

Dinosauria*

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The term, meaning awesome reptiles, that was coined by the British comparative anatomist R. Owen in 1842 to represent three partly known, impressively large fossil reptiles from the English countryside: the great carnivore *Megalosaurus*, the plant-eating *Iguanodon*, and the armored *Hylaeosaurus*. They were distinct, Owen said, not only because they were so large but because they were terrestrial (unlike mosasaurs, plesiosaurs, and ichthyosaurs); they had five vertebrae in their hips (instead of two or three like other reptiles); and their hips and hindlimbs were like those of large mammals, structured so that they had to stand upright (they could not sprawl like living reptiles). Owen's diagnosis was strong enough to be generally valid, with some modification, 150 years later. His intention in erecting Dinosauria, though, as A. J. Desmond noted, seems to have been more than just the recognition of a new group: By showing that certain extinct reptiles were more "advanced" in structure (that is, more similar to mammals and birds) than living reptiles, he was able to discredit contemporary evolutionary ideas of the transmutation of species through time into ever-more-advanced forms (progressivism).

Over the next several decades, dinosaurs were discovered in many other countries of Europe, for example, *Iguanodon* in Belgium and *Plateosaurus* in Germany, but rarely in great abundance. The first dinosaur discoveries in the United States were from New Jersey as early as the 1850s [*Trachodon*, 1856; *Hadrosaurus*, 1858; *Laelaps* (= *Dryptosaurus*), 1868]. The genus *Troodon*, based on a tooth from Montana, was also described in 1856, but at the time it was thought to be a lizard. Spectacular discoveries of dinosaurs from the western United States and Canada began in a great rush in the 1870s and 1880s and continued into the early 1900s. From 1911 to 1914, expeditions into German East Africa discovered some of the largest dinosaurs ever collected: *Brachiosaurus* and *Tornieria*, among many others. In the 1920s, expeditions into the Gobi desert of Mongolia brought back new and unusual dinosaurs such as *Protoceratops*, and the first eggs immediately recogniz-

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able as dinosaurian. For various reasons, such grand expeditions dwindled until the late 1960s, when renewed activities in the western United States and Canada, Argentina, southern Africa, India, Australia, China, Mongolia, and even Antarctica uncovered dozens of new dinosaurs. The rate of new discoveries reached an estimate of one new find every 6 weeks (intriguing new ones include *Microraptor*, *Mononykus*, *Eoraptor*, and *Brachytrachelopan*) during the mid-1990s, a pace of discovery that has continued (or possibly been exceeded) in the early twenty-first century. The finds since the 1960s may represent up to 50% of all dinosaurs currently known to have existed.

HIP STRUCTURE

As dinosaurs became better known, their taxonomy and classification developed, as well as their diversity. In 1887, H. G. Seeley recognized two quite different hip structures in dinosaurs and grouped them accordingly. Saurischia, including the carnivorous Theropoda and the mainly herbivorous, long-necked Sauropodomorpha, retained the generalized reptilian hip structure in which the pubis points down and forward and the ischium points down and backward. The remaining dinosaurs have a pubis that has rotated to point down and backward, thus extending parallel to the ischium; this reminded Seeley of the configuration in birds, and so he named this group Ornithischia. However, the ornithischian pubis is only superficially similar to that of birds, which are descended from, and are thus formally grouped within, Saurischia. Seeley's discovery, in fact, only recognized the distinctiveness of Ornithischia, and he concluded that Saurischia and Ornithischia were not particularly closely related. Even within Saurischia, there were general doubts that Sauropoda and Theropoda had any close relationship; eventually, the word "dinosaur" was used mainly informally by paleontologists.

However, this situation has been reversed. In 1974, Robert Bakker and Peter Galton argued that there were a great many unique features, including warm-bloodedness, which characterized the dinosaurs as a natural group (also including their descendants, the birds). Although this scheme was debatable in some particulars, it spurred renewed studies anchored in the new methodology of cladistic analysis of phylogenies (evolutionary relationships). A 1986 analysis listed nine uniquely derived features (synapomorphies) of the skull, shoulder, hand, hip, and hindlimb that unite Dinosauria as a natural group; this analysis has been since modified and improved, and today Dinosauria is universally accepted as a natural group, divided into the two monophyletic clades, Ornithischia and Saurischia.

EARLIEST DINOSAURS

Dinosaurs are archosaurs, a group that comprises living crocodiles, birds, and all of the living and extinct descendants of their most recent common ancestor (**Fig.**

1). The closest relatives of dinosaurs, which evolved with them in the Middle and Late Triassic (about 240–225 million years ago), include the flying pterosaurs and agile, rabbit-sized forms such as *Lagosuchus* and *Lagerpeton*. The common ancestor of all these forms was small, lightly built, bipedal, and probably an active carnivore or omnivore. Somewhat larger, with skulls ranging 15–30 cm (6–12 in.) in length, were *Eoraptor* and *Herrerasaurus* from the Late Triassic of Argentina and *Staurikosaurus* from the early Late Triassic of Brazil (**Fig. 2**). When the latter two genera were first described in the 1960s, they were thought to be primitive saurischian dinosaurs. The relationships of these animals are contentious, however, with some authors placing them within Theropoda, others positioning them at the base of Saurischia, and a further group of specialists suggesting that they were outside the group formed by Saurischia plus Ornithischia. These Late Triassic genera testify to a burst of evolutionary change at this interesting time in vertebrate history, and show that a variety of taxa very close to the origin of dinosaurs appeared during this interval. The first definite ornithischians and saurischians appear at almost the same time, though dinosaurs remained generally rare and not very diverse components of terrestrial faunas until the beginning of the Jurassic Period (about 200 million years ago).

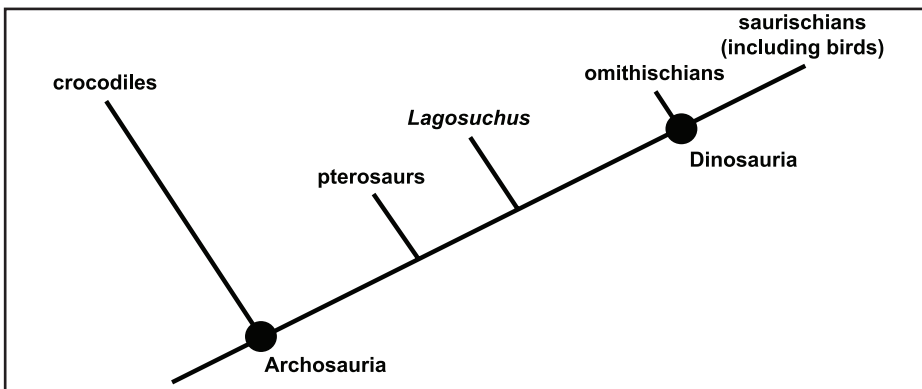


Fig. 1 Simplified phylogenetic tree of the archosaurian reptiles.



Fig. 2 *Eoraptor*, an early dinosaur or dinosaurian relative from the Late Triassic of Argentina.

An area of great interest is how the dinosaurs and their closest relatives differ from their contemporaries. Their posture and gait hold some important clues. Like *Lagosuchus*, *Lagerpeton*, and their other close relatives, the first dinosaurs stood upright on their back legs. The head of the thigh bone (femur) angled sharply inward to the hip socket, which was slightly open (not backed by a solid sheet of bone as in other reptiles). The femur moved like a bird's, in a nearly horizontal plane; the shin bone (tibia) swung back and forth in a wide arc, and the fibula (the normally straplike bone alongside the tibia) was reduced because the lower leg did not rotate about the knee, as a crocodile's or lizard's does. The ankle, too, had limited mobility: it formed a hinge joint connecting the leg to long metatarsals (sole bones), which were raised off the ground (in a stance called digitigrady, or "toe-walking"). All of these features can be seen today in birds, the living descendants of Mesozoic dinosaurs. Because the first dinosaurs were bipedal, their hands were free for grasping prey and other items, and the long fingers bore sharp, curved claws. The neck was long and S-shaped, the eyes large, and the bones lightly built and relatively thin-walled.

ORNITHISCHIA

Ornithischians (**Fig. 3**) are a well-defined group characterized by several unique evolutionary features; the entire group was analyzed cladistically in 1986, and the resulting phylogeny has been the basis of all later work. Ornithischians have a pre-dentary bone, a toothless, beaklike addition to the front of the lower jaw that, like the front of the upper jaw, probably had a horny covering in life (**Fig. 4**). This appears to have been an adaptation for plant eating. The jaw joint was set below the occlusal plane, a nutcracker-like arrangement interpreted as increasing leverage for crushing plant material. The teeth were set in from the side of the jaw, suggesting the presence of fleshy cheeks to help sustain chewing. The cheek teeth were broad, closely set, and leaf-shaped, and were often ground down to a shearing surface. In the hip, the pubis pointed backward. In all but the most generalized ornithischians, a new prong on the pubis was developed from the hip socket, upward, forward, and outward. This may have provided a framework to support the guts or to anchor the hindlimb muscles.

The most generalized ornithischians known are the fragmentary *Pisanosaurus* from the Late Triassic of Argentina and the small *Lesothosaurus* from the Early Jurassic of South Africa. In the major ornithischian radiation, Thyreophora branch off first, and Cerapoda are divided into Ornithopoda and Marginocephalia. All known ornithischians are either omnivores or herbivores.

Fig. 3 Relationships of the ornithischian dinosaurs. The base of this diagram is linked to Fig. 12. (Modified from P. C. Sereno, *The evolution of dinosaurs*, *Science*, 284:2137–2147, 1999)

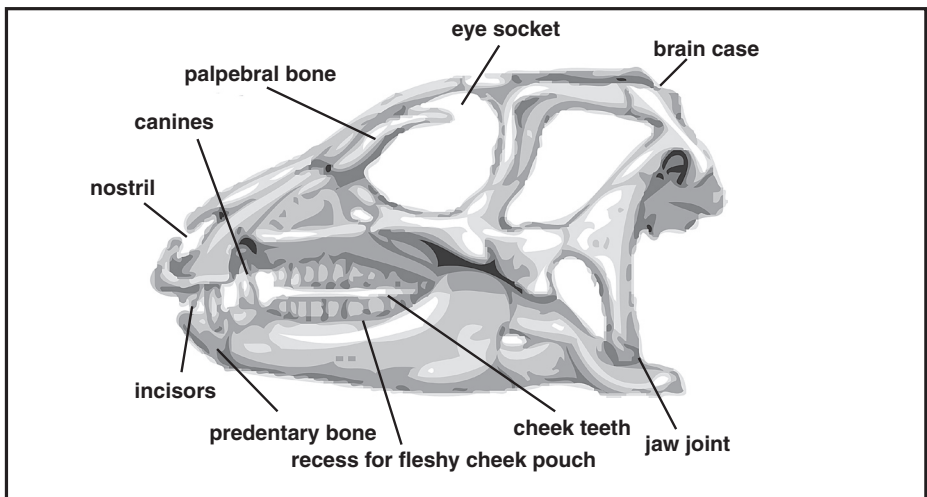
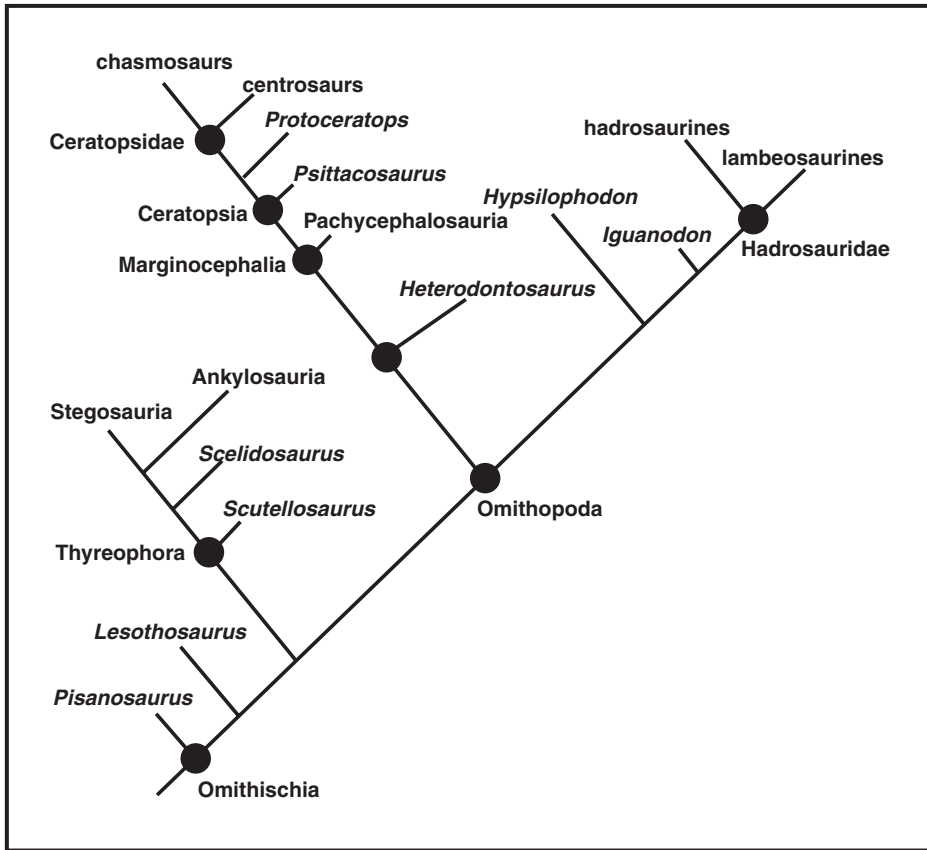


Fig. 4 Skull of *Heterodontosaurus*, showing typical ornithischian features.

THYREOPHORA

Stegosaurus and ankylosaurs were distinguished by their elaborate armor of modified dermal bone. The earliest thyreophorans, such as the small, bipedal *Scutellosaurus* and the slightly larger, probably quadrupedal *Scelidosaurus* (both from the Early Jurassic), had such scutes all over their bodies, but not as elaborate or distinctive as those of the larger, fully quadrupedal stegosaurs and ankylosaurs.

Stegosaurus

Stegosaurus first appear in the Middle Jurassic of China and Europe, and were undoubtedly widespread by then, though the group never seems to have been particularly diverse: 14 genera are known, mostly from the Late Jurassic and Early Cretaceous. They had the reduced ancestral armor pattern of Thyreophora, losing the scutes on the sides of the body and retaining only a row along either side of the vertebral column (**Fig. 5**). Originally this paravertebral armor was spiky or conelike (*Huayangosaurus*), but in some forms (*Kentrosaurus*) the armor forward of the middorsal region became platelike polygons, and in *Stegosaurus* the now much-enlarged, subtriangular plates occupied all but the last two terminal tail positions, which were still spiky. All well-known stegosaurs (except *Stegosaurus* itself) seem to have had a long spine projecting upward and backward from the shoulder as well. *Stegosaurus* also had a complement of bony ossicles in its throat region. In all stegosaurs the heads were relatively small and the teeth few and diamond-shaped. Stegosaurs had small brains, ranging from a walnut to a billiard ball in size. An expansion of the neural canal in the hip region was once interpreted as a “second brain” to control the hindlimbs and tail, but it is only a cavity to accommodate the sacral nerve plexus and a large glycogen (“fat”) storage organ like those of birds and some other reptiles.

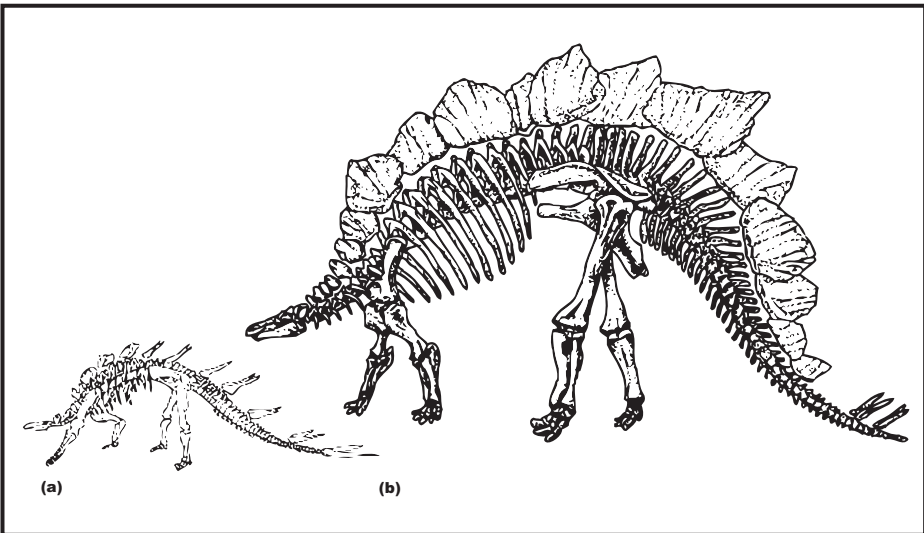


Fig. 5 Stegosaurs. (a) *Kentrosaurus*. (b) *Stegosaurus*.

The distinctive armor of stegosaurs has long fueled speculation about its position, arrangement, and function. The spikes appear to have been primitively paired, though the 17 plates of *Stegosaurus* form a single alternating, nearly medial row. Sharpey's fibers, which reflect the direction of muscle attachment to bone, show that these plates stood upright, not flat, and could not have been moved up and down. Defense is a possible function, although it must be asked why stegosaurs lost all but their paravertebral row of armor. Stegosaurs were not fast runners: the lower limbs were long and the feet and upper limbs were short, so they would have had to stand and deliver. The spikes and plates, like the shoulder spines, could have had a passive function in defense, and the terminal tail spikes, which dragged along the ground, might have made a formidable weapon. However, the plates are relatively weak "sandwiches" of latticelike bone internally, not optimal for defense. In some large stegosaurs, the broad surface area of the plates may have contributed to thermoregulation, though this hypothesis has been challenged. However, it is most likely that they were used in species recognition: no two stegosaurs have identical armor.

Ankylosaurs

Ankylosaurs are distinctive dinosaurs (**Fig. 6**). Their skulls are short, low, and flat, always wider than high in rear view, and a complement of dermal ossicles covers the skull and closes the antorbital and mandibular fenestrae. There is an S-shaped row of small, uncomplicated teeth, which sometimes display wear. The body is broad and squat, and the limbs short. Armor covers much of the body, as in Thyreophora primitively, and appears in several shapes, including keeled or spined plates, polygonal pustules, spikes, and rows of symmetrical ovals or rounded rectangles.

Ankylosauria is divided into Nodosauridae and Ankylosauridae, based on a number of distinctive but subtle features of the skull and its plating, plus several postcranial characteristics. Several authors now recognize a third group, Polacanthidae. There are not many gross differences, though ankylosaurids have a tail club (four armor plates envelop the last series of tail vertebrae, which are deeply internested and partly fused). Both groups are primarily Cretaceous, though several

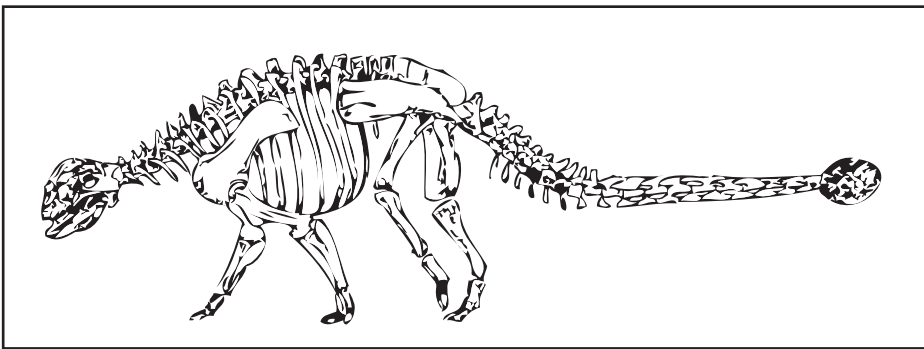


Fig. 6 *Euoplocephalus*, an ankylosaur.

genera are now known from the Jurassic. Ankylosaurs, like stegosaurs, seem never to have been very diverse, and they may have been solitary or have traveled in small family groups. They could not have been fast runners, and may have depended on camouflage, squatting, or slashing with lateral spines or tail club to repel predators.

CERAPODA: ORNITHOPODA

In many ways, Ornithopoda includes the most generalized ornithischians, which retain the bipedal posture of ancestral dinosaurs while lacking the horns, frills, spikes, and armor of other ornithischians. Nonetheless, they have their own specializations, and through the Mesozoic Era a general progression in size and adaptation can be seen from heterodontosaurs through hypsilophodonts to iguanodonts and hadrosaurs. In ornithopods, the upper front (premaxillary) teeth are set below the cheek (maxillary) teeth, and the jaw joint is set substantially below the occlusal plane of the teeth. *Heterodontosaurus* (**Fig. 4**), a fox-sized, lightly built form from the Early Jurassic of South Africa, shows these general characters and a few unusual ones, including protruding “canine” teeth presumably for defense or display.

The remaining three ornithopod groups are somewhat larger in size; they lose progressively all the front (premaxillary) teeth, reduce and/or lose the antorbital and maxillary fenestrae, and reduce the third finger (the fourth and fifth are already reduced in ornithischians). *Hypsilophodon* is a generalized member of this group. It still has five pairs of premaxillary teeth, and there is a gap between its front and cheek teeth, but the cheek teeth are now closely set and their crowns are typically worn flat. It was once thought that *Hypsilophodon* lived in trees, but this was based on the presumption that the first toe was reversed (as in birds) to serve as a perching adaptation. Actually, the anatomy of the foot is normal, and there are no additional reasons to put *Hypsilophodon* in trees.

More derived (advanced) ornithopods, such as *Dryosaurus* and *Tenontosaurus*, approach the condition of iguanodonts and hadrosaurs in many respects: the front teeth are completely lost; the front of the beak begins to flare; the cheek teeth become larger and more closely set, creating a single grinding battery of teeth; and the “bridge” of the nose (the area between the eyes and nostrils along the skull midline) becomes more highly arched. The forward prong of the pubis begins to grow outward until it reaches farther forward than the front of the ilium. As the cheek teeth begin to unify into opposing dental batteries, the internal kinesis (mobility) of the skull bones against each other also evolves to resist and redirect the forces of chewing.

The iguanodonts (**Fig. 7**) and hadrosaurs (**Fig. 8**) are the most familiar ornithopods, and were among the first dinosaurs discovered; they are still among the best represented in the fossil record. These two groups continue the trends already seen in the hypsilophodonts and dryosaurs, gaining larger size, losing the front teeth,

flaring the snout further, and arranging the cheek teeth in a long, straight row for efficient crushing and slicing. In iguanodonts and hadrosaurs, the pubis changes somewhat: its original (backward) prong is reduced to a splint, and the forward prong enlarges and flares. This may reflect support for the intestinal tract, which is thought to have needed an extensive system of fermentation for the tough, low-nutrient plants that the animals ate. The claws on the fingers and toes are flattened and broadened into spoon-shaped hooves, and the middle three fingers, as with the middle three toes, may have functioned as a unit in walking on four legs. The fifth finger in these dinosaurs is quite distinctive: it points to the side, much like a thumb, and was similarly opposable to the other fingers, probably for manipulating food. The thumb is extraordinary in iguanodonts: the thumb phalanx, its terminal ungual, and its supporting metacarpal bone are fused together into a conelike spike, and this in turn is articulated tightly to the blocky, nearly immobile wrist bones. Whatever function this had in scratching, procuring food, or even defense, it had no function at all in hadrosaurs, which lost the thumb altogether.

Hadrosaurs (known as duckbills) dominated most of the Late Cretaceous of the Northern Hemisphere in numbers and diversity; their bones are found by the thousands in some deposits, suggesting mass deaths, perhaps during seasonal migrations or droughts. Their jaws were formidable food processors. Four or five rows of replacement teeth accompany each cheek tooth, and all of them are closely set, so as the teeth wore down they formed a single cutting and crushing surface of hundreds of teeth in each quadrant of the jaws. As in all cerapodans, the enamel was thicker on the oral side of the lower teeth and the cheek side of the upper teeth, so the teeth wore down unevenly: the cutting surface of the dental batteries was not horizontal, but beveled for better slicing as well as crushing.

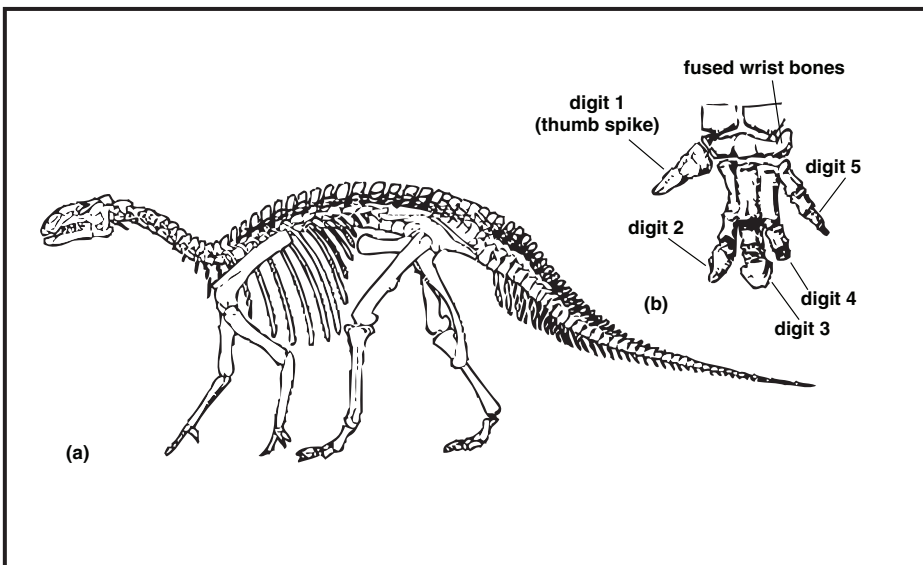


Fig. 7 *Iguanodon*, an ornithomimid. (a) Skeleton. (b) Hand.

Hadrosaurs are generally divided into two groups (**Fig. 8**): the more conservative hadrosaurines and the more derived lambeosaurines, which are noted for their profusion of skull crests and ornaments. Some crests were solid and spikelike (*Saurolophus*), while others were partly hollow and resembled bizarre hats or helmets (*Lambeosaurus*, *Corythosaurus*) or even snorkels (*Parasaurolophus*). The partial hollowness in the crests, which were formed of the premaxillary and nasal bones, was to accommodate the nasal passages that normally run through these bones. Many explanations have been proposed for this great variety in skull structure, including functions in head butting, underwater feeding, or improvement in sense of smell, but most have little support. Because lambeosaurines vary little in other skull and postcranial features, a plausible explanation is that the crests were for display and species recognition, like the horns of present-day hoofed mammals. Experimental analysis and acoustical modeling of hollow-crested forms suggested that the chambers in the crests could have served as vocal resonators to create distinctive and far-reaching sounds for species recognition and communication. This idea has contributed to the picture of sophisticated social organization that is developing for many groups of dinosaurs.

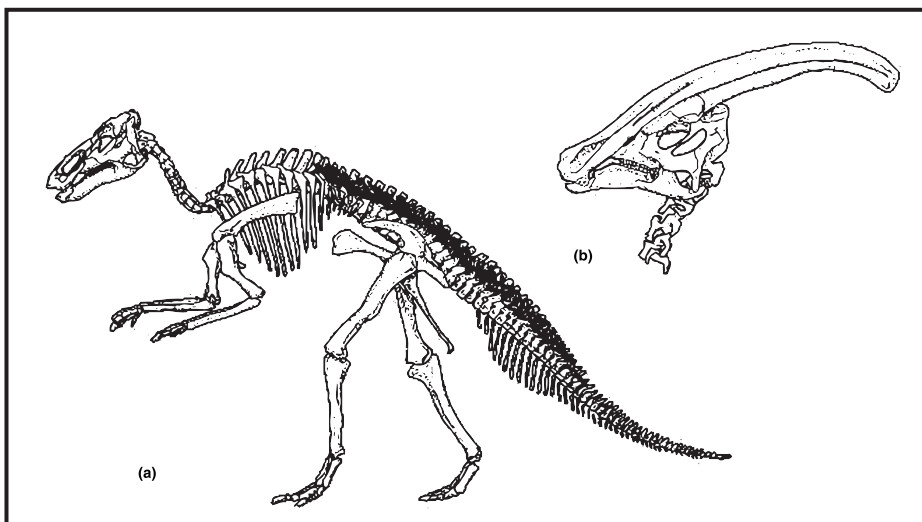


Fig. 8 Hadrosaurs. (a) Skeleton of the hadrosaurine *Edmontosaurus*. (b) Side view of skull of the lambeosaurine *Parasaurolophus*.

CERAPODA: MARGINOCEPHALIA

Marginocephalia includes the dome-headed Pachycephalosauria (**Fig. 9**) and the frilled, usually horned Ceratopsia (**Fig. 10**). Both groups are almost exclusively Cretaceous, though a few Late Jurassic forms are now known. Marginocephalia are recognized by a small shelf or incipient frill that overhangs the back of the head; also, their hips are wider than in most other forms, though ankylosaurs have extremely wide (but very different) hips. The small shelf on the skull was the basis for