N. Jb. Geol. Paläont. Mh.	**1996**, H. 12	739–750	Stuttgart, Dezember 1996

Agamid lizards (Reptilia, Sauria, Agamidae) from the Early Eocene of Kyrgyzstan

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With 8 figures in the text

AVERIANOV, A. & DANILOV, I. (1996): Agamid lizards (Reptilia, Sauria, Agamidae) from the Early Eocene of Kyrgyzstan. – N. Jb. Geol. Paläont. Mh., **1996** (12): 739–750; Stuttgart.

Abstract: Lizard jaw fragments belonging to Uromastycinae and 2 specimens of Agamidae from the Early Eocene (Ypresien) Alay beds at Andarak 2 locality in Kyrgyzstan are the first remains of agamid lizards known from the Early Eocene of Asia. The majority of them belong to the uromastycines. They represent the oldest fossil record for this subfamily and demonstrate their abundance in the Paleogene of Asia.

Zusammenfassung: Aus den untereozänen Alay-Schichten der Fundstelle Andarak 2 (Kirgisien) werden Eidechsen-Unterkieferfragmente von Uromastycinen sowie Agamiden indet. beschrieben. Sie sind die ersten Nachweise von Agamen aus dem Untereozän von Asien. Die Mehrzahl von ihnen gehört zu Uromastycinae. Sie repräsentieren die ältesten Funde dieser Unterfamilie überhaupt und zeigen deren häufiges Auftreten im Paläogen Asiens.

Introduction

Findings of lizards of Early Eocene age in Asia are exceptionally rare. Among them there are lizard remains from the Bumban Member of the Naran Bulak Svita at Tsagan Khushu, Mongolia (DASHZEVEG et al. 1987; ALIFANOV 1993). The age of this member is not Middle Eocene, as was ascribed by ALIFANOV (1993), but basal Early Eocene, Early Ypresien, possibly equivalent to the MP 7 mammal Paleogene reference level in Europe (SCHMIDT-KITTLER 1987). A jaw fragment with a single tooth is referred to *Tinosaurus* sp. known from the Early-Middle Eocene Kuldana Formation at Chorlakki in Pakistan (RAGE 1987). Another Early Eocene Asian locality bearing lizard remains is Andarak 2 in Kyrgyzstan. The age of this locality was previously considered to be Middle Eocene (RUSSELL & ZHAI 1987 and references therein), but recently is reconsidered as Early Eocene, Late Ypresien (AVERIANOV & UDOVICHENKO 1993; AVERIANOV 1994), approximately equivalent to the MP 10 mammal reference level in Europe.

0028–3630/96/1996–0739 $ 3.00

The Andarak 2 locality produces a rich and diverse fauna of marine as well as terrestrial vertebrates, including elasmobranch and teleost fishes, turtles, crocodiles, squamates, birds and mammals. Among squamates serpents are quite abundant, and the presence of two types of jaw fragments of large lizards, as well as a vertebra tentatively assigned to *Varanus* sp. were reported (Reshetov et al. 1978; Chkhikvadze 1984). In another paper (Zerova & Chkhikvadze 1984) two of the jaw fragments mentioned above were tentatively referred to Lacertidae.

The aim of this paper is to describe lizard remains from the Andarak 2 locality collected by the first author since 1988.

Described material is housed in the Paleoherpetological collection of the Zoological Institute, Russian Academy of Science, St. Petersburg (ZIN PH).

Systematic paleontology

Order Sauria McCartner, 1802
Suborder Lacertilia Wagler, 1830
Infraorder Iguania Cuvier, 1807
Family Agamidae Gray, 1827
Subfamily Uromastycinae Theobald, 1868

Uromastycinae gen. et sp. indet.

Material: Six jaw fragments (ZIN PH 1–4/1, 6/1 and 8/1). Andarak 2, Kyrgyzstan. Lower Alay beds, Early Eocene (Late Ypresien).

Description: Two more complete jaw fragments (ZIN PH 1/1 and 2/1) are definitely from the dentary. ZIN PH 1/1 is the anterior portion of the dentary with a squarish anterior profile. Total length of the fragment is 5.6 mm, it bears 10 teeth. The lateral surface is slightly convex and marked by well formed nutrient foramina lying at a sharp angle to the tooth row (Fig. 1a). There are three closely spaced foramina on the preserved surface. In lingual view (Fig. 1b) the specimen shows the subpleurodont teeth and widely opened Meckelian groove, which terminates below the fifth tooth from the front. The groove seems to be rotated to the ventral border of the dentary approaching the symphysis as it occurs in *Uromastyx* and some other agamid genera. The subdental ridge is robust, of equal thickness along the fragment. The tooth row is homodont. Teeth are slightly increased in size posteriorly. Three teeth occupy a space of 1.5–2 mm. The teeth have a rounded crown without a central cusp. They are closely attached but do not overlap.

ZIN PH 2/1 is the posterior portion of the dentary bearing the three last teeth and the coronoid process of the dentary. The depth of the dentary just anterior to this process is more than three times the height

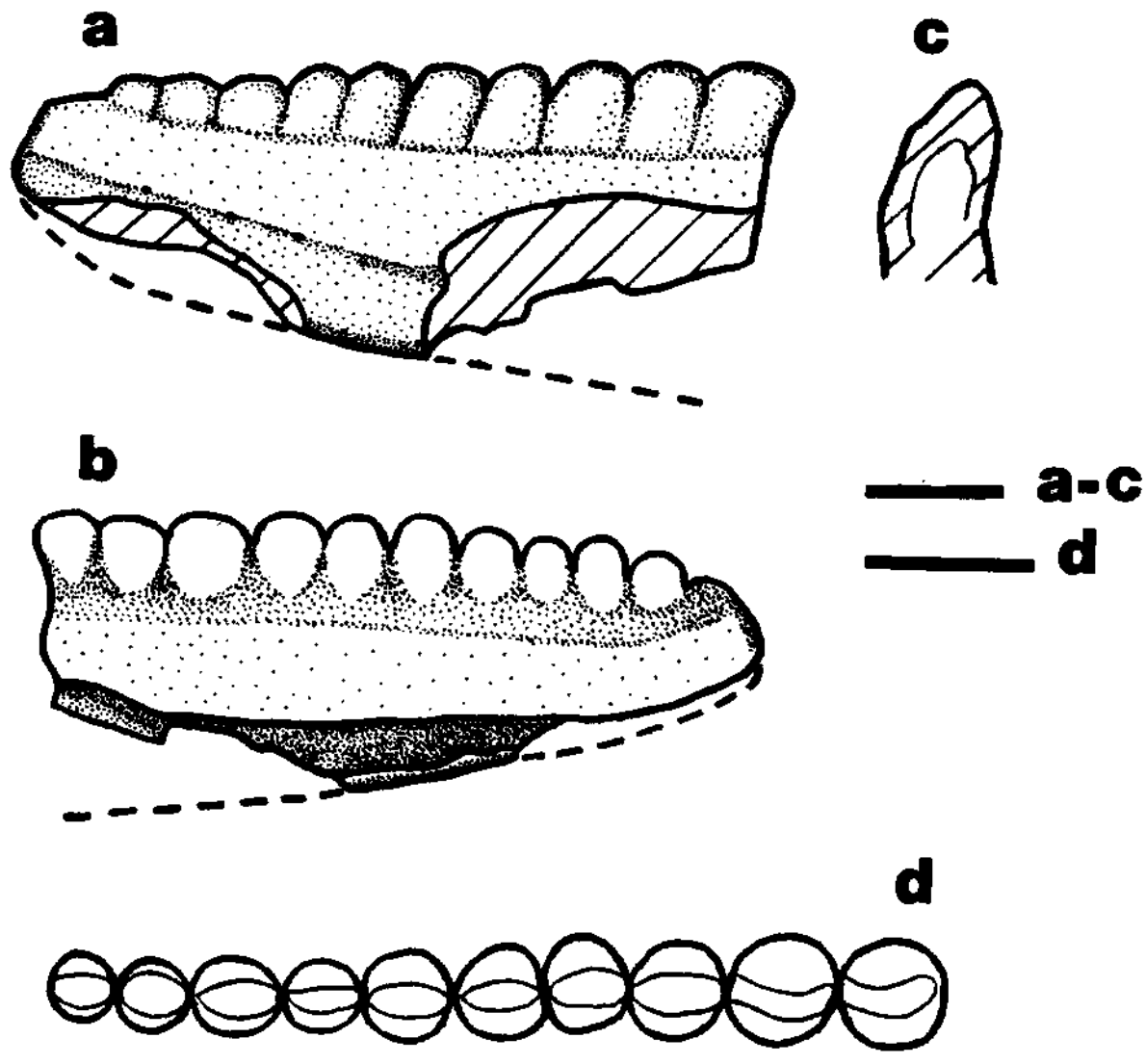

Fig. 1. Uromastycinae gen. et sp. indet. Anterior portion of dentary, ZIN PH 1/1. Scale bar: 1 mm. a – labial view, b – lingual view, c – cross section, d – occlusal view of teeth.

of the last tooth. The last three teeth occupy a space of 3 mm. The slightly elevated central cusp can be recognized on each tooth. In lingual view (Fig. 2b) below the posterior tooth a ridge for attachment of coronoid and spleniale is visible. The coronoid process of the dentary was of considerable height, apparently elevated above the tooth row. In labial view (Fig. 2a) there is a well developed groove between supraangular and angular projections of the dentary: it marks a sharp angle between these projections.

The jaw fragment ZIN PH 3/1 is a small portion of the dentary with four teeth (Fig. 3). In tooth size and morphology it closely approximates ZIN PH 1/1. In labial view it bears two widely spaced nutrient foramina (Fig. 3a), which form a sharp angle with the tooth row. In lingual view (Fig. 3b) the anterior part of the Meckelian groove can be recognized; it does not reach the symphysis and rotates on the ventral border of the dentary.

ZIN PH 4/1 is a maxilla(?) fragment with three teeth (Fig. 4) approximating in size ZIN PH 2/1. The tooth crowns have a slightly elevated central cusp, or are almost flat (Fig. 4d). Teeth slightly overlap in occlusal view. The lingual surface shows nutrient foramina (Fig. 4b).

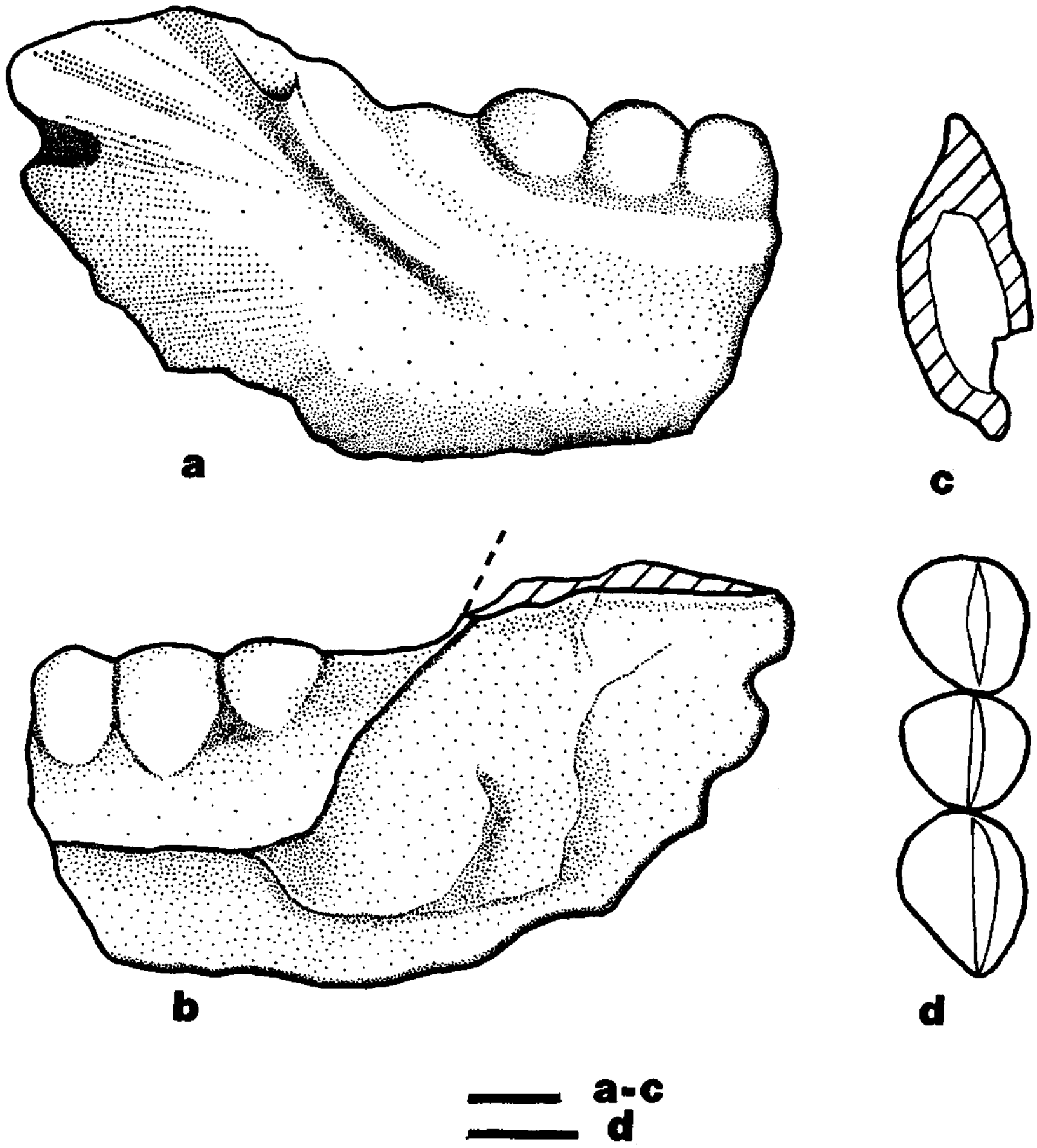

Fig. 2. Uromastycinae gen. et sp. indet. Posterior portion of dentary, ZIN PH 2/1. Scale bar: 1 mm. a – labial view, b – lingual view, c – cross section, d – occlusal view of teeth.

ZIN PH 6/1 is a dentary(?) fragment with three teeth that increase in size to the posterior end (Fig. 5). Possibly this fragment comes from the posterior portion of the dentary. Three teeth occupy a space of 2.7 mm. Teeth do not overlap in occlusal view.

ZIN PH 8/1 is a part of the dentary with three teeth (Fig. 8). The depth of the bone increases posteriorly. The Meckelian groove is wide open (Fig. 6b, c). This fragment comes from the posterior portion of the dentary. Three teeth occupy a space of 2.3 mm.

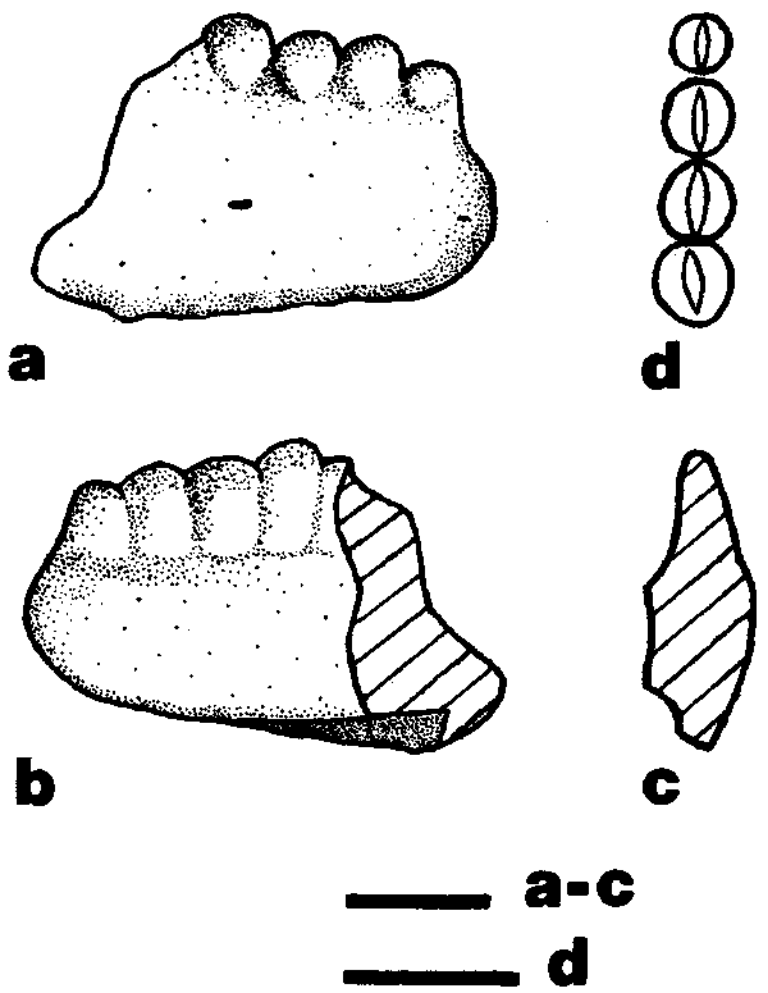

Fig. 3. Uromastycinae gen. et sp. indet. Dentary fragment, ZIN PH 3/1. Scale bar: 1 mm. a – labial view, b – lingual view, c – cross section, d – occlusal view of teeth.

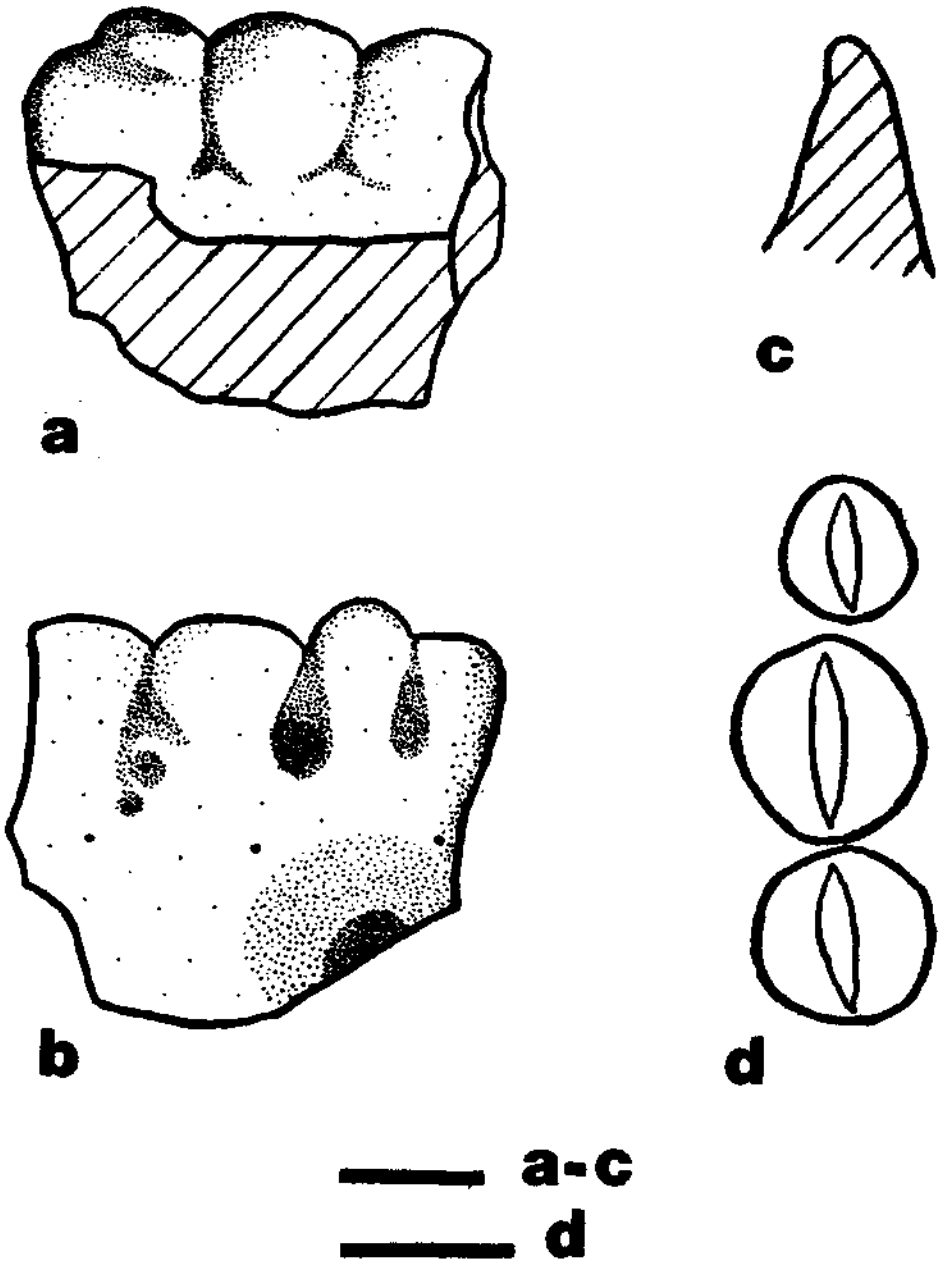

Fig. 4. Uromastycinae gen. et sp. indet. Maxilla(?) fragment, ZIN PH 4/1. Scale bar: 1 mm. a – lingual view, b – labial view, c – cross section, d – occlusal view of teeth.

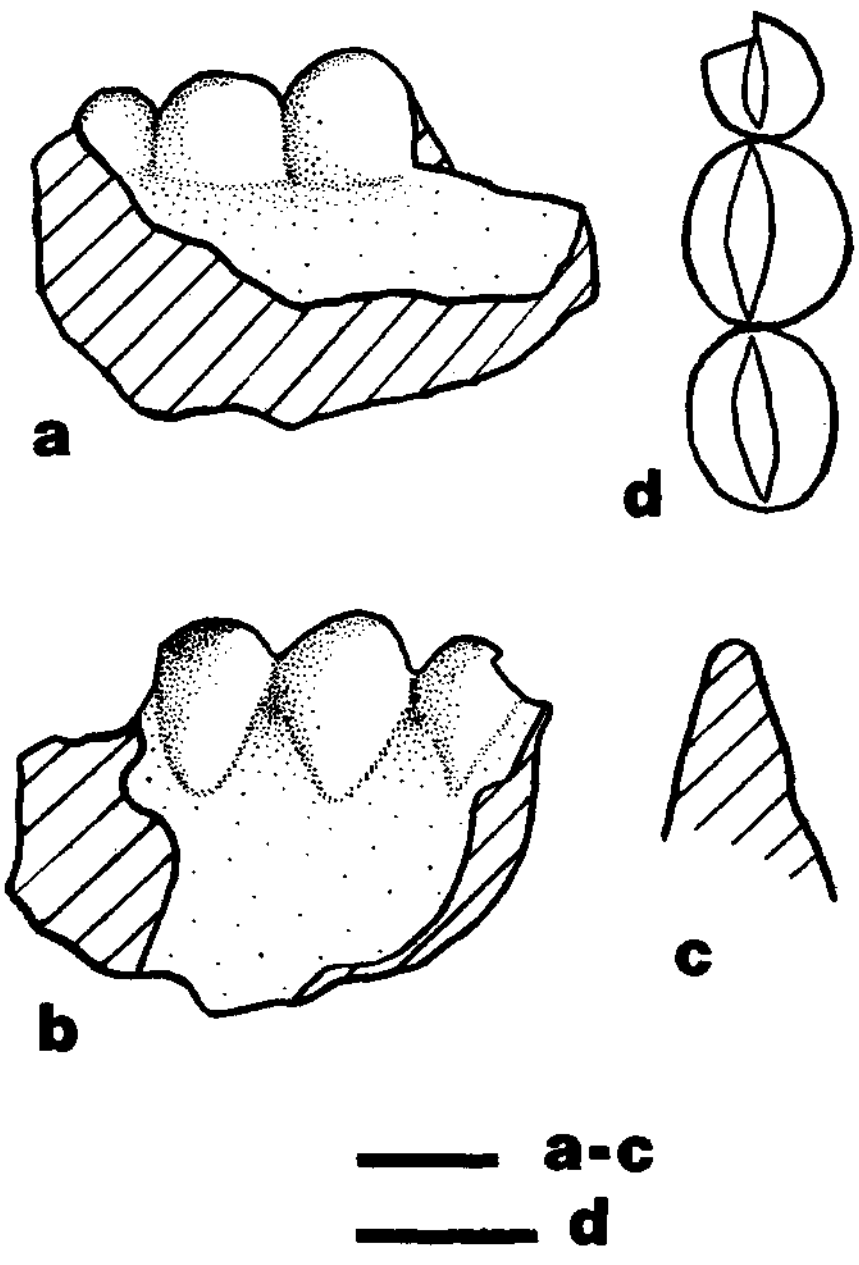

Fig. 5. Uromastycinae gen. et sp. indet. Dentary(?) fragment, ZIN PH 6/1. Scale bar: 1 mm. a– lingual view, b – labial view, c – cross section, d – occlusal view of teeth.

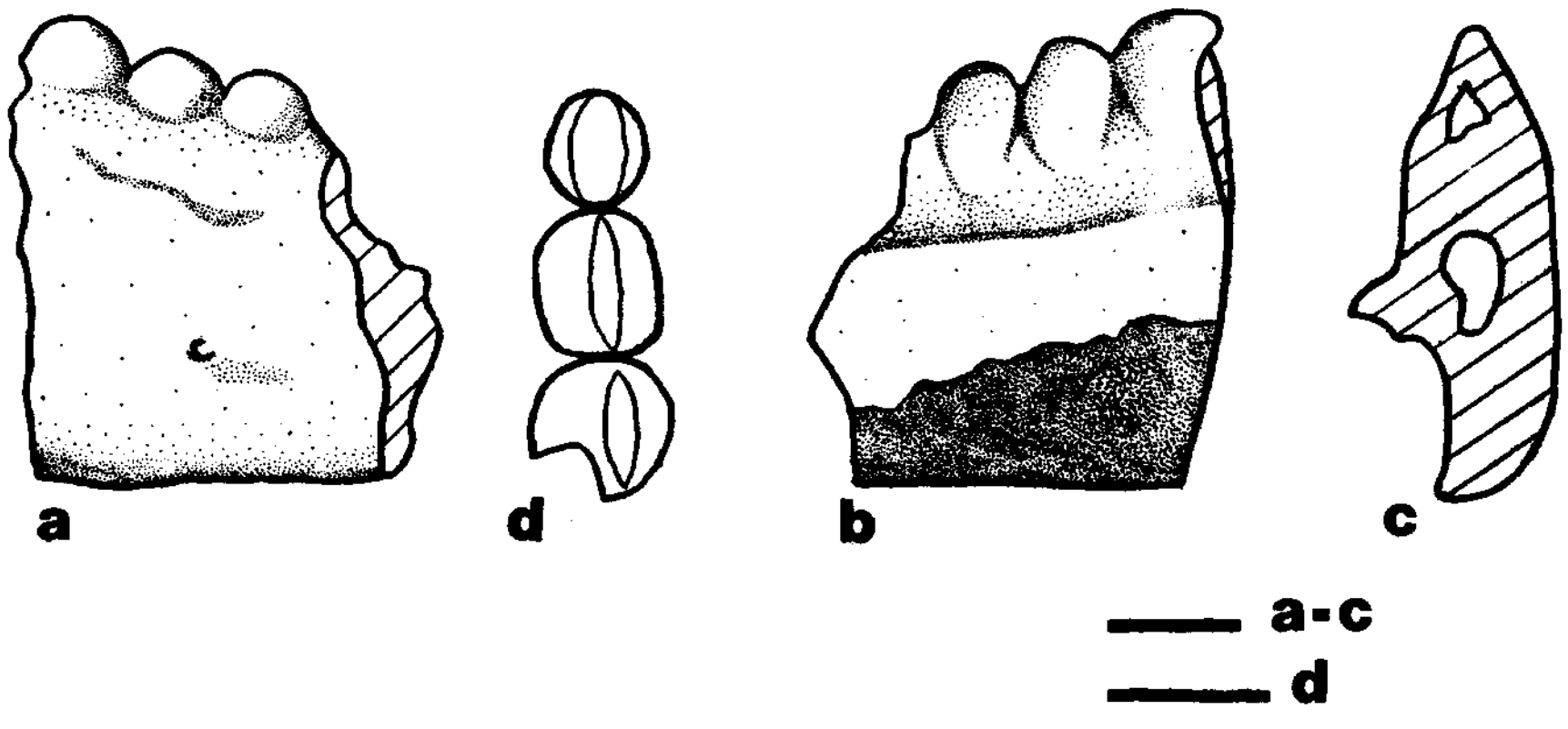

Fig. 6. Uromastycinae gen. et sp. indet. Dentary fragment, ZIN PH 8/1. Scale bar: 1 mm. a – labial view, b – lingual view, c – cross section, d – occlusal view of teeth.

Agamidae subfamily, gen. et sp. indet. 1

Material: One dentary fragment (ZIN PH 5/1). Andarak 2, Kyrgyzstan. Lower Alay beds, Early Eocene (Late Ypresien).

Description: ZIN PH 5/1 is the anterior portion of a dentary (Fig. 7), which is anteriorly complete, showing a weak symphysis. It carries four teeth and spaces for three more teeth and has an intact length 5.6 mm. The teeth have pointed apices and two accessory cusplets separated by distinct vertical notches. Their crowns are inclined anteriorly at an angle of approximately of 55° to the subdental shelf. Three more anterior teeth have higher crowns. They are similar to the pleurodont canine teeth of other agamids. The first preserved tooth shows a resorption pit developed at the center of its base, indicating tooth replacement. The ventral border of the dentary forms a slight thickening below the sixth tooth from the front, probably bearing a pocket for the anterior end of the angulare. The subdental shelf is straight and thinner than in ZIN PH 1/1. It is noticeably decreasing in width anterior to the fifth tooth from the front (Fig. 7b).

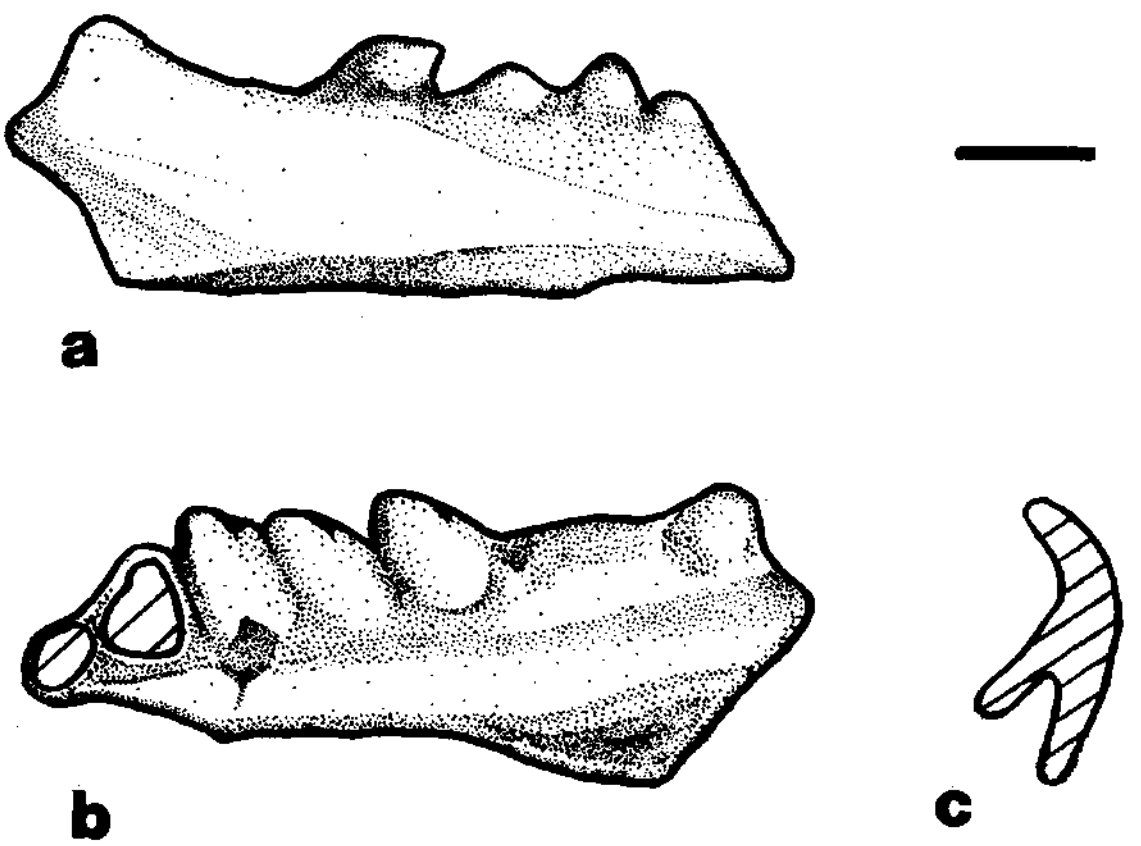

Fig. 7. Agamidae subfamily, gen. et sp. indet. 1. Anterior portion of dentary, ZIN PH 5/1. Scale bar: 1 mm. a – labial view, b – lingual view, c – cross section.

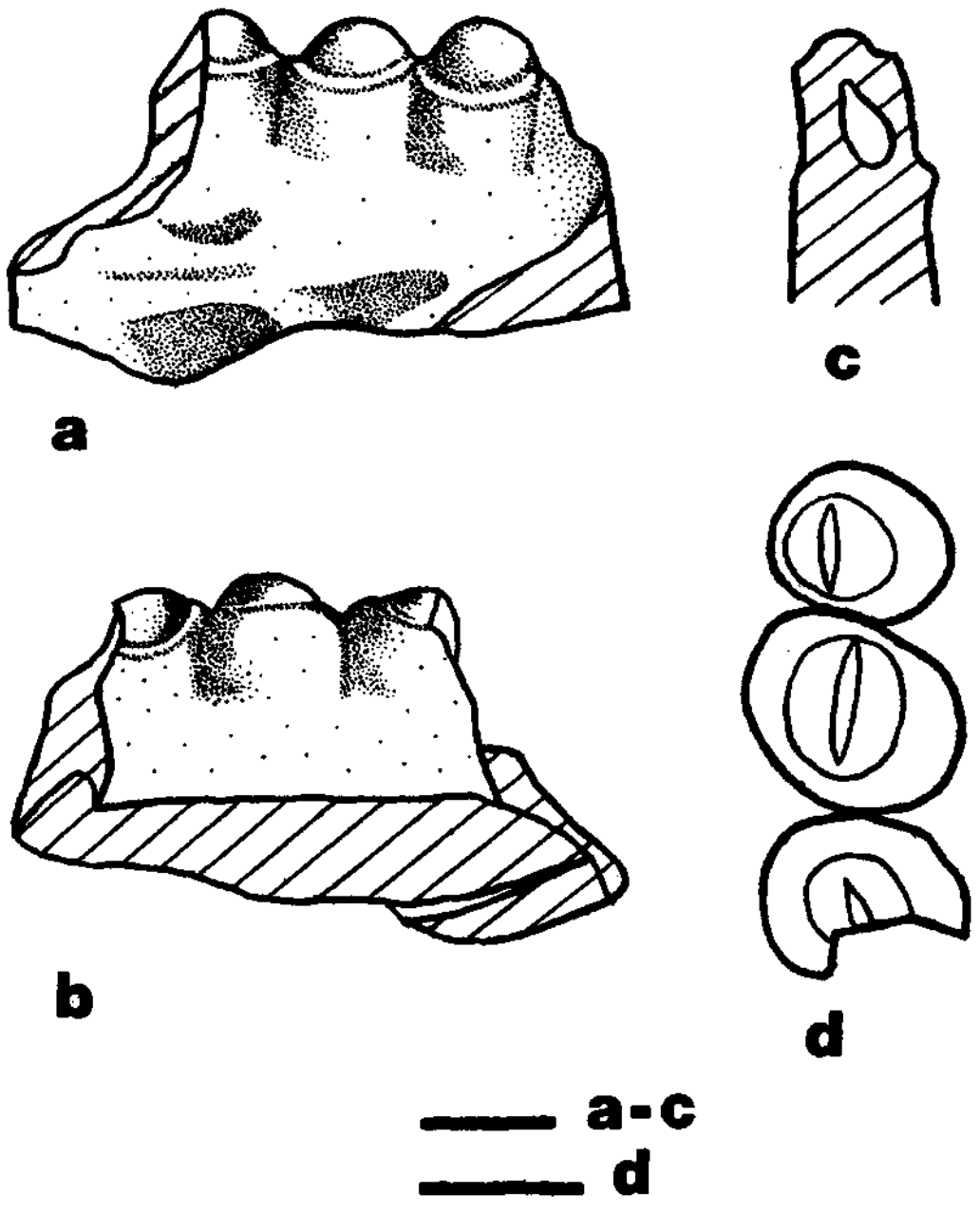

Fig. 8. Agamidae subfamily, gen. et sp. indet. 2. Maxilla(?) fragment, ZIN PH 7/1. Scale bar: 1 mm. a – lingual(?) view, b – labial(?) view, c – cross section, d – occlusal view of teeth.

Agamidae subfamily, gen. et sp. indet. 2

Material: One jaw fragment (ZIN PH 7/1). Andarak 2, Kyrgyzstan. Lower Alay beds, Early Eocene (Late Ypresien).

Description: ZIN PH 7/1 is a maxilla(?) fragment bearing two and a half teeth. The teeth differ greatly from those of the fragments described above by more rounded crowns, stretched transversely, and bearing a nearly complete cingulum (Fig. 8).

Discussion

By its coronoid process of the dentary elevating above the tooth row and by closely spaced teeth, "Uromastycinae gen. et sp. indet." resembles mostly the representatives of the Middle Eocene Asiatic genera *Pseudotinosaurus* Alifanov, 1991 and *Brevidensilacerta* Li, 1991, the Early Oligocene European genus *Palaeochamaeleo* De Stefano 1903 (generic status retained after Alifanov 1991) and the modern Asiatic and African

genus *Uromastyx* MERREM 1820 (all belonging to the Uromastycinae). Assignment of ZIN PH 1–4/1, 6/1 and 8/1 jaw fragments to the Uromastycinae is based on their resemblance to the modern genus *Uromastyx* in having a wide open Meckelian groove, a coronoid process elevating above the teeth, closely set teeth with blunt crowns, and the outline of the dentary.

Uromastycinae in the traditional context (including *Leiolepis*) has no apomorphic character states in the structure of the dentary. Moreover, the structure of the dentary and teeth is rather different in *Uromastyx* and *Leiolepis*. For the Uromastycinae, without *Leiolepis,* the coronoid process of the dentary and the closely set teeth with blunt crowns apparently are the apomorphic characters (ALIFANOV 1991). *Pseudotinosaurus* was based on *Tinosaurus asiaticus* GILMORE 1943 from the Middle Eocene (Lutetian, Irdinmanhan) Ulan Shirech Formation at Shara Murun area, Inner Mongolia. ALIFANOV (1991) referred to the type species new material from the Middle Eocene (basal Lutetian) Khaychin Svita at Khaychin Ula II locality (Mongolia) and described another species, *P. ascriptivus* from this and the contemporaneous locality Khaychin Ula III. Very close to, if not congeneric with *Pseudotinosaurus,* is *Brevidensilacerta xichuanensis* LI 1991 from the Middle Eocene (Lutetian) Hetaoyan Formation in Xichuan basin, Henan Province, China (LI 1991a). *Brevidensilacerta* differs from *Pseudotinosaurus* by the shape of the posterior teeth which have no pointed central cusp and are rounded. In the latter character, which is also characteristic for *Uromastyx* and *Palaeochamaeleo,* it resembles Uromastycinae gen. et sp. indet. described here. The Andarak uromastycine differs from *Pseudotinosaurus, Brevidensilacerta, Uromastyx,* and *Palaeochamaeleo* by the much lower anterior portion of the dentary and by lacking caniniform teeth on the dentary. At present, Uromastycinae gen. sp. indet. from Andarak cannot be assigned to any known genus of the subfamily. Apparently this is a new genus and species, the description of which is postponed until more complete material is found.

Agamidae gen. et sp. indet. 1 from Andarak resembles *Tinosaurus lushihensis* DONG 1965 from the Middle Eocene (Lutetian) Lushi Formation in Henan Province, China (DONG 1965) and *Tinosaurus* sp. cf. *T. lushihensis* from the contemporaneous Hetaoyan Formation (LI 1991a) by its size, by its tricuspid, anteriorly inclined anterior teeth, with distinct grooves that separate denticles from the main cusp, and by the lack of caniniform teeth, but differs from the Lushi specimens by lower tooth crowns. The generic attribution of the Chinese species merits additional investigation (ESTES 1983; ALIFANOV 1991).

Agamidae gen. et sp. indet. 2 differs from all known agamid lizards by possessing a cingulum on the teeth.

Both *Tinosaurus doumuensis* Hou 1974 and *Agama sinensis* Hou 1974 from the Upper Paleocene Doumu Formation in Qianshan Basin, Anhui Province, China (Hou 1974) apparently belong to the Agamidae, but their generic attribution requires confirmation.

Tinosaurus yuanquensis Li 1991 from the Middle Eocene (Bartonian, Sharamurunian) Hedi (=Heti) Formation in Yanqu basin, Shanxi Province, China (Li 1991b), having low dentary with Meckel's groove terminating at the anterior end of the bone, large caniniform anterior teeth and conical distantly spaced posterior teeth with outer wear facets on the bone between them, possibly belongs to the subfamily Agaminae s. str.

Undeterminate remains of agamid lizards were reported from the Middle Eocene (Lutetian, Irdinmanhan) locality Shinzhaly in eastern Kazakhstan (Zerova & Chkhikvadse 1984). It was assumed by these authors that agamids from this locality were arboreal lizards, like modern *Calotes*, because a number of mammals living in forest's and swamps were found there. In actuality the faunal list of the Shinzhaly locality (Russell & Zhai 1987; Emry et al. 1995, Tjutkova et al. 1995) does not contain any mammal whose habitat can be interpreted as arboreal. Moreover, a majority of them clearly indicate primarily open landscapes. Remains of a large agamid lizard (*Tinosaurus* sp.) were reported from the Middle Eocene (Lutetian) Sargamyss Svita in the Zayssan Depression (Chkhikvadze 1985).

The agamid jaw fragments described above are the first material of Early Eocene Agamidae in Asia and the oldest uromastycines in the fossil record, which confirm the wide distribution and variety of uromastycine agamids in the Paleogene of Asia. They document the abundance and diversity of this lizard group on an island in the Fergana Gulf of the Tethys, the area of Andarak 2 locality, which apparently is characterized by open landscapes with xerophytic vegetation in some places and warm and at least semiarid climatic conditions.

Acknowledgements

We thank Drs. Nikolai Udovichenko and Marc Godinot for assistance in the field, Dr. Natalia Ananjeva for reading the manuscript and providing useful comments, Dr. Jörg Erfurt for the Zusammenfassung translation and help with the manuscript preparation.

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Bei der Tübinger Schriftleitung eingegangen am 25. April 1996.

Anschrift der Verfasser:

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