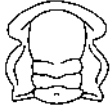


A eutherian mammal from the Early Cretaceous of Russia and biostratigraphy of the Asian Early Cretaceous vertebrate assemblages

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Prokennalestes abramovi n.sp. is described based on M2 from the upper Barremian–middle Aptian (Early Cretaceous) Mogoito locality in Transbaikalia, Russia. It differs from the Mongolian species of *Prokennalestes* (Khoboor, early Albian) by a combination of one primitive character (steeper and shorter lingual slopes of the paracone and metacone), one more derived character (larger size), and some characters of uncertain polarity (small preparastyle, lack of labial cuspules along the ectoflexus). *P. abramovi* n.sp. is the oldest eutherian mammal so far described, and its discovery extends the known geological range of Eutheria by 10–15 Ma. The Tsagantsabian land-vertebrate biochron can be defined by a dominance of sinemyid turtles; the Khukhtekian by a dominance of macrobaenids. □ *Biostratigraphy, China, Early Cretaceous, Eutheria, Mongolia, Prokennalestes, Russia, vertebrates.*

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In a now classic summary of Mesozoic mammals distribution, published 20 years ago, Clemens *et al.* (1979, p. 28) remarked that the ‘Asiatic records of Early Cretaceous mammalian life are exceptionally tantalizing, but unfortunately very little really usable information is yet available’. Three mammalian localities in the Asian Early Cretaceous were known at that time: two Chinese sites, each producing single mammal specimens (*Endotherium niinomii* and *Manchurodon simplicidens*), and a site from Mongolia (Khoboor), which was known to include a diverse and important mammal fauna, although most of this fauna had not yet been described. The past 20 years have witnessed some improvement in our knowledge of Early Cretaceous mammals from Asia (Fig. 1): the Khoboor fauna has been described (Dashzeveg 1975, 1979, 1994; Trofimov 1978, 1980, 1997; Dashzeveg & Kielan-Jaworowska 1984; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska & Dashzeveg 1989, 1998; Sigogneau-Russell *et al.* 1992; Wible *et al.* 1995) and 10 new mammal localities have been reported from the Early Cretaceous of Asia (Fig. 1). These are as follows: (1) Khamryn-Uls in Mongolia (Albian), yielding a single undescribed amphilestine ‘triconodont’ dentary fragment with m2-3 (Reshetov & Trofimov 1980; Tumanova 1987); (2) Khodzhaikul in Uzbekistan (latest Albian?), producing the holotype and only

known specimen of the eutherian *Bobolestes zenge* and several edentulous dentary fragments, first found in 1978 (Nessov 1985); (3) Huang-Ni-Tang in Xinjiang, China, producing a dentary fragment with five broken teeth found in 1980 (Chow & Rich 1984); the locality was dated as early? Cretaceous by Chow & Rich (1984) or early Cretaceous by Zhang (1984); (4) Elesitai in Inner Mongolia, China (Aptian–Albian or ?Albian), where a well-preserved jaw with three teeth of ‘a new genus of mammal’ was found in 1988, but not yet described (Dong 1993a, p. 1999; Russell & Zhao 1996, p. 646 cite also ‘mammals’ for this locality); (5) Badaohao in Liaoning Province, China (Aptian–early Albian), where upper and lower jaws of multituberculates, anterior parts of two dentaries of symmetrodonts, a dentary of an aegialodontid, and a dentary of a ‘possible eutherian’ were found in 1994 (Wang *et al.* 1995); (6) Xindi and a nearby locality in Liaoning Province, China (Albian), produced an isolated multituberculate tooth and a mammal tooth fragment, respectively, both found in 1994 (Wang *et al.* 1995); (7) Shestakovo in Western Siberia, Russia (early–?middle Albian), producing remains of amphilestid ‘triconodonts’ (first found in 1995) and possible symmetrodonts, of which only the dentary of *Gobiconodon borissiaki* has been described (Maschenko & Lopatin 1998; Novikov *et al.* 1998); (8) the Lao-



Fig. 1. Localities of the Early Cretaceous mammals in Asia. 1. Xinqiu; 2. Khoboor; 3. Khamryn-U; 4. Khodzhakul; 5. Huang-Ni-Tang; 6. Elesitai; 7. Badaohao; 8. Xindi; 9. Shestakovo; 10. Laolonghuoze; 11. Yanhaizi; 12. Xinminbao; 13. Jehol; 14. Mogoito.

longhuoze locality in Inner Mongolia, China, yielding an undescribed mammal humerus (Brinkman & Peng 1993a, b; Dong 1993a; and D. Brinkman, pers. comm.); (9) the Yanhaizi locality in Inner Mongolia, China, producing an undescribed mammal maxilla (D. Brinkman, pers. comm.); (10) the Xinminbao Group of western Gansu, China, from where a 'triconodont' mammal is known (Lucas & Estep 1998); and (11) the Jehol localities (Sihetun and others), Liaoning, China (latest Barremian: Swisher *et al.* 1999), producing spectacular mammal materials, including complete skeletons (a symmetrodont *Zhangheotherium quinquecuspidens*, a 'triconodont' *Jeholodens jenkinsi*) (Hu *et al.* 1997, 1998; Ji *et al.* 1999).

The age of *Manchurodon simplicidens* is considered now as Late (Zhang 1984) or Middle Jurassic (Zhou *et al.* 1991). Where taxa have been described or identified, the mammals from most of these localities are non-tribosphenic (multituberculates, 'triconodonts' and symmetrodonts). The remains of the oldest eutherians, which are the most tantalizing for understanding the origin of this now biotically significant group, have been described so far from the Xinqiu [*Endotherium*], Khoboor [*Prokennalestes*] and Khodzhakul [*Bobolestes*] faunas only. The dentary of a possible eutherian from Badaohao, China (Wang *et al.* 1995) was further referred to as '*Endotherium* or closely related form' (Wang *et al.* 1998, p. 777); unfortunately, it remains undescribed. It comes from the Shahai Formation, overlying the latest Barremian (124.6 Ma., Swisher *et al.* 1999) Yixian Formation, and thus cannot be dated as ?Valanginian or ?Hauterivian, as was originally suggested (Wang *et al.* 1995). It is best dated as Aptian–early Albian (Lucas & Estep 1998, fig.

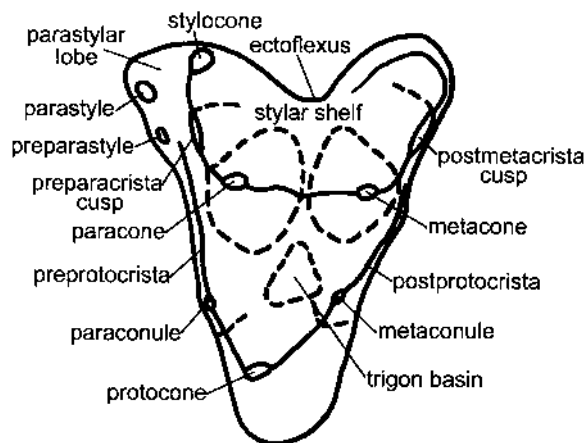


Fig. 2. Dental terminology of an archaic eutherian upper molar, based on ZIN 34834, left M2 of *Prokennalestes abramovi* n.sp. (holotype).

3). The *Endotherium niinomii* holotype comes from the Fuxin [= Fushin] Formation (Wang *et al.* 1995), which overlies the Shahai Formation. The age of the Fuxin Formation is probably Albian or even younger, Late Cretaceous (*versus* Wang *et al.* 1999). In North America the oldest eutherian might be *Montanalestes keeblerorum* Cifelli, 1999, recently discovered associated dentaries with placental dental formula (three molars) from the Aptian–Albian Cloverly Formation in Montana, USA (Cifelli 1999). This is a fully tribosphenic mammal with a derived structure of the dentary, but it has a very high paraconid, exceeding the metaconid in size, which is not characteristic for eutherians.

Here we announce the discovery of a new early Cretaceous mammalian locality in Asia, the Mogoito locality in Transbaikalia, Russia (Fig. 1), which is only the fourth site producing remains of eutherian mammals of this age. We describe this new taxon below as *Prokennalestes abramovi* n.sp. The Mogoito locality is in upper Barremian–middle Aptian strata; we shall argue that *P. abramovi* is the oldest eutherian known, antedating *Prokennalestes* from Khoboor (early Albian) by some 10y–15 Ma (in contrast with Rich *et al.* 1997, we do not consider the Aptian *Ausktribosphenos nyktos* from Australia as a eutherian mammal; see Kielan-Jaworowska *et al.* 1998). We use this discovery as an opportunity to discuss the biostratigraphy of the better known early Cretaceous vertebrate assemblages of Asia.

The nomenclature of molar crown morphology adopted here follows that of Bown & Kraus (1979) with slight emendations (Fig. 2). Capital and lower-case letters, I/i (incisor), C/c (canine), P/p (premolar) and M/m (molar), refer to upper and lower teeth, respectively.

Institutional abbreviation: ZIN – Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia. *Measurements:* AW – anterior crown width; L – crown length; PW – posterior crown width; PRW – width of the protocone. Way of measurements is after Butler (1990). All measurements are in millimetres.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Infraclass Eutheria Gill, 1872

Superfamily Kennalestoidea Kielan-Jaworowska, 1981

Family Kennalestidae Kielan-Jaworowska, 1981

Genus *Prokennalestes* Kielan-Jaworowska & Dashzeveg, 1989

Type species. – *Prokennalestes trofimovi* Kielan-Jaworowska & Dashzeveg, 1989.

1974 *Prokennalestes* Trofimov 1974, [nomen nudum] – Trofimov (in Beliajeva *et al.* 1974), p. 20.

1979 *Prokennalestes* Beliajeva, Trofimov & Reshetov

1974 [nomen nudum] – Kielan-Jaworowska *et al.*, pp. 223, 224, 242.

1989 *Prokennalestes* gen. n. Kielan-Jaworowska & Dashzeveg, p. 348.

1992 *Prokennalestes* Kielan-Jaworowska & Dashzeveg 1989 – Sigogneau-Russell *et al.*, p. 205.

Revised diagnosis (based on Kielan-Jaworowska & Dashzeveg (1989) and Sigogneau-Russell *et al.* (1992) with emendations). – Estimated skull length varies between 20 and 35 mm. Mandibular foramen situated very low. Dentary symphysis goes below posterior root of p2. Dental formula I?/? C 1/1 P 5/5 M 3/3. P4 strong, piercing. P5 semimolariform, without metacone. p3 shorter than p2 and lower than p4. p5 with single main cusp. Upper molars with large parastylar area; preparastyle and postmetacrista cusp present; paracone larger than metacone; no pre- and postcingula. c1 double rooted [hypothesized]. Paraconid lowest of trigonid cusps, connate at its base with metaconid. Three talonid cusps; distance between hypoconulid and entoconid smaller than between hypoconulid and hypoconid. Anterolingual cuspule and anterolabial cingulid are present.

Differential diagnosis. – Differs from *Kennalestes* by five premolars in adults, upper molar pre- and postcingulum lacking, postmetacrista cusp-like, p5 less molariform; from *Otlestes* by upper molar parastylar lobe larger and stylar shelf wider, preparacrista

and postmetacrista cusp-like, lower canine two-rooted, p5 less molariform; from *Bobolestes* by upper molar stylar shelf wider, preparacrista and postmetacrista cusp-like; from *Montanalestes* by a Meckelian groove present, paraconid much more reduced; from *Asioryctida* by metastylar region unreduced.

Remarks. – We accept here the ‘two-rooted lower canine hypothesis’ for *Prokennalestes* (as was originally suggested by Kielan-Jaworowska & Dashzeveg 1989, see discussion in Sigogneau-Russell *et al.* 1992) on the basis of comparison of its anterior alveoli with those in *Kennalestes gobiensis* Kielan-Jaworowska 1969. Subsequently, we remove *Prokennalestes* from Otlestidae as it shares with the *Otlestes* Nessov 1985 only symplesiomorphic similarity (e.g. five premolars) and lacks the apomorphic characters of the latter (single-rooted lower canine, larger talonid on p5, reduced parastylar lobe on M1-2, reduced preparacrista). Similarly, *Prokennalestes* differs from *Kennalestes* Kielan-Jaworowska 1969 mainly in retention of plesiomorphic traits (distinct Meckelian groove, five premolars in adults [four in adults of *K. gobiensis*, but five in juveniles, see Kielan-Jaworowska 1981], ultimate lower premolar with only incipient talonid, penultimate upper premolar with less developed talon, M1-3 without pre- and postcingula, postmetacrista cusp-shaped, metaconule minute). However, *Prokennalestes* possess at least one derived trait which is not characteristic for *Otlestes*, but could be ancestral for *Kennalestes*: p3 is somewhat reduced. Other similarities (synapomorphies?) between *Prokennalestes* and *Kennalestes* are the strong piercing penultimate upper premolar, semimolariform ultimate upper premolar, and possessing of a preparastyle on M1–3. All this advocates for inclusion of *Prokennalestes* in Kennalestidae rather than Otlestidae. We agree with Kielan-Jaworowska & Dashzeveg (1989) that *Kennalestes* could be easily derived from *Prokennalestes*. We do not consider appearance of pre- and postcingula as an apomorphy or an important diagnostic feature for the Kennalestidae (*contra* Kielan-Jaworowska & Dashzeveg 1989), as they were easily derived in parallel (independently) in a number of the lineages of Cretaceous therians, e.g., in *Falepetrus*, *Bistius*, *Asiatherium*, *Sailestes Kulbeckia*, ‘Zhelestidae’ and Leptictidae (Kielan-Jaworowska *et al.* 1979; Clemens & Lillegraven 1986; Szalay & Trofimov 1996; Nessov 1997; Nessov *et al.* 1998).

Prokennalestes abramovi n.sp.

Fig. 3

1999 *Prokennalestes* sp. nov. Averianov & Skutschas, p. 6.

Etymology. – Named in honour of our friend Dr Alexei Abramov in recognition of his generous assistance during the 1998 fieldwork at Mogoito.

Holotype. – ZIN 34834, left M2 (Figs 2, 3).

Type horizon and locality. – The Mogoito Member of the Murtoi Formation (upper Barremian–middle Aptian). The Mogoito locality is the source of the specimen and is on the west coast of the Gusinoe Osero (Geese Lake), Buryatiya, Russia (N 51°12'03", E 106°17'06") (Fig. 1, no. 14).

Diagnosis. – Size relatively large (M2 length 2.09 mm), preparastyle small, cusps on ectocingulum except stylocone lacking, paracone and metacone with lingual slopes vertically oriented.

Differential diagnosis. – Differs from *P. trofimovi* Kielan-Jaworowska & Dashzeveg 1989 and *P. minor* Kielan-Jaworowska & Dashzeveg 1989 [both from the Albian of Mongolia] in being of somewhat larger size, in having a smaller preparastyle, in lacking additional cusps posterior to the stylocone on the ectocingulum, and in having more vertically oriented and shorter lingual slopes of paracone and metacone.

Description. – The holotype is considered to be M2 rather than M1 because of its deep ectoflexus. The parastylar lobe is prominent but not as wide labiolingually as in the Mongolian species because of considerable reduction of the preparastyle [in the Mongolian species the preparastyle is missing on some specimens of M2 (Kielan-Jaworowska & Dashzeveg 1989; personal observation); this was interpreted as a possible artifact caused by the state of wear or preservation]. The stylocone is smaller than the parastyle; both cusps are worn on the holotype. There are no styles along the ectoflexus. The preparacrista does not reach the stylocone labially. Both preparacrista and postmetacrista are cusp-shaped, the latter being the larger of the two. The paracone is larger than the metacone. They are slightly connate at their bases and do not protrude very far lingually, with relatively steep, nearly vertical lingual slopes. The trigon basin is larger than in the Mongolian species, being relatively very deep at the centre (this may indicate a greater height of the hypoconid with respect to the Mongolian species). The protocone is lower than the paracone and metacone. There is a prominent, cone-shaped paraconule and a much smaller, more labially situated metaconule. The preprotocrista reaches the preparastyle labially.

Remarks. – The two nominal species of Mongolian *Prokennalestes* may represent sexual morphs within

one species (Kielan-Jaworowska & Dashzeveg 1989). The Russian *Prokennalestes* combines at least one character that can be considered as primitive compared with the Mongolian species (steeper, shorter lingual slopes of the paracone and metacone), at least one more derived character (larger size) and some characters of uncertain polarity (reduced preparastyle, lack of the labial cuspules along the ectoflexus; a similarity with the Cenomanian *Otlestes meiman* Nesso 1985 from Uzbekistan). This may indicate a complex and mosaic evolutionary history, now virtually unknown, of the earliest Asian eutherians. Kielan-Jaworowska & Dashzeveg (1989) indicated the presence of a third, unnamed and still undescribed, eutherian taxon in the Khoboor fauna, represented by a single worn lower molar. It is 2.8 mm long and apparently does not fit the size of *P. abramovi* n.sp. The specimens of *Prokennalestes* in the Paleontological Institute, Russian Academy of Sciences, Moscow (comprising a reported 80% of the 500 mammal teeth and jaw fragments in that sample; see Reshetov & Trofimov 1980) were collected during the 1969–1973 field seasons in Khoboor and have remained undescribed for 30 years.

The holotype is the only known specimen of the species. It was found on 31st August, 1998 by P. Skutschas.

Measurements. – See Table 1.

Biostratigraphy of the Early Cretaceous Asian vertebrate assemblages

We selected several of the better known Tsagantsabian and Khukhtekian vertebrate assemblages and some taxa that appear to have biostratigraphic utility (Fig. 4; see Appendix for more detailed information) in order to elucidate the relative stratigraphic position of the Mogoito locality. The turtles, when well studied, are of special importance, as was shown for the Cretaceous of Soviet Middle Asia (Nesso 1997). We subsequently present all data that are relevant for the age assessment of these assemblages and use this information to elucidate the geological age for the Mogoito locality.

Relative stratigraphic position of selected Early Cretaceous Asian vertebrate assemblages

A faunal parsimony analysis was used to avoid circular reasoning in considering the age relationships of

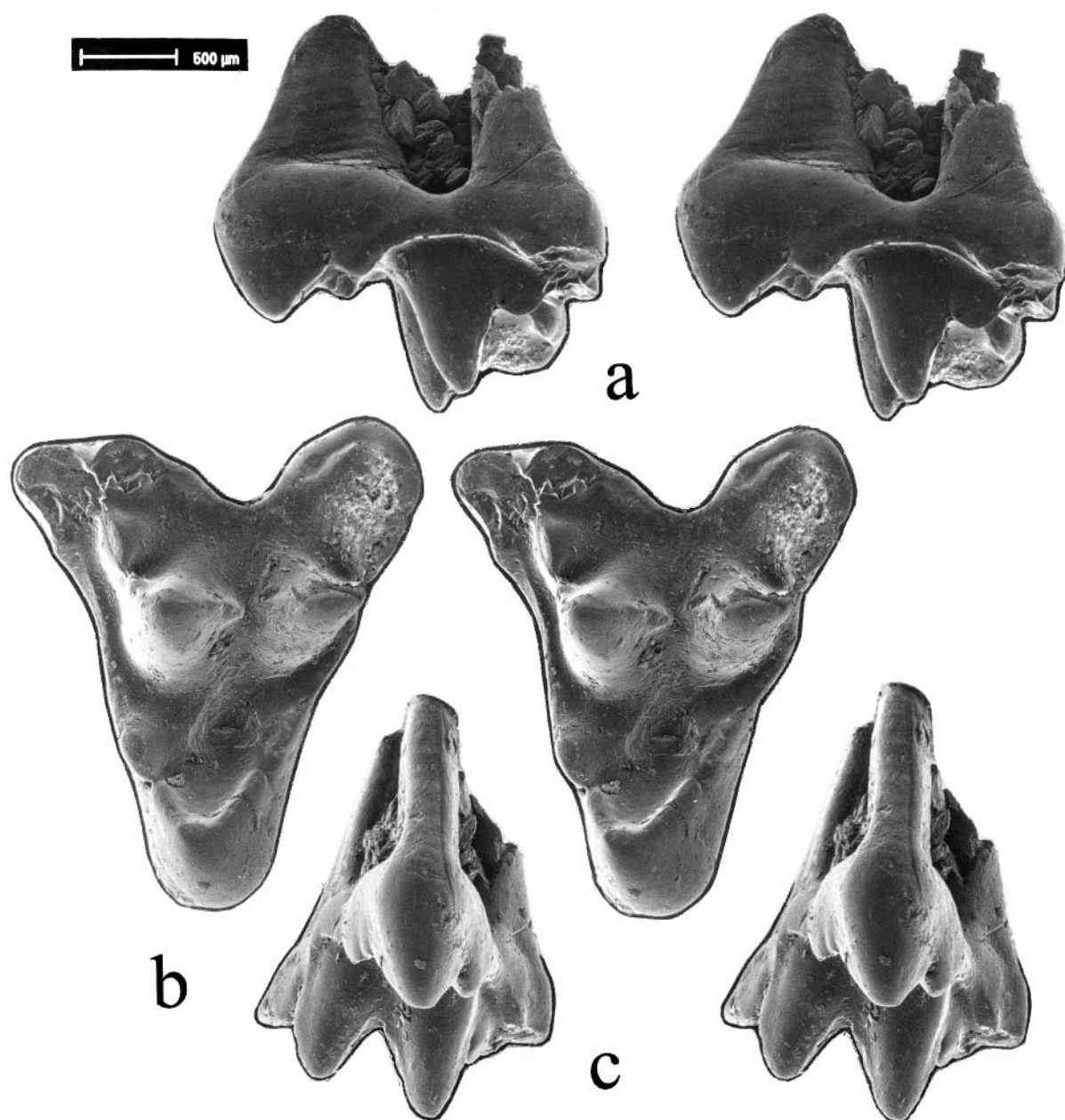
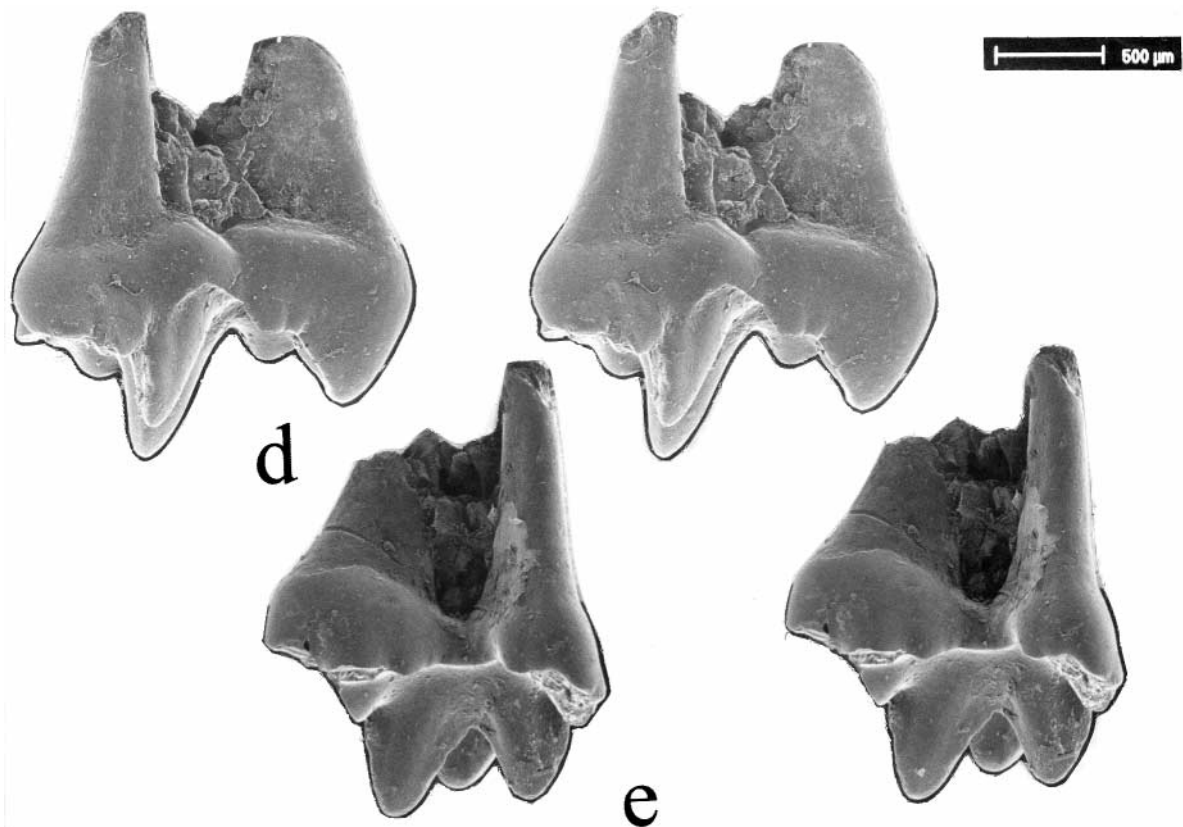


Fig. 3. SEM micrographs of ZIN 34834, left M2 of *Prokennalestes abramovi* n.sp. (holotype). a – anterior, b – occlusal, c – lingual, d – posterior, e – labial views. Stereopairs. Scal bar is 0.5 mm.

vertebrate assemblages (for examples of such an approach, see Hooker 1996 and Averianov & Godinot 1998). Use of the implicit enumeration* option in HENNIG 86 (Farris 1988) produced one tree (Fig. 5; length, 12 steps; consistency index, 0.75; retention index, 0.75). A hypothetical assemblage with 0 for each taxon was used as an outgroup. On this tree there are following groups of localities: A) Shestakovo + B (Khamryn Us + Khoboor, united by *Shamosaurus*), united by *Gobiconodon* [or ‘amphilestine triconodonts’]; C) Mogoito and Khuren Dukh, united by

Kirgizemys; E) Ejinhoru + F (Upper Tugulu + Laolonghuoze, united by crocodiles), united by *Sinemys*; and D) C + E, united by champsosaurs. We interpret this sequence of localities as stratigraphic (Fig. 4). The Tsagantsabian land-vertebrate biochron can be defined by dominance of sinemyid turtles (*Sinemys*), the Khukhtekian by dominance of macrobaenids (*Kirgizemys* and *Hangaiemys*). An important biostratigraphic boundary could lie within the Khukhtekian biochron (assemblages with and without choristoderes). Choristoderes, as possibly thermopho-



bous animals, could have disappeared from the region owing to a considerable warming that occurred within the Aptian (Sun 1995). *Khurendukhosaurus bajkalensis* from Mogoito is half the size of *K. orlovi* from Khuren Dukh (Efimov 1996), which suggests a lower stratigraphic position of Mogoito relative to Khuren Dukh and, possibly, a large temporal gap between these localities. We conclude that the Mogoito locality is the oldest among Khukhtekian assemblages considered.

Table 1. Measurements of M2 in *Prokennalestes* species (AW – anterior crown width; L – crown length; PW – posterior crown width; PRW – width of the protocone).

Measurements	<i>P. trofimovi</i> (<i>n</i> = 5)*	<i>P. minor</i> (<i>n</i> = 4)*	<i>P. abramovi</i> sp. n. (holotype)
L	1.6–1.8	1.3–1.5	2.09
AW	2.4–2.5	1.7–1.9	2.44
PW	2.2–2.4	1.7–1.9	2.61
PRW	–	–	1.12

*After Kielan-Jaworowska & Dashzeveg (1989).

Data for assessment of the age for Early Cretaceous Asian vertebrate assemblages

(1) The Tebch basalts at Tebch, Inner Mongolia, China, overlying deposits with *Psittacosaurus mongoliensis*, were dated by the Ar 40 / Ar 39 analysis as 110 ± 0.52 Ma [early Albian] (Eberth *et al.* 1993). In the Shandong Province of China the Shuimutou Formation of the Qingshan Group, lying between the Doushan and Zhujiashuang formations, both containing remains of *Psittacosaurus*, has a K/Ar date 122 Ma (early Aptian; Cheng *et al.* 1995). The range of the *Psittacosaurus* biochron has been estimated as Barremian–early Albian (Lucas & Estep 1998). The absolute age of effusives from different layers of Tsagantsab and Khukhtek formations was determined by K/Ar analysis as 119–141 Ma [Valanginian–Aptian] and 108–113 Ma [Aptian–Albian], respectively (Shuvalov & Nikolaeva 1998).

(2) The hybodontid shark *Asiadontus* is found in the marine upper Aptian Mogolsai beds in Kirghisia and

Age	LVF	Locality	<i>Sinemys</i>	<i>Kirgizemys</i>	<i>Hangatemys</i>	champsosaurus	crocodiles	<i>Stamosaurus</i>	<i>Psittacosaurus</i>	<i>Grobicomodan</i>	
Albian	Khukhtekian	Shestakovo					+		+	+	
		Khoboor			+				+	+	+
		Khamryn-Us							+	+	+
Aptian	Khukhtekian	Khuren Dukh		+	+	+			+		
		Mogoito		+		+			+		
Barremian	Tsagantsabian	Ejinhoro	+			+			+		
		Laolonghuoze	+			+	+		+		
		Upper Tugulu	+				+		+		

Fig. 4. Distribution of some vertebrate taxa among selected Early Cretaceous Asian vertebrates assemblages. LVF – land-vertebrates

in the Mongolian locality Tushilge Ula, Khukhtek Formation (Nessov 1997). From Tushilge Ula, remains of osteichthyan fishes (?Acipenseriformes and Sinamiidae) and champsosaurs are also known, so it corresponds to the Khukhtekian localities Mogoito and Khuren Dukh in Fig. 4. The hybodontid sharks more probably were not exclusively freshwater fishes, as usually believed, but were anadromous, entering rivers for breeding (J.D.Ward. pers. comm.) and feeding in coastal marine waters and brackish-water lagoons. Thus, the appearance of *Asiadontus* in the southeastern Gobi (Tushilge Ula) could be explained by the late Aptian (Clansean) sea transgression. Appearance of the hybodontid shark *Thaiodus* in the Aptian–Albian Khot Kruat Formation in Thailand and in the Takena Formation in Tibet, China (Cappetta *et al.* 1990) may also be connected with the same transgression, and this event may be used for more precise dating of these formations.

(3) The late Aptian sea transgression was reflected in

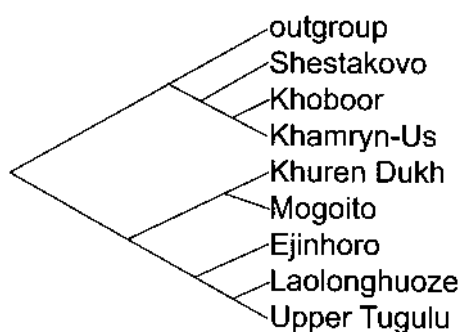


Fig. 5. A parsimony tree for the selected Early Cretaceous Asian vertebrates assemblages. See text for discussion of taxa supporting each node.

mainland Asia by the formation of extensive lake basins, where ‘paper’ shales with *Lycotera* remains were deposited (Andakhuduk Formation in Mongolia, Zaza Formation in eastern Transbaikalia, and lower Selenga Formation in western Transbaikalia). In Mongolia, at the Ondai Sair locality (Andakhuduk Formation), the tetrapod fauna of turtles, sauropods (*Asiatosaurus*), theropods, and *Psittacosaurus mongoliensis* is situated above the ‘paper’ shales with *Lycotera* (Kalandadze & Kurzanov 1974) and thus is not older than late Aptian. The level of the locality Mogoito (Murtoi Formation) in western Transbaikalia is more than 1000 m stratigraphically below the ‘paper’ shales with *Lycotera* of the lower Selenga Formation (Nessov & Starkov 1992), so the age of this locality could be considerably older than late Aptian.

In conclusion, the Mogoito locality should be referred to as late Barremian–early Aptian in age.

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Appendix. List of selected Early Cretaceous Asian vertebrate assemblages

Upper Tugulu Group (Shenjinkou and Lianmuqin Formations), Xinjiang, China. Vertebrates. – Fishes: *Dsungarichthys bilineatus*, *Neobaleichthys chikuensis*, *Siyuichthys ornatus*, *S. pulcher*, *S. pulchellus*, *Bogdaichthys fukangensis*, *B. serratus*, *Manasichthys elongatus*, *M. tuguluensis*, *Uighuroniscus sinkiangensis*, and *Wukan-gia houyanshanensis*. Turtles: *Sinemys wuerhoensis* and *Dracochelys bicuspis*. Protosuchian crocodilian: *Edentosuchus tianshanensis*. Pterosaurs: *Noripterus complicidens* and *Dsungaripterus weii*. Coelurosaur: *Tugulusaurus facies* and *Phaedrolosaurus ilikensis*. Carnosaur: *Kelmayisaurus petrolicus*. Sauropod: *Asiatosaurus mongoliensis*. Stegosaurid: *Wuerhosaurus homheni*. Ceratopsian: *Psittacosaurus* sp.

Reference. – Lucas & Estep (1998).

Age. – Barremian (accepted here).

Laolonghuoze, Inner Mongolia, China. Luohandong Formation of Zhidan Group. Vertebrates. – Amiid fish: *Sinamia* [sp.]^{1, 2}. At least three new turtles¹: *Ordosemys leios*¹, *Sinemys gamera*² and undetermined genus¹. Crocodiles: *Eotomistoma* [sp.]^{1, 2} and *Shantungosuchus* [sp.]^{1, 2} or *Shantungosuchus hangjinensis*⁶ [holotype comes from the Yanhaizi locality within the same formation]. Stegosaur^{1, 2, 4}, sauropods^{1, 2}, psittacosaur^{1, 2, 4}, large ornithopods^{1, 2}, an iguanodontid (a tooth)⁴, a pterosaur^{1, 2}, choristodere *Ikechosaurus* [sp.]^{1, 2} or *Ikechosaurus sunailinae*³, a mammal (humerus)^{1, 2, 4}.

Close to the Chabu Sumu locality in the Luohandong Formation remains of a fish *Lycoptera* [sp.]³, *Ikechosaurus sunailinae*³ [could be the type locality for this species], a bird *Enantiornithes* indet.⁵ were found.

References. – 1. Brinkman & Peng (1993a); 2. Brinkman & Peng (1993b); 3. Brinkman & Dong (1993); 4. Dong (1993a); 5. Dong (1993c); 6. Wu *et al.* (1994).

Age. – Barremian (accepted here).

Ejinhoro Formation (localities Alouchaideng, Yangpujie, Ahmalongqui), Inner Mongolia, China.

Vertebrates. – Turtles *Sinemys*^{1, 2}, champsosaurs *Ikechosaurus* n.sp.¹, or *I. sunailinae*², dinosaurs *Psittacosaurus*, numerous skeletons^{1, 3}, or *P. mongoliensis*², or *P. neimongoliensis*, *P. ordosensis*, and *Psittacosaurus* sp.⁴, stegosaur *Wuerhosaurus ordosensis*^{2, 3, 5}, small troodontid¹, or *Sinornitholestes youngi*^{3, 5}, a sauropod¹, or Diplodocidae indet.² and Brachiosauridae indet.², or teeth cf. *Chiayasaurus* sp.⁴, a pterosaur^{3, 5}.

References. – 1. Dong (1993a); 2. Dong (1993b); 3. Russell & Dong (1993); 4. Russell & Zhao (1996).

Age. – Barremian (accepted here).

Mogoito, Buryatian Republic, Russia. Murtoi Formation.

Vertebrates. – Fishes³, acipenseriform *Stichopterus*⁷, or cf. *Stichopterus* sp.⁹, teleostean and holostean fishes, Holosteii indet.⁹, cf. *Irenichthys* sp.⁹, acipenseriform and primitive teleostean fishes¹⁰, turtles³, turtles *Kirgizemys dmitrievi*^{5, 7, 9}, *Kirgizemys* sp.^{5, 6, 10}, ?Toxochelyidae gen. et sp. indet.⁵, ?Plesiochelyidae gen. et sp. nov.⁵ [two latter taxa later referred to as cf. *Sinemys* sp.], cf. Adocidae⁷, dinosaurs³, a dinosaur, probably theropod¹ [possible based on a sauropod phalanx or metapodial], a sauropod^{2, 10}, or sauropods, similar with *Chiayasaurus* and *Mongolosaurus*⁷, or cf. *Chiayasaurus* sp.⁸, cf. *Mongolosaurus*¹¹, Armatosauria (?Ankylosauria)⁷ [based on osteoderms which may actually belong to sauropods⁸], Ornithomimidae⁶, or small ornithomimid dinosaur⁷, or small Ornithomimidae either Oviraptorosauria⁸, very small theropod⁸, a dromaeosaurid¹¹, a large theropod^{2, 7}, or [Therizinosauridae]⁴, or a segnosaurid either spinosaurid⁸, or carnosaur¹⁰, a bird^{6, 7}, *Psittacosaurus* sp.¹¹, an ornithopod² (actually absent, determination was incorrect⁸), crocodiles³ [actually absent, material belongs to choristoderes⁹], choristoderes *Khurendukhosaurus* sp.^{6, 7, 9}, or *Khurendukhosaurus bajkalensis*^{10, 11}, a scincomorph lizard cf. *Paramacellodus* sp.¹¹, an eutherian mammal *Prokennalestes abramovi* sp. n.¹¹.

References. – 1. Riabinin (1937); 2. Dmitriev (1960); 3. Dmitriev & Rozhdestvensky (1968); 4. Rozhdestvensky (1970, 1976); 5. Nessov & Khozatskyi (1981); 6. Nessov (1992); 7. Nessov & Starkov (1992); 8. Nessov (1995); 9. Nessov (1997); 10. Efimov (1996); 11. our data.

Age. – Late Barremian–middle Aptian^{7–9}, 'Neocomian'¹⁰, late Barremian–early Aptian (accepted here).

Khuren Dukh [= Khooren Dukh], Mongolia. Dzunbain Formation².

Vertebrates. – Large-sized ganoid fishes^{1, 2}, turtles *Kirgizemys kansuensis*⁹, *Hangaiemys hobuensis*¹, or *Hangaiemys 'leptis'* [nomen nudum]⁹, and *Asiachelys perforata* [nomen nudum]⁹, small carnivorous dinosaurs^{1, 2}, ornithomimids^{1, 4}, *Harpymimus okladnikovii*⁶, *Psittacosaurus* sp.¹, *Iguanodon orientalis*¹, an ankylosaur¹, choristoderes *Tchoiria namsarai*^{3, 8}, *Irenosaurus egloni*⁸ [= *Tchoiria egloni*], and *Khurendukhosaurus orlovi*^{7, 8}.

References. – 1. Kalandadze & Kurzanov (1974); 2. Nowodworskaja (1974); 3. Efimov (1975); 4. Barsbold 1983; 5. Efimov (1983); 6. Barsbold & Perle (1984); 7. Sigogneau-Russell & Efimov (1984); 8. Efimov (1988); 9. P. Narmandakh (1991, unpublished dissertation).

Age. – Middle-late Aptian (accepted here).

Khamryn-Uus [= Gashuny-Khuduk], Mongolia. Dzunbain⁵ or Khukhtyk³ Formation.

Vertebrates. – *Psittacosaurus* sp.^{1–3, 5}. Large ankylosaur², *Shamosaurus scutatus*⁵, sauropods^{3, 5}, small carnosaur^{2, 3, 5}, Troodontidae indet.⁴, turtles², lizards², Iguanidae⁵, Varanidae⁵, an amphilestine 'triconodont' mammal^{2, 5}.

References. – 1. Kalandadze & Kurzanov (1974); 2. Reshetov & Trofimov (1980); 3. Suslov (1983); 4. Barsbold *et al.* (1987); 5. Tumanova (1987).

Age. – Aptian-Albian^{3, 4}, early Albian (accepted here).

7) Khoboor [= Khovboor, = Gouchin Us, = Hobur], Mongolia. Dzunbain^{9, 14}, Khulsyngol¹¹, or lower Dushiulin Formation.

Vertebrates. – Pisces: isolated teeth of fishes¹⁵. Anura: *Eodiscoglossus* sp.²². Testudinata: turtles¹, *Hangaimeys hoburensis*^{3, 5, 7} [= *Sinemydiidae*², = *Changaimeys hoburensis*⁴], *Mongolemys* [sp.]⁵ [= *Dermatomydidae*, sic², = *Mongolemys* sp. nov.³]. Dinosauria: psittacosaur¹, *Psittacosaurus mongoliensis*^{2-4, 7, 15}, small theropods^{1, 3, 4, 7, 15}, large theropods^{1, 4, 15}, dromaeosaurids¹¹, sauropods^{1, 3, 4, 7, 15}, an ankylosaur? *Shamosaurus* [sp.]¹⁵. Aves: Aves indet. (teeth, a feather)¹⁶. Sauria: lizards^{1, 2, 15}, five new forms of lizards⁴, 10 species of lizards¹⁷, *Priscagamidae*²¹. Gekkonidae: *Hoburogekko suchanovi*^{17, 21}, *Paramacellodidae*²¹? *Xantusidae*²¹, *Slavoiiidae*: *Slavoia* [sp.]²¹? *Xenosauridae*²¹, *Dorsetisauridae*: *Dorsetisaurus* [sp.]²¹, *Amphisbaenia*? *Hodzhakulia* [sp.] [= *Hodzhaculia* [sic]²¹]. Mammalia: Mammalia indet.²⁴, 'Triconodonta': *Gobiconodontidae* [= *Triconodonta*^{1, 9, 15}, = triconodonts (2 species)¹⁸]: *Gobiconodon borissiaki*^{7, 13, 26} [= *Triconodonta* gen. et sp. nov.⁷, = *Gobiconodon borissiaki* [nomen nudum]^{3, 4}, = *Neoconodon borissiaki* [nomen nudum]³, = *Gobioconodon* [sic] *borissiaki* [nomen nudum]⁶] and *Gobiconodon hoburensis*²⁶ [= *Guchinodon hoburensis*^{7, 13}]. Docodonta: *Docodonta* [indet.]²⁷. Multituberculata [= *Multituberculata*^{4, 9, 15}, = multituberculates (3 species)¹⁹]: *Arginbaataridae*: *Arginbaatar dmitrievae*¹⁰ [= *Plagiaulacidae* gen. et sp. nov.^{2, 3}, = *Arguinbaatar* [sic] *dmitrievae*¹³, = *Arginbaatar dmitrievae* [sic]¹⁴]. *Eobaataridae*: *Eobaatar magnus*¹⁴, *E. minor*¹⁴, family incertae sedis: *Monobaatar mimicus*¹⁴. Symmetrodonta: *Amphidontidae*: *Gobiotheriodon infinitus*²⁵ [= *Symmetrodonta*^{1, 9, 15}, = *Symmetrodonta* gen. et sp. nov.², = *Gobiodon infinitus* [nomen nudum]^{3, 4}, = *Gobion infinitus* [nomen nudum]^{3, 6}, = *Gobiodon infinitus*^{10, 13}, = symmetrodonts (1 species)¹⁹]. Eupantotheria: *Peramurida*: *Arguimus khosbajari*^{8, 23} [? = *Trituberculata*¹, = *Arguimus khosboyari* [sic]¹³, = eupantotherians (two species)¹⁹, ? = *Arguitherium cromptoni*²³]. *Aegialodonta*: *Kielantherium gobiensis*^{6-8, 12, 13} [? = *Prodeltheridium kalandadzei* [nomen nudum]¹³, ? = deltatherians (1 species)¹⁹]. Eutheria: *Kennalestoidea*: *Prokennalestes trofimovi*^{18, 20} and *P. minor*^{18, 20} [= *Insectivora*^{1, 9, 15}, = *Insectivora* (two new genera)², = *Prokennalestes kozlovi* [nomen nudum]^{3, 4, 6, 7, 13}, = *Prozalambdalestes simpsoni* [nomen nudum]^{3, 4, 6}, = *Prozalambdalestes* [sic] *simpsoni*

[nomen nudum]⁷, = *Prozalambdalestes simpsoni* [sic] [nomen nudum]¹³, = eutherians (two species)¹⁹].

References. – 1 Kalandadze & Reshetov (1971); 2 Trofimov (1972); 3. Beliajeva *et al.* (1974); 4. Kalandadze & Kurzanov (1974); 5. Sukhanov & Narmandakh (1974); 6. Dashzeveg (1975); 7. Trofimov (1978); 8. Dashzeveg (1979); 9. Reshetov & Trofimov (1980); 10. Trofimov (1980); 11. Barsbold (1983); 12. Dashzeveg & Kielan-Jaworowska (1984); 13. Reshetov & Trofimov (1984); 14. Kielan-Jaworowska *et al.* (1987); 15. Tumanova (1987); 16. Kurochkin (1988); 17. Alifanov (1989); 18. Kielan-Jaworowska & Dashzeveg (1989); 19. Reshetov (1989); 20. Sigogneau-Russell *et al.* (1992); 21. Alifanov (1993); 22. Gubin (1993); 23. Dashzeveg (1994); 24. Wible *et al.* (1995); 25. Trofimov (1997); 26. Kielan-Jaworowska & Dashzeveg (1998); 27. Agadjanian (1999).

Age. – Aptian-Albian^{1, 15}, early Albian (accepted here).

8) Shestakovo, Kemerovo Province, Western Siberia, Russia. Ilek [= Shestakovo] Formation.

Combined list for Shestakovo 1–3 sites: amniiform fishes^{5, 8, 9}, or *Sinamiidae* (scales)¹⁰, turtles^{5, 8, 9}, crocodiles^{5, 8, 9}, or two proto-suchian forms – *Sichuanosuchus* and a new, undescribed genus⁶, a small theropod^{5, 8, 9}, a dromeosaurid (teeth)¹⁰, deinonycho-saurians (*Troodontidae* gen. indet.)⁶, a large sauropod^{5, 8, 9}, or sauropods (*Titanosauridae* gen. indet.)⁶, or cf. *Euhelopus* (tooth)¹⁰, *Psittacosaurus* sp.^{1-4, 8}, or *Psittacosaurus mongoliensis*³, or two ceratopsian forms (*Psittacosaurus*)⁵, or *Psittacosaurus mongoliensis* and *Psittacosaurus* cf. *xinjiangensis*⁶, or *Psittacosaurus* aff. *mongoliensis*⁷, lizards⁵, a tritylodontid synaspid^{5, 6} *Xenocretosuchus sibiricus*⁹, a 'triconodont' mammal *Gobiconodon borissiaki*^{5, 6, 8-10}, mammals (symmetrodonts, 'triconodonts')⁶.

References. – 1. Rozhdestvensky (1960a); 2. Rozhdestvensky (1960b); 3. Nessov (1995); 4. Nessov (1997); 5. Maschenko & Lopatin (1998); 6. Novikov *et al.* (1998); 7. Voronkevich (1998); 8. Maschenko (1999); 9. Tatarinov & Maschenko (1999); 10. own (unpublished) observation.

Age. – Aptian–Albian², late Barremian–Aptian, more probably, late Aptian^{3, 4}, Berriasian⁶, early-? middle Albian (accepted here).