THE PROSAUROPOD DINOSAUR *AMMOSAURUS*, THE CROCODILE *PROTOSUCHUS*, AND THEIR BEARING ON THE AGE OF THE NAVAJO SANDSTONE OF NORTHEASTERN ARIZONA

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ABSTRACT—Analysis of the anatomy of *Ammosaurus* specimens from Upper Triassic rocks of Connecticut and Arizona shows this taxon to be a prosauropod and not a primitive coelurosaur. Dermal armor and a pes from the Navajo Sandstone are referred to the crocodilian genus *Protosuchus*. On sound stratigraphic criteria the age of the Kayenta Formation and most of the Navajo Sandstone is Late Triassic rather than Early or Middle Jurassic.

INTRODUCTION

VERY few skeletons of prosauropod dinosaurs have been found in North America, and most of these are from the Upper Triassic of the Connecticut Valley (Lull, 1953). An exception is the specimen described by Brady (1935) from the Navajo Sandstone of northeastern Arizona. Brady (1935) referred this specimen to *Ammosaurus*, a prosauropod genus hitherto known only from the Connecticut Valley. His description is rather brief, and Brady later (1936) mentioned undescribed material. The Navajo Sandstone is an aeolian deposit (see Gregory, 1917, p. 59; Camp, 1936, p. 40; Baker et al. 1936, p. 52) that outcrops extensively in Utah, Arizona, Nevada, Colorado and New Mexico (see Heaton, 1950, fig. 9) and reaches a thickness of at least 2100 feet in southern Utah. Only one other reptile has been described from this formation, the coelurosaurian dinosaur *Segisaurus* (Camp, 1936), but Dr. C. L. Camp also collected two undescribed partial skeletons, one referable to *Ammosaurus* and the other to the crocodilian genus *Protosuchus* (see below).

There has been some confusion about whether *Ammosaurus major* from the Connecticut Valley is a primitive coelurosaur or a prosauropod, so a discussion of the relevant features of the Connecticut Valley specimens is necessary. The Navajo specimens are relevant to this problem and also to the age of the Navajo Sandstone. The Navajo is usually considered Early Jurassic, but Lewis et al. (1961) have suggested that at least part of it is Late Triassic.

Specimens mentioned in this paper are preserved in institutions which are identified by the following abbreviations:

AM Amherst College Museum, Amherst, Mass.

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AMNH American Museum of Natural History, New York.

MNA Museum of Northern Arizona, Flagstaff, Ariz.

UCMP University of California Museum of Paleontology, Berkeley, Calif.

UT1 University of Tübingen, Germany; skeleton of *Plateosaurus* designated as no. 1 by Huene (1932).

YPM Yale Peabody Museum, Yale University, New Haven, Conn.

SYNONOMY OF THE CONNECTICUT VALLEY PROSAUROPODS

There are two genera of prosauropods reported from North America for which postcranial material is available; these are *Anchisaurus* and *Ammosaurus* from the Upper Triassic rocks of the Connecticut Valley. The synonomy of the Connecticut Valley prosauropods will be dis-

cussed in detail elsewhere. I recognize two monospecific genera: the slender-footed *Anchisaurus* of Marsh (1885) and the broad-footed *Ammosaurus* of Marsh (1891). *Yaleosaurus colurus* Huene 1932 (= *Anchisaurus colurus* Marsh 1891, YPM 1883) is a junior synonym of *Anchisaurus polyzelus;* I can find no diagnostic characters by which YPM 1883 can be distinguished from *A. polyzelus* (AM 41/109–118). Huene (1906) referred *Anchisaurus polyzelus* to the genus *Thecodontosaurus* of Riley and Stutchbury (1836) as *T. polyzelus* but this is incorrect. The holotype of *Thecodontosaurus antiquus* Morris (1843, p. 211) is an incomplete dentary with teeth [see Riley and Stutchbury (1840, pl. 29, figs. 1, 2, and p. 352) ; Riley and Stutchbury (1836) proposed the genus *Thecodontosaurus* from the Magnesian Conglomerate of Bristol, England but they did not give a specific name]. There is no articulated association between teeth of *Thecodontosaurus* and the postcranial material referred to this genus. In addition, there is no such association for any of the postcranial material apart from some vertebrae (Huene 1907–8, figs. 214, 218–220) and a forelimb (YPM 2195, Marsh 1892, pl. 15, fig. 2; Huene 1914b, fig. 46). There are no teeth with AM 41/109–118 and those of YPM 1883 are not well enough preserved for comparison with those of *Thecodontosaurus*. In addition, *Anchisaurus* differs in certain important postcranial characters from the Bristol material referred to *Thecodontosaurus*. Huene (1932) correctly referred *Anchisaurus solus* (YPM 209) of Marsh (1892) to the genus *Ammosaurus*. However, the small size of the skeleton and its poor ossification indicate a young individual. Although almost complete (see Huene, 1906, pl. 4) the specimen is poorly preserved and it is best regarded as a young *Ammosaurus major* rather than a separate species, *A. solus,* as Huene (1932) proposed.

SPECIMENS FROM THE NAVAJO SANDSTONE
Prosauropod dinosaurs

MNA G2 7233.—Brady (1936, p. 150) stated that this specimen was found about two and a half miles east of Inscription House Lodge (on the road between Tuba City and Navajo Mountain) on the plateau between Navajo and Shonto Canyons. The stratigraphic occurrence was in typically cross-bedded Navajo Sandstone that Brady estimated to be about 80 to 100 feet below the top of the formation. Brady (1935, p. 213) noted that "the animal appears to have been buried entire in the position in which it died, prone with the hind limbs doubled under it, and with the feet extended and the claws bent

downward as though gripping the sand. The upper parts . . . seem to have been entirely removed by recent erosion." A photograph of the specimen as found was given by Brady (1935, fig. 1).

There are several incomplete caudal vertebrae, the centra of which are not as high as in *Plateosaurus* (Huene, 1926) and resemble those of *Ammosaurus* (YPM 209). Brady (1935, fig. 3) figured the block containing many of the gastralia. Only the apron-like anterior part of the pubes is preserved as an impression of the ventral surface with a partial layer of thin bone (Text-fig. 1A). The pubes are broad and at the distal end of each there is a well marked swelling of the ventral surface similar to that on the pubis of *Plateosaurus* (Text-fig. 1C, D). At the proximal end of the left pubis there are indications of a small obturator foramen (Text-fig. 1A), and the adjacent bony surface is obliquely inclined, facing posteromedially and dorsally as does the equivalent area in *Plateosaurus* (Text-fig. 1B).

Brady (1935, p. 213) wrote that "the femur has a marked sigmoidal curve and is about 30 cm. in length" but this bone was not collected. The tibia measures 28 cm in length. Brady (1935, fig. 2) illustrated the left pes, the more complete and undescribed right pes was collected later (Brady, 1936). The bones of both
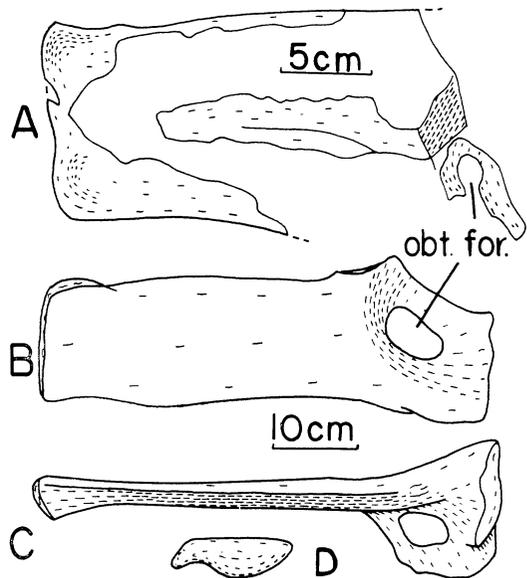
TEXT-FIG. *1—A,* dorsal view of pubes of *Ammosaurus,* MNA G2 7233. *B-D,* left pubis of *Plateosaurus,* after Huene (1926). *B,* dorsal view. *C,* lateral view. *D,* distal end.

feet are rather crushed and some of the pha-
langes are missing but all the proportions in
Text-figure 2 are approximately correct. The
ungual phalanges of digits I to IV show a pro-
gressive decrease in size (Text-figs. 2, 3) and
that of the first digit has a large ventral area
for the flexor tendons (Text-fig. 3A).

UCMP 82961.—This specimen was found in
1938 by M. Wetherill on the Navajo Indian
Reservation 300 yds. east of the road to the Be-
tatakin Ruin 7.7 miles from the Kayenta-Tuba
City road. There are two cervical vertebrae that
are similar to the sixth and eighth cervical
vertebrae of *Plateosaurus* (Huene 1926 and
AMNH 6810). From the position of the associ-
ated pieces of ribs it would appear that the cer-
vical ribs were about twice the length of the
centrum, as is the case in *Plateosaurus*.

The right manus is well preserved and is ex-
posed in palmar view (Text-fig. 4). The first
metacarpal is slightly crushed but its general
appearance is not distorted. The lateral surface
of the proximal part is concave to receive the
second metacarpal and the ginglymus is assym-
metrical. The enormous ungual has a large ven-
tral area for flexor tendons and a prominent
dorsal process for extensor tendons (Text-fig.
6E). The appearance and proportions of the
other metacarpals and phalanges are shown in
Text-figure 4. The ungual phalanges of the sec-
ond and third digits are much smaller and less
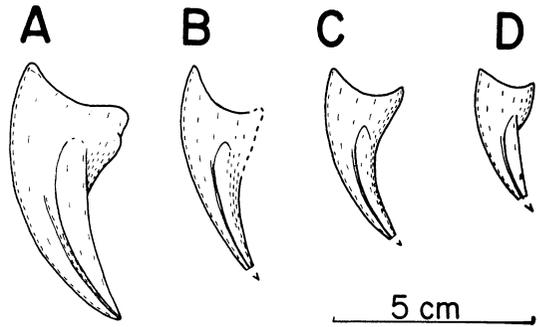
TEXT-FIG. 3—Ungual phalanges of pes of *Ammosaurus*
MNA G2 7233, ×½. *A*, digit 1 from right pes, in
medial view. *B*, digit 2 from left pes, in lateral view.
C, digit 3 from left pes, in lateral view. *D*, digit 4
from left pes, in lateral view.

trenchant than that of the first digit. The
crushed distal ends of four metatarsals are simi-
lar to those of the Flagstaff specimen and the
best preserved are shown in Text-figure 5.
There are several isolated and rather flattened
phalanges from the talus slope debris that re-
semble those of the Flagstaff specimen. The
eight ungual phalanges are of four sizes that
correspond to those of the Flagstaff specimen
(compare Text-figs. 3 and 6A–D).

MNA G2 7092.—Baird (personal communica-
tion) has informed me that another specimen, a
trackway, was undoubtedly made by a prosauro-
pod dinosaur walking quadrupedally.
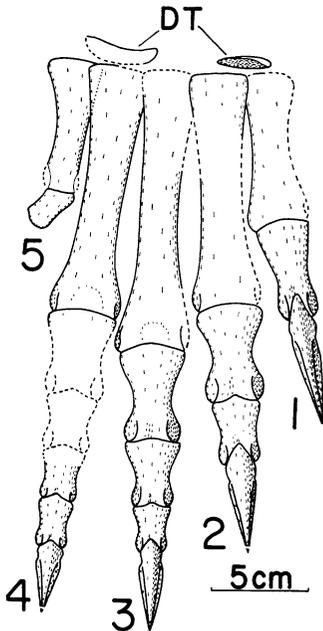
TEXT-FIG. 2—Right pes of *Ammosaurus*, MNA G2
7233 in dorsal view. Abbreviation: DT, distal tarsal.
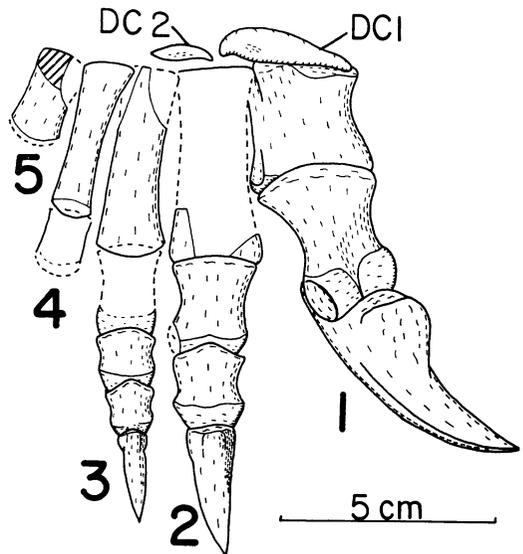
TEXT-FIG. 4—Left manus of *Ammosaurus* in ventral
view, UCMP 82961, ×½. Abbreviations: DC,
distal carpal; 1–5, digits.

TEXT-FIG. 5—Metatarsals of right pes of *Ammosaurus* in dorsal view. UCMP 82961, ×½. *A*, metatarsal I. *B*, metatarsal II.

TEXT-FIG. 6—Ungual phalanges of *Ammosaurus*, UCMP 82961 ×½. *A*, digit 1 from right pes, in medial view. *B*, digit 2 from right pes in medial view. *C*, digit 3 from right pes, in medial view. *D*, digit 4 from left pes, in lateral view. *E*, digit 1 from left manus, in lateral view.

Identity of the Navajo prosauropod

The manus of the Berkeley specimen (Text-fig. 4) is clearly that of a prosauropod dinosaur (see below) and, on the basis of the similarity between the pedal ungual phalanges of the Berkeley and Flagstaff specimens (Text-figs. 3, 6A–D), it is reasonable to refer both to 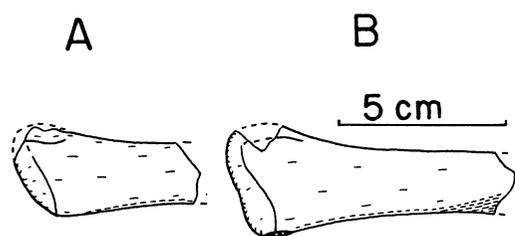a single genus. The other prosauropod characters of the Navajo specimens are indicated in Table 1 and these characters are discussed more fully below for the Connecticut Valley specimens.

Brady (1935) noted that the pes of the Flagstaff specimen resembled that of *Ammosaurus major* as figured by Marsh (1896) and this is shown in Text-figures 7A and 7B. In both specimens the foot is broad and stout with expanded distal ends of metatarsals I to IV, and the ungual phalanx of the first digit is the largest. In contrast, the foot of *Anchisaurus* (Text-fig.

7C) is more slender, the distal ends of metatarsals I to IV are not so expanded, and the ungual phalanx of the first digit is small. The fifth metatarsal of the Flagstaff specimen bore a phalanx and this was probably the case in *Ammosaurus major* (a fragment of bone near the left fifth metatarsal of YPM 208 is probably part of this phalanx) but it may not have done so in *Anchisaurus*.

It is reasonable to refer the Navajo specimens to the genus *Ammosaurus*. The Navajo specimens may represent a new species; one difference from *A. major* is that the obturator foramen of the pubis (Text-fig. 1A) appears to be much smaller (Text-fig. 9). There are also dif-
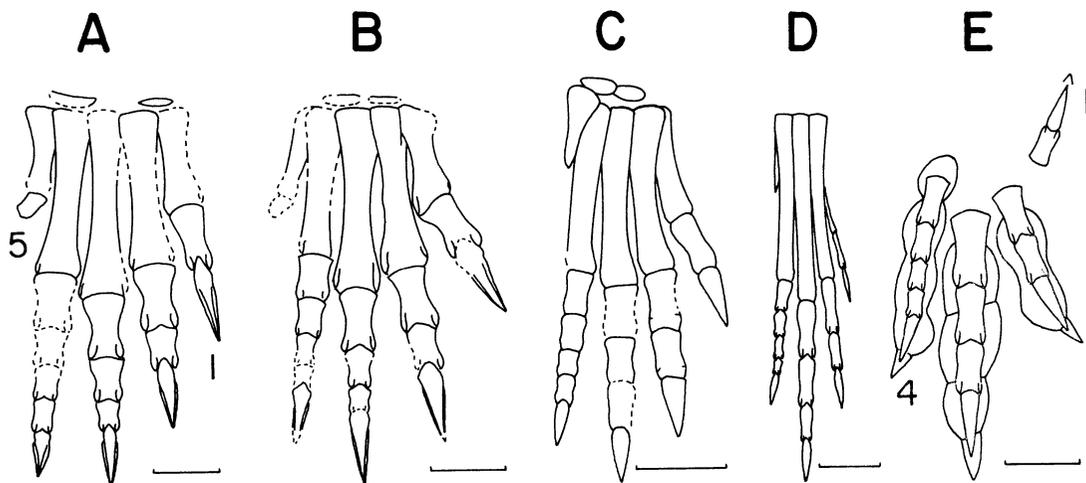
TEXT-FIG. 7—Comparison of the structure of the pes. *A, Ammosaurus* MNA G2 7233, right pes in dorsal view. *B, Ammosaurus major* YPM 208, right pes in dorsal view. *C, Anchisaurus polyzelus* YPM 1883, left pes in ventral view. *D, Coelophysis,* right pes in dorsal view, adapted from Ostrom (1969, fig. 81A). *E, Anchisauripus exsertus,* reconstruction of right pes in dorsal view, outline of footprint reverse of Lull (1953, fig. 41). *A-D* drawn so that the length of the third digit is the same; *E* is at same scale of reduction as *B*. Scale in each case represents 5 cms.

ferences between the relative proportions of the metatarsals and phalanges of the feet of the Flagstaff specimen and *Ammosaurus major* (Text-figs. 7A, 7B). However, both specimens are crushed and damaged, with these proportions differing slightly on opposite sides of the same animal. Bearing in mind the incompleteness of the three specimens concerned and the questionable nature of the differences, I consider it inadvisable to erect a new species on the basis of the material available. The Navajo specimens are best regarded as *Ammosaurus* cf. *major*.

Coelurosaurian dinosaur *Segisaurus*

UCMP 32101.—The holotype of *Segisaurus halli* was found about 1 mile north of Keet Seel Ruin on the west side of Keet Seel Canyon, the north branch of Segi Canyon about 14 miles by trail northwest of Marsh Pass on the Kayenta-Tuba City road, Navajo Indian Reservation. The specimen is unique and it was described by Camp (1936) who erected the family Segisauridae for it.

Crocodile *Protosuchus*

UCMP 61299.—This specimen of the primitive crocodile *Protosuchus* was found by a party led by Dr. C. L. Camp in the Navajo Sandstone of Cobra Head Canyon, a tributary of Segi Canyon about three miles above Marsh Pass, Arizona (UCMP locality no. V69146). The specimen consists of two pieces of matrix with no contact surface between them. The first block contains parts of 24 dorsal scutes of the dermal armor from the left side. The first four scutes are almost complete (Text-fig. 8A), the next 12 are represented mainly as a natural mold as are the last eight that become progressively less complete medially. The entire series is visible in ventral view, but the first four scutes have also been exposed in dorsal view (Text-fig. 8A). The medial part of the corresponding four scutes of the right side are preserved, but in Text-figure 8A the right side has been restored as a mirror image of the left and as if there were no median ridge along the middle of the back.

The scutes closely resemble those of *Protosuchus* and, to judge from the figures in Colbert and Mook (1951, fig. 4; pl. 11; pl. 14, fig. 2), the four most anterior plates (Text-fig. 8A) are from about the sixth to ninth cervical segments with the series as preserved extending to about the third caudal vertebra. Colbert and Mook (1951) noted that on most of the dorsal scutes the dorsal part was separated by a distinct keel
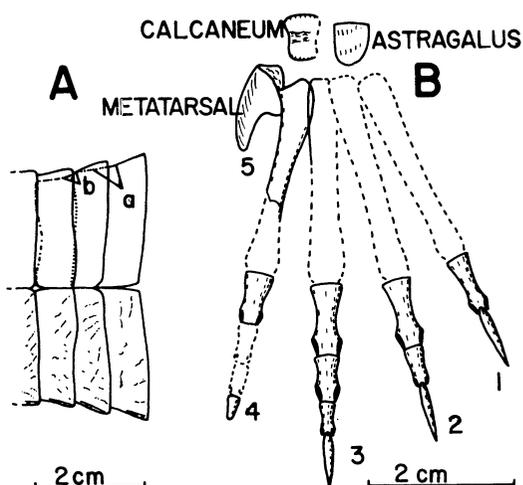
TEXT-FIG. 8—*Protosuchus* UCMP 61299. *A,* dorsal scutes of dermal armor from about cervical segments 6 to 9. a and b represent two separate plates, ×2/3. *B,* right pes in dorsal view, ×1.

from the lateral part. They emphasized that this lateral part was an integral part of the dorsal scute, and this is also the case in the Navajo specimen (especially clear in ventral view). Each scute overlapped about half of the scute behind it (compare two sides of Text-fig. 8A), but in the Navajo specimen the scutes have been displaced anteroposteriorly. The posterior limit of overlap is indicated medially by a transverse depression on the dorsal surface of the overlapped scute. Laterally the keel disappears in the overlapped portion and transversely the lateral part is gently convex, the curve matching that of the ventral surface in this region.

Walker (1968, 1970) has reinterpreted the pseudosuchian thecodont *Stegomosuchus* of Huene (1922; = *Stegomus longipes* Emerson and Loomis 1904, description in Lull 1953) as a primitive crocodile closely related to *Protosuchus*. Walker (1968) noted that the dorsal scutes of *Stegomosuchus* are very similar to those of *Protosuchus* and that an examination of casts suggested that the lateral dorsal row of scutes described by Emerson and Loomis (1904) are not discrete elements. A study of the specimen in the Museum of Amherst College confirms that these lateral scutes are an integral part of the dorsal scutes. This is especially clear from the ventral block (see Lull 1953, pl. 6A). There is no trace of a lateral suture, and a latex peel gives the ventral surface of the dorsal scutes that closely resemble those of the Navajo specimen of *Protosuchus*.

The second block contains fragments of bone

from about 15 segments of dermal armor of the tail plus the right pes (Text-fig. 8B). The astragalus and calcaneum resemble those of *Protosuchus* as described by Colbert and Mook (1951), but the proximal end of the fifth metatarsal is much broader. As illustrated by Colbert and Mook (1951, fig. 12) the fifth metatarsal is proportionally more reduced than in the living *Alligator*. The phalanges are very similar to those of *Protosuchus* (see Colbert and Mook, 1951, fig. 12) but, judging from their position as preserved, the metatarsals were displaced along their length relative to each other. In the reconstruction (Text-fig. 8B) the length of the third metarsal is the same as that of the series of phalanges it bore, and the relative proportion of the other metatarsals is as shown by Colbert and Mook (1951, fig. 12).

THE SYSTEMATIC POSITION OF
AMMOSAURUS

Introduction.—The prosauropod specimens from the Navajo Sandstone are referred to the genus *Ammosaurus*. When Huene (1914a) erected the Ammosauridae he regarded it as the most primitive family of coelurosaurs (reasons given in 1932, 1956). This conclusion has been accepted by most workers (e.g., Romer, 1956; Kuhn, 1965; Camp et al., 1968; Colbert 1961; Reig, 1970) but recently some doubts have been expressed. Romer (1966) listed *Ammosaurus* as Theropoda *incertae sedis,* Appleby et al. (1967) noted that its classification as a coelurosaur was doubtful, while Colbert and Baird (1958, p. 3) said that it was probably a prosauropod related to *Anchisaurus*. Colbert (1964) contrasted the structure of the pelvic girdle of Triassic carnosaurs and prosauropods with that of coelurosaurs and post-Triassic carnosaurs. He concluded that the Triassic carnosaurs, including the Ammosauridae, represented an early radiation of carnivores that were restricted to the Triassic and were completely separate from the Coelurosauria and the true Carnosauria. His taxonomic conclusions were summarized as follows:

Order Saurischia
Suborder Paleopoda
  Infraorder Palaeosauria: Families Ammosauridae, Palaeosauridae, Teratosauridae
  Infraorder Plateosauria: Families Thecodontosauridae, Plateosauridae, Melanorosauridae
Suborder Theropoda
  Infraorders Coelurosauria, Carnosauria
Suborder Sauropoda

Walker (1964) noted that the postcranial material of Triassic carnosaurs was not definitely associated with the skull material and should be referred to the Prosauropoda. Charig et al. (1965) came to the same conclusion and dis-

cussed the resemblances between the postcranial material of Triassic carnosaurs and prosauropods in detail. They noted that the geographical distribution of the postcranial material of the carnosaurian families Gryponychidae (= Palaeosauridae) and Teratosauridae was the same as that of the prosauropod families Thecodontosauridae and Plateosauridae respectively. Charig et al. (1965) correctly combined these two pairs of families that, on the basis of priority, became the Thecodontosauridae and Plateosauridae. The carnosaur skull material was retained in the family Teratosauridae?, Theropoda *incertae sedis*. Charig et al. (1965, p. 213) noted that *Ammosaurus* did not seem to fit satisfactorily into any of the existing taxa of saurischians.

The modifications summarized above mean that the Infraorder Palaeosauria of Colbert's (1964) classification would be represented by one family, the Ammosauridae. The osteology, synonymy and systematic position of the prosauropod skeletons from the Upper Triassic of the Connecticut Valley will be discussed in detail elsewhere, and a summary of the synonomies is given above. In the following discussion the anatomy of YPM 208 (type of *Ammosaurus major*) and YPM 209 (see Text-fig. 11A) will be considered in relation to the characters of prosauropods discussed by Colbert (1964) and Charig et al. (1965). The specimen concerned is indicated in parenthesis and the characters are listed in Table 1 with an indication of the occurrence of each in the four specimens of *Ammosaurus* (columns A–D), *Anchisaurus* (E) and *Plateosaurus* (F).

Prosauropod characters of Ammosaurus.— There appear to have been 25 presacral vertebrae in YPM 209 (Text-fig. 11A), a count typical of prosauropods and in contrast to the 23 or 24 of theropods (see Charig et al. 1965), and the third sacral vertebra is a modified caudal vertebra (YPM 208). The pelvic girdle of both specimens is the brachyiliac type characteristic of prosauropods (Text-figs. 9, 10A, 11) and rather different from the dolichoiliac type characteristic of theropods (Text-fig. 10B, C, see Colbert, 1964). The pubic peduncle of the ilium is broad and is much longer than the ischiadic head and the acetabulum is large with an elliptical outline (Text-fig. 9A; YPM 208, 209). The size of the anterior process of the ilium cannot be determined in YPM 209, but that of YPM 208 is long (Text-fig. 9A). As a result the ratio of the length of the ilium to its height at the ischiadic head is about 2.0 in YPM 208 as against 1.3 in *Plateosaurus* (Text-fig. 10A) and 2.5 in *Coelophysis* (Text-fig. 10C). The anterior process of YPM 208 is rather different from the

small triangle that Colbert (1964) and Charig et al. (1965) considered characteristic of prosauropods. However, the process is slender, resembling that of ornithischians in this respect (a reason why Huene referred *Ammosaurus* to the Ornithopoda in 1906) and it is not the deep plate so characteristic of theropods. In addition, the anterior process of *Anchisaurus* (YPM 1883), an undoubted prosauropod, has recently been prepared and it is almost identical to that of YPM 208. Although damaged, the anterior process of *Gyposaurus* (Broom 1913; see Broom 1906, pl. 3, fig. 1 where described as *Hortalotarsus*) is also long. This elongation indicates that a large M. ilio-tibialis 1 was differentiated as in ornithischians (see Galton 1969, 1970a). I regard the elongation of the anterior process in these genera as a modification of the usual prosauropod ilium.

The distal part of the pubes forms a broad, transversely orientated apron (Text-fig. 9) but more proximally the bones are twisted (YPM 208, 209). Ventral to the acetabular region there is a deep plate with a large obturator foramen (YPM 208, this region not preserved in YPM 209). These features are characteristic of prosauropods (Text-fig. 10A) and are in marked
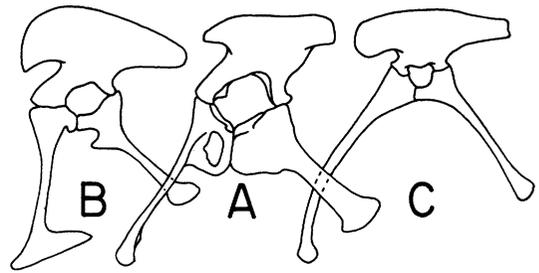
TEXT-FIG. *10*—Pelvic girdles of saurischians in lateral view, not to same scale. *A*, brachyiliac type, the prosauropod *Plateosaurus,* after Huene (1926). *B*, dolichoiliac type, the carnosaurian theropod *Allosaurus,* after Gilmore (1920, fig. 46). *C*. dolichoiliac type, the coelurosaur *Coelophysis*, after Colbert (1964, fig. 2).

contrast to the straight, rod-like pubis of theropods (Text-fig. 10B, C) in which there is usually only a small plate ventral to the acetabulum and no obturator foramen (a *small* obturator foramen has been reported in only *Ceratosaurus,* see Gilmore 1920, pl. 23. and *Syntarsus,* see Raath, 1969, fig. 4B).

The proximal part of the ischium of YPM 208 (Text-fig. 9) is not typically prosauropod because, ventral to the acetabulum, it is not plate-like but is quite shallow so that there is a relatively short union with the pubis. There are indications of an obturator process and the ischium is rather theropod-like (see Text-figs. 9, 10B, C). However, I consider that this is a convergent feature resulting from the emargination of the anteroventral part of an ordinary prosauropod ischium (Text-fig. 10A). The pubis of *Anchisaurus* (YPM 1883) lacks an obturator foramen because the posteroventral border has been emarginated and the subacetabular part is quite similar to that of theropods (Text-fig. 10B, C). The proximal part of the ischium may have been shallow as in *Ammosaurus* but this cannot be determined because so little of the proximal end is preserved. It should be noted that in the figures of the ischium of *Anchisaurus* (AM 41/109–118) given in Marsh (1892, pl. 17, fig. 6; 1896, pl. 3, fig. 4), Huene (1914b, fig. 29), and Lull (1915, fig. 17; 1953, fig. 14a) the proximal part is based on the ventral third of the left scapula.

The femur lacks the prominent lesser trochanter (YPM 208) so characteristic of theropods, and it is longer than the tibia (YPM 208, 209, Text-fig. 11A). Charig et al. (1965) pointed out that the astragalus of prosauropods has a central ascending process that keys into the distal end of the tibia that backs the astragalus with a descending flange. There are indications of such a central ascending process on
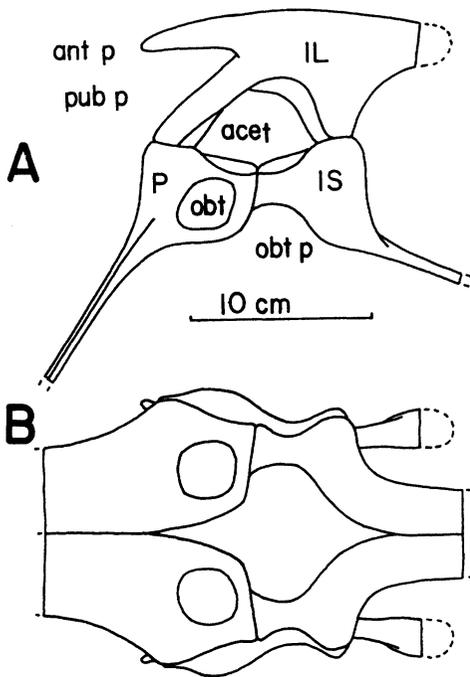
TEXT-FIG. *9*—Reconstruction of pelvic girdle of *Ammosaurus major* YPM 208. *A,* lateral view. *B,* ventral view. Abbreviations: acet, acetabulum; ant p, anterior process; obt f, obturator foramen; obt p. obturator process; pub p, pubic process; IL, ilium; IS, ischium; P, pubis.
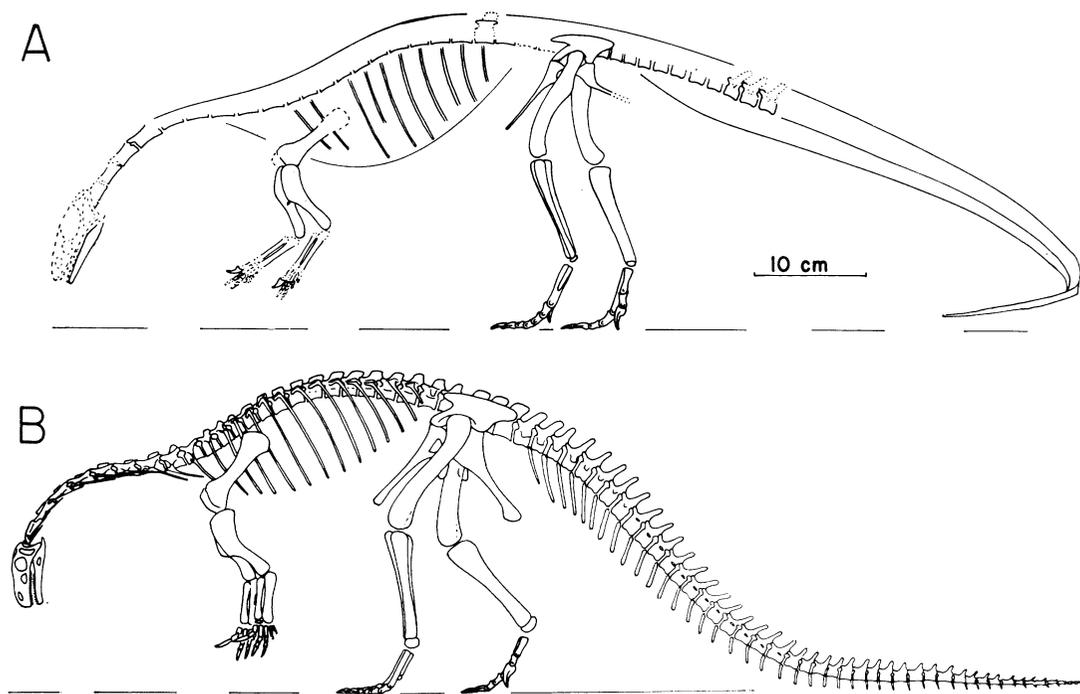
TEXT-FIG. 11—Skeletal reconstructions of prosauropods. A, Ammosaurus major, based mainly on YPM
    209 with pelvis and pes from YPM 208 and skull outline from Anchisaurus (YPM 1883). The length
    of YPM 209 was about 1 meter while YPM 208 was about 3 meters. B, Plateosaurus, based on AMNH
    6810. Original about 6.5 meters long; for photograph see Colbert (1961, pl. 28).

the astragalus of YPM 208. In theropods the
anterior process fits against the anterior surface
of the tibia. However, the structure of the ankle
is not so diagnostic as Charig et al. (1965)
thought because the coelurosaur Syntarsus from
the Late Triassic of Rhodesia has a typically
"sauropodomorph" tibia and astragalus (see
Raath, 1969, fig. 6).

The structure of the pes (Text-fig. 7B) is
that of typical prosauropods, being broad with a
shortened but complete first metatarsal (YPM
208, 209). In theropods the first metatarsal is
long but slender with the proximal section of
the shaft unossified (Text-fig. 7D). In the car-
nivorous bipedal theropods the first digit proba-
bly aided the others in gripping the prey so that,
although it was not used for supporting the
weight, it was not shortened as in the herbivo-
rous prosauropods and ornithischians (see Gal-
ton, 1970a). The ungual phalanx of the first
digit is the largest (YPM 208), and it is anteri-
orly directed (YPM 208, 209) rather than pos-
teriorly directed as in carnosaurs. Lull (1915,
1953) considered that the first digit of Ammo-
saurus could have been posteriorly directed, but
this was based on the assumption that the foot-
prints of Anchisauripus exsertus (Text-fig. 7E)

were made by Ammosaurus major (Text-fig.
7B). However, this is physically impossible be-
cause, as in all prosauropods, the third digit of
YPM 208 (Text-fig. 7B) is short relative to the
second and fourth digits whereas in the foot-
print (Text-fig. 7E) the central digit is elon-
gated as in theropods (but not in Syntarsus, see
Raath 1969, fig. 6). In addition the structure of
the first metatarsal of YPM 208 shows that it
was held alongside the second metatarsal and
that the digit could not have been posteriorly di-
rected. The footprints of Anchisauripus could
not have been made by any prosauropod and
were probably made by a carnosaurian thero-
pod.

On the basis of the above analysis (see Table
1 and Text-fig. 11) I conclude that Ammosaurus
is a prosauropod (= Palaeopoda sensu Colbert,
1964).

The Prosauropod Manus.—Confirmatory ev-
idence that Ammosaurus is a prosauropod is
provided by the manus of the Navajo specimen
(Text-fig. 4). Charig et al. (1965) mentioned
the massive and strong pollex in their list of
prosauropod characters. I am studying the func-
tional anatomy of the saurischian manus and
have concluded that the manus of prosauropods,

including those genera of Triassic "carnosaurs" correctly referred to the Prosauropoda by Charig et al. (1965), are all very similar in form and are identical to that of the Navajo *Ammosaurus* (Text-fig. 4).

I suggest that the uniformity of manus structure of prosauropods was correlated with the development of an enormous and trenchant first ungual (Text-figs. 4, 6E, 12) that was used while bipedal for offence or defence in a group that was only facultatively bipedal. During quadrupedal locomotion with the digits of the manus in full extension (Text-fig. 12) the weight was taken by digits II to IV (mostly II and III), and the enormous first ungual phalanx was held clear off the ground (Text-fig. 12B). The lateral surface of this phalanx would only have touched the ground if it was irregular or soft and even then the point of the claw would not have been damaged.

The main variation is that metacarpals II to IV are more slender in some genera (e.g., *Anchisaurus*, see Huene 1906, pl. 2; 1914b, fig. 9; *Thecodontosaurus* YPM 2195, see Huene 1914b,
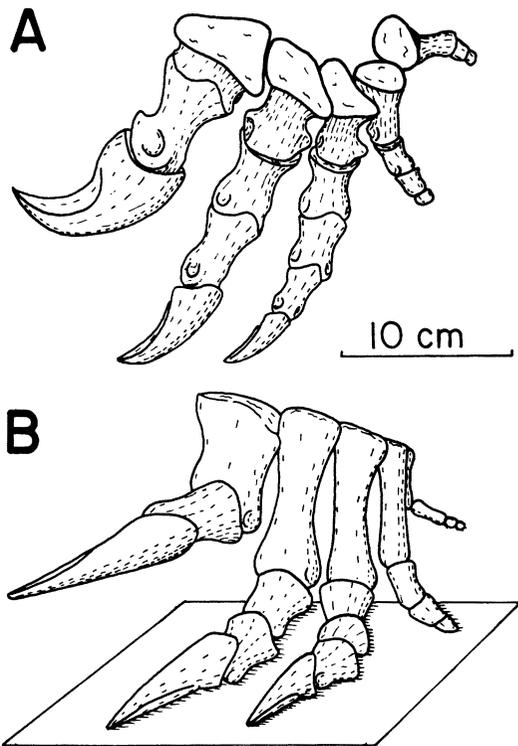
TEXT-FIG. *12*—Left manus of *Plateosaurus* (UT 1) on the ground with the digits mounted in full extension. *A*, from above. *B*, from in front.

TABLE *1*—Prosauropod Characters of *Ammosaurus*

Character	A	B	C	D	E	F
1. Teeth spatulate	+				+	+
2. Twenty five presacral vertebrae 3. Third sacral from caudal series	3	2				+
4. Enormous pollex on manus	−			+	+	+
5. Long pubic peduncle to ilium, elliptical acetabulum	+	+			+	+
6. Small triangular anterior process to ilium	×				×	+
7. Proximal part of pubis deep, large obturator foramen	+	−			×	+
8. Pubis twisted with broad apron distally	+	+	+		+	+
9. Proximal part of ischium deep	×					+
10. Small lesser trochanter to femur	+		+		+	+
11. Tibia shorter than femur	+	−	+		+	+
12. Central ascending process of astragalus keying into tibia	−				+	+
13. Pes broad and distal end of metatarsals expanded	+	+	+	+	×	+
14. Metatarsal I complete, digit anteriorly directed	+	+	+		+	+
15. First ungual phalanx largest on pes	+		+	+	×	+
16. Digit III not elongated relative to digits II and IV	+		+		+	+
17. Metatarsal V quite large, 18. bears phalanx	+	17	+		17	+

Abbreviations: A, YPM 208. B, YPM 209. C, MNA G2 7233. D, UCMP 82961. E, *Anchisaurus* YPM 1883. F, *Plateosaurus* (see Huene, 1926). +, yes. −, possibly so. ×, no. No entry indicates that this region is not known.

fig. 46; *Palaeosaurus* (?) *diagnosticus*, see Huene 1932, pl. 5, fig. 6) in which the metatarsals are also more slender (*Anchisaurus*, Text-fig. 7C; *Thecodontosaurus*, see Huene 1907–08, pl. 90, fig. 1; *Palaeosaurus* (?) *diagnosticus*, see Huene 1932, pl. 6, fig. 8). Most prosauropods were quite large and the more massive nature of the metacarpals was a graviportal adaptation that was unnecessary in the smaller forms.

That most prosauropods were only facultatively bipedal is shown by the hind-limb to trunk ratio of *Anchisaurus* (1.02; YPM 1883, AM 41/109–118), *Ammosaurus* (1.09, YPM 209) and *Plateosaurus* (1.10, AMNH 6810; 1.07, UT 1). These values are lower than those of truly bipedal dinosaurs (e.g., hadrosaurs 1.22–1.44, *Iguanodon* 1.35, *Gorgosaurus* 1.37, *Struthiomimus* 1.9; see Galton 1970b, table 1) but higher than those of undoubtedly quadrupedal dinosaurs (e.g., *Ankylosaurus* and *Scolosaurus* 0.69, *Stegosaurus* 0.9, *Kentrurosaurus* 0.86, *Triceratops* 0.9, *Apatosaurus* 0.85, see Galton 1970b, table 2). The manus shows more variety of form in the fully quadrupedal sauropods (cf. *Brachiosaurus* and *Torniera*, see Janensch, 1961, pl. C) in which the first phalanx is large, but it is non-

trenchant, broad and helped to support the weight (see Galton 1970b, fig. 4). The first ungual phalanx of the manus of theropods is trenchant but the structure of the manus is extremely variable (see Ostrom 1969, fig. 82). This group was fully bipedal, consequently the structure of the manus was not limited by locomotory adaptations.

Systematic status of the family Ammosauridae.—Colbert (1964, p. 20) referred the family Ammosauridae to the Infraorder Palaeosauria (see above) that he characterized as follows: "small to rather large palaeopods, skull varying from moderate to large size with sharp teeth. Astragalus and calcaneum closely appressed to tibia and fibula." The corresponding characters of the Infraorder Plateosauria (= Prosauropoda) were "medium to large sized palaeopods, with relatively small skull and lanceolate or blade-like teeth. Astragalus and calcaneum distinct elements."

Ammosaurus cannot be classified on the basis of its size, and the ratio of the length of the mandible to the presacral length of YPM 209 is 0.137 as against 0.134 for *Plateosaurus* (calculated from Huene, 1926, pl. 7) and 0.23 for *Coelophysis* (calculated from Colbert, 1961, fig. 8). The teeth of YPM 209 are spatulate rather than lanceolate or blade-like and the astragalus (YPM 208) and calcaneum (MNA G2 7233) are distinct elements. Certain features of the anatomy of *Ammosaurus* are unusual for a prosauropod, *viz.,* the long anterior process of the ilium (YPM 208) and the ventral emargination of the proximal part of the ischium (YPM 208). However, the first feature also occurs in *Anchisaurus* (YPM 1883) and *Gyposaurus* of Broom (1913, see 1906, pl. 3, figs. 1, 4), and the pubis of *Anchisaurus* (YPM 1883) shows an emargination that may also have affected the ischium. I conclude that there is no justification for isolating *Ammosaurus* in a family of its own. Its affinities lie with the non-melanorosaurid prosauropods currently placed in the families Thecodontosauridae and Plateosauridae (for genera see Romer 1956, 1966), both of which contain broad-footed forms. However, all the genera of these two families are very similar and I consider that the few differences do not warrant the retention of the family Plateosauridae. This conclusion is based on an examination of the material of *Ammosaurus, Anchisaurus, Palaeosaurus* and *Plateosaurus* in conjunction with descriptions of the other genera. Consequently there are four familial names available for the non-melanorosaurid prosauropods: Anchisauridae Marsh (1885), Plateosauridae Marsh (1895), Thecodontosauridae

Huene (1906) and Ammosauridae Huene (1914a). As noted above, Huene (1906) was incorrect in referring *Anchisaurus polyzelus* to the genus *Thecodontosaurus* and Anchisauridae has priority. The following classification is modified from Charig et al. (1965).
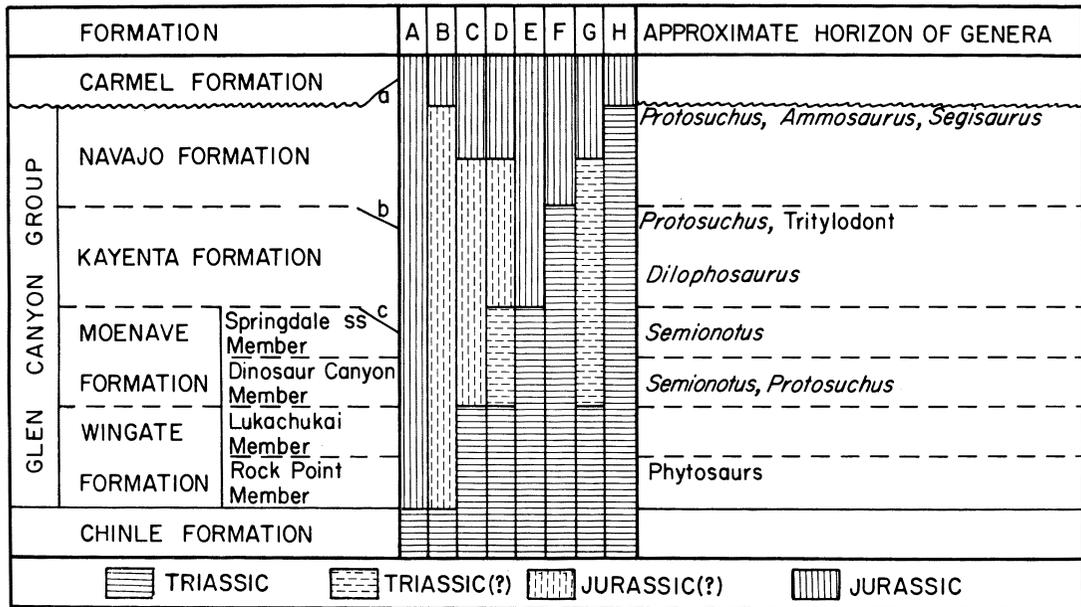
Order Saurischia
  Suborder Sauropodomorpha
    Infraorder Prosauropoda
      Family Anchisauridae (including Ammosauridae, Plateosauridae and postcranial material ascribed to Gryponychidae = "Palaeosauridae" and Teratosauridae)
      Family Melanorosauridae
    Infraorder Sauropoda
  Suborder Theropoda
Saurischia *incertae sedis*
      Family Teratosauridae? (late Triassic)

It should be noted that, although most prosauropods have the characters considered by Colbert (1964) and Charig et al. (1965) to be diagnostic (see Table 1) some variation exists, but this does not debar the genus concerned from being a prosauropod. Thus the anterior process of the ilium may be long, the subacetabular part of the pubis or ischium may be shallow, the pes may be slender, and the first ungual phalanx of the pes need not be the largest. In fairness to Marsh (1885, 1891, 1895, 1896) it should also be noted that he placed *Ammosaurus* in the family Anchisauridae and that it was subsequently moved to the Ornithischia (Huene, 1906), Coelurosauria (Huene, 1914a) and the Palaeosauria (Colbert, 1964).

AGE OF THE NAVAJO SANDSTONE

The Navajo Sandstone is the youngest formation of the Glen Canyon Group. The various levels at which the Jurassic-Triassic boundary has been placed are shown in Text-figure 13. The fauna of the Glen Canyon Group has been discussed in detail by Colbert and Gregory (1957), Gregory (1957, p. 22), Harshbarger et al. (1957, p. 25–30) and Lewis et al. (1961). On the basis of the evidence assessed in these papers it is reasonable to place the Moenave Formation in the Triassic, but it is uncertain whether the Kayenta and the Navajo are Triassic or Jurassic.

Lewis (1955, 1958, *in* Harshbarger et al. 1957, Lewis et al. 1961) reported a new genus of tritylodont from near the top of the Kayenta Formation. According to Lewis (1958) this tritylodont is more closely related to *Bienotherium* from the Lower Lufeng Series (Keuper, Upper Triassic) of China (Young, 1947) and *Tritylodon* of the Stormberg Series of South Africa than it is to the known Rhaetic to Early Jurassic *Oligokyphus* or the Middle Jurassic *Stereognathus*. Lewis (1958) reported *Protosuchus*

FORMATION		A	B	C	D	E	F	G	H	APPROXIMATE HORIZON OF GENERA
CARMEL FORMATION										
NAVAJO FORMATION										*Protosuchus, Ammosaurus, Segisaurus*
KAYENTA FORMATION										*Protosuchus,* Tritylodont / *Dilophosaurus*
MOENAVE FORMATION	Springdale ss Member									*Semionotus*
	Dinosaur Canyon Member									*Semionotus, Protosuchus*
WINGATE FORMATION	Lukachukai Member									
	Rock Point Member									Phytosaurs
CHINLE FORMATION										

Legend: ▤ TRIASSIC   ▦ TRIASSIC(?)   ▨ JURASSIC(?)   ▥ JURASSIC

TEXT-FIG. *13*—The different ages assigned to the formations of the Glen Canyon Group of northern Arizona. Authors for the ages: *A*, Gregory (1917). *B*, Baker et al. (1935), Heaton (1950). *C*, Averitt et al. (1955). *D'*, Harshbarger et al. (1957). *E*, Imlay (1952), Welles (1954a, b, c, 1970), Colbert and Gregory (1957). *F*, Gregory (1957), Colbert (1965b), Cox (1967), Appleby et al. (1967). *G*, Lewis et al. (1961), Cooley et al. (1969). *H*, Camp et al. (1947), this paper. a, b, and c represent intertonguing, for details see Lewis et al. (1961). The data for the last column is from Welles (1954a, 1970), Colbert and Gregory (1957), Lewis et al. (1961) and this paper. For fauna of the Chinle Formation see Colbert and Gregory (1957).

from the same locality and, as Lewis et al. (1961) noted, this suggests a correlation of the Kayenta with the Stormberg Series of South Africa that is probably Keuper to Rhaetic (Haughton 1924, Watson 1942, Charig et al. 1965, Attridge and Charig 1967, Appleby et al. 1967). Lewis et al. (1961, p. 1437) noted that the Stormberg Series "contains *Tritylodon longaevus,* related to the tritylodont found in the Kayenta, associated with the protosuchian species *Notochampsa istedena* and *Erythrochampsa longipes,* and with species of *Semionotus*." Walker (1968) reinterpreted the interorbital region of *Protosuchus* as being narrow and, as a result, this genus is much closer to *Notochampsa* than had been thought (see Colbert and Mook 1951, Welles 1954b, c). Walker (1968, p. 6) noted that "the near-contemporaneity of the Longmeadow Sandstone (Portland Arkose, Newark Group) of the Connecticut Valley with the Dinosaur Canyon Sandstone of Arizona is a justifiable deduction from the close relationship between *Stegomosuchus* and *Protosuchus.* Furthermore, the enhanced resemblance between *Protosuchus* and *Notochampsa* reinforces the allocation of a late Triassic, rather than early Jurassic, horizon to the former, since

Notochampsa occurs in the same bed as prosauropod dinosaurs which have close affinities with those of the late Keuper of Germany."

The material described above of *Protosuchus* and the prosauropod *Ammosaurus* (the coelurosaur *Segisaurus* is of no biostratigraphic use because it is unique and was assigned to a family of its own by Camp, 1936) suggests that the Navajo Sandstone of northeastern Arizona was closely contemporaneous with the Portland Arkose, the uppermost formation of the Newark Series (Upper Triassic) of the Connecticut Valley. The following skeletal remains have been described from this formation: the crocodile *Stegomosuchus longipes* (see comments above), the coelurosaur *Coelophysis* (Colbert and Baird 1958, Colbert 1964; *Coelophysis* is well represented by material from the Chinle Formation of New Mexico) and the prosauropods *Anchisaurus polyzelus* and *Ammosaurus major.*

Prosauropods have been described from the Rät (Upper Triassic, Rhaetic) of Germany (Huene, 1932) and from other beds, such as the Lower Lufeng Series of China (Young, 1951), the Cave Sandstone of the Stormberg Series, South Africa (Huene 1932, Charig et al. 1965,

Attridge and Charig 1967), the Tranquilo Formation of Argentina (Sill 1969, p. 809), and the Portland Arkose of Connecticut (Lull 1953), the youngest of which are regarded as Rhaetic in age. No prosauropods have been described from deposits younger than Rhaetic (Romer 1956, 1966, Appleby et al. 1967) and this suggests a Triassic age for most of the Navajo Sandstone of northeastern Arizona. However, very few dinosaurs have been described from deposits that are definitely Early Jurassic. The richest fauna is from the Lias of England that has provided theropods (*Sarcosaurus,* various elements, see Huene 1932; "*Scelidosaurus harrisoni*" knee region, see Newman 1968) and ornithischians (*Scelidosaurus harrisoni,* a complete skeleton, see Owen 1861, 1863; Newman 1968 and two specimens ? young *Scelidosaurus,* see Owen 1861, Rixon 1968, Newman 1968). Another ornithischian has been described from the Lias of Portugal (jaw *Lusitanosaurus,* Lapparent and Zbyszeski, 1957). The sauropod *Rhoetosaurus* is from the Wallon Coal measures of Australia (Longman 1926) and sauropod bones have been reported from the Kota Formation of India (Jain et al. 1962). This is an extremely fragmentary sample, that of the Middle Jurassic is almost as bad (see Colbert, 1965a), and it is not until the Upper Jurassic that there is a reasonable representation of the terrestrial fauna (see Colbert, 1965a). Consequently there is insufficient evidence to tell whether or not prosauropods actually became extinct at the end of the Triassic. It is also possible that the tritylodont and *Protosuchus* could be Early Jurassic.

The stratigraphic evidence concerning the age of the Navajo Sandstone, as discussed by Baker et al. (1936) and Harshbarger et al. (1957, p. 31), seems to indicate an Early Jurassic age. Imlay (1952, p. 964) noted that "most geologists who have studied these formations agree that the Navajo Sandstone resembles the overlying Jurassic sandstones lithologically, in distribution, and in westward thickening, whereas the Kayenta and Wingate in these respects resemble the underlying Chinle Formation of Triassic age." The top part of the Navajo Sandstone intertongues with the Carmel Formation (Middle to Upper Jurassic) near Bryce Canyon and near Zion National Park in southwestern Utah (see Lewis et al., 1961). These parts at least must be Jurassic, but the Navajo Sandstone may be very time-transgressive because the lower part intertongues with the Kayenta in northern Arizona and south western Utah (see Harshbarger et al. 1957, p. 18 and Averitt et al. 1955, p. 2520).

Welles (1954a) described a carnivorous dinosaur, *Megalosaurus wetherilli,* from the basal part of the Kayenta and compared the relative proportions of the limb bones with those of other megalosaurs. He concluded that the Kayenta form was much closer to *Megalosaurus bucklandi* (Middle Jurassic, Europe) and *M. cuvieri* (Late Jurassic, Europe) than it was to the megalosaurs from the Late Triassic of Europe. Welles (1954a) also noted that the ascending process of the astragalus of *Megalosaurus wetherilli* was well developed and represented a stage considerably more advanced than that of Late Triassic theropods. Welles (1954a, b, c) concluded that the Kayenta Formation was Lower or Middle Jurassic.

Welles (1954a, table 2) took his ratios for Triassic megalosaurs from Huene (1932). However, all these ratios are based on postcranial material that, as Charig et al. (1965) have shown, should be referred to the Prosauropoda. It must also be noted that the ascending process of the astragalus of prosauropods is low in comparison to that of theropods. Swinton (1955, p. 134) pointed out that "the main elements of the skull, the scapula, and the pelvic bones [of *Megalosaurus wetherilli*] are not those of typical megalosaurs . . . it is not *Megalosaurus.*" Welles (1970) has recently erected the genus *Dilophosaurus* for "*Megalosaurus*" *wetherilli* and has referred it to the theropod family Coeluridae. Baird (personal communication) pointed out several years ago that the limb ratios of the coelurosaur *Halticosaurus* from the Middle Keuper (Upper Triassic, Norian) of Germany are closer to the Kayenta theropod than are those of the Jurassic *Megalosaurus* (Table 2). Consequently the specimen described by Welles (1954a) does not necessarily indicate a Jurassic age for the Kayenta but, on the contrary, could be used as evidence for a Triassic age. However, for the following reasons I consider that these limb ratios should not be used for any age determination. Firstly, we know so little about the Triassic to Middle Jurassic theropods. Secondly, the various indices used by Welles (1954a, Table 2) differ considerably in the three Triassic coelurosaurs for which corresponding material is available (see Table 2). Thirdly, these ratios probably varied in different lines, depending on the locomotory adaptation, and the evolutionary rate can vary within one line.

Welles (1970) gives the age of the lower beds of the Kayenta Formation as Late Early Jurassic or Early Middle Jurassic. Welles (personal communication) is still impresssed by the advanced condition of the skull and astragalus of *Dilophosaurus* and says that "it is a good descendant of *Coelophysis,* but rather far removed. The Kayenta footprints are far advanced over anything from the Eastern Trias

TABLE 2—Skeletal indices of species of *Megalosaurus* and Triassic coelurosaurs

		1	2	3	4	5	6	7	8	9
Age	Genus and Species	$\dfrac{H+R+MCIII}{F+T+MTIII}$	Total of 1 in cms	Index of 1	H.F index	R.H	T.F	MT III.T	MT III.F	ΣD
Upper Jurassic	*Megalosaurus cuvieri*	$\dfrac{24+14+7}{52+52+24}$ $\dfrac{45}{126}$		36	46	58	96	48	46	32
Middle Jurassic	*Megalosaurus bucklandi*	$\dfrac{38+21+10}{70+65+39}$ $\dfrac{69}{174}$		40	54	55	93	60	56	22
Upper Triassic	*Halticosaurus*[1]	$\dfrac{20.5+15+6.8}{42+40+22}$ $\dfrac{42.3}{104}$		41	49	73	95	55	52	17
	Syntarsus[2]	$\dfrac{10+6.1+2.6}{20.8+22.3+13.2}$ $\dfrac{18.7}{56.3}$		33	48	61	107	60	63	34
	Coelophysis[3]	$\dfrac{12+8+4}{20+22+12}$ $\dfrac{24}{54}$		44	60	67	110	54	60	35
	Dilophosaurus wetherilli	$\dfrac{28+17.5+10}{54+53+29}$ $\dfrac{55.5}{136}$		41	52	62	98	55	54	—

Data for *Megalosaurus* and *Dilophosaurus* is taken from Welles (1954a, table 2), and the corresponding values for Triassic coelurosaurs are given for comparison (sources: 1, Huene 1934; 2, Raath 1969; 3, YPM 5705). In columns 3 to 9 the value of the index represents the quotient ×100. Column 9 shows the total amount, regardless of sign, by which the indices of *Megalosaurus* and Triassic coelurosaurs differ from those of *Dilophosaurus wetherilli*. Abbreviations: F, femur; H, humerus; MCIII, third metacarpal; MT III, third metatarsal; R, radius; T, tibia.

and should also be Jurassic. We have several ? new unprepared small things that include what seem to be aetosaur, tritylodont, crocodile, and another small reptile. This assemblage sounds like Keuper, but it will be several years before we get them cleaned up and studied. I am inclined toward Middle Jurassic for the Kayenta unless, as E. H. Colbert says, I have a very precocious dinosaur."

Colbert and Gregory (1957, p. 1462) noted that the Triassic of Northern Arizona "seems to merge into the Jurassic, so that it is difficult to draw a distinct line of demarcation between the sediments of the two periods." However, on the basis of sound biostratigraphic practice I consider that the Kayenta Formation and most of the Navajo Sandstone should be assigned to the Late Triassic. Of special importance here is the fact that the Navajo Sandstone has yielded the only well preserved North American prosauropod specimens outside of the Connecticut Valley. The rocks of the Portland Arkose of the Connecticut Valley are hard, bone is exceedingly rare (see Lull, 1953), there are very few exposures, and the rock is no longer quarried commercially. In contrast the Navajo Sandstone

is soft, there are numerous exposures, and a small area on the Navajo Indian Reservation yielded four skeletons in only a few years. The Navajo fauna would be especially important if it could be proved of Lower Jurassic age because, in addition to the rarity of terrestrial faunas of this age, it would indicate that the massive extinctions presumed to have occurred at the end of the Triassic (see Colbert 1965a, Cox 1967) were spread over a greater time span than has been supposed.

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