A SURVEY OF CRETACEOUS TRIBOSPHENIC MAMMALS FROM MIDDLE ASIA (UZBEKISTAN, KAZAKHSTAN AND TAJIKISTAN), OF THEIR GEOLOGICAL SETTING, AGE AND FAUNAL ENVIRONMENT

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ABSTRACT

This paper is an English concentrate of various Russian publications by the senior author presenting the mammalian taxa from the Cretaceous (Albian through Santonian) of the region termed Middle Asia by Soviet geographers. The diagnoses are the unmodified, literal translation of the original version, but are followed with short complementary remarks; most of the species are illustrated anew with SEM photographs, others are by normal photography. The fossiliferous formations are cited and arguments for their dating are given. Finally, the main vertebrate groups accompanying mammals are listed and the environment and climate at the time of deposition are suggested. In conclusion, an hypothesis on the origin and high diversity of tribosphenic mammals on the Cretaceous coastal plains of southwest Asia is proposed. In appendix the taxon *Khuduklestes bohlini* nov. gen. nov. sp. is formally defined.

RESUME

Cet article constitue un résumé, en langue anglaise, de plusieurs travaux publiés en russe par le premier auteur, concernant les taxons mammaliens du Crétacé (Albien à Santonien) d'Asie occidentale. Les diagnoses reproduites ici représentent la traduction littérale de la version originale, mais elles sont suivies de courtes remarques complémentaires. La plupart des taxons sont illustrés par de nouvelles photographies effectuées au MEB, les autres par des photos classiques. Un chapitre fournit les arguments qui ont permis la datation des formations fossilifères; le suivant détaille les assemblages fauniques qui accompagnent les mammifères dans ces formations, d'où sont déduites des considérations sur l'environnement et le climat au moment du dépôt. En conclusion est présentée une hypothèse sur l'origine et la diversité des mammifères tribosphéniques dans les plaines côtières crétacées de l'Asie du sud-ouest. En appendice le taxon *Khuduklestes bohlini* nov.gen. nov. sp. reçoit une diagnose formelle.

INTRODUCTION

For decades, Asiatic Cretaceous mammals —spectacular as they are— were essentially limited to the upper Cretaceous (late Santonian? or early Campanian) of Mongolia (Kielan-Jaworowska 1984 and references therein). Then 20 years ago came to light, also in Mongolia, the now famous locality of Khovbur, of late Aptian age (Kielan-Jaworowska & Nessov 1990). The new genera of mammals yielded by Khovbur (Dashzeveg 1975 and 1979, Trofimov 1978 and 1980) include the oldest placental known, *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989). Finally, tribosphenic mammal remains, including skull materials, were found by members of the American Museum Natural History expeditions to Mongolia in 1991, 1992 (Clark 1992).

From China, only scarce material is published: part of a lower jaw with M_1–M_3 was found in the coal-bearing bed of the "Hsinchiu" or in the Hsinch'iuyao (Xinqiuyao) coal mine near the city of Fuhsin, Lianing Province and published as *Endotherium niinomii* by Shikama (1947). A series of data contributes to the resolution of the dating problem concerning this taxon: the advanced morphology of the dentition (Lillegraven *et al.* 1979); the relation of the specimen to coal deposits and the presence of similar deposits in the Cretaceous of the Transbaikal region, both corresponding to an increase in humidity; the presence, in the two areas, of lycopterid fish (Shikama 1947, p. 76; Nessov & Starkov 1992); better knowledge of the climato-stratigraphic time scale of Asia; and finally the known time of the establishment of the Asian basins in which black shales were formed. From all these considerations it can be suggested that the age of *Endotherium* should most probably be situated between latest Barremian-Late Aptian.

Moreover, the fused first and second cervical vertebrae of a relatively large mammal were discovered near the Tsondolein Khuduk locality in Gansu Province (Bohlin 1953, fig. 20). A cast of this fossil was examined by LAN in the Paleontological Institute of Uppsala and mentioned in Nessov 1982 as *Khuduklestes bohlini* and in 1987 as "*Khuduklestes*", but not redescribed (see appendix p. 84). The composition of the fossil assemblage, which includes very primitive protoceratopsid dinosaurs (Nessov *et al.* 1989 and references therein), allows a Cenomanian age to be proposed.

Finally, an undetermined partial lower jaw with broken teeth from the District of Klamelia of the Xinjiang Uygur Autonomous Region of the People's Republic of China has been described (Chow & Rich 1984); the age of the Tukoura Group is most probably early Cretaceous.

It should also be mentioned that abundant unpublished material (20 to 30 mammalian skulls) has been collected by the Sino-Canadian expeditions of the 1990s from Bayan Manduhu (a Barun Goyot equivalent) and is under study by Dr. Qiu Zhanxiang (pers.com. D.A. Russell 1992).

From Middle Asia, in Kazakhstan, only one specimen was known before 1978, a partial lower jaw with three broken teeth and a few more alveoli (Bazhanov 1972). This mammal, called *Beleutinus* by Bazhanov 1972, poorly preserved as it is, was nevertheless the incentive for the senior author —who had previously discovered sites containing assemblages of lower vertebrates similar to those of the Late Cretaceous of North America which also contained mammals— to launch himself on a search for Cretaceous mammals in the then Soviet Union; this led him, through more than 10 years of prospecting, to the discovery of a series of new mammals ranging from Albian through Santonian (9 different levels), thus filling the gap between those of the early Cretaceous and the oldest of the Late Cretaceous mammalian sites of Mongolia (Nessov & Kielan-Jaworowska 1991). The filling of this hiatus in the mammalian record is important, since the time of divergence of many eutherian groups is presumed to have taken place in the first half of the Late Cretaceous (Lillegraven *et al.* 1979).

These finds have been the subject of several short publications, mostly in Russian journals, the accessibility and readibility of which are not easy for occidental workers. So, during a common stay in the Mesozoic niche that Professor Kielan-Jaworowska has founded in Oslo, the present authors united their efforts to offer a synthesis of these data in English, accompanied by mostly new illustrations, in order to make them more exploitable for comparisons and to enter them conspicuously in the constantly reshaping image of the mammalian world of the Cretaceous.

Three points should be stressed before going any further:

1) The diagnoses given here between brackets represent the scrupulous translation of the Russian version (translation by LAN, except where mentioned otherwise),

without any effort to emend them, even though the authors recognize the necessity of such an enterprise for several cases at least; only some of the envisaged changes are mentioned in the remarks following the diagnoses. In the case of *Khuduklestes*, the first formal diagnosis is proposed.

2) The new illustrations presented here have been taken from the casts of the originals made by one of us in Oslo (DER) (photos URA 12 CNRS, except where mentioned otherwise).

3) This work does not include the "archaic ungulates", some of which figured in Nessov & Kielan-Jaworowska (1991, fig. 1); these mammals are the subject of a study in preparation by these two authors.

Unless indicated differently, all the Cretaceous mammals treated here are stored in the Chernyshev Central Museum of Geological Exploration (CCMGE) of Saint Petersburg, Russia.

MIDDLE ASIAN MAMMALIAN TAXA CREATED BEFORE THE END OF 1992

(in chronological order of description)

N.B. Middle Asia and Central Asia are two distinct geographic regions recognized by Soviet geographers. Middle Asia embraces the Republics of Turkmenistan, Uzbekistan, Kazakhstan, Tajikistan and Kyrgystan, which are in fact situated in the south-western part of Asia, while Central Asia refers to Mongolia and the northern part of China.

BELEUTINUS BAZHANOV 1972

Type species: *B. orlovi* BAZHANOV 1972 (and not 1971 as in 1972, p. 76). See also Nessov 1987, p. 200 and pl. 1, fig. 10.

Material: Holotype (Pl. 1, fig. 1): posterior part of right dentary (as mentioned in Lillegraven *et al.* 1979, and not anterior part of left dentary as written in the original publication) with posterior roots of M_1–M_2 and both roots of M_3, and two alveoli of two teeth immediately anterior. Specimen is housed in the Institute of Zoology, Academy of Sciences of Kazakhstan, Alma-Ata.

Locality: Baybolat Well area (Fig. 2, **8**, p. 72), on the slope of the margin of the plateau near Zhalmauz Well, western part of the Dzhalagash Region, Kzyl-Orda District, Kazakhstan.

Formation: Bostobe Formation, possibly lower part of the formation (and not Beleuty Formation, as mentioned in the original publication: this unit has not been recognized in the area).

Age: Santonian-lower Campanian (most probably, lower Santonian: Nessov & Khisarova 1988), and not Coniacian as noted in Bazhanov 1972.

Attribution: Theria, infraclass, order and family unknown in Bazhanov 1972; Eutheria, Mixotheridia in Nessov 1987 (for the diagnosis of this suborder, created in Nessov 1985a, see p. 61), possibly Zalambdalestidae "... as has small angle between the anterior margin of coronoid process; roots of teeth not wide; M_3 situated relatively far from the anterior margin of the masseteric fossa. In connection with this, only very provisionally it is possible to refer this mammal to Zalambdalestidae" (in comparison with forms described in Kielan-Jaworowska 1975a).

Diagnosis: see Remarks.

Remarks. As the type and only specimen was misinterpreted and inverted anteroposteriorly and left and right, only a few features of the original description remain valid: jaw "with somewhat sharpened ridge on the top", which means that a ridge crosses the area situated between the coronoid process and the tooth row; "the enamel covering of the masticatory surfaces strongly worn because of old age of specimen; the result is that, at the base of the crowns is visible the cross section of the pulp cavity... roots of teeth relatively long in relation to the height of the jaw and somewhat raised above the alveoli"; "the animal was somewhat larger than a water shrew" (*Neomys*).

The attribution, proposed in Nessov 1987, to the Zalambdalestidae (as well as to mixotheridians) can be reinforced by some additional information on the shape and lingual position of the bony ridge just behind the tooth row. No feature of this fossil justifies its attribution to "mammals of metatherian-eutherian grade " as in Lillegraven *et al.* 1979 (it should be stressed here that this expression constitutes a contradiction in itself, since the mammals for which this group was erected (Patterson 1956) are precisely of a grade below that reached either by eutherians or metatherians). But given its poor state of preservation, the main interest of the specimen is historical.

N.B. A small cervical centrum was recognized in 1982 in the microvertebrate material from the area close to the Zhalmauz Well (Nessov & Khisarova 1988, fig. 7), the type area of *Beleutinus*, and at a level possibly corresponding to that where, in the Bostobe Formation, was found the holotype of *Beleutinus orlovi*.

DAULESTES TROFIMOV & NESSOV 1979 *in* Nessov & Trofimov 1979

Type species: *D. kulbeckensis* TROFIMOV & NESSOV 1979, fig. 1. See also Nessov 1981, fig. 10 (18) and Nessov 1982, pl. 1, fig. 6.

Material: Holotype (Pl. 1, fig. 2): part of right half of the mandible, with M_1 and canine, 3 last (broken) premolars, two alveoli behind canine; CCMGE 1/11758.

Locality: Dzhyrakuduk (Fig. 2, 6, p. 72), NNW of Kulbecke Spring, central Kyzylkum Desert, Uzbekistan.

Formation: lower part of the Bissekty Formation (unit previously known as Taykarshi Beds), site CDZH-17a.

Age: Late Turonian.

Attribution: Eutheria, Zalambdalestidae *in* Nessov & Trofimov 1979 but Palaeoryctidae *in* Nessov 1982 and 1987.

Diagnosis: [The dimensions are small (the size of a small shrew). The mandible is blunt, gently ascending from C to the P_4 and slightly concave in the region of the M_1. The for. mentale is situated under P_4. The canine is small. The premolars have two roots. There are small diastems between C and P_1, P_1 and P_2, P_2 and P_3. The P_4 is molarized very weakly, and is significantly smaller than the M_1. The protoconid of the M_1 is hefty, high and pointed, with the apex slightly bent posteriorly. The metaconid is larger than the paraconid. The talonid, narrower than the trigonid, is low. The hypoconid is significantly larger than the hypoconulid and the entoconid. The crista obliqua is well expressed, while the cingulum is not.] (Translation G.V. Shkurkin; see reference for Nessov & Trofimov 1979).

Remarks. The alveolus immediately following the canine was not figured in the original drawing of the specimen. Now several hypotheses can be proposed: either *Daulestes* had 5 premolars, the three anterior teeth having only one root; or there were only 4 premolars; or the "canine" was in fact a P_1; finally the respective sizes of the last two premolars might suggest that the antepenultimate could be a milk-tooth...

The absence of zalambdalestid specializations in this specimen motivated its inclusion in palaeoryctids, these forms representing eutherians of a more primitive grade.

CRETASOREX NESSOV & GUREYEV 1981

Type species: *C. arkhangelskyi* NESSOV & GUREYEV 1981, fig. 1; also Nessov 1981, fig. XI (30), Nessov 1982, pl. 2, fig. 6; Nessov 1985b, pl. 2, fig. 4.

Material: Holotype (Pl. 1, fig. 3): posterior part of the left mandible with the articular area and part of last alveolus; CCMGE 2/11758.

Locality: site CBI-4, Dzhyrakuduk (north of Kulbecke Spring), central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation (originally "unformally a unit of Taykarshi Beds").

Age: Coniacian (originally attributed to "Late Turonian-Santonian").

Attribution: Eutheria, Lipotyphla, Soricidae.

Diagnosis: [The posterior part of the mandible is massive. The exterior side of the apex of the coronoid process is smooth, having no bump or hollow, the anterior margin of its base is moved back from the M_3 farther than in contemporary and in known fossil genera. The fossa between the superior and inferior facets on the posterior side of the articular process of the mandible is weakly expressed. The superior facet is well developed in a vertical direction]. Translation G.V. Shkurkin 1981.

Remarks. The mineralized specimen was found by LAN embedded in a locally soft spot (about 3 cm in diameter) in an otherwise relatively dense, yellowish, crossbedded sandstone consisting of small to middle sized grains and containing Cretaceous mammals of the level 6b (see p. 78). Two interpretations are possible: either the fossil is contemporaneous with the formation; the subhorizontal disposition of the layers of the formation (dipping 2-4° NW, N and NE) and the position of the jaw tens of meters below the base of the marine Paleocene would support a Coniacian age; or this inclusion is a contaminant, filling a fossil or subfossil hole of the hard sandstone. Any age between late Cretaceous and late Cenozoic is excluded: indeed no fossorial mammal could have dug through the whole thickness of the upper part of Late Cretaceous and Tertiary deposits; it is true that these deposits are now greatly cut by ravines (on the edge of which is the fossiliferous hole) but the rate of eolian erosion, approximately 10-12mm per year for a soft sandstone, testifies to the youth of such ravines. If the contaminant hypothesis is retained, the age of the specimen can only be late Cenozoic, but probably not Recent: the shape of the jaw does not correspond to that of the Recent Soricidae, such as *Sorex* and *Diplomesodon* which live now in the Kyzylkum, and the coloration of the specimen indicates that it must be a fossil form at least from the latest Cenozoic.

TASLESTES NESSOV 1982

Type species: *T. inobservabilis* NESSOV 1982, pl. 1, fig. 4; also Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 1, fig. 4): poorly preserved right mandibular fragment with M_2 (protoconid broken) and alveoli of M_1 and M_3; CCMGE 8/11758.

Locality: site CDZH-17b, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: lower part of the Bissekty Formation (formerly Taykarshi Beds).

Age: late Turonian.

Attribution: Eutheria, Proteutheria, Palaeoryctidae(?) (Nessov 1982), but Zhelestidae according to LAN, this paper.

Diagnosis: [rather small size (that of the European mole). Lower jaw high (twice as high as wide between M_1 and M_2), internal side not flattened at that level. Very deep masseteric fossa, sharply delimited anteriorly. Talonid of M_2 low, narrower than trigonid. Metaconid relatively weakly protruding lingually. Paraconid small. Hypoconid weakly protruding labially. Hypoconulid and entoconid of this tooth somewhat protruding backwards, very small (much smaller than hypoconid), entoconid the smallest].

Remarks. The important fact is the moderately lingual situation of the hypoconulid; also the short paraconid appressed to the metaconid suggests that *Taslestes* could be a mixotheridian. This badly preserved specimen might not deserve a generic distinction were it found now and not in 1979. However it is the only described mixotheridian of this size in Asia.

OXLESTES NESSOV 1982

Type species: *O. grandis* NESSOV 1982, pl. 1, fig. 1; also Nessov 1981, fig. 9 (23), and Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 1, fig. 5): vertebral body of C1 and C2 (as in original determination and not C2 and C3 as in Nessov & Kielan-Jaworowska 1991); CCMGE 6/11758; possibly also large parietal bone (Pl. 7, fig. 1) (also in Nessov 1985a, pl. 2, fig. 1) and perhaps large fragment of a large canine (mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1).

Locality: site SSHD-8a, Sheikhdzheili (Fig. 2, 3, p. 72), southwestern part of the Kyzylkum Desert, Karakalpakian Autonomous Republic, Uzbekistan.

Formation: upper part of the Khodzhakul Formation.

Age: lower Cenomanian.

Attribution: originally as Eutheria, Palaeoryctidae (?); but LAN thinks it might be also a large deltatheroid, one of the largest mammals with *Khuduklestes bohlini* nov. gen. nov. sp. (see Appendix p. 84) among known forms of the Mesozoic of the CIS and Asia.

Diagnosis: [Among larger mammals known until now for the beginning of the Late Cretaceous. Epistropheus relatively narrow, with long, somewhat sharpened anteriorly, well individualized tooth-like process. The length of the anterior part of the epistropheus, which is the homolog of the centrum of the atlas, is more than half the length of the vertebra. Anterior paired articular surfaces elongated horizontally and somewhat narrowing anteriorly. Unpaired articular surfaces on the ventral side of the odontoid process slightly widening posteriorly. Ventral median crest is interrupted in front of the line of the transversal suture of the epistropheus; the part of this crest situated on the centrum of the atlas has its spine oriented backwards and downwards. On the ventral side of the epistropheus, the lateral ridges are situated not far from the median line of the vertebra and are separated from the lower margin of paired articulated surfaces by a relatively large space. The upper margin of the somewhat concave posterior articulating surface of the vertebra is almost horizontal. Two large, symmetrically situated openings for blood vessels are disposed dorsally, approximately in the middle of the length of the centrum of the epistropheus; those of the atlas centrum are smaller.]

Remarks. The parietal bone with a strong sagittal crest, and the large canine are of a size compatible with the type vertebrae of *Oxlestes* and therefore are provisionally referred to this taxon. If this association is correct, *Oxlestes* could well be a deltatheroid, or a palaeoryctid predator.

The very small primitive protoceratopsid dinosaur *Asiaceratops* NESSOV *et al.* 1989 (of which the largest known thoracic centrum, among more than 100 specimens belonging to different individuals, is only 16 mm) was part of the living assemblage that included *Oxlestes* at the beginning of the Late Cretaceous. Young specimens of *Asiaceratops* could very well have been preyed upon by an adult *Oxlestes*, which had the size of a young badger. The evolution of large carnivorous mammals could have begun in the earlier Cenomanian of western Asia and the supposed descendants of *Oxlestes* would have coevolved with their prey, the plant-eating dinosaurs of the beginning of the Late Cretaceous. This hypothesis is sustained by the association in China of the axis of another quite large mammal, *Khuduklestes,* with the relatively small protoceratopsid, *Microceratops.*

SAILESTES NESSOV 1982

Type species: *S. quadrans* NESSOV 1982, pl. 2, fig. 8; also Nessov 1981, fig. XI (29) and Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 1, fig. 6): isolated upper M^1 or M^2; CCMGE 7/11758.

Locality: site CBI-4a, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: originally as Eutheria Kennalestidae, but now suspected (LAN) to belong to the peculiar group of kennalestids with two weak cingula and a strong C cusp on the ectoflexus (in *Kennalestes*, an incipient C cusp only on M^2).

Diagnosis: [Upper molars subtriangular and only moderately widened transversally. M^1 with relatively low proto-, meta- and paracones; the latter is the most pronounced. Protocone connected by crests to small paraconule and well developed metaconule. Parastyle and metastyle present. Hypocone incipient.]

Remarks. It may be of interest to note a certain resemblance between M^1/M^2 of *Sailestes* and the M^1 of the European Late Paleocene *Bustylus* GHEERBRANT & RUSSELL 1991, in the general shape, the position of the conules, the slightly proclined protocone and especially in the development of a C cusp, which is unusual for an adapisoriculid; but the stylar shelf, narrow in *Sailestes*, remains wider in the more recent *Bustylus*.

KUMSUPERUS NESSOV 1984

Type species: *K. avus* NESSOV 1984, figs. e, j and z; also Nessov 1982, pl. 2, fig. 2 ("remnant of advanced eutherian"); and Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 2, fig. 1): partial left mandible with very worn M_1–M_3; CCMGE 13/11758.

Locality: site CBI-4, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan. Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: originally as Eutheria incertae sedis, with some characters shared with primitive primates and condylarths; now considered (Nessov & Kielan-Jaworowska in preparation) as a mioclaenid condylarth.

Diagnosis: [Lower molars close to one another. M_3 approximately as long as M_2, with small trigonid, talonid narrowing strongly backwards. Paraconid of $M_{2\text{-}3}$ strongly reduced, considerably displaced towards the lingual side and towards the metaconid. Protoconid and metaconid of $M_{2\text{-}3}$ situated on a line approximately perpendicular to the longitudinal axis of the jaw. Entocingulid weakly developed. Long diastema between M_3 and the steep anterior border of the coronoid process; at that level jaw not high; however height increases considerably towards M_1.]

Remarks. The extreme wear of the teeth could be attributed partly to old age and partly to the hardness of food (plants?).

KUMLESTES NESSOV 1985a

Type species: *K. olzha* NESSOV 1985a, pl. 2, fig. 15; also Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 2, fig. 2): part of left lower jaw with ?dP_{3-4} or M_{1-2}; CCMGE 1/12176.

Locality: site CBI-4, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: Tribotheria *incertae sedis* in Nessov 1985a; Eutheria? this paper.

Diagnosis: [Talonid of the preserved teeth narrow, hypoconid very high, sharp, much higher than hypoconulid, which is displaced strongly backwards; hypoconulid is approximately twice as high as the entoconid, which differs from *Kermackia* SLAUGHTER. Crista obliqua pronounced, high and thick. Hypoflexid not wide.]

Remarks. The trigonid of M_2 was originally partly preserved and showed pronounced ridges on the paracristid and protocristid. Cristae of the tooth form a "W". Entoconid somewhat abraded but probably low; large hypoconid; talonid basin deeper, hence more derived, than in *Prokennalestes*: this leads to a doubt concerning the tribotherian status of the genus.

BOBOLESTES NESSOV 1985a

Type species: *B. zenge* NESSOV 1985a, pl. 1, fig. 1; also Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 2, fig. 3): fragment of right maxillary with M^2–M^3; CCMGE 2/12176.

Locality: site SKH-20, Khodzhakul (Fig. 2, **1**, p. 72), southwestern Kyzylkum Desert, Karakalpakian Autonomous Republic, Uzbekistan.

Formation: lower or middle part of the Khodzhakul Formation.

Age: latest Albian (Vrakonian).

Attribution: originally as Theria, Pappotheriidae suborder incert., but the strong winged conules are more advanced than in pappotheriids; Nessov (1989) then referred it to the proteutherian subfamily Bobolestinae, which became Bobolestidae in Nessov 1992a.

Diagnosis: (also valid for the family created in 1992a, as the family is monotypic) [Paracone of M^{2-3} notably larger than metacone; both cusps situated slightly labial to the middle of the distance between protocone and ectoflexus, and separated by a deep furrow situated between postparaconule and premetaconule cristae. Postparacrista and premetacrista considerably reduced. Stylocone and cusp B1 weak. Parastyle on M^2–M^3 moderately developed, considerably shifted forward. Behind parastyle is a deep and narrow transversal groove. Preparaconule crista long, and extended labially beyond the paracone. Protocone not large, preprotocrista and postprotocrista disposed relatively widely far apart. Paraconule and metaconule well developed. Hypocone absent.]

Suborder MIXOTHERIDIA NESSOV 1985a

Diagnosis: [Lower molars with somewhat approximated entoconid and "hypoconulid", as quite clearly opposed to the hypoconid. The latter usually somewhat displaced in front of entoconid. Paraconid not large, displaced lingually, situated not far from metaconid; in relation with this, the angle between the trigonid cristae is not wide. Upper molars with stylar shelf not wide, with or without incipient hypocone.]

Remarks. The quotation marks surrounding "hypoconulid" refer to the idea of LAN (1985a, 1987) that the homology of the talonid cusps of this taxon may be questioned; but the present authors now further question this homology within therian mammals, as at least 4 cusps can be found on the talonid of some primitive therians of the Cretaceous of North America (*Potamotelses* FOX 1972; one Trinity mammal, Slaughter 1965, fig. 2, for example).

Originally included in the Mixotheridia were *Gallolestes* LILLEGRAVEN 1976 (Campanian, Mexico), *Sorlestes, Taslestes* and *Aspanlestes,* all genera grouped in an unnamed family. In the same paper as the Mixotheridia (Nessov 1985a) was created the genus *Zhelestes* on an upper jaw, and the subfamily Zhelestinae (Zhelestidae NESSOV 1990). Many years of work at the locality produced, among other mammalian remains, lower teeth of mixotheridian morphology and upper teeth of zhelestine morphology; this led to the conclusion that the latter represent the upper mixotheridian dentition.

Now together with the Zhelestidae (which also includes some genera in press, see Table 3 with the stratigraphic position of published and unpublished genera), the Zalambdalestidae and possibly Tupaiidae (Averianov & Nessov in press) are also considered as Mixotheridia. Finally, this suborder may have to be elevated to an ordinal rank (Nessov 1989) as an ancestral group for the Order Scandentia WAGNER 1855 *sensu* McKenna 1975, or as a junior synonym of the Scandentia, if tupaiids are indeed a member of this group. In fact, the possibility that the "preungulates" were the source for tupaiids as well as for condylarths may be worthy of investigation.

N.B. The upper tooth that was attributed to *Aspanlestes* may in fact not belong to the Zhelestidae (see p. 62).

SORLESTES NESSOV 1985a

Type species: *S. budan* NESSOV 1985a, pl. 2, fig. 13; also Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 1, fig. 7): right mandibular fragment with M_2 and alveolus of

M_3; CCMGE 3/12176; material attributed to the genus, see remarks for *?Zalambdalestes mynbulakensis*.

Locality: main level of site CBI-14, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: Eutheria, Mixotheridia.

Diagnosis: [paraconid not very strongly appressed to metaconid; entoconid and hypoconulid strongly appressed one against the other, and large (in comparison with this condition in *Taslestes*). Precingulid has the shape of a relatively strong ridge.]

Remarks. The features displayed by this specimen are typical of the branch of mixotheridians with pre-condylarth affinities.

ASPANLESTES NESSOV 1985a

Type species: *A. aptap* NESSOV 1985a, pl. 2, figs. 10 and 11; also mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype of *A. aptap* (Pl. 4, fig. 1): right mandibular fragment with P_3–P_4 (or P_4–P_5), and M_1–M_2; CCMGE 4/12176; *Aspanlestes* sp. cf. *A. aptap*: part of left mandible with half M_2 and M_3, CCMGE 20/12176, Nessov 1985a, pl. 2, fig. 7; and upper molar (M^1 or M^2), CCMGE 23/12176, Nessov 1985a, pl. 2, fig. 10, initially considered as belonging to the type genus and species.

Locality: type and upper molar: site CDZH-17a, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan; for *Aspanlestes* sp. cf. *A. aptap*, the site is CBI-4.

Formation: type and upper molar: lower part of the Bissekty Formation; for *A.* sp. cf. *A. aptap*, middle part of the Bissekty Formation.

Age: late Turonian for holotype and upper molar; Coniacian for *Aspanlestes* sp. cf. *A. aptap*.

Attribution. Eutheria, Mixotheridia.

Diagnosis: [Paraconid strongly appressed to metaconid, protoconid short anteroposteriorly. Cusps sharper than in *Gallolestes*; precingulid in the shape of a relatively strong ridge; protocristid oriented almost strictly transversally.]

Remarks. Now that the fauna becomes better known, it can be questioned whether the upper molar is congeneric with the type of *Aspanlestes aptap*, or even belongs to the Mixotheridia. Also, the latter shares strong similarities with the type of *Sorlestes*; but differences between the two M_2s concern the shape of the protoconid, the protocingulid, stronger in *Sorlestes* and the general size (approximately 2/3 in *Sorlestes);* this, added to the difference in time (estimated at about 700,000 years if one accepts that all the late Turonian and all the Coniacian are represented in the Bissekty Formation and that the rate of sedimentation was relatively stable), allows the two taxa (*Sorlestes* and *Aspanlestes*) to be maintained.

OTLESTES NESSOV 1985a

Type species: *O. meiman* NESSOV 1985a, pl. 1, figs. 4, 12 and 13.

Material: Holotype (Pl. 3): left mandible with P_4–M_3; CCMGE 7/12176. Left mandibular fragment with P_5 and talonid of M_3, CCMGE 9/12176; left maxilla with M^{1-2}, Nessov & Kielan-Jaworowska 1991, fig. 1.

Locality: site SSHD-8, Sheikhdzheili, southwestern Kyzylkum Desert, Karakalpakian Autonomous Republic, Uzbekistan.

Formation: upper part of the Khodzhakul Formation.

Age: Lower Cenomanian.

Attribution: Eutheria, Proteutheria, Otlestidae KIELAN-JAWOROWSKA & DASHZEVEG 1989, and Nessov 1989 (originally considered as subfamily Otlestinae of Palaeoryctidae, Nessov 1985a).

Diagnosis (of the subfamily and genus): [Mammals with 8 two-rooted teeth behind large one-rooted tooth (canine?) in the lower jaw. There are remnants of a coronoid bone and a Meckelian groove. Talonid of M_{1-3} very low, trigonid high. Protoconid considerably bigger than metaconid. Paraconid present on the last premolar (P_5).]

Remarks. The emended diagnosis for the Otlestidae was published by Kielan-Jaworowska & Dashzeveg 1989.

The posterior groove, situated on the labial surface, that was considered at the time of the above diagnosis as the remnant of the Meckelian groove, possibly does not represent this structure, as, according to T. Rowe (pers. com. to LAN 1991), the opening situated above this same groove and leading to a channel could represent the location of the Meckelian cartilage.

The relations between Otlestidae and *Prokennaletes* have been discussed in Sigogneau-Russell *et al.* 1992.

ZHELESTES NESSOV 1985a

Type species: *Z. temirkazyk* NESSOV 1985a, pl. 3, fig. 14: also mentioned Nessov & Kielan-Jaworowska 1991, fig. 1.

Material attributed to the genus: holotype of *Z. temirkazyk* (Pl. 5, fig. 1): left maxilla with partly preserved alveolus of canine, alveolus of P^1, teeth P^{2-5}, M^{1-3} (crown of small P^3 was broken after the original description and figuration); CCMGE 10/12716.

Zhelestes sp. cf. *Z. temirkazyk*, right maxillary with P^5, M^{1-2}, CCMGE 11/12176, Nessov 1985a, pl. 3, fig. 5.

Locality: holotype: uppermost part of the site CBI-17 of Dzhyrakuduk (10 meters above the main level of site CBI-14). Specimen of *Zhelestes* sp. cf. *temirkazyk*: middle part of site CBI-14, Uzbekistan.

Formation: holotype: upper part of the Bissekty Formation. Specimen attributed to the genus: middle part of the same formation.

Age: Coniacian.

Attribution: Eutheria, originally ascribed to Kennalestidae, Zhelestinae, now Zhelestidae.

Diagnosis of the subfamily and genus: [Canine one-rooted, small; P^1 large, two-rooted. P^2 or P^3 missing, but the other one small. P^4 large, two-rooted, with long axis notably inclined backwards. Metacone of P^5 not individualized or very weak. P^5–M^2 with antero-labial projection short, narrow, with a relatively wide protocone area. M^1–M^2 not very wide, with talon weak, narrow. Palatal surface of the maxillary presents long antero-median projection].

Remarks. The change in the designation of the canine and anterior premolars results from the identification (McKenna, pers. com. to LAN 1991) of the large canine alveolus, and the removing, by LAN, of a tooth-like particle of matrix lodged in the diastema. In this new interpretation, the upper dentition of this genus consists of a very large probably one-rooted canine, a small and one-rooted P^1, a much larger two-rooted P^2, a very reduced two-rooted (?) P^3 followed by a diastema, and a large two-rooted P^4 whose anterior border is strongly sloping forwards and downwards, P^5 molarized, and molars with a very narrow stylar shelf.

If the animal was really old, it is very improbable that the tooth in the position of P^3 is a persistent deciduous tooth. It resembles *Prokennalestes* in that 5 premolars were present during the life of the animal; this feature seems to be more primitive than in *Kennalestes* where only young specimens keep 5 teeth in the premolar position (Kielan-Jaworowska 1984). But the type of the genus *Zhelestes*, in comparison to *Kennalestes* (which is geologically younger), shows peculiar, advanced features in the size reduction of the tooth in the P^3 position and in the related development of a diastema, as well as in the strong reduction of the stylar shelf. Furthermore, *Zhelestes* differs from *Kennalestes* by the presence, possibly, of a single-rooted upper canine. Finally the genus is closer to zalambdalestids, but it differs from them as well as from kennalestids in the morphology of P^4: this tooth is practically devoid of a protocone, as is the same tooth in *Prokennalestes*, and it has cingula, not present on the same tooth of zalambdalestids.

BULAKLESTES NESSOV 1985a

Type species: *B. kezbe* NESSOV 1985a, pl. 3, fig. 6.

Material: Holotype (Pl. 4, fig. 2): upper left M^3; CCMGE 12/12176.

Locality: site CBI-4, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: Eutheria, Proteutheria *inc. sed.* Nessov 1985a.

Diagnosis: [M^3 with high, sharply pointed paracone. Apex of metacone somewhat projecting backwards. Lingual part of the tooth narrow and long. Protocone high, with additional cuspule on the postmetacrista. Metaconule and paraconule well developed, with paraconule larger. Parastyle (?) large, only separated from smaller stylocone by short groove].

Remarks. Short anterior cingulum. "Lingual part of the tooth narrow and long" should be understood "short and wide", in conformity with the usual fashion of regarding a tooth. This M^3 is more derived than that of *Bobolestes*, which is of course much older, and could represent an early kennalestid.

SULESTES NESSOV 1985b

Type species: *S. karakshi* NESSOV 1985b, pl. 2, fig. 1. Also Nessov 1985a, pl. 3, fig. 15; Kielan-Jaworowska & Nessov 1990, fig. 3 and Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 4, fig. 3): left maxillary fragment with M^1–M^2; CCMGE 35/12000. Nessov figured (1987, tab. I, fig. 5) from another but close level of the same locality, a left mandibular fragment with M_1 and root of P_4 (CCMGE 5/12455) as *Sulestes* sp.; this specimen is also figured and described in Kielan-Jaworowska & Nessov 1990.

Locality: site CBI-4, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: Deltatheroida, Deltatheriidae, Sulestinae.

Diagnosis (for the subfamily and for the genus): [Small predators. Metastyle area of M^{1-2} with 5-6 cusps. Parastyle and stylocone sharp, long, the second much thicker and longer, the first showing labially a nearly straight anterior border. Stylocone followed posteriorly by one very weak additional cusp (B1) on M^1 and a series of small cuspules on M^2. Ectoflexus medially incised, emarginated. Paracingulum narrow, long; preparaconule crista with a series of small cusps (4-6) and one larger cusp situated near the junction of this crista with parastyle; same crista uninterrupted on M^2; on same tooth, two additional cuspules between paracone and stylocone, preceded medially by small emargination of preparacrista. Postmetacrista long, almost straight, emarginated by a fissure lingual to the area of additional cusps and showing a series of small prongs labially. Deep fissure between paracone and metacone. Protoconid small, sharp.]

Remarks. The tip of the stylocone of both molars and the paracone of M^1 are now broken.

Other deltatheroidans have been found in the middle part of the formation, which belong to a new genus, larger than *Sulestes* and with a stronger reduction of metaconid, but with other cusps much higher and sharper. *Sulestes*, which is older than *Deltatheridium* from Mongolia (Kielan-Jaworowska 1975b), appears more advanced, as already noted in Nessov 1985b; it represents a different phyletic line than *Deltatheridium*, a line which underwent a more rapid evolutionary rate.

ZALAMBDALESTES GREGORY & SIMPSON 1926

?Z. mynbulakensis NESSOV 1985b; also mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 5, fig. 2): fragment of left dentary with M_2; CCMGE 36/12000.

Locality: site CBI-4b, Dzhyrakuduk, central Kyzylkum Desert, Uzbekistan.

Formation: middle part of the Bissekty Formation.

Age: Coniacian.

Attribution: originally Eutheria, Zalambdalestidae (more primitive than those from Mongolia, Kielan-Jaworowska 1975a), though in fact it may represent a specimen of *Sorlestes budan* with a strongly worn talonid.

Diagnosis: none given in the original presentation; original description as follows: [lower jaw low at the level of tooth row, coronoid process not steep anteriorly. Length of M_2: 2.3 mm. Trigonid high. Metaconid and protoconid relatively close together; a line through them is oriented perpendicular to the jaw. Protoconid larger than metaconid. Paraconid not large and appressed against metaconid. Talonid somewhat worn and considerably wider than trigonid. In occlusal view, region of hypoconulid looks somewhat truncated posteriorly near the contact with M^3. Hypoflexid not wide. Presence of an oblique projection on precingulid and postcingulid].

Remarks. This species, which LAN regards as a junior synonym of *Sorlestes budan*, underlines the resemblances between this genus and zalambdalestids, in the shape of the talonid (closeness of hypoconulid and entoconid) and in the common approximation of the protoconid and the strongly reduced paraconid; these resemblances translate their common status as mixotheridians, of which however they represent two different lines of evolution.

ZHELESTES NESSOV 1985a

?Z. bezelgen NESSOV 1987, pl. 1, fig. 1; also Nessov & Kielan-Jaworowska 1991, fig. 1.

Material: Holotype (Pl. 6, fig. 1): fragment of left maxillary with P^5–M^2; CCMGE 1/12455; supplementary material: upper M^2, unpublished.

Locality: slightly above the main level of the site CBI-14, Dzhyrakuduk, Uzbekistan.

Formation: middle or upper part of the Bissekty Formation.

Age: Coniacian.

Attribution: Eutheria, Zhelestidae.

Diagnosis: only the following description was given: [animal smaller than *Zhelestes temirkazyk* NESSOV. Length $P^{4?}$–M^2 (see below) = 6.7 mm as opposed to 8.1 mm in the holotype of the latter. Relatively narrower molars. Postcingulum of new species extends somewhat farther labially, stylar shelf on the preserved teeth slightly wider].

Remarks. The change in the dental formula of the type species (see p. 63) permits the interpretation of the last premolar as P^5, and not P^4.

This species might be attributed to a new genus of Zhelestidae. There are several differences between the two type specimens, for example, P^5 is slightly longer labially in *?Z. bezelgen*, more pinched in the middle in occlusal view, hence has a shorter lingual part. But, in the absence of the anterior part of the maxillary, and, in consequence, of the dental formula, it is not possible to make a definite decision concerning this problem.

ALYMLESTES AVERIANOV & NESSOV in press

Type species: *A. kielanae* AVERIANOV & NESSOV in press.

Material: Holotype (Pl. 6, fig. 2): crown of left lower M_1 or M_2; ZIN (Zoological Institute of the Russian Academy of Sciences, St. Petersburg) C. 78332.

Locality: site "Grey Mesa", northeast of Alymtau Range, Sary-Agach Region, Chimkent District, southern Kazakhstan (Fig. 2, **9**, p. 72).

Formation: lower Darbaza Formation, grey sands.

Age: lower?-middle Campanian.

Attribution: Eutheria, Mixotheridia, Zalambdalestidae.

Diagnosis: [Crown of lower molars higher than in other known members of the family, labial part of the talonid very high. Trigonid and talonid basins relatively smaller and deeper. Difference in height between trigonid and talonid of lower molars relatively small.]

Remarks. This is a very advanced form among Zalambdalestidae (displaying the same evolutive trend as other Mixodontia). If age determinations are correct, this mammal could also be a little younger than other members of the family.

Also found in the Coniacian levels were condylarths (approximately 5% of the mammalian jaws and teeth) (for example Nessov 1987, pl. 1, fig. 2 and Nessov & Kielan-Jaworowska 1991, fig. 1: the largest upper molar and one lower molar) and multituberculates (1%) (Kielan-Jaworowska & Nessov 1992). Note that no mutituberculates have been found in other levels. One enigmatic unpublished small mammalian edentulous lower jaw with hystricognathy comes from the upper Turonian of Dzhyrakuduk.

List of mammalian genera treated in this paper, in systematic order

?Tribotheria, family unknown
Kumlestes

Metatheria, Deltatheroida, Deltatheridiidae, Sulestinae NESSOV 1985b
Sulestes

Eutheria, Proteutheria, Otlestidae (Nessov 1985a) Kielan-Jaworowska & Dashzeveg 1989
Otlestes

Eutheria, Proteutheria, Bobolestidae (Nessov 1989), 1992a
Bobolestes

Eutheria, Proteutheria, Palaeoryctidae (Winge 1917), Simpson 1931
Bulaklestes
Daulestes
Oxlestes

Eutheria, Proteutheria, Kennalestidae Kielan-Jaworowska 1975a
Sailestes

Eutheria, Mixotheridia, Zalambdalestidae Kielan-Jaworowska 1975a
Beleutinus
?Zalambdalestes mynbulakensis
Alymlestes

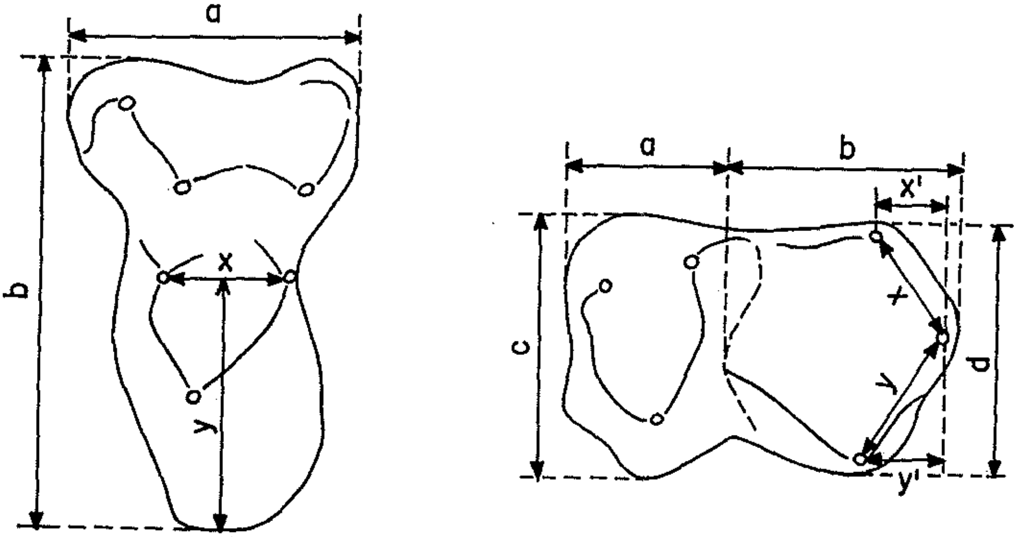

Figure 1.— Measurements on upper molars:
a = maximum labial length
b = maximum width
x = distance between the lingual points of the Vs of the two conules
y = distance between the level of x and the lingual extremity of the crown
Abbreviations: meta, metacone; mu, metaconule; pa, paracone; pu, paraconule.

Measurements on lower molars:
a = length of the trigonid from the anterior extremity of the crown to the point of contact of the oblique crest
b = length of the talonid, between the anterior end of the oblique crest and the posterior extremity of the crown
c = maximum width of the trigonid
d = maximum width of the talonid
x = real distance between the hypoconulid and the entoconid
y = real distance between the hypoconulid and the hypoconid
x' = distance between the hypoconulid and the entoconid measured along longitudinal axis
y' = distance between the hypoconulid and the hypoconid measured along longitudinal axis
Abbreviations: ento, entoconid; hu, hypoconulid; hy, hypoconid; mctd, metacristid; md, metaconid; pd, paraconid.

	measurements	trigonid	size & situation pd/md	cingula	hu/ento	hy	ant. end of obl. crest
Daulestes M/1	lg total :	prot. high, recurved	smaller	anterior ?	?	> ento and hu	
Taslestes M/2	a=0,65;b=0,67 c=0,90;d=0,84 x=0,26;y=0,37 x'=0,22;y'=0,16	md sligthly distal/proto	slightly labial	anterior ?	ento=hu (double) ; ento faces hy	big ; arms unequal	slightly lingual
Kumsuperus M/2 (worn)	a=1,11;b=1,30 c=1,76;d=1,67 x & y unmeasurable	very compressed ; post. wall tranverse	labial ? very reduced ?	anterior ?	?	?	?
Kumlestes M/2	a=0,55?;b=0,56 c=0,70;d=0,64 x=0,27;y=0,32 x'=0,20;y'=0,25	md slightly distal	more labial	anterior ? post. 0	hu hooked sup. to ento; 3 cusps ~ equidistant	high	mi-trigonid
Sorlestes M/2	a=1,10;b=1,53 c=1,80;d=1,80 x=0,56;y=0,95 x'=0,43;y'=0,48	post. wall transverse	small but hardly labial	ant. and post.	relatively close	2 arms almost =	slightly labial
Aspanlestes M/2	a=1,04;b=1,22 c=1,53;d=1,60 x=0,64;y=0,79 x'=0,50;y'=0,49	high ; post. wall transverse	small but hardly labial	ant. and post.	relatively close	2 arms almost =	mi-trigonid or slightly labial
Otlestes M/2	a=0,61;b=0,69 c=1,02;d=0,76 x=0,34;y=0,35 x'=0,21;y'=0,32	very high; post. wall transverse	smaller ; more labial	anterior	close ; ento slightly distal/hyp	2 arms almost =	mi-trigonid
Zalambdalestes mynbulakensis M/2	a=1,01;b=1,30 c=1,66; d=1,79 x=0,48;y=1,21 x'=0,32;y'=0,55	v. narrow ; post. wall almost inverted	more labial	ant. and post.	twinned		labial
Alymlestes M/1 or M/2	a=0,98;b=1,28 c=1,85;y=1,97 x=0,50? y=0,70? x'=0,25? y'=0,48?	very high, narrow ; post. wall transverse	very small; not labial	0 but anterior cuspules	ento slightly distal/hy		far labially
Prokennalestes trofimovi (PSS10-40) M/2	a=0,92;b=0,76 c=1,01; d=0,93 x=0,30;y=0,43 x'=0,10;y'=0,23	md slightly distal/proto	very small ; slightly more labial	anterior	close; ento almost terminal	close to hu	lingual; mctd separated
Kennalestes (MgM I/5) M2	a=0,75;b=0,85 c=1,00;b=0,94 x=0,24;y=0,56 x'=0,15;y'=0,31	high; post. wall transverse	slightly smaller and more labial	weak anterior	close?	2 arms = lowest of 3 cusps	mi-trigonid
Asioryctes M/2 (I/134)	a=0,96;b=0,82 c=1,30;d=0,99 x=0,58;y=0,45 x'=0,23;y'=0,30	very narrow; post. wall almost inverted	very reduced;more labial	anterior	distal; 3 cusps ~ equidistant	2 arms = highest of 3 cusps	mi-trigonid
Zalambdalestes lechei M2 (P/43)	a=1,00;b=1,30 c=1,89;d=1,85 x=0,76? y=1,02 x'=y'=0,49	narrow; post. wall transverse	much < but hardly more labial	0 ?	quite close? badly defined	quite distal;lower than ento	somewhat labial
Barunlestes M2 (MgM I/135)	a=1,10;b=1,10? c=1,75; d=1,70 x=0,87;y=0,80 M1:x'=0,35;y'=0,31	very short; post. wall transverse	much smaller	?	ento distal	compressed	more labial

Table 1.— Comparison of lower molar characters in Cretaceous Middle and Central Asian genera.

	measurements	protocone	pa/meta	pu/mu	parast. sulcus	stylar shelf	cusp C	stylocone	cingula	peculiarities
Sulestes M2	a=2,43; b=2,86 x=0,77; y=0,60	narrow, deflected	equal	small, V, close to protocone	discrete	very wide ; long metast. wing	0	+	anterior	deep ectoflexus
Bobolestes M2 M3	a=1,60; b=1,88 x=0,63; y=0,64 a=1,22; b=1,79 x=0,54; y=0,51	narrow, low	slightly >	V, equal	definite	narrow but metast wing	0	not distinct	0	deep ectoflexus
Sailestes M1 or M2	a=1,47;b=1,69 x=0,55; y=0,67	narrow, low, deflected	higher	V, subequal	definite	narrow, but metast.wing	+	very small	ant., incipient post.	ectoflexus
Bulaklestes M3	a=1,40; b=2,23 x=0,38;y=0,63	low, short,	much >	V, pu bigger	0	0	0	small	ant. very short	big parastyle; specialized /*Bobolestes*
Zhelestes t. M2	a=2,80; b=4,00 x=?;y=? (wear)	big	slightly >	? (worn)	definite	0	0	definite ?	post.	no ectoflexus
Z. bezelgen M2	a=2,39; b=2,98 x=1,10; y=1,39	slightly dissymetrical	slightly >	strong, equal, close to cones	definite	0	0	not definite	ant. & post. strong	ectoflexus moderate
Prokennalestes trofimovi M2 (GI PST 10-18)	a=1,46; b=1,92 x=0,47; y=0,61	relatively short	>	pu slightly >	definite	moderate	0 or incipient	moderate	0	deep ectoflexus ; parast. double
Kennalestes M2 (ZPal MgM I/5) (I/2) M2	a=1,66; b=2,51 x=0,66? y=1,13 a=1,86; b=2,50 x=0,73; y=1,05	deflected, wide	very >	V, pu >	not clear	moderate, wider in parast. area	hardly incipient on M2	small	ant. & post. strong	deep ectoflexus ; parast. prominent
Asioryctes M2 (I/134)	a=1,72; b=2,76 x=0,59? y=1,00?	shorter, wide	very >	?	not clear	moderate	0	< to parast	0	ectoflexus moderate ; long parast. wing
Zalambdalestes M2 (P/43)	a=2,08; b=3,10 x=0,95?;y=1,70?	wide, long	slightly >	?	not definite	narrow except parast. wing	0	very small ?	0	moderate ectoflexus; shorter wings

Table 2.— Comparison of upper molar characters in Cretaceous Middle and Central Asian genera.

Eutheria, Mixotheridia, Zhelestidae (NESSOV 1985a), 1990

Aspanlestes
Sorlestes
Taslestes
Zhelestes

Eutheria, Condylarthra, Mioclaenidae OSBORN & EARLE 1895

Kumsuperus

Eutheria, Lipotyphla, Soricidae GRAY 1821

Cretasorex?

FORMATIONS AND DETERMINATIONS OF THEIR AGE

(Fig. 2)

The authors are well aware that the restriction to Asian deposits of several of the taxa invoked below undermines the determination of the geologic age; also, as far as sharks are concerned, there can exist, in a same locality, forms of a quite different evolutionary stage (H. Cappetta, pers. com. 1993); as a result, when species attribution is not possible, their use in age determination is weakened. The indications given below are thus often only tentative.

• 1. The Khodzhakul locality is situated in the lower or middle part of the **Khodzhakul Formation** (Schultz 1967; see also Schultz 1972) (the lower limit of this formation is not clear at the locality itself but it is clear 4-6 km SSE of the northern margin of the Sheikhdzheili Range). The uppermost Albian age is based mainly on sharks (*"Eoanacorax" dalinkevichiusi* and *"Eoanacorax"* sp. [Pl. 8, fig. 5], *Paraisurus macrorhiza* [Pl. 9, fig. 5] and *Paraisurus* sp.). The genus *"Eoanacorax"* (grade taxon, most primitive among Anacoracidae, see Pl. 8, figs. 5-11 and Pl. 9, figs. 1-4) is characteristic of the late Albian; the genus *Paraisurus* is known from uppermost Aptian (Clansean) up to latest Albian and is unknown from the upper Cretaceous. In the adjacent geological section at Karakul Lake, (i.e. approximately 14 km east of the Khodzhakul locality), a level with uppermost Aptian ammonites (e.g. *Hypacanthohoplites nolani*) is situated far below the mammalian level. Finally, about 45 km NW of Khodzhakul in the Beshtyube Hills and approximately 110 km east, near the Kokcha Range, lower Turonian ammonites (*Mammites nodosoides*) have been found far above this level (Schultz 1972).

• 2 and 3. The Khodzhakulsay and Sheikhdzheili localities are situated in the upper part of the **Khodzhakul Formation** (approximately 14 m above locality 1) and far below the above mentioned level with lower Turonian ammonites. The first locality is situated on the right slope of the Khodzhakulsay Ravine and the second close to the border of the plateau; the early Cenomanian age of both is based on the turtle assemblage (*Ferganemys itemirensis, Tienfucheloides undatus, Kizylkumemys schultzi*) which typifies the Cenomanian in western Asia (younger than the late Albian turtle assemblage

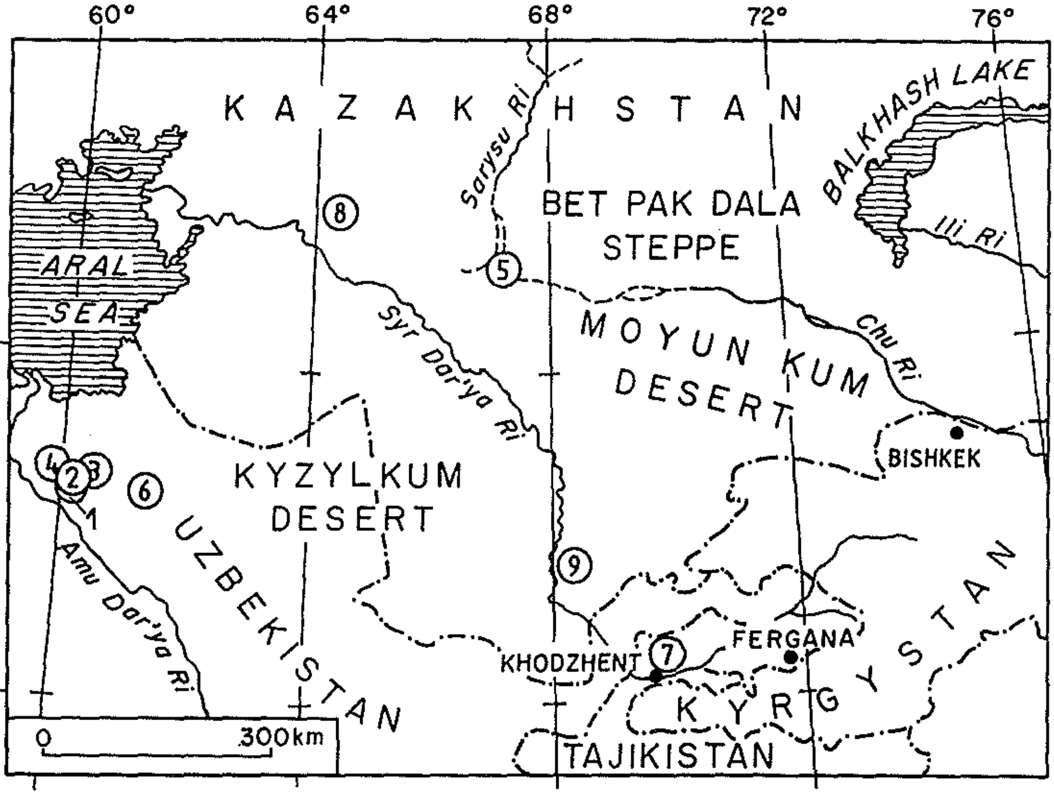

Figure 2.— Map of the localities mentioned in this paper.

1: **Khodzhakul** (name of a recently dried lake); uppermost Albian (Vrakonian) – Autonomous Karakalpakian Republic of Uzbekistan.
2: **Khodzhakulsay** (name of a ravine); Cenomanian – Autonomous Karakalpakian Republic of Uzbekistan.
3: **Sheikhdzheili** (name of a mountain range); lower Cenomanian – Karakalpakian Autonomous Republic of Uzbekistan.
4: **Chelpyk** (name of a hill); lower? Cenomanian – Karakalpakian Autonomous Republic of Uzbekistan.
5: **Ashchikol** (on the eastern margin of the Ashchikol Lakes, 10 km south of the Besmolla Well); lower Turonian – Suzak Region, Chimkent District, Kazakhstan Republic.
6: **Dzhyrakuduk** (name of a well) = Bissekty (well) = Kulbecke Spring; upper Turonian and several levels of the Coniacian – Uchkuduk Region of the Bukhara District, Republic of Uzbekistan.
7: **Kansay** (in fact, Kyzylbulak, situated 3-4 km east of Kansay; lower Santonian – Khodzhant (Khodzent) District of the Republic of Tajikistan.
8: **Zhalmauz** (name of a well in area of the Baybolat Well); Santonian-lower Campanian? – Dzhalagash Region of the Kzyl-Orda District, Republic ot Kazakhstan.
9: **Alymtau** (name of a ridge); lower-middle Campanian – Sary-Agach Region of the Chimkent District, Republic of Kazakhstan.

and older than the early Turonian); note that *Ferganemys itemirensis* is much larger and must belong to a possibly somewhat younger species than that from the late Albian of Fergana (*F. verzilini*); the genus itself is not known after the Cenomanian-Turonian boundary. The early Cenomanian age is also based on the regressive nature of the deposits (the regression occurred in the early Cenomanian in this area), and their situation close to the uppermost Albian, i.e. between the two transgressive layers of the latest Albian and late Cenomanian-early Turonian. True *Scapanorhynchus* and

Ptychodus are missing, these two genera appearing in the European part of Russia (Volga River Basin, Belgorod District) and in Middle Asia only in the mid-Cenomanian. Somewhat above in the Khodzhakul Formation of this area, Cenomanian bivalves have been found (Schultz 1972).

- 4. The Chelpyk (=Cholpyk) locality is also situated in the **Khodzhakul Formation**, either in the same level as 2 or 3, or somewhat higher, but in any case below the Cenomanian-Turonian boundary. This datation is based on the various vertebrate elements which are similar to those of 2 and 3. As there was an important turnover of terrestrial, brackish and marine ecosystems and vertebrate assemblages at the Cenomanian-Turonian boundary of the region, as well as in many other areas of the world (Nessov &Khisarova 1988), the assemblage 4 has to be situated before this boundary. The turnover of hybodont sharks at the Cenomanian-Turonian boundary of the region occurred between two species (without lateral cusps on the crown, Pl. 8, fig. 1), one with strong and long lateral cusps (Pl. 8, fig. 2), and another species with moderate development of these relatively wide cusps (Pl. 8, fig. 3). For the turtles, the assemblage 4 includes the above-mentioned *Kizylkumemys schultzi*, which is known also from the lower Bainshire Formation of Mongolia (e.g. Khara-Kutul, Amtgay, Shine-Usu-Khuduk), again of Cenomanian age and not Cenomanian-Turonian as stated in Shuvalov & Chkhikvadze 1975. It is important to remark that remains of the ray *Myledaphus*, which are known in the Turonian and Coniacian of the Kyzylkum (*Myledaphus tritus* NESSOV) and in the Iren Dabasu Formation of northern China (D.A. Russell, pers. com. to LAN), and those of the turtle *Lindholmemys*, which was common in Middle Asia and in Mongolia after the Cenomanian/Turonian boundary, are absent at the localities Chelpyk, Khodzhukulsay and Sheikhdzheili; this admittedly negative argument nevertheless also supports a pre-Turonian age.

- 5. The Ashchikol "locality" is situated in an unnamed geological unit (20 m of alluvial and lacustrine greyish sands, silts, clays and gravels, sometimes with thin coal layers, obtained by a drilling core, about 500 meters under the surface). This unit lies under a thicker (also unnamed) unit of green and grey silts and clays, which was dated near its base by spores and pollen as lower Turonian (L.G. Rusinova, pers. com. to LAN). Moreover, the reduction of the paraconid, the trenchantness of the precingulid (hence of the postcingulum) and the twinning of the hypoconulid and the entoconid of the mammal jaw from the drilling core suggest an earlier age than the Cenomanian/Turonian boundary, as no mammal has been found below this boundary in Middle Asia with these features similarly developed.

- 6. The Dzhyrakuduk fossils come from different levels situated from 26 m above the bottom of the **Bissekty Formation** (formerly **Taykarshi Beds**) (Nessov 1990; see also Sochava 1968) to near the top of the formation; the latter has a total thickness of approximately 88-103 m. The series is divided here into a level 6a, situated 26-27 meters above the top of the lower Turonian marine unit (dated by forams), and underlying the Bissekty Formation, itself terrestrial, freshwater or semi-marine; levels grouped as 6b, situated nearly 26 meters above 6a; levels grouped here as 6v, which consist of a series of closely set levels; locality 6g, situated 7 meters above 6v; and finally 6d, situated 3 meters above 6g, and 6e. The presence of the turtles *Lindholmemys* and *Shachemys* and of the ray *Myledaphus tritus* (Pl. 9, fig. 6) indicates that these levels are situated above the Cenomanian-Turonian boundary. The upper Turonian age of 6a (sites CDZH-17a and -25) is based on the presence of certain anacoracid sharks (Pl. 8, figs. 6-9) and, mostly; on its situation above the level with early Turonian forams; the latter indicate an important transgression of the sea in the middle latitudes of both Asia and North America (e.g. lower members of Mancos and Tropic Shales of Utah); the Coniacian age of 6b (site CBI-4, -4a, -4b and -4d), 6v (sites CBI-14 and others), 6g (sites CBI-17 and -17a), and 6d (site CBI-5 and -5a) is based on sharks (*Ptychocorax aulaticus*, Pl. 9, fig. 3) known in other areas of Middle Asia with ammonites, belemnites and other marine invertebrates (Aulat settlement at the limit of Uzbekistan and Tajikistan, Bzoubay settlement in southwestern Kyzylkum, also Sheikh-Aryk and Sultan-Sandzhar areas of northern Turkmenistan [Pl. 9, figs. 1-2]); anacoracids are of a Coniacian evolutionary stage (Pl. 8, fig. 10). The presence of the ray *Myledaphus tritus* (Pl. 9, fig. 6) places the sites below the Santonian, as this form is unknown in the Santonian of Middle Asia (though the genus reaches the K/T boundary in North America where many vertebrates persist longer than in Asia, e.g. polyacrodontids, dicamptodontoids, chelydrids, amiids, gars). In Middle Asia and at the Coniacian-Santonian boundary, *Myledaphus* was replaced by *Parapalaeobates* (Pl. 9, fig. 7), *Protoplatyrhina* and *Baibishia* (Pl. 9, fig. 8) (see however the diverging opinion of Cappetta 1992); sharks of the genus *Polyacrodus* with numerous subvertical striae of the crown were replaced by another species with rare irregular striae, and the base of the main cusp of the crown of *Hybodus* became wider in the Santonian (Pl. 8, fig. 4). The upper part of the Coniacian component of the Dzhyrakuduk section is correlated by LAN with a brief and timid transgression, on the basis of the partial replacement of brackish water hybodontids by the very common *Hispidaspis*, *Cretolamna*, anacoracids with serrated teeth, and *Heterodontus*, an assemblage indicating higher salinity. Approximately 6-8 m above the higher level with mammals of the Bissekty Formation, anacoracids (Pl. 8, fig. 11) occur which are much smaller and much more primitive than those of the Lower Campanian: *Squalicorax kaupi* (well dated, for instance, in the southern Swedish locality of Ivö-Klack).

- 7. The Kansay mammalian locality is situated in the lower half of the local section of the **Yalovach Formation** (Solun 1937; see also Vialov 1945a and b; Sochava 1968) dated as lower Santonian by large sculptured brackish water pelecypods (determinations G.G. Martinson, pers. com. to LAN). Its geochronological situation above the Coniacian-Santonian boundary is based on the following evidence: the red color of the sediments (in comparison with those below), reflecting the increase of aridity in the region above the Coniacian-Santonian boundary; the presence of a tyrannosaurid theropod with thick teeth replacing the Albian-Coniacian torvosaurid-like theropod with flatter teeth; the presence of a relatively large crocodile advanced beyond that of the Coniacian ecological analog; the presence of advanced species of the turtle genera *Lindholmemys* and *Shachemys*; the appearance of the rays *Protoplatyrhina*, *Parapalaeobates* and *Baibishia* (Pl. 9, figs. 7-8) as well as the absence of *Myledaphus* Species of *Hybodus* of this age and area differ from Coniacian forms by the wider base of the main cusp (in lateral view) (Pl. 8, fig. 4).

- 8. The Zhalmauz locality is situated in the **Bostobe Formation** (Samodurov 1958; see also Shilin 1986, Nessov & Khisarova 1988) (and not in the Beleuty Formation as erroneously mentioned in the first description of *Beleutinus*). This formation has been dated as Santonian-Campanian after the study of floras from many sites in this formation (Shilin 1986), also by the presence of *Parapalaeobates* as well as peculiar *Polyacrodus* (with thin, irregular, widely spaced striae) and by the absence of *Myledaphus* in the fossil assemblage. An upper Campanian age is excluded from this interval as no evidence of transgression could be found in this level, but only higher, above the formation; therefore the age of the level containing the two mammals would be Santonian-lower Campanian. As the excavations for the screening done in 1962 was made mostly in the lower part of the formation (LAN observation 1980, 1982), the age of *Beleutinus* and of the unnamed cervical vertebra centrum is most probably Santonian.

- 9. The Alymtau locality is situated in the lower part of the **Darbaza Formation** (Minakova 1941; see also Byelyen'kii 1961), only two or several meters below the transgressive middle part of this formation and corresponds to the upper Campanian. The sharks *Scapanorhynchus armenicus* and *Paraanocorax obruchevi* found with the mammalian teeth, may also indicate a Campanian age (determinations L.S. Glickman, pers. com. to LAN), but their restriction to Asian deposits limits their stratigraphic value.

N.B. We know of one additional locality related to Cretaceous mammals: it is not in middle Asia but in Russia, and it has yielded only mammal hair (V.V. Zherikhin, pers. com. to LAN) included in amber. This locality is that of Yantardakh (Fig. 3, *), situated on the banks of the Maymecha River, Kha Langer River basin, Dolgan-Nenets Autonomous District, Northern Siberia. There, yellowish sands of the Khets Formation contain pieces of lignite and amber (Nessov 1992a and b); these sediments were first dated as lower Cretaceous, but the inoceram molluscs found in adjacent lateral layers indicate a Santonian age. The interest of this discovery is in extending the northern range of Asiatic mammals during a warm episode (the latitude, 70°N, is about the same as that of the Northern Slope of Alaska (Clemens 1991), and the climate in Yantardakh at that time was temperate to cold temperate and humid): it thus seems that, at least in particularly warm intervals of the Cretaceous, almost all of Asia was inhabited with mammals.

FOSSILIFEROUS CONTENTS OF THE MENTIONED LOCALITIES

(For figures of holotypes [Pl. 1 to 6], see systematic part)

- 1. Khodzhakul locality (site SKH-20). – Type of *Bobolestes zenge*. – Edentulous posterior part of a small lower jaw, found in 1978 and first for locality (Nessov 1984, fig. d). – Upper edentulous jaw (mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1) approximately two times larger than the type of *Bobolestes*. – Part of a large rectangular tooth with thick enamel (mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1). In the same assemblage were small gastropods, ammonites, crabs, crayfish, many species of sharks (with a dominance of lamnoids), rare holocephalians, holostean fishes: Lepidotidae, Gyrodontidae, Aspidorhynchidae, Pholidophoriformes, different teleosts; primitive marine turtles (including peculiar plesiochelyid-like "macrobaenids"), plesiosaurs (mostly young) and numerous coprolites; many of the forms indicate an open marine bay of normal or near-normal salinity and high bioproductivity. On the other hand, an assemblage consisting of primitive discoglossid and pelobatid frogs, numerous well preserved remains of scapherpetontid salamanders, non-marine turtles including trionychids and the oldest record of the Carettochelyidae *Kizylkumemys*, rare bones and teeth of a very small hadrosaur, small crocodiles and birds testify to a brackish water lake environment behind the shore bar and the existence of a channel connecting the sea and the lake. On the lake shores (Rocek & Nessov 1993, fig. 2) thrived araucarian gymnosperms, sycamore-like angiosperms, ankylosaurs, diverse lizards and small theropods. The climate was semi-humid and temperate to warm, cooler though than in the Santonian or early Campanian of the region.

Originally, mammals from this locality were the oldest known for Middle Asia, but in 1992 scarce and still unpublished mammal material was found in the upper Bathonian of the Balabansay Formation of the Kokart River in the northeastern part of the Fergana Depression, Kyrgystan.

• 2. Khodzhakulsay locality (site SKH-5). – Rare and undescribed bones, mostly edentulous lower jaws of small therians, found in 1979. The accompanying fossil assemblage is also very rich, with a dominance of the gastropod *Mathildella* and non-marine vertebrates. There are no ammonites and the plesiosaurs and holocephalians are rare; sharks are dominated by brackish forms (Hybodontidae, Polyacrodontidae). Among the vertebrates, holosteans, scapherpetontids, trionychids, adocids and carettochelyids are dominant. Finally, middle-sized theropods with relatively flattened teeth, the primitive protoceratopsid *Asiaceratops* and small shamosuchid crocodiles are also abundant. Sycamores and cypress-like conifers lived near the shore. The concentration of fossils in this site comes from an accumulation in a channel connecting two brackish reservoirs, one of them linked to the more open saline embayment (Nessov 1990, fig. 1; Rocek & Nessov 1993, fig. 2)

• 3. Sheikhdzheili locality (sites SSHD-8 and -8a). – Type of *Oxlestes grandis*, found in 1979 as the first mammal for the locality. – Type of *Otlestes meiman*. – Several teeth and edentulous jaws, one of which figured in Nessov 1984 (figs. a and b) (Pl. 7, fig. 3); note the reduction of P_2 opposed to the relatively large P_1 and P_3; large P_1–P_3 relative to P_2 is a common feature in Cenomanian and Coniacian mammals of the area (possibly corresponding to a peculiar mode of replacement). – Another lower jaw with two teeth and upper jaw with 2 teeth attributed to the same species (Nessov 1985a, pl. 1, fig. 4). – Lower premolar (Nessov 1985a, pl. 1, fig. 11). – Lower molar of a possibly primitive mixotheridian (Nessov 1985a, pl. 1, fig. 3) (Pl. 7, fig. 2). – Parietal bone (of *Oxlestes*?) with a strong sagittal crest (Nessov 1985a, pl. 2, fig. 1) (Pl. 7, fig. 1). – The distal extremity of a femur figured in Nessov 1985a (pl. 1, fig. 5) as a Cenomanian form from the Khodzhakul Formation comes in fact from the middle part of the Coniacian Bissekty Formation at Dzhyrakuduk (see below). – Part of a large canine (of *Oxlestes*?) (mentioned by Nessov & Kielan-Jaworowska 1990): height of preserved part of crown and root is 21.7 mm, but there is some doubt as to its mammalian nature. The assemblage of other groups of vertebrates is quite the same as for 2.

- 4. Chelpyk locality (SKH-1). (The upper molar in Nessov 1985a, pl. 2, fig. 10, was found not at this locality as then indicated, but in 6a, see below). – Several mammal bones, the best preserved being a calcaneum of a primitive eutherian found in 1980 (Nessov 1985a, pl. 2, fig. 2). The faunal assemblage is very similar in composition and in the dominant groups to those of 2 and 3. With respect to assemblage 1, brackish water sharks prevail (lamnoids are much rarer), lepidotid and pycnodontid holosteans dominate among actinopterygians, turtles are especially diverse with nine species ("macrobaenids", adocids, nanhsiungchelyids, lindholmemydids, carettochelyids, two species of trionychids and one species of an undescribed family). Also present are amphibians and a small and primitive hadrosaur (*Gilmoreosaurus?* sp.) and the very small protoceratopsid *Asiaceratops salsopaludalis*, theropods, ankylosaurs, a small shamosuchid crocodile, pterosaurs and birds. Leaves of sycamores and cones of cypress-like conifers have also been found. These localities were formed near the channels, themselves connected to brackish reservoirs. The climate was semi-humid (Rocek & Nessov 1993, fig. 2).

- 5. Ashchikol locality. – A single mammalian lower jaw with the last premolar and molars (Pl. 7, fig. 4) was found in 1989 in a well core (mentioned Nessov & Kielan-Jaworowska 1991, fig. 1). Spores, pollen, diatoms and possible sponge spicules (extracted from the core by Dr. Björklund from the Paleontological Museum, Oslo University) were found inside the same sample, testifying to a near-shore semi-marine environment.

- 6. Dzhyrakuduk locality. The first mammal was found in 1978 after the discovery, during the preceding year, of a faunal assemblage approaching, at the familial and generic levels, those of the Campanian and Maastrichtian of North America (Estes 1964 and references therein). In this assemblage were rays (*Myledaphus*, *Ischyrhiza* and *Ptychotrygon*) and sharks (*Brachaelurus* and *Squatirhina* and others), gars, amiid, peculiar pholidophoriform and aspidorhynchid holosteans, elopomorph teleosteans, frogs (with sculptured skull roof), scapherpetontid and batrachosauroidid salamanders, adocids of the genus *Adocus* and trionychid turtles, teeid lizards, *Paronychodon*-like theropods and tyrannosaurids. North American coastal plain faunas have Campanian and Maastrichtian mammals, but at first no mammals were found in the Coniacian of Dzhyrakuduk. However, after an intensive search in the site CDZH-17a, the jaw of *Daulestes kulbeckensis* was found and, later in the laboratory, an edentulous lower jaw, overlooked in 1977 because of its poor preservation: these represented the first mammals in that level and locality.

  - 6a (group of sites CDZH-17a, -17g, -25). – Type of *Daulestes kulbeckensis,* site CDZH-17a. – Type of *Aspanlestes aptap*, site CDZH-17a. – Type of *Taslestes inobservabilis*, site CDZH-17g. – A canine, site CDZH-17a, possibly of a deltatheroid (Nessov 1981, fig. 9 (26); Nessov 1982, pl. 1, fig. 8 and Nessov & Kielan-Jaworowska 1991, fig. 1). – Short fragment of an edentulous lower jaw (Nessov 1982, pl. 1, fig. 7). – Upper molar with incipient posterior cingulum

(Nessov 1985a, pl. 2, fig. 10) (this site, and not CDZH-3 nor SCH-1 as indicated in 1985a) (Pl. 7, fig. 5). – Also at the same level in CDZH-25 was found the anterior part of a lower jaw with a replacing canine (Nessov 1984, figs. e, d), several unpublished teeth, a lower jaw with part of the dentition, and postcranial elements, some of which are as big as cranial and postcranial elements of condylarths from the Coniacian levels (see below).

Therefore it is possible that remains of condylarths will be discovered later in deposits that are a little older (upper Turonian), that is, in the lower part of the Bissekty Formation.

- 6b (sites group CBI-4, -4a, -4b, -4d and others). Site CBI-4: – Type of *Sailestes quadrans*. – Type of *Kumsuperus avus*. – Type of *Kumlestes olzha*. – Type of *Sulestes karakshi*. – Type of *Bulaklestes kozbe*. – Femur of a peculiar morphology, possibly cursorial or climbing mammal (Nessov 1982, pl. 2, fig. 1). – Small edentulous lower jaw (Nessov 1982, pl. 2, fig. 3). – Two pelvis fragments (Nessov 1982, pl. 2, figs. 4 and 5). – Edentulous deltatheroid lower jaw (Nessov 1982, pl. 3, fig. 7). – Mixotheridian lower trigonid (Nessov 1985a, pl. 2, fig. 4). – Small incisor (Pl. 7, fig. 7) with sharp anterior border and oblique ridge on the lingual side of the crown, possibly of a plant-eating mammal (Nessov 1985a, pl. 2, fig. 3) (now lost). – Lower jaw with very unequal teeth (milk dentition?) (Nessov 1985a, pl. 2, fig. 17). – Peculiar premolar, possibly therian (Nessov 1985a, pl. 3, fig. 2), with sharp posterior margin of main cusp. – Upper last premolar of a mioclaenid condylarth (Nessov 1985a, pl. 3, fig. 1 as Kennalestidae). – Anterior part of lower jaw with very large canine alveolus (Nessov 1985a, pl. 3, fig. 3). – Proximal part of a femur indicating a much faster mode of locomotion than the above-mentioned femur from the same site (site CBI-4b; not SSHD-8) (Nessov 1985a, pl. 1, fig. 5). – Part of squamosal (Nessov 1985a, pl. 2, fig. 6). – Posterior part of an edentulous lower jaw with subhorizontal and strongly deflected angular process (Nessov 1985a, pl. 2, fig. 5). – Frontal with partial cast of endocranial and nasal cavities and remnants of turbinalia (Nessov 1985b, pl. 2, fig. 6). – Small and wide upper tooth (Pl. 7, fig. 6), either deciduous or a new genus (Nessov 1987, pl. 1, fig. 4). – Upper and lower teeth of a small species of a new genus of mioclaenid condylarth (Nessov & Kielan-Jaworowska in prep.). – Two isolated lower molars of a new species of deltatheroid. – Several dozen unpublished specimens (mostly postcranials), among which are the jaws and teeth of "preungulates" (peculiar mixotheridians).

- 6v (sites CBI-14, -14a, -50 and others). – Type of *?Zalambdalestes mynbulakensis*. – Part of lower jaw with last molar and part of M_2 of *Aspanlestes* sp. cf. *A. aptap* (Nessov 1985a, pl. 2, fig. 7). – Type of *Sorlestes budan*. – Type of *?Zhelestes bezelgen*. – Upper jaw with P^5–M^2 of *Zhelestes* sp. cf. *Z. temirkazyk* (Nessov 1985a, pl. 3, fig. 5) (Pl. 7, fig. 8). – Distal 2/3 of a humerus (Nessov 1985a, pl. 2, fig. 9). – Proximal end of ulna of Theria (Nessov 1985a, pl. 2, fig. 8). – Fragment of lower jaw of *Sulestes* sp., with M_1 and part of root of another tooth (Nessov 1987, pl. 1, fig. 5 and Kielan-Jaworowska & Nessov 1990, figs. 1, 2a-e). – Upper and lower teeth of a periptychid condylarth of a new genus (upper tooth figured in Nessov 1987, pl. 1, fig 2 and both upper and lower in Nessov & Kielan-Jaworowska 1991, fig. 1; Nessov & Kielan-Jaworowska in prep.). – Several teeth belonging to preungulate mixotheridians, some tending toward condylarth molar morphology. – Two (upper and lower) molars of a larger species of a new mioclaenid condylarth (Nessov & Kielan-Jaworowska in prep.). – More than 100 teeth, jaws and postcranials of proteutherians, preungulate mixotheridian and condylarths. Here has also been found a lower jaw with the ultimate molar (undescribed) characterized by a wide talonid and paraconid strongly protruding anteriorly; it belongs to a group previously unknown in the first half of the Late Cretaceous of Asia.

N.B. P_4, incisor? and two edentulous lower jaws, proximal part of humerus and one or two femora of non-tribosphenic mammals (multituberculates) were also found at this level (Kielan-Jaworowska & Nessov 1992). Rare multituberculates have been found only during this interval of the geologic section of Middle Asia.

- 6g (sites CBI-17 and -17a). – Type of *Zhelestes temirkazyk.*

The faunal assemblage of 6b, 6v and 6g includes numerous vertebrate remains representing approximately 70 families. Among them are heterodontid, odontaspidid, mitsukurinid, cretoxyrhinid and other sharks; polyodontid, acipenserid?, albulid, elopid and enchodontid actinopterygian fishes, albanerpetontid, gobiatid and many other amphibians, chelydrid-like turtles, priscagamid, teeid-like, scincid-like, necrosaurid and varanid-like lizards, azhdarchid pterosaurs, three genera of crocodiles, dromaeosaurid, ornithomimid, segnosaur, sauropod, ankylosaurid, hadrosaurid, protoceratopsid? and ceratopsid dinosaurs, alexornithiform, zhyraornithid, ichthyornithid and kuszholiid (patagopterygiform) birds and many others. Remains of sycamores, Lauraceae- and *Viburnum*-like angiosperms, manganesed paleosols and standing-up groups of tree trunks (Nessov 1980, fig. 1 and Nessov 1992a, fig. 3) with remains of brackish water vertebrates between them, were found at the level near 6g and 6d. This led to the visualization of a mosaic of water-basins and lowlands in the area of contact of these forested coastal plains and brackish water embayments. The climate was semi-humid and the environment close to a brackish water channel with sycamore forests covering the banks (Nessov 1990, fig. 1). It should be added that three-fourths of this fauna (excluding acipenserid?, polyodontid, many lizards and birds) is also found in 6a and many of the groups also occur in 6d and 6e.

6g is estimated by LAN to be approximately 270,000 years younger than 6v.

- 6d (sites CBI-5, -5a and others; these are close to the level containing the type of *Zhelestes temirkazyk* [6g] but the exact relation of 6g and 6d is difficult to determine. – Skull of a small eutherian under study (large part of braincase including the otic region of one side, two upper and lower jaws with most of the cheek teeth), mentioned in Nessov & Kielan-Jaworowska 1991, fig. 1. – Two lower teeth and one upper molar of a particular eutherian (unpublished). – Several other remains including postcranials.

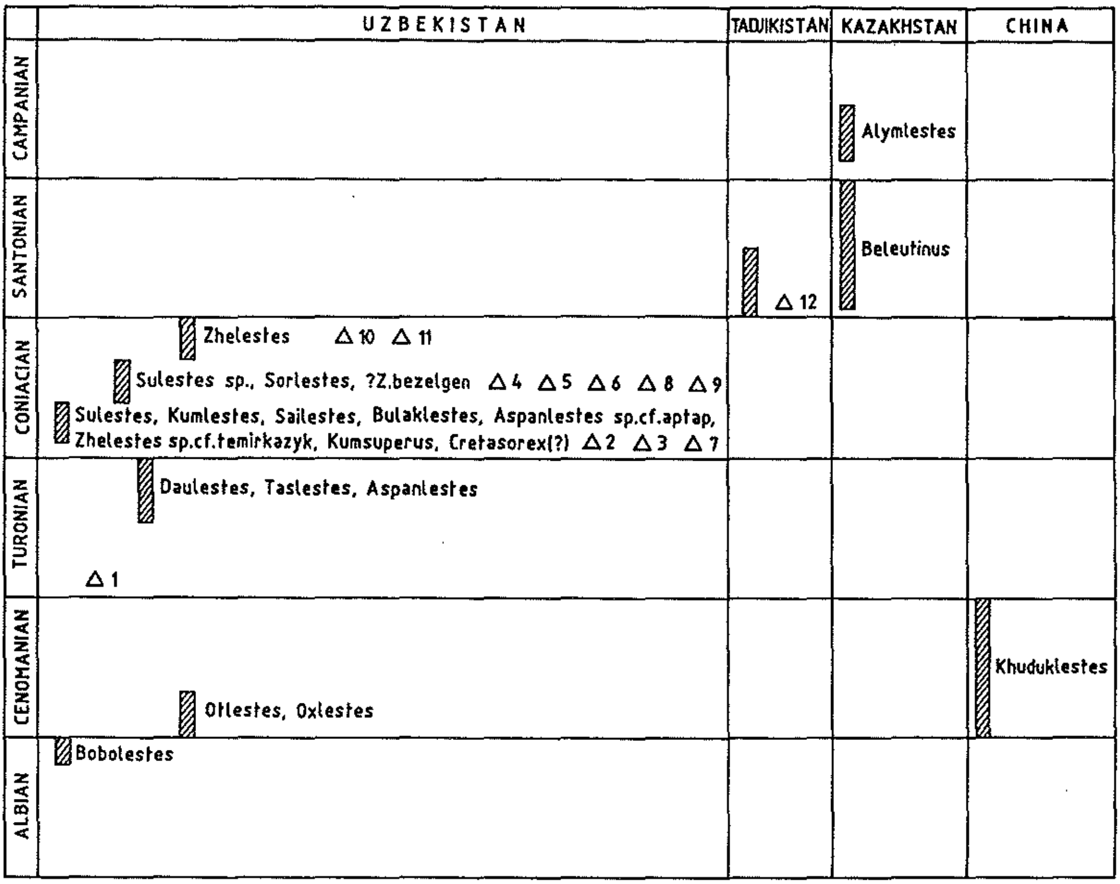

Table 3.— Stratigraphic and geographic ranges of the Albian and Late Cretaceous mammals of middle Asia and China reviewed or cited in this work; geological intervals not to scale; bars represent the time intervals for genera or species mentioned.

Δ1 – lower jaw of an unnamed eutherian from a drilling core (Ashchikol)

Δ2 – undescribed species of deltatheroid (Dzhyrakuduk)

Δ3 – undescribed genus and species of a small mixotheridian with very short trigonid on lower molars (Dzhyrakuduk)

Δ4 – undescribed species of *Zhelestes* or another zhelestid (Dzhyrakuduk)

Δ5 – undescribed genus and species of therian with paraconid relatively far anteriorly on lower molars (Dzhyrakuduk)

Δ6 – undescribed species of Lipotyphla (Dzhyrakuduk)

Δ7 and Δ8 – undescribed genus and two species of mioclaenid condylarths (Dzhyrakuduk)

Δ9 – undescribed genus and species of a periptychid condylarth (Dzhyrakuduk)

Δ10 – undescribed species of proteutherian with long labial wings on upper molars (Dzhyrakuduk)

Δ11 – skull with both lower jaws of an undescribed genus and species of small eutherian (Dzhyrakuduk)

Δ12 – undescribed species of eutherian with long labial wings on upper molars (Dzhyrakuduk)

- 6e (site CBI-7a) 3-4 kms east of the other Coniacian mammalian sites of the Dzhyrakuduk locality; it may be the same level as 6d or slightly higher. – Proximal part of a large femur (Nessov 1985a, pl. 3, fig. 13), possibly a condylarth as the biggest teeth and jaws of Coniacian mammals are condylarths. – Unpublished lower molar with a vertical carious cavity in the upper part of the crown.

Climate for the levels 6a, 6b, 6v, 6g, 6d, and 6e was semi-humid (as attested by floras, by sandstones and sands without carbonate cement, and by the formation of siderite concretions around the plant fossils) and near-tropical (high diversity of reptiles and small amphibians, Rocek & Nessov 1993).

- 7. Kansay locality (site FKA-7a). – Two eutherian molars, both found in 1984 (at least one belonging to a new genus (Nessov 1987, pl. 1, fig. 9) (Pl. 7, fig. 9).

- 8. Zhalmauz locality of the Baybolat Well area. – Type of *Beleutinus orlovi* found in 1962 (Bazhanov 1972; Nessov 1987, pl. 1, fig. 10). – Cervical vertebra (Nessov & Khisarova 1988, fig. 7).

The fossil assemblage includes *Astenopodichnium* sp. (trace fossils of May-fly larvae on the wood surface), the ray *Parapalaeobates glickmani,* sharks (*Polyacrodus* sp. cf. *P. brabanticus,* and the very common *Hybodus kansaiensis*), amiid and ichthiodectiform holosteans, scapherpetontid salamanders, lindholmemydid and trionychid turtles, lizards, crocodiles, large theropod and small dromaeosaurid and hadrosaurid dinosaurs. The environment is unknown, but brackish waters were not far.

- 9. Alymtau locality (site "Grey Mesa"). – A lower molar of *Alymlestes kielanae* AVERIANOV & NESSOV in press, was located there in 1991.

Also found in this site were thousands of shark teeth (mostly Mitsukurinidae, Anacoracidae, large Sclerorhynchidae), testifying to the beginning of the transgression in the last half of the Campanian. Other groups of vertebrates are also well represented; among them is the first Asiatic record for the crocodile *Brachychampsa.* As the latest Santonian -latest Early Campanian was the warmest period in the high latitudes of the Northern Hemisphere (as indicated in western Beringia by floras, Nessov & Golovneva 1990) it is quite possible that this time interval was important for the migration of *Brachychampsa* from North America where this genus is known from the Albian to the Paleogene.

The presence, in the assemblage 9, of sclerorhynchid teeth (of a bigger species than in assemblages 6a-v and 7) shows the salinity to be lower than that of the ocean, as these and all other pristioid chondryichtians are characteristic of the relatively low salinity of estuaries.

In the latest Early Cretaceous and early Late Cretaceous, the southwestern part of Asia (Fig. 3) was influenced by large scale (planetary) winds from the northeast (Nessov 1992c). These air masses, crossing Asia (the biggest landmass of the Northern Hemisphere), arrived there as very dry masses, but western breezes from the Tethys increased the degree of moisture in these coastal plains; this was in contrast with the situation in more inland areas. In consequence, synchronous sediments of the upper Cretaceous in the Kyzylkum Desert appear very different when going from southwestern coastal plains towards the northeast, and this over a distance of only several dozen of km. This phenomenon is materialized by the strong increase in frequency of red-colored sediments, by the presence, in more inland sediments, of concretions of strontium sulphate, by the disappearance of manganese and siderite around the wood remains, mostly replaced by silicification.

Moreover, the composition of floras and faunas (Nessov 1988, 1992b) leads to the conclusion that the climate on these coastal plains of southwest Asia, which was mostly semi-humid in the Late Albian, early Cenomanian, Late Turonian and Coniacian, became semi-arid in the early Santonian and remained so at least up to the early Campanian (possibly up to middle Campanian).

Thus the environmental conditions (temperature, moisture and dynamics of these factors) which reigned on the coastal plains of southwest Asia, in comparison to those prevailing on more central areas of Asia, led to a greater diversity of mammals (as immigrants from various mountainous areas and from colder, more northern coastal plains had the possibility to attain empty niches); this resulted in a more intense competition between ecologically similar forms and in a faster evolutionary rate, especially in the late Early Cretaceous-Coniacian interval. On the contrary, the increase in aridity and possibly continentalisation of climates in the same coastal plains in the Santonian-Campanian (thermic maximum occurred probably in the Late Santonian-Early Campanian) led to the simplification of these theriofaunas and to the replacement of many strictly specialized forms by fewer species with a wider range of ecological niches, arid biotopes included.

It is possible that the rarity of multituberculates in humid and semi-humid coastal plains of southwest Asia led to the faster evolution of therians toward plant consumption; all the more so that the insectivorous niche there must have been close to saturation, and hence subject to fierce biological competition: southern Asia was problably the region where precondylarths and condylarths evolved before the Coniacian.

Then, the same warm conditions that favored the migration of some sharks, rays, turtles and dinosaurs at the end of the Santonian could have facilitated that of precondylarths, condylarths and possibly some other mammals from Asia to North America. Just after the late Campanian in high latitudes, the climate became cooler (with a warm period again in the middle Maastrichtian). In these relatively cool intervals, precondylarths and condylarths may have lived in southern parts of North America, from where they moved up to northern USA and Canada in Bug Creek times

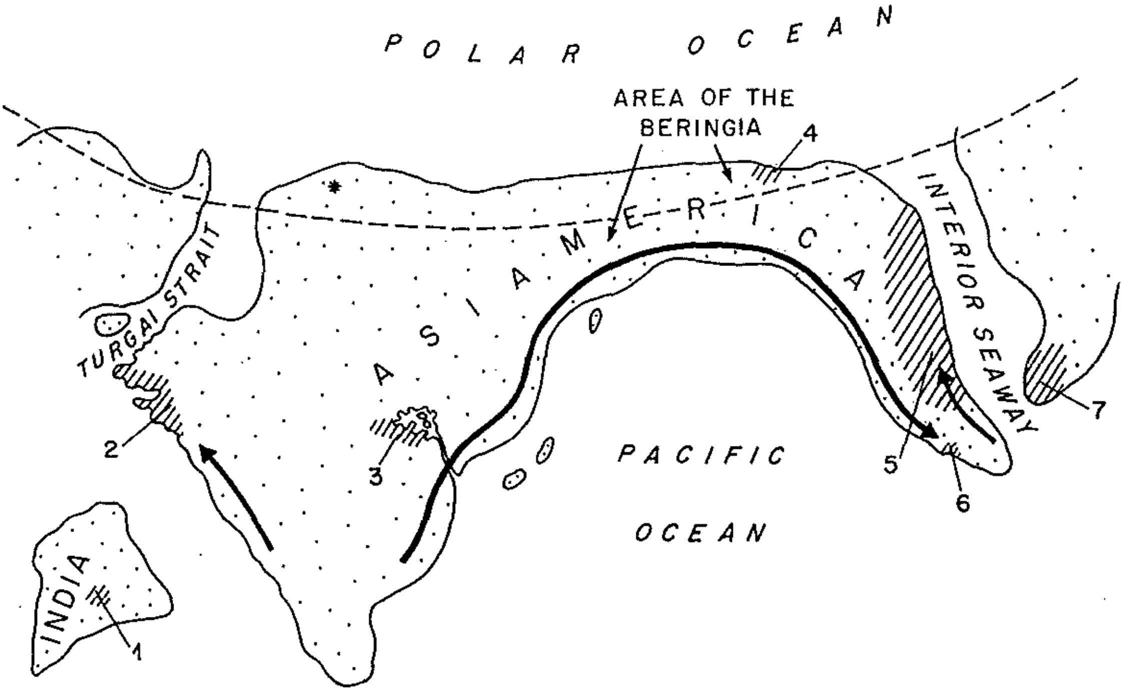

Figure 3.— Very simplified outline of Asiamerica and adjacent lands of the Northern Hemisphere, showing localities with mammalian remains and the principal migrational routes of advanced eutherians during the Late Cretaceous.

1: Andrea Pradesh (fresh or brackish water environment)
2: Uzbekistan, Kazakhstan and Tajikistan (coastal plains and estuaries, with semi-humid, near tropical climate, Nessov 1992a)
3: Mongolia and Gansu Province of the People's Republic of China (lacustrine estuaries with low salinity and relatively dry areas with semi-arid and arid climate, Jerzykiewicz 1989, Mertiniene & Nessov 1991)
4: Alaska (cold temperate climate, Clemens 1991)
5: Alberta, Saskatchewan, Montana, Wyoming, Utah, Colorado, New Mexico, etc. (coastal plains with freshwater and brackish water basins, subtropical climate, Winkler et al. 1990)
6: Mexico (coastal plains, lakes and estuaries, low salinity: semi-humid climate, temperate to warm and subtropical forested areas; Brodkorb 1976; Lillegraven 1976)
7: Texas, Mississippi... (mostly coastal plains, semi-humid temperate to warm climate in the north, semi-humid subtropical in the south, Caldwell 1975)
*: Yantardakh

(last part of the Maastrichtian). Another possibility is that condylarths emigrated from Asia to North America only in the warm interval of the middle Maastrichtian; but the presence of *Gallolestes*, related to Asiatic precondylarth forms, in the Campanian of Northern Mexico (Lillegraven 1976) and the record of a condylarth-like talonid in the Santonian of Texas (Emry *et al.* 1981) support the possibility of an earlier migration.

Finally, marsupials may have been present in the late Cretaceous of northeastern Asia (at least in the mid-Maastrichtian if not already in the latest Santonian and early Campanian): marsupials are known from Alaska (Clemens 1991) and the flora and dinosaur assemblages of the middle Maastrichtian are similar in North America (e.g. the common presence of the genus *Troodon*) and in the Kakanant locality of the Chukotka area (NE Russia) (Nessov & Golovneva 1990): this indicates comparable environmental conditions; moreover the Beringian bridge was operational. The discovery of marsupials in these levels of northeast or eastern Russia is thus to be expected.

APPENDIX

KHUDUKLESTES gen. nov.

Type species: *K. bohlini* sp. nov.

Material: Holotype: axis, Bohlin 1953, fig. 20. Specimen in I.V.P.P. Museum, Beijing, China; cast in Paleontological Institute of Uppsala, Sweden.

Locality: Tsondolein-Khuduk, Gansu Province, People's Republic of China.

Age: Cenomanian.

Attribution: Eutheria incert. sed.

Diagnosis (by comparison with *Oxlestes*): Base of odontoid process without pronounced neck-like area; same process more strongly pointed anteriorly. Anterior part of the ventral ridge not so strongly marked. Width of axis narrowing (more so than in *Oxlestes*) behind the paired articular surfaces, so that the lateral ridges are much closer to the edges of the posterior half of the centrum.

For more complete description, see Bohlin, 1953, pp. 41-42.

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LEGENDS OF PLATES

PLATE 1

Fig. 1.— *Beleutinus orlovi*, fragment of right dentary with remains of three molars; a, labial view: x 3.2; b, lingual view: x 3.2; c, occlusal view: x 4.

Fig. 2.— *Daulestes kulbeckensis*, fragment of right dentary CCMGE 1/11758, with M_1 and other fragmentary teeth; a, labial view; b, lingual view: x 10.

Fig. 3.— *Cretasorex arkhangelskyi*, posterior part of left dentary CCMGE 2/11758; posterior view: x 8.

Fig. 4.— *Taslestes inobservabilis*, fragment of right mandible 8/11758 with M_2; a, occlusal view: x 30; b, labial view: x 10.

Fig. 5.— *Oxlestes grandis*, partial axis CCMGE 6/11758; a, ventral view; b, dorsal view of ventral part: x 2.

Fig. 6.— *Sailestes quadrans*, upper right molar CCMGE 7/11758; a, occlusal view; b, labial view; c, anterior view: x 20.

Fig. 7.— *Sorlestes budan*, right M_2 CCMGE 3/12176; a, lingual view; b, occlusal view: x 20.

PLATE 2

Fig. 1.— *Kumsuperus avus*, fragment of left dentary CCMGE 12/11758 with M_1–M_3; a, labial view: x 4.3; b, occlusal view: x 15; c, posterior view: x 6.4.

Fig. 2.— *Kumlestes olzha*, fragment of left dentary CCMGE 1/12176 with two molariform teeth; a, lingual view; b, occlusal view: x 20.

Fig. 3.— *Bobolestes zenge*, fragment of right maxilla CCMGE 2/12176 with M^2–M^3; a, occlusal view; b, anterior view; c, labial view; d, posterior view: x 20.

PLATE 3

Otlestes meiman, left dentary CCMGE 9/12176; a, labial view: x 8; b, the same: x 20; c, lingual view: x 8; d, the same: x 20; e, occlusal view: x 20.

PLATE 4

Fig. 1.— *Aspanlestes aptap*, right dentary CCMGE 4/12176 with 2 premolars and the two first molars; a, labial view: x 15; b, occlusal view: x 20.

Fig. 2.— *Bulaklestes kezbe*, right upper M^3 CCMGE 12/12176; occlusal view: x 20.

Fig. 3.— *Sulestes karakshi*, fragment of left maxilla CCMGE 35/12000 with M^2–M^3; a, occlusal view; b, posterior view; c, labial view: x 20.

PLATE 5

Fig. 1.— *Zhelestes temirkazyk*, left maxilla CCMGE 10/12176 with P^2–M^3; a, lateral view: x 6; b, labial view: x 15; c, occlusal view: x 15.

Fig. 2.— *?Zalambdalestes mynbulakensis*, left M_2 CCMGE 36/12000; a, lingual view; b, occlusal view: x 20.

PLATE 6

Fig. 1.— *?Zhelestes bezelgen*, fragment of left maxilla with P^5–M^2 CCMGE 1/12455; a, occlusal view; b, labial view; c, anterior view: x 20.

Fig. 2.— *Alymlestes kielanae*, left M_2 ZIN C. 78332; a, labial view; b, anterior view; c, posterior view; d, lingual view; e, occlusal view: x 15.

PLATE 7

Fig. 1.— Parietal (possibly of *Oxlestes*), lower Cenomanian SSHD-8a; a, dorsal view; b, ventral view: x 2.

Fig. 2.— Gen. indet., left lower molar, lower Cenomanian SSHD-8; a, labial view: X8; b, occlusal view: x 10.

Fig. 3.— Gen. indet., edentulous lower jaw, lower Cenomanian SSHD-8; a, labial view; b, occlusal view: x 2.

Fig. 4.— Gen. indet., fragment of right lower jaw in drilling core, upper Turonian; labial view: about x 4.5.

Fig. 5.— Gen. indet., left upper molar, late Turonian CDZH-17a; posterior view: x 10.

Fig. 6.— Gen. indet., left upper molar, Coniacian CBI-4; a, occlusal view; b, anterior ? view: x 8.5.

Fig. 7.— Gen. indet., incisor, Coniacian CBI-4; a, medial view; b, lingual view: x 10.

Fig. 8.— Gen. indet., fragment of right maxilla, Coniacian CBI-14; occlusal view: x 10.

Fig. 9.— Gen. indet., upper molar, lower Santonian FKA-7a; posterior view: x 10.

PLATE 8

Fig. 1.— *Hybodus* sp. cf. *H. kodzhakulensis*; a, labial view; b, occlusal view (note: almost no lateral cusps). From Khodzhakul, site SKH-20, uppermost Albian.

Fig. 2.— *Hybodus sp.* cf. *H. nukusensis*, labial view (note: long labio-lingually flattened lateral cusps). Same locality, site, formation and age as 1.

Fig. 3.— *Hybodus kansaiensis*, labial view (note: moderately developed lateral cusps). From Dzhyrakuduk, site CDZH-17a, upper Turonian.

Fig. 4.— *Hybodus sp.* cf. *H. kansaiensis*, labial view (note: advanced form with wide base of the main cusp). From Kansay, site FKA-6, lower Santonian.

Fig. 5.— Primitive anacoracid ("*Eoanacorax*"), labial view. Locality, formation and age as for 1.

Figs. 6-9.— Anacoracids, labial view. Locality, site, formation and age as for 3.

Fig. 10.— Anacoracid; a, labial view; b, lingual view. From Dzhyrakuduk, site CBI-14, Coniacian.

Fig. 11.— Anacoracid, labial view. From Dzhyrakuduk, site CBI-8, upper Coniacian or Santonian.

All x 5.

PLATE 9

Fig. 1.— *Ptychocorax aulaticus*, anterior tooth; a, lingual view; b, labial view; c, occlusal view. From Sultan-Sandzar, Coniacian: x 5.

Fig. 2.— *Ptychocorax aulaticus*, lateral tooth; a, occlusal view; b, labial view. Locality, formation and age as for 1: x 5.

Fig. 3.— *Ptychocorax aulaticus*, lateral tooth; a, lateral view; b, occlusal view. From Dzhyrakuduk, site CBI-14, Coniacian: x 5.

Fig. 4.— *Ptychocorax aulaticus*, occlusal view. From Dzhyrakuduk, site CBI-18a, Coniacian: x 5.

Fig. 5.— *Paraisurus macrorhiza*, anterior tooth; a, lateral view; b, anterior view. From Khodzakul, site SKH-20, uppermost Albian: x 3.

Fig. 6.— *Myledaphus tritus*; a, occlusal view; b, anterior or posterior view. From Dzhyrakuduk, site CBI-14, Coniacian: x 6.

Fig. 7.— *Parapalaeobates glickmani*; a, occlusal view; b, anterior or posterior view. From Kansay, site FKA-7a, lower Santonian: x 6.

Fig. 8.— *Baibishia baibishe*; a, occlusal view; b, anterior or posterior view. Locality, site, formation and age as for 7: x 7.

Pl. 1, fig. 1 (*Beleutinus*) by B.S. Pogrebov, Saint Petersburg University.

Pl. 1, fig. 5 (*Oxlestes*) by D. Serrette, URA 12 CNRS.

Pl. 1, fig. 2a and b (*Daulestes*), Pl. 1, fig. 3 (*Cretasorex*), Pl. 3, fig. 1a and 1c (*Otlestes*), and Pl. 7, figs. 1-3 and 5-9, by G.I. Pustynina (All Union Geological Institute).

Pl. 5, fig. 1a (*Zhelestes*), Pl. 6, fig. 2 (*Alymlestes*) and Pl. 7, fig. 4 (gen. indet.), by LAN with help of H.A. Nakrem and P. Aas from Oslo University.

All others by C. Weber-Chancogne, URA 12 CNRS.

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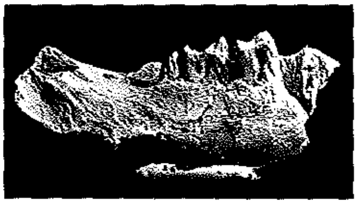
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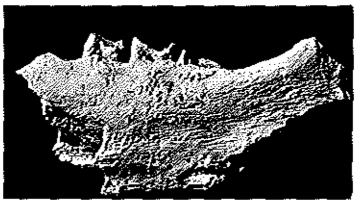
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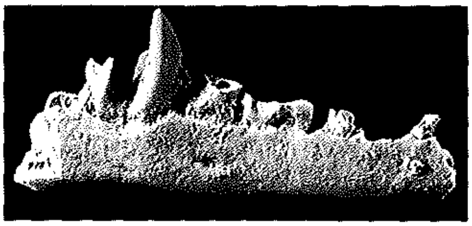
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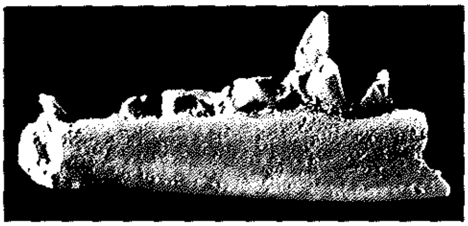
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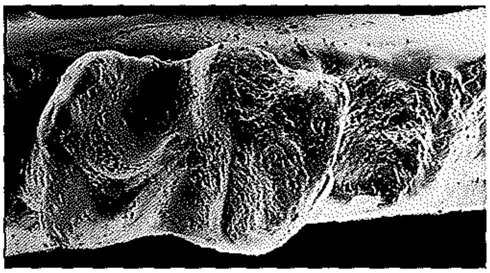
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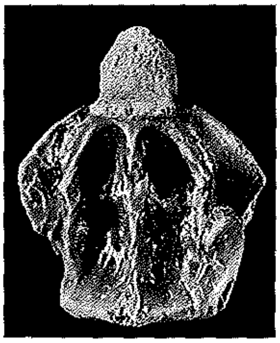
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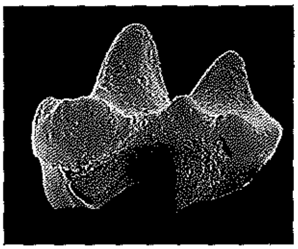
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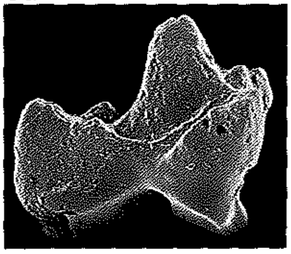
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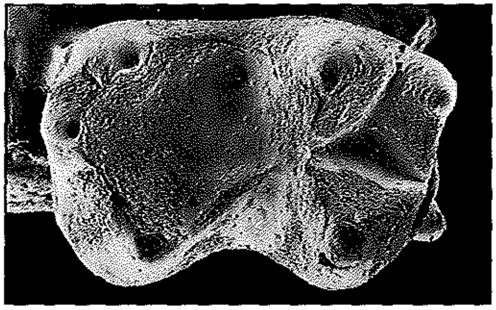
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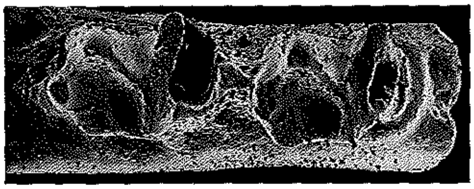
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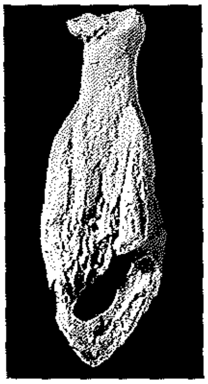
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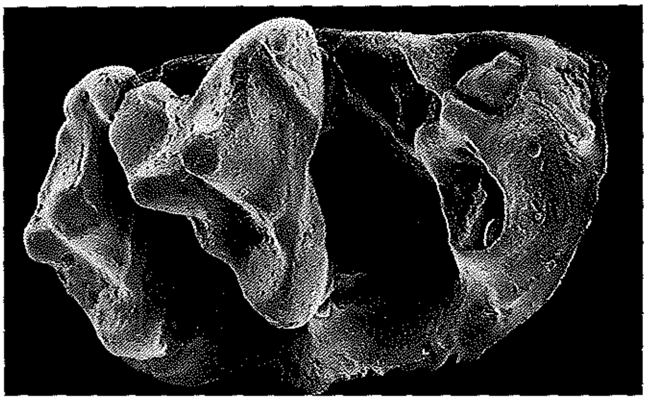
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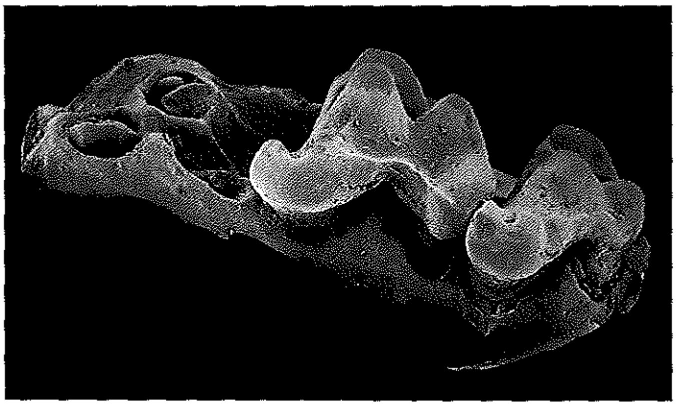
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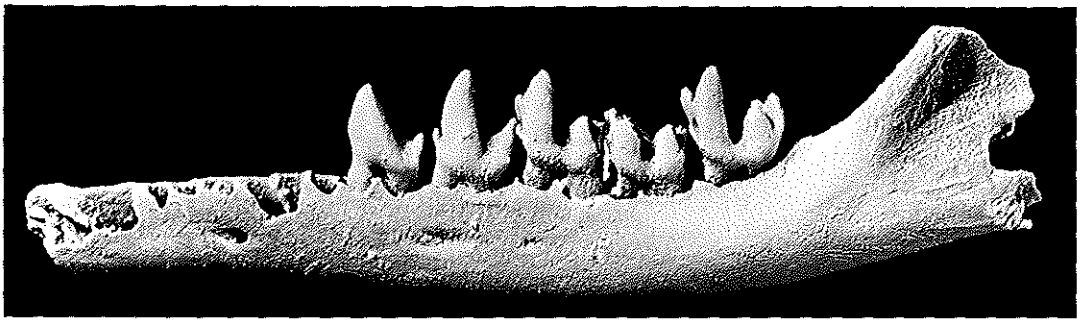
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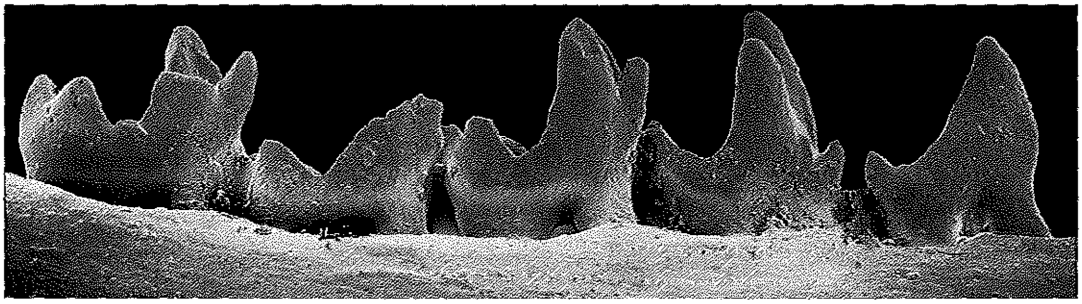
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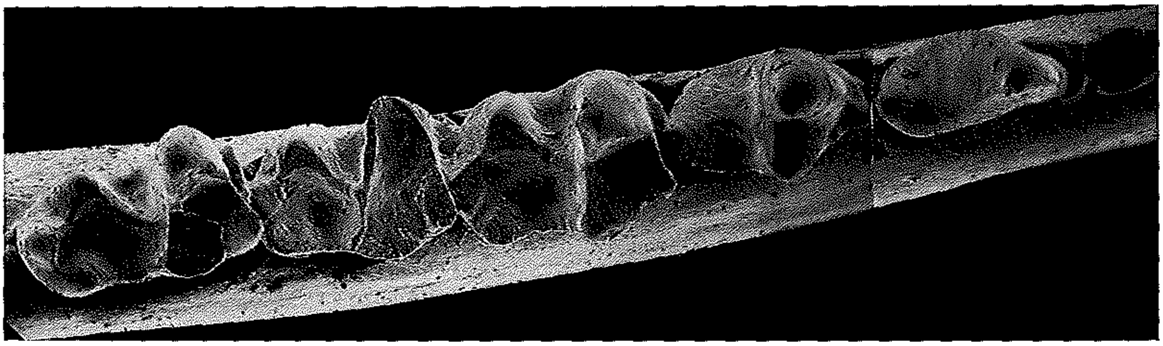
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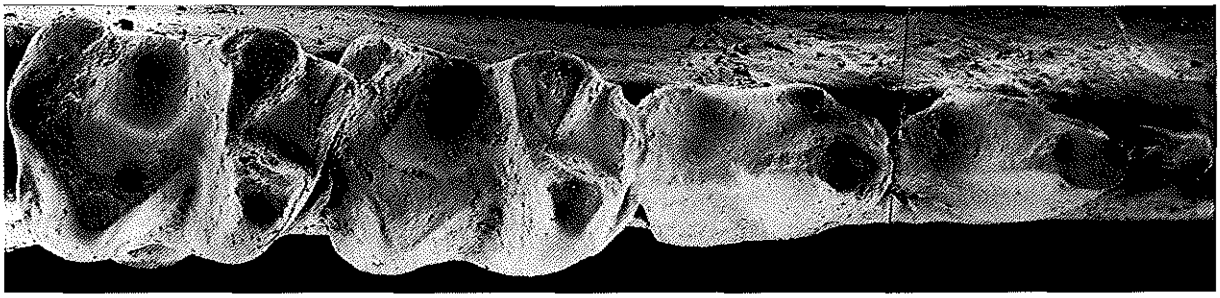
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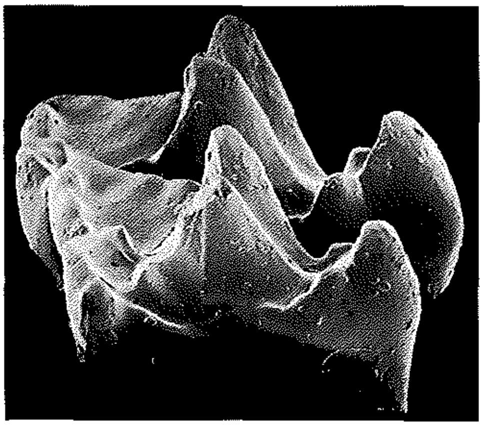
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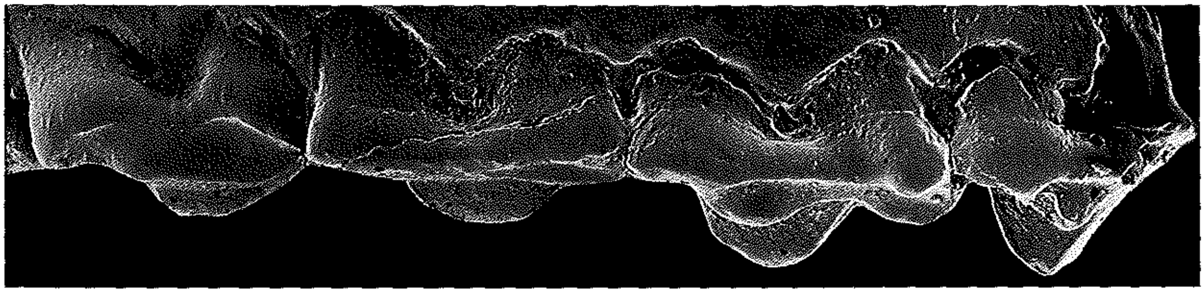

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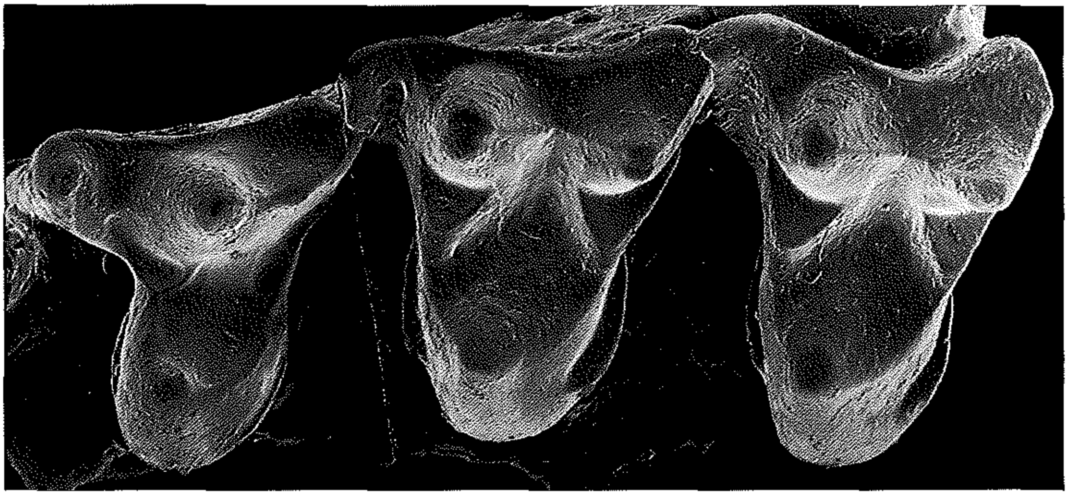
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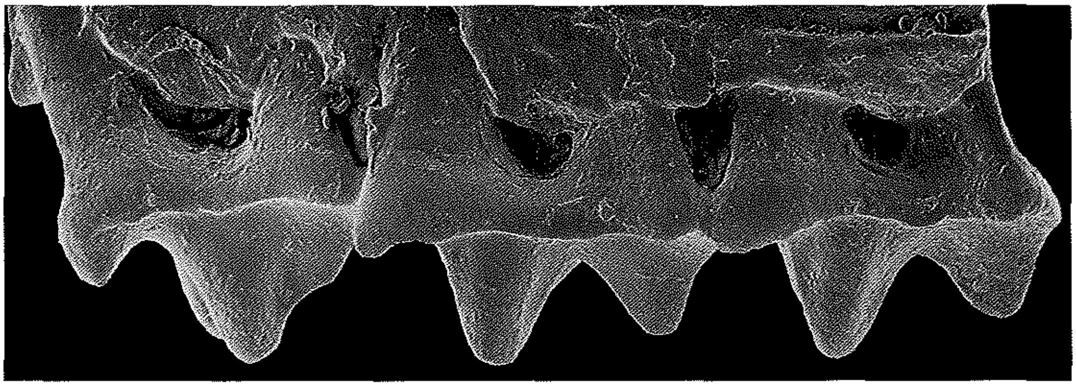
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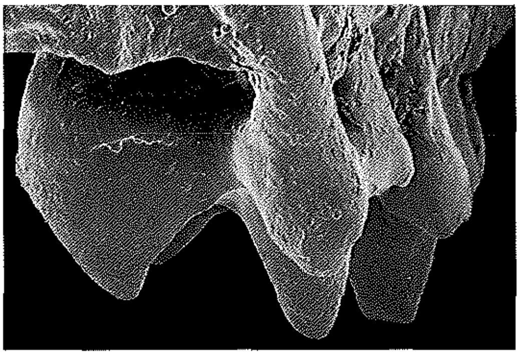
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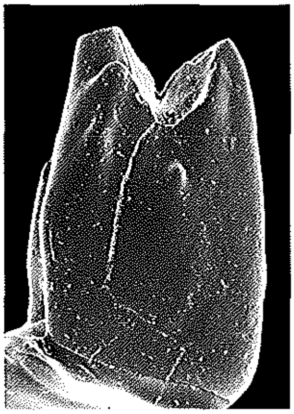
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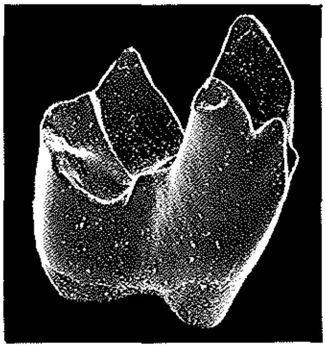
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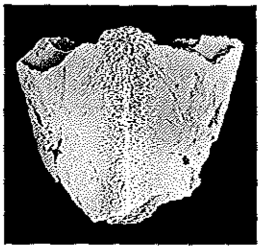
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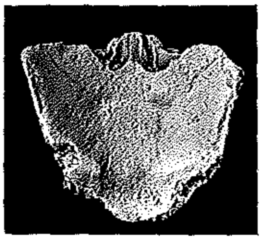
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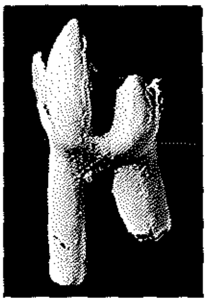
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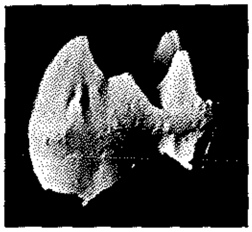
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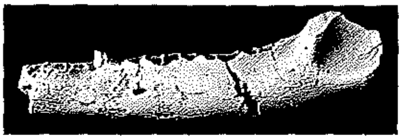
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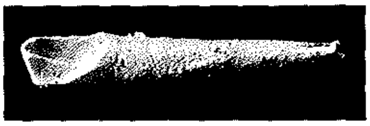
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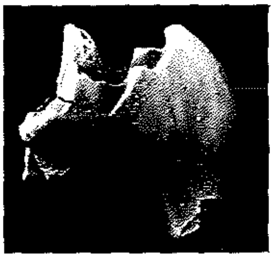
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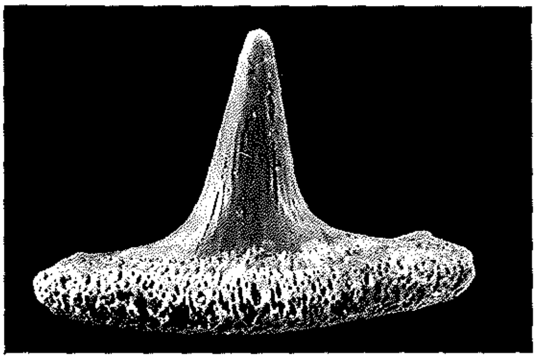
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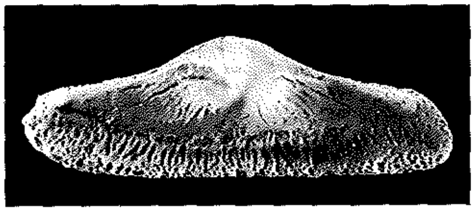
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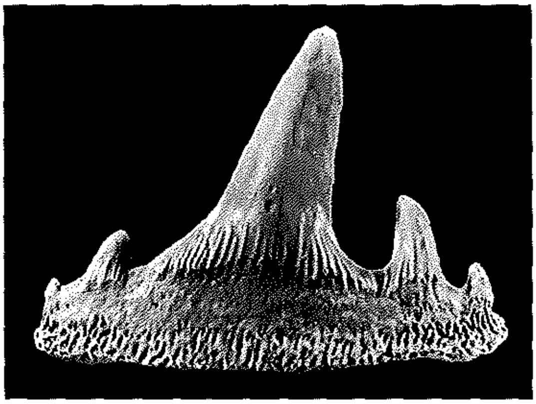
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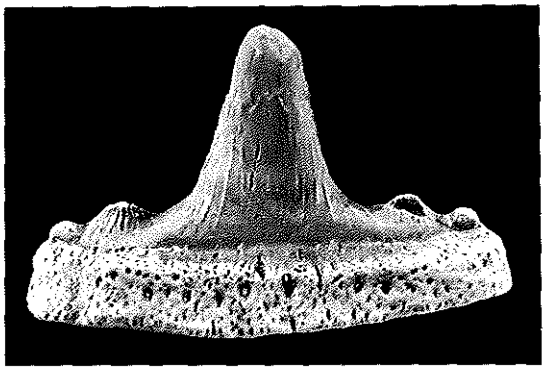
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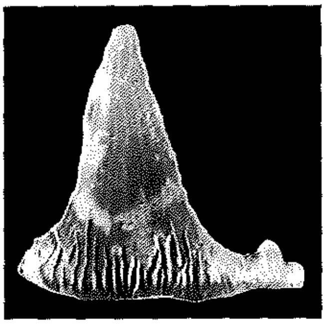
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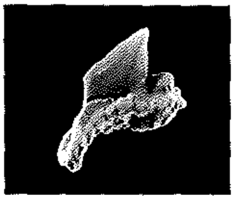
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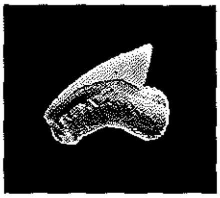
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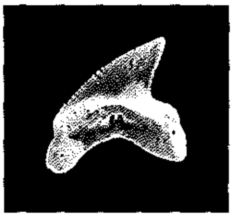
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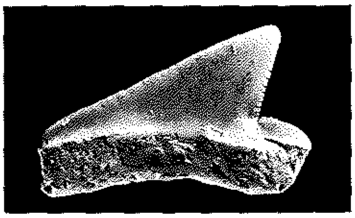
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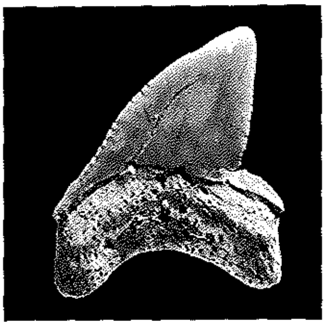
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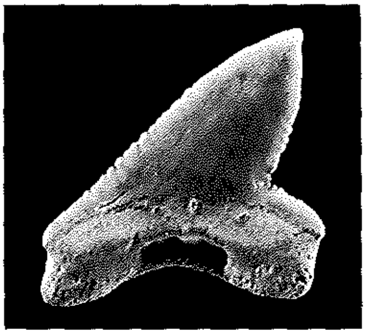
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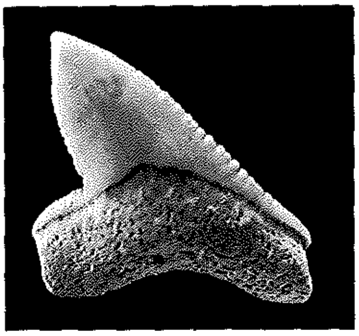
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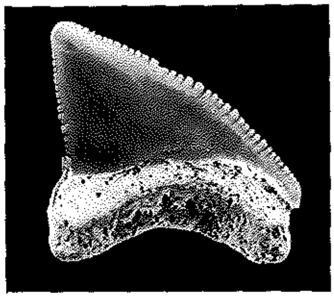
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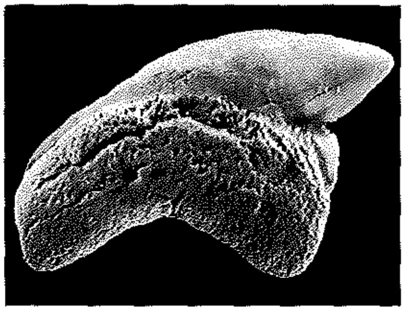
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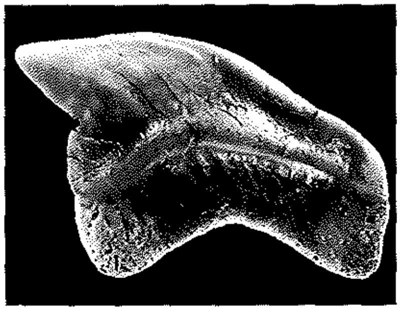
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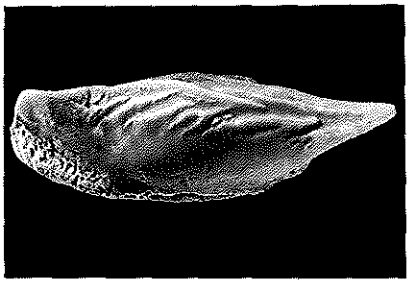
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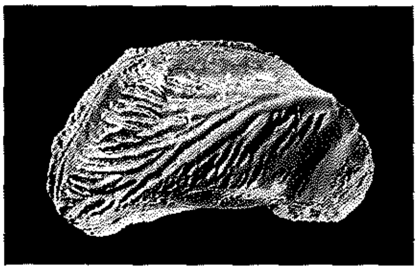
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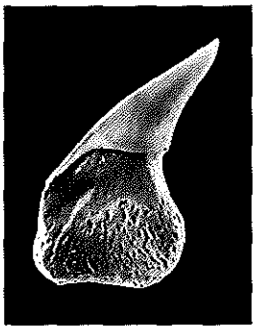
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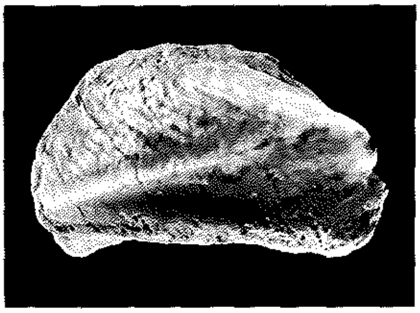
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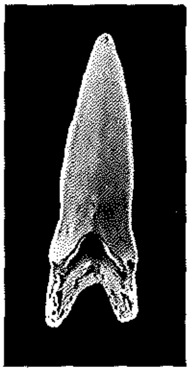
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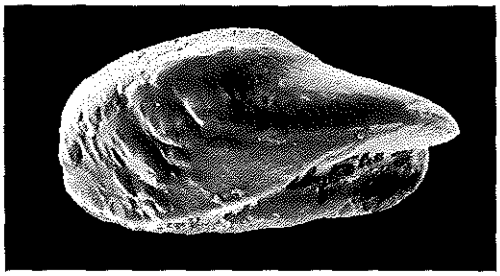
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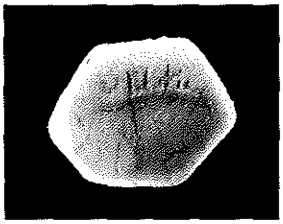
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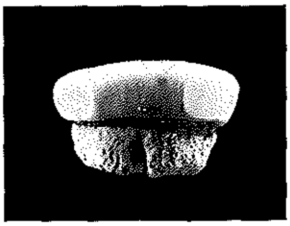
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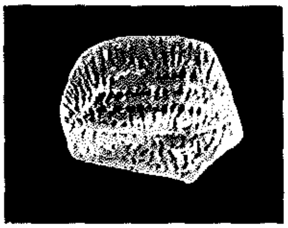
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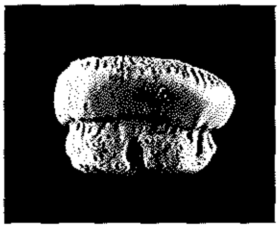
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