

## THE FORAMEN OVALE IN THE RHINOCEROTIDAE

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PHYLOGENETIC significance has been accorded to the individualization of cranial foramina (Hecker and Grünwald, 1926) and taxonomic importance to the foramen ovale (Weber and Abel, 1928; Adams and Eddy, 1949). The separate passage of the mandibular branch of the trigeminal nerve has been considered an advanced morphological character, and its alleged absence in Perissodactyla has been accounted (Weber and Abel, 1928) an ordinal distinction from the Artiodactyla. A somewhat confused literature on the subject has been reviewed by Edinger and Kitts (1954) and clarified by their submission of additional palaeontological evidence. These authors demonstrated that a discrete foramen ovale obtains in the Condylarthra, that its mode of manifestation varies widely in different mammalian groups, that it is wanting in many extant artiodactyls and that, in some stocks, it tends to merge with the foramen lacerum medium. They regarded the foramen ovale as neither a constant nor an advanced character, but a primitive mammalian cranial feature present in the earliest mammals, retained in various extant forms or secondarily lost in others.

Osborne (1898) regarded a tendency for the foramen ovale to become confluent with the foramen lacerum as characteristic of fossil rhinoceroses: Edinger and Kitts (1954) adduced supportive evidence and described the nature of the foramen in *Subhyracodon*, *Caenopus*, *Hyracodon*, *Teleoceras*, *Chilotherium* and other extinct forms. Regarding modern forms they stated categorically that "No extant rhinoceros has a foramen ovale", meaning thereby a separate, intra-alisphenoidal aperture for the mandibular nerve. This statement was based on the reported examination of 4 skulls (viz. 1 *Rhinoceros*, 1 *Diceros*, 1 *Dicerorhinus*, 1 *Ceratotherium*). It is not wholly supported by independent examination of 104 modern rhinoceros crania (viz. 20 *Rhinoceros unicornis*, 16 *R. sondaicus*, 18 *Dicerorhinus sumatrensis*, 30 *Diceros bicornis*, 20 *Ceratotherium simum*) ranging in age from birth to senescence and comprising males and females. (The majority of the specimens so examined are in the collections of the British Museum (Natural History).)

This more extensive range of material reveals generic and specific differences of foramen ovale constitution among the extant Rhinocerotidae. By this criterion the Asiatic forms are distinguished sharply from the African, the Sumatran Rhinoceros proving morphologically variable.

In *Rhinoceros unicornis*, a ridge (crista alisphenoidalis, crista Eustachii)



runs postero-laterally from the base of the pterygoid process (ectopterygoid) towards a post-sphenoidal gap in the cranial base, the confluent foramina lacerum et ovale. This ridge invariably ceases before gaining the anterior edge of the conjoint foramen, whose anterior rim is in consequence, of smooth, uninterrupted contour. A sharp petrosal process projects forwards and is connected to the foramen's anterior rim by a ligament. Thus in life the foramina ovale and lacerum are separated principally by fibrous tissue.

In *Rhinoceros sondaicus* conditions are somewhat similar but the Eustachian ridge gains the anterior margin of the conjoint foramen and impinges thereon as a sharp spicule. In life, a ligament passes backwards thence to an anteriorly-directed process of the petrosal, thus dividing the common foramen of the macerated skull into a lateral compartment (foramen ovale) and a medial compartment (foramen lacerum). In *R. sondaicus*, therefore, bone enters more fully into the common foraminal partition than is the case in *R. unicornis*.

In *Dicerorhinus sumatrensis* arrangements are curiously variable. In five-sixths of specimens the "common" foramen is again compartmented by an osseo-ligamentous partition. The Eustachian ridge encroaches on the anterior rim of the foramen as a largish, blunt, triangular tubercle, the petrosal sends relatively far forwards an irregular, substantial process, and the two are united by intervening ligament. Arrangements recall those in *R. sondaicus*, save that the anterior foraminal tubercle is relatively larger and blunter and the petrosal process relatively longer. But one-sixth of specimens show a wholly different configuration, one indeed exactly similar to that characteristic of *Diceros bicornis*. That is, the foramen ovale is not a compartment of a "common" foramen, but is instead a recognizably discrete and wholly intra-alisphenoidal opening, separated from the more medial foramen lacerum by a wide and deep osseous plate, which is not an ossified ligament.

In *Diceros bicornis* the foramen ovale is invariably discrete and intra-sphenoidal. A projecting petrosal process may contact posteriorly the osseous lamina circumscribing the foramen: this lamina, however, is never composite, but is always wholly alisphenoidal in constitution.

In *Ceratotherium simum* the foramen ovale is discrete and separated medially from the foramen lacerum by an osseous but composite (temporo-sphenoidal) bar. The Eustachian ridge is prolonged antero-posteriorly between the foramina upon a long, stout, prismatic, freely-ending alisphenoid spur, to whose medial aspect is applied an equally robust, forwardly-projecting blade from the petrosal. These two osseous processes never fuse, but remain in harmonic sutural apposition.

Thus a "true" (i.e. discrete) foramen ovale does exist in the extant Rhinocerotidae—in all specimens of the two African species and in a minority of specimens of the Sumatran species.

In Asiatic rhinoceroses (all *R. unicornis*, all *R. sondaicus*, most *Dicerorhinus*) the foramen ovale is circumscribed medially in part by ligament.



In African rhinoceroses (and in some *D. sumatrensis* specimens) the foramen is circumscribed medially by bone. This circumscribing bony bar is anatomically simple (i.e. wholly sphenoidal) in all *Diceros bicornis* specimens and in the "aberrant" *Dicerorhinus* specimens: it is composite and bipartite (i.e. temporo-sphenoidal) in all *Ceratotherium* specimens.

These findings assist in the specific recognition of skulls and afford some minor evidence bearing upon the phylogeny and taxonomy of the Rhinocerotidae.

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