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continued inside back cover)

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ANCHISAURUS CAPENSIS (BROOM) AND A REVISION OF THE ANCHISAURIDAE (REPTILIA, SAURISCHIA)

by

P. M. GALTON & M. A. CLUVER

Cape Town Kaapstad

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&

M. A. Cluver

South African Museum, Cape Town

(With 13 figures and 3 tables)

[*MS accepted 22 October 1975*]

ABSTRACT

A complete description of the skeleton of the type specimen (SAM-990) of the prosauropod dinosaur *Gyposaurus capensis* Broom is given. Comparison with other prosauropods indicates that this dinosaur represents a valid South African species of *Anchisaurus* Marsh, 1885 from the Upper Triassic of North America. It is considered that the infra-order Prosauropoda should be divided into three families, viz. Anchisauridae, Plateosauridae and Melanorosauridae. It is proposed that the family Anchisauridae be restricted to prosauropods with relatively slender feet, and that broad-footed forms previously assigned to the Anchisauridae be transferred to the Plateosauridae. The Family Anchisauridae is therefore considered to include the genera *Anchisaurus*, *Efraasia*, *Thecodontosaurus* and several indeterminate species. The genera *Ammosaurus*, *Aristosaurus*, *Massospondylus* (including *Gryponyx*, *Aetonyx* and *Dromicosaurus*), and *Lufengosaurus* (including *Yunnanosaurus*) are included in the Plateosauridae, while *Arctosaurus* and *Ischisaurus* are referred to the suborder Theropoda. '*Thecodontosaurus*' *gibbidens*, *Spondylosoma absconditum* and *Teleocrater alphos* are placed within the Thecodontia, and *Tanystropheus primus* and *T. latespinatus* in the order Lacertilia. Thus constituted, the family Plateosauridae becomes the dominant and most widespread prosauropod family, while the Anchisauridae, in contrast, is known from a geographically and numerically restricted fossil record.

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Ann. S. Afr. Mus. **69** (6), 1976: 121–159, 13 figs, 3 tables.

INTRODUCTION

Broom (1906) described a specimen (SAM-990) from the Cave Sandstone, Stormberg Series (Upper Triassic) of Ladybrand, Orange Free State, South Africa, and referred it to the prosauropod taxon *Hortalotarsus skirtopodus* Seeley, 1894. The holotype of *Hortalotarsus skirtopodus* was referred to the genus *Thecodontosaurus* Riley & Stutchbury, 1836, by Huene (1906) as *T. skirtopodus* and, because SAM-990 differed in several aspects from *Thecodontosaurus*, Broom (1911) made it the holotype of *Gyposaurus capensis*. Broom (1906) noted several resemblances between SAM-990 and *Anchisaurus* Marsh, 1885, from the Upper Triassic of North America, so he referred *Gyposaurus capensis* (SAM-990) to the Family Anchisauridae Marsh, 1885. Galton (1973, in press) provisionally accepted the validity of *Gyposaurus capensis* but noted that the holotype should be carefully compared with *Anchisaurus polyzelus* (Hitchcock) to determine whether or not these species are generically distinct. A comparison of photographs of SAM-990 with a specimen of *Anchisaurus polyzelus* (YPM 1883) showed that *Gyposaurus* is a junior synonym of *Anchisaurus* and that SAM-990 should be redescribed.

Huene in several papers between 1906 and 1932 made important contributions to an understanding of the Family Anchisauridae (as Thecodontosauridae Lydekker, 1890). Charig *et al.* (1965) considerably enlarged the family by referring to it genera of Triassic theropods (Family Gryponychidae = 'Palaeosauridae') based solely on postcranial material which was indistinguishable from that of prosauropods. The generic list of Romer (1966: 370) includes these changes and the comprehensive list given by Steel (1970) faithfully but rather uncritically records all the genera and species referred to the family.

A taxonomic revision of the Family Anchisauridae is necessary for several reasons:

1. Several of the suggested and generally accepted synonymies are probably incorrect. In assessing these the recognition of slender- and broad-footed types (Galton 1971, 1973, in press) is useful.

2. The skeletal anatomy of prosauropods is remarkably uniform, so taxa should be based on specimens which include either most of the specimen or bones which are diagnostically different from those of other prosauropods. Because of the limited number of skeletal variations it is necessary to diagnose taxa on the basis of a combination of characters which, if each was taken in isolation, would not be diagnostic. Unfortunately several of the taxa listed by Steel (1970) are based on specimens which are generically and specifically indeterminate.

3. The group has been over-classified and insufficient account has been taken of the range of individual variation possible within a dinosaurian species; this can be quite extensive, as shown by the prosauropod *Lufengosaurus huenei* Young (see Rozhdestvensky 1966) and the ornithopod *Hypsilophodon foxii* Huxley (see Galton 1974).

4. A few of the taxa included within the family are not prosauropods.

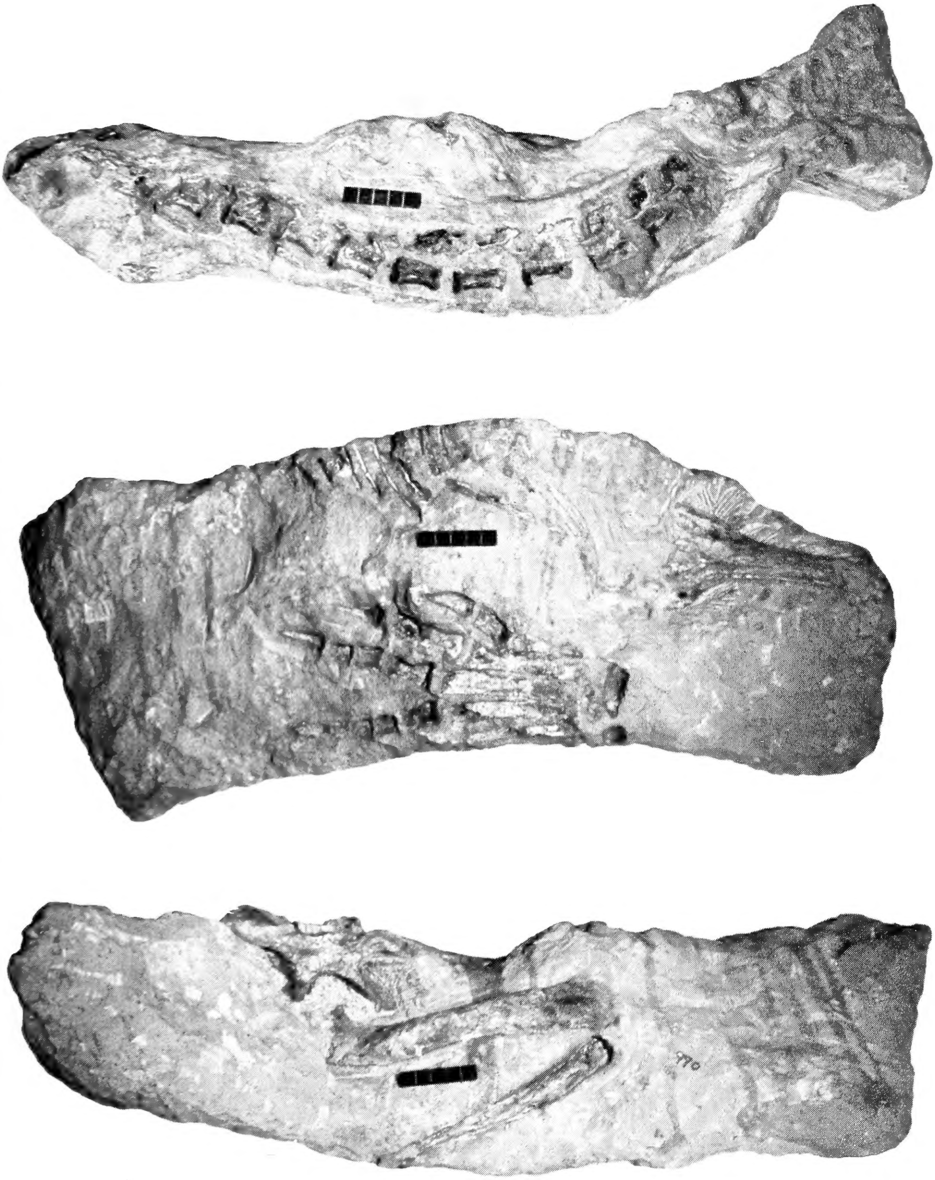


Fig. 1. *Anchisaurus capensis* (Broom). Type specimen (SAM-990) showing vertebral column (top), pubis, ischia and pes (middle) and ilium, femur and fibula (bottom).

Summaries of certain aspects of the revision of the family Anchisauridae have been published earlier (Galton 1971, 1973, in press). The first author (P. M. G.) is responsible for all sections except the description and illustration of SAM-990, which is the work of the second author (M. A. C.).

REDESCRIPTION OF *ANCHISAURUS CAPENSIS* (BROOM)

The specimen (SAM-990) is preserved in a soft sandstone matrix (Fig. 1). The bone is generally not well preserved and is inclined to crumble during preparation. Much of the specimen (including most of the vertebral column) is preserved as bone impression, and details of certain of these portions were obtained from silicone rubber positives. Chief portions of the preserved skeleton are 17 vertebrae (including, probably, dorsals, sacrals and caudals), an incomplete left pubis, the right ilium and pubis and both ischia, and the right femur, fibula and pes. Several other fragmentary bones, mostly seen as impressions, are scattered through the block: anteriorly a portion of the right scapula blade can be made out, while impressions of 13 ribs lie ventral to the dorsal vertebrae.

VERTEBRAL COLUMN (Fig. 2)

Altogether 17 vertebrae are preserved, some very incompletely. Eleven of these are in articulation and consist of a number of dorsals and possibly two sacrals. A space separates the last of these from the first of the posterior group, which have been displaced to the right of the anterior series. The space is sufficient to accommodate three vertebrae of the size of those on each side of it, and there is thus the possibility that this gap was originally filled by three sacral vertebrae. However, as will be shown below, it is more likely that a parting of the vertebral column between two sacral vertebrae occurred prior to fossilization of the specimen.

The anterior three vertebrae, imperfectly seen, are not in natural articulation, although still in relatively close association with each other. The centrum of the second vertebra is opisthocoelous and slightly convex anteriorly, while the third centrum is concave anteriorly and posteriorly. The fourth vertebra has a procoelous centrum and is markedly convex posteriorly. This convex rear meets the apparently convex anterior surface of the fifth vertebra's centrum, which also appears to be opisthocoelous. The sixth vertebra is provided with a biconcave centrum, the neural spine is broad in lateral view, and its postero-dorsal edge overhangs the postzygapophysis so that a posterior embayment is formed above the postzygapophysis. The seventh vertebra resembles the sixth and the succeeding eighth in the shape of the neural spine, and both the seventh and eighth vertebrae have biconcave centra, similar to that of the sixth vertebra. The eighth vertebra shows the neural spine clearly, and probably represents the condition which existed in the less complete sixth and seventh vertebrae. The spine, posteriorly situated, is antero-posteriorly lengthened and fairly low.

The neural spine of the ninth vertebra is shorter antero-posteriorly. The

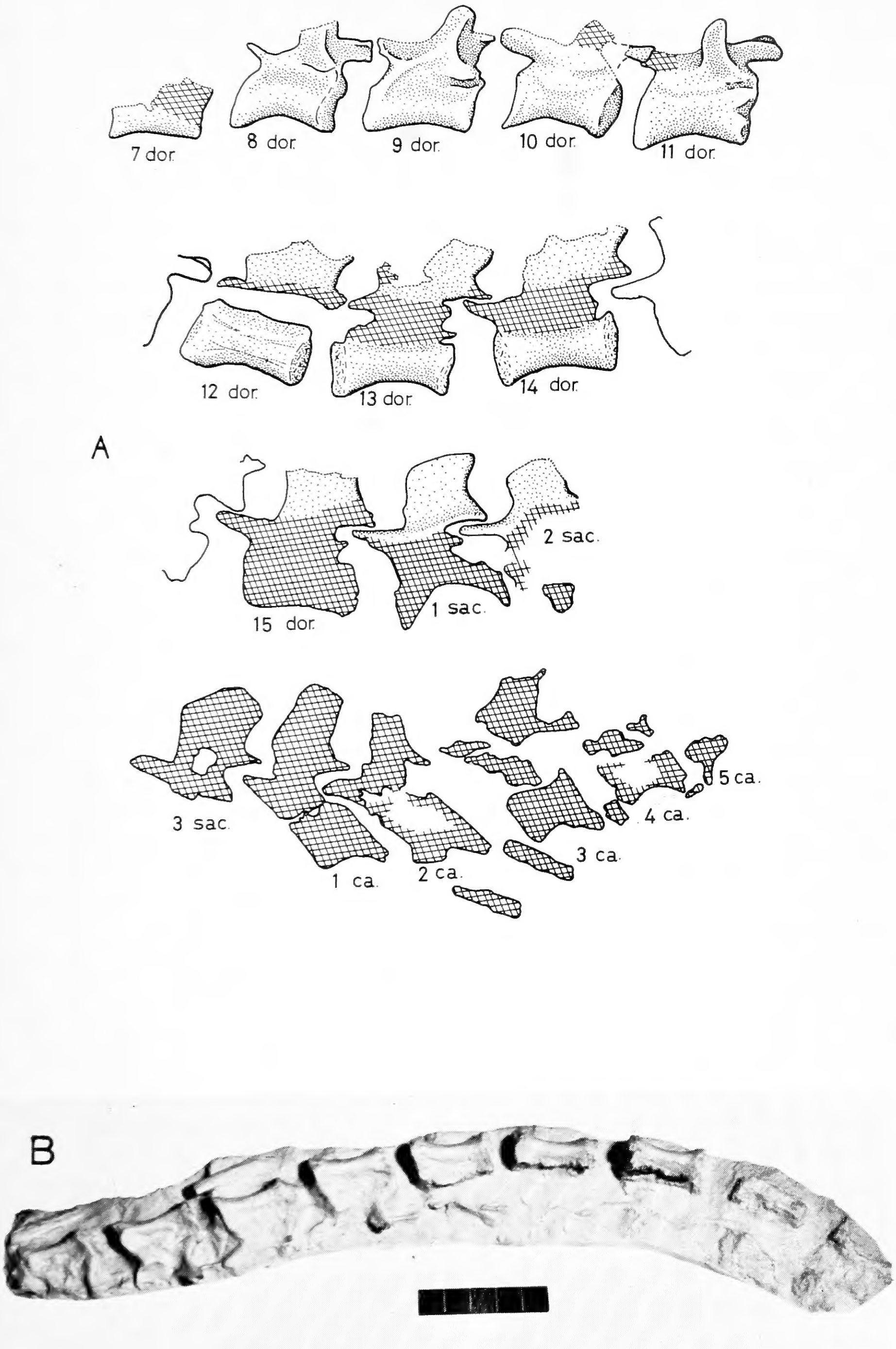


Fig. 2. *Anchisaurus capensis* (Broom). SAM-990. A. Vertebral column in lateral view. Broken edges shown in dashed outline, hatched areas seen in section only. × 0,5. B. Mould of centra of dorsal vertebrae.

tenth vertebra has the only complete neural spine and there is a shallow notch above the postzygapophysis. The ninth and tenth vertebrae are possibly procoelous, with a convexity on the posterior articular surface.

The posterior group of six vertebrae lies slightly to the right of the anterior row, and appears to be in near-natural association with the right ilium. The spine of the most anterior vertebra (the twelfth in the column as preserved) is fairly high and slightly rounded anteriorly; there is only a slight posterior notch above the postzygapophysis. The spine resembles that of the tenth (and eleventh?) vertebra of the anterior row fairly closely. The thirteenth vertebra has a high and narrower spine, posteriorly inclined, and a chevron can be seen extending back and down from below its centrum. The fourteenth and fifteenth vertebrae are similar, as far as can be seen. Remnants of chevrons are seen between the centra of vertebrae fourteen to seventeen.

Identification of vertebral types

Caudal vertebrae are fairly clearly represented by nos. 13 to 17 in the rear series, with narrower, obliquely inclined spines and a series of chevrons. The last two vertebrae (10 and 11) of the anterior row have narrower and possibly higher spines than the preceding ones, and they resemble the first member of the posterior group. From this it can be argued that the tenth, eleventh and twelfth vertebrae of the column as a whole are sacrals, separated by the disintegration of the pelvic girdle. Vertebra 12 is in fairly natural association with the right ilium, and 10 and 11 are close to the ilium of the left side. The left ilium has been displaced sideways and forward relative to the right side, and this could account for the gap in the series. Moreover, no recognizable loose vertebral portions can be identified in the surrounding matrix.

In *Efraasia* (Galton 1973) and *Plateosaurus* (Huene 1926) there are fifteen dorsal vertebrae so, if the above interpretation is correct, the specimen as preserved probably includes dorsal vertebrae 7 to 15, sacral vertebrae 1 to 3, and caudal vertebrae 1 to 5.

Dimensions of the vertebrae, numbered according to their above identification, are given in Table 1.

PELVIC GIRDLE

The pelvic girdle is represented by the right ilium, both ischia, and an incomplete left and almost complete right pubis. The right side of the pelvis (Figs 3, 5) is preserved in almost natural association. The ilium is well preserved, but both pubis and ischium are incomplete distally, and do not make any clear contact with each other. The areas of articulation between ischium, pubis and ilium are imperfectly preserved and could not be determined.

Ilium

The ilium (Figs 3A, 5) of the right side is uncrushed and complete except for a portion of the dorsal crest. It is characterized by long anterior and posterior

TABLE 1.
Dimensions of Vertebrae (mm). *Anchisaurus capensis* (Broom) SAM-990

Vertebra	*Length of centrum ventrally*	*Maximum height*	*Length between pre- and post-zygapophysis*	*Height of spine above post-zygapophysis*	*Length of spine*
7th dorsal . .	27	—	—	—	—
8th dorsal . .	29	—	—	—	—
9th dorsal . .	±30	—	—	—	—
10th dorsal . .	30	—	—	—	—
11th dorsal . .	31	—	—	—	—
12th dorsal . .	31	40	—	13	30
13th dorsal . .	33	42	40	16	32
14th dorsal . .	33	40	48	14	30
15th dorsal . .	32	38	44	13	20
1st sacral . .	31	43	39	19	18
2nd sacral . .	—	—	—	—	—
3rd sacral . .	—	—	35	18	21
1st caudal . .	18	51	34	22	13
2nd–5th caudals .	±18	—	—	—	—

processes, and a pre-acetabular process considerably longer than the post-acetabular process. The anterior process lies slightly external to the more posterior surface of the bone, and extends as far forwards as the anterior edge of the pre-acetabular process. The slender finger-like form of the anterior process (Fig. 10B) is similar to that of *Anchisaurus polyzelus* (Fig. 10A) and *Ammosaurus* (Galton 1971) and in contrast to the small triangle of other prosauropods (Fig. 10C–D).

A prominent pre-acetabular buttress is developed, arising from close above the tip of the pre-acetabular process and flaring out laterally before merging with the body of the ilium at the base of the postacetabular process. The body of the ilium is expanded to a certain extent above the buttress. The postacetabular process is considerably shorter than the pre-acetabular, and takes no part in the formation of the buttress. Above the postacetabular process the ilium is continued posteriorly as a short crest, medial to the base of the posterior process. The maximum length of the ilium is 130 mm.

Pubis

The proximal part of the pubis (Fig. 3A) is incomplete, and the areas of articulation with the ilium and, to a lesser extent, the ischium are not fully preserved. The ventral edge of the bone is deeply notched below the proximal end, and this appears to be a natural condition. Below this embayment, which represents an open obturator foramen, the pubis curves medially and forwards to terminate as a horizontal plate with an average width of 24 mm. The length of the pubis, as preserved, is 145 mm.

For prosauropods an open obturator foramen is described to date only

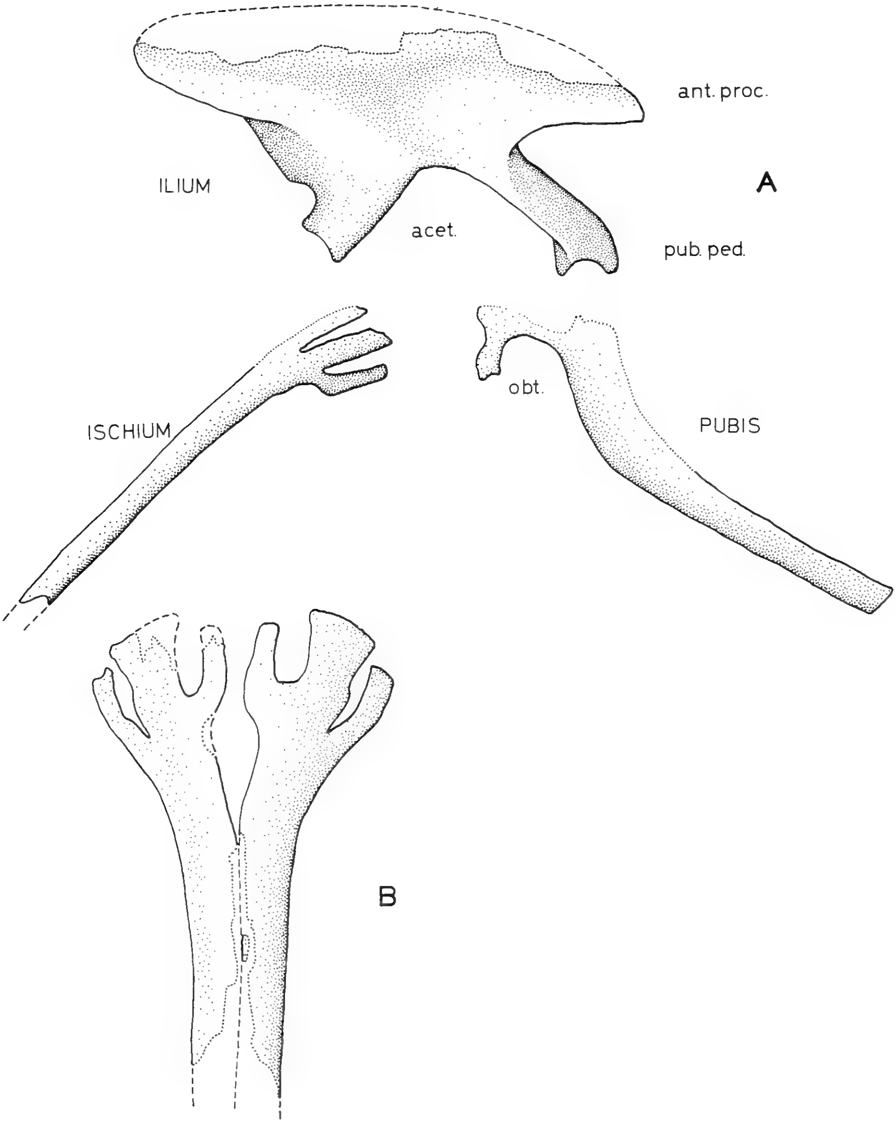


Fig. 3. *Anchisaurus capensis* (Broom), SAM-990. A. Pelvic girdle in right lateral view. B. Ischia in ventral view. × 0,5.

in SAM-990 (Fig. 10H) and *Anchisaurus polyzelus* (Fig. 10G, K); in all other prosauropods it is enclosed ventrally as in *Efraasia* (Fig. 10J, N). A similar open obturator foramen is present in most theropods (for *Allosaurus* and *Ceratosaurus* see Gilmore 1920). Romer (1923) noted that as a result of the more vertical orientation of the archosaurian femur there is a trend amongst archosaurs to reduce that part of the pelvis equivalent to the central portion of the pubo-ischiadic plate of primitive reptiles. The loss of the ventral border of the obturator foramen in *Anchisaurus* (Fig. 10G, H, K) and most therapods probably represents the loss of that portion of the m. pubo-ischio-femoralis externus 2 which originated ventral to the acetabulum in most prosauropods and in all sauropods (see Romer 1923: fig. 2, *Camarasaurus*).

Ischium

Both ischia (Fig. 3), with a preserved length of 136 mm, are present, but are incomplete posteriorly. In each the widened proximal portion is curved outwards and carries two embayments, one above a ventral hook-shaped keel and the other, less clearly defined, lying more dorsally. The proximal portions of the ischia are separated by an ovoid space, but the shafts are closely appressed and form a dorsally open trough.

HIND LIMB

Femur

The femur (Fig. 4A), which is seen in dorsal (anterior) view, is broad and fairly powerful but, with a preserved length of 194 mm, it is incomplete proximally and distally. The proximal end, as shown by what is still preserved, was inclined fairly sharply inwards. Below the proximal end the femur is strongly built and raised to a smooth crest, which runs from proximo-laterally to disto-medially where it merges into the flat distal end. No condyles are preserved, and only an indication of the base of the fourth trochanter can be made out, high in the upper half of the bone.

Fibula

The right fibula (Fig. 4B) lies in its natural position between the femur and the pes and is seen in lateral (external) view. The proximal half is stoutly built and leads to a crest formed in the middle of the bone, directed sideways and forwards. The distal part of the bone is slender and tapers off to the articulation with the pes. Both proximal and distal ends are incomplete and the preserved length of the bone is 176 mm.

Pes

The pes (Figs 4C, 6, 11K) is seen in ventral view, the bones being either eroded or indicated by bone impressions. The calcaneum is incomplete laterally, and probably extended out slightly farther than shown. The astragalus is transversely elongated, with a rounded anterior surface curving back to the

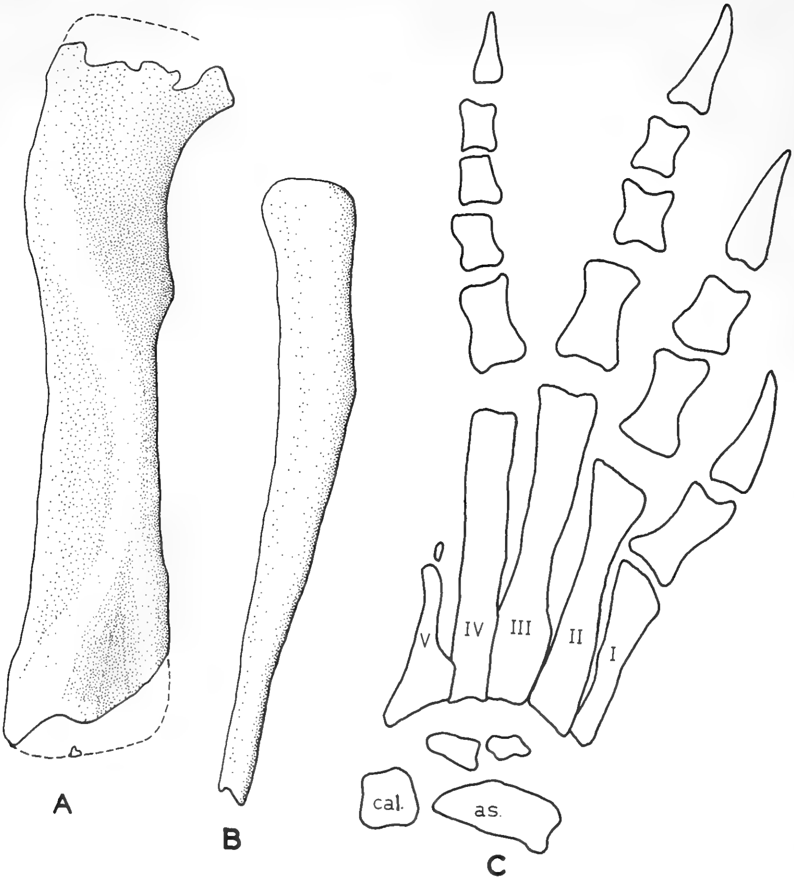


Fig. 4. *Anchisaurus capensis* (Broom), SAM-990. A. Right femur in dorsal (anterior) view. B. Right fibula in lateral view. C. Right pes in ventral view. × 0,5.

narrow lateral corner of the bone. Both calcaneum and astragalus are preserved as impressions, both approximately 15 mm long.

Two small distal tarsal elements are preserved, probably nos 3 and 4. No. 3 is no more than a bony nodule, while 4 is more robust with posterior and medial surfaces at right angles to each other and a convex anterior surface facing metatarsals IV and V. The considerable space between the astragalus and the proximal ends of metatarsals I and II suggests that the two distal tarsals are laterally displaced.

All five metatarsals are preserved, in several cases as somewhat imperfect impressions. There is the usual overlapping of the proximal ends with each metatarsal slightly underlying its medial fellow. Metatarsal V is short and narrow but provided with a strong and wide base. Metatarsal IV is about twice as long and of more or less equal width over its entire length. Metatarsal III is the longest and most robust of the series, while II is slightly shorter than IV. The distal ends of metatarsals III and IV are squarely truncated but metatarsal II terminates in an oblique surface, so that the medial inclination of the row of phalanges seems to be a natural one. This could be true, too, of the short metatarsal I, although this element is incomplete distally.

A small fragment of bone in front of the fifth metatarsal probably represents a vestigial phalanx. The form and degree of preservation of the phalanges are apparent from Figures 4C and 6, and from Table 2.

TABLE 2.
Anchisaurus capensis (Broom), SAM–990. Dimensions of pes (in mm).

Metatarsal length			*Phalanx length (proximal to distal)*				
Metatarsal I	44	Digit I	30	34			
II	76	II	30	22	31		
III	86	III	30	17	14	30	
IV	75	IV	24	16	12	12	21
V	48	V	—				

SLENDER- AND BROAD-FOOTED PROSAUROPODS

When the feet of anchisaurids and plateosaurids are drawn so that digit II of the manus (Fig. 7) or digit III of the pes (Fig. 8) are reduced to unit length then two groups are distinguishable, those with slender feet (Figs 7A, C–D, I, 8D–G, 8I) and those with broad feet (Figs 7B, E–H, J–Q, 8A–C, H, J–S).

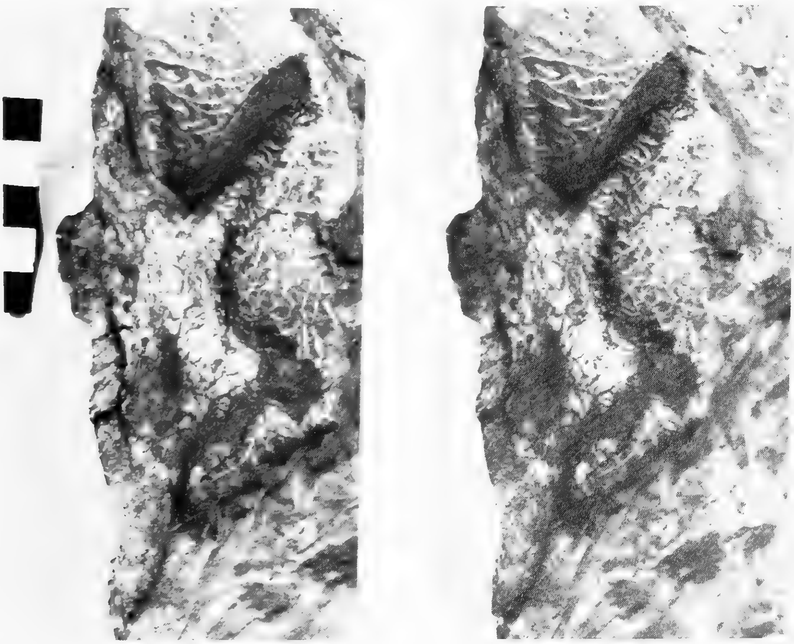


Fig. 5. *Anchisaurus capensis* (Broom), SAM-990. Stereophotograph of right ilium.

The difference is clearest for the manus (digits II to IV) and, where both fore- and hind feet are known, the manus and pes are both slender (Figs 7C, E, I, 8D) or broad (Figs 7B, 8H; 7E, 8K; 7G, 8L; 7J, 8N; 7K, 8O; 7Q, 8Q). The difference between slender and broad feet is not growth related since there are small prosauropods with broad feet (Figs 7B, 8A–C, H). These appear to be juveniles of species that grew much larger (Figs 7B, H, K, 8H, O–P—all *Ammosaurus major*, see Galton 1971) and all the larger prosauropods are broad-footed. The prosauropod families Plateosauridae (Figs 7–8) and Melanorosauridae (see Bonaparte 1972*a*: figs 62, 70; Raath 1972: figs 9f, 10a–b) are all broad-footed, whereas the Anchisauridae as currently classified include both slender and broad-footed forms (Figs 7–8). '*Gyposaurus*' *capensis* (Figs 3C, 5, 7G, 10K) and *Thecodontosaurus antiquus* (Figs 8F, 11G) are both slender-footed species but broad-footed species have been incorrectly referred to both genera.

SYSTEMATIC DISCUSSION

Order SAURISCHIA

Suborder SAUROPODOMORPHA

Infra-order PROSAUROPODA

Family **Anchisauridae** Marsh, 1885

Diagnosis

Smaller forms, skull lightly built, shallow posterior half of lower jaw with articulation in line with tooth row, manus and pes slender.

Genus *Anchisaurus* Marsh, 1885

(includes *Megadactylus* Hitchcock, *Amphisaurus* Marsh, *Gyposaurus* Broom)

Diagnosis

Centra of dorsal vertebrae low, broad bases to neural spines of anterior caudal vertebrae, ilium with long anterior process, pubis with open obturator foramen and a relatively narrow distal part that is not apron-like.

The characters of the skull, neck and manus listed below (p. 133) for *Anchisaurus polyzelus* may also be diagnostic of the genus, but these regions are not known in *A. capensis*.

Anchisaurus polyzelus (Hitchcock, 1865)

Megadactylus polyzelus Hitchcock, 1865: 40, pl. 9 (fig. 6). Cope, 1870: 122A–G, pl. 13 (preocc.).
Amphisaurus polyzelus Marsh, 1882: 84 (preocc.).
Anchisaurus polyzelus Marsh, 1885: 169; 1892: pl. 16 (fig. 3) pl. 17 (fig. 6); 1896: 147, pl. 3 (figs 4–5). Lull, 1915: 119, figs 14–17; 1953: 99, figs 12–14a. Galton, 1971: 782, fig. 7C; 1973: fig. 1F, H, M, O, P, S.
Anchisaurus colurus Marsh, 1891: 267; 1892: 543, pl. 15, 16 (figs 1, 2); 1893: 169, pl. 6; 1896: 148, pl. 2 (figs 1–3), pl. 3 (figs 1, 2), pl. 4. Huene, 1906: 6, figs 1–6, pls 1–3; 1914*b*: 69, figs 1–11; Lull, 1912: 414, figs 2–3; 1915: 130, figs 18–21, pls 4, 10.
Thecodontosaurus polyzelus Huene, 1906: 19, figs 10, 10a; 1914*b*: 75, figs 23–24; 1932: 116.
Yaleosaurus colurus Huene, 1932: 119, pl. 14 (fig. 1), pl. 54 (fig. 3). Lull, 1953: 107, figs 15–18, pl. 4.

Types

Incomplete skeleton (AM 41/109) from Longmeadow Sandstone, upper part of Newark Series (Upper Triassic) of Springfield, Massachusetts, U.S.A. (*A. polyzelus*). Almost complete skeleton (YPM 1883) from Portland beds, upper part of Newark Series near Manchester, Conn., U.S.A. (*A. colurus*).

Diagnosis

$\pm$ 9 maxillary teeth, 16 dentary teeth, basipterygoid processes very small, cervical vertebrae elongate, metacarpal I broad, digits II and III of manus subequal in length, ungual I of pes smaller than ungual II.

Discussion

Megadactylus Hitchcock being preoccupied, Marsh (1882) replaced it with *Amphisaurus* (also preoccupied) and then *Anchisaurus* (Family Anchisauridae also proposed). Huene (1906) referred the material of *Megadactylus polyzelus* Hitchcock to *Thecodontosaurus* as *T. polyzelus* (Hitchcock) and used the Family Thecodontosauridae (originally proposed by Lydekker, 1890: 246) to replace Anchisauridae. Marsh (1891) made YPM 1883 the holotype of a new species of *Anchisaurus*, *A. colurus*, but he did not indicate how it differed from *A. polyzelus* (AM 41/109). Huene (1906) suggested that *Anchisaurus polyzelus* resembled *Thecodontosaurus* and differed from *Anchisaurus colurus* in several features, discussed here together with others noted later by Huene (1907–08, 1932) (for full discussion see Galton, in press):

1. *Shortness of cervical vertebrae.* Huene (1932) noted that AM 41/109 resembled *Thecodontosaurus* (Fig. 11A) in the shortness of the anterior cervical vertebrae, which are elongate in YPM 1883 (Figs 9H, 11B). However, this comparison was based on misidentification of part of the neural arch of a dorsal vertebra (Galton in press, fig. 3a–c) as a cervical vertebra (Huene 1914*b*: fig. 23a).

2. *Shortness of dorsal vertebrae.* Huene (1906) originally noted that AM 41/109 differed from *Thecodontosaurus* and resembled YPM 1883 in having very elongate dorsal vertebrae. Later Huene (1914*b*) figured an extremely short centrum of AM 41/109 as that of a dorsal vertebra. Although not stated, this implied that the dorsal vertebrae of AM 41/109 are extremely short as in *Thecodontosaurus*. The isolated centrum figured by Huene (1914*b*) could not be located but judging from the proportions it was probably part of an anterior caudal vertebra. The proportions of an isolated neural arch (Galton in press, fig. 3a–c) and of a centrum (Galton in press, fig. 5c) show that the dorsal vertebrae of AM 41/109 were probably elongate (i.e. the centra were low) as in YPM 1883 (Fig. 9K).

3. *Slenderness of neural spines of anterior caudal vertebrae.* This comparison by Huene (1906) was based on misleading figures given by Cope (1870) and Marsh (1893, 1895, 1896). Cope (1870: pl. 8 (fig. 7): see Lull 1953:

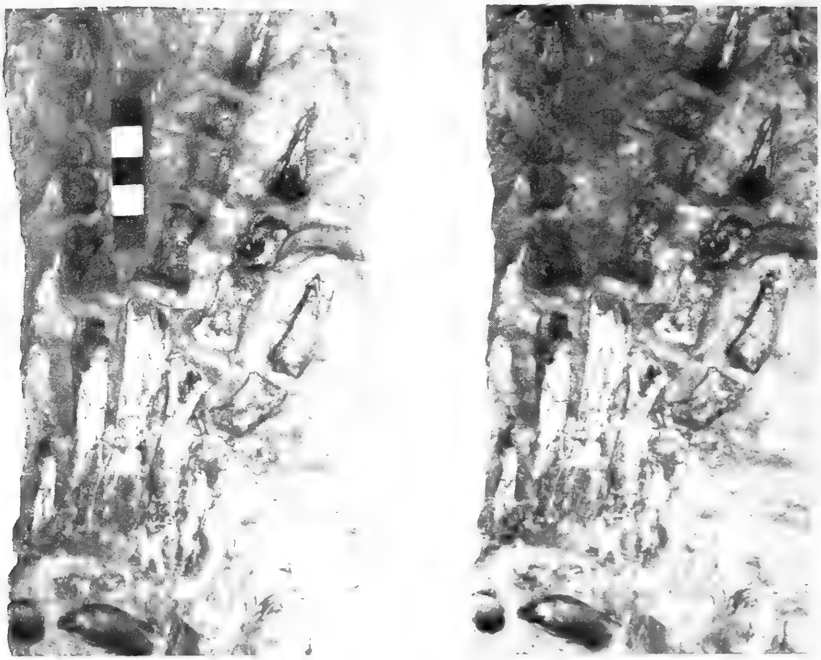


Fig. 6. *Anchisaurus capensis* (Broom), SAM-990. Stereophotograph of right pes in ventral view.

fig. 12a) did not indicate that the neural spines of the anterior caudal vertebrae of AM 41/109 were damaged and incomplete (Fig. 9P); originally the neural spines were broader and not as narrow as in the vertebrae referred to *Thecodontosaurus* (Fig. 9S) by Huene (1907–08: pl. 77 (fig. 4); 1914*b*: fig. 40).

Most of the supposed differences between AM 41/109 and YPM 1883 were either the result of misinterpretation (1–3 above, different position of fourth trochanter of femur) or the result of differences in preservation (form of radius, metacarpals, tibia, fibula: see Galton in press). YPM 1883 does differ from AM 41/109 in having a proportionally long centrum to the last dorsal vertebra (but this might be sacral vertebra 3) and a proportionally smaller manus with a less trenchant first ungual phalanx (Fig. 7A, C). However, these differences probably represent individual variations within a species because individuals of the ornithopod dinosaur *Hypsilophodon foxii* show a much wider range of morphological variation (see Galton 1974). YPM 1883 should be referred to *Anchisaurus polyzelus* because, on the basis of available material, it cannot be distinguished from AM 41/109 by any characters of taxonomic significance and, in addition, AM 41/109 does not show any unique resemblance to *Thecodontosaurus*. Consequently, *Anchisaurus colurus* Marsh is a junior synonym of *Anchisaurus polyzelus* (Hitchcock) and, as *A. colurus* is the type species of the

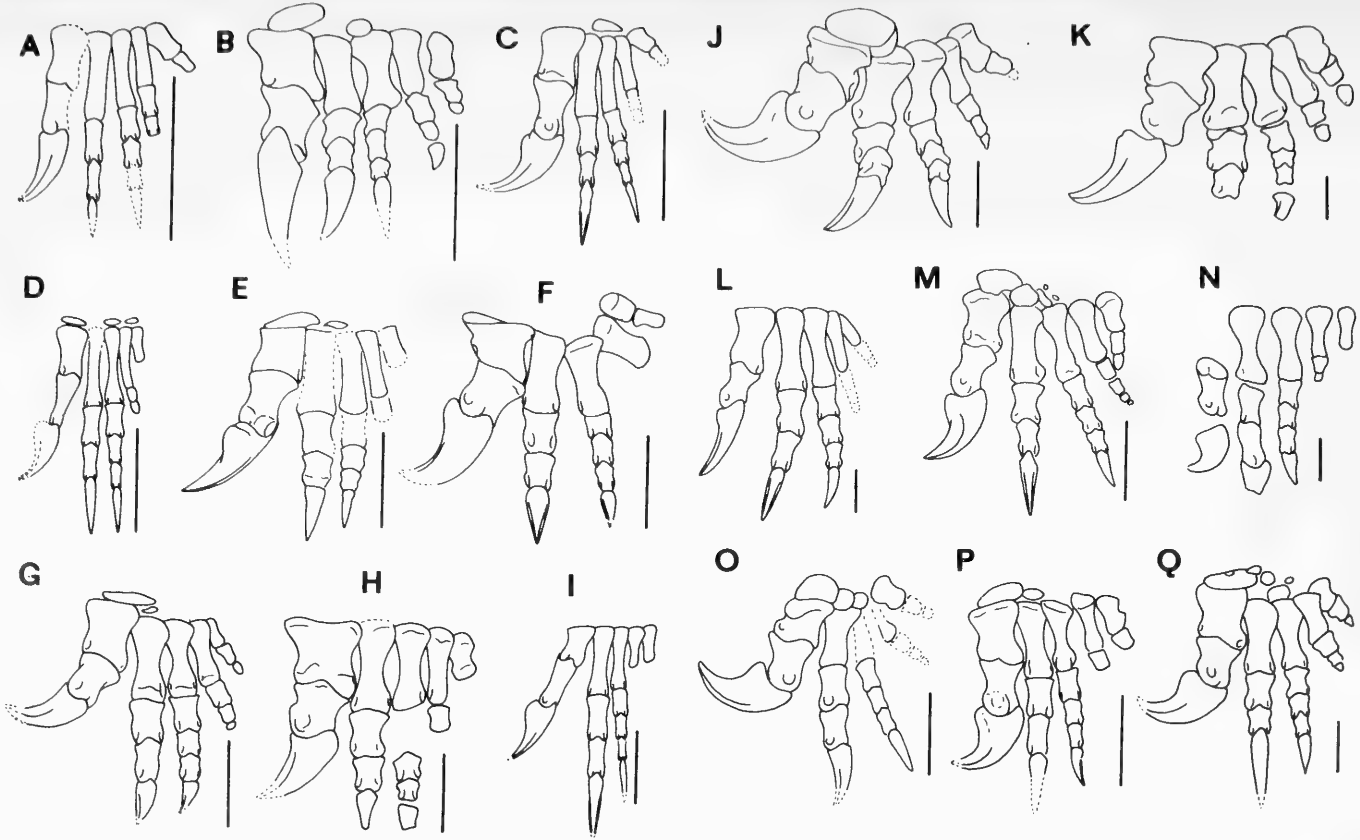


Fig. 7. Comparison of the manus of prosauropods, either right in dorsal view or left in ventral view (E), all drawn to digit II unit length, scale = 5 cm. These genera are divided by Romer (1966) between the families Anchisauridae (A–D, F, J, O–Q) and Plateosauridae (H, K–N). A. *Anchisaurus polyzelus* AM 41/109. B. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). C. *Anchisaurus polyzelus*, YPM 1883. D. *Thecodontosaurus antiquus*, YPM 2195. E. *Ammosaurus* cf. *major*, Galton (1971). F. *Massospondylus harriesi*, figured as *M. browni* by Van Hoepen (1920*b*). H. *Lufengosaurus huenei*, figured as *Yunnanosaurus huangi* by Young (1942). I. *Efraasia diagnostica*, SMNS 12667. J. *Massospondylus harriesi*, from Broom (1911). K. *Lufengosaurus huenei*, figured as *L. magnus* by Young (1947). L. *Plateosaurus erlenbergiensis*, after Galton (1971). M. *Plateosaurus* sp., figured as *Pachysaurus ajax* by Huene (1932). N. *Plateosaurus* sp., figured as *Teratosaurus minor* by Huene (1907–08). O. *Aetonyx palustris*, from Broom (1911). P. *Aetonyx palustris*, AMNH 5624. Q. *Gryponyx africanus*, from Broom (1911).

genus *Yaleosaurus* (Huene 1932: 122), *Yaleosaurus* is a junior synonym of *Anchisaurus* Marsh, 1885.

Anchisaurus capensis (Broom, 1911)

Hortalotarsus skirtopodus (*non* Seeley, 1894) Broom, 1906: 201, pl. 3.
Gyposaurus capensis Broom, 1911: 293.

Type

Partial skeleton (SAM-990) from the Cave Sandstone, Stormberg Series (Upper Triassic) of Ladybrand, Orange Free State, South Africa.

Diagnosis

Ungual 1 largest on pes.

Discussion

Because of its nature, SAM-990 can be distinguished from *Anchisaurus polyzelus* (YPM 1883) only by the relative size of ungual 1 of the pes—large in SAM-990 and small in YPM 1883. *Anchisaurus capensis* (Broom) is distinguishable from all prosauropods other than *A. polyzelus* (Hitchcock) by the following combination of characters:

1. Centra of posterior dorsal vertebrae (about the tenth) are proportionally low so that the ratio of central length to height $(\frac{L}{H})$ is 2,1 (Figs 2, 9L).
2. Anterior process of ilium is elongate (Figs 3, 5, 10B).
3. Subacetabular part of pubis is emarginated ventrally so that the obturator foramen is open (Figs 3, 10H).
4. The pes is slender (Figs 4C, 6C, 11K).
5. Broad bases to neural spines of anterior caudal vertebrae (Figs 2, 9Q).

The form of these elements in the species of Anchisauridae is summarized in Table 3 to facilitate comparisons. The systematic position of other species incorrectly referred to '*Gyposaurus*' are discussed below (pp. 141, 143, 147).

TABLE 3.
Comparison of species attributed to '*Gyposaurus*' with other anchisaurids.

	Dorsal Centra: length/ height	*Neural spine of anterior caudal*	*Anterior process of ilium*	*Proximal pubis/ obturator foramen*	*Pes*
'*Gyposaurus*' *capensis*	2,1	wide	long	shallow/open	slender
'*Gyposaurus*' *erectus*	1,4	wide	short	deep/closed	broad
'*Gyposaurus*' *sinensis*	1,1	—	short	deep/closed	broad
Anchisaurus polyzelus	2,1	wide	long	shallow/open	slender
Thecodontosaurus antiquus	1,7	narrow	short	—	slender
Efraasia diagnostica	2,5	narrow	short	deep/closed	slender

Genus *Efraasia* Galton, 1973

Diagnosis

Basipterygoid processes of medium length, cervical vertebrae elongate, centra of dorsal vertebrae low, narrow bases to neural spines of anterior caudal vertebrae, slender metacarpal I, digit II of the manus robust and appreciably longer than digit III, ilium with short triangular anterior process, pubis with closed obturator foramen with an apron-like distal part, ungual 1 largest in pes.

Efraasia diagnostica (Huene)

Thecodontosaurus diagnosticus Fraas, 1913: 1098 (*nomen nudum*).
Palaeosaurus (?) *diagnosticus* Huene, 1932: 52, 73, figs 1, 2, 7–8, pls 4–6.
Palaeosauriscus diagnosticus Charig, 1967: 712.
Efraasia diagnostica Galton, 1973: 247, figs 1A–E, 2–15, 16A, 17C–D.

Syntypes

An almost complete skeleton (SMNS 12667) (Berckhemer 1938) together with additional material (SMNS 12668) from the Stubensandstein (Upper Triassic) of Pfaffenhofen, Württemberg, West Germany (see Galton 1973).

Diagnosis

As for genus.

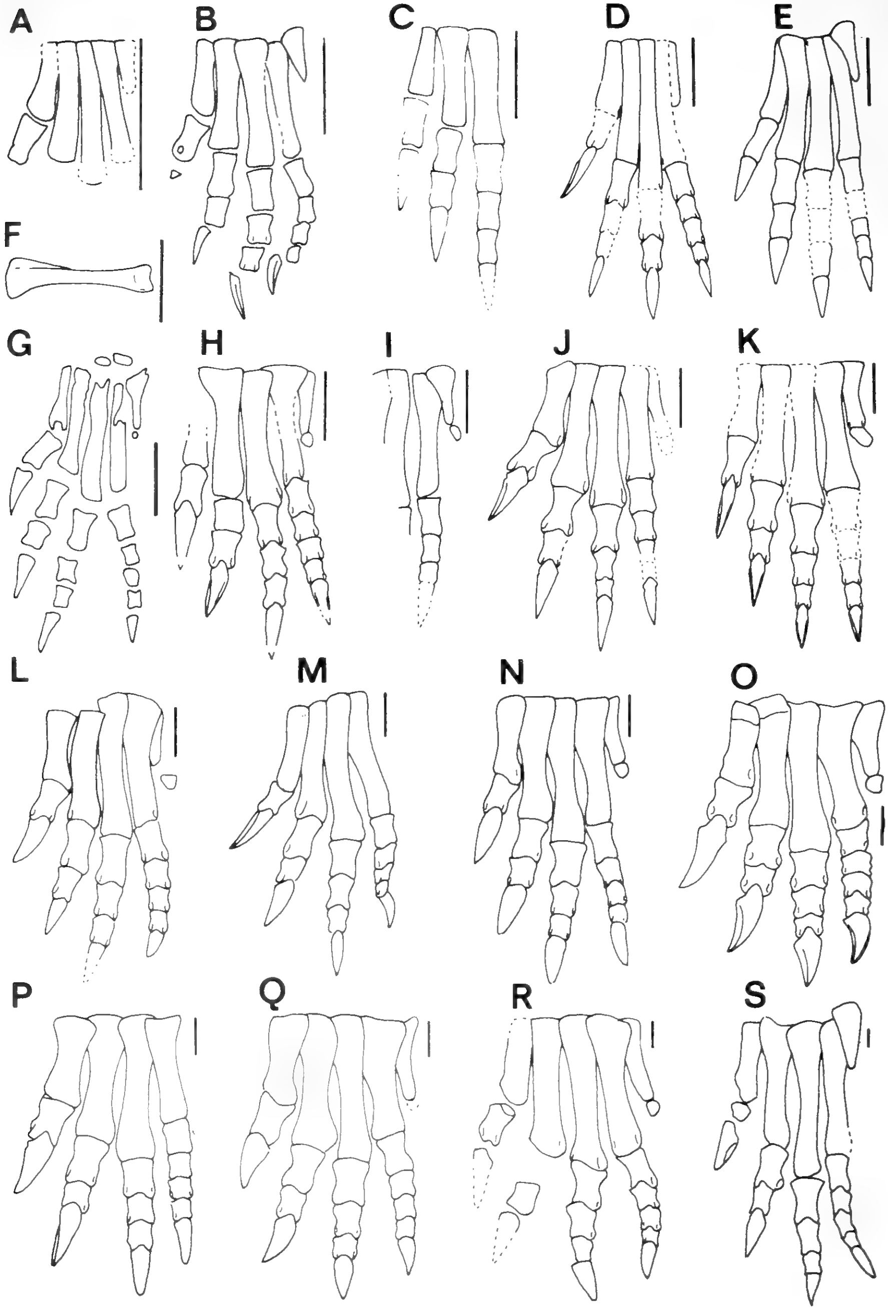
Discussion

As shown by the manus (Fig. 7I) and the pes (Figs 8D, 11M), *Efraasia diagnostica* undoubtedly represents a slender-footed prosauropod. Apart from that of *Anchisaurus polyzelus* (YPM 1883, Fig. 12B; Huene 1906: pl. 1), this is the only reasonably complete and well-preserved skeleton (Fig. 12A; Berckhemer 1938) of a slender-footed prosauropod described to date. *Efraasia diagnostica* (Figs 7I, 8D, 9I, M, 10D, J, N, 11M) resembles *Anchisaurus capensis* in several features (Table 3) but differs in three important respects, viz. the ilium has a short triangular anterior process (Fig. 10D), the subacetabular part of the pubis is deep with a complete obturator foramen (Fig. 10J, N), and the bases of the neural spines of the anterior caudal vertebrae are narrow (Fig. 9R).

Genus *Thecodontosaurus* Riley & Stutchbury, 1836

Diagnosis

At least 21 dentary teeth (in holotype, Fig. 9B); from referred specimens without teeth diagnosis tentatively expanded as follows: elongate basipterygoid processes, cervical vertebrae proportionally short compared with other anchisaurids, high centra to dorsal vertebrae, narrow base to neural spines of anterior and caudal vertebrae, high placed deltopectoral crest on proximal third of humerus, manus with slender metacarpal I and digits II and III subequal in length, short triangular anterior process to ilium.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Thecodontosaurus antiquus Morris

Thecodontosaurus Riley & Stutchbury, 1836: 398; 1840: 352, pl. 29 (figs 1–2).
Thecodontosaurus antiquus Morris, 1843: 211.

Type

Incomplete dentary with teeth from the Magnesian Conglomerate (Upper Triassic) near Bristol, England.

Diagnosis

As for genus.

Discussion

Riley & Stutchbury (1836, 1840) did not give a specific name for *Thecodontosaurus* and this oversight was rectified by the proposal of *T. antiquus* Morris, 1843.

Thecodontosaurus was the first genus of prosauropod to be described so it is unfortunate that there is no articulated association between teeth of the type and the postcranial material referred to the genus by Seeley (1895*a*) and Huene (1907–8, 1914*b*). Indeed, the only articulated bones referred to *Thecodontosaurus* are a few short sequences of vertebrae (Huene 1907–8: figs 214, 218–220) and a fore limb with scapula, cervical vertebra and dorsal ribs (Fig. 11A–G). The description and skeletal reconstruction of *Thecodontosaurus antiquus* given by Huene (1932: 116, pl. 54 (fig. 1)) are based on many specimens. However, the postcranial remains from Bristol indicate the presence of a slender-footed prosauropod (Fig. 11A–G) and it is reasonable to refer this material to *Thecodontosaurus antiquus*. Species of *Thecodontosaurus* from other parts of the world (see next section and pp. 145, 147, 152, 153) are incorrectly referred to this genus.

Fig. 8. Comparison of the pes in various prosauropods, either right in dorsal view or left in ventral view (A, C, E, G, I,), all drawn to digit III unit length, scale lines represent 5 cm. These genera are divided by Romer (1966) between the families Anchisauridae (B, C, E–I, L, N, Q) and Plateosauridae (M, O, P, R, S). A. *Ammosaurus major*, YPM 209. B. *Aristosaurus erectus*, from Van Hoepen (1920*a*). C. *Thecodontosaurus browni*, from Huene (1932). D. *Efraasia diagnostica*, SMNS 12668. E. *Anchisaurus polyzelus*, YPM 1883. F. *Thecodontosaurus antiquus*, metatarsal III, from Huene (1907–08). G. *Anchisaurus capensis*, SAM-990. H. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). I. *Hortalotarsus skirtopodus*, figured as *Thecodontosaurus skirtopodus* by Huene (1906). J. *Ammosaurus major*, YPM 208. K. *Ammosaurus* cf. *major*, from Galton (1971). L. *Massospondylus harriesi*, figured as *M. browni* by Van Hoepen (1920*b*). M. *Plateosaurus gracilis*, from Berckhemer (1938). N. *Massospondylus harriesi*, from Broom (1911). O. *Lufengosaurus huenei*, figured as *Yunnanosaurus magnus* by Young (1947). P. *Lufengosaurus huenei*, figured as *Yunnanosaurus robustus* by Young (1951). Q. *Gryponyx africanus*, from Broom (1911). R. *Plateosaurus robustus*, from Huene (1932). S. *Plateosaurus* sp., figured as *Pachysaurus wetzelianus* by Huene (1932).

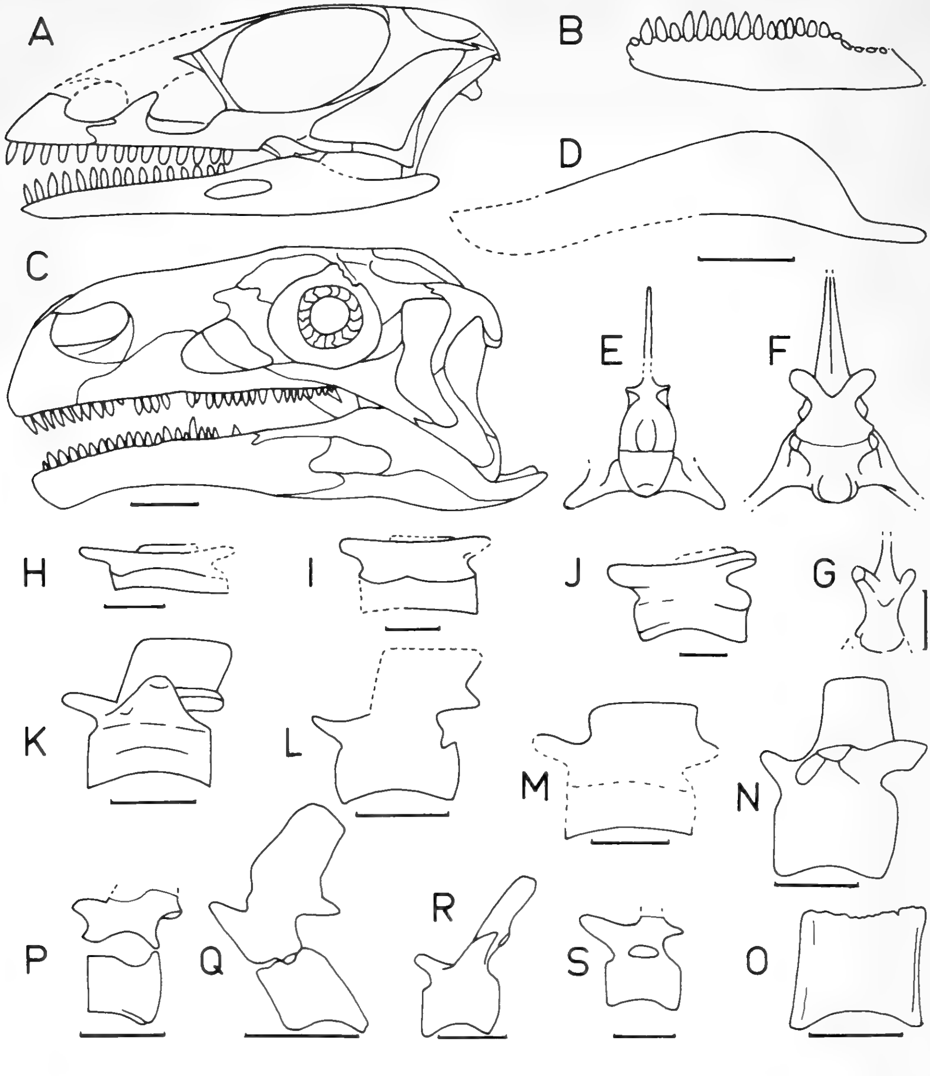

Fig. 9. Comparison of skulls and vertebrae of prosauropods, scale = 2,5 cm, A, B, D–F × 0,5. A. Skull of *Anchisaurus polyzelus*, YPM 1883, lateral view. B. *Thecodontosaurus antiquus*, left partial dentary in lateral view, from Riley & Stutchbury (1840). C. Skull of *Plateosaurus* in lateral view, from Romer (1966). D. *Massospondylus harriesi*, left partial lower jaw in lateral view, from Haughton (1924). E–G. Braincases in ventral view: E. *Anchisaurus polyzelus*, YPM 1883. F. *Thecodontosaurus antiquus*, YPM 2192. G. *Efraasia diagnostica* basisphenoid, SMNS 12667. H–J. Third cervical vertebra in lateral view: H. *Anchisaurus polyzelus*, YPM 1883. I. *Efraasia diagnostica*, SMNS 12667. J. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). K–O. dorsal vertebrae (tenth to twelfth) in lateral view: K. *Anchisaurus polyzelus*, YPM 1883. L. *Anchisaurus capensis*, SAM-990. M. *Efraasia diagnostica*, SMNS 12667. S. *Thecodontosaurus antiquus*, from Huene (1907–08).

Anchisauridae *nomina dubia*

Hortalotarsus skirtopodus Seeley, 1894

Hortalotarsus skirtopodus Seeley, 1894: 411, figs 1–3.
Thecodontosaurus skirtopodus Huene, 1906: 44, figs 72–78, pls 13, 14. Haughton, 1924: 370. Huene, 1932: 117. Haughton & Brink, 1954: 35.
Gyposaurus skirtopodus Charig, 1967: 712.

Type

Incomplete hind limb in the Albany Museum, from the Cave Sandstone, Stormberg Series, of Barkly East Division, Cape Province, South Africa.

Discussion

The assignment of *Hortalotarsus skirtopodus* to *Thecodontosaurus* by Huene (1906) was based in part on the characters of isolated bones found at localities different from that of the type specimen. The pes of the type (Fig. 8I) is obviously that of a slender-footed prosauropod, and Huene (1906) could not distinguish it from the pes of *Thecodontosaurus*. However, this pes (Fig. 8I) is also indistinguishable from those of *Anchisaurus capensis* (Fig. 11K), *Anchisaurus polyzelus* (Fig. 11L) and *Efraasia diagnostica* (Fig. 11M). This specimen is generically and specifically indeterminate so *Hortalotarsus skirtopodus* Seeley is a *nomen dubium*.

Thecodontosaurus browni (Seeley, 1895*b*)

Massospondylus browni Seeley, 1895*b*: 118, figs 13–14.
Thecodontosaurus browni Huene, 1906: 141, pl. 12 (figs 7–8); 1932: 118. Broom, 1911: 293. Haughton, 1924: 370.

Type

Limb bones (BMNH R3302) from the Red Beds, Stormberg Series of Telle River, Herschel, Cape Province, South Africa.

Discussion

Seeley (1895*b*) noted that the proportions of the phalanges of the pes are very similar to those of *Hortalotarsus* (Fig. 8H) so this is probably another generically and specifically indeterminate specimen of a slender-footed prosauropod.

Thecodontosaurus minor Haughton, 1918

Thecodontosaurus minor Haughton, 1918: 468; 1924: 376, fig. 21.
Thecodontosaurus browni: Huene, 1932: 118.

Type

Left tibia, a cervical vertebra and a portion of a left ilium (SAM-3451) from the Red Beds, Stormberg Series, from road-cutting at Naude's Nek, Pitsing, Maclear District, Cape Province, South Africa.

Discussion

The tibia is slender so this may be a slender-footed prosauropod but, on

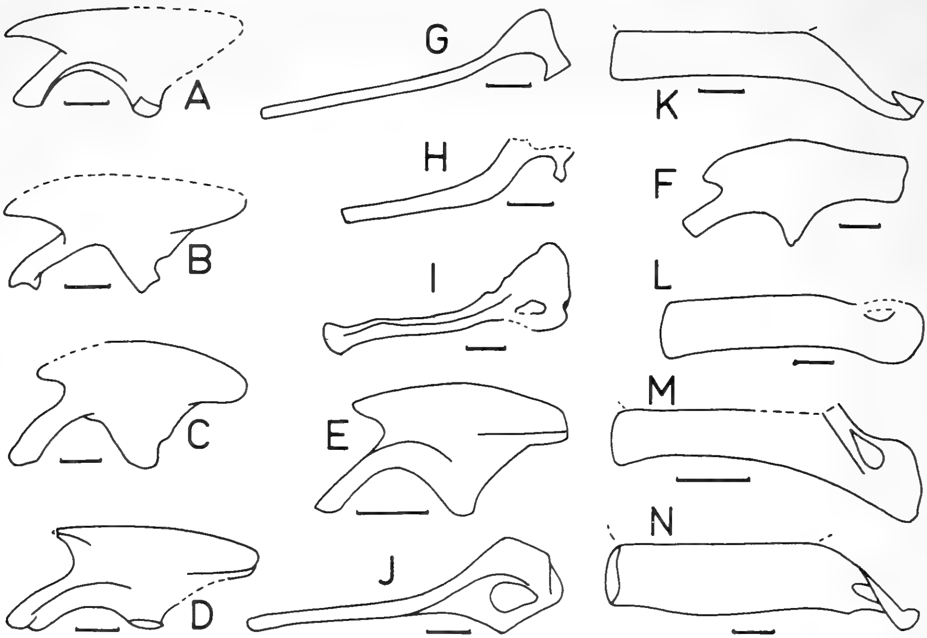

Fig. 10. Comparison of ilium and pubis of prosauropods. Scale = 2,5 cm. A–F. Lateral view of left ilium: A. *Anchisaurus polyzelus*, YPM 1883. B. *Anchisaurus capensis*, SAM-990. C. *Lufengosaurus huenei*, figured as *Gyposaurus sinensis* by Young (1941). D. *Efraasia diagnostica*, SMNS 12667. E. *Aristosaurus erectus*, fromVan Hoepen (1920*a*). F. *Thecodontosaurus antiquus*, from Huene (1907–08). G–J. lateral view of left pubis: G. as A. H as B. I as C. J as D. K–N. Ventral view of right pubis (L, M) or dorsal view of left pubis (K, N): K as A, G. L as C, I. M as E. N as D, J.

the basis of available material, this specimen is a generically and specifically indeterminate prosauropod and *Thecodontosaurus minor* is a *nomen dubium*.

Thecodontosaurus macgilivrayi (Seeley)

Agrosaurus macgilivrayi Seeley, 1891: 161, figs 1–6.
Thecodontosaurus macgilivrayi Huene, 1906: 147, figs 86–90; 1932: 52.

Type

Tibiae, radius, an ungual and tooth (BMNH 49984) from York Peninsula, Queensland, Australia.

Discussion

Huene (1932: 52) subsequently referred *Agrosaurus macgilivrayi* to the Theropoda (Coelurosauria) as do Romer (1956, 1966), Steel (1970) and White (1973). However, the latero-distal surface of the tibia is notched (Fig. 11H–J) (Huene 1906: fig. 86a, d–e) to receive the central ascending process of the astragalus in typical prosauropod fashion. This material undoubtedly represents a prosauropod but is generically and specifically indeterminate, so *Agrosaurus macgilivrayi* is a *nomen dubium*; it may represent a slender-footed prosauropod.

PROSAUROPOD SPECIES INCORRECTLY ASSIGNED TO ANCHISAURIDAE

Family **Plateosauridae** Marsh, 1895

Diagnosis

Larger forms, skull massively built, deep posterior half to lower jaw with articulation offset ventral to line of tooth row, manus and pes broad.

Ammosaurus major Marsh, 1889

Anchisaurus major Marsh, 1889: 331, fig. 1.
Ammosaurus major Marsh, 1891: 267; 1892: 545, pl. 16 (fig. 4), pl. 17 (fig. 3); 1896: 150, pl. 3 (figs 3, 6). Huene, 1906: 15, pls 5–9; 1907–08: 303–04, figs 297–298; 1914*a*: 13; 1914*b*: 74, figs 20–22; 1932: 26. Lull, 1915: 148, figs 24–25; 1953: 123, figs 19–20. Galton, 1971: 786, figs 9, 11A.
Anchisaurus solus Marsh, 1892: 545; 1896: 149. Huene, 1914*b*: 72, figs 12–19. Lull, 1915: 144, figs 22–23; 1953: 120.
Anchisaurus (?) *solus* Huene, 1906: 14, pl. 4.
Ammosaurus solus Huene, 1932: 27, pl. 49 (fig. 1).

Type

Pelvis and hind limbs (YPM 208) from the Portland Beds, upper part of Newark Series near Manchester, Connecticut, U.S.A. (*Ammosaurus major*). Almost complete skeleton (YPM 209) from the same locality and horizon (*Anchisaurus solus*).

Discussion

Ammosaurus has long been regarded as a primitive theropod dinosaur but it is considered as an anchisaurid by Steel (1970) and by Galton (1971), who provides a detailed discussion of the taxonomic position of this genus (Galton in press). The pes of the holotype (Fig. 8J) and of the referred specimens (Fig. 8A, K) plus a referred manus (Fig. 7E) are of the broad type. *Ammosaurus* is a broad-footed prosauropod characterized by the following combination of characters: centra of dorsal vertebrae low, slender sacral rib 3, elongate anterior process to ilium, subacetabular part of the ischium emarginated ventrally (Galton, in press).

Aristosaurus erectus van Hoepen, 1920*a*

Aristosaurus erectus van Hoepen, 1920*a*: 82, figs 1–6, pls 9–10. Haughton 1924: 379. Haughton & Brink, 1954: 33.
Gyposaurus capensis Huene, 1932: 123, pl. 54 (fig. 2).
Gyposaurus erectus Charig, 1967: 712. Steel, 1970: 49.

Type

An almost complete skeleton as slab and counterpart (TM 130) from the Cave Sandstone, Stormberg Series, near Roosendal, Senekal District, Orange Free State, South Africa.

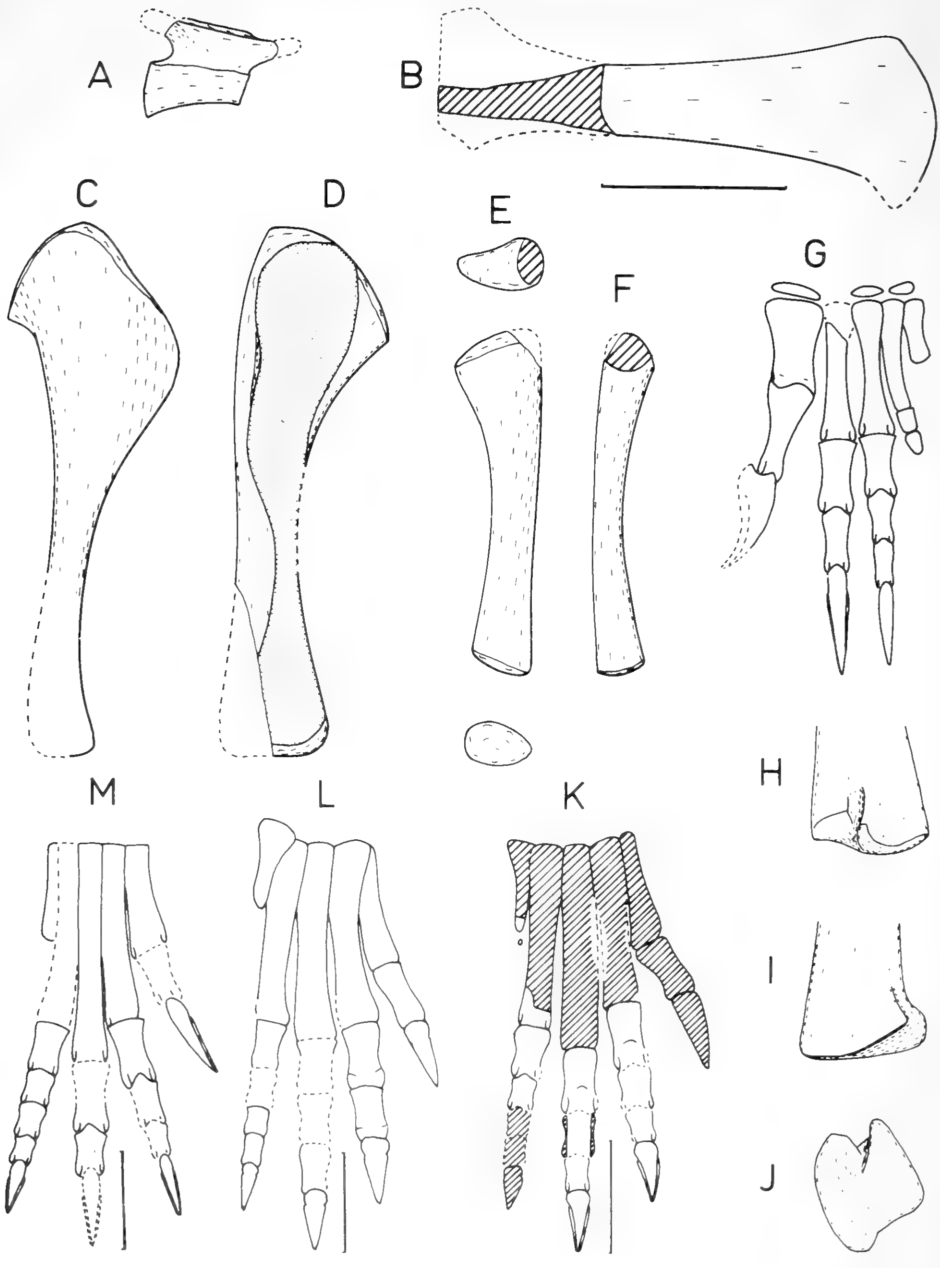

Fig. 11. *Thecodontosaurus*, *Agrosaurus* and comparisons of the anchisaurid pes. Scale = 5 cm, A–J ± × 0,45. A–G. *Thecodontosaurus antiquus*, YPM 2195, from Durdham Down, Bristol, England. Matrix indicated by stipple, broken bone by diagonal shading: A. Right side of anterior cervical vertebra. B. Right scapula in lateral view. C. Left humerus in medial view. D. As C, in anterior view. E. Left ulna in proximal, lateral and distal views. F. Left radius in lateral view. G. Left manus in lateral or dorsal view. H–J. *Agrosaurus macgillivrayi*, distal end of left tibia in lateral view (H), anterior view (I), and distal view (J), all from Huene (1906). K–M. Anchisaurid pes, drawn to digit III unit length: K. *Anchisaurus capensis*, SAM-990, compare with Fig. 5. L. *Anchisaurus polyzelus*, YPM 1883. M. *Efraasia diagnostica*, SMNS 12668.

Discussion

Romer (1956, 1966), Charig (1967), Steel (1970) and White (1973) follow Huene (1932, 1956) in regarding *Aristosaurus* as a junior synonym for *Gyposaurus* but this is unlikely because, in contrast to the situation in *Gyposaurus capensis* (Table 3):

1. In photographs of the skeleton of *Aristosaurus erectus* in Van Hoepen (1920*a*: pls 9–10) and in the reconstruction (Fig. 12D) given by Huene (1932) the dorsal vertebrae are proportionally higher with a central length to height ratio of about 1,4 for dorsal 10.
2. The anterior process of the ilium is short (Fig. 10E).
3. The obturator foramen of the pubis is closed ventrally (Fig 10M).
4. The hind feet of *Aristosaurus erectus* appear to be of the broad type.

There is no reason why *Aristosaurus erectus* should be referred to the genus *Anchisaurus*. *Aristosaurus erectus* appears to be a valid taxon of broad-footed prosauropod, but further preparation and illustration of the holotype is needed.

Genus *Massospondylus* Owen, 1854

(includes *Leptospondylus* Owen, *Pachyspondylus* Owen, *Aetonyx* Broom, *Gryponyx* Broom, *Dromicosaurus* Van Hoepen)

Massospondylus carinatus Owen, 1854

Massospondylus carinatus Owen, 1854: 97. Seeley, 1895*b*: 102, figs 1–12. Huene, 1906: 36, figs 43–70, pls 13–16. Broom, 1911: 241. Haughton, 1924: 383. Huene, 1932: 124.
Leptospondylus capensis Owen, 1854: 97.
Pachyspondylus orpenii Owen, 1854: 97.

Type

Isolated bones from the Red Beds, Stormberg Series of Beaucherf, Harrismith, Orange Free State, South Africa. The holotype in the Museum of the Royal College of Surgeons in London was destroyed during World War II but casts of this material are in the National Museum of Southern Rhodesia, Bulawayo (J. Attridge, pers. comm.).

Massospondylus harriesi Broom, 1911

Massospondylus harriesi Broom, 1911: 299, pls 15–17. Haughton, 1924: 384, figs 21–29. Huene, 1932: 125.
Massospondylus browni (*non* Seeley, 1895*b*): Van Hoepen 1920*b*: 118, pls 17–22.
Aetonyx palustris Broom, 1911: 304, figs 20–23. Haughton, 1924: 404, fig. 30. Huene, 1932: 91.
Gryponyx africanus Broom, 1911: 294, figs 1–9. Haughton, 1924: 417, figs 36–38. Huene, 1932: 88, pl. 7 (figs 1–4).
Gryponyx taylori Haughton, 1924: 420, fig. 39. Huene, 1932: 90.
Dromicosaurus gracilis Van Hoepen, 1920*b*: 103, figs 8–21, pls 13–16. Haughton, 1924: 405.
Thecodontosaurus dubius Haughton, 1924: 377.

Types

Massospondylus harriesi: Bones of the fore limb (SAM-3394) from the top of the Red Beds, Stormberg Series of Foutanie, Fouriesburg, Orange Free State, South Africa.

Aetonyx palustris: Partial skeleton (SAM-2768, 2769, 2770) from the top of the Red Beds (but listed as from Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series from Foutanie, Fouriesburg, Orange Free State, South Africa.

Gryponyx africanus: Pelvis and hind limb, right and left manus, vertebrae (SAM-3357–9) from the top of the Red Beds (but listed as from the Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series of Foutanie, Fouriesburg, Orange Free State, South Africa.

Gryponyx taylori: Pelvic girdle and sacral vertebrae (SAM-3453) from the top of the Red Beds (but listed as from Cave Sandstone by C. E. Gow *in* Anderson & Anderson 1970), Stormberg Series of Fouriesburg, Orange Free State, South Africa.

Dromicosaurus gracilis: Partial skeleton (TM 123) from Red Beds of Naaupoort Nek, Bethlehem, Orange Free State, South Africa.

Thecodontosaurus dubius: Larger portion of a skeleton (SAM-3712) from the Cave Sandstone, Stormberg Series of Ladybrand, Orange Free State, South Africa.

Discussion

On the basis of the phalanges Seeley (1895*b*) stated that *Massospondylus carinatus* had a broad hind foot and Huene (1906) separated this genus from *Plateosaurus* mainly because of its *Thecodontosaurus*-like tibia. *Massospondylus* was the first genus of broad-footed prosauropod to be described from South Africa.

The manus (Fig. 7F–G, J) and the pes (Fig. 8L, N) of *Massospondylus harriesi* (SAM-3394) are obviously of the broad type. The material (Figs 7G, 8L, 12E) described by Van Hoepen (1920*b*) as *Massospondylus browni* should be referred to this species (Haughton 1924). The manus of *Aetonyx palustris* Broom (Fig. 7O) is of the broad type and the pes is similar, as indicated by the measurements given by Huene (1932: 92). J. Attridge (pers. comm.) regards *Aetonyx palustris* as a junior synonym for *Massospondylus harriesi*. The manus (Fig. 7Q) and pes (Fig. 8Q) of *Gryponyx africanus* are of the broad type and *Gryponyx africanus* is probably a junior synonym for *Massospondylus harriesi*.

Gryponyx taylori Haughton is a *nomen dubium* because the material is generically and specifically indeterminate; it probably represents another specimen of *Massospondylus harriesi*.

The manus and pes of *Dromicosaurus gracilis* Van Hoepen are not preserved but were probably of the broad type because *Dromicosaurus* was regarded as being closely allied to *Aetonyx* and *Massospondylus* by Van Hoepen (1920*b*), Haughton (1924) and Huene (1932). J. Attridge (pers. comm.) regards *Dromico-*

saurus gracilis as a junior synonym for *Massospondylus harriesi*. The type specimen of *Thecodontosaurus dubius* Haughton has never been figured, but Huene (1932: 92) referred it to *Aetonyx palustris* so it is presumably a broad-footed form; J. Attridge (pers. comm.) refers this specimen to *Massospondylus harriesi*.

Stratigraphically and geographically, *Massospondylus harriesi* is the most ubiquitous prosauropod in southern Africa.

Plateosaurus gracilis (Huene, 1907)

Thecodontosaurus (?) *hermannianus* Huene, 1907–08: 216, fig. 236, pl. 144 (fig. 1).
Plateosaurus gracilis Huene, 1932: 303.

Type

Right maxilla with teeth from the Stubensandstein (Upper Triassic) of Heslach, in Stuttgart, West Germany.

Lufengosaurus huenei Young, 1941*a*

Lufengosaurus hueni Young, 1941*a*: 1, figs 1–25, pls 1–6; 1947: 41; 1951: 50, fig. 11, pl. 12. Rozhdestvensky, 1965.
Gyposaurus sinensis Young, 1941*b*: 205, pls 1–9; 1948: 91, pls 1–5; 1951: 49.
Yunnanosaurus huangi Young, 1942: 64, figs 1–17; 1951: 56.
Lufengosaurus magnus Young, 1947: 2, figs 1–14.
Yunnanosaurus robustus Young, 1951: 58, figs 12–14, pls 7–10.

Types

Several incomplete skeletons from the lower Lufeng Series (Upper Triassic, Rhaetic) of Lufeng, Yunnan, China.

Discussion

Rozhdestvensky (1966) restudied 70 specimens from the Lufeng Series and decided that *Lufengosaurus huenei*, *L. magnus*, *Yunnanosaurus huangi*, *Y. robustus* and *Gyposaurus sinensis* of Young were all differentiated only on size-related characters and are conspecific (as *Lufengosaurus huenei* Young, 1941*a*). Rozhdestvensky (1966) noted that, judging from the original diagnosis of Young (1941*b*), *Gyposaurus sinensis* is hardly distinguishable from *G. capensis*, but that without visual comparisons or more detailed descriptions it is impossible to decide the relationship between these two species. Galton (1973, in press) noted that '*Gyposaurus*' *sinensis* was incorrectly referred to the genus *Gyposaurus*, and may represent a new genus or be based on juveniles of either *Lufengosaurus* or *Yunnanosaurus*. '*Gyposaurus*' *sinensis* should not be referred to the genus *Gyposaurus* (or *Anchisaurus*) because of the following anatomical features (Table 3):

1. Centra of posterior dorsal vertebrae are proportionally high with a central length to height ratio of 1,1 (Fig. 9O).
2. Anterior process of ilium is short and triangular (Fig. 10C).
3. Subacetabular part of pubis is broken but originally this region was

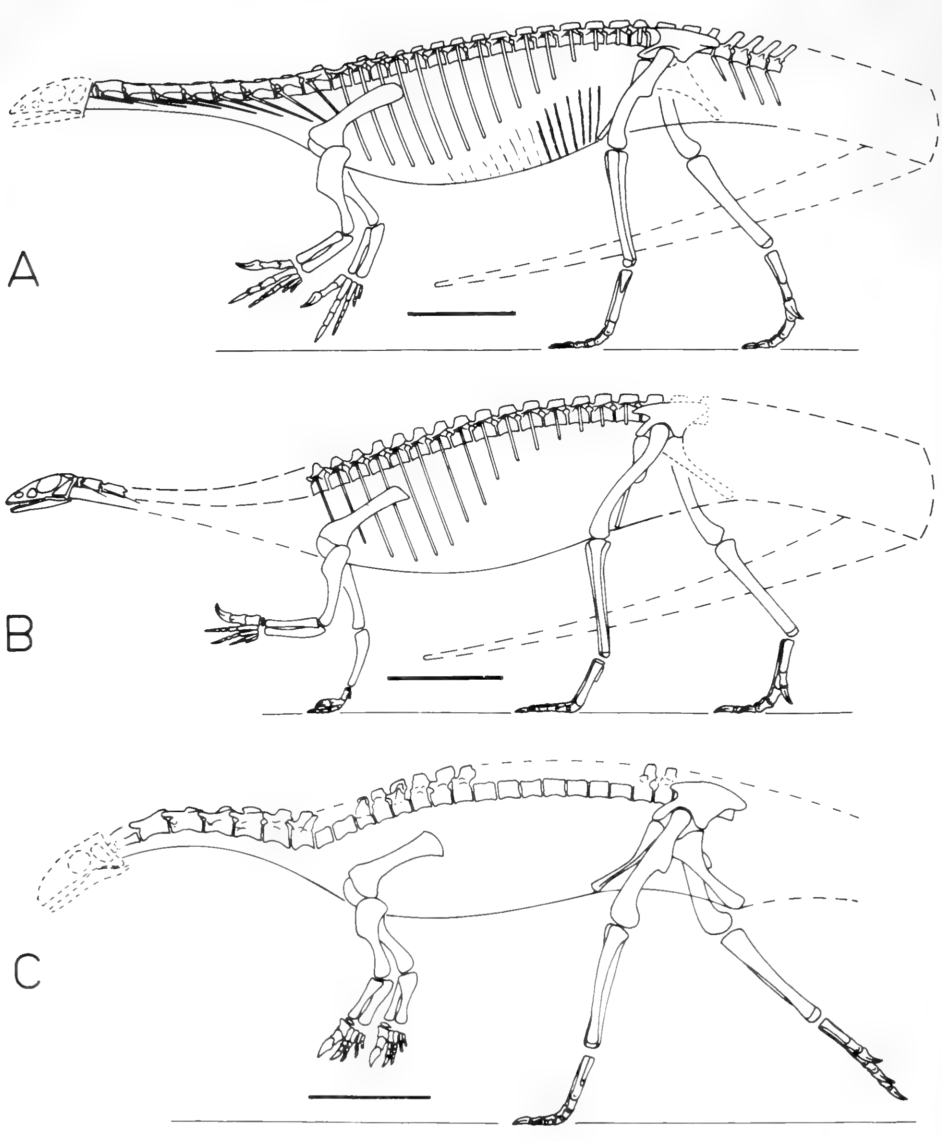

Fig. 12. Skeletal reconstructions of prosauropods. Scale = 20 cm. Tails of A and B diagrammatically folded over. A. *Efraasia diagnostica*, SMNS 12667, 12668, from Galton (1973). B. *Anchisaurus polyzelus*, YPM 1883, AM 41/109, from Galton (1973). C. *Lufengosaurus huenei*, based on figures of individual bones given by Young (1941*b*) as *Gyposaurus sinensis*.

D

E

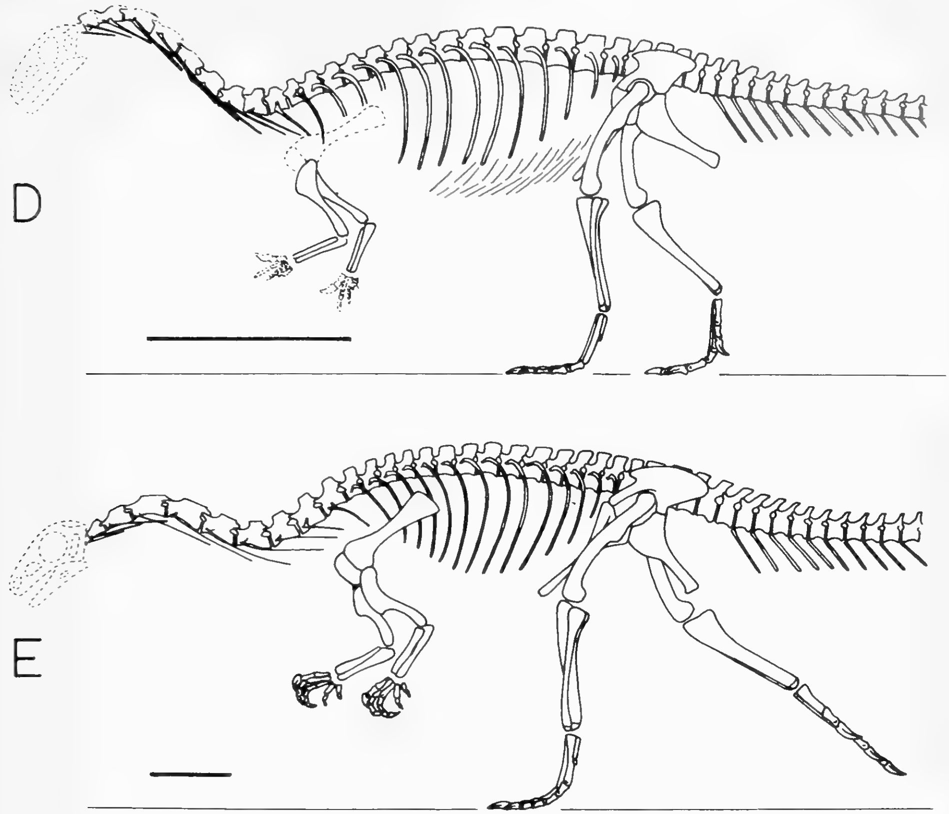

Fig. 12. (*cont.*)
D. *Aristosaurus erectus*, modified from *Gyposaurus capensis* of Huene (1932). E. *Massospondylus harriesi*, modified from *Thecodontosaurus browni* of Huene (1932), based on specimen described as *Massospondylus browni* by Van Hoepen (1920*a*).

deep with a complete obturator foramen (Young 1941*b*: 222; 1948: 96) (Figs 10I, L).

4. Pes (Fig. 8H) and manus (Fig. 7B) are broad.

Young (1941*b*) did not cite the papers of Broom (1906, 1911) so the assignment as *Gyposaurus sinensis* was probably based on the skeletal reconstruction of *Aristosaurus erectus* given by Huene (1932) as *Gyposaurus capensis*. However, the skeleton of '*Gyposaurus*' *sinensis* (Fig. 12C) differs greatly in several aspects from that of *Aristosaurus erectus* (Fig. 12D) and this is especially true for the form of the neck vertebrae (Fig. 9J) and fore limb. It should be noted that the skeletal reconstruction of '*Gyposaurus*' *sinensis* given by Young (1941*b*, pl. 9) bears practically no resemblance to a reconstruction (Fig. 12C) based on figures of the bones of the same specimen given by Young (1941*b*). The correctness of the contention of Rozhdestvensky (1966) that *Gyposaurus sinensis*

Young, 1941*b* is a junior synonym of *Lufengosaurus huenei* Young, 1941*a* is shown by the proportionally short neck and proportionally massive manus of the two types.

Prosauropoda *nomina dubia*

Gryponyx transvaalensis Broom, 1912

Gryponyx transvaalensis Broom, 1912: 82, figs 3–4. Van Hoepen, 1920*b*: 102. Haughton, 1924: 420. Huene, 1932: 91, pl. 7, fig. 5.

Type

Ungual 1 of the manus and a metatarsal (in the Transvaal Museum) from the Bushveld Sandstone (Cave Sandstone), Stormberg Series of Wiepe 1258, northern Transvaal, South Africa.

Discussion

This material is probably prosauropod but is generically and specifically indeterminate.

NON-PROSAUROPOD SPECIES INCORRECTLY ASSIGNED TO ANCHISAURIDAE

Order SAURISCHIA

Suborder THEROPODA

Arctosaurus osborni Adams, 1875

Arctosaurus osborni Adams, 1875: 177. Lydekker, 1889: 352.

Type

Isolated cervical vertebra (NMI 62 1971) from Heiberg Formation (Upper Triassic) of north-west extremity of Cameron Island, Bathurst Group, Arctic Archipelago, Canada.

Discussion

Arctosaurus was described as reptilian by Adams (1875) but subsequently Lydekker (1889) referred it to the family Anchisauridae. Regarded as a turtle by Huene (1906) and White (1973) but referred to the prosauropod family Melanorosauridae (as Plateosauravidae) by Huene (1956) and to the Anchisauridae (as Thecodontosauridae) by Romer (1966). The region of the diapophysis is slightly damaged (Fig. 13B, F) but from the adjacent curves of the neural arch (Fig. 13E) it is obvious that the diapophysis was very small and, as a result, this vertebra is from the anterior part of the series and is probably either the third or fourth cervical vertebra. It is proportionally very much shorter than the equivalent vertebrae of *Anchisaurus* (Figs 9H, 12B), *Efraasia* (Figs 9I, 12A) and *Plateosaurus* (Huene 1926). The only prosauropods with cervical vertebrae proportionally as short are *Thecodontosaurus* (Fig 11A) and *Lufengosaurus* (Figs 9J, 12C) but in both cases the vertebrae are proportionally much lower, the neural spines are not so well developed and there is no pleurocoel (exaggerated in *Arctosaurus* because of crushing). *Arctosaurus osborni* is

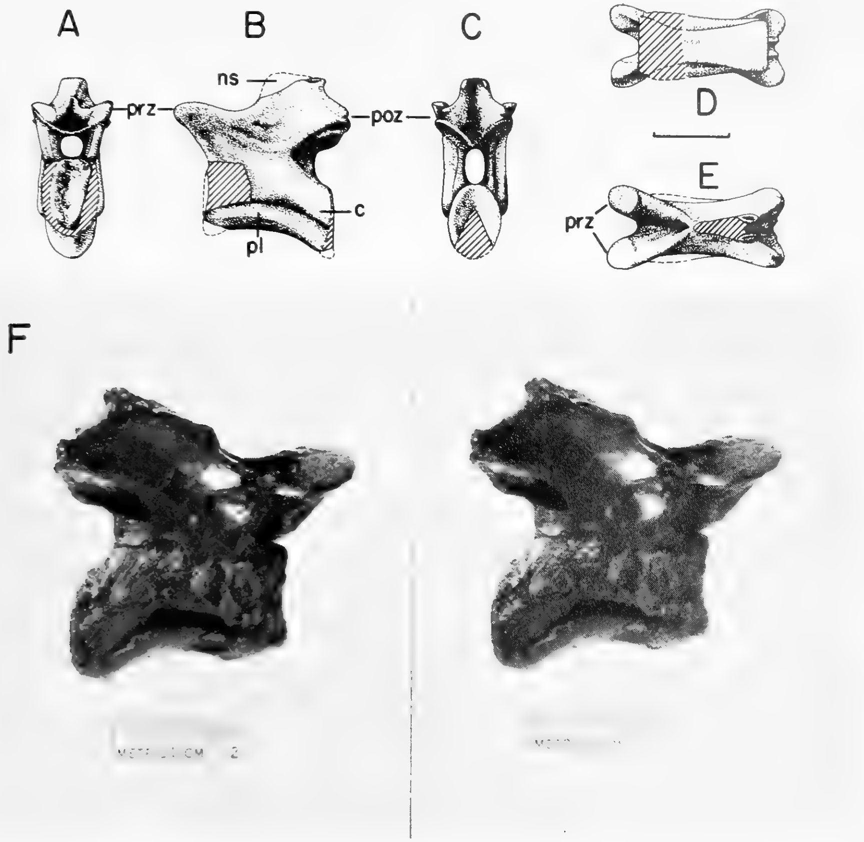

Fig. 13. *Arctosaurus osborni* Adams, holotype NMI G2 1971, anterior cervical vertebra in: A. Anterior view. B. Left lateral view. C. Posterior view. D. Ventral view. E. Dorsal view. F. Stereo photograph of left side, compare with B. Scale = 2,5 cm. Broken bone indicated by diagonal shading.

not a prosauropod and, on the basis of the general form of the vertebra and the presumed presence of a pleurocoel, this specimen is tentatively regarded as Theropoda *incertae sedis* as listed by Steel (1970).

Ischisaurus cattoi Reig, 1963

Ischisaurus cattoi Reig, 1963: 10, figs 4B, 5. Colbert, 1970: 27. Bonaparte, 1972*b*: 673, fig. 22.

Type

Two incomplete skeletons from the Ischigualasto Formation (lower Upper Triassic) of Argentina.

Discussion

Ischisaurus is listed as an anchisaurid by Steel (1970) and as Saurischia *incertae* by Bonaparte (1972*b*: 674), who notes that 'the suggested affinities with the Coelurosauria appears as one of the possible relationships'. Romer (1966) and Colbert (1970) list *Ischisaurus* as a coelurosaurian theropod.

Order THECODONTIA

'*Thecodontosaurus*' *gibbidens* Cope, 1878

Thecodontosaurus gibbidens Cope, 1878: 177. Huene, 1921: 571, figs 14–15.

Type

Isolated teeth from the Upper Triassic of Pennsylvania, U.S.A.

Discussion

The isolated teeth are almost circular rather than oval in cross-section as in prosauropods (*Thecodontosaurus antiquus* Riley & Stutchbury, 1840; *Anchisaurus*, YPM 1883; *Plateosaurus*. AMNH 6810), so these teeth are provisionally referred to the Ornithischia (Galton, in press).

Spondylosoma absconditum Huene, 1935

Spondylosoma absconditum Huene, 1935: 247, pl. 30, figs 1–13. Charig, 1967: 712. Colbert, 1970: 19. Bonaparte, 1972*b*: 674.

Type

Scapula, humerus, femur, tibia (all incomplete) and eight vertebrae from the Santa Maria Formation (Upper Triassic) of Brazil.

Discussion

Huene (1935, 1942) regarded *Spondylosoma* as a saurischian but did not make a more specific assignment for this genus. Romer (1956, 1966) referred *Spondylosoma* to the Anchisauridae (as Thecodontosauridae) as did Colbert (1970) and Charig (1967), who noted at the same time the possibility of its being a prestosuchid pseudosuchian. Bonaparte (1972*b*: 674) notes that 'there are doubts regarding its assignment to the Saurischia, or even to Prosauropoda. Unfortunately there are not sufficient diagnostic pieces to define better its taxonomic position' and *Spondylosoma* is listed as Saurischia *incertae*.

Teleocrater alphos (Haughton, 1932)

Thecodontosaurus (?) *alphos* Haughton, 1932: 662, fig. 19.
Teleocrater alphos Charig, 1967: 712.

Type

Two cervical vertebrae (SAM-10654) from the Manda Formation (Upper Triassic, Anisian) of Tanzania.

Discussion

Charig refers this material to the pseudosuchian *Teleocrater*.

Subclass LEPIDOSAURIA

Order LACERTILIA

Huene (1932, not 1931 as cited by Steel 1970) considered that the following Middle Triassic (Muschelkalk) species were based on specimens which should be referred to the eosuchian *Tanystropheus*, a lacertilian according to Wild (1974); the non-prosauropod nature of these species is also discussed by Colbert (1970):

Tanystropheus primus (Huene, 1907–08)

Thecodontosaurus primus Huene, 1907–08: pl. 42 (figs 8–9).
Tanystropheus primus Huene, 1932: 6.

Tanystropheus latespinatus (Huene, 1907–08)

Thecodontosaurus (?) *latespinatus* Huene, 1907–08: figs 237–245.
Tanystropheus latespinatus Huene, 1932: 6.

NOTES ON THE FAMILIES ANCHISAURIDAE AND PLATEOSAURIDAE

The infra-order Prosauropoda is currently divided into three families: Anchisauridae (= Thecodontosauridae), Plateosauridae and Melanorosauridae (see Romer 1956; Colbert 1964; Charig *et al.* 1965; Bonaparte 1972*a*). Postcranially the separation is clearest between melanorosaurids and non-melanorosaurids (Romer 1956: 617; Bonaparte 1972*a*: 160). Galton (1971, 1973) suggests that the range of morphological variation is insufficient to warrant the retention of two families of non-melanorosaurid prosauropods. However, the skulls of *Anchisaurus* (Fig. 9A) and *Plateosaurus* (Fig. 9C) are very different and, because of this, Galton (in press) now considers that they should not be included in the same family. Fortunately the genera concerned are the basis for the first two valid prosauropod family names to be proposed: Anchisauridae Marsh, 1885, and Plateosauridae Marsh, 1895.

In only one case (*Anchisaurus polyzelus*, YPM 1883) is a well-preserved skull found in natural association with a skeleton of a slender-footed prosauropod. Consequently the referral of *Efraasia* and *Thecodontosaurus* to the Family Anchisauridae is tentative. Contrary to the impression given by Huene (1932: fig. 7; 1956: fig. 10), the skull of *Efraasia* is very incomplete but, as noted by Galton (1973), *Efraasia* is an ideal ancestor for the more recent *Anchisaurus*. The holotype of *Thecodontosaurus antiquus* is an incomplete dentary but, judging from what is preserved (Fig. 9B), the complete lower jaw was probably more like that of *Anchisaurus* (Fig. 9A) than that of *Plateosaurus* (Fig. 9C). Although considered unlikely, the discovery of additional material may show that the restriction of the family Anchisauridae to slender-footed forms is artificial. However, the criterion is practical and with it most taxa and specimens of non-melanorosaurid prosauropods are readily referable to either the Family Anchisauridae or the Family Plateosauridae.

Plateosaurus engelhardti Meyer, 1837 from the Keuper (Upper Triassic) of Germany is the earliest taxon of plateosaurid to be described, but since then a multitude of taxa have been erected for material from the Triassic of Germany (Steel (1970) lists 9 species as *Plateosaurus*, 8 species as *Gresslyosaurus*). However, this material is probably extremely overclassified and all the taxa of European plateosaurids listed by Steel (1970: 53–56) should be provisionally regarded as junior synonyms of *Plateosaurus engelhardti* Meyer, 1837. All the European plateosaurid material can probably be referred to (at the most) three species of *Plateosaurus*, but a restudy of all the holotypes is needed to determine the other valid species.

Lufengosaurus (see Young 1941*a*, *b*, 1942, 1947, 1951) and *Plateosaurus* (see Huene 1907–8, 1926, 1932) possess the features listed above as characteristic of plateosaurids. The skulls of *Ammosaurus* (see Galton, in press) and *Aristosaurus* (see Van Hoepen 1920*a*) are not well enough preserved to tell anything about the form of the skull. However, the holotype of *Massospondylus harriesi* includes a lower jaw (Fig. 9D), the posterior part of which is deep with the articulation offset ventral to the line of the tooth row. J. Attridge is studying two skulls of *Massospondylus harriesi* (SAM- K388 and K1314) and has found that both skulls show the features listed above (pers. comm.).

Massospondylus is the most ubiquitous prosauropod in southern Africa and its previous classification as an anchisaurid made the prosauropod fauna of Africa unique, because in other areas with abundant, well-preserved prosauropod skeletons, plateosaurids are the most common form. However, Cox (1973: 213) notes that 'it is clear that land connections between all the continents existed for much, at least, of the Triassic'. As regards prosauropods the presence of *Anchisaurus* in North America and South Africa and the presence of *Plateosaurus* in Germany and South America (Casamiquela 1964; Bonaparte 1972*b*) indicated that this was the case for the continents on either side of the Atlantic. With the transfer of broad-footed forms, previously listed under the Anchisauridae, to the Plateosauridae, this family becomes the dominant and cosmopolitan prosauropod family of the world. In marked contrast, the Anchisauridae have an extremely restricted fossil record (total of about 10 articulated specimens for North America, Europe and South Africa) with no remains discovered to date from Asia (Young 1951; Rozhdestvensky 1966) or South America (Bonaparte, pers. comm.). Haughton (1924) noted that the Stormberg Series of South Africa was deposited under conditions of progressively increasing aridity, and it is interesting that skeletal remains of melanorosaurids occur in the lowermost levels (Passage Beds, Charig *et al.* 1965; basal Red Beds, Haughton 1924), most plateosaurid skeletons occur higher in the Red Beds, and those of anchisaurids are found in the overlying Cave Sandstone (Charig *et al.* 1965; Haughton 1924; Haughton & Brink 1956). Charig *et al.* (1965) report the presence of small tridactyl footprints in the Passage Beds and in the lower Red Beds and note (p. 204) that these '. . . may indicate the movement of thecodontosaurids from one upland region to another via a lowland area'. The world-wide rarity of anchisaurid skeletal remains is presumably because these species occupied the drier upland areas, which are rarely represented in the fossil record.

SUMMARY

The holotype (SAM-990) of the prosauropod dinosaur *Anchisaurus capensis* (Broom, 1911) is characterized by the following combination of characters: low centra to posterior dorsal vertebrae, broad bases to neural spines of anterior caudal vertebrae, ilium with long anterior process, pubis with open obturator foramen, and with slender pes with first ungual phalanx the largest. SAM-990 differs from the North American *Anchisaurus polyzelus* (Hitchcock) only in the large size of the first ungual of the pes, and SAM-990 is referred to *Anchisaurus* Marsh, 1885 as *Anchisaurus capensis* (Broom). Taxa which have been incorrectly referred to the genus *Gyposaurus* (= *Anchisaurus*) are *Gyposaurus erectus* (Van Hoepen) (= *Aristosaurus erectus* Van Hoepen), *Gyposaurus sinensis* Young (= *Lufengosaurus huenei* Young) and *Gyposaurus skirtopodus* (Seeley) (= *Hortalotarsus skirtopodus* Seeley, *nomen dubium*). The Family Anchisauridae is restricted to those species with slender feet, *viz. Anchisaurus polyzelus*, *A. capensis*, *Efraasia diagnostica*, and *Thecodontosaurus antiquus*. Taxa with broad feet previously classified as anchisaurids (*Aristosaurus, Ammosaurus, Gyposaurus sinensis* (as *Lufengosaurus huenei*), *Massospondylus* (including *Aetonyx*, *Dromicosaurus*, *Gryponyx africanus*, *G. taylori*, *Thecodontosaurus dubius*), *Yunnanosaurus* (= *Lufengosaurus*) are transferred to the family Plateosauridae, the dominant and cosmopolitan family of prosauropods.

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ABBREVIATIONS

acetabulum	acet
anterior process of ilium	ant proc
astragalus	as
centrum	c
caudal vertebra	ca
calcaneum	cal
chevron	ch
dorsal vertebra	dor
neural spine	ns
pleurocoel	pl
postzygapophysis	poz
prezygapophysis	prz

pubic peduncle	pub ped
sacral vertebra	sac
Amherst College Museum, Amherst, Massachusetts	AM
American Museum of Natural History, New York	AMNH
British Museum (Natural History), London	BMNH
National Museum of Ireland, Dublin	NMI
South African Museum, Cape Town	SAM
Staatlichen Museum für Naturkunde in Stuttgart	SMNS
Yale Peabody Museum, New Haven, Connecticut	YPM

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'
'. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit
Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

P. M. GALTON & M. A. CLUVER

ANCHISAURUS CAPENSIS (BROOM)
AND A REVISION OF THE ANCHISAURIDAE
(REPTILIA, SAURISCHIA)