THE
Complete
DINOSAUR

Edited by James O. Farlow and M. K. Brett-Surman

Ornithopods

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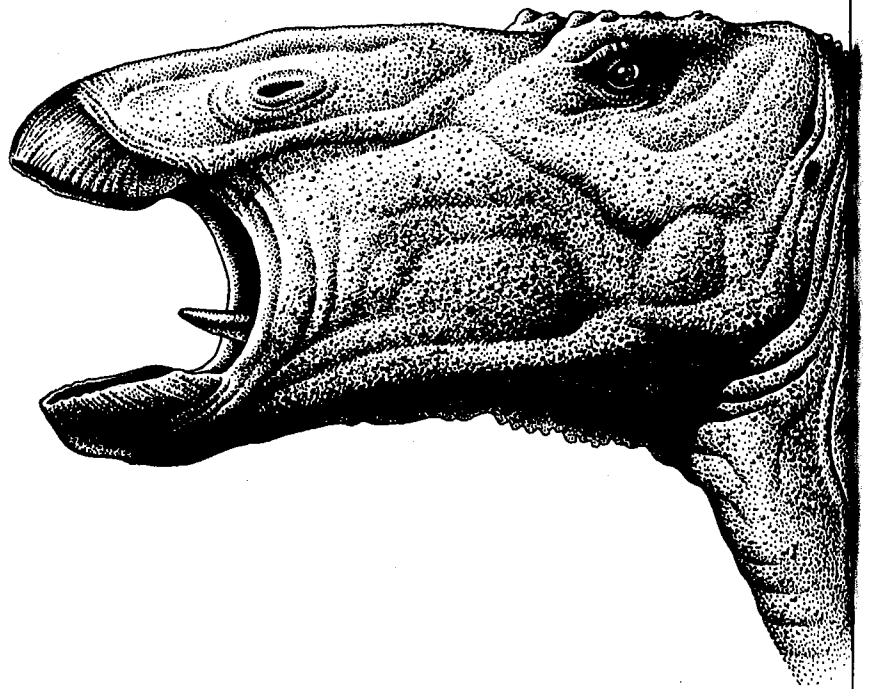
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The Ornithopoda ("bird-feet"), commonly called the ornithopods, were small (less than 1 meter tall and 2 meters long) to large (about 7 meters tall and 20 meters long) bipedal herbivorous dinosaurs that existed from the earliest Jurassic to the end of the Cretaceous. The groups that make up the ornithopods are, more or less in the sequence of their appearance in the fossil record, from the Jurassic: the heterodontosaurids, hypsilophodontids, dryosaurids, camptosaurids, tenontosaurs, iguanodontids, and hadrosaurs. They lived on every continent, including Antarctica. In a world dominated by theropods, the ornithopods had neither armor like the Thyreophora, nor horns like the Ceratopsia. They were the first herbivorous dinosaurs to have multiple tooth rows, cheek pouches, and true mastication ("chewing"). At the time that they were alive, they were the most derived herbivores on Earth. They occupied the niches occupied today by such medium-sized herbivores as antelopes, tapirs, moose, and horses. They were the first herbivorous dinosaurs to engage in "selective feeding" because they had very narrow muzzles that could selectively crop specific parts of plants. They were the first bipedal herbivores to occupy nearly every size range. From the Jurassic to the end of the Cretaceous, they continued to diversify and were the most successful of the herbivorous dinosaurs, both in the numbers of individuals per fauna and in the total number of ornithischian species.

History of Knowledge of the Group

O. C. Marsh of Yale University first named the Ornithopoda in 1881. A revised diagnosis published one year later (Marsh 1882) is paraphrased as follows: ornithopods walked on their toes (not flat-footed), and have five functional fingers on the hand and three on the foot; the pre-pubic bone projects forward and away from the midline of the body (in contrast to the theropods, where the pubes meet and fuse in the midline), and a post-pubic bone is present; the vertebrae are not hollowed out (as in saurischians); the front limbs are small and all the limb bones are hollow; the premaxillary bone (the upper lip bone) has no teeth. In Marsh's scheme, the group included the "camptonotids" (later renamed the camptosaurids), the iguanodonts, and the hadrosaurs.

Because the ornithopods showed none of the elaborate horns, frills, spikes, or body armor found in other ornithischians, they were once considered to be the basic, or stem, group from which other ornithischian lineages arose. Originally, when *Iguanodon* was only the second dinosaur known (1825), it was assumed that this animal was a quadruped. It was Joseph Leidy of Philadelphia who first suggested in the 1860s that *"Trachodon"* (1856), *Hadrosaurus* (1858), and *Iguanodon* might be bipedal (see Torrens, chap. 14 of this volume). This seemed to be confirmed in 1878 when multiple complete skeletons of *Iguanodon* were unearthed in Bernissart, Belgium.

As the years progressed, it became clear that the features used to define ornithopods were also present in other ornithischians. Consequently the ornithopods gradually came to be regarded as "essentially bipedal ornithischians" (Steel 1969). All bipedal ornithischians were therefore assigned to the ornithopods, including pachycephalosaurs, *Stenopelix*, psittacosaurids, and the "fabrosaurs." It was not until the 1970s, and later in Sereno's (1986) cladistic classification, that a reclassification of all the ornithischians resulted in a redefinition of the ornithopods. It became apparent that bipedalism was simply an ancestral character shared with many other dinosaurs. The pachycephalosaurs were pulled out and placed into their own group, united with the Ceratopsia (including the Psittacosauridae) as the Marginocephalia (Maryańska and Osmólska 1974, 1985; Cooper 1985; Sereno 1986; Dodson 1990).

Classification

Today the ornithopods may be partially diagnosed as follows: premaxillary teeth (if present) are on a level lower than the maxillary teeth; the jaw joint is lower than the tooth rows so that the jaws come together like nutcrackers instead of like scissors; the premaxillary bone has a process that extends backward (caudally) toward the orbit (eye); and there is a very large fourth trochanter on the femur for the attachment of the caudifemoralis muscle group. For a more complete classification, with a discussion of the many characters used to define the member clades, see Fastovsky and Weishampel 1996.

Within the Ornithopoda are the Euornithopoda (literally "true ornithopods"), which are distinguished by loss of the fenestrae (windows or holes) in the lower jaw (present in heterodontosaurids; Fig. 24.1); by elongation of the prepubic bone, which extends farther forward than in non-euornithopods; and by the presence of an obturator process on the
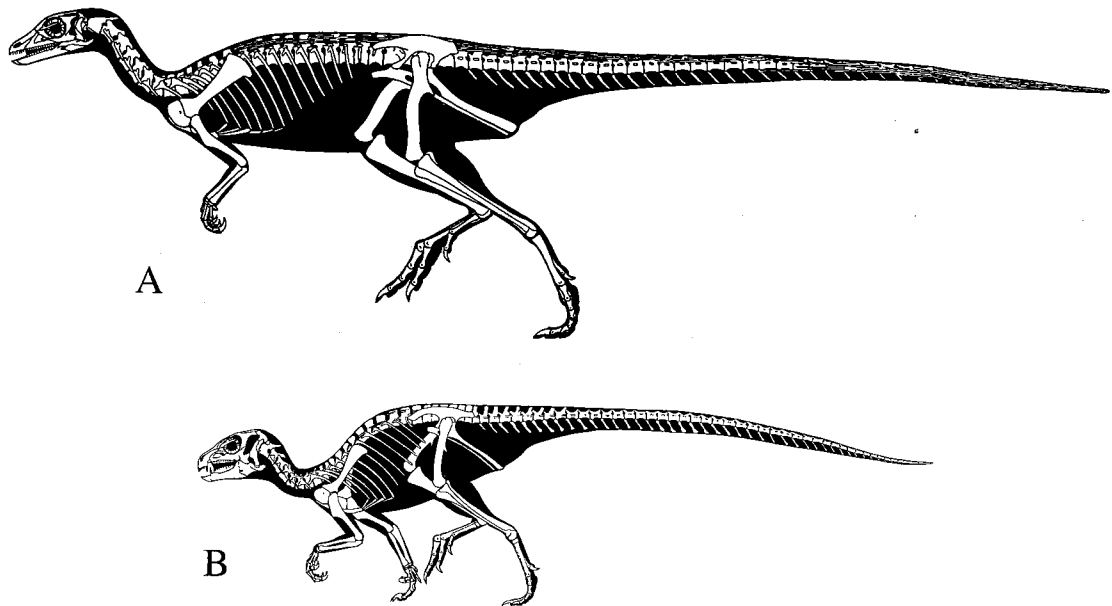
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Figure 24.1. (A) *Lesothosaurus,* a fabrosaurid (?), and (B) *Hetero-dontosaurus.* Length of each animal about 1 m. This and other drawings in this chapter by Gregory S. Paul, who retains the copyright.

ischium. Within the euornithopods are the Hypsilophodontidae and the Iguanodontia. This latter group includes the iguanodontids and hadrosaurs, and is defined by loss of the premaxillary teeth; having a small antorbital fenestra in front of the eye (Fig. 24.2, 24.3A, B), or none at all; an enlarged nasal opening; and a predentary bone with two processes that project backward. All euornithopods have a pleurokinetic skull (discussed below; Norman and Weishampel 1990).

Figure 24.2. *Hypsilophodon* skull. Abbreviations as follows:
AF = antorbital fenestra (fenestra = "window"); AN = angular; CP = coronoid process; D = dentary; EN = external nares; FR = frontal; J = jugal; L = lacrimal; MX = maxilla; N = nasal; P = pal-pebral bone; PD = pre-dentary; PF = prefrontal; PM = premaxilla; PO = post-orbital; Q = quadrate; QJ = quadratojugal; SA = sur-angular; SQ = squamosal; SR = sclerotic rings; TF = temporal fenestra.
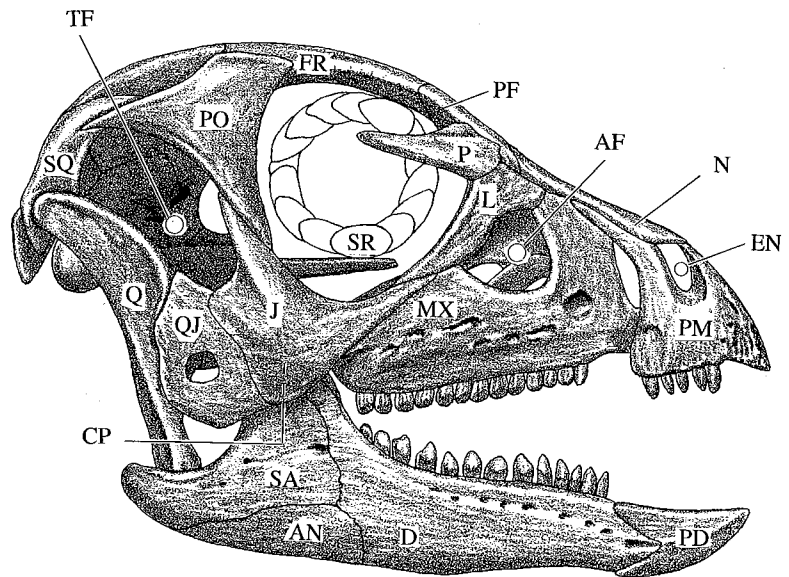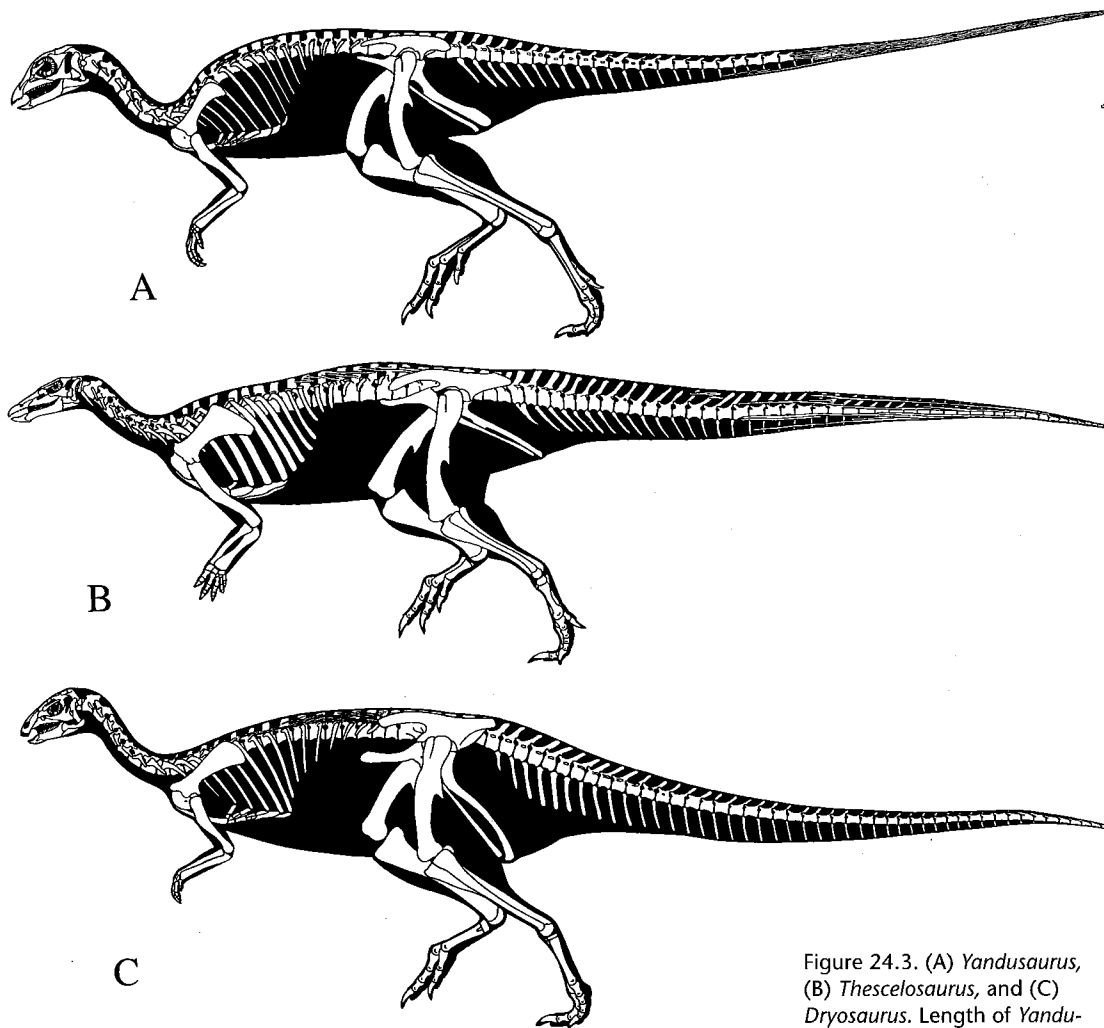
Figure 24.3. (A) *Yandusaurus,* (B) *Thescelosaurus,* and (C) *Dryosaurus.* Length of *Yandusaurus* and *Thescelosaurus* about 1.5 m, and of *Dryosaurus* about 2 m.

The heterodontosaurids (Fig. 24.1B) have several unique features, such as canine-like teeth and relatively long arms with large hands. This was the earliest ornithopod group in which all the cheek teeth are close enough together to form a solid dental battery and the teeth are designed for cutting, instead of "grabbing," vegetation. With a body length of about 1 meter, heterodontosaurs were about half the size of an adult human.

The hypsilophodontids (Figs. 24.2, 24.3A, B) are about 2 meters long and include such famous genera as *Thescelosaurus* and *Hypsilophodon.* This clade was the first ornithopod group to occur worldwide. They retained their premaxillary teeth and had chisel-shaped cheek teeth, and they were lightly built but had relatively heavy hind legs, probably for stability while running. Although about a dozen genera are known, there are only a few complete skeletons known for one genus. New finds in the United States, especially of a new hypsilophodontid from Texas (Winkler et al. 1997), will add new information, especially about growth processes in these dinosaurs. It may turn out that only a subset of this family is monophyletic.

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One of the early clades of the Jurassic Iguanodontia, the dryosaurs (Figs. 24.3C, 24.4A), comprises small (just over 2 meters long), lightly built bipedal herbivores—probably the first ornithopod group to exceed 100 kilograms in live body mass. The dryosaurs were the last ornithopod group to have relatively short arms, and this may have prevented them from being functionally quadrupedal. They are the first ornithopods to have a distal expansion on the end of the ischium.

Camptosaurs were the first heavily built ornithopods that were more than 3 meters long, and had relatively longer arms than the dryosaurs. *Camptosaurus* (Figs. 24.4A, 24.5A) is the first ornithopod to have a noticeably elongated muzzle, presumably to increase the amount of food taken and processed per bite. Camptosaurs were also the first group with two functional rows of teeth in each jaw, arranged one above the other in an alternating pattern to form a single chewing unit. Camptosaurs have a very wide pelvis and thick hind limbs. Their front limbs were much shorter than their hind limbs, but could nonetheless reach the ground, permitting four-footed walking. The first metacarpal was reduced to a spur on the

Figure 24.4. Flesh restorations of (A) *Camptosaurus* (left) and *Dryosaurus* (right) and (B) *Muttaburrasaurus*.
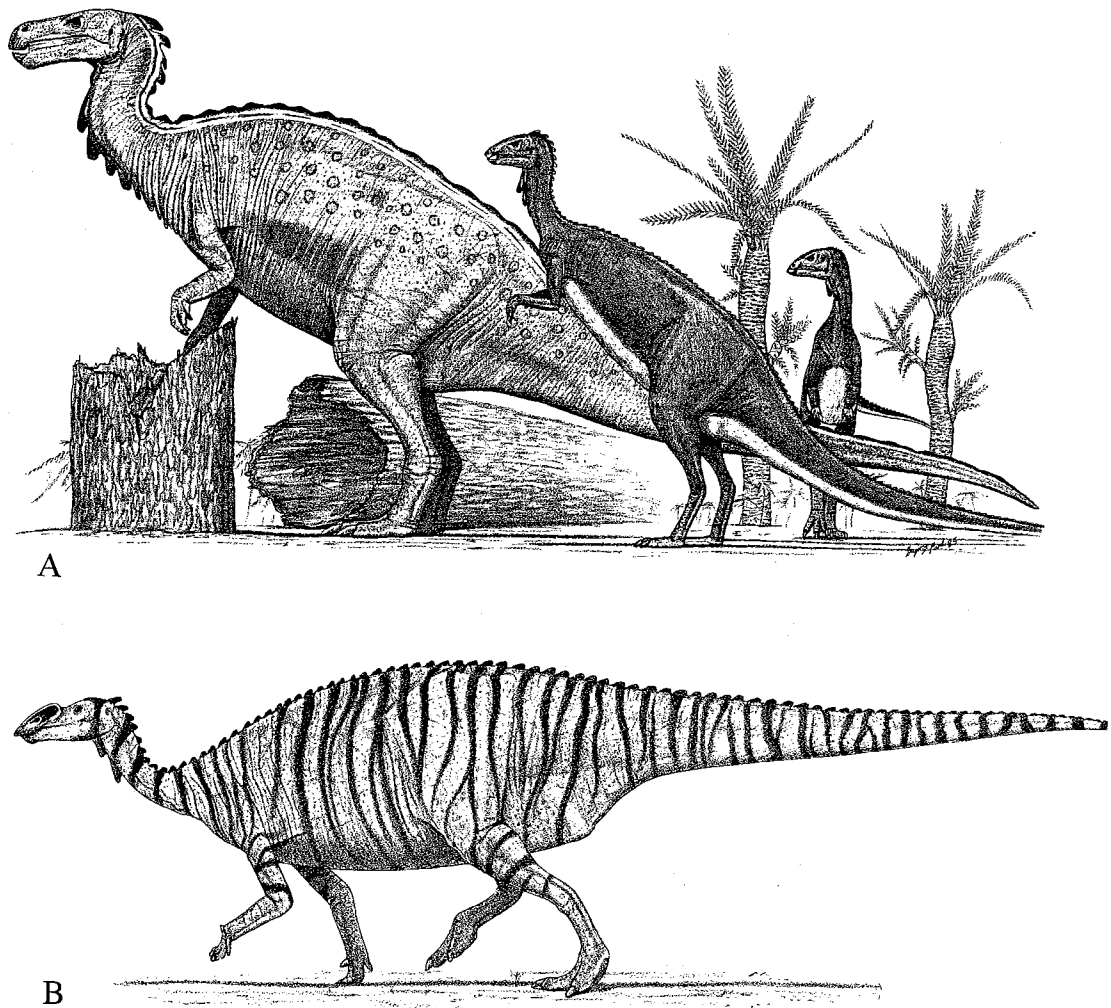
A

B

Figure 24.5. (A) *Camptosaurus* and (B) *Tenontosaurus.* Length of *Camptosaurus* about 2.5 m, and of *Tenontosaurus* about 4.5 m.

hand, and there was considerable fusion of carpals in the wrist. One rare genus, *Muttaburrasaurus* (Fig. 24.4B) from Australia, is as large as the later iguanodontids, but has not yet been described in detail.

Tenontosaurus (Fig. 24.5B) is an enigmatic genus that has been classified both as a hypsilophodontid and as an iguanodontid (Weishampel and Heinrich 1992). It is about 7 meters long and has a very high skull, an edentulous (toothless) beak, and four digits on the hind foot. One would expect it to be intermediate between the Jurassic camptosaurs and the later Cretaceous hadrosaurs, but it has features that do not place it firmly in either group, such as a relatively more robust pelvis than in other ornithopods. *Tenontosaurus* is famous for being the prey of *Deinonychus* (Maxwell and Ostrom 1995). New finds made in the early 1990s in Montana, Wyoming, Oklahoma, and Texas (Winkler et al. 1997) will finally clarify its phylogenetic position.

The most derived group within the Iguanodontia is the Iguanodontoidea, which includes two groups: the iguanodonts, such as *Iguanodon* and the sail-backed *Ouranosaurus* (Figs. 24.6, 24.7A), and the hadrosaurians, such as *Anatotitan* and *Parasaurolophus* (Figs. 24.7B, 24.8). Hadrosaurs can be characterized as having a wider and more elongated snout than other ornithopods, interlocking teeth in multiple rows or dental batteries, the relatively longest forelimbs of all the ornithopods, and hoof-like unguals on the pes. Some genera are noted for expanded nasal crests. Hadrosaurs were the largest of the ornithopods, some forms (*Shantungosaurus,* Fig. 24.8A) approaching sauropods in size. They were mostly Laurasian (that is, occupying the northern continents) in distribution, and have the best fossil record of all the ornithischians.

In previous classifications of the group, the family Hadrosauridae is subdivided into the subfamilies Hadrosaurinae (solid-crested and non-crested genera) and Lambeosaurinae (hollow-crested forms), plus some
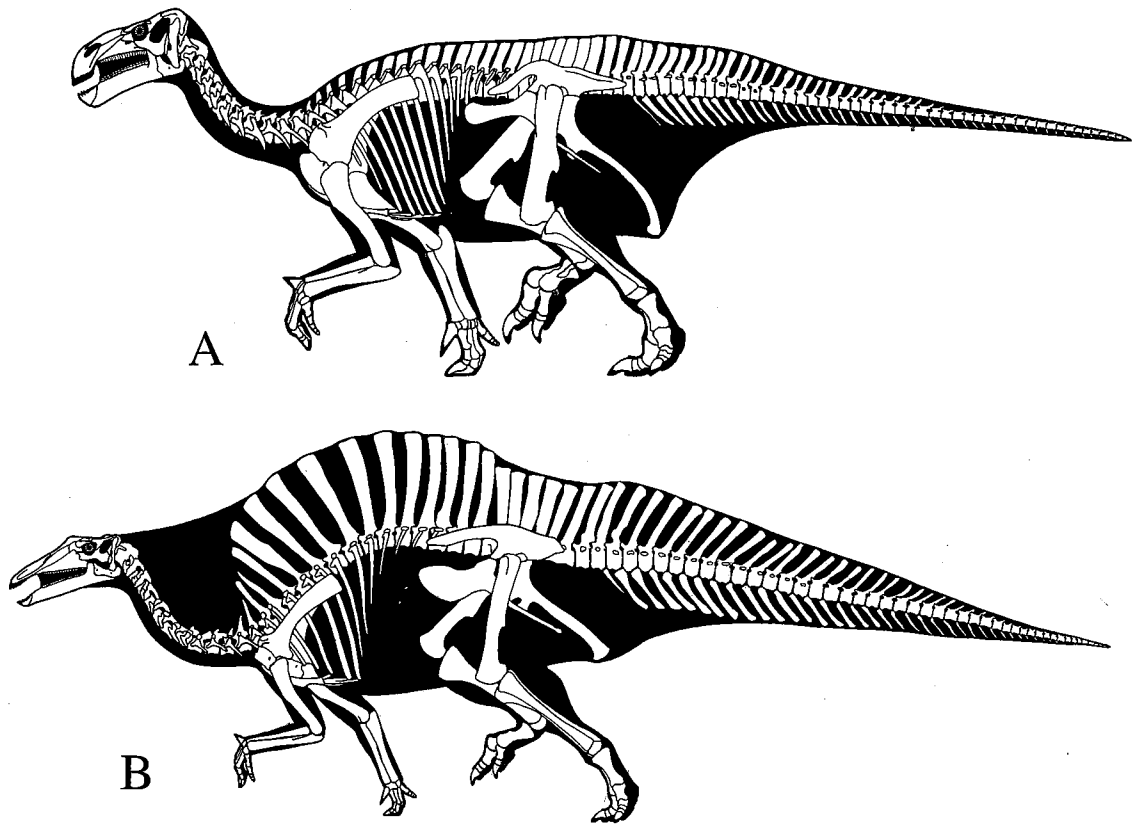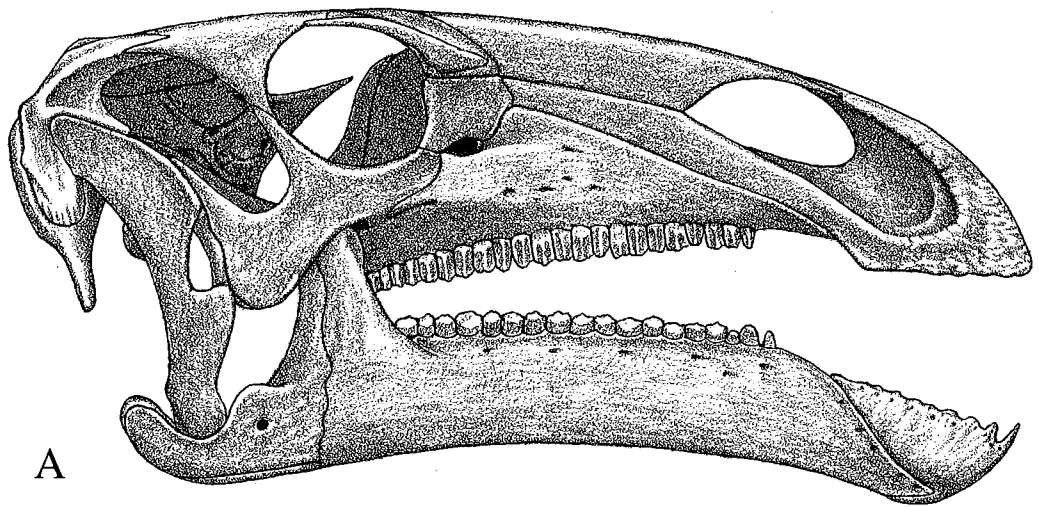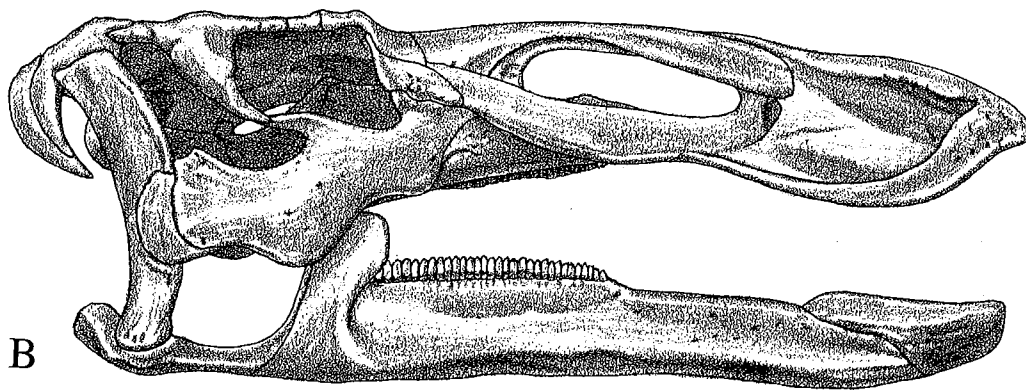
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Figure 24.6. (A) *Iguanodon* and
(B) *Ouranosaurus*. Length of
Iguanodon about 9 m, and of
Ouranosaurus about 6 m.

early forms that do not fit easily into the aforementioned two subfamilies. In recent classifications (Weishampel et al. 1993; Fastovsky and Weishampel 1996), the clades Hadrosaurinae and Lambeosaurinae were placed into the Euhdarosauria, and the earlier forms incorporated into the redefined Hadrosauridae. The clade Hadrosauridae is now used to include the Euhadrosauridae plus *Telmatosaurus, Secernosaurus,* their common ancestor, and all of its descendants. Although there is still no universally accepted classification of the ornithopods as a whole, one classification scheme is as follows (see Fig. 24.9):

Ornithopoda
    Heterodontosauridae
    Euornithopoda
        Hypsilophodontidae
        Iguanodontia
            Dryomorpha
            Tenontosaurus
                Dryosauridae
                Ankylopollexia
                    Camptosauridae
                    Iguanodontoidea
                        Iguanodontidae
                        Hadrosauridae

Figure 24.7. Skulls of (A) *Igua-nodon* and (B) *Anatotitan*.

The "Fabrosaur" Problem

"Fabrosaurs" are a Late Triassic and Early Jurassic group of small (less than 2 meters long) bipedal ornithischians that were long placed within the ornithopods (Gow 1981). They were removed from the ornithopods after this group was reclassified in 1986 because they lacked two key features that define ornithopods: an obturator process on the ischium and a tooth row fully recessed from the outer margin of the jaws. This means that fabrosaurids may not have had cheeks. On the other hand, Thulborn (1992) proposed that *Lesothosaurus*, the best-known form to date (Fig. 24.1A), is a fabrosaur, and that this group therefore does have both a recessed tooth row and an obturator process, thereby making these dinosaurs ornithopods. Because there are no complete and associated skulls with skeletons at this time, I have taken the conservative approach and treated the fabrosaurs as outside the ornithopods. A new restoration of *Lesothosaurus* (Fig. 24.1) is presented here to contrast it with the ornithopods.

It is important to note, however, that both the fabrosaurids and the more derived heterodontosaurids and hypsilophodontids establish an early
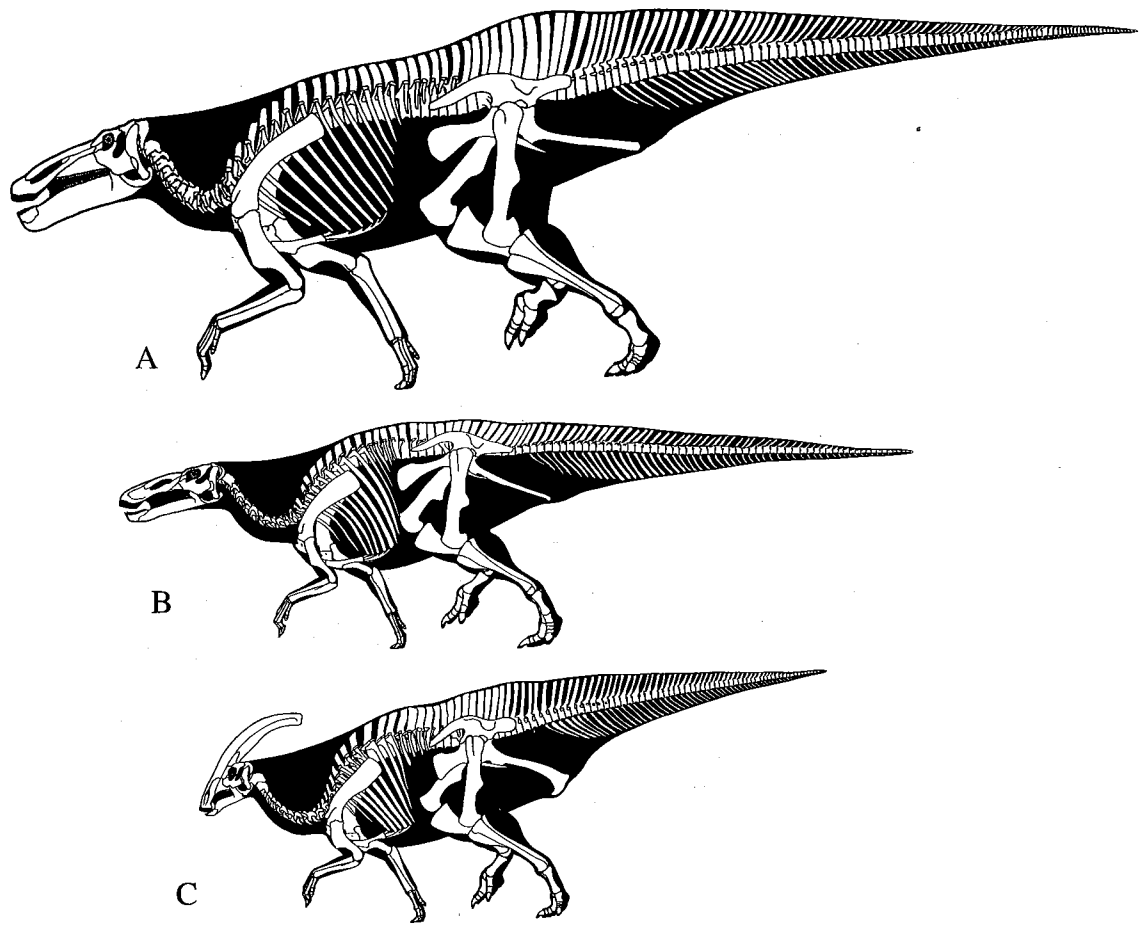
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Figure 24.8. (A) *Shantungo-saurus*, (B) *Anatotitan*, and (C) *Parasaurolophus*. Length of *Shantungosaurus* about 17 m, of *Anatotitan* about 12 m, and of *Parasaurolophus* about 9 m.

trend for Jurassic ornithopods—small, lightly built, fast herbivores with narrow snouts for selective feeding on the undergrowth.

Geographic Distribution

Ornithopods occurred in both Gondwana and Laurasia during the Triassic and Jurassic. Only in the Cretaceous do we see evidence of possible provinciality or endemism, with certain groups restricted to particular areas—except for the hypsilophodontids, which continued to occur on every major continent. *Tenontosaurus* seems to have been a Laurasian genus, but this may be an artifact of its limited fossil record; it is known only from certain lower Cretaceous deposits in the United States. Dryosaurs are known from Africa and both South and North America. Iguanodonts are known from both Gondwana and Laurasia, and so are the hadrosaurs, although most forms in the latter group are restricted to Laurasia. During the Late Cretaceous, the continents were breaking apart, making migration routes for land animals increasingly harder to traverse, and this may be responsible for the suggestions of provinciality seen in the distribution of
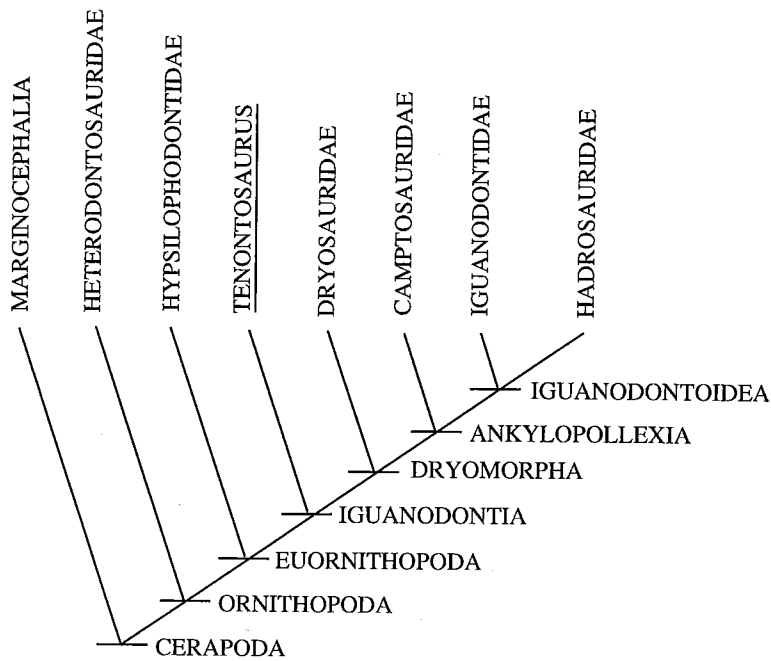
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Figure 24.9. Tentative cladogram of the ornithopods. Ornithopod classification changes frequently with new discoveries and better character analysis, and so our understanding of their phylogenetic relationships is in a state of flux. This cladogram draws upon information from several workers on the group. For an alternative classification, see Sereno 1997.

Late Mesozoic ornithopods. On the other hand, the number of presently known fossiliferous sites representing the latest Cretaceous in Gondwana is quite poor; the terrestrial fossil record is heavily biased in favor of Asiamerican (eastern Asia plus western North America) sites. Thus the Late Cretaceous provinciality of ornithopods may be more apparent than real, and ornithopod families may have remained worldwide in their distribution.

## Origins and Evolutionary Trends

The evolutionary origins of ornithopods remain obscure. There are fewer than ten species total of ornithischians known from the Triassic. By the Jurassic, only *Heterodontosaurus* (Fig. 24.1B) and *Lesothosaurus* (Fig. 24.1A) are reasonably well known.

When one traces the history of the ornithopods from the Jurassic through the Cretaceous, and from hypsilophodonts through hadrosaurs, several consistent trends appear. The snout becomes progressively longer and broader, and toothless at its front end. This allowed the animal to gather in more food per mouthful and to reach deeper into the vegetation.

There is an increase in the number of cheek teeth for more efficient grinding and slicing. Early ornithopods have just one row of teeth in each jaw, whereas hadrosaurs have three interlocking rows in their jaws, forming a grinding pavement or battery.

A most remarkable elaboration can be seen in the nasal apparatus of some of the iguanodonts and most of the hadrosaurs. In these animals the premaxillary and nasal bones extended backward over the nasal opening and sometimes over the entire length of the skull. This may reflect modifications of the nasal region for vocalization (see below).

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Figure 24.10. The hand (manus) of several ornithopods. (A) The primitive ornithopod *Heterodontosaurus*, showing the details of metacarpal I and the natural medial articulation of the first digit, which might have allowed some grasping ability.
(B) *Camptosaurus*, also showing details of metacarpal I, with slightly less medial orientation of the first digit. (C) *Iguanodon*.
(D) *Anatotitan*. Note the trend over time (that is, from *Heterodontosaurus* through progressively more derived forms) for a shift from a grasping ability of digit I to a stronger support function for the entire hand. There is also a loss of elements in digit I, loss of carpals, and an elongation of the median metacarpals. Not to scale.
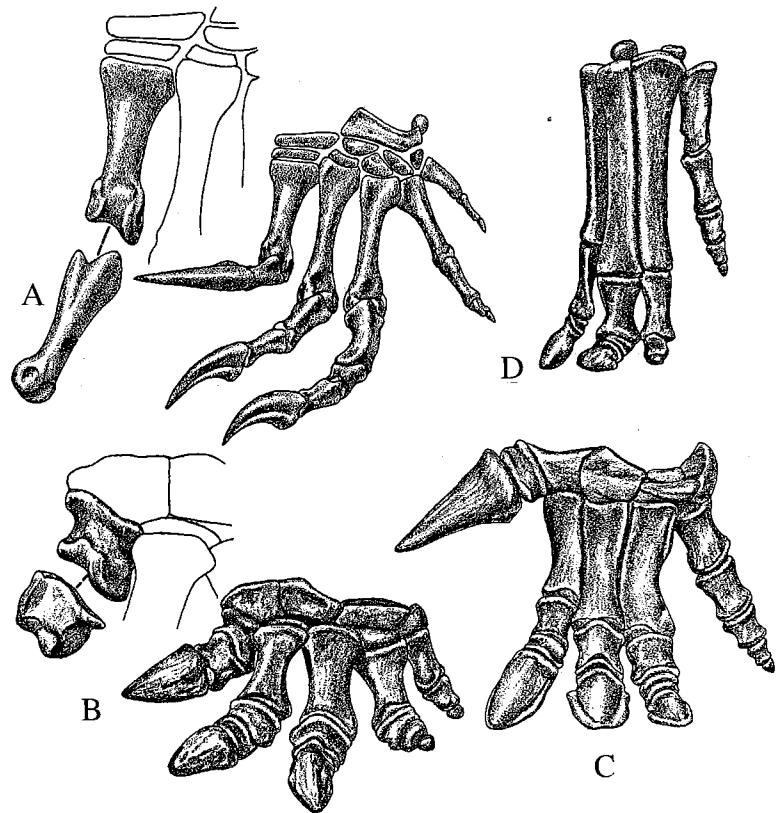
Ornithopods nicely illustrate two of the "laws" of evolution recognized by paleontologists. Cope's Rule states that over geologic time, in a lineage, size will increase. This is obviously true for ornithopods: The Early Jurassic *Heterodontosaurus* is about 1 meter long, while the Late Cretaceous *Shantungosaurus* is into the sauropod size range (more than 20 meters long). Marsh's "Law" states that over geological time, the encephalization quotient (EQ) of a lineage will increase. EQ is defined as the ratio of the actual brain mass to the expected brain mass for a reptile of a certain size, based on samples of modern animals. The brain size is estimated by measuring the volume of the brain cavity. Early ornithopods have EQs well within the range of other ornithischians, but the later ornithopods have the highest EQs of all the ornithischians (Hopson 1977).

The forelimbs became progressively longer with the appearance of each successive ornithopod group. Eventually this allowed the later ornithopods to become what can be called "facultative quadrupeds" or "non-obligatory bipeds." This means that when the arms became long enough relative to the hind limbs, these ornithopods could walk, or in some cases trot, as quadrupeds. At higher speeds, however, these ornithopods probably reverted to bipedalism. Accompanying forelimb elongation, the hands of later ornithopods became more robust, and the claw-like fingers became more hoof-like (Fig. 24.10). Beginning with the iguanodonts, the first and fifth digits of the hands were reduced, and the middle three fingers became elongated to bear the weight of the front limb when touching the ground.

In order to support the weight of the body with increasing size, the number of sacral vertebrae (which connect the pelvis to the backbone) increased. In hadrosaurs, the number of sacral vertebrae can be as many as ten. The pelvic girdle also became somewhat broader, presumably to provide more space for the digestive system, to allow a wider stance for stability, and to provide firmer support for the increased mass of the animal.

Functional Morphology

The ornithopod chewing apparatus was in some ways functionally superior to that of many present-day herbivorous animals. Early ornithopods had slender jaws with small teeth in a single row that could cut vegetation but did not grind or mash the plant fodder. During ornithopod evolution, the cheek teeth became larger, with thicker enamel for increased strength. The edges of the tooth along the crown had denticles to assist in cutting, and ridges were present on the enameled face of the tooth. By the Late Jurassic, when the camptosaurs appeared, there were two staggered rows of teeth positioned one atop the other in both the upper and lower jaw, the two vertical rows of teeth forming a single chewing unit. By the latest Cretaceous, hadrosaurs had three vertical tooth rows with perfectly interlocking diamond-shaped teeth in a massive tooth battery. These teeth were ever-replacing, which means that they emerged from the jaw as though riding on a conveyor belt, to be gradually worn away at the top of the dental battery. The jaws are deep because they were producing hundreds of teeth at any one time. The teeth are enameled on one side only, with softer dentine exposed on the other side, the side that formed the actual chewing surface. As the upper and lower tooth batteries ground against each other, the dentine wore away faster than the enamel, so that the teeth were self-sharpening.

The jaws of derived ornithopods were kinetic, which means that they had the ability to rotate with respect to one another (Norman 1984; Norman and Weishampel 1985; Weishampel and Norman 1989; and Weishampel and Horner 1990). The lower jaw could slide forward and backward slightly on its articulation with the upper jaw. At the same time, the upper jaws were hinged against the skull, enabling them to swing outward independently (like paired trap doors opening in opposite directions), a condition known as pleurokinesis. All of this allowed for more effective grinding of plant food, and gave the jaws some ability to serve as shock absorbers of chewing forces (see Weishampel 1984).

As in other advanced ornithischians, the tooth row of ornithopods was medially recessed from the jawbones, indicating that in life there were fleshy cheeks. The occlusal plane (the surface along which upper and lower teeth met) slanted downward and outward, so that the plant bolus dropped into the cheek pouch during chewing.

The front part of the mouth of later ornithopods had no teeth, and the front end of the cheek teeth was well behind the beak. This gap behind the beak and in front of the teeth, the diastema, allowed the tongue to slide around into the cheeks and manipulate the food bolus back toward the dental battery. The elongation of the jaws in succeeding clades can be partly explained by the addition of the increased number of tooth rows (more than sixty in hadrosaurs).

The beak became wider and was covered by a horny covering. Constant abrading and cutting of resistant plant material acted to sharpen the cutting edge of the beak, enhancing its value as a cropping device.

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If iguanodontian ornithopod jaws are compared to those of the other prominent group of Late Cretaceous Asiamerican large herbivores, the ceratopsians, two things are noteworthy: ornithopod jaws are relatively weaker than ceratopsian jaws, and ornithopod jaws are specialized for grinding, as opposed to the slicing action of ceratopsian jaws. Such differences in the way they processed their fodder may be indicative of ways in which ornithopods and ceratopsians avoided direct competition for food. Ornithopods may have preferentially fed on softer vegetation, while ceratopsians may have concentrated on tougher-fiber plants. The interaction of plants and herbivorous dinosaurs undoubtedly affected the evolutionary pathways of both groups (Wing and Tiffney 1987; Tiffney, chap. 25 of this volume).

The snouts and nasal crests of hadrosaurs have long been interpreted in terms of improvement of their owners' vocal abilities (Abel 1924; Weishampel 1981). There are two basic kinds of nasal crests in hadrosaurs—solid and hollow. Solid-crested (saurolophines) and non-crested (edmontosaurines and kritosaurines) hadrosaurs had enlarged external nasal chambers. This enlargement was the result either of simple expansion, as in *Kritosaurus,* or of the formation of expanded and folded pockets of bone at the front of the nose, as in *Edmontosaurus.* Soft tissues in the nasal chambers probably could resonate in a manner analogous to reed instruments such as oboes. Hollow-crested hadrosaurs (lambeosaurines), such as *Corythosaurus* and *Parasaurolophus* (Fig. 24.8), had nasal chambers that functioned like French horns or trombones.

Such elaborate crests probably served many simultaneous functions, such as species recognition, species-specific "hooting" to maintain contact with fellow hadrosaurs when direct visual contact was not possible, possible sexual identification, and age indication. The crests may also have increased the surface area for olfactory tissues, improving the sense of smell.

The vast variety of hadrosaur cranial crests prompted pioneering paleontologists to put these dinosaurs into a plethora of named species, but Dodson (1975), in one of the first major morphometric studies of dinosaurs using multivariate statistical analyses, showed that many of the differences in shape of the crests were due to growth and sexual variation, and were therefore of limited taxonomic use.

Large ornithopods have sometimes been pictured as semi-aquatic animals. Even the name "duckbill" suggests a duck-like proficiency in water. Without armor, or faster-than-theropod speeds, ornithopods are often pictured as running into the water to get away from theropods. Unfortunately, ornithopods were probably poorer swimmers than theropods.

There are three basic means of propulsion in water for a terrestrial vertebrate: paddling with the forearms, sculling with the tail like a crocodile, and using the hind legs as the main propulsive organ. The first two methods would have been very inefficient for the larger dinosaurs because of the speed of resistance from the water. The arms and hands of ornithopods are small compared to the cross-section of the body, so an ornithopod could not generate much forward propulsion. Picture a cross-section of the body of the hadrosaur *Anatotitan* (Fig. 24.8) compared to a cross-section of its hand. For this dinosaur, attempting to paddle with its hands would have been like trying to row a wide canoe with a spoon for a paddle.

The hands of some ornithopods, especially hadrosaurs, are sometimes pictured as webbed, hence an aquatic adaptation. Mummified hands of hadrosaurs, however, show that they were not webbed but padded, a terrestrial adaptation.

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Efficient tail sculling is also ruled out for ornithopods because their backbones and the proximal third of their tail had ossified tendons that severely restricted side-to-side movement (but see Coombs 1975 for an alternative hypothesis). These ossified tendons form a tight bundle surrounding the tail in some primitive ornithopods, and a rhomboid latticework of overlapping tendons in advanced ornithopods. There can be as many as nine tendons in two overlapping series per neural spine (in hadrosaurs), but fewer tendons per bundle in less advanced ornithopods. These ossified tendons are well developed on the dorsal part of the tail (epaxial series), but are less well developed on the ventral side of the tail (hypaxial series). Bony processes that project laterally from the tail vertebrae (caudal transverse processes), and that act as the attachment points for muscles that moved the tail from side to side, are small in hadrosaurs, and disappear entirely about vertebra number 16 as one moves backward along the tail. In large theropods, in contrast, these transverse processes, and the tail as a whole, lack ossified tendons, are larger, and extend for more than two-thirds of the length of the tail. Theropod tails were probably much better propulsive devices than were hadrosaur tails.

This leaves leg propulsion as the most likely method for ornithopod swimming, but once again, ornithopods had less powerful (forceful) legs than theropods of a similar size. Even if retreat to water was not an effective way of escaping theropod predators, however, the larger ornithopods probably could swim at least as well as any of the modern terrestrial large herbivores, such as deer or horses.

Most ornithopods were not as well designed for running as theropods. When it came to defense, they had no armor, and they could not depend upon running into the water to escape. So how did they defend themselves? There are two possible answers. The first is safety in numbers. Many living ungulates travel in herds for safety. At least one species of hadrosaur (*Maiasaura*) probably traveled in herds of thousands of individuals. The second possibility is that ornithopods may have been more maneuverable than theropods. This is because ornithopods have a wider pelvis, so they may have been more stable. They also have wider feet for firmer contact with the ground, and a lower center of gravity, which may have given them a smaller turning radius at full speed. Thus the basic method of defense for ornithopods was probably herding behavior on land, where ornithopods could use their advantage of better maneuverability than the theropods.

Large ornithopods were probably quadrupedal walkers and bipedal runners. The forelimb is only two-thirds the length of the hind limb, and the forelimb did not have a wider excursion arc than the hind limb to counteract this difference in size. The scapula could not rotate and thus act as an additional limb element to increase the stride length, as it does in horses, for example. Consequently the ornithopod forelimb could not maintain the same stride length as the hind limb. Whenever an ornithopod went into a full run, it had to retract its forelimbs and run bipedally (see Bennett and Dalzell 1973; Thulborn 1990). (For an alternative hypothesis, see Paul 1987.)

Skin and Eggs

Ornithopods had thick, wrinkled skin with bony knobs of various sizes embedded throughout. This can be seen in "mummified" hadrosaurs at the American Museum in New York and at the Senckenberg Museum in Germany. The hand in later ornithopods was padded much like a snow

mitten. One species had a small "dragon frill" down the back that resembled a picket fence in appearance (Horner 1984). There is no evidence for feathers or lizard-like, overlapping scales.

Most of the known ornithopod eggs are, represented by the hypsilophodont *Orodromeus* and the hadrosaurs *Maiasaura* and *Hypacrosaurus* (Horner and Currie 1994). Eggs came in many size ranges and were laid in many differing patterns. There are now enough dinosaur nesting sites that a full text has appeared devoted just to the topic of eggs and babies (Carpenter et al. 1994; Hirsch and Zelenitsky, chap. 28 of this volume). On the basis of studies of juvenile *Maiasaura,* it has been suggested that hatchling hadrosaurs were altricial and not precocial (Weishampel and Horner 1994), but this conclusion has been challenged (Geist and Jones 1996).

The Future of Ornithopod Studies

Because ornithopods, especially hadrosaurs, have one of the most complete fossil records known for dinosaurs, representing hatchlings to adults, they are one of the best groups to use in studies of growth series and life histories. The two most fruitful areas for future research will be the often neglected studies of allometry and postcranial functional morphology, and how they relate to ontogeny and phylogeny (Dunham et al. 1989). For example, in some hadrosaurs, characters that appear only in the adult stages of stratigraphically early genera eventually begin to appear in the juvenile stages of stratigraphically later genera (an example of peramorphosis). Paedomorphosis and neoteny are two additional topics that will form the core of future populational studies of dinosaurs. Certain taxonomic characters appear only in the adult stages of development, and this will affect future taxonomies (Brett-Surman 1989).

The largest ornithopods may have lived for so long, and passed through so many size ranges, that they functionally occupied several different niches during their lifespan. This "niche assimilation" would be ecologically equivalent to multiple species of modern mammals. The resulting reduced community structure (as compared to modern mammalian faunas) may have been a factor in dinosaur extinction, because communities with few species are more susceptible to extinction than communities with many species.

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