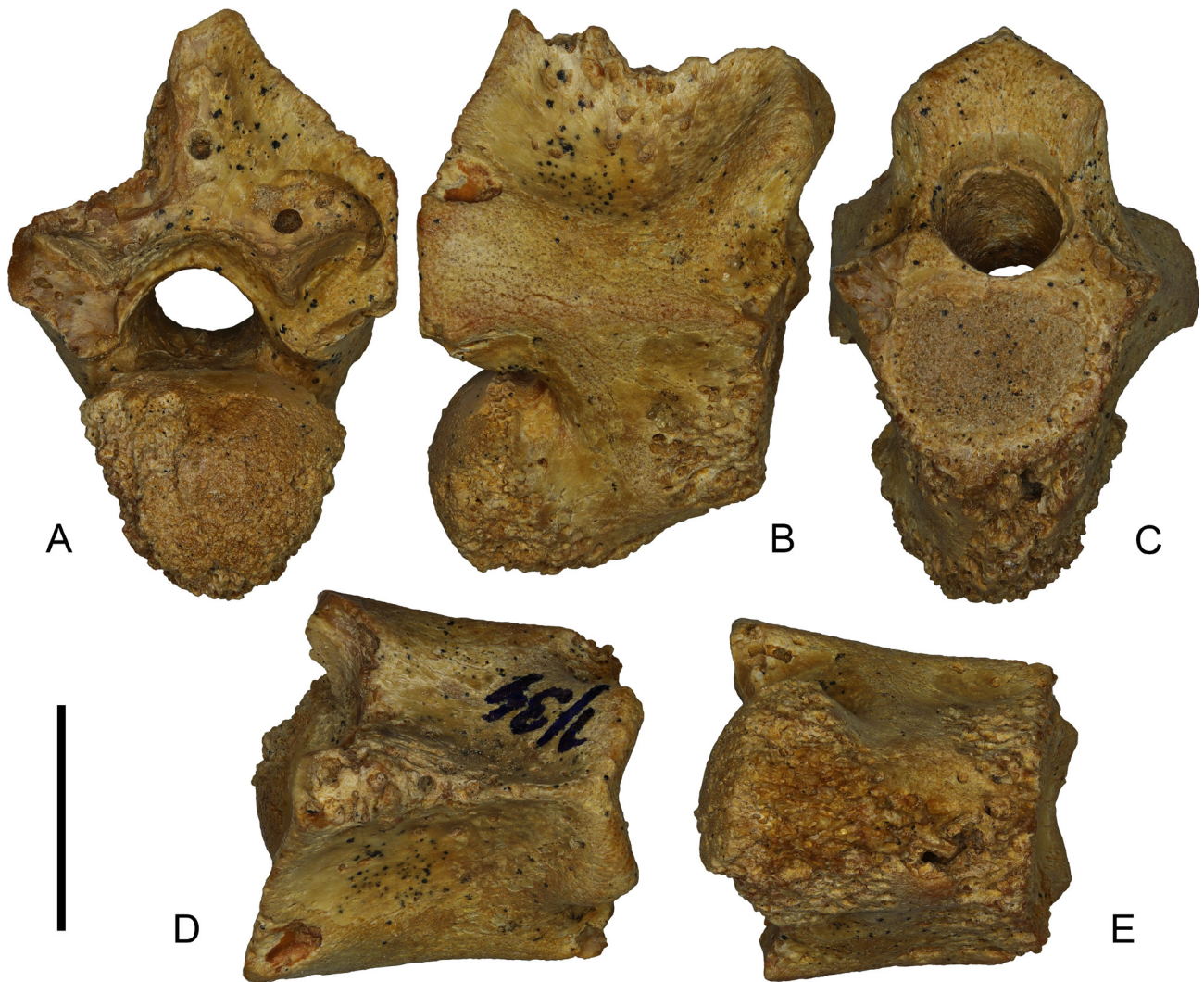


Fig. 1. *Pterosphenus muruntau* Averianov, 1997 (ZIN PC 1/34, holotype), anterior trunk vertebra, in posterior (A), lateral (B), anterior (C), dorsal (D), and ventral (E) views. Scale bar: 10 mm.

from the top of the anterior border of the zygosphene (Rage et al., 2003). *Pterosphenus muruntau* differs from other species of *Pterosphenus* in the less laterally compressed vertebrae and lower pterapophyses. Additionally it differs from *P. kutchensis* Rage et al., 2003 from the early Eocene of India (Rage et al., 2003) in the left and right synapophyses not originating from a common base, anterior hypapophysis present, much smaller neural canal, oblique prezygapophyseal articular facets, the zygosphene narrower than the cotyle, concave anterior surface of the zygosphene, prominent interzygapophyseal ridge, and thin base of the neural spine above the zygosphene. *Pterosphenus muruntau* additionally differs from

P. biswasi Rage et al., 2003 from the early Eocene of India (Rage et al., 2003) in the much smaller neural canal, the zygosphene narrower than the cotyle, and anterior surface of the zygosphene more deeply concave.

Redescription. For description of holotype (Fig. 1) and paratype (Fig. 2), see Averianov (1997).

ZIN PH 4/287 (Fig. 3): Almost complete anterior trunk vertebra, missing dorsal part of neural spine and left pterapophysis. Cotyle cordiform in shape, with concave dorsal margin below neural canal and ventral margin narrowing towards anterior hypapophysis. Condyle narrower than cotyle, subtriangular in shape, with convex dorsal margin. Axis of condyle horizontal. Centrum

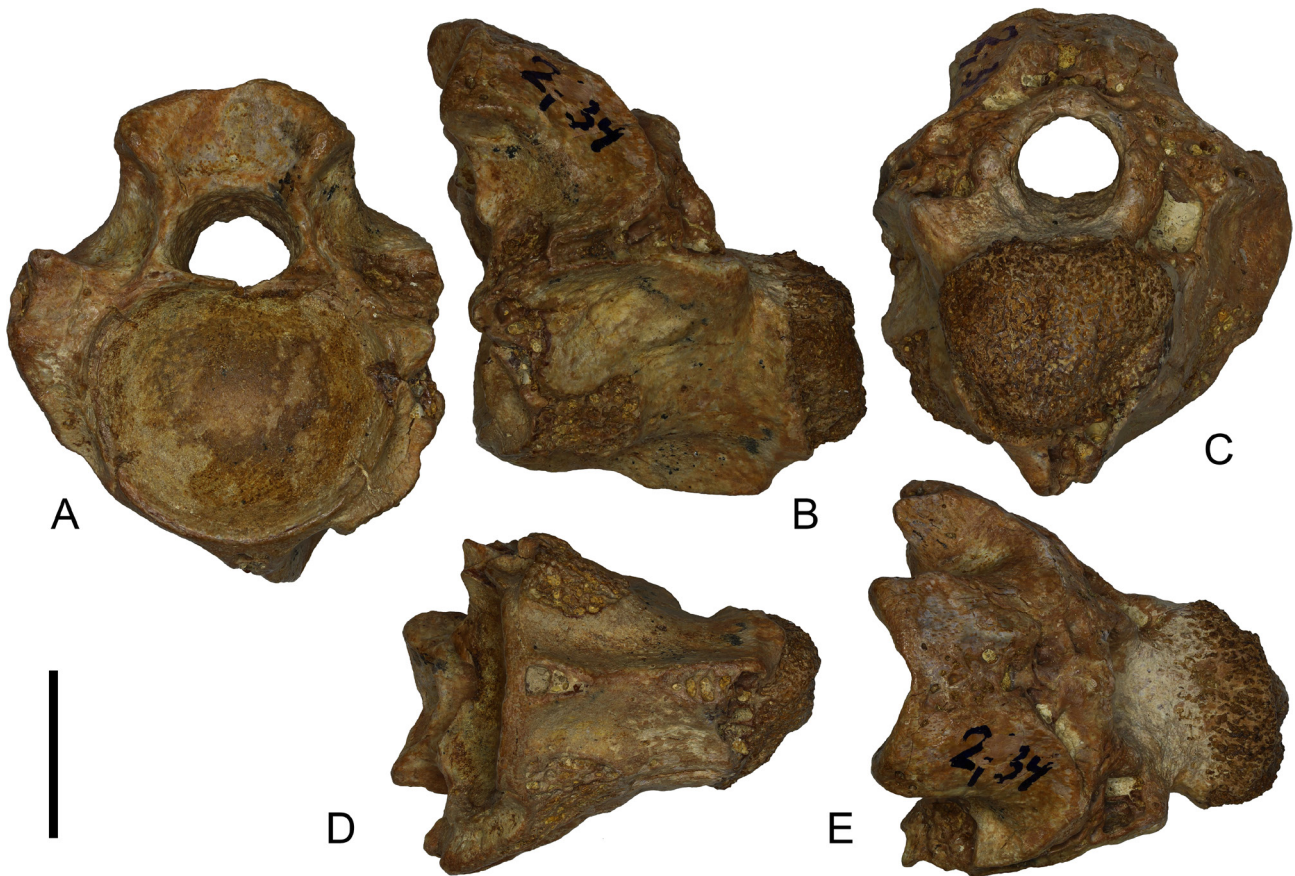


Fig. 2. *Pterosphenus muruntau* Averianov, 1997 (ZIN PC 2/34, paratype), middle trunk vertebra, in anterior (A), lateral (B), posterior (C), ventral (D), and dorsal (E) views. Scale bar: 10 mm.

constricted close to condyle. Only basal parts of synapophyses preserved. They positioned close to cotyle and below to mid-height on centrum, but not projecting ventrally to centrum. Anterior surface of left synapophysis with tiny foramen similar to that in *P. kutchensis* (Rage et al., 2003: fig. 2a). Subcentral ridge poorly defined. Two hypapophyses developed and connected by a ventral keel: smaller anterior and larger, thicker posterior. Anterior hypapophysis hook-like, pointed anteriorly. Posterior hypapophysis about twice as high as anterior one. Small subcentral foramen present on right side. Neural canal small, about one-third of cotyle width. Its anterior opening D-shaped, with dorsal margin more convex than ventral margin. Posterior opening of neural canal nearly round. Neural arch similar in length to centrum, with prezygapophyses projecting anteriorly beyond cotyle and postzygapophysis not projecting posteriorly beyond condyle. Zygapophyses great-

ly reduced. Transverse width of prezygapophysis about one-third of cotyle width. Zygapophyseal articular surfaces oval and horizontal, located slightly above level of neural canal floor. Their long axis oblique in prezygapophyses and transverse in postzygapophyses. Prezygapophyses connected to synapophyses by sharp vertical ridges. Interzygapophyseal ridge stout. Transverse width of zygosphene about 85% of cotyle width. Anterior margin of zygosphene convex. Dorsal margin of zygosphene triangular in anterior view, pointing dorsally and continuing into neural spine whose anterior border coinciding with that of zygosphene. Articular surfaces of zygosphene oval, facing ventrolaterally. Zygantrum consisting of two depressions housing articular surfaces and separated by elevated midline surface. Zygantral articular surfaces oval, facing dorsomedially. Irregular tiny neurovascular foramina present dorsal to these surfaces. A large zygantral foramen placed

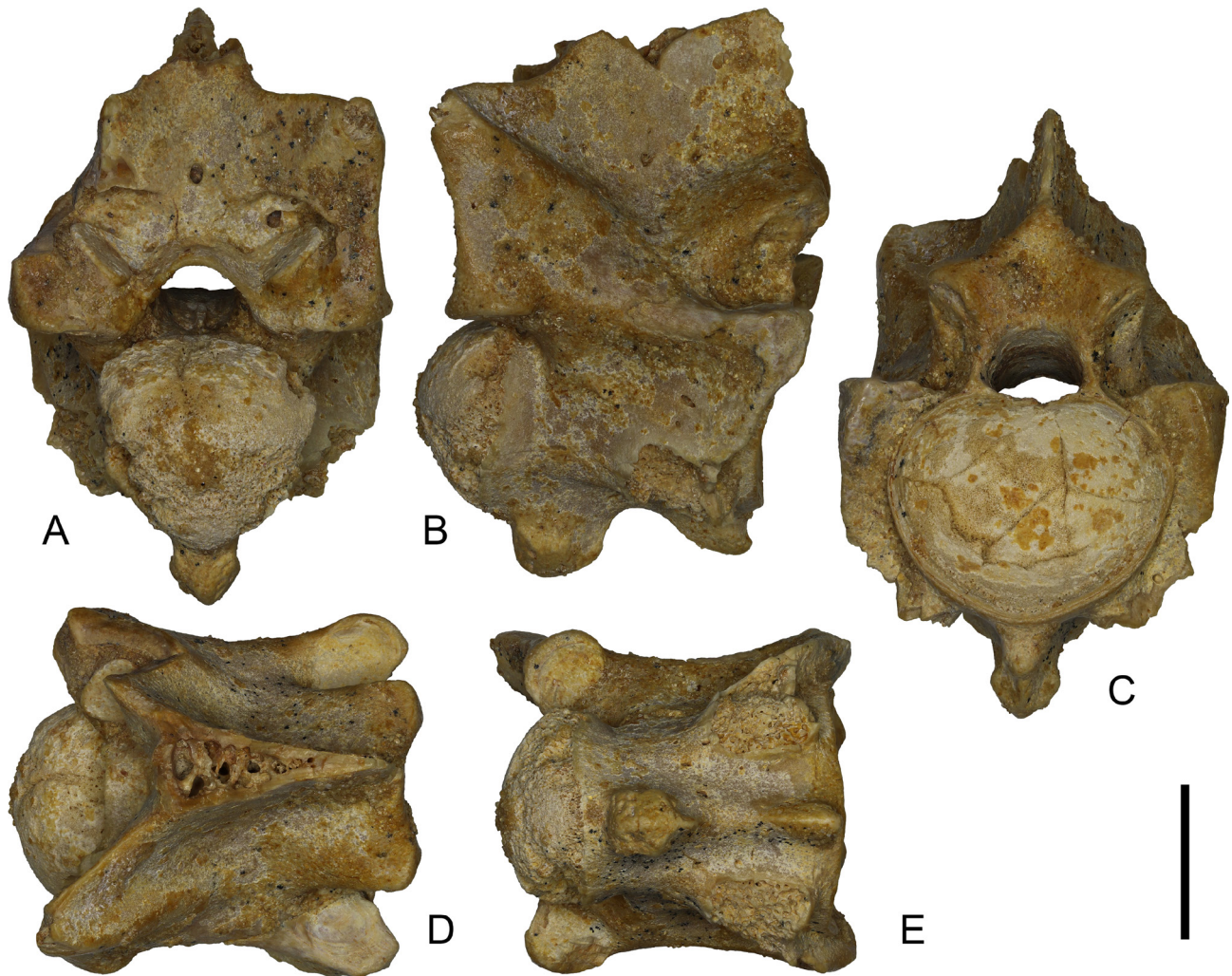


Fig. 3. *Pterosphenus muruntau* Averianov, 1997 (ZIN PH 4/287), anterior trunk vertebra, in posterior (A), lateral (B), anterior (C), dorsal (D), and ventral (E) views. Scale bar: 10 mm.

on midline within zygantrum as in some other palaeophiids (Rage et al., 2003; Georgalis et al., 2021). Neural spine extending for entire length of neural spine. Its base triangular in cross-section, wide posteriorly and tapering anteriorly where neural spine as a thin vertical plate. Pterapophyses low, only slightly higher than dorsal margin of zygosphenes. Pterapophyseal ridge directed towards zygosphenes parallel to interzygapophyseal ridge.

ZIN PH 5/287 (Fig. 4): Unusual posterior trunk vertebra with nearly absent zygapophyses and reduced zygosphenes and zygantrum. Neural spine absent. Specimen referred to *Pterosphenus* because of reduction of zygapophyses and zygosphenes. It is not clear if it is an aberrant specimen

or it represents a previously unknown positional variation for *Pterosphenus*.

Measurements. For measurements, see Table 1.

Discussion

According to Rage et al. (2003), the characters cited in the original diagnosis of *P. muruntau* by Averianov (1997) are either characters diagnosing the genus *Pterosphenus* or characters related to ontogeny (neural canal small, external walls of vertebrae relatively thick) or not taxonomically significant (lateral and pterapophyseal marrow cavities present). Rage et al. (2003) described the juvenile specimens of *P. kutchensis* from the early Eocene of India, which have the neural canal

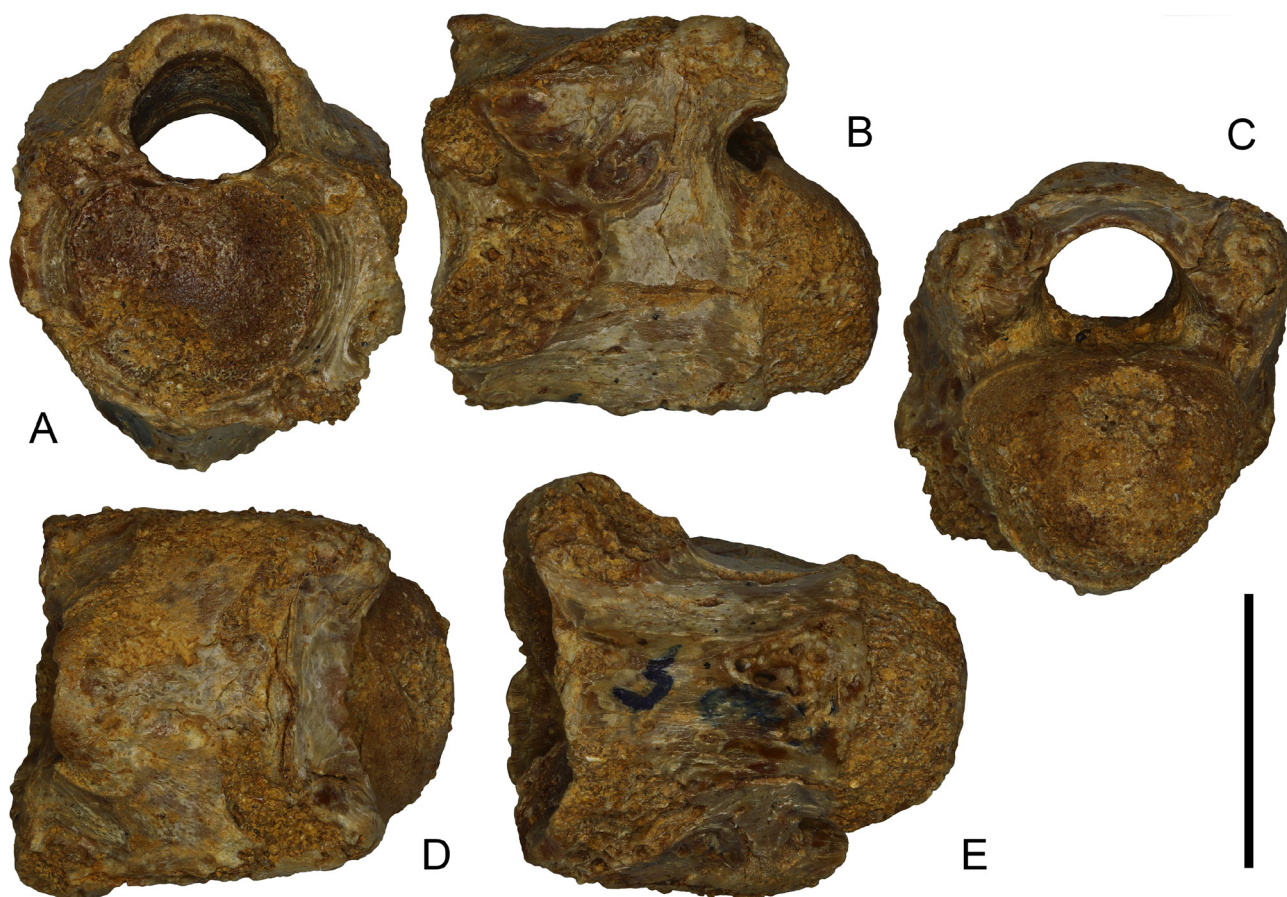


Fig. 4. *Pterosphenus muruntau* Averianov, 1997 (ZIN PH 5/287), posterior trunk vertebra, in anterior (A), lateral (B), posterior (C), dorsal (D), and ventral (E) views. Scale bar: 10 mm.

wider than in adults. However, in adult specimens of *P. muruntau* the neural canal is much smaller (less than the half of the cotylar width) than in adult specimens of *P. kutchensis* and other species of *Pterosphenus*. This character is considered here a valid diagnostic feature distinguishing *P. muruntau* from other species. *Pterosphenus* sp.

from the late Eocene of Morocco (Zouhri et al., 2018: fig. 8a, g) approaches *P. muruntau* in the size of the neural canal but is still relatively larger than in Uzbek species. The Moroccan species clearly differs from *P. muruntau* in the relatively larger zygosphene, which is similar in width with the cotyle, as in other species of *Pterosphenus*.

Table 1. Measurements (in mm) of trunk vertebrae in *Pterosphenus muruntau* Averianov, 1997 (Dzheroi, Uzbekistan; middle Eocene).

Specimen	CL	Co	Pr	Zy
ZIN PC 1/34*	15.4	8.6	–	9.3
ZIN PC 2/34**	23.7	18.9	–	13.7
ZIN PH 4/287	21.9	17.3	23.4	13.3
ZIN PH 2/287	–	–	–	11.3

Abbreviations: CL, length of vertebral centrum (from the ventral surface); Co, width of cotyle; Pr, distance between the tips of prezygapophyses; Zy, width of zygosphene.

* Holotype.

** Paratype.

Among the palaeophiid snakes, the enlarged lateral and pterapophyseal marrow cavities are present among the species of *Pterosphenus* (Hutchison, 1985; Houssaye et al., 2019). This character, “taxonomically nonsignificant” according to Rage et al. (2003), could be a diagnostic character of the genus *Pterosphenus*.

Rage et al. (2003: 701) noted that the small size of the pterapophyses in *P. muruntau* would be “a feature of interest” because in other species of *Pterosphenus* they are high. However, Rage et al. (2003) decided that the state of preservation of the pterapophyses in the two known specimens of *P. muruntau* does not permit inference that they were small or incipient and concluded that this species should be considered a *nomen dubium*. Although the right pterapophysis is broken on the holotype of *P. muruntau* (Fig. 1B), the broken area is very small suggesting that the pterapophysis was also small. A larger pterapophysis would have left a large damage area. The pterapophysis is well preserved in the specimen ZIN PH 4/287 described in this paper. It is higher than in species of *Palaeophis* Owen, 1841 and similar in height (level with the dorsal margin of the zygosphenes) to that of the holotype of *P. kutchensis* (Rage et al., 2003: fig. 2l), but distinctly lower than in other specimens of *P. kutchensis* (Rage et al., 2003: fig. 3A) and in other species of *Pterosphenus*. A small size of the pterapophyses is considered here a valid diagnostic character of *P. muruntau*.

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* Lev Nesov himself preferred the transliteration of his family name as “Nessov” and this is widely used in the literature. However, the correct transliteration of this Russian name is “Nesov”, which I use here and also in my other papers.