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Braincase Anatomy

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The braincase is generally one of the most poorly understood regions of the dinosaur skeleton. It is often partially or completely obscured by other skull bones. Parts of it do not ossify or are fragile and easily destroyed, and it is a complex of numerous bones pierced by nerves, blood vessels, and pneumatic diverticula. Nevertheless, braincases have been described for each of the major dinosaurian lineages. Increased use of noninvasive computerized tomography (CT) scanning (see COMPUTERS AND RELATED TECHNOLOGY) has also revealed details that could previously only have been visible through serial sectioning, which would invariably result in the destruction of most of the specimen.

Because the braincase is not directly subject to the same selective pressures as parts of the skeleton involved in the acquisition and processing of food (teeth, limb proportions, etc.), in the protection of the animal from predators (i.e., defensive horns, spikes, and armor), or in sexual or other display structures, its morphology tends to be conservative within a lineage. Comparison of braincases among taxa can therefore provide clues to relationships that may otherwise be obscured in more rapidly evolving parts of the body.

The braincase houses the brain; study of the endocranial cavity can approximate the overall size of the brain (see INTELLIGENCE) and show the relative development of different parts of the braincase. Because most cranial nerves and blood vessels pass through foramina and canals in the braincase, and the positions of these openings are conservative in all tetrapods, most of the openings can be identified in fossil skulls. The positions and sizes of these openings can provide information on interrelationships and can give clues about sensory abilities. Because the braincase also forms the inner walls of the middle ear, adjacent bones are often invaded by pneumatic diverticula from the middle ear air sac. These openings are less regular than those of the nerves and blood vessels and can be asymmetrical.

The ossified braincase can develop from as many as 23 separate centers of ossification, from bones of both dermal and endochondral origin. Some of the braincase components are paired, some are medial and singular, and others are complexes of several bones that are co-ossified in even the youngest animals. Braincases usually fuse up completely in mature animals, and most of the sutures are difficult to see. Dermal bones include the frontals and parietals on the skull roof and the parasphenoid, which fuses with the basisphenoid. Specific endochondral bones ossify in particular regions of the chondrocranium and can be identified by their consistent relationships to the cranial nerves and to the inferred positions of the cartilages.

The braincase is roofed by the frontals and parietals in a consistent manner. The ventral surface of the frontal usually has well-defined impressions of the olfactory tract and the cerebral hemispheres, and depressions in the ventral surface of the paired parietals show what the top of the back part of the brain looked like. In dinosaurs such as troodontids (Russell, 1969), the enlarged cerebral hemispheres mostly covered the midbrain so that it left no impression in the frontals. Hadrosaurs were relatively large-brained animals (Hopson, 1979), which is reflected by the doming of the frontal bones.

The occiput is normally formed by four bones (supraoccipital, basioccipital, and a pair of exoccipitals), all of which form the margins of the foramen magnum. The supraoccipital generally makes a contribution to the dorsal margin of the foramen magnum, the sides are formed by the paired exoccipitals, and the basioccipital makes a small contribution to the ventral margin. The supraoccipitals of *Lesothosaurus* (Weishampel and Witmer, 1990a), heterodontosaurids (Weishampel and Witmer, 1990b), hypsilophodonts (Galton, 1989), stegosaurs (Gilmore, 1914), and protoceratopsians (Brown and Schlaikjer, 1940) are larger than normal and contribute to the entire dorsal margin of the foramen magnum. In iguanodonts (Taquet, 1976; Norman, 1986; Galton, 1989), hadrosaurs (Langston, 1960; Weishampel and Horner, 1990), ceratopsids (Hatcher *et al.*, 1907), and possibly *Pachycephalosaurus* (Maryanska and Osmólska, 1974), the supraoccipital is excluded from the margin of the foramen magnum by the exoccipitals, which meet on the midline. The supraoccipital normally makes only a narrow contribution to the dorsal margin of the foramen magnum in the vast majority of dinosaurs, including *Camptosaurus* (Gilmore, 1909), sauropods (Madsen *et al.*, 1995), and most pachycephalosaurids (Maryanska and Osmólska, 1974). An anterior extension of the supraoccipital contacts the prootic and laterosphenoid in all neoceratopsians.

The two epiotic bones probably form from separate centers of ossification than the supraoccipital. They can make a small contribution to the occiput, but in most specimens they have fused indistinguishably to the supraoccipital (Currie and Zhao, 1993a).

In all known dinosaurs the exoccipital is fused without a trace of sutures to the opisthotic, and together they form a conspicuous paroccipital process. The paroccipital process meets the squamosal, parietal, and quadrate in a loose butt joint in most dinosaurs but fuses to the quadrate and squamosal in nodosaurid ankylosaurs. In neoceratopsians, the distal end of the paroccipital process is expanded and is embedded in a slot in the squamosal (Brown and Schlaikjer, 1940). The passages of the 12th cranial nerves are completely enclosed within the exoccipital, which also forms the posteromedial margin of the metotic fissure, through which passed the internal jugular vein and cranial nerves X and XI. The jugular and associated nerves can be diverted posteriorly to exit on the occiput in some dinosaurs (Currie and Zhao, 1993b). The skull has a prominent knob-like process, known as the occipital condyle, that articulates with the first cervical vertebra (the atlas). It is formed by the basioccipital and both exoccipitals. Usually more than two-thirds of the condyle is formed by the basioccipital, which separates the dorsolateral contributions from the exoccipitals. In neoceratopsians (Hatcher *et al.*, 1907; Brown and Schlaikjer, 1940), the basioccipital is excluded from the foramen magnum by the exoccipitals, which can form up to two-thirds of the ball-like occipital condyle in ceratopsids.

The otic capsule is formed from three centers of ossification, although only the outer two—the prootic and opisthotic—can generally be distinguished. As previously mentioned, the epiotic ossifies with the supraoccipital in the tectum synoticum of the chondrocranium. In protoceratopsians and probably ceratopsids (Brown and Schlaikjer, 1940), part of the epiotic is exposed on the lateral surface of the braincase between the prootic, opisthotic, laterosphenoid, and parietal. The facial nerve (VII) and the anterior (vestibular) and posterior (cochlear) branches of the eighth cranial nerve pass through the prootic, which also forms the posterior margin of the exit for cranial nerve V. The prootic sends a tongue-like process posteriorly to extensively overlap the opisthotic above the stapedial recess. The crista prootica often extends ventrolaterally into a wing-like process that forms the anterior wall of a pneumatic cavity in the side of the basisphenoid. This process, referred to by S. Welles (personal communication, 1996) as the preotic pendant, is usually formed in part by the basisphenoid, but in some cases can be formed almost entirely by the basisphenoid (in which case it is called the *ala basisphenoidalis*). The opisthotic co-ossifies with the exoccipital within the occipital arch of the chondrocranium. It forms the anteroventral borders of the opening for the ninth and tenth cranial nerves and for the stapedial recess. The otic capsule encloses the inner ear and semicircular canals and forms a conspicuous bulge on the inner wall of the endocranial cavity. The floccular recess invades the capsule anteromedially and tends to be relatively large in small animals. These and other bones adjacent to the middle ear sac are invaded by pneumatic diverticula in theropods such as ornithomimids (Osmólska *et al.*, 1972), troodontids (Currie, 1985; Currie and Zhao, 1993b), and tyrannosaurs (Russell, 1970) (Fig. 1).

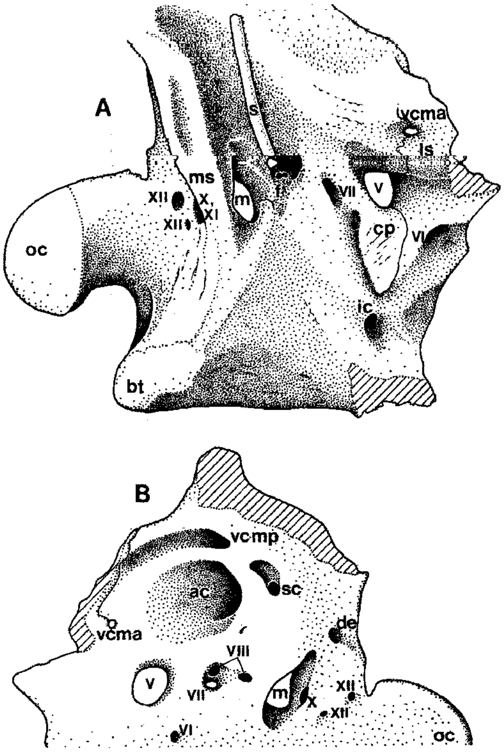

FIGURE 1 Braincase of *Dromaeosaurus albertensis* from right posteroventral (A) and medial (B) views. ac, fossa auriculae cerebelli; bt, basal tubera; de, ductus endolymphaticus; f, fenestra ovalis and fenestra pseudorotunda; ic, internal carotid; ls, laterosphenoid; m, metotic fissure; ms, metotic strut; oc, occipital condyle; pn, pneumatic space, s, stapes; vcma, anterior canal of middle cerebral vein. Roman numerals represent cranial nerves. (From Currie (1995) with permission.)

The floor of the braincase ossifies within the basal plate of the chondrocranium into the basioccipital posteriorly and the basisphenoid anteriorly. The basioccipital forms the floor of the metotic fissure and effectively makes up the lower margins of the exit foramina for cranial nerves IX to XI. Beneath the occipital condyle are a pair of processes called the basal tubera, formed primarily by the basioccipital but supported anteriorly by the basisphenoid. Primitively, a large pneumatic sinus (known by many names, including the basisphenoidal recess and Rathke's Pouch) opens ventrally. Although bounded mostly by the basisphenoid, the posterior wall is formed primarily by the basioccipital. The basicranial complex is pierced on the midline by a eustachian opening in most neoceratopsians (Dodson and Currie, 1990), except in *Bagaceratops* in which the opening passes between the basioccipital and basisphenoid. The sixth cranial nerve passes anteroventrally through the basisphenoid behind the dorsum sellae. In coelurosaurian dinosaurs (Currie and Zhao, 1993b), including birds, cranial nerve VI exits the basisphenoid lateral to the pituitary, whereas in most dinosaurs (including allosaurids, sauropods, hadrosaurs, and pachycephalosaurids) it enters the hypophyseal fossa in primitive fashion. The pituitary is nested in the fossa (which is also called the hypophyseal recess or pituitary fossa) anterior to the dorsum sellae.

The basisphenoid and parasphenoid are indistinguishably fused in all dinosaurs, with the possible exception of pachycephalosaurids (Maryanska and Osmólska, 1974). Anteriorly they taper into the distinctive cultriform process (parasphenoid rostrum), which supports the interorbital septum. In ornithomimids, therizinosaurids, and troodontids (Barsbold, 1983), the parasphenoid is expanded into a pneumatic, balloon-like structure referred to as the bulbous parasphenoid. Ventrally the same bones form the paired basipterygoid processes, which articulate with the pterygoids. Posterodorsal to the basipterygoid process, the lateral wall of the basisphenoid is invaded by the internal carotid. This artery passes anteromedially to meet its counterpart on the midline in the hypophyseal recess.

Like other archosaurs, including crocodiles and birds, the laterosphenoid (pleurosphenoid of some authors) of dinosaurs is ossified in the pila antotica. It extends dorsolaterally in a wing-like process that contacts the frontal, parietal, and postorbital. Ventrally it forms the margin of the foramen for the various branches of the fifth cranial nerve. One of these branches—the ophthalmic—is usually expressed on the laterosphenoid either by a groove on the lateral surface or by a canal enclosed within the bone. The ophthalmic branch of the trigeminal is separate in *Allosaurus* (Hopson, 1979), protoceratopsids (Brown and Schlaikjer, 1940), ceratopsids (Brown, 1914), troodontids (Currie and Zhao, 1993b), and tyrannosaurids (Bakker *et al.*, 1988), but the branches exit from a single opening in all other dinosaurs. Anteriorly, the laterosphenoid forms the posterior border of the foramen for the third cranial nerve, and the fourth passes through its upper regions.

Anterior to the laterosphenoid is a series of ossifications within the interorbital cartilages that show great ontogenetic and taxonomic variability. They are either absent or unknown in most smaller and primitive dinosaurs, including ceratosaurs (Welles, 1984; Raath, 1985), protoceratopsids (Brown and Schlaikjer, 1940), and psittacosaurids (Sereno, 1987). There is also considerable confusion concerning what each of these ossifications should be called. The orbitosphenoids, which develop late in the pila metotica of the chondrocranium, are a pair of small ossifications that form around the common (carcharodontosaurids, troodontids, and tyrannosaurids) or separate openings (allosaurids) on the midline for the second (optic) cranial nerves. The orbitosphenoid also borders the opening for the third cranial nerve and probably the fourth in at least some cases. Other than theropods, the orbitosphenoid is also known in sauropods (Madsen *et al.*, 1995), hadrosaurs (Lull and Wright, 1942), iguanodontids (Norman, 1986), and pachycephalosaurids (Maryanska and Osmólska, 1974). Dorsally, the sphenethmoid can ossify to form an elongate tube or pair of tubes beneath the frontal for the olfactory tracts and bulbs. According to S. Welles (personal communication, 1996), there is a separate ossification, which he calls the septosphenoid, in some theropods beneath the parietal and behind the sphenethmoid. The interorbital septum can also ossify into a thin, vertical sheet of bone between the sphenethmoid and the cultriform process (Maryanska, 1977; Madsen *et al.* 1995; Coria and Currie, 1997).

Despite the complexity of braincases and lack of much comparative information about them, they provide much information about individual dinosaurs. One research area where they have been particularly useful in elucidating relationships has been in the origin of birds debate. Differences in terminology are slowly being resolved, and with the advent of CT scanning, braincases have become more accessible. It is therefore highly likely that the number of publications describing braincases will steadily continue to increase in coming decades.

See also the following related entries:

PALEONEUROLOGY • SKULL, COMPARATIVE ANATOMY

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