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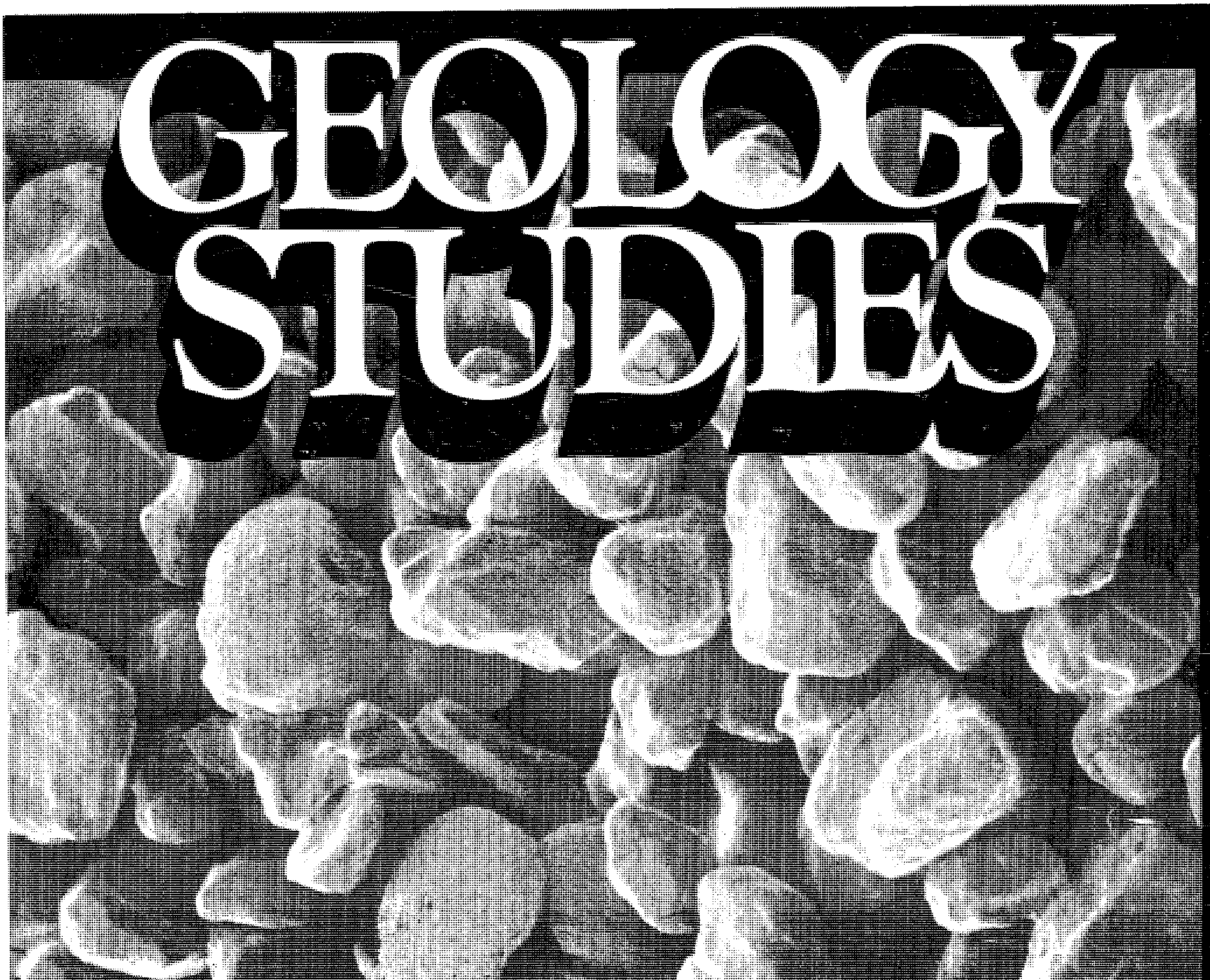

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Additional Specimens of the Hypsilophodontid Dinosaur *Dryosaurus altus* from the Upper Jurassic of Western North America

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Abstract.–Specimens of the hypsilophodontid dinosaur (Reptilia: Ornithischia: Ornithopoda) *Dryosaurus altus* (Marsh) are described from the Morrison Formation (Upper Jurassic) of Colorado, Utah, and Wyoming. As shown by these specimens, the postcranial anatomy of *Dryosaurus altus* (Marsh) is very similar to that of *Dryosaurus lettow-vorbecki* Pompeckj from the Tendaguru Formation (Upper Jurassic) of Tanzania, East Africa.

INTRODUCTION

The purpose of this paper is to describe four specimens (AMNH 834, CM 1949, CM 21786, DNM 1016)* of an ornithopod dinosaur (Reptilia: Ornithischia) from the Morrison Formation (Upper Jurassic) of Colorado, Utah, and Wyoming. Comparisons with YPM 1876 (holotype of *Laosaurus altus* Marsh, 1878, the type species of genus *Dryosaurus* Marsh, 1894) show that these four specimens are referable to the hypsilophodontid *Dryosaurus altus* (Marsh). A summary of previous work on hypsilophodontid dinosaurs from the Upper Jurassic of North America is given by Galton and Jensen (1973:137–38).

Data on Specimens

AMNH 834.–From Bone Cabin Quarry, Medicine Bow anticline, Wyoming; specimen consists of one cervical and several fragmentary dorsal and caudal vertebrae; right scapula, coracoid, humerus, ilium, ischium and pubis, both femora, incomplete left tibia, pes and some phalanges (figs. 1A-D, 2A-D, 3F, 4A-C, 5A-B). Length of right femur 222 mm and original length of animal about 2.0 m.

CM 1949.–Collected by W. H. Utterback in 1905 from the Elk Mountains near Brown's Ranch, Johnson County, Wyoming; specimen consists of several dorsal and caudal vertebrae, right ilium, femur and tibia (figs. 3I, 4D-E, 5N-O). Length of tibia 496 mm and original length of animal about 3.8 m.

CM 21786.–Collected by J. L. Kay and A. C. Lloyd in 1955 from Lily Park, Moffat County, Colorado; specimen consists of 41 vertebrae, incomplete left ilium, ends of all long bones (left tibia with intact calcite core, length 356 mm, and original length of animal about 2.7 m) with both pes almost complete (figs. 1E-V, 2E-H, 3G-H, 4F-O, 5C-M).

DNM 1016.–Collected by J. Adams from the exhibit cliff at Dinosaur National Monument near Jensen, Uintah County, Utah (White 1964, fig. 1); left ilium (fig. 3A-E), length of original animal about 2.4 m.

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We thank the following people for all their assistance while studying specimens under their care: Dr. D. S. Berman, Carnegie Museum; Dr. E. S. Gaffney, American Museum of Natural History; Dr. J. H. Ostrom, Peabody Museum of Yale University; and Dr. T. E. White and Mr. J. Adams of Dinosaur National Monument. NSF grant DEB 76-09769 to P. M. Galton partly supported this work and provided $250 toward the publication of this paper.

DESCRIPTION AND COMPARISONS

No attempt is made to describe the specimens in detail because there are several good descriptions of the bones of cursorial ornithopods in the literature. Instead comparisons have been drawn primarily with the following taxa: the fabrosaurid *Fabrosaurus australis* (Thulborn 1972) from the Upper Triassic of Lesotho, southern Africa; the hypsilophodontids *Hypsilophodon foxii* (Galton 1974) from the Lower Cretaceous of England; *Dysalotosaurus lettow-vorbecki* (Janensch 1955) from the Tendaguru Formation (Upper Jurassic) of Tanzania, East Africa, and *Othnielia* (Galton 1977, based on *Nanosaurus rex* Marsh, 1887; see Galton & Jensen 1973) from the Morrison Formation of western North America; and the iguanodontid *Camptosaurus dispar* (Gilmore 1909; the several Morrison species described are probably all referable to *C. dispar*) from western North America. Unless stated to the contrary, data for comparisons with these taxa are taken from the papers indicated above.

Vertebral Column

Using the vertebral column of *Hypsilophodon foxii* (Galton 1974, figs. 19-22) as a guide, the vertebrae of *Dryosaurus* represented by centra in CM 21786 (fig. 1E-V) are identified as shown. The two cervical centra (fig. 1E-H) are tentatively identified as cervicals four and seven, with the seventh showing a stouter medioventral keel than does the fourth (fig. 1F, H). A well-preserved cervical of *Dryosaurus* (fig. 1A-D) is tentatively identified as the ninth, and presumably it is the last of the cervical keels and, on the basis of *Hypsilophodon,* are identified as dorsals one and three. The remaining seven centra are tentatively identified as shown (fig. 1J-M). The dorsal centra of CM 21786 increase in width passing posteriorly to culminate in a heavy, squat centrum that is wider than long (fig. 1N, O), and clearly this is the last dorsal. The sacrum of *Dryosaurus* probably consisted of six vertebrae as in *Hypsilophodon.* The last four are preserved in CM 21786 (fig. 1P; first four vertebrae, unnatural hyperflexion between sacrals 3 and 4 not compensated for). In the caudal series (fig. 1P-V) the first chevron was borne between the centra of the first two caudals as indicated by the presence of ventral articular facets. Starting with about the twentieth caudal, the transverse process is represented by a small ridge on the side of the centrum (fig. 1S-V).

*Institutional names cited in this paper have been abbreviated as follows: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; DNM, Dinosaur National Monument Quarry, Jensen, Utah; YPM, Peabody Museum, Yale University, New Haven.

Pectoral Girdle

The scapula and coracoid (fig. 2A) of *Dryosaurus* (AMNH 834) are not well preserved, but are typically hypsilophodontid in form. The ratio of the maximum length of humerus to that of scapula is 0.7 and, judging from the measurements given by Gilmore (1925), the corresponding ratio for another specimen of *Dryosaurus* (CM 3392) is about 0.8. In *Hypsilophodon, Othnielia, Dysalotosaurus, Thescelosaurus neglectus* (Gilmore 1915) and *Parksosaurus warreni* (Parks 1926, as *Thescelosaurus warreni*), this ratio is 1.0. The scapula of *Dysalotosaurus,* as figured by Janensch (1955), is slightly shorter than the humerus, but with the anteroventral process for the clavicle restored as in other hypsilophodontids, the scapula and humerus of *Dysalotosaurus* are of equal length.

Fore Limb

The deltopectoral crest of the humerus (fig. 2D, E) is low but stout as in *Othnielia, Dysalotosaurus, Camptosaurus,* and in young individuals of *Hypsilophodon,* rather than high and slender as in mature individuals of *Hypsilophodon.* The anterior aspect of the distal outer condyle of *Dryosaurus* (CM 21786) is flat with a groove on its median surface (fig. 2E, H). The form of this condyle is the same as in *Dysalotosaurus* (Janensch 1955, fig. 34d) and is in contrast to the well-rounded condyles of the humeri of *Othnielia, Hypsilophodon* and *Camptosaurus.* The distal end of the humerus of AMNH 834 is badly damaged, but the form of the condyles of YPM 1876, the holotype of *Dryosaurus altus,* are identical to those of CM 21786. Posteriorly in CM 21786 there is a well-defined intercondylar groove (fig. 2F, H) with a foramen at the end of the indented nonarticular surface (fig. 2F, H). Only the ends of the radius and ulna of CM 21786 are preserved and, although flattened, are similar to those of other hypsilophodontids.

Pelvic Girdle

The ilia of AMNH 834 (fig. 3F), CM 1949 (fig. 3I), DNM 1016 (fig. 3A-E), and the posterior portion of CM 21786 (fig. 3G, H) are hypsilophodontid in form. They differ from the ilia of *Hypsilophodon* (Galton 1969, 1974) in being proportionally low in lateral view (fig. 3B, F, G, I) with a much broader brevis shelf (fig. 3C, D). However, the brevis shelf of DNM 1016 (fig. 3A, D) and its preserved proximal portion in AMNH 834 (fig. 3F) are as in the specimens referred to *Dryosaurus* by Gilmore (1925, fig. 5) and to *Dysalotosaurus* by Janensch (1955, pl. 13, fig. 19). The brevis shelf is wide, thin, and at an acute angle to the main body of the ilium (fig. 3C) to give the V-shaped appearance noted by Gilmore (1925). Although damaged, the brevis shelf of CM 1949 was obviously thin and wider than the main body of the ilium. The form of the posterior part of the main body of the ilium is identical in the ilia of DNM 1016 (fig. 3A-E), AMNH 834 (fig. 3F), CM 1949 (fig. 3I), CM 21786 (fig. 3G), YPM 1884, and those of *Dysalotosaurus.* The posterior portion of the ilium becomes very broad and contrasts with the thinness of the brevis shelf. In this respect these specimens differ from *Hypsilophodon* and *Othnielia* in which the posterior end is much deeper, and the termination is gently rounded. The dorsal edges of AMNH 834 and DNM 1016 have a distinct lateral bevel (fig. 3B, F, G). Posteriorly this beveled surface becomes deeper to include most of the height of the ilium. This feature is also shown quite clearly in the ilia of *Dryosaurus* (YPM 1884 and Gilmore 1925, fig. 6) and *Dysalotosaurus* (Janensch 1955, fig. 37a). The posterior surface of the ilium of CM 21786 (fig. 3G, H) has a matt finish, and in life this part was covered in cartilage.

The ischium of *Dryosaurus* (fig. 3F) has a proximally placed obturator process, and posterior to it the two ischia are in contact for the rest of their length. The distal half of

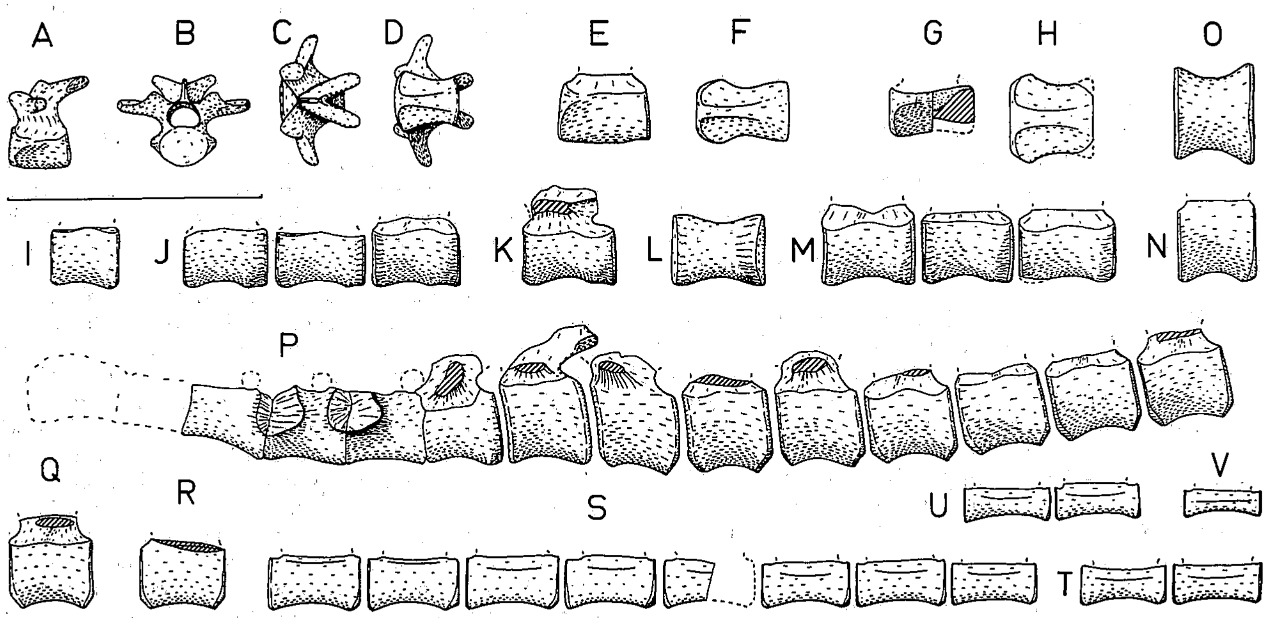

FIGURE 1.—*Dryosaurus altus,* referred specimens, vertebrae X ⅓. A-D.—Ninth cervical vertebra, AMNH 834, in A, lateral; B, anterior; C, dorsal; D, ventral views; E-V.—vertebral centra of CM 21786: E, cervical 4 in lateral view; F, as E in ventral view; G, cervical 7 in lateral view with posterior half sectioned along midline; H, cervical 7 in ventral view; I-O, dorsal vertebrae: I, dorsal 1 in lateral view; J, dorsals 3 to 5 in lateral view; K, dorsal 7 in lateral view; L, as K in ventral view; M, dorsals 10 to 12 in lateral view; N, last dorsal in lateral view; O, as N in ventral view; P, three sacral vertebrae conjoined with cando-sacral vertebrae; Q-V, caudal vertebrae in lateral view, tentatively identified as follows: Q, 9; R, 15; S, 20 to 27; T, 31 and 32; U, 36 and 37; V, 42. Scale line represents 10 cm.

the ischium is bar-shaped (fig. 3F, sections) and gently curved in lateral view (fig. 3F). The ischia of *Dryosaurus* (Marsh 1896, pl. 55, fig. 4), *Dysalotosaurus* (Janensch 1955, pl. 13, figs. 21, 22) and, apart from the distal half being more curved with the end more expanded, the ischia of *Camptosaurus* (Gilmore 1909, 1912) are also very similar. In *Othnielia, Parksosaurus* (Parks 1926), and *Thescelosaurus* (Gilmore 1915) the obturator process is also proximally placed, but the distal half of the ischium is dorsoventrally flattened and bladelike. This is also the case in the ischia of *Hypsilophodon* in which the obturator process is at midlength (Galton 1969, 1974).

The preserved part of the right pubis (fig. 3F) of *Dryosaurus* is similar to the corresponding region of the pubis of YPM 1876 (Marsh 1896, pl. 55, fig. 4), *Othnielia, Dysalotosaurus,* and *Hypsilophodon.* In *Dryosaurus* (AMNH 834, YPM 1876) and *Othnielia* the prepubic process is long and in marked contrast to the short and sharply pointed prepubis, as figured by Marsh (1894, 1896) for *Laosaurus consors,* and to the very short prepubic process of *Fabrosaurus.*

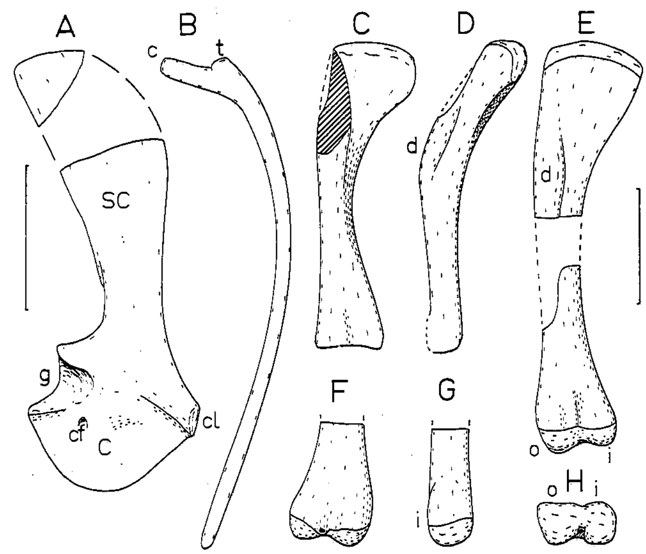

FIGURE 2.–*Dryosaurus altus,* pectoral girdle and forelimb, referred specimens. A, right scapula and coracoid in lateral view, AMNH 834 X0.38, dashed line based on impression in plaster jacket into which specimen fits. B, dorsal rib, AMNH 834, X0.38; C-D, right humerus, AMNH 834, X0.38 in C, anterior and D, medial views; E-H, right humerus CM 21786, X0.3 in E, anterior view; F, posterior view of distal end; G, medial view of distal end; H, distal end. c, capitulum; C, coracoid; cf, coracoid foramen; cl, facet for clavicle; d, deltepectoral crest; g, glenoid cavity; i, inner condyle; o, outer condyle; SC, scapula. Scale lines represent 5 cm.

Hind Limb

The femora of hypsilophodontids are the most diagnostic postcranial bones for taxonomic identification. The femora of CM 21786 (fig. 4J-O), AMNH 834 (fig. 4A-C), and CM 1949 (fig. 4D, 5O) are almost identical to that of YPM 1876 (Galton 1975, fig. 2G-L), the holotype of *Dryosaurus altus.* In particular all the femora show the following combination of characters: a deep cleft between the greater and lesser trochanters (fig. 4A, B, D, J), the fourth trochanter is on the

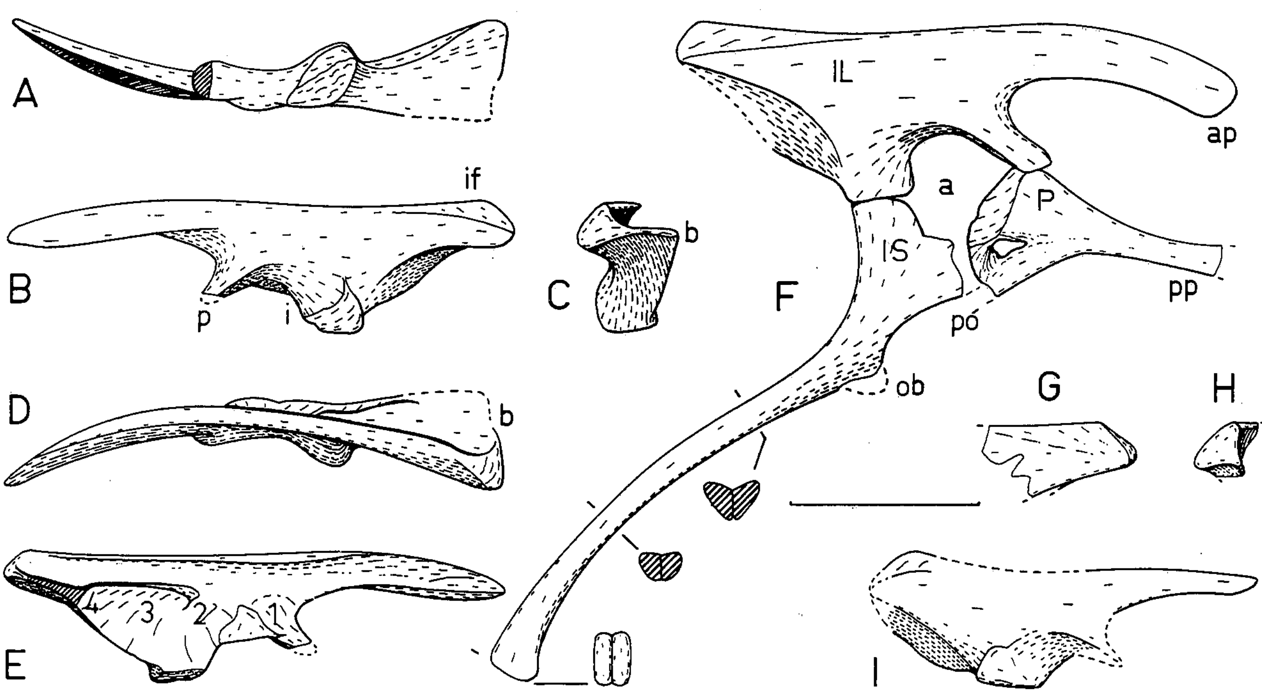

FIGURE 3.–*Dryosaurus altus,* referred specimens, pelvic girdle. A-E.–Ilium DNM 1016, X0.25 in A, ventral; B, lateral; C, posterior; D, dorsal; E, medial views; F, pelvic girdle of AMNH 834 in lateral view, X0.5; G, lateral and H, posterior views of posterior portion of ilium, CM 21786, X0.25; I, ilium, CM 1949 in lateral view X0.125. Scale line represents 20 cm for I, 10 cm for A-E, G-H, and 5 cm for F. a, acetabulum; ap, anterior process; b, brevis shelf; i, ischiadic head; if, area for M. iliotibialis; IL, ilium; IS, ischium; P, pubis; p, pubic peduncle; po, postpubic rod; pp, prepubic rod or anterior process; 1, 2, 3, 4, attachment areas for sacral ribs 1 to 4 (area for 5 broken).

proximal half of the femur (fig. 4A, B, D), the deep depression for the M. caudi-femoralis longus (Galton 1969) is set well on the shaft (fig. 4A), the distal end is nearly square (fig. 4C, O) with a well-developed anterior intercondylar groove (fig. 4C, O, 5O), and posteriorly a proportionally small lateral condyle (fig. 4C, O). The femora of *Dysalotosaurus* (Janensch 1955, pl. 14, figs. 1, 2) are very similar. The femora of *Camptosaurus* have a much more anteroposteriorly expanded lesser trochanter and a more distally placed fourth trochanter. Distally the femora of *Othnielia, Hypsilophodon, Parksosaurus* (Parks 1926) and *Thescelosaurus* (Gilmore 1915) lack an anterior intercondylar groove.

The slender tibia of CM 1949 is longer than the femur (fig. 4D, E) as in all other hypsilophodontids. The form of the tibia (fig. 4E-I, 5B, N) of *Dryosaurus* is almost identical to that of YPM 1876, *Dysalotosaurus, Othnielia,* and *Hypsilophodon.* In *Camptosaurus* and *Thescelosaurus* the tibia is much

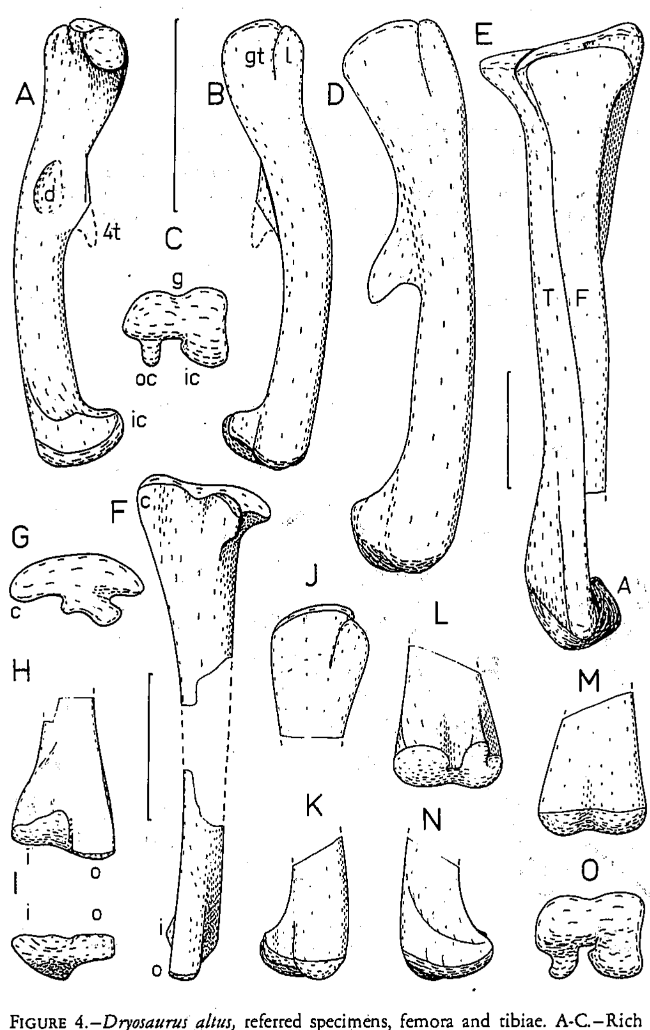

FIGURE 4.–*Dryosaurus altus*, referred specimens, femora and tibiae. A-C.–Rich femur, CM 1949, in lateral view, X0.2. E.–right tibia, fibula, CM 1949, lateral view, X0.2. F-I.–Left tibia, CM 21786, X0.25 in F, medial view; G, proximal end; H, anterior view of distal end; I, distal end. J-O.–Right femur, CM 21786, X0.25; J, proximal end in lateral view; L, distal end in posterior view; M, distal end in anterior view; N, distal end in medial view; O, distal end. A, astragulus; c, cnemial crest; d, deep depression for insertion of M. caudi-femoralis longus; F, fibula; g, anterior intercondylar groove; gt, greater trochanter; i, inner malleolus; ic, inner condyle; o, outer malleolus; oc, outer condyle; 4t, fourth trochanter. Scale lines represent 10 cm.

stockier and shorter than the femur. The fibula of CM 1949 is incomplete (fig. 4E), and it is of normal hypsilophodontid form. The fibulae of CM 21786 are represented by crushed ends that are not well preserved.

Only three metatarsals (fig. 5A) and some phalanges are represented in AMNH 834, but the pes of CM 21786 (fig. 5C-J) is the most complete pes of *Dryosaurus* discovered to date. CM 21786 possesses two incomplete right distal tarsals (fused 2-3, 4), the preserved parts of which are of the standard hypsilophodontid type (Galton 1974, figs. 57F, G). Although the shafts of the metatarsals are rather crushed, all the articular surfaces are well preserved (fig. 5H-J). The general form of the pes is shown (fig. 5C, D), and it is obviously slender. In *Hypsilophodon* (Galton 1974, fig. 58), *Parksosaurus* (Parks 1926, figs. 15, 16), and *Othnielia* (Galton and Jensen 1973, fig. 6D) the first metatarsal is relatively large. In *Dryosaurus* the pes of YPM 1884, AMNH 834, and CM 21786 (fig. 5C) all have associated phalanges, but there is no trace of a good-sized metatarsal I or of any phalanges referable to this digit. However, in the case of CM 21786, metatarsal I is probably represented by a dimunitive element (fig. 5C, D, K-M). This element has a convex proximal articular surface, so it is not a phalanx; and it shows a well-defined distal articular surface with two separate condyles (fig. 5M). It cannot be a fifth metatarsal because where known, as in *Hypsilophodon* (Galton 1974, fig. 58B) and in *Othnielia* (Galton and Jensen 1973, fig. 6A), it is a slender, tapering rod with a rounded distal end without condyles. This small element of CM 21786 (fig. 5C, D, K-M) is very similar in form and size to an element preserved with the pes of *Dysalotosaurus* (Janensch 1955, fig. 40) and identified as metatarsal I. The pes of *Camptosaurus* and *Thescelosaurus* (Gilmore 1915) are much shorter and stockier than are those referred to *Dryosaurus.*

DISCUSSION

On the basis of the comparisons made above, it is apparent that the postcranial anatomy of *Dryosaurus altus* (Marsh) is most similar to that of *Dysalotosaurus lettow-vorbecki* Pompeckj, 1920, from the Upper Jurassic of Tanzania. As noted earlier (Galton 1973), a comparison of the skull of CM 3392 from the Morrison Formation of Utah with the holotype of *Dryosaurus altus* confirms the provisional identification by Gilmore (1925). However, the skull of CM 3392 does not have a supraorbital bar as described by Gilmore (1925, fig. 3). Instead, the supraorbital tapers gently to a point lateral to the postorbital with no suture between these bones. Apart from the longer supraorbital, the skull of CM 3392 (Galton 1977) is almost identical to that of *Dysalotosaurus* (Janensch 1955, fig. 1). In all other genera of hypsilophodontids no two skulls are alike.

In addition to general hypsilophodontid characters, *Dryosaurus* and *Dysalotosaurus* show the same combination of postcranial features. The humeri (fig. 2C-H) are very similar with a low delto-pectoral crest (also shown by *Othnielia*) and a uniquely flat lateral condyle, but in *Dryosaurus* the scapula is longer than the humerus whereas in *Dysalotosaurus* these bones are subequal in length. The ilia are very similar; the ilium of AMNH 834 is almost identical to that of *Dysalotosaurus* as figured by Janensch (1955). In particular both show a very low main body to the ilium, an obliquely truncated posterior end, and a broad brevis shelf (fig. 3A-C). In the ischia (fig. 3F) the obturator process is proximal in position (also shown in *Othnielia, Parksosaurus*), and the distal halves are bar-shaped and curved in lateral view. In the hind limb

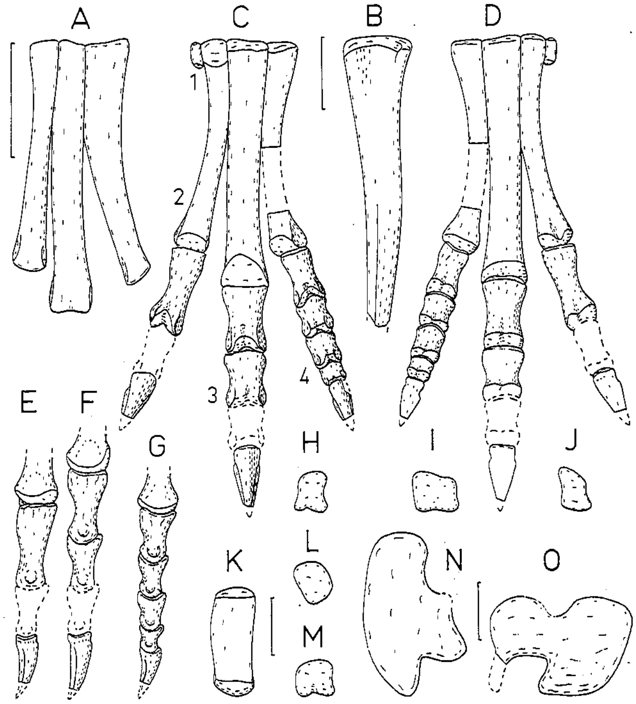

FIGURE 5.—*Dryosaurus altus,* referred specimens, pes. A, metatarsals 2-4, AMNH 834, dorsal view, X0.3. B, left tibia, AMNH 834, X0.3; C-M, left pes of CM 21786, X0.2; C, dorsal; D, ventral views; E-G, medial view of digits: E, 2; F, 3; G, 4; H-J, distal view of metatarsals: H, 2; I, 3; J, 4; K-M, metatarsal 1 in K, dorsal; L, proximal; M, distal views; N, proximal end of left tibia, CM 1949, X0.15; O, distal end of right femur, CM, 1949, X0.15. 1-4, digits 1 to 4. Scale lines represent 5 cm except K-M where 1 cm.

the femora of *Dryosaurus* (figs. 4A-D, J-O, 5O; Galton 1975, fig. 2G-L) and *Dysalotosaurus* are nearly identical and possess the following combination of characters: lesser trochanter is rodlike and separated from the greater trochanter by a deep cleft, the deep depression level with the fourth trochanter is set well anteriorly on the shaft, and the distal end is square with a well-developed anterior intercondylar groove. In the pes metatarsal I is rudimentary (figs. 5C, K) and is represented by a small nubbin of bone in both genera.

Dryosaurus altus and *Dysalotosaurus lettow-vorbecki* are very similar and, as discussed elsewhere (Galton 1977, in press), these species are congeneric and are referred to the genus *Dryosaurus* Marsh 1894 as *Dryosaurus altus* (Marsh 1878) and *Dryosaurus lettow-vorbecki* (Pompeckj 1920). The occurrence of *Dryosaurus* in the Upper Jurassic of North America and East Africa provides good evidence of the presence of a land route between Laurasia and Gondwanaland in the early Upper Jurassic (Galton 1977, in press).

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