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EVOLUTION OF THE THERIAN MAMMALS
IN THE LATE CRETACEOUS OF ASIA. PART III. POSTCRANIAL
SKELETON IN ZALAMBDALESTIDAE

(Plates 1—11)

Abstract. — Postcranial skeletons of the Asiatic Late Cretaceous eutherian mammals *Zalambdalestes lechei* and *Barunlestes butleri* (Zalambdalestidae) are described and figured. The skeleton of zalambdalestids shows a mosaic of primitive and advanced characters. Its characteristic features are: long spinous process of the axis; short spinous processes of thoracic vertebrae; sacrum of two vertebrae; scapuloideum and lunatum fused as scapholunatum; tibia and fibula strongly fused; calcaneal fibular facet lacking; tibial trochlea on astragalus well developed; hind limbs (especially metatarsals) very long. The length ratio of forelimb to hindlimb resembles that of present-day Macroscelididae. Locomotion of the zalambdalestids was probably similar to that of macroscelidids, which is dominantly quadrupedal walking, running and jumping. Similarities of skeletons and probable mode of life do not, however, imply close phylogenetic relationship. It is also unlikely that zalambdalestids are a sister group of lagomorphs.

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INTRODUCTION

The purpose of this paper is to describe the postcranial skeletons of Late Cretaceous eutherian mammals of the family Zalambdalestidae from the Gobi Desert of Asia and to evaluate, in-so-far as possible, their habits. Functional anatomy of the Zalambdalestidae has not yet been studied in detail and only the most obvious conclusions can be drawn.

The Zalambdalestidae consist of two monotypic genera, *Zalambdalestes* (represented by *Z. lechei* GREGORY and SIMPSON, 1926) and *Barunlestes* (represented by *B. butleri* KIELAN-JA-

WOROWSKA, 1975). SZALAY and MCKENNA (1971) have shown that *Z. grangeri* GREGORY and SIMPSON, 1926 and *Z. sp.* KIELAN-JAWOROWSKA, 1969 are junior synonyms of *Z. lechei*. *Zalambdalestes* derives from the ?late Santonian and/or early Campanian Djadokhta Formation (see GRADZIŃSKI *et al.* 1977) at the locality of Bayn Dzak, Mongolian People's Republic. *Barunlestes* has been found in the ?middle Campanian Barun Goyot Formation of several localities within the Nemegt Basin. It also occurs within the red beds of Khermeen Tsav (previously referred to as Khermeen Tsav formation, e. g. KIELAN-JAWOROWSKA 1974), a stratigraphic equivalent of the Barun Goyot Formation, at the locality of Khermeen Tsav II. See GREGORY and SIMPSON 1926, SIMPSON 1928, KIELAN-JAWOROWSKA 1969, 1974, 1975a and SZALAY and MCKENNA 1971 for miscellaneous background information.

Of the seven therian genera known from rocks of Late Cretaceous age in the Gobi Desert, parts of postcranial skeletons were found in *Asioryctes* and *Kennalestes* (in the latter only an atlas and a fragment of an axis) and in both genera of the Zalambdalestidae. The skeleton of *Asioryctes* shows many primitive characters and in some way is more similar to that of *Didelphis* than to present-day eutherians (KIELAN-JAWOROWSKA 1977). Skeletons of the Zalambdalestidae, however, show a mosaic of primitive and advanced characters. Although *Zalambdalestes* has been found in beds older than those yielding *Asioryctes*, it is more specialized.

Zalambdalestes and *Barunlestes* differ in dental formulae and skull proportions (KIELAN-JAWOROWSKA 1975a), but significant differences in their postcranial skeletons have not been recognized. Thus the postcranial skeletons of both genera are described herein together, and the reconstruction of *Zalambdalestes* given as fig. 17 is based in part upon skeletal elements of *Barunlestes*.

Preliminary comparisons indicate that skeletons of the Zalambdalestidae are similar in general proportions to those of present-day Macroscelididae; thus comparisons are made with *Elephantulus* and *Rhynchocyon*. It was also instructive to make certain comparisons with *Didelphis*, other marsupials, and *Tupaia*, *Rattus* and *Oryctolagus*.

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Abbreviations of institutional names:

MCZ Museum of Comparative Zoology, Harvard University, Cambridge.

ZPAL Institute of Paleobiology (Zakład Paleobiologii), Polish Academy of Sciences, Warsaw.

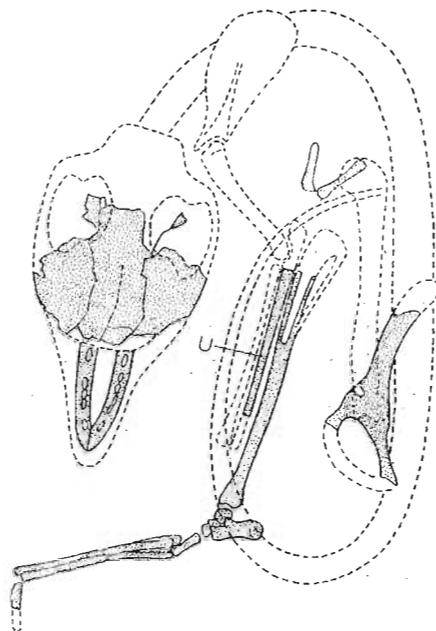
MATERIAL

Zalambdalestes lechei (ZPAL MgM-I/43), Djadokhta Formation, Bayn Dzak (Main Field), Gobi Desert. The following elements of the postcranial skeleton have been found in association with skull and mandibles: incomplete left pelvis, left tibia lacking the proximal part, and then in articulation incomplete left tarsus (calcaneus, astragalus, navicular and medial cuneiform), five metatarsals (proximal parts of second and third ones are broken off, the first metatarsal is obscured by the remaining ones and not developed from the rock due to the state

of preservation), first phalanges of all the digits (distal parts of fourth and fifth broken off), displaced fragment of the left ulna, situated along the left tibia; fragment of right pelvis with proximal part of femur preserved in acetabulum, incomplete right pes consisting of cuboideum, lateral cuneiform and five metatarsals (distal parts of fourth and fifth broken off), first and second phalanges of the first digit, incomplete first phalanges of second and third digits, complete first phalanges of fourth and fifth digits; two caudal vertebrae.

The recognition of the fragmentary longitudinal bone (see fig. 1, U), situated on the inner side of the left tibia, as a part of an ulna, is based on the following premises: as all the details

Fig. 1
Zalambdalestes lechei (ZPAL MgM-I/43) reconstruction of the position of the buried animal. The shadowed areas denote the bones, which have been preserved. Right foot preserved in a different level in the same piece of rock is not shown. U — ulna. Natural size.



and proportions of postcranial skeletons in *Zalambdalestes* and *Barunlestes* are similar, one has to presume that the fused tibia and fibula, characteristic of *Barunlestes*, occurred also in *Zalambdalestes*; the bone in question (U) is too long for a fibula, as compared with *Barunlestes*; it cannot be a metatarsal as it is too long and all the metatarsals are in place in both feet. It appears from the reconstruction of the position of the skeleton (fig. 1) that this is one of the forearm bones, possibly ulna.

(ZPAL MgM-I/166), Djadokhta Formation, Bayn Dzak (Main Field) Gobi Desert. Second to seventh cervical vertebrae and first thoracic vertebra, preserved together. The assignment of this specimen to *Z. lechei* is based on the following premises: the axis of this specimen has the same structure as in *Barunlestes butleri*, having the anterior part of the dorsal edge of the spinous process flattened dorsoventrally, to form a tear-shaped area. Such a structure is known only in the Zalambdalestidae, which suggests that the specimen in question is a zalambdalestid. *Z. lechei* is the only representative of the Zalambdalestidae in the Djadokhta Formation.

Barunlestes butleri (ZPAL MgM-I/77) holotype, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert. The following elements of the postcranial skeleton have been found in association with skull and mandibles: atlas, axis, three isolated thoracic vertebrae, six lumbar vertebrae (probably first to fifth) found dispersed and the seventh associated with first sacral, two sacral and four and a half coccygeal vertebrae, preserved in association with the pelvis (right side of the pelvis almost complete, left without posterior part); part of the left forelimb in articulation, consisting of the distal end of the humerus, radius and ulna, almost complete

carpus (without capitatum and/or pisiform), five metacarpals, first phalanges of the first and fifth digits; right femur (without the medial part), associated with the proximal extremity of the ulna; left femur without the distal end, proximal part of the left tibia with broken off distal and proximal extremities of the fused fibula, distal ends of second to fifth metatarsals, associated with first phalanx of the fourth digit and proximal part of the first phalanx of the third digit.

(ZPAL MgM-I/104), red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert. Left humerus lacking the distal end, distal part of the right scapula, found in association with skull and mandibles.

DESCRIPTIONS

VERTEBRAL COLUMN

Atlas (pl. 2: 1; fig. 2) has been preserved only in *Barunlestes*. It has the form of a narrow ring. The vertebral foramen is wide and rounded in its dorsal part, much narrower and roughly quadrangular ventrally. The transverse processes are broken, only the bases are preserved. The dorsal arch is 1.8 mm long in the middle and 1.4 mm long laterally; its anterior edge is pointed in the middle. A hardly discernible medial dorsal tubercle is present anteriorly. The posterior border of the dorsal arch is straight. The ventral arch is very narrow — 0.7 mm long, without a ventral tubercle. The fovea dentis is flat. The sutures between the ventral arch (intercentrum) and lateral masses are present. The anterior articular cavities are oval, converging ventrally, moderately deep, and with distinct dorsal edges. The posterior articular cavities are smaller than the anterior ones, almost flat, oval and confluent with the ventral arch. The inter-

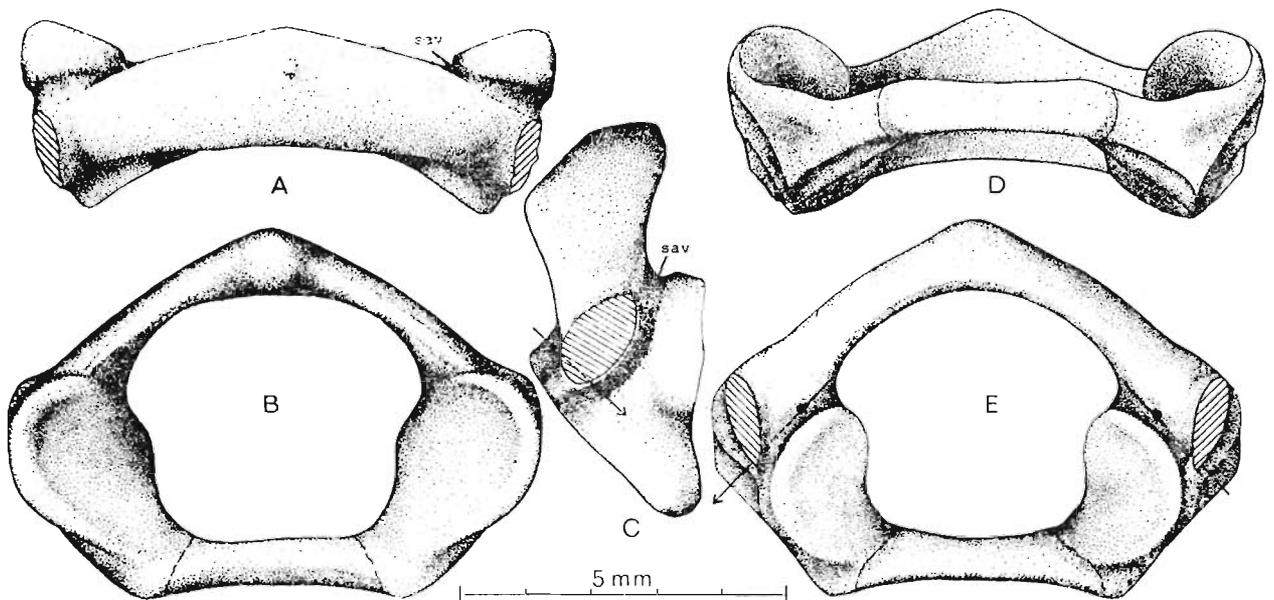


Fig. 2

Barunlestes butleri, reconstruction of the atlas, based on ZPAL MgM-I/77. A — dorsal, B — anterior, C — lateral, D — ventral, E — posterior views. The hatched areas denote the broken bases of the transverse process, the arrows denote the course of the transverse canal, sav — sulcus arteriae vertebralis.

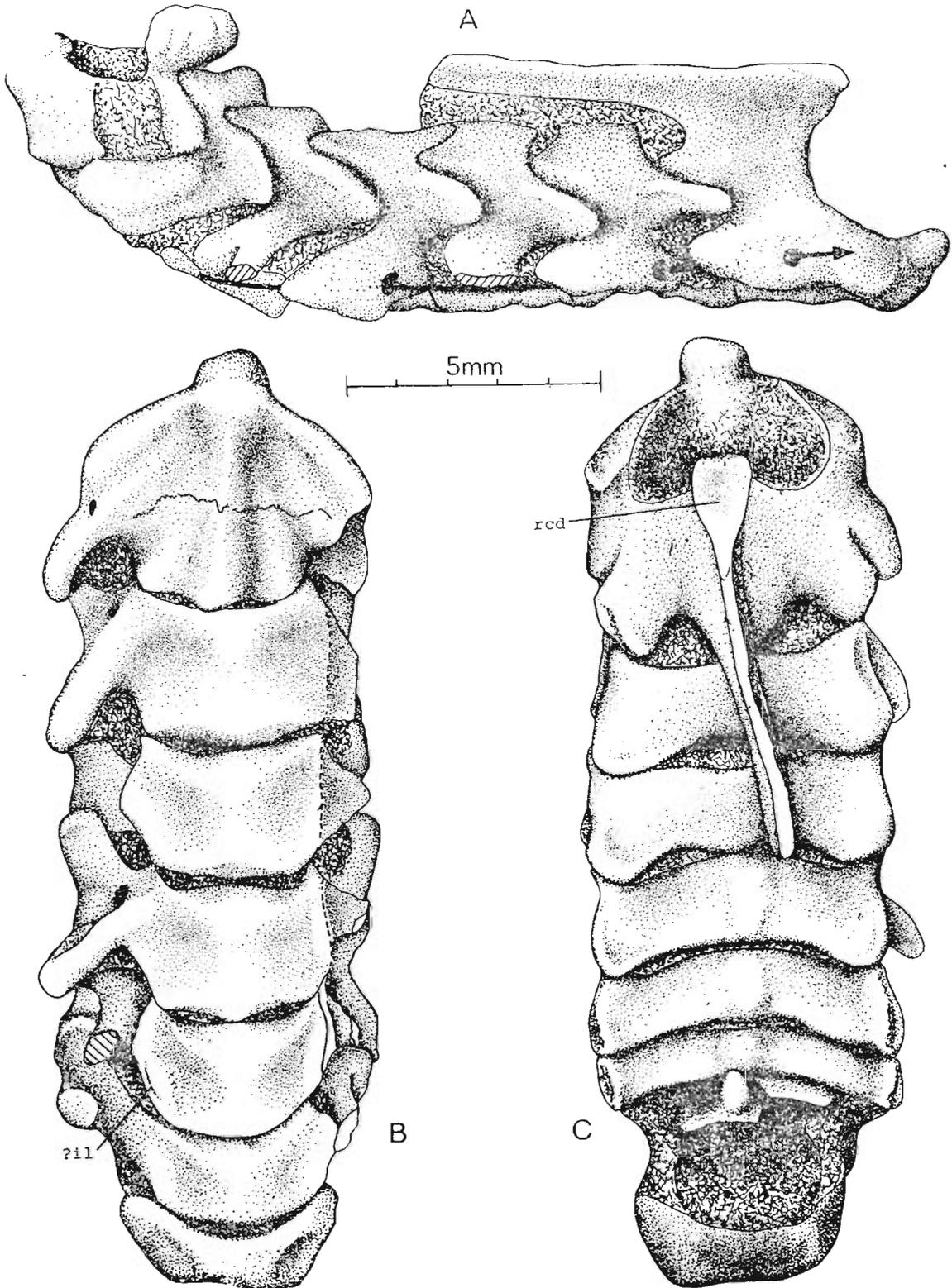


Fig. 3

Zalambdalestes lechei (ZPAL MgM-I/166), second to seventh cervical vertebrae and first thoracic vertebra, drawn as they have been preserved. The arrow denotes the course of arteria vertebralis. The transverse processes are preserved on the right side of the axis, of C_3 and C_6 , ?il — incipient inferior lamella on C_6 , rcd — attachment area for rectus capitis dorsalis muscle. A — right lateral, B — ventral, C — dorsal views.

vertebral (arcual) and alar foramina are absent. Sulcus arteriae vertebralis is seen in dorsal view as a notch at the lateral part of the dorsal arch, adjacent to the anterior articular cavity. The transverse canal (foramen) is present. Its posterior opening is situated in the middle of the shallow groove (for arteria vertebralis) which separates the transverse process from the posterior articular cavity. The anterior opening of the transverse canal is a foramen situated at the posterior end of the atlantis fossa. Extending anterodorsally from this foramen is a distinct groove for the continuation of arteria vertebralis along the base of the transverse process. The groove passes anteriorly into the sulcus arteriae vertebralis.

Axis (pl. 2: 2; pl. 3, pl. 4: 2; figs. 3 and 4) is almost completely preserved in *Zalambdalleste* (ZPAL MgM-I/166), where only the transverse process on the left side is missing; in *Barunlestes* (ZPAL MgM-I/77) it is less complete, as the posterior part of the spinous process, the transverse processes and the middle part of the ventral wall of the body are missing; it is also slightly deformed.

The body is longer in *Zalambdalestes* than in *Barunlestes*. Its length (without dens) in *Zalambdalestes* is 4.4 mm, whereas in *Barunlestes* it measures 3.8 mm. A median ventral ridge extends along the body. The lateral depressions are uneven, bordered laterally by faint ridges which converge slightly anteriorly. The body is divided into atlantal and axial parts by a transverse suture, visible on the ventral surface. The axial part is shorter than the atlantal. The dens is somewhat damaged in *Zalambdalestes*, where it is directed anterodorsally, but in *Barunlestes* it appears to be somewhat more horizontally directed. The anterior articular surfaces are not very prominent and are confluent ventrally with the articular surface of the dens. The transverse

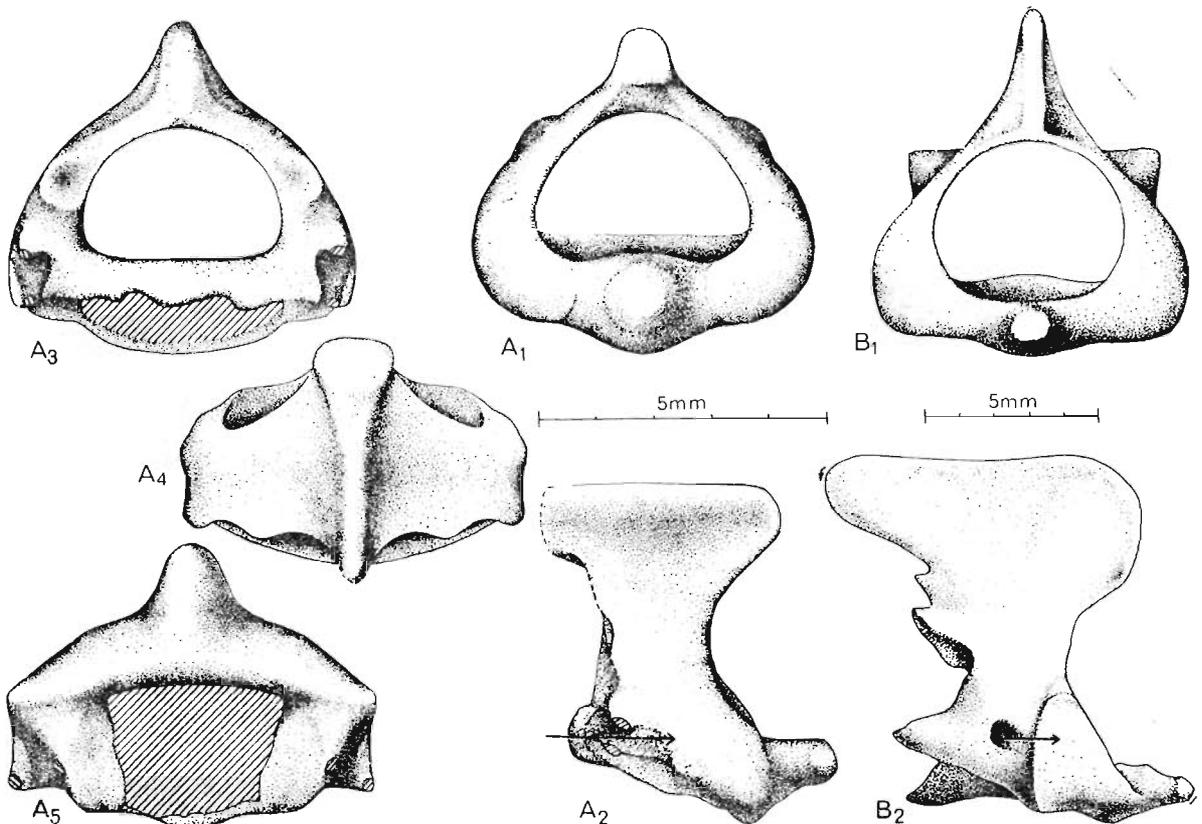


Fig. 4

Axis of *A* — *Barunlestes butleri* (partly reconstructed, on the basis of ZPAL MgM-I/77) and *B* — *Rhynchocyon cirnei hendersoni* MCZ 43735. *A*₁, *B*₁ — anterior, *A*₂, *B*₂ — lateral, *A*₃ — posterior, *A*₄ — dorsal, *A*₅ — ventral views. The hatched areas denote the broken bases of the transverse processes and the damaged ventral surface of the body. The arrows denote the transverse canal. Posterior margin of the arch is in *Barunlestes* broken.

process is preserved only on the right side of *Zalambdalestes*. It is small and pierced by a transverse foramen. The arch is comparatively high. Its anterior margin is regularly concave. The posterior articular process is in *Zalambdalestes* extensive and directed horizontally; in *Barunlestes* it is broken off. The most characteristic feature of that axis of the Zalambdalestidae is the structure of the spinous process. This is very long, rather slender, longitudinally directed process which reaches posteriorly to above the posterior edge of the fourth vertebra. Its lateral surface is slightly concave. Anteriorly the dorsal edge of the spinous process is flattened dorsoventrally, forming a tear-shaped area.

Third vertebra (pl. 3 and fig. 3) has been preserved only in *Zalambdalestes*. The body (in ventral view) is comparatively short and wide, concave in both longitudinal and transverse directions. The posterior edge of the body is more prominent than the anterior one. The arch is very low and the spinous process is not developed. It cannot be stated whether the dorsal tubercle was present, as the middle part of the body is obscured by the spinous process of the axis. The arch, when examined in dorsal view, appears flat, narrow along the mid-line and widens laterally, due to the extensive articular processes, which are arranged roughly horizontally. The short transverse process is directed nearly horizontally and obliquely posterolaterally. The interarticular space between the axis and the third vertebra is comparatively large; between the third and fourth vertebrae it is very short.

Fourth to seventh cervical vertebrae (pl. 3 and fig. 3) have been preserved only in *Zalambdalestes*. The bodies of the cervical vertebrae decrease in length from the second to the seventh. When examined in ventral view, the bodies of fourth and fifth vertebrae resemble that of the third vertebra: the ventral crest is absent, but the midline is somewhat raised, and the anterior and posterior edges are also raised. The arches of the cervical vertebrae are flat, as the spinous processes are not developed. Whether a median dorsal tubercle is present in the fourth vertebra is unknown, but such a tubercle occurs on the fifth vertebra and increases in prominence on the sixth and seventh. The body of the sixth vertebra differs from the remaining ones in being more truncated posteriorly and in having raised lateral margins. The prominent lateral margin, is interpreted as an incipient inferior lamella (HOWELL 1926, KIELAN-JAWOROWSKA 1977), which, however, is much less prominent than in *Asioryctes* and in modern therian mammals. The seventh vertebra is very short; its transverse process, only the base of which has been preserved, is not perforated by a foramen.

First thoracic vertebra (pl. 3 and fig. 3). A badly damaged first thoracic vertebra has been preserved together with the cervical vertebrae in *Zalambdalestes*. Its characteristic feature is the presence of a prominent dorsal tubercle, much higher than on the preceding cervical vertebrae.

Unidentified thoracic vertebrae (pl. 4: 1a; figs. 5 and 16). Three damaged thoracic vertebrae have been preserved in *Barunlestes* (ZPAL MgM-1/77) in front of the lumbar, but not in articulation. They have short and rounded spinous processes. Their supposed position in the vertebral column is illustrated on pl. 4: 1a and in fig. 17, the most anterior one being obscured in fig. 17 by the scapula.

The most posterior of the preserved thoracic vertebrae (see pl. 4: 1a, and fig. 5) is the longest and highest. In anterior view, the greatest diameter of the body is transverse. The anterior surface of the body is slightly concave, the posterior is flat. The medial crest is absent, but the ventral surface of the body is irregularly furrowed. The transverse process is very short, placed very low on the body, and is more prominent anteriorly than posteriorly. Above the transverse process there is an accessory process, very prominent posteriorly, narrowing anteriorly, and disappearing in about the mid-length of the arch. Its posterior free end is broken on both sides. Of the costal foveae, only the posterior one is present; anterior costal fovea and transverse costal foveae are absent. However, it cannot be excluded that in *Barunlestes* the absence of the

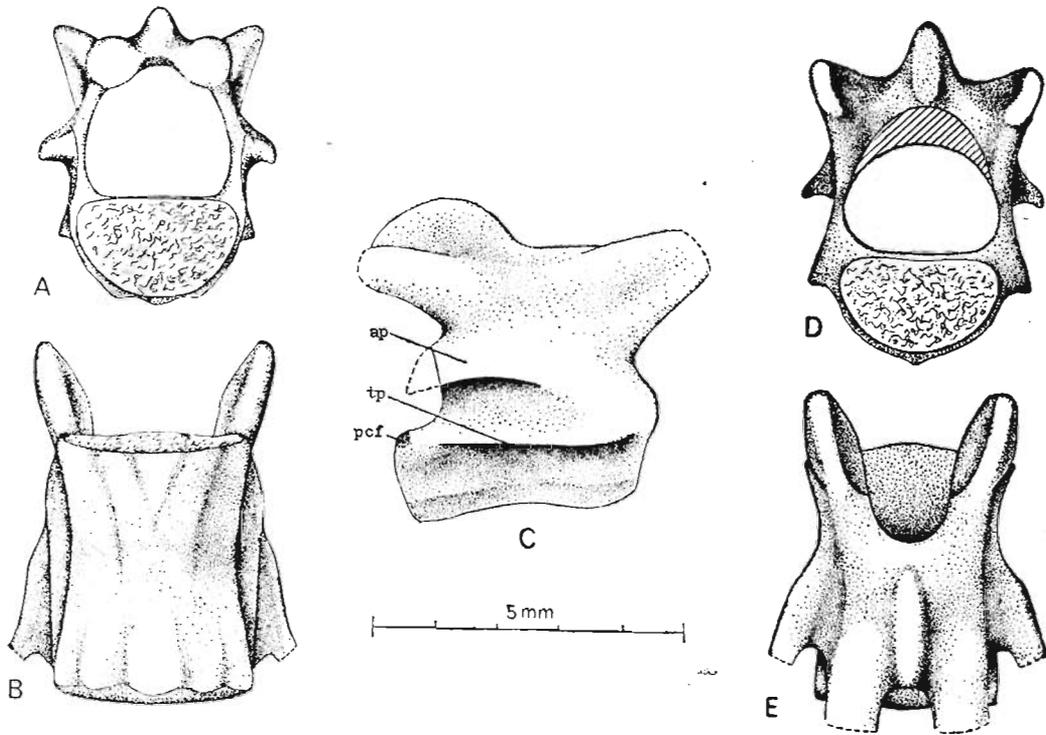


Fig. 5

Barunlestes butleri (ZPAL MgM-1/77), unidentified thoracic vertebra, (third one from the top on pl. 4:1a); A — posterior, B — ventral, C — lateral, D — anterior, E — dorsal views; ap — accessory process, pcf — posterior costal fovea, tp — transverse process.

anterior costal fovea and the transverse costal fovea on the preserved thoracic vertebrae is due to the damaged state of the specimen. The anterior articular processes are larger than the posterior ones. They have concave articular surfaces, facing medially. The posterior articular surfaces form rounded knobs. The spinous process is short and crescent-shaped. Two other thoracic vertebrae (see pl. 4: 1a) are strongly damaged. They are smaller than the one described and differ from it in having relatively wider accessory processes. The costal foveae are not discernible due to the poor state of preservation.

Lumbar vertebrae (pl. 4: 1, pl. 5, pl. 6: 1c-f; figs. 6, 7, 8). Six lumbar vertebrae have been preserved in *Barunlestes*, but it is possible that one is missing. The last is still in anatomical position, articulated with the sacrum. The other five, the first two of which are distorted, lie in front. The last of these (i. e. L5) differs in many respects from the vertebra attached to the sacrum and has a body whose posterior aspect does not fit the anterior aspect of the other, so it appears that at least one vertebra has been lost between them. This would then make seven lumbar vertebrae in *Barunlestes*, the penultimate being lost. The bodies increase in length posteriorly as far as the third lumbar vertebra, and then decrease posteriorly again. The last one is much shorter than the others.

As an example of the lumbar vertebrae, the third is described in detail (fig. 7). The body is strongly elongated, with a concave ventral surface provided with strong ventral crest. In ventral view, about two thirds along the body, an oblique, weak furrow extends from the ventral crest posterolaterally. In anterior and posterior views the greatest diameter of the body is transverse. The comparatively short transverse processes are placed relatively low on the upper part of the body, and extend all along the length of the body; they are more prominent anteriorly than posteriorly. In ventral view they form roughly crescent-shaped wings, with the greatest diameter

at about one quarter of the body length from the front; they taper posteriorly, and have slightly undulating free margins. The shape and size of the vertebral foramen is more or less similar to that of the body. Accessory processes are absent. The anterior articular processes are very strong, with deep, concave articular facets, and embrace the posterior facets from below, laterally, and also partly from above. The posterior articular processes are much less prominent, and are rounded. The spinous process is comparatively long, pointed, and bent.

The first lumbar vertebra (fig. 6) differs from the third in having a higher arch, in the shape of the spinous process (which is straight, roughly rectangular, and projects upwards), in the presence of a prominent accessory process, and in having narrower and differently shaped transverse processes. The upward direction of the spinous process is characteristic of the diaphragmatic vertebra (first lumbar) in modern mammals, and this is characteristic also of *Barunlestes*.

The second lumbar (pl. 4: 1) is intermediate in some respects between the first and the third. Its arch is comparatively high, accessory processes are present, but the spinous process is bent anteriorly as in the third one. The transverse processes are broken, and it is impossible to state whether they are shaped as in the first or in the third lumbar. The fourth and fifth lumbar are similar to the third, becoming gradually shorter and lower posteriorly, and having the transverse processes relatively wider and shorter. The last lumbar vertebra (pl. 6: 1c—f and fig. 8) differs from the preceding in being distinctly shorter and lower, in having the spinous process directed backwards and slightly bent posteriorly, and in having wider transverse processes.

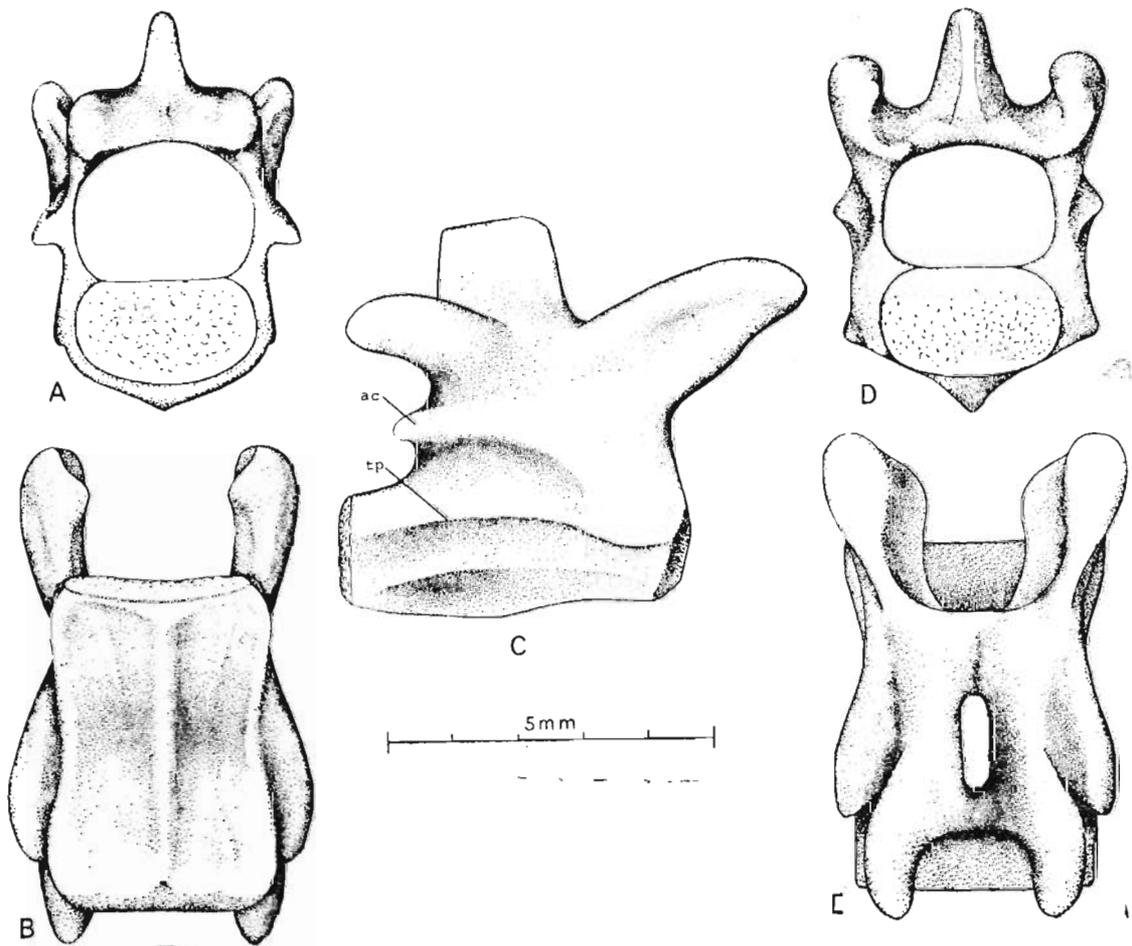


Fig. 6

Barunlestes butleri (ZPAL MgM-I/77), first lumbar vertebra; *A* — posterior, *B* — ventral, *C* — lateral, *D* — anterior, *E* — dorsal views; *ac* — accessory process, *tp* — transverse process.

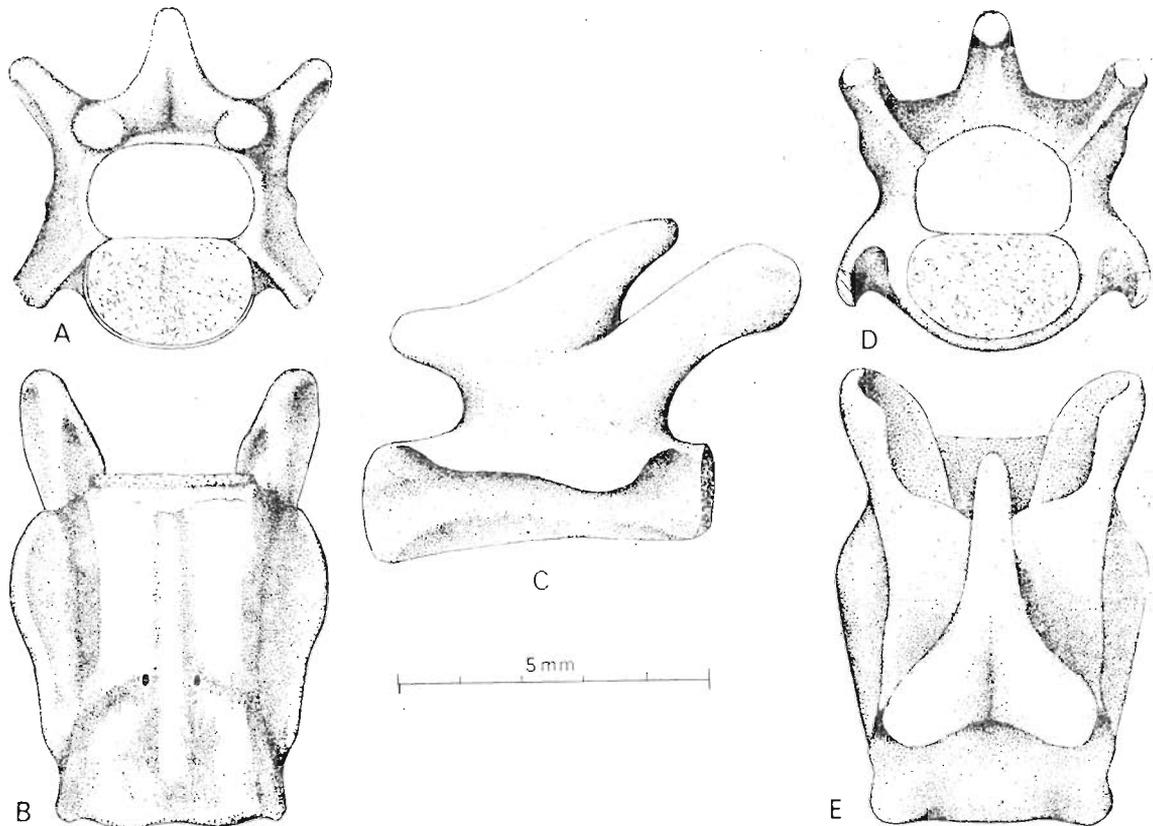


Fig. 7

Barunlestes butleri (ZPAL MgM-I/77), third lumbar vertebra; *A* — posterior, *B* — ventral, *C* — lateral, *D* — anterior, *E* — dorsal views.

Sacrum (pl. 5 and pl. 6: 1a—b; fig. 8) has been preserved only in *Barunlestes*. The sacrum consists of two vertebrae, only the first of which articulates with the ilium. The posterior articular processes of the first vertebra and the anterior ones of the second are not preserved. Judging from the small area left for them between the spinous process and the sacral foramen, they were reduced, and probably fused. The sacrum in dorsal view forms a strongly elongated triangle. In dorsal view, starting about half way along the first sacral, there extends a median sacral crest, from which a narrow, pointed spinous process rises posterodorsally; the tip of it overhangs the second sacral. The anterior processes of the first sacral are prominent and face medially. Lateral to them the anterior margin of the sacrum is concave. A wide longitudinal groove, bordered laterally by the raised edge of the articular surface, extends from this concave margin to the sacral foramen. The sacral foramen is large and more elongated transversely than longitudinally. On the level of the anterior margin of the sacral foramen, between it and the base of the spinous process, there is a deep furrow, convex anteriorly and surrounded anteriorly by a prominent margin. To the rear of this furrow, the bone is missing on both sides. The auricular surface consists of a high, rounded anterior part and a roughly triangular posterior part, which narrows posteriorly. The auricular surface is irregularly furrowed. About the middle of it there is a vertical ridge, convex posteriorly, and bounded anteriorly by a deep groove, in front of which there is a series of perpendicular furrows; in the posterior part, the furrows are shallower than in the anterior.

The second sacral vertebra is longer than the first, and longer than the first coccygeal. The transverse processes arise from only the anterior part of the vertebra, and are roughly triangular. The transverse processes are partly broken on both sides; they are reconstructed (fig. 8) as meet-

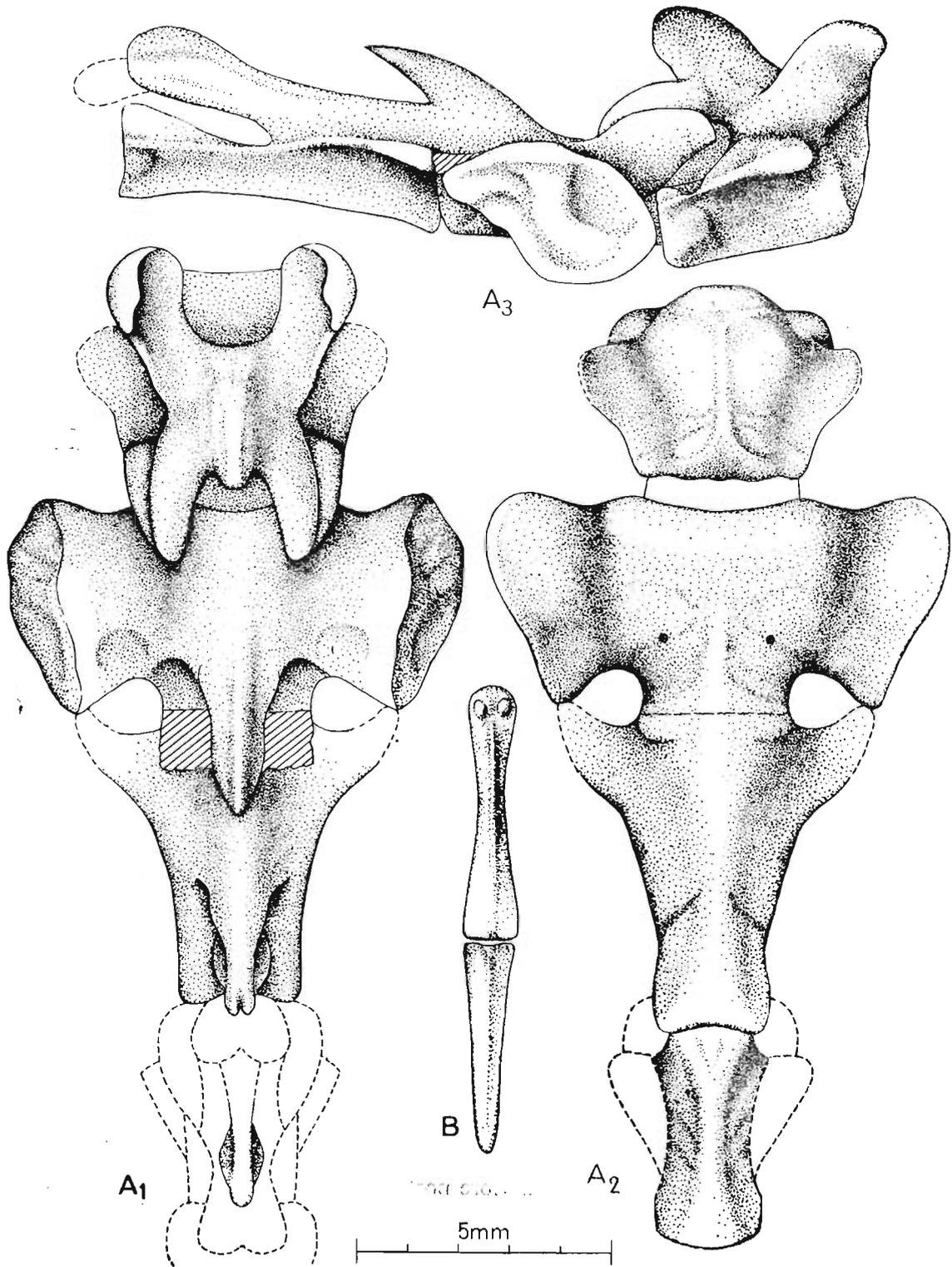


Fig. 8

*A*₁ — *Barunlestes butleri* (ZPAL MgM-I/77), last lumbar vertebra, sacrum and first coccygeal vertebra partly reconstructed; *A*₁ — dorsal, *A*₂ — ventral, *A*₃ — lateral views. In *A*₃ first coccygeal vertebra is not figured. *B* — *Zalambdalestes lechei* (ZPAL MgM-I/43), coccygeal vertebrae, possibly penultimate and ultimate.

ing the wings of the first vertebra. Along the second sacral vertebra extends a comparatively narrow and high median crest, in the posterior part of which rises a second spinous process, directed obliquely upwards. This is stouter than the first one, and is probably bifurcated at the end. Half way along, the spinous process is enlarged transversely by roughly triangular plates on its lateral walls. The posterior articular processes are not preserved. They have been reconstructed in fig. 8, on the basis of a comparison with the second and third coccygeal vertebrae, in which the articular processes are preserved (pl. 6: 1c—f).

In ventral view the middle part of the first sacral vertebra, corresponding to the body, is elevated and bounded laterally by wide, longitudinal grooves, which separate the body from the strongly raised wings. The ventral side of the body is longitudinally concave. An extremely faint body crest extends along the posterior half of the body. Faint furrows extend posterolaterally from the body crest towards the sacral foramina, with small vascular openings present in the middle of their lengths. In the second sacral vertebra, the body crest is more strongly pronounced than in the first one. The body is concave in a longitudinal sense, with raised anterior and posterior borders. In the posterior part of the body, oblique furrows extend posterolaterally from the crest. The wings are separated from the body by small, shallow furrows.

Coccygeal vertebrae. The first four and a half coccygeal vertebrae are preserved in *Barunlestes* in articulation with the sacrum (ZPAL MgM-I/77 pl. 6: 1c—f; fig. 8A), and two, probably from the posterior part of the tail, in *Zalambdalestes* (ZPAL MgM-I/43, pl. 10: 2; fig. 8B). The bodies of the first coccygeals in *Barunlestes* are distinctly shorter than those of the last coccygeals in *Zalambdalestes*. This points to different proportions of the tail in the two genera, that of *Zalambdalestes* being probably longer.

The structure of the preserved four vertebrae in *Barunlestes* also indicates a rather short tail. The neural process, which is high and prominent on the first coccygeal in *Barunlestes*, becomes obsolete on the third. The first three vertebrae are provided with wide, flattened, and rounded anterior articular processes, which articulate with much narrower posterior ones. On the fourth vertebra, the posterior articular processes are reduced, and the anterior ones of the fifth are strongly flattened. The transverse process is preserved only on the right side of the fourth vertebra and on the left side of the fifth. It extends only along the first half of the body length, as reconstructed in fig. 8A.

REMARKS ON VERTEBRAL COLUMN

The atlas in *Barunlestes* (unknown in *Zalambdalestes*) is similar in general shape to that of *Asioryctes*, which occurs in Mongolia in the same beds as *Barunlestes* (KIELAN-JAWOROWSKA 1977). The intercentrum is probably not synostosed with the lateral arches in *Asioryctes*, but it is synostosed in *Barunlestes*. The sutures between the ventral arch (intercentum) and lateral arches are present in *Barunlestes* (see fig. 2), which is a primitive character, not present in most adult modern eutherian mammals. The transverse processes are relatively larger in *Barunlestes* than in *Asioryctes*. The main difference is the presence of the transverse foramen on the atlas of *Barunlestes*; this is absent in *Asioryctes*, which retains the more primitive condition (KIELAN-JAWOROWSKA 1977). The transverse foramen in *Barunlestes* is relatively smaller than in present-day mammals of similar size. It is situated more posteriorly and pierces the posterior part of the transverse process. *Barunlestes* is the oldest known eutherian mammal in which the transverse foramen in the atlas makes its appearance.

A primitive feature of the axis of *Zalambdalestes* and *Barunlestes* is the presence in adult condition (as in *Asioryctes*) of a joint between the atlantal and axial parts of the axial body. The most characteristic feature of the neck in the *Zalambdalestidae* is the structure of the spinous process of the axis, which is unusually long and rather slender, directed horizontally. This process is very different from those of present-day and fossil mammals known to me. In most mammals the spinous process is high and strong, more or less rounded (see e. g. fig. 346 in

LESSERTISSEUR and SABAN 1967, and fig. 41 in KRÜGER 1958). In certain large rodents (e. g. *Borhyaena*, see SINCLAIR 1906) the axial spine is very strong, projecting posteriorly beyond the margin of the axial body. In both these genera it is, however, very different from that in *Barunlestes*, being relatively shorter, more robust and directed posteriorly upwards. In these genera, as in most large mammals, the spinous process of the axis serves as an area of attachment of the first, strong digitation of the lamellar part of the ligamentum nuchae (see SISSON and GROSSMAN 1953: 214). The shape of the spinous process of the axis and those of the first thoracic vertebrae indicate that the ligamentum nuchae was probably wanting in the *Zalambdalestidae*. It follows from the observation of SLIJPER (1946) that this ligament rarely occurs in mammals of a small size. The presence of a large, tear-shaped area on the anterior part of the dorsal side of spinous process of *Zalambdalestes*, interpreted here as an area of origin of the rectus capitis dorsalis muscle, indicates that this muscle was probably well developed. The side of the axial spine and the posterior articular process usually serve in mammals as origin for the obliquus capitis posterior, which inserts on the dorsal surface of the wing of the atlas. Its main function is to rotate the atlas and with it the head. The lateral sides of the axial spines are in *Zalambdalestes* concave and may have served as extensive attachment for the obliquus capitis posterior. Because of the immobility of the anterior part of the neck between C2 and C4 (due to the elongation of the spinous process of the axis), all the movements of the head are limited to the region lying in front of the axis. This, as well as the lack of a ligamentum nuchae explain the strong development of the rectus capitis dorsalis and obliquus capitis posterior.

The spinous processes of the thoracic vertebrae are in *Barunlestes* small and rounded as in numerous small mammals (SLIJPER 1946). The lumbar vertebrae are similar to those of *Didelphis* in that both have very short transverse processes. Differences exist, however, in the shape of the spinous processes, which are short and straight in *Didelphis*, but longer and bent anteriorly in *Barunlestes*.

A primitive feature of the zalambdalestid skeleton is the structure of the sacrum, which consists of two vertebrae, only the first articulating with the ilium. In this respect the *Zalambdalestidae* are more primitive than present-day eutherian mammals. An unusual feature of the structure of the sacrum is the length of the second sacral vertebra, which is longer than the first sacral and longer than the first coccygeal.

PECTORAL GIRDLE AND FORELIMB

Scapula (pl. 7: 2; fig. 9) has been preserved only in *Barunlestes*. The shape of the scapula cannot be estimated. In outer view, the glenoid border is concave, and its medial part strongly projects downwards into a small tuber scapulae, medial to which there is a large, prominent coracoid process. The ventral border between the tuber scapulae and coracoid process is deeply incurved. The spine starts 1.7 mm above the glenoid border. Its free margin is broken off. The broken surface of the spine in the ventral part is greatly enlarged, being 0.7 mm wide and narrowing dorsally. The enlargement of the ventral part of the spine indicates the presence of a rather extensive acromion, the shape of which cannot be estimated. It also cannot be estimated whether the supraspinous fossa is larger than the infraspinous fossa. In inner view, the coracoid process is very prominent, and overhangs the medial part of the glenoid angle. The margin of the glenoid fossa is thickened and rounded; a longitudinal ridge extends from the middle part of it dorsally for a distance of about 2 mm. Laterally to this, there is a longitudinal furrow, and further laterally the surface of the scapula is convex again; in the middle of the preserved part of this last convexity there is a large, oval, nutrient foramen. The remainder of the preserved part of the inner surface is rather flat.

Humerus (pl. 8: 4, pl. 9: 2; figs. 10, 11) has been preserved only in *Barunlestes*. The length of the humerus, estimated on the basis of two specimens in which only the proximal or distal

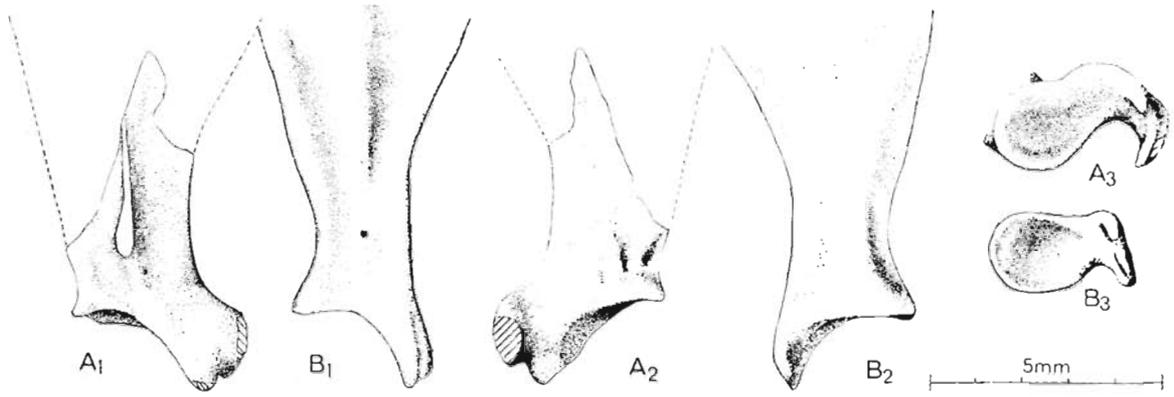


Fig. 9

Distal part of the right scapulae of *A* — *Barunlestes butleri* (ZPAL MgM-I/104); *B* — *Elephantulus myurus* (ZPAL Mw/1); *A*₁ *B*₁ — outer, *A*₂ *B*₂ — inner, *A*₃ *B*₃ — end views.

parts were preserved, is about 22 mm. In its proximal half (fig. 10) the shaft is curved, convex in front, and along the proximal one third of its length somewhat compressed laterally. The deltoid tuberosity is small, triangular and distinctly separated from the greater tubercle (tuberculum majus) by a transverse groove. The deltoid tuberosity is continued by a crest which runs downwards and forms the medial boundary of the very shallow musculo-spiral groove. The lesser tubercle (tuberculum minus) is relatively large and flattened, forming in anterior aspect (fig. 10A₃) a flat semi-circular surface, separated from the shaft by a distinct groove. The head is moderately curved and the neck well marked. A shallow undivided intertubercular groove extends at the front of the medial side. The lesser tubercle which is not very prominent, is separated from the head by a shallow groove.

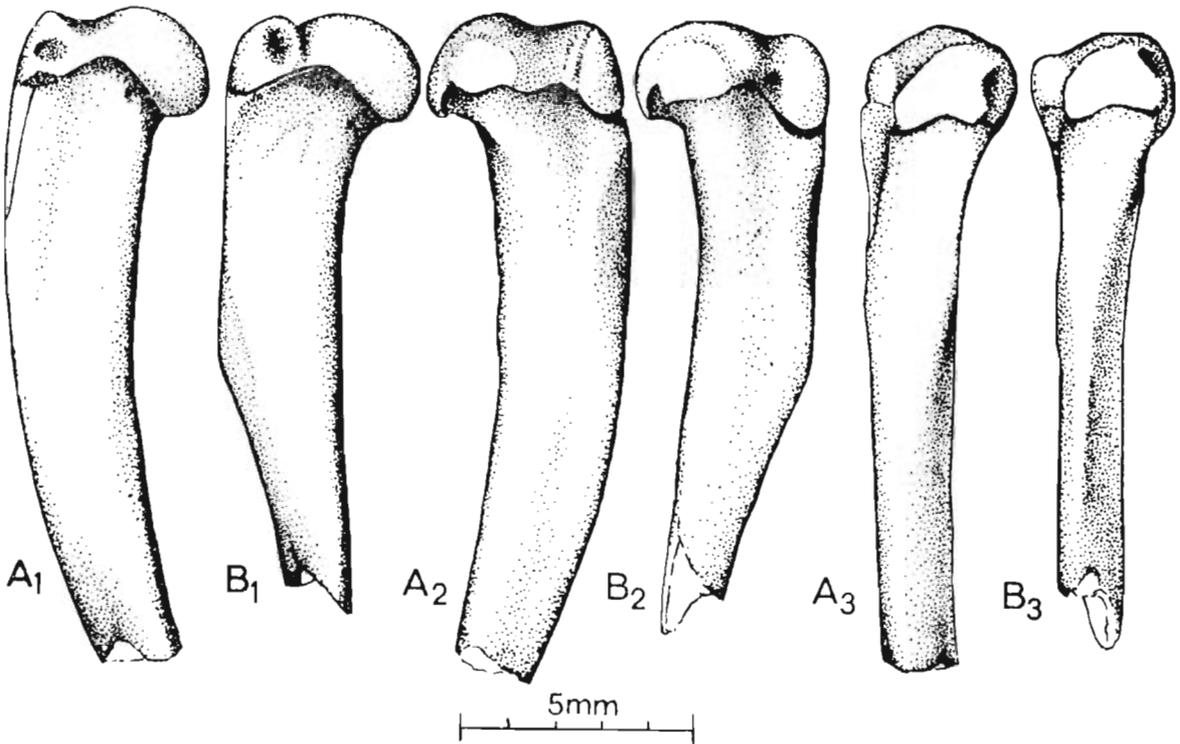


Fig. 10

Proximal part of the left humerus of *A* — *Barunlestes butleri* (ZPAL MgM-I/104) and *B* — *Elephantulus myurus* (ZPAL Mw/1); *A*₁ *B*₁ — posterolateral, *A*₃ *B*₁ — anteromedial, *A*₂ *B*₃ — anterior views.

The distal part of the shaft is strongly compressed anteroposteriorly. The medial epicondyle (fig. 11) is very prominent, the lateral condyle much smaller. Above the medial epicondyle there is a large oblique entepicondylar foramen. A shallow furrow extends from the entepicondylar foramen towards the medial epicondyle, with a distinct nutrient foramen at the end of the furrow. The radial and olecranon fossae communicate with each other, to form a supratrochlear foramen, relatively large in the described specimen, perhaps due to distortion.

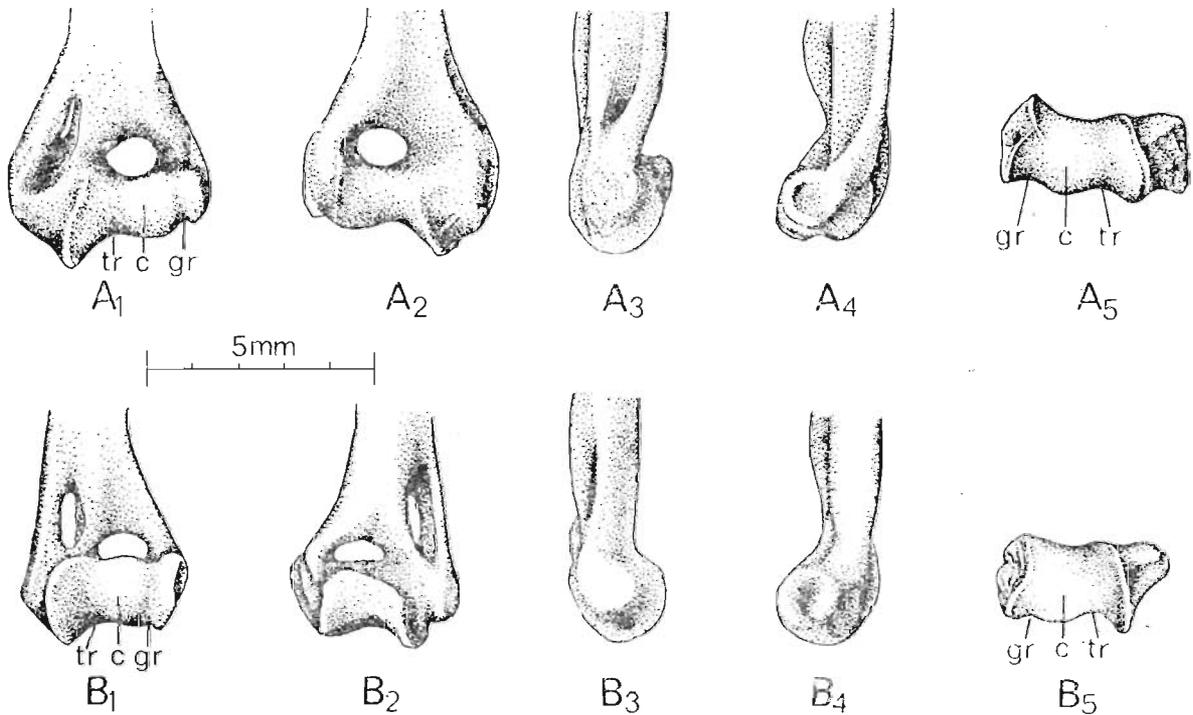


Fig. 11

Distal part of the right humerus of *A* — *Barunlestes butleri* (ZPAL MgM-1/77); *B* — *Elephantulus myurus* (ZPAL Mw/1); *A*₁ *B*₁ anterior, *A*₂ *B*₂ posterior, *A*₃ *B*₃ lateral, *A*₄ *B*₄ medial, *A*₅ *B*₅ end views; *tr* — trochlea, *c* — capitulum, *gr* — groove for the margin of the radial head.

The medial edge of the distal extremity (vestige of the ulnar condyle, see JENKINS 1973) projects strongly downwards and forms a prominent, sharp crest. The trochlea is confluent with the capitulum. Lateral to the capitulum (in anterior and ventral aspects — see fig. 11A₁ and A₅) there is shallow groove (*gr*). Extending laterally to the groove, is the lateral crest which projects downwards, but is less prominent than the medial crest.

Forearm (pl. 1: 1a, pl. 8: 1, pl. 10: 1; figs. 12, 13) has been preserved only in *Barunlestes*. The two bones of the forearm are very long and slender. Estimated length of the ulna (in ZPAL MgM-1/77, the middle part of which is missing), is 30 mm, and that of the radius about 24.5 mm. Radius and ulna contact each other proximally and distally, but are separated in the middle. The radius is arranged in the proximal part entirely in front of the ulna (see pl. 8: 1d).

Radius. The preserved fragment of the proximal part shows the head which is elongated transversely and flattened from front to back (pl. 8: 1d). The oval articular surface for the capitulum is situated almost in the middle of this surface, somewhat more medially than laterally and is confluent with the trochlear notch on the ulna. Lateral to the cavity, a large semilunar wing is directed obliquely downwards and anterolaterally, to match the groove and the lateral ridge on the distal extremity of the humerus. The large size of this wing forces the head to project strongly laterally over the shaft of the radius. The head also projects medially over the shaft, but to a smaller degree than laterally. The margin of the head along the contact with the ulna

forms a straight line. The neck is very well marked. In the middle part the shaft is flattened; distally it becomes more robust and roughly quadrangular in cross section. The distal articular surface (pl. 10: 1c, 1e) forms a single, insignificantly concave, roughly rectangular facet for articulation with the scapholunatum. The styloid process is not developed.

Ulna. The ulna is almost complete, broken in the middle. The olecranon process projects upwards and is slightly bent inwards. In this last respect it differs from that in *Elephantulus* (fig. 12A₁ and B₁) where it projects straight upwards. The olecranon process consists of a triangular tuberosity, strongly elongated longitudinally, tapering distally, and of a small tubercle on the upper margin of the olecranon. Its shape is different from that in the Macroscelididae, where on the proximal margin of the olecranon process there are two tubercles. The medial surface between the tuber olecrani and the semilunar surface is deeply concave. The anterior

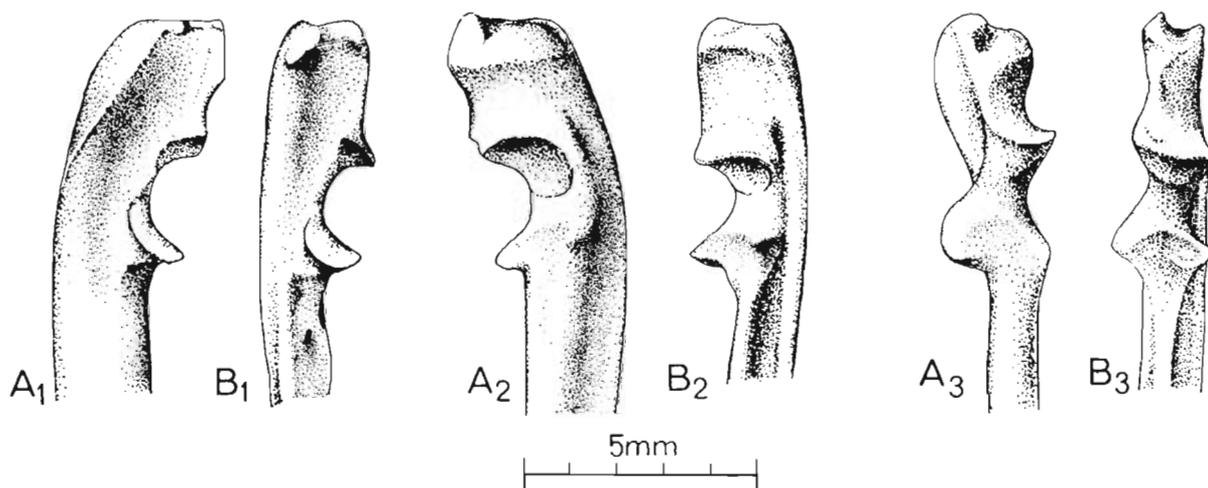


Fig. 12

Proximal part of the right ulna in A — *Barunlestes butleri*; B — *Elephantulus myurus*; A₁ B₁ — lateral, A₂ B₂ — medial, A₃ B₃ — anterior views.

margin of the olecranon, when seen in medial view, is straight in the upper part and forms a semilunar depression in the lower part, just above the anconeus process, which strongly overhangs the semilunar notch. The latter is concave from above downwards, narrow in the upper part and strongly enlarged transversely in the lower part. The medial semilunar wing projects medially over the medial surface of the ulna. The shaft is strongly compressed laterally, oval on cross section; it recalls that of *Rhynchocyon*, but differs from other Macroscelididae, where it is reduced distally and fused with the radius. At the distal end the ulna becomes more robust; it is rounded in cross section and articulates with the triquetrum. The styloid process is absent.

Carpus (pl. 10: 1; fig. 13) has been preserved only in *Barunlestes*. Of nine bones, which probably constituted the carpus, seven have been preserved in ZPAL MgM-1/77, possibly the capitatum and pisiform being lacking. A damaged bone, preserved in abnormal position on the ventral side of the carpus (seen on pl. 10: 1c) may be either of these bones. As may be seen from fig. 13A₁ the third to fifth metacarpals in the studied specimen have been moved proximally, the triquetrum is partly obscured by the hamatum, while the distal part of the ulna (due to displacement) is almost entirely obscured by the radius. Because of the small size of the bones of the carpus, it was decided not to separate them from each other. A characteristic feature of the carpus in *Barunlestes* is fusion of the scaphoideum and lunatum, which form a large crescent-shaped scapholunatum. The proximal convex surface of the scapholunatum articulates with almost all of the distal surface of the radius. The concave distal surface of the scapholunatum surrounds the centrale. On the dorsal surface of the scapholunatum an oblique, distinct furrow is visible,

which might show the line of fusion of the scaphoideum and lunatum. At the junction of the radius, the triquetrum and the scapholunatum, there is a minute bone, rounded proximally and tapering distally, designated here a sesamoid bone (os Daubentoni — see LESSERTISSEUR and SABAN 1967). The triquetrum is roughly quadrangular, but poorly preserved.

Three carpals of the distal row have been preserved. The trapezium tapers proximally, the trapezoideum is roughly rectangular, the size of the capitatum is reconstructed in fig. 13A₂,

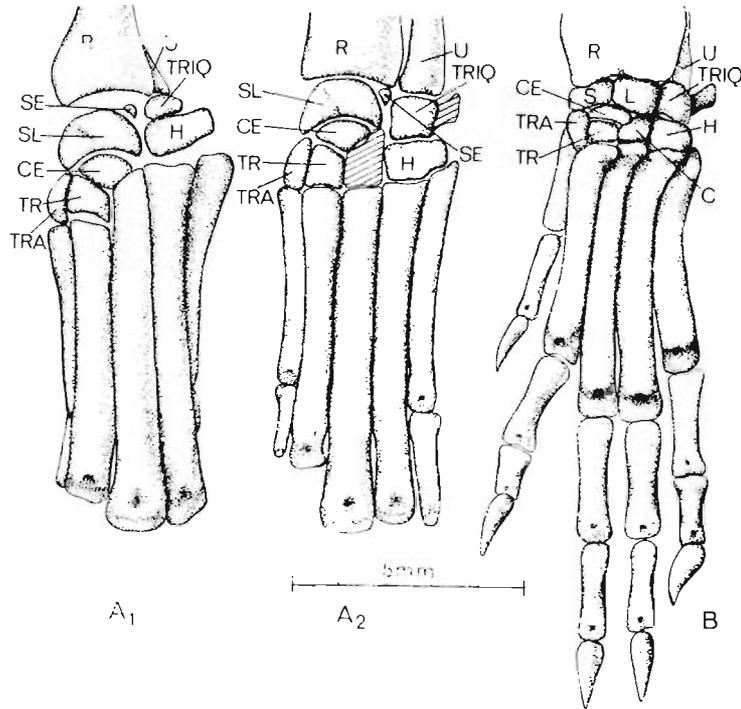


Fig. 13

Left carpus and metacarpals of *A* — *Barunlestes butleri* (ZPAL MgM-1/77); *A*₁ — the bones as they have been preserved, *A*₂ — reconstruction; *B* — *Elephantulus myurus* (ZPAL Mw/1); *C* — capitatum, *CE* — centrale, *H* — hamatum, *L* — lunatum, *R* — radius, *S* — scaphoideum, *SE* — sesamoid bone, *SL* — scapholunatum, *TR* — trapezium, *TRA* — trapezoideum, *TRIQ* — triquetrum, *U* — ulna.

while the hamatum is elongated transversely and narrows laterally. The pisiform has not been preserved, unless a fragmentary bone, seen on pl. 11: 1c on the ventral side of the carpus is a part of it.

Metacarpals. Five metacarpal bones are preserved in *Barunlestes* (ZPAL MgM-1/77). The first is the shortest, the third and fourth are the longest and the third is the widest of all the metacarpals. In the second, third and fourth metacarpals the distal ends are wider than the shafts and the proximal ends. In the first and fifth metacarpals the proximal ends are enlarged and protrude medially in the first, and laterodistally in the fifth. The metacarpals are so arranged as to form a convex dorsal surface and a concave volar surface. The shafts of all the metacarpals are compressed from front to back. The proximal ends articulate with each other and with the corresponding carpal bones. The proximal articular surface is concave from side to side. The distal ends have articular surfaces of the nature of a head, provided with a distinct pit on the dorsal side.

Phalanges. Of the digit phalanges only the first one of the first digit and first of the fifth digit are preserved in situ in *Barunlestes* (ZPAL MgM-1/77). They have the proximal ends slightly enlarged and taper distally.

REMARKS ON THE PECTORAL GIRDLE AND FORELIMB

The glenoid (articular) angle in the scapula of *Barunlestes* differs from those of most modern clavicate mammals in the presence of a very extensive coracoid process, which together with a small tuber scapulae strongly projects ventrally beyond the glenoid fossa. In some present-day primitive clavicate eutherians such as *Solenodon*, *Tenrec*, *Elephantulus* and *Tupaia*, the glenoid angle is reminiscent of that in *Barunlestes*. Also in *Didelphis* and some other marsupials (e. g. *Philander*) the tuber scapulae and the coracoid process recall those of *Barunlestes*. Although the acromion and clavicle are not preserved in *Barunlestes*, on the basis of the above comparisons, as well as on the basis of similar proportions of fore- and hindlims in *Barunlestes* to those in the Macroscelididae (see below), one can presume the presence of a clavicle in *Barunlestes*.

The proportionate lengths of the segments of the forelimb in *Barunlestes* are reminiscent of those of the modern Macroscelididae (see reconstruction of *Zalambdalestes* skeleton, fig. 17, and that of *Elephantulus*, in GRASSÉ, 1955, fig. 1579, after de BLAINVILLE). The difference concerns the metacarpal bones, which are relatively longer in *Barunlestes* than in *Elephantulus*.

The humerus of *Barunlestes* shows strong similarity to that of the Macroscelididae (see figs. 10 and 11). In the proximal part the similarities concern proportions of the tuberculum majus and tuberculum minus, and the presence of the entepicondylar and supratrochlear foramina. The distal extremity is also generally reminiscent of those of the Macroscelididae and to a smaller degree of other primitive extant mammals such as *Tupaia* (see JENKINS 1973, fig. 171); e. g. a groove (fig. 11, gr.) on the distal extremity, characteristic of *Barunlestes* and Macroscelididae does not occur in *Tupaia*.

In *Barunlestes*, in the Macroscelididae and in *Tupaia* the radius is situated in its proximal end fully anterior to the ulna, not anterolaterally, and the articulating surface of the radius is confluent with the trochlear notch on the ulna (see pl. 8: 1d, 2 and 3). In this respect the radius and ulna in these three groups represent the form figured by TORNIER (1886, fig. 1b), as characteristic of the Marsupialia. Consequently, the capitulum (which forms the central part of the distal extremity and is not separated from the trochlea by a ridge), articulates in extension with the radius and in flexion with the ulna.

The carpus of *Barunlestes* differs from that of the Macroscelididae in the presence of a scapholunatum, whereas in the Macroscelididae the scaphoideum and lunatum are not fused (fig. 13). The centrale characteristic of *Barunlestes* occurs in the Macroscelididae (and in many other mammals). The metacarpals are relatively longer in *Barunlestes* than in *Elephantulus*, but the differences are not striking.

The carpus of *Barunlestes* has a structure typical of the convergent hand (defined also by ALTNER 1971 as a "Spreizhand") of small mammals. In numerous primitive marsupials (e. g. in *Didelphis*), the scaphoideum and lunatum are fused as in *Barunlestes*. However, the carpus in *Didelphis* shows a quite different arrangement of bones, characteristic of a grasping hand with opposable pollex (see ALTNER 1971).

PELVIC GIRDLE AND HINDLIMB

Pelvis (os coxae) (pl. 1: 2a—b, pl. 5 and pl. 6: 1a—b). Incomplete pelvis has been preserved in *Zalambdalestes* (ZPAL MgM-I/43) and almost complete in *Barunlestes* (ZPAL MgM-I/77). The sutures between ilium, ischium and pubis are present in acetabular region and are better seen on the inner than on the outer surface of the pelvis. The position of the sutures agrees in general with that in *Didelphis*. The ilium is narrow and strongly elongated, concave longitudinally, and with a rounded anterior margin. The tuber coxae and tuber sacrale are not developed. Above the anterior part of the acetabulum on the upper margin of the pelvis there is a small tubercle through which passes the suture between the ilium and ischium. In front of this tubercle

the upper margin of the ilium is concave, forming the greater sciatic notch, and in front of the notch there is a crescent-shaped prominence, the posterior iliac spine. From the spine forwards, the ilium forms an elongated shaft, slightly narrowing anteriorly, its inner side forming the surface that articulated with the sacrum.

The ventral margin of the ilium in front of the acetabulum is slightly concave. A prominent tubercle for the rectus femoris muscle is present near the anterior margin of the acetabulum. Extending anteriorly from this tubercle towards the anterosuperior corner of the ilium, a ridge delimits the gluteal surface from the pelvic surface. The inner (pelvic) surface of the ilium is convex in a longitudinal direction. The auricular surface is small and poorly discernible, delimited posteroventrally by an indistinct, rounded ridge.

The body of the ischium forms a straight shaft, which widens posteriorly to form a poorly defined tuber ischii. The ischiatic spine is very small, marked only by the presence of the greater sciatic notch. The dorsal margin between the suture with the ilium and the ischiatic spine forms

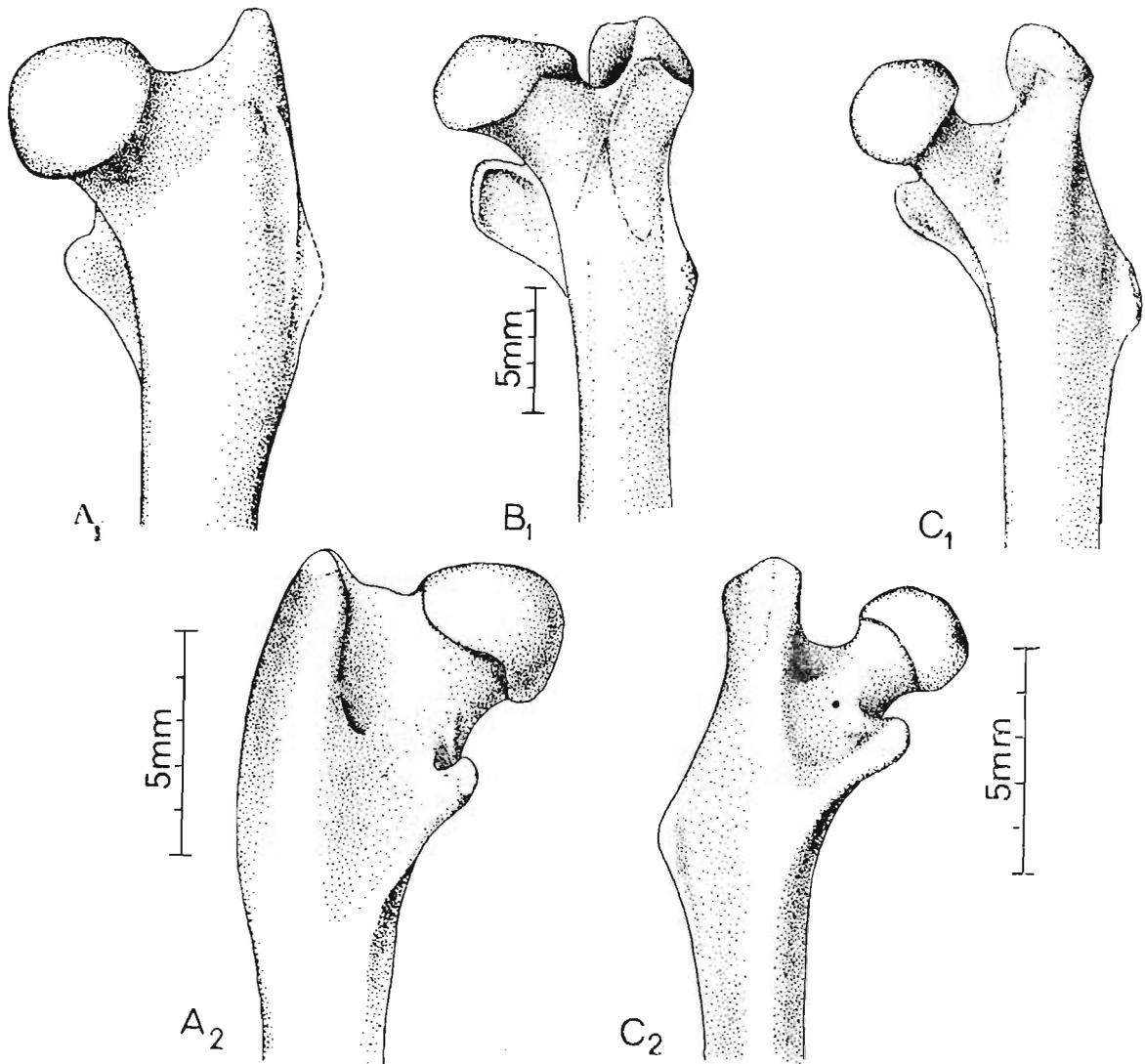


Fig. 14

Proximal part of the femur of *A* — *Barunlestes butleri* (ZPAL MgM-1/77), *B* — *Rhynchocyon cirnei hendersoni* MCZ 43735. *C* — *Elephantulus myurus* (ZPAL Mw/1); *A*₁, *B*₁, *C*₁ — anterior, *A*₂, *C*₂ — posterior views. The broken line in *A*₁ denotes reconstructed third trochanter, not figured in fig. *A*₂.

a straight line; the greater sciatic notch is very shallow, extending posteriorly for one third of the ischium length. The body and ramus of the ischium are almost at right angles. The suture between ischium and pubis is not visible in the posterior part of the pelvis.

The acetabular and symphyseal processes of the pubis meet at a right angle. On the lower part of the anterior margin of the pubis there is a small triangular surface, tapering downwards, recognized (KIELAN-JAWOROWSKA 1975c) as an articular surface for the marsupial bone. It has been claimed (KIELAN-JAWOROWSKA *l. c.*) that it is highly possible that the marsupial bones existed in *Barunlestes* and were characteristic of all primitive mammals, including Eutheria. The acetabulum is a deep hemispheric cavity of which about one-sixth is formed by the pubis, one-sixth by the ilium and two-thirds by the ischium. The articular part is circumferential except for a deficiency of one quarter of the ring posteroventrally. It is moderately deep anteriorly, shallow dorsally and most deep posteriorly where it forms a prominent rounded wing. There is a small, deep notch behind and below the wing. The nonarticular part is formed exclusively by the ischium. The obturator foramen is large, elongated longitudinally, and roughly oval in outline.

Femur (pl. 1: 1b, pl. 5, pl. 7: 1, pl. 11: 2, 4; fig. 14) has been preserved only in *Barunlestes*. It is long and slender. In ZPAL MgM-I/77 the estimated length of the femur (measured along the distal and proximal parts of the right femur, which were preserved in situ, the middle part being missing) is 34.5 mm. The head forms more than a hemisphere; its upper (proximal) surface is flattened. The neck is stouter than in the Macroscelididae (fig. 14), less elongated, and most distinct anteriorly and medially. It forms an angle of about 60° with the body. The anterior surface of the neck is in the same plane as the anterior aspect of the body. The upper margin of the neck forms an almost straight line, very different from that in *Elephantulus* and more reminiscent of *Rhynchocyon*. The greater trochanter is rather short, roughly triangular, much less prominent than in *Elephantulus*. The lateral surface of the greater trochanter is broad proximally and slightly narrowed distally. The trochanteric crest overhangs a very deep and elongated trochanteric fossa. The third trochanter in the studied specimens is not preserved. In the Macroscelididae the third trochanter forms a delicate, roughly triangular wing. It cannot, however, be excluded that the third trochanter was present in *Barunlestes* and had a structure similar to that in the Macroscelididae. If this is true it must have become broken during fossilization. It is tentatively reconstructed in fig. 14A₁. This hypothesis is partly confirmed by the study of the lateral surface of the shaft, below the greater trochanter. In the left femur of ZPAL MgM-I/77 there is on this surface a delicate ridge, the middle part of which is broken off. Judging from the size of the broken ridge, the third trochanter in *Barunlestes* would probably be less prominent than in *Elephantulus*.

The distal extremity is flattened anteroposteriorly. The condyles are of almost equal size, the inner slightly larger. They are separated by a narrow and deep intercondyloid fossa. The fossa is bounded proximally by a distinct intercondylar line, which forms a sharp, transverse ridge. The patellar groove is asymmetrical. The groove of the trochlea is wide and extensive, not very deep. Of the two ridges, that surround it, the medial is more prominent and extends up higher than the lateral one. The lateral epicondyle is somewhat more prominent than the medial. The medial epicondyle is surmounted by the adductor tubercle.

Tibia and fibula (pl. 1: 2a—b, pl. 5: 1a, pl. 7: 1d, pl. 11: 1 and 3). In *Barunlestes* (ZPAL MgM-I/77) are preserved: a part of the left tibia, 34 mm long, lacking the distal extremity, and a 13 mm long proximal part of the right tibia. In *Zalambdalestes* (ZPAL MgM-I/43) and incomplete left tibia is preserved, its distal end (i. e. the tibiofibular) articulates with a partial tarsus and foot. The proximal extremity is missing, and the lateral wall of the proximal part, together with the place of fusion with the fibula, is not preserved. The length of the preserved part of the tibia is 34 mm. In the same specimen, along the inner side of the tibia, there is the shaft of the fine, long bone, interpreted as an ulna (fig. 1).

The fibula is fused with the tibia along about two thirds of its distal extent and consists only of the proximal part. No trace of the lower part can be distinguished. The lower end of the fragment is fused to the tibial shaft and the upper extremity is fused or jointed by a synovial joint to the tuberosity of the tibia. The length of the free part is in *Barunlestes* (ZPAL MgM-I/77) about 9.6 mm. This free part is not preserved. Judging from the preserved proximal and distal extremities fused with the tibia, the free part of the fibula was a very slender bone.

The length of the tibia is unknown, it may measure around 40 mm. The shaft of the tibia is thick, prismatic and roughly triangular in cross section proximally. It becomes gradually thinner distally and oval in cross section. At the distal end it strongly widens again. The anterior margin is prominent only proximally, along about one third of the length of the tibia; distally it is gently rounded. The medial margin is rounded. The lateral margin forms a sharp crest above the fusion with the fibula and is rounded below. The lateral surface is wide and concave along one third of its proximal extent and rounded below. Extending along the lateral margin of the posterior surface there is a wide groove which becomes narrower and shallower near the fusion with the fibula. The popliteal line is not discernible proximally; it is visible only as a faint, oblique crest extending over a distance between the mid-line of the posterior surface and the medial border. The distal extremity of the tibia is not preserved in *Barunlestes* but it is partly preserved in *Zalambdalestes* (see pl. 1: 2b—c). In this specimen both lateral and medial malleoli are broken off; the cochlea tibiae is well preserved. The medial groove is smaller than the lateral one, which is associated with a great asymmetry of the astragalus. The medial groove is arranged roughly horizontally; the large lateral groove, quadrangular in shape, is arranged very obliquely. The intermediate ridge is prominent. Due to these characters and the absence of the malleoli caused by damage, the preserved distal end of the tibia appears in anterior view to be roughly triangular and tapering downwards.

The proximal extremity of the tibia is in *Barunlestes* in superior aspect roughly triangular. The medial articular surface is smaller than the lateral, gently concave and elongated anteroposteriorly. The lateral surface is roughly circular. The two surfaces are separated by the intercondylar eminence, which forms a smooth, not very prominent ridge, widening anteriorly. Extending in front of the intercondylar eminence, the intercondylar area is rough and depressed. A posterior intercondylar area is not discernible. Anteriorly the two articular surfaces are confluent and form a wide subtriangular elevation. Separated from this elevation by a transverse groove, and situated lower is the tuberosity of the tibia. The lateral articular surface has an overhanging outer margin, which in the posterolateral corner projects downwards and fuses or makes a synovial joint with the fibula.

Tarsus (pl. 1: 2b—c, pl. 9: 1, and fig. 15) has been preserved only in *Zalambdalestes* (ZPAL MgM-I/43).

Calcaneus is 6.6 mm long, narrow, strong and compressed laterally. Examined in dorsal view it is constricted at about one third of its length from the upper margin. The length of the proximal part of the body above the astragalo-calcaneal facet exceeds a half of the calcaneal length (measures 4 mm). The tuber calcanei forms a prominent, rounded knob, 1.3 mm long in plantar view. The astragalo-calcaneal facet in dorsal aspect is obscured by the astragalus. In lateral aspect it is seen as a sharp triangular process (processus cochlearis of Sisson and Grossman 1953, or processus coracoideus of Nickel *et al.* 1968), projecting obliquely downwards, entirely surrounded by the lateral ridge of the astragalus. The sustentacular facet examined in plantar view forms a narrow process, which widens upwards. In medial view it appears more extensive, triangular, and provided with an oblique ridge. The medial surface of the body below the tuber is distinctly concave.

The lateral surface is slightly concave, and the plantar surface forms a slightly concave ridge. The distal surface of the calcaneus is arranged at right angle to the length of the body. In its medial half it bears a cuboid facet surrounded laterally by a ridge. The cuboid facet faces downwards and consists of a flat anterior part and concave posterior part. The articular

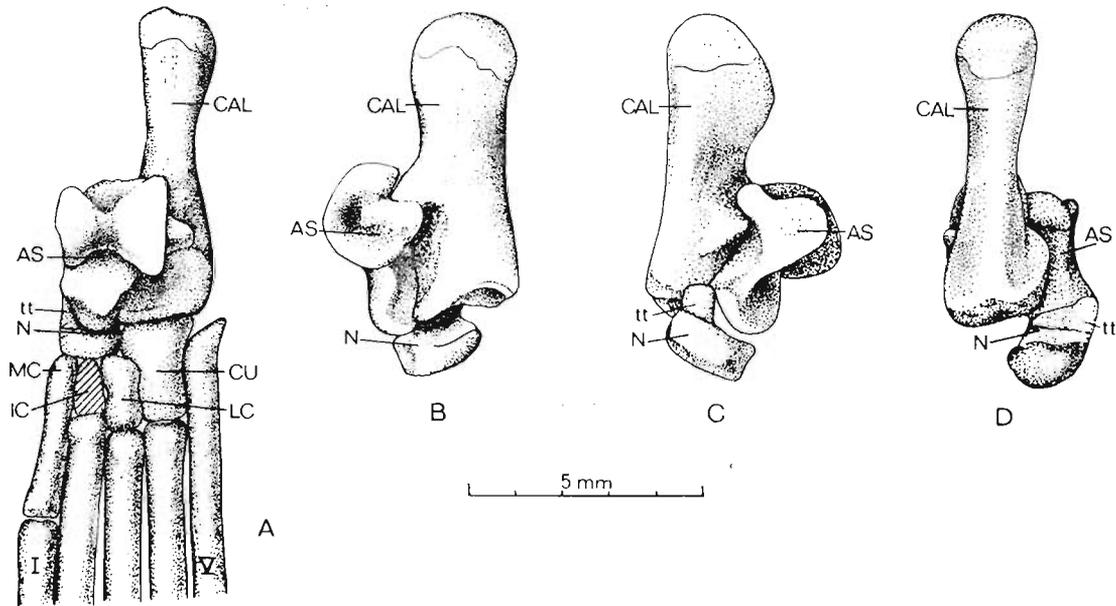


Fig. 15

Zalambdalestes lechei (ZPAL MgM-I/43); A — reconstruction of the left tarsus and proximal ends of metatarsals in dorsal view, B — calcaneus, astragalus and navicular of the same specimen, as they have been preserved in lateral view, C — the same in medial view, D — the same in plantar view; AS — astragalus, CAL — calcaneus, CU — cuboideum, IC — intermedial cuneiform, LC — lateral cuneiform, MC — medial cuneiform, N — navicular, tt — tuber tibialis.

surface for the lateral malleolus of the tibia (tibio-calcaneal facet) is not developed on the calcaneus; the tibia articulates exclusively with the astragalus (see below). The peroneal tubercle is not developed.

Astragalus has a deep trochlea and a head separated from the trochlea by a short, unstricted neck. The trochlea is arranged parallel with regard to the body of the calcaneus, but the distal part of the astragalus is arranged obliquely.

The trochlea is markedly asymmetrical. The lateral ridge is very large, strongly convex, the medial ridge much smaller. The lateral ridge forms in lateral view an almost regular circle. The trochlear groove, in the only specimen in which the astragalus has been preserved (ZPAL MgM-I/43) is deeper than it was in life, because of damage, possibly partly due to the preparation. An examination of the photograph of this specimen on pl. 9: 1e may give a wrong impression that the groove of the tibial trochlea was much deeper in *Zalambdalestes* than in any known present-day mammal, which in fact is not the case. The shape of the groove of the tibial trochlea is in *Zalambdalestes* unknown and it is only tentatively reconstructed in fig. 15. Extending laterally from the lateral ridge is a very prominent lateral malleolar surface, triangular in dorsal view. This serves as an area for articulation with lateral malleolus of the tibio-fibula. In lateral view the lateral malleolar surface has an appearance of a prominent, rounded ridge. The plantar surface is in large part obscured by the calcaneus. The dorsal astragalar foramen (SZALAY 1971) was probably absent, but as the surface of the bone is in this area damaged, its presence cannot be excluded. On the exposed part of the plantar surface the plantar astragalar foramen is not discernible.

Navicular is a small bone, consisting of the main body which articulates with the astragalar head and the medioproximal tuber (tuber tibialis). An indistinct joint is tentatively recognized between the main body and tuber tibialis. It is, however, not certain whether the line, recognized herein as a joint (very distinct in dorsal and medial views, but much less distinct in ventral view) is not a crack. The main body is irregularly quadrilateral in dorsal view, 1.2 mm long and 0.9 mm high. Its proximal surface is concave. The distal surface is convex in the anterior part and flat posteriorly, not divided into separate fossae for the cuneiforms.

Cuboideum is 2.1 mm long, wide proximally along one third of its length, opposite the contact with the navicular, and narrower distally. The medial border of the cuboideum is incurved to house the lateral cuneiform.

Lateral cuneiform is 1.5 mm long, roughly rectangular, with sigmoid lateral margin contacting the cuboideum.

Intermedial cuneiform, which is not preserved, is (as appears from the reconstruction in fig. 15) about 1.1 mm long, roughly rectangular.

Medial cuneiform is strongly elongated, 3.4 mm long and about 0.6 mm wide.

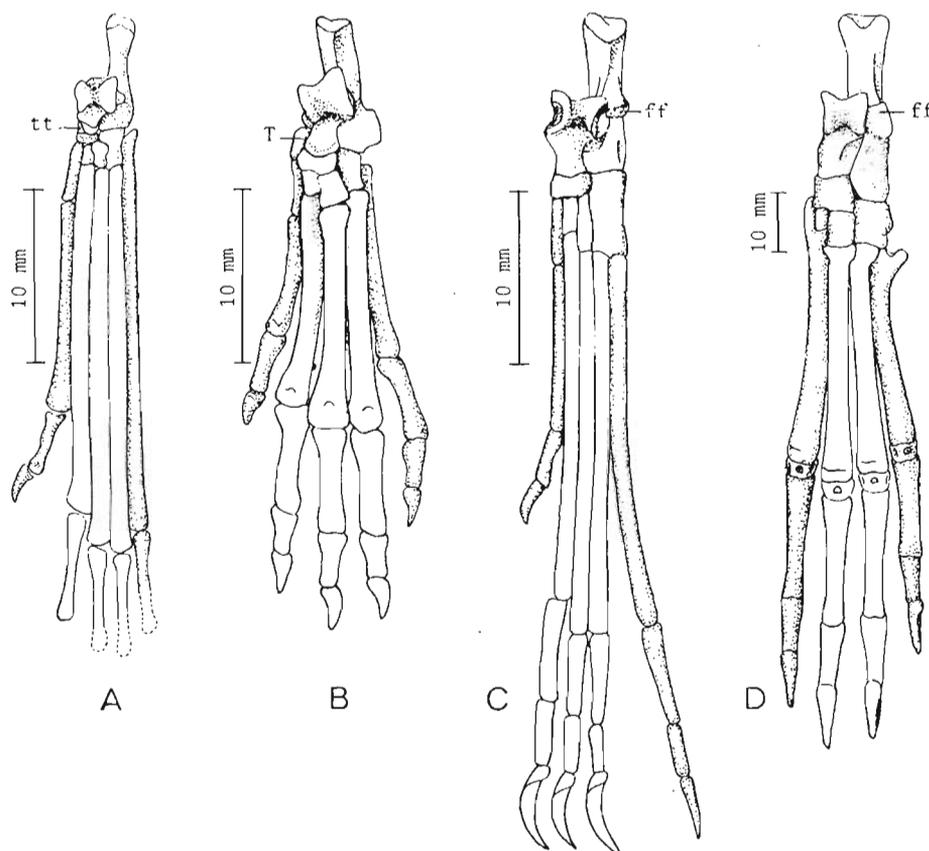


Fig. 16

Diagrammatical drawings of the left feet of A — *Zalambdalestes*, B — *Rattus*, C — *Elephantulus*, D — *Oryctolagus*; T — tibiale, tt — tuber tibialis, ff — calcaneal fibular facet.

Metatarsals (pl. 1: 1c and 2b—e, and fig. 16A) have been almost completely preserved in *Zalambdalestes* (ZPAL MgM-1/43) and distal ends of second to fifth in *Barunlestes* (ZPAL MgM-1/77). They are very long and thin, with strongly enlarged distal ends. The first, the shortest, is in *Zalambdalestes* (ZPAL MgM-1/43) 12.5 mm long, the second 21 mm long, the third 22.5 mm long, the fourth (estimated length) 23.5 mm long, the fifth (estimated length) 23.5 mm long. The second metatarsal is the widest. The fifth is pointed proximally and protrudes laterally along the cuboideum.

Phalanges. The first and second phalanges of the first digit are preserved in *Zalambdalestes* (ZPAL MgM-1/43), where the first is 3 mm long, the second (sharp claw) is 2 mm long. The first phalanx of the second digit is 5.4 mm long. Of the other digits only the proximal parts of the first phalanges are preserved. The first phalanx of the fourth digit in *Barunlestes* (ZPAL MgM-1/77) is 4 mm long.

REMARKS ON THE PELVIC GIRDLE AND HINDLIMB

The possible existence of epipubic bones in the Zalambdalestidae has been discussed elsewhere (KIELAN-JAWOROWSKA 1975c). The femur resembles in general those of the Macroscelididae and comparisons with that family have been made throughout the description. A characteristic feature of the hindlimb of the Zalambdalestidae is a strong degree of fusion of the tibia and fibula. Tibia and fibula are fused in numerous mammals, among which the Macroscelididae, Leporidae, Tarsiidae and Dipodidae display a manner of fusion similar to that in the Zalambdalestidae, (MCKENZIE 1911, BARNETT and NAPIER 1953). In all these groups no trace of the lower half of the fibular shaft can be distinguished. The lower end of the fragment is fused to the tibial shaft, whereas the superior tibio-fibular joint is either fused (e. g. *Rhynchocyon*, *Petrodromus*, *Elephantulus*, *Dipus*) or synovial (e. g. *Macroscelides*, *Lepus*, *Tarsius*, *Jaculus*, *Allactaga*). BARNETT and NAPIER (1953) stated that mammals with thin, flexible fibula, fused or incorporated with the tibia at its lower end and articulating with it at the upper end by means of synovial joint, are capable for rapid, sudden movements. It is impossible to state whether the superior tibio-fibular joint in the Zalambdalestidae was synovial or fused. However, the preserved parts of the tibia and fibula speak for the capacity for rapid movements.

The tarsus of *Zalambdalestes* has a structure in general similar to those of the present-day eutherian mammals and very different from that of the Late Cretaceous *Asioryctes*. KIELAN-JAWOROWSKA (1977) has shown that the tarsus of *Asioryctes* represents the most primitive type found in the therian mammals intermediate between that of Triassic triconodonts (JENKINS and PARRINGTON 1976) and modern therian mammals. The primitive features of the tarsus of *Asioryctes* are the lack of the tibial trochlea and the position of the proximal body of the astragalus medial to the calcaneus. *Zalambdalestes*, which occurs in beds older than *Asioryctes* has a very advanced structure of the tarsus. The astragalus is here supported by the calcaneus, the tibial trochlea on the astragalus is well developed and the tibio-fibula articulates only with the astragalus. The astragalo-calcaneal complex of *Zalambdalestes* is also more advanced than in the Late Cretaceous eutherian genera from North America *Protungulatum* and *Procerberus* described by SZALAY and DECKER (1974). The primitive features of these genera are the presence of a distal peroneal tubercle (absent from *Zalambdalestes*), the cuboid facet oblique to the long axis of the calcaneus (perpendicular in *Zalambdalestes*), the low tibial trochlea (deep in *Zalambdalestes*) and the presence of a calcaneal fibular facet (absent from *Zalambdalestes*). The other specialized feature of *Zalambdalestes* tarsus is the long and laterally compressed calcaneal body posterior to the astragalo-calcaneal facet. The astragalo-calcaneal complex of *Zalambdalestes* is also more specialised than that of the Paleocene leptictid *Prodiacodon* described by SZALAY (1966) in its lack of the peroneal tubercle (broken off but possibly present in *Prodiacodon*) and probably in the absence of the astragalular foramen.

Since Gegenbaur's paper (1864) anatomists have commonly believed that the mammalian astragalus represents a fused tibiale and intermedium. The question has been discussed by various authors (see LEWIS 1964 for summary). LEWIS (*l. c.*) argued that there is no evidence to support GEGENBAUR'S view and demonstrated that the free tibiale, which occurs in rodents and monotremes, is homologous with the tuber tibialis of the navicular of certain mammals. Consequently according to LEWIS the navicular is homologous with centrale plus tibiale. In a majority of present-day mammals the navicular is irregularly quadrilateral with a concave proximal surface to receive the astragalular head. However, in some mammals, e. g. in marsupials (see *Thylacinus*), in the Felidae and in some insectivores the navicular is provided with a large medio-proximal tuber tibialis. The tuber tibialis is well developed in *Zalambdalestes* and there is an uncertain joint between it and the quadrilateral part of the navicular. If this interpretation is correct, the structure of the navicular in *Zalambdalestes* may serve as an additional argument supporting LEWIS' (1964) idea.

The tarsus of *Zalambdalestes* may be superficially compared with that of rodents (see fig. 16),

from which it differs in the lack of a free tibiale, in the lack of a peroneal tubercle, in having the astragalar trochlea arranged parallel to the calcaneus (oblique in rodents) and in the differently shaped astragalar head. The similarities concern the presence of the lateral malleolar surface on the astragalus, the lack of the calcaneal fibular facet and the general proportions of the cuneiforms. The metatarsals are, however, proportionally more elongated in *Zalambdalestes* than in quadrupedal rodents.

Neither does the tarsus of lagomorphs invite a close comparison with that of *Zalambdalestes*. There are certain similarities such as lack of the peroneal tubercle (absent also in most present-day mammals) and the nearly longitudinal arrangement of the astragalar trochlea in lagomorphs (entirely longitudinal in *Zalambdalestes*). The differences concern the presence of extensive calcaneal fibular facet in lagomorphs (absent in *Zalambdalestes*) which results in a quite different contact of the tibio-fibula with the tarsus in the two groups, and the different shape of the astragalar head. In Recent leporids the calcaneus extends more distally than the astragalus making possible the calcaneo-navicular contact. This is a new feature as in the Oligocene leporid *Megalagus* the astragalus reaches the same distance distally as the calcaneus (DAWSON 1958). The tarsus of *Megalagus* is very different in details from that of *Zalambdalestes* and with the exception of the relative lengths of the astragalus and calcaneus does not differ essentially from those of the modern leporids. The navicular in *Megalagus* as in the modern leporids, is provided with an extensive tuber, directed distally, very different from that in *Zalambdalestes*.

The long metatarsals, comparable with those of *Zalambdalestes* occur in the Macroscelididae, but there are important differences in the structure of the tarsus (see fig. 16). The latter is more elongated in Macroscelididae, the calcaneal fibular facet is present, and the distinctive structure of the macroscelidid astragalus, with the ridges strongly bent toward the middle of the trochlea, is very different from that in *Zalambdalestes*.

It is interesting to compare the tarso/metatarsal index $\left(\text{length of } \frac{\text{tarsus} \times 100}{\text{metatarsal III or IV}} \right)$ of *Zalambdalestes* and other mammals. I have measured as the length of the tarsus the distance between the proximal end of the calcaneal tuber and the distal end of the cuboideum, or lateral cuneiform, depending on which one protrudes farther distally. The tarso-metatarsal index so obtained is 39 in *Zalambdalestes*, 63 in *Elephantulus*, 83 in *Rattus* and 90 in *Oryctolagus*. These differences in the proportionate lengths of the tarsus and metatarsals are also clearly seen from fig. 16. The tarsus in *Zalambdalestes* is unusually short in comparison with strongly elongated metatarsals. In *Elephantulus* in which the metatarsals are of about the same absolute length as in *Zalambdalestes*, the tarsus is almost twice as long. The proportions between tarsal and metatarsal lengths in *Rattus* and *Oryctolagus* are very different from those in *Zalambdalestes*.

It follows from the foregoing comparisons that although the tarsus of *Zalambdalestes* is generally on the level of organization of modern eutherian mammals, it has a specific structure, not known to occur as a whole in any group of present-day mammals.

HABITS OF THE ZALAMBDALESTIDAE

(fig. 17)

The structure of the spinous process of the axis of *Zalambdalestes* indicates that the anterior part of the neck was immobile. This structure, together with short spinous processes of the thoracic vertebrae, suggest the lack of a ligamentum nuchae. An immobile neck region is characteristic of mammals of various habits, including aquatic (not an appropriate comparison with the Zalambdalestidae), fossorial, and ricochet adaptations (HATT 1931, LULL 1948, LESSERTISSEUR and SABAN 1967). It is improbable that the zalambdalestids were strongly fossorial as limb structure shows no appropriate adaptations. The neck in *Zalambdalestes* is not greatly shortened, and thus differs from the common condition in ricochet small mammals. The axis of *Barunlestes*

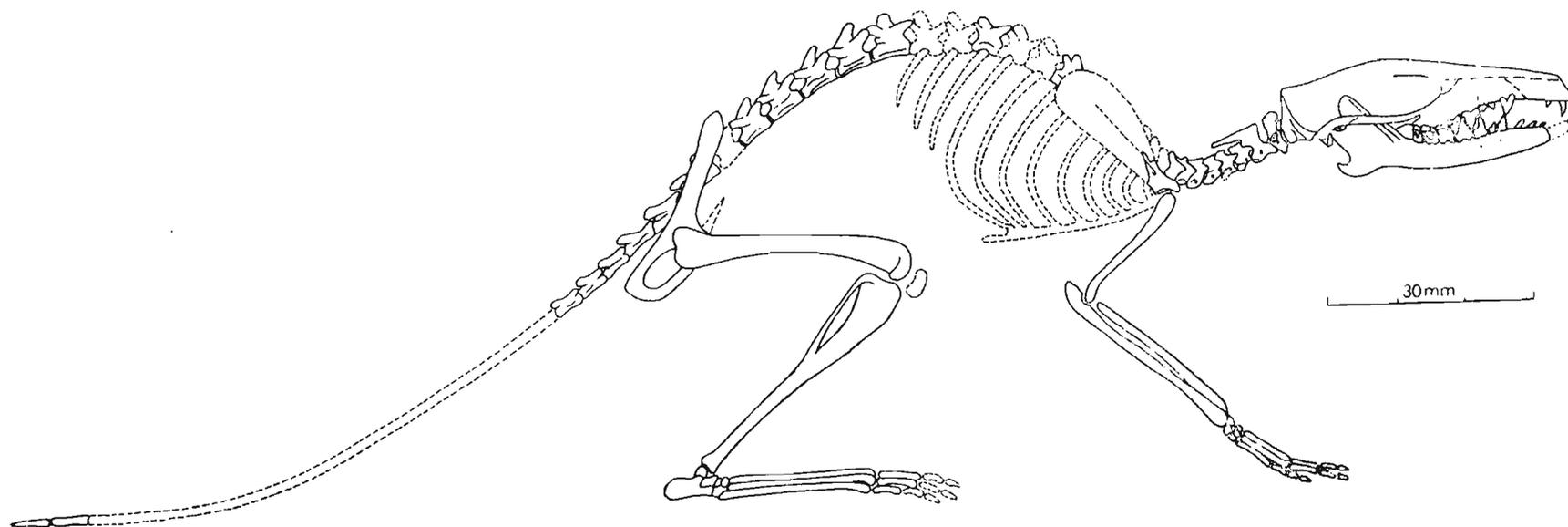


Fig. 17

Reconstruction of the skeleton of *Zalambdalestes lechei*, partly based on skeletal parts of *Barunlestes butleri*.

is distinctly shorter than in *Zalambdalestes*, however, and might hint to a tendency toward shortening of the neck region through the history of the Zalambdalestidae. Unfortunately, the remaining neck vertebrae of *Barunlestes* are unknown. It seems possible that the partial immobility of the anterior part of the neck is indicative of a tendency toward ricochetal behaviour, although the Zalambdalestidae presumably did not leap bipedally (see below).

The estimated value of the intermembral index $\left(\text{lengths of } \frac{\text{humerus} + \text{radius} \times 100}{\text{femur} + \text{tibia}} \right)$ is 63 in the Zalambdalestidae. As complete tibiae and humeri are unknown in *Barunlestes* and *Zalambdalestes*, their lengths have been estimated from preserved fragments.

The values of the intermembral index are 96 in *Lepus*, 62 in *Rhynchocyon*, 75 in *Petrodromus*, 65 in *Elephantulus*, 68 in *Macroscolides*, 45 to 48 in *Macropus*, 46 in *Dipodomys*, 39 in *Pedetes*, 33 in *Jaculus*, and 36 in *Allactaga* (EVANS 1942, HOWELL 1933). Thus the Zalambdalestidae fall within the range of variation of macroscolidid genera, being similar in intermembral index to *Rhynchocyon* (62) and *Elephantulus* (65).

MARLOW (1969) has shown that the desert-living Australian mammals *Antechinomys spenceri* (Dasyuridae) and *Notomys cervinus* (Muridae) occupy the same habitat and are similar in general appearance, but differ in modes of locomotion. *Antechinomys* leaps quadrupedally, while *Notomys* leaps bipedally at fast speeds, but runs quadrupedally at lower speeds. He also provided detailed osteological measurements for both genera. Unfortunately he chose to measure the ulna in the forearm rather than the radius; thus estimation of intermembral indices is difficult. Having no specimens of *Antechinomys* or *Notomys* available, I estimated the length of the radius to be about 78% of that of the ulna, as calculated from measurements taken on the radiographs by MARLOW (1969, Table II), and on the basis of comparisons with other murids and dasyurids. The estimated intermembral index is 65 in *Antechinomys* and 44 in *Notomys*. This agrees with the data discussed above, and shows that *Notomys*, which leaps bipedally, has a low intermembral index, that falls within the range of variation observed in ricochetal small mammals. The quadrupedal *Antechinomys* has an intermembral index similar to those of the Zalambdalestidae and Macroscolididae.

The data provided by MARLOW (1969) show that the intermembral index may serve as a reasonable indication of the mode of progression in small mammals with elongated feet, although MARLOW does not draw this conclusion.

The value of the metatarsal/femoral index $\left(\text{lengths of } \frac{\text{metatarsal III} \times 100}{\text{femur}} \right)$ is 55 in *Rhynchocyon*, 60.7 in *Petrodromus*, 53.6 in *Elephantulus*, and 70.8 in *Macroscolides* (see EVANS 1942). The same index is probably about 65 in the Zalambdalestidae, estimated tentatively from length of femur in *Barunlestes* and length of third metatarsal in *Zalambdalestes*. This means that the metatarsals in zalambdalestids are relatively longer than in most macroscolidid genera.

Persistent repetition of misinformation that the elephant shrews hop bipedally occurs in the literature (e. g. LESSERTISSEUR and SABAN 1967, VAUGHAN 1972, GUNDERSON 1976), despite EVANS' (1942: 104) statement that: "The Macroscolididae, in spite of their apparent adaptation for hopping, do not do so". BROWN (1964) and BROWN and YALDEN (1973) again demonstrated that the Macroscolididae do not have completely bipedal locomotion. The usual form of progression in members of this family is to walk quadrupedally or run with all four feet frequently clear of the ground. The intermembral index ranges between 33 and 48 in ricochetal mammals and thus is lower than in the quadrupedal Macroscolididae and in the Zalambdalestidae¹⁾.

On the basis of intermembral and metatarsal/femoral indices, and other proportions of particular segments of the limbs, I conclude that locomotion by the zalambdalestids was similar to that of present-day macroscolidids. While it seems reasonable also to conclude that they were not bipedal leapers, it is perhaps too much to expect a mode of progression identical with that

¹⁾ The estimation assumes *Zalambdalestes* and *Barunlestes* to have been roughly comparable in body size and body proportions, an assumption borne out by the known scattered parts.

of any other living or extinct group of mammals. For example the structure of the tarsus, and in particular of astragalus, is very different in between the zalambdalestids and macroscelidids, thus providing indirect evidence that functions, as well, differed in detail.

Geological evidences (LEFELD 1971, GRADZIŃSKI and JERZYKIEWICZ 1974, see also KIELAN-JAWOROWSKA 1977) suggest that known zalambdalestids lived in semi-desert habitats. As they do not show specialization peculiar to fossorial life, it seems likely that they scurried quickly under the cover of vegetation or among the rocks, as do the macroscelidids today (SAUER and SAUER 1972). Their molars (KIELAN-JAWOROWSKA 1969, CROMPTON and KIELAN-JAWOROWSKA 1978), are adapted for crushing and shearing and indicate a diet of insects. It is possible that they used the procumbent, strongly enlarged first lower incisors for picking their prey.

PHYLOGENETIC CONSIDERATIONS

The skeleton of the Zalambdalestidae has been compared throughout the foregoing description with those of various present-day mammals and in particular, the Macroscelididae. The conclusion has been drawn that the mode of life of the zalambdalestids was similar to that of the macroscelidids. This conclusion does not imply, however, a particularly close phylogenetic relationship between the two families. The dentition of the macroscelidids is very different from that of the zalambdalestids and the fossil forms (BUTLER and HOPWOOD 1957, PATTERSON 1965) are not more similar to the zalambdalestids than living species. The similarities in the postcranial skeleton of the two families either concern characters considered primitive, also found among various other groups of modern mammals, or characters which are connected with a similar mode of locomotion and are probably convergent in origin. The carpus and tarsus are different in the Zalambdalestidae and Macroscelididae and show that the former in some respects, were more advanced than the latter. For example, the zalambdalestids have a scapholunatum and have lost the articulation of the tibio-fibula with the calcaneus.

VAN VALEN (1964) suggested a remote relationship of the Zalambdalestidae with the Lagomorpha. He pointed out some similarities in the dentition of the Mongolian Paleocene genera *Pseudictops* and *Eurymylus* (see WOOD 1942) with the lagomorphs and with *Zalambdalestes*. SULIMSKI (1969) claimed that *Pseudictops* is close to the Anagalidae but that any similarity with *Eurymylus* is superficial. SYCH (1971) described new material of *Eurymylus*, including previously unknown upper incisors, and demonstrated that the genus possesses only one pair; all definitive lagomorphs have two pairs of upper incisors. Taking this into account and noting differences in structure of the enamel on the lower incisors (plus some other characters), he removed *Eurymylus* from the order Lagomorpha and created for it the order Mixodontia. SZALAY and MCKENNA (1971) created the order Anagalida to include the Anagalidae, Pseudictopidae, Eurymylidae, Zalambdalestidae, and possibly also Didymoconidae. They claimed that the closest known relatives of the Anagalida are the Lagomorpha. KIELAN-JAWOROWSKA (1975a) demonstrated that the type of tooth wear in *Zalambdalestes* and *Eurymylus* is different.

MCKENNA (1975) proposed for the Anagalida a new rank (grandorder), which he placed within a cohort Epitheria. He included within the Anagalida two orders, the Macroscelidea and Lagomorpha. Families included within the various new ranks are not specified in MCKENNA'S (1975) classification, but it appears from his fig. 3 that the Lagomorpha would include the Zalambdalestidae, Pseudictopidae, and Duplicidentata. He also states (*l. c.*: 34—35): "I believe that *Zalambdalestes* is cladistically a Cretaceous lagomorph. A *Zalambdalestes*-like animal, possibly still with the tibia and fibula unfused, could have given rise to later lagomorphs by loss of I^1 , I^2 , I_3 , C_1^1 , dP_1^1 and P_2 , to yield the dental formula $I_1 I^2 I^3 P_4^1 P_5^2 M_1^1 M_2^2 M_3^3$, from which both ochotonids and leporids could have been derived".

To verify that *Zalambdalestes* or Zalambdalestidae are cladistically lagomorphs, by which

understand that they represent a sister group of the Duplicidentata, one should demonstrate the existence of synapomorph lagomorph characters shared both by the Zalambdalestidae and Duplicidentata. I see no such characters in the dentition, skull, or postcranial skeleton. MCKENNA (1975), however, argued for similarities in dentition. He stated that *Zalambdalestes* possesses enlarged incisors I_1 and I^2 and compared them with the corresponding teeth in the Duplicidentata. This comparison appears to me superficial, because although I_1 and I^2 are enlarged in *Zalambdalestes*, they are different both in structure and in function from those in lagomorphs. In the lagomorphs, upper and lower incisors are ever growing and adapted for gnawing (see WOOD 1957). There is no indication in specimens of *Zalambdalestes* and *Barunlestes* that the upper incisors were evergrowing. Lower incisors I_1 in the Zalambdalestidae, however, are greatly enlarged, almost completely procumbent, and evergrowing, although they were clearly not modified for gnawing.

Among other "lagomorph-like" features of the Zalambdalestidae, MCKENNA pointed out the prismatic structure of the trigonids and talonids, lack of anterior and posterior cingula on upper molars, and the quintet of cheek teeth (P_4^1 P_3^1 M_1^1 M_2^1 M_3^1) which contrast sharply in morphology from more anteriorly placed teeth.

Lingual cingula are wanting in Theria of metatherian-eutherian grade such as all the Trinity therians (see SLAUGHTER 1971), Deltatheridiidae (see KIELAN-JAWOROWSKA 1975b), *Potomatelses* (see FOX 1972) and most marsupials (see CLEMENS 1966). They are also lacking in the most primitive of known eutherian mammals ("*Prokennalestes*" from the Early Cretaceous of Mongolia²⁾). Lingual cingula are first seen in eutherians in the Late Cretaceous *Kennalestes* from Mongolia (KIELAN-JAWOROWSKA 1969). They are lacking in a wide variety of eutherians such as *Asioryctes* (see KIELAN-JAWOROWSKA 1975a), Didelphodontinae (see CLEMENS 1973), *Pseudictops* and *Eurymylus* (discussed above), Zalambdalestidae and many others. The lack of lingual cingula in Cretaceous therians is probably in most cases a primitive (plesiomorph) feature; their absence in the zalambdalestids and lagomorphs thus cannot unequivocally be taken as evidence of special relationship for these groups.

There is indeed a certain similarity in molar structure between the zalambdalestids and lagomorphs, referred to by MCKENNA (1975) as "prismatic structure of the trigonids and talonids"; the type of wear, however, in these groups is quite different. CROMPTON and KIELAN-JAWOROWSKA (1978) demonstrated that in *Zalambdalestes*, in order for matching shearing surfaces to remain in contact during the power stroke, it was necessary for the upper surface of the lower jaws to rotate in a medial direction about their longitudinal axes (when viewed from behind), before the beginning of the power stroke. To my knowledge such rotation of the lower jaws does not occur in the lagomorphs. CROMPTON and KIELAN-JAWOROWSKA (*l. c.*) on the basis of studies on molar occlusion in *Zalambdalestes* also suggested that zalambdalestid molars were adapted for crushing and shearing rather than for grinding. Thus they functioned in a manner quite different from those of lagomorphs.

SZALAY and MCKENNA (1971) mentioned that in the order Anagalida the foot is "somewhat lagomorph-like". MCKENNA (1975) also cited as one of the features characteristic of the grand-order Ernotheria, a "lagomorph-like foot structure". Unfortunately neither SZALAY and MCKENNA (1971) nor MCKENNA (1975) explained what they meant by "lagomorph-like foot structure". The foot is poorly known in the Leptictida, a group assigned by MCKENNA (1975) to Ernotheria. The astragalo-calcaneal complex of known forms, however, reminds one of that of a cat (SZALAY 1966) and is not lagomorph-like.

One of the features characteristic of lagomorphs is the retention of fibular facet on the calcaneus for articulation with tibio-fibula (WOOD 1957). Additional to lagomorphs, such a facet is present in the Macroscelididae (see fig. 16) and Pseudictopidae (see SULIMSKI 1969), but pro-

²⁾ "*Prokennalestes*" has been named (but not described) by BELIAJEVA *et al.* (1974) and information concerning its morphology is cited herein with the kind permission of Dr. B. A. TROFIMOV of the Palaeontological Institute in Moscow.

bably not in the Anagalidae (see SIMPSON 1931) among the groups discussed above. The calcaneus has not been described in *Anagale*, but the structure of the astragalus suggests a tibio-astragal contact similar to that in *Tupaia*. The Zalambdalestidae in this respect are also more specialized than the lagomorphs, as the tibio-fibula has lost contact with the calcaneus and articulates only with the astragalus. The structure of the astragalus, the arrangement of the other bones in the tarsus, and the structure of metatarsals are different in the Zalambdalestidae and in lagomorphs (see fig. 16). Again, in other features of postcranial anatomy I recognize no characters that could unequivocally be regarded as specifically common to zalambdalestids and lagomorphs; to the contrary, there are many important differences. The axial spine for example has a very different structure in the two groups. The transverse foramen in the seventh cervical vertebra is absent from *Zalambdalestes*, but present in lagomorphs. The transverse processes of the lumbar vertebrae are extremely narrow in the Zalambdalestidae, in contrast to their considerable width in lagomorphs. The listing could go on.

In conclusion, I see no reason to regard the Zalambdalestidae as a sister group of the Duplicitata, except in the sense that both may have been derived from such generalized forms as the Early Cretaceous "*Prokennalestes*". It is possible, on dental morphological grounds, however, to agree that all groups of eutherians may be derived from such creature.

The Zalambdalestidae show a peculiar mosaic of specialised and primitive characters. They are strongly specialised in the structure of hindlimbs and dentition, whereas in other parts of the skeleton they retain generally primitive features. To these latter belong, among others, sutures between the ventral and lateral arches of the atlas, the joint between the axial and atlantal parts of the axial body, the sacrum consisting of two vertebrae and the presumed presence of marsupial bones. The specializations seen in the Zalambdalestidae do not suggest a special relationship with any other known group of mammals.

It could be argued in such a situation, that the Zalambdalestidae would merit ordinal rank. However, I am personally opposed to the practice of creating high rank taxa for poorly known, monotypic or almost monotypic families. For the present, therefore, I classify the Zalambdalestidae as family *incertae sedis* in order Proteutheria (ROMER 1966), NOVACEK 1977, *faute de mieux*.

ADDENDUM

Since this paper was submitted to publication a classification of eutherian mammals has been published (Szalay 1977), in which the Zalambdalestidae are classified as Lagomorpha *incertae sedis*. In the view of the foregoing argument such assignement cannot be accepted.

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EXPLANATIONS OF THE PLATES

PLATE 1

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. The specimen as it has been found, showing the skull, partial left forelimb and three thoracic vertebrae, $\times 1$.
- 1b. Other side of the same specimen, showing partial right and left femora, $\times 1$.
- 1c. Distal ends of the second to fifth metatarsals, associated with first phalanx of the fourth digit and the proximal part of the first phalanx of the third digit, $\times 6$.

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/43

- 2a. The specimen as it has been found, showing partial skull, left tibia and partial left os coxae, $\times 1$.
- 2b. The same specimen after the removal of the skull, partly developed from the rock, showing left os coxae, partial left tibia, partial tarsus and pes, $\times 1$.
- 2c. Stereo-photograph of the left hindlimb of the same specimen in dorsal view. Fragmentary bone on the inner side of the tibia is probably the left ulna (see text-fig. 1). In the upper part of this photograph two coccygeal vertebrae are visible, $\times 2$.
- 2d. Left metatarsals second to fifth and indeterminate phalanx of the same specimen, $\times 4$.
- 2e. Distal ends of the left metatarsals and incomplete first phalanges of the same specimen, $\times 6$.

Photo: E. Wyrzykowska

PLATE 2

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. The atlas in right lateral view.
- 1b. The same in dorsal view.
- 1c. The same in ventral view.
- 1d. The same in anterior view.
- 1e. The same in posterior view.
- 2a. The axis in right lateral view.
- 2b. The same in dorsal view.
- 2c. The same in ventral view.
- 2d. The same in anterior view.
- 2e. The same in posterior view.

All stereo-photographs $\times 6$

Photo: E. Wyrzykowska

PLATE 3

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/166

- 1a. Stereo-photograph of the cervical vertebrae first to seventh and first thoracic vertebra in ventral view.
- 1b. Stereo-photograph of the same in dorsal view.
- 1c. The same in right lateral view.
- 1d. The same in left lateral view.

All $\times 6$

Photo: E. Wyrzykowska

PLATE 4

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. Three thoracic and five lumbar vertebrae (possibly first to fifth) in right lateral view.
- 1b. The lumbar vertebrae of the same specimen in dorsal view.
- 1c. The same in ventral view.

All stereo-photographs $\times 3$

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/166

- 2. Stereo-photograph of the axis in front view, $\times 6$.

Photo: E. Wyrzykowska

PLATE 5

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. Last lumbar vertebra, sacrum, two coccygeal vertebrae, partial pelvis, proximal parts of femora and proximal part of left tibia, partly developed from the rock, $\times 3$.
- 1b. Stereo-photograph of the same specimen, completely developed from the rock, after the removal of the left hind-limb, in dorsal view, $\times 2$.
- 1c. Stereo-photograph of the same in ventral view, $\times 2$.

Photo: E. Wyrzykowska

PLATE 6

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. Stereo-photograph of the right os coxae in ventral view.
- 1b. Stereo-photograph of the same in dorsal view.
- 1c. Stereo-photograph of the last lumbar vertebra, sacrum and four and a half coccygeal vertebrae of the same specimen in dorsal view.
- 1d. Stereo-photograph of the same in ventral view.
- 1e. The same in left lateral view.
- 1f. The same in right lateral view.

All $\times 3$

Photo: E. Wyrzykowska

PLATE 7

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin; holotype, ZPAL MgM-I/77

- 1a. Proximal part of the left femur in posterior view.
- 1b. The same in anterior view.
- 1c. The same in lateral view.
- 1d. Right knee of the same specimen, as it has been preserved, in anterior view.
- 1e. Distal part of the right femur of the same specimen in anterior view.
- 1f. The same in posterior view.
- 1g. The same in end view.
- 1h. The same in medial view.

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia; ZPAL MgM-I/104

- 2a. Distal part of the right scapula in end view.
- 2b. The same in lateral view.
- 2c. The same in anterior view.
- 2d. The same in inner view.

All stereo-photographs $\times 4$

Photo: E. Wyrzykowska

PLATE 8

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1a. Stereo-photograph of the proximal part of the left ulna in medial view, $\times 4$.
- 1b. Stereo-photograph of the same in anterior view, $\times 4$.
- 1c. Stereo-photograph of the same in lateral view, $\times 4$.
- 1d. Stereo-photograph of the same ulna and radius in anterior view, $\times 4$.

Tupaia sp.

Recent, Borneo; MCZ 35614

2. Stereo-photograph of the proximal part of the left ulna and radius, $\times 3.5$.

Rhynchocyon cirnei hendersoni THOMAS

Recent, West Africa; MCZ 43735

3. Stereo-photograph of the proximal part of the left ulna and radius in anterior view, $\times 3.5$.

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia; ZPAL MgM-I/104

- 4a. Stereo-photographs of the proximal part of the left humerus in posterolateral view, $\times 4$.
 4b. Stereo-photograph of the same in anterior view, $\times 4$.
 4c. Stereo-photograph of the same in anteromedial view, $\times 4$.

Photo: E. Wyrzykowska

PLATE 9

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/43

- 1a. Right cuboideum, lateral cuneiform and all metatarsals (the first one not visible in this view), the distal parts of fourth and fifth broken off, in dorsal view, $\times 4$.
 1b. The same in inner view showing complete first digit and broken off first phalanges of the fourth and fifth digit, $\times 4$.
 1c. Partial left tarsus of the same specimen (calcaneus, astragalus and navicular fused with tibiale), in inner view, $\times 6$.
 1d. The same in ventral view, $\times 6$.
 1e. The same in dorsal view, $\times 6$.
 1f. The same in outer view, $\times 6$.

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia: holotype, ZPAL MgM-I/77

- 2a. Distal part of the left humerus, in medial view, $\times 6$.
 2b. The same in anterior view, $\times 6$.
 2c. The same in lateral view, $\times 6$.
 2d. The same in posterior view, $\times 6$.
 2e. The same in end view, $\times 6$.

All stereo-photographs

Photo: E. Wyrzykowska

PLATE 10

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype, ZPAL MgM-I/77

- 1 a. Distal part of the left humerus, ulna, broken off radius, incomplete carpus, metacarpals and first phalanges of the first and fifth digit in outer view, $\times 2$.
- 1 b. The same in inner view, $\times 2$.
- 1 c. Distal part of the radius and ulna, carpus and incomplete hand of the same in inner view, $\times 6$.
- 1 d. The same in outer view, $\times 6$.
- 1 e. The same in dorsal view, $\times 6$.

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/43

- 2. Coccygeal vertebrae (possibly penultimate and ultimate), $\times 2$.

All stereo-photographs

Photo: E. Wyrzykowska

PLATE 11

Barunlestes butleri KIELAN-JAWOROWSKA

Upper Cretaceous Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, Mongolia; holotype ZPAL MgM-I/77

- 1 a. Stereo-photograph of the left tibia in posterolateral view, $\times 4$.
- 1 b. Stereo-photograph of the same in anterior view, $\times 4$.
- 1 c. The same in medial view, $\times 4$.
- 1 d. Stereo-photograph of the same in top view, $\times 4$.
- 2 a. Stereo-photograph of the proximal part of the right femur in anterior view, $\times 4$.
- 2 b. The same in top view, $\times 4$.
- 2 c. The same in posterior view, $\times 4$.
- 2 d. The same in lateral view, $\times 4$.

Zalambdalestes lechei KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgM-I/43

- 3. Stereo-photograph of the left tibia in end view, $\times 6$.
- 4 a-b. Incomplete right os coxae with the proximal part of the femur in two views, $\times 4$.

