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The skull and mandible of the African elephant (*Loxodonta africana*)

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ABSTRACT

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In the present study the bones of the skull, excluding the hyoid apparatus, are described. All the bones are aerated by sinuses. In the occipital bone the squamous part is aerated from the sinus of the parietal bone, the lateral part is aerated from the tympanic bulla and the basal part from the sinus of the basisphenoid bone. Condylar foramens and hypoglossal canals are absent. A small interparietal bone is present at birth. At an early age it fuses with the surrounding cranial bones. The squamous part of the temporal bone lies sagittally in young animals, but moves progressively to a transverse plane as the animals age. A foramen lacerum is represented by jugular and oval foramens and the carotid canal. The body of the basisphenoid bone is excavated by the massive maxillary tuberosity. The latter extends to the oval foramen and contains the developing molar teeth. The ethmoturbinate, nasal and lacrimal bones are exceptionally small. In old bulls the palatine processes of the incisive bones and their sinuses are gradually displaced by the palatine processes of the maxillae.

The incisive part of the mandible does not carry any teeth and both lateral and medial mental foramina are present.

Keywords: African elephant, *Loxodonta africana*, mandible, skull

INTRODUCTION

The first publication on the osteology of the elephant is a comprehensive study on a female by Blair (1706). However, he did not say whether it was an African or an Indian elephant. Mayer (1847, cited by Güssgen 1988) described the bones of the skull of both the African and the Indian elephants. Eales (1928) reported on the bones of an African elephant foetus and Mariappa (1986) on those of an Indian elephant foetus. Sikes (1971) gave an overview of the bones of the African elephant. Owing to the dearth of material these studies were often undertaken on single specimens, with the result that illustrations are often inadequate and inaccurate. This study was therefore undertaken to illustrate and describe the bones of the skull of the African elephant accurately, by making use of animals of different ages and of both sexes.

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MATERIALS AND METHODS

The skulls of five adult elephants and four juveniles of both sexes were examined. The skulls were compared, and dorsal, ventral, lateral, caudal and medial views of both young and adult animals were illustrated. All the animals originate from the Kruger National Park. The nomenclature used is based on the *Nomina Anatomica Veterinaria* (1994).

RESULTS

Bones of the cranium (*Ossa cranii*)

OCCIPITAL BONE (*Os occipitale*) (Fig.1–4)

The occipital bone consists of squamous, basal and lateral parts. The large, oval *Foramen magnum* is bounded dorsally by the lateral parts, laterally by the occipital condyles and ventrally by the basal part. The squamous part of the occipital bone is pneumatized from the paranasal sinus of the parietal bone, while the lateral part contains an extension of the tympanic bulla of the temporal bone. The area just dorsal to the *Foramen magnum,* however, remains unpneumatized.

Externally, the unpaired squamous part (*Squama occipitalis*) forms two thirds of the caudal surface of the skull, while internally, it forms the roof and lateral part of the caudal cranial fossa. The squamous part fuses ventrally with the lateral part, ventrolaterally with the temporal bone (squamous part and mastoid process), and ventrolaterally and dorsally with the parietal and interparietal bones. The latter two fusion lines are the first to ossify and disappear from the surface of the skull, while the suture between the parietal and occipital bones forms a transverse nuchal line (*Linea nuchae*). The external surface of the squamous part is divided into a rough dorsal part and a smooth ventral part. Its dorsal part contains two deep median fossae that are separated from each other by a median ridge (*Crista occipitalis externa*). Laterally, the ventral part bears two large, tuberous enlargements that continue onto the lateral part of the occipital bone. Small mastoid foramina (*Foramina mastoidea*) are sometimes present in the suture between the squamous occipital bone and the mastoid process of the temporal bone.

The lateral part (*Pars lateralis*) is paired and forms the ventral part of the caudal surface of the skull. Each part bounds the *Foramen magnum* dorsally and laterally, and bears two oval condyles (*Condylus occipitalis*) for articulation with the atlas. The lateral parts fuse dorsally with the squamous part, laterally with the squamous temporal bones and ventrally with the tympanic temporal bones and basi-occipital bone. The occipital condyles are longitudinally orientated and extend onto the basi-occipital bone. Their articular surfaces face caudally and ventrally. The jugular foramen (*Foramen jugulare*) lies in the fissure between the lateral part of the occipital, basi-occipital and tympanic temporal bones. The stylomastoid foramen (*Foramen stylomastoideum*) lies in a deep fossa on the fissure between the squamous temporal, tympanic temporal and lateral part of the occipital bones. The lateral part bears two large tubercles, one laterally along its lateral margin and one medially between the lateral tubercle and the occipital condyle. The medial tubercle is continuous with the tubercle of the squamous occipital bone. It is noteworthy that the lateral parts of the occipital bone lack both condylar and hypoglossal canals.

The unpaired base of the occipital bone (*Pars basilaris*) is wedge-shaped and forms the caudal part of the floor of the cranium. It has a prominent median ridge, bounds the *Foramen magnum* ventrally and bears two depressions laterally. The depressions lie immediately medially to the jugular foramens. The basi-occipital bone fuses rostrally with the basisphenoid bone and caudally with the lateral part of the occipital bone. Medially, it lies against the tympanic temporal bone, forming the tympano-occipital fissure (*Fissura tympano-occipitalis*). The carotid canal (*Canalis caroticus*) lies laterally to the latter fissure, and is surrounded by the medial part of the tympanic bulla. Intracranially, the basi-occipital bone lies against the petrous temporal bone to form the petro-occipital fissure (*Fissura petro-occipitalis*). In older animals, the entire base of the occipital bone is aerated by a caudal extension of the sinus of the basisphenoid bone.

PARIETAL BONE (*Os parietale*) (Fig. 2, 4, 5)

The paired parietal bones form the middle part of the dorsal and dorsolateral walls of the cranium. They fuse rostrally with the frontal bones, laterally with the squamous temporal bones, caudally with the squamous occipital bones and medially with each other. The small interparietal bone is wedged in between the parietal and occipital bones. In some animals, a distinct tubercle is present at the caudal end of the sagittal (interparietal) suture. Externally, the dorsal and lateral parts of the bone are separated by a ridge, the temporal line (*Linea temporalis*). Intracranially, the spheno-orbital crest extends onto the parietal bone, resulting in a clear separation of the rostral and middle cranial cavities. The greater part of the parietal bone is pneumatized by a caudal extension of the frontal sinus.

INTERPARIETAL BONE (*Os interparietale*) (Fig. 2)

The unpaired interparietal bone lies on the caudal midline of the skull, wedged in between the parietal and squamous occipital bones. It is a small, rectangular bone that can be distinguished only in very young animals. On the surface of the skull, it fuses with the parietal and occipital bones to such an extent that its boundaries cannot be seen. Intracranially, it forms a small tentorial process (*Processus tentoricus*). The latter lies on the midline and completes the separation of the middle and caudal cranial cavities dorsally.

TEMPORAL BONE (*Os temporale*) (Fig. 1–4)

The paired temporal bones consist of squamous, tympanic and petrous parts. The squamous part (*Pars*

squamosa) forms the ventrolateral part of the cranium. In young animals it is placed sagittally, while in mature animals it lies transversely. Externally, it fuses dorsally with the parietal bone, rostrally with the frontal bone, ventrally with the wing of the basisphenoid and the tympanic temporal bones and, in some specimens, also caudally with the petrous temporal bone as well as with the lateral and squamous occipital bones. Intracranially, it fuses dorsally and dorsorostrally with the parietal bone, ventrally with the basisphenoid bone and caudally with the petrous temporal bone. It has a zygomatic process (*Processus zygomaticus*) that projects rostrally to join the temporal process of the zygomatic bone. The two processes, together with the zygomatic process of the maxilla, form the zygomatic arch (*Arcus zygomaticus*). The ventral surface of the root of the zygomatic process is concave to form the mandibular fossa (*Fossa mandibularis*) that bears an articular surface (*Facies articularis*) for articulation with the condyle of the mandible. The caudal border of the articular surface ends on a low retro-articular process (*Processus retro-articularis*). Caudally to the zygomatic process is the large tympanic incisure (*Incisura tympanica*). The caudal part of the incisure forms the retrotympanic process (*Processus retrotympanicus*). Together, the retro-articular process, tympanic incisure and retrotympanic process form a bony canal that leads to the external acustic meatus. (The latter is part of the tympanic temporal bone.) The greater part of the squamous temporal bone is aerated by extensions of the frontal sinus.

The tympanic part (*Pars tympanica*), forms the caudoventral part of the cranium. Externally, it is bulbous in young animals, whereas it is rostrocaudally flattened and caudally somewhat triangular with the apex in mature animals. The bulbous nature of the bone is due to the tympanic bulla (*Bulla tympanica*), that is incompletely subdivided internally by many septae. Furthermore, the cavity of the bulla extends into the lateral part of the occipital and the petrous temporal bones. The tympanic temporal bone is bounded medially by the basi-occipital and basisphenoid bones, caudally by the lateral and squamous parts of the occipital bone and rostrally by the squamous temporal bone and the wing of the basisphenoid bone. Three foramina and one canal are associated with the external boundaries of the tympanic temporal bone. These are the carotid canal along its medial border, the jugular foramen along the caudomedial border, the stylomastoid foramen along the caudolateral border and the oval foramen along the cranial border. Furthermore, the medial angle of the bone contains the *Canalis musculotubarius* for the Eustachian tube and the lateral angle contains the external acustic meatus (*Meatus acusticus externus*) that leads to the cavity of the middle ear. The tympanic temporal bone also bears a muscular process (*Processus muscularis*). The latter is long and slender, and lies in the rostral wall of the musculotubular canal.

The petrous part of the temporal bone (*Pars petrosa*) forms the caudoventral part of the cranium. It fuses medially and caudally with the tympanic temporal bone, dorsally with the occipital and parietal bones and cranially with the squamous temporal and basisphenoid bones. A vertical ridge, the *Crista partis petrosa*, divides its inner (medial) surface into a rostral part that forms the ventrocaudal part of the middle cranial fossa, and a caudal part that forms the rostroventral part of the caudal cranial fossa. The caudal surface bears the internal acustic meatus (*Meatus acusticus internus*) and the rostral part is deeply grooved by the middle meningeal artery. Ventromedially, the rostral border is notched to form the caudal wall of the oval foramen and its medial border contains the carotid canal. The opening into the temporal canal lies along the dorsal border of the bone, in the fissure between the squamous and petrous temporal bones. Externally, the styloid process that lies medially to the stylomastoid foramen, is the only part of the petrous temporal bone that is visible on the surface of the skull. In some young specimens, however, a small, oval area of the bone is visible on the surface between the squamous occipital bone, lateral part of the occipital bone and squamous temporal bone. The petrous temporal bone is aerated from the tympanic bulla.

FRONTAL BONE (*Os frontale*) (Fig. 2, 4, 5)

The paired frontal bones consist of squamous, temporal, and orbital parts, each with external and internal (intracranial) surfaces.

Externally, each bone fuses rostrodorsally with the nasal and incisive bones, rostroventrally with the maxilla and lacrimal bones, caudoventrally with the squamous temporal and parietal bones and caudodorsally with the parietal bone. The left and right frontal bones fuse with each other along the dorsomedian plane. The caudoventral part of the frontal bone does not fuse with the maxillary tuberosity, but forms a large and deep fissure. The *Foramen rotundum* opens into the caudal part of the fissure. Furthermore, the external openings of the ethmoidal foramen (*Foramen ethmoidale*), the optic canal (*Canalis opticus*) and the orbital fissure (*Fissura orbitalis*) are located in a notch along the caudoventral part of the bone, just dorsally to the fissure. A vertical plate of bone from the wing of the presphenoid bone separates the optic canal from the orbital fissure.

The squamous part (*Squama frontalis*) is narrow and lies transversely across the roof of the skull. The lateral part of the frontal bone lies vertically and is divided by a very prominent ridge, the *Crista orbitotemporalis*, into a narrow, caudally situated, temporal part (*Facies temporalis*), and a wider, rostrally

situated orbital part (*Facies orbitalis*). The junction between the squamous and orbital parts forms a rounded supraorbital ridge (*Margo supraorbitalis*), and the junction between the squamous and temporal parts forms the rostral part of the short, temporal line (*Linea temporalis*). The temporal line, supraorbital ridge and orbitotemporal crest meet to form a small zygomatic process (*Processus zygomaticus*).

Intracranially, the frontal bones form the dorsal and lateral parts of the rostral cranial fossa. They fuse caudally with the parietal bones, caudoventrally with the presphenoid bone, rostroventrally with the ethmoid bones and along the dorsal and rostral median planes, with each other. The intracranial opening of the ethmoidal foramen lies on the suture between the frontal, ethmoid and presphenoid bones. A prominent ridge along the ventral part of the bone forms the lateral border of the ethmoidal fossa.

BASISPHENOID BONE (*Os basisphenoidale*) (Fig. 2, 3)

The basisphenoid bone forms the floor of the middle cranial cavity and consists of a body, two wings and two pterygoid processes. The body (*Corpus*) fuses caudally with the basi-occipital bone and rostrally with the presphenoid bone. The caudal part of its dorsal surface is slightly concave and, together with the concavity of the basi-occipital bone, it forms the hypophyseal fossa (*Fossa hypophysialis*). The body of the basisphenoid bone is excavated rostrally by the left and right maxillary tuberosities. The two excavations or hollows are separated from each other by a median septum and the maxillary tuberosities within them contain the developing molar teeth. Furthermore, the rostral border of the body bears a median incisure and, just caudally to that, a foramen that leads to the hollows and developing teeth. The body is aerated from the presphenoid sinus.

Each wing (*Ala*) of the basisphenoid bone is small and projects laterally from the body. Intracranially, it fuses laterally with the squamous temporal bone and rostrally, over a short distance, with the presphenoid bone. Caudally, the wing is separated from the petrous temporal bone by a wide notch that forms the rostral border of the oval foramen. Its rostral border contains the large round foramen and it forms the floor of the orbital fissure.

Each pterygoid process (*Processus pterygoideus*) is large and extends rostrally and ventrally as a thin plate of bone. It covers the greater part of the maxillary tuberosity, but does not fuse with it. Dorsally, it fuses with the squamous temporal bone, and its rostral edge is continuous with the orbitotemporal crest of the frontal bone. Ventrolaterally, it fuses with the pterygoid bone and ventromedially, with the perpendicular part of the palatine bone. In old animals its caudal border fuses with the tympanic temporal bone. A large foramen that leads to the space between the maxillary tuberosity and the pterygoid process is present close to its caudodorsal border.

PRESPHENOID BONE (*Os presphenoidale*) (Fig. 2, 3)

The presphenoid bone consists of a body (*Corpus*) and two small wings (*Alae*). Intracranially, it forms the caudal floor of the rostral cranial cavity. It fuses rostrally with the frontal and ethmoid bones and caudally with the parietal bone and with the wings and body of the basisphenoid bone. The ventral border, at the junction between the body and the wings, is notched to form the roofs of the orbital fissures. Furthermore, the ventral border of the body covers the maxillary tuberosities, but do not fuse with them. The body is aerated by the sphenoidal sinus (also see ethmoid bone). Each wing extends laterally and dorsally from the body and bears the optic canal (*Canalis opticus*). Externally, it divides the ventral incisure of the frontal bone so that the optic canal lies medially, and the orbital fissure laterally, to the wing (see frontal bone).

PTERYGOID BONE (*Os pterygoideum*) (Fig. 2, 3, 4)

The paired pterygoid bones are thin, perpendicular plates of bone that project rostroventrally from the basisphenoid bone. The rostral extremity of each bone is slightly enlarged and free to form the hamulus (*Hamulus pterygoideus*). The pterygoid bone presents two surfaces, an external surface that is free, and an internal surface that is related to the maxillary tuberosity. Externally, it fuses rostrally with the perpendicular part of the palatine bone, caudodorsally, with the body of the basisphenoid, and ventrally, with the pterygoid process of the basisphenoid.

ETHMOID BONE (*Os ethmoidale*) (Fig. 2)

The ethmoid bone forms the rostral border of the cranial cavity. It consists of two cribriform plates (*Lamina cribrosa*) separated from each other by a perpendicular plate (*Lamina perpendicularis*) and two ethmoidal labyrinths of turbinate bones (*Labyrinthus ethmoidalis*). In older animals, the rostral border of the perpendicular plate fuses with the ossified caudoventral part of the nasal septum. Intracranially, the caudal, free edge of the perpendicular plate forms a prominent crest, the *Crista galli*, and rostrally, it extends into the nasal cavity to separate the left and right ethmoidal labyrinths. The dorsal surface of each labyrinth is covered by a thin plate of bone, the *Lamina tectoria*, that extends laterally from the perpendicular plate. The ventral surface is covered by the *Lamina basalis* and the lateral surface is covered by the *Lamina orbitalis*. Each ethmoidal labyrinth, therefore, is covered laterally, ventrally, medially and dorsally by plates of ethmoid bone. The ethmoidal turbinate bones, compared with those of domestic animals, are surprisingly small. The perpendicular plate of the ethmoid bone is aerated from the nasal cavity via two small openings situated between the ventral ethmoid

turbinates and the basal laminas. The sinus extends caudally into the presphenoid and basisphenoid bones and rostrally, into the sinus of the vomer and the ossified part of the nasal septum.

VOMER (*Vomer*) (Fig. 2, 3)

The vomer is a thin, perpendicular keel-shaped bone that divides the floor of the nasal cavity and roof of the nasopharynx into left and right parts. Its caudodorsal part is attached to the presphenoid, ethmoid and perpendicular parts of the palatine bones and its rostroventral part lies in a groove between the palatine processes of the maxillary bones. The caudodorsal surface of the vomer is grooved to accommodate the perpendicular lamina of the ethmoid bone. The caudal part of the vomer is aerated from the ethmoidal and presphenoidal sinuses.

Bones of the face (*Ossa faciei*)

NASAL BONE (*Os nasale*) (Fig. 2–5)

The paired nasal bones are small and pyramid-shaped with caudal bases and rostral apexes. The base of each pyramid fuses with the frontal bone; its ventrolateral border fuses with the incisive bone; the ventromedial border fuses with the ethmoid bone; and the medial surfaces fuse with each other in the median plane. Rostromedially, the apexes fuse along the midline to form a single, pronounced nasal process. One or more large openings along the ventrolateral borders lead from the nasal cavity to the sinusus of the nasal bones. Each sinus extends into the incisive, maxillary, lacrimal, frontal, parietal, temporal and occipital bones.

LACRIMAL BONE (*Os lacrimale*) (Fig. 4, 5)

The paired lacrimal bones are small and elongated, each with a prominent dorsal process and wedged in between the maxilla and the frontal bone. Its medial surface fuses with the maxilla and its caudal border fuses for some distance with the frontal bone. The caudal part of the bone is aerated from the maxillary sinus.

INCISIVE BONE (*Os incisivum*) (Fig. 2–5)

The paired incisive bones are large and, together with the palatine processes of the maxillary bones, form the most rostral part of the skull. Each bone consists of a body with a rostrolateral alveolar process, a rostromedial palatine process and a caudal nasal process. The bones fuse laterally and ventrally with the maxillae, caudolaterally with the frontal bones, caudally with the nasal bones and along the median plane with each other. Together, they form the ventral and lateral walls of the bony entrance to the nasal cavity.

The dorsomedial surfaces of the palatine processes are concave, forming a large, oval depression rostrally to the osseous nasal opening. In bulls, the sinus between the external and internal laminae of the palatine process becomes progressively smaller until the two laminae eventually fuse with each other. The resultant solid plate of bone is progressively replaced by the underlying palatine process of the maxilla until, in old bulls, the maxilla breaks through to the surface so that the medial part of the oval nasal depression is formed by the maxilla and not by the incisive bone.

Laterally, the alveolar process bears a large alveolus for the second incisor or tusk. The alveolus extends caudally into the body of the incisive bone and, in the adult, is separated from the nasal cavity by only a thin plate of bone. In the adult male, the incisive bone is more massive than in the female and much more expanded rostrally (Fig. 5B, 5C).

The body and nasal process of the incisive bone is aerated via the frontal sinus, while the palatine process is aerated via a separate opening situated in the dorsal part of the nasomaxillary aperture.

PALATINE BONE (*Os palatinum*) (Fig. 2, 3)

The paired palatine bones are small and carry perpendicular and horizontal laminae. The horizontal lamina (*Lamina horizontalis*) fuses rostrally and laterally with the palatine process of the maxilla, and along the median plane with each other, to form the caudomedial part of the hard palate. The perpendicular lamina (*Lamina perpendicularis*) consists of a thin plate of bone that fuses laterally with the maxillary tuberosity, caudolaterally with the pterygoid process of the basisphenoid bone and caudomedially with the pterygoid bone. A single palatine foramen (*Foramen palatinum majus*) is present along the lateral border of the horizontal lamina, or on the suture between the horizontal lamina and the palatine process of the maxilla.

MAXILLA (*Maxilla*) (Fig. 2–4)

The paired maxillae are large and irregularly shaped. Each bone consists of a body, with frontal, palatine, zygomatic, and alveolar processes. It fuses rostrodorsally and rostroventrally with the incisive bone, caudodorsally with the frontal and lacrimal bones, ventromedially with the incisive and palatine bones, dorsomedially with the ethmoid bone and laterally with the zygomatic bone. The caudal parts of the left and right maxillary palatine processes (*Processus palatinus*) fuse with each other along the median plane to form the middle part of the hard palate. The rostral part of the palatine processes do not fuse with each other, therefore the rostral part of the hard palate is incomplete along the median plane.

The body (*Corpus maxillae*) has orbital, facial, pterygopalatine and nasal surfaces. Caudally, it bears a

massive maxillary tuberosity (*Tuber maxillae*) that extends to the level of the oval foramen and contains the developing molar teeth. The tuberosity is covered laterally by the pterygoid process of the basisphenoid bone, caudally by the pterygoid bone and medially by the perpendicular lamina of the palatine bone. Laterally, the large infraorbital canal (*Canalis infraorbitalis*) connects the maxillary foramen (*Foramen maxillare*), that lies in the pterygopalatine fossa, with the infraorbital foramen, (*Foramen infraorbitale*). A foramen along the ventromedial wall of the infraorbital canal, leads to the incisive canal that contains the blood vessels and nerves of the tusk. In addition, numerous small foramina are also present in the canal. The nasal surface of the body forms the ventrolateral wall of the nasal cavity and the lateral wall of the nasopharynx, and its surface contains many vascular grooves. It has a large nasomaxillary aperture (*Apertura nasomaxillaris*) along its dorsal border and one or more smaller openings along its ventrorostral part. All the openings lead from the nasal cavity to the maxillary sinus.

The frontal process (*Processus frontalis*) extends dorsomedially from the body of the maxilla and fuses with the frontal and lacrimal bones. It lies dorsally to the infraorbital foramen and forms the ventromedial part of the bony orbit.

The zygomatic process (*Processus zygomaticus*) projects caudolaterally from the lateral wall of the infraorbital canal, fuses caudally with the zygomatic bone and forms the ventrolateral part of the bony orbit.

The horizontal palatine process (*Processus palatinus*) is large and projects rostrally and medially from the body of the maxilla. The left and right caudal parts fuse with each other to form the hard palate between the cheek teeth. Rostrally to the cheek teeth, the palatine processes do not fuse with each other, but with the incisive bones. The rostrolateral part of the palatine process is concave to accommodate the incisive bone and tusk (see also Incisive bone), while the medial part is flat, to form the rostral part (rostrally to the cheek teeth) of the hard palate.

The alveolar process (*Processus alveolaris*) projects ventrally from the body and bears the alveolus of the cheek teeth.

The entire maxilla, excluding the alveolar process, is aerated from the nasal cavity.

ZYGOMATIC BONE (*Os zygomaticum*) (Fig. 3–5)

The paired zygomatic bones are long and flat. In the young animal, the bones are straight, but in old animals, they curve gently from lateral to medial. Each bone fuses rostrally with the zygomatic process of the maxilla and caudally with the zygomatic process of the squamous temporal bone. The line of fusion with the zygomatic process of the temporal bone is oblique dorsoventrally, whereas the line of fusion with the zygomatic process of the maxilla is perpendicular.

MANDIBLE (*Mandibula*) (Fig. 6)

The mandible consists of left and right halves that are fused rostrally. Each half consists of a horizontal body (*Corpus mandibulae*) and a vertical ramus (*Ramus mandibulae*).

The body of the mandible consists of a rostral incisive part (*Pars incisiva*) and a caudal molar part (*Pars molaris*). Rostrally, the left and right incisive parts fuse with each other in the midline. A thin process projects rostrally from the fusion line. The incisive parts do not carry any teeth.

The molar part contains the alveolus for the cheek teeth. One or more lateral mental foramina (*Foramina mentalia lateralia*) are present on the lateral surface of the incisive and molar parts, while a single medial mental foramen (*Foramen mentale mediale*) is present mostly on the medial surface of the incisive part of the mandible.

The mandibular ramus is trapezoid in outline. Its caudal border is thick and curves dorsally from the ventral border of the mandibular body, forming a rounded mandibular angle (*Angulus mandibulae*). It meets the rostral border at the condylar process (*Processus condylaris*). The condylar process bears the smooth articular surface, *Caput mandibulae*. The thin rostral border of the ramus bears the coronoid process (*Processus coronoideus*). The latter lies midway between the junction of the ramus and body ventrally, and the condylar process dorsally (almost at the level of the cheek teeth). Laterally, the ramus is concave, to form the masseteric fossa (*Fossa masseterica*). The medial surface of the ramus is divided into rostral and caudal parts by a vertical ridge. Rostrally to the ridge is a concave area, the pterygoid fossa (*Fossa pterygoidea*), for the attachment of the medial pterygoid muscle. Caudally to the ridge, lies the large mandibular foramen (*Foramen mandibulae*) that leads to the mandibular canal (*Canalis mandibulae*) for the mandibular nerves and blood vessels. A shallow depression, the pterygoid fovea (*Fovea pterygoidea*) for the attachment of the lateral pterygoid muscles, lies dorsally to the mandibular foramen.

The skull as a whole

In the mature African elephant, the skull takes the form of a four-sided pyramid with its base at the nuchal surface of the occipital bone and its apex at the rostral part of the incisive bone.

The skull is divided into cranial and facial regions. The occipital, parietal, temporal, interparietal, basi-

sphenoid, presphenoid, pterygoid, frontal, ethmoid and vomer bones contribute to the cranial region, whereas the nasal, lacrimal, maxilla, incisive, palatine, zygomatic and mandibular bones form the facial region.

The division between the cranial and facial regions is determined by the position of the cribriform plate of the ethmoid bone which lies deep within the skull. Externally, it corresponds to the rostral border of the temporal fossa.

The cranial part of the roof of the skull is formed by the parietal and frontal bones. The roof merges into the lateral surface of the skull at the temporal line. The broadest part of the roof is caudal.

The lateral surface of the cranial region consists of bones forming the temporal fossa, i.e. the caudolateral part of the frontal bone, lateral part of the parietal bone, the squamous part of the temporal bone, the zygomatic process of the temporal bone, the zygomatic bone and the zygomatic process of the maxilla. The latter also contributes to the face. The temporal fossa is situated dorsally and medially to the zygomatic arch. It is bordered rostrally, dorsally and caudally by the temporal line that extends from the frontal bone over the parietal bone onto the squamous temporal bone. In young animals, the caudal part of the line is indistinct and has a rostrocaudal orientation, whereas in old animals, it lies transversely.

In the facial region of the skull, the nasal bones are situated dorsocaudally and are very small. Ventrally and rostrally to the nasal bones, the incisive bones extend rostrally to form the apex of the pyramid. The osseous external nares are large. They are bounded dorsally by the nasal bones and laterally and ventrally by the incisive bones. In the midline, the nares are confluent, i.e. there is no bony separation between the two. The bony orbit lies rostrally to the temporal fossa. It is caudally incomplete. The orbit is bounded dorsally and medially by the frontal and lacrimal bones and ventrally by the zygomatic process of the maxilla and rostral part of the zygomatic bone. Caudo-medially, it contains the ethmoid foramen, optic foramen and orbital fissure. All these foramina are laterally covered by the pterygoid crest. The pterygopalatine fossa lies ventrally to the orbit. Its medial wall is formed by the maxilla, including the maxillary tuber. Three foramina are present: the maxillary foramen leading to the infraorbital canal, the phenopalatine foramen opening into the nasal cavity and the caudal palatine foramen which connects with the palatine canal.

The basal surface of the skull is divided into cranial and palatine regions. The choanae are situated at the border between these two regions.

Externally, the base of the cranial region is bounded by the lateral and basal parts of the occipital bone, the tympanic part of the temporal bone and the basisphenoid bone. All the foramina lie around the periphery of the tympanic temporal bone. They are from caudal to rostral: the jugular foramen, the carotid canal, the musculotubural canal, the oval foramen and the spinous foramen. The facial part of the base of the skull (hard palate) is formed from caudal to rostral by the palatine, maxillary and incisive bones.

The cavities of the skull

The skeleton of the skull forms two cavities, the cranial cavity in the cranial region and the nasal cavity in the facial region. The cranial cavity is divided into three fossae: rostral, middle and caudal. The caudal fossa houses the cerebellum; the middle and rostral fossae, the cerebrum. The walls of the cranial cavity bear negative impressions of the gyri and sulci of the cerebrum. The rostral fossa contains the ethmoidal fossae for the olfactory bulbs.

The nasal cavity is relatively small compared with the cranial cavity. It extends rostrally from the external nasal opening and ventrocaudally to the choanae. It is divided into two halves by the nasal septum.

Caudally, the ethmoturbinate bones project rostrally and laterally into the nasal cavity. All the turbinate bones originate from the cribriform plate. However, the inner five (endoturbinates) do not reach the surrounding bones, whereas the outer 30 (ectoturbinates) do. The turbinate bones emerge from the cribriform plate as a single process, but soon divide into primary, secondary and even tertiary processes, so that a very complicated labyrinthine space is formed.

The paranasal sinuses are cavities in the skull bones between the inner and outer laminae. Numerous thin plates of bone span these cavities to connect the inner and outer laminae. All the bones of the cranium and face are involved, except for a small area dorsal to the foramen magnum. In young animals, communication of these cavities with the nasal cavity is through one or two foramina situated in the nasal bone. In adult animals three to four foramina are present. A large foramen in the caudomedial part of the maxillary bone connects the maxillary sinus with the nasal cavity.

The ratio between the length (taken from the *Foramen magnum* to the rostral tip of the incisive bone) and height (taken from the basi-occipital bone to the highest point of the cranium) of the skull in young animals is 1,66:1, whereas in adult animals it is 0,75:1.

DISCUSSION

Sikes (1971) and Eales (1928) noted the absence of the hypoglossal and condylar canals as was reported in this study. The communication between the sinus

KEYS: FIG. 1–6

1 Occipital bone

1a *Squama occipitalis*
1b *Pars basalis*
1c *Pars lateralis*
1d *Foramen magnum*
1e *Linea nuchalis*
1f *Crista occipitalis externa*
1g *Condylus occipitalis*
1h *Foramina mastoidea*
1i *Fissura petro-occipitalis*
1j *Foramen jugulare*
1k *Foramen stylomastoideum*
1l *Canalis caroticus*

2 Parietal bone

2a *Linea temporalis*
2b *Crista spheno-orbitalis*

3 Interparietal bone

3a *Processus tentoricus*

4 Temporal bone

4a *Pars squamosa*
4b *Pars tympanica*
4c *Pars petrosa*
4d *Processus zygomaticus*
4e *Fossa mandibularis*
4f *Facies articularis*
4g *Processus retro-articularis*
4h *Incisura tympanica*
4i *Processus retrotympanicus*
4j *Meatus acusticus externus*
4k *Bulla tympanica*
4l *Canalis musculotubarius*
4m *Processus styloideus*
4n *Processus muscularis*
4o *Crista partis petrosa*
4p *Meatus acusticus internus*

5 Frontal bone

5a *Squama frontalis*
5b *Facies temporalis*
5c *Facies orbitalis*
5d *Crista orbitotemporalis*
5e *Margo supra-orbitalis*
5f *Processus zygomaticus*
5g *Foramen rotundum*
5h *Fissura orbitalis*
5i *Foramen ethmoidale*

6 Basisphenoid bone

6a *Corpus*
6b *Ala*
6c *Processus pterygoideus*
6d *Fossa hypophysealis*
6e Median septum between the two bones
6f Developing molar tooth
6g *Foramen ovale*
6h Round foramen in the pterygoid process of the basisphenoid

7 Presphenoid bone

7a *Corpus*
7b *Ala*
7c *Canalis opticus*

8 Pterygoid bone

8a *Hamulus pterygoideus*

9 Ethmoid bone

9a *Lamina cribrosa*
9b *Lamina perpendicularis*
9c *Labyrinthus ethmoidalis*
9d *Crista galli*
9e *Lamina tectoria*
9f *Lamina basalis*
9g *Lamina orbitalis*
9h Ossified part of the nasal septum

10 Vomer

11 Nasal bone

11a *Processus nasalis*
11b Foramen leading to the sinus in the nasal bone

12 Lacrimal bone

12a *Processus dorsalis*

13 Incisive bone

13a *Corpus*
13b *Processus alveolaris*
13c *Processus palatinus*
13d *Processus nasalis*

14 Palatine bone

14a *Lamina horizontalis*
14b *Lamina perpendicularis*
14c *Foramen palatinum major*

15 Maxilla

15a *Corpus*
15b *Processus frontalis*
15c *Processus palatinus*
15d *Processus zygomaticus*
15e *Processus alveolaris*
15f *Canalis infraorbitalis*
15g *Foramen maxillare*
15h *Foramen infraorbitale*
15i *Tuber maxillae*
15j *Aperturae nasomaxillaris*

16 Zygomatic bone

17 Mandible

17a *Corpus mandibulae*
17b *Ramus mandibulae*
17c *Pars incisiva*
17d *Pars molaris*
17e *Foramina mentalia lateralia*
17f *Foramen mentalia mediale*
17g *Angulus mandibulae*
17h *Processus condylaris*
17i *Caput mandibulae*
17j *Processus coronoideus*
17k *Fossa masseterica*
17l *Fossa pterygoidea*
17m *Foramen mandibulae*
17n *Canalis mandibulae*
17o *Fovea pterygoidea*

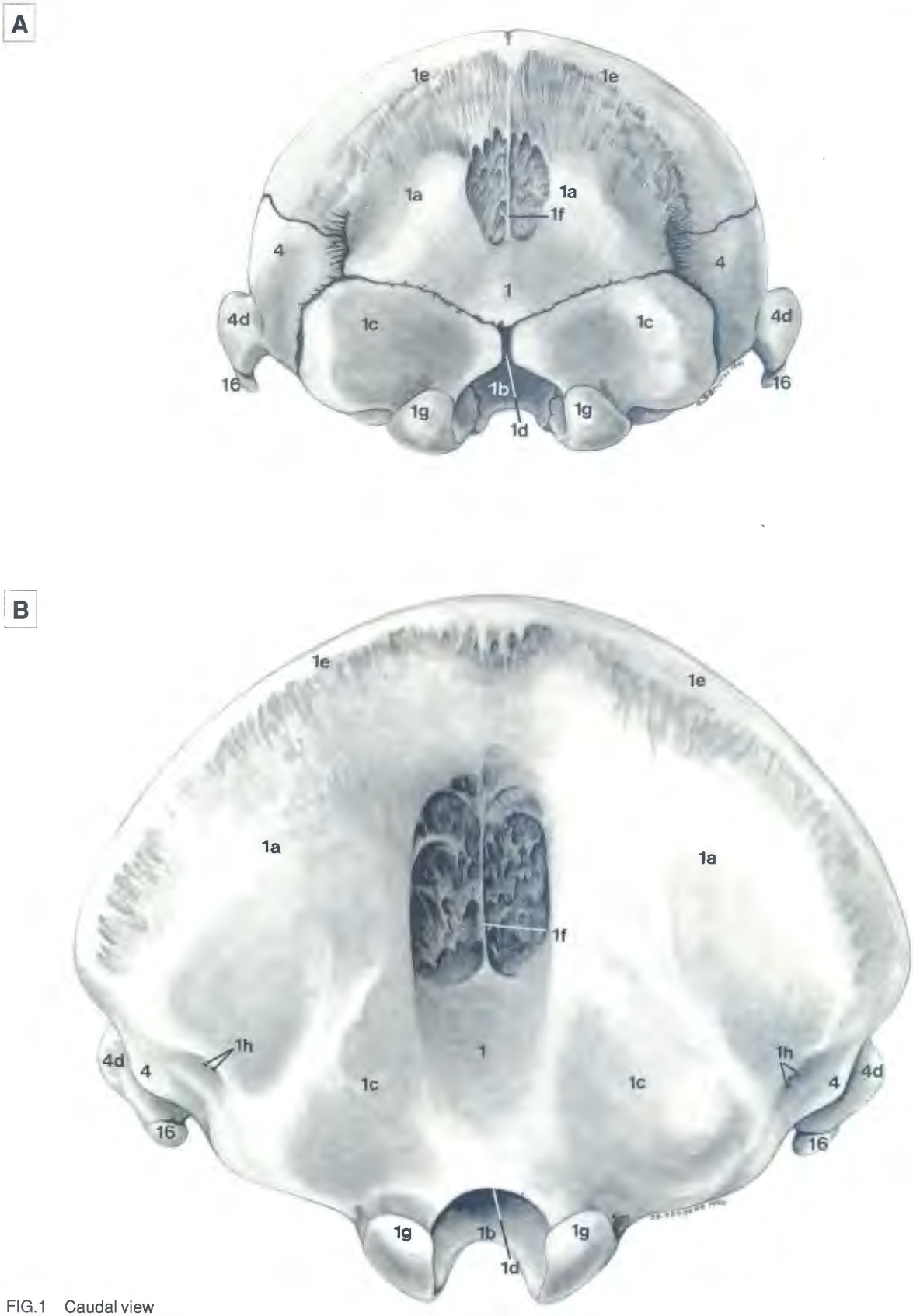

FIG.1 Caudal view
A. Juvenile
B. Adult

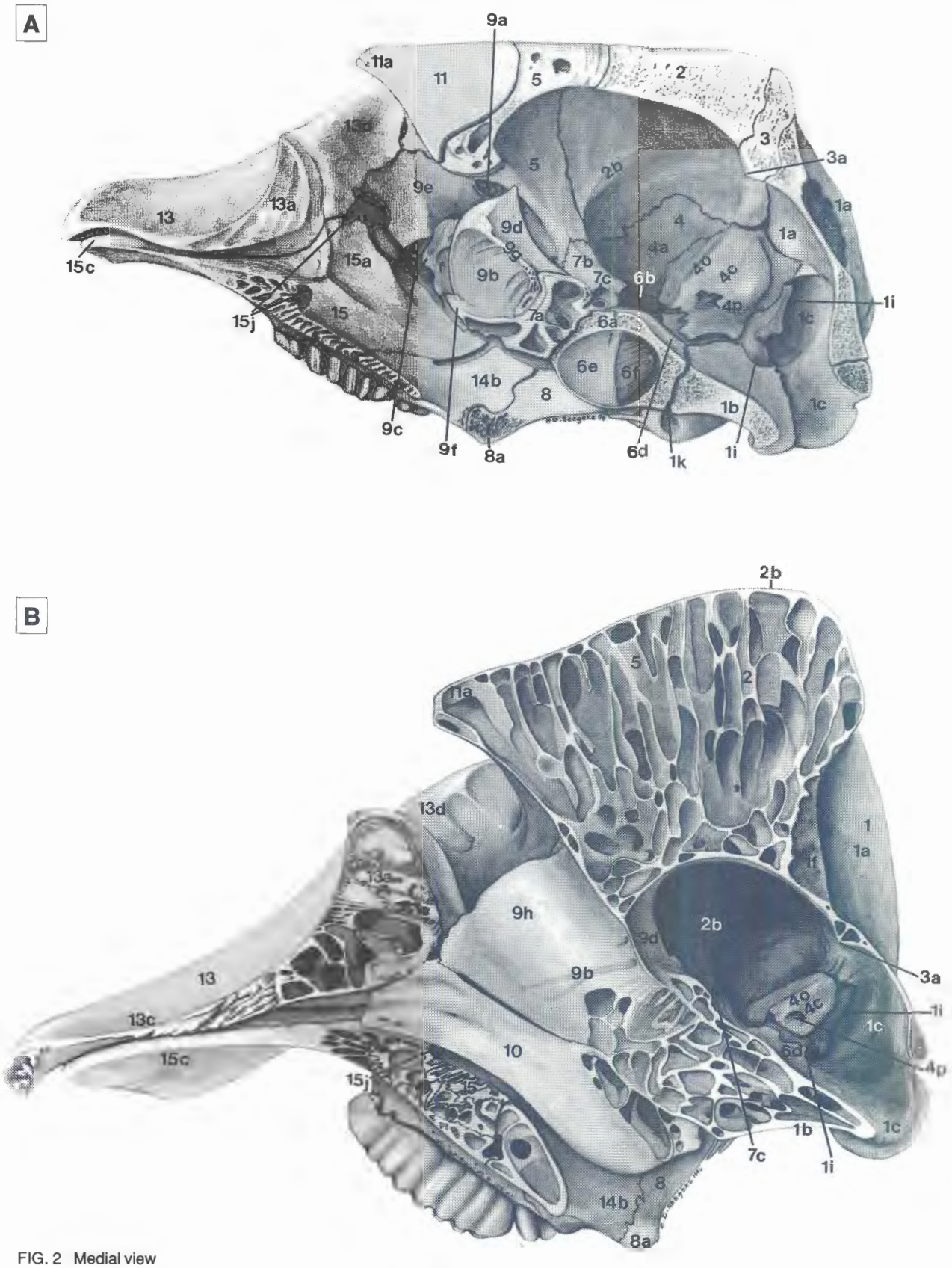

FIG. 2 Medial view
A. Juvenile
B. Adult

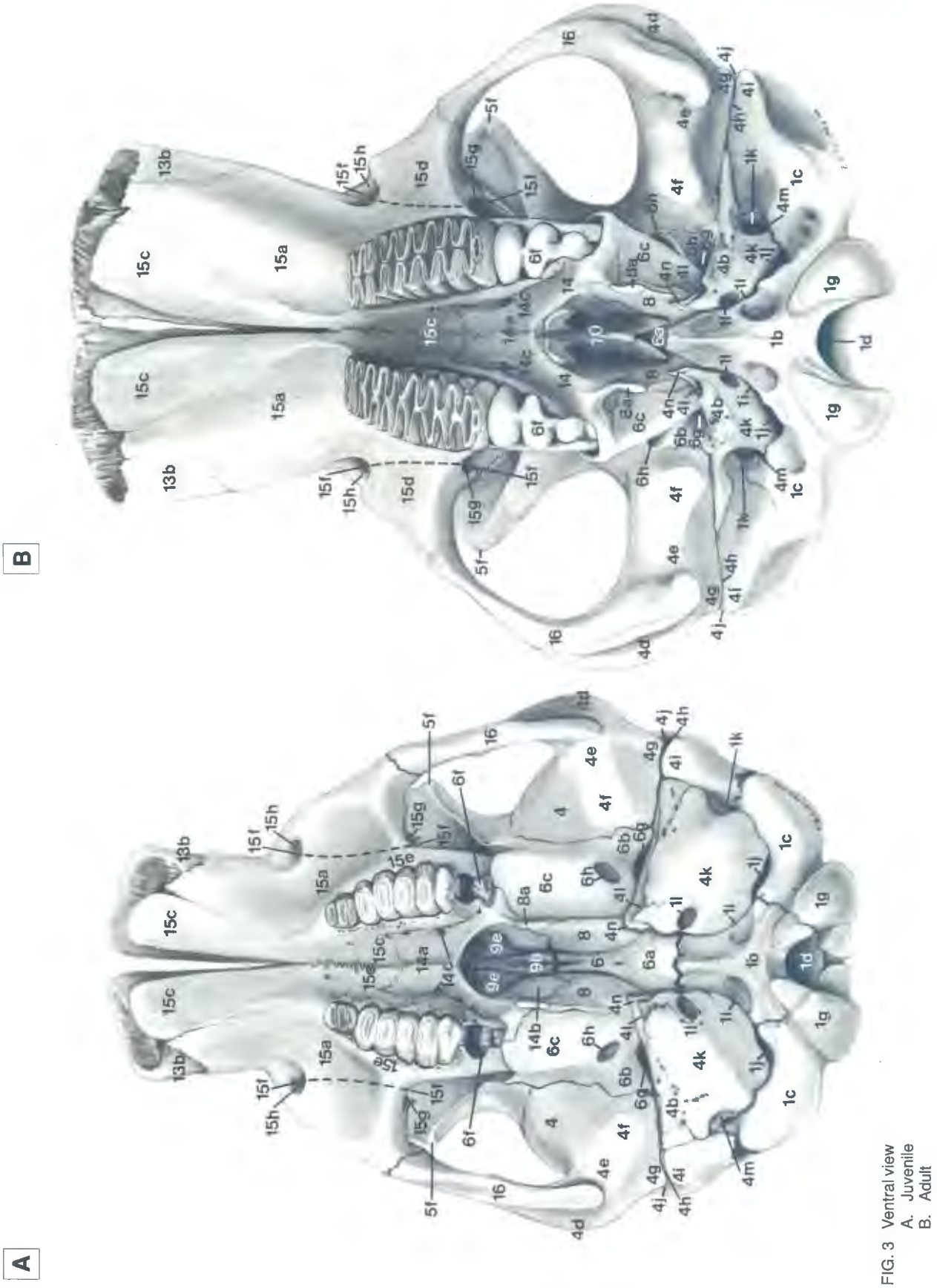

FIG. 3 Ventral view
A. Juvenile
B. Adult

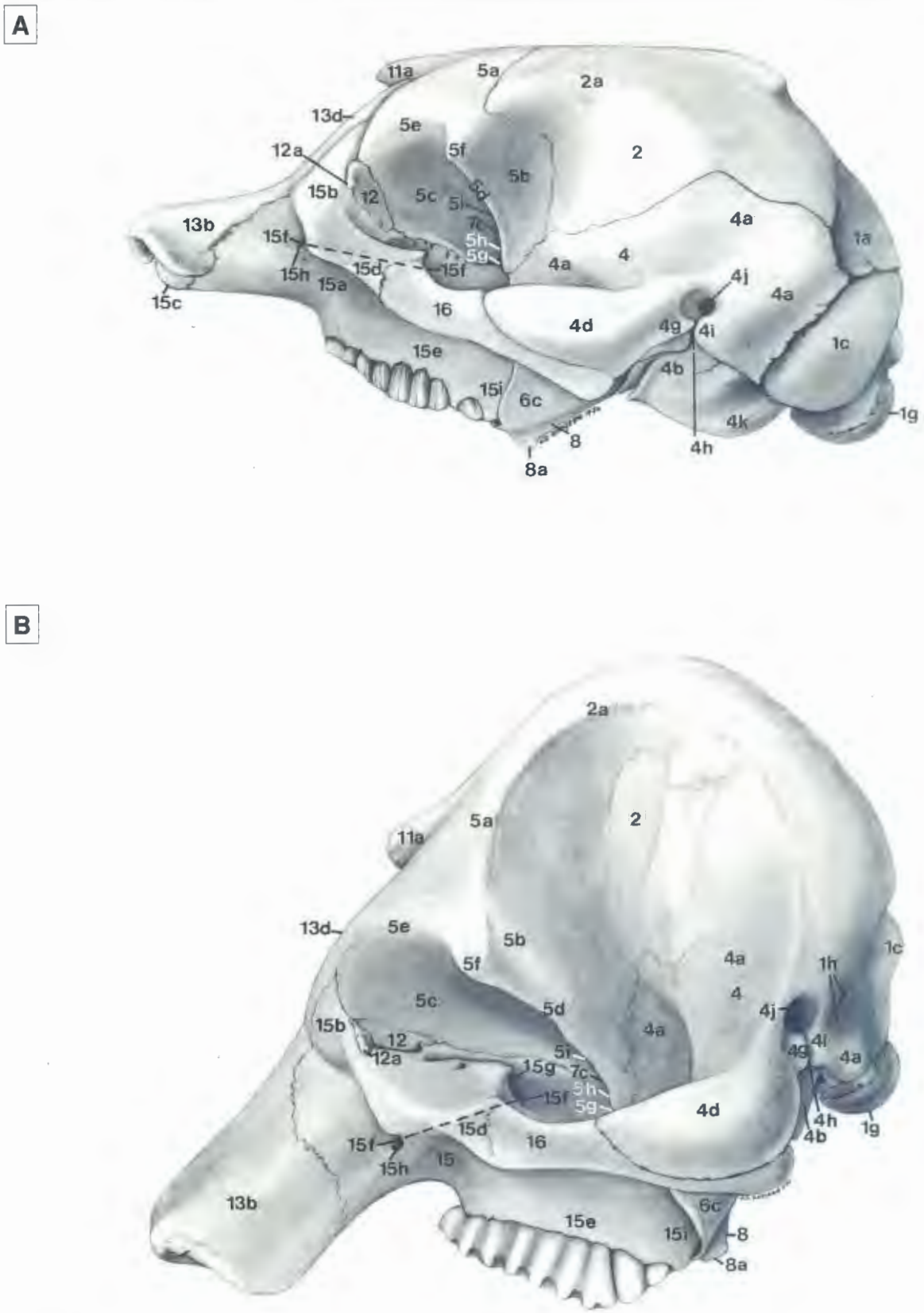

FIG. 4 Lateral view
A. Juvenile
B. Adult

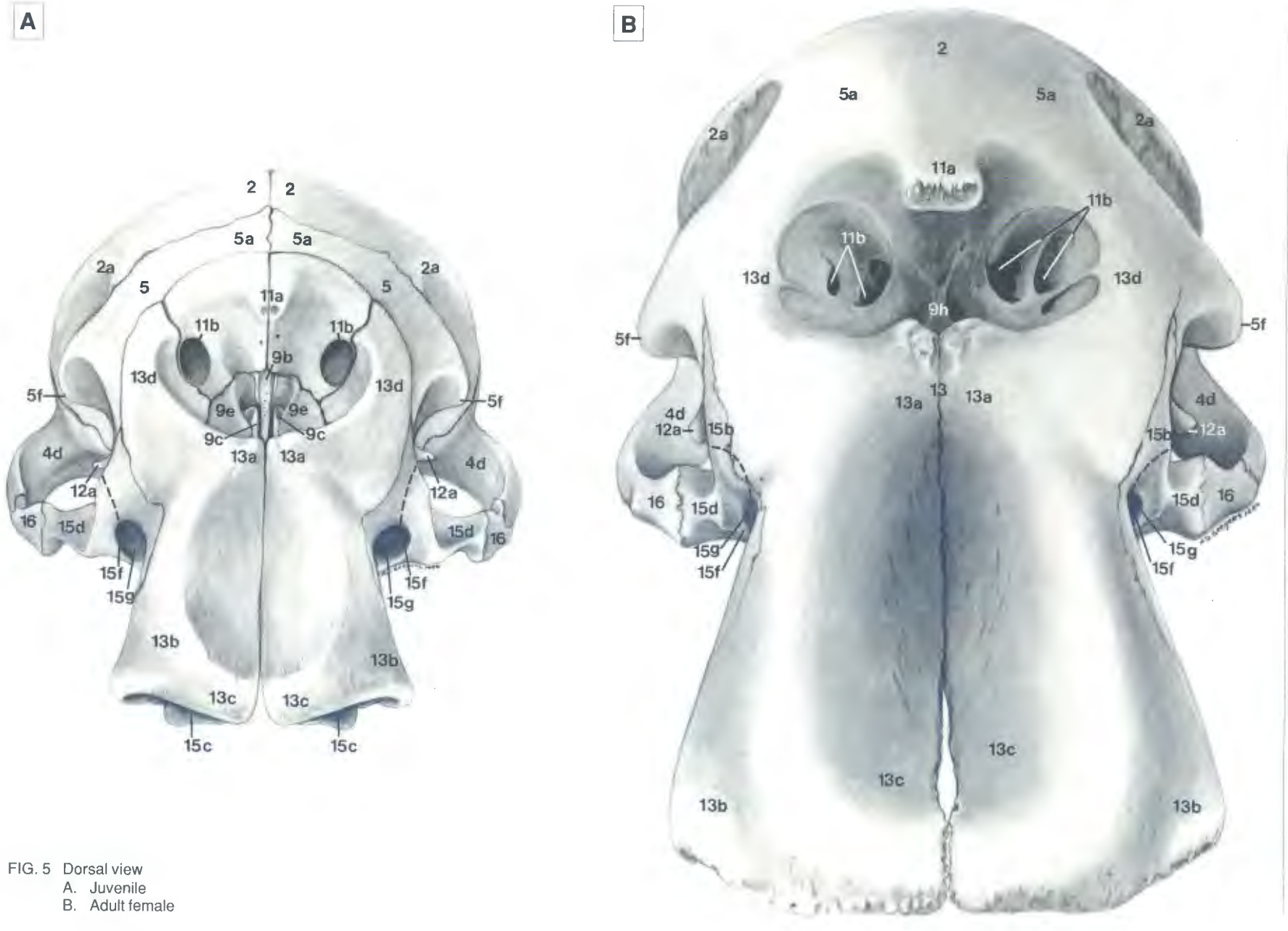

FIG. 5 Dorsal view
A. Juvenile
B. Adult female

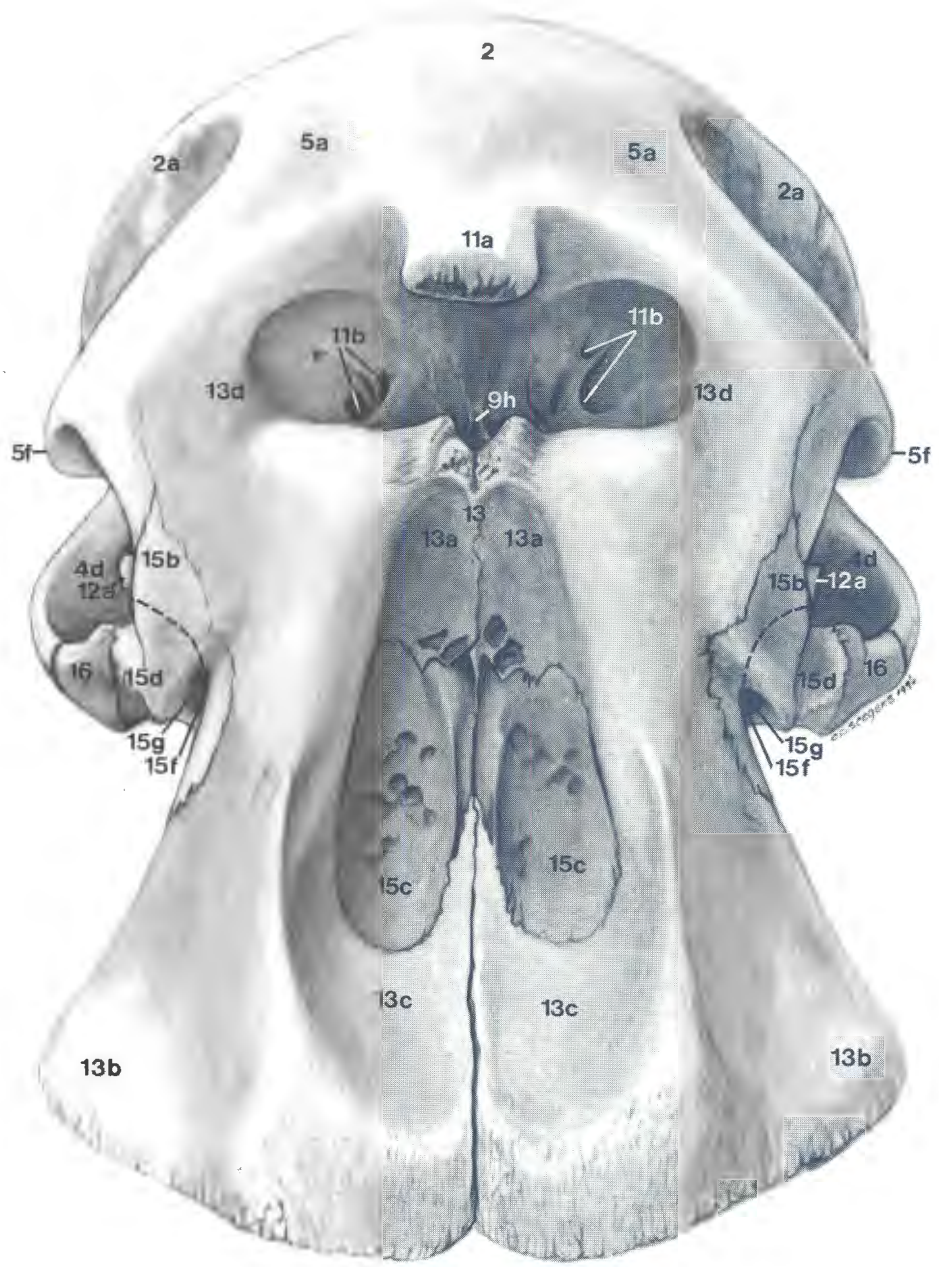

FIG. 5 Dorsal view
C. Adult male

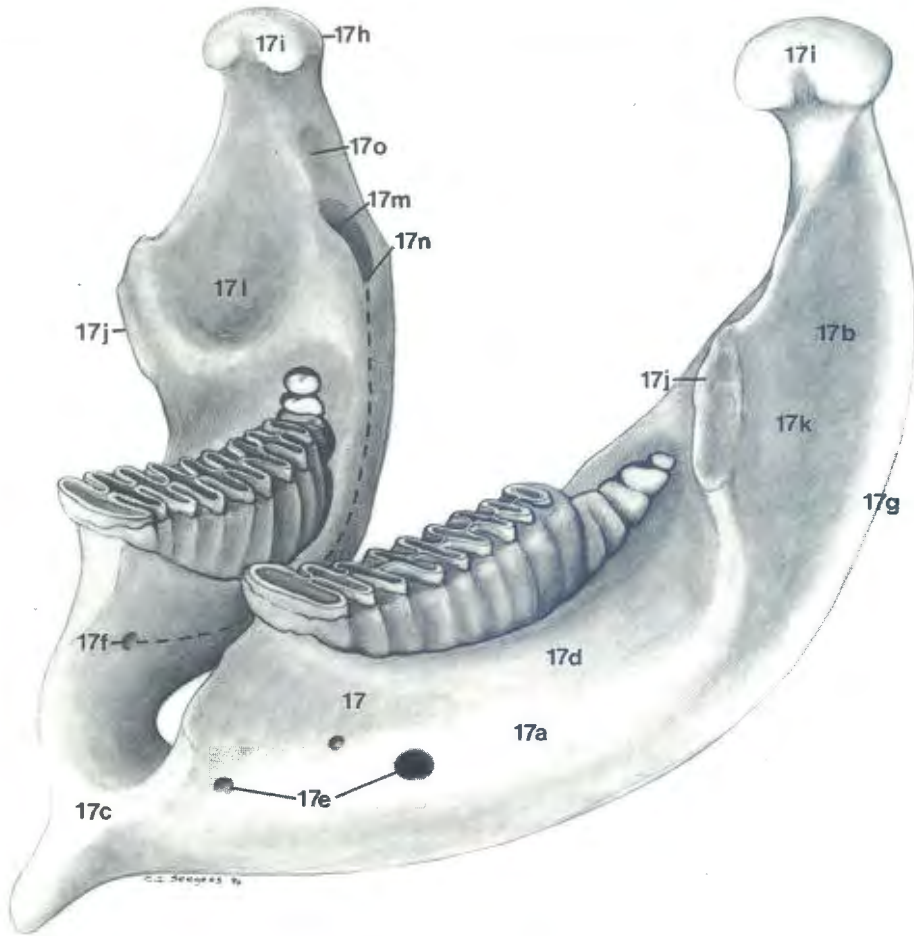

FIG. 6 Mandible

in the occipital bone and the tympanic bulla has not been reported before.

The parietal bones are the largest of the cranial bones and, in young animals, the sutures between them and the neighbouring bones are clearly visible, with the exception of the borders with the interparietal bone, (Boas & Paulli 1925; Eales 1928; Mariappa 1986). These results correspond to the findings in this study.

Boas & Paulli (1925) reported that the interparietal bone could be distinguished only in very young animals, as was also found in the present study.

The change in direction, relative to the long axis of the skull, found in the squamous part of the temporal bone, is described for the first time in this study. Sikes (1971) reported the absence of a "post-glenoid process", but the present study showed the presence of a small retro-articular process. Mariappa (1986) mentioned the *Foramen lacerum,* but the present study reported the exact anatomical positions of the carotid canal, the jugular foramen, the stylomastoid foramen, the oval foramen and the musculotubural canal.

The relationships of the frontal bone with the surrounding bones, as reported in this study, correspond to the descriptions of Eales (1928), but the topography of the ethmoidal foramen, optic canal and the orbital fissure is described for the first time.

The relationship of the pterygoid process of the basisphenoid bone to the maxillary tuberosity, as reported in this study, corresponds to the description of Mariappa (1986). He also described the foramen rotundum and foramen ovale, present in the wing of the basisphenoid bone, but in this study the foramen ovale was found to be situated on the border with the petrous temporal bone.

Mariappa (1986) described the wings of the presphenoid bone as large, whereas in this study they were found to be small.

The results obtained in this study on the pterigoid, vomer, ethmoid, nasal and lacrimal bones are in agreement with those of Boas & Paulli (1925), Eales (1928) and Mariappa (1986).

The concavity on the dorsomedial aspect of the palatine processes of the incisive bone has been de-

scribed before (Eales 1928), but the thinning and disappearance of the bone in older bulls was described for the first time in this study.

The findings on the palatine, maxillary and zygomatic bones and the mandible, are in accordance with the findings of Eales (1928) and Mariappa (1986).

Boas & Paulli (1925) described the extensive pneumatization of the bones of the skull of an Indian elephant. However, they reported that the area ventral to the nuchal crest remains solid, whereas this study showed that only a small area dorsal to the foramen magnum remains unpneumatized. The change in shape of the elephantine skull as the animal ages, as seen in the differences in the length: height ratio between the skull in young and adult animals, is due to a greater emphasis in growth in height. This finding corresponds to those of Boas & Paulli (1925).

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