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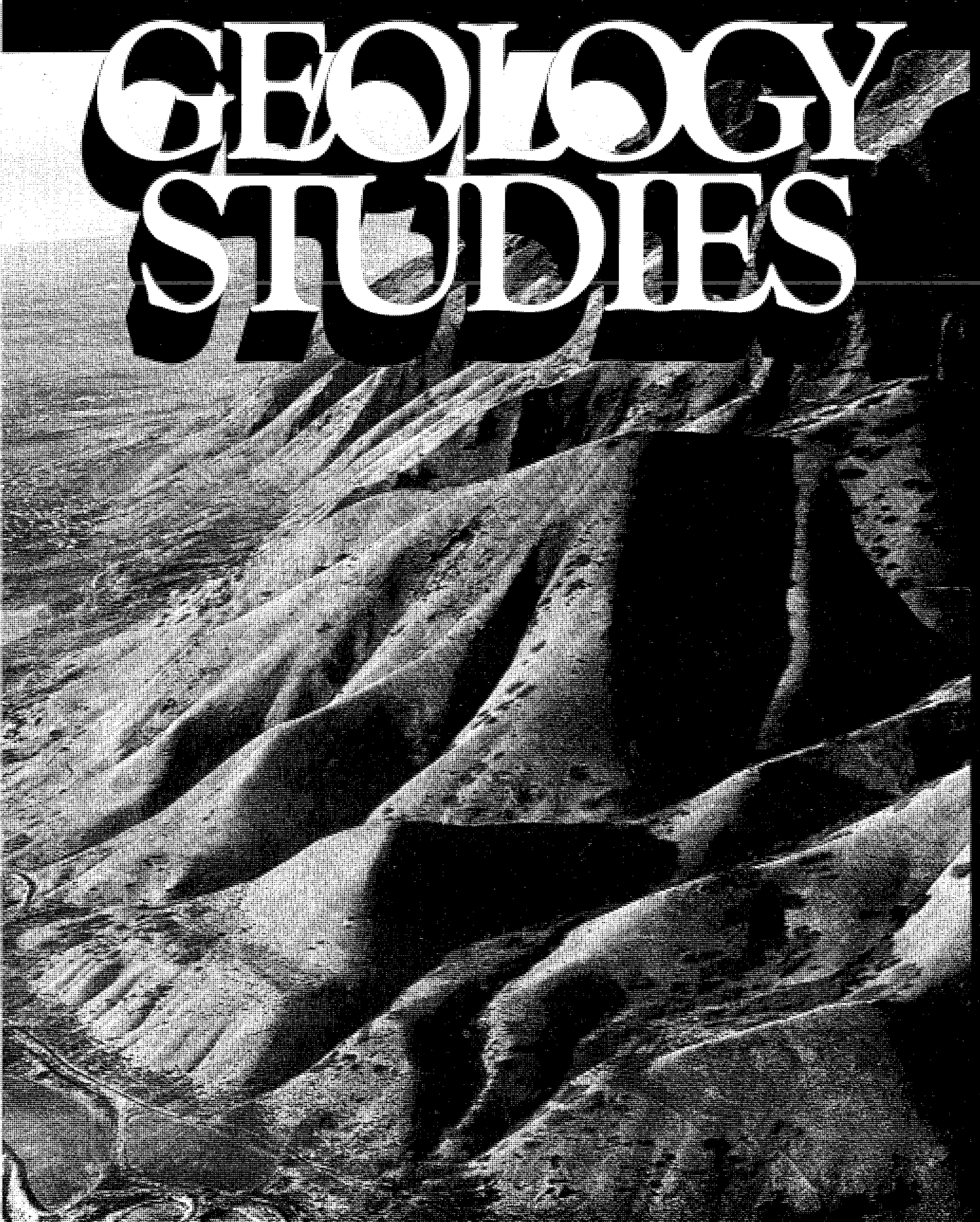

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THE GLORY OF GOD IS INTELLIGENCE

Cover: Compound faceted spurs along the Wasatch Mountains indicate alternating periods of fault displacement and tectonic stability.

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Remains of Ornithopod Dinosaurs from the Lower Cretaceous of North America

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ABSTRACT.—Two new species of ornithopod dinosaurs (Reptilia: Ornithischia) described from the Lower Cretaceous of the western interior of the United States are referred to European genera (*Hypsilophodon, Iguanodon*). *Camptosaurus depressus* may be a valid taxon on the basis of a dentary tooth referred to this species. The geographic range of *Tenontosaurus* is tentatively extended to Arizona and Maryland. A femur from Utah is probably hadrosaurian and represents the earliest record of this family to date. The transatlantic distribution of *Hypsilophodon* and *Iguanodon* indicates that there was a land connection between Europe and North America at the beginning of the Cretaceous.

INTRODUCTION

The purpose of this paper is to describe several specimens of herbivorous ornithopod dinosaurs of Lower Cretaceous age from the western interior of North America (Utah, Colorado, South Dakota, and Nebraska) and a tooth from Maryland. Two specimens are particularly important because they represent new species of *Hypsilophodon* and *Iguanodon,* two characteristically European species.

Previous Work

Remains of terrestrial vertebrates are extremely rare from the Lower Cretaceous of North America (see survey in Ostrom 1970, p. 124; Langston 1974), with only a few taxa of bipedal ornithopod dinosaurs described to date. A partial skeleton from the Lakota Sandstone (Neocomian) of Calico Canyon, near Buffalo Gap, western South Dakota, was described by Gilmore (1909) as *Camptosaurus depressus.* Many skeletons from the somewhat earlier Cloverly Formation (upper Aptian-lower Albian) of Wyoming and Montana have been described as *Tenontosaurus tilletti* by Ostrom (1970). Langston (1974) describes material of *Tenontosaurus* sp. from the Comanchean Series of Texas and Oklahoma plus a small hypsilophodontid tooth from Texas. A femur from the Aptian-Albian of Arizona that was described as a camptosaur by Miller (1964) is probably also referable to *Tenontosaurus* (see p. 00). Galton and Jensen (1975) give a preliminary description of American specimens referred to two European genera—a femur of *Hypsilophodon* (Lakota Sandstone, South Dakota) and maxillary teeth of *Iguanodon* (Cedar Mountain Formation, Utah). Galton and Jensen (1975) also refer to *Iguanodon* the distal end of a femur from the Dakota Sandstone of Nebraska which Barbour (1932) considered as hadrosaurian.

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SYSTEMATIC PALEONTOLOGY

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family Hypsilophodontidae

Hypsilophodon Huxley 1869

Type species.—*Hypsilophodon foxii* Huxley 1869

Type locality.—Isle of Wight, England

Known distribution.—Restricted to Wealden Marls (Berriasian) of Isle of Wight (Galton 1974, 1975).

Hypsilophodon wielandi, new species

Etymology.—*Hypsilophodon wielandi,* named for Prof. G. R. Wieland, who worked the Black Hills of South Dakota so extensively and who collected this specimen in 1900.

Type specimen.—AMNH 2585[1], a left femur (figs. 1A–1F).

Type locality.—4.8 km north of Piedmont, western South Dakota.

Horizon.—38 m above Morrison beds in Lakota Sandstone (Lower Cretaceous, ?Aptian *sensu* Cobban and Reeside 1952).

Diagnosis.—The femur of *Hypsilophodon wielandi* is characterized by a couple of minor differences from that of *H. foxii*: the ratio of the minimum distance between the proximal end of the femur and the distal edge of the fourth trochanter is 0.45 (0.43 in *H. foxii*), and distally there is a slight anterior intercondylar groove. For the principal measurements of the femur see table 1.

Comparisons.—As in femora of *Hypsilophodon foxii* (Galton 1969, 1974, 1975), there is a small cleft separating the lesser and greater trochanters (figs. 1C, 1I), an S-shaped ridge on the lateral surface of the greater trochanter (figs. 1A, 1G), and posterodistally the lateral and medial condyles are subequal in size (figs. 1F, 1L). The other hypsilophodontid femora described from North America differ from that of *Hypsilophodon wielandi* in several respects. In the femora of *Othnielia* (Galton 1977, described as *Nanosaurus* (?) *rex* by Galton and Jensen 1973) and

[1]Institutional names cited in this paper have been abbreviated as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; BYU, Brigham Young University Earth Sciences Museum, Provo, Utah; UA, University of Arizona Geological Collections, Tucson; UNSM, University of Nebraska State Museum, Lincoln; USGS, United States Geological Survey, Denver; USNM, United States National Museum, Washington, D.C.; YPM, Peabody Museum, Yale University, New Haven.

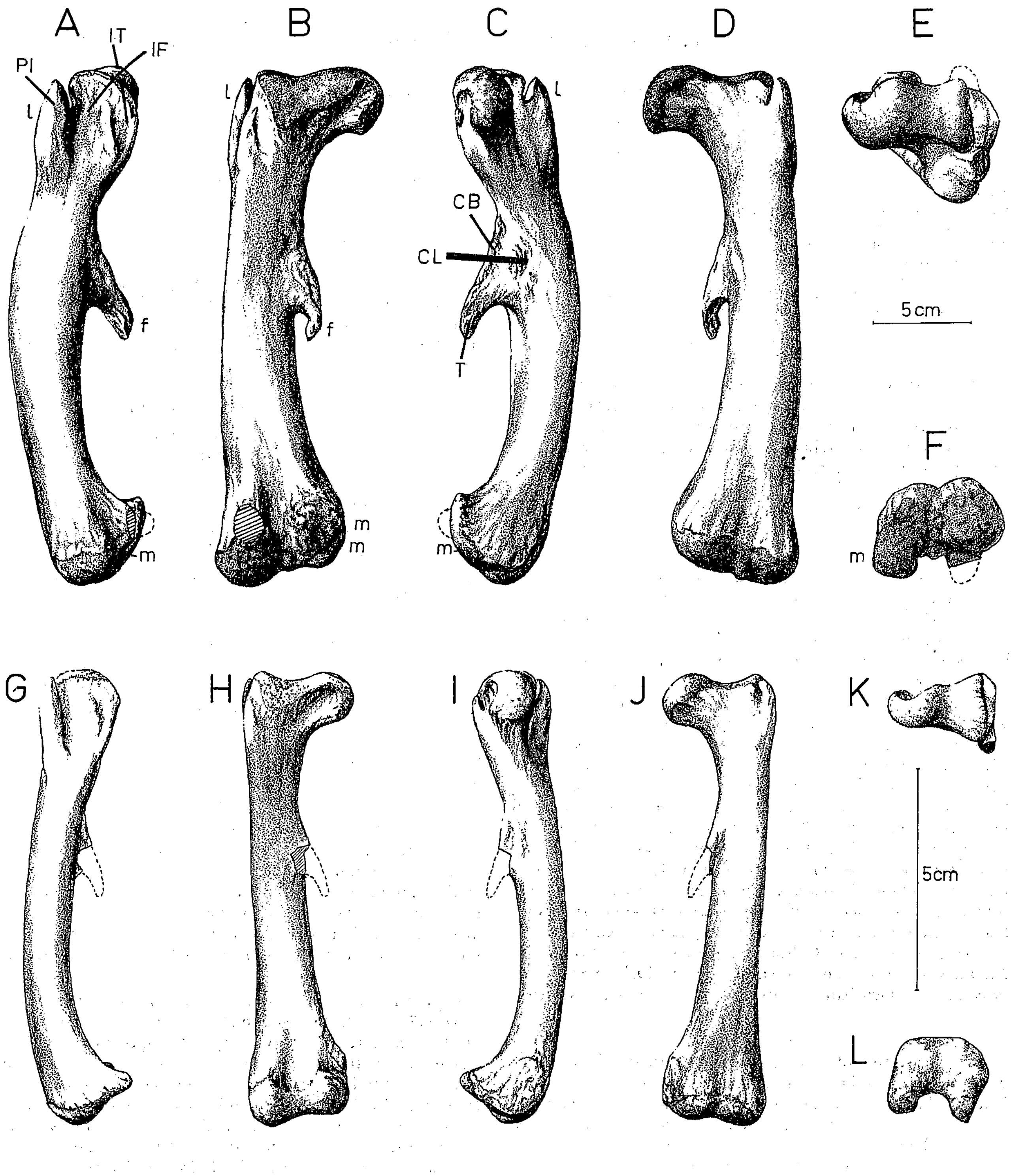


FIGURE 1.—Left femora of *Hypsilophodon*: A–F, *Hypsilophodon wielandi*, n. sp., holotype AMNH 2585, X0.33; distal end crushed, but outlines as restored are probably correct; G–L, *Hypsilophodon foxii*, BMNH R5830, X0.75. A,G, lateral view; B,H, posterior view; C,I, medial view; D,J, anterior view, E,K, proximal end; F,L, distal end. Muscles after Galton (1969, 1975). The more robust appearance of AMNH 2585 is a function of its much larger size in comparison to BMNH R5830; different sized femora of *Dryosaurus altus* show a comparable difference in proportion. CB, M. caudi-femoralis brevis; CL, M. caudi-femoralis longus; f, fourth trochanter; g, greater trochanter; IF, M. ilio-femoralis; IT, M. iliotrochantericus; l, lesser trochanter; m, medial condyle; PI, dorsal part of M. puboischiofemoralis internus; T, tendon inserting on fibula.

Dryosaurus (Galton 1975, 1977) from the Upper Jurassic, there is a deep cleft separating the lesser and greater trochanters whereas in *Parksosaurus* from the Upper Cretaceous no such cleft is present (Parks 1926). In *Othnielia* there is no anterodistal intercondylar groove, but in *Dryosaurus* it is well developed, and posteriorly the lateral condyle is thin as is also the case in *Parksosaurus.*

Langston (1974, pl. 2, fig. 3) and Thurmond (1974, fig. 14) refer two small teeth from the Comanchean Series of Texas to the Hypsilophodontidae, but they are completely unlike the teeth of any member of this family. The crown is very simple with very faint vertical ridges, and there is practically no cingulum. These teeth may be those of a fabrosaurid ornithopod.

Family Camptosauridae

Camptosaurus Marsh 1885

Type species.—*Camptosaurus* (=*Camptonutus*) *dispar* (March, 1879).

Type locality.—Quarry 13, 13 km east of Como, Albany County, Wyoming.

Known distribution.—? Middle Jurassic: Oxford Clay of Peterborough, England (Galton 1975); Upper Jurassic: Kimmeridge Clay of Oxford, England (Galton 1975); Morrison Formation of Wyoming and Colorado; Lower Cretaceous: Lakota Sandstone of South Dakota.

Camptosaurus depressus Gilmore

Camptosaurus depressus Gilmore 1909

Type specimen.—USNM 4753, ilia, pubis, and vertebrae.

Type locality and horizon.—Lakota Sandstone from Calico Canyon near Buffalo Gap, Custer County, South Dakota.

Referred specimen.—USGS D262, partial crown of a right dentary tooth (figs. 2E–2G) collected by Mr. D. E. Wolcott in 1957.

Horizon and Locality.—Lakota Sandstone 1 m above base, NW ¼ NW ½ sec. 15, T. 7 S, R. 6 E, Hot prings Quadrangle, Fall River Co., South Dakota.

Comparisons.—The thickly enamelled and ornamented surface of the crown (fig. 2E) is notable for the sparcity of vertical ridging with only one long ridge plus two others, neither of which extends further than the middle of the crown. The tubercules of the anterior and posterior edges are not extended into vertical ridges as are some of those on the teeth of *Camptosaurus* (Gilmore 1909) and *Tenontosaurus* (Ostrom 1970). The single long ridge is larger than the others, but it is small in comparison with the prominent keel present on maxillary teeth of *Camptosaurus* (Gilmore 1909; Ostrom 1970, pl. 15G) and on dentary teeth of *Tenontosaurus* (Ostrom 1970, Langston 1974). At midcrown level the thickly enamelled medial surface of the dentary teeth of *Camptosaurus* have from two to four vertical ridges (Gilmore 1909, fig. 2). These teeth also differ from USGS D262 (figs. 2E–2G) in having several tubercules along the tip of the unworn tooth. This is also true for unworn maxillary teeth of *Tenontosaurus* (YPM 5456) in which there are up to nine ridges near the tip of the lateral surface and still four or five ridges halfway down the crown (Ostrom 1970, pl. 16C, D; Langston 1974). A short ridge is present on the thinly enamelled surface of USGS D262 opposite the long ridge of the other side (figs. 2F, 2G). In the teeth of *Camptosaurus* there are several comparable ridges, but none are present in *Tenontosaurus* (YPM 5456).

USGS D262 is similar to the dentary teeth of *Camptosaurus,* and, as the holotype of *C. depressus* is from the Lakota Sandstone of South Dakota, this crown (figs. 2E–2G) is tentatively identified as a right dentary tooth of *C. depressus.* If correctly referred, this tooth supports the contention of Ostrom (1970) that *C. depressus* is a valid taxon.

Associated fauna.—The femur of *Hypsilophodon wielandi* and the partial skeleton (Gilmore 1914, p. 114–21) of the ankylosaur *Hoplitosaurus marshi* (Lucas 1901) are the only dinosaurs reported to date from the Lakota Sandstone. The latter was discovered alongside the holotype of *Camptosaurus depressus.*

TABLE 1
MEASUREMENTS (IN MM) OF *HYPSILOPHODON* FEMORA

	L	Wp	Wd	Mw	F	TL
BMNH R5830	101	26.5	25	10.5	43	0.9
BMNH R196	150	–	–	14	65	1.36
BMNH R5829	200	52	56	–	87	1.8
AMNH 2585	270	80	84*	35	115	2.43

F, minimum distance from proximal end to distal edge of fourth trochanter; L, maximum length; Mw, minimum width of shaft; TL, estimated total length (in m) of body based on size of BMNH R196; Wd, maximum width of distal end; Wp, maximum width of proximal end; *, crushing.

Family Iguanodontidae
Iguanodon

Iguanodon Mantell 1825

Type species.—*Iguanodon mantelli* Meyer 1832.

Type locality.—Near Brighton, Sussex, England.

Known distribution.—Neocomian (Lower Cretaceous) of western Europe, Tunisia, and eastern Mongolia (see below, p. 10).

Iguanodon ottingeri, new species

Etymology.—*Iguanodon ottingeri,* named for Mr. Lin Ottinger who collected the holotype in 1968.

Type specimen.—BYU 2000, posterior part of right maxilla with teeth (figs. 2A–2D, 3A).

Type locality.—North of Arches National Park boundary 3.22 km, 1.2 km east of Dalton Well south of U.S. 160 in section 22, T. 24 S, R. 20 E, Grand County, southeastern Utah.

Occurrence.—Specimen was recovered from a thinly bedded deposit of reworked dinosaur bones in the ? Basal Cedar Mountain Formation (Bodily 1969, Stokes 1952). Other materials collected from the deposit includes scutes and other bones of an ankylosaur. At first sight the fossiliferous zone appears to occur within the upper member of the Morrison Formation (Brushy Basin Member), but *Iguanodon* and ankylosaurs are both characteristically Cretaceous vertebrates. The Cedar Mountain sediments interfinger with the early Mancos Shale sediments in this area and, in some cases, fine Mancos-like but tinted sediments lie directly upon the lower or Salt Wash Member of the Morrison Formation without any intervening resistant sand channels, conglomerates, or hard shales or other sediments characteristic of the Dakota Sandstone, the Cedar Mountain Formation, or the Brushy Basin Member of the Morrison Formation. Because of these local complications in the stratigraphy, the vertebrate remains are used to date the horizon for BYU 2000 which is tentatively regarded as Lower Cretaceous (Neocomian).

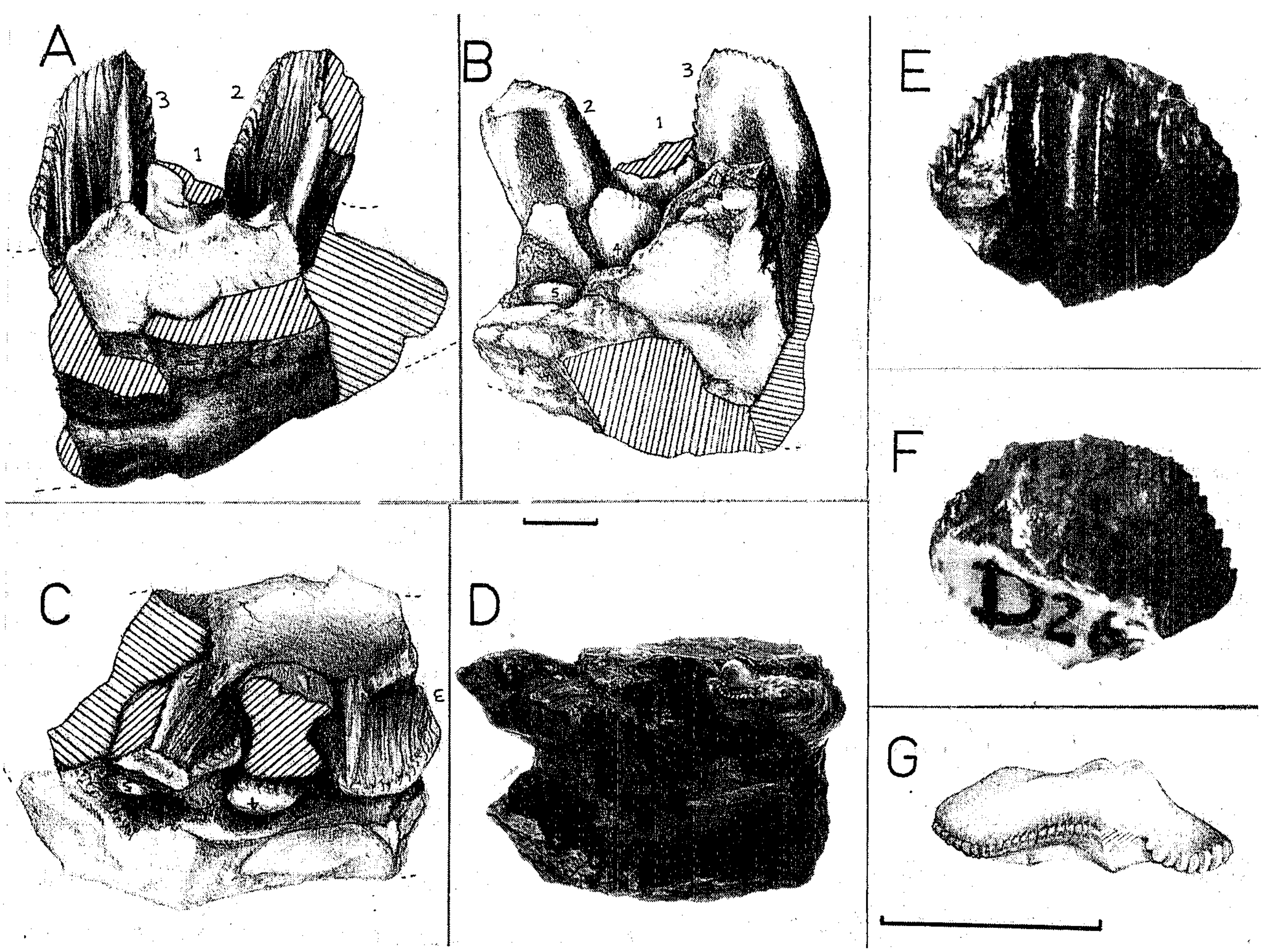
Diagnosis.—*Iguanodon*-like teeth with prominent vertical depressions on the anterior and posterior edges of the root and the base of the crown.

Description and comparisons.—Two replacement teeth identify the medial side of BYU 2000 (fig. 2B), so the thickly enamelled and strongly ornamented surface of the crown of the functional teeth is the lateral surface (figs. 2A, 3A) and, as a result, BYU 2000 is part of the maxilla. The slope of the dorsal surface is natural (figs. 2A, 2B, 3A), and as the prominent keel (figs. 2A, 3A) is posterior to the median line in ornithopod teeth (Hulke 1885, Gilmore 1909), BYU 2000 is part of the posterior end of the right maxilla. The morphology of the lateral surface of the bone (figs. 2A, 3A) is very similar to this region of an isolated maxilla (BMNH R754) of *Iguanodon* described by Hulke (1886).

On the posterolateral edge of the crown of the complete tooth there are at least nine well-developed tubercules, each of which continues as a short ridge (figs. 2A, 3A). Along the obliquely inclined ventral edge of the crown there are five small tubercules, the most anterior (i.e., furthest from the prominent keel) of which extends as a short ridge, and then four tubercules that extend as ridges which traverse the height of the crown (figs. 2A, 3A). Along the anterolateral edge (figs. 2A, 3A) there are twelve tubercules of which three extend onto the crown as ridges. The lower part of the medial surfaces of the crowns (fig. 2B) is covered with a thin layer of enamel.

The prominent keel on the lateral surface (figs. 2A, 3A) readily separates the teeth from those of *Tenontosaurus,* in which such a keel is present only on the dentary teeth (Ostrom 1970, Langston 1974). The complete crown of BYU 2000 differs from those of the maxillary teeth of *Camptosaurus* (Gilmore 1909; Ostrom 1970, pl. 15G) in its larger size, more angular outline (figs. 2A, 3A), and much more prominent keel. In addition, the broken and well-erupted tooth (figs. 2A–2D) shows that there is a deep vertical depression on both the anterior and the posterior edges of the root and the base of the crown which receives the upper part of the crowns of the adjacent teeth. No comparable depressions are present on the teeth of *Camptosaurus,* in which each crown slightly overlaps the one behind it (Gilmore 1909, fig. 7).

There is a lot of variation in the form of the maxillary teeth of *Iguanodon* (e.g., Mantell 1825, 1848; Owen 1855, 1861; Hulke 1886), but those of BYU 2000 are similar to those of BMNH 40100 (figs. 2A–2D; 3A, 3C, 3D) and almost identical to the posterior tooth of BMNH R754 (fig. 3B). In *Iguanodon* each tooth usually overlaps the one posterior to it (Hulke 1886), but sometimes the anterior edge of the crown and root has a vertical depression to receive the crown of the more anterior tooth (figs. 3C, 3D). However, no tooth of *Iguanodon* seen by the senior author in the collection of the British Museum (Natural History) has a deep depression on both the anterior and the posterior edges as in BYU 2000 (figs. 2A–2D). An unusual example of tooth replacement for *Iguanodon* is shown (fig. 3D) where the root of the functional tooth extends dorsally lateral to the replacement tooth (fig. 3C), but medially it does not (fig. 3D). Instead, the replacement tooth fits into a recess at the base of the crown so that it is immediately above the functional tooth but, unlike the situation in hadrosaurs



(Lull and Wright 1942), adjacent tooth series do not show the same feature, and the teeth are not closely packed to form a dental battery.

Tenontosaurus Ostrom

Tenontosaurus Ostrom 1970

Type species.—*Tenontosaurus tilletti* Ostrom 1970

Type locality.—AMNH 33-1, SW ¼ section 26, T. 7 N, R. 16 E, Wheatland County, Montana.

Known distribution.—Cloverly Formation (Aptian-Albian) of Montana and Wyoming (Ostrom 1970); Comanchean Series (Neocomian-Albian) of Texas and Oklahoma (Langston 1974).

Tenontosaurus sp.

Referred Specimens.—UA 22, nearly complete right femur (fig. 4O); UA 23, two fragments of left femur, described by Miller (1964; pl. 61, figs. A,B; pl. 62, Fig. E).

Locality.—South of Empire Mountains,about 64 km southeast of Tucson, southern Arizona.

Horizon.—Nonmarine facies of Aptian-Albian age.

Comparisons.—The femur is 700 mm long so it is from an animal with a total body length of about 5.2 m. The femur is bowed in medial view (fig. 4O) rather than straight as in hadrosaurs (fig. 4G; Parks 1920, Lull and Wright 1942). Miller (1964, p. 380) noted that this "femur resembles *Iguanodon atherfieldensis*; however, it differs from members of that genus in that the head is not at right angles to the shaft, the width of the femur is too great, and the shaft is concave distally on the posterior surface." Although not cleared of matrix, the anterodistal intercondylar groove appears to be not nearly so well developed as in *Iguanodon* and more comparable to the femora of *Camptosaurus*. However, the lesser trochanter of UA 20 is not markedly expanded anteroposteriorly as in the femora of *Camptosaurus* (Gilmore 1909, Galton 1975). In *Tenontosaurus* the lesser trochanter is not expanded (Ostrom 1970), and the form of the rest of the femur is similar to UA 22 (fig. 4P). The more massive construction of the bone and the lower position of the fourth trochanter of UA 20 may be attributed to the difference in size: the femur of *Tenontosaurus* figured is 480 mm (Ostrom 1970; longest femur listed, 580 mm). The femur UA 20 is tentatively regarded as a large femur of *Tenontosaurus*, and its age (Aptian-Albian) is certainly correct. However, it may represent an as yet undefined genus.

? *Tenontosaurus* sp.

Referred Specimen.—USNM 244564, incomplete crown of a right dentary tooth (Text.-figs. 2H, 2I).

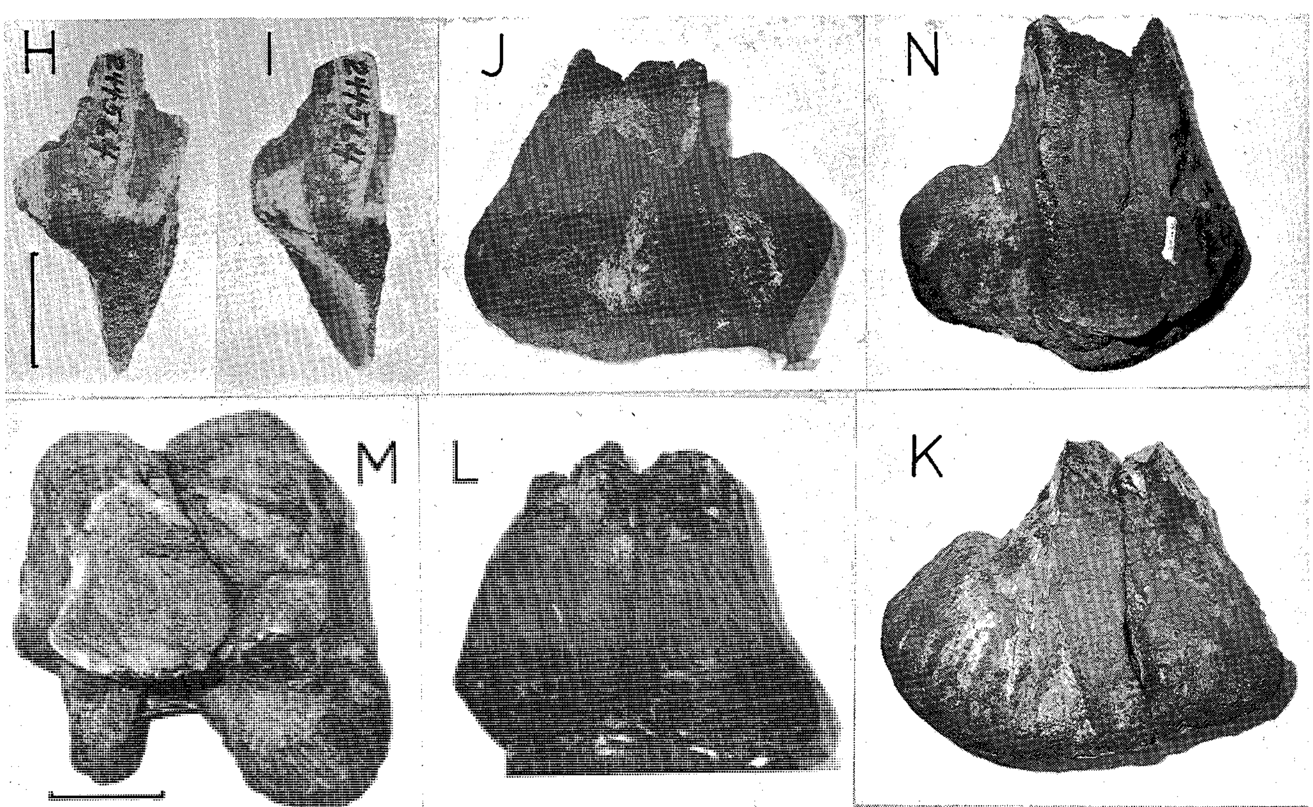


FIGURE 2.—Iguanodontid teeth and a femur; A–D, posterior part of right maxilla with teeth of *Iguanodon ottingeri* n. sp., holotype BYU 2000 approximately X1. Note that A and B illustrated upside down. A, lateral view, compare with figure 4A; B, medial view; C, ventral view with lateral surface lowermost; D, ventromedial view looking along teeth. E–G, right dentary tooth referred to *Camptosaurus depressus*, USGS D262, X3, E, medial view; F, lateral view; G, dorsal view with medial surface lowermost. H,I, right dentary tooth, ?*Tenontosaurus*, USNM 244564, X0.5, in H, medial view; I, anteromedial view; J–N, distal end of left femur UNSM 1200, X0.15, ? hadrosaurian (see also figures 4I–4N), J, lateral view; K, medial view; L, posterior view; M, proximal view; N, lateral view of shaft section to show medial condyles. Broken surfaces shown by cross hatching. Scale lines represent 1 cm in A–I, 10 cm in J–N. 1–5, teeth numbered in order of age: 1, oldest tooth with most of crown broken; 2, functional tooth with obliquely inclined occlusal surface; 3, unworn functional tooth; 4, replacement tooth for 1; 5, replacement tooth for 2.

Horizon and Locality.—Arundel Formation (Neocomian) at the Jessop Police Barracks, Laurel, Maryland.

Comparisons.—The extreme degree of development of the central ridge (fig. 2H, 2I) is matched only among ornithopod taxa described to date by the dentary teeth of *Tenontosaurus* (Langston 1974, pl. 2, fig. 4; Ostrom 1970, pl. 17, fig. 17). However, USNM 244564 differs from the teeth of *Tenontosaurus* in two respects. Firstly, it lacks a secondary vertical ridge on the lower half of the crown either side of the central ridge (fig. 2H). Secondly, the central ridge does not extend to the base of the crown so there is a vertically concave area at the base (figs. 2H, 2I). In *Tenontosaurus*, the central ridge extends to the base of the crown (Ostrom 1970, Langston 1974).

Discussion.—Lull (1911) described the ornithopod *Dryosaurus grandis* from the Arundel Formation, but Gilmore (1921) showed that the holotype represented a theropod dinosaur, *Ornithomimus affinis*. Consequently, the dentary tooth (fig. 2H, 2I) is the first evidence for an ornithopod dinosaur from the Arundel Formation, the fauna of which is also discussed by Vokes (1949), Ostrom (1970), and Langston (1974).

Family Hadrosauridae

Hadrosaur femora

BYU 2000.—Badly damaged right femur (figs. 4A–4D).

Locality.—East of Canyonlands Airport 3.22 km, section 28 in T. 23 S, R. 20 E, Grand County, southeastern Utah.

Occurrence.—In the uppermost sediments of the Lower Cretaceous Cedar Mountain Formation in a region of fluctuating early Cretaceous shorelines which generated an interfingering

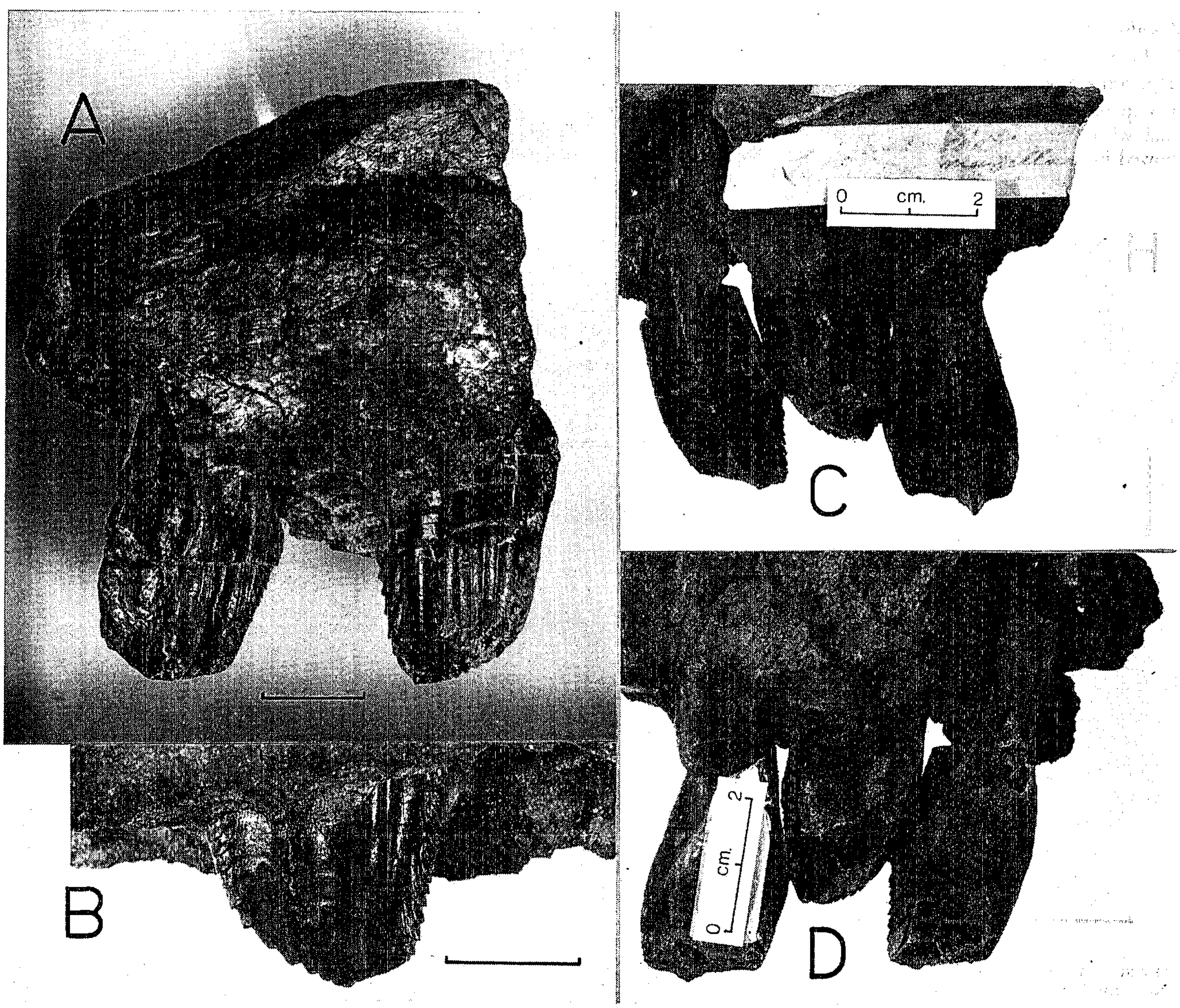


FIGURE 3.—Maxillary teeth of *Iguanodon*: A, *Iguanodon ottingeri* n. sp., holotype BYU 2000, X1.5, lateral view of posterior part of right maxilla; compare with figure 2A; B, *Iguanodon mantelli*, posterior tooth of left maxilla BMNH R754, X2, Tilgate Forest (Wealden) of Cuckfield, Sussex, England, complete maxilla figured by Hulke (1886); C–D, *Iguanodon mantelli*, middle teeth of left maxilla BMNH 40100, X1, Lower Greensand Formation (Aptian) of Blackgang Chin, Isle of Wight, England; other teeth of this specimen illustrated by Owen (1861, pl. 7); C, lateral view; D, medial view. Scale lines represent 20 mm in A, C, D; 10 mm in B.

of the Lower Mancos Formation shales with the siltstones and sands of the Cedar Mountain Formation.

Description.—The right femur (figs. 2J–2N, 4A–4D) is represented by the globular head and the inner condyle, but most of the shaft is badly eroded. The two sections of the femur measure a total length of 1070 mm with probably about 50 to 100 mm missing so this femur is from an animal with a body length of at least 9 m. Distally the anterior intercondylar groove (figs. 4C–4D) is very deep with a maximum depth of about 65 mm, and it is partly covered by a prominent lateral lip from the inner condyle (fig. 4D) as in hadrosaurs (fig. 4H, Parks 1920, Lull and Wright 1942). The shaft also appears to have been fairly straight in medial view (fig. 4B) with a slight anterior bow in the distal third as is also the case in hadrosaurs (figs. 4B, 4G), and posteriorly the medial condyle is large and upwardly hooked (fig. 4B). However, the anterior intercondylar groove is also very deep in *Iguanodon* (fig. 4F), and the shaft may be almost straight (fig. 4E). Anteriorly the distal condyles appear to be more pronounced in BYU 2001 (fig. 4B) than in *Iguanodon* (fig. 4E).

UNSM 1200 (=6-8-28).—Distal and end of left femur (figs. 2J–2N, 4I–4N) described by Barbour (1932).

Locality.—Collected by J. B. White in 1928 on his farm 3.22 km south of Decatur, northeastern Burt County, near the Missouri River, eastern Nebraska.

Horizon.—Dakota Sandstone, Lower Cretaceous, Aptian-Albian (Cobban and Reeside 1952); the correctness of the conclusion by Barbour (1931) that this femur was found in place rather than after transportation is shown by the fact that the consolidated matrix in the anterior intercondylar groove is typical Dakota Sandstone.

Comparisons.—The anterior intercondylar groove is deep (figs. 2M; 2N; 4M, 4O) with a maximum depth of 80 mm. The complete femur was very large for an ornithopod because the anterior-posterior diameter of the inner condyle is 356 mm as against 292 mm for a femur of the hadrosaur *Kritosaurus* with a length of 1045 mm and from an animal with a total length of about 8.2 m (Parks 1920). Consequently, this distal end is from an animal with a total body length of about 9.7 m. UNSM 200 (figs. 2J–2N, 4I–4N) is similar to the distal ends of the femora of hadrosaurs (figs. 4G, 4H; Parks 1920, Lull and Wright 1942), and it was referred to the hadrosaur *Trachodon* by Barbour (1931). However, it is also similar to the distal ends of the femora of *Iguanodon* (figs. 4E, 4F) so this femur is identified as hadrosaurian with less certainty than BYU 2000.

Discussion

The femur (fig. 4A–4D) is definitely hadrosaurian, and that described by Barbour (1931) (figs. 2J–2N; 4I–4N) may also be hadrosaurian. The problem of distinguishing the femora of *Iguanodon* from those of hadrosaurs is not helped by the fact that, as shown by Rozhdestvensky (1967) and Taquet (1975), hadrosaurs probably originated from *Iguanodon*-like iguanodontids. The oldest hadrosaur previously described from North America is from the Eutaw Formation (Upper Cretaceous, Santonian; see Kaye and Russell 1973) of Mississippi. Older Hadrosaurian remains are known from the Upper Cretaceous of England (Cenomian, Lydekker 1888); Kazakhstan (Cenomian, Rozhdestvensky 1968); and the eastern Gobi Desert, Mongolia (? Albian, Gilmore 1933, Rohzdestvensky 1967). If correctly identified, the femur (figs. 4A–4D) represents the first remains of a hadrosaur of Lower Cretaceous age and opens up the possibility that more complete remains of a hadrosaur will be excavated from the Cedar Mountain Formation.

Hypsilophodon and *Iguanodon* are the best known genera of ornithopod dinosaur from the Lower Cretaceous of England. Remains of *Iguanodon* are widespread with many specimens from the Lower Cretaceous of southern England (Mantell 1848, Owen 1855, Hulke 1886, Hooley 1925), Belgium (Casier 1960), and France (Lapparent 1967) plus very fragmentary material from Spain (Lapparent 1966) and Portugal (Lapparent and Zbyszewski 1957). *Iguanodon* was probably also present in Tunisia (Lapparent 1960), the eastern Gobi Desert of Mongolia (Rozhdestvensky 1952), and possibly Spitzbergen (Lapparent 1962) as well, but the last record is necessarily tentative because it is based on footprints (fig. 5).

The North Atlantic started to open between North America and Africa in the Lower Jurassic (Le Pichon and Fox 1971), and the second stage of expansion, which corresponds to the Bermuda discontinuity, probably ended sometime between the Upper Jurassic and the Lower Cretaceous (Le Pichon and Fox 1971). The presence of a land connection between Laurasia and Gondwanaland is clearly shown by the great similarity of the dinosaurian faunas of the Upper Jurassic which are best known from the Morrison Formation of North America and the Tendaguru of Tanzania, East Africa (Colbert 1973, Galton 1977). However, Ostrom (1970) found no taxa common to the Cloverly Formation (Aptian-Albian) of North America and the Wealden (Neocomian) of Europe, but in part this is probably a result of the age difference between the two faunas. Ecological differences are also apparent as shown by the different relative abundances of the tetrapod elements of the faunas, and this is particularly true of the fauna of the Arundel Formation of Maryland (see Ostrom 1970 for details) which, although of about the same age as the Wealden beds, has only one very fragmentary remain of an ornithopod (p. 00).

The specimens of *Hypsilophodon* and *Iguanodon* described above show that the presumed absence of these genera from North America reflected the lack of material from beds of the appropriate age and/or ecology. The presence of these characteristically European genera in North America indicates a northern land connection sometime in the Lower Cretaceous. *Valdosaurus* (Galton 1977) from the lower Cretaceous (Wealden) of England is similar to *Dryosaurus* from the Upper Jurassic (Morrison) of western United States (Galton 1975, 1977), so *Valdosaurus* may also have crossed the Lower Cretaceous land connection. Reconstructions of the northerly limit of the North Atlantic at this time vary (fig. 5) from south of Newfoundland (Cox 1974) to a connection with the Arctic Ocean via an epicontinental seaway betwen Greenland and Scandinavia (Hallam 1971, Berggren and Hollister 1974).

Epicontinental seas, shallow and liable to local retreats and advances, are not such an absolute barrier to terrestrial animals as are true oceans. Allen (1975) has recently reinterpreted the "deltaic" nature of the Wealden (Lower Cretaceous) of southern England as a subsiding graben-basin spasmodically open to the sea and marginated by active horsts. Hallan and Sellwood (1976) reconstruct continuous land between eastern North America and western Europe during the Berriasian (Lower Cretaceous). The presence of two characteristically European genera in North America indicates that a northern land route was present between these two areas in the Lower Cretaceous. Future discoveries in the Neocomian of North America will probably increase the number of genera common to both areas. During the Lower Cretaceous the midcontinental seaway of central North America (fig. 5) had not extended far enough north to separate two distinct dinosaurian faunas in the northern hemisphere (Asia America, Asia plus western North America; Euramerica, Europe plus eastern North America) as occurs in the Upper Cretaceous (Cox 1974).

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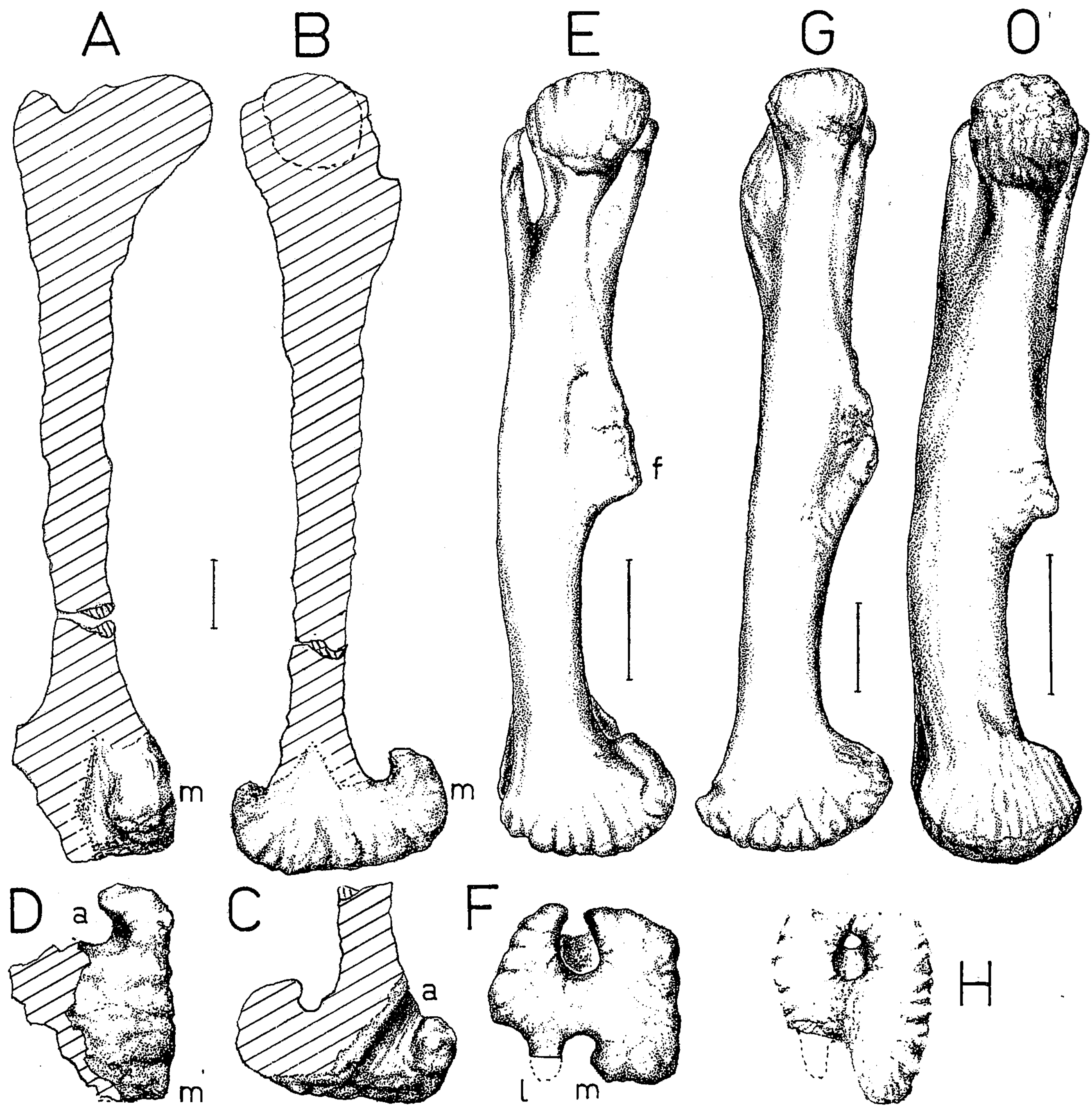

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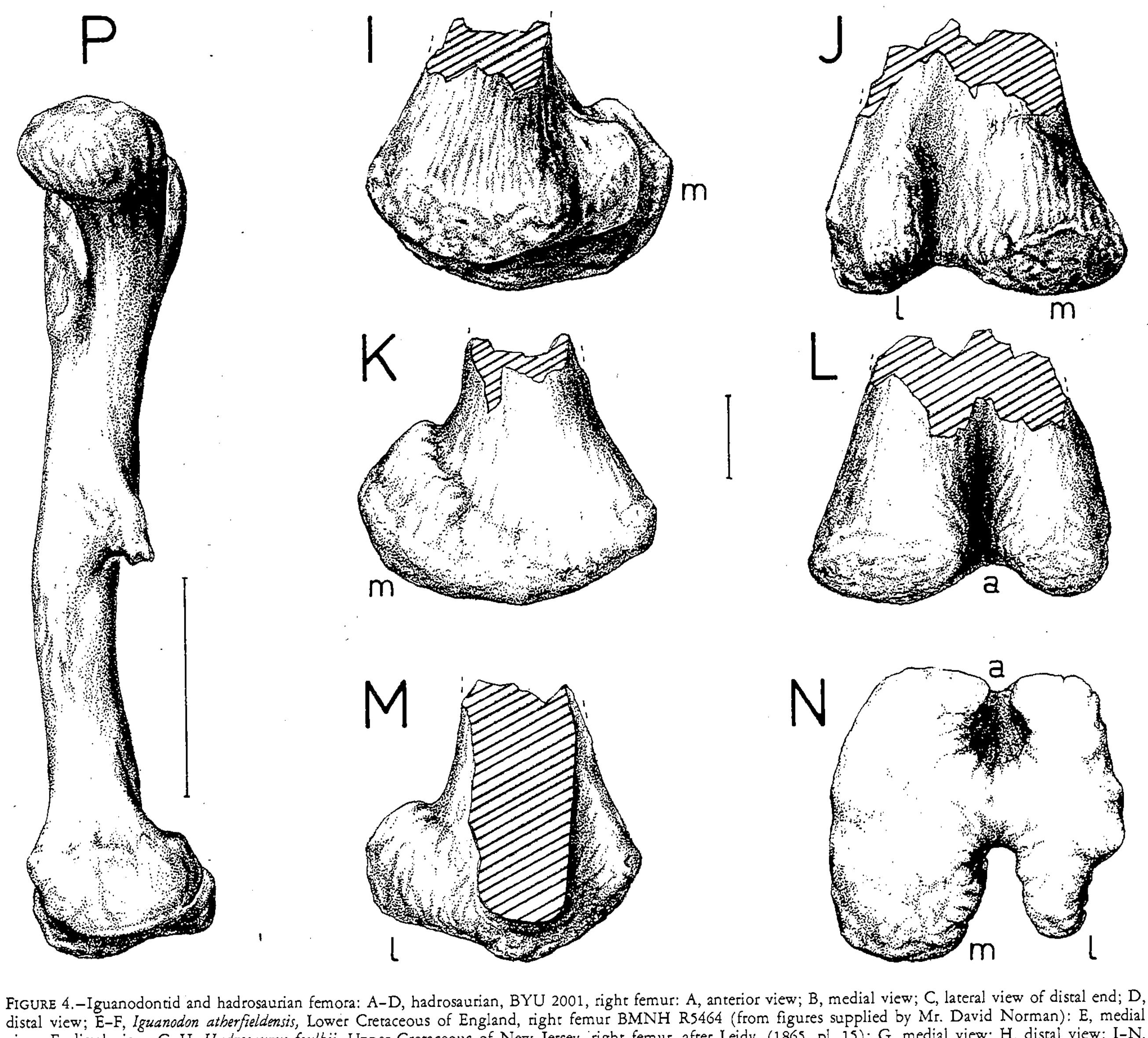

FIGURE 4.–Iguanodontid and hadrosaurian femora: A–D, hadrosaurian, BYU 2001, right femur: A, anterior view; B, medial view; C, lateral view of distal end; D, distal view; E–F, *Iguanodon atherfieldensis*, Lower Cretaceous of England, right femur BMNH R5464 (from figures supplied by Mr. David Norman): E, medial view; F, distal view; G–H, *Hadrosaurus foulkii*, Upper Cretaceous of New Jersey, right femur, after Leidy, (1865, pl. 15): G, medial view; H, distal view; I–N, hadrosaurian (or ? iguanodontid), distal end of left femur UNSM 1200: I, lateral view; J, posterior view; K, medial view; L, anterior view; M, section in medial view; N, distal view; O, *Tenontosaurus* sp., UA 21 right femur in medial view, P. *Tenontosaurus tilletti*, right femur in medial view, after Ostrom (1970, pl. 20). Scale lines represent 10 cm, broken bone shown by mechanical shading. a, anterior intercondylar groove; f, fourth trochanter; l, lateral condyle; m, medial condyle.

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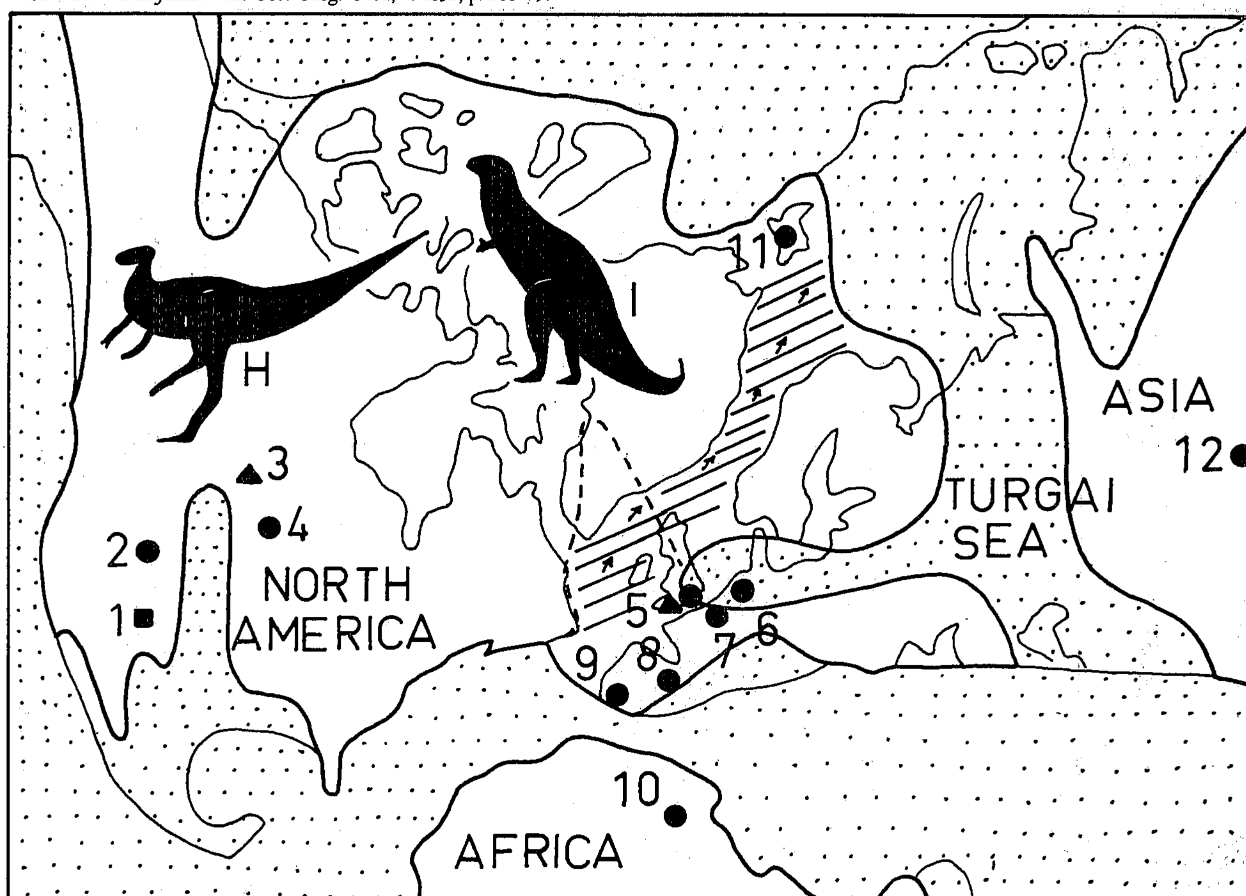

FIGURE 5.–Map to show localities and the distribution of land in part of the northern hemisphere during the Lower Cretaceous, after Galton and Jensen (1975) and modified from Cox (1974). —— reconstructed coastlines; ———, present coastlines; ---, northern extent of North Atlantic after Dietz and Holden (1970); →→, circulation currents, after Berggren and Hollister (1974); cross hatching, epicontinental sea, after Hallam (1971); H,I, flesh reconstructions of *Hypsilophodon* and *Iguanodon* with body lengths of up to 2.3 meters and 9 meters, respectively; ▲, *Hypsilophodon* localities; ●, *Iguanodonon* localities; ■, *Tenontosaurus* locality; 1, southern Arizona; 2, southern Utah; 3, western South Dakota; 4, eastern Nebraska; 5, southern England; 6, Belgium; 7, France; 8, Spain; 9, Portugal; 10, Tunisia; 11, Spitzbergen; 12, eastern Gobi Desert (symbol shifted slightly left).