8. Discussion of Character Analysis of the Appendicular Anatomy in Campanian and Maastrichtian North American Hadrosaurids— Variation and Ontogeny

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Abstract

Over 50 morphological characters commonly have been used for defining and diagnosing the hadrosaurids, and these are reevaluated in terms of data from ontogeny, paleopathology, and postcranial studies. Features once used to define supraspecific taxa are also reevaluated in the light of population and ontogenetic variation.

The hadrosaur postcranium becomes more robust with age, expressed as more rugose muscular attachments and greater deposition of bone on articular surfaces. Most ridges and bumps on the long bones are smooth, short, and do not project far from the shafts in small specimens. In the largest animals, ridges may become exaggerated, and trochanters and muscular insertion scars become large, pitted, and rugose, with a tendency to look pathological.

Four size classes in hadrosaurids are identified on the basis of gross morphology that may reflect individual age. The first class (hatchling) represents hadrosaurids with little or no expansion of the muzzle, small and smooth articular surfaces, five or six sacrals, and less than 20 tooth rows. The second class (juvenile) has a no-

ticeable muzzle, 20 to 40 tooth rows, articulations with some ru-gosities on the long bones, six or seven sacrals, and in the Lam-beosaurinae, the appearance of incipient cranial crests and an is-chial foot. (Loss of the ischial "foot" is a derived condition.) The third size class (adult) is the size range in which all of the features useful for diagnosis of hadrosaurs are fully developed. The fourth class (old age) is characterized by 10 or more sacrals, all bony pro-jections greatly increased in size and rugosity, fusion of the distal femoral condyles anteriorly, pitting of the articular ends of the long bones, frilling or pitting of the ends of the unguals, and clubbing of the apices of the neural spines. Some of these features may appear pathologically in younger specimens.

Introduction

In the summer of 1973, while visiting the Field Museum of Natural History in Chicago, one of us (M. B.-S.) found the postcranial re-mains of a hadrosaur from the Rio Chico area of Argentina (Brett-Surman 1979). Brett-Surman set out to compare the specimen to known hadrosaurs. Despite the ubiquitous nature of hadrosaurian postcrania in relevant paleontological collections, little attempt had been made to use them in hadrosaur systematics because of the er-roneous belief that they were of little systematic value. Brett-Surman (1975, 1989) summarized the results of his investigations and included a detailed discussion of characters useful in distin-guishing groups of hadrosaurs from postcrania alone. Davies (1983) and Wagner (2001) expanded Brett-Surman's work on hadrosaurs from Trans-Pecos Texas, with Wagner including taxa outside of Hadrosauridae.

We analyze the taxonomic characters of hadrosaurids on the basis of their appendicular elements and demonstrate features that represent ontogenetic stages in taxa and valid taxonomic synapo-morphies for other genera. Where possible, only articulated skele-tons were used in this study to ensure the accuracy of appendicular ratios and other associations. Individual elements were also drawn from photographs using a camera lucida. We review the earlier work on hadrosaurid postcrania by Brett-Surman (1975, 1989) and Wagner (2001). For a more complete list of character states, see Sereno (1999), Norman (2002), and Head (2001); and for dis-cussions of resultant phylogenies, see Norman (2004), Horner et al. (2004), Head (2001), and Godefroit et al. (2000). A complete list-ing of all scientific papers on hadrosaurids can be found at http://www.nmnh.si.edu/paleo/collections.html. For simplicity, the informal term "iguanodontoids" refers to taxa more closely related to *Iguanodon* than to Hadrosauridae.

Institutional Abbreviations. AMNH: American Museum of Natural History, New York; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMNH: Denver Museum of Nature & Science (formerly Denver Museum of Natural History), Denver, Colorado; FMNH: Field Museum of Natural History,

Chicago, Illinois; IVPP Institute of Vertebrate Palaeontology and Palaeoanthropology, Academic Sinica, Beijing; NMC: Canadian Museum of Nature (formerly the National Museum of Canada), Ottawa; ROM: Royal Ontario Museum, Toronto; TMM: Texas Memorial Museum, Austin; UCMP: Museum of Paleontology, University of California, Berkeley; USNM: National Museum of Natural History (formerly United States National Museum), Washington, D.C.; YPM: Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Analysis of Hadrosaurid Appendicular Elements

Pectoral Girdle

The hadrosaur pectoral girdle has only rarely been considered as a source of systematic information (Brett-Surman 1989). Interpretation of pectoral girdle morphology is difficult, especially because these elements, although essentially flat, are curved to fit against the ribcage. Differing perspective in illustrations, distortion, and (especially in the scapula) damage to the thinned margins of elements may all exacerbate interpretation.

Scapula. In hadrosaurids, two regions of the scapula (Fig. 8.1A) show morphological variations across a continuum. The proximal part includes the suture for the coracoid, as well as the deltoid ridge, which arises on the dorsal margin and angles in a posteroventral direction to the ventral border. Anterior to this ridge is the deltoid fossa, the posterior border of which terminates at the narrowest part, or scapular neck. The second or posterior part of the scapula consists of the blade, which is laterally flattened and rectangular in shape. In correct anatomical position, the scapula is parallel to the vertebral column. Two morphs are recognized representing a morphological continuum, the hadrosaurine scapula and the lambeosaurine scapula (Fig. 8.1).

In the hadrosaurine scapula (Fig. 8.1), the blade is relatively longer (anteroposteriorly) and not as wide (dorsoventrally) as compared to the condition in lambeosaurines. *Brachylophosaurus* (NMC 8893) is the most extreme in that the blade is relatively the longest of any known hadrosaurid, while the width (measured dorsoventrally) is relatively the smallest. This results in a length/width ratio greater than in any other genus. In the lambeosaurine scapula (Fig. 8.1), the blade is relatively shorter (anteroposteriorly in natural position) and wider (dorsoventrally) than in most hadrosaurines. An extreme of this is seen in *Parasaurolophus cyrtocristatus* (see especially Ostrom 1963), where the blade is short and robust, with a length/width ratio smaller than in any other genus. The only exception to this morphological variety is seen in one specimen of *Lambeosaurus* (ROM 1218), which more closely resembles the hadrosaurine variety.

The scapula displays considerable variation within clades and even within genera. There is much overlapping of shapes among
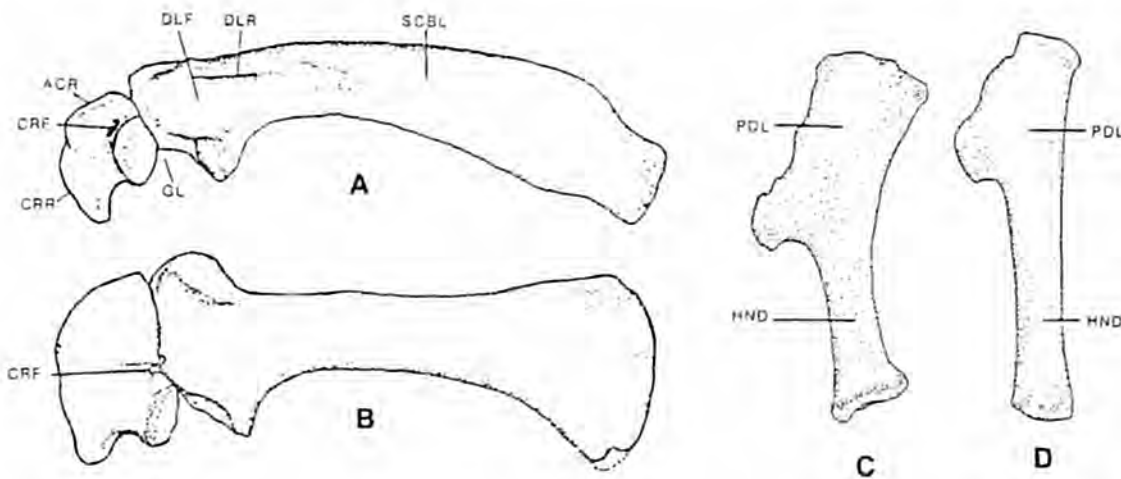
Figure 8.1. Comparison of the left scapulae and coracoids in lateral view: (A) Kritosaurus AMNH 5465 (length = 792 mm); (B) Camptosaurus USNM 4282 (length = 482 mm). Left sternals in ventral view: (C) Tsintaosaurus IVPP V-125 (length = 420 mm); (D) Shantungosaurus (length = 705 mm); redrawn from Hu (1973). See Appendix 8.1 for abbreviations.

genera; therefore, it is impossible to diagnose scapulae to the generic level or to use length/width ratios to separate taxa. As noted above, *Brachylophosaurus* stands out from the other genera with its unique length/width ratio of the blade, but a sample size of less than five does not justify the delineation of its own morphotype. It is only possible to state that a scapula is either long and thin (most likely a hadrosaurine) or it is shorter and wider (most likely a lambeosaurine). Some blades expand abruptly just distal to the neck and have parallel dorsal and ventral borders, or convex dorsal borders (e.g., *Prosaurolophus*, ROM 787).

During ontogeny, the deltoid ridge becomes elongate and more robust until it finally reaches the lower scapular border in adults. In juveniles, the area of the glenoid is larger than the area for the suture with the coracoid (e.g., *Bactrosaurus* AMNH 6577), while in adults (e.g., *Anatotitan copei* AMNH 5730) the area of the glenoid and the area of the coracoid suture are about equal in extent. In juveniles the suture for the coracoid is slightly roughened, but in adults it is extremely rugose and massive (e.g., USNM 2413, a coracoid showing the scapular sutural area). In many juveniles, the dorsal and ventral borders of the blade diverge slightly posterior (as in the iguanodontids), whereas in adults the dorsal and ventral borders are parallel so that the blade appears rectangular in lateral aspect.

The scapular blade of adults is proportionally longer than that of juveniles. The major area of ossification is at the distal end of the blade, an area for the ossification of the suprascapular cartilage, possibly to increase the area for muscle attachment in supporting a larger mass. Hadrosaurids of the same age group maintain the same scapular proportions relative the body throughout life. It would appear that this is accomplished solely by increasing the length and width of the scapular blade relative to the proximal por-

tion of the scapula. Distal flaring of the scapula also occurs, and is exceptional well developed in *Parasaurolophus*, some of the scapulae described by Young (1958), and the paratype of *Corythosaurus casuarius*. It is quite reduced in the type of *Brachylophosaurus*, and scapulae referred to *Shantungosaurus* and *Tanius sinensis*. Illustrated scapulae of *Corythosaurus* (Brown 1916; Lull and Wright 1942) and *Edmontosaurus* (Gilmore 1924a; Lull and Wright 1942; Parks 1935) show significant variability in the degree of flaring of the scapula, and this is reported for *Brachylophosaurus* as well (Prieto-Marquez 2000, and this volume).

It is impossible at this time to distinguish morphological types that may be referred to specific genera or clades because of inadequate sample size.

Coracoid. In *Iguanodon*, the coracoid is crossed ventromedially by a low, arcuate, dorsally convex ridge extending from the tip of the ventral hook to a lateral process on the craniodorsal margin of the bone. This angular, slightly everted rugosity is the coracoid "acromion process"; its cranial end is the biceps tubercle (Dilkes 2000; Norman 1986). In hadrosaurids, the biceps tubercle is folded lateroventrally, producing an overhanging ridge that is most pronounced dorsally where it is continuous with the craniodorsal margin, but which overhangs and scallops that margin ventrally. Development of this process gives the dorsocranial margin of the coracoid a slight concavity, which is accentuated in lateral view by the lateral concavity of this region in articulated specimens.

In hadrosaurids, the coracoid (Fig. 8.1A) terminates anteriorly in a large hooklike process. Arising from this hook is the coracoid ridge that forms the anterior border of the coracoid and ends at the juncture with the dorsal border. The coracoidal ridge is deflected medially on the dorsal surface where the acromion ridge originates. This ridge extends posteriorly to the suture with the scapula. The glenoid is at the base of the coracoid-scapular suture and has a hyperbolic cone-shaped depression at its center. The scapular suture is rugose with rounded knobs and deep depressions. The main body of the coracoid is three to four times as thick as the coracoid ridge and hook.

Midway between the dorsal and ventral borders of the coracoid and anterior to the scapular suture is the coracoid foramen. The position of the coracoid foramen appears to be somewhat variable (Davies 1983; Brett-Surman 1989), but with a few exceptions, it is generally farther than its own diameter from the scapular articulation in hadrosaurids. The foramen is entirely enclosed by the coracoid in adult hadrosaurids, but it lies partly open to the suture in some juveniles and in iguanodontids as a "coracoid notch" (Parks 1919, 1920). Progressive ossification of the cartilaginous pad that presumably connected the coracoid and scapula may have eventually closed the notch during hadrosaurid ontogeny. The coracoid foramen (Fig. 8.1A) passes through the bone at a slight angle, opening toward the scapula on both sides. A shallow trough is sometimes present that approaches (Young 1958, fig. 21-1) or opens into the scapular suture (UCMP 94475).

The coracoid in hadrosaurids appears to be elongate relative to that of nonhadrosaurids as measured perpendicular to the scapular facet in lateral view. The coracoid hook, where the bone articulates with the sternals, is longer and oriented subparallel to the margin of the coracoidal glenoid. The dorsocranial region of the coracoid below the scapular facet appears to be slightly longer in specimens that possess a plesiomorphically cranially directed acromion process of the scapula.

The coracoid does not display sufficient variation among the lineages to make it diagnostic at the species level. Most coracoids are crushed flat, which makes it difficult to ascertain their original shape. It appears, however, that in hadrosaurines the coracoid is longer (anteroposteriorly) and lower (dorsoventrally) than in lambeosaurines, but the sample size is too small to justify this proposed dichotomy. It is possible that this feature may be end points on a morphological continuum.

The only difference between the early forms, such as *Bactrosaurus* (AMNH 6577) and *Gilmoreosaurus* (AMNH 6581), and the more derived late Cretaceous forms, is that the coracoidal hook is smaller and pointed more ventrally than anteroventrally.

Ontogenetically, the coracoidal hook is small and points ventrally in juveniles. The coracoid foramen is entirely enclosed within the coracoid, unlike some nonhadrosaurid ornithopods. Dorsally, the knob at the end of the acromion ridge is small and rounded and generally smooth. The glenoid is deep as in adults but the depression is symmetrically shaped. The scapular suture is slightly rugose. The main body of the coracoid is slightly thicker than that of the coracoidal hook. One growth feature of interest is that with ontogeny, the coracoid abruptly becomes thicker (lateromedially) and more rugose, especially at the suture with the scapula.

Sternals. Sternal are the most difficult elements to study. They are rarely preserved or prepared and are virtually ignored in the literature (see Parks 1920 for the first complete description of a hadrosaurid sternal). There is no literature on the ontogenetic or population variation of this element.

In hadrosaurids, the ventral segments of the sternal ribs apparently coalesced into a single, caudolaterally directed prong that is fused to the caudolateral margin of the sternal plate. Part of this process may be analogous or homologous with a portion of the "xiphisternum" of *Crocodylus* (Romer 1956); the neutral term "handle" is preferred by us (Fig. 8.1C, D). The shaft of the handle tapers somewhat distally and then flares to the tip. The tip of the handle is usually rounded and has an everted rim for the joint capsule that articulates it with the sternal ribs. The remaining portion of the sternum, the "paddle" (Fig. 8.1C, D) is apparently homologous with the sternal plate of nonhadrosaurids and has an everted rim for the joint capsule that articulates it with the sternal ribs.

Of the sternal elements examined, there appear to be two morphs that correspond to the two hadrosaurid subfamilies (Fig. 8.1C, D). The "paddle" is relatively longer (dorsoventrally) in lam-

A   B   C   D   E   F   G
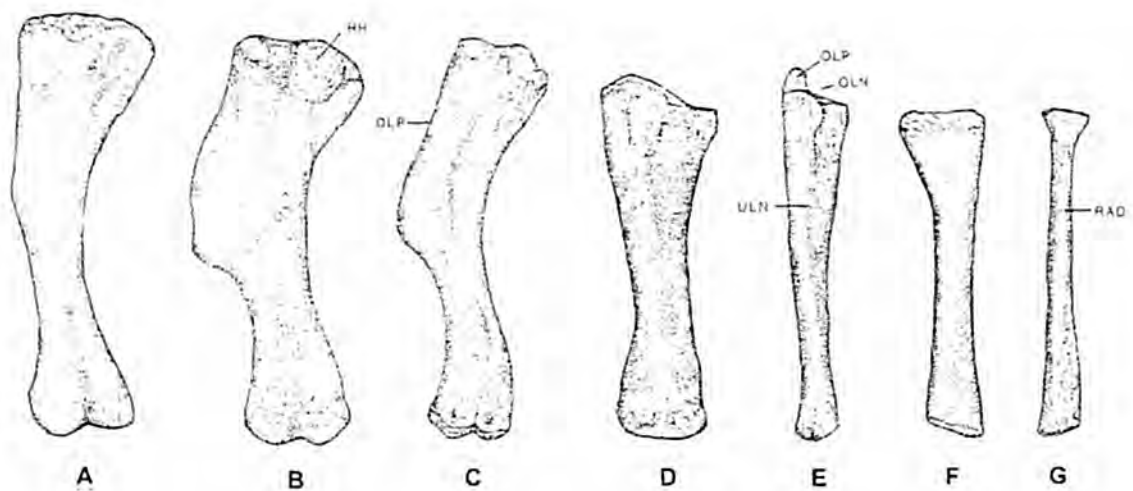
beosaurines. The "handle" is relatively longer and thinner in hadrosaurines. The handle appears to lengthen during ontogeny, but the sample size is too small at present for a definitive statement. Curvature of the handle may represent postmortem distortion.

Sternals of *Iguanodon* are much closer in shape to hadrosaurids than they are to camptosaurids in which the handle is absent. As restored by Dollo (1883a, 1883b) and Norman (1980), there is space between the coracoids and sternals for a cartilaginous xiphisternum. This may also have been true for hadrosaurids.

Humerus. The humerus (Fig. 8.2B, C) is divided into two parts. The dorsal part contains the head, which fits into the glenoid formed by the scapula and coracoid. Immediately below the humeral head, the proximal part of the shaft expands anterolaterally to form the deltopectoral crest. The lateral border of this crest is parallel to the medial border of the proximal part of the humeral shaft. At midshaft, the deltopectoral crest abruptly ends and the shaft narrows to its minimum width. At the distal end of the humerus, the element expands into lateral and medial condyles for articulation with the radius and ulna.

As with the scapula, two morphotypes of humeri can be distinguished (Fig. 8.2), but there are many intermediate forms along a continuous morphocline. Only the most extreme morphotypes are useful to distinguish hadrosaurines from lambeosaurines. In hadrosaurines (Fig. 8.2C), the deltopectoral crest is slightly less than three times as long (dorsoventrally) as it is wide (lateromedially). The asymptote of the ventrolateral border is at or just above the midpoint of the humerus. The overall aspect of the humerus is long and gracile compared to the thicker and more robust lambeosaurine humerus. The best example of the "gracile" morphotype is seen in type specimen of *Brachylophosaurus canadensis*.

In lambeosaurines (Fig. 8.2B), the deltopectoral crest is about

Figure 8.2. Comparison of the left humeri in posterior views. (A) Camptosaurus USNM 4282 (length = 360 mm); (B) Parasaurolophus ROM 768 and AMNH 5893 (length = 520 mm); (C) Kritosaurus AMNH 5465 (length = 764 mm). Comparison of the right ulnae in lateral view. (D) Camptosaurus USNM 4282 (length = 262 mm); (E) Parasaurolophus FMNH P27393 (length = 665 mm). Comparison of the right radii in lateral view. (F) Camptosaurus USNM 4282 (length = 232 mm); (G) Parasaurolophus FMNH P27293 (length = 585 mm).

twice as long as wide. The asymptote of the ventrolateral border is at or just below the midpoint. The overall aspect is that of a thicker and more robust element than in hadrosaurines. Because the deltopectoral crest is relatively wider in lambeosaurines, the length/width ratio of the crest is generally smaller than in hadrosaurines. The best example of the "robust" morphotype is in the type specimen of *Parasaurolophus walkeri*.

Several growth characteristics of the humerus are observed. In juveniles, the lateral tuberosities at the proximal end are poorly developed, if present at all. The head is relatively smaller compared to adults, and the deltopectoral ridge is thinner measured anteroposteriorly in articulation. The distal condyles are relatively smaller, and there is little difference in size between the lateral and medial tuberosities. In adults, the medial (ulnar) distal condyle enlarges as the condyles increase in size (Brett-Surman 1975).

The relative length of the humerus, as compared with the femur, shows a wide range of variability. The range for all hadrosaurids is from 47% to 63%, with hadrosaurines in general having a longer relative humeral length. The relative thickness of the shaft is also greater in lambeosaurines than in hadrosaurines (Brett-Surman 1975; Egi and Weishampel 2002). The ratio of the deltopectoral width to length ranges from 19% to 33% with lambeosaurines, in general, having a wider deltopectoral crest. The relative size of the hadrosaurid distal condyles, as compared to minimum shaft diameter, was used by Sereno (1999) to diagnose hadrosaurids (condyle width 120% to 130%). Hadrosaurids range from 160% to 200%; therefore, this character is not used in this study. In juveniles, the radial and ulnar condyles are similar in degree of development, but the ulnar condyles are far more developed in adults. Extreme caution must be taken when considering thickness as a taxonomic character. As in the coracoid, thickness is more a product of ontogeny than of taxonomy.

Radius. The radius (Fig. 8.2G) is long and straight, with a circular cross section at midshaft. The proximal end, which articulates with the medial-distal condyle of the humerus, abruptly expands into a circular, cup-shaped process, and resembles the top of a Doric column in anterior view. The distal end is flattened and is rectangular in anterior view.

Brown (1913a) and Lull and Wright (1942) stated that the radius/humerus length ratio is diagnostic at the subfamily level, the humerus being longer in the hadrosaurines and the radius longer in lambeosaurines. This hypothesis is no longer valid (Brett-Surman 1975; Egi and Weishampel 2002). The radius (Fig. 8.2) is longer than the humerus in the hadrosaurines *Saurolophus osborni* (AMNH 5220), *Edmontosaurus edmontoni* (NMC 2288), and *Anatotitan copei* (AMNH 5730) and in the lambeosaurine *Hypacrosaurus altispinus* (NMC 8501). The radius is shorter than the humerus in the hadrosaurines *Kritosaurus* (=*Gryposaurus*?) *incurvimanus* (ROM 764), *Prosaurolophus maximus* (ROM 787), and *Edmontosaurus annectens* (YPM 2182) and in the lam-

beosaurine *Parasaurolophus walkeri* (ROM 768). The length of the radius increases with ontogeny relative to the length of the humerus. The result is that hadrosaurine radii approach the relative lengths of lambeosaurines when the femur length approaches 140 cm. The radius/humerus ratio is not consistent within any clade and is therefore useless for taxonomic purposes.

Ulna. The ulna (Fig. 8.2F) has the overall shape of an inverted, triangular bone, with a conical cross section. The proximal end forms a three-pronged process, with each prong radiating at 90 degrees from the other prongs. The medially and anteriorly projecting processes form a cradlelike structure (radial notch) that receives the radius. The proximally projecting olecranon process articulates with the posterior side of the humerus between the two distal condyles, which sit in the olecranon notch of the ulna. The distal end of the ulna is flattened like that of the radius.

The transition from juvenile to adult results in a great enlargement of the olecranon notch of the ulna and an increase in robustness of the olecranon process (Dilkes 2001; Brett-Surman 1975, 1989). The lateral process becomes thicker. The distal end does not show any great increase in width compared to its circumference, but the shaft undergoes a tremendous increase in length compared to its circumference. This results in the forelimb becoming relatively thinner with increasing age.

The only variation observed among the ulnae of hadrosaurids is that most hadrosaurines appear to have limb elements that are more slender and less thick than those of lambeosaurines of the same size, but this feature is not consistent enough to have taxonomic validity.

Carpals. The blocklike carpals (Fig. 8.3B) resemble an ice-hockey puck. They are circular in cross section and about one-half as tall (dorsoventrally) as wide (lateromedially). They have also been reported as tetrahedral (Davies 1983; Prieto-Marquez 2000) and as ovoid (Prieto-Marquez 2000).

Hadrosaurid carpals are rare in collections, probably because they are rarely recognized because of their irregular appearance, may go uncollected, or may be inadvertently destroyed during preparation. Hadrosaurid carpals have been restored in a colinear arrangement above metacarpal III since Brown's (1912) redescription of the manus in *Edmontosaurus annectens*. In a specimen of *Anatotitan* (Fig. 8.3B, AMNH 5886), they are mounted on top of one another, both over the third metacarpal. In a specimen of *Corythosaurus casuarius* (CM 9461), the radiale and the intermedium are mounted next to each other, both under the radius and each over a different metacarpal, and other specimens (Lambe 1913; Parks 1920) suggest a side-by-side arrangement. Homologies of these elements are uncertain. The recent consensus (e.g., Erickson 1988; Norman and Weishampel 1990; Rasmussen 1998) is that the radiale, intermedium, carpal I (if present), and metacarpal I fuse to form a larger block, while the ulnare and distal carpal five fuse to form a smaller block.
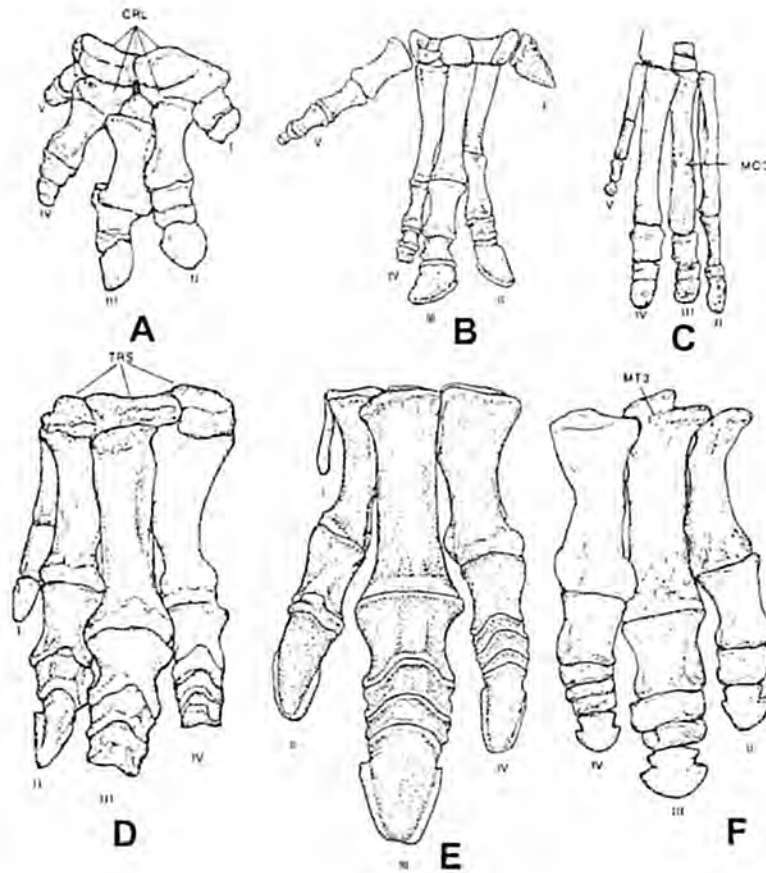
Figure 8.3. Comparison of the right mani in anterior views: (A) Camptosaurus USNM 4277 (metacarpal III length = 78 mm); (B) Iguanodon (redrawn from Norman 1986); (C) Anatotitan AMNH 5886 (length of metacarpal III = 310 mm). Comparison of the right pedes in anterior view: (D) Camptosaurus USNM 4277 (metatarsal III length = 234 mm); (E) Iguanodon (redrawn from Norman 1986); (F) Saurolophus AMNH 5270 (length of metatarsal III = 340 mm).

The sample of carpals is insufficient to determine the range of variation present in hadrosaurids. The intermedium (provisional designation) is slightly larger than the radiale (provisional designation), which, in one specimen (AMNH 5886), has an overhanging lateral process that fit over the second metacarpal. Only two carpals are consistently seen among hadrosaurs, and what is termed the "intermedium" here could very well be the ulnare.

Little variation in morphology of the carpals was noted among the genera. Variations in relative lengths of metacarpals II and III vary widely between 76% to 91%. Measurements of these elements did not prove to be of diagnostic value. It is common for the hand not to be preserved in most specimens. There appears to be a taphonomic pattern such that the head, manus, and pes are the first parts to become separated from the main portion of the skeleton (Dodson 1971). None of the bones of the manus or pes is fused to another or to the limbs, thus making separation quite easy before final burial.

Metacarpals. The metacarpals (Fig. 8.3B) are pencil shaped and have smooth, featureless articular ends. Metacarpal I is lost

and metacarpal V is reduced. The manus is functionally tridactyl, with metacarpal III slightly longer than metacarpal II and metacarpal IV, which are equal in length.

As noted by Maryańska and Osmólska (1984), digit IV is somewhat divergent in hadrosaurids. In most cases, this divergence is associated with an axial twisting in the first phalanx, whereby the metacarpal joint is convex in two dimensions. The distal articulation is laterally compressed and arcuate in extensor view, and apparently allowed the digit to splay laterally. The distal articulation of the first phalanx is twisted as well, such that its hinge line is almost in the same plane. In *Edmontosaurus annectens* (Osborn 1912) and *Hypacrosaurus altispinus* (Brown 1913b), metacarpal IV is slightly divergent laterally, although this is not apparently true of all specimens of *Edmontosaurus* (Lambe 1913; Marsh 1892).

In *Iguanodon*, metacarpal V is laterally compressed proximally and was apparently somewhat divergent from the rest of the manus. In *Iguanodon* and hadrosaurs, this digit is elongate and may have been prehensile (Norman 1980). In contrast to the morphology seen in *Iguanodon*, metacarpal V may have been appressed to metacarpal IV in at least some hadrosaurs (Wagner and Lehman, personal communication; q.v. Maryańska and Osmólska 1984: plate 20-8; Parks 1920).

Digit V is absent in two well-preserved, articulated specimens of hadrosaurs from the Aurisino Limestone of Italy (Dalla Vecchia 2001).

We were unable to detect any differences in metacarpals among the genera of hadrosaurids. The sample size of the specimens with a complete manus is too small at this time to detect any trends even at the level of subfamily.

Phalanges. The phalanges of hadrosaurids are most similar to *Iguanodon* (fide Norman 1980). They are longer (proximal distally) than wide (lateromedially) and flattened. The general formula is 0-3-3-3-3. The unguals are hoof shaped but relatively less developed and laterally flared than the pedal phalanges. Some hadrosaurs had wedge-shaped phalanges, whereas others did not. One slight difference exists between the phalanges (Fig. 8.3B) of some hadrosaurines and lambeosaurines. In the hadrosaurines, the second row of phalanges (distally from the metacarpals) of digits II, III, and IV generally consists of well-developed elements that are proportionally as large as the proximal row of phalanges. In the lambeosaurines, this row generally consists of elements that are considerably reduced and often pebblelike. Sereno (1999) allied *Iguanodon*, hadrosaurs and *Ouranosaurus* on the presence of manual digits in the second rank of the three middle digits that are more than twice the length of phalanx 1. This is probably a typographical error because the appropriate derived state is for the second-rank phalanges to be 50% or less of the first rank in length.

In *Saurolophus angustirostris* (Rozhdestvensky 1957), phalanx IV-1 is unusually short, and its proximal and distal articular surfaces are set at an angle to one another. Slight asymmetry in pha-
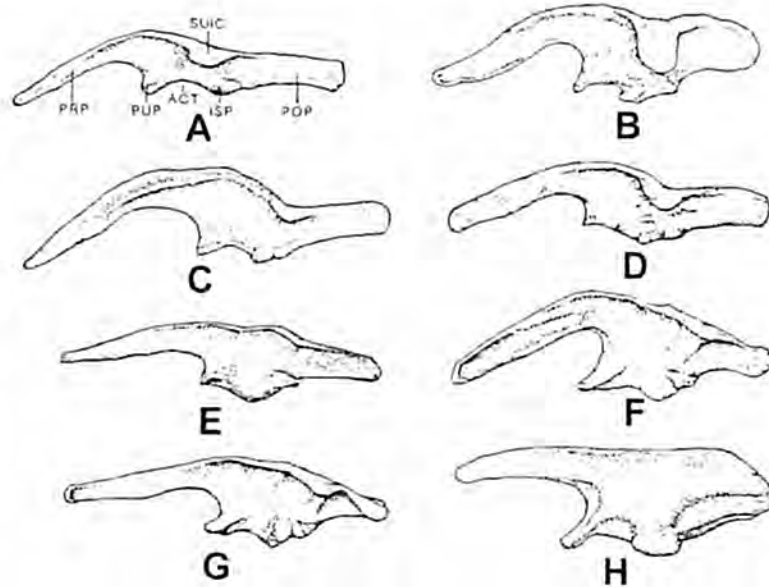
Figure 8.4. Comparison of the left ilia in lateral views. (A) Edmontosaurus DMNH 1493 (right in reverse; length = 1160 mm); (B) Parasaurolophus FMNH P27393 (length = 975 mm); (C) medial view of Kritosaurus USNM 8058 (length = 900 mm); (D) Lambeosaurus ROM 1218 (length = 1003 mm); (E) Tanius (length = 920 mm) (redrawn from Wiman 1929); (F) Bactrosaurus AMNH 6577 (length = 690 mm); (G) Gilmoreosaurus AMNH 6551 (length = 650 mm); (H) Camptosaurus USNM 5473 (length = 642 mm).

lanx IV-2 is evident in specimens of *Kritosaurus incurvimanus* (Parks 1919) and *Edmontosaurus annectens*. Phalanx V-4 has been recovered with specimens of *Kritosaurus incurvimanus* (Parks 1920) and *Brachylophosaurus goodwini* (Prieto-Marquez 2000). Unguals are generally smooth along the anterior edges. In some very large animals, the unguals are pitted, have roughened edges, and have deep gouges at the leading anterior edge resulting in a "frilling" (*Bactrosaurus*, AMNH 6553; Gilmore 1933). The latter is a growth-related feature and is not systematically useful (Brett-Surman 1975, 1989).

Pelvis and Hindlimb

Ilium. The ilium (Fig. 8.4) is composed of three distinct sections. The preacetabular process curves ventrally and is a flat, vertical blade in all but the oldest individuals (see below). The midsection of the ilium contains the acetabulum, and the dorsal margin bears the "antitrochanter" (or, more properly, the suprailiac crest, fide Rowe 1986). The middle area between the dorsal and ventral margins contains the concave depression for the M. iliofemoralis (see Dilkes 1993). The medial side of the ilium contains the articulations for the sacral ribs. The postacetabular process is paddlelike and rectangular in lateral view. Iliac length is isometric during ontogeny and is approximately 93% of femur length. In iguanodontids, this ratio is nearer to 100%. Iliac height compared to length is between 16% and 25%, with much variation between taxa.

The preacetabular process appears to be deeper, as measured at its minimum depth nearest to midshaft, relative to the height of the ilium at the pubic peduncle in some iguanodontians than in others.

However, the limited data available suggest that the average ratio for hadrosaurs is around 33% ± 7%. It is unclear if this ratio changes with growth. Among hadrosaurs, the angle of the preacetabular process in lateral view relative to the main body is greater in taxa with particularly deep ilia, ~35 degrees or more (e.g., *Bactrosaurus, Parasaurolophus, Hypacrosaurus*), and it is shallower, 20–27 degrees, in taxa with shallow ilia (e.g., *Edmontosaurus*). As discussed below, apomorphic reduction of the pubic peduncle in some taxa may increase this angle to near 40% (e.g., *Kritosaurus*). However, the difference between ilia from two sides of the same animal may be 5 degrees or more (e.g., Morris 1978). Individual variation is also high, ranging from 20 to over 30 degrees in juvenile *Maiasaura* (Carpenter 1999: fig. 12.29), and from 25 to over 35 degrees in *Corythosaurus* (Brown 1916; Parks 1935; possibly Gilmore 1946). The degree of deflection of the preacetabular process is much greater than in any other iguanodontians, but the degree of deflection is too variable to be of taxonomic use.

In *Iguanodon*, the medial surface of the ilium is relatively shallowly embayed for the acetabulum, while the lateral surface is deeply embayed ventrally by an acetabular fossa having a steeply sloping caudal margin and a slightly produced marginal "lip" dorsally. This process is more properly termed the "antitrochanter." The iliac acetabular fossa extends laterally, almost to the level of the base of the preacetabular process, and "cups" the femoral head medially as well as dorsally. In hadrosaurids, both the medial and lateral margins of the acetabular fossa are lower such that they are nearly at the same level, and the acetabular margin of the ilium is only slightly arched in lateral view. The acetabular surface of the ilium contacts the femoral head only dorsally, and the acetabular articular surface is only barely visible in lateral view. In *Ouranosaurus, Bactrosaurus, Altirhinus, Probactrosaurus gobiensis*, and possibly *Iguanodon*, an intermediate state is observed where the lateral margin of the acetabular surface is lower such that it extends only about halfway to the level of the base of the preacetabular process, and the medial margin is barely arched.

In early hadrosaurids, the suprailiac crest is distinctly triangular, with a nearly vertical caudal margin in lateral view. It is somewhat pendant and elongate, often traversing nearly half of the distance from the dorsal to the ventral border of the postacetabular process in lateral view. The suprailiac crest in these taxa has a low, rounded ventral buttress extending from the lateral surface of the iliac blade, probably representing the intermuscular line between M. iliofemoralis and M. iliofibularis (Dilkes 2000). In *Barsboldia, Claosaurus, Secernosaurus, "Kritosaurus" australis*, unnamed ilia illustrated by Young (1958), and all hadrosaurids, the suprailiac crest is more cranially located such that its caudal edge is over the ischial tuberosity on the lateral face of the ischiadic peduncle, and the cranial edge is nearly over the center of the acetabulum, as it is in hadrosaurids. In all of these taxa except *Claosaurus*, the "antitrochanter" is strongly developed, the postacetabular process is

TABLE 8.1.
Relative comparison of the hadrosaurid ilium morphocline.

Characteristic	Hadrosaurine	Lambeosaurine
Preacetabular process relatively deflected ventrally	Less (average, 32 degrees)	More (average, 42 degrees)
L/H ratio of ilium, average (SD)	5.41 (0.05)	4.43 (0.5)
Postacetabular process L/H ratio, average (SD)	2.46 (0.14)	1.88 (0.25)
Iliotibialis process extends to meet peduncle	Rarely	Often
Ischial and pubic peduncle	Less robust	Relatively more robust

slightly displaced ventrally, and the dorsal margin of the ilium is strongly "notched" accordingly. The development of the suprailiac crest is size related with a strong overprint of individual variation (Brett-Surman 1989; Lull and Wright 1942).

Five morphotypes of ilia are recognized among the five clades of hadrosaurids ("tribes" fide Brett-Surman in Chapman and Brett-Surman 1990). These morphotypes grade into one another along a morphocline and are not useful taxonomically (Morris 1978). The two extremes on the morphocline are the ilium of *Edmontosaurus* and that of *Parasaurolophus*. Both display heterochronic and onto-genetic trends (Table 8.1).

The first morphotype is represented by *Bactrosaurus* and *Gilmoreosaurus* (Fig. 8.4F, G). The preacetabular process is ventrally deflected as in later hadrosaurids. Both ischial and pubic pe-duncles are structured in typical hadrosaurid fashion, as is the M. iliofemoralis depression. The postacetabular process has been greatly modified from the camptosaurid (Gilmore 1909) and *Iguanodon* (Norman 1980) condition where this process is rudi-mentary (if present at all), but it is not as well developed as in the more advanced hadrosaurids *Edmontosaurus* and *Parasaurolo-phus*. The suprailiac crest is rudimentary and is more of a laterally projecting lip on the dorsal margin of the ilium as in *Iguanodon*. In other hadrosaurids, it is a massive process (compare *Bactrosaurus* in Fig. 8.4F to *Parasaurolophus* in Fig. 8.4B). The dorsal margin is curved in the typical hadrosaurid fashion.

A second mophotype is exemplified by *Edmontosaurus* (Fig. 8.4A) and *Anatotitan*. In these genera, the ilium is greatly elon-gated and not relatively as high as in other genera, resulting in a length/height (L/H) ratio that is greater than in any other iliac type. In lateral view, the ilium is thin and greatly elongated, in contrast to the more robust appearance as in *Parasaurolophus*. The postac-

etabular process also has the greatest L/H ratio of any clade, and the body is relatively shallow.

The third morphotype is seen in *Kritosaurus* (Fig. 8.4C), where the ilium is somewhat similar to the second morphotype in lateral view but has a relatively taller body, and the ventral deflection of the preacetabular process is greater. This deflection is more pronounced than in any other clade. The postacetabular process also appears to be deflected dorsally, giving the overall aspect of the ilium in this clade an accentuated "sigmoidal" curve. This feature is common to this clade and to the saurolophs.

A fourth type of ilium is exemplified by *Corythosaurus* and *Saurolophus* (Fig. 8.4D), in which the L/H ratio is smaller than that of the previous types. The preacetabular process is usually more ventrally deflected as in the *Kritosaurus* clade. The postacetabular process has a smaller L/H ratio than in any other hadrosaurine clade.

The fifth morphptype of ilium is represented only by *Parasaurolophus* and *Tsintaosaurus* (Fig. 8.4B). As in the previous type, the preacetabular process is strongly deflected ventrally, but it is thicker and wider than in all other clades. The body is the deepest of any lineage, and the postacetabular process has the smallest L/H ratio of any lineage. The suprailiac crest is relatively more massive and extends farther laterally than in any other clade.

In summary, in morphotypes 2 through 5, the ilium becomes progressively more massive. The L/H ratio of the element as a whole decreases while the suprailiac crest and the postacetabular process increase in robustness. This is a consequence of an increase in the relative and absolute size of the suprailiac crest. The result is increased surface area for the attachment and size of the M. iliotibialis, M. iliofemoralis, and M. caudifemoralis externus complexes in the lambeosaurines. This would make the legs relatively more powerful than those of hadrosaurines with the same femoral length, but it does not imply greater speed.

Finally, ontogenetic characters among the ilia are surprisingly few considering the diversity of forms. The ilium maintains its general shape and dimensions throughout life. Juveniles can be recognized only by their absolute size. In very old individuals, for example USNM 3814, the preacetabular process has thickened, as has its dorsal rim and the medial ridge that extends onto the preacetabular bar (Fig. 8.5C, shown in medial view) for articulation with the sacrum and the origin of M. puboiliofemoralis internus. This has proceeded to such an extent that preacetabular bar has changed from a narrow cross-sectioned blade to a thickened bar with a T-shaped cross section.

Pubis. The hadrosaur pubis is one of the thinnest, most fragile bones in the skeleton, and an undamaged specimen is very rare. The thin, frail prepubic margin and the shaft of the postpubis are rarely preserved intact. Postmortem distortion and perspective differences exaggerate an apparent high degree of individual variation in this element. Fortunately, the small sample of juvenile and
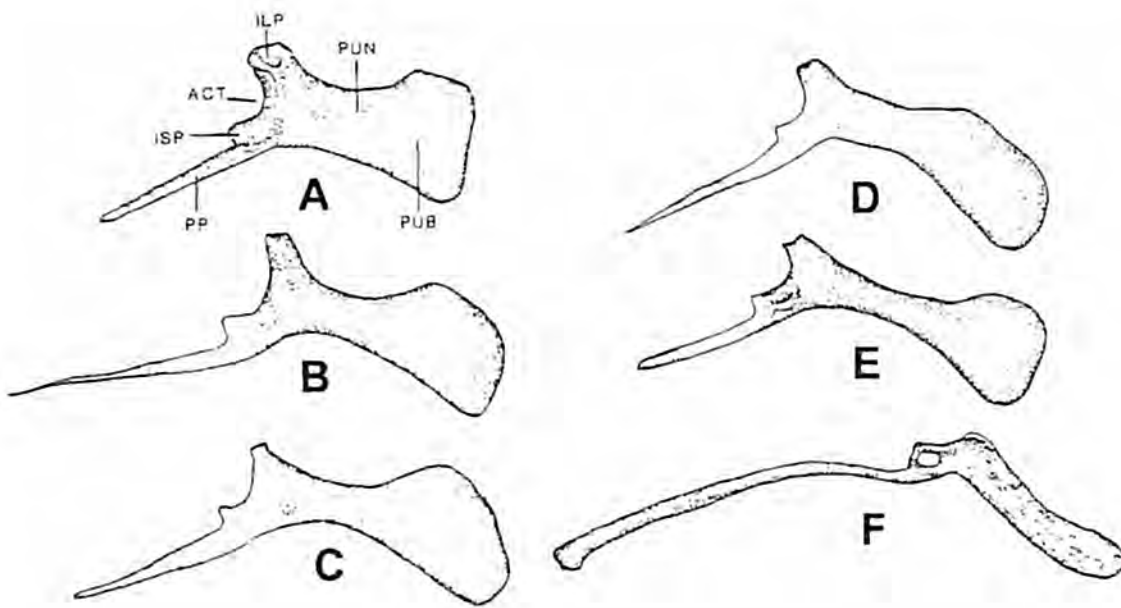
Figure 8.5. Comparison of right pubes in lateral view. (A) Parasaurolophus FMNH P27393 (length of prepubic blade = 430 mm); (B) Corythosaurus AMNH 5240 (length of prepubic blade = 490 mm); (C) Prosaurolophus ROM 787 (length of prepubic blade = 533 mm); (D) Kritosaurus ROM 764 (length of prepubic blade = 534 mm); (E) Edmontosaurus DMNH 1493 (length of prepubic blade = 630 mm); (F) Camptosaurus YPM 1880 (length of prepubic blade = 336 mm).

subadult prepubes available suggests that prepubic morpohology in juveniles is consistent with that in adults. Unfortunately, specimens on exhibit have a substantial amount of restoration of the pubis and may easily mislead researchers (Brett-Surman 1975, 1989; Dilkes 1993).

The pubis (Fig. 8.5) is divided into three portions. The most posterior section contains the postpubic process, which extends posterioventrally along the ventral margin of the ischium. It is rod-like and often vestigial. The middle section forms the acetabular margin, with the posteriorly projecting ischial peduncle and the dorsally projecting iliac peduncle. The most anterior portion is the prepubic process, comprising a "neck" and "blade" (Fig. 8.5A).

The prepubis is likely the origin of hypaxial musculature and M. ambiens (Hutchinson 2001a; Romer 1927). Carrier and Farmer (2000) proposed that the prepubic process had a role in mechanical respiration among ornithischians, a connection previously proposed by Brett-Surman (1975) for hadrosaurs. Crocodiles use their M. rectus abdominis to push the liver toward the lungs as a pseudo diaphragm, and if hadrosaurs breathed in a similar manner, then a correlation may exist between complexity of the narial apparatus and size of the M. rectus abdominis and its origin on the prepubis. This correlation is exactly what is found in hadrosaurids. The *Parasaurolophus* clade has the most complex nares and the thickest, shortest, and widest prepubic blade. The orientation of the blade is directly in line with the ribcage so that the force on the prepubis from muscular contraction is transmitted along its longitudinal axis, thereby minimizing lateral components of force. The lat-

eral forces that exist as a result of the actions of the ambiens and the puboischiofemoralis externus muscles are braced by the sacral ribs and cartilage (Maryańska and Osmólska 1981).

The length of the prepubis averages 50% the length of the ilium in hadrosaurids. There is noted variability, especially in *Edmontosaurus*, from 46% to 60% of iliac length. The ratio of the prepubic length to height is quite variable, ranging from 26% to 62%. Hadrosaurines on average have a ratio less than 47%; that of lambeosaurines is more than 47%. There is too much overlap to delineate clades.

There are five different pubic morphologies (Fig. 8.5) corresponding to five clades. All these types grade into one another; therefore, comparisons can only be made between the extremes along a morphocline.

The first type is exemplified by *Edmontosaurus* (Fig. 8.5E) and also by the hadrosaurine *Gilmoreosaurus*. The neck is relatively longer and thinner than in other clades. The blade is symmetrically expanded in most cases, with a slight emphasis of the dorsal side. The surface area of the blade (in lateral view) is relatively the smallest of any clade.

Kritosaurus characterizes the second type of pubis (Fig. 8.5D). This type is notable for having a blade with parallel dorsal and ventral borders. The prepubic part of this element is strongly deflected ventrally. The neck is relatively shorter and wider than in *Edmontosaurus*.

The third type is typified by *Saurolophus* (Fig. 8.5C). The blade contains a dorsally projecting asymmetrical bulge, which gives this portion an overall triangular shape in lateral view. The anterior border projects sharply in the ventral direction. The tip is well rounded, grading gradually into the ventral border, which is straight. The neck is relatively shorter and wider than in other hadrosaurines.

Corythosaurus represents the fourth type of pubis (Fig. 8.5B). The blade closely resembles that of *Saurolophus* but the dorsally projecting bulge is more flattened, giving this portion of the element a more trapezoidal aspect in lateral view rather than a triangular one. The dorsal border is deflected ventrally but not as abruptly as in *Saurolophus*. The dorsal and ventral borders are subparallel, almost as in *Kritosaurus*, but the blade is relatively much shorter. The anterior border is well rounded and longer than in the other clades, and the neck is shorter and wider.

Parasaurolophus and *Bactrosaurus* represent the fifth type of pubis (Fig. 8.5A). In this type, the blade is relatively shorter and wider than in other clades. In lateral view, the blade resembles a rectangle with the longer axis of the rectangle oriented vertically. The dorsal and ventral borders are subparallel in most cases. The anterior border is perpendicular to the dorsal and ventral borders and is relatively longer than in the *Corythosaurus*-like pubis. The neck is very short and relatively wider than in other clades, giving it a robust appearance. One unique difference of this clade is the mas-
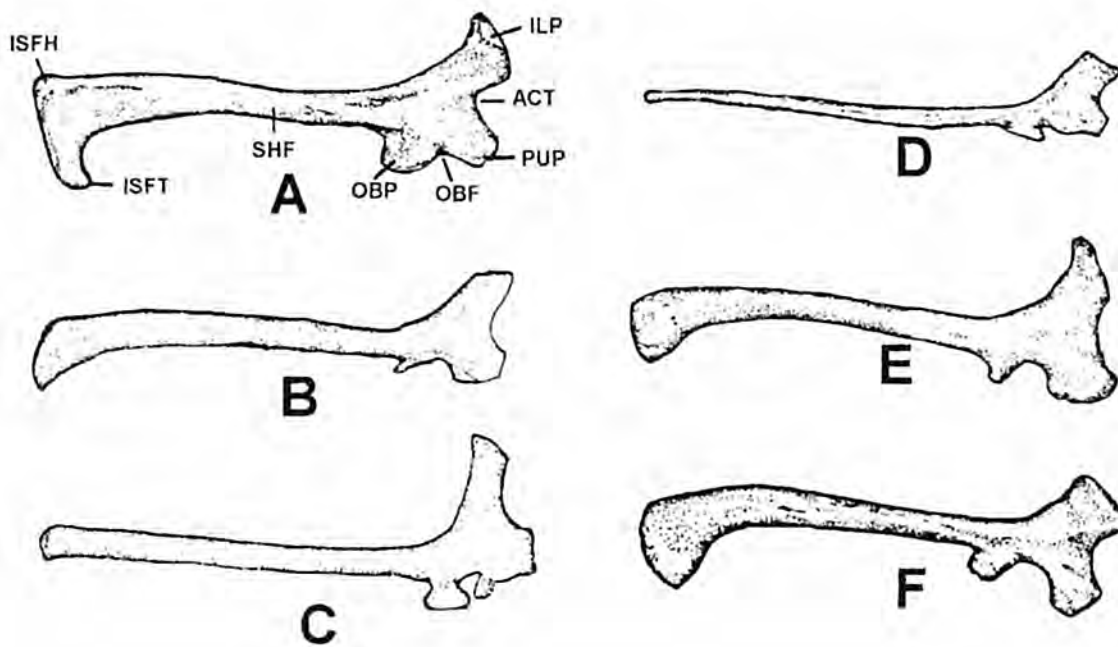
Figure 8.6. Comparison of the right ischia in lateral view. (A) Parasaurolophus FMNH P27393 (length = 1078 mm); (B) Corythosaurus AMNH 5240 (length = 1030 mm); (C) Shantungosaurus (length = 1602 mm) redrawn from Hu (1973); (D) Anatotitan AMNH 5730 (length = 1160 mm); (E) Gilmoreosaurus AMNH 6551 (length = 718 mm); (F) Camptosaurus YPM 1878 (length = 553 mm).

siveness of the iliac peduncle. The articular surface is deep, cuplike, and well rounded. In other clades, the iliac peduncle is long and thin, with a shallow cup. Parasaurolophus cyrtocristatus (FMNH P27393) displays a large ridge that extends from the iliac peduncle to the ischial peduncle. This ridge is not as well developed as in the other genera. The type of Parasaurolophus walkeri has a pathological fusion of the pubis and ilium at the pubic peduncle.

In summary, the pubis increases in robustness with each of the clades by increasing the surface area of the blade and enlarging the attachment with the prepubic neck by increasing its width and decreasing its length. The most gracile forms (the edmontosaurs) have the most elongate prepubis compared to animals of comparable size in other clades. The most robust forms (the parasaurolophs) have the shortest prepubis.

Juveniles have pubes with the same morphology as the adults. It is remarkable that hadrosaurids show such a uniformity of pattern throughout the ontogeny of the individual. The postpubis, because of its lack of distinctive features and rare preservation, proved to be of no value for the diagnosis of suprageneric clades.

Ischium. The ischium projects at approximately a 45-degree angle posterioventrally from the acetabulum and is composed of three portions. The most proximal portion contains the acetabulum, the iliac and pubic peduncles, and the obturator process and fenestra. The middle portion contains the ischial shaft, which is columnar and featureless. The most distal portion contains the terminal knob or "foot" (Fig. 8.6E), composed of the "heel" and "toe" (Fig. 8.6A).

Use of the ischium in hadrosaur systematics dates to Brown (1914), and the "footed" ischium is often used and misused in hadrosaur systematics, the. The presence of a "footed ischium" is the peromorphic condition (Brett-Surman 1989). Distal expansion of the caudal end is found in all iguanodontians. Lack of a "footed ischium" is the derived, neotenic condition that characterizes the hadrosaurines. Although other features of the hadrosaur ischium are frequently obscured or altered by distortion, damage, and incomplete ossification, the ischium is the most resistant bone in the hadrosaur pelvis.

The degrees of development of the "foot" has been discussed by Brett-Surman (1975, 1989), Godefroit et al. (2000), and Casanovas-Cladellas (1999). With increasing size, the distal expansion acquires certain characteristics in a moderately consistent order. In gracile ischia, the minimal thickness is approximately three-quarters down the shaft. In robust taxa with very low length/foot ratios, the foot is very small, often appears flat-bottomed, and may form an acute angle with the shaft (possibly related to the shallowing of the ischial-vertebral angle in hadrosaurs). In ischia with a ratio of 8:1 to 6:1, the curved "ball" of the foot develops, and there may be a small inflection of the dorsal ridge of the ischial shaft where it curves into the sole of the foot, forming a slight "heel" in larger specimens. In larger specimens in this range (ischial ratio 7:1 to 6:1), the "ball" of the foot may migrate ventrally, beveling the "heel" area. In ischia of adults with ratios between 6:1 and 4:1, the "heel" may increase in prominence as a slight flange, but it is still relatively small. At around 5:1, the tip of the foot may extend cranioventrally past the "ball" of the foot as a straight, dorsoventally narrow, elongate "toe." At his point, authors seem to be in agreement that the distal expansion is to be termed "club-shaped" as opposed to "footed" (e.g., Casanovas-Cladellas et al. 1999), although this distinction is arbitrary. These ischia have a "sock," a thickening of the distal half of the shaft that accentuates the dorsal curvature of the bone and shifts the location of minimal shaft thickness to near the middle of the shaft. In ischia with length/foot ratio of less than 4:1, the heel is expanded and protrudes dorsally and distally in lateral view, the toe is well developed, and the "sock" extends about two-thirds up the shaft, such that the thinnest point is just distal to the obturator process, and the entire distal shaft is a thickened club. Stem hadrosaurs and iguanodontians therefore cover the entire range of ischial foot size. Because the relative size of the ischial foot is ontogenetically variable and the shape of the foot is dependent on relative size, comparisons of "clubbed" versus "footed" ischia (e.g., Casanovas-Cladellas et al. 1999) will not unequivocally separate a stem hadrosaur from a nonhadrosaur.

The ischial symphysis is reduced to a plate of bone surrounding the ischial obturator foramen (Hutchinson 2001a). In many taxa, including tetanuran theropods and ornithischians, the obturator foramen was "opened" by reduction in the ossification of its outer margin; its ventral margin became the obturator process, and this is

separated from the ischiadic peduncle by the obturator notch (Hutchinson 2001a; Novas 1996). In iguanodontians, the obturator process is somewhat variable in development, but shows such remarkable consistency in shape that one suspects a process of progressive ossification of a cartilaginous or other connective tissue precursor. Ossification takes place in discrete stages: in the first stage, the obturator process is a low, triangular fin, and there is a low fin extending ventrally from the pubic peduncle (e.g., Norman 2002). Following this, the distal end of the obturator process swells ventrolaterally into a rugose "postpubic peduncle," diamond shaped in lateral view, that projects somewhat laterally from the tip (e.g., Taquet 1976) and apparently contacted the postpubis (Dilkes 1993). The lateral surface of the portion of the obturator process separating the postpubic peduncle from the ischial shaft is excavated by a trough parallel to the shaft. Development of a postpubic peduncle often, but not always, creates a slight notch between the ventral margin of the obturator process and the shaft of the ischium as in some theropods. This notch is variable among individuals, dependent on the degree of ossification of the caudal end of the postpubic peduncle. At around the same stage of development of this structure, the ventral fin on the pubic peduncle produces a mediolaterally thin, hook-shaped spur that grows around the obturator notch, partially enclosing it (e.g., Brinkmann 1984; Dilkes 1993; Gilmore 1917; Rozhdestvensky 1957). This hook is smaller in taxa where the pubic peduncle makes a shallower angle with the shaft (see above). In some cases (e.g., Sternberg 1935), the postpubic peduncle grows craniodorsally toward the ischiadic peduncle.

In the final stage, a thin, slightly everted, rugose bar, apparently a continuation of the postpubic peduncle, closes the obturator foramen ventrally (e.g., Gilmore 1924b). Systematic variation in this character was not observed. Closure of the ischial obturator notch appears to have set in at smaller sizes in some specimens with more "robust" ischia (e.g., Boyd and Ott 2002), but closure also appears to progress with age, such that moderate to large specimens of unfooted ischia have closed or nearly closed obturator foramina (e.g., Brett-Surman 1989; Brown 1913a; Gilmore 1917; Hu 1973; Mateer 1981). However, even smaller unfooted ischia may have a completely enclosed foramen (Maryańska and Osmólska 1984), and the presence or preservation of this feature is variable within species (cf. Maryańska and Osmólska 1984 with Rozhdestvensky 1957). However, a rather small, "gracile" ischium from Big Bend has over half of the foramen encircled, with broken edges indicating more bone was present in a small-size individual (TMM 42309; Davies 1983).

The ventral edge of the ischium is quite thin, probably more so in gracile ischia. In taxa with a shallow angle between the shaft and the pubic peduncle, the flange beneath the latter responsible for closing the obturator foramen is somewhat less robust. Often closure is accomplished by a thin arm of bone that appears particularly vulnerable to damage and may be broken off in many speci-

mens (e.g., Gilmore 1924b). Even in truly robust specimens, such as the type of *Parasaurolophus cyrtocristatus* (Ostrom 1963) in which the obturator process is a large, rectangular flange that nearly occludes the obturator notch, the bar enclosing the foramen is either unossified or unpreserved. It is also conceivable that pathology may have caused early ossification of this structure in some specimens. However, closure of the ischial obturator notch appears to be so variable as to be systematically useless (Brett-Surman 1975, 1989).

Four types of ischia can be recognized. Three are represented by Late Cretaceous forms. The first type is exemplified by *Gilmoreosaurus* (Fig. 8.6E) and displays an intermediate morphology between *Iguanodon* (Norman 1980) and hadrosaurines. In this type, the obturator notch is open in adults. The shaft is relatively more decurved than in other hadrosaurids, but the degree of curvature is less than that of most specimens of *Iguanodon*. Distally, the shaft terminates in a rounded knob that protrudes asymmetrically to the ventral side.

The second type of ischium is represented by the hadrosaurines; exemplified by *Anatotitan copei* (Fig. 8.6D). In this type, the relative size of the peduncles is considerably reduced in most forms. The obturator notch is open, except in old adults. The shaft is long, straight, and relatively thinner than in any other type of ischium. The distal end usually tapers to a rounded point. A knob is rarely present. If present, however, it is rudimentary and always considerably smaller than in other types.

Corythosaurus and *Lambeosaurus* exemplify the third type of ischium (Fig. 8.6B), where the pubic and ischial peduncles are equal in size or the iliac peduncle is slightly larger. The shaft is long, straight, and generally much thicker than in hadrosaurines of the same size. Posteriorly, the diameter of the shaft gradually increases distally, where it terminates in an abrupt expansion into a structure resembling a foot in lateral view. This expansion is totally in a ventral direction when the ischium is viewed laterally in natural articulation. There is no "heel," but there is a slight tapering of the foot at the "toes" (see Fig. 8.6A).

The fourth type of ischium is represented by *Hypacrosaurus* and *Parasaurolophus* (Fig. 8.6A), which is most distinctive for its robustness. All landmarks previously cited are relatively larger in size and thicker than in any other type of ischium. The iliac peduncle displays a prominent "lip" that projects posteriorly on its articular surface. The pubic peduncle is a large roughened process with a broad articulation. The obturator notch is closed in adults, but this area is frequently damaged during fossilization, creating the impression that the notch is normally open. The shaft is long and straight, and it does not increase in diameter for the proximal half of its length. The distal half gradually increases in diameter until the abrupt expansion into a large footlike process that is up to 50% larger than in the other forms displaying this structure. This foot has a distinctive "heel" and "toes" (Fig. 8.6A) that are more

prominent and massive, and that project farther posteriorly than related forms. A ridge extends from the pubic peduncle across the shaft to the posterior side and continues onto the foot. This ridge has not been noted in other ischial types, but it may be a growth feature rather than a generic characteristic.

One growth feature is noticeable in the ischium. The distally enlarged knob or "foot" is ontogenetically variable. Excellent examples of this are present in the Two Medicine faunal collection (Campanian) housed in the U.S. National Museum (lot number USNM 358593). In this fauna, as well as the Iren Dabasu fauna (e.g., specimens of *Bactrosaurus* and *Gilmoreosaurus* housed at the AMNH), there are three size or age groups. The first may be termed hatchlings and are individuals of hindlimb length less than 30 cm. The second age group may be called juveniles and have a hindlimb length of 30–90 cm. The adult age group consists of the largest animals with hindlimb lengths of more than 90 cm. There is no indication of an ischial foot in any of the hatchlings. The juveniles have a distal enlargement that is not quite a foot but that is definitely too large to be from a hadrosaurine. The true foot appears suddenly in this group—within the time it takes the ischium to grow another 5 cm in length (USNM lot number 358593). Perhaps this signals the attainment of sexual maturity. This is the only major growth feature noted in an appendicular element that appears after the hatchling stage.

In summary, only pelvic elements have clear characteristics that can be of diagnostic value to the level of subfamily and clade. All other postcranial elements display either a complete intergradation of form with only the extremes exhibiting subfamilial features (such as the humerus as discussed above), or the postcrania are too similar in all the genera to be of taxonomic use.

Femur. The femur (Fig. 8.7) is a long, cylindrical element. The head of the femur is cylindrical and relatively larger than in other ornithopods. The greater trochanter is massive and covers the entire lateral aspect of the proximal part of the femur. The lesser trochanter is relatively much smaller and often fuses to the greater trochanter in old adults (Fig. 8.7G). The greater and lesser trochanters are usually separated from each other by a small cleft. The shaft of the femur is straight and circular in cross section, with the fourth trochanter at midpoint. The distal condyles are larger and more robust than in any ornithopod clade and project posteriorly. The anterior condyles may fuse to form an anterior condylar canal in old adults (e.g., USNM 7582, 7948).

The lesser trochanter displays considerable variation in size, orientation, and degree of fusion to the greater trochanter. This is individual variation, for virtually every skeleton examined shows differences between the right and left sides. Variability of the lesser trochanter thus is of no value in the diagnosis of species. The lesser trochanter is sometimes fused to the greater along the dorsal margin of the femur in large, evidently older specimens. The two are also fused in the modest-size type specimens of *Kritosaurus incurvi-*
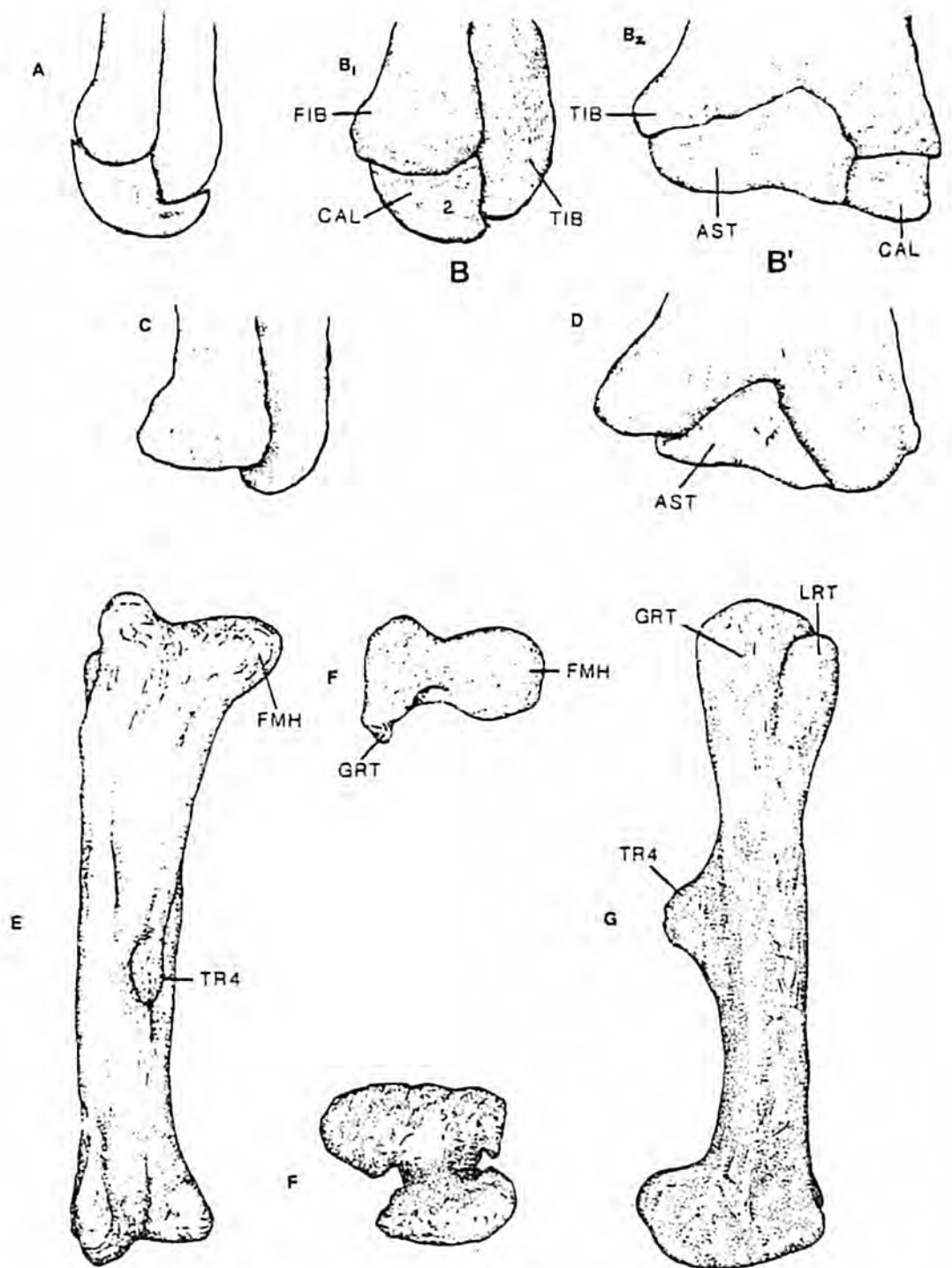
Figure 8.7. Comparison of hindlimb elements. Distal end of the tibiae, fibulae, and calcanea for (A) Camptosaurus USNM 2210 in left lateral view; (B) Anatotitan AMNH 5730 in lateral view and (B') in anterior view; (C) Lambeosaurus ROM 1218; (D) Parasaurolophus FMNH P27393 (without calcaneum); (E) posterior view of the femur of Anatotitan AMNH 5730 (length = 1135 mm); (F) proximal view and distal view of the femur of Gilmoreosaurus AMNH 6551; (G) lateral view of the femur of Corythosaurus CM 9461 (length = 760 mm).

manus and *Hadrosaurus*, although Pinna (1979) describes a specimen of *Kritosaurus notabilis* in which the two trochanters are completely separate. Dilkes (1993) reports no ontogenetic fusion in the trochanters of *Maiasaura*, and Davies (1983) described the presence and absence of this fusion over a broad size range in femora from Big Bend.

The degree to which the distal condyles approach each other on the cranial side of the femur appears to be size related (P. Galton, personal communication). Weishampel and Horner (1990) suggest that closure of the condylar groove may be species dependent, not ontogenetic. The condyles are reported to approach one another during growth in *Maiasaura* (Dilkes 1993), but they are joined even in small individuals of *Telmatosaurus* (Weishampel et al. 1993) and *Bactrosaurus* (Godefroit et al. 1998).

Generally, smaller hadrosaur femora appear concave cranially. With growth, the cranial margin becomes straighter, and some femora even appear somewhat bowed cranially, although the shaft is straight to slightly convex caudally. These changes are caused in part by the development of a low, rounded ridge, the linea intermuscularis cranialis of Hutchinson (2001b), that passes mediolaterally down the femoral shaft. This has been interpreted as the intermuscular line between the M. femorotibialis externus and internus (Hutchinson 2001b), and sometimes a distinct scar for the latter appears on the lateral side of bone caudal to this structure (Dilkes 1993; Young 1958, fig. 30). This ridge is only prominent in some hadrosaur femora, often those possessing a strongly developed fourth trochanter, and no systematic pattern is evident in its distribution.

In smaller hadrosaurs, the fourth trochanter is low and rounded, and the ventral margin of the fourth trochanter tapers into the femoral shaft. With increasing body size, the fourth trochanter is farther from the femoral shaft (Dilkes 2001), and the ventral margin forms an abrupt angle with the shaft, eventually developing a horizontal ventral margin distally. Sereno (1999) lists a "subtriangular," or nonpendant, fourth trochanter as an apomorphy of Hadrosauridae, whereas Norman (2002, character 63) distinguishes between a triangular trochanter and a rounded trochanter, with the latter diagnosing hadrosaurids and *Bactrosaurus*. In *Iguanodon*, the fourth trochanter is a caudoventrally directed prong associated with the secondary tendon of the M. caudifemoralis longus (Hutchinson 2001a).

Individual variation is manifest in the hadrosaurian femora, but the general morphology is identical in all clades (Fig. 8.7). Ontogenetic variation is relatively small and is confined to those features associated with increasing size, such as muscle scars, expansion of the base of the fourth trochanter, and in some cases, closure of the anterior condylar canal (Brett-Surman 1989).

Tibia. The tibia (Fig. 8.7) is long and straight, with a proportionally larger cnemial crest than in other ornithopods. The distal end is notched for the astragalus. The tibia is remarkably consistent

in shape ontogenetically, except for the cnemial crest. The crest exhibits positive allometry in its extent down the shaft relative to shaft length (although quantifying this relationship is difficult), and transforms from a small triangular nubbin in small individual to a triangular flange, then to a trapezoidal wing in progressively larger individuals. The ends of the fibula expand somewhat with growth, producing a cranially directed bulbous process distally and a short cranial process proximally.

No variation was observed between the genera of hadrosaurids; however, Godefroit et al. (1998) and Xu et al. (2000) diagnose hadrosaurs on the widening of the proximal head extending down the shaft of the tibia. The proximal ends of the tibiae of all large ornithopods are slightly flared.

Fibula. The fibula (Fig. 8.7B) is extremely similar to that of *Iguanodon* (fide Norman 1980). It is long and straight, and the proximal end forms a concave cup that receives the lateral projections of the proximal tibial crest. The distal end of the fibula is expanded into a knob that sits in the dorsally projecting cup of the calcaneum.

Two morphs are observed. The first morph (Fig. 8.7B) is typified by all genera except *Parasaurolophus*. In this type, the distal end of the fibula is moderately expanded into the shape of a ball. The second morph (Fig. 8.7C) is represented by the type specimen of *Parasaurolophus cyrtocristatus* in which the distal end is greatly expanded compared to all other hadrosaurids, possibly because of the loss of the calcaneum (see discussion below).

In general, fibula length is highly correlated with tibia length (averaging 95%), appears to be isometric with respect to tibia length across the hadrosaurids and shows no systematic distribution of variation. Expansion of the distal end occurs with increased size in ornithopods, as is clearly evidenced in *Iguanodon* (Norman 1980, 1986) and *Hypacrosaurus* (e.g., Brown 1913b; Horner and Currie 1994). The distal end of the fibula is expanded in all adult hadrosaurs, and there is no evidence that it is any more pronounced in any taxon relative to any other.

Astragalus. The astragalus of hadrosaurids (Fig. 8.7D) is similar to *Iguanodon* (fide Norman 1980), but has a relatively higher anterior ascending process. This process is proportionally larger and distinctly triangular in juveniles of hadrosaurids. A juvenile hadrosaurid astragalus from Big Bend (part of TMM 42534) shows an unusual indentation and a change in the character of the bone between the intercondylar portion below the ascending process and the cap over the medial malleolus of the tibia. Others appear to have smaller, perhaps incompletely formed cranial edges (Dilkes 1993; Horner and Currie 1994). It is possible that expansion of the astragalus over the medial condyle occurs during postnatal ontogeny in hadrosaurs.

One source of apparent variation in the astragalus involves positioning in mounted skeletons. Brown's (1913b, fig. 7) comparative illustration shows seemingly different astragali with the left in

articulation with the tibia, whereas the right is displaced down and is viewed from a different angle. The astragalus of all hadrosaurs is notched on the lateral side to receive a peglike process from the calcaneum (contra Chatterjee 1982).

In the hadrosaurids, two types of astragali were observed. The first type (Fig. 8.7B) is represented by all the genera except *Parasaurolophus*. In this type, the astragalus is triangular in shape when viewed anteriorly, but skewed laterally into a 25-50-105 degree configuration rather than the equilateral shape of *Parasaurolophus*. The outer malleolus of the tibia is relatively smaller and less rugose in this type. The second type (Fig. 8.7D) is represented solely by the type specimen of *Parasaurolophus cyrtocristatus*. In this type, the astragalus is also triangular in shape when viewed anteriorly, but it is much reduced in size and thickness compared to other hadrosaurids, and it does not extend as far medially under the inner malleolus. To compensate for the reduced astragalus in *Parasaurolophus*, the inner malleolus of the tibia is relatively more rugose and expanded than in the other genera. This increase is related to the possible loss of the calcaneum in *Parasaurolophus* as discussed below.

Small, presumably juvenile, specimens of hadrosaurines and lambeosaurines, especially *Corythosaurus*, with tibiae 60 cm or less in length, tend to have astragali resembling the first type but with a more triangular ascending process. Except in *Parasaurolophus*, the astragali of larger individuals enlarge and expand medially. This suggests that the form of the astragalus changes with growth. The sample size is too small at this time for any definitive conclusions.

Calcaneum. In profile, the calcaneum (Fig. 8.7B) forms a quarter section of a circle. The arc of the circle forms the articulation for the metatarsals and faces anteriorly in natural position. The two radii marking this quarter section form two cups, one facing proximally to receive the fibula and one facing posteriorly to receive the tibia. The calcaneum is small and does not extend ventroposteriorly beneath the tibia to the posterior side. The distal end of the tibia fits in a slight concavity on the posterior side of the calcaneum. In *Camptosaurus* (USNM 4282), the calcaneum forms the entire surface of articulation for the distal tarsals on the lateral side. In hadrosaurids, the calcaneum and the posterior side of the tibia both articulate with the distal tarsals on the lateral side. A peglike process inserts into a notched on the lateral side of the astragalus. This condition is opposite of what has been reported elsewhere for ornithopods (Chatterjee 1982).

The possible loss of the calcaneum in *P. cyrtocristatus* deserves comment. The enlarged knob at the distal end of the fibula may represent the fusion of the calcaneum to the fibula. The calcaneum may also have failed to ossify and the fibula has enlarged to compensate. Because the sample is based only on the type of *P. cyrtocristatus*, there is a distinct possibility that the calcaneum simply was not fossilized. But this is doubtful because of the lack of space

for the calcaneum to occupy and the absence of any articular feature on the astragalus.

Metatarsals and Distal Tarsals. The metatarsals (Fig. 8.3C, D) of all hadrosaurids resemble one another closely. No consistent variation was observed among the genera; however, the sample size for complete and articulated metatarsals is insufficient at this time for any definitive statement.

Sereno (1999, character 96) lists loss of distal tarsals 3 and 4 as an apomorphy of hadrosaurids + *Ouranosaurus.* "Iguanodontians" have two or three ossified distal tarsals, and hadrosaurids appear to have only the fourth. This bone has been reported in only four instances (Brett-Surman 1975; Godefroit et al. 1998; Horner 1979; Lull and Wright 1942; see also Weishampel and Horner 1990). Because any inference for the loss of distal tarsals in other forms (e.g., *Ouranosaurus nigerensis*) relies heavily on negative evidence, this character should be scored only for particularly well-known taxa and is probably of limited use.

Several changes in pedal form occurred during the evolution of hadrosaurs. These appear to be related to maximum adult body size because they are broadly paralleled in ceratopsians, but some appear even in juvenile hadrosaurs (Dilkes 1993). These include splayed metatarsals II and IV, the presence of axially foreshortened phalanges (up to four times wider than long), dorsoventral compression of the phalanges, and axial shortening of the unguals. Some of these changes may represent scoreable characters, but they are not discussed in detail here because of difficulties in quantification.

The repeated failure to identify a metatarsal I in articulated hadrosaurids, including "mummies" (e.g., Osborn 1912) and the Aurisino Limestones stem hadrosaurid (Dalla Vecchia 2001), is problematic. Continued use of this character in attempting to resolve the relationships of hadrosaurs and close outgroups is inadvisable.

Phalanges. In hadrosaurids, the pedal phalanges (Fig. 8.3) are of similar shape except in *Gilmoreosaurus,* in which the unguals are more clawlike and are therefore similar to the camptosaurid pattern. This is peculiar in light of the fact that *Bactrosaurus johnsoni,* a species sympatric with *Gilmoreosaurus,* has typical hadrosaurid phalanges with more hooflike unguals. The most proximal row of phalanges is longer (proximodistally) than wide (lateromedially). The reverse condition is true for all other phalanges of the pes. The proximal row is noticeably larger and more robust than the more distal rows. The general phalangeal formula is 0-3-4-5-0(?). See Gregory (1948) for a discussion of whether the fifth digit is present. (The formula for the Aurisino Limestone hadrosaur is 0-3-4-4-0 [Dalla Vecchia 2001].) The lack of any material unquestionably articulated and possessing a fifth digit requires that the fifth digit be regarded as absent. The pedal unguals of *Maiasaura* and *Brachylophosaurus* have an axial keel on the plantar face of the bone (Fiorillo 1990; Prieto-Marquez 2000).

Dilkes (1993) noted that *Maiasaura* has similar prominent extensor bumps on the phalanges in that taxon.

Although it appears that the pes is not diagnostic to subfamily level, differences have been noted (Brown 1913a). In a comparison of the types of "*Diclonius mirabilis*" (=*Anatotitan*) and *Hypacrosaurus*, Brown (1913b, fig. 7) observed that the hadrosaurine pes has relatively less robust metatarsals but wider, flatter, and sometimes longer phalanges. Lambeosaurines, in contrast, have relatively more robust metatarsals but less robust phalanges. This results in a hadrosaurine foot that is shorter and wider than the more elongated lambeosaurine foot. Perhaps they represent an adaptation of the hadrosaurines to their more heavily overgrown lowland environments, in contrast to the more open lambeosaurine environments where cursorial abilities would be at a premium.

References Cited

Boyd, C., and C. J. Ott. 2002. Probable lambeosaurine (Ornithischia, Hadrosauridae) specimen from the Late Cretaceous Hell Creek Formation of Montana. *Journal of Vertebrate Paleontology* 13(3, Suppl.): 32A.

Brett-Surman, M. K. 1975. The appendicular anatomy of hadrosaurian dinosaurs. M.S. thesis. University of California, Berkeley.

———. 1979. Phylogeny and paleobiogeography of hadrosaurian dinosaurs. *Nature* 277: 560–562.

———. 1989. Revision of the Hadrosauridae (Reptilia: Ornithischia) and their evolution during the Campanian and Maastrichtian. Ph.D. diss. George Washington University. Available at http://www.nmnh. si.edu/paleo/bib/hadrobib.htm.

Brown, B. 1912. The osteology of the manus in the Family Trachodontidae. *Bulletin of the American Museum of Natural History* 31: 105–108.

———. 1913a. The skeleton of *Saurolophus*, a crested duck-bill dinosaur from the Edmonton Cretaceous. *Bulletin of the American Museum of Natural History* 32: 387–393.

———. 1913b. A new trachodont dinosaur, *Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 32: 395–406.

———. 1914. *Corythosaurus casuarius*, a new crested dinosaur from the Belly River Cretaceous with provisional classification of the family Trachodontidae. *Bulletin of the American Museum of Natural History* 33: 559–565.

———. 1916. *Corythosaurus casuarius*, skeleton, musculature, and epidermis. *Bulletin of the American Museum of Natural History* 35: 709–716.

Brinkmann, W. 1984. Erster nachweis eines hadrosauriers (Ornithischia) aus dem unteren Garumnium (Maastrichtium) des Beckens von Tremp (Provinz Lérida, Spanien). *Palaeontologische Zeitschrift* 58: 295–305.

Carpenter, K. 1999. *Eggs, Nests, and Baby Dinosaurs*. Bloomington: Indiana University Press.

Carrier, D. R., and C. G. Farmer. 2000. The evolution of pelvic aspiration in archosaurs. *Paleobiology* 26: 271–293.

Casanovas-Cladellas, M. L., X. P. Pereda-Suberbiola, J. V. Santafe, and D. B. Weishampel. 1999. First lambeosaurine hadrosaurid from Europe: Paleobiogeographical implications. *Geological Magazine* 136: 205–211.

Chapman, R. E., and M. K. Brett-Surman. 1990. Morphometric observations on hadrosaurid dinosaurs. In K. Carpenter and P. J. Currie (eds.), *Dinosaur Systematics: Approaches and Perspectives*, pp. 163–177. Cambridge: Cambridge University Press.

Chatterjee, S. 1982. Phylogeny and classification of Thecodontian reptiles. *Nature* 295: 317–320.

Dalla Vecchia, F. M. 2001. Terrestrial ecosystems on the Mesozoic peri-Adriatic carbonate platforms: The vertebrate evidence. *Proceedings of the Seventh Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires 1999*: 77–83.

Davies, K. L. 1983. Hadrosaurian dinosaurs of Big Bend National Park. M.S. thesis. University of Texas, Austin.

Dilkes, D. W. 1993. Growth and locomotion in the Hadrosaurian dinosaur *Maiasaura* from the Upper Cretaceous of Montana. Ph.D. diss. University of Toronto.

———. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura* from the Late Cretaceous (Campanian) of Montana. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 90: 87–125.

———. 2001. An ontogenetic perspective on locomotion in the Late Cretaceous dinosaur *Maiasaura* (Ornithischia: Hadrosauridae). *Canadian Journal of Earth Sciences* 38: 1205–1227.

Dodson, P. D. 1971. Sedimentology and taphonomy of the Oldman For-
mation, Dinosaur Provincial Park, Alberta. *Palaeogeography,
Palaeoclimatology, Palaeoecology* 10: 21–74.

Dollo, L. 1883a. Troisieme note sur les dinosauriens de Bernissart. *Bulletin
du Musée Royal d'Histoire Naturelle de Belgique* 2: 85–126.

———. 1883b. Quartieme note sur les dinosaurines de Bernissart. *Bulletin
du Musée Royal d'Histoire Naturelle de Belgique* 2: 223–252.

Egi, N., and D. B. Weishampel. 2002. Morphometric analysis of humeral
shapes in hadrosaurids (Ornithopoda, Dinosauria). *Senckenber-
giana Lethaea* 82: 43–58.

Erickson, B. R. 1988. Notes on the postcranium of *Camptosaurus. Scien-
tific Publications of the Science Museum of Minnesota* 6(4): 3–13.

Fiorillo, A. R. 1990. The first occurrence of Hadrosaur (Dinosauria) remains
from the Marine Claggett Formation, Late Cretaceous of South Cen-
tral Montana. *Journal of Vertebrate Paleontology* 10: 515–517

Gilmore, C. W. 1909. Osteology of the Jurassic reptile *Camptosaurus,*
with a review of the species and genus, and description of two new
species. *Proceedings of the U.S. National Museum* 36: 197–332.

———. 1917. *Brachyceratops,* a ceratopsian dinosaur from the Two Med-
icine Formation of Montana. *U.S. Geological Survey Professional
Paper* 103: 1–45.

———. 1924a. A new species of hadrosaurian dinosaur from the Edmon-
ton Formation (Cretaceous) of Alberta, Canada. Geological Series
43. *Bulletin of the Department of Mines, Geological Survey of
Canada* 38: 13–26.

———. 1924b. On the skull and skeleton of *Hypacrosaurus,* a helmet-
crested dinosaur from the Edmonton Cretaceous of Alberta. Geo-
logical Series 43. *Bulletin of the Department of Mines, Geological
Survey of Canada* 38: 49–64.

———. 1933. On the dinosaurian fauna of the Iren Dabasu formation.
Bulletin of the American Museum of Natural History 67: 23–78.

———. 1946. Notes on recently mounted fossil skeletons in the United
States National Museum. *Proceedings of the U.S. National Mu-
seum* 96: 201–203.

Godefroit, P., Dong Z.-M., P. Bultynck, Li H., and Feng L. 1998. Sino-
Belgian Cooperative Program. Cretaceous dinosaurs and mammals
from Inner Mongolia. 1. New *Bactrosaurus* (Dinosauria: Hadro-
sauroidea) material from Iren Dabasu (Inner Mongolia, P. R.
China). *Bulletin des Institutes Royal des Science Naturalles Bel-
gique* 68(Suppl.): 1–70.

Godefroit, P., Zan S., and Jin L. 2000. *Charonosaurus jiayinensis* n.g.,
n.sp., a lambeosaurine dinosaur from the Late Maastrichtian of
northeastern China. *Compte Rendu de l'Academie du Sciences Na-
turelles, Paris, series 2, Sciences de la Terre et des planètes* 330:
875–882.

Gregory, J. T. 1948. The type of *Claosaurus*(?) *affinis* Wieland. *American
Journal of Science* 246: 29–30.

Head, J. J. 2001. A reanalysis of the phylogenetic position of *Eolambia
caroljonesa* (Dinosauria: Iguanodontia). *Journal of Vertebrate Pale-
ontology* 21: 392–396.

Horner, J. R. 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale
(marine) of south-central Montana with a checklist of Upper Creta-
ceous dinosaur remains from marine sediments in North America.
Journal of Paleontology 53: 566–577.

Horner, J. R., and P. J. Currie. 1994. Embryonic and neonatal morphology of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur Eggs and Babies*, pp. 312–336. Cambridge: Cambridge University Press.

Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, pp. 438–463. Berkeley: University of California Press.

Hu C. 1973. A new hadrosaur from the Cretaceous of Chucheng, Shantung. *Acta Geologica Sinica* 2: 179–206.

Hutchinson, J. R. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131: 123–168.

———. 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131: 169–197.

Lambe, L. M. 1913. The manus in a specimen of *Trachodon* from the Edmonton Formation of Alberta. *Ottawa Naturalist* 27: 21–25.

Lull, R. S., and N. E. Wright. 1942. Hadrosaurian dinosaurs of North America. *Geological Society of America Special Papers* 40: 1–242.

Marsh, O. C. 1892. Restorations of *Claosaurus* and *Ceratosaurus*. *American Journal of Science* 44: 343–349.

Maryańska, T., and H. Osmólska. 1981. First lambeosaurine dinosaur from the Nemegt Formation, Upper Cretaceous, Mongolia. *Acta Palaeontologica Polonica* 26: 243–255.

———. 1984. Postcranial anatomy of *Saurolophus angustirostris* with comments on other hadrosaurs. *Palaeontologica Polonica* 46: 119–141.

Mateer, N. 1981. The reptilian megafauna from the Kirtland Shale (Late Cretaceous) of the San Juan Basin. In S. G. Lucas, J. K. Rigby Jr., and B. S. Kues (eds.), *Advances in San Juan Basin Paleontology*, pp. 49–75. Albuquerque: University of New Mexico Press.

Morris, W. J. 1978. *Hypacrosaurus altispinus?* Brown from the Two Medicine Formation, Montana, a taxonomically indeterminate specimen. *Journal of Paleontology* 52: 200–205.

Norman, D. B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* 178: 1–103.

———. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 56: 281–372.

———. 2002. On Asian ornithopods (Dinosauria: Ornithischia). 4. *Probactosaurus* Rozhdestvensky, 1966. *Zoological Journal of the Linnaean Society* 136: 113–144.

———. 2004. Basal Iguanodontia. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, pp. 413–437. Berkeley: University of California Press.

Norman, D. B., and D. B. Weishampel. 1990. Iguanodontianide and related Ornithopoda. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, pp. 510–533. Berkeley: University of California Press.

Novas, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* 16: 723–741.

Osborn, H. F. 1912. Integument of the iguanodontian dinosaur *Tra-*

chodon. *Memoirs of the American Museum of Natural History* 1: 33–54.

Ostrom, J. H. 1963. *Parasaurolophus cyrtocristatus*, a crested hadrosaurian dinosaur from New Mexico. *Fieldiana Geology* 14: 143–168.

Parks, W. A. 1919. Preliminary description of a new species of trachodont dinosaur of the genus *Kritosaurus*, *Kritosaurus incurvimanus*. *Transactions of the Royal Society of Canada*, ser. 3, 13: 51–59.

———. 1920. The osteology of the trachodont dinosaur *Kritosaurus incurvimanus*. *University of Toronto Studies, Geological Series* 11: 1–74.

———. 1935. New species of trachodont dinosaurs from the Cretaceous formations of Alberta with notes on other species. *University of Toronto Studies, Geological Series* 37: 1–45.

Pinna, G. 1979. Osteologia dello scheletro di *Kritosaurus notabilis* (Lambe, 1914) del Museo Civico di Storia Naturale di Milano. *Memorie della Societa Italiana di Scienze Naturali Museo Civico Milano* 22: 33–56.

Prieto-Marquez, A. 2000. On the postcrania of *Brachylophosaurus goodwini* (Dinosauria: Ornithopoda): Implications for hadrosaur morphology. *Journal of Vertebrate Paleontology* 20(3, Suppl.): 63A.

Rasmussen, M. E. 1998. Notes on the morphology and the orientation of the forelimb of *Ouranosaurus*. *Oryctos* 1: 127–130.

Romer, A. S. 1927. The pelvic musculature of ornithischian dinosaurs. *Acta Zoologica* 8: 225–275.

———. 1956. *Osteology of the Reptiles*. Chicago: University of Chicago Press.

Rowe, T. 1986. Homology and evolution of the deep dorsal thigh muscles in birds and other Reptilia. *Journal of Morphology* 189: 327–346.

Rozhdestvensky, A. K. 1957. Duck-bill dinosaur—*Saurolophus* from the Upper Cretaceous of Mongolia. *Vertebrata PalAsiatica* 1: 129–149.

Sereno, P. C. 1999. The evolution of dinosaurs: Supplementary material. *Science*. Available at http://www.sciencemag.org/feature/data/1041760.shl.

Sternberg, C. M. 1935. Hooded hadrosaurs of the Belly River Series of the Upper Cretaceous. *Bulletin of the National Museum of Canada* 77: 1–37.

Taquet, P. 1976. Geologie et palaeontologie du gisement de Gadoufaoua (Aptian du Niger). *Cashiers de Paléontologie du Centre National Recherche Scientifique, Paris*, pp. 1–191.

Wagner, J. R. 2001. The hadrosaurian dinosaurs (Ornithischia: Hadrosauria) of Big Bend National Park, Brewster County, Texas, with implications for Late Cretaceous paleozoogeography. M.S. thesis. Texas Tech University.

Weishampel, D. B., and J. R. Horner. 1990. Hadrosauridae. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, pp. 534–561. Berkeley: University of California Press.

Weishampel, D. B., D. Grigorescu, and D. B. Norman. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: The most basal hadrosaurid dinosaur. *Palaeontology* 36: 361–385.

Wiman, C. 1929. Die Kriede-Dinosaurier aus Shantung. *Palaeontologia Sinica* n.s.c., 6: 1–67.

Xu Z., Zhao X.-J., Lu J.-C., Huang W.-B., Li Z.-Y., and Dong Z.-M. 2000. A new Iguanodontian from Sangping Formation of Neixiang,

Henan and its stratigraphical implications. *Vertebrata PalAsiatica* 38: 179–191.

Young, C. C. 1958. The dinosaurian remains of Laiyang, Shantung. *Palaeontologica Sinica*, n.s., C, 16: 53–138.

Appendix 8.1. List of abbreviations.

ACF—acromion fossa
ACR—acromion ridge
ACT—acetabulum
AST—astragalus
CAL—calcaneum
CRF—coracoid fossa
CRL—carpals
CRR—coracoid ridge
DE—dentary
DLF—deltoid fossa
DLP—deltopectoral crest
DLR—deltoid ridge
FEM—femur
FIB—fibula
FMH—femoral head
GL—glenoid
GTR—greater trochanter
H—height
HH—humeral head
HL/FL—hindlimb/forelimb ratio
HND—sternal handle
HUM—humerus
ILP—iliac peduncle
ISFH—ischial foot—heel
ISFT—ischial foot—toe
ISP—ischial peduncle
JU—jugal
L—length
LA—lacrimal
LTR—lesser trochanter
MC3—metacarpal III
MC3/H—metacarpal III/humerus ratio
MT3—metatarsal III
MT3/F—metatarsal III/femur ratio
NA—nasal
OBF—obturator fossa
OBP—obturator process
OLN—olecranon notch
OLP—olecranon process
PBH—pubic blade height
PBL—pubic blade length
PD—predentary
PDL—sternal paddle
PF—prefrontal
PM1—premaxilla—1
PM2—premaxilla—2
PO—postorbital
POEP—postorbital eye pocket
POP—postacetabular process
PP—postpubis
PRP—preacetabular process
PUB—pubic blade
PUN—pubic neck
PUP—pubic peduncle
QJ—quadratojugal
QU—quadrate
R/H—radius/humerus ratio
RAD—radius
RPL—reflected premaxillary lips
SCAP—scapula
SCBL—scapular blade
SHF—shaft
SQ—squamosal
STB—sternal body (paddle)
STH—sternal handle
SUIC—suprailiac crest
T/F—tibia/femur ratio
TIB—tibia
TR3—third trochanter
TR4—fourth trochanter
TRS—tarsals
U/H—ulna/humerus ratio
ULN—ulna
UNG—ungual
W—width

Appendix 8.2. System of standardized measurements.

See Figure 8.8 for location of measurements.

Humerus

Length from 'a' to 'b'
Length of deltopectoral process from 'e' to 'f'
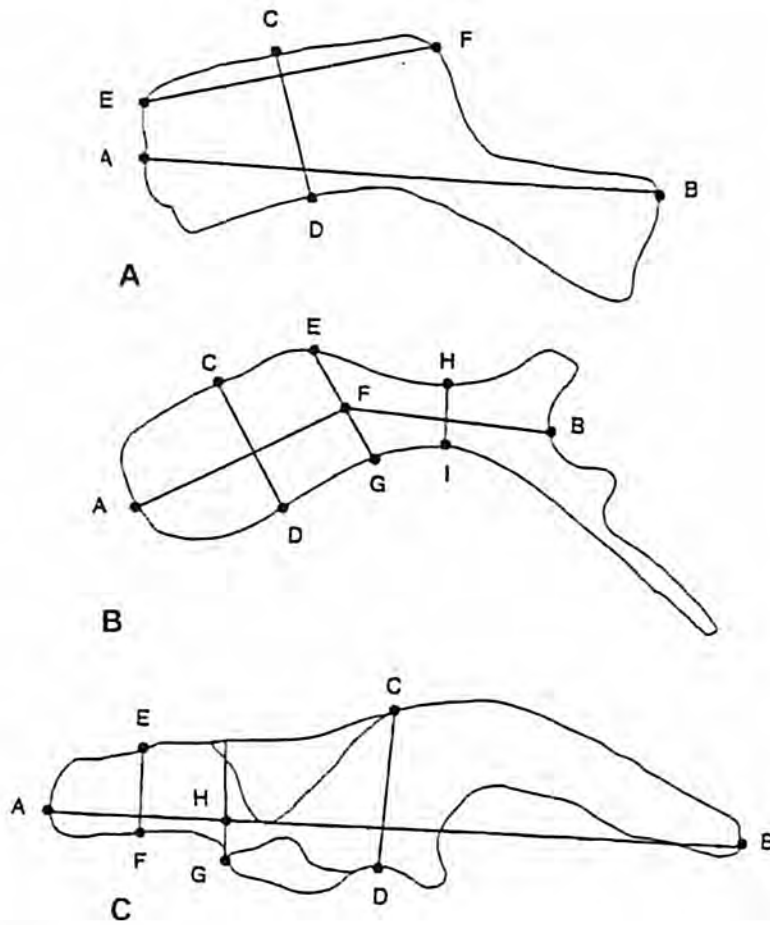Width of deltopectoral process from 'c' to 'd'

Figure 8.8. Location for standardized measurements (see Appendix 8.2). (A) Humerus; (B) pubis; (C) ilium.

Pubis

> Length from 'a' to 'b'
> Length of blade from 'a' to 'f'
> Width of blade from 'c' to 'd'
> Width of neck from 'h' to 'i'

Ilium

> Length from 'a' to 'b'
> Length of postacetabular process from 'a' to 'h'
> Width of postacetabular process from 'e' to 'f'
> Width of iliac body from 'c' to 'd'

The placement of points for measurements are as follows: On the humerus, line 'ab' indicates the maximum distances where 'a' falls on the midpoint of the head and 'b' is on the asymptote of the distal trochlea. Line 'ef' defines the deltopectoral crest, and each point falls on the asymptote. Line 'cd' is perpendicular to 'ef.' Other measurements proved to be taxonomically useless.

On the pubis: Line 'ab' is the length where line 'af' bisects the blade into dorsal and ventral segments. Point 'b' is on the asymptote of the ace-

tabulum. Line 'cd' is perpendicular to 'af' and bisects it. Line 'eg' is perpendicular to 'af' where point 'e' is on the asymptote. Line 'ih' is the minimum width of the neck. Line 'af' is the blade length, and line 'cd' is the height.

On the ilium: Line 'ab' is the maximum length between perpendiculars. Line 'cd' is perpendicular to 'ab' where 'd' is on the asymptote of the acetabulum. Point 'c' may or may not fall on the anterior border of the antitrochanter. Point 'g' lies on the posterior border of the ischial peduncle. Line 'hg' is drawn perpendicular to line 'ab' at this point. Line 'ah' now defines the postacetabular process length. Line 'ef' bisects this line and is perpendicular to it, thus defining the height. Line 'cb' usually bisects the preacetabular process, thus forming angle ∠DCB, which is a good measure of the preacetabular process deflection. These are the most diagnostic elements.

Measurements for other elements are simply the maximum length between perpendiculars and the minimum diameter of the shaft at its midpoint except in the case of the femur where it is taken halfway between the fourth trochanter and the extreme distal end of the femur. The length of the scapula is taken along the dorsal border from the coracoid ridge to the asymptote of the dorsal border at the end of the scapular blade (Fig. 8.1A). A line halfway along this line perpendicular to the trend of the scapular blade defines the height. This is not possible in camptosaurids because of the exaggerated development of the acromial ridge. The length is therefore measured between perpendiculars (Fig. 8.1B). The height is now the diameter of the blade midway between these two points.

Cautionary Note. We have found during these studies that many of the measurements in Lull and Wright (1942) are taken directly from previous publications. Many measurements that were made from photographs varied from actual measurements that one of us (M. B.-S.) made from the same bone. They seem to vary in direct proportion to the increasing size of the bone. The reader is cautioned against relying totally on photographs.