ZOFIA KIELAN-JAWOROWSKA

EVOLUTION OF THE THERIAN MAMMALS IN THE LATE CRETACEOUS OF ASIA. PART VII. SYNOPSIS

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The Late Cretaceous Asian therian faunas described in parts I—VI of this paper consist of four eutherian and three (one tentatively assigned) deltatheroidan genera. Main anatomical and phylogenetic results obtained from the study of the dentition, skull structure, postcranial skeleton and endocranial casts of eutherians, and the dentition and skull structure of deltatheroidans are summarized. Early and Late Cretaceous Asian therian mammals are compared. It is concluded that Late Cretaceous genera: *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes* derive from the Early Cretaceous "*Prokennalestes*" which is the oldest and most generalized known eutherian mammal. *Kennalestes* and *Asioryctes* retained many primitive characters, while the Zalambdalestidae acquired by the Late Cretaceous a high degree of specialization. It is presumed that the Eutheria originated in Asia. The place of origin of the Deltatheroida is not known, but it is possible that they originated also in Asia from *Kielantherium*-like forms in pre-Coniacian times.

Key words: Mesozoic mammals, Cretaceous, Eutheria, Deltatheroida, Asia.

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EWOLUCJA SSAKÓW THERIA W PÓŹNEJ KREDZIE AZJI. CZĘŚĆ VII. PODSUMOWANIE

Streszczenie. — Późnokredowe fauny ssaków Theria Azji, opisane w częściach I—VI niniejszej pracy, obejmują cztery rodzaje łożyskowców i trzy rodzaje deltateroidów. W pracy streszczono główne wnioski anatomiczne i filogenetyczne, wyciągnięte w częściach I—VI, w oparciu o zbadanie uzębienia, budowy czaszki, szkieletu pozaczaszkowego i odlewów jamy czaszki ssaków łożyskowych, oraz uzębienia i budowy czaszki deltateroidów. Porównano wczesno- i późnokredowe ssaki Theria Azji. Cztery rodzaje łożyskowców: *Kennalestes*, *Asioryctes*, *Zalambdalestes* i *Barunlestes* pochodzą od wczesnokredowego rodzaju "*Prokennalestes*", który jest najprymitywniejszym znanym łożyskowcem. Rodzaje *Kennalestes* i *Asioryctes* charakteryzują się prymitywną budową, gdy natomiast Zalambdalestidae osiągnęły w późnej kredzie wysoki stopień specjalizacji. Przeprowadzone badania wskazują, że ssaki łożyskowe najprawdopodobniej powstały w Azji. Miejsce powstania Deltatheroida jest nieznane, aczkolwiek wydaje się możliwe że wyodrębniły się one również w Azji, przed koniakiem, z form zbliżonych do *Kielantherium*.

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INTRODUCTION

In a series of papers entitled: „Evolution of the therian mammals in the Late Cretaceous of Asia" of which the present one is the seventh and the last, I have described the therian mammals collected by members of the Polish-Mongolian Palaeontological Expeditions between 1963 and 1971, from the rocks of the Upper Cretaceous age in the Gobi Desert, Mongolian People's Republic. The six papers of this series so far published (KIELAN-JAWOROWSKA 1975*b*, 1977, 1979, 1981, 1984*a*, 1984*b*) were confined respectively to: 1) the family Deltatheridiidae; 2) postcranial skeleton in *Kennalestes* and *Asioryctes*; 3) postcranial skeleton in *Zalambdalestidae*; 4) skull structure in *Kennalestes* and *Asioryctes*; 5) skull structure in Zalambdalestidae; 6) endocranial casts of eutherian mammals; (see also KIELAN-JAWOROWSKA 1969, 1975*a*, 1982, CROMPTON and KIELAN-JAWOROWSKA 1978, KIELAN-JAWOROWSKA and TROFIMOV 1980, 1981).

The collection described in the above mentioned papers and discussed in the present one, housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, derives from the rocks of the Djadokhta Formation (locality of Bayn Dzak), Barun Goyot Formation (localities of Nemegt and Khulsan) and the red beds of Khermeen Tsav (locality of Khermeen Tsav II). The ages of these formations are disputable; that of the Djadokhta Formation has been estimated by GRADZIŃSKI *et al.* (1977) as ?late Santonian and/or ?early Campanian, and that of the Barun Goyot Formation and of the red beds of Khermeen Tsav as ?middle Campanian. These estimates generally concur with those of FOX, who stated (1978: 577): „Also inconclusive, the available evidence suggests that east Asian Djadokhta and Barun Goyot Formations are Campanian in age". However, recently KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO (1983) claimed on charophytan evidence that the Nemegt Formation which overlies conformably the Barun Goyot Formation is not younger than the Lower Campanian Stage. It follows that the Barun Goyot Formation may belong to the ?upper part of the Santonian Stage and the Djadokhta Formation to the ?lower part of the Santonian or ?upper part of the Coniacian Stage. All these estimates should be regarded as tentative.

Late Cretaceous Asian therian mammals were collected earlier from the rocks of the Djadokhta Formation by members of the Central Asiatic Expeditions of the American Museum of Natural History in New York. This material is housed in the American Museum of Natural History and consists of 8 therian specimens (GREGORY and SIMPSON 1926, SIMPSON 1928, SZALAY and MCKENNA 1971).

The Soviet-Mongolian Palaeontological Expeditions have conducted, since 1970, excavatory work in the territory of Mongolia. They assembled, among others, a spectacular collection of Early Cretaceous mammals (BELIAJEVA *et al.* 1974), housed in the Palaeontological Institute, USSR Academy of Sciences in Moscow. Late Cretaceous therian mammals have been found by members of these expeditions in Toogreeg beds at the locality of Toogreeg (one specimen of *Zalambdalestes lechei*, see KIELAN-JAWOROWSKA and TROFIMOV 1981) and in the red beds of Khermeen Tsav at the locality of Khermeen Tsav II. The therian collection from Khermeen Tsav II housed in the Palaeontological Institute in Moscow consists, to the best of my knowledge, of 2 specimens of *Barunlestes butleri*, one of which has been described (KIELAN-JAWOROWSKA and TROFIMOV 1980).

Outside Mongolia the record of Late Cretaceous therian mammals of Asia is very scanty and consists of only 3 specimens. BOHLIN (1953) described one specimen (the body of an axis) of a mammal from the Late Cretaceous rocks of northern Kansu province in China, but one cannot even be sure whether this specimen belongs to a therian or non-therian mammal. BASHANOV (1972) described one specimen designated *Beleutinus orlovi*, which is a lower jaw with heavily damaged teeth plus alveoli, found in Kazakhstan (Soviet Union) in beds of presumable Coniacian age. The specimen is badly damaged and its affinity is uncertain (see

CLEMENS *et al.* 1979: 37, for discussion). TROFIMOV and NESOV (*in*: NESOV and TROFIMOV 1979) described a new genus and species *Daulestes kulbeckensis*, based on a single fragmentary lower jaw with incomplete dentition, from the Late Turonian of the Central Kyzyl Kum Desert in the Uzbek SSR and assigned it to the Zalambdalestidae. The zalambdalestid affinities of this species are uncertain (see KIELAN-JAWOROWSKA 1984*a*). As all of these three specimens are poorly preserved and their affinities are not clear, I shall not discuss them further.

The Late Cretaceous therian mammals of Mongolia are of special interest because of their unusual state of preservation. North American, South American and European Late Cretaceous therian faunas (ARCHIBALD 1982, CLEMENS 1966, 1968, 1973, CLEMENS and RUSSELL 1965, FOX 1970, 1971, 1972, 1974, 1976, 1979*a*, 1979*b*, 1979*c*, GRAMBAST *et al.* 1967, LEDOUX *et al.* 1966, LILLEGRAVEN 1969, 1972, 1976, MARSHALL *et al.* 1983*a*, 1983*b*, SAHNI 1972, SIGÉ 1972, SLOAN and VAN VALEN 1965, VAN VALEN and SLOAN 1965; see also CLEMENS 1979, KIELAN-JAWOROWSKA, EATON and BOWN 1979 and KIELAN-JAWOROWSKA, BOWN and LILLEGRAVEN 1979 for reviews), are usually represented by isolated teeth, fragments of jaws with teeth and rarely isolated fragments of brain cases or isolated bones from the postcranial skeletons. In contrast the Late Cretaceous therian mammals of Asia are often preserved as entire skulls, sometimes associated with articulated postcranial skeletons. A few endocranial casts have also been found.

EARLY CRETACEOUS ASIAN THERIAN MAMMALS

The roots of the Late Cretaceous Asian therian mammals are to be found among the Early Cretaceous therians from the same continent. The latter are known only from two localities. The first is the „Hsinchiu" coal mine (see CLEMENS *et al.* 1979 for full references and discussion), where only one therian mammal, possibly a eutherian, *Endotherium niinomii* SHIKAMA, has been found. The specimens of *Endotherium* have been lost, but the drawing of the lower jaw (SHIKAMA 1947) shows that this was a relatively advanced ?eutherian mammal. The age of the beds yielding *Endotherium* is uncertain, late Early Cretaceous (possibly Aptian or Albian) has been suggested (PATTERSON 1956).

The second, much more rich locality is that of Khovboor near Guchin Us in Mongolia (KALANDADZE and RESHETOV 1971). The age of the Khovboor beds is uncertain, it has been refered to as Aptian or Albian (BARSBOLD *et al.* 1971). The mammals in KHOVBOOR were collected by members of the Soviet-Mongolian Palaeontological Expeditions (and are housed in the Institute of Palaeontology, USSR Academy of Sciences, Moscow) and by Mongolian palaeontologists (housed in the Stratigraphy and Palaeontology Laboratory, Institute of Geology, Academy of Sciences of the Mongolian People's Republic in Ulan Bator). These collections comprise about 500 specimens (TROFIMOV 1978), including isolated teeth, jaws with teeth and fragments of postcranial skeletons.

So far five species have been described from these collections. These are: *Kielantherium gobiensis* DASHZEVEG, a member of the Aegialodontia and *Arguimus khosbajari* DASHZEVEG, an eupantothere (DASHZEVEG 1975, 1979); *Gobiconodon borissiaki* TROFIMOV and *Guchinodon hoburensis* TROFIMOV, triconodonts, and *Arginbaatar dimitrievae* TROFIMOV, a multituberculate (TROFIMOV 1978, 1980).

In addition BELIAJEVA *et al.* (1974) published a list of mammals found in Khovboor, which includes among others two eutherian species „*Prokennalestes kozlovi*" and „*Prozalambdalestes simpsoni*". Both these species are here cited enclosed by quotation marks, because they have been named but not described or figured (as other species listed by BELIAJEVA *et al.* 1974) and may be cited only as *nomina nuda*. Of the species so far described or named from Khovboor

beds, only *Kielantherium gobiensis*, „*Prokennalestes kozlovi*" and „*Prozalambdalestes simpsoni*" are relevant to this discussion. However, „*Prozalambdalestes simpsoni*", as identified by Dr. B. A. TROFIMOV in the PIN collection in Moscow, is represented there only by one lower jaw of an old individual (with worn teeth) and is poorly known. Therefore in the discussion that follows I will not refer to „*Prozalambdalestes*".

Kielantherium gobiensis DASHZEVEG, 1975, assigned to the Aegialodontidae, is known from a single lower molar, which is similar to the oldest known common ancestor of eutherian and metatherian mammals: *Aegialodon* from the Wealden of England (KERMACK *et al.* 1965). FOX (1976) argued that *Kielantherium* should be considered a junior synonym of *Aegialodon*. However, because of temporal differences, geographic separation and incomplete knowledge of both genera, it would seem premature to synonimise them.

RELATIONSHIPS OF LATE CRETACEOUS ASIAN THERIAN MAMMALS

The collections of Late Cretaceous therians of Mongolia include seven genera: *Deltatheridium*, *Deltatheroides*, *Hyotheridium*, *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes* (GREGORY and SIMPSON 1926, SIMPSON 1928, KIELAN-JAWOROWSKA 1969, 1975*a*, 1975*b*, 1977, 1979, 1981, 1984*a*), of which the latter four are recently classified as undoubted eutherian mammals.

The Deltatheridiidae, assigned to Theria of metatherian-eutherian grade (BUTLER and KIELAN-JAWOROWSKA 1973, KIELAN-JAWOROWSKA 1975*b*) are now regarded as belonging to a separate order Deltatheroida, erected by me (KIELAN-JAWOROWSKA 1982), in Theria *incertae sedis*. The family includes two genera: *Deltatheridium* and *Deltatheroides*. *Hyotheridium* is reminiscent of the Deltatheridiidae, but as it is known only from a single, badly damaged specimen, its features cannot be distinguished and its assignment to the Deltatheridiidae is only tentative.

The brain case structure and postcranial skeleton are unknown in the members of the Deltatheridiidae. As I pointed out earlier (KIELAN-JAWOROWSKA 1975*b*), the structure of the snout and dentition are quite different between the Deltatheridiidae and the Mongolian Late Cretaceous eutherian mammals (Fig. 1). The Deltatheridiidae are characterized by a short snout (suggesting a carnivorous specialization), strong zygomatic arches, and differ from eutherian mammals which have slender, elongated snouts with slender zygomatic arches. The dentition is also very different. In the Deltatheridiidae there is a strong single-rooted canine, followed by the non-molariform premolars and 3—4 molars, whereas in eutherian mammals the canine (except for *Barunlestes*) is double-rooted, there are 4 premolars (5 in juvenile *Kennalestes*) and 3 molars.

The premolars are trenchant and not molariform in the Deltatheridiidae and there is a sharp morphological change between the premolars and the molars, whereas the premolars become gradually more and more molariform in eutherian genera and the fourth premolars do not differ (or differ very little) from the molars. The coronal structure of the molars is different in two groups discussed. The upper molars of the Deltatheridiidae are relatively shorter transversely, the conules are not winged, the talonids are very narrow and situated in one line with paraconid-metaconid. In contrast the paraconid is taller than the metaconid in eutherian genera, the conules are winged (poorly expressed in Zalambdalestidae), the upper molars are more elongated transversely, the talonids are comparatively wide and the paraconid is shorter than the metaconid. There are only 5 shearing surfaces on the molars of the Deltatheridiidae, whereas 6 in the eutherian mammals (CROMPTON and KIELAN-JAWOROWSKA 1978).

It seems that the Deltatheroida arose from the Aegialodontia in Asia in pre-Coniacian times and the ?Albian *Kielantherium* may reside close to their ancestors.

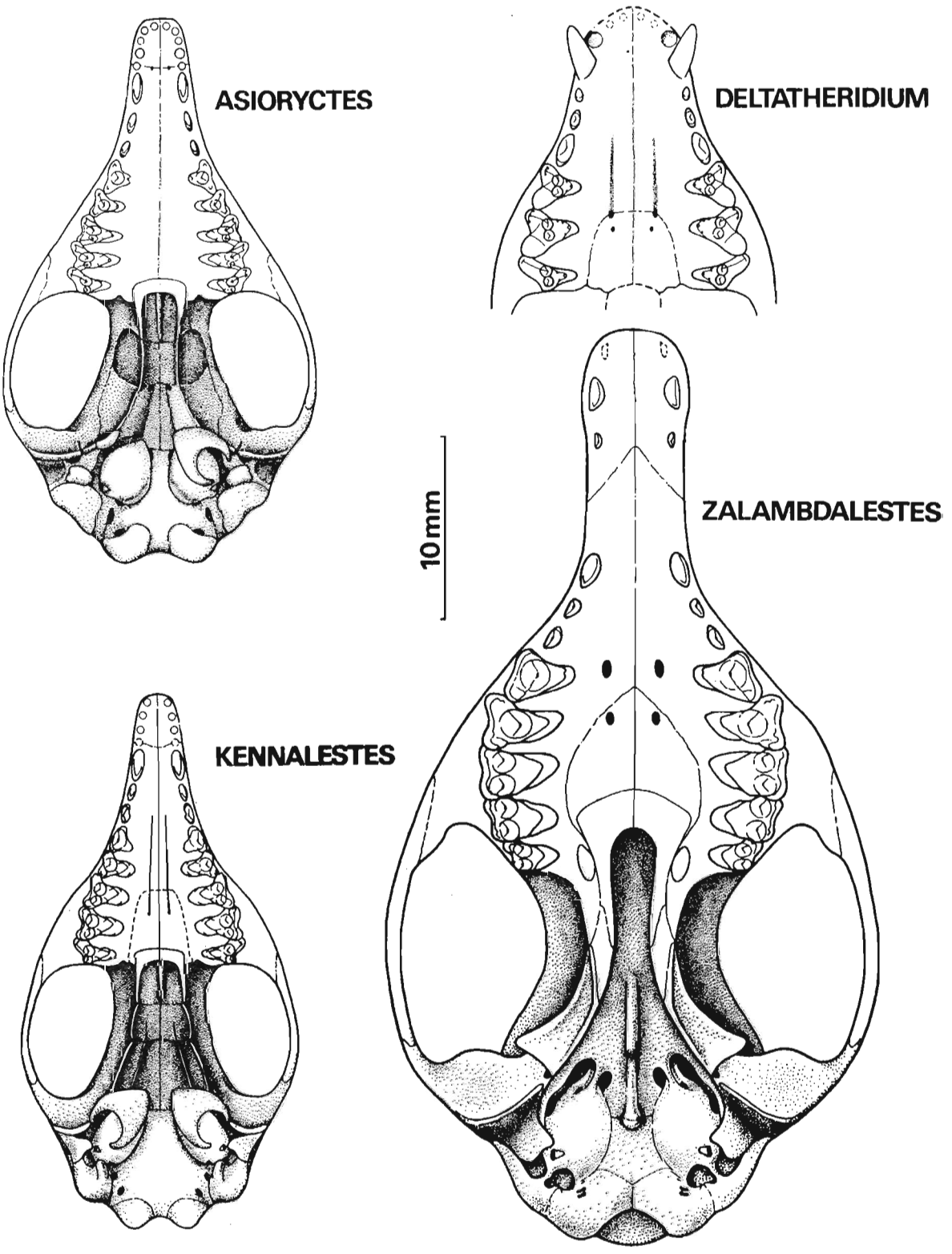

Fig. 1
Reconstruction of the skulls of four Late Cretaceous Asian therian mammals in ventral view: *Kennalestes gobiensis* and *Zalambdalestes lechei* (both from the Djadokhta Formation); *Asioryctes nemegetensis* and *Deltatheridium pretrituberculare tardum* (both from the Barun Goyot Formation).

The Late Cretaceous eutherian Asian genera have been assigned to three different families within Proteutheria ROMER 1966: *Kennalestes* to the Kennalestidae, *Asioryctes* to the subfamily Asioryctinae within the Palaeoryctidae, *Zalambdalestes*, *Barunlestes* and (tentatively) *Daulestes* to the Zalambdalestidae. The genera discussed, differing so much from each other that they may be assigned to three different families, still have several characters in common, suggesting that they were derived from a common, not very distant ancestor. The possible candidate for such an ancestor is „*Prokennalestes*" from the Early Cretaceous Khovboor beds of Mongolia.

It appears from personal information from Dr. B. A. TROFIMOV (see KIELAN-JAWOROWSKA, BOWN and LILLEGRAVEN 1979 : 242) that „*Prokennalestes*" has 5 premolar loci and 3 molars. The upper molars have paracone larger than the metacone, wide stylar shelf, small, winged conules, prominent protocone and lack pre- and postcingula. As far as the dentition is concerned, „*Prokennalestes*" is the most generalized eutherian mammal known.

CROMPTON and KIELAN-JAWOROWSKA (1978 : fig. 1) basing on the structure of *Aegialodon*, *Kielantherium*, *Pappotherium*, other primitive therians, and *Kennalestes*, reconstructed the molars of a hypothetical, generalized Early Cretaceous therian mammal, which is placed in the line of evolution leading to the Eutheria. It seems that „*Prokennalestes*" is on the level of organization represented by this hypothetical form.

The molars of *Kennalestes* are very close to those of „*Prokennalestes*", from which they differ in having pre- and postcingula, the postcingulum being considerably longer and wider than the precingulum. Another difference is the presence of 4 premolars in adult *Kennalestes* (but 5 in juvenile form), whereas 5 are retained in adult „*Prokennalestes*". It is easy to derive the postcanine dentition of *Kennalestes* from forms close to „*Prokennalestes*".

The molars of the remaining Late Cretaceous Asian eutherian genera, although differing from *Kennalestes*, may be derived with some modification from „*Prokennalestes*" — like forms. The upper molars of *Asioryctes* lack pre- and postcingula and thus retain the primitive feature of „*Prokennalestes*". They are, however, strongly specialized beyond the level of „*Prokennalestes*" in being short longitudinally, strongly elongated transversely, having a narrow stylar shelf, an enlarged paracone in contrast to a small metacone and lacking (or having small) metaconule.

Similarly the upper molars of *Zalambdalestes* and *Barunlestes* (unknown in *Daulestes*), although highly specialized, retain the primitive feature of „*Prokennalestes*" such as the lack of pre- and postcingula. They are characterized by a very short stylar shelf with a small metastylar area, poorly pronounced conules, great enlargement of the talonid in the lower molars with a very large hypoconid, which is correlated with a large groove between the paracone and metacone.

As has already been pointed out elsewhere (KIELAN-JAWOROWSKA 1975*b*) the Late Cretaceous Asian eutherian genera, although differing from each other in the coronal structure of the molars, are similar in the general appearance and organization of the dentition, when seen in lateral view. All have a strong double-rooted upper canine (secondarily single-rooted in *Barunlestes*), situated some distance to the rear of the premaxillary-maxillary suture, followed, after a short space, by small P^1 and P^2 that are double-rooted and do not come into occlusion with the lower premolars. In all genera P^3 is the strongest tooth of the whole series, with a high, piercing paracone and P^4 is semi-molariform. Upper canine, and upper premolars except for the last, have, to my knowledge, not been found in „*Prokennalestes*", but I presume that they would have been of the same pattern as in the above cited Late Cretaceous eutherian genera. P^5 in „*Prokennalestes*", (corresponding to the tooth designated P^4 in *Kennalestes*) is semi-molariform as in *Kennalestes*.

The number of the incisors is not known in „*Prokennalestes*", but as it is 4/3 in *Kennalestes* and 5/4 in *Asioryctes* (which is a metatherian dental formula), one can presume that in „*Prokennalestes*" there were more than 3/3 incisors characteristic of modern Eutheria. For the time being the comparisons with „*Prokennalestes*" have to be limited to post-canine dentition only.

The skull structure in the Late Cretaceous Asian eutherian mammals is comparatively well known. The common features of the four eutherian genera in which the skulls are known, are as follows: slender snout, slender zygomatic arch, inclination of the occipital plate forwards from the condyles, ectotympanic inclined to the horizontal, large promontorium, no entotympanic, long jugal, no paroccipital process, medial inflection of the angular process of the dentary. The internal carotid and stapedial arteries are present, but there is no promontory artery. This pattern of internal carotid circulation supports in my opinion (KIELAN-JAWOROWSKA 1981), PRESLEY'S (1979) idea, that the medial internal carotid and promontory arteries are not separate vessels, but the same one which may move in ontogeny and phylogeny laterally or medially over the promontorium. The skulls of *Kennalestes* and *Asioryctes* are more similar to each other than either of them is to the representatives of the Zalambdalestidae. They differ from the Zalambdalestidae in having moderately elongated snouts (strongly elongated in Zalambdalestidae) and a relatively longer mesocranial region. The basisphenoid wing, homologous to the basipterygoid process of cynodonts is characteristic of *Kennalestes* and *Asioryctes*, but is absent from the Zalambdalestidae. In *Asioryctes* (and possibly also *Kennalestes*) f. rotundum is confluent with the sphenorbital fissure, whereas in the Zalambdalestidae it is separated.

The endocranial casts in *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes* (KIELAN-JAWOROWSKA and TROFIMOV 1980, KIELAN-JAWOROWSKA 1984*b*) represent the casts of primitive therian lissencephalic brains with very large olfactory bulbs, cerebral hemispheres widely separated posteriorly, large midbrain exposure on the dorsal side and a comparatively short and wide cerebellum. The rhinal fissure has not been found in *Kennalestes* and *Barunlestes*, it is tentatively recognized in *Asioryctes*, in which the neocortex is very small, while in *Zalambdalestes* it is situated low down on the lateral side of the hemisphere, suggesting the presence of an extensive neocortex. The encephalization quotient could not be evaluated for *Barunlestes butleri*; it is tentatively 0.36 for *Kennalestes gobiensis*, 0.56 for *Asioryctes nemegetensis* and 0.70 for *Zalambdalestes lechei*. The four genera in question were probably more macrosmatic than most Tertiary and recent mammals, and favoured nocturnal niches in which olfaction and hearing were important senses.

The great differences between *Asioryctes* and the representatives of the Zalambdalestidae concern the postcranial skeleton (in *Kennalestes* only an atlas has been preserved). The preserved parts did not allow reconstruction of the entire skeleton of *Asioryctes*. However, a comparison of the preserved parts with the skeleton of *Didelphis* has allowed me (KIELAN-JAWOROWSKA 1977) to define the list of features which are characteristic of *Asioryctes* and at the same time may be regarded as symplesiomorph therian character states. The most important of these are the following: primary lack of the transverse foramen in the atlas; the suture between the synostosed axial and atlantal parts of the second cervical vertebra; three bones in the proximal row of the carpus; centrale and praepollex present; incipient superimposition of the astragalus on the calcaneus; tibial trochlea on the astragalus not developed; astragalo-cuboid contact present. The pelvis in *Asioryctes* has not been preserved and it is not known whether marsupial bones were present. As, however, there is an indirect evidence (KIELAN-JAWOROWSKA 1975*c*) that the marsupial bones were present in the Zalambdalestidae, it is possible that they were also present in *Kennalestes* and *Asioryctes*. Their presence may be regarded as a symplesiomorph therian character state.

The postcranial skeleton is in the Zalambdalestidae much more advanced than that in *Asioryctes* and shows a mosaic of primitive and advanced characters (KIELAN-JAWOROWSKA 1979). The transverse foramen in the atlas, absent in *Asioryctes* is present in *Barunlestes* (unknown in *Zalambdalestes*). *Barunlestes* is the oldest known eutherian mammal in which the transverse foramen in the atlas makes its appearance. The specialized feature of the neck in the Zalambdalestidae is the structure of the spinous process of the axis, which is unusually long and horizontally directed. A primitive feature of the zalambdalestid vertebral column is the structure

of the sacrum (unknown in *Asioryctes*), which consists of two vertebrae, only the first articulating with the ilium. In the carpus of *Barunlestes*, in contrast to *Asioryctes*, the scaphoideum and lunatum are fused into scapholunatum. Specialized features of the hindlimb of the Zalambdalestidae are a strong degree of fusion of the tibia and fibula and very long metatarsals. The tarsus in Zalambdalestidae has a structure characteristic of modern Eutheria, having astragalus supported by the calcaneus and a well developed tibial trochlea (in contrast to *Asioryctes*).

It has been concluded that the locomotion of the Zalambdalestidae was similar to that of the present-day Macroscelididae and that all the Late Cretaceous Mongolian eutherian genera studied lived in a semi-desert habitat (KIELAN-JAWOROWSKA 1977, 1979).

The above comparisons show that although *Kennalestes*, *Asioryctes* and the Zalambdalestidae have many features in common, which show that they derive from a common ancestor, they differ very much in details of their structure, *Kennalestes* and *Asioryctes* retaining numerous primitive characters, the Zalambdalestidae evolving faster and acquiring by the Late Cretaceous a high degree of specialization.

I have discussed the paleogeography of Cretaceous Theria elsewhere (KIELAN-JAWOROWSKA 1982, see also LILLEGRAVEN 1974 and LILLEGRAVEN *et al.* 1979) and I argued that in the late Early Cretaceous, when seaway between the main continents appeared, three (or four) geographically isolated centres of development of the therian mammals were formed in the Northern Hemisphere: eastern North America; western North America; Asia and possibly Europe. I also presumed that from the common *Aegialodon*-like ancestors the following groups originated: the Eutheria in Asia, the Marsupialia (CLEMENS 1977) in western North America (or in South America, but see also KIRSCH 1977) and the Pappotherida in eastern North America (BUTLER 1978, but see also SLAUGHTER 1965, 1968*a*, 1968*b*, 1971). The place of origin of the Deltatheroida is not known, but it seems probable that they originated in Asia in pre-Coniacian times. The new estimates of the age of the Nemegt Formation (KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO 1983), and consequently of the ages of the Barun Goyot and Djadokhta Formations, although inconclusive, speak in favour of my earlier hypothesis that the eutherian mammals and taeniolabidoid multituberculates (KIELAN-JAWOROWSKA 1974, 1980, KIELAN-JAWOROWSKA and SLOAN 1979) and possibly also the Deltatheroida (KIELAN-JAWOROWSKA 1982) originated in Asia and dispersed to North America in pre-Campanian times.

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