CONTRIBUTIONS TO THE DESCRIPTIVE AND COMPARATIVE
ANATOMY OF THE CRANIUM OF THE CAPE FRUIT-BAT
ROUSETTUS AEGYPTIACUS LEACHI SMITH

by

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(With 15 text-figures)

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ABSTRACT

An account of the chondrocranium and dermocranium of
Rousettus aegyptiacus leachi is presented. It is based
on a near-term embryo and a young adult. Comparison
with other mammals, especially Chiroptera, is given.
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INTRODUCTION

Only one species of the genus *Rousettus* Gray 1821 is found in South Africa (Roberts, 1951) and its distribution ranges along the coastal belt from the southern Cape Province northeastward to Natal (Roberts, 1951; Ellerman et al., 1953). Beyond the borders of South Africa the same species is found northwards in Portuguese East Africa, Tanganyika, Kenya, Uganda and the Congo (Allen, 1939), (Ellerman, 1953). This form of *Rousettus*, popularly known as the Cape Fruit-Bat, was first named *Pteropus leachii* by Andrew Smith in 1829. Later, however, most workers recognized this bat as *Rousettus leachii* (e.g. Andersen, 1912; Roberts, 1913, 1951; Godfrey, 1923; Loveridge, 1923; Hewitt, 1931 and Allen, 1939), an exception being Solater who called it *R. collaris* in 1901. Ellerman, Morrison-Scott and Hayman (1953) regard the South African form of *Rousettus* as a sub-species of the Egyptian Fruit-Bat, and therefore name it *R. aegyptiacus leachi*. This name is adopted in the present paper.

Although Grosser (1902), Fawcett (1919), Sitt (1943), Koch (1950) and Frick (1954) and others described several aspects of the chondrocranium of *Microchiroptera*, a great hiatus in our knowledge of the skull of *Megachiroptera* existed.
existed up to 1943 when the work by Starck on the chondro-
cranium of *Pteropus semindus* appeared. Unfortunately
there seems to be some doubt as to whether the two embryos
used by Starck were correctly identified. Frick suggests
that Starck's material actually belonged to the genus
*Rousettus*. The material used in the present investigation
(near-term embryo and young adult) is much older than that
of Starck thus making comparison difficult, but it seems
certain that what Starck described could not have been
*R. aegyptiacus* if *Rousettus* at all.

As for *Rousettus* itself, very little is known as far
as its chondrocranium is concerned. Though the oldest
known pictures of bats viz. those from Tomb 15 at Beni
Hasan, dating from about 2,000 B.C., are probably of *R.
aegyptiacus* (Allen, 1940), the only scientific research
on the skull of this genus are the investigations of van
der Klaauw (1922) on *Rousettus amplexicaudatus*, that of
Wassif (1948) on *R. aegyptiacus* (and possibly that of
Starck (1943)). The work both of van der Klaauw and
Wassif, however, is limited in extent treating of the
endotympanic and the auditory ossicles respectively.

The present investigation is based on the skulls of a
relatively late male embryo and of a young adult male.
Unless mentioned otherwise, the description and illustra-
tions given are all based on the conditions found in the
skull of the embryo.
Fig. 1. — Graphic reconstruction of the skull x approx. 5.5. Dorsal view. The dermal bones of the left side are omitted.

AL.SPH., alisphenoid; BAS. OCC.FIS., basicochlear fissure; BAS.Occ., basioccipital; BAS.SPH., basisphenoid; CAV.INT. NAS., cavum internasale; EXOCC., exoccipital; FOR.AL.SPH., foramen alisphenoidale; FOR.MAG., foramen magnum; FOR. OPT., foramen opticum; FOR.OV., foramen ovale; FOR.SPH., ORB., foramen sphenorbitale; FR., frontal; FOS.HY.PH., fossa hypophyseos; FOS.SUBARC., fossa subarculata; HY./
Fig. 1, cont.

HY.GL.FOR., hypoglossal foramen; INT.PAR., interparietal; JUG., jugal; LACR., lacrimal; LAM.CR., lamina cribrosa; MEAT.AC.INT., meatus acusticus internus; NAS., nasal; ORB.SPH., orbitosphenoid; PAR., parietal; P.MAX., pre-maxillary; PR.AL., processus alaris; PR.SPH.ETHM., processus sphenethmoidalis; P.SPHEN., presphenoid; SUP.FAC.COMM., suprafacial commissure; SUP.OCC., supraoccipital; TEC.NAS., tectum nasi; TEGM.TYMP., tegmen tympani; ZYG.PR.MAX., zygomatic process of maxillary; ZYG.PR.SQ., zygomatic process of squamosal.
MATERIAL AND TECHNIQUE

A late male embryo, removed from the mother which had been preserved in formalin, measured 125 mm. from snout to tip of tail. After removal of the skin of the head and the lenses of the eyes, the material was decalcified in a 6% solution of concentrated nitric acid in 70% alcohol for two months. An alcoholic solution of borax-carmine was used as a bulk-stain and paraffin wax (M.P. 52° C) for embedding. The anterior half of the head was microtomized at 15 μ and the rest at 20 μ. Counter-staining with anilin blue and orange G proved to be successful.

Another skull, viz. that of a young adult male obtained in the Helderberg mountains above Somerset West and measuring 175 mm. from snout to tip of tail, was treated in the same way except that it was preserved in Bouin's Fluid, decalcified in Ebner's solution for three months, and sectioned at 25 μ.

Graphic reconstructions were made from projection drawings of the sections.
I would like to express my sincerest appreciation to Dr. M.E. Malan, under whose direction this investigation has been carried out. For technical aid, I am indebted to Mr M.H.C. Visser and Dr J.H. Skinner. I am also very grateful to Professor C.A. du Toit, for his valuable advice, and to Professor C.M. van der Westhuizen of the Zoological Department, University College Western Cape, for his continued interest.
Fig. 2.— Graphic reconstruction of the skull x approx. 5.5. Ventral view. The dermal bones of the left side are omitted.

AL.MIN., ala minima; AL.SPH., alisphenoid; ANN.TYMP., anulus tympanicus; ATR.TURB., atrioturbinal; BAS.GCC. FIS., basicochlear fissure; BAS.LAM.MAX.TURB., basal lamella of the maxilloturbinal; BAS.GCC., basioccipital; CART.PAL., cartilago palatini; CART.PAR.S.ANT., cartilago paraseptalis anterior; CART.PAR.S.POST., cartilago para-

septalis posterior; CR.PAROT., crista parotica; CAUD.

END.TYMP., caudal endotympanic; CAV.INT.NAS., cavum internasale/
nasale; ETH.TURB., ethmoturbinal; EXOCC., exoccipital; FEN.NAR., fenestra narina; FOR.AL.SPH., foramen alisphenoidale; FOR.JUG., foramen jugulare; FOR.MAG., foramen magnum; FOR.OPT., foramen opticum; FOR.OV., foramen ovale; FOR.SPH.ORB., foramen sphenorbitale; JUG., jugal; LAM.AL., lamina alaris; LAM.TR.ANT., lamina transversalis anterior; MAX., maxillary; MAX.TURB., maxilloturbinal; OCC.COND., occipital condyle; ORB.SPH., orbitosphenoid; PAL., palatine; PAR., parietal; PARS CAN.AUD., pars canadicularis of auditory capsule; PARS COCH.AUD., pars cochlearis of auditory capsule. PLEURETHM., pleurethmoid; POSTGL.FOR., postglenoid foramen; POSTGL.PR., postglenoid process; PR.AL., processus alaris; PREMAX., premaxillary; PR.PAR.COND., processus paracondylideus; P.SPHEN., pre-sphenoid; PR.SPH.ETHM., processus sphenethmoidalis; PTER., pterygoid; PR.UNC., processus uncinatus; PR.ZYG.SQ., processus sygomaticus of squamosal; ROS.END.TYMP., rostral endotympanic; SEPT.NAS., septum nasi; SQ., squamosal; SULC.M.ST., sulcus musculi stapedii; SUP.OCC., supraoccipital; TEGM.TYMP., tegmen tympani; TYMP.HY., tympanohyal; ZYG.PR.MAX., zygomatic process of maxillary.
THE CHONDROCRANIUM

ETHMOIDAL REGION

The nasal capsule of *Rousettus aegyptiacus leachi* follows the general pattern of that of placental mammals and is without the marked specialization shown by the Microchiroptera. As is typical of Megachiroptera, the nasal capsule is very long and in general shape resembles that of Insectivora. It occupies about half of the total length of the cranium. Viewed from the dorsal side, the posterior part is much widened. A lateral view shows a gradual increase in height, the capsule ending in the processus sphenethmoidalis (= vestige of the commissura sphenethmoidalis) where it reaches its maximum height. (Fig. 3).

In the dorsal midline the two nasal capsules are fused to the septum nasi and here a shallow sulcus supraseptalis is formed. The fenestra narina is situated antero-laterally, and medio-ventral to it a deep sulcus infraseptalis is constituted by the downward and outward expansion of the two processus laterales ventrales from the nasal septum.

The anterior wall of the nasal capsule is formed by the cupula nasii anterior (cartilago cupularis, cupola anterior) while the cupula posterior (cupola posterior) together with the oblique lamina cribrosa forms the hind wall. Dorsally the nasal sac is supported by a complete cartilaginous/
Fig. 3.— Graphic reconstruction of the ethmoidal region x approx. 6.6. Lateral aspect. The dermal bones are omitted.

AL.MIN., ala minima; AL.SPH., alisphenoid; BAS.LAM.MAX.TURB., basal lamella of maxilloturbinal; CART.DUCT.NAS.PAL., cartilago ductus nasopalatinus; CART.PAL., cartilago palatini; CART.PAR.S.ANT., cartilago paraseptalis anterior; CEN.STEM, central stem; CR.GALLI, crista galli; ETH.TURB., ethmoturbinal; FEN.NAR., fenestra narina; FOR.OPT., foramen opticum; LAM.TR.ANT., lamina transversalis anterior; MAX.TURB., maxilloturbinal; ORB.SPH., orbitosphenoid; PAR.NAS., paries nasi; PLEURETHM., pleurethmoid; PR.AL., processus alaris; PR.LAT.VENT., processus lateralis ventralis; PR.SPH.ETHM., processus sphenethmoidalis; PR.UNC., processus uncinatus; SEPT.NAS., septum nasi; VOM., vomer.
roof or tectum nasi. The side-wall and floor, or paries nasi and solum nasi respectively, are very incomplete.

SEPTUM NASI The nasal septum is without any inter-narial foramina. It is approximately of the same thickness throughout, except at the back where it thickens gradually, especially ventrally, to meet the broad cranial base. The height gradually increases to where the oblique cribiform plate meets the tectum nasi. From here the height of the septum decreases again towards the cylindrical central stem. Its lower edge is fairly straight.

ANTERIOR WALL In front, between the two cupulae nasi anteriores, there is a deep cavum internasale, accommodating the strong ligaments connecting the cupulae. Ventrally each cupula is continuous with the processus lateralis ventralis, dorsally with the tectum nasi and dorso-laterally with the paries nasi (Fig. 4a). With the alar cartilage making up the hind wall an almost complete ring is thus formed around the fenestra narina.

POSTERIOR WALL The planum antorbitale forms an oblique floor beneath the olfactory lobes. It forms an angle of about 55 degrees with the lower edge of the septum nasi and in this way the posterior quarter of the nasal capsule occupies a subcerebral position. The primitive large foramen olfactorium advehens is subdivided into the many foramina of the lamina cribrosa through which the olfactory nerves/
nerves enter the nasal capsule. A crista galli extends as a low and insignificant ridge into the supracribrous recess (de Beer, 1937). In this region a central mesethmoidal ossification centre has already spread into the cribiform plate and crista galli. This ossified part, however, is still separate from the lateral mesethmoidal ossification in the paries nasi namely the pleurethmoid (Figs. 1, 2 and 7).

A mesethmoid, when present, originates as the most anterior centre of ossification in the mammalian central stem which as a rule ossifies from either three or four centres. They are, beginning posteriorly, the basioccipital, the basisphenoid, the presphenoid, and when present, the mesethmoid. According to Broom (1926) there are never more than three bones in the basicranial axis of the mammal-like reptiles. These are, in Broom's (1935) words: "... the basioccipital, the basisphenoid and a third bone placed well forward which has usually been regarded as the ethmoid or sphenethmoid. In position it seemed to agree rather with the mammalian mesethmoid than with the presphenoid but was probably homologous with the bone called sphenethmoid in the frog" (p.33). In an earlier paper (1927) he is more definite and considers the three elements as: "... manifestly homologous with the three in Marsupials and Artiodactyls, and are thus the basioccipital,
the basisphenoid, and the presphenoid, that, consequently, the fourth element when present in mammals must be looked upon as a neomorph" (p. 233). Furthermore Broom's investigations (1926, 1927, 1935) show that a mesethmoid does not exist in all mammals and he therefore divides them into two subclasses: the Palaeotherida with no mesethmoid, and the Neotherida with a mesethmoid. According to the condition in the epauletted fruit-bat, *Epomophorus wahlbergi* in which a large independent mesethmoid is present (1927), he classifies the Chiroptera as Neotherida. As will be shown later *R. aegyptiacus* also has four centres of ossification.

A lamina transversalis posterior is formed by the forwardly projecting continuation of the ventral edge of the cupula posterior. It is free from the nasal septum (Figs. 5c & d) as, for instance, in *Trichosurus, Halmaturus, Canis, Lepus* and *Talpa* (de Beer, 1937). In *Myotis* the nasal septum and the lamina transversalis posterior are continuous (Frick, 1954).

**TECTUM NASI** The roof of the nasal capsule is complete without even a foramen epiphaniale. The absence of the latter corresponds with Starck's findings (1943) in *Pteropus semindus* and with the condition in *Myotis* (Frick, 1954). As the tectum nasi increases in height to meet the processus sphenethmoidalis, it causes a backward deepening/
flation of the sulcus supraseptalis.

**PARIES NASI** The paries nasi of *R. aegyptiacus* is very incomplete at this stage of development. Even the fairly well-developed posterior half is interrupted by four large fissures (Fig. 3) between the parallel basal lamellae of some of the ethmoturbinals. There is a dorsal fissure above the secondary ethmoturbinal; a second fissure between the secondary ethmoturbinal and the first primary ethmoturbinal, and lastly two fissures between the first and second primary ethmoturbinals. All these apertures are closed over by the maxillary. In the late ontogeny of many mammals extensive resorption of cartilage occurs in the paries nasi, and it may well be that it (the paries nasi) is more extensive in younger stages of *R. aegyptiacus* as it is in the stages of *Pteropus semindus* described by Starck (1943). In front of the fissures a large part of the paries nasi is ossified as the pleurethmoid.

**SOLUM NASI AND BASAL CARTILAGES** The dorso-lateral edge of the cupula nasi anterior rolls in to form the small atrioturbinal (Fig. 4a) which runs horizontally in a postero-medial direction towards the septum nasi. Before it reaches the latter, it turns backwards and becomes a rod with one slightly concave face facing latero-ventrally. It stretches towards the antero-dorsal edge of the lamina transversalis anterior. Ventrally the latter is fused/
Fig. 4 (a, b, c, d and e).—Successive transverse stereograms of the nasale capsule, anterior view.

ANT. TIP ETH. TURB., anterior tip of the ethmoturbinal; ATR. TURB., atrioturbinal; BAS. LAM. MAX. TURB., basal lamella of the maxilloturbinal; CART. DUCT. NAS. PAL., cartilago ductus nasopalatini; CART. PAL., cartilago palatini; CART. PAR. S. ANT., cartilago paraseptalis anterior;
Fig. 4, cont.

CR. SEM. CIRC., crista semicircularis; CUP. NAS. ANT., cupula nasi anterior; LAM. TR. ANT., lamina transversalis anterior; MAX. TURB., maxilloturbinal; PAR. NAS., paries nasi; P. ETH. TURB. i, first primary ethmoturbinal; P. ETH. TURB. ii, second primary ethmoturbinal; P. ETH. TURB. iii, third primary ethmoturbinal; PR. AL., processus alaris; PR. LAT. VENT., processus lateralis ventralis; PR. UNC., proc. uncinatus; SEPT. NAS., septum nasi; S. ETH. TURB., secondary ethmoturbinal; SUL. INF. SEPT., sulcus infraseptalis; SUL. SUP. SEPT., sulcus supraseptalis; TEC. NAS., tectum nasi.
fused to the base of the nasal septum and thus, together with the atrioturbinal, a complete cartilaginous ring is formed. The lamina transversalis anterior lies almost vertically (Fig. 4b) and may perhaps more correctly be considered as part of the side-wall as is the case in Myotis (Frick, 1954). Behind the alar cartilage there is no zona annularis. A relatively short and small process extends from the paries nasi towards the dorsal edge of the lamina transversalis anterior but does not fuse with it.

The lamina transversalis anterior itself is not fused to the processus lateralis ventralis. This does not correspond with Sturm's description (1937) of the general condition in mammals. He states: "Vorn geht sie gleichmäßig in den Processus lateralis ventralis über oder wird von diesem durch eine kleine Einkerbung geschieden" (p.218). This could have been the case during earlier stages of development, but in the late embryo of R. aegyptiacus examined, the hind edge of the processus lateralis ventralis lies against the front edge of the praemaxillary and does not extend backwards to fuse with the lamina transversalis anterior. Fawcett (1919) too, found in Miniopterus schreibersi in contrast with the condition in Myotis (Frick, 1954), the following: "The anterior basal angle of the lamina transversalis anterior is prolonged forwards as a long slender process as far as the processus lateralis ventralis/
ventralis, but it does not fuse with that structure" (p. 333).

The lamina transversalis anterior of R. aegyptiacus therefore does not possess an anterior process that fuses with the processus lateralis ventralis, but from its vertical part a cartilaginous process stretches antero-dorsally to meet the atrioturbinal.

From the ventral edge of the lamina transversalis anterior a very small process projects downwards and forwards (Figs. 3 and 4b). It is the cartilago ductus nasopalatini which lies immediately in front of the ductus nasopalatinus.

In several Chiroptera e.g. in "die Vespertilionen" (Schwink, 1888), Vespertilio and Vesperugo (Simonetta et Magnoni, 1939), Pteropus semindus (Stark, 1943), and in Myotis myotis and M. capaccinii (Frick, 1954), an organ of Jacobson is absent. It is also absent in R. aegyptiacus. This fact, however, does not prevent the development of the anterior paraseptal cartilage which, therefore, is not tube- or U-shaped as in those mammals where it supports the organ of Jacobson (Stadtmüller, 1936), but is merely an oval rod which extends backwards from the lamina transversalis anterior. Anteriorly it is continuous with the latter, and its front half lies against the septum nasi with only the perichondrial lamellae between them.
them. This is in contrast with the condition in Pteropus semindus where: "... ein allseits freier vorderer Parasep	alknorpel ist vorhanden" (p. 597). The anterior para-
septal cartilage reaches as far back as a point dorsal to
the anterior end of the vomer.

Directly in front of the lamina transversalis posterior
the cartilago paraseptalis posterior is represented by
a small detached piece of cartilage. It is syndesmotic-
ally connected with the nasal septum and with the lamina
transversalis posterior. The ductus nasolacrimalis fol-
lows a typical course lateral to the lamina transversalis
anterior and opens immediately in front of the latter,
dorsal to the first upper incisor, into the nasal sac.

A cartilago papillae palatinae is absent in the two
developmental stages investigated.

Posterior, postero-lateral and lateral to the ductus
nasopalatinus lies a small piece of cartilage. Its lat-
eral and posterior sides are supported by the maxillary
but otherwise it lies free. Sturm (1937) gives a good
synoptic description of the basal cartilages, and of the
cartilago palatina. He says, inter alia: "Dieser Knor-
pel liegt im Gegensatz zur Cartilago ductus nasopalatini im
hinteren Bereich des Foramen incisivum" (p. 219). Accord-
ing to this definition the cartilage described above could
be regarded as a cartilago palatina — a structure which is
homologous with the cartilago ectochoanalisis of lower
tetrapods/
tetrapods because in mammals Stenson's duct marks the anterior end of the primary choana (de Beer, 1937). Regarding its function Ärnböck Christie-Linde (1914) says: "Its function, originally related to the canalis naso-palatinus, has in the course of development been considerably reduced. In higher mammals the cartilago palatina is probably in general of a more or less rudimentary character. Yet it may be of some use as partially supporting the nasal cavity in foetal stages" (p. 364).

ALAR CARTILAGE The fenestra narina is bounded posteriorly by an alar cartilage which is confluent with the atrioturbinal. It runs downwards to the level of the processus lateralis ventralis and then turns outwards and broadens to form a flat cartilaginous strip. At a point outside the general lateral plane of the paries nasi, it turns upwards again to terminate at more or less the same height as the tectum nasi (Fig. 4b). It is difficult to decide definitely whether this structure is a processus alaris superior or a processus alaris inferior.

Hans Sturm (1937), and later Starck (1943) tried to create order out of the confusion which had existed in the past regarding the relations of the mammalian alar cartilages. Starck gives the following summary: "Im allgemeinen wird bei Säugern das Einmündungsgebiet des Ductus nasolacrimalis durch besondere Knorpelstützen – die Processus
Fig. 5 (a, b, c and d).—Successive transverse stereograms of the nasal capsule. Posterior view.

CR. GALLI, crista galli; CR. SEM. CIRC., crista semicircularis; LAM. CR., lamina cribrosa; LAM. TR. POST., lamina transversalis posterior; P. ETH. TURB. i, first primary ethmoturbinal; P. ETH. TURB. ii, second primary ethmoturbinal; P. ETH. TURB. iii, third primary ethmoturbinal; PL. ANTORB., planum antorbitale; PLEURETHM., pleurethmoid; PR. SPH. ETHM., processus sphenethmoidalis; SEPT. NAS., septum nasi; S. ETH. TURB., secondary ethmoturbinal; SULC. SUP. SEPT., sulcus supraseptalis; TEC. NAS., tectum nasi; VOM., vomer.
alares gekennzeichnet. Der Processus alaris superior entspringt in der Regel vom oberen Rand der Fenestra naris und umfaßt von oben her den Tränennasengang. Er hat keine Verbindung mit den Basalknorpeln" (p. 597). Further on he continues: "Ein Proc. alaris inferior, der im Zusammenhang mit den Basalknorpeln stehen müste und den Tränennasengang von unten her umfaßt, fehlt bei Pteropus völ-
lig" (p. 597). Concerning the topography of the same cartilages, Sturm states: "In der Ausbildung der Processus alaris superior und inferior können wir das Bestreben sehen, den hintersten Abschnitt der Fenestra naris, in der den Ductus nasolacrimalis einmündet, nach vorn zu abschließen. Das kann durch eine Überbrückung von oben her oder von unten her erfolgen, allerdings ist das nicht immer an den bisher modellierten Kranien einwandfrei zu erkennen" (p. 200). Later on, after mentioning his doubt about the accuracy of Fawcett's terminology for the alar cartilages of Erinaceus, he concluded: "Klarheit wäre hier nur durch die Untersuchung der jüngsten Entwicklungsstadien zu erhalten. Wo diese fehlen, ist es vielleicht besser, wenn man den Knorpel einfach Processus alaris nennt" (p. 200).

The processus alaris in R. aegyptiacus is U-shaped. The medial arm is dorsally continuous with the atrio-turbinal and the lateral one extends upwards, outside the paries nasi to form the posterolateral margin of the fenestra/
fenestra narina. The opening of the ductus nasolacrimalis into the nasal cavity immediately in front of the lamina transversalis anterior, lies medially to the inner arm of the processus alaris. In view of the fact that the atrioturbinal is formed by the rolled-in paries nasi, the processus alaris actually then derives from the upper edge of the fenestra narina and may, if anything, be considered as a processus alaris superior. Another reason for this assumption is the fact that in some mammals e.g. in Sorex (de Beer, 1929) and Sus scrofa domestica (Sturm, 1937), the processus alaris superior is by exception attached to the processus lateralis ventralis. However, since the early development of the cranium of R. aegyptiacus is not known, and keeping Sturm's advice in mind, the non-committal term processus alaris seems safer.

THE TURBINALS As previously described, a small cartilaginous atrioturbinal, absent in Myotis (Frick, 1954), is formed by inrolling of the anterior part of the paries nasi (Fig. 4a).

The maxilloturbinal, primarily an inrolling of the ventral edge of the side-wall is at this stage of development already almost completely ossified and is synostotically continuous with the maxillary by means of a basal lamella. Contact with the side-wall has been lost completely, probably as a result of resorption. The maxilloturbinal/
turbinal is very large and projects backwards from a point dorsal to the lamina transversalis anterior. A foramen through which the ductus nasolacrimalis passes forwards and downwards, perforates the horizontal lamella connecting the maxilloturbinal with the maxillary. The slender hindmost part of the maxilloturbinal loses its contact with the maxillary and becomes a cartilaginous plate which sharply increases in size and which borders the ductus nasopharyngeus for a short distance laterally. Strictly speaking, this part of the maxilloturbinal is therefore extracapsular.

Postero-dorsally the nasopharyngeal duct is separated from the nasal sac by the pleurethmoid (see also p. 2) which extends inwards to fuse for a relatively short distance with the dorsal edge of the lateral lamella of the vomer (Figs. 2, 3, 5a & b). Actually this bony plate serves as a floor for the nasal sac and at the same time as a roof for the nasopharyngeal duct (Fig. 7b). Further back the pleurethmoid goes over into the cartilaginous lamina transversalis posterior which, although lying against it, does not fuse with the nasal septum. Between the lamina transversalis posterior and pleurethmoid laterally, and the straight septum nasi medially, a semicircle is formed around the posterior paraseptal cartilage.

The posterior half of the ethmoturbinal (Figs. 4b and
5a to d) is still cartilaginous, but its anterior part shows increasing ossification. This turbinal is composed of three primary ethmoturbinals (endoturbinals) and one bilaminar secondary ethmoturbinal (ectoturbinal). The latter springs from the dorso-lateral aspect of the paries nasi and is still, except for a short ossified anterior part, cartilaginous. From the basal lamella one dorsal and one ventral lamella arises vertically.

Parallel to the root of the secondary ethmoturbinal arises the horizontal septum or medial root (Roux, 1947) of the well-developed first primary ethmoturbinal. It is typically bilaminar and built up by a dorsal lamella which projects in a medio-dorsal direction, and a ventral lamella, extending medio-ventrally from the basal lamella. Its foremost third ends freely, dorsal to the maxilloturbinal in the lumen of the nasal sac. Further back it gradually merges into the paries nasi, lateral to the cribiform plate.

In front, the second primary ethmoturbinal springs from the ventro-lateral aspect of the paries nasi as a uni-lamellar plate. A little further back, however, it becomes bilaminar, being composed of a medial and a lateral lamella. Posteriorly it is attached to the lateral part of the paries nasi, and to a certain extent, also to the planum antorbitale.
Fig. 6.— Transverse section through the ala minima and the hindmost part of the cupula posterior.

AL.MIN., ala minima; CUP.POST., cupula posterior; DUCT. NAS.PH., ductus nasopharyngeus; ORB.SPH., orbitosphenoid; PAL., palatine; SCL., sclera; II, nervus opticus; Vb, maxillary division of trigeminal nerve.
The third primary ethmoturbinal is rooted to the cribiform plate, the cupula posterior and further forward, to the ventrao-lateral aspect of the paries nasi (actually to the pleurethmoid). It is relatively short and reaches only as far as the hind edge of the fenestra basalis. Rostrally it is ossified and unilamellar but caudally it is still cartilaginous consisting of three small lamellae, springing from the basal lamella.

The crista semicircularis (Figs. 4d, 4e and 5a) is well developed. Posteriorly it arises from the tectum nasi, close to the nasal septum. Continuing forwards, the root of the crista shifts gradually outward towards the paries nasi where it completes its parabolic course by turning ventrally and then backwards to terminate as a short processus uncinatus (Figs. 3 and 4d).

A nasoturbinal, the reduction of which is typical in Chiroptera (Paulli, 1900), is entirely absent.

ORBITOTEMPORAL REGION

In the late embryo studied the orbitotemporal region has already undergone extensive ossification. An interorbital septum is represented only by the very small crista galli (Figs. 3, 5c and 4d). In the opinion of various workers, amongst others Weber (1904), Voit (1909), Terry (1917), Stadtmüller (1936) and Lindahl (1946), the mammal-
ian nasal capsule compared with that of the reptile has become extended, pushing itself posteriorly along the interorbital septum - a step which has resulted in the primary loss of the mammalian interorbital septum. De Beer (1937) too suggests that the existence of the interorbital septum seems to be correlated with the degree of development of the nasal capsule, rather than with the size of the eye.

A well-developed interorbital septum occurs in the primates where the nasal capsule is least developed. In R. aegyptiacus on the other hand the nasal capsule is very well developed and may perhaps be the reason for the virtual absence of an interorbital septum.

The anterior part of the central stem in the orbito-temporal region is already ossified as the presphenoid. This ossification is still separated from that of the mesethmoid by a considerable tract of cartilage. Its posterior end can be distinguished from the basisphenoid behind it by the presence of a strip of cartilage which cuts right across the central stem. Anteriorly the latter is more or less circular in cross section but in passing posteriorly it becomes more and more flattened as far as the post-optic root of the orbitosphenoid.

The orbital cartilage is completely ossified as the orbitosphenoid and is synostotically continuous with the presphenoid by means of two roots bordering the foramen

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opticum. They are respectively the preoptic root (pila prooptica) and the postoptic root (pila metoptica).

Immediately in front of the preoptic root and ventral to the hindmost end of the nasal capsule, a small cartilaginous process projects sideways from the central stem (Figs. 2 and 6). Its postero-lateral tip is fused to the preoptic root against which it is closely applied over its whole length and from which it is separated only by connective tissue. The process has no connexion at this stage with the lamina orbitonasalis; whether it represents an ala minima or not is therefore not quite clear. Starck (1943) describes a somewhat similar process in Pteropus semilunaris which he calls an ala minima. I cannot, however, quite agree with his interpretation of the incisure between his ala minima and the paries nasi as an "abgesprengten Rest der Fenestra orbitonasalis (Foramen prächiasmaticum)" (p. 602). If anything it ought to be called an incisura infracribrrosa since a foramen prechiasmaticum has no connexion with the ala minima, but with the ala hypochiasmatica. In R. aegyptiacus the latter is possibly represented by a small laterally projecting process which springs from the central stem and the postero-medial edge of the preoptic root of the orbitosphenoid.

There is no connexion (commissura sphen-ethmoidalis) between the nasal capsule and the ossified ala orbitalis
at this stage. This is quite probably due to extensive resorption of cartilage in this region, as is usual in late mammalian embryos. Probably, for the same reason, there is no orbitoparietal commissure.

Behind the presphenoid the central stem is ossified as the basisphenoid. The latter is separated from the anterior margin of the basioccipital by a transverse cartilage, the sphenoccipital synchondrosis, while the anterior margin is indicated by the intersphenoidal synchondrosis. The anterior part of the basisphenoid, is oval in cross section but becomes broader and dorsally depressed towards its posterior end. The depression results in a shallow fossa, the fossa hypophyseos. A prominent dorum sellae is not formed.

The alisphenoid is fully ossified and is in bony continuity with the processus alaris (basitrabecularis) of the basisphenoid. It is thus impossible to determine the limits between the ala temporalis and the processus alaris. The whole structure is more or less fan-shaped with the apex fused to the central stem whence it extends laterally before curving upwards. In this way it serves as a lateral wall and, together with the processus alaris, as a floor for the cavum epiptericum in which the large Gasserian ganglion lies.

The antero-dorsal part of the alisphenoid overlaps
the orbitosphenoid with which it is in a syndesmotic connection for a short distance medially and in this way the fissura sphenoidalis is enclosed as a foramen sphenorbitalis (foramen lacerium anterius). This enormous foramen transmits the oculomotor, the trochlear, and the abducens nerves, as well as the ophthalmic and maxillary divisions of the trigeminal nerve. The mandibular branch of the latter leaves the cranium through the foramen ovale.

Since the ophthalmic and maxillary branches are not separated by a skeletal bridge, a typical processus ascendens must either be regarded as being absent (de Beer, 1926) or we must accept Fuchs' (1910) theory that the maxillary branch slipped forward over the processus ascendens. The alisphenoid in any case is an ossification of the ala temporalis which has been shown by embryological, morphological and palaeontological evidence to be a derivation of the processus ascendens of the palatoquadrate (see de Beer, 1937).

In front of the foramen ovale, the alisphenoid is pierced by a relatively small foramen alisphenoidale through which the arteria maxillaris interna, a branch of the external carotid, enters the braincase, only to leave again through the foramen sphenorbitalis. A similar canal in Pteropus semindicus, Starck (1943) identifies as a canalis alisphenoides.
Fig. 7.— Transverse section through the unidentified cartilage in the orbit and through the pleuro-ethmoid-vomer synostosis.

CART. "N", cartilage "N" (See page 23); CR. SEM. CIRC., crista semicircularis; DUCT. NAS. PH., ductus nasopharyngeus; FR., frontal; MAX., maxillary; PAL., palatine; P. ETH. TURB. i, first primary ethmoturbinal; P. ETH. TURB. ii, second primary ethmoturbinal; P. ETH. TURB. iii, third primary ethmoturbinal; PLEURETHM., pleurethmoid; SCL., sclera; S. ETH. TURB., secondary ethmoturbinal; VOM., vomer.
The hind edge of the alisphenoid is joined to the front edge of the pars cochlearis by means of the alicochlear commissure.

No vestiges of the pila antotica could be found.

Perhaps the most peculiar feature of the orbitotemporal region is the presence of a discrete convex cartilaginous plate in the orbit (Cart. "N" in fig. 7). It lies medio-dorsally to the anterior part of the sclera with its dorsal edge in the upper eyelid and its ventral part embedded in glands. In this way it forms a small "cup" entirely outside the sclera, and its curvature corresponds more or less to that of the latter. From its position it is clear that the structure does not represent a sclerotic cartilage. The only mammals in which the sclera condries, and that only partly, are the Monotremata.

The most acceptable interpretation seems to be that this cartilaginous plate in Rousettus, although it is very large and does not lie inside the nictitating membrane, probably represents a modified cartilage of the third eyelid ("Nickhautknorpel"). The latter is quite common among mammals (Franz, 1934; Weber, 1927). The possibility that the structure is a tarsal cartilage can be excluded, as the tarsus in mammals is always without any cartilage-cells (Franz, 1934). Moreover according to Argaud and Falloney (no date given), a tarsus itself is absent in bats.
Whatever this cartilage in *R. aegyptiacus* may be, it will be interesting to know more of its ontogeny. The retina and choroid of *Megachiroptera* also show certain deviations from the general mammalian plan (Kolmer, 1912).

In contrast with the nasal region, the orbitotemporal region has undergone extensive ossification. At the stage investigated it consists of two discrete bony structures: the presphenoid which is anchored to the orbitosphenoid, and the basisphenoid which is in bony continuity with the alisphenoid. Cartilage remains only in the tract between mesethmoid and presphencid, in the intersphenoidal synchondrosis, and in the sphenoccipital synchondrosis (Fig. 2).

OTIC REGION

The auditory capsule is relatively large. Its size, as in *Pteropus semindus* (Starck, 1943), results in a restriction of the basal plate to a typical triangular shape (Fig. 2), but not to the same extent as in *Myotis myotis* (Frick, 1954) and *Miniopterus schreibersi* (Fawcett, 1919). Starck (1943) points out that the ratio of the volume of the otic capsule to that of the braincase in the two specimens of *Pteropus* investigated by him, is more or less 1:20. He compares it with the condition in *Manis* (1:16), *Lepus* (1:20), *Rhinolophus* (1:11), and *Homo* (1:70).

The anterior division of the cochlear capsule, the
pars cochlearis, contributes to the cranial floor, while
the pars canalicularis, which lies posteriorly and dorso-
laterally to the cochlear part, plays an important part
in the formation of the postero-ventral portion of the
side-wall, as well as of the ventro-lateral aspect of the
hind-wall. In front, the pars cochlearis is attached to
the alisphenoid by means of the alicochlear commissure.
Connexion with the planum basale is effected by the post-
erior basicochlear commissure, and further back, the broad
occipito-capsular commissure unites the exoccipital with
the pars canalicularis.

Although Starck (1943) could not find a tegmen tympani
in Pteropus semindus, this structure is well developed in
R. aegyptiacus (Figs. 1, 2 and 8) and, according to van de
der Klaauw (1922), occurs also in Roussettus amplexicauda-
tus. Of the absence of a tegmen tympani in Pteropus
Starck (1943) says: "Das Tegmen tympani ist zweifellos
eine Neubildung der höheren Säuger (van Kampen, 1905,
Matthes 1921, Starck 1941)", and then concludes: "Pteropus
schließt sich in diesem Punkte also an die niedersten Zu-
stände an, ein Befund, der für die Beurteilung des Craniums
im ganzen zu beachten bleibt", (p. 609). The genus Rou-
settus, however, cannot be regarded as primitive in this
respect.

In front, the tegmen tympani which forms the secondary
suprafacial/
suprafacial commissure (lateral suprafacial or lateral prefacial commissure of de Beer, 1937) establishes a close syndesmotic connexion with the pars cochlearis and in this way a "foramen" faciale secundarium is enclosed. From the tegmen tympani, the crista parotica is produced backwards and downwards as a lateral wall for the deep sulcus musculi stapedii, but does not end in a mastoid process. The cartilaginous tympanochyale of the hyoid arch is fused to the ventral edge of the crista.

A large fossa subarcuata (Figs. 2 and 9) lodges the paraflocculus of the cerebellum. Although very deep, it does not penetrate right through to the outside surface of the capsule as in Microtus (see de Beer, 1937), and some Microchiroptera e.g. Miniopterus schreibersi (Fawcett, 1919), and Myotis myotis (Frick, 1954). The condition in R. aegyptiacus is similar to that in Pteropus semindus (Starck, 1943). The jugular vein runs forward in a shallow trough on the dorso-lateral aspect of the auditory capsule before descending over the antero-lateral region of the latter and entering the squamosal on its way to the foramen postglenoideum. Antero-ventral and slightly to the fossa subarcuata a large meatus acusticus internus is present (Fig. 2). From this deep depression branches of the auditory nerve enter the capsule through the foramen acusticum superius and, separated from the latter by
Fig. 8.- Transverse section through the otic region of the young adult.

ANN.TYMP., anulus tympanicus; A.ST., arteria stapediais; CART."X", cartilage "X" (See page 38); CH.T., chorda tympani; END.TYMP., endotympanic; L.J.V., lateral jugular vein; MALL., malleus; MAN.MAL., manubrium mallii; M.T.T., musculus tensor tympani; SQ., squamosal; STY.HY., stylohyal; TEGM.TYMP., tegmen tympani; TYMP., tympanum.
the crista falciformis, through the foramen acusticum inferius. The ramus ampullaris posterior of the eighth nerve, however, runs through a separate foramen, the foramen singulare, in the postero-medial aspect of the internal auditory meatus from where it enters the canalis singulare on its way to the ampulla posterior. In this respect too, R. aegyptiacus differs from Pteropus seminuss where a foramen singulare is absent (Starck, 1943). The foramen is present also in Miniopterus schreibersi (Fawcett, 1919).

The facial nerve leaves the internal auditory meatus through the primary facial foramen which is confluent with the foramen acusticum superius. The latter lies medially and slightly posteriorly, to the former. The primary facial foramen leads to the primary facial canal which is bridged over by the suprafacial commissure (true prefacial commissure of de Beer, 1937). Between the latter and the secondary suprafacial commissure, is the cavum supracochlearis from where the facial nerve descends through the "foramen" faciale secundarium into the sulcus facialis which is posteriorly continued as the sulcus musculi stapedii (Fig. 2). The nerve then runs for a short distance immediately above the stapedial artery, before descending laterally to the musculus stapedialis.

The fenestra ovalis lies in the lateral wall of the pars cochlearis and it lodges the footplate of the stapes.
It is situated postero-ventrally to the secondary facial "foramen" and antero-ventrally to the sulcus facialis. Postero-ventral to the fenestra ovalis a comparatively large fenestra rotunda is present. It faces downwards and is separated from the aquaeductus cochleae by the processus recessus which connects the ventro-medial wall of the pars cochlearis with that of the pars canalaris. The aquaeductus cochleae faces medially into the foremost part of the jugular foramen.

In the medial wall of the canalar part, and ventral to the fossa subarcuata, the ductus endolymphaticus opens through a slit-like foramen endolymphaticum.

THE ENDOTYMPANIC (Figs. 2 and 8). This structure forms a floor to the tympanic cavity. In the stage investigated it is still cartilaginous. Its front part lies between the ventral ramus of the tympanic ring and the base of the skull, while the narrower central portion lies between the tympanic and the auditory capsule. Posteriorly, behind the tympanic ring, the lateral edge of the endotympanic finds connexion with the ventral edge of the medial wall of the sulcus facialis, posterior to the styl-oid process. The latter is in cartilaginous continuity with the lateral edge of the broad posterior part of the endotympanic. The inner side of this part, partly covers the fenestra rotunda from the ventral side. The endo-
tympanic/
tympanic is connected by fibrous tissue to the anulus tympanicus, the base of the skull, and the auditory capsule.

Van der Klaauw (1922) describes two endotympanics on each side in Rousettus amplexicaudatus, namely a caudal endotympanic which fuses with the styloid process and a rostral endotympanic which acquires continuity with the Eustachian tube cartilage. Both these elements are distinguishable in R. aegyptiacus. The rostral division is continuous with the cartilage of the tuba auditiva and in this region is not noticeably separated from the caudal endotympanic. Posteriorly, however, a strip of connective tissue, unrecognisable in some sections, indicates the margin between the rostral and caudal elements of the endotympanic.

Among Chiroptera an endotympanic has been shown to be present in Miniopterus (Fawcett, 1919), in Rousettus and Pteropus (van der Klaauw, 1922), and in Myotis (Frick, 1954). The two embryos of Pteropus studied by Starck (1943), were apparently too young to show an endotympanic, which always arises relatively late in ontogeny (van Kampen, 1905). The occurrence of an endotympanic element (or elements) is widespread in mammals and, according to van Kampen (1905), it has evolved within the class Mammalia. Fawcett (1919) in describing his findings in Miniopterus states: "To my mind from the fact that it resembles/
les very much in its structure the auricular cartilage, in the cartilage of the Eustachian tube and that of the younger nasal cartilages, it seems fair to assume that it is really a provision for support of the outer end of the first pharyngeal pouch more especially protecting it from the pressure of the digastric muscle which at this stage is of large size," (p. 346). Van Kampen on the other hand, seeks the reason for its presence in the degree of development of the floor of the tympanic cavity. Therefore he says: "Hierfür spricht namentlich die Tatsache, daß man annehmen muß, daß die ventrale Wand der Paukenhöhle der Säugetiere bei deren Voreltern noch nicht entwickelt gewesen ist (s. S. 337) und das Entotympanicum in seiner jetzigen Gestalt erst beim Auftreten dieser Wand entstanden sein kann," (p. 704). Reinbach (1952) does not agree.

Reinbach does not agree with van der Klaauw's terminology for the two endotympanic elements. He proposes the term "Tubotympanicum" for van der Klaauw's "Rostrales Entotympanicum" and gives as his reason Fawcett's findings (1919) in Miniopterus where the rostral endotympanic and the Eustachian tube cartilage chondrify at the same time in the same strand of connective tissue surrounding the first pharyngeal pouch.
OCCIPITAL REGION

The exceptionally large foramen magnum (Fig. 2) is bounded in the usual way by the supraoccipital postero-dorsally, by the exoccipitals laterally, and by the basi-occipital anteriorly. These four elements are all completely ossified and the basioccipital is ankylosed to the exoccipitals. On each side of the foramen magnum a narrow strip of cartilage extends laterally and indicates the site of the exoccipital-supraoccipital union.

The basioccipital arises from the hindmost centre of ossification in the central stem. It is typically triangular in shape with the apex fused to the basisphenoid. Posteriorly it is directly continuous with the exoccipitals and together they form the anterior and antero-lateral margins of the foramen magnum. The jugular foramen is separated from the basicochlear fissure by a very slender and inconspicuous cartilaginous posterior basicochlear commissure (chordo-cochlear commissure of Fawcett). The basicochlear fissure between the basioccipital and otic capsule is long and slit-like and is confluent with the foramen caroticum in front. This means that there is no commissura basicochlearis anterior. Similar conditions obtain in Miniopterus schreibersi (Fawcett, 1919) and in Myotis/
Fig. 9. - Transverse section through the lamina alaris and the large fossa subarcuata.

ATLAS; CAN.AUD.CAPS., canalicular part of auditory capsule; CART.AUR., cartilago auricularis; FOS.SUBARC., fossa subarcuata; LAM.AL., lamina alaris; L.J.V., lateral jugular vein; OC.CAPS.COMM., occipito-capsular commissure; PR.PAR.COND., processus paracondyloideus; REC.SUPR.AL., recessus supra-alaris; SQ., squamosal; IX & X, glosso-apharyngeal and vagus nerves.
Myotis capaccinii (Frick, 1954).

Each occipital condyle is cartilaginous and is situated antero-laterally to the foramen magnum. It is formed mainly by the exoccipital, but the basioccipital also contributes to its formation. Immediately lateral to each condyle the hypoglossal nerve leaves the cranium through a comparatively small hypoglossal foramen which indicates the line of union between the basioccipital and the exoccipital. There is only one foramen on each side and although Koch (1950) finds two foramina in Scotophilus temmincki, the usual number in Chiroptera appear to be one, since it is the case also in Miniopterus schreibersi (Fawcett, 1919), Pteropus seminundus (Starck, 1943), Myotis myotis and M. capaccinii (Frick, 1954).

Behind the jugular foramen the exoccipital spreads outwards as a distinct lamina alaris which ends laterally in a paracondylar process (Figs. 2 and 9). It extends laterally as far as the medio-ventral and ventral aspect of the pars canalicularis of the auditory capsule. In this way a groove, the recessus supra-alaris, is formed (Fig. 9).

Of this lateral wing in mammals, Stadtmüller (1936) says: „Eine Lamina alaris findet sich bereits bei Reptilien (Krokodil). Die Lamina alaris der Säuger ist aber nicht auf sie zurückzuführen, sondern ist eine erst inner-
halb des Säugerstammes sich herausbildende, parallel gerichtete Neuerwürbung", (p. 865). It is absent in lower mammals e.g. *Echidna* (Stadtmüller, 1936), *Tachyglossus* and *Ornithorhynchus* (Reinbach, 1952). Concerning the condition in higher mammals, Reinbach (1952), after mentioning the condition in some *Marsupialia* and *Insectivora*, states: "Chiropteren, Carnivoren, Cetaceen, Ungulaten, Sirenen und Primaten zeigen im allgemeinen eine mehr oder minder stark ausgeprägte Lamelle" (p. 22). In *Chiroptera* PWCcett (1919) describes a lamina alaris for *Miniopterus schreibersi*, Starek (1943) one for *Pteropus semindus*, and and Sitt (1943) one for *Rhinolophus rouxii*. Frick (1954), however, could find no such lamina in *Myotis myotis* and *M. capaccinii*. He also says that although PWCcett (1919) describes a lamina alaris in *Miniopterus*, he could not recognize it with any certainty from PWCcett's illustrations. He also regards it as absent in *Rhinolophus* and in *Rousettus*. As far as *Rousettus* (*R. aegyptiacus* in any case) is concerned Frick is wrong, as figure 9 clearly illustrates.

The supraoccipital is very large and serves as a hind-wall for the braincase. In addition to being fused to the exoccipitals, it is syndesmatically connected with the small interparietal above it, with the parietals dorsolaterally, and with the auditory capsule ventro-laterally.
Fig. 10. - Graphic reconstruction of the posterior part of the dentary to show Meckel's cartilage and associated structures x approx. 11.

ANN.TYMP., anulus tympanicus; DENT., dentary; FOR.MAND., foramen mandibulare; MALL., malleus; MAN.MALL., manubrium mallii; MECK.CART., Meckel's cartilage; PR.GRAC., processus gracilis.
THE VISCERAL ARCH SKELETON

MANDIBULAR ARCH In the embryonic stage investigated the cartilage of Meckel is represented by a relatively short bar of cartilage (Fig. 10). The malleus is present as a discrete osseous element with only its manubrium or tympanic process still cartilaginous. The anterior part of the processus gracilis of the malleus lies medio-ventrally to the posterior tip of Meckel’s cartilage (Fig. 11). This anterior part therefore represents the prearticular which at this stage has already been incorporated by the gracilart process. The malleus is large and articulates with the anterior and antero-ventral surface of the incus. The large and well developed musculus tensor tympani is attached to a small processus muscularis on the medial side of the neck of the malleus. The incus too, is fully ossified and shows a stout crus brevis. The ascending process of the palatoquadrate is discussed on page 22.

HYOID ARCH The osseous stapes is typically stirrup-shaped and pierced by the stapedial artery. (A more detailed description of the stapes of the young adult will be given later). A large and well-developed musculus stapedialis is attached to the head of the stapes. The tympanohyal is proximally fused to the crista parotica (page 26) while the tympanosquamous ligament connects its distal/
distal end with the proximal tip of the stylohyal. The latter is thus not incorporated in the styloid process as, for example, in Myotis, Miniopterus and Rhinolophus. The stylohyal is long and slender and is followed by the shorter and thicker ceratohyal. Antero-ventral to the anterior end of the ceratohyal, the hypohyal lies in an almost vertical position with its ventral end in contact with the basihyal. A backward extension of the basihyal, the thyrohyal or cornu branchiale, is situated medio-ventrally to the cornu hyale. The thyrohyals are continuous with the basihyal without any histological line of demarcation (Fig. 13). The whole structure therefore, viewed from above (Fig. 13), forms a semicircle antero-dorsal and dorso-lateral to the horseshoe-shaped thyroid cartilage. The posterior end of each ala of the latter is much flattened in a vertical plane (Fig. 13) and partly covers the lamina dorsalis of the cricoid cartilage from the lateral side (Fig. 12). This lamina bears a well defined crista mediana on its dorsal midline. The two lateral plates of the cricoid cartilage are fused with each other in front, so that the whole structure forms a complete ring beneath the arytenoids.

Ossification in the hyoid arch is limited to the stapes, the central part of the thyrohyal, a small median centre in the basihyal, a very small portion of the cerato-
hyal/
Fig. 11.— Transverse section through the dentary to show its relation to Meckel's cartilage and to the gracilar process.

DENT., dentary; MECK.CART., Meckel's cartilage; PR.GRAC., processus gracilis; ZYG.PR.SQ., zygomatic process of squamosal.
hyal, and a larger part of the stylohyal. In the young adult ossification is much more extensive. With the exception of small proximal and distal cartilaginous parts, the whole stylohyal is already ossified. The same is true of the ceratohyal. Only the ventral part of the hypohyal which is in contact with the basihyal, is cartilaginous. The basihyal, as well as the cornu branchiale, is osseous except for that part of the basihyal which is in contact with the hypohyals, and for the posterior end of the cornu branchiale.

A good summary of the hyoid apparatus in Chiroptera is given by Sprague (1943) who says that this apparatus in the Megachiroptera shows much less specialization than that of the Microchiroptera, while among the Megachiroptera that of Rousettus is the least specialized. This opinion is confirmed by a comparison of the condition in R. aegyptiacus with that in Pteropus semindus (Starck, 1943) and some Microchiroptera (Elias, 1908).

AUDITORY OSSICLES OF THE YOUNG ADULT. WASSIF described the auditory ossicles of R. aegyptiacus in 1948. The results of the present investigation confirm his work in practically all respects. The posterior crus of the stapes (Figs. 14 and 15) is slightly thicker than the anterior one. They enclose an intercrural foramen which transmits the stapedial artery. A large and well-developed "capillary channel" extends from the capitulum steto-
opposed musculus stapedialis extends from the capitulum stapedis backwards into the fossa musculi stapedii. As Wassif (1948) points out, no skeletal element of Paauw is embedded in the tendon of the stapedial muscle. According to him Paauw's cartilage, the retention of which may be regarded as a primitive feature, frequently occurs in Chiroptera.

A short and stout crus brevis extends postero-dorsally from the body of the incus (Figs. 14 and 15). The crus longum incudis (stapedial process) points ventrally before curving in a posterior direction and ending in a comparatively large and well-developed Sylvian apophysis which articulates with the head of the stapes. The body of the incus articulates with the malleus with nearly the whole of its anterior and antero-ventral face.

An ossified manubrium (processus tympanicus), which is attached to the tympanum, points antero-ventrally from the ventral tip of the neck of the malleus (Figs. 14 and 15) where a small orbicular apophysis is present. Only the foremost tip of the manubrium mallei is still cartilaginous. This process as a whole is much shorter than the large processus gracilis (processus Polii or anterior process) which is partly fused with the tympanic. The prominent inner lamella of this gracilis process is perforated by a foramen for the chorda tympani nerve (Figs. 8 and 15). The outer lamella is less extensive. From
Fig. 12.— Graphic reconstruction of the hyoid apparatus x approx. 11. Lateral view.

AL.CART.THYR., ala of cartilago thyroidea; BAS.HY., basihyal; CART.ARYT., cartilago arytenoidea; CART.CRIC., cartilago cricoidea; CART.THYR., cartilago thyroidea; CER.HY., ceratohyal; HYP.HY., hypohyal; STYL.HY., stylohyal; THYR.HY., thyrohyal; TRACH., trachea.
the upper anterior part of the neck a lateral shelf extends forward towards the processus cephalicus which lies dorsally to the basis of the anterior process. Nearly the whole of the postero-dorsal surface of the head of the malleus articulates with the indus. The musculus tensor tympani (Figs. 8 and 15) is attached to a small tubercle, the processus muscularis, on the medial side of the neck of the malleus. The tendon of this muscle lies dorsally to the chorda tympani. According to Bondy (1907) the chorda tympani pierces the tendon in Sciurus and Equus. Wassif (1948) describes a similar condition in Tadarida teniotis and Rhinopoma microphyllum in which the tensor tympani muscle is two-headed. In these cases the nerve passes between the two tendons. The same condition obtains in Miniopterus schreibersi (Fawcett, 1919).

An apparently peculiar feature is a fairly large cartilaginous rod (Cart. "X" in Fig. 8) which lies ventro-laterally and laterally to the musculus tensor tympani. It arises from the antero-ventral edge of the bony tegmen tympani and extends forward laterally to and close to the tensor tympani muscle. Further forward it broadens laterally and finds connexion with the osseous inner lamella of the processus gracilis of the malleus and with the tympanic bone in this region. This connexion stretches over a short distance and then the rod decreases in size to/
to end anteriorly dorsally to the Eustachian tube, postero-
laterally to the Eustachian tube cartilage, and ventro-
laterally to the musculus tensor tympani.

Van der Klauw (1922) describes a somewhat similar
cartilage (actually consisting of two elements) in Rousset-
tus amplexicaudatus. Of its connexion with the tegmen
tympani he says: "Obgleich der Übergang ununterbrochen
ist, ist der Knorpel des eigentlichen Processus tegminis
tympani so viel älter, daß dieser Knorpelstab meines Erach-
tens kein unterer Ast eines sich spaltenden Processus teg-
minis tympani sein kann" (p. 11). Likewise in R. aegypt-
ianus the transition is uninterrupted although the tegmen
tympani is already osseous. The function and homology
of this seemingly double (see van der Klauw, 1922) piece
of hyalin cartilage is unknown. Without knowledge of its
ontogeny, its morphological significance cannot be determ-
ined. It seems to serve as a support to and place of
attachment for the large tensor tympanic muscle.
Fig. 13. - Graphic reconstruction of the hyoid apparatus x approx. 8.3. Dorsal view.

BAS.HY., basihyal; CART.ARYT., cartilago arytenoidea; CART.CRIC., cartilago cricoidea; CART.THYR., cartilago thyroidea; CER.HY., ceratohyal; CR.MED., crista mediana; HYP.HY., hypohyal; LAM.DORS., lamina dorsalis; STYL.HY., stylohyal.
THE DERMOCRANIUM

The premaxillary (os incisivum) (Figs. 1 and 2) is relatively small and lodges the two incisor teeth. Posteriorly it lies against the anterior border of the maxillary. From a broad base this bone tapers antero-dorsally to meet the anterior tip of the nasal. In the ventral midline, antero-ventrally to the lamina transversalis anterior, the premaxillaries form a strong syndesmosis.

The maxillary (Figs. 1, 2 and 7) is large and it covers a considerable area of the ventral and lateral parts of the nasal capsule. Its wide palatine process constitutes more than the half of the secondary palate. Posterior and slightly ventral to the infraorbital foramen in the alveolar part, the maxillary bears a long zygomatic process which ends posteriorly against the jugal.

The jugal (zygomaticum) (Figs. 1 and 2) is a short and slender rod-like element which connects the zygomatic process of the maxillary with that of the squamosal. Its posterior end is overlapped laterally by the zygomatic process of the squamosum, while the jugal itself overlaps the zygomatic process of the maxillary for a short distance laterally. A complete zygomatic arch is therefore present.

The lacrimal (Fig. 1) is a small element on the side of the nasal capsule. Its broad base rest on the maxillary dorsal/
dorsal and postero-dorsal to the foramen infraorbitalis, while its dorsal edge overlaps the corresponding part of the frontal. The small lacrimal is pierced by a fairly large foramen for the nasolacrimal duct. Neither Myotis nor Rhinolophus possesses a lacrimal (Frick, 1954). Frick expresses the opinion that the lacrimal of these forms may have been incorporated in the maxillary.

The palatine (Fig. 2) consists of a vertical plate and a larger horizontal or palatine plate. The latter stretches from the pterygoid to the posterior border of the palatine process of the maxillary. The posterior edges of the palatine plates form the anterior border of the apertura nasalis interna. The vertical lamina or pars perpendicularis is much longer than high and lies obliquely its dorsal edge facing dorso-medially. In this way a deep trough which lodges the ductus nasopharyngeus, is formed. This trough is partly roofed by the dorsally situated lamina transversalis posterior and by the pleurethmoid structure.

The corpus of the vomer (Figs. 3 and 7) is trough-shaped with its upper surface folded around the lower edge of the nasal septum. It reaches forwards as far as the posterior end of the anterior paraseptal cartilage. Here the corpus splits into two short rostral limbs which reach forwards as far as the posterior end of the cartilago palatino/
Fig. 14.— Graphic reconstruction of the auditory ossicles of the right side of the young adult. Lateral view.

ANN. TYMP., anulus tympanicus; A. ST., arteria stapedialis; CH. T., chorda tympani; CRUS B., crus brevis; CRUS L., crus longum; C. ST., capitulum stapedis; F. PL., footplate; INC., incus; MALL., malleus; MAN. MALL., manubrium mallei; M. ST., musculus stapedialis; ORB. APH., orbicular apophysis; OUT. LAM. PR. GRAC., outer lamella of processus gracilis; PR. CEPH., processus cephalicus; PR. GRAC., processus gracilis; SYLV. APH., Sylvian apophysis.
palatini. The two caudal limbs are very long and reach backwards as far as the alaminima. The dorsal edge of the lateral lamella of the corpus is ankylosed to the pleuroethmoid of the corresponding side (Fig. 7).

The pterygoid (Fig. 2) is relatively small. Its posterior tip lies more or less dorsally to the Eustachian tube cartilage, and its lamina perpendicularis is a posterior continuation of the vertical lamina of the palatine, lateral to the ductus nasopharyngeus. The pterygoid is fused for a very short distance to the alisphenoid. No pterygoid cartilage is present in the embryonic stage investigated.

The nasal (Fig. 1) has the usual shape. It reaches backwards as far as the middle of the nasal capsule where it overlaps the anterior end of the frontal. Laterally it borders on the maxillary and antero-laterally on the premaxillary.

The frontal (Figs. 1, 2 and 7) is very large. The nasal overlaps a considerable part of its anterior end. It is further bordered by the maxillary, lacrimal, palatine, and parietal. The fontanelle between the frontals and parietals is small at this stage. A stout postorbital process, pierced by a supraorbital foramen, is present. It is absent in all Phyllostomatoidea, Rhinopomatidae and Noctilionidae (Stadtmüller, 1931).
The parietal (Fig. 1) is very large and borders on the frontal anteriorly, the small interparietal postero-medially, and the squamosal ventro-laterally. The anteriorly situated ventro-lateral process reaches the alisphenoid and completely separates the frontal and squamosal. The parietal bears two less prominent lateral crests.

The interparietal (Fig. 1) is a small unpaired element which lies between the medio-dorsal edge of the supraoccipital and the two parietals. In this respect *Pteropus semindus* is rather peculiar, for Starck (1943) could find no interparietal, a bone which is commonly found in *Megachiroptera*.

The squamosal (Fig. 2) is horizontally elongated. The zygomatic process passes outwards before turning forwards to meet the jugal, overlapping it laterally. The outwardly directed part of the zygomatic process bears at its base the glenoid fossa for articulation with the dentary. The postglenoid process is not very prominent and lies anteriorly to the foramen postglenoides through which the lateral jugular vein passes.

The tympanic (ectotympanic) (Figs. 2, 3 and 10) forms a complete ring. The broader antero-dorsal limb is closely related to the gracilis process of the malleus and later becomes fused to it.

The prearticular cannot be distinguished as a discrete element/
Fig. 15.— Graphic reconstruction of the auditory ossicles of the left side of the young adult. Medial aspect.

ANN.TYMP., anulus tympanicus; AN.T.CRUS, anterior crus; A.ST., arteria stapedialis; CART."X" (See page 38); CH.T., chorda tympani; CRUS B., crus brevis; CRUS L., crus longum; F.PL.REM., footplate removed; INC., incus; IN.LAM, PR.GRAC., inner lamella of processus gracilis; MALL., malleus; MAN.MALL., manubrium mallei; M.ST., musculus stapedialis; M.T.T., musculus tensor tympani; POST.CRUS, posterior crus; PR.CEPH., processus cephalicus; PR.GRAC., processus gracilis.
element being already incorporated in the processus gracilis of the malleus.

The dentary reaches from the anterior end of the skull to the glenoid fossa in the squamosal. Near its anterior end the lateral side is perforated by a mental foramen, while the inner side is pierced by the mandibular foramen at a point immediately posterior to the anterior end of Meckel's cartilage (Fig. 10).
The author realizes that in view of Frick's (1954) suggestion that the specimens which Starck (1943) described as *Pteropus seminudus* were probably *Roussettus*, most of his comparison in the text between *Pteropus* and some microchiropteran genera are suspect. A comparison between *Pteropus* and *Roussettus* would therefore provide the same situation. It could, however, be useful in order to support the suggestion of Frick (1954) as most differences can probably be ascribed to difference in age (see Introduction p. 2).

There are a few exceptions such as the presence of a foramen singulare and a tegmen tympani in *Roussettus* compared with the absence of the same characteristics in *Pteropus*. The same applies to the presence of a very deep fossa hypophyseos and of a cartilago dorsi sellae in the latter in contrast to the shallow fossa hypophyseos and the absence of a dorsum sellae in *Roussettus*.

The author is at present collecting embryological material of *Roussettus aegyptiacus leachi* for a comprehensive study of the skull development. Knowledge of the stages corresponding to Starck's specimens would of course help to settle the matter.

For a good account of the interrelationships of the interrelationships of the *Megachiroptera*, *Microchiroptera* and/
and Insectivora the reader is referred to Starck (1943). In his opinion both mega- and microchiropteran cranial characteristics can be traced back to a common ancestral stock -- a view which does not support the theory of a dichotomous origin of the Chiroptera. Simonetta (1960) compares the most important cranial features of Megachiroptera and Microchiroptera with those of the Menotyphla and of the true Insectivora and comes to the conclusion that there is a closer affinity between the Menotyphla and the Chiroptera than between the latter and the Insectivora (S.S.).
SUMMARY

ETHmoid REGION

1 The septum nasi has no foramina.
2 A deep cavum internasale is present between the two cupulae nasi anteriores.
3 The mesethmoid still consists of three discrete ossified centres.
4 The pleurethmoid is ankylosed to the dorsal edge of the corpus of the vomer.
5 The lamina transversalis posterior is not fused to the nasal septum.
6 There is no zona annularis.
7 The lamina transversalis anterior lies almost vertical and is not continuous with the processus lateralis ventralis.
8 A cartilago ductus nasopalatini is represented by a small process which projects antero-ventrally from the ventral edge of the lamina transversalis anterior.
9 An organ of Jacobson is entirely absent.
10 The anterior paraseptal cartilage is rod-shaped and fused to the lamina transversalis anterior.
11 The ductus nasolacrimalis passes laterally to the lamina transversalis anterior, before it opens, immediately in front of this structure.
A cartilago papillae palatinae is absent.

A small cartilago palatina is present in the postero-lateral region of the ductus nasopalatinus.

An alar cartilage, probably a processus alaris superior, borders the fenestra naria posteriorly.

The atrioturbinal is well developed, but a nasoturbinal is entirely absent.

The posterior part of the maxilloturbinal borders the ductus nasopharyngeus laterally.

The ethmoturbinal is composed of three primary ethmoturbinals and one bilaminar secondary ethmoturbinal.

ORBITAL REGION

1. An insignificant crista galli represents the inter-orbital septum.

2. The ala orbitalis is completely ossified as the orbitosphenoid, the latter being continuous with the presphenoid by means of two roots which enclose the optic foramen.

3. A laterally projecting process which extends from the central stem immediately antero-ventral to the preoptic root of the orbitosphenoid, probably represents an ala minima.

4. The fossa hypophyseos is shallow and no dorsum sellae is formed.
5 The alisphenoid is in bony continuity with the processus alaris of the basisphenoid.
6 The ophthalmic and maxillary divisions of the trigeminal nerve are not separated by a skeletal bridge.
7 A small foramen alisphenoidale in the alisphenoid transmits the internal maxillary artery.
8 A peculiar feature is the presence of a cup-like cartilaginous plate which lies on the medio-dorsal and anterior part of the sclera.

OTIC REGION
1 A tegmen tympani is present.
2 The crista parotica does not end in a mastoid process.
3 The large fossa subarcuata is not perforated by a foramen to the outside.
4 There is a separate foramen singulare for the ramus ampularis posterior.
5 The rostral and caudal endotympanics form a cartilaginous floor to the tympanic cavity.

OCCIPITAL REGION
1 The foramen magnum is exceptionally large.
2 A commissura basicochlearis is absent.
3 There is only one hypoglossal foramen.
4 The exoccipital extends laterally as a distinct lamina alaris which ends in a paracondylar process.
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