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THE POSTURE OF HADROSAURIAN DINOSAURS

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ABSTRACT—Comparisons of hadrosaurs with undoubtedly quadrupedal dinosaurs and graviportal mammals show that hadrosaurs were bipedal. Arguments used to show that hadrosaurs were quadrupedal indicate only that most of the thoracic and caudal sections of the vertebral column were held more or less horizontally as in many birds.

INTRODUCTION

HADROSAURIAN DINOSAURS are represented by a large number of complete skeletons from the Upper Cretaceous. Many of these are displayed in museums of North America but the animal is usually shown in a resting position. The pose is either quadrupedal or bipedal with the vertebral column at an angle of about 45° and the tail touching the ground. Lull and Wright (1942) concluded that although hadrosaurs probably were bipedal the vertebral column was held more or less horizontally. More recently Ostrom (1964) reached the same conclusion but Sternberg (1965) suggested that they were completely quadrupedal. Hadrosaurs are usually regarded as aquatic animals (e.g. Osborn 1912, Brown 1916, Lull and Wright 1942, Colbert 1961, Sternberg 1965) but recently Ostrom (1964) has made a convincing case that they were terrestrial herbivores. Ostrom (1964) concluded that hadrosaurs may have migrated across rivers and swamps or retreated into these waters to escape from predators. In this paper I have attempted to bring together as many facets as possible that bear on the posture of hadrosaurs while on land. Institution names have been abbreviated as follows:

AMNH—American Museum of Natural History
CM—Carnegie Museum, Pittsburgh, Pa.
NMC—National Museum of Canada, Ottawa
ROM—Royal Ontario Museum, Toronto
USNM—United States National Museum, Washington, D.C.
YPM—Peabody Museum, Yale University

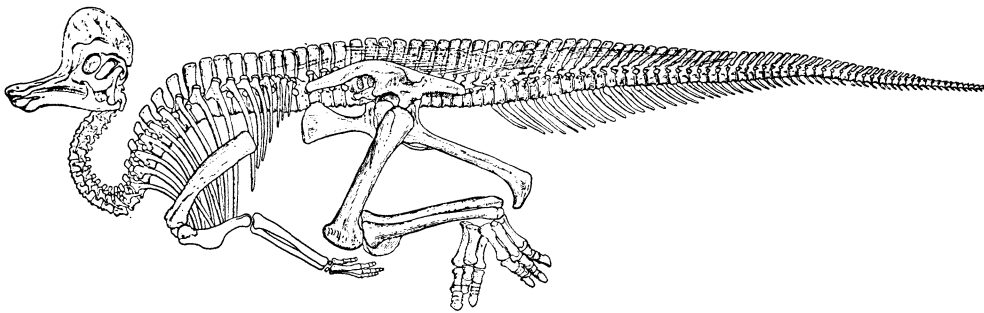
I am grateful to Dr. C. B. Cox of King's College London; Dr. W. Langston of the Texas Memorial Museum, Austin; Dr. T. E. White, Dinosaur National Monument, Jensen; Dr. J. H. Ostrom and R. T. B. Bakker of Yale University for their criticisms and suggestions. The American Museum of Natural History kindly allowed me to reproduce the drawing used for text-figure 1 and W. Coombs, Jr. helped with ankylosaurs and provided the photograph used for text-figure 4C. The photograph for text-figure 3 was taken by A. H. Coleman and the manuscript was typed by Louise Holtzinger. Travel funds

from the Peabody Museum enabled me to see the mounted skeletons of hadrosaurs cited. Dr. A. J. Charig of the British Museum (Natural History) kindly provided ratios for two ankylosaurs.

THE ATTITUDE OF THE VERTEBRAL COLUMN IN HADROSAURS

Lull and Wright (1942), Ostrom (1964) and Sternberg (1965) have emphasized that in all naturally articulated skeletons of hadrosaurs the vertebral column, from dorsal 7 back through the proximal two-thirds of the tail, is preserved remarkably straight (text-figs. 1, 5, see also plates in Lull and Wright, 1942). This condition apparently is due to an extensive series of ossified tendons that would have inhibited any arching or lateral bending of much of the back and tail during life. Sternberg (1965) objected to the extremely upright bipedal pose of *Corythosaurus* as reconstructed in Brown (1916, fig. 16, see also *Kritosaurus*). To this he could have added the mounted skeletons of *Corythosaurus* (ROM 5505, see Lull and Wright 1942, pl. 28A) and *Anatosaurus* (AMNH 5886, see Lull and Wright 1942, pl. 15) and reconstruction of *Anatosaurus* by Osborn (1912, figs. 3, 13). In each of these the vertebral column is reconstructed at an angle that ranges from 65° to 75° to the horizontal with a distinct bend in the tail so that the posterior half or two thirds lies on the ground. Because most of the vertebral column is preserved "ramrod" straight in so many specimens we must conclude a straight and rigid column in life. The sacrum then must have been held close to the horizontal if the tail was to clear the ground while the animal walked.

The structure of the ilium shows that the sacrum must have been held horizontal (text-figs. 1, 2, 5). Lull and Wright (1942, p. 87) wrote that "the acetabulum—is a shallow curve forming not more than 105° of arc as compared with upward of 180° in the Saurischia (*Creosaurus*, *Morosaurus*). It is this relative shallowness of the acetabulum, together with the lightness of the pubic peduncle [text-fig. 2], that renders doubtful the assumption of anything like the



TEXT-FIG. 1—*Corythosaurus casuarius*, AMNH 5240, as preserved, about $\times 1/45$ natural size. From Brown (1916, pl. 13, fig. 2) and reproduced by courtesy of the American Museum of Natural History.

erect posture of the body often seen in mounted and restored skeletons of hadrosaurian dinosaurs. For in such an attitude the upward thrust of the femoral head would bear, not upon the acetabulum and the acetabular bar [formed by the sacral ribs], but partly against the light pubic peduncle and against the pubis itself. The whole ilium is strong enough for the weight it had to carry if the long axis were inclined but slightly from the horizontal." From the figures of *Corythosaurus* (text-fig. 1) *Anatosaurus* (text-figs. 2A, 5) and *Hypacrosaurus* (text-fig. 2B) it is apparent that the vertebral column need only be 20° above the horizontal for the femur to bear on the weak pubic peduncle.

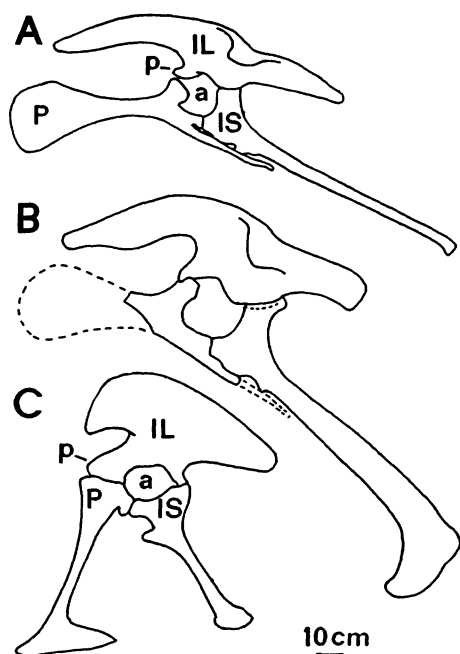
The ramrod straight posterior dorsal, sacral and anterior caudal vertebrae, the slender pubic peduncle and the shallow curve of the acetabulum show that the straight part of the vertebral column must have been held more or less horizontally and that any other position would have been difficult or even impossible. Sternberg's conclusion (1965) that hadrosaurs were always quadrupedal does not necessarily follow.

ATTITUDE OF THE VERTEBRAL COLUMN IN LIVING BIPEDS

The usual reconstruction of hadrosaurs in bipedal pose with the vertebral column at 45° to the horizontal is based on the erroneous assumption that bipedalism is correlated with an upright vertebral column. Admittedly this is the case in man, but here the vertical column with fully extended hind limbs was attained by considerable modifications of the foot, knee, pelvis, vertebral column, thorax and head (see Brul 1962). Bipedal mammals other than primates are saltators. Most of the published photographs of kangaroos show them resting on the tail with the vertebral column held at about 45° to the horizontal. The kangaroo pose is rather different while moving; the body is carried well for-

ward and the tail, acting as a counterbalance, is stretched out behind. This nearly horizontal pose is shown in Barnett (1963, p. 216), Carrington (1963, p. 69) and Walker (1964, p. 85). Hatt (1932) reviewed the genera of ricochettal rodents and noted that while resting, the fore part of the body is rather vertical and the center of gravity is behind acetabula with the tail acting as a prop. However, "during ricochet the fore part of the body is lowered, and the center of gravity thrown well forward of the acetabula. The tail acts to balance the anterior part of the body . . ." (Hatt, p. 702). He also noted (p. 610) that "during the bipedal run as practiced by the jerboas, the body is held nearly horizontal during rapid progress." Bartholomew and Caswell (1951, figs. 2, 3) illustrate this horizontal pose for a fast moving kangaroo rat *Dipodomys* as does Marlow (1969, fig. 2) for *Notomys*.

Several lizards are facultatively bipedal (see Snyder 1949, 1952, 1954, 1962) and the speed gait is the trot (Snyder 1952) with the femur held laterally. Snyder (1952, p. 67) noted that the iguanids *Crotaphytus*, *Gambelia* and *Basiliscus* can "assume the bipedal gait directly from a resting position or from slow or rapid quadrupedal progression." The body of *Crotaphytus* is inclined at about 45° and *Gambelia* at 75° to the horizontal. He noted that in some aspects bipedal locomotion is better developed in the agamid *Amphibolurus* in which the head and trunk may be inclined at 25° with the tail tip dragging or the body and tail may be carried parallel to the ground with the head and neck upraised. In the first instance the body as a whole is carried higher above the ground and the feet strike the ground closer to the midline with a reduced amount of lateral swinging of the hind limb during recovery. In this case the angling of the body appears to be an adaptation to achieve a more pendulum-like action of the hind limb. I consider that the angling of the body in faculta-



TEXT-FIG. 2—Bones of the pelvic girdle from the left side. A. *Anatosaurus copei*, AMNH 5730, after Lull and Wright (1942, fig. 22). B. Pelvic girdle of *Hypacrosaurus altispinus*, AMNH 5204, after Lull and Wright (1942, fig. 23). C. *Androdemus valens*, USNM 4734, after Gilmore (1920, fig. 46). Abbreviations: IL, ilium; IS, ischium; P, pubis; a, acetabulus; p, pubic peduncle.

tively bipedal lizards probably results from their imperfect adaptations for this mode of locomotion because the femur is normally laterally directed.

At first sight the posture of birds while walking on the ground appears to be upright but this is because of the relative shortness of the trunk region and the long mobile neck which is strongly flexed with the long axis of the skull set almost perpendicular to it. Actually the dorsosacral region of many birds is held at only a small angle to the horizontal (eg. see Romer 1966, fig. 251 for *Columba*, the pigeon). This is especially true for ground living birds such as road runners, pheasants and ratites (text-fig. 3). This horizontal pose is surprising considering that birds lack the heavy counterbalance of a long and fleshy tail. However, the center of gravity is over the feet because the femur is held nearly horizontal, the trunk region is short and much of the abdomen is ventral to the pelvic girdle. I consider that the attitude of the vertebral column in birds, the only living "bipedal archosaurs," is particularly relevant to the posture of hadrosaurs.

EVIDENCE FOR BIPEDALITY IN HADROSAURS

Bipedal reptiles have a tail that is long relative to the trunk and the hind limb is long relative to both the trunk and the fore limb. The tail provides the necessary counterbalance as Snyder (1949) has shown. Loss of the distal third of the tail restricts bipedal running to a few imperfect steps in *Basiliscus basiliscus*. The long and deep tail of hadrosaurs (text-fig. 1, 5 and Lull and Wright, 1942, pls. 13A, 17B, 23B, 27B for specimens with reasonably complete tails) with its musculature would have provided an adequate counterbalance for bipedal running. In addition much of the abdomen was undoubtedly slung ventral to the pelvic girdle (Galton 1969, in press a) as is the case in birds today. In tables 1 and 2 the trunk length is the distance between the glenoid cavity and the acetabulum, the fore limb is the combined lengths of the humerus, radius and metacarpal III and the hind limb is the combined lengths of the femur, tibia and metatarsal III. The length of the phalanges of digit III is not included because neither Lull and Wright (1942) nor Gregory (1912) gave the necessary data and this digit is rarely complete in ankylosaurs, sauropods and stegosaurs (text-fig. 4). It is apparent that the hind limbs of hadrosaurs were long enough relative to the fore limbs and trunk for bipedal locomotion (table 1). The separation between undoubtedly quadrupedal dinosaurs (table 2) and hadrosaurs (table 1) is clearest for the hind limb to trunk ratio (1.22 to 1.44 cf. 0.69 to 1.08). The large hind limb to fore limb ratio in *Stegosaurus* shows that a great disparity in limb length is not in itself indicative of bipedality. However, the fore limb of *Stegosaurus* (text-fig. 4B) resembles those of other undoubtedly quadrupedal dinosaurs (text-figs. 4A-D, 4F, table 2) and of those mammals, considered by Gregory (1912) to be graviportal (table 2), much more closely than that of hadrosaurs (text-fig. 4E, table 1).

Undoubted quadrupedal dinosaurs (table 2) have a robust fore limb with a relatively short radius and ulna, with a radius to humerus ratio ranging from 0.49 to 0.72. In contrast, the radius and ulna of hadrosaurs (text-fig. 5) are slender and elongated with a radius to humerus ratio ranging from 0.75 to 1.18. The metacarpals of the quadrupedal forms are short and stout (metacarpal III to humerus ratio ranging from 0.17 to 0.26) with a broad manus having five short metacarpals in *Monoclonius* (text-fig. 4A), *Stegosaurus* (text-fig. 4B), *Nodosaurus* (text-fig. 4C), *Apatosaurus* (text-fig. 4D) and *Talarus* (text-fig. 4F) or four as in *Triceratops* (Osborn 1933, fig. 4).

TABLE 1—Various ratios for hadrosaurs and other bipedal dinosaurs

Species	Hind limb: Fore limb	Hind limb: trunk	Radius: humerus	Meta-carpal III: humerus	Tibia: femur	Meta-tarsal III: femur	Length hind limb in cms.	Total length in feet
<i>Claosaurus agilis</i> ¹ YPM 1190	—	1.44	.75	—	.82	.31	148	17
<i>Edmontosaurus regalis</i> ROM 5167	1.70	1.30	.92	.48	.81	.33	265	—
<i>Anatosaurus annectens</i> YPM 2182	1.62	1.22	.93	.46	.89	.26	229	29
<i>Anatosaurus annectens</i> USNM 2414	—	1.29	.86	—	.90	.36	232	26
<i>Kritosaurus incurvimanus</i> ROM 4514	1.67	1.38	.88	.36	.90	.35	235	27
<i>Saurolophus osborni</i> AMNH 5220	1.66	1.40	1.02	.54	.89	.37	259	32
<i>Corythosaurus casuarius</i> AMNH 5338	1.68	1.42	1.06	.44	.94	.38	229	26
<i>Lambeosaurus clavinitialis</i> NMC 8703	1.65	—	1.18	.51	.98	.29	232	—
<i>Hypacrosaurus altispinus</i> NMC 8501	—	—	1.22	—	.93	.36	245	—
<i>Procheneosaurus praeceps</i> AMNH 5340	1.74	1.44	1.05	.49	.93	.36	135	14
<i>Iguanodon atherfieldensis</i> ²	1.98	1.35 ³	.71	.30	.88	.35	151	18
<i>Gorgosaurus libratus</i> ⁴ NMC 2120	4.80	1.37	.48	.20	.96	.57	263	28
<i>Antrodemus valens</i> ⁵ USNM 4734	2.93	—	.70	.34	.80	.35	187	—
<i>Struthiomimus altus</i> ⁶ AMNH 5339	2.17	1.90	.74	.32	1.12	.77	139	13

¹ Hadrosaur ratios calculated from measurements and plates in Lull and Wright, 1942, p. 225–229, only specimens with most of required measurements or the extreme value for one of the ratios included.

² Hooley, 1925

³ Casier, 1960 pl. 11 for *Iguanodon bernissartensis*

⁴ Lambe, 1917

⁵ Gilmore, 1920

⁶ Osborn, 1916

In hadrosaurs the central three metacarpals are slender and elongated (text-fig. 4E) with a metacarpal III to humerus ratio ranging from 0.36 to 0.54. As Brown (1912, p. 107) noted, “the extreme elongation of the metacarpals, the loose articulation of the phalanges and the reduction of the unguals to two functional hoofs indicate that the manus [AMNH 5060 of *Anatosaurus*] was no longer used to any extent in progression.” Osborn (1912) described the mummified manus of *Anatosaurus* [AMNH 5060] in which the digits are enclosed in a mitten-like integument. Osborn concluded that *Anatosaurus* was completely aquatic because of the absence of any trace of epidermal callouses, tubercle enlargements or hoof-like unguals. Lull and Wright (1942) and Ostrom (1964) followed Osborn (1912) in considering that the manus lacked hoof-like unguals. However, as Brown (1912, p. 107) noted “the integument in this specimen [AMNH 5060] extends over all

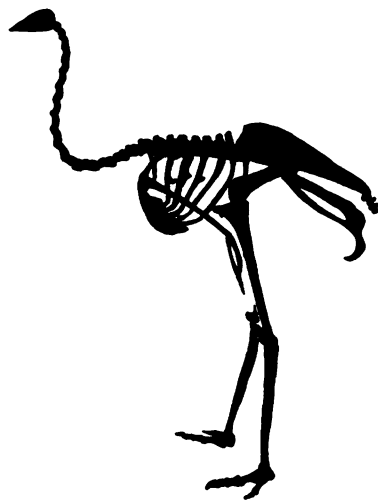
the phalanges but the terminal hoofs of digits II and III are as well formed as those in the pes and were undoubtedly covered by a nail.” Lull and Wright (1942) and Ostrom (1964) have pointed out that most of the features cited by Osborn (1912) only show that the fore limbs were not used for walking on land. Ostrom (1964) noted that the pronounced reduction of ossification in the wrist with only two very small carpal bones, even without the evidence presented by Osborn, made it very unlikely that the manus could have borne any significant weight. However, it should be noted that the two carpal bones of *Monoclonius* (text-fig. 4A) are quite small so a lack of ossification in the wrist region need not have impeded the weight-carrying capacity of the fore limb. However, the significance of the different arrangement of the carpals in *Anatosaurus* (text-fig. 4D) is not clear. As regards the aquatic theory the digits of the manus are very short (text-fig. 4D) and,

TABLE 2—Various ratios for quadrupedal dinosaurs and graviportal mammals

Taxa	Hind limb: fore limb	Hind limb: trunk	Radius: humerus	Meta-carpal III: humerus	Tibia: femur	Meta-tarsal III: femur	Length hind limb in cms.	Total length in feet
Stegosaurs:								
<i>Stegosaurus stenops</i> ¹	1.71	.90	.70	.21	.62	.12	181	15
<i>Kentrurosaurus aethiopicus</i> ²	1.40	.86	.67	.19	.68	—	—	—
Ankylosaurs:								
<i>Ankylosaurus</i> ³	1.26	.69	—	—	—	—	—	—
<i>Scolosaurus cutleri</i> ⁴	1.46	.69 ¹⁵	.61	.20	.69	.25	116	—
<i>Hierosaurus coleii</i> ⁵	—	—	.72	—	.75	.20	94	—
<i>Talarus</i> ⁶	1.51	—	.49	.20	.53	.19	86	—
<i>Palaeoscincus</i> AMNH ⁷	—	—	.70	.26	—	—	—	—
<i>Nodosaurus</i> AMNH 3036 ⁸	—	—	.66	.26	—	—	—	—
Ceratopsians:								
<i>Monoclonius flexus</i> ⁹	1.45	1.08	.59	.23	.70	.26	155	13
<i>Triceratops elatus</i> ¹⁰	1.29	.90	.50	.19	.64	.20	175	19
Sauropods:								
<i>Apatosaurus</i> ¹¹	1.35	.85	.69	.17	.62	.13	313	76
<i>Diplodocus</i> ¹²	1.38	.80	.70 ¹³	—	.70 ¹³	—	—	—
Graviportal Mammals: ¹⁴								
<i>Uintatherium mirabile</i>	1.09	—	.71	.20	.52	.10	112	—
<i>Coryphodon lobatus</i>	1.11	—	.66	.19	.61	.15	74	—
<i>Mastodon americanus</i>	.96	—	.76	.19	.69	.11	184	—
<i>Elephas indicus</i>	1.06	—	.85	.22	.60	.14	177	—
<i>Elephas africanus</i>	.95	—	.87	.21	.72	.14	195	—
<i>Brontotherium gigas</i>	1.14	—	.90	.41	.55	.26	141	—

¹ Gilmore, 1914, 1920; ² Hennig, 1924; ³ Brown in Huene, 1956, fig. 587a; ⁴ Nopcsa, 1928; ⁵ Mehl, 1936; ⁶ Maleev, 1956; ^{7,8} Coombs, personal communication; ⁹ Lull, 1933; ¹⁰ Osborn, 1933; ¹¹ Gilmore, 1936; ¹² Holland, 1906; ¹³ Mook, 1917; ¹⁴ Gregory, 1912; ¹⁵ Charig, personal communication—this ratio is .85 in the lower Jurassic ankylosaur *Scelidosaurus* at the British Museum.

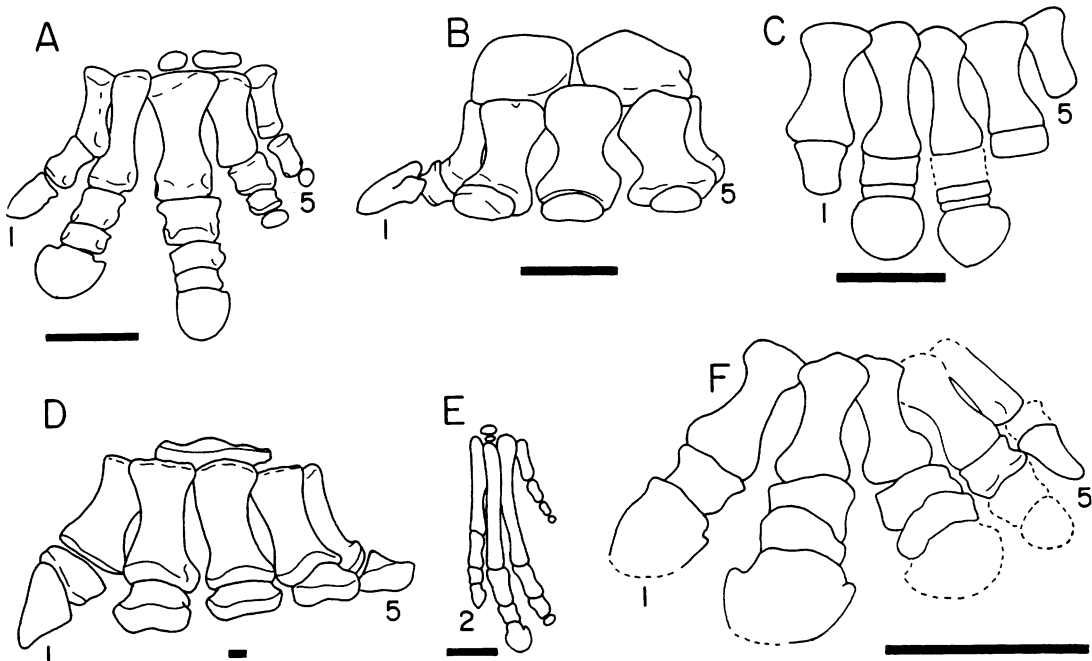
as a result, the fully spread web would have added little to the effectiveness of the forelimb as a sculling or steering organ.



TEXT-FIG. 3—*Struthio camelus*. YPM Osteol. Colln. 2125. Height 160 cm or 5 ft. 3 ins.

As shown by text-figure 4 the structure of the hadrosaurian manus is completely different from that of the undoubtedly quadrupedal dinosaurs. Lower Cretaceous trackways from Glen Rose, Texas (Bird 1941, 1944; sauropod) and Peace River, British Columbia (Sternberg, 1932; *Tetrapodosaurus*, probably an ankylosaur) show that in at least two groups of quadrupedal dinosaurs the digits of the manus were enclosed in a fleshy pad which acted as a weight absorbing cushion. This was also probably the case in the larger ceratopsians and stegosaurs as it is in graviportal mammals today in which the manus is broad with short metacarpals (Young, 1962, fig. 475, Indian elephant; fig. 484, Indian rhinocerus; fig. 497, hippopotamus).

The hind limb of hadrosaurs is much longer than the forelimb (table 1) and the individual bones are much more robust (text-fig. 5). The tibia to femur ratio ranges from 0.81 to 0.98 and the metatarsal III to femur ratio from 0.26 to 0.38. These ratios are not as low as in undoubtedly quadrupedal dinosaurs (0.53–0.75; 0.12–0.26) or graviportal mammals (0.52–0.72; 0.10–0.26). However, they are lower than in the un-



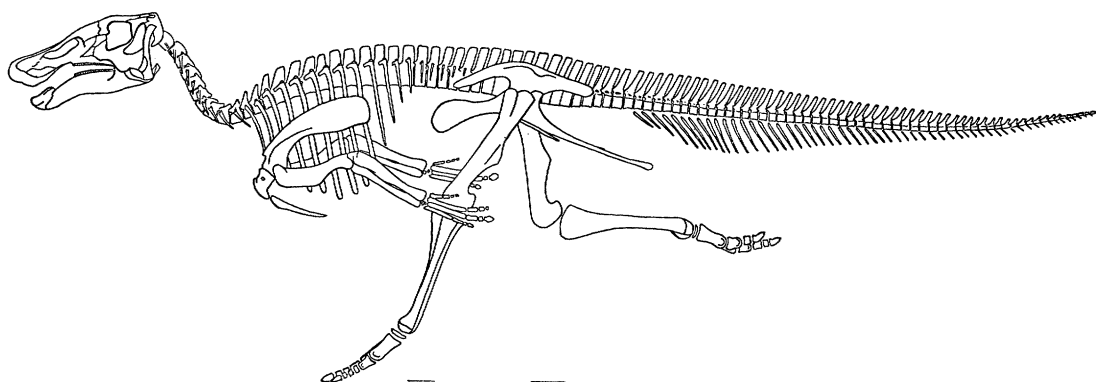
TEXT-FIG. 4.—Left manus of different dinosaurs with metacarpal III reduced to the same length. Scales in each case represent 10 cm. A. *Monoclonius flexus* YPM 2015, after Lull (1933, fig. 24). B. *Stegosaurus sulcatus* USNM 4397, after Gilmore (1914, fig. 38). C. *Nodosaurus* sp.?, AMNH 3036, after photograph supplied by Coombs, scale only approximate. D. *Apatosaurus excelsus* CM 563, after Gilmore (1936, fig. 35). E. *Anatosaurus annectens* YPM 2182, USNM 2414, after Lull and Wright (1940, fig. 24). F. *Talarus* after Maleev (1956, fig. 18).

doubtably bipedal *Gorgosaurus* (0.96, 0.57; Lambe 1917). Hadrosaurs have a very prominent fourth trochanter which, as noted by Ostrom (1964), is better developed than it is in some other ornithischians whose bipedal abilities have never been questioned. As discussed elsewhere (Galton 1969) the fourth trochanter probably provided an increased leverage for the *M. caudi-femoralis brevis* during the initial part of femoral retraction. I believe the hind limbs carried all the weight and that hadrosaurs were bipedal except when resting.

The vertebral column on either side of the sacrum appears to be ramrod straight but this is only true of the line formed by the tops of the neural spines. As shown particularly clearly in certain skeletons (text-figs. 1, 5; Lull and Wright 1942, pl. 19C, *Kritosaurus* ROM 4514; pl. 23B *Saurolophus* AMNH 5220 and pl. 27 *Corythosaurus* AMNH 5340 and 5338) the line formed by the ventral edges of the centra of the caudal vertebrae curves gently dorsally for the first 10 or so vertebrae. This duplicates the equivalent curve of the dorsal centra and indicates that the tail was held well off the ground to increase its efficiency as a counterbalance to the trunk. The vertebral column is symmetrical

about the sacrum with a progressive change in the structure both anteriorly and posteriorly so that there is a progressive decrease in the height of the neural spines and centra (see text-fig. 5; Lull and Wright 1942, pls. 13A, 17B, 18, 19C, 27). These changes are greatest for the dozen or so vertebrae on either side of the sacrum and are more pronounced than is the case in the undoubtedly quadrupedal dinosaurs (see figures in Colbert 1961, Romer 1956, 1966).

The system of ossified tendons in hadrosaurs is developed to a degree that, apart from the distal part of the tail of ankylosaurs, is not matched by any of the definitely quadrupedal ornithischians. The tendons in hadrosaurs form a rhomboidal lattice on the sides of the neural arches of the dorsal, sacral and caudal vertebrae (see text-fig. 1 and plates in Lull and Wright 1942). The extreme development of these ossified tendons was undoubtedly an adaptation for bipedal posture with the straight part of the vertebral column held more or less horizontally. The hind limbs acted as pillars with the vertebral column as an antigravity beam, the structure of which resisted any tendency to sag. The neural spines were longest where the tensional forces were greatest and the centra were deep-



TEXT-FIG. 5—Reconstruction of *Anatosaurus annectens* in a hurry; based on YPM 1190 and USNM 2414 an animal 29 feet long.

est where the compressive forces were greatest. Concerning the tendons, Ostrom (1964, p. 993) wrote that "Mechanically, the rhomboidal tendon arrangement is a highly efficient design for resisting tension entirely comparable to the rhomboidally arranged tensile struts of a balanced cantilever bridge. The ossification of the tendons would seem to be one further step in the efficient resistance of tensile stresses because bone has much greater tensile strength than does tendon (see Koch 1917)".

POSE OF THE LIMBS

In the reconstruction of *Lambeosaurus* by Sternberg (1965, fig. 2) the humerus is shown horizontal and pointing laterally from the glenoid cavity with the radius and ulna held vertically. Sternberg considered that the figure of *Anatosaurus* in Lull and Wright (1942, fig. 20) was incorrect because the head of the vertically held humerus is not in the glenoid cavity. Gregory (in Osborn 1916) used this argument with reference to *Struthiomimus* as did Sternberg (1940) for *Thescelosaurus* and most other ornithischians. The whole of the proximal end of the humerus of dinosaurs was an articular surface, as in crocodiles, so part of it is still in contact with the glenoid cavity even when all of the head is visible in lateral view (text-fig. 5). The proximal end did not form a ball and socket joint as in mammals so its convex articular surface must be considerably larger than that of the glenoid cavity if the humerus was to have a reasonable range of movement. The glenoid articular surface of the scapula in all dinosaurs faces ventrally, as was noted by Bakker (1968), indicating that the humerus was normally held in a vertical position as in most mammals.

Sternberg (1965, p. 3) noted that "in all naturally articulated skeletons, the femora point forward and downwards, never backward and

downward. The well developed articulating surface on the posterior part of the distal condyle [of the femur] suggests that the knee was strongly flexed." The first point may show that the femur had a limited range of movement anteroposteriorly. In his reconstruction Sternberg (1965, fig. 2) shows both femora pointing anteriorly at an angle of about 45° to the sacrum. This position may represent the most anterior position the femur could have assumed. However, in some articulated skeletons still in the matrix the other femur is more posteriorly placed so that it makes an angle of about 85–110° with the sacrum (see Lull and Wright 1942, pls. 10A, 12B, 13A, 13B, 17B, 23B). In showing the femora as he did Sternberg was probably impressed by his second point, but this only shows that the knee could have been strongly flexed and, because the articular surface extended anteriorly across the whole of the distal end of the femur, it is apparent that the knee could also be straightened. Sternberg (1965) also argued that if the tibia was held vertically it would not articulate properly with the foot. However, the astragalus was firmly attached to the distal end of the tibia as was the calcaneum to the fibula. The distal articular surface of the astragalus and calcaneum was extensive and convex anteroposteriorly consistent with a digitigrade pose; I fail to see why the foot should not articulate properly even with the tibia held vertically. I believe that the supposedly typical quadrupedal pose of the reconstruction of *Lambeosaurus* given by Sternberg (1965, fig. 2) actually shows the animal in a half-squatting position.

ATTITUDE OF THE VERTEBRAL COLUMN IN OTHER BIPEDAL DINOSAURS

In *Iguanodon* there is a well-developed set of ossified tendons which formed a rhomboidal net-

work comparable to that in hadrosaurs. As a result, most of the back and tail was preserved straight in the skeletons discovered at Bernisart (see Casier 1960, pls. 3, 4, 9). The acetabulum is shallow and the pubic peduncle of the ilium slender (Casier 1960, Hooley 1925). The radius, ulna and metacarpals II to IV are slender and elongated (table 1). Consequently the straight part of the column was probably held rather horizontally. It is interesting that Heilmann (1926, fig. 111), although he did not discuss the problem, reconstructed two running individuals with the column in such a pose. The column of *Camptosaurus* may have been held more horizontally than shown by Gilmore (1909, pl. 18, 19; 1912, pls. 59, 61) and, to judge from the heavily ossified carpus and the short but broad manus with five stout metacarpals (Gilmore 1909, fig. 28), *Camptosaurus* was probably more quadrupedal (Gilmore 1912, pls. 56, 57, 58) than the other ornithopods. As regards *Thescelosaurus* it is perhaps significant that the skeleton as preserved (Gilmore 1915, pl. 79) with a practically horizontal column, looks much more life-like and dynamic than the reconstruction (Gilmore 1915, pl. 80) with the column at 45° and half the tail trailing on the ground. I have reconstructed *Hypsilophodon* (Galton, in press *a* and *b*, for discussion see in press *b*) and *Thescelosaurus* (Galton, in press *c*) running with the column held horizontal. Although evidence is lacking for many ornithopods I consider that the sacrum was probably carried more or less horizontally in all of them.

I have not looked specifically at the pose in saurischians but, to judge from the much deeper acetabulum and the massive pubic peduncle of the ilium (text-fig. 2C), the posture on many occasions must have been more upright than was possible in hadrosaurs. Gregory (1950, fig. 14, 20) reconstructed *Tyrannosaurus* in a much less erect pose than did Osborn (1916). A skeleton of *Tyrannosaurus* was recently mounted at the British Museum (Natural History) as shown in Kurtén (1968, fig. 35, also includes a picture of the *Ceratops* mount at the United States National Museum) and Newman (personal communication) has several reasons for regarding Osborn's pose as incorrect. The column was shown more or less horizontal while running in reconstructions of *Struthiomimus* (Gregory in Osborn 1916; Gregory 1950, which is given by Romer 1966, fig. 233), *Megalosaurus* (Parker in Swinton, 1962, pl. 2) and *Deinonychus* (Ostrom 1969). This was probably the normal pose for bipedal saurischians while running and the tail was long enough to have acted as an adequate counterbalance. In this pose the upwardly directed thrust from the femur would be

perpendicular to the long axis of the ilium and adjacent part of the vertebral column with the hind limbs and viscera in the "normal quadrupedal position." In addition the tail would be well clear of the ground and its steering and balancing functions would be enhanced.

A NEW RECONSTRUCTION OF *ANATOSAURUS ANNECTENS*

The holotype (USNM 2414) and plesiotype (YPM 2182) of *Anatosaurus annectens* Lull and Wright (1942) were collected by J. B. Hatcher in 1891 from the Lance Formation of Niobara County, Wyoming. Marsh (1892a) originally named them *Claosaurus annectens* and used data from both specimens for his reconstruction (1892b, 1896). Beecher (1901, 1902) mounted the Yale specimen, which was the first skeleton of a dinosaur to be mounted in North America. The earlier mount of *Hadrosaurus foulkii* at the Philadelphia Academy of Natural Sciences (see Lull and Wright 1942, pl. 10B), as restored by Waterhouse Hawkins, consisted mainly of plaster replicas rather than bones and it has since been dismantled. Although Beecher (1902, p. 312) noted that "the subject lies wholly outside [his] particular field of research," this is still the best mounted skeleton of a hadrosaur in a fast running posture (see plates in Beecher 1901, 1902, and Lull and Wright 1942, pl. 13B). In text-figure 5 the vertebral column is shown nearly horizontal and the fore limbs are backwardly directed. The outlines of the vertebrae, ribs and chevrons, which are based on USNM 2414 (Lull and Wright 1942, pl. 13A), are rather generalized. The outlines of the skull, pectoral girdle and fore limbs, pelvic girdle and femur are based on Lull and Wright (1942, figs. 53, 20, 24).

SUMMARY

That hadrosaurs were bipedal is clearly shown by the following combination of characters: the length of hind limb relative to the trunk and to the fore limb; the non-graviportal nature of the fore limb with an elongated radius, ulna and metacarpals; the absence of any epidermal callouses or tubercle enlargements on the mittened manus; the well-developed fourth trochanter on the femur; the progressive changes in the size of the centra and the height of the neural arches on either side of the sacrum; the upward turn of the centra at the base of the tail and the rhomboidal network of ossified tendons. However, the ramrod straight vertebral column, the shallow iliac part of the acetabular curve, the slender pubic peduncle and the pose in living bipeds other than primates shows that while running bipedally the straight

part of the column was probably held more or less horizontal. This was probably the case in all ornithopods and possibly in theropods as well.

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