

Albanerpetontid amphibians from the Upper Cretaceous of Middle Asia

JAMES D. GARDNER and ALEXANDER O. AVERIANOV



Gardner, J.D. & Averianov, A.O. 1998. Albanerpetontid amphibians from the Upper Cretaceous of Middle Asia. — *Acta Palaeontologica Polonica* **43**, 3, 453–467.

We review the fossil record of Asian albanerpetontids. The three dentaries previously attributed to the two species of *Nukusurus* Nessov, 1981 (lower Cenomanian and Coniacian, Uzbekistan) are from albanerpetontids, but none are distinctive below the familial level. We thus designate the names *Nukusurus*, *N. insuetus* Nessov, 1981, and *N. sodalis* Nessov, 1997 as *nomina dubia* within the Albanerpetontidae. Two dentaries (lower Cenomanian, Uzbekistan) described herein for the first time supplement the known record of Asian albanerpetontids. The holotype atlas and only specimen of the supposed albanerpetontid *Bishara backa* Nessov, 1997 (upper Santonian–?Campanian, Kazakhstan) is shown to be from a salamander, not an albanerpetontid. Our study recognizes *Albanerpeton* (Cretaceous–Miocene, North America and Europe) and *Cel- tedens* (Middle Jurassic–Lower Cretaceous, Europe) as the only valid albanerpetontid genera. Limited evidence favors one or more dispersals from Europe or North America to Asia in the medial Cretaceous as the major biogeographic event in the history of Asian albanerpetontids.

Key words: Albanerpetontidae, *Bishara*, Cretaceous, Kazakhstan, Kirghizia, *Nukusurus*, Uzbekistan.

James D. Gardner [gardner@odum.biology.ualberta.ca], Laboratory for Vertebrate Paleontology and Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada.

Alexander O. Averianov [sasha@AA1923.spb.edu], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab 1, Saint Petersburg, 199034 Russia.

Introduction

The Albanerpetontidae are small-bodied, superficially salamander-like amphibians known almost exclusively by rare articulated skeletons and abundant bones from the Middle Jurassic–Miocene of Laurasia (e.g., Estes & Hoffstetter 1976; Estes 1981; Fox & Naylor 1982; Milner 1994; McGowan & Evans 1995; Nessov 1997). The higher level affinities of the Albanerpetontidae are unresolved (Milner 1988, 1993a, 1994).



Fig. 1. Map of Middle Asian fossil localities mentioned in text. Inset map shows locations of Kazakhstan, Kirghizia, and Uzbekistan and approximate area shown in larger map. Symbols: ● – Upper Cretaceous locality; ▲ – Jurassic locality. Distance between localities 1 and 2 is exaggerated. Localities: 1 – Chelypk locality, Uzbekistan, Upper Cretaceous (lower Cenomanian) Khodzhakul Formation; 2 – Sites SSHD-8 and -8a, Sheikdzheili locality, Uzbekistan, Upper Cretaceous (lower Cenomanian) Khodzhakul Formation; 3 – Sites CBI-4v and -17, Dzhyrakuduk locality, Uzbekistan, Upper Cretaceous (Coniacian) Bissekty Formation; 4 – Tashkumyr locality, Kirghizia, Middle Jurassic (Callovian) Balabansay Formation; 5 – Baybishe locality, Kazakhstan, Upper Cretaceous (upper Santonian–?Campanian) Bostobe Formation. Map modified from Nesson (1988: fig. 1) and Nesson *et al.* (1994: fig. 2).

Originally they were regarded as prosirenid salamanders (e.g., Estes & Hoffstetter 1976; Estes 1981; Duellman & Trueb 1986; Trueb & Cloutier 1991), but it is more likely that they are a distinct lissamphibian lineage not otherwise closely related to the Caudata (Fox & Naylor 1982; McGowan & Evans 1995). Four albanerpetontid genera have been recognized to date. These are *Albanerpeton* Estes & Hoffstetter, 1976 (Aptian–Paleocene, North America; Miocene, France), *Celtdens* McGowan & Evans, 1995 (Bathonian–Albian, Europe), '*Nukusurus*' Nesson, 1981 (lower Cenomanian and Coniacian, Uzbekistan), and *Bishara* Nesson, 1997 (upper Santonian–?Campanian, Kazakhstan) (e.g., Estes & Hoffstetter 1976; Estes 1981; Nesson 1981, 1988, 1997; Fox & Naylor 1982; McGowan & Evans 1995; McGowan 1996; McGowan & Ensom 1997; Gardner 1996). The two Asian genera are known by only three jaws and an atlas, none of which have been adequately described, figured, or compared with homologous bones from other albanerpetontid taxa. The status of these supposedly endemic Asian taxa is thus unclear, a situation that frustrates attempts to examine the phylogenetic and paleobiogeographic history of the Albanerpetontidae.

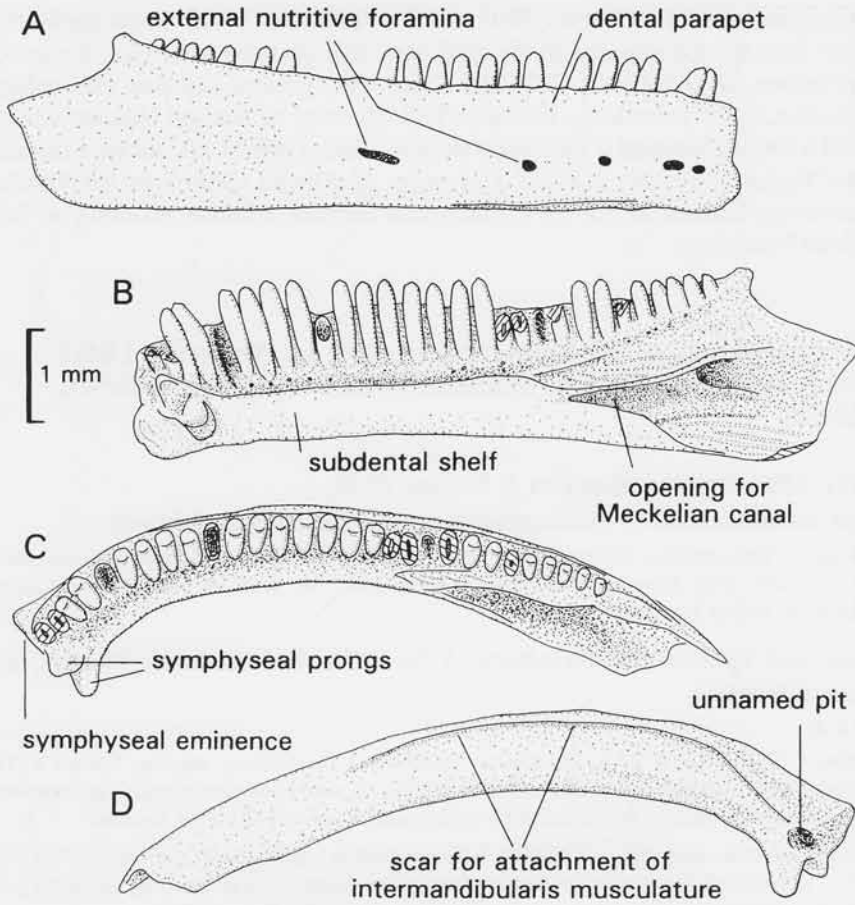


Fig. 2. Osteological terms for albanerpetontid dentaries. A-D. MNHN.LGA 49, *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976; nearly complete right dentary lacking posteriormost end, labial, lingual, dorsal, and ventral views; La Grive-St. Alban, France, middle Miocene.

In this paper we (1) redescribe and refigure the three dentaries attributed by Nesson (1981, 1988, 1997; Nesson & Udovichenko 1986) to the two species of '*Nukusurus*', (2) critically examine the status of '*Nukusurus*' and its two species, (3) describe two recently identified albanerpetontid dentaries from the Cretaceous of Uzbekistan, (4) examine the identity of the holotype atlas and only specimen of the supposed albanerpetontid *Bishara*, (5) review other reports (Nesson 1981, 1988, 1997) of albanerpetontid fossils from Asia, and (6) speculate on the history of Asian albanerpetontids.

Terms, conventions, and institutional abbreviations: We follow Nesson *et al.* (1994) for names of localities and formations and in using the term 'Middle Asia' for the region encompassing Kazakhstan, Kirghizia, Tajikistan, Turkmenistan, and Uzbekistan (Fig. 1). A taxonomic name in quotes (e.g., '*Nukusurus*') denotes a taxon as it was understood by earlier authors. Fig. 2 shows osteological terms for dentaries; terms

for other elements follow Estes (1981) and Fox & Naylor (1982). Tooth positions are counted from the anterior end of the tooth row, unless stated otherwise. Institutional abbreviations are as follows: CCMGE, Chernyshev Central Museum of Geological Exploration, Saint Petersburg; FMNH, Field Museum of Natural History, Chicago; MNHN Muséum National d'Histoire Naturelle, Paris; OMNH, Oklahoma Museum of Natural History, Norman; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton; and ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Redescription of *Nukusurus insuetus* Nessov, 1981 nomen dubium and *N. sodalis* Nessov, 1997 nomen dubium

Family Albanerpetontidae Fox & Naylor, 1982

Genus indeterminate (= *Nukusurus* Nessov, 1981 nomen dubium)

Remarks. — Two species, '*Nukusurus insuetus*' Nessov, 1981 (Nessov's type species) and '*N. sodalis*' Nessov, 1997, have been included in '*Nukusurus*'. We consider these three names to be *nomina dubia* within the Albanerpetontidae.

Genus and species indeterminate A (= *Nukusurus insuetus* Nessov, 1981 nomen dubium)

Fig. 3A–H.

Material. — ZIN PHA K 77-4, incomplete dentary and fragmentary angular, Nessov's (1981) holotype of '*Nukusurus insuetus*'; and CCMGE 241/12177, nearly complete dentary and fragmentary angular, referred by Nessov & Udovichenko (1986) and Nessov (1988) to '*N. insuetus*'.

Localities, horizon, and age. — ZIN PHA K 77-4: Chelpyk locality; and CCMGE 241/12177: site SSHD-8, Sheikdzheili locality; Kyzylkum Desert, north-central Uzbekistan (Fig. 1); upper part of Khodzshakul Formation; lower Cenomanian (Nessov *et al.* 1994; Nessov 1997).

Description. — ZIN PHA K 77-4 (Fig. 3A–D) is an incomplete left dentary and the anterior tip of a left angular. The angular is displaced labial to its point of articulation, in the opening for the Meckelian canal, with the dentary. The dentary is missing much of the area for attachment of the postdentary bones and all but the base of the symphyseal prong. The dentary is moderately robust and small, 4.8 mm long as preserved. The dental parapet is relatively uniform in height along its length and its dorsal edge is nearly straight in labial view. The dentary is smooth externally, except for a row of five small external nutritive foramina. The posteriormost foramen is lateral to the sixteenth tooth position. The symphyseal eminence is not prominent. Internally, the anterior edge of the opening for the Meckelian canal is in line with the twenty-first locus. The posterior end of the tooth row is broken, and we estimate that at least the posteriormost six loci are missing. The 23 preserved loci include 16 tooth bases, six empty tooth slots, and at the first locus a tooth slot containing an *in situ* replacement crown. Judging by the broken pedicles and empty tooth slots, the teeth were relatively gracile and those located about one-third of the distance along the ramus were only slightly enlarged relative to other teeth along the tooth row.

CCMGE 241/12177 (Fig. 3E–H) is a more nearly complete left dentary that lacks the posterior part of the area for articulation with the postdentary bones and preserves the anterior end of the angular in articulation. This specimen is 5.4 mm in preserved length, and came from an individual about one-quarter again as large as the individual represented by ZIN PHA K 77-4. Like the latter dentary, CCMGE 241/12177 is elongate, moderately robust, and the dental parapet is relatively uniform in height along its length. A row of four small external nutritive foramina penetrates the

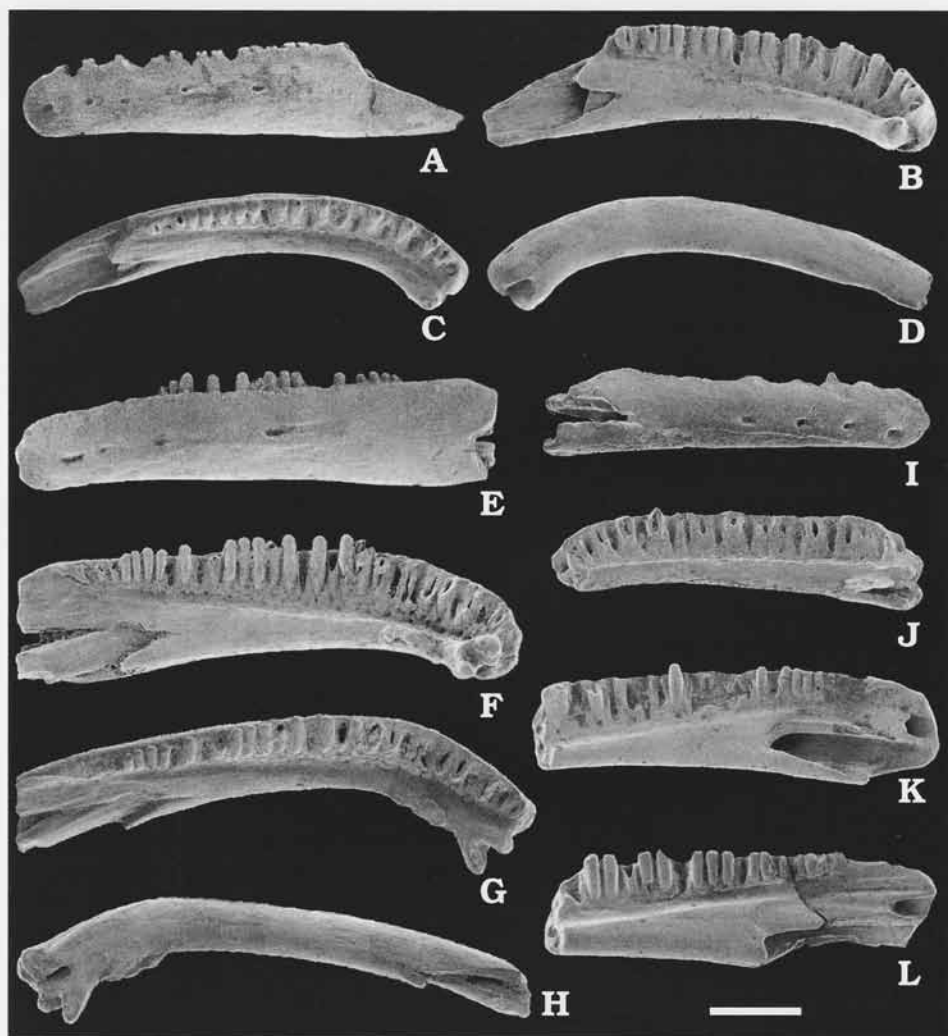


Fig. 3. Dentaries of *Nukusurus* Nessov, 1981 *nomen dubium* and Albanerpetontidae indeterminate from the Upper Cretaceous of Uzbekistan. **A–D.** ZIN PHA K 77-4, *Nukusurus insuetus* Nessov, 1981 *nomen dubium*; incomplete left dentary and angular, labial, lingual, occlusal, and ventral views; Chelpyk locality, Khodzhaikul Formation, lower Cenomanian. **E–H.** CCMGE 241/12177, *N. insuetus* Nessov, 1981 *nomen dubium*; nearly complete left dentary and incomplete angular, labial, lingual, occlusal, and ventral views; Sheikdzheili locality, Khodzhaikul Formation, lower Cenomanian. **I, J.** CCMGE 111/12177, *Nukusurus sodalis* Nessov, 1997 *nomen dubium*; fragmentary right dentary, labial and lingual views; Dzhyrakuduk locality, Bissekty Formation, Coniacian. **K.** ZIN PC 1/46, Albanerpetontidae indeterminate; posterior end of right dentary, lingual view; Sheikdzheili locality, Khodzhaikul Formation, lower Cenomanian. **L.** ZIN PC 2/46, Albanerpetontidae indeterminate; posterior end of right dentary, lingual view; Sheikdzheili locality, Khodzhaikul Formation, lower Cenomanian. Scale bar 1 mm. All SEM micrographs.

dentary externally, with the posteriormost foramen situated lateral to the seventeenth tooth position. The dentary ventrally and ventrolaterally bears a shallow and anteroposteriorly elongate scar, bounded labially by a low ridge, for attachment of the intermandibularis musculature. The sym-

physeal eminence is more prominently developed than on ZIN PHA K 77-4 and two symphyseal prongs are preserved intact. Just posterior to the bases of the symphyseal prongs, an unidentified small and flattened fragment of bone adheres to the lingual edge of the subdental shelf. More posteriorly, the anterior margin of the opening for the Meckelian canal is in line with the twenty-third tooth position, or the ninth locus from the posterior end of the tooth row. The intact tooth row consists of 32 loci, including 11 nearly complete teeth, 12 broken teeth, and nine empty tooth slots. Teeth are highly pleurodont, non-pedicellate, closely spaced, gracile, and not particularly elongate. Tooth apices are abraded, but are clearly labiolingually compressed and chisel like. Broken tooth bases and empty tooth slots indicate that the teeth were largest about one-third of the distance along the tooth row, but not markedly so.

Genus and species indeterminate B
(= *Nukusurus sodalis* Nesson, 1997 *nomen dubium*)

Fig. 3I, J.

Material. — CCMGE 111/12177, fragmentary dentary, designated by Nesson (1997) as the holotype and only specimen of '*Nukusurus sodalis*'.

Locality, horizon, and age. — Site CBI-17, Dzhyrakuduk locality, Kyzylkum Desert, north-central Uzbekistan (Fig. 1); upper part of Bissekty Formation; Coniacian (Nesson *et al.* 1998).

Description. — CCMGE 111/12177 (Fig. 3I, J) is a fragment of a right dentary missing the symphyseal region and all of the bone posterior to the opening of the Meckelian canal. The preserved part of the dentary is 4.0 mm long, and appears to be from an individual that was about the same size as that represented by ZIN PHA K 77-4. The dorsal edge of the dental parapet is horizontal along its preserved length, but it is lower than in the two dentaries described above. A row of four tiny external nutritive foramina is present labially and a faint scar for the intermandibularis musculature is developed ventrally. The tooth row is incomplete anteriorly and posteriorly. The preserved section of the tooth row includes about 21 tooth positions, consisting of approximately equal numbers of broken tooth bases and empty slots.

Remarks. — Although Nesson & Udovichenko (1986) used the name '*Nukusurus sodalis*', the first valid publication of this name was by Nesson (1997). Nesson (1988) previously listed CCMGE 111/12177 as belonging to a 'new form of albanerpetontid' (p. 478) and a 'new albanerpetontid amphibian' (caption for pl. 14: 31).

Evaluation of *Nukusurus* Nesson, 1981 *nomen dubium* and its included species

Status of *Nukusurus* Nesson, 1981 *nomen dubium*. — Nesson (1981) diagnosed '*Nukusurus*', then known only by ZIN PHA K 77-4, using 11 features of the dentary. We consider each of these features below.

(1) Dentary small. Albanerpetontids were small animals and had correspondingly small bones. For example, articulated skeletons of *Celtesdens megacephalus* and *C. ibericus* from the Lower Cretaceous of Europe have snout-vent lengths of about 50 mm (McGowan & Evans 1995; Gardner pers. obs.). Dentaries attributed to '*Nukusurus*' are small in absolute terms, but they are comparable in size to dentaries known for most other albanerpetontid species. There is no evidence that body size, and by implication element size, differs among genera. However, body size does differ among species of *Albanerpeton* (Gardner in preparation).

(2) Ornament absent. Ornament develops ontogenetically on the labial surface of the dentary in *Albanerpeton inexpectatum*, and this feature is diagnostic for larger

individuals of this species (Gardner in preparation). The labial surface of the dentary is smooth and unornamented in all other albanerpetontids, indicating that lack of ornament on the dentary is not diagnostic for '*Nukusurus*' nor for any other albanerpetontid taxon.

(3) Dental parapet low. In absolute terms, the dental parapet in albanerpetontid dentaries is low. Even in dentaries of large-bodied species such as *Albanerpeton inexpectatum* and *A. galaktion*, the dental parapet is rarely higher than about 1.5 mm. Relative to overall dentary size, however, the dental parapet in albanerpetontid dentaries is actually rather high. The dental parapet in dentaries of '*Nukusurus*' is comparable in height to the parapet in similar-sized dentaries of other albanerpetontids; hence, a low dental parapet is not diagnostic for '*Nukusurus*'.

In labial outline, the dorsal edge of the dental parapet is straight to shallowly convex dorsally on the three dentaries of '*Nukusurus*'. This is the condition seen in dentaries of most other albanerpetontids, and it is clearly not diagnostic for genera. The only appreciable variation in this feature occurs at the specific level within *Albanerpeton*, where in dentaries of *A. nexuosus* the dorsal edge of the dental parapet is strongly convex to angular dorsally (see Estes 1964: figs 43e, 44c).

(4) Symphyseal prongs present. Albanerpetontid dentaries each bear one or two prongs that arise from the posterior part of the symphysis and project medially. In life, these prongs formed a mortise-in-tenon joint with complementary prongs on the opposite dentary. Symphyseal prongs are an autapomorphy for the Albanerpetontidae (Milner 1988, 1994), and their presence is diagnostic only at the familial level.

(5) Size of symphyseal prongs. Nesson (1981) stated that dentaries of '*Nukusurus*' differ from those of '*Prodesmodon*' (= *Albanerpeton nexuosus*) in having smaller symphyseal prongs. Differences in the relative sizes of the symphyseal prongs between these two taxa reflect nothing more than the larger size of the two dentaries of *A. nexuosus* figured by Estes (1964: figs 43e, 44a-c) and thus are not taxonomically significant.

(6) Pit on ventral surface of symphysis. Albanerpetontid dentaries have a small, unnamed pit on the ventral surface of the symphysis, between the bases of the symphyseal eminence and symphyseal prongs. An unnamed foramen in this pit opens dorsally into the Meckelian canal. As this pit and foramen occur in all albanerpetontid dentaries, their presence is neither diagnostic for genera nor for species.

(7) Size of pit on ventral surface of symphysis. According to Nesson (1981), dentaries of '*Nukusurus*' differ from those of '*Prodesmodon*' (= *Albanerpeton nexuosus*) in having a smaller pit on the ventral surface of the symphysis. The size of this pit varies ontogenetically and this variation is not taxonomically significant.

(8) Meckelian canal long. The Meckelian groove in albanerpetontid dentaries is enclosed as a bony canal along most of its length. The relative length of the Meckelian canal does not differ among albanerpetontid taxa, because the anterior edge of the opening for the canal consistently lies below the seventh to ninth loci from the posterior end of the tooth row. ZIN PHA K 77-4 lacks the posterior end of the tooth row, which creates the impression that the opening for the Meckelian canal lies more posteriorward in this dentary.

(9) Number of teeth. Nesson (1981) estimated that ZIN PHA K 77-4 had 17-23 teeth when complete, and on this basis he proposed that dentaries of '*Nukusurus*'

differed from those of '*Prosiren*' (= *Albanerpeton arthridion*) in having fewer teeth. Given that ZIN PHA K 77-4 lacks the posterior section of the tooth row, the original number of loci for this dentary, when it was complete, cannot be estimated with any confidence. The only '*Nukusurus*' dentary with a complete tooth row is CCMGE 241/12177, and this specimen has 32 tooth positions. This neither differs appreciably from the 33 loci in FMNH PR806 (Estes 1969: fig. 2i), the only dentary of *A. arthridion* with a complete tooth row, nor from tooth counts in larger dentaries of other albanerpetontid taxa.

(10) Teeth largest near anterior end of dentary. In albanerpetontid dentaries, the largest teeth occur about one-third of the distance along the tooth row from the anterior end, and become smaller anteriorward and posteriorward along the tooth row. This pattern occurs in all albanerpetontid dentaries and it is clearly not diagnostic for genera. Variation in the relative heterodonty of the anterior teeth is seen within *Albanerpeton*, with *A. nexuosus* having dentaries in which the largest teeth are considerably enlarged relative to others along the tooth row (Estes 1964: figs 43e, 44c).

(11) Teeth less pleurodont in posterior part of tooth row. As tooth size decreases posteriorward along the albanerpetontid dentary, the posteriormost teeth become little more than tiny denticles. Due to their shortened pedicles and therefore reduced area for attachment, these posteriormost teeth are less firmly attached to the inner wall of the parapet. Nevertheless, these teeth retain their pleurodont attachment. This pattern is not taxonomically significant because it occurs in all albanerpetontids.

In short, none of the 11 features used by Nesson (1981) to diagnose '*Nukusurus*' are informative at the generic level among albanerpetontids. We see no other features in the three dentaries from Uzbekistan that can be interpreted as being diagnostic for albanerpetontid genera. Given that it is uncertain which albanerpetontid genus is represented by these dentaries, we designate the name '*Nukusurus*' a *nomen dubium*.

Specific status of *Nukusurus insuetus* Nesson, 1981 *nomen dubium* and *N. sodalis* Nesson, 1997 *nomen dubium*. — It is evident from the preceding section that neither of the dentaries attributed by Nesson (1981, 1988) and Nesson & Udovichenko (1986) to '*Nukusurus insuetus*' are distinctive at the specific level. There is also no compelling morphological evidence that these dentaries are from conspecific individuals. As it is uncertain which species is represented by Nesson's (1981) holotype dentary, we designate the name '*N. insuetus*' a *nomen dubium*.

Nesson (1997: p. 161) stated that his holotype dentary of '*Nukusurus sodalis*' differed from dentaries of '*N. insuetus*' in having a lower dental parapet and larger teeth. We offer the following comments about these features: (1) The dental parapet in CCMGE 111/12177 is indeed low in absolute and relative terms, but it is comparable in height to the parapet in most other albanerpetontid dentaries of similar size. In albanerpetontids, the dental parapet typically is low in small dentaries and becomes relatively taller with increased dentary size. Other features of CCMGE 111/12177, such as its small size and weakly developed scar for the intermandibularis musculature, further suggest that this dentary is from a subadult. As such, we interpret the low dental parapet on this specimen as an ontogenetic feature of no taxonomic significance. (2) Tooth size is difficult to determine for CCMGE 111/12177, because the specimen lacks intact teeth. Examination of the original

photographs (see Nesson & Udovichenko 1986: pl. 2, fig. 22) of the dentary show that this damage was not inflicted after Nesson described the specimen. Judging by the broken tooth bases and empty tooth slots, teeth on this dentary were probably similar in size to those on the two dentaries attributed to '*N. insuetus*'. CCMGE 111/12177 cannot be identified more precisely than to the familial level, and for this reason we designate the name '*N. sodalis*' a *nomen dubium*.

New albanerpetontid fossils from Middle Asia

Material. — ZIN PC 1/46 and 2/46, incomplete dentaries.

Localities, horizon, and age. — ZIN PC 1/46: site SSHDa; and ZIN PC 2/46: site SSHD-8; Sheikdzheili locality, Kyzylkum Desert, north-central Uzbekistan (Fig. 1); upper part of Khodzshakul Formation; lower Cenomanian (Nesson *et al.* 1994; Nesson 1997).

Description. — ZIN PC 1/46 and 2/46 (Fig. 2K, L, respectively) are incomplete right dentaries, comparable in size to CCMGE 241/12177. Each lacks the anterior one-third or so of the ramus, but retains more of the area for attachment of the postdentary bones than do the other three dentaries from Uzbekistan. The anterior margin of the opening for the Meckelian canal is in line with the seventh (ZIN PC 2/46) and about the ninth (ZIN PC 1/46) locus from the posterior end of the tooth row, as it is in other albanerpetontid dentaries. In ZIN PC 1/46, the dorsal margin immediately behind the tooth row is intact and horizontal in lingual or labial view.

Remarks. — Neither dentary can be identified below the familial level. One of these may be the same specimen (CCMGE 203/11657) reported by Nesson (1981) as a small 'prosirenid' dentary from an unspecified site at the Sheikdzheili locality.

Re-interpretation of *Bishara* Nesson, 1997

Nesson (1997: p. 161) named a new albanerpetontid genus and species, *Bishara backa*, on an incomplete atlantal centrum, CCMGE 240/12177. This is the only specimen known for the taxon. The holotype was collected from the upper Santonian–?Campanian (Nesson *et al.* 1994; Nesson 1997) Baybishe locality (Fig. 1), located in south-central Kazakhstan in the middle or upper part of the Bostobe Formation.

One of us (Averianov) has not been able to locate CCMGE 240/12177 in the collections of the CCMGE or ZIN. Nevertheless, we can comment on the identity of this specimen based on published photographs (Nesson 1988: pl. 16, fig. 12; 1997: pl. 10, fig. 3) that depict the fossil in anterior and ventral views. These photographs show an odontoid process flanked to either side by a vertical cotyle – features that confirm CCMGE 240/12177 is an atlantal centrum. These photographs further demonstrate, however, that CCMGE 240/12177 lacks characteristic features that are plainly visible in anterior and ventral views on unequivocal albanerpetontid atlantes. These features include the following: odontoid process broad (width equal to or greater than one-half the width across the outer edges of the anterior cotyles), gutter-like in anterior view, with concave dorsal surface and lateral edges confluent with dorsal margins of anterior cotyles; anterior cotyles slightly compressed dorso-medially–ventrolaterally and kidney-shaped in anterior outline, with concave margin facing odontoid process; and deep notch below odontoid process separating anterior cotyles (Seiffert 1969: fig. 1B, C; Estes & Hoffstetter 1976: text-fig. 1A, E; Fox & Naylor 1982: fig. 1f; McGowan 1996: fig. 9a, c). CCMGE 240/12177 compares favorably with salamander atlantes, and we identify it as such. Consequently, the name *Bishara backa* denotes a salamander, not an albanerpetontid.

Purported albanerpetontid fossils from Middle Asia

?Albanerpetontid frontal. — Nesson (1988) reported an uncatalogued albanerpetontid frontal from the Upper Jurassic (Callovian) Tashkumyr locality (Fig. 1), western Kirghizia, in the upper part of the Balabansay Formation. We cannot confirm the identity of this fossil, because it was never described or figured and one of us (Averianov) has not been able to locate it in collections of the CCMGE or ZIN. If the reported geological age and identity of this specimen are correct, it would be among the geologically oldest known albanerpetontid fossils (see below).

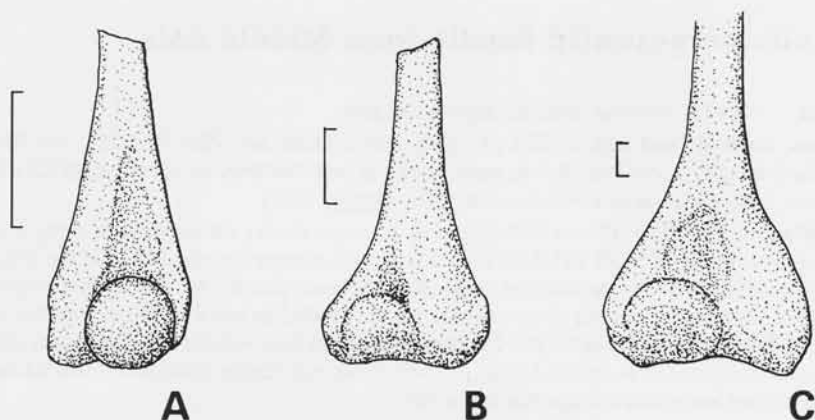


Fig. 4. Distal ends of selected albanerpetontid and caudate humeri in ventral view. A. OMNH 33516, *Albanerpeton arthridion*, left humerus; OMNH locality V706, Oklahoma, Antlers Formation, uppermost Aptian–lowermost Albian. B. CCMGE 183/11657, Caudata indeterminate, right humerus; Dzhyrakuduk locality, Bissekty Formation, Coniacian. C. UALVP unnumbered, *Ambystoma tigrinum* (Caudata; Ambystomatidae), right humerus; southern Alberta, Canada, Recent. Scale bars 1 mm.

Salamander humerus. — CCMGE 183/11657 is the distal end of a right humerus (Fig. 4B) that has been referred to the Prosirenidae and Albanerpetontidae (Nesson 1981, 1997, respectively). This humerus was collected from site CBI-4v, Dzhyrakuduk locality, Kyzylkum Desert, north-central Uzbekistan (Fig. 1), which lies in the middle part of the Coniacian-aged Bissekty Formation (Nesson *et al.* 1998). Unequivocal albanerpetontid humeri are characterised by features such as having the shaft in line with the radial condyle, the distal end moderately wide, the radial condyle a relatively large hemispherical ball, and the ulnar condyle smaller than the radial condyle (Estes & Hoffstetter 1976: pl. 9, figs 6, 7; McGowan & Ensom 1997: fig. 2b; here: Fig. 4A). We interpret CCMGE 183/11657 as a salamander humerus (Fig. 4B, C), because the shaft is offset from the radial condyle, the distal end is relatively wider, the radial condyle is a small ball with a flattened distal end, and the ulnar condyle is larger than the radial condyle.

Speculations on the Mesozoic history of Middle Asian albanerpetontids

The five dentaries described above from Uzbekistan provide little direct information about the evolution of albanerpetontids, aside from confirming that the group was widespread across Laurasia during the Late Cretaceous. The record of albanerpetontids

elsewhere is better, but significant temporal and geographic gaps remain. In general, these gaps correspond to intervals and areas from which nonmarine microvertebrate assemblages as a whole are poorly documented. This suggests that breaks in the albanerpetontid fossil record are attributable at least in part to taphonomic and collecting biases, and should not be interpreted as reflecting an actual absence of albanerpetontids in time and space. Despite these limitations, some constrained speculations can be made about the Mesozoic history of Asian albanerpetontids based on the distributions of fossils, land masses, and marine barriers shown in Fig. 5.

The geologically oldest albanerpetontid fossils date from the lower Bathonian (Kriwet *et al.* 1997) of France (Estes 1981) and the upper Bathonian of England (Evans & Milner 1994; McGowan 1996). These occurrences likely underestimate the time of origin for the family, an event that Milner (1994) suggested occurred no later than the Early Triassic. This date is supported by hypotheses of higher level relationships of the Lissamphibia (e.g., Milner 1988, 1990, 1993b; Trueb & Cloutier 1991; McGowan & Evans 1995; Laurin & Reisz 1997) constrained against fossil occurrences (e.g., Milner 1993a).

Except for a Lower Cretaceous record in Morocco (Broschinski & Sigogneau-Russell 1996), albanerpetontids are known only from Laurasia and most likely originated there. Continental tetrapod assemblages of Triassic–Early Jurassic age are relatively cosmopolitan, indicating that there were few barriers to overland dispersal during this time (e.g., Shubin & Sues 1991; Russell 1993; Sues 1997). In the absence of fossils, the extent to which albanerpetontids were able to disperse across Laurasia during this interval obviously remains unknown. However, judging by distributions of other contemporaneous amphibians (Milner 1994), it would not be surprising if albanerpetontids also broadly distributed across Laurasia by at least the Middle Jurassic.

Regardless of when and where albanerpetontids originated and what the early undocumented biogeographic history of the group might have been, the European Bathonian occurrences show that albanerpetontids were in Europe when the Turgai Straits first opened between Europe and Asia in the late Middle to early Late Jurassic. With the opening of these straits, Asia was isolated from the remainder of Laurasia for about 50 million years (Gradstein *et al.* 1995), until about the late Early Cretaceous. While it is possible that albanerpetontids were already in Asia prior to the opening of the Turgai Straits and could have evolved vicariantly on the continent during its subsequent isolation, fossil evidence that this occurred is lacking.

Albanerpetontids are reliably known from Asia when the continent was connected first with Europe from about the Aptian–Coniacian by a series of intermittent land bridges across the Turgai Straits, and then across the Bering Isthmus with the western subcontinent of North America continuously from the latest Albian or earliest Cenomanian to Maastrichtian. Fossils in Europe and North America predate the establishment of these land bridges, and thus argue against albanerpetontids having dispersed from Asia into Europe or North America. Evidence for faunal interchange of any kind across the Turgai Straits during the Aptian–Coniacian is lacking, in large part because the European record of nonmarine vertebrates from this interval is sparse (Buffetaut *et al.* 1981; Le Loeuff & Buffetaut 1995). By contrast, considerable faunal interchange occurred across the Bering Isthmus between western North America and Asia during the Late Cretaceous (e.g., Russell 1993; Sereno 1997). This interchange need not have been limited to large tetrapods, as evidenced by occurrences of the

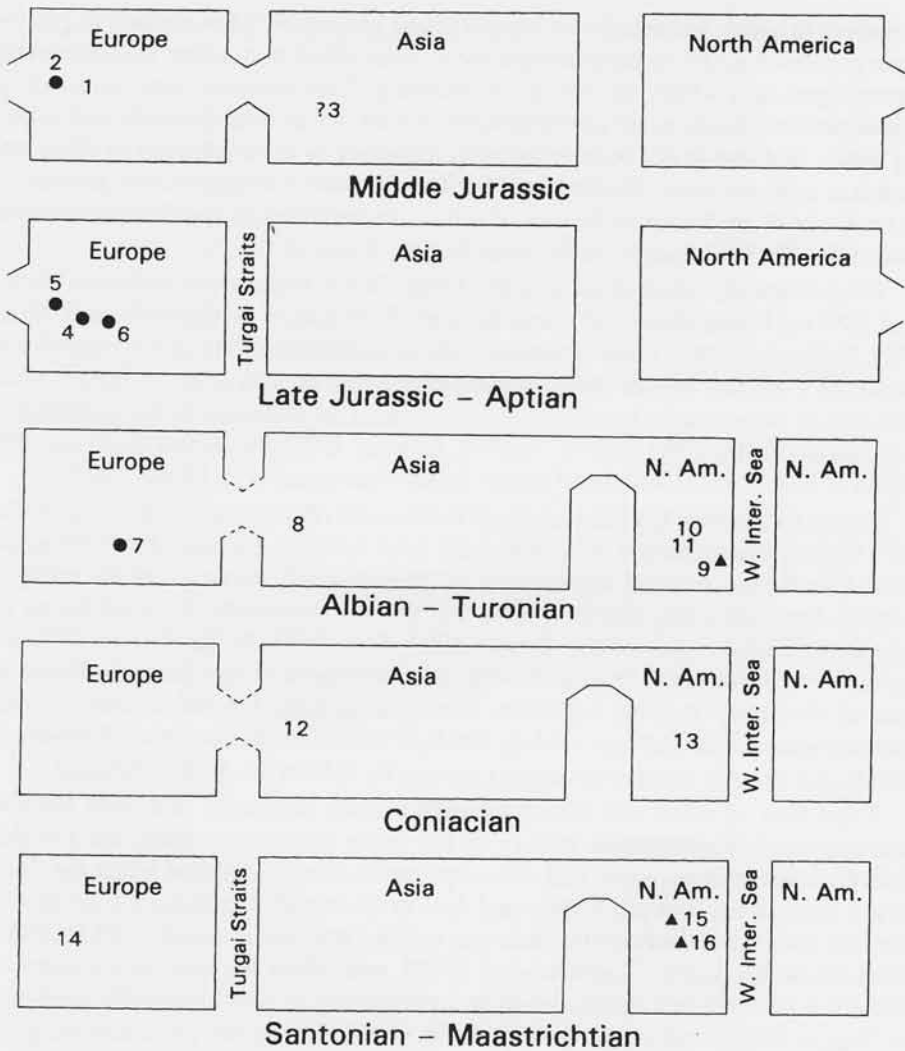


Fig. 5. Diagrammatic representation of Laurasian continents and distribution of albanerpetontid fossils from the Middle Jurassic–Cretaceous. Continental reconstructions based on Barron (1987), Funnell (1990), and Smith *et al.* (1994). Dashed lines are intermittent land connections; abbreviations: N. Am. – North America and W. Inter. Sea – Western Interior Seaway; symbols: ● and numeral – *Celtedens*, ▲ and numeral – *Albanerpeton*, '?' and numeral – unverified occurrence, and numeral – *Albanerpetontidae* indeterminate. Localities: 1 – lower Bathonian, France; 2 – upper Bathonian, England; 3 – Callovian, Kirghizia; 4 – Kimmeridgian, Portugal; 5 – Berriasian, England; 6 – Barremian, Spain; 7 – Albian, Italy; 8 – lower Cenomanian, Uzbekistan; 9 – Aptian–Albian, USA; 10 – upper Albian–lower Cenomanian, USA; 11 – Turonian, USA; 12 – Coniacian, Uzbekistan; 13 – lower or middle Coniacian, USA; 14 – upper Campanian–lower Maastrichtian, Spain; 15 – lower and middle Campanian, Canada; and 16 – upper Maastrichtian, USA.

earliest scapherpetontid salamanders in the upper Albian of Uzbekistan (Nessov 1981) and uppermost Albian–lowermost Cenomanian of Utah (Cifelli *et al.* in press). If albanerpetontids dispersed into Asia from Europe or western North America during the

late Early and Late Cretaceous, as is implied by continental reconstructions and limited fossil occurrences, we would expect Asian albanerpetontids to show close affinities with European or North American taxa.

Testing of the ideas we have presented here must await the recovery from Asia of fossils that are more systematically informative and sample a broader temporal range than the five dentaries presently available. Prospects for recovering such fossils are promising, judging from the abundant and occasionally well-preserved amphibian bones that have already been collected from Middle Jurassic–Cretaceous localities in Middle Asia (e.g., Nessov 1988, 1997).

Conclusions

- The Asian record of albanerpetontids is limited to five indeterminate dentaries from the Upper Cretaceous (lower Cenomanian and Coniacian) of Uzbekistan.
- There are no endemic Asian albanerpetontids. The names *Nukusurus*, *N. insuetus*, and *N. sodalis* are *nomina dubia* within the Albanerpetontidae. The name *Bishara* denotes an indeterminate salamander, not an albanerpetontid. These findings leave *Albanerpeton* (Aptian–Paleocene, North America; Miocene, Europe) and *Celtedens* (Bathonian–Albian, western Europe) as the only valid albanerpetontid genera.
- Limited evidence suggests that a Cretaceous dispersal from Europe or North America, rather than vicariance within Asia, may have played the more prominent role in the evolution of Asian albanerpetontids, but evidence for either scenario remains weak.

Acknowledgements

Our study was possible because Dr. N.B. Ananjeva carried the fossils described here from Saint Petersburg to Gardner in Prague. For access to comparative specimens we thank Drs. D. Goujet and J.-C. Rage (MNHN), Dr. R.L. Cifelli and R.L. Nydam (OMNH), Dr. R.C. Fox (UALVP), Dr. S.E. Evans (University College London), and Drs F. Barattolo, S. Bravi, C. Barbera, and P. De Castro (Dipartimento di Paleontologie dell' Università di Napoli). We also thank B. Badzio for translating part of Nessov's (1981) paper, G.D. Braybrook for taking the scanning electron micrographs, and Drs G.E. Ball, M. Borsuk-Bialynicka, R.C. Fox, Gao K., and A.R. Milner for reviewing earlier versions of our paper. Gardner's funding was provided by a University of Alberta Recruitment Scholarship and Dissertation Fellowship, and more recently by his wife, N.J. Marklund, and parents-in-law, G.T. and G.F. Marklund. Averianov thanks I.G. Danilov (ZIN) for various help during our study.

References

- Barron, E.J. 1987. Global Cretaceous paleogeography – International Geologic Correlation Program Project 191. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **59**, 207–214.
- Broschinski, A. & Sigogneau-Russell, D. 1996. Remarkable lizard remains from the Lower Cretaceous of Anoual (Morocco). — *Annales de Paléontologie (Vert.-Invert.)* **82**, 147–175.
- Buffetaut, E., Cappetta, H., Gayet, M., Martin, M., Moody, R.T., Rage, J.-C., Taquet, P., & Wellhofer, P. 1981. Les vertébrés de la partie moyenne du Crétacé en Europe. — *Cretaceous Research* **2**, 275–281.
- Cifelli, R.L., Nydam, R.L., Gardner, J.D., Weil, A., Eaton, J.G., Kirkland, J.I., & Madsen, S.K. In press. Medial Cretaceous vertebrates from the Cedar Mountain Formation, Emery County: The Mussentuchit

- local fauna; In: D.D. Gillette (ed.), *Vertebrate Fossils of Utah*. — *Utah Geological Survey Special Publication*.
- Duellman, W.E. & Trueb, L. 1986. *Biology of Amphibians*. 670 pp. McGraw-Hill Inc., New York.
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. — *University of California Publications in Geological Sciences* **49**, 1–180.
- Estes, R. 1969. Prosiromphidae, a new family of fossil salamanders. — *Nature* **224**, 87–88.
- Estes, R. 1981. Gymnophiona. Caudata. In: P. Wellnhofer (ed.), *Encyclopedia of Paleoherpetology*, Part 2, 1–115. Gustav Fischer Verlag, Stuttgart.
- Estes, R. & Hoffstetter, R. 1976. Les Urodèles du Miocène de La Grive-Saint-Alban (Isère, France). — *Bulletin du Muséum National d'Histoire Naturelle*, 3^e série, no. 398, *Sciences de la Terre* **57**, 297–343.
- Evans, S.E. & Milner, A.R. 1994. Middle Jurassic microvertebrate assemblages from the British Isles. In: N.C. Fraser & H.-D. Sues (eds), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 303–321. Cambridge University Press, New York.
- Fox, R.C. & Naylor, B.G. 1982. A reconsideration of the relationships of the fossil amphibian *Albanerpeton*. — *Canadian Journal of Earth Sciences* **19**, 118–128.
- Funnell, B.M. 1990. Global and European Cretaceous shorelines, stage by stage. In: R.N. Ginsburg and B. Beaudoin (eds), *Cretaceous Resources, Events and Rhythms*, 221–235. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Gardner, J.D. 1996. The North American fossil record of *Albanerpeton* (Lissamphibia, Albanerpetontidae). — *Journal of Vertebrate Paleontology* **16** (supplement to 3), 36A.
- Gradstein, F.M., Agterberg, F.P., Ogg, J.G., Hardenbol, J., Veen, P. van, Thierry, J. & Huang, Z. 1995. A Triassic, Jurassic and Cretaceous time scale. In: W.A. Berggren, D.V. Kent, M.-P. Aubry, & J. Hardenbol (eds), *Geochronology, Time Scales and Global Stratigraphic Correlation*. — *SEPM Special Publication* **54**, 95–126.
- Kriwet, J., Rauhut, O.W.M. & Gloy, U. 1997. Microvertebrate remains (Pisces, Archosauria) from the Middle Jurassic of southern France. — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **206**, 1–28.
- Laurin, M. & Reisz, R.R. 1997. A new perspective on tetrapod phylogeny. In: S.S. Sumida & K.L.M. Martin (eds), *Amniote Origins: Completing the Transition to Land*, 9–59. Academic Press, San Diego.
- Le Loeuff, J. & Buffet, E. 1995. The evolution of Late Cretaceous non-marine vertebrate fauna in Europe. In: A. Sun & Y. Wang. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*, 181–184. China Ocean Press, Beijing.
- McGowan, G.J. 1996. Albanerpetontid amphibians from the Jurassic (Bathonian) of southern England. In: M. Morales (ed.), *The Continental Jurassic*. — *Museum of Northern Arizona Bulletin* **60**, 227–234.
- McGowan, G.J. & Evans, S.E. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. — *Nature* **373**, 143–145.
- McGowan, G.J. & Ensom, P.C. 1997. Albanerpetontid amphibians from the Lower Cretaceous of the Isle of Purbeck, Dorset. — *Proceedings of the Dorset Natural History and Archaeological Society* **118**, 113–117.
- Milner, A.R. 1988. The relationships and origin of living amphibians. In: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*. — *Systematics Association Special Volume* **35A**, 59–102. Clarendon Press, Oxford.
- Milner, A.R. 1990. The radiations of temnospondyl amphibians. In: P.D. Taylor and G.P. Larwood (eds.), *Major Evolutionary Radiations*. — *Systematics Association Special Volume* **42**, 321–349. Clarendon Press, Oxford.
- Milner, A.R. 1993a. Amphibian-grade Tetrapoda. In: M.J. Benton (ed.), *The Fossil Record* **2**, 665–679. Chapman and Hall, London.
- Milner, A.R. 1993b. The Paleozoic relatives of lissamphibians. — *Herpetological Monographs* **7**, 8–27.
- Milner, A.R. 1994. Late Triassic and Jurassic amphibians: fossil record and phylogeny. In: N.C. Fraser & H.-D. Sues (eds), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, 5–22. Cambridge University Press, New York.
- Nessov, L.A. (Nesov, L.A.) 1981. Cretaceous salamanders and frogs of Kyzylkum Desert [in Russian with English abstract]. — *Trudy Zoologičeskogo Instituta, Akademiâ Nauk SSSR* **101**, 57–88.
- Nessov, L.A. (Nesov, L.A.) 1988. Late Mesozoic amphibians and lizards of Soviet Middle Asia. — *Acta Zoologica Cracoviensia* **31**, 475–486.

- Nessov, L.A. (Nesov, L.A.) 1997. *Cretaceous Nonmarine Vertebrates of Northern Eurasia* [in Russian with English abstract]. 218 pp. Izdatel'stvo Sankt-Peterburgskogo Universiteta, Sankt-Peterburg.
- Nessov, L.A. (Nesov, L.A.), Archibald, J.D., & Kielan-Jaworowska, Z. 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. In: K.C. Beard & M.R. Dawson (eds), *Dawn of the Age of Mammals in Asia – Bulletin of the Carnegie Museum of Natural History*, **34**, 40–88.
- Nessov, L.A. (Nesov, L.A.), Sigogneau-Russell, D., & Russell, D.E. 1994. A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. — *Palaeovertebrata* **23**, 51–92.
- Nessov, L.A. (Nesov, L.A.) & Udovichenko, N.I. (Udovičenko, N.I.) 1986. New findings of Cretaceous and Paleogene vertebrate remains of Soviet Middle Asia [in Russian]. — *Voprosy Paleontologii* **9**, 129–136.
- Russell, D.A. 1993. The role of Central Asia in dinosaurian biogeography. — *Canadian Journal of Earth Sciences* **30**, 2002–2012.
- Seiffert, J. 1969. Urodelen-Atlas aus dem obersten Bajocien von SE-Aveyron (Südfrankreich). — *Paläontologische Zeitschrift* **43**, 32–36.
- Sereno, P.C. 1997. The origin and evolution of dinosaurs. — *Annual Review of Earth and Planetary Sciences* **25**, 435–489.
- Shubin N.H. & Sues, H.-D. 1991. Biogeography of early Mesozoic continental tetrapods: patterns and implications. — *Paleobiology* **17**, 214–230.
- Smith, A.G., Smith, D.G., & Funnell, B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. 99 pp. Cambridge University Press, New York.
- Sues, H.-D. 1997. Continental tetrapods of the Early Mesozoic. In: J.O. Farlow & M.K. Brett-Surman (eds), *The Complete Dinosaur*, 627–643. University of Indiana Press, Indianapolis.
- Trueb, L. & Cloutier, R. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: H.-P. Schultze & L. Trueb (eds), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*, 223–313. Cornell University Press, Ithaca.

Płazy z rodziny Albanerpetontidae z górnej kredy Azji Środkowej

JAMES D. GARDNER i ALEXANDER O. AVERIANOV

Streszczenie

Rewizja azjatyckiego zapisu kopalnego albanerpetontydów pozwoliła potwierdzić obecność tej grupy na podstawie dwóch żuchw z dolnego cenomanu Uzbekistanu, opisanych tu po raz pierwszy, oraz trzech okazów opisanych wcześniej przez Nesowa z dolnego cenomanu i koniaku Uzbekistanu. Materiał nie wykazuje jednak cech diagnostycznych pozwalających go określić poniżej szczebla rodzajowego. Dlatego nazwy *Nukusurus*, *N. insuetus* Nessov, 1981 i *N. sodalis* Nessov, 1997 wypada uznać za *nomina dubia*. Holotyp domniemanego albanerpetontyda *Bishara backa* Nessov, 1997 (górnym santon–?kampan Kazachstanu) – pojedynczy dźwigacz – należy natomiast do salamandry, a nie albanerpetontyda. Tak więc jedynymi ważnymi rodzajami albanerpetontydów pozostają *Albanerpeton* (kreda–miocen, Ameryka Północna i Europa) oraz *Celtdens* (środkowa jura–dolna kreda, Europa). Na podstawie ograniczonego materiału kopalnego można przypuszczać, że w połowie kredy doszło do jednorazowego lub kilkakrotnego zasiedlenia Azji przez albanerpetontydy z Europy lub Ameryki Północnej.