Marsupials from the Late Cretaceous of Uzbekistan

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A fragment of dentary with m4, showing characters of some Late Cretaceous North American marsupials, is assigned to *Marsasia* sp. *Marsasia* Nessov, 1997 from the Coniacian of Uzbekistan, represented by *M. aenigma* known from edentulous dentaries with inflected angular processes, was attributed by Nessov to ?Marsupialia. *Marsasia* sp., found in the same horizon as the type species, resembles it in size and structure of the masseteric fossa, but differs in having a less steep coronoid process. We assign *Marsasia* to Marsupialia on the basis of the following characters: inflected angular process, shape of the dentary similar to that in *Asiatherium*, postcanine dental formula, inferred from alveoli for p1-3, m1-4, and structure of m4 more similar to Cretaceous marsupials than eutherians. The phylogenetic position of *Marsasia* may be between the Albian *Kokopellia* and Campanian *Asiatherium*. *Marsasia* is tentatively referred to the order Asiadelphia, which may represent an endemic Asian marsupial clade.

Key words: Asiadelphia, Cretaceous, *Marsasia*, Marsupialia, paleobiogeography, Uzbekistan.

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Introduction

It was generally accepted during the late 1970s and early 1980s that marsupials originated in North or South America and reached Europe during the Tertiary, but never reached Asia (Lillegraven 1969, 1974; Hoffstetter 1970; Cox 1974; Kielan-Jaworowska 1982). At that time, the oldest marsupials were known from the Late Cretaceous (Campanian) of North America, while the oldest uncontested placentals were from the ?early Campanian of Asia. New finds changed this view. Undoubted marsupials are now known from the Cenomanian (Cifelli & Eaton 1987), and probable marsupials from the Albian (Cifelli 1993; Cifelli & Muizon 1997) of North America, while

placentals are known from the ?late Aptian or ?early Albian of Asia (Kielan-Jaworowska & Dashzeveg 1989).

Marsupials have been also reported from the Tertiary of Asia. Gabunia *et al.* (1990, see also Emry *et al.* 1995) discovered didelphids (*Asiadelphis*) in the Oligocene of Kazakhstan, Ducrocq *et al.* (1992) reported didelphids (*Siamoperadectes*) from the Miocene of Thailand, and Qi *et al.* (1996) noted the presence of *Asiadelphis*-like opossum in the Middle Eocene of China. These finds obviously represent Tertiary invasions to the Asian continent, as *Asiadelphis* and *Siamoperadectes* have affinities with taxa known from the Tertiary of Europe and Australia, respectively.

Kielan-Jaworowska & Nessov (1990) suggested the sister-group relationships of Marsupialia and Deltatheroida (a predominantly Asian group with limited invasion to North America), both belonging to the clade Metatheria. Muizon (1994), who argued that the alisphenoid bulla, regarded by Kielan-Jaworowska & Nessov (1990) as a synapomorphy of Metatheria, made its appearance several times in the evolution of marsupials, has criticized this idea. Rougier *et al.* (1998), however, found in *Deltatheridium* stapedial system of marsupial pattern, marsupial tooth replacement, and an inflected angular process, a feature regarded as a marsupial synapomorphy (Sánchez-Villagra & Smith 1997). Rougier *et al.* (1998: p. 73A) concluded: 'A phylogenetic analysis of most Mesozoic tribosphenidans employing craniodental features shows deltatheroidans as a basal branch of Metatheria.'

It is relevant to the discussion on the site of marsupial origin and paleogeography to note the presence in the Late Cretaceous of Mongolia of the Asian marsupial order Asiadelphia, based on *Asiatherium reshetovi* from beds at Udan Sayr, correlative with the ?upper Campanian Barun Goyot Formation (Trofimov & Szalay 1994; Szalay & Trofimov 1996). The only other Asian Cretaceous therian assigned to Marsupialia (albeit with a question mark), is *Marsasia aenigma* from the Upper Cretaceous (Coniacian) Bissekty Formation in Uzbekistan, described in the posthumous monograph of L.A. Nessov (1997). The modest new material of *Marsasia*, described in this paper, casts some light on the relationships of Asian marsupials.

Abbreviation. — ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Description

Cohort Marsupialia Illiger, 1811
Order ?Asiadelphia Trofimov & Szalay, 1994
Asiadelphia *incertae sedis*
Marsasia Nessov, 1997

Marsasia Nessov, gen. nov.; Nessov 1997: p. 164.
Type species: *Marsasia aenigma* Nessov, 1997.
Species assigned: Type species and *Marsasia* sp.

Revised diagnosis. — Shares with *Asiatherium* the shape of the dentary, having the horizontal ramus of almost equal depth along the tooth row (subparallel alveolar and ventral borders), and similar shape of a large and very deep masseteric fossa (known also

in other groups, e.g., in zhelestids). Differs from *Asiatherium* in having the condylar process situated very low, only slightly above the level of the molars, and deeper masseteric fossa, probably the deepest among known Cretaceous marsupials. Shares with *Kokopellia*, *Asiatherium*, *Pariadens*, *Glasbius*, and several other Cretaceous marsupials relatively low cusps of the lower molars, and a small difference between the height of the trigonid and the talonid. Differs from *Asiatherium* in having the talonid (at least in m4) slightly longer than the trigonid, and shares this character with *Kokopellia*, as well as with some Cretaceous eutherians, such as zhelestids. Shares with *Kokopellia* and *Asiatherium*, and with many Cretaceous and Paleogene eutherians, the posterior (rather than lingual) position of the hypoconulid, and the entoconid and hypoconulid slightly approximated (but not strongly twinned as in Late Cretaceous marsupials). The characteristic feature of *Marsasia* is extremely small and low entoconid, probably the lowest among the known Cretaceous marsupials; it is also small in *Kokopellia*, while high in *Asiatherium*.

Marsasia aenigma Nessov, 1997

Figs 1, 2.

'Lower jaw of Theria'; Nessov 1985: p. 16, pl. 2: 5.

Marsasia aenigma Nessov, sp. nov.; Nessov 1997: p. 164, pl. 47: 1, 2.

Material. — ZIN C.82620 – holotype (Fig. 1), incomplete left dentary with alveoli for seven double-rooted postcanine teeth. Upper-middle part of the Bissekty Formation, locality CBI-51.

ZIN C.83130 – paratype (Fig. 2), right dentary fragment with alveoli of three last molars. Middle part of the Bissekty Formation, locality CBI-4b. Both specimens are from Dzharakuduk (referred to also sometimes as Dzhyrakuduk) in Uzbekistan, found by L.A. Nessov in 1989 and 1980 respectively. The age of the Bissekty Formation is Coniacian (Nessov 1997).

Diagnosis. — See part of the generic diagnosis concerning the dentary. The dentition is unknown.

Description. — The body of the dentary is of the same depth along the tooth row, without any constriction at the juncture with the ascending ramus. The condyle is situated low, only slightly above the level of the alveoli. The masseteric fossa is very large, extending posteriorly to the condyle; it is very deep, sharply limited by the coronoid and condyloid crests. The condyloid crest extends from the condyle anteroventrally and then anteriorly, parallel to the ventral border of the dentary. There are two mental foramina (one in *Asiatherium*); the anterior one is more pronounced, situated below the p1–p2 embrasure, whereas the less pronounced posterior one is situated below m1. The coronoid process has a very steep anterior border, and is relatively high (the uppermost part of the coronoid process is broken in both specimens; it may be seen on an earlier photo of the paratype ZIN 83130 in Nessov 1985: pl. 2: 5). The angular process (better preserved in the paratype) forms a thin, narrow plate, oriented at about 90° to the plane of the coronoid process, i.e. completely inflected medially. The mandibular foramen is relatively large, situated immediately above the angular process, at the midlength of the latter. The symphysis (Fig. 1A) extends posteriorly to below the alveolus for the supposed p2, and has a marked medial projection. As the anteriormost part of the dentary is unknown, the total length of the

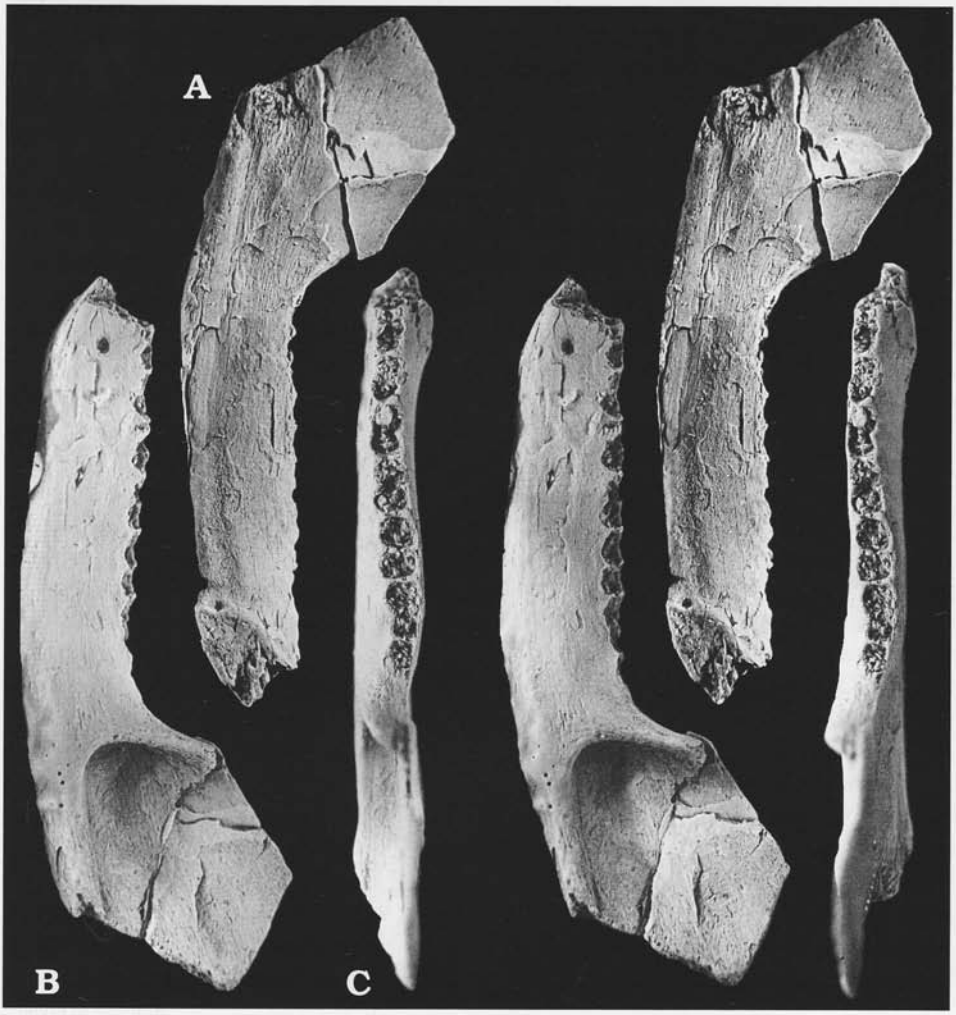

Fig. 1. *Marsasia aenigma* Nessov, 1997. ZIN C.82620 – holotype. Incomplete left dentary with alveoli for seven double-rooted postcanine teeth. Upper-middle part of the Bissekty Formation (Coniacian), locality CBI-51, Dzharakuduk, Uzbekistan. In medial (**A**), lateral (**B**), and dorsal (**C**) views. All stereo-photographs coated with ammonium chloride, × 8.

symphysis cannot be estimated. On the lingual side, parallel to the ventral margin of the dentary, there is a remnant of Meckel's groove, extending posteriorly above the angular process to the mandibular foramen (Figs 1A, 2B), best seen in the paratype, where it extends along the whole preserved length of the dentary. In the holotype the Meckel's groove disappears below the alveolus for ?m2. The groove is shallower than in *Kokopellia* (Cifelli & Muizon 1997).

In the holotype there are alveoli of six double-rooted teeth and anteriorly an alveolus for the posterior root of seventh tooth. The alveoli for the posteriormost molar are relatively small, with a larger posterior root. Alveoli for the next two more anterior molars (?m3 and

Fig. 2. *Marsasia aenigma* Nessov, 1997. ZIN C.83130 – paratype. Fragment of right dentary with alveoli for three last molars. Middle part of the Bissekty Formation (Coniacian), locality CBI-4b, Dzharakuduk, Uzbekistan. In lateral (**A**), medial (**B**), dorsal (**C**), and posterior (**D**) views. All stereo-photographs coated with ammonium chloride; **A**–**C** × 8, **D** × 15.

?m2) are larger and nearly equal in size, with the posterior root only slightly larger than the anterior one in both. The alveolus for the next more anterior molar is slightly smaller. Alveoli for two next more anterior teeth (?p3 and ?p2) are somewhat smaller and similar in size. Only the posterior portion of an alveolus for the anteriormost tooth is preserved.

Marsasia sp.

Figs 3, 4.

Material. — ZIN C.83131, left dentary fragment with presumed m4, from the upper-middle part of the Bissekty Formation, locality CBI-14 at Dzharakuduk, found by L.A. Nessov in 1990.

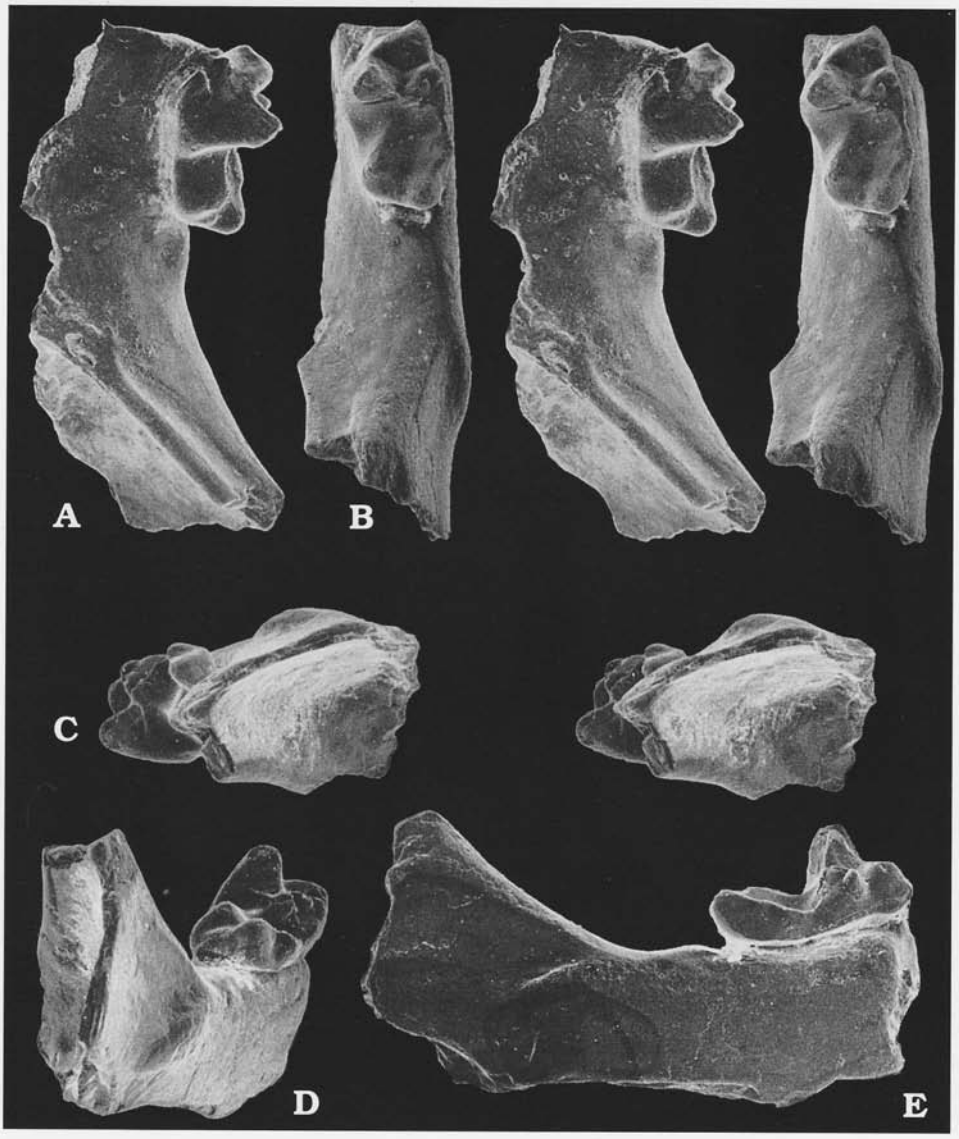

Fig. 3. *Marsasia* sp. ZIN C.83131, left dentary fragment with m4, from the upper-middle part of the Bissekty Formation, locality CBI-14 at Dzharakuduk, Uzbekistan. All SEM micrographs, in lateral (**A**), dorsal (**B**), posterior (**C**), oblique posterolateral (**D**), and medial (**E**) views, **A–C** stereo-pairs, all × 15, see also Fig. 4.

Description. —The m4 in ZIN C.83131 is 1.6 mm long. The trigonid is slightly shorter than the talonid, being 0.77 mm long, the talonid 0.83 mm long. The trigonid is slightly wider than the talonid being 0.9 mm wide, while the maximum width of the talonid is 0.83 mm. The tips of the protoconid and metaconid are broken; the paraconid is slightly worn. The metaconid and the paraconid are lower than the protoconid, in spite of the break of the tip of the latter. The paraconid is relatively large, its base is wider both

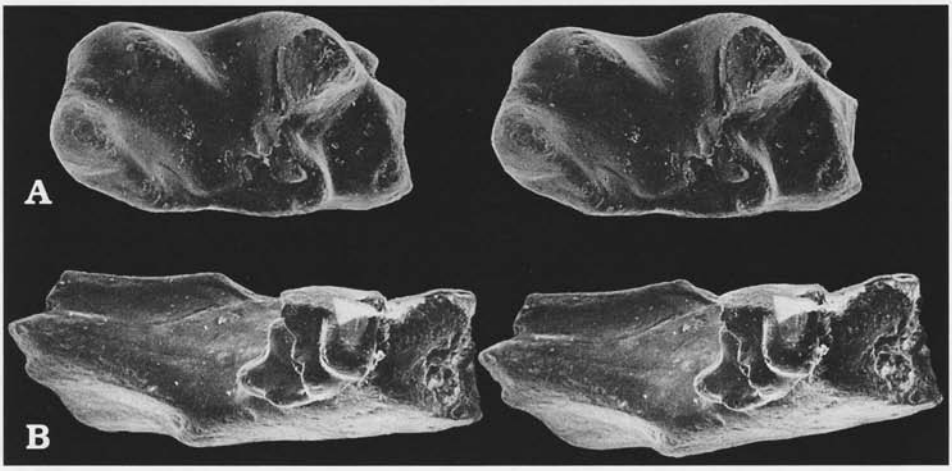

Fig. 4. *Marsasia* sp. ZIN C.83131. Upper-middle part of the Bissekty Formation, locality CBI-14 at Dzharakuduk, Uzbekistan. SEM stereo-micrographs. **A**. The m4, occlusal view, × 30. **B**. Antero-occlusal view of the dentary fragment with m4, × 15, see also Fig. 3.

lingually and transversely than the base of the metaconid. There is a short anterior cingulid below the paraconid. The talonid basin is relatively deep and well defined, although the talonid cusps are very low. The hypoconid is the largest of the talonid cusps. The hypoconulid is smaller, situated at the posterior border, and forms the posterior projection of the tooth but is asymmetrically arranged, being closer to the lingual than to the buccal margin. There is a deep, obliquely directed valley between the hypoconid and hypoconulid. The entoconid is the smallest of the talonid cusps. It is joined to the hypoconulid by a rounded ridge. The distance between the tips of the hypoconulid and entoconid is much shorter than between the hypoconid and hypoconulid, although hypoconulid and entoconid are not clearly twinned. The cristid obliqua contacts the trigonid at the notch between the protoconid and the metaconid.

Allocation to *Marsasia* and variation. — The three specimens assigned to *Marsasia* are of comparable size, the holotype of *M. aenigma* being the largest and ZIN C.83131 the smallest. The length of m4 is 1.6 mm in ZIN C.83131; the length of the alveoli for m4 is 2.0 mm in ZIN C.82620 (holotype), and 1.9 in ZIN C.83130. In ZIN C.83131 the anterior margin of the coronoid process forms a very prominent ridge, flanking a very deep masseteric fossa, as in *M. aenigma*. The coronoid process is less steep in ZIN C.83131 than in *M. aenigma*. In ZIN C.83131 the last molar is separated from the base of the coronoid process by a greater distance (slightly less than the tooth length) than in *M. aenigma*. In *M. aenigma* the alveolus for the posterior root of the last molar is placed closer to the base of the coronoid process. These differences may be within the range of the ontogenetic variation of one species. In younger specimens the last molar is usually situated very close to the coronoid process or sometimes even located on its horizontal slope, while in older specimens this tooth is well separated from the coronoid process because of the continuous growth of the dentary.

Marsasia sp. and the holotype of *M. aenigma* come from the same level within the Bissekty Formation, whereas ZIN C.83130 was found approximately 6 m below the level of CBI-14 and CBI-51, which yielded the two first specimens (Nessov 1997). It cannot be excluded that *Marsasia* sp. belongs to *M. aenigma*, but because of the incompleteness of the material we prefer to assign it to *Marsasia* sp.

Dental formula. — In archaic placentals (e.g., *Prokennalestes*, *Otlestes*) there is no sharp difference between the size of the alveoli for the molars and premolars and teeth are not crowded. In zhelestids, the dominant placental group in Dzharakuduk assemblage (Nessov *et al.* 1998), the p3 (the sixth tooth from the back) and its alveolus are considerably reduced. This is not the case in *Marsasia*, where the fifth and sixth teeth are of nearly equal size.

In aegialodontids and deltatheroidans the posterior root of the molars is smaller than the anterior one, because of the small size of the talonids. In *Marsasia* we observe a different situation. The size variation of teeth/roots along the tooth row is similar to that in *Kokopellia* (i.e. the ultimate tooth is small, the two penultimate teeth are larger and of the same size, the fourth tooth again is smaller, the two next teeth are of the same size and approximate also the size of the fourth tooth from behind, while the seventh tooth possibly was reduced). On the basis of these similarities we interpret the dental formula in *Marsasia* as p1-3, m1-4.

Allocation to Marsupialia

It has long been considered that in some Cretaceous placentals (e.g., *Kennalestes, Asioryctes, Barunlestes, Gypsonictops*, and others) the angular process is slightly inflected medially, resembling the condition in marsupials; this effaces the distinction between Placentalia and Marsupialia. Sánchez-Villagra & Smith (1997), however, demonstrated, that the structure of the angular process in marsupials is clearly distinct from that in Cretaceous placentals. We agree. In all Cretaceous placentals housed at the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, at the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, and at the Institute of Zoology of the National Academy of Sciences in Tashkent, the angular process is rod-like and projects ventrally (see e.g., the zhelestids figured by Nessov *et al.* 1998: fig. 17). Although in some forms the angular process is inflected not only downwards but also medially (e.g., in *Kennalestes*, figured by Kielan-Jaworowska 1969: pl. 23: 1c), it never forms a horizontal plate as in marsupials, and is always seen in buccal view of the dentary. *Marsasia*, in contrast to Cretaceous placentals, has a typical, plate-like, horizontal marsupial angular process. In contrast to *Asiatherium*, where the angular process is incomplete and has been reconstructed by Szalay & Trofimov (1996: fig. 3), the angular process in *Marsasia* is not visible from the buccal side. If the reconstruction of Szalay & Trofimov is correct, *Marsasia* would be more derived in this respect than *Asiatherium*. As the plate-like, horizontal angular process is a synapomorphy of Marsupialia (Sánchez-Villagra & Smith 1997), *Marsasia* may be regarded as a marsupial.

The postcanine dental formula of *Marsasia aenigma*, inferred from alveoli, is p1-3, m1-4. If true, *Marsasia* is a marsupial not only because of the structure of the angular

process, but also because of its premolar and molar counts. We thus assign *Marsasia* to Marsupialia.

Allocation within Marsupialia

Among the known Cretaceous metatherians, *Marsasia* most closely resembles the Late Cretaceous Asian *Asiatherium* and the Early Cretaceous North American *Kokopellia*. It shares with *Asiatherium* a nearly identical shape of the body of the dentary, with subparallel alveolar and ventral borders and a large, deep masseteric fossa. The shape of the dentary differs from *Kokopellia* (as well as from *Kielantherium*, *Deltatheridium*, *Alphadon*, *Pediomys*, *Pucadelphys*, and other marsupial genera), where the body is convex ventrally. It shares with *Asiatherium* and *Kokopellia* a steep coronoid process, although in *Marsasia* sp. it is slightly less steep than in the latter genera. It shares with *Kokopellia* the position of the medial projection of the symphysis, which in both forms starts beyond the supposed p2.

In the structure of m4, *Marsasia* differs from most Cretaceous marsupial genera in having less twinned hypoconulid and entoconid. It shares this character with *Asiatherium*, *Kokopellia*, and *Deltatheridium*, but differs from the latter in having a large talonid (very small in Deltatheroida, see e.g., Kielan-Jaworowska & Nessov 1990, and references therein). *Kielantherium* does not invite a comparison in this respect, as it has a very small talonid with only two cusps, the entoconid not being developed (Dashzeveg & Kielan-Jaworowska 1984). It should be mentioned, however, that the twinning of the hypoconulid and entoconid also occurs in some placental genera, e.g., in the 'Zhelestidae' (Nessov *et al.* 1998: figs 15, 16). The difference, however, is that while in most marsupials the twinned cusps tend to be arranged along the lingual border of the talonid, in placental mammals the hypoconulid is always situated posteriorly, and the line of the twinned cusps is arranged obliquely in respect to the longitudinal axis of the tooth. This condition is also characteristic of *Kokopellia*, *Asiatherium* and *Marsasia*. *Marsasia* resembles *Kokopellia* and *Asiatherium* in having low cusps and small difference between the height of the trigonid and talonid cusps (also characteristic of some other Cretaceous marsupials, such as *Pariadens* and *Glasbius*), and similar proportions between the cusps of the trigonid. It differs, however, from *Asiatherium* in having a longer talonid than the trigonid, and a very low entoconid, which is high in *Asiatherium*. The most characteristic feature of the *Marsasia* m4, the small and low entoconid, is shared with *Kokopellia*, as is the proportion between the trigonid and talonid lengths, and the arrangement of cusps on the talonid. *Marsasia* resembles *Asiatherium* structure of the dentary and shares some characters of the dental structure with it, but in details of m4 morphology (especially the talonid) it is more similar to *Kokopellia*.

Conclusions

On the basis of the above comparisons, we tentatively assign *Marsasia* to Asiadelphia and suggest that its phylogenetic place may lie between the Albian *Kokopellia* and

Campanian *Asiatherium*, a finding that is consistent with the ages of the three taxa. We disagree with McKenna & Bell (1997), who excluded Asiadelphia from Marsupialia, and we support Cifelli & Muizon's (1997) conclusion on the marsupial affinities of *Asiatherium*. *Marsasia* and *Asiatherium* increase our knowledge of the diversity of basal marsupials and suggest that some radiation of early marsupials took place in Asia.

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Сумчатые из позднего мела Узбекистана

АЛЕКСАНДР АВЕРЬЯНОВ и ЗОФИЯ КЕЛЯН-ЯВОРОВСКА

Резюме

Фрагмент зубной кости с m4, имеющим признаки некоторых позднемеловых Северо-Американских сумчатых, отнесен к *Marsasia* sp. *Marsasia* Nessov, 1997 из коньяка Узбекистана представления *M. aenigma*, которая известна по зубным костям без зубов с отогнутым медиально угловым отростком. Этот род был отнесен Несовым к ?Marsupialia. *Marsasia* sp., найденная в том же горизонте, что и типовый вид рода, напоминает последний по размерам и структуре массетерной ямы, но отличается менее круто поднимающимся венечным отростком. Мы относим *Marsasia* к Marsupialia на основании следующих признаков: отогнутый угловой отросток, форма зубной кости сходная с таковой у *Asiatherium*, зубная формула заклыковых зубов, восстановленная по альвеолам как p1–3 m1–4, и строение m4, более сходное с таковым меловых сумчатых, чем плацентарных. Филогенетическое положение *Marsasia* может быть между альбской *Kokopellia* и кампанским *Asiatherium*. *Marsasia* предварительно отнесена к отряду Asiadelphia, который может представлять эндемичную группуАзиатских сумчатых.