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EVOLUTION OF THE THERIAN MAMMALS IN THE LATE
CRETACEOUS OF ASIA. PART II. POSTCRANIAL SKELETON IN
KENNALESTES AND *ASIORYCTES*

(plates 15—18)

Abstract. — The oldest known eutherian postcranial skeleton, belonging to the Late Cretaceous paleoryctid *Asioryctes* and an atlas of a (?) leptictid *Kennalestes* are described and figured. The structure of the manus and pes of *Asioryctes*, in which the pollex and hallux are not opposable, together with sedimentological data, indicate terrestrial habits of Cretaceous eutherian mammals. The theory of arboreal origin of the therian mammals is rejected. It is shown that in the postcranial anatomy *Asioryctes* is more similar to *Didelphis* than to the present-day eutherian mammals, although it differs from *Didelphis* in the structure of the pollex and hallux. Features of the mammalian postcranial anatomy, which may be regarded as symplesiomorph therian characters are discussed.

Contents

	Page
Introduction	65
<i>Kennalestes</i>	66
Atlas	66
<i>Asioryctes</i>	67
Vertebral column	67
Fore limb	71
Hind limb	73
Habits of Cretaceous eutherian mammals.	75
Phylogenetic considerations	78
References	80

INTRODUCTION

Of the seven therian genera known from the Late Cretaceous of Asia (*Kennalestes*, *Asioryctes*, *Zalambdalestes*, *Barunlestes*, *Deltatheridium*, *Deltatheroides* and *Hyotheridium*) only the first four have been classified recently as undoubted eutherian mammals (KIELAN-JAWOROWSKA, 1975a, 1975b, 1975d). *Kennalestes* is tentatively assigned to the Leptictidae; *Asioryctes* is assigned to the Palaeoryctidae; *Zalambdalestes* and *Barunlestes* are both assigned to the Zalambdalestidae. Postcranial skeletons of *Deltatheridium*, *Deltatheroides* and *Hyotheridium* have not been found. The postcranial skeleton of *Kennalestes* is unknown, except for an incomplete atlas and the body of an axis found in an immature specimen. This is especially regrettable, as judging from the tooth structure, (CROMPTON & KIELAN-JAWOROWSKA, 1977), *Kennalestes* is the most primitive of the true eutherian mammals so far described. The postcranial skeleton of *Asioryctes* is represented by the cervical and first thoracic vertebrae, an incomplete

hand and an incomplete hind limb. Skeletal elements of *Kennalestes* and *Asioryctes* are described in the present paper.

More complete postcranial skeletons have been preserved in *Zalambdalestes* and *Barunlestes*. In contrast to *Asioryctes*, which in various respects is extremely primitive for an eutherian mammal, the *Zalambdalestidae* show in their skeleton a combination of primitive and advanced characters. They will be described in the forthcoming paper.

The fragments discussed herein are the oldest described skeletons of eutherian mammals. Postcranial skeletons of Cretaceous eutherian mammals from North America have not been described except for the astragalo-calcaneal complex of *Procerberus* and *Protungulatum* from the Hell Creek Formation of Montana (SZALAY & DECKER, 1974; SZALAY, 1977). A rich collection of isolated bones assembled from this formation has not been described.

The two genera described here are monotypic. *Kennalestes* is represented by *K. gobiensis* KIELAN-JAWOROWSKA, 1969, *Asioryctes* by *A. nemegetensis* KIELAN-JAWOROWSKA, 1975. For the sake of brevity in the descriptions I use only the generic names. The skeleton of *Asioryctes* is compared with those of *Didelphis* and *Tupaia*, regarded frequently as most primitive extant marsupial and eutherian mammals, and occasionally also with the skeleton of *Tenrec*.

The age of the Djadokhta Formation yielding *Kennalestes* has been recognized as ?late Santonian, and/or ?early Campanian, that of the Barun Goyot Formation yielding *Asioryctes* as ?Middle Campanian (KIELAN-JAWOROWSKA, 1974, GRADZIŃSKI *et al.*, 1977).

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Abbreviations used for institutions:

MCZ Museum of Comparative Zoology, Harvard University, Cambridge

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

ISEZ Institute of Systematic and Experimental Zoology (Zakład Zoologii Systematycznej i Doświadczalnej) of the Polish Academy of Sciences, Cracow.

KENNALESTES

Material. — The postcranial skeleton is unknown except for the damaged dorsal arch of an atlas and the body of an axis, associated with the skull of an juvenile individual from the Djadokhta Formation, Bayn Dzak, Gobi Desert (ZPAL MgM-I/1). The axis fragment is poorly preserved and does not merit description.

Atlas (pl. 16, fig. 1). The dorsal arch is 1.3 mm long in the middle and 0.7 mm long laterally. Its anterior margin is strongly sigmoid, its posterior margin straight. The sulcus arteriae vertebralis is indistinct. The intervertebral, alar and transverse foramina are probably absent, but this cannot be stated with certainty due to the damage. Only on the left side the base of the transverse process (which is broken) is present. A shallow groove runs below the transverse process. Because of the poor state of preservation the entire course of the arteria vertebralis cannot be recognized.

ASIORYCTES

Material. — In the holotype ZPAL MgM-I/56, (Barun Goyot Formation, Nemegt, Gobi Desert) an incomplete atlas and axis are preserved with the skull; in ZPAL MgM-I/98, (Khermeen Tsav „formation”, Khermeen Tsav II, Gobi Desert), which is somewhat smaller than the holotype and is tentatively regarded herein as juvenile specimen, the skull is associated with all the cervical vertebrae, first thoracic vertebra, incomplete right fore limb: radius and ulna, both without proximal ends, nearly complete carpus without pisiform, five metacarpals without distal ends and incomplete right hind limb. The latter consists of two parts, preserved in the same piece of rock. The proximal part (pl. 18, figs 2*c*, 2*d*) consists of the tibia and fibula without proximal ends, calcaneus, astragalus and cuboideum somewhat displaced medially. The distal part (pl. 18, figs 2*a*, 2*b*) consists of three cuneiforms, a fragment of the distal end of the navicular, five metatarsals, first phalanges of the first, second and third digits, and damaged second phalanx of the first digit. The reconstruction (text-fig. 4*A*₂) is based on both parts. In the specimen as preserved the tibia and fibula do not contact each other distally; it seems probable that the tibia has been moved downwards and medially. The metatarsals of the fourth and fifth digits were displaced to the plantar side of the other metatarsals and are seen only in ventral view.

The skulls of both specimens (ZPAL MgM-I/56 and /98) have been figured by KIELAN-JAWOROWSKA, 1975*a*.

VERTEBRAL COLUMN

(pl. 15, figs 1, 2, pl. 16, fig. 2, pl. 17, text-figs 1, 2)

Atlas. The ventral arch of the atlas (intercentrum) is not preserved. The dorsal arch is about 1.7 mm long in the middle. Because of damage one cannot state with full certainty whether the medial dorsal tubercle was present. The anterior margin of the dorsal arch is convex anteriorly. A deep notch (sulcus arteriae vertebralis) is present on the lateral side of the anterior margin, near the anterior articular cavity. The transverse processes are broken; their preserved

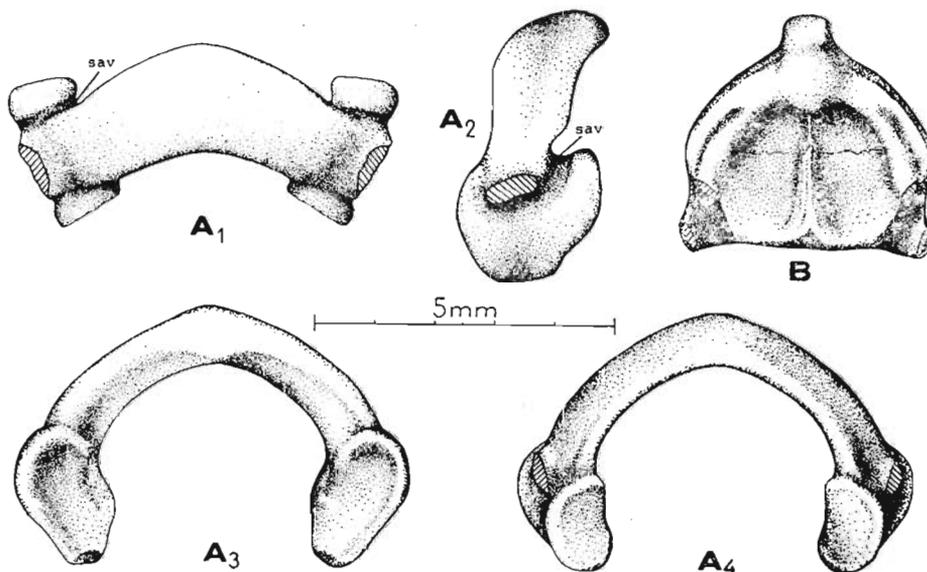


Fig. 1

Asioryctes nemegetensis. *A* — Reconstruction of the atlas (without intercentrum), based on ZPAL MgM-I/56, *A*₁ — dorsal, *A*₂ — right lateral, *A*₃ — anterior, *A*₄ — posterior views, *B* — reconstruction of the axis in ventral view, based on ZPAL MgM-I/56 and ZPAL MgM-I/98, the scale is of ZPAL MgM-I/56. *sav* — sulcus arteriae vertebralis. The hatched areas denote the broken bases of transverse processes.

bases are short. The anterior articular cavities are roughly oval with prominent dorsal edges. The posterior articular cavities are distinctly smaller and flat. The intervertebral, alar and transverse foramina are absent. The base of the transverse process is surrounded from behind and ventrally by a distinct groove, which indicates the course of the arteria vertebralis. The groove is especially deep along the atlantis fossa. Anteriorly it passes into the sulcus arteriae vertebralis.

Axis. In ZPAL MgM-I/98, which is a young individual, the axis is deformed; in ZPAL MgM-I/56 the posterior part of the arch is missing. The reconstruction of ventral view of the axis on text-fig. 1B is based on both specimens, and the given scale is of the adult one.

In ZPAL MgM-I/56 the transverse process is broken. In ZPAL MgM-I/98 it is preserved, except that on the left side its tip is missing. As far as can be seen the process is not pierced by a foramen; the arteria vertebralis appears to run in an open groove below the process. The dens is peg-like, its ventral margin (in lateral view) is directed anterodorsally, the dorsal margin more horizontally. The anterior articular surfaces are oval, more prominent posteriorly than anteriorly. They are orientated more horizontally than vertically. Their ventral edges form raised ridges, which meet each other anteriorly, and in ventral view they surround anteriorly the lateral depressions of the body. A median ridge extends along the ventral wall of the body. The lateral depressions are surrounded laterally by longitudinal ridges which converge slightly anteriorly. Lateral depressions and lateral ridges are more prominent in the adult (ZPAL MgM-I/56) specimen. Extending transversely across the body, the transverse joint is recognized on the ventral surface. It divides the body into the atlantal and axial parts. In the juvenile specimen (see pl. 17, fig. 1c) the posterior axial part of the body is somewhat displaced with regard to the atlantal part, which is best seen in the midline where the course of the median ridge is interrupted. The atlantal part of the body is shorter than the axial. On the dorsal side of the body there are oval nutrient foramina (pl. 15, fig. 2b).

The arch is strongly expanded dorsally into a long anvil-shaped spinous process. The edge of its anterior extremity is broken, the posterior extremity is pointed (pl. 17, fig. 1e). The upper

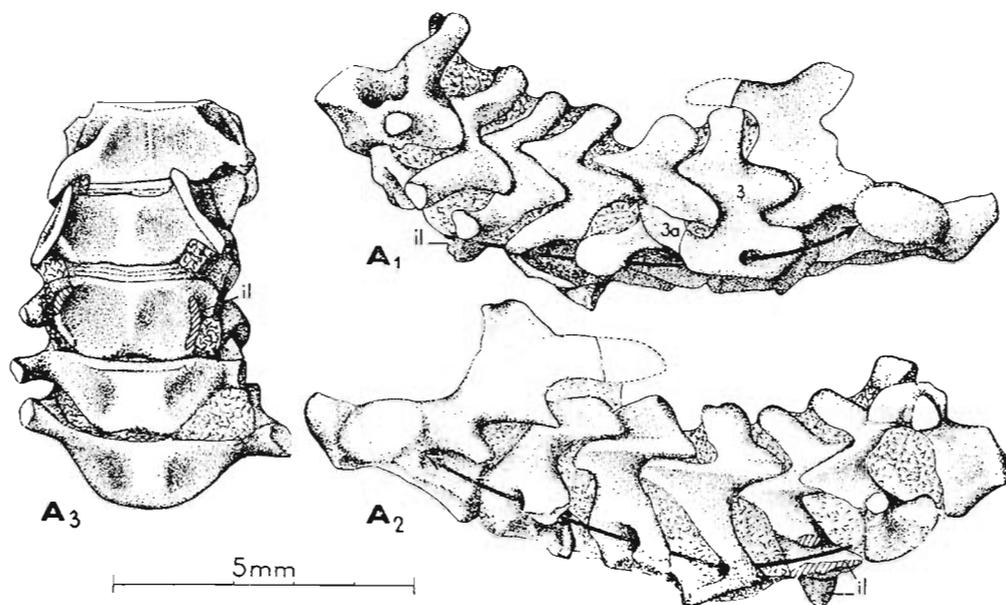


Fig. 2

Asiorcytes nemegetensis. A_1 — A_2 The second cervical to first thoracic vertebrae of ZPAL MgM-I/98, drawn as they have been preserved, not reconstructed, in right and left lateral views, A_3 — the fourth cervical to first thoracic vertebrae of the same specimen in ventral view. 3 and 3a the third cervical vertebra, il — interior lamella. The hatched areas denote the broken bases of the inferior lamella and of the transverse process of the sixth vertebra. In A_3 the shape of the inferior lamella is on the right side partly reconstructed. Note, that the inferior lamella in *Asiorcytes* appears somewhat asymmetrical.

margin of the spinous process is incurved in the middle. The anterior margin of the arch is deeply concave, and the intervertebral foramen is absent. Posterior margin of the arch is concave in the dorsal part. The posterior articular process is extensive and situated low. It is associated with a deep incurvature on the posterior margin, which lodges the anterior articular process of the third vertebra.

Third vertebra. The body (in ventral view) is short and wide, narrower anteriorly than posteriorly. The ventral crest is not very prominent, tuberculate at its posterior end; it separates two lateral depressions, delimited laterally by transverse processes. Anterior and posterior extremities of the body are probably low and wide, crescent-shaped. The arch is low. The spinous process is not developed, but there is a low crest. The articular processes are large, nearly horizontal; the anterior ones are directed dorsally, the posterior ventrally. The transverse processes are directed obliquely, more posteriorly than laterally. Each arises by two roots: one from the body, visible in ventral view as an oblique crest, convex outwards, directed (in lateral aspect) more horizontally and one from the arch, directed more obliquely downwards. Between these is the large transverse foramen. On the right side (pl. 17, fig. 1*b*) in the posterior prolongation of the rounded margin of the transverse process is a small bony plate, pointed posteriorly, designated 3*a* on text-fig. 2. This might be a slightly displaced posterior extremity of the transverse process.

Cervical vertebrae fourth to seventh. The bodies of the cervical vertebrae decrease in length from the third to the seventh. The lengths of the arches also decrease and consequently those of the interarcual spaces increase.

The ventral tubercle, present at the caudal end of the third vertebra, is not discernible on the fourth and the following vertebrae, perhaps due to the state of preservation. The fourth vertebra differs from the third in being shorter and in having the ventral branch of the transverse process more prominent. On the fifth vertebra this branch becomes very prominent and projects ventrally as a distinct plate. Beginning with the fifth vertebra the arches become very faint and the dorsal crests are developed merely as tubercles. The sixth differs from the remaining ones in the development of an inferior lamella (HOWELL, 1926). In the described specimen it is broken on both sides, but its base, which is better preserved on the left side shows, that it appears from the preserved parts, that it was somewhat asymmetrical. The inferior lamella is not confluent with the transverse process. It is directed parasagittally, unlike the obliquely directed ventral root of the transverse process in the preceding vertebra. The ventral branch of the transverse process of the fifth vertebra is on the left side completely preserved and very prominent, but the inferior lamella of the sixth vertebra is missing. Consequently the photographs of the specimen in ventral and left lateral views (pl. 16, fig. 2*a*, pl. 17 fig. 1*c*, 1*d*) may give a wrong impression that the inferior lamella in *Asioryctes* was associated with the fifth vertebra. The posterior part of the transverse process, to the rear of the transverse foramen, in the sixth vertebra is missing on both sides, but the preserved parts indicate that the transverse canal was here shorter than in the preceding vertebrae. The seventh vertebra has no ventral crest, but there are two symmetrical depressions on the body. The transverse process is not perforated by the transverse foramen. It is short in a longitudinal sense, situated opposite the anterior part of the body and directed more transversely than in the preceding vertebrae. It is peg-like and tuberculate at the end. A costal facet for the first rib is discernible on the body.

First thoracic vertebra. The body is short, low and crescent-shaped in posterior view. The ventral crest is absent, but there are symmetrical depressions on the body, similar to those on the seventh vertebra. The arch is poorly preserved. It is low and narrow. The spinous process is not developed, but there is a tubercle, which is higher than on the cervical vertebrae. Anterior articular processes are similar to those on the cervical vertebrae, but posterior ones are not preserved. The transverse process is rather short, directed entirely transversely, with rounded extremity when examined in posterior view, situated rather high. The costal pits are hardly discernible due to the small size of the specimen and the state of preservation.

Discussion. — In cynodonts and in Triassic triconodonts the atlas consists of four separate ossifications: right and left arches, an intercentrum and an atlas body, synostosed to the axis body (JENKINS, 1971, JENKINS & PARRINGTON, 1976). In *Kennalestes* and in both specimens of *Asioryctes* the intercentrum is not preserved and it is possible that it was not synostosed to the arches as in the Triassic mammals. Right and left arches are preserved together and probably were synostosed.

In *Kennalestes* and *Asioryctes* the transverse foramen is wanting, as in the Triassic triconodonts. Among the modern mammals the transverse foramen is absent from the Monotremata Marsupialia, Cetacea, Sirenia, Ruminantia (except the Tylopoda) and Rhinocerotidae (RÜEGER, 1938, LESSERTISSEUR & SABAN, 1967), but only in the Monotremata and Marsupialia its absence is primary. In these groups, the arteria vertebralis after leaving the second cervical vertebra, passes by the root of the transverse process of the atlas, grooving, the bone around it (GAUPP, 1907, COUES, 1878). In eutherian modern mammals the lack of the transverse foramen in the atlas is either connected with special adaptations of the cervical vertebrae (Cetacea, Sirenia) or with a different course of the arteria vertebralis. In Ruminantia (SISSON & GROSSMAN, 1947) the arteria vertebralis enters the vertebral canal between the third and second cervical vertebrae, and transverse foramina are very small or absent on the axis and absent from the atlas. *Kennalestes* and *Asioryctes* differ from modern eutherian mammals in this, that the lack of the transverse foramen is here primary. In this respect they are on *Didelphis* level of organization. In *Tupaia* the transverse foramen is developed in the atlas as in most modern eutherian mammals. In *Asioryctes* the transverse foramen is probably wanting in the axis, although there is a groove for arteria vertebralis.

In *Megazostrodon* and *Eozostrodon* there is a distinct joint between the atlantal and axial bodies, which are not completely synostosed (JENKINS & PARRINGTON, 1976). Such a joint is also present in juvenile eutherian mammals, as well as in adult Monotremata and Marsupialia (RÜEGER, 1938, JENKINS, 1969). In *Asioryctes* a trace of the joint is visible between the atlantal and axial bodies, especially well seen in a juvenile specimen, in which the atlantal part of the body is arranged at an angle with regard to the axial part (pl. 17, fig. 1c).

Cervical ribs, characteristic of cynodonts, were probably also present in Triassic triconodonts (JENKINS & PARRINGTON, 1976). The transverse foramina are lacking in these forms. Among the modern mammals the cervical ribs occur in monotremes, and on the axis of a marsupial, *Perameles*. They occur also on the last cervical vertebrae in some Cetacea, Edentata, and have been described as an anomaly in man and in numerous domestic mammals. In modern mammals the cervical ribs may be best studied in *Ornithorhynchus* and *Tachyglossus*. The ribs are here synostosed with the transverse processes, but the suture which crosses the transverse foramen is well visible. This suture may disappear in adult individuals. In *Asioryctes* the transverse foramina on the third to sixth cervical vertebrae are very distinct. The transverse processes of the cervical vertebrae are long, and cracked in various places, but these cracks are irregularly placed and none of them could be unequivocally interpreted as a remnant of a synostosis. The conclusion is that the cervical ribs in *Asioryctes* are absent.

The sixth cervical vertebra in therian mammals is characterized by a special development of the ventral branch of the transverse process, which loses the contact with the rest of the transverse process and is arranged longitudinally as a lamella strongly projecting downwards. This structure has been called the carotid tubercle, CHASSAIGNAC's tubercle, transverse ventral tubercle (see LESSERTISSEUR & SABAN, 1967) or inferior lamella (HOWELL, 1926).

The inferior lamella does not occur in Triassic triconodonts and in the monotremes. Neither have I found it in the multituberculates from the Late Cretaceous of the Gobi Desert. It seems that the inferior lamella on the sixth vertebra is a distinctive character of therian mammals. It is a constant character in primitive marsupials and placentals and disappears only in some specialised forms. In both *Didelphis* and *Tupaia* (pl. 16, fig. 3a, 3b) the inferior

lamella is well developed. The inferior lamella in *Asioryctes* is less prominent than in modern therian mammals.

The neural spines on the cervical vertebrae in *Asioryctes* are lacking, which may be explained by the small size of the animal. SLIJPER (1946) has shown the existence of a correlation between the length of the cervical spines and the absolute size of the animals. Among the mammals studied by him the cervical spines were wanting in most small insectivores and rodents, of very different habits. The galesaurid cynodonts, presumable ancestors of the mammals (JENKINS, 1970, 1971, CROMPTON & JENKINS, 1973) had well developed cervical spines. But these were comparatively large animals, more or less of *Didelphis* size. In Triassic triconodonts (JENKINS & PARRINGTON, 1976) the cervical spines are short. In *Tupaia* they are comparatively well developed (see pl. 16, fig. 3a), in spite of the statement of SLIJPER (1946, table 7) that in *Tupaia* there are practically no cervical spines. In *Asioryctes*, in contrast to *Tupaia*, the cervical spines are completely lacking, as in very small mammals such as e.g. *Sorex*, *Pitymys*, *Talpa* and numerous others. In the lack of the cervical neural spines *Asioryctes* differs strongly from *Didelphis*, in which the cervical spines are enlarged. In *Didelphis* they closely adhere each other and the second to the seventh vertebrae act as a very rigid structure almost as one bone.

FORE LIMB

(pl. 15, fig. 3, pl. 18, fig. 1, text-fig. 3)

Radius and ulna. The preserved part of the radius and ulna is 6 mm long. The radius is circular in cross section proximally, strongly flattened anteroposteriorly distally. Its diameter in the proximal part is 0.6 mm, in the distal part 1.2 mm. The distal end bears on the medial side a distinct tubercle. The styloid process is poorly developed. The distal facet is roughly oval, obscured. The ulna is 0.6 mm wide proximally. Its maximal distal diameter is 0.85 mm. The distal articular facet is roughly circular. In both the radius and ulna the epiphyses are well defined.

Carpus. The reconstruction of the carpus in text fig. 3A is tentative, because its bones are strongly coalesced with the matrix, which cannot be completely removed. It is also possible that some carpal bones were not entirely ossified. The width of the carpus is 3.6 mm, the length about 0.8 mm. Measurements of the individual bones are not given, because of the poor definition of their shape. The carpus is slightly convex dorsally in longitudinal and transverse directions. It consisted probably of ten bones, of which the pisiform is not preserved. In the proximal row there are three bones; scaphoideum, lunatum and triquetrum. The distal margins of these form an arch, which embraces the bones of the distal row. The scaphoideum is comparatively large, more extensive in palmar view, where it partially covers the trapezium. At the disto-lateral corner of the palmar side, the scaphoideum is provided with a large tubercle (tuberculum ossi scaphoidei). The lunatum is small, roughly rectangular. The triquetrum is large, in dorsal view elongated transversely, with rounded proximal margin. An articulating surface for the pisiform is visible on the ventral side of the triquetrum (text-fig. 3A₂).

Wedge medially between the scaphoideum and trapezium is a small triangular bone, recognized tentatively as the praepollex. Two phalanges of the praepollex are recognized on ventral side. The centrale is only tentatively recognized. It is a very small, short bone, transversely elongated, situated between the lunatum and trapezoideum. Of the bones of the distal row, the trapezium and hamatum are large, whereas the trapezoideum and capitatum are small roughly quadrangular. The trapezoideum is smaller than the capitatum. The trapezium is roughly triangular, projecting somewhat distally beyond the distal margins of the other carpal bones. Its distal margin is wedged between the first and the second metacarpals. The joint between the trapezium and first metacarpal is arranged obliquely. The hamatum is transversely elongated, with concave distal margin. Extending obliquely across the hamatum is an indistinct line. It

cannot be decided whether it is due to a damage, or is a remnant of fusion between the fourth and fifth carpal bones. The hamatum articulates with both the fourth and fifth metacarpals. The fifth does not project laterally beyond the hamatum. There is a distance between the capitatum and trapezoideum, filled with the matrix, due probably to distortion.

Metacarpals. The metacarpals are arranged subparallel. Their distal ends are broken off. The first is the widest.

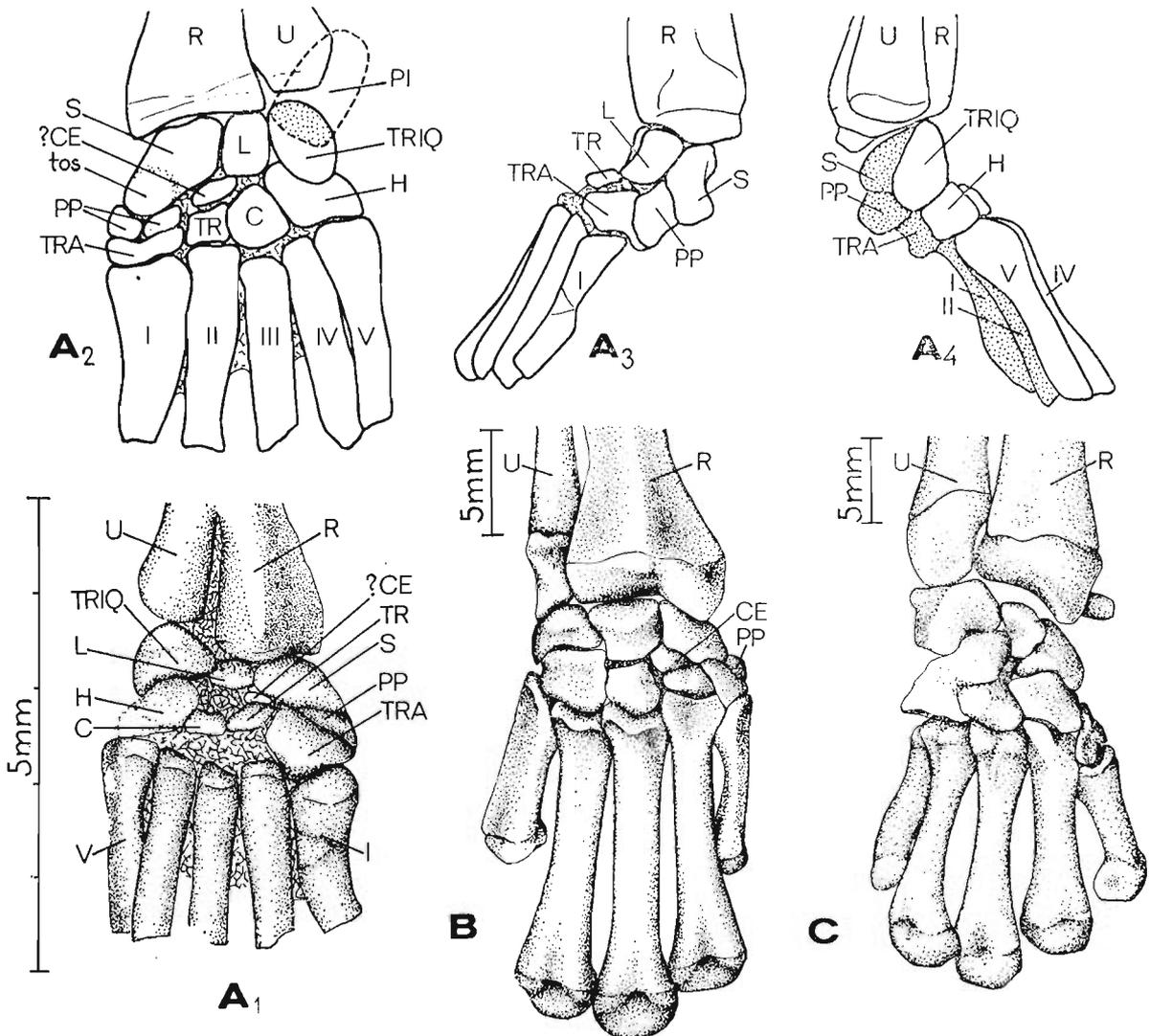


Fig. 3

Comparison of the right carpus and metacarpals in *A* — *Asioryctes nemegetensis* (ZPAL MgM-I/98), *A*₁ — dorsal view (the dorsal part of the carpus covered by the matrix, is reconstructed), *A*₂ — ventral view (the shadowed area on the triquetrum denotes the articulating surface for the pisiform, which is reconstructed), *A*₃ — left lateral view, *A*₄ — right lateral view; *B* — *Tenrec ecaudatus* (MCZ 44967), dorsal view, *C* — *Didelphis marsupialis* (ISEZ 7/3019), dorsal view. *C* — capitatum, *CE* — centrale, *H* — hamatum, *L* — lunatum, *PI* — pisiform, *PP* — praepollex, *R* — radius, *S* — scaphoideum, *T* — triquetrum, *TR* — trapezoideum, *TRA* — trapezium, *tos* — tuber ossi scaphoidei, *U* — ulna.

Discussion. — The hand of *Asioryctes* agrees in the arrangement of the carpal bones with the "Spreizhand" of modern mammals (insectivores and rodents) described by ALTNER (1971). Of the modern primitive small mammals which I had an opportunity to study it reminds one most of the hand of the Tenrecidae (see *Tenrec* on text-fig. 3*B*). The similarities concern the position of the centrale and the general arrangement of the carpal bones, although there are

some differences in proportions. The fifth metacarpal more strongly projects laterally beyond the hamatum in *Tenrec* than in *Asioryctes*. The hand of *Tupaia* although retaining primitive characters differs from that of *Asioryctes*. The centrale in *Tupaia* is situated not between the proximal and distal rows, but opposite the enlarged capitatum in the distal row, and the fifth metacarpal more strongly projects laterally beyond the hamatum. The hand of *Didelphis* does not invite a comparison with that of *Asioryctes*. It differs not only in having an opposable pollex and a saddle-type hinge between the trapezium and the first metacarpal, which is not the case in *Asioryctes*, but also in a quite different arrangement of the carpal bones. The centrale in *Didelphis* is fused with the scaphoideum, as in all the marsupials. In the arrangement of the remaining carpal bones (see text fig. 3C) it shows the pattern characteristic of the grasping hand defined by ALTNER (1971) and by YALDEN (1972), and is very different from the primitive type characteristic of *Asioryctes*.

SCHMIDT-EHRENBERG (1942) recognized in the embryological development of the carpus in various mammals (e.g. in *Hemicentetes*), four centralia. This agrees with STEINER'S conception (1935, 1942) of the structure of the vertebrate carpus. In *Asioryctes*, only one centrale is recognized. In the carpus of *Asioryctes* there are four distal carpals, and on the fourth is a distinct oblique line, dividing it into two parts. This line might be very tentatively recognized as the line of fusion between the fifth and fourth carpals. The carpus of Triassic mammals is not known. Five distal carpals occur in cynodonts, although in some cases the fourth and fifth may be fused, (for discussion see JENKINS, 1971), and the suture of synostosis is not preserved. Therefore it is more probable that the above discussed line on the fourth carpal of *Asioryctes* is due to damage.

HIND LIMB

(pl. 18, fig. 2, text-fig. 4)

Tibia. The preserved part of the tibia is 7 mm long. It is a thin bone, flattened antero-posteriorly, and oval in cross section. The diameter is 0.7 mm proximally, widening to 1.2 mm distally. The anterior margin of the preserved part is rounded. The shaft presents no sulci or ridges. The epiphysis at the distal end is very distinct. It is extended medially into an obtuse, conical process that forms the inner malleolus. The articular surface consists of a nearly flat lateral part and a very obliquely placed medial part, resulting from the downward extension of the malleolar prominence. The tibia overlaps the medial convexity of the astragalar proximal body.

Fibula. The fibula is more slender than the tibia, nearly round in cross section in the upper part, (the diameter is 0.6 mm), becoming flattened anteroposteriorly in the distal part. The diameter of the epiphysis is 0.9 mm. Extending along the anterior side of the tibia, on a distance of about 3.7 mm, a distinct groove widens distally. The epiphysis is well defined. The articular surface is probably flat or slightly concave. The fibula articulates with the lateral portion of the astragalar trochlea and with the calcaneus.

Tarsus. The characteristic features of the astragalo-calcaneal complex of *Asioryctes* are as follows:

1. Proximal body of the astragalus does not override the calcaneus and is situated entirely medial to it.

2. The sustentacular facet is well developed, but extends only beneath two thirds of the width of the astragalar head.

The calcaneus is anteroposteriorly elongate, 3.4 mm long, dorsoventrally compressed. In dorsal aspect it has a slightly raised lateral border and concave central portion. The plantar surface is concave in both the longitudinal and transverse directions. Projecting strongly posterolaterally an extensive peroneal tubercle is located lateral to the cuboid facet. On the lateral border, above the peroneal tubercle, there is another crescent-shaped process. As the lateral

margin is somewhat damaged, the size and shape of this process cannot be recognized with full certainty. The cuboid facet is oblique to the long axis of the calcaneus. It faces downwards and ventrally, and a large part of its articular surface is exposed in plantar view. The cuboid facet is confluent with a small facet on the astragalus head, suggesting a presence of an astragalo-cuboid contact.

The tuber of the calcaneus is bent medially, at an angle of 37° with the calcaneal body. It is comparatively short: its length, measured from the upper margin of the astragalo-calcaneal facet is 1.1 mm, which is about one third of the calcaneal length. The calcaneal fibular facet is obscured in the studied specimen by the fibula. It is placed above the astragalo-calcaneal facet, which is situated on the medial border of the calcaneus. In dorsal view the astragalo-calcaneal facet has an appearance of a prominent crescent. Its articulating surface faces medially and articulates with the lateral surface of the proximal body of the astragalus. The calcaneal sustentacular facet cannot be studied in dorsal aspect, being entirely obscured by the astragalus head. Laterally it is surrounded by a prominent ridge. The sustentacular facet when studied in plantar aspect is roughly rectangular and flat. Above the cuboid facet, in plantar aspect there is a distinct oval foramen of unknown function.

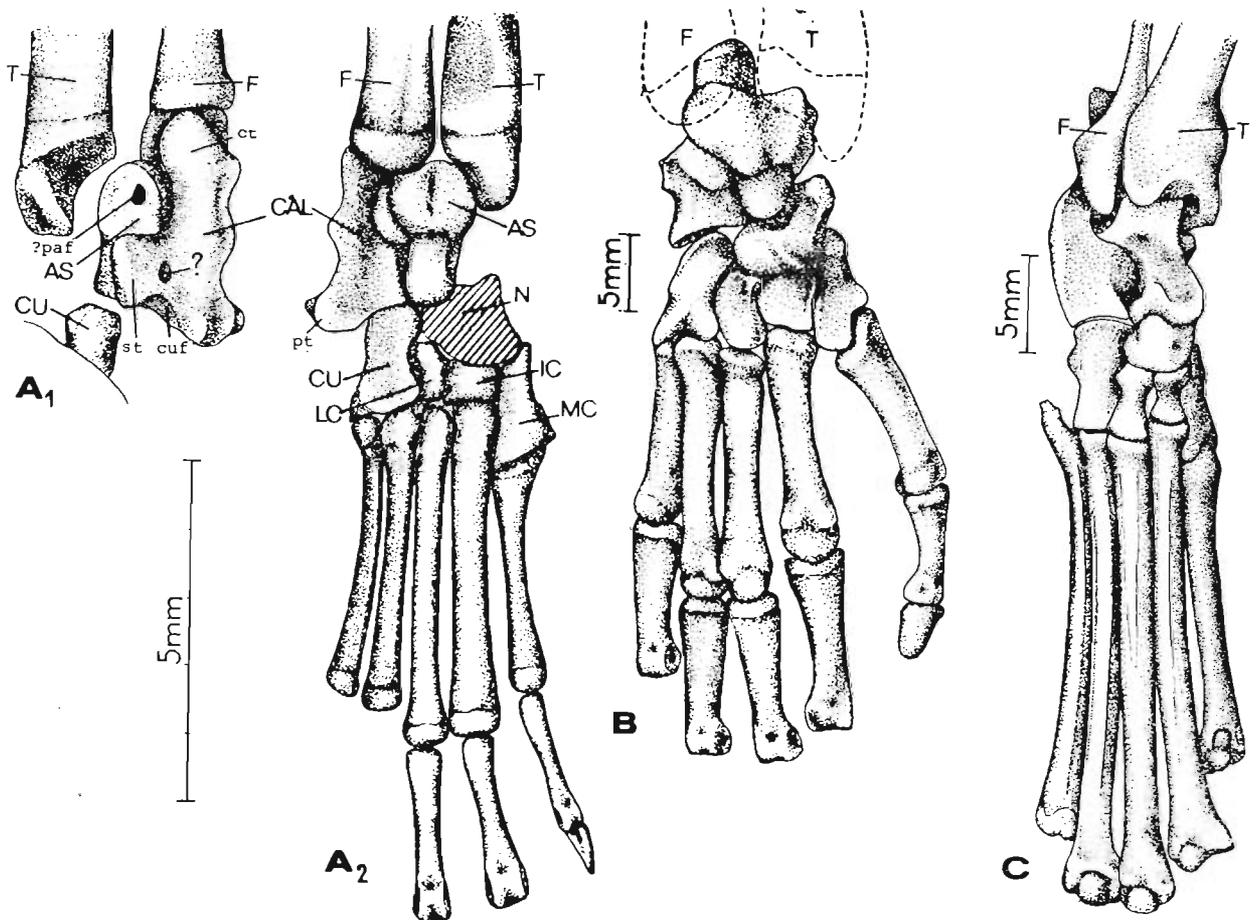


Fig. 4

Comparison of the right tarsus and metatarsals in A — *Asioryctes nemegetensis* (ZPAL MgM-I/98), B — *Didelphis marsupialis* (ISEZ M/3019), and C — *Tupaia* sp. (MCZ 35614). A₁ — proximal part of the tarsus, as it has been preserved, in ventral view. A₂ — reconstruction of the tarsus and partial foot of the same specimen in dorsal view, based on two parts, found in the same piece of rock. The naviculare is reconstructed. First and fifth metatarsals were probably in life less exposed in dorsal view than it is figured. AS — astragalus, CAL — calcaneus, ct — calcaneal tuberosity, CU — cuboideum, cuf — cuboid facet, F — fibula, IC — intermedial cuneiform, LC — lateral cuneiform, MC — medial cuneiform, N — naviculare, paf — plantar astragalus foramen, pt — peroneal tubercle, T — tibia, st — sustentacular facet.

The astragalus is anteroposteriorly elongate, 2.2 mm long. It consists of a well defined proximal body (1.3 mm wide and 1.1 mm long) and a distal head (0.4 mm wide). The gently rounded head is separated from the body by a constricted neck. The proximal body is asymmetrical, shorter laterally than medially. On the lateral part of its proximal border there is an extensive, concave, fibular facet. The medial facet for articulation with the tibia is convex. The tibial trochlea is not developed. The proximal body is generally inflated, with a faint longitudinal groove along the middle. The medial wall opposite the neck is concave and is partly visible in dorsal aspect. The plantar surface of the proximal body is less convex than the dorsal. There is probably a plantar astragalal foramen (SZALAY, 1966), placed asymmetrically, more laterally than medially. It cannot be excluded that this foramen is due to the distortion. The superior astragalal foramen is probably absent.

The cuboid is elongate anteroposteriorly, 1.5 mm long, constricted in the middle. The proximal margin is rounded, the distal margin sends a triangular process laterally. The medial wall is concave to fit the lateral cuneiform. The latter is elongated anteroposteriorly, 0.8 mm long. Its proximal part sends a lateral process, wedged between the cuboid and navicular. The lateral margin of the process is convex. The intermedial cuneiform is rectangular, 0.7 mm wide and 0.5 mm long. It projects far distally beyond the distal margin of the remaining cuneiforms. The medial cuneiform is large, roughly triangular, 1.9 mm long and 0.85 mm wide. Its proximal margin is oblique, with a lateral process. The distal margin is strongly oblique and has a lateral tubercle. Only the distal part of the navicular is preserved, surrounded by three cuneiforms. Its tentative shape is reconstructed on text-fig. 4A.

Metatarsals. Of the five metatarsals the first is the shortest. Its length (including medial process) is 3.5 mm. The second metatarsal is the widest, it is 4.8 mm long. The third metatarsal is the longest, 5 mm long, but less stout than the second. The fourth 4.3 mm long and the fifth (4 mm long) are thinner than the third. The fourth and fifth metatarsals articulate with the distal surface of the cuboideum, and the fifth does not protrude laterally beyond it. In all the metatarsals the epiphyses are very distinct.

Phalanges. — The length of the first phalanx of the first digit is 2.1 mm, of the second and third digit 2.5 mm. The second phalanx of the first digit is sharply pointed, 0.7 mm long.

Discussion. — The tarsus of *Asioryctes* represents the most primitive type found in the therian mammals. SZALAY and DECKER (1974) described the astragalo-calcaneal complex of the Late Cretaceous eutherian genera *Protungulatum* and *Procerberus*, the latter identical with *Cimolestes*. In all these genera, the astragalo-calcaneal complex is of typical eutherian pattern, in spite of certain primitive features such as the presence of distal peroneal tubercle, a cuboid facet oblique to a long axis of calcaneus and a low tibial trochlea. In all of them the astragalus is completely supported by the calcaneus and has no plantar contact, the tibial trochlea is shallow, but completely developed and the calcaneal body anterior to the astragalo-calcaneal facet is comparatively long, extending for about a half of the calcaneal length. All hitherto known fossil and extant eutherian mammals have the astragalo-calcaneal complex more advanced than in *Protungulatum* and *Procerberus*. A more primitive type is characteristic of metatherians, where e.g. in *Didelphis* the proximal body of the astragalus is inflated, with a shallow groove in the middle and the tibial trochlea not fully developed, as in *Asioryctes*. The similarities with *Asioryctes* concern also the shape of the calcaneus, which has a short and inclined tuber calcanei, extensive peroneal tubercle, and a process on the lateral border above the peroneal tubercle. The calcaneo-astragal contact in *Didelphis* is more extensive than in *Asioryctes*, for in *Didelphis* not only the astragalal head, but also a large part of the proximal body is superimposed on the calcaneus.

In *Asioryctes* the proximal body of the astragalus lies medially to the calcaneus, and the astragalo-calcaneal contact is limited to the sustentacular facet. With regard to the superposition of the astragalus, *Asioryctes* is intermediate between the reptiles (astragalus situated medial to calcaneus) and therian mammals (astragalus supported by calcaneus). The Triassic trico-

nodonts in the structure of the astragalo-calcaneal articulation are on the cynodont level of organization (JENKINS & PARRINGTON, 1976). Among the therapsid reptiles, the astragalo-calcaneal articulation is more extensive in cynodonts (JENKINS, 1971) than in bauriamorphs (SHAEFFER, 1941). However, in the shape of the calcaneus, astragalus and cuboideum, the tarsus of *Asioryctes* is more similar to that of *Bauria* than that of cynodonts and of Triassic triconodonts. The similarities concern the short and strongly medially inclined tuber of the calcaneus, the widely enlarged distal part of the calcaneus, with prominent peroneal tubercle projecting laterally beyond the contact with cuboideum and the presence of an astragalo-cuboid contact. These similarities are, however, not strong enough to suggest a relationship. The calcanea of cynodonts, of *Oligokyphus* (KÜHNE, 1956) and of Triassic triconodonts, having rounded lateral margins, and lacking prominent peroneal tubercles are different from that in *Asioryctes*.

Asioryctes is similar to *Didelphis* also in the arrangement and structure of the cuboideum and lateral and intermedial cuneiforms. The only important difference between these genera concerns the mesocuneiform, and the joint between it and the first metatarsal. In *Didelphis* this joint is of saddle type and the hallux is opposable, whereas in *Asioryctes* the joint is of hinge type and the hallux does not show any degree of opposability.

The astragalo-calcaneal complex of *Tupaia* is highly specialised, of the typical eutherian pattern and does not invite a comparison with *Asioryctes*. But in the structure of the distal part of the tarsus, *Tupaia* retains certain primitive characters. In cynodonts (JENKINS, 1971) and in *Megazostrodon* (JENKINS & PARRINGTON, 1976) the medial cuneiform projects distally beyond the level of other cuneiforms, which is also characteristic of *Asioryctes*. This feature is retained in some degree in *Tupaia*, where the medial cuneiform projects distally more strongly than in most modern mammals and has a roughly triangular shape as in *Asioryctes*. The fifth metatarsal in *Tupaia* projects laterally beyond the cuboideum, whereas in *Asioryctes* (as in *Didelphis*) it articulates with the facet on the distal margin of the cuboideum.

HABITS OF CRETACEOUS EUTHERIAN MAMMALS

The old idea that both marsupial (HUXLEY, 1880, DOLLO, 1899, BENSLEY, 1901 *a*, 1901 *b*) and placental mammals (MATTHEW, 1904, 1909, 1937) had an arboreal origin has for a long time ruled in textbooks of vertebrate palaeontology and zoology. Among the modern authors it has been supported by LEWIS (1964), STEINER (1965) and MARTIN (1968), while GIDLEY (1919) and HAINES (1958) were the main opponents. Also the data discussed by NAPIER (1961) and ALTNER (1971) speak implicitly against the arboreal origin of the therian mammals. Until now the discussion could be only speculative, as there was no direct evidence relating to the structure of fore and hind limbs in ancestral therians. The Cretaceous skeleton described herein for the first time provides such evidence.

In the discussion on terrestrialism versus arborealism in the ancestors of eutherian mammals, the structure and habits of *Tupaia* have played an important part. JENKINS (1974), who studied the locomotion of *Tupaia glis*, concluded that with regard to primitive mammals terrestrialism and arborealism are not discrete phenomena. He stated (1974, p. 110): "With possible exception of a few species, all tree shrews can and do move freely between ground and trees". The same idea had been expressed earlier by ALTNER who stated (1971, p. 89): "Die eigentliche Anpassung von *Tupaia glis* besteht darin, dass die Anpassung des Tiers an das Baumleben relativ ungenau ist, so dass die quadrupede Lokomotion zu ebener Erde wie auch in der buschförmigen Übergangszone durchaus möglich und üblich ist".

ALTNER (1971), who studied the embryology of the *Tupaia* hand, compared its structure with those of semiarboreal (*Sciurus*) and terrestrial (*Xerus*) rodents, as well as those of terrestrial insectivores, *Erinaceus* and *Nesogale* (the latter is a subgenus of *Microgale* — see WALKER,

1964). He has shown that in *Sciurus*, *Xerus*, *Erinaceus* and *Nesogale*, despite their different modes of life, the structure of the hand is essentially the same. This type of hand has been designated by ALTNER as "Spreizhand", which corresponds to the convergent hand of HAINES (1958) and NAPIER (1961).

The carpus of *Tupaia* is according to ALTNER in some respects intermediate between the "Spreizhand" and the "Greifhand", characteristic of e.g. *Microcebus*. The "Spreizhand" as characterized by ALTNER, may be defined as follows:

1. The proximal row of the carpal bones is concave distally and embraces the distal row.
2. The centrale may be incorporated either in the proximal row (Insectivora) or in the distal row (Rodentia).
3. The trapezoideum and capitatum are small in comparison with the trapezium and hamatum.
4. The fifth digit projects laterally beyond the hamatum and may contact the triquetrum.
5. The trapezium is longitudinally elongated and projects distally beyond the distal margin of the remaining carpal bones.
6. The carpo-metacarpal joint of the pollex is of a hinge type. The first digit is not opposable.

In connection with the last character it should be noted that HAINES (1958) described the carpo-metacarpal joint of *Tupaia* as saddle-shaped and regarded this digit as in some measure opposable. It has been shown by NAPIER (1961), NAPIER and NAPIER (1967), ALTNER (1971) and JENKINS (1974) that this is not the case and that the *Tupaia* hand does not show any degree of opposability.

The hand of *Asioryctes*, as far as can be seen, agrees with most of the above characteristics. It shows certain primitive features which are also retained in numerous modern mammals, such as the presence of three bones in the proximal row of the carpus (lunatum not fused with scaphoideum), presence of the centrale and of the praepollex. It differs from the hands of modern mammals in, that the trapezium is not elongated longitudinally, although it projects somewhat distally, and also in that the fifth metacarpal does not project laterally. As in modern mammals with convergent hands the pollex of *Asioryctes* is not opposable.

The pes has been less widely discussed than the manus in connection with arborealism. The hallux is certainly not opposable in the foot of *Asioryctes*. The medial cuneiform is triangular, very strongly elongated and protrudes distally beyond the level of other cuneiforms. This is probably a primitive feature, because an elongated medial cuneiform, which projects distally beyond the distal margin of other cuneiforms, occurs also in the Triassic *Megazostrodon*. JENKINS and PARRINGTON (1976, p. 427), interpreted its foot as follows: „As preserved, the foot of *Megazostrodon* appears to indicate an absence of hallucal divergence. However, the skeletal posture is similar to that typically seen in ligament preparation of tupaiid feet: the digits are more or less parallel and in the same plane except for the hallux which lies somewhat to the plantar side of metatarsal II". In *Asioryctes* they are rather metatarsals IV and V that lie somewhat to the plantar side of the other metatarsals, but this is interpreted as due to the state of preservation. The small divergence of the hallux probably occurs also in *Asioryctes*, where the distal margin of the medial cuneiform is arranged obliquely. This might or might not be an arboreal adaptation, as a similar tendency to divergence occurs also in the feet of numerous exclusively terrestrial small mammals. It is concluded that *Asioryctes* has a convergent, non-prehensile hand and a moderately elongated foot with non-opposable hallux.

The question arises whether *Asioryctes* was a tree-runner adapted to semi-arboreal life, like *Tupaia* and *Sciurus*, or whether it was an exclusively terrestrial mammal. On the basis of comparisons given by ALTNER (1971) it is evident that such a conclusion cannot be drawn from the hand structure. Comparison of the feet of small modern mammals of different habits leads to a similarly negative result. However, additional information may be obtained from studies of the environment in which the skeletons *Asioryctes* were found. Late Cretaceous mammals on the Gobi Desert have been found in three formations: the Djado-

khta Formation, the Barun Goyot Formation and the Khermeen Tsav "formation", not designated formally, being a stratigraphic equivalent of the Barun Goyot Formation. Sedimentological investigations carried out in the Djadokhta and Barun Goyot Formations (LEFELD, 1969, GRADZIŃSKI & JERZYKIEWICZ, 1974) show that both formations are composed of the deposits of sand dunes, intercalated by lacustrine sediments. No remnants of trees were found in these sediments, although tree trunks are very common in the sandy, dinosaur-bearing sediments of the younger Nemegt Formation (GRADZIŃSKI, 1970), in which mammals have not been found. When collecting mammals in the Late Cretaceous sediments of the Gobi Desert, I have been struck by the ecological similarity of the faunistic assemblages of the Djadokhta and Barun Goyot Formations, to those living now in steppe and semi-desert habitats of the Gobi Desert. In both the Djadokhta and Barun Goyot Formations we find terrestrial, medium-sized dinosaurs: protoceratopsids, ankylosaurids, coelurosaurids and pachycephalosaurids (the latter found only in the Barun Goyot Formation), accompanied by diversified lizards and mammals. The mammals are represented by the multituberculates, deltathridiids, primitive insectivores (*Kennalestes* and *Asioryctes*) and larger specialized zalambdalestids. In the present-day steppe and semi-desert habitats of the Gobi Desert the dinosaurs are replaced ecologically by large mammals such as horses, camels, goats and sheep, accompanied as in the Cretaceous time by numerous lizards and small mammals. Among the latter are the rodents and lagomorphs, replacing ecologically the multituberculates and zalambdalestids, while *Asioryctes* and *Kennalestes* are replaced by modern insectivores. Although the above comparison is rather superficial, when taken in conjunction with the sedimentological evidence it strongly indicates that the Late Cretaceous mammals from Mongolia lived in a semi-desert environment, and were certainly not tree-runners.

It may be argued that *Asioryctes* is secondarily adapted to semi-desert environment, but it derived from the ancestors possessing an opposable pollex and hallux (as e.g. MARTIN, 1968 has argued in the case of *Tupaia*). Taking such a possibility into account, it should be remembered that Early Cretaceous therian mammals were of *Asioryctes* size or even smaller, and because of this they had no need for opposable hands and feet. This has been clearly shown by NAPIER for the primates, who stated (1961, p. 130): "Below a critical size, clawed, convergent hands offer little or not disadvantage, but once the ratio of average branch diameter to the size of animal has reached a critical point, clawed and convergent extremities are not longer adequate to maintain stability in an arboreal environment, and some form of grasping mechanism is required". The tree climbing phase of primate evolution commenced about the Middle Eocene (NAPIER, 1961). We do not know when it commenced in marsupials, but it is evident that opposability had to evolve independently in primates and marsupials.

It would be naïve to presume that *Asioryctes* should be regarded as an ancestor or near-ancestor of all the Tertiary and modern eutherian mammals. The fact that it was a terrestrial mammal does not preclude the possibility that there existed other contemporaneous semi-arboreal eutherian mammals, which might have lived in forest habitats. These, I believe, were small tree-runners with convergent hands.

PHYLOGENETIC CONSIDERATIONS

Although this paper does not deal with problems of classification, the conclusions drawn from it may help in recognising which characters of the postcranial anatomy may be regarded as symplesiomorph (HENNIG, 1965) for the Theria. MCKENNA (1976) in an attempt at the cladistic classification of mammals, when reviewing marsupial-eutherian dichotomy did not discuss the postcranial anatomy, because there was little factual evidence for it. The discussion that follows would be more convincing if the complete skeleton of *Asioryctes* could be compared with that of Cretaceous marsupial. As this is impossible, the incomplete skeleton of *Asioryctes*

is compared herein with that of the present-day *Didelphis*. Although *Didelphis* in its physiological functions does not display primitive features (TYNDALE-BISCOE, 1973) there is no doubt that it has retained in its skeleton various primitive (symplesiomorph) characters. The structures which are shared by *Asioryctes* and *Didelphis* may be with some confidence regarded as characteristic for the common ancestors of the Eutheria and Metatheria, and are recognized as symplesiomorph therian character states. These are as follows:

1. Primary lack of the transverse foramen in the atlas. This feature is retained in modern Marsupialia, but not in Eutheria. The transverse foramen is present in such primitive eutherian mammals as *Tupaia* and *Tenrec*. Its absence in the atlas in certain extant Eutheria is secondary.

2. The suture between the synostosed axial and atlantal parts of the second cervical vertebra. It occurs in *Didelphis* and in *Asioryctes*. Among the modern eutherian mammals it is recognizable only in the early stages of ontogeny.

3. Presence of the transverse foramina in the third to sixth cervical vertebrae, correlated with the disappearance of cervical ribs, which are completely fused with transverse processes.

4. Lack of the transverse foramen in the seventh cervical vertebra.

5. Incipient development of the inferior lamella on the sixth cervical vertebra. This structure is characteristic for extant therian mammals. It occurs in *Asioryctes* but is less prominent than in the modern mammals. As it is present also in the marsupials, it must have developed in an incipient stage in the common ancestor of the therian mammals.

6. In the carpus: three bones (scaphoideum, lunatum and triquetrum) in the proximal row; centrale and praepollex present. In present-day marsupials, including *Didelphis*, the centrale is fused with the scaphoideum, but as it existed in cynodonts and in *Asioryctes*, it must have occurred in the common ancestor of the therian mammals.

7. Pollex and hallux not opposable. This is a controversial question. The arguments that it is a symplesiomorph therian character are as follows: pollex and hallux are not opposable in cynodonts, in Triassic triconodonts (only the hallux is known) and in Cretaceous eutherian mammals. Common ancestors of the therian mammals were very small, and as such had no need for opposability (see NAPIER, 1971). In the light of the above the opposable pollex and hallux in primitive extant marsupials must be regarded as autapomorph marsupial characters.

8. Fifth carpal not protruding laterally beyond the hamatum.

9. Marsupial bones present. This is not certain as the pelvis in *Asioryctes* is not known. As, however, there is indirect evidence that the marsupial bones were present in the Cretaceous eutherian Zalambdalestidae (KIELAN-JAWOROWSKA, 1975c), I believe that their presence is a symplesiomorph character of therian mammals.

10. In the astragalo-calcaneal complex: incipient superimposition of the astragalus on the calcaneus; tibial trochlea on the astragalus not developed; astragalo-cuboid contact present.

11. Medial cuneiform long, projecting far distally beyond the level of other cuneiforms.

12. Fifth metatarsal not protruding laterally beyond the cuboideum.

It follows from the foregoing discussion that the Cretaceous eutherian *Asioryctes* in its postcranial anatomy shares more characters with *Didelphis* than with any present-day eutherian mammal. This supports the idea that the eutherian mammals evolved much faster than the marsupials, and not only in physiology but also in postcranial anatomy went far away from the common therian ancestors.

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EXPLANATION OF PLATES

Photo: E. Wyrzykowska

PLATE 15

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Barun Goyot Formation, Nemegt, Southern Monads, Gobi Desert, Mongolia, ZPAL MgM-I/56

- 1a. The incomplete atlas in dorsal view, holotype.
- 1b. The same in right lateral view.
- 1c. The same in left lateral view.
- 1d. The same in posterior view.
- 1e. The same in anterior view.
- 2a. The axis of the same specimen in ventral view.
- 2b. The body of the axis after removal of the arch, in dorsal view.
- 2c. The same specimen with the arch in place, in dorsal view.
- 2d. The same specimen (before the preparation) in anterior view.
- 2e. The same specimen in left lateral view.

All stereophotographs $\times 6$

Upper Cretaceous, Khermeen Tsav "formation", Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/98

- 3a. Incomplete right hand in ventral view (see also plate 18).
3b. The same specimen in dorsal view.

Both stereophotographs $\times 8$

PLATE 16

Kennalestes gobiensis KIELAN-JAWOROWSKA

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia, ZPAL MgM-I/1

1. Stereophotographs of the skull of a juvenile specimen in posterior view, showing incomplete atlas, $\times 6$.

Asioryctes nemegetensis KIELAN-JAWOROWSKA

Upper Cretaceous, Khermeen Tsav "formation", Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/98

- 2a. Stereophotograph of the second cervical to first thoracic vertebrae in left lateral view, $\times 8$, (see also plate 17).
2b. Stereophotograph of the same in dorsal view, $\times 8$.

Tupaia sp.

Recent, Borneo, MCZ 35614

- 3a. Second cervical to first thoracic vertebrae in left lateral view, showing prominent inferior lamella on the sixth vertebra, $\times 4.5$.
3b. The same in ventral view, $\times 4.5$.

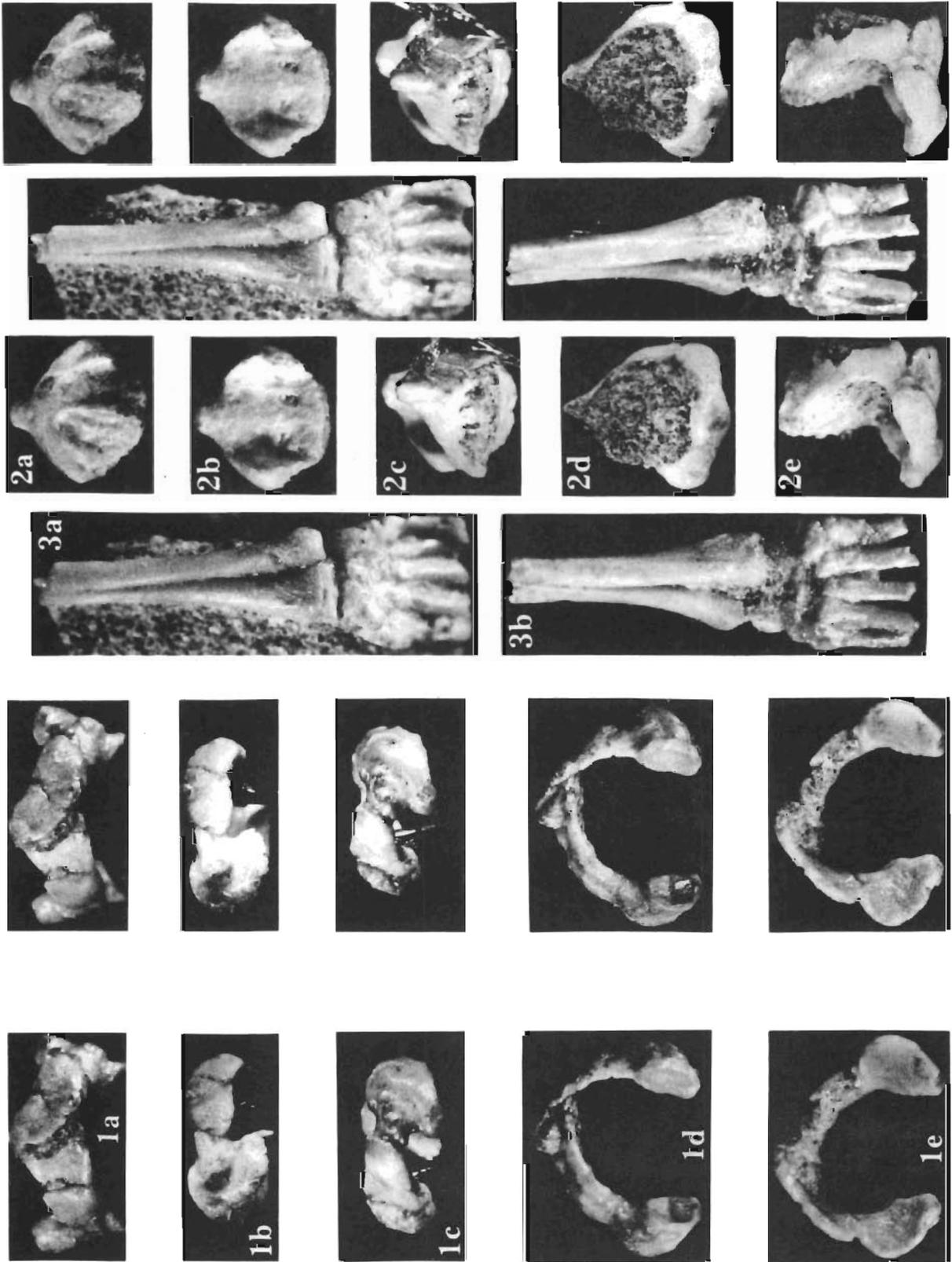
PLATE 17

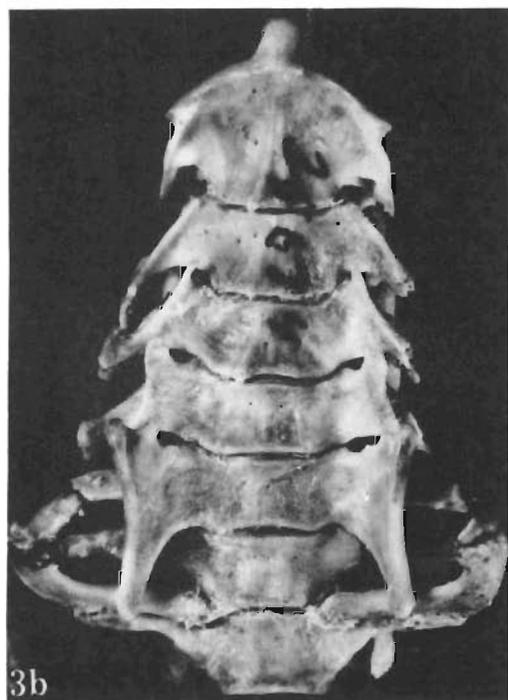
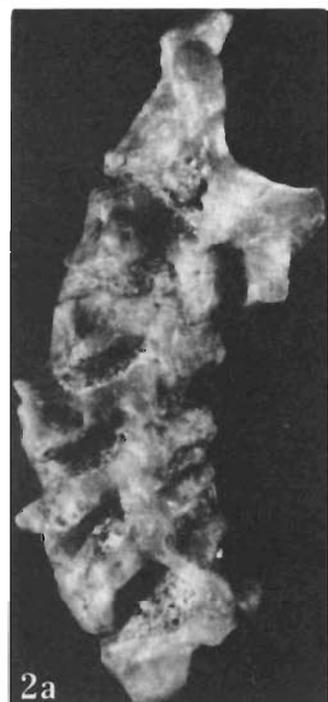
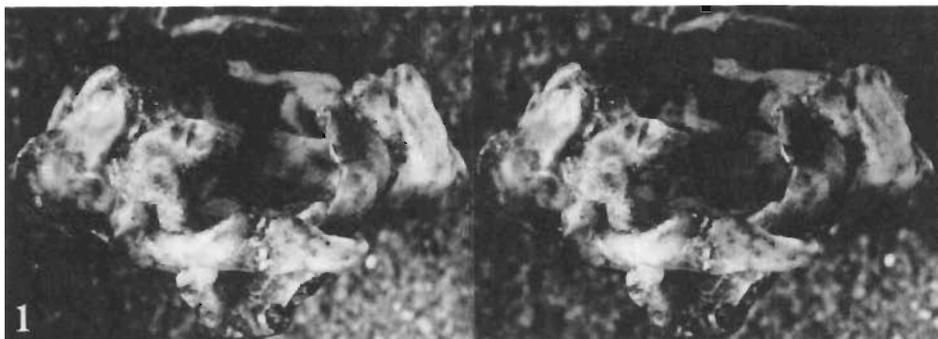
Asioryctes nemegetensis KIELAN-JAWOROWSKA

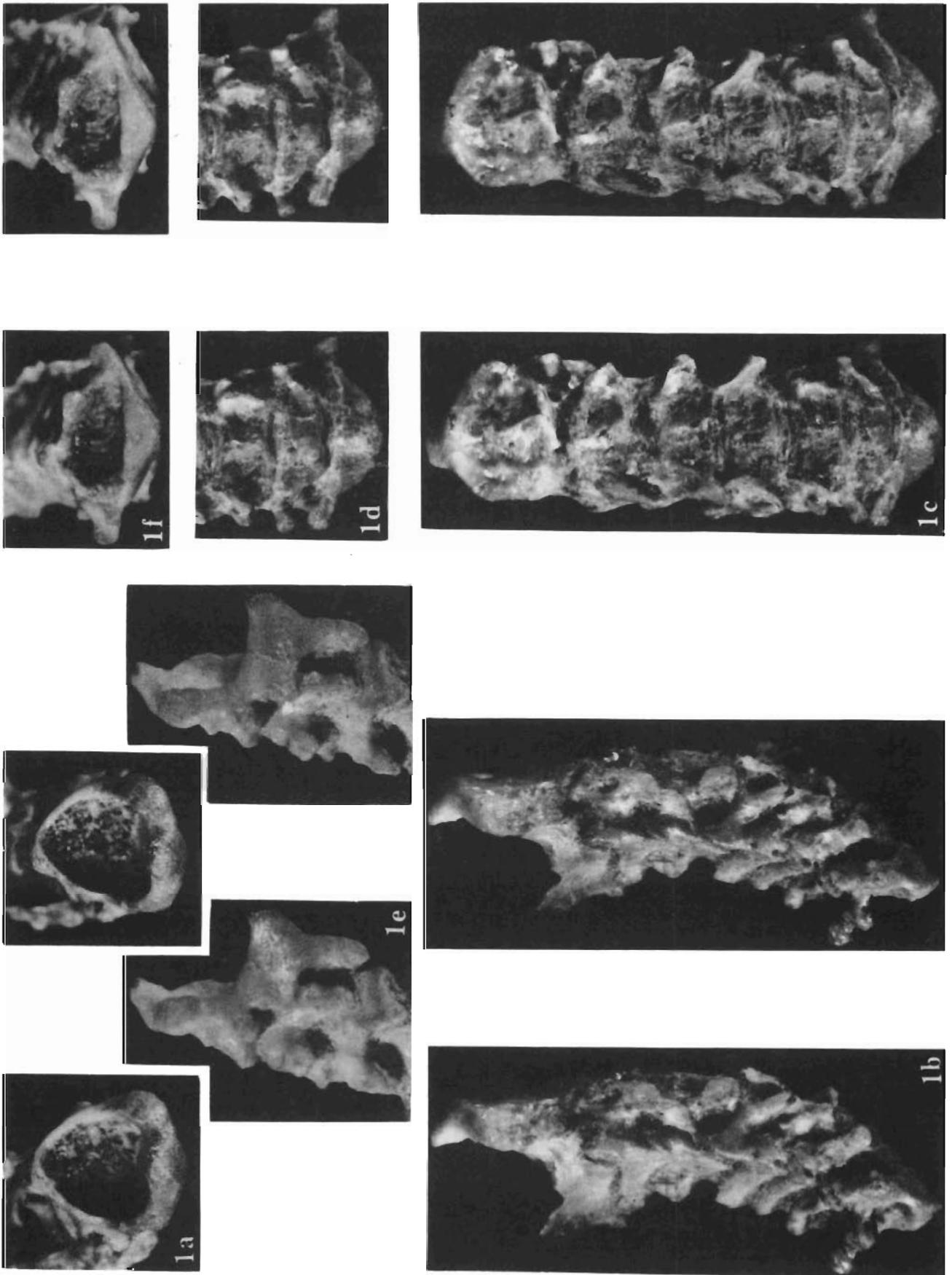
Upper Cretaceous, Khermeen Tsav "formation", Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/98

- 1a. The axis in anterior view, (see also plate 16).
1b. The same specimen in right lateral view. The photograph shows in addition to the axis third through seventh cervical vertebrae and first thoracic vertebra.
1c. The same specimen in ventral view, showing axis arranged horizontally.
1d. The same specimen in ventral view showing posterior three vertebrae arranged horizontally.
1e. Anterior part of the same specimen in left lateral view, before the complete preparation, and before the damage of the posterior part of the axial neural spine.
1f. First thoracic vertebra of the same specimen in posterior view.

All stereophotographs $\times 8$







Z. KJELAN-JAWOROWSKA: POSTCRANIAL SKELETON IN *KENNALESTES* AND *ASIORYCTES*

