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AFFINITIES OF THE MONGOLIAN CRETACEOUS INSECTIVORES[1]

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The unique series of Mesozoic mammal remains found by the Third Asiatic Expedition in Mongolia has now been completely described in a series of three papers.[2] The affinities of the one known multituberculate, *Djadochtatherium matthewi*, were as thoroughly discussed as the material warrants in the first paper, and no additional remarks seem necessary. The relationships of the more important insectivores, however, were only briefly discussed in the second paper and a review of the evidence, especially including the important new details given in the third paper, suggests some modification and amplification of the views already presented.

Not only are these mammal remains by far the most complete ever discovered in the Mesozoic, but they also occupy a very strategic position in time and in space which makes close scrutiny of their relationships essential. In time they occur in the Cretaceous, when, according to theories formed before their discovery and based largely on early Tertiary mammals, the differentiation of the placental orders should be in progress and not yet far advanced. In space they occur in Central Asia in or near the region which a number of students, especially Osborn and Matthew, have considered as an important center of radiation and probably the very one whence came the groups of mammals which appear to have entered North America and Europe suddenly at the beginning of the Tertiary and which must have been undergoing an important deployment during upper Cretaceous time. The Mongolian Cretaceous insectivores are thus actual representatives, so long hoped for but so little expected, of a group hitherto hypothetical and known only by its presumed descendants.

[1]Publications of the Asiatic Expeditions of the American Museum ofNatural History. Contribution No. 85.

[2]Simpson, G. G. 1925. A Mesozoic Mammal Skull from Mongolia. American Museum Novitates, No. 201.
Gregory, W. K. and Simpson, G. G. 1926. Cretaceous Mammal Skulls from Mongolia. American Museum Novitates, No. 225.
Simpson, G. G. 1928. Further Notes on Mongolian Cretaceous Mammals. American Museum Novitates, No. 304.

These insectivores have been placed in two families, four genera, and five species:

DELTATHERIDIIDAE Gregory and Simpson
Deltatheridium pretrituberculare Gregory and Simpson
Deltatheroides cretacicus Gregory and Simpson
Hyotheridium dobsoni Gregory and Simpson
ZALAMBDALESTIDAE Gregory and Simpson
Zalambdalestes lechei Gregory and Simpson
Zalambdalestes grangeri Simpson

Zalambdalestidæ

PARATYPE SKULL OF *Zalambdalestes lechi*:—The classification of the specimens referred to Z. *lechei* is minor relative to the broader relationships here chiefly under consideration, but essential to the taxonomy of the group. In our joint paper Dr. Gregory and I referred to this species, as a paratype, a second nearly complete but badly preserved skull and lower jaws. Space prohibited thorough discussion of the peculiarities of this individual and no explanation of its reference to the same species as the type, of rather different aspect, was given.

The two skulls agree in the following chief particulars: (1) the general shape of brain case and interorbital region is the same; (2) the snout is narrow and elongated; (3) the known features of the lambdoid crest, glenoid and ear regions are the same; (4) so far as known in both, the dental formula is the same; (5) the morphology of the teeth is the same so far as known; (6) the measurements of the teeth are the same so far as accurately obtainable. The paratype (No. 21704) differs from the type (No. 21708) in the following principal particulars: (1) Both cranial and facial regions are shorter, the facial relatively more so; (2) the orbit is larger relative to the skull; (3) the snout is less elongate, the diastemata shorter; (4) the jaw is more slender; (5) the lateral incisor may be smaller, but this is uncertain.

In weighing these resemblances and differences it will at once be seen that the resemblances are those upon which valid taxonomic conclusions are usually based, while the differences are without exception just such as are often seen between the young and the adult of the same species. It is true that the material is imperfect and that further discoveries may indicate specific separation, but this seems improbable. It is a sounder practice to refer specimens to the same species when they cannot be proven to be distinct on the basis of known homologous parts than to create separate species for them because they cannot be rigidly proven to be the same.

EVIDENCE OF THE DENTITION.—Gregory and Simpson provisionally considered the Zalambdalestidæ as ancestral to zalambdodont insectivores, although clearly stating that the paracone and metacone are more separate and more buccal than in any undoubted zalambdodonts and that the skull is almost devoid of the peculiarly zalambdodont specializations. We considered the separation of the two phyla represented by the Cretaceous families to be slight and emphasized (p. 14) the many resemblances of the Zalambdalestidae to the Leptictidae, suggesting that the zalambdodont and leptictid groups were possibly not yet distinct. Largely on the basis of a much improved knowledge of the details of molar structure, it now seems more probable that the zalambdodont and leptictid lines were distinct at this time and that *Zalambdalestes* stands closer to the latter, while the true zalambdodonts were derived from a group closer to the Deltatheridiidae.

Most of the characters of *Zalambdalestes* fall into four different categories: (1) primitive characters; (2) points of special resemblance to the zalambdodonts; (3) points of special resemblance to the leptictids; (4) specializations peculiar to the genus or family. The main conclusion here drawn is that the third of these categories is more indicative of true affinities than the second.

The anterior part of the dentition is the most highly specialized. The long diastemata and the enlarged lateral upper and median lower incisors are specializations of definitely insectivore character but not leading to any one group of later Insectivora, indeed excluding this genus from direct ancestry of any known later form. The relatively small two-rooted upper and incisiform lower canines are possibly primitive, but they do resemble those of some zalambdodonts (cf. *Limnogale, Microgale, Potamogale*) although not very closely. The absence of $P\frac{1}{1}$ points in the same direction, although this again is a specialization so common and so readily acquired as to afford no really good evidence. These teeth are absent in all zalambdodonts and are also absent in the Erinaceinae, but are present in the Gymnurinae and in the Leptictidae, save *Acmeodon*. P^2 is a small tooth of purely primitive character.

P^{3-4} are becoming molariform. Each has a protocone, parastyle and metastyle, but a single undivided cusp represents both paracone and metacone. The closest analogy, although not exact, is seen in *Potamogale*, but here we begin to encounter difficulties in the comparison with undoubted zalambdodonts, for in the very ancient and primitive *Palaeoryctes* (cf. also *Limnogale*) P^3 is definitely more primitive and the chief cusp of P^4 is more central, as in *Potamogale*. In all other zalambdodonts this cusp is almost or quite internal. P^3 of the Cretaceous genus is also more molariform than in *Leptictis*, but the conditions in this Oligocene form may be secondary for the earlier forms of the same family approach *Zalambdalestes* as closely as does *Potamogale*. P^4 in the leptictids always has the paracone and metacone distinct so far as known, but the conditions in the much older *Zalambdalestes* could readily give rise to those in the leptictids.

The crucial evidence of the molars continues this confusing resemblance to two groups now widely separate, but points much more definitely toward the erinaceomorphs. The molars are short and wide, and in badly worn teeth, such

as the only ones available when the joint paper was written, the resemblance to zalambdodonts is impelling. The structure revealed in *Zalambdalestes grangeri*, however, changes this. It is impossible to consider these teeth as structurally similar to those of such genera as *Ericulus*, *Centetes*, *Solenodon*, or *Chrysochloris*, before the upgrowth of the internal cingulum. Not only would this oppose the view, so strongly supported by comparative anatomy, embryology, and paleontology, that this cingulum is vestigial, not rudimentary,[1] but it is strongly contradicted by the actual morphology of the teeth in question. With their two large buccal cusps and strong cingulum external to these, the teeth of *Zalambdalestes* are obviously closer to those of *Palaeoryctes* or of *Potamogale* than to any other zalambdodonts. But even here the morphological gap is large, for in these two genera the paracone and metacone are median and nearly confluent and the external shelf is wide, with strong styles, while in the Cretaceous genus paracone and metacone are quite distinct and buccal, while the external shelf is represented only by a strong but narrow cingulum and the styles are vestigial.

On the other hand, the molars of *Zalambdalestes* are almost identical with those of the leptictids in ground plan. They differ only in being shorter, more transverse, without hypocone or anterior cingulum. The absence of these two features of the later leptictid molars is primitive and the more transverse development, not in any event a fundamental difference, is approached by such leptictids as *Palaeolestes* and *Gypsonictops*. The molars of *Zalambdalestes grangeri* are longer than those of *Z. lechei*, furthermore, and the differences from the leptictidae are really slight. The small M^3 also resembles the homologous tooth in leptictids closely and is quite unlike that of any true zalambdodont.

The lower cheek teeth confirm the evidence of the uppers. P_{3-4} are strikingly leptictid in general character, P_4 being quite as molariform as in many leptictids. Nor does any character of the lower molars exclude them from the structural ancestry of the latter. The only approach to zalambdodont structure lies in the short trigonids, but this is not very distinctive, is simply complementary to the short upper molars, and is not, as invariably in zalambdodonts, accompanied by a shortening of the heels. *Palaeoryctes* and *Potamogale* are the most primitive zalambdodonts in this respect, as in other dental characters, but in neither is the heel structure like that of *Zalambdalestes* and in both the high trigonid towering above the small, low heel is quite unlike the condition seen in *Zalambdalestes* and in the Leptictidae.

OSTEOLOGICAL EVIDENCE.—Turning to the skull and jaws, the evidence tends in the same direction as that of the dentition. The resemblances to the Zalambdodonta are largely those in which this group most

[1]This problem is much too large to discuss here. Valuable discussions with references to the most important literature will be found in the following studies:

Gregory, W. K. 1922. The Origin and Evolution of the Human Dentition. Baltimore. Esp. p. 101–107.

Leche, W. 1907. Zur Entwicklungsgeschichte des Zahnsystems der Säugetiere, etc. 2ter Teil, 2ter Heft: die Familien der Centetidae, Solenodontidae, und Chrysochloridae. Chun's Zoologica, XLIX. (This work contains a great wealth of information on zalambdodonts and to it and to Leche's other papers on Insectivora the writer is deeply indebted.)

Matthew, W. D. 1913. A Zalambdodont Insectivore from the Basal Eocene. Bul. A. M. N. H., XXXII, 307–14. (Full description of *Palaeoryctes*, to which reference is frequently made in the present paper.)

approaches the primitive conditions for all insectivores. The basicranial structure is poorly known but, as already pointed out by Gregory and

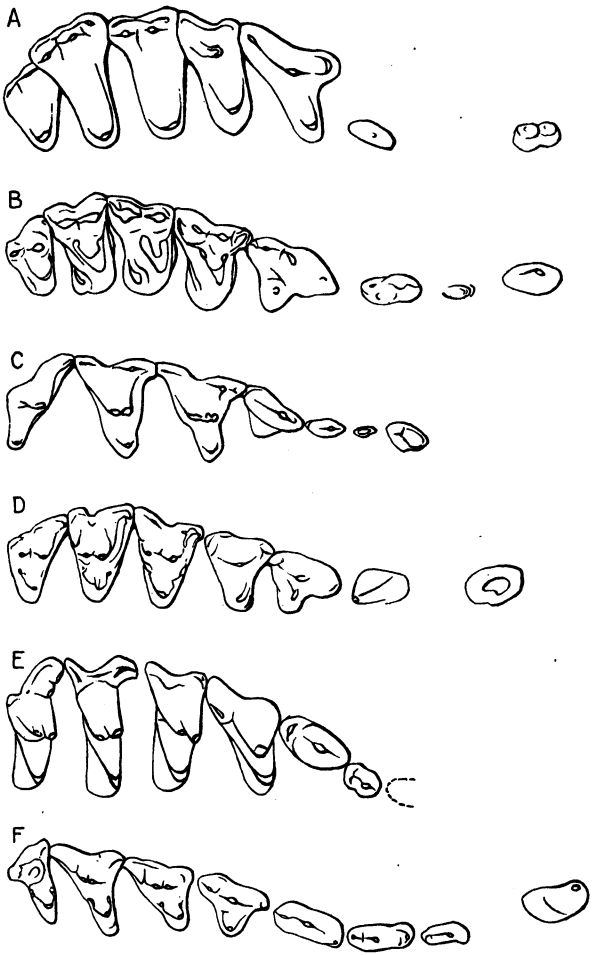

Fig. 1. Comparative diagrams of right upper cheek. A, *Zalambdalestes grangeri*. B, *Diacodon bicuspis*. C, *Deltatheridium pretrituberculare*. D, *Didelphodus absarokae*. E, *Palæoryctes puercensis*. F, *Sinopa strenua*. Not to scale. Drawn by John Germann.

Simpson, is devoid of characteristically zalambdodont characters so far as can be determined. The complete zygomata and unfused nasals are, of course, primitive, but the loss of these characters was a very early and universal specialization of zalambdodonts. The general

aspect of the skull is somewhat like some zalambdodonts (although the postorbital constriction is slight or lacking in the matter) but is equally, or rather more, like some leptictids (cf. *Diacodon*, for example) and really furnishes no convincing evidence of affinities beyond strongly confirming reference to the Insectivora.[1]

The posterior region of the lower jaw with its hook-like, non-inflected angle and long slender coronoid also is a slight modification of a type occurring in most groups of insectivores. The femur is more like that of *Ictops* than of any known zalambdodont, but is too generalized to cast much light on the problem.

The pelvis also is primitive in general features, suggesting the basic type seen with many variations in the Insectivora and retained in modified form in many other primitive placentals. The resemblance of this pelvis to that of some creodonts, such as *Tritemnodon*, is marked, but in the latter forms the crista lateralis is generally more ventral and the ventrolateral surface of the ilium reduced. The pelvis is not exactly like that of any other known insectivore. The probable participation of the pubis in the acetabulum rim and the median crista lateralis distinguish it from that of any soricid or talpid and the strong development of the gluteus medius area differs sharply from any zalambdodont. The position of crista lateralis, of the spina anterior inferior ilii, and of the tuberculum iliopectineum are all paralleled in the leptictids and the expanded anterosuperior plate of the ilium and its outward extension anteriorly are largely due to greater emphasis of characters also occurring in less extreme form in erinaceomorphs. The fact that this modification is very like that seen in some creodonts is interesting but is probably not indicative of special affinity.

Deltatheridiidæ

The characteristic members of this family are *Deltatheridium* and *Deltatheroides*, two closely related genera which differ chiefly in that in the former P^1 is lacking, P^2 is one rooted, P^3 is shorter than P^4, and P^4 has only a slight basal internal heel, while in the latter P^1 is present, P^2 two-rooted, P^3 as long as P^4, and P^4 has a distinct internal heel. Unfortunately *Deltatheroides*, in some respects the more interesting, is less adequately known, but its general structure was probably close to that of the other genus. *Hyotheridium* was referred to the family doubtfully; it is sharply distinct in its slender elongate snout, and the cheek tooth structure is very little known so that its true relationships are open to question.

Gregory and Simpson considered this family as structurally "in a very central position, ancestral to the creodonts and to many or all

[1]The reference of the Zalambdalestidae to the Insectivora does not rest largely on primitive characters, as in so many supposed Eocene insectivores or as in the Deltatheridiidae, but on numerous positive resemblances to undoubted insectivores. It hardly appears necessary to debate this point, but Pfeffer, in a recent study (Pfeffer, G. 1927. Die Frage d. Grenzbestimmung zwischen Kreide und Tertiär in zoogeographischen Betrachtung. Jena), denies that they are even placentals, suggesting that they are an extinct group of stragglers from the Pantotheria. Without wishing to slight Dr. Pfeffer's elaborate and valuable summaries of much other material, the main thesis of his paper may be said to be that the placentals suddenly came into being at the beginning of the Tertiary, which is supposed to be chiefly delimited by this event. Rather than recognizing that the Mongolian mammals put the last nail in the coffin of this theory, moribund for fifty years, and on no evidence save that they refute his arguments, Pfeffer gives these mammals a position absolutely opposed by every feature of their anatomy.

of the dilambdodont insectivores and possibly also to other orders." Reconsideration enlarges and strengthens the main points of this view and adds the suggestion that divergence from the zalambdodonts is really less in this family than in the Zalambdalestidae.

RELATIONSHIP TO DIDELPHODUS.—It was also suggested that *Didelphodus*, of the American lower Eocene, might belong to this family. *Didelphodus* differs from *Deltatheroides* in the absence of P^1, from *Deltatheridium* in the larger 2-rooted P^2 and submolariform P^4, and from both Cretaceous genera in the heeled P^3 and more distinct paracone and metacone of the molars. Except for these points, which indicate merely that *Didelphodus* is more advanced than either of the earlier genera, the upper teeth are very closely similar. The lower teeth of *Deltatheroides* are unknown. *Didelphodus* differs from *Deltatheridium* in the lower dentition by the presence of P_1, the stouter and more complex P_{3-4}, the slightly wider molar heels, the shorter trigonid on M_1, the smaller paraconids, and the shorter heel on M_3. The absence of P_1 and long heel of M_3 are certainly specializations in *Deltatheridium* and they exclude it from the direct ancestry of *Didelphodus*, although not profound differences. The heel is narrow in both, although more so in the Cretaceous form, and it is impossible to say which is the more primitive condition. The same is true of the relative sizes of paraconids and metaconids. The genera appear to be related, although showing incipient specialization along slightly divergent lines. *Deltatheroides* has no known character excluding it from the ancestry of *Didelphodus*, but is insufficiently known for a positive conclusion on this point.

The reference of *Didelphodus* to the Deltatheridiidae seems warranted by the facts in hand and is convenient. It has been referred to the Leptictidae, both as a creodont and as an insectivore, and also to the Proviverridae, but its resemblances are not at all close to either family.[1] *Phenacops*, from the middle Eocene, is apparently related to *Didelphodus*.[2] It is known only from an imperfect lower jaw, but is

[1]Despite its name, *Didelphodus* has nothing to do with the marsupials. On this genus see especially:
Cope, E. D. 1881. The Temporary Dentition of a New Creodont. Am. Nat., XV, 667–9. (Here referred to *Deltatherium*.)
. . . 1882. Notes on Eocene Mammalia. Am. Nat., XVI, 522.
. . . 1885. Tertiary Vertebrata. Rept. U. S. Geol. Surv. Ter. (Hayden), III, 284.
Matthew, W. D. 1918. Insectivora, etc., in Matthew & Granger, A Revision of the Lower Eocene Wasatch and Wind River Faunas. Bul. A. M. N. H., XXXVIII, 579–85.
Scott, W. B. 1892. A Revision of the North American Creodonta, etc. Proc. Ac. Nat. Sci. Phila., 1892, 311.
[2]Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin. Mem. A. M. N. H., IX, 535–6.
. . . 1918, loc. cit., p. 582.

interesting as having P_1 reduced and the heel of M_3 very narrow and long—convergences toward *Deltatheridium*.

Aside from these two Eocene genera, there appear to be no other mammals which show special affinity with the Deltatheridiidae and none with which generic comparison is necessary.

RELATIONSHIP TO ZALAMBDODONTS AND CREODONTS.—Turning to the broader aspects of the problem, *Deltatheridium*, *Deltatheroides*, probably *Hyotheridium*, and apparently also *Didelphodus* and *Phenacops* form a group of distinct genera which may be provisionally united into a single family. The characters of this family suggest closer comparison especially with zalambdodont insectivores and with creodonts, two ancient and primitive groups widely divergent in their more specialized members.

Matthew (1913, loc. cit.) was the first to point out the resemblances between the molars of *Didelphodus* and those of the zalambdodonts and to suggest that this genus, which he referred to the Leptictidae but which then occupied a position apart from any other known form, might afford a clue to the origin of the peculiar teeth of this division of the Insectivora.

Structurally, the family Deltatheridiidae does offer an almost ideal point of departure for the zalambdodonts. The molars are not unlike those of *Potamogale*, still closer to those of *Palaeoryctes*. The high trigonids and low narrow talonids are as typical of the ancestral zalambdodont condition as of the more central carnivores. The premolars are less specialized than in any known zalambdodont and could give rise to the conditions in the latter. The upper molars with their wide external shelves and central, almost connate paracone and metacone are also closer to those of *Palaeoryctes* than are those of any other known mammal not definitely a zalambdodont. There are no specializations sufficiently profound to exclude the family, as a broad unit, from a position very close to the ancestry of the zalambdodonts.

Nevertheless there is reason to believe that the known members are advancing more in the direction of the Carnivora Their departure from a primitive, very central position is slight but seems to indicate that their phylum lay closer to the creodont line than to any other arising at this time. The canines are much enlarged and single-rooted, the molars do not tend to shorten but seem to be approaching such types as *Proviverra*, *Deltatherium*, and others, the talonids are

narrow but are not short and that of M_3 is unusually long—a specialization independent from the similar one which appears in some later carnivores but nevertheless of creodont type and directly opposed to the tendencies which gave rise to the zalambdodonts. It is conceivable that *Hyotheridium* is closer to the zalambdodonts than are the typical genera, but too little is known of it. The creodont and zalambdodont lines may tentatively be visualized as diverging at a time somewhat earlier than that of the Djadokhta Formation and the Deltatheridiidae as arising in or near the base of a focal Asiatic protocreodont group, within the order Insectivora.

BROADER RELATIONSHIPS

These relationships, while inevitably subject to radical revision when other discoveries make advances possible, do rest on resemblances of a definite sort. Beyond them are other broader and less definite but not less important inferences which may be stated without too much insistence. The structure of the deltatheridiids agrees with their position in time between the pre-placental, pre-marsupial pantotheres and the close but distinct array of placental orders in the early Tertiary and with their position in space near the center of the land masses later dominated by placentals in suggesting that they, of all known mammals, stand closest to the common point of divergence of many or all placental mammals. In the skull and dentition they come very near to showing all the features which the most competent students of Paleocene and early Tertiary mammals have believed would characterize such a central group when found.

Of the important characters of the family as a whole, only one is unexpected or could be considered as widely aberrant, namely, the great width of the shelf external to the paracone and metacone, but this feature also, while possibly more highly developed in this particular line than in some others then diverging from the insectivorous proto-placentals, is apparently to be considered as primitive.

Winge, in an early and important paper on molar evolution, long ago suggested that the external styles and cingulum of the upper molar are extremely ancient structures.[1] For his extreme view that they are the *most* ancient part of the tooth there seems no real evidence and a vast body of facts now opposes it, but more and more items of evidence, of which these Cretaceous mammals are not the least, are

[1]Winge, H. 1882. Om Pattedyrenes Tandskifte, etc. Vidensk. Meddel. f.d. naturh. Foren. i Kjöbenhavn, 1882, p. 15–69.

appearing to demand a greater antiquity and importance for the part of the upper molar external to the paracone and metacone than has been commonly granted. In the most primitive living mammals and in the majority of the early Tertiary forms the upper molars usually have a strong external shelf, in some cases, which may offer a real clue to the whole process, agreeing with the Deltatheridiidae in occupying nearly half the total width. Not only is such a structure seen in ancient and primitive zalambdodonts, but also relatively little modified in many creodonts, which are the most primitive and central members of a group including carnivores and ungulates and related to the ancestry of other orders. The soricoids and bats also have a specialized molar structure which could be derived from that of the Deltatheridiidae by wider separation of paracone and metacone, their acquisition of a lambdoid shape, and the upgrowth of a hypocone. In the more primitive members of many groups of mammals the paracone and metacone are not really external and there appears to be no real evidence that in these groups they have migrated inward from a strictly buccal position.

It is not to be assumed that no new styles have arisen, or that all which occupy analogous positions are homologous. It is suggested only that the ancestral condition, the condition in the Cretaceous insectivores which gave rise to all higher mammals, was near that of the Deltatheridiidae, with a large bifid central cusp, an internal heel, and a more or less broad external cingulum or shelf. These are probably the only elements which were present in the common ancestry and which are strictly homologous (when correctly identified, of course) throughout all placentals. Within each line of descent the teeth went their own way, hypocones (not really homologous in the different orders), conules, styles, supplementary cusps arose or were lost, paracone and metacone became more distinct (most mammals) or fused (zalambdodonts and some carnivores), premolars became molarized by steps which followed the general history of the molars but, since they started from a different basis, could not be expected to recapitulate the exact history. But enough has been said on this very complex subject, to which the writer hopes to return in more detail, to indicate its probable bearing on the immediate question.

CONCLUSIONS

1. The Zalambdalestidae and Deltatheridiidae are not widely different but are related to diverging groups.

2 The Zalambdalestidae are the more specialized and, contrary to the opinion first expressed, are more distant from the zalambdodonts than are the members of the other family

3. The closest affinities of the Zalambdalestidae are with the erinaceomorphs, of which group they represent a very early and non-ancestral branch.

4. The Deltatheridiidae are on a very primitive plane and show but little specialization from a condition structurally ancestral to the majority of placental mammals.

5. Such specialization as they do show is tending in the creodont direction and they strongly suggest the hitherto hypothetical group of Cretaceous insectivores inferred, especially by Matthew, to be the immediate ancestors of the Carnivora.

6. The evidence further suggests that the zalambdodont insectivores had their origin very near this group, although probably not specifically in the family Deltatheridiidae.

7. Both Zalambdalestidae and Deltatheridiidae, although on a very low evolutionary level, are definitely placentals and Insectivora and a break still remains between them and the Jurassic pantotheres, a break which is not profound and which can now be filled by inference more surely than before but which is not actually bridged by any known mammals.