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# The Postcranial Skeletons of The Triassic Mammals Eozostrodon, Megazostrodon and Erythrotherium

F. A. Jenkins and F. R. Parrington

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# THE POSTCRANIAL SKELETONS OF THE TRIASSIC MAMMALS *EOZOSTRODON*, *MEGAZOSTRODON* AND *ERYTHROTHERIUM*

By F. A. JENKINS, Jr† and F. R. PARRINGTON, F.R.S.‡
† *Department of Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.*
‡ *University Museum of Zoology, Cambridge, England*

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Abundant but dissociated postcranial materials assignable to *Eozostrodon* (from Pont Alun quarry, Glamorgan, Wales) are described together with the associated, partial skeletons of *Megazostrodon rudnerae* and *Erythrotherium parringtoni* (from the Red Beds of southern Africa). The postcranial skeletons of these Triassic triconodonts are evaluated in both comparative and functional terms.

Triassic triconodonts inherited from cynodonts specializations in the atlas-axis complex (e.g. double occipital condyles, a dens, reduction of the atlanto-axial zygapophyses) which permitted extensive cranial flexion–extension at the atlanto-occipital joint and rotation at the atlanto-axial joint. Marked differentiation of the major vertebral regions appears for the first time among mammals. In *Megazostrodon*, post-axis cervical vertebrae bear relatively narrow laminae and pedicles, broadly spaced zygapophyses, and rod-like, posteriorly recurved spinous processes; this pattern appears to be basic to mammals, and is retained among many later, generalized groups. The structure of the cervical vertebrae reveals that a cervico-thoracic flexure and an ascending posture of the neck were present. The large size of cervical vertebral foramina is evidence of a marked enlargement of the spinal cord at levels corresponding to the origin of the brachial plexus; this relationship may be interpreted as evidence of a greater neuromuscular control of the forelimb and a freedom of neck movement typical of mammals. An 'anticlinal' region in the thoracolumbar vertebral series has been identified in *Eozostrodon*; this musculoskeletal specialization is related to axial flexion and extension characteristic of the posture and locomotor movements in mammals. The sacrum consists of at least two (and possibly three) vertebrae. The tail is moderately long and incorporates approximately twelve vertebrae.

The shoulder girdle of *Eozostrodon* is little modified from the basic cynodont pattern; a **T**-shaped interclavicle, the lack of a supraspinous fossa, and the presence of both coracoids are features retained by monotremes. Both the coracoid and the scapula participate in the narrow, semi-lunar glenoid. The humero-ulnar joint is condylar, rather than trochlear, a condition retained by monotremes and other non-therian groups. The pelvic girdle represents a fully mammalian grade of organization; there is no evidence of epipubic bones. The limb skeleton, and particularly the joints, show various features consistent with an interpretation of well-developed mobility. The claw structure is suggestive of prehensility and an ability to climb. The hallux, at least, was probably somewhat divergent, and its joint structures indicate that abduction and extension (independent of the other digits) were possible.

Triassic mammals as now known were all small, insectivorous forms; *Megazostrodon* was approximately 10 cm in head–body length, probably weighed between 20 and 30 g, and was proportioned similarly to medium-sized shrews (e.g. *Suncus murinus*, *Blarina blarina*). A skeletal reconstruction of a Triassic triconodont is depicted, and an interpretation of their habits is presented.

## 1. INTRODUCTION

The purposes of this monograph are to describe the postcranial skeletons of the earliest known mammals, and to probe, in so far as possible by osteological study, biological questions concerning the habits and adaptations of these late Triassic forms. In this context, information on the background of this investigation is useful.

Studies of Mesozoic mammals, begun some 150 years ago, are based on rare and fragmentary fossils, principally jaws and teeth. These investigations have yielded a bare outline of some 120 million years of mammalian evolution – about two-thirds of mammalian history. No assessment of the important biological changes occurring during this time can ever be complete, but major advances are possible as new discoveries provide material that is more complete or that represents a previously unknown evolutionary stage. So tenuous is the evidence that at least some concepts are re-evaluated with each discovery. Postcranial anatomy offers especially intriguing prospects for investigation because associated material (that can be positively assigned to a taxon below subclass) has been for the most part unknown, and indeed even dissociated bones are a rarity.

Since G. G. Simpson's monographs of 1928 and 1929, progress in the study of Mesozoic mammals has been largely dependent on new finds. A major impetus to renewed investigation came from the discoveries of Mesozoic mammals by Walter Kühne in 1939 and during the immediate post-war years. Kühne first worked on fissures in the Carboniferous limestone quarries at Frome, Somerset, in southwest England where he collected a series of teeth of the problematical form *Haramiya* and two triconodont teeth which were placed in the genus *Eozostrodon* (Parrington 1941, 1946). The fissure faunas are generally thought to be of Upper Triassic (Rhaetic) age (Kühne 1946), although Kermack, Mussett & Rigney (1973) believe that the evidence is insufficient to determine whether the deposits are Rhaetic or Lower Liassic. After the war Kühne carried his explorations farther west, eventually reaching the quarries at Bridgend in Glamorgan, Wales, where he not only found more triconodont teeth in some quantity (Kühne 1958) but also a symmetrodont tooth (Kühne 1950). Shortly after making these discoveries, Kühne returned to Germany and the work was continued by a team from University College, London, under the leadership of Dr K. A. Kermack.

About 1956, during routine quarry operations in Pont Alun quarry, near Bridgend, Glamorgan, a fissure was exposed which yielded tonnes of clay containing the remains of both triconodonts and symmetrodonts, the former in great abundance (Kermack, Kermack & Mussett 1956). In 1966 Mr A. Baynes, then a Cambridge graduate student, happened upon some fresh material in Pont Alun quarry and approximately 9 tonnes of fossiliferous clay which had been discarded and left to weather for some years in the neighbouring Ewenny quarry.

The abundant material discovered in Wales has given rise to a series of papers confined almost entirely to detailed descriptions of the dentitions and jaws of this and related materials as well as to the phylogenetic position of these forms (for a detailed summary, see the introduction in Parrington 1971). The taxonomic question of whether this material should be referred to *Eozostrodon parvus* or *Morganucodon watsoni* has been debated extensively; in any case, this question is not relevant here, and the name *Eozostrodon* will be used.

The material from the Welsh quarry fissures is significant not only in terms of its phyletic position and preservation, but also because of the associated postcranial bones. Initially, with the focus of attention on dental anatomy, the postcranial materials had been accorded only preliminary study. Kermack & Mussett (1959) figured a scapulocoracoid and Parrington (1971) described an ilium and several femoral heads. At present, however, both the quality and quantity of available postcranial bones justifies a monographic study.

Bones from the fissures at Pont Alun are abundant but in nearly all cases were disarticulated before burial. The presence of charcoal in the clay has been interpreted as the product of periodic scrub fires (Harris 1958) and it seems possible that, at intervals, a mixture of clay, charcoal and bones was washed into underground fissures by surface water. Some of the bones were broken and variably water-worn at this stage; further breakage resulted from weathering after the clay was abandoned at the quarry, and undoubtedly some damage occurred when the clay was processed to extract the bones. The interpretation of the material is further complicated by certain problems of association. Completely intermixed with the mammalian remains are abundant fragments of a small lizard and probably several archosaurs, all as yet undescribed. The mammals and lizard were of similar size (an estimated head and body length of about 8 cm) and positive allocation of some bones (e.g. ribs) is impossible. In such cases of doubt, clear indication of the authors' uncertainties are given in the text.

*Eozostrodon* teeth and jaws are mixed with the teeth of a second mammal, *Kuehneotherium praecursoris*, but this form is comparatively rare (judged by the number of teeth recovered). Since two types of mammalian postcranial materials have not been recognized, it is assumed that the mammalian material belongs to *Eozostrodon*. Alternatively, the apparent inability to distinguish the two genera on the basis of postcranial anatomy may tend to confirm our opinion that the two mammals are closely related.

Although preservation of the bone in the *Eozostrodon* collection is excellent, complete specimens of individual bones are rare. Accordingly, most of the figures in this paper are based on two or more specimens; in every case the degree of overlap between fragments ensured continuity and accuracy, and the number of specimens used in the reconstruction is indicated in the legend. All of these specimens are in the University Museum of Zoology, Cambridge.

The discovery of two additional triconodont mammals (Crompton 1964; Crompton & Jenkins 1968; Crompton 1974) in the Upper Triassic Red Beds of southern Africa, each with most of the postcranial skeleton preserved, provided evidence critical to interpreting the dissociated *Eozostrodon* collection. The positive association of the Red Bed specimens and their apparently close relationship to *Eozostrodon* are compelling reasons to include all of this material in one study. *Megazostrodon rudnerae* (B.M.N.H. M 26407) appears to be an essentially complete skeleton, although not all the postcranial bones have been identified. Some parts of the skeleton are slightly crushed and fragmented. *Erythrotherium parringtoni* (S.A.M. K 359) is almost certainly a juvenile specimen (Crompton 1974), and as such the ends of the long bones are generally poorly preserved. Nevertheless, this specimen is also nearly complete and serves to corroborate interpretations based on *Eozostrodon* and *Megazostrodon*.

In the following sections a brief account is given of the material representing each element and is followed by a detailed morphological description.

## 2. Osteology of the postcranial axial skeleton

### (*a*) *Atlas-axis complex*

#### *Material*

Occipital condyles are known in both *Eozostrodon* and *Megazostrodon*. The atlas of Triassic triconodonts, like that of cynodonts, is composed of four ossicles: a right and left arch (each representing a pedicle and lamina), an intercentrum, and an atlas body (synostosed to the axis body). The atlas arches, the atlas and axis bodies and possibly the intercentrum of the atlas are preserved among the *Eozostrodon* materials. The atlas body and somewhat crushed atlas arches have been identified on the specimen of *Megazostrodon*.

#### *Morphology*

Triassic triconodonts possess two occipital condyles situated at the ventrolateral aspects of the foramen magnum (figures 1*a*, *b*). Oval in outline, the condyles extend along the ventral margin of the foramen nearly to the midline where they are separated by a shallow notch. The curvature of the articular surface is markedly greater dorsoventrally than mediolaterally, indicating that movements at the atlanto-occipital joint were largely restricted to flexion-extension as is typical of mammals.

The atlas arch in *Eozostrodon* bears two articular facets (figure 1*c*). The smaller and more transversely oriented of the two faces posteromedially and articulates with the atlas body. This shallowly concave facet is piriform in outline. The larger facet faces anteromedially and articulates with one of the two occipital condyles. Approximately kidney-shaped in outline, this facet bears an inflected dorsal margin that makes the surface distinctly concave. Between the dorsal margins of these facets is a pit (and in larger specimens a slight degree of rugosity) that probably marks the attachment of a transverse atlantal ligament. The remainder of the atlas arch is comprised of a dorsal plate, representing a lamina, and a transverse process, possibly for an atlantal rib. The dorsal plate, constricted and thick at its base and broad and thin along its dorsal margin, was joined to the plate on the other arch by connective tissue. The transverse process is damaged in all specimens, but as preserved resembles that in *Megazostrodon* described below. On the lateral aspect of the atlas arch are two sulci (figure 1*d*), one on either side of the base of the dorsal plate, which represent the course of neurovascular structures traversing the atlanto-occipital and first intervertebral foramina. (There is no evidence of a proatlas as in cynodonts.)

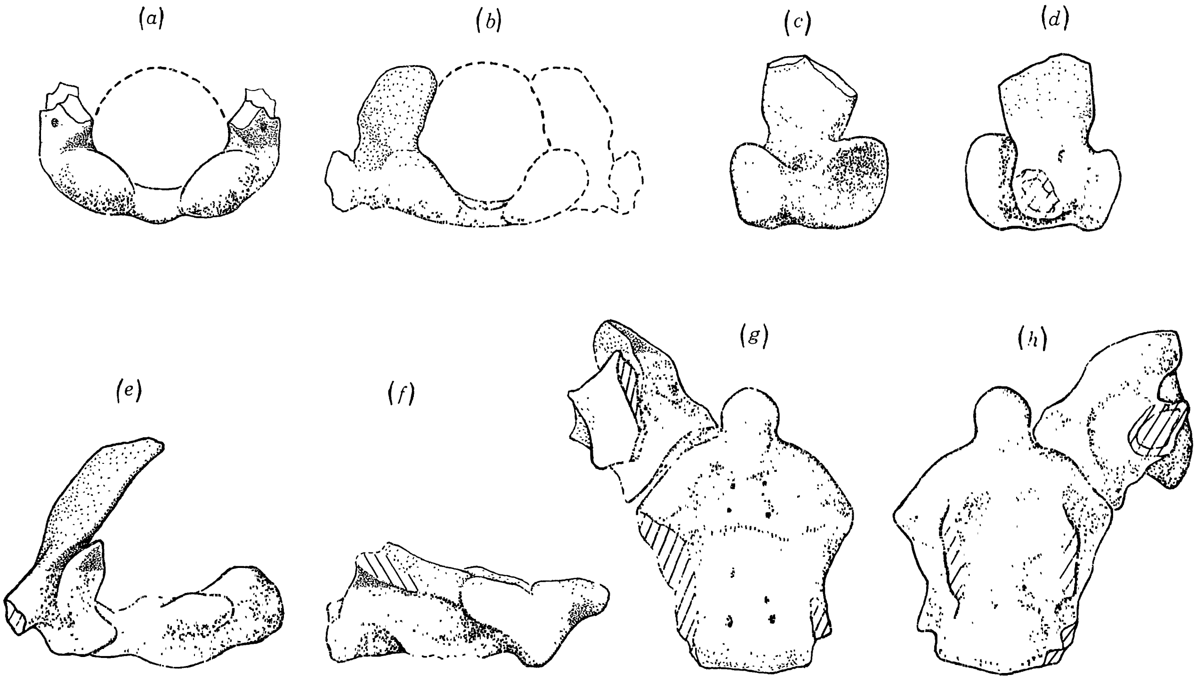

FIGURE 1. Atlas-axis complex of Triassic triconodonts. (*a*) Partial left exoccipital of *Eozostrodon* (the right side has been restored as a mirror image), in occipital view, showing left occipital condyle. (*b*) The same in *Megazostrodon*. (*c*) Medial view of a left atlas arch in *Eozostrodon* showing two facets; the anterior (right) and posterior (left) facets articulate with the left occipital condyle and atlas body, respectively. (*d*) Lateral view of same showing sulci leading from atlanto-occipital (left) and first intervertebral (right) foramina for neurovascular structures. (*e*) Anterolateral view of the detached atlas body and right atlas arch of *Megazostrodon*. (*f*) Lateral view of the atlas body, dens and axis body in *Eozostrodon*. The neural arch of the axis has been lost in this specimen. (*g*) The same in dorsal view, together with a left axis arch which is depicted in normal anatomical relationship (but was not found in association). Note the facet on the dorsal aspect of the dens for the atlantal transverse ligament, and the sutural joint separating atlantal and axial bodies. The atlantal lamina is broken, but presumedly formed part of an osseoligamentous bridge over the vertebral canal (as in cynodonts) and did not synostose with its counterpart (as in mammals). (*h*) The same in ventral view. The suture between atlantal and axial bodies is clearly seen. (*a–e*, approximately × 8; *f–h*, approximately × 11.)

The atlas arches of *Megazostrodon*, although somewhat crushed, appear to conform to the *Eozostrodon* pattern (figure 1*e*). Preserved are the complete dorsal margin of the lamina and the transverse process. The latter is short and approximately rectangular in section; in general form, it resembles that of cynodonts, although the superior margin is anterior to the posterior margin – the reverse of the cynodont orientation.

The atlas arches in *Eozostrodon* undoubtedly were joined ventrally by an intercentrum, as in cynodonts, because there is a facet for an intercentrum on the atlas body ventral to the dens. The identification of the atlantal intercentrum is problematical, however. A number of small crescentic ossicles possibly represent atlantal intercentra, but they lack double facets for the two occipital condyles; alternatively, these ossicles may be post-axis cervical intercentra such as occur in cynodonts, occasionally in mammals and commonly in reptiles.

The body of the atlas in *Eozostrodon* and *Megazostrodon* is a hemicircular ossicle bearing a prominent dens of mammalian proportions (figures 1*e*–*h*); in *Megazostrodon* and in many *Eozostrodon* specimens, the atlas body has separated from the axis body with which it was only incompletely synostosed. These features confirm Jenkins's (1969) conclusion that the mammalian dens evolved as an addition to the atlas body, and is not simply a vestige of the body. The atlas body is dorsoventrally compressed and considerably wider than the axis body (figures 1*f*, *g*). On either side of the dens are broadly convex facets for the atlas arches. A saddle-shaped facet can be seen on the dorsal aspect of the dens in well preserved specimens; across this facet played the transverse ligament of the atlas.

The axis body of *Eozostrodon*, known from only two incomplete specimens, is as dorsoventrally compressed as the atlas body. In both the pedicles are broken and the arch is missing. However, the pedicle base is short anteroposteriorly and is located on the caudal half of the axis body (right side, figure 1*g*). The atlanto-axial intervertebral foramen was therefore large, a feature associated with rotational movements of the atlas arches on the axis (Jenkins 1971*a*). Another feature of morphological importance is the slight degree to which the notochordal fossa is developed on the posterior aspect of the body. In contrast, the axis of the associated lizard is deeply notochordal. The depth of the notochordal fossa is therefore a critical feature in distinguishing mammalian from reptilian post-axial vertebrae in the Pont Alun collection.

### (*b*) *Vertebral column*

*Material*

Articulated vertebrae, including segments from the cervical, thoracic, lumbar, sacral and caudal regions, are present in *Megazostrodon*, although almost all vertebrae are fragmented or crushed to some degree. In *Erythrotherium*, at least part of the thoracolumbar and sacral series has been preserved, but owing to the exceedingly delicate nature of the bone only minimal preparation was undertaken. Both these specimens, however, provide sufficiently detailed information that some disarticulated vertebrae in the Pont Alun quarry collection can be assigned to *Eozostrodon*. Furthermore, *Eozostrodon* vertebrae are distinguished by their platycoelous centra from those of the associated lizard which are amphicoelous. Partial vertebrae of *Eozostrodon* from all the major vertebral regions have been identified except the post-axis cervicals. The absence of post-axis cervicals from the collection may be attributed to their fragile construction; if they resembled the lightly built cervicals of *Megazostrodon*, they would be prone to destruction during burial, weathering and subsequent preparation.*

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* Since the foregoing was written a cervical vertebra referable to *Eozostrodon* has been found. See addendum, p. 430.

### *Morphology*

The post-axis cervical vertebrae in *Megazostrodon* bear relatively narrow laminae and pedicles, with zygapophyses set widely apart (figure 6*a*, plate 1). The neural spines, broken off at their bases, are narrow, rod-like and slightly recurved posteriorly (figure 6*b*). The pedicles appear to articulate only with the dorsolateral margin of the bodies, thus creating a wide vertebral canal. Transverse processes are well developed, as are longitudinal flanges along the ventrolateral aspects of the bodies (figure 6*c*). Possibly cervical ribs articulated with these; a few associated fragments may be interpreted as cervical ribs. Intercentra are not present.

Thoracic vertebrae of *Eozostrodon* are known from fewer than ten specimens (figures 2*a–d*). The vertebral bodies are wider than deep, and are deeper at the posterior than at the anterior end. On the lateral aspect of the pedicle is an elongate, slightly raised facet (diapophysis) for the rib tubercle; in some specimens the facet for the rib head is confluent with the tubercular facet, whereas in others it occurs separately at the anterior junction between the pedicle and body. Intervertebral notches, which border on the intervertebral foramina, are present on the anterior and posterior margins of the pedicles. The posterior notch is the more deeply incised and is bounded superiorly by a small anapophysis, as in cynodonts. The articular surfaces of the zygapophyses are more or less horizontally oriented. On the prezygapophyses the surfaces are slightly concave from side to side, the lateral half being somewhat upturned. The spinous processes are narrow and inclined posteriorly.

Thoracolumbar differentiation in *Eozostrodon* is demonstrated by three vertebrae from the posterior thoracic and anterior lumbar region that are preserved in articulation (figure 6*d*, *e*, plate 1). The most anterior of these possesses a posteriorly inclined, attenuated spinous process, nearly horizontally oriented zygapophyseal facets, and a diapophysis which, although damaged, resembles that of the thoracic vertebrae described above. On this evidence, the vertebra appears to belong to the thoracic series. On the second and third vertebrae the spinous processes are successively more robust and vertical, and the articular facets on the zygapophyses become oriented obliquely rather than horizontally (approximately from 35° to 45° from horizontal on the postzygapophyses of the third vertebra). The zygapophyses are situated also successively closer to the median plane; on the anterior-most vertebra, the distance between the lateral margins of the prezygapophyses is 2.5 mm, whereas on the last vertebra the comparable measurement is 2.0 mm. The short transverse processes of the second and third vertebrae are directed anterolaterad and taper to a thin point; the transverse process of the third vertebra appears to be somewhat shorter and more robust, but poor preservation leaves this point uncertain. Small anapophyses are present on the first two vertebrae, but are absent on the last. Lumbar vertebrae of *Eozostrodon* thus possess a number of distinctive features similar to those of higher mammals; the reconstruction in figure 2*e* may be compared to the imperfectly preserved lumbar vertebrae in *Megazostrodon* (figure 9*a*, plate 4) in which some of the same features can be identified.

The sacrum of *Eozostrodon* is composed of at least two and possibly three vertebrae (figures 2*f*, *g*). The neural arch of the first sacral vertebra bears prezygapophyses set narrowly together. The zygapophyseal articular surfaces are slightly concave from side to side and are oriented as a whole at approximately 45° to the median plane; in contrast to dorsal vertebrae, the surfaces are inclined somewhat posteriorly. The transverse process of the first sacral vertebra is directed posteriorly and somewhat ventrally, and meets (and apparently synostoses with) the transverse process of the second sacral which is directed anteriorly. The anterior aspect of the first sacral body (centrum) bears the evenly pitted texture characteristic of other vertebral surfaces that adjoin intervertebral disks. The posterior aspect of the second sacral body, however, is uneven and rugose, evidence of a possible third sacral vertebra. Furthermore, at least part of the articular surface for the ilium is missing; relative to the elongate surface on the medial aspect of *Eozostrodon* ilia, this surface is short and may well have been extended by a third sacral rib.

*Eozostrodon* caudal vertebrae show marked morphological gradation (figure 2*h*). Anterior

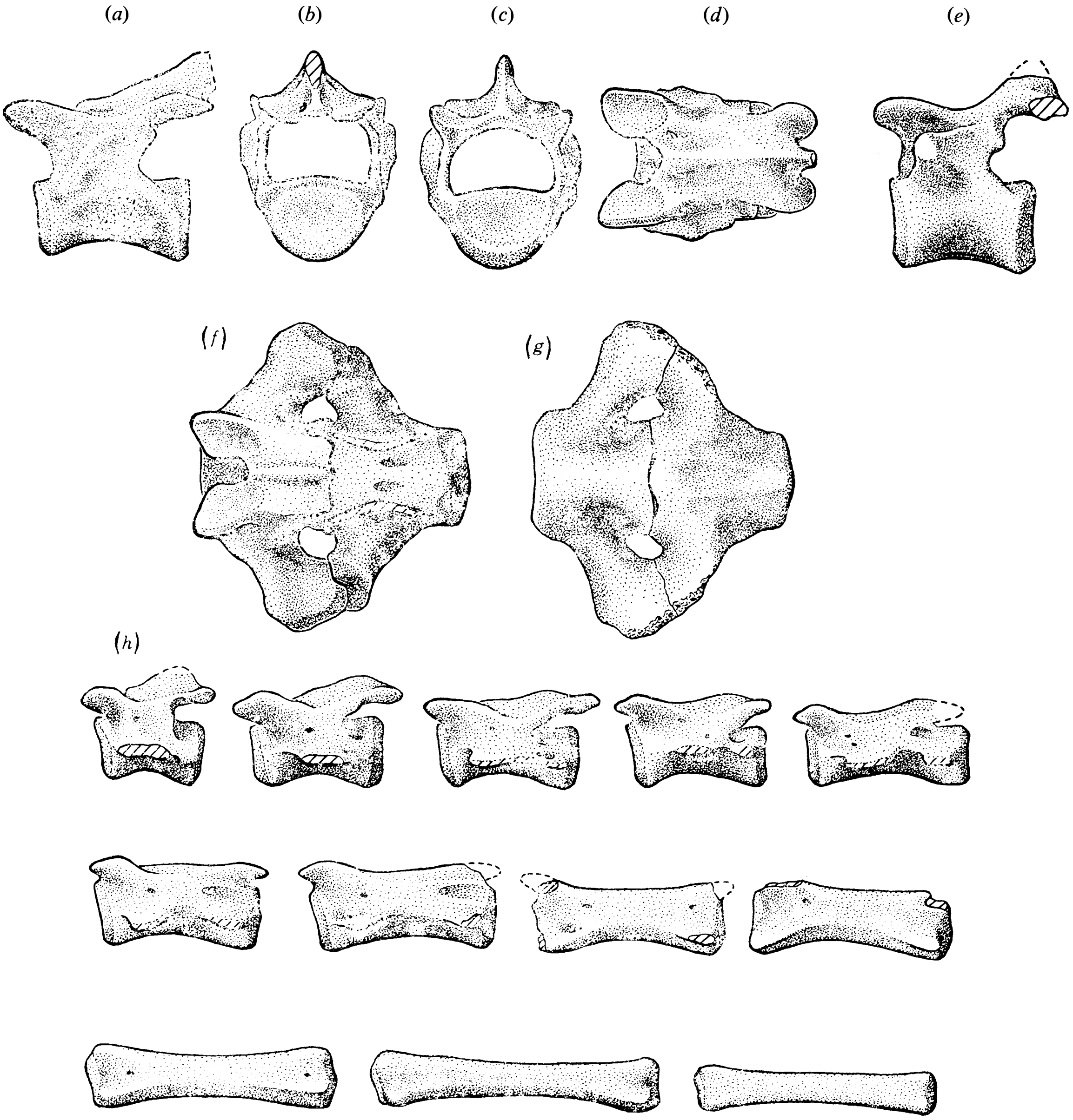

FIGURE 2. (*a*) Lateral, (*b*) posterior, (*c*) anterior and (*d*) dorsal views of a thoracic vertebra of *Eozostrodon*, a reconstruction based on two specimens. (*e*) Lateral view of a lumbar vertebra of *Eozostrodon*, a reconstruction based on three specimens. (*f*) Dorsal view of a partial sacrum of *Eozostrodon*; neural arch and zygapophyses of the most anterior vertebra are drawn from two additional specimens. (*g*) Ventral view of same. (*h*) Lateral view of dissociated *Eozostrodon* caudals, here reconstructed in sequence. (All approximately × 8.)

caudals have relatively short centra and an unmodified arch structure with processes resembling those of the dorsal series. The major difference is that the transverse process is a thin, horizontally oriented blade located between the pedicle and centrum (rather than centrally on the pedicle, as is the case on lumbar vertebrae). Passing posteriorly, the principal morphological changes are the following: elongation of the centrum; elongation of the transverse process; incorporation of a foramen, probably vascular, running dorsoventrally through the process (e.g. on the third, seventh and eighth vertebrae; figure 2*h*); reduction and loss of the spinous process, and incorporation of the intervertebral foramen into the pedicle. The distal caudal vertebrae are a simple dumb-bell shape, lack any processes, and bear a narrow, dorsal groove that carried the terminal caudal nerves. Nutrient foramina, variably positioned, are commonly found on the centra and arches.

Although the number of caudal vertebrae in *Eozostrodon* is unknown, the degree to which caudals are differentiated indicates a moderately long tail composed of at least 12 vertebrae. A reconstructed series of caudal vertebrae is depicted in figure 2*h*. The tail in cynodonts appears to have been relatively shorter (see Jenkins 1971*a*), although the tail in the advanced mammal-like reptile *Oligokyphus* (as restored by Kühne 1956) is relatively long.

Haemal arches are present in the Pont Alun collection, but they cannot be assigned positively to *Eozostrodon*. A distinct morphological gradient is shown by the seven specimens available. Proximal elements have a stirrup-shaped arch and four tubercles, two on each side, protruding ventrally; although the arch is symmetrical, the position, shape and size of the tubercles are asymmetrical. The arch diminishes to a small, round canal in the more distal specimens, and the anterior and posterior pairs of tubercles respectively coalesce to form rod-like processes grooved dorsally by vasculature.

## 3. Osteology of the appendicular skeleton

### (*a*) *Interclavicle*

#### *Material*

Two types of interclavicle are present in the Pont Alun collection; inasmuch as they are similar in structure and the interclavicle has not been identified among the *Megazostrodon* and *Erythrotherium* materials, the assignment of one of these forms to *Eozostrodon* is only tentative. The more gracile of the two is here interpreted as belonging to *Eozostrodon* because comparison of other homologous bones indicates that the lizard is somewhat more robust in build.

#### *Morphology*

The interclavicle is **T**-shaped with elongate lateral processes (figure 3). Distinct sulci are developed for reception of the proximal ends of the clavicles (figure 3*c*). The posterior process of the interclavicle is narrow and elongate, widening only slightly toward its caudal end. The lateral and posterior processes curve dorsally to a slight degree, but on the whole the interclavicle is flat. The articular surface for contact with the sternum is not preserved in any specimen. At the intersection between each lateral process and the posterior ramus is a shallow groove (figure 3*a*); in monotremes this area is occupied by the articulation between the procoracoid and interclavicle, but no sulcus is present. However, it is unlikely that the procoracoids articulated here in *Eozostrodon* (see §4*b*). The groove may represent the proximity of neurovascular structures or the attachment of ligaments.

The second type of interclavicle in the Pont Alun collection, tentatively identified as belonging to the lizard, is characterized by a more pronounced dorsal curvature of the lateral processes, the presence of bulbous, irregular exostoses at the proximal end of each lateral process, and relatively deeper clavicular sulci. In no specimen of this type is more than the base of the posterior process preserved. Grooves at the intersection between the lateral processes and the posterior ramus are absent.

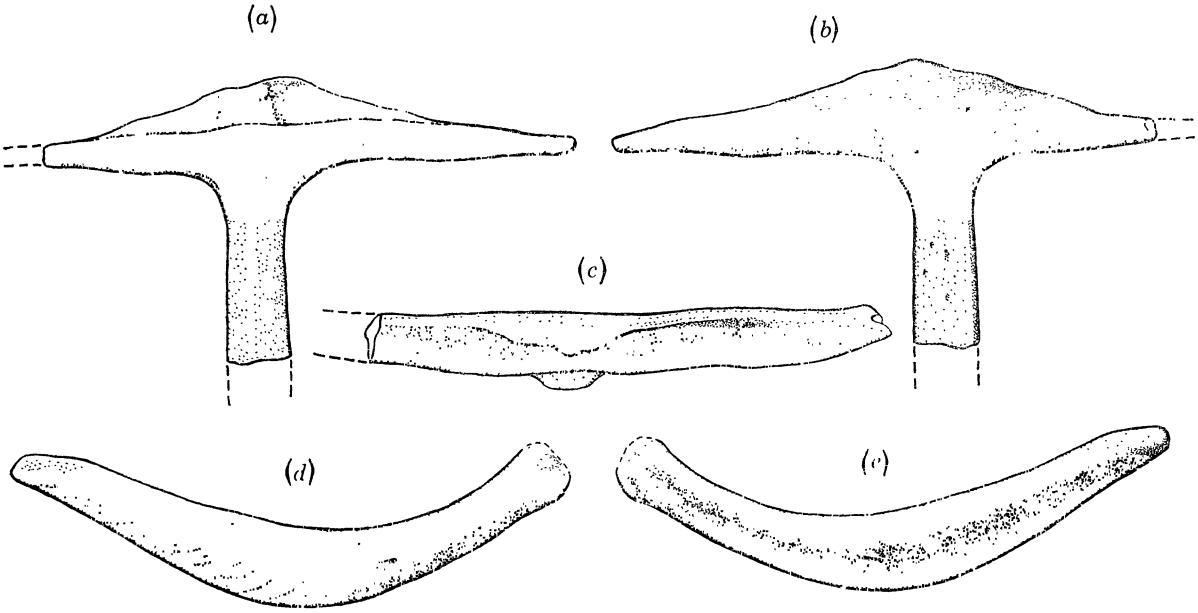

FIGURE 3. Interclavicle and clavicle referred tentatively to *Eozostrodon*. (*a*) Interclavicle in ventral view showing two lateral processes (for articulation with the clavicles) and a posterior process. (*b*) The same in dorsal view. (*c*) Anterior view of the lateral processes showing the sulci for reception of the medial ends of the clavicles. Reconstruction based on three specimens. (*d*) Left clavicle in anterior view. (*e*) The same in posterior view. Reconstruction based on six specimens. (All approximately × 9.)

The interclavicle of *Eozostrodon* differs from that typical of cynodonts in the narrowness of both the lateral and posterior processes. Monotremes have elongate lateral processes with a clavicular sulcus similar to that in *Eozostrodon*; however, in monotremes the joint between clavicle and interclavicle is interlocking and immovable, whereas in *Eozostrodon* the joint was not so firmly fixed judging from the disarticulated state of all specimens. The relatively narrow posterior process in *Eozostrodon* contrasts with the broader, plate-like processes of cynodonts. In monotremes the anterior part is similar to that in *Eozostrodon*, but posteriorly broadens substantially to form a wide contact with the sternum.

### (*b*) *Clavicle*

*Material*

Clavicles are known only from the *Eozostrodon* collection and here only by incomplete specimens. The assignment of some of this material to *Eozostrodon* is tentative, for there are no features which certainly distinguish them as mammalian. As in the case of the interclavicle, the distinction between apparently similar elements in the lizard and mammal is based on the somewhat more robust build of other bones that are known to belong to the lizard. On this criterion, however uncertain, the clavicle of *Eozostrodon* is identified as being the more gracile of the forms represented.

### *Morphology*

The slender clavicle, bowed with the convex margin directed anteriorly as in monotremes, possesses little of the sinusoidal curvature characteristic of therians (figures 3*d*, *e*). The anterior surface is relatively flat, more so medially than laterally. The relatively straight medial half of the clavicle tapers to a narrow point, and lodges in the sulcus on the lateral process of the interclavicle, much as in monotremes. Along the ventral margin of the anterior surface are faint lineations (figure 3*d*), representing either muscular or ligamentous attachments.

The posterior aspect of the clavicle (figure 3*e*) reveals a longitudinal groove separating a ventral flange from the shaft proper. The flange is broadest in the middle of the clavicle. Nutrient foramina are variably positioned between the flange and shaft.

In all available specimens the distal end is at least partially damaged and thus the structure of the articular surface cannot be determined precisely. However, details are sufficiently preserved in several specimens to show that the articular surface is not spatulate, as in typical therians, but blunt as in monotremes.

The clavicle in *Eozostrodon* differs from the cynodont and tritylodontid pattern in which the proximal end is spatulate and the shaft does not bear a ventral flange. Substantial similarity exists between the proximal ends of the clavicles of *Eozostrodon* and monotremes, especially *Ornithorhynchus*. In monotremes, however, the clavicle articulates with the interclavicle for nearly its entire length, whereas in *Eozostrodon* this articulation probably extended for no more than half the length of the clavicle.

## (*c*) *Scapulocoracoid*

### *Material*

The scapulocoracoid of *Eozostrodon*, represented by about two dozen incomplete specimens, is composed of a scapula, coracoid, and procoracoid. From *Megazostrodon* only the scapulae have been recovered. In no specimen of *Eozostrodon* is the dorsal half of the scapular blade preserved, although the blade is nearly complete in *Megazostrodon*. An incomplete scapulocoracoid of *Eozostrodon* has been figured and briefly discussed by Kermack & Mussett (1959).

### *Morphology*

In *Megazostrodon* the infraspinous fossa is extremely deep (figure 7*b*), although some post-mortem crushing may have exaggerated this feature. The anterior half of the scapular blade is a laterally reflected flange, homologous with the scapular spine of therian mammals. The acromion, or site of clavicular articulation, is represented as a slight thickening along the ventral margin of the flange. A supraspinous fossa is not developed; however, the anterior half of the scapular blade, being laterally reflected, presents an extensive, anteriorly facing surface (figure 7*a*, plate 2) that undoubtedly provided origin for the supraspinous muscle. This surface appears to have been slightly concave. There is no trace of further remodelling of the blade to indicate that a supraspinous fossa of the therian type was developing. On the base of the scapula is a hemicircular articular surface that represents approximately one half the glenoid, and a small process that articulates with the procoracoid. Between the glenoid and the infraspinous fossa, the scapula is slightly constricted.

Although only the base of the scapula is known in *Eozostrodon* (figure 4; figures 8*a*, *b*, plate 3), the general structure is similar to that in *Megazostrodon*, particularly the depth of the infraspinous fossa and the degree to which the anterior flange (scapular spine) is laterally reflected.

The glenoid in *Eozostrodon* is formed by scapular and coracoid facets of which the latter is slightly the larger of the two (figures 4*a*, *d*; figure 8*a*, plate 3). The procoracoid does not participate in the glenoid articulation. The glenoid is oval and approximately symmetrical in outline. However, the posteroventral margin of the glenoid typically bears a slight indentation, and the anterior (or lateral) margin extends forward onto the lateral aspect of the scapulocoracoid.

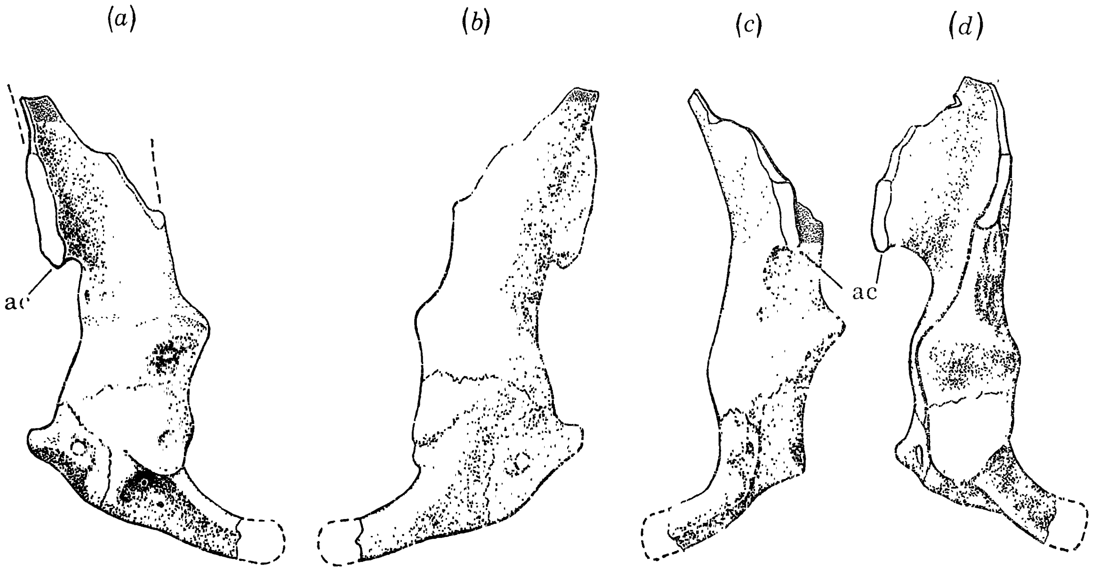

FIGURE 4. The left scapulocoracoid of *Eozostrodon*, a reconstruction based on one nearly complete specimen and four additional fragments. The dorsal half of the scapula is missing in all available specimens, and is not reconstructed here. ac, acromion. (*a*) Lateral view showing sutural joints between scapula, procoracoid (with foramen), and coracoid. (*b*) Medial view of same. (*c*) Anterior view. (*d*) Posterolateral view; note triceps rugosity above the glenoid, and the shallow pits on the glenoid. (Approximately × 8.)

The surface is smooth and of uniform curvature except for two shallow indentations, one in the centre of the scapular half of the glenoid, the other adjacent to the ventral margin of the coracoid facet. With the exception of the lack of procoracoid participation in the glenoid, these features are also found in cynodonts (figures 19*a*, *b*) (Jenkins 1971*a*).

In both *Megazostrodon* and *Eozostrodon*, a narrow groove occurs above the glenoid fossa along the posteromedial margin of the scapular blade (figure 4*d*; figure 7*b*, plate 2). In some specimens of *Eozostrodon* this area is also somewhat rugose, resembling a point of musculotendinous attachment. Jenkins (1971*a*) interpreted a similar feature on the scapular blade of cynodonts as representing the origin of the scapular head of the triceps.

The small, irregularly shaped procoracoid of *Eozostrodon* is pierced by a procoracoid foramen and bears an anteriorly projecting process (figure 4*a*; figure 8*a*, plate 3). The procoracoid is synostosed principally to the coracoid, its suture with the scapula being relatively short. The procoracoid and its sutures are preserved intact in only a few specimens. In most cases, the procoracoid is broken away, with only the scapulocoracoid junction (and glenoid) intact. Although neither procoracoid nor coracoid is preserved in *Megazostrodon*, an articular surface for both these elements is preserved on the base of the scapular blade.

The coracoid of *Eozostrodon* bears half the glenoid (figures 4*a*, *d*). Ventrally, the coracoid is thin and plate-like, and posteriorly tapers to a narrow process. In general the form is similar to that in cynodonts although the coracoid has extended anteriorly and invaded the area which, in cynodonts, is occupied by the procoracoid (figure 19). The tip of the coracoid process is missing in all available specimens, but probably was occupied by a tuberosity for the coracoid head of the triceps as in cynodonts and monotremes.

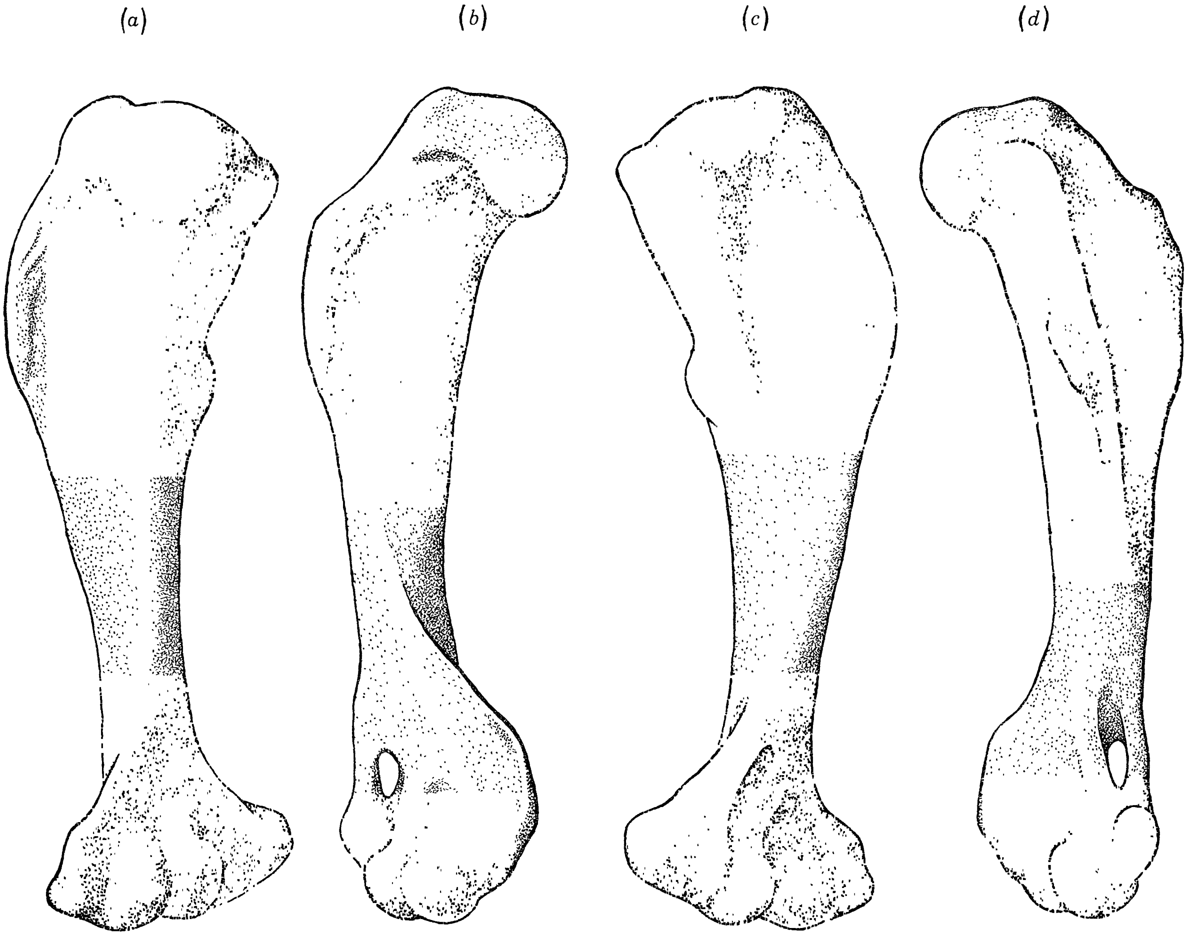

FIGURE 5. The left humerus of *Eozostrodon*, a reconstruction based on six incomplete specimens. (*a*) Dorsal, (*b*) lateral, (*c*) ventral and (*d*) medial views. (Approximately × 8.)

### (*d*) *Humerus*

#### *Material*

More than fifty humeral fragments in the Pont Alun collection are referable to *Eozostrodon*, and they preserve detailed features of the articular surfaces. A few specimens are nearly complete, permitting an accurate reconstruction of the entire bone. The left humerus associated with *Megazostrodon* is somewhat crushed, and its proximal and distal ends are poorly preserved. In most major features, however, it resembles the humerus of *Eozostrodon*.

### *Morphology*

The proximal and distal ends of the *Eozostrodon* humerus are twisted relative to one another; an imaginary plane through the tubercles and deltopectoral crest lies at approximately 50° to a plane through the epicondyles and elbow joint. *Megazostrodon* appears to have been similar, but due to crushing this feature cannot be verified with certainty.

The humeral head in *Eozostrodon* is bulbous and nearly hemispherical (figure 5; figures 8*a*, *b*, plate 3). The greater tubercle is confluent with the humeral head and is less prominent than the lesser tubercle which stands apart from the head as a major prominence. The relatively large deltopectoral flange has a thickened, rugose margin which is evenly rounded in outline (figure 5*a*). A small, shallow fossa occurs in the broad bicipital groove beneath the humeral head (figure 5*c*). Opposite the deltopectoral flange, on the medial aspect of the shaft, is a prominent tubercle (figure 5*d*; figure 8*b*, plate 3); this feature occurs in cynodonts and in primitive mammals and may represent the attachment of the teres major muscle.

As preserved, the sphericity of the humeral head in *Megazostrodon* is less than that in *Eozostrodon*; however, the head is crushed out of position and is almost certainly distorted (figure 7*c*, plate 2). The relative proportions of the greater and lesser tubercles, the shallow fossa beneath the head, and the small tuberosity on the medial aspect of the shaft all resemble the *Eozostrodon* pattern. However, the deltopectoral crest appears to be only about half as wide as that in *Eozostrodon* – a feature which may have resulted from post-mortem deformation. The margin of the flange is reflected ventrally, very possibly an artifact.

In *Eozostrodon*, a crest runs along the dorsal aspect of the humeral shaft from a point near the head to the ectepicondyle (figure 5*a*). The shaft in cross-section through the middle is mediolaterally compressed, but distally expands to the large entepi- and ectepicondyles. The ectepicondylar flange is large and reflected somewhat dorsally. There is a large entepicondylar foramen but no ectepicondylar foramen. The capitulum is bulbous with an articular surface that appears to extend onto the dorsal aspect of the bone (figure 5*a*; figure 8*c*, plate 3). An ulnar condyle wraps completely around the distal end from ventral to dorsal aspects; inasmuch as the dorsal half of the condyle is more laterally situated relative to the shaft than is the ventral half (figure 8*c*, plate 3), the configuration of the condyle as a whole is slightly spiral. The condyle extends farther proximally on the dorsal aspect than on the ventral aspect. An intercondylar groove, apparently occupied principally by the lateral margin of the proximal articular surface of the ulna, separates the ulnar condyle from the capitulum.

The distal half of the *Megazostrodon* humerus resembles that of *Eozostrodon* in general structure. Although the distal articular surfaces are not preserved in *Megazostrodon*, there appears to have been an ulnar condyle. As in *Eozostrodon*, the entepicondyle is robust and protuberant.

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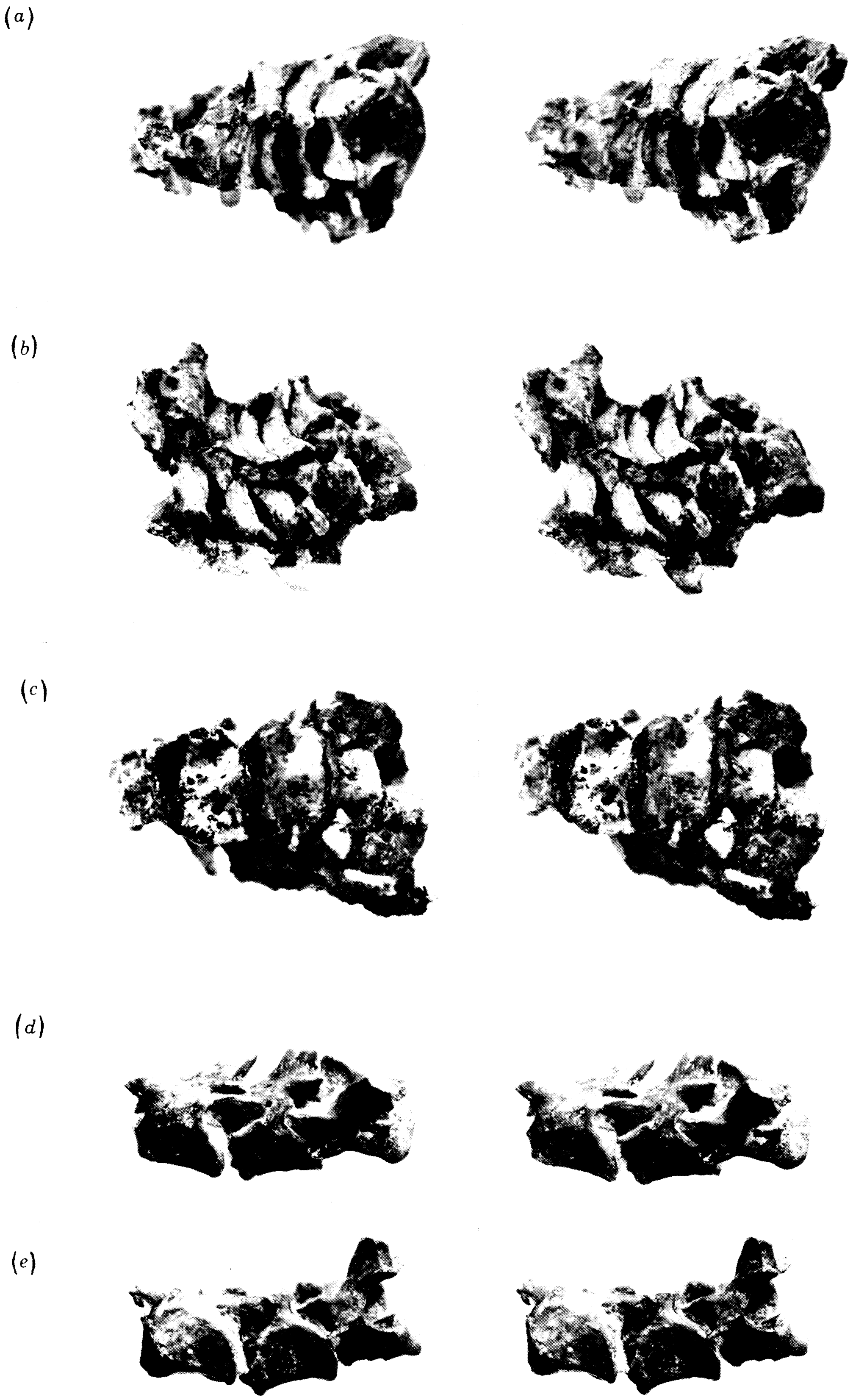
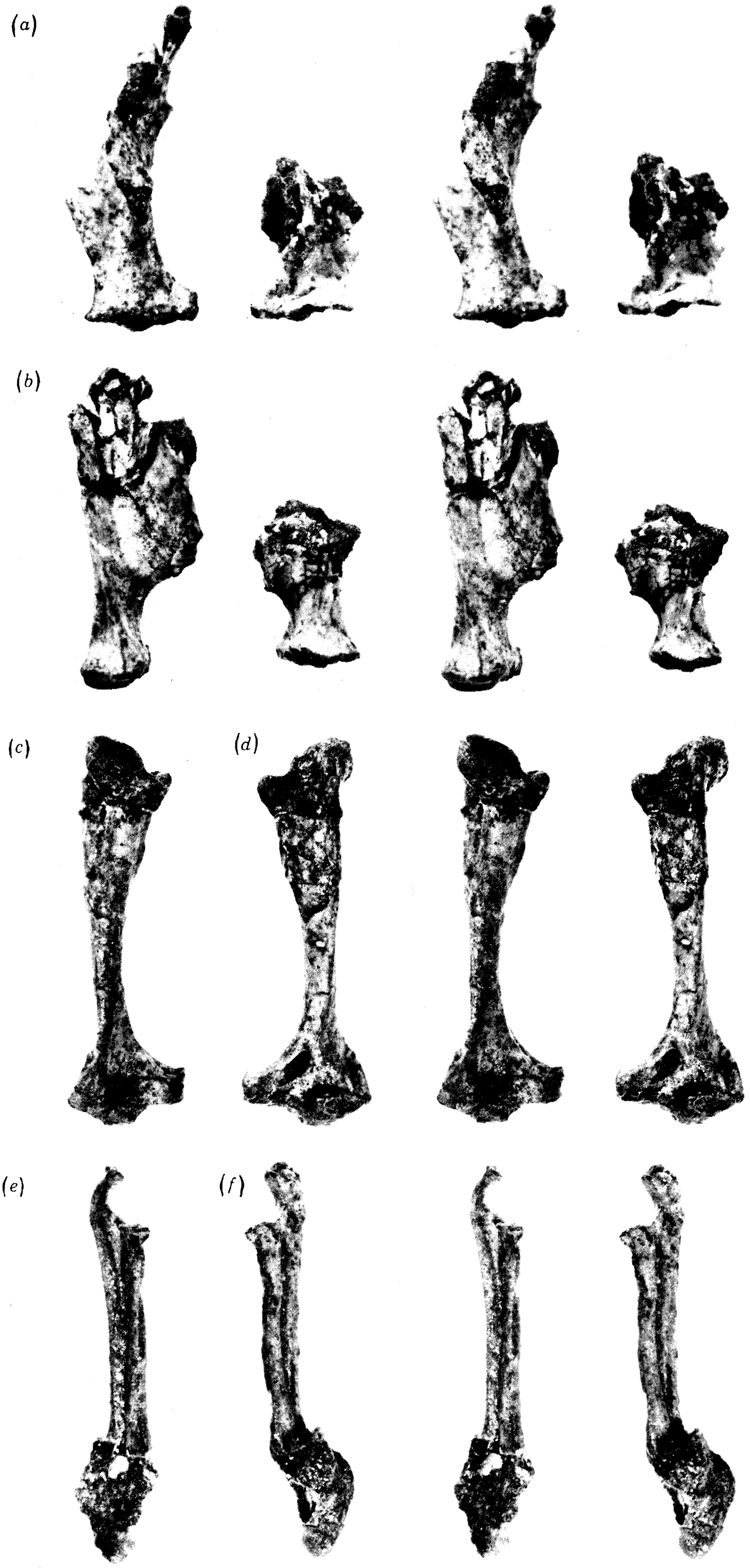
## Description of plate 1

Figure 6. (*a*–*c*) Stereophotographs of articulated posterior cervical and possibly anterior thoracic vertebrae of *Megazostrodon rudnerae* (B.M.N.H. M 26407) in (*a*) dorsal, (*b*) lateral and (*c*) ventral views. (× 7) (*d*–*e*) Stereophotographs of three articulated vertebrae from the thoracolumbar region of *Eozostrodon*. The vertebra on the left is probably the last thoracic or first lumbar, and is shown in lateral (*d*) and ventrolateral (*e*) views. (× 5.3.)



FIGURES 6 (*a*–*e*). For description see opposite.



FIGURES 7 (*a–f*). For description see opposite.

### (*e*) *Radius*

#### *Material*

The radius in *Eozostrodon* is known from an almost complete specimen of a young individual, as well as about three dozen fragments. Both radii of *Erythrotherium* have been recovered in articulation with the ulnae; these tiny bones, with shaft diameters of 0.7 mm, have been somewhat crushed post-mortem and do not preserve the detailed features seen in *Eozostrodon*.

#### *Morphology*

The proximal end of the radius in *Eozostrodon* bears an oval, concave articular surface that is oblique, rather than transverse, to the shaft (figure 8*f*, plate 3; figure 10). The medial margin of the articular surface which lies against the ulna is only slightly convex, and the facet just distal to the medial margin (figure 8*f*; right specimen) which articulates with the radial notch of the ulna is confined to the posteromedial aspect of the proximal end; these features are evidence that pronation-supination movements of the radius were relatively limited. A ridge passes from the ulnar facet down the shaft and curves medially before disappearing at about the middle of the bone (figure 10*c*). A similar ridge occurs on the cynodont radius and was interpreted by Jenkins (1971*a*) as being associated with the attachment of the forearm flexors and the radio-ulnar interosseous ligament.

The somewhat sigmoidal curvature of the *Eozostrodon* radius allows for the passage of the bone across the ulna. On the anterior aspect of the shaft, at the junction between the middle and distal thirds, is a slight groove flanked by two short ridges (figure 10*a*). Distal to the lateral ridge, on the lateral aspect of the shaft, is a low and rather indistinct tubercle. A similar groove and single ridge are found on the anteromedial aspect of the radius in monotremes, especially *Ornithorhynchus*, which apparently divides the extensor and flexor surfaces. In *Eozostrodon* the ridges and groove may have had a similar significance, although their position on the anterior aspect of the shaft as well as their substantial build is suggestive of an extensor muscle attachment or a close relationship between a tendon and the shaft. In monotremes, the comparable area is occupied by the insertion of the m. extensor radialis profundus (Haines 1939).

The distal end of the radius in *Eozostrodon* is expanded mediolaterally. The articular surface is slightly concave, the principal curvature being anteroposterior to accommodate flexion–extension movements at the wrist (figure 8*f*, plate 3, left specimen). A blunt styloid process is developed on the medial aspect of the distal end (figures 8*f*, 10*a*, *b*) and on the lateral margin is a small, raised facet for articulation with the ulna (figure 10*d*).

The articulated right radius and ulna of *Erythrotherium* (figures 7*e*, *f*, plate 2) show that the radius crosses the anterior aspect of the ulna. Both radii have been somewhat crushed, and the surface details known from *Eozostrodon* cannot be identified.

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### DESCRIPTION OF PLATE 2

FIGURE 7. (*a*–*b*) Stereophotographs of the scapulae of *Megazostrodon rudnerae* (B.M.N.H. M 26407). Most of the right scapula is preserved; the dorsal (vertebral) margin is lost. Both scapulae are shown in (*a*) lateral and (*b*) posterior views. (×6.7.) (*c*) Dorsal and (*d*) ventral views of the left humerus of *Megazostrodon*. (Approximately ×4.25.) (*e*) Lateral and (*f*) medial views of the right radius and ulna of *Erythrotherium parringtoni* (S.A.M. K 359). (×5.)

### (*f*) *Ulna*

*Material*

The ulna of *Eozostrodon* is represented by over 40 incomplete specimens. In *Erythrotherium*, both ulnae are preserved in articulation with the radii.

*Morphology*

The bulbous olecranon process of the *Eozostrodon* ulna is the principal feature that distinguishes it from the ulnae of various cynodonts (figure 8*e*, plate 3; figure 10). In one specimen with an almost complete proximal end (figure 8*e*, middle), the olecranon is asymmetrical, being higher and more robust medially than laterally. An olecranon is not present in *Erythrotherium*; inasmuch as the specimen represents an immature individual, this process may have been cartilaginous or incompletely developed.

The proximal articular surface on the *Eozostrodon* ulna bears three facets (figures 8*e*, 10*e*). The largest of these articulates with the ulnar condyle of the humerus; its surface is shallowly concave mediolaterally and is sharply curved proximodistally. The proximal part of the surface is characterized by a smaller radius of curvature and is more laterally positioned than is the distal part; this complex configuration conforms to the spiral or 'worm-screw' geometry of the ulnar condyle on the humerus. A second facet, narrow and more or less laterally oriented, is found lateral to the proximal part of the facet for the ulnar condyle (figure 10*h*); this facet articulates with the radial condyle (capitulum) of the humerus. The crest separating these two facets articulates with the intercondylar groove of the humerus. Distal to the facet for the radial condyle is a third facet for contact with the head of the radius, homologous with the radial notch of later mammals. In *Erythrotherium* the proximal articular surface clearly possesses the radial and ulnar condyle facets (figures 7*e*, *f*, plate 2), but the preservation is not good enough to determine the presence of the radial condyle facet or other details for comparison with *Eozostrodon*.

The ulnar shaft of *Eozostrodon* and *Erythrotherium* is transversely compressed, as in mammals and cynodonts, and bears a longitudinal sulcus on the medial and lateral sides from which flexor and extensor musculature took origin (figures 7*e*, *f*, plate 2; figures 10*f*, *h*). An ulnar flange, presumedly for attachment of the radio-ulnar interosseous ligament, is not as wide in the Triassic mammals as in cynodonts, giving the ulna a more slender appearance. Otherwise, the general configuration of the bone is similar in the two groups.

The distal end of the ulna in *Eozostrodon* is known from only one specimen. The articular surface appears to have been oval in outline with the long axis oriented anteroposteriorly, and only one half the size of the distal articular surface of a comparably sized radius.

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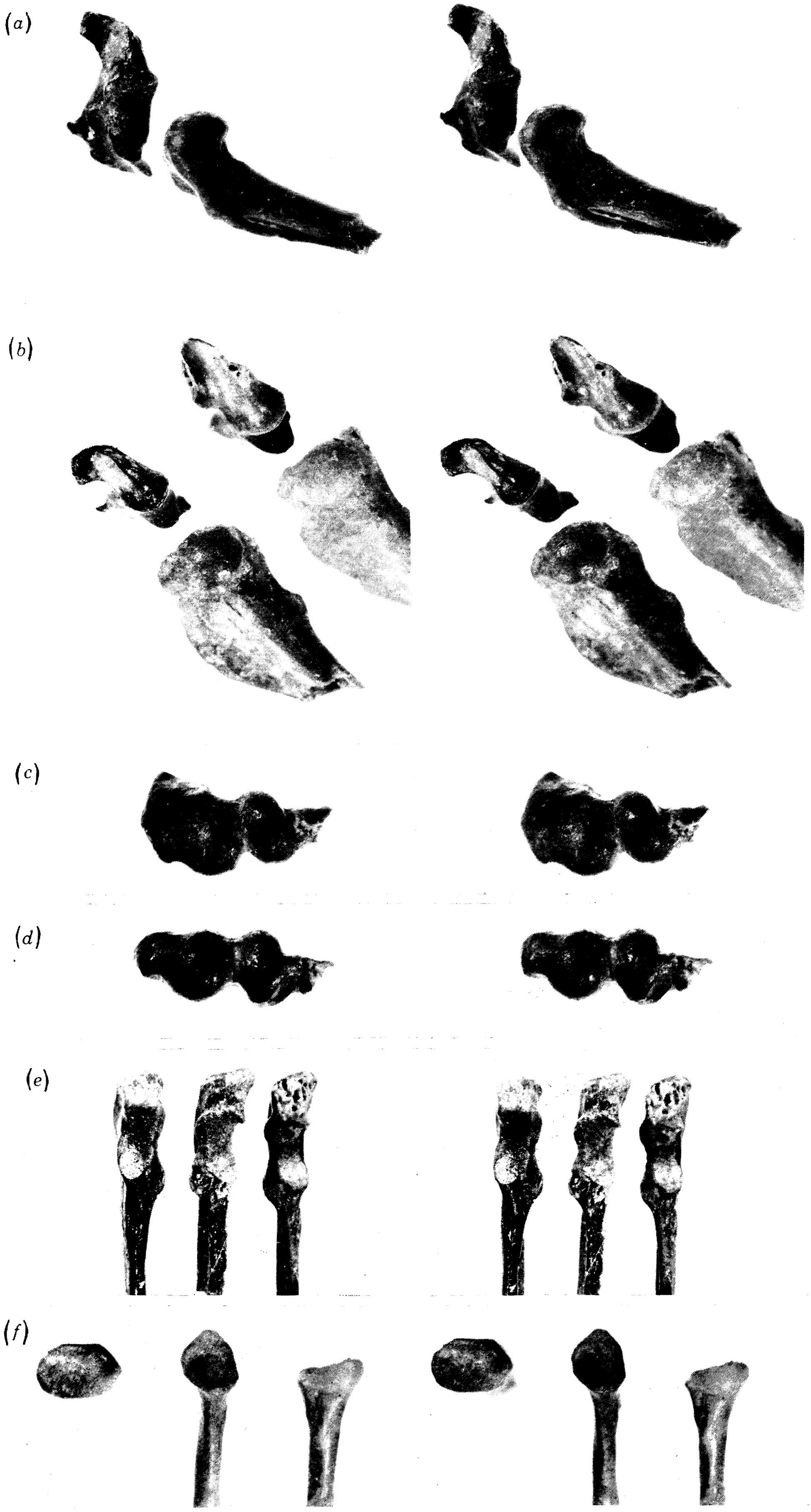
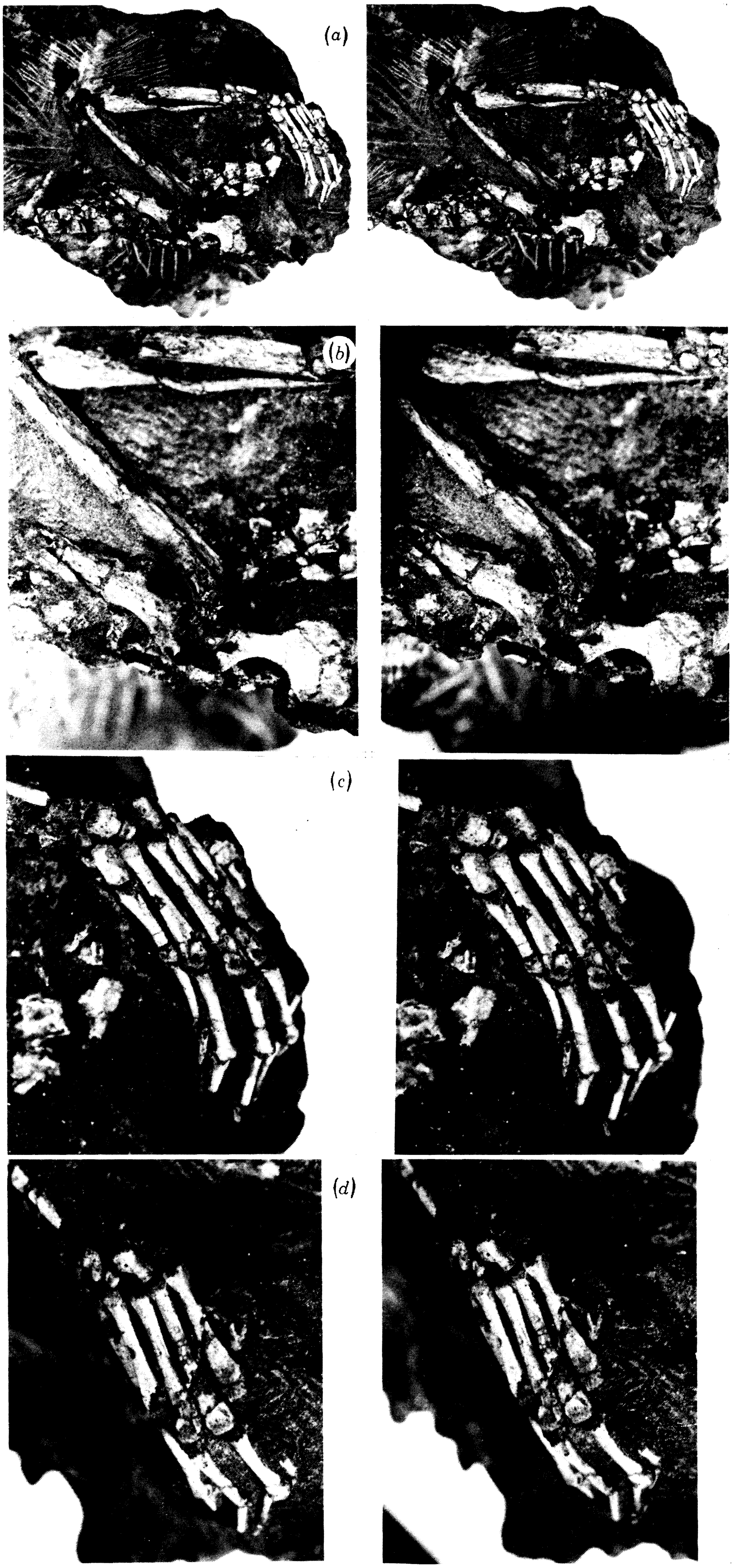
### Description of plate 3

Figure 8. Stereophotographs of some articular surfaces of the forelimb in *Eozostrodon*. (*a*) Posterolateral view of a left glenoid and anterolateral view of a proximal humerus; the bones have been separated from their normal articular relationship to show the curvature of the articular surfaces. (*b*) Dorsal view of two left glenoids and proximal humeri to show the approximate articular relations; none of the bones illustrated were associated. (× 5.) (*c*) End on view of a distal left humerus, seen slightly from the dorsal aspect, to show the shape of the bulbous radial condyle (left) and ulnar condyle (right). (*d*) The same seen from a more ventral aspect. (× 7.5.) (*e*) A left and two right proximal ulnae showing the articular surface for the ulnar condyle. (Approximately × 5.5.) (*f*) Articular surfaces of the radius of *Eozostrodon*: (left) distal articular surface; (middle) proximal articular surface; (right) proximal facet for articulation with the ulna. (× 6.1.)



FIGURES 8 (*a*–*f*). For description see opposite.



FIGURES 9 (*a–d*). For description see opposite.

### (*g*) *Manus*

#### *Material*

A few incomplete metacarpals and phalanges were recovered next to the jaw of *Megazostrodon* and are the only elements positively attributable to the manus. On the basis of this material there is no evidence of substantial differences from the comparable pedal elements which are well preserved and nearly complete. The metacarpals of *Megazostrodon* appear to be only slightly shorter than metatarsals, but even this is uncertain because of breakage. In the Pont Alun collection, numerous metapodials, carpals and tarsals are present. Some of these can be identified as belonging to the pes by comparison with the hindfoot in *Megazostrodon*; small ossicles that cannot be so identified may represent *Eozostrodon* carpals or foot bones from the associated lizard. Our knowledge of the manus in Triassic mammals thus remains unsatisfactory.

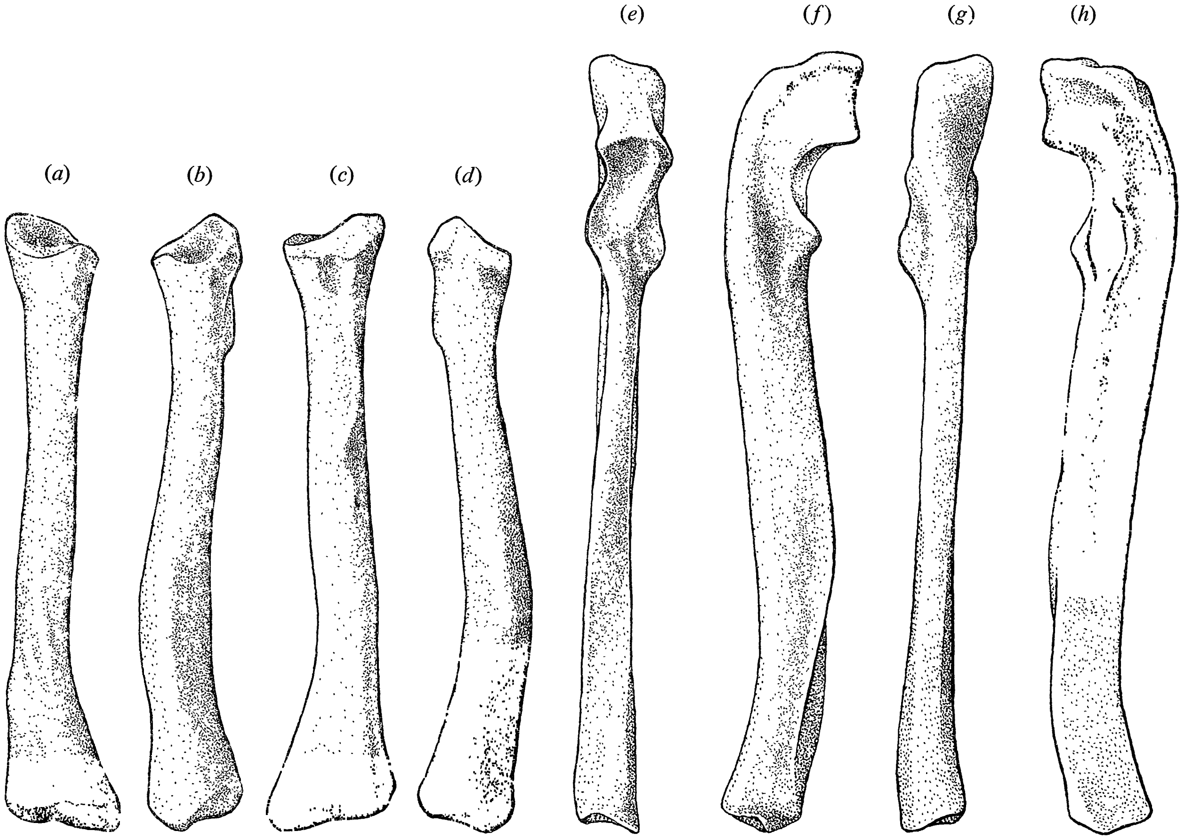


FIGURE 10. (*a–d*) A right radius of *Eozostrodon*, drawn from a nearly complete specimen of a small individual. Additional details have been taken from three fragments of larger individuals. (*a*) Anterior, (*b*) medial, (*c*) posterior and (*d*) lateral views. (*e–h*) A left ulna of *Eozostrodon*, a composite drawing based on seven specimens. (*e*) Anterior, (*f*) medial, (*g*) posterior, (*h*) lateral views. (Both bones are approximately × 8.)

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### DESCRIPTION OF PLATE 4

FIGURE 9. Stereophotographs of the pelvis and hindlimb of *Megazostrodon rudnerae* (B.M.N.H. M 26407). (*a*) Lateral view of left pelvis and hindlimb; the limb has been displaced from its normal position and lies above the vertebral column. (× 1.5.) (*b*) Enlargement of the pelvis and proximal femur. (× 3.5.) (*c*) Enlargement of the dorsum of the pes from medial aspect. (*d*) The same from lateral aspect. (× 4.7.)

### (*h*) *Ilium*

#### *Material*

The ilium is known in *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. In *Megazostrodon* and *Erythrotherium* the ilia are essentially complete although crushed. The anterior end of the ilium of *Eozostrodon* is missing in the more than four dozen specimens known, although in other features that can be compared it is similar to *Megazostrodon* and *Erythrotherium*. The ilium of *Eozostrodon* has been described and figured by Parrington (1971).

#### *Morphology*

The ilium of *Eozostrodon* is narrow and elongate, and during life was oriented anterodorsally as is the typical condition in mammals (figure 11*a*; figure 13*d*, plate 5). In cross section the anterior part is more or less blade-like. On the lateral aspect of the blade a low, longitudinal ridge separates a superior and larger concave area from a smaller one below. The dorsal and ventral margins of the blade are thin, slightly everted flanges, the dorsal flange being approximately twice the length of the ventral flange. A shallow and rugose depression, located just anterior to the acetabulum, is comparable to that in many living mammals and represents the attachment of the rectus femoris. The rugosity on the medial aspect of the iliac blade is evidence of a relatively extensive sacroiliac articulation (figure 11*b*). This articulation appears to have occupied the anterior extent of the blade beginning at a point where the dorsal and ventral marginal flanges are developed. How far the sacroiliac articulation extended anteriorly on the ilium is unknown, for the anterior tip of the blade is missing in all specimens. In *Megazostrodon*, however, the ilium appears to extend above the level of the sacral transverse processes (figure 9*a*, plate 4). Posterior to the sacroiliac articular surface, the ilium of *Eozostrodon* is constricted as seen in lateral view and has an oval cross section.

The right iliac blade of *Erythrotherium* is preserved nearly complete (figure 13*a*, plate 5). Thin, everted flanges arise along the dorsal and ventral margins as in *Eozostrodon*. The ventral flange arises between the middle and posterior thirds of the blade, somewhat more posteriorly than is apparently the case in *Eozostrodon*, and continues to the truncated anterior extremity of the blade. The dorsal flange begins closer to the acetabulum than in *Eozostrodon*; its anterior half has been broken away, but presumedly it continued to the anterior end also. The anterior third of the blade is markedly everted. The medial surface is convex and rugose as in *Eozostrodon*.

The iliac blade of *Megazostrodon* (figure 9*b*, plate 4) bears all the structural features that can be seen on the ilium of *Eozostrodon* from lateral aspect; because the anterior end of the blade is poorly preserved, the extent of the flanges, as well as the eversion of the tip, cannot be determined.

In *Eozostrodon*, the posterior part of the ilium bears a large, semicircular and slightly concave acetabular facet positioned perpendicularly to the long axis of the iliac blade. Dorsomedial to the facet is a protuberant process for articulation with the ischium (figure 11*a*). The ilio-ischial joint surface, along which separation has invariably occurred in available specimens, is narrow and vertical in orientation. In contrast, the process articulating with the pubis bears a large triangular area which faces posteroventrally and slightly medially (figure 11*b*). The structure of the acetabular part of the ilium in *Megazostrodon* and *Erythrotherium* appears to be similar, although the latter specimen is fragmented and somewhat distorted in this region.

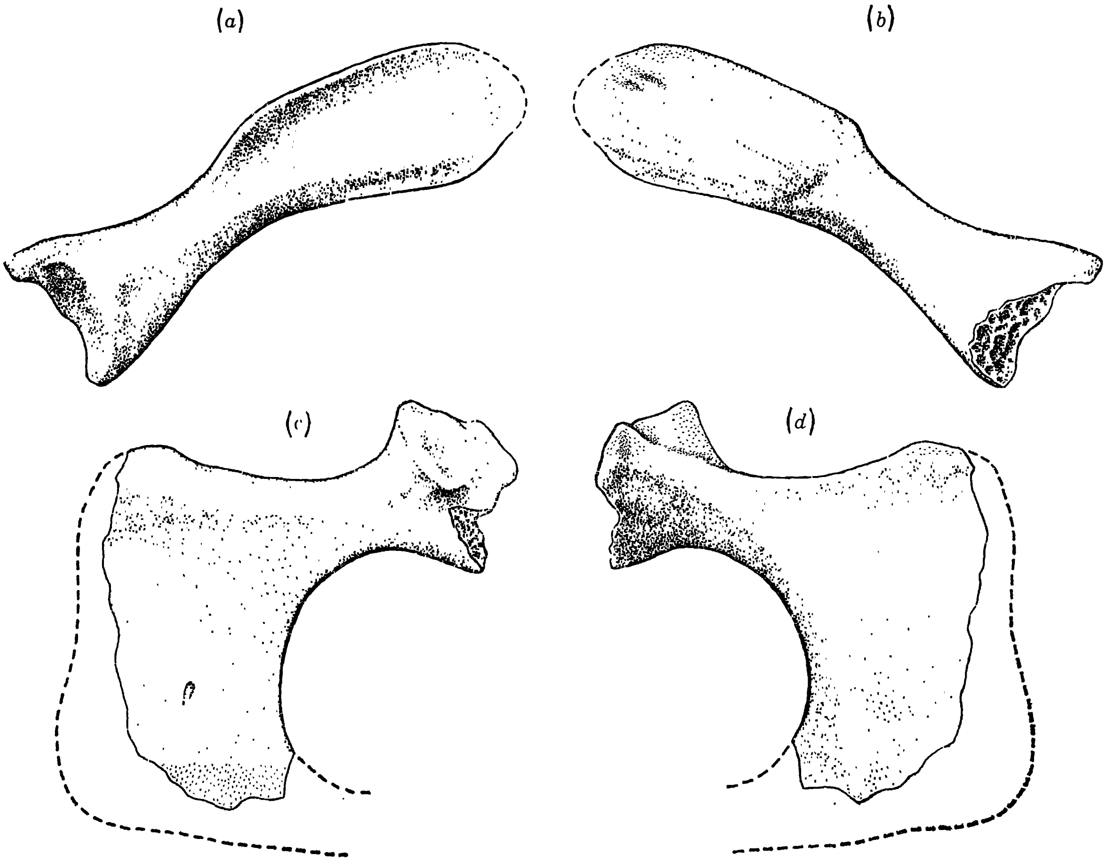

Figure 11. Dissociated pelvic bones of *Eozostrodon*. (*a*) Lateral view of a right ilium, based on several nearly complete specimens. (*b*) Medial view of same, showing rugosity on the blade representing the area of the sacroiliac articulation, and the exposed trabeculae where the ischium and pubis have broken away. (*c*) Lateral view of a right ischium of *Eozostrodon*, based on three specimens. The inferior margin of the obturator foramen has been broken away. (*d*) The same in medial view. (*a*, *b*, approximately × 8; *c*, *d*, approximately × 10.)

### (*i*) *Ischium*

#### *Material*

The ischium is known in *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. In *Megazostrodon* the bone is nearly complete, preserving most of posterior, blade-like part. In no case is the ischiopubic ramus preserved, and thus the ventral margin of the obturator foramen is unknown.

#### *Morphology*

In all three genera the ischial blade is essentially flat; *Eozostrodon* specimens show a very shallow concavity on the external surface (figure 11*c*), and a medial curvature of the ventral part of the blade that meets its counterpart along the ischiopubic symphysis. In *Megazostrodon* the dorsal margin is nearly completely preserved; it is concave in lateral view and terminates posteriorly in a rounded ischial tuberosity (figure 9*b*, plate 4). The posterior margin appears to be indented in the middle (figure 9*b*), but this is almost certainly the result of breakage and the margin in *Eozostrodon* is here interpreted as being more or less straight (cf. figure 11*c*). In both *Megazostrodon* and *Eozostrodon* the posterior part of the ischial blade appears to have a large surface area, comparable to that in monotremes and larger than that in primitive therians. The obturator margin formed by the ischium is almost perfectly hemicircular in *Megazostrodon* and *Eozostrodon*; in *Erythrotherium* (figure 13*a*) this region has been distorted through crushing.

In all three genera, the ischial 'neck' between the blade and the acetabulum is triangular in cross section. The dorsal margin of the 'neck' bears a longitudinal groove similar to that seen in cynodonts (Jenkins 1971*a*).

The acetabular part of the ischium in all three genera bears a shallow, piriform acetabular facet and two processes for articulation with the ilium and pubis, respectively. Between the acetabular facet and the pubic process is a deep incisure that represents the acetabular notch (figure, 9*b*, plate 4; figure 13*d*, plate 5); this feature is typically mammalian (although some mammals, including monotremes, lack a notch), and contrasts with the cynodont condition in which a similar notch occurs between the ischial and iliac parts of the acetabulum.

### (*j*) *Pubis*

#### *Material*

An essentially complete pubis is known in *Erythrotherium*, but because the specimen is immature certain bony features (e.g. articular surfaces) are not completely preserved. Only the acetabular facet of the pubis has been identified positively in *Megazostrodon*; the major part of both pubes have been broken away, and one displaced fragment has been tentatively identified as pubic. In *Eozostrodon*, the only known pubic fragment is an articular facet preserved with a partial acetabulum.

#### *Morphology*

The anterior half of the pubis in *Erythrotherium* is transversely broadened by two processes (figure 13*a*, plate 5). Laterally is a relatively large pubic tubercle which appears to have been directed laterad and somewhat ventrad. The posterior margin of the tubercle is continuous with the inferior margin of the pubis. Medially is a somewhat larger process bearing the acetabular facet as well as the joint surfaces contacting the ilium and ischium. These features, as preserved, are rather amorphous and do not present a clear picture of the acetabular structure. The posterior half of the pubis is a thin, more or less vertically oriented blade; it is broken, presumedly along the pubo-ischial joint. The posterior end of the pubic blade expands dorsoventrally, and appears to delineate part of the posterior margin of the obturator foramen; if the pubo-ischial joint has been correctly identified, then it is evident that the inferior margin of the obturator margin (the so-called ischiopubic ramus) was formed principally by the pubis.

The pubis of *Eozostrodon* bears a well-developed acetabular facet as well as extensive contacts with the ilium and ischium (figure 13*d*, plate 5). The anterior half of the bone is highly cancellous and the posterior half, if comparable to that in *Erythrotherium*, was probably a thin plate; the fragile nature of the bone may explain why pubes are poorly represented in the Pont Alun collection. Ventral to the acetabular facet is the beginning of a prominence which, although broken off, appears to represent a well developed pubic tubercle.

A fragment tentatively identified as belonging to the left pubis of *Megazostrodon* (figure 9*b*, plate 4) occurs below the acetabulum. Other than an articular surface comparable to that in *Eozostrodon*, the fragment reveals little useful information.

### (*k*) *Femur*

#### *Material*

Complete femora are known from the *Megazostrodon* and *Erythrotherium* specimens, although in both cases the proximal and distal ends are variably crushed or distorted. More than three dozen femoral fragments of *Eozostrodon*, including the two proximal ends figured by Parrington (1971), permit an accurate reconstruction.

*Morphology*

In all three genera the structure of the head and trochanters appears to be similar. The following description is based on *Eozostrodon* which is represented by the best preserved material. The hemispherical femoral head is reflected dorsally and somewhat medially relative to the shaft (cf. figure 9*b*, plate 4; figure 12; figure 13*b*, *e*, plate 5), a condition found also in cynodonts and in some primitive living mammals. The margin of the femoral head is hemicircular along the dorsal aspect (figure 12*a*), but ventrally it is irregular because of the prolongation of the articular surface onto a ridge between the head and greater trochanter (figure 12*c*). A shallow and, in some specimens, a rugose depression on the ventromedial aspect of the head is evidence of the attachment of a ligamentum capitis femoris (figures 12*b*, *c*; figure 13*e*, plate 5). On the

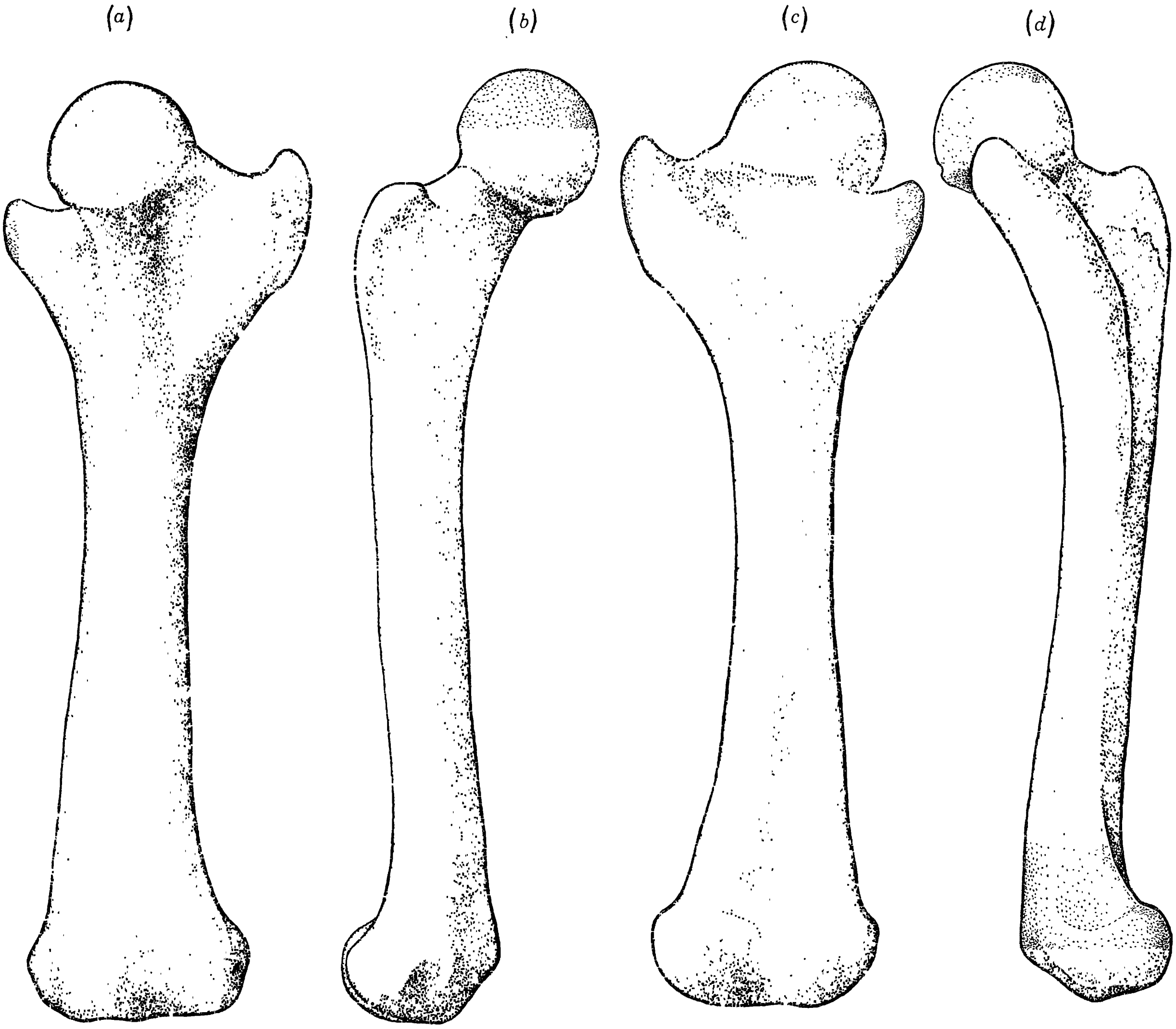

FIGURE 12. The left femur of *Eozostrodon* in (*a*) dorsal, (*b*) medial, (*c*) ventral, and (*d*) lateral views; this reconstruction is based on seven incomplete specimens. (Approximately × 8.)

dorsal aspect of the articular surface is a narrow sulcus that closely parallels the margin of the head for nearly half its circumference (figures 12*a*, *b*). On the best preserved specimens this feature can be seen to continue to the lateral and medial aspects of the head around the margin, either as a shallow sulcus or a slightly rugose line. Possibly the sulcus represents the site of attachment of the articular capsule; however, a capsular attachment on the articular part of the head, rather than the neck, would be unusual. The short neck is moderately constricted except where a distinct ridge joins the greater trochanter and head.

The prominent trochanters of *Eozostrodon* are triangular in outline (figures 12*a*, *c*) and arise in relatively ventral positions from the medial and lateral aspects of the shaft (figure 13*e*, plate 5). Both are reflected dorsally and terminate in blunt apices. The greater trochanter, almost twice the size of the lesser, has a large, rugose area for musculotendinous attachment principally on its lateral and ventral aspect. A comparable rugosity on the lesser trochanter is confined to the apex. On the ventral aspect of the shaft between the trochanters is an oval intertrochanteric fossa. In the *Megazostrodon* (figures 9*a*, *b*, plate 4) and *Erythrotherium* (figures 13*b*, *c*, plate 5) femora the structure of the proximal end is similar to that in *Eozostrodon*, although the preservation is not sufficiently complete to allow delicate details, such as the curvature and sulcus on the head, to be compared.

In all three genera, the middle of the femoral shaft is oval in cross section, being somewhat compressed dorsoventrally. (This feature is exaggerated in *Megazostrodon*, probably as a result of crushing.) There is no trace of a linea aspera. The shaft widens at the distal end, more abruptly along the lateral aspect than the medial.

In *Eozostrodon*, the patellar groove is asymmetrical and runs a complex course. On the dorsal aspect of the distal end, the patellar groove is situated lateral to the shaft mid-line (figure 12*a*). Its course around the distal end is oblique, terminating on the lateral condyle rather than at the intercondylar groove (figure 14*a*, plate 6). The lateral condyle is approximately twice the size of the medial condyle and has a broadly convex surface that slopes gradually into the popliteal fossa. The medial condyle, in contrast, bears a more sharply curved articular surface which does not extend quite as far toward the popliteal fossa. The articular surface for the head of the fibula is apparently represented by a distinct facet on the lateral epicondyle (figure 12*b*). As a whole the distal end and especially the condyles are rather flat, reminiscent of the exaggerated condition in monotremes. The epicondyles bear slight depressions and rugosities which may be interpreted as representing the attachment of collateral ligaments. The distal ends of the femora in *Erythrotherium* (figures 13*b*, *c*, plate 5) and *Megazostrodon* (figure 9*a*, plate 4) are poorly preserved, but appear to conform to the *Eozostrodon* pattern.

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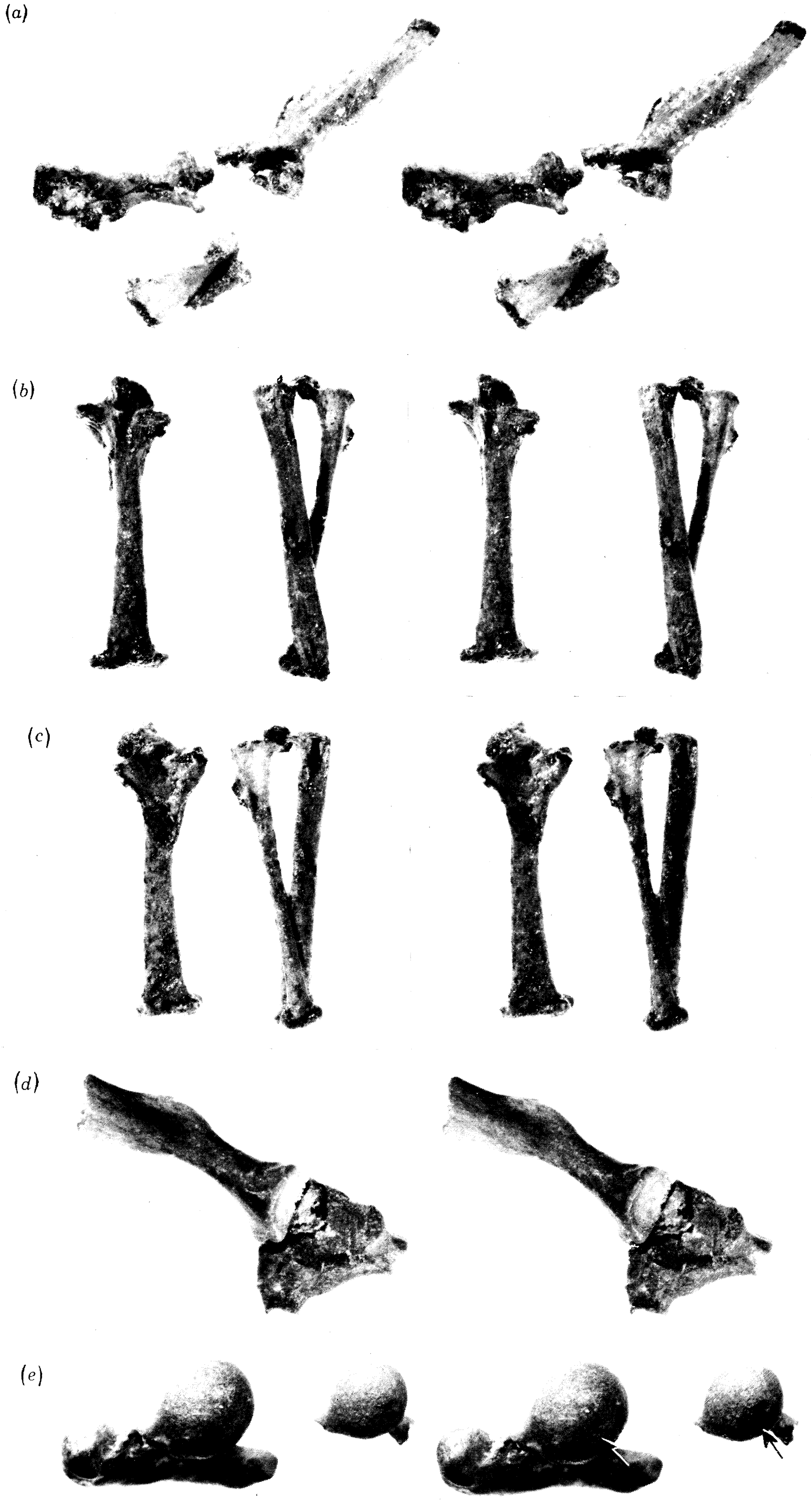
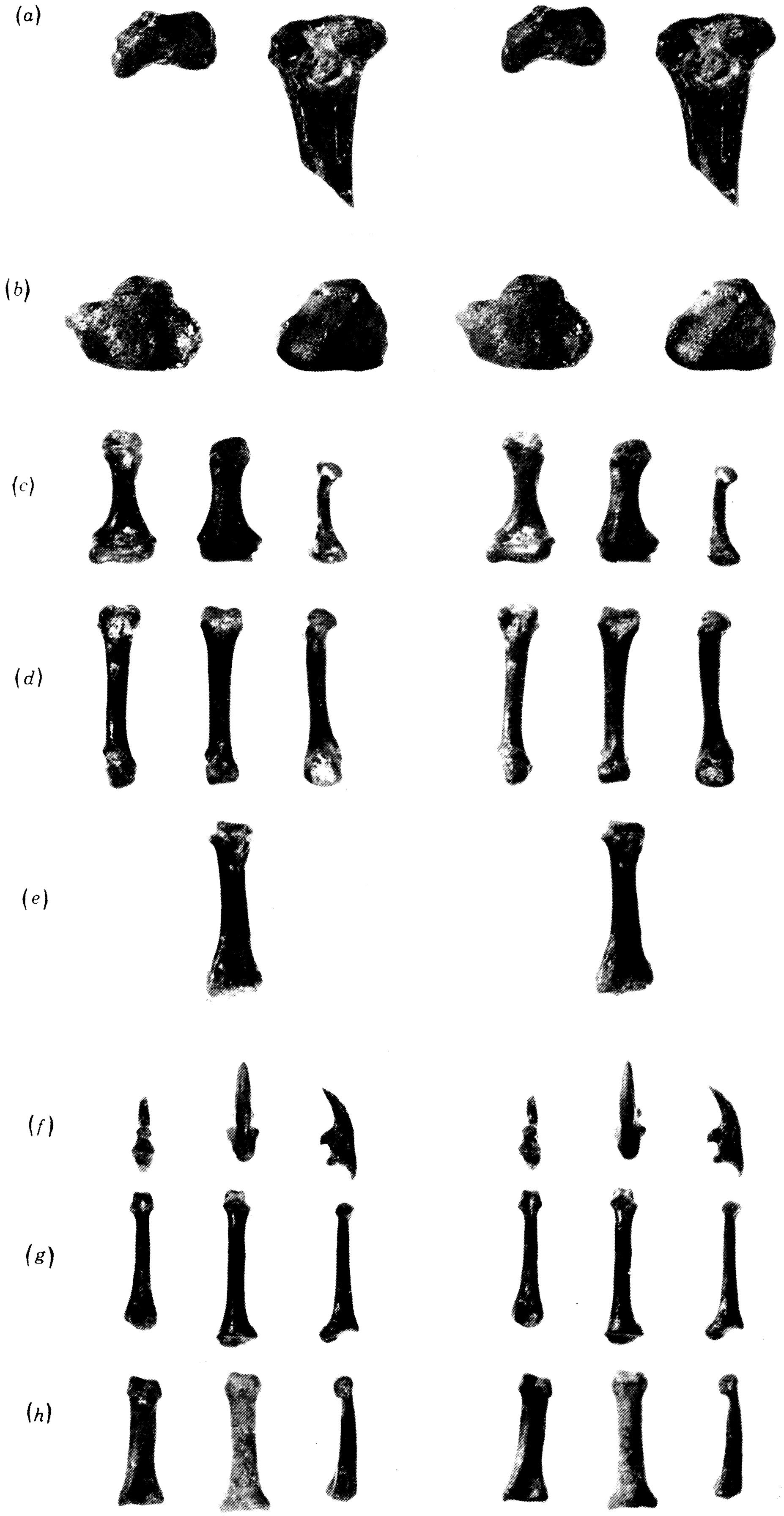
## Description of plate 5

Figure 13. Stereophotographs. (*a*) Lateral view of the disarticulated right pelvis of *Erythrotherium parringtoni* (S.A.M. K 359). The bones are placed in their approximate relationship only. Much of the acetabulum and posteroventral part of the ischium has been lost. (× 7.4.) (*b*) Right femur, tibia and fibula of *Erythrotherium*. The femur is shown in dorsal view. The tibia is shown in approximately medial view, but the proximal end of the fibula has been displaced postmortem and is not in a comparable position. (*c*) The same femur in ventral view and the tibia in lateral view. (× 5.1.) (*d*) Lateral view of a partial left acetabulum of *Eozostrodon*, preserving the pubic (left) and ischial (right) facets. A dissociated ilium has been added. (× 6.2.) (*e*) End on view of a nearly complete proximal femur (left) and a dissociated femoral head (right) to show the articular surface and the fovea (arrow). (× 7.)



FIGURES 13 (*a*–*e*). For description see opposite.



FIGURES 14 (*a–h*). For description see opposite.

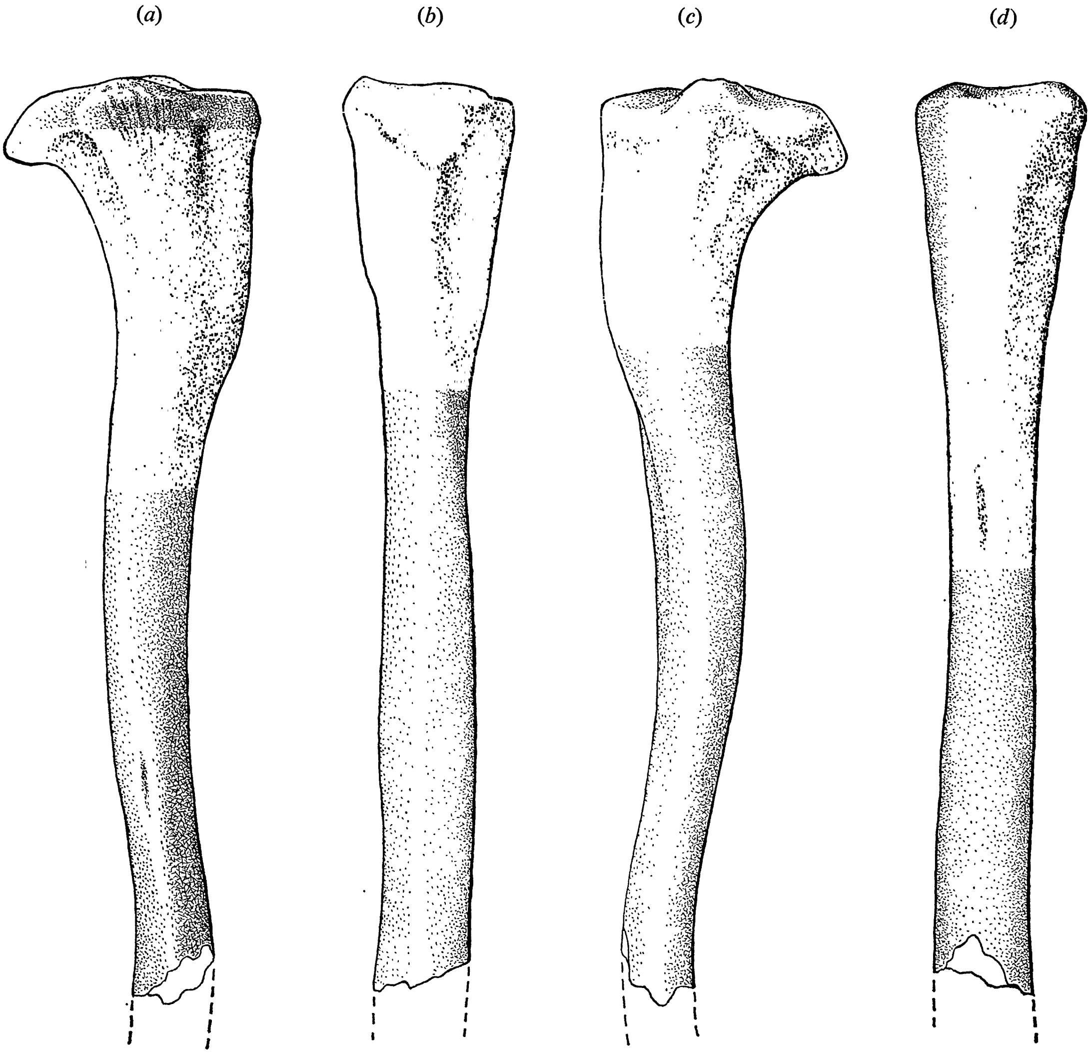


FIGURE 15. The right tibia of *Eozostrodon* in (*a*) anterior, (*b*) lateral, (*c*) posterior, and (*d*) medial views. Reconstruction based on five incomplete specimens. (Approximately × 8.)

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## DESCRIPTION OF PLATE 6

FIGURE 14. Stereophotographs. (*a*) The distal end of the left femur in *Eozostrodon* in distal (left) and ventral (right) views. (× 5.3.) (*b*) The proximal articular surface of the tibiae in *Eozostrodon*; anterior is toward the top of the page, and the left tibia is placed on the left. The right tibia is missing its lateral process for articulation with the fibula. (× 6.9.) (*c*) Representative first metatarsals (?metacarpals) of *Eozostrodon* in ventral (left), dorsal (middle) and side (right) views. (*d*) Representative middle (i.e. II, III, or IV) metatarsals (?metacarpals) of *Eozostrodon* in views comparable to that in (*c*). (*e*) A representative fifth metatarsal (?metacarpal) of *Eozostrodon* in dorsal view. (All × 6.6.) (*f–h*) Representative terminal, middle and proximal phalanges, respectively, of *Eozostrodon* in ventral (left), dorsal (middle) and side (right) views. (All × 6.6.)

### (*l*) *Tibia*

#### *Material*

Tibiae are known from *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. In *Erythrotherium* the right tibia is preserved complete, although the distal and proximal ends have been crushed. The proximal half of the single tibia known from *Megazostrodon* is missing, and the distal end is crushed. More than two dozen tibial fragments in the Pont Alun collection have been identified as belonging to *Eozostrodon*, but in no available specimen is the distal end preserved.

#### *Morphology*

The proximal articular surface is best preserved in *Eozostrodon*. The well-delineated articular facets for the femoral condyles are separated by an articular eminence (figure 14*b*, plate 6). The medial facet is relatively narrow and runs an oblique course across the tibial plateau from the posteromedial margin, where the articular surface is concave, to the anterior margin adjacent to the tibial tuberosity; here the surface is slightly convex. The lateral facet is more or less circular; the surface contour is somewhat saddle-shaped, being convex anteroposteriorly and concave mediolaterally. A large, laterally projecting process for the fibula gives the proximal end of the tibia a highly asymmetrical outline.

Viewed anteriorly, the proximal end of the tibia of *Eozostrodon* is bowed medially (figure 15*a*). In part this appearance results from a large excavation on the medial side of the shaft (possibly for extensor muscle origin) and the protuberant process for the fibula. The tibial tuberosity for the insertion of the patellar ligament is moderately developed, and is continued distally as a cnemial crest. Along the medial aspect of the middle of the shaft is a narrow, longitudinal groove (figure 15*d*). At this point the shaft is narrowest and is approximately circular in cross section; distally the shaft slightly enlarges and becomes oval in cross section, the largest diameter being oriented anteroposteriorly.

The distal articular surface of the *Eozostrodon* tibia has not been positively identified in the Pont Alun collection. The tibiae of *Megazostrodon* (figures 9*a*, *b*, plate 4) and *Erythrotherium* (figures 13*b*, *c*, plate 5), although imperfectly preserved, show the distal part of the shaft to be compressed mediolaterally. Several long bone fragments in the *Eozostrodon* collection possibly represent distal tibiae; the articular surface is elongate (presumedly anterposteriorly), convex, and bears no malleolus.

### (*m*) *Fibula*

#### *Material*

The proximal half of the fibula of *Eozostrodon* is known from about a dozen fragments, but the identification of the distal end remains problematical. From *Megazostrodon* and *Erythrotherium* almost complete fibulae have been recovered, although they are somewhat damaged.

#### *Morphology*

The proximal third of the fibula in all three genera is flattened mediolaterally (figure 9*a*, plate 4; figures 13*b*, *c*, plate 5; figure 16), with thin, flange-like anterior and posterior margins. The lateral surface bears a concavity which is deepened by the lateral reflection of the posterior margin (figures 16*b*, *c*). In *Eozostrodon* the proximal articular surface has a complex configuration. Anteriorly is a round, bulbous facet for articulation with the femur (figure 16*a*);

its shape is evidence of fibular mobility. Posteriorly, this facet is continuous with a protuberant, complexly contoured surface, apparently for musculotendinous attachment. The flattening of the proximal end and the differentiation of musculotendinous and articular processes are similar to the specialized condition in monotremes; such features are not present in cynodonts.

The fibular shaft is slender and round. The fibulae of *Erythrotherium* (figures 13*b*, *c*, plate 5) and *Megazostrodon* show a slight enlargement in shaft diameter toward the distal end which in the former bears a circular and slightly convex surface. Fragments tentatively identified as distal fibulae of *Eozostrodon* show two facets separated by a low ridge.

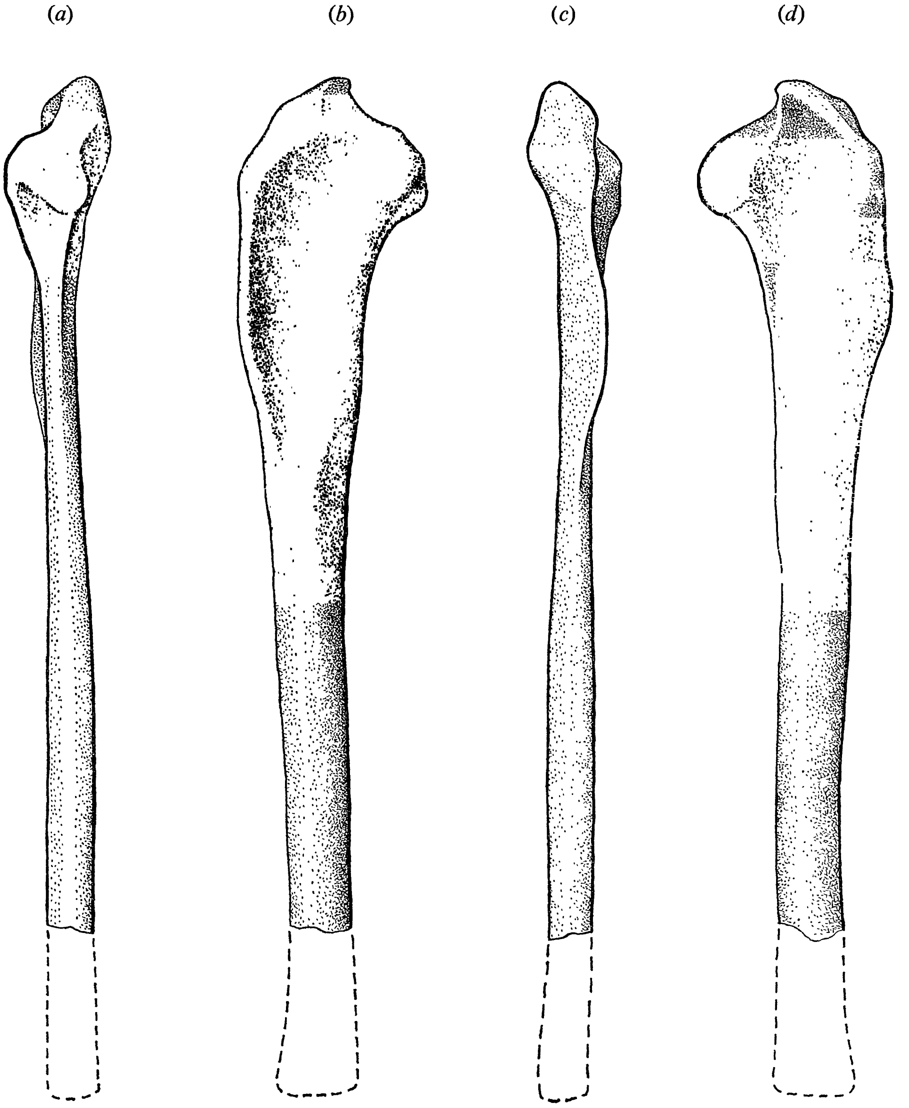

FIGURE 16. The right fibula of *Eozostrodon* in (*a*) anterior (*b*) lateral, (*c*) posterior and (*d*) medial views. Reconstruction based on four incomplete specimens. (Approximately × 9.)

### (*n*) *Pes*

*Material*

A nearly complete left pes is known from *Megazostrodon*, although some of the tarsals (calcaneus and astragalus in particular) are in damaged condition. The incomplete and partly disarticulated pes of *Erythrotherium* is too poorly preserved to be useful for comparison. In the Pont Alun collection are numerous *Eozostrodon* foot bones, of which the calcanea and astragali can be positively identified. The navicular is tentatively identified on the basis of similarity to the navicular in *Megazostrodon*. At least six other kinds of ossicles have been recovered, but their identity as tarsals or carpals is uncertain. Metapodials and phalanges are also present, and many of these are essentially identical to those in the *Megazostrodon* pes. However, some metapodials and phalanges may represent manual elements. Lacking evidence to the contrary, it is likely that the bony anatomy of the pedal and manual digits in *Eozostrodon* was quite similar.

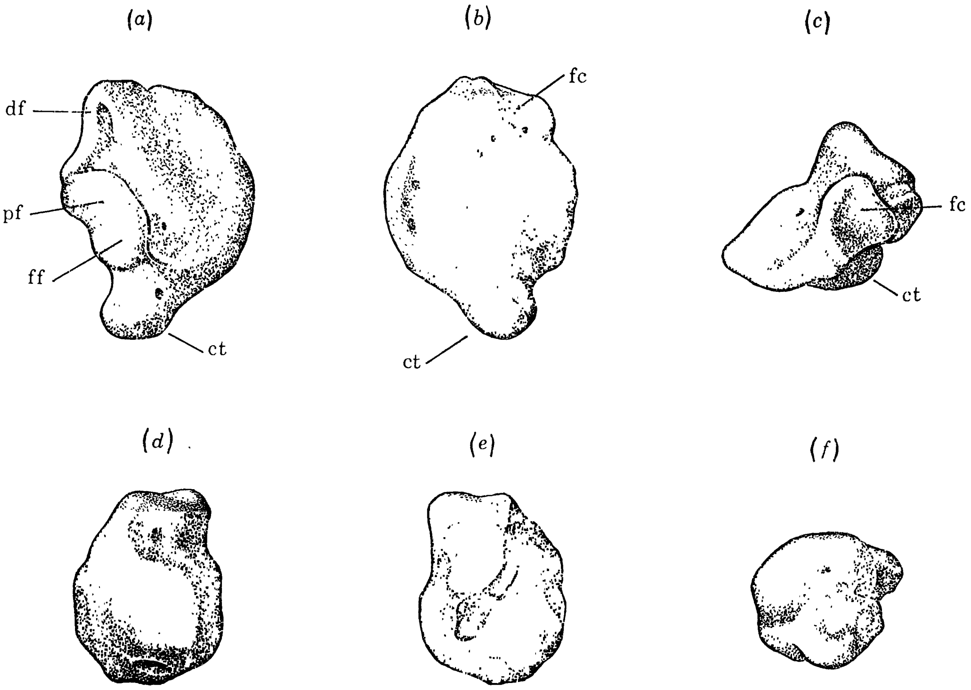

Figure 17. The calcaneus and astragalus of *Eozostrodon*. (*a*) Dorsal, (*b*) plantar, and (*c*) distal views of the right calcaneus, showing, ct, calcaneal tuberosity; df, distal (sustentacular) facet for the astragalus; fc, facet for the cuboid; ff, fibular facet; and pf, proximal facet for the astragalus. (*d*) Dorsal, (*e*) plantar, and (*f*) distal views of the left astragalus. (*a–c*, Approximately × 9; *d–f*, approximately × 8.)

*Morphology*

The pes of *Megazostrodon* is relatively long. The estimated length, measured along the third digit, is *ca.* 15.5 mm, which compares with a crural length of 18 mm and a femoral length of 19 mm. The proportions of the foot in *Erythrotherium* appear to have been similar.

The calcaneus of *Eozostrodon* is broad and relatively thin (figures 17*a–c*). The small calcaneal tuberosity is reflected medially and toward the plantar aspect; this feature, together with the slight proximodistal curvature of the remainder of the calcaneus, gives the bone a distinctly bowed appearance. A large part of the calcaneus is a broad, lateral flange with thickened proximal and distal margins. In life, this flange was probably not exactly horizontal, but was inclined somewhat toward the plantar aspect of the foot (as illustrated in figure 17*c*). On the medial margin of the calcaneus is a dorsally directed tubercle that bears two indistinctly separated articular facets (figure 17*a*). On the apex and posterior aspect of the tubercle articulated the fibula, and on the anteromedial aspect articulated the proximal of the two plantar facets of the astragalus. The sustentaculum tali is extremely narrow, considerably less developed than that in cynodonts. The sustentacular facet, for the distal of the two plantar facets on the astragalus, faces dorsomedially. On the distal end of the calcaneus is a well-defined facet for the cuboid (figure 17*b*, *c*). The calcaneus of *Megazostrodon* has proportions similar to that in *Eozostrodon*; no additional structural details are evident in this specimen.

The astragalus of *Eozostrodon*, approximately hemispherical in shape, bears a bulbous dorsal surface. On the dorsal surface is an oval tibial facet (figure 17*d*), the long axis of which is oriented at approximately 30° to the proximodistal axis of the bone (from distomedial to proximolateral aspects). The facet as a whole is convex; a ridge along the long axis represents a narrow zone where the curvature is sharpest. On the truncated end of the short but distinct astragalar head is a circular, shallowly concave facet for the navicular (figure 17*f*). On the plantar aspect are two facets for articulation with the calcaneus (figure 17*e*). Between these runs a deep sulcus that passes to the dorsal surface around the medial side; posteriorly the sulcus is continuous with a canal that opens by a large foramen onto the posterior (distal) surface. Preservation of the astragalus in *Megazostrodon* is sufficient to confirm only some of the gross details known in *Eozostrodon*.

The navicular of *Megazostrodon* is preserved in articulation with the astragalar head (figure 9*c*, plate 4). Roughly cuboidal in shape, the bone bears a concave facet for the astragalus and articulates distally with at least two cuneiforms. The dorsal surface is somewhat saddle-shaped, being convex transversely and concave proximodistally. The same features are present in the navicular of *Eozostrodon*; the facets for the cuneiforms are oriented distoventrally.

The tarsus of *Megazostrodon* as preserved is partially disarticulated and therefore some identifications of the remaining elements are tentative. The most lateral ossicle, here identified as the cuboid, is L-shaped and articulates principally with metatarsal IV (figure 9*d*, plate 4). Medial to the cuboid and proximal to metatarsal III is a space, presumedly once occupied by an ectocuneiform. The cuboidal mesocuneiform is the smallest of the ossicles; apparently displaced as preserved, the mesocuneiform probably articulated principally with metatarsal II. The entocuneiform is a large, rectangular ossicle which articulates distally with metatarsal I and medially with metatarsal II. Proximally, the meso- and entocuneiforms articulated with the navicular; the missing ectocuneiform probably did also. Proximal to the entocuneiform occurs a small, pea-shaped ossicle which is very likely a sesamoid.

Metatarsals and pedal phalanges are well preserved in the left pes of *Megazostrodon* (figures 9*c*, *d*, plate 4) and may be compared with similar elements recovered among the *Eozostrodon* materials. Metatarsal I in *Megazostrodon*, which is the shortest (see table 1), has a broad proximal end with an articular surface that is convex in a dorsoplantar direction; the joint with the entocuneiform is therefore ginglymoid. The proximal half of the bone is asymmetrical, viewed dorsally, with a protuberance on the proximomedial corner and a semilunar groove (possibly for an extensor tendon attachment) on the dorsal surface of the shaft. The distal end has been crushed. Comparable bones in the *Eozostrodon* collection are slightly more robust, being shorter in overall length and wider at the proximal end (figure 14*c*, plate 6).

As in *Megazostrodon*, the proximal articular surface extends onto the dorsal aspect of the bone; the asymmetry of the proximal end and the semilunar groove on the dorsal surface of the shaft also occur. The distal articular surface is convex, permitting substantial flexion and extension. However, the convexity is greater on the medial than on the lateral side, so that the flexion–extension axis is not perpendicular to the shaft. The proximal phalanx of the hallux apparently diverged medially and may have been slightly medially rotated also.

Metatarsals II, III and IV of *Megazostrodon* are of approximately the same size and characteristic shapes (table 1, figures 9*c*, *d*, plate 4). They are compressed mediolaterally at the proximal end where intermetatarsal articulations are developed (except on the medial side of II which contacts the entocuneiform). The distal ends are somewhat crushed, but reveal a moderate degree of mediolateral expansion for the metatarsophalangeal articulation. On this evidence, the comparable metatarsals from the *Eozostrodon* collection may be identified although their assignment to positions II, III or IV remains uncertain.

TABLE 1. MEGAZOSTRODON PEDAL MEASUREMENTS/mm

| | digit | | | | |
|---|---|---|---|---|---|
| | I | II | III | IV | V |
| metatarsal length | 3.3 | 5.2 | 6.0 | 5.9 | 5.3 |
| mid-shaft width | 0.5 | 0.6 | 0.5 | 0.5 | 0.6 |
| proximal phalanx length | 2.4 | 3.5 | 3.4 | 3.4 | missing |
| mid-shaft width | 0.3 | 0.5 | 0.5 | 0.5 | missing |
| middle phalanx length | — | broken | 2.6 | 2.2 | broken |
| mid-shaft width | — | *ca.* 0.4 | 0.3 | 0.3 | 0.3 |
| distal phalanx length | 1.6 | missing | 1.7 | 1.6 | 1.5 |
| mid-shaft width | 0.25 | missing | 0.25 | 0.25 | 0.25 |

In *Eozostrodon* the proximal articular facet of a middle metatarsal is essentially flat from medial to lateral aspect; in the best preserved specimens the surface is actually very slightly concave from side to side (figure 14*d*, plate 6). In dorsoplantar dimension the articular surface is convex and extends from the dorsum of the proximal end, which is relatively broad, to the ventral surface which is relatively narrow. The relative difference in width between the dorsal and plantar surfaces is evidence of a transverse tarsal arch, known also from cynodonts (Jenkins 1971*a*) and common among pentadactyl mammals. Intermetatarsal articulations are well developed proximally. In a typical metatarsal (e.g. III or IV) the medial surface of the proximal end bears a flat facet, more or less in the same plane as the medial surface of the shaft, as well as a shallow concavity. The comparable surface on the lateral side is usually somewhat irregular and protrudes beyond the plane of the lateral surface of the shaft. Slight variations in this pattern apparently represent features peculiar to metatarsals in specific positions II, III or IV; however, the precise identification of these metatarsals cannot be made on the basis of the presently available material.

Metatarsal V in *Megazostrodon* (figure 9*d*, plate 4) is slightly shorter than III and IV and further differs in the breadth of its proximal end. On the medial side of the proximal end is a raised intermetatarsal facet for contact with IV; on the lateral side is a protuberance, a feature probably homologous with the similarly placed tuberosity of living mammals where the part of the peroneal musculature inserts. The distal end is poorly preserved. A single metatarsal from among the *Eozostrodon* materials displays comparable features at the proximal end, and is interpreted to be a fifth metatarsal (figure 14*e*, plate 6). The distal end is slightly asymmetrical, as in the case of metatarsal I, with a flexion–extension axis which provides for slight medial deviation of the proximal phalanx upon flexion, and lateral deviation upon extension.

Proximal phalanges in the *Megazostrodon* foot are preserved on all but the fifth digit (figures 9*c*, *d*, plate 4). The proximal ends are moderately expanded and bear concave articular facets; the distal ends are also expanded (except for I, which is of reduced size to accommodate the terminal phalanx) and bear trochlear articular surfaces. Along the ventromedial and ventrolateral margins of the distal third of each shaft (except I) is a thin, low flange for the attachment of the digital fibrous sheaths for the flexor tendons. Comparable elements among the *Eozostrodon* materials reveal some additional features (figure 14*h*, plate 6), and do not appear to differ from those of *Megazostrodon*. The proximal facet is shallow and hemicircular in outline; the plantar margin is nearly straight. On the distal end, the trochlea is very slightly asymmetrical. The functional interpretation of this asymmetry is dependent upon a correct identification of left and right elements; comparison with the imperfectly preserved *Megazostrodon* phalanges does not allow a certain identification, but it appears that flexion was accompanied with a small degree of medial deviation. The fossae on either side of the trochlea are positioned eccentrically toward the dorsal side, so that the collateral ligaments at the proximal interphalangeal joint tightened upon flexion. Flanges for attachment of the digital fibrous sheaths are well developed.

Complete middle phalanges are preserved only on digits III and IV of *Megazostrodon*. Details of the proximal end cannot be determined satisfactorily, although it is evident that the proximal end is mediolaterally expanded and is the widest part of the bone. The slender shaft tapers slightly toward the distal end which bears a well-developed trochlea. Comparable elements among the *Eozostrodon* materials (figure 14*g*, plate 6) reveal that the proximal end is somewhat asymmetrical; in dorsoventral view, the medial surface is more protuberant than the lateral. The articular surface is a simple concavity. Between well-developed tuberosities on the flexor aspect of the proximal end is a large groove in which runs the continuation of the flexor tendon to the distal phalanx. The articular surface of the trochlea on the distal end extends farther proximally on the flexor aspect than on the extensor aspect, and is evidence that the terminal phalanges could be extensively flexed. The pits on either side of the trochlea, which marked the attachment of the collateral ligaments, are eccentrically located toward the dorsal aspect; thus, as in the case of the proximal interphalangeal joint, the ligaments tightened during flexion and enhanced the stability of the joint.

Two kinds of terminal (ungual) phalanges occur in the Pont Alun collection. One form (figure 14*f*, plate 6) is identical to the terminal phalanges in the *Megazostrodon* foot and therefore may be referred confidently to the pes of *Eozostrodon*. The articular surface bears a median keel that fits into the opposing trochlea. On the plantar surface is a prominent flexor tubercle and, between the tubercle and the articular surface, a large nutrient foramen. The distal, claw-bearing part of the phalanx is a slender, tapering cone; slightly recurved, it has a deep sulcus on both sides that extends to the tip.

The second type of terminal phalanx found among the *Eozostrodon* materials differs in all respects from the above. Without either a median keel on the articular surface or a prominent flexor tubercle, this phalanx has a claw-bearing process that is mediolaterally compressed and bears shallow sulci. Although there exists no positive evidence of the structure of manual unguals in Triassic mammals, it is here assumed that the manual unguals were similar to those of the pes and this second type of phalanx pertains to the associated lizard.

## 4. Evaluation of the postcranial adaptations of Triassic mammals

### (a) *Axial skeleton*

In the atlanto-occipital and atlanto-axial joints Triassic mammals had achieved nearly all the major adaptations for movement and stability characteristic of later mammals. The double occipital condyles, situated at the ventrolateral margins of the foramen magnum, are a mechanism principally for flexion and extension; because the axis of the movement passes through the spinal medulla, deformation of that structure is less than would be the case were the condyle or condyles situated ventral to the foramen magnum (Jenkins 1971*a*). The fact that the atlas arches and intercentrum of Triassic mammals are not synostosed to form an atlas ring is probably of little significance. These elements were undoubtedly conjoined by ligaments to form functionally the same unit. The dens (or odontoid process) is of typical mammalian proportions. Together with the apical, alar and transverse atlantal ligaments, the dens in recent mammals serves to stabilize the atlanto-axial joint which has become specialized for rotation through loss of the atlanto-axial zygapophyses (Jenkins 1969). In Triassic mammals the stout dens, the apparent absence of atlanto-axial zygapophyses, and the enlarged atlanto-axial intervertebral foramen are all evidence that rotatory movements of the head were as developed as in recent mammals. The body of the axis is flattened dorsoventrally, a shape characteristic of later mammals which is of uncertain functional significance.

In relatively generalized mammals, post-axial cervical vertebrae are characterized by: narrow, thin laminae; short spinous processes; enlarged vertebral foramina; zygapophyses set widely apart; and short, commonly robust transverse processes with dorsal and ventral apophyses; transverse foramina; and parallelepiped, dorsoventrally flat bodies. The cervical series of *Megazostrodon* demonstrates that most of these features, with the exception of transverse foramina, were present or incipiently developed by Triassic times. Reduction of the laminae and spinous processes among recent mammals appears to be related in part to the typically ascending (rather than horizontal) posture of the neck. Elongate spinous processes and anteroposteriorly broad laminae would interfere structurally with the characteristic cervicothoracic flexure of the axial skeleton, and especially with extension of the neck. The presence of similar features in a Triassic mammal is evidence that a cervicothoracic flexure and an ascending posture of the neck had already been developed (figure 18).

The apparent enlargement of the cervical vertebral foramina in *Megazostrodon* warrants special attention. The cervical vertebral foramina among living mammals are substantially enlarged at levels corresponding to the cervical enlargement of the spinal cord (at the origin of the brachial plexus). The spinal cord does not completely fill the vertebral canal at any level, of course, and therefore canal size cannot be construed as a direct measurement of cord diameter. None the less, canal size usually varies roughly with the bulk of its contents. Furthermore, the spaciousness of the mid-cervical vertebral canal is probably also an adaptation to avoid impinging on the spinal cord over a wide range of neck movements. Reptiles also possess a cervical enlargement of the spinal cord, but generally do not have a marked enlargement of the vertebral canal at corresponding levels. The difference may be due to the fact that the reptilian spinal cord occupies the entire length of the vertebral canal, whereas in mammals the spinal cord is relatively shorter because it reaches its definitive size before the vertebral column stops growing (Kappers, Huber & Crosby 1936). The cervical (as well as lumbar) enlargement in mammals is thus represented within a proportionally shorter distance in the canal. This fact, together with an increase in neurons mediating sensory input and motor control, may account for the disparity of cervical canal size characteristic of mammals. In *Megazostrodon* the apparent enlargement of the cervical canal may be interpreted as evidence that the spinal cord had developed to mammalian proportions; the enlargement probably developed concomitantly with an increase in neuromuscular control of the forelimbs and with greater freedom of neck movement. The wide spacing of the zygapophyses may have developed as a result of the enlargement of the vertebral canal, although an increase in the bulk of transversospinalis musculature (medial to the zygapophyses) was possibly also a factor. The relative flattening of the vertebral bodies among modern mammals and in *Megazostrodon* is not readily interpreted in functional terms except as it may relate to cervical canal enlargement; if such is the case, the dimensional change is a relative broadening rather than a dorsoventral flattening.

The lack of transverse foramina in *Megazostrodon* is probably of minor significance and reveals nothing about the disposition of the vertebral arteries. Transverse foramina are created where costal rudiments synostose to vertebrae, leaving a gap between the capitular and tubercular articulations. Although in most cases the vertebral artery and accompanying veins are thus enclosed, among recent mammals transverse foramina are commonly absent on C 7, or the vertebral arteries may fail to pass through one or more of these foramina.

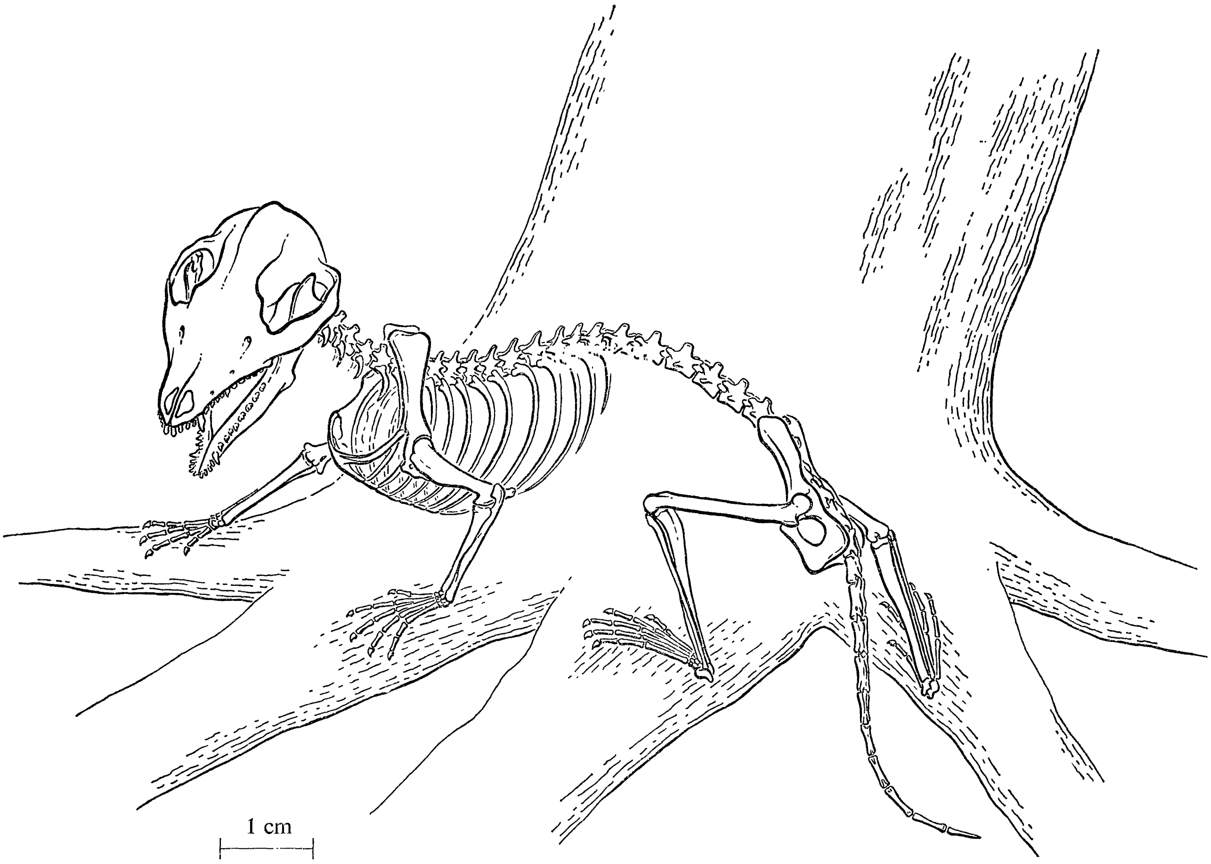

Figure 18. Skeletal reconstruction of a Triassic triconodont based principally on the proportions of *Megazostrodon rudnerae* (B.M.N.H. M 26407). The accuracy of this restoration is limited to those skeletal parts that are well known from the *Megazostrodon* and *Eozostrodon* materials. The exact number of vertebrae remains unknown. Details of the braincase structure, the manus, and the position of the shoulder girdle are uncertain.

In *Eozostrodon* the transition from thoracic to lumbar vertebral structure appears to occur relatively abruptly (over three vertebrae) and involves a reorientation of the spinous processes and zygapophyseal facets as well as an increase in the transverse distances between zygapophyses (see § 2*b*, figure 18). Similar features occur among modern mammals. Commonly, an anticlinal vertebra may be recognized as having a spinous process with an orientation intermediate between the caudally inclined pre-anticlinal processes and the cranially inclined post-anticlinal processes. Similarly, the diaphragmatic vertebra possesses an intermediate orientation of the zygapophyses. From a comparative anatomical analysis, Slijper (1946) concluded that these features were specializations for axial mobility. Mammals that employ extensive flexion and extension of the trunk during locomotion localize the movement in the diaphragmatic region where maximum mobility is permitted by the zygapophyseal orientation. Furthermore, the anticlinal arrangement of vertebrae reflects the specialization of epaxial musculature around this region to effect such movement. The fact that *Eozostrodon* possesses at least the basic structures of both anticlinal and diaphragmatic types of vertebrae is evidence that truncal flexion was already part of the locomotor behaviour among early mammals. Thoracolumbar differentiation was not present in advanced cynodonts (Jenkins 1971*a*) although *Oligokyphus*, as reconstructed by Kühne (1956), apparently possessed some incipient development of such an adaptation.

### (*b*) *Shoulder girdle*

The shoulder girdle of Triassic triconodonts retains the basic pattern established among advanced cynodonts. The shape of the scapular blade, the infraspinous (supracoracoideus) fossa, and the posteriorly projecting coracoid process are similar to the cynodont condition (figures 19*a*, *b*). Certain modifications of the pattern are evident, however. The procoracoid is smaller and is completely excluded from the glenoid. Reduction of the anterior margin of the procoracoid and adjacent scapula creates a substantial gap beneath the clavicle and protuberant acromion for a muscle to pass to the humerus from the anterior (or anteromedial) aspect of the scapula; a similar condition exists in monotremes. The glenoid fossa is narrower and more symmetrical than in cynodonts.

Comparison of the reconstructed shoulder girdles of a cynodont and *Eozostrodon* with that of an echidna reveals the degree to which monotremes have modified a pattern inherited from the reptile–mammal transition (figure 19*c*). The basic structural plan of the girdle, including lateral extension of the clavicular processes of the interclavicle, was established among Triassic triconodonts. Major specializations of monotremes are the lateral orientation of the glenoid (originally directed posterolaterad and somewhat ventrad), the shallowness of the infraspinous fossa, the caudal extension of the vertebral border and, apparently, the establishment of an articulation between the coracoids and interclavicle. Many of the structural peculiarities undoubtedly evolved in conjunction with digging habits. The lateral orientation of the glenoid is related to the abducted posture of the humerus, a fossorial specialization, and changes in scapular shape may be likewise related. It is also likely that the articulation between both coracoids and the interclavicle is a fossorial specialization that provides additional stability to the girdle.

The multituberculate scapula, as described by McKenna (1961), appears to be similar to that in Triassic triconodonts, possessing a laterally projecting, anteriorly positioned spine, a relatively deep infraspinous fossa, and no appreciable development of a supraspinous fossa. Although the scapulocoracoid joint was not observed in available material, McKenna concluded that the coracoid contributed to the glenoid fossa and that the dorsal part, at least, was an anteroventromedial projection. This projection is broken at its distal (ventral) extremity, but appears sufficiently robust to have supported a substantial ventral component. Thus, the coracoid also may have been structurally similar to that in Triassic triconodonts. In this regard, it is interesting that the interclavicle from the late Cretaceous Lance Creek Formation tentatively referred to as multituberculate by McKenna is very similar to that described for *Eozostrodon*.

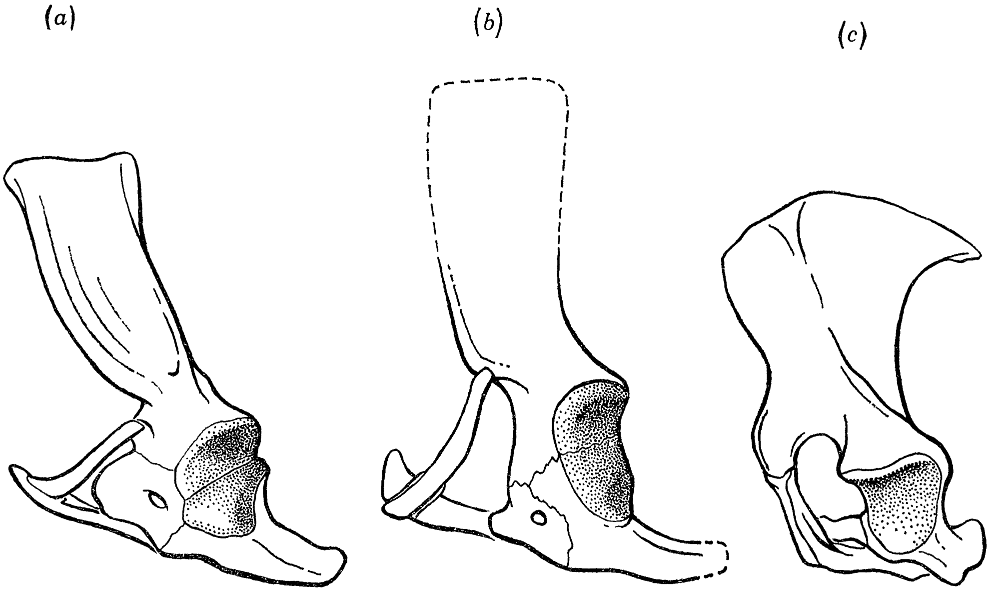

FIGURE 19. The reconstructed pectoral girdles of (*a*) a cynodont (in part after Jenkins 1971 *a*) and (*b*) *Eozostrodon* compared with that of an echidna (*c*). (Not to scale.)

The position and orientation of the scapulocoracoid in Triassic triconodonts has important functional as well as phylogenetic implications, although neither can be precisely determined from available materials. A central question concerns how closely the coracoids adjoined the midline, and thus approximated the coracoid–procoracoid–interclavicle buttressing typical of monotremes. On the present tenuous evidence from the general proportions of the clavicle, interclavicle and scapulocoracoid assigned to *Eozostrodon*, a reconstruction of the coracoids not impinging upon the interclavicle appears most likely (figure 18). Even if there were no direct articulations involved, the coracoids and interclavicle may have been joined by ligaments or other connective tissue. The scapulocoracoid may have occupied a relatively high position on the thorax (as depicted in figure 18, for example), but at this time a monotreme-like position anterior to the first rib cannot be excluded. The orientation of the scapulocoracoid may have directed the glenoid posterolaterad and (by virture of the curved scapular half of the glenoid) slightly ventrad (as depicted in figure 19*b*); conversely, the scapulocoracoid may be envisioned as rotated on the acromioclavicular articulation so as to direct the glenoid more ventrad. Associated material is required to solve these problems.

On present evidence, only a limited functional analysis can be made for the shoulder girdle. The extensive articulation between the clavicles and interclavicle limits girdle movement and promotes stability. This stability is augmented among living monotremes by the addition of coraco-interclavicular articulations, thus creating a yoke which is intrinsically braced against forces from powerful, digging forelimbs. There is no evidence that Triassic triconodonts were fossorial or possessed coraco-interclavicular articulations, so that other implications of their shoulder structure must be considered. In therians, the mobile clavicle serves both as a strut (maintaining the lateral position of the shoulder against medially directed forces) and as a spoke (guiding the shoulder in an arcuate pathway during locomotor movements) (Jenkins 1974*b*). The tongue and groove articulation between clavicles and interclavicle in *Eozostrodon* essentially prohibits anteroposterior or dorsoventral sliding of the scapulocoracoid, eliminating any spoke effect. Some rotation of the scapulocoracoid at the acromioclavicular joint is still theoretically possible. However, the strut effect is certainly present and is, if anything, augmented by the lateral expansion of the interclavicle and the tongue and groove articulation between clavicle and interclavicle. The significance of this arrangement (not present in cynodonts, but further developed in monotremes) may be that in non-therians an osseoligamentous stabilization of the pectoral girdle developed concomitantly with an increase in forelimb mobility. Therians, in contrast, evolved a shoulder mechanism which participates in forelimb movements, although the arrangement of musculature and clavicle is capable of fixing the shoulder in a stable position.

### (*c*) *Forelimb*

The shoulder joint of *Eozostrodon* is constructed on the basic pattern established among cynodonts, but also possesses several advanced features retained by monotremes. The glenoid is narrower and shallower than that in cynodonts. Comparison of representative glenoids and humeral heads of *Eozostrodon* reveals that the glenoid is wider and has a larger radius of curvature than the humeral head when measured in a dorsoventral plane, but is distinctly narrower than the head in a mediolateral plane (figures 8*a*, *b*, plate 3). Exact measurements of this apparent disparity cannot be made because no complete, associated shoulder joint is yet known. However, this disparity consistently appears among all available materials, and may be interpreted as an adaptation to increase the range of movement at the shoulder. The anterior extension of articular surface onto the lateral surface of the scapulocoracoid (figure 4*a*; figure 8*a*, plate 3) is a related adaptation, and occurs also in cynodonts. Peterson (in press) interpreted a similar extension of the glenoid in certain lizards as an adaptation to increase the anterior excursion of the humerus.

The humeral head of Triassic triconodonts is fully hemispherical and is flanked by trochanters resembling those of therians. Furthermore, the articular surfaces of the glenoid and head are smoothly contoured, evidence of a thin lamina of articular cartilage as in modern mammals. These features are also consistent with an interpretation of well-developed shoulder mobility. Monotremes retain many of these features, but have become specialized in the lateral orientation of the glenoid which accommodates the horizontal, transverse posture of the humerus (Jenkins 1970). Furthermore, the glenoid has become deeper and broader, possibly as an adaptation for shoulder stability during fossorial activity.

As in the shoulder, the articular surfaces at the elbow are well defined and thus provide some evidence of the possible movements. The ulna articulates with a condyle (rather than a trochlea as in therians) that wraps around the distal end of the humerus from dorsal (extensor) to ventral (flexor) aspects; the dorsal half of the condyle is positioned farther laterally than the ventral half, so that the condyle as a whole forms part of a spiral. An ulnar condyle is found among cynodonts and was retained by multituberculates and, in somewhat modified form, by monotremes (Jenkins 1973). Functionally, the spiral configuration may be interpreted as an adaptation to accommodate a complex displacement between the humerus and ulna moving in different planes. In the primitive mammalian condition the humerus is oblique to the median plane, and the forearm is approximately sagittal. During a propulsive movement, the humerus rotates, adducts, and elevates, whereas the ulna is simply extended in a sagittal plane (see Jenkins 1973 for further details). The dimensions of the ulnar condyle reveal that the range of forearm flexion and extension was large, probably on the order of 90°. Extension beyond a right-angle humero-ulnar position was made possible by the greater extension of the ulnar condyle onto the extensor surface than onto the flexor surface. Pronation and supination, however, appear to have been limited by the following features. First, the outline of the radial head is oval rather than circular; the facet for the capitulum is an oval concavity set obliquely to the shaft rather than a round concavity set transversely as in mammals that have developed pronation–supination ability. Secondly, the facet for the radial notch of the ulna is only slightly convex, and occupies no more than one quarter of the circumference of the head. In mammals with developed pronation–supination ability, the comparable facet conforms to the circular outline of the head and may extend around one half or more of the head's circumference.

### (*d*) *Pelvis*

The pelvis of Triassic triconodonts possesses many structural features retained among later mammals, both therian and non-therian (figure 20). The narrow, elongate iliac blade is directed anterodorsad. The low, longitudinal crest between concave areas on the lateral aspect of the blade appears to represent an incipient acetabular (or lateral) border separating the gluteal (superior) from the iliacus (inferior) origins as, for example, in monotremes and many therians (figure 20*d*, *e*). An acetabular notch is present, together with a characteristic incisure beneath the ischial facet. None of these features are known in cynodonts although they were present in tritylodontids such as *Oligokyphus* (figure 20*b*) (Kühne 1956). Other features, such as the enlarged obturator foramen and the apparent reduction of the anterior part of the pubis, represent a further continuation of trends established among cynodonts. As a result of these developments, the pelvis of Triassic triconodonts had attained a grade of structural organization basic to all mammals; from this fact may be inferred a basically mammalian pattern of pelvic musculature.

Only in acetabular structure do Triassic triconodonts retain vestiges of a primitive and cynodont-like pattern. The acetabulum is composed of three more or less separate bony facets – iliac, ischial and pubic. Their round, laterally protruding margins create an irregular (emarginate) acetabular rim (figure 13*d*, plate 5; figure 20*c*). Medially the margins merge with the floor of the acetabulum. This arrangement is similar to that in cynodonts (figure 20*a*) except for the position and orientation of the iliac facet. In cynodonts the iliac facet is located superiorly and faces ventrad, whereas in tritylodontids (figure 20*b*) and Triassic triconodonts the iliac facet assumes an anterodorsal position and faces posteroventrad. The emargination in the acetabular rim between iliac and ischial facets, which in cynodonts is posterosuperior, broadly opens the entire superior margin of the acetabulum in Triassic triconodonts and tritylodontids (figure 13*d*, plate 5; figures 20*b*, *c*). The multituberculates *Eucosmodon* (Granger & Simpson 1929) and *Kryptobaatar* (Kielan-Jaworowska 1969) also possess a deep emargination superiorly between the iliac and ischial facets, and in *Eucosmodon*, at least, the pubic and iliac facets remain differentiated. In all these cases the incisures separating the facets along the acetabular rim were probably filled with fibrocartilage. Thus, the socket was completed by the addition of connective tissue around an osseous framework. In contrast, higher mammals typically possess a more extensive bony support of the acetabulum. The circular acetabular rim is smooth and unbroken except by the acetabular notch; the facets of the three bones merge into a continuous articular surface (figure 20*e*). The socket is completed simply by the addition of a transverse ligament bridging the acetabular notch and a narrow fibrocartilaginous labrum. Monotremes have advanced to this structural level, although the loss of the acetabular notch and the perforate acetabulum (in *Tachyglossus*) are undoubted specializations (figure 20*d*).

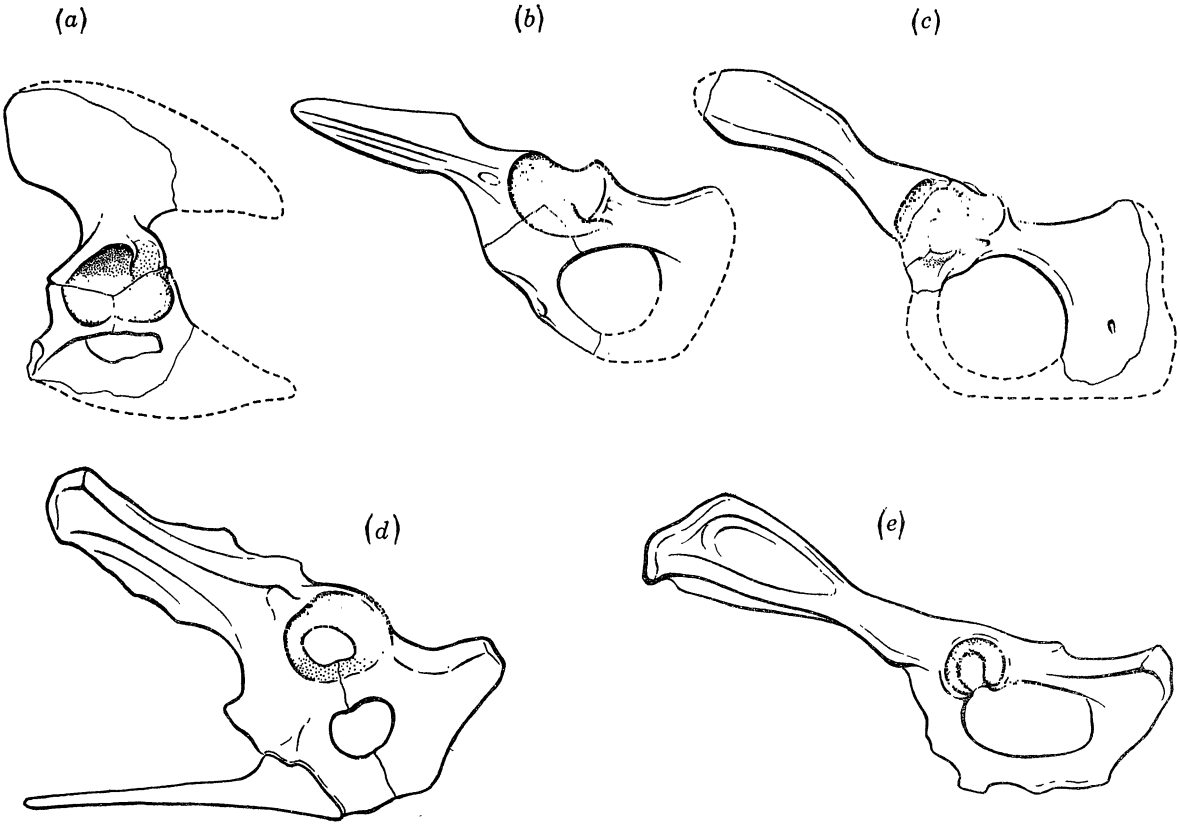

FIGURE 20. The pelvic girdles of (*a*) a cynodont (after Jenkins 1971*a*), (*b*) *Oligokyphus* (after Kühne 1956), (*c*) *Eozostrodon*, (*d*) echidna and (*e*) tree shrew (*Tupaia* sp.). (Not to scale.)

The dimensions of the acetabulum in Triassic triconodonts cannot be determined precisely on the basis of available material. The sphericity of the femoral head favours an interpretation of an essentially round socket which may be reconstructed on the basis of two dissociated fragments of *Eozostrodon* (figure 13*d*, plate 5). Even in this case, however, the anteroposterior dimension is somewhat greater than the dorsoventral dimension, a feature which is also characteristic of cynodonts, tritylodontids and, to a lesser extent, monotremes (figures 20*a*, *b*, *d*). In view of the fact that part of the pubic facet is missing from the specimen represented in figure 13*d*, plate 5, the acetabulum might be reconstructed with an even greater disparity between anteroposterior and dorsoventral dimensions (figure 20*c*).

The existence of epipubic bones in Triassic mammals remains a possibility which cannot be conclusively settled on the basis of the available material. Epipubes are not rigidly conjoined with the pubes in living mammals, and they may be expected to have been rapidly disarticulated from all but the best preserved fossils. The presence of epipubes in a tritylodontid (Fourie 1962) and a multituberculate (Kielan-Jaworowska 1969), as well as in monotremes and marsupials, would appear to increase the possibility that these bones might also occur in Triassic non-therians. However, the pubes of *Megazostrodon* and *Erythrotherium* are disarticulated and partially damaged, and no conclusions can be drawn on the basis of the available Pont Alun material.

### (*e*) *Hindlimb*

The proximal end of the femur in Triassic triconodonts possesses a number of advanced features not seen in cynodonts. Considered together, these features are evidence that the hip joint was functionally comparable to that in later mammals. First, the head is almost entirely spherical, permitting a wide excursion of the hindlimb. The extension of articular surface onto the ventrolateral aspect of the neck (figure 12*c*) is also characteristic of generalized, non-cursorial mammals (in the sense of Jenkins 1971*b*), and represents an area of acetabular contact at the end of a propulsive movement when the femur is fully extended and abducted. A short but definitive neck offsets the head from the shaft. The presence of a fovea on the head and an incisure beneath the ischial facet is evidence of a ligamentum capitis femoris and a non-articular area in the centre of the acetabulum as in most living mammals. In modern mammals, the ligament carries part of the blood supply to the head; this secondary pathway perhaps originated in conjunction with the gradual separation, both in structure and development, of the head from the shaft. The general orientation of the femur may be interpreted from the position of the fovea inasmuch as the fovea and the attached ligament must move within the acetabular fossa (i.e. the non-articular area) in the centre of the acetabulum. In *Eozostrodon* the fovea is eccentric, i.e. on the ventromedial aspect of the head; in order for the fovea to lie within the central and deepest part of the acetabulum, the femur must have been directed anteriorly at about 45° to sagittal. Such a posture is comparable to that observed in some living mammals (Jenkins 1971*b*).

The trochanters in *Eozostrodon* and *Megazostrodon* are flat, triangular processes arising from the medial and lateral aspects of the shaft. In their shape and position they represent a primitive pattern of trochanteric structure found in *Oligokyphus* (Kühne 1956), in Jurassic mammals from Stonesfield and the Purbeck (Simpson 1928), and in monotremes. The most characteristic feature is that the trochanters diverge proximally, more or less on opposite sides of the neck; each trochanter appears to have been formed by muscular forces resolved at roughly 40° to the shaft. This arrangement differs from that in cynodonts, in which the lesser trochanter is aligned with the shaft along its ventral aspect, or that in multituberculates and therians, in which the greater trochanter is more or less a proximal continuation of the shaft. Phylogenetic shifts in trochanters have been reviewed by Parrington (1961) and Jenkins (1971*a*), but the adaptive significance of the Triassic triconodont pattern, and the possible derivation of other patterns from it, can be evaluated only with additional evidence from fossil and comparative anatomical studies.

On the articular surfaces of the knee joint in *Eozostrodon* are preserved a number of features useful for osteological comparison. The asymmetry of the condyles and the proximal tibial facets is characteristic. The medial condyle is narrower and more protuberant than the lateral. The medial facet on the tibia is correspondingly narrower than the lateral, and being longer provides for a greater range of anteroposterior movement; furthermore, the medial facet is concave, whereas the lateral is slightly convex. Similar features are found in the knees of therians which exhibit a generalized pattern of mammalian limb posture (e.g. *Didelphis*, *Tupaia*). The functional significance of these features is far from clear, for no detailed, comparative analysis of knee mechanics is available other than Haines' (1942) primarily anatomical study. However, cineradiographic records of walking *Didelphis*, *Tupaia*, and other non-cursorial mammals give some evidence of rotation at the knee during the propulsive, weight-bearing movement (Jenkins 1971*b*). The femur, oriented obliquely to sagittal at the beginning of a step, adbucts during the propulsive movement (i.e. the angle between the femur and a sagittal plane increases). The crus, however, remains in or near a sagittal plane. Such a change in relative orientation of the femur and tibia may be accommodated by a mechanism permitting rotation at the knee. The mechanism possibly consists of a greater anteroposterior excursion of the medial condyle which is guided by the grooved tibial facet; the axis of rotation would pass close to or through the rounded, convex lateral tibial facet.

A second characteristic feature of the *Eozostrodon* knee is the course of the patellar groove which ends on the lateral condyle rather than in the intercondylar notch. A similarly eccentric position is found in such therians as *Didelphis* which shares with *Eozostrodon* a relatively broad distal end of the femur and participation of the fibula in the knee joint. The effect is to position the quadriceps tendon across the middle of the tibio-fibular half of the knee joint. Thus, quadriceps activity is balanced with respect to the entire lower leg. In those forms in which the fibula does not participate in the knee joint, the patellar groove evenly bisects the distal femur.

As Haines (1942) recognized, monotremes have undergone considerable specialization in knee joint structure. The condyles are relatively flat, subequal in size, and widely separated. The patellar groove is so broad as to cover most of the dorsal surface of the distal end of the femur. Monotremes have furthermore added an elongate proximal process on the fibula. An incipient development of a similar process appears to have been present in *Eozostrodon* and possibly in *Megazostrodon*, but there is no other substantial evidence that monotremes preserve much of the primitive knee structure and function of Triassic non-therians.

The tarsus of Triassic triconodonts retains the basic pattern established among cynodonts, but also shows development of several advanced features found among later mammals. The astragalus is somewhat hemispherical, as in cynodonts. The tibial facet shows no development of a trochlea like that in advanced therians, but rather is convex from side to side as well as proximodistally. The division of the tibial facet into medial and lateral halves by a low, proximodistal ridge is another feature apparently inherited from cynodonts, although a similar condition is present in certain therians (e.g. *Didelphis*). The precise boundaries of the fibular facet are not clear. The articulation appears to have been shared between the astragalus and calcaneum, as in cynodonts and (in a specialized form) in monotremes. There are two features, however, that appear here for the first time among mammals. First, an astragalar head occurs as a well ossified, distinct process for articulation with the navicular. Secondly, the sulcus between the calcaneal facets on the astralagus is enclosed posteriorly to form an astragalar canal (and foramen). Astragalar canals are also present in tritylodontids (Kühne 1956), in multituberculates (Granger & Simpson 1929), and in some therians. The broad, flat shape of the calçaneus, a well-developed tuber calcis and a posteromedial process for the astragalus (and possibly for the fibula) are all features established in cynodonts. Curiously, the sustentaculum tali is not as prominent as in cynodonts. A degree of superposition appears to have been accomplished by the elevation of the medial margin of the calcaneus which allowed the 'ventral' face of astragalus to lie against it. Kühne (1956) interpreted a similar condition in *Oligokyphus*.

In neither the ankle nor subtalar joints is there evidence that Triassic triconodonts had progressed substantially toward a therian level of organization. However specialized the tarsus of monotremes may be, the unusual ankle and calcaneo-astragalar articulations appear to be more readily derived from that in Triassic triconodonts than one in which recognizably therian characters had developed.

The phalanges of Triassic triconodonts provide evidence of well-developed prehensile abilities, specifically considering the flanges for digital fibrous sheaths of the flexor tendons, the extensive trochleae at the distal interphalangeal joints, the large ungual flexor tubercles, and the structure of the distal phalanges which surely supported narrow, pointed claws.

## 5. The habits of Triassic mammals

The habits of primitive, early mammals, reconstructed on the basis of both palaeontological and comparative anatomical evidence, have figured prominently in theories concerning the origin and basic adaptations of the class as a whole. A recurring and central question is whether early mammals were arboreal or terrestrial. Review of the major contributions on this subject (Jenkins 1974*a*) reveals that the theories proposed to date have relied largely on indirect evidence. Arguments from the standpoint of comparative anatomy have not demonstrated convincingly that the structures in question were special adaptations of the earliest mammals. At best, the comparative approach may identify anatomical patterns basic to all mammalian phylogenies, but seldom can any one structure be shown to be positively indicative of terrestrialism or arborealism. Arguments based on palaeontological evidence have likewise failed because the fossils cited were too recent or too specialized to represent a primitive mammalian condition.

With the Triassic fossils now known, another attempt at interpreting primitive mammalian habits seems warranted. However, recent behavioural and physiological studies necessitate a re-evaluation of the traditional question of arborealism versus terrestrialism in mammalian ancestry. In a review of the locomotor behaviour and adaptations of tree shrews (Tupaiidae), Jenkins (1974*a*) concluded that the categories 'arborealism' and 'terrestrialism' have only limited applicability. Among tree shrews, the difference between 'arboreal' and 'terrestrial' species is principally behavioural; even the most persistently ground dwelling forms can climb, and many species so freely frequent the forest floor, low vegetation and trees that these habitats can scarcely be considered discrete (Jenkins 1974*a*). Therefore an animal may reasonably be classified as arboreal or terrestrial only by habitat preference. However, the degree to which different locomotor repertoires for arboreal and terrestrial settings must be employed is in part dependent on size. The important factors are the physical dimensions of the substrate in relation to the animal's size, and the bioenergetic consequences of size. For mammals such as tree shrews, and indeed for small mammals in general, most terrestrial and arboreal habitats (except very flat, sparsely vegetated terrain) offer a similar set of physical challenges. First, in terms of foot emplacement, the small mammal faces a disordered and discontinuous spatial array of support surfaces. At ground level, obstacles that require climbing are common, and vegetation provides a continuum of substrate possibilities between the 'terrestrial' and the 'arboreal'. For most small mammals, the spatial complexity of possible locomotor substrates requires adaptations for both body stability and limb mobility. Typically, the humerus and femur are abducted from a sagittal plane, and the elbow and knee is flexed (Jenkins 1971*b*); the centre of gravity is thus held low with a relatively wide stance. The ball-and-socket shoulder and hip joints provide the freedom necessary to position the supporting limbs over a wide range. Flexion and extension of the vertebral column offer further possibilities for adjusting the position of forelimbs and hindlimbs. A second feature of the physical environment for small mammals is that substrate surfaces are seldom level; pronation–supination of the manus and inversion–eversion of the pes, together with the frictional effect of plantar pads and claws, are critical to stability. From the perspective of the small mammal which possesses the basic adaptations to move on discontinuous, spatially complex and uneven surfaces, arboreal and terrestrial surfaces are not only intergradational, but everywhere require basically the same locomotor repertoire.

In physiological terms, arboreal and terrestrial substrates do not make comparable energetic demands on mammals of different size. Relative to body mass, smaller mammals have a relatively higher energetic cost for level running than do larger forms, but the incremental increase for running on progressively more inclined (including vertical) surfaces is far less (Taylor, Caldwell & Rowntree 1972). However, as pointed out above, small mammals seldom move on 'level' surfaces; relative to their size, the terrain normally presents obstacle-filled, inclined substrates. Thus, smaller mammals pay only a smaller increase in metabolic cost for arboreal climbing, but the energy they expend in moving through a 'terrestrial' setting may not be appreciably different than that in an 'arboreal' setting.

The question of arboreal versus terrestrial specialization in the diminutive Triassic mammals is probably invalid in view of the fact that the anatomical and physiological requirements for locomotion in both settings are similar for animals of small size. However, inquiry can be appropriately directed to the question of whether Triassic mammals possessed adaptations for moving on spatially complex, uneven, and even steep surfaces.

Cartmill (1974) provided a thorough biomechanical and comparative analysis of the role that mammalian claws play in climbing and in various arboreal activities. Inasmuch as the possession of sharp, laterally compressed claws is a crucial adaptation for small mammals in gaining stability on nonhorizontal surfaces, the occurrence of similarly developed claws (and prominent flexor tubercles) in Triassic mammals is evidence that they were similarly adapted. Furthermore, the clambering style of locomotion in small mammals requires limb movement over a wide range of postures; as in modern forms, the ball-and-socket shoulder and hip joints of Triassic mammals appear to provide for ample excursion. A better understanding of the comparative and functional anatomy of the distal limb joints is needed to evaluate this viewpoint more fully, although some aspects are suggestive. For example, the degree of pronation and supination possible in *Eozostrodon* appears to have been relatively modest, but the curvature of the proximal radio-ulnar joint is comparable to that present in agile modern mamals (e.g. *Tupaia*). The evidence for inversion and eversion of the foot is moot, inasmuch as the functional relationships between the astragalus, calcaneus, and other tarsals are incompletely understood.

Two lines of evidence support the view (based on claw structure) that prehensility was developed in the foot of Triassic triconodonts. Lewis (1964), reviewing the flexor muscles in the mammalian leg and foot, noted that the peroneus longus tendon typically is displaced from the base of the fifth metatarsal (where it inserts in lower tetrapods) to the base of the hallucal metatarsal; both insertions occur in monotremes. Lewis interpreted this shift as providing hallucal adduction, and ascribed a similar function to the flexor accessorius. The widespread occurrence of these muscles in living mammals lead Lewis to conclude that the common ancestor of mammals possessed a 'widely divergent', 'opposable' hallux. Plausible as this argument may be, a divergent, opposable hallux in early mammals cannot be reconstructed with absolute certainty on the basis of comparative myology alone; muscles that act across several joints may have had different or multiple functions in the primitive condition (in the case of peroneus longus, for example, pronation at the transverse tarsal joint is a possibility). Evidence for independent action of the hallux, however, is available directly from the Triassic fossils. 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 preparations 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 (figure 9*c*, plate 4). In the weight-bearing foot of *Tupaia*, digital divergence from III is typically 5° for II and IV, 10° for V, and 20° for the hallux (Jenkins 1974*a*). A comparably modest degree of digital spreading was probably also present in Triassic mammals. Aside from the similarity in post-mortem postures, the halluces of *Tupaia* and the Triassic mammals appear to be similarly adapted for independent movement. High-speed cinematography of arboreal locomotion in *Tupaia* reveals that the hallux is positioned across the top of a branch by abduction and extension, and thus may secure an active grip by opposing the remaining digits on the side of the branch (Jenkins 1974*a*, Figure 7). Independent movement takes place principally at the metatarsophalangeal joint which incorporates an asymmetrical condyle, and possibly to a lesser degree at the tarsometatarsal joint which is saddle-shaped. In *Eozostrodon*, the asymmetry of the distal articular surface of metatarsal I (figure 14*c*, plate 6) is the same adaptation for abduction–adduction. The prolongation of the proximal articular facet onto the dorsum of metatarsal I in both *Eozostrodon* (figure 14*c*, plate 6) and *Megazostrodon* (figure 9*c*, plate 4), in contrast to the condition in the other metatarsals, is evidence of independent flexion–extension at this joint. Furthermore, some abduction may have been possible at this site, although the evidence in *Megazostrodon* is not entirely clear.

Body size and proportions are relevant to interpreting the habits of early mammals. Approximately the size of medium-sized modern shrews (e.g. *Crocidura baluensis*, *Suncus murinus*), *Megazostrodon* was approximately 10 cm in head–body length and probably weighed between 20 and 30 g. *Eozostrodon* was on the order of 20 % smaller. A reconstruction of a Triassic triconodont, utilizing the proportions of the associated skeleton of *Megazostrodon*, depicts a gracile build and a relatively large head (figure 18). The lengths of the skull, pelvis, hindlimb and humerus are represented accurately enough in *Megazostrodon* to warrant comparison with those in modern shrews. Measurements were taken from a sample of twelve individuals representing *Blarina blarina*, *Crocidura baluensis*, *Crossogale phaeura* and *Suncus murinus*, all shrews of approximately the same size as *Megazostrodon*. Certain fundamental differences between these shrews and *Megazostrodon* are masked by the use of skull length as a simple index of head size. In *Megazostrodon* (and undoubtedly in other Triassic mammals as well) the lower jaw is nearly as long as the skull and articulates near the back of the skull. The infratemporal fossa is large and the braincase relatively small. Comparably sized modern shrews typically have a broadly expanded braincase caudad to the jaw articulation, a relatively shorter jaw, and a smaller infratemporal fossa. Despite these differences, the proportionate relation of tooth row to skull length is similar in *Megazostrodon* and comparably sized shrews. In the species sampled, the distance from $P^4$ to the last molar ranges from 22 to 27 % of skull length; in *Megazostrodon* (with a skull length estimated at 27.5 mm) this relation is 26 %. Similarly, the shrew $P^3$ to $I^1$ length ranged from 18 to 21 % of skull length, and in *Megazostrodon* this relation is estimated to be the same (20 %). Small differences are apparent in the proportionate relations of the limbs. In the shrew sample, the humeri are variably 5–10 % shorter than the femora, whereas in *Megazostrodon* the humerus is about 21 % shorter. The range for humeral length in shrews is from 43 to 50 % of skull length (as against 55 % in *Megazostrodon*), and for femoral length is from 47 to 57 % (as against 67 % in *Megazostrodon*). Finally, the anteroposterior length of the shrew pelvis relative to skull length varies from 61 to 76 %; in *Megazostrodon* the pelvis is 60 %. Other than the slightly greater length of the proximal limb segments, *Megazostrodon* appears to have had skeletal proportions much like those in some living shrews. Some caution must be applied to this conclusion, however, in view of the fact that slight post-mortem distortion of the *Megazostrodon* skeleton has occurred, and the body length of this and related forms can only be estimated.

The molars of both Triassic triconodonts and their symmetrodont relatives, the Kuehneotheriidae, were capable of shearing; the relatively long, sharp canines were suited for prehension and penetration. That these small mammals existed on a primarily insectivorous diet appears certain (Kermack, Mussett & Rigney 1973). Insectivory as a dietary specialization, however, was an opportunity open to land vertebrates well before the appearance of mammals in the late Triassic (Rohdendorf 1970). Terrestrial invertebrates, and notably the insects, are well diversified and abundant in the fossil record of the late Carboniferous. Olson (1966), in reconstructing food chains utilized by late Paleozoic amphibians and reptiles, discussed the increasingly important role of terrestrial invertebrates in evolving vertebrate assemblages. The mammals of the late Triassic thus were not the first occupants of an insectivorous niche, but rather appear to have possessed special adaptations for exploiting this food source which were unlike those of any previous vertebrates.

Several factors may have contributed to the origin of insectivory among the earliest mammals. First, extensive faunal and floral changes occurred at the close of the Permian. Numerous groups of amphibians and reptiles, some of which were small and may have been predominantly insectivorous, became extinct; competition among vertebrates for invertebrate foods may have diminished accordingly, although some diapsid reptiles, notably the eosuchians, underwent a modest radiation in this niche. However, the composition of invertebrate faunas also changed; approximately one third of Permian insect orders, for example, have no post-Palaeozoic record (Riek 1970; F. M. Carpenter, personal communication). Compositional changes in the invertebrate fauna may have been related to some degree to the Permian extinction of smaller vertebrates, but in any case the Triassic was not impoverished in terms of terrestrial invertebrates as a potential food source (one half of all known insect orders, for example, had Triassic representatives (Riek 1970; F. M. Carpenter, personal communication). A second factor influencing the development of mammalian insectivory stems from the phylogenetic history of synapsid reptiles themselves. During the Permo-Carboniferous the pelycosaurs and therapsids were the major terrestrial carnivores. The cynodonts surviving into Triassic times inherited from them anatomical adaptations for ingesting animal prey, and probably sensory and locomotor adaptations for hunting as well. Dietary specialization on an abundant and diverse invertebrate food supply was accompanied by selective reduction in body size, and thus many cynodonts of the middle and late Triassic were as small as their insectivorous counterparts in late Palaeozoic faunas. However, the preadaptation that cynodonts and their mammalian descendants exploited as insectivores (*sensu lato*) was to hunt prey, rather than to feed opportunely as do most insectivorous amphibians and reptiles.

Some aspects of the biology of the earliest mammals may be plausibly inferred from comparative anatomical and physiological studies of modern forms, as well as from geological data. The problem of temperature regulation offers an interesting example. All living mammals normally maintain body temperature at relatively constant levels. However, the level at which temperature is regulated, and the degree to which activity and ambient temperatures affect the capacity to regulate it, varies significantly between groups of mammals. Monotremes, for example, maintain body temperature at 31 ± 2 °C, marsupials at 36 ± 2 °C, and placentals at 38 ± 2 °C; monotremes maintain their body temperatures as effectively in low ambient temperatures as do therians, but are unable to tolerate high ambient temperatures (for a review, see Schmidt-Nielsen 1975). A conservative conclusion from these facts is that the earliest mammals metabolically regulated body temperature *at some possibly modest level*, although certain control mechanisms (i.e. providing for heat loss in high ambient temperatures) were specializations developed later. The palaeontological evidence for the evolution of mammalian musculoskeletal features in advanced mammal-like reptiles (summarized by Parrington 1967) has also been used to infer that the earliest mammals were physiologically advanced. On the basis of the geological evidence, Crompton (1968) suggested that the metabolic control of body temperature and an insulating pelage may have originated among mammal-like reptiles adapted to relatively cold climates. The fact that nocturnal habits are widespread among living mammals, and that most species are colour-blind, prompted Jerison (1971, 1973) to infer that mammals were primitively nocturnal; the ability to maintain body temperature would be a critical adaptation for activity in the lower range of fluctuating ambient temperatures. As plausible as these hypotheses may be, further resolution of such questions requires more taphonomic and anatomical information about Triassic mammals than is currently available.

At present, the available cranial and postcranial evidence supports an interpretation of Triassic mammals as having acquired basic adaptations for a diet and locomotor repertoire characteristic of many small, insectivorous mammals today. They may be envisaged foraging for insects and grubs among litter and fallen plant debris, and clambering upward through low vegetation and even trees to seek out bark-dwelling and leaf-eating insects. Rather than being the unsuccessful competitors of archosaurs, Mesozoic mammals from Triassic times onward probably dominated a major ecological niche. From small beginnings, their adaptive radiation produced a significant diversity of forms (of which the teeth alone are rather meager evidence) and were probably as specialized in habitat and behaviour as were many of their reptilian contemporaries.

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## *Addendum*, 19 *November* 1975

A nearly complete cervical vertebra referable to *Eozostrodon* was recovered recently. This specimen confirms conclusions based on the articulated cervical vertebrae of *Megazostrodon*, and furthermore displays features which are not visible in that series. The body, dorsoventrally compressed and oval in cross section, is 2 mm wide, 1.25 mm deep, and 1.5 mm long. A small, pit-like notochordal fossa occurs in the centre of the anterior aspect of the body; posteriorly, the notochordal fossa is broader and possesses less steeply inclined sides. The neural arch, although somewhat distorted as preserved, is similar to those in *Megazostrodon* in being narrow anteroposteriorly. Both the pedicles and laminae are approximately 0.75 mm in this dimension, and therefore about half the length of the body which is the same as in *Megazostrodon*. Furthermore, the relative size of the vertebral foramen (and cervical vertebral canal), which could only be estimated in *Megazostrodon* from the interzygapophyseal breadth, can here be seen. The pedicles articulate with the dorsolateral margins of the body and are bowed laterally. Allowing for some distortion in this specimen, the transverse dimension of the vertebral foramen is at least 2 mm, and very probably slightly larger than the width of the body itself. The specimen therefore provides confirmation of our interpretation of cervical canal enlargement in Triassic triconodonts as a result of the development of a cervical enlargement of the spinal cord of mammalian proportions.

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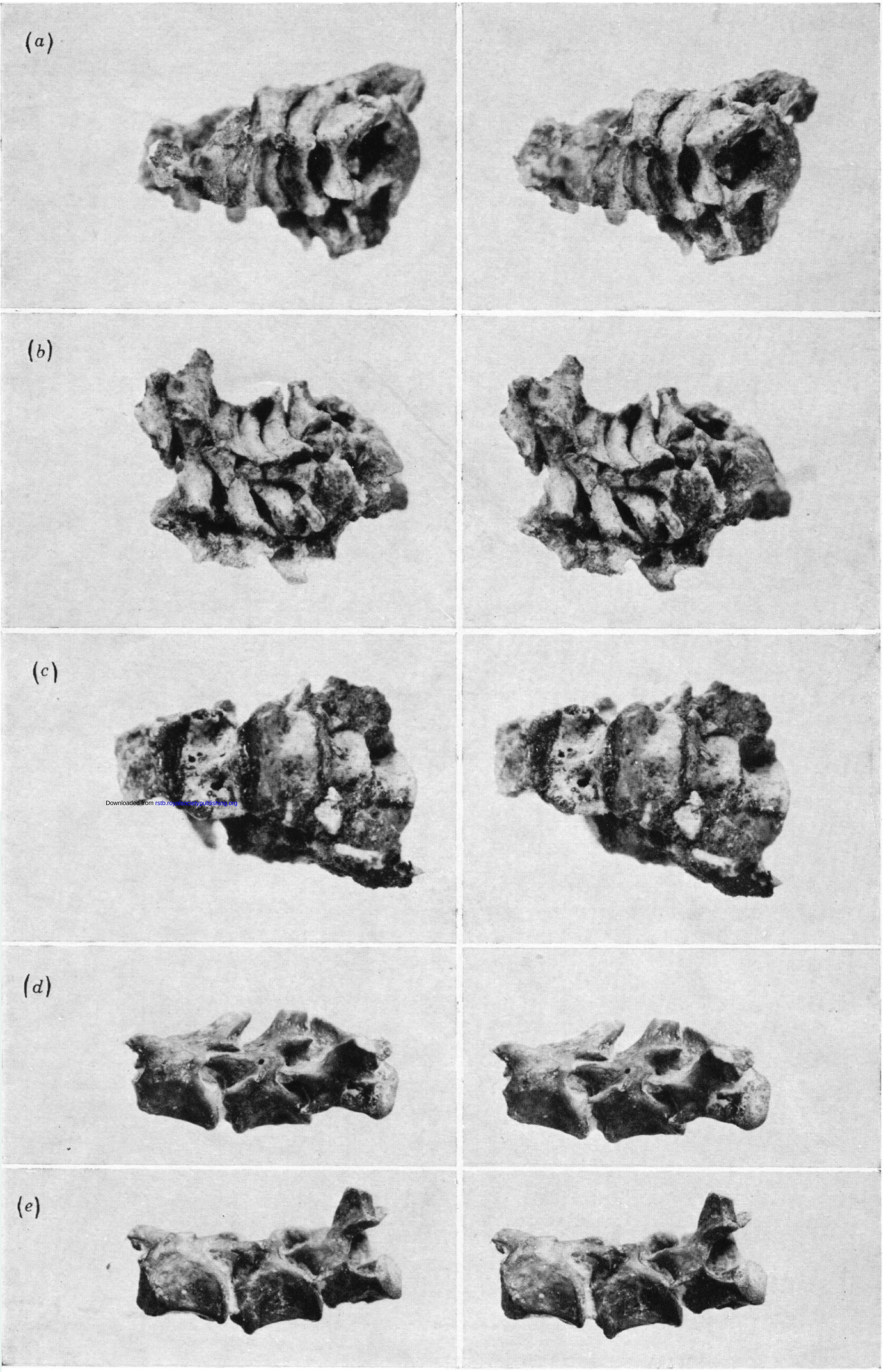

FIGURES 6 (*a*–*e*). For description see opposite.

Figures 7 (*a–f*). For description see opposite.

FIGURES 8 (*a–f*). For description see opposite.

Figures 9 (*a–d*). For description see opposite.

FIGURES 13 (*a–e*). For description see opposite.

FIGURES 14 (*a*–*h*). For description see opposite.