THE PARANASAL SINUSES OF THE ANTHROPOID APES

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INTRODUCTION

From time to time various writers have given some account of the anatomy of the nasal fossae and associated paranasal sinuses of anthropoid apes. Thus Seydel (1891) has given an excellent account of the structure of the nasal fossa in Primates, while Paulli (1899, 1900) has not only provided a clear (though unillustrated) account of the primate arrangement of parts, but has also worked out in considerable detail its morphology in subprimate mammals. Between them, these two authors have presented a tolerably complete picture of the form and evolution of the paranasal sinuses, from their initial appearance in eutherian phylogeny to their greatest elaboration in various extant specialized forms. Nevertheless, in their study of anthropoid apes both authorities were seriously handicapped by scarcity of material, particularly of the gorilla and chimpanzee, and it is impossible from their descriptions, accurate as they are, easily to comprehend the interrelationships of the various structures present in the anthropoid ape group.

The gaps in our knowledge have been partially filled by Keith (1902), Bolk (1917), Weidenreich (1924), Wegner (1936), Wood Jones (1938), and others, but none of these later authors has attempted any re-assessment of the anthropoid ape types as a whole, though the possible phylogenetic significance of the paranasal sinuses has been not infrequently suggested. Further, since for no anthropoid ape are figures or descriptions available showing all the sinuses in their detailed relationships to individual cranial bones, it becomes necessary first to give a short account of these structures in each genus of anthropoid apes, and only thereafter to attempt the institution of comparisons between them or any appreciation of their phylogenetic history.

Herein the ordinary terminology of the conchae as employed in comparative anatomy is adopted, i.e. nasoturbinal, maxilloturbinal and ethmoturbinals I, II and III, corresponding respectively to the agger nasi, inferior concha, and the middle, superior and supreme conchae of man. The terms "inferior", "middle" and "superior meatus" are applied in their human connotation to lower Primates. Though anatomical and clinical custom has sanctioned the application of the term "processus uncinatus" both to the ethmoidal bony process itself and to the ridge of mucous membrane which covers it, we have here preferred Peter's (1902) term "plica semilunaris" for the mucous ridge alone. "Bulla ethmoidalis", though not ideally descriptive of the homologous structure in anthropoid apes, has been retained to designate both the relevant mucosal elevation and the underlying osseous formation. "Hiatus semilunaris" is used (in Zuckerkandl's sense) as meaning the gap between the bulla ethmoidalis and the plica semilunaris, and as excluding any cavity to which that gap may lead (Layton, 1934). The cavity in the lateral nasal fossa wall into which the hiatus semilunaris leads is called by His (1895) and Schaeffer (1910 *a*) the "infundibulum ethmoidale", but, as Layton has pointed out, this term has been too indiscriminately employed in the past to have retained any definite meaning, and we have therefore preferred instead a latinization of Layton's own term "semilunar groove", namely "sulcus semilunaris". (Admittedly "semilunar" is not strictly descriptive of certain of the several varieties of form which the sulcus may assume: nevertheless the term is retained here partly because it is already established in nasal anatomy and partly to avoid the pedantry inseparable from the adoption of a more precisely descriptive label.)

Further, in human descriptive anatomy, the term "concha nasalis inferior" is applied both to an intranasal elevation of mucous membrane and to the underlying, causative skeletal element, and with some justice, since in man the two are approximately co-extensive. In the anthropoid ape nasal fossa, however, matters are otherwise, the equivalent of the processus lachrymalis et ethmoidalis of the human skull taking the form of a large vertical bony plate (pars verticalis) in the lateral nasal wall. Hence the distinction is herein made between the skeletal element itself ("inferior turbinate") and the less extensive conchal elevation ("maxillo-turbinal").

THE GIBBONS AND THE PRIMITIVE ANTHROPOID APE TYPE

The structure of the gibbon nasal fossa is variable: of two specimens discussed here in detail, one manifests relatively elaborate nasal structures, the other a more simplified arrangement.

In the first specimen, *Hylobates lar leuciscus* (R.C.S. 30 A) the intact but rather shrunken mucous membrane reveals the structures in the middle meatus particularly well without need of conchal disturbance. The nasoturbinal, maxilloturbinal and ethmoturbinals I, II and III, are well-developed; the smooth-walled inferior meatus receives the nasolachrymal duct: the wide middle meatus bears on its lateral wall two ridges (*a*) the plica semilunaris, formed by the mucous membrane overlying the processus uncinatus of the ethmoid, and above this, (*b*) the bulla ethmoidalis. Between the two the semilunar gap (hiatus semilunaris) leads to the shallow semilunar groove (sulcus semilunaris), in the floor of which, at its posterior part, lies the opening (ostium maxillare) of the maxillary sinus. Thus the sinus opens, not directly but indirectly, into the middle meatus, by way of the semilunar groove and semilunar gap. Posteriorly a large sphenoidal sinus is present but ethmoidal and frontal sinuses are wanting.

A second specimen of the same species (R.C.S. 30 B) reveals on examination a precisely similar condition of parts.

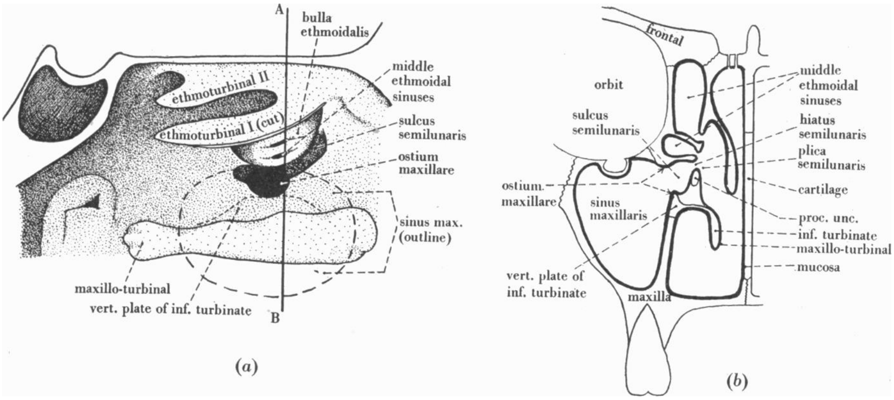


Fig. 1. Schemata of human lateral nasal fossa wall to illustrate structure and the terminology employed: (*a*) surface view, ethmoturbinal I (concha media) cut to expose bulla ethmoidalis, etc., (*b*) vertical section along A–B.

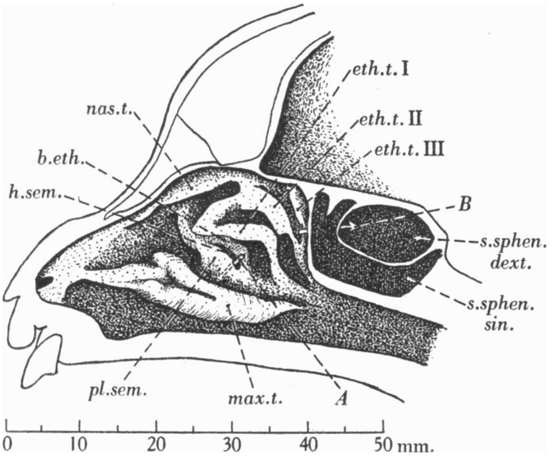


Fig. 2. Lateral nasal fossa wall in *Hylobates lar leuciscus* (R.C.S. 30 A), wet specimen. Arrow *A* passes through hiatus semilunaris and sulcus semilunaris into maxillary sinus: B enters sphenoidal sinus.

In a macerated skull of a different species, *H. hoolock* (R.C.S. D 1), the main turbinals are developed as before, though in different relative proportions. The middle meatus, again wide but here quite smooth-walled, presents neither bulla ethmoidalis nor uncinate process, so that in the fresh state a plica semilunaris was presumably wanting. In this specimen therefore the maxillary sinus opens directly into the middle meatus without the intervention of a sulcus and hiatus semilunaris. The meatal lateral wall is constituted by the maxilla, the nasal surface of the lachrymal, the large vertical plate of the inferior turbinate, and a small part of the ethmoid, all of which participate in the formation of the bony opening into the maxillary sinus. The sinus itself is confined to the maxilla, which it fills, and does not invade the frontal, sphenoid or other adjacent bones.

The sphenoidal sinus is relatively large, with its ostium situated in the normal primate position, i.e. in that part of the ethmoid which forms the posterior wall of the nasal cavity. It invades the frontal bone and the lateral mass of the ethmoid, and over a limited area reaches the vertical plate of the palatine.

A second skull of the same species (D 2) is essentially similar in its details of nasal structure. The conformation of the lateral nasal fossa wall described for *Hylobates hoolock* appears to be identical with that of a macerated specimen of *Symphalangus syndactylus* (R.C.S. 60).

The variation in degree of development of the plica semilunaris and of the bulla ethmoidalis in different specimens or species of gibbon is also attested in the literature. In Zuckerkandl's (1887) skull of *Hylobates concolor* both these structures were well-developed, but in Seydel's (1891) wet specimen, *Hylobates* sp., although the bulla and plica were present in rudimentary fashion, they were situated too far forward to have direct relationship to the ostium maxillare, so that this opening was formed by the same series of elements as obtains in our specimen of *H. hoolock*. The number of gibbon ethmoturbinals is also variable, for ethmoturbinal III may be absent (Selenka, 1898; Paulli, 1900) and even ethmoturbinal II may be rudimentary (Seydel, 1891).

There can be no doubt that the presence, rather than the absence, of a well-developed plica semilunaris and bulla ethmoidalis is to be regarded as the more primitive feature. Paulli's (1900) extended studies of mammalian material have shown that the Primates as a whole, being microsmatic animals, manifest a reduced olfactory apparatus, so that a more complex arrangement is likely to have given place phylogenetically to a more simple. Thus the three ethmoturbinals result from the reduction of the typical mammalian set of four or more, and the bulla ethmoidalis is the last remnant of the numerous ectoturbinals characteristic of osmatic animals. The morphology of the plica semilunaris is doubtful. Most authors, following Zuckerkandl (1887), have interpreted it as a part of the nasoturbinal, but Peter (1902) has claimed that it develops as an independent structure. It is clear, at least, that it forms part of the primitive primate inheritance, since Seydel (1891) has shown that it is already developed in platyrrhine and catarrhine monkeys. Hence in the possession of a plica semilunaris separated by a hiatus semilunaris from an ethmoidal bulla, and of a maxillary sinus opening into a sulcus semilunaris, the first gibbon described above (R.C.S. 30 A) is to be regarded as primitive. It is possible that the earliest anthropoid apes possessed a still more complex nasal

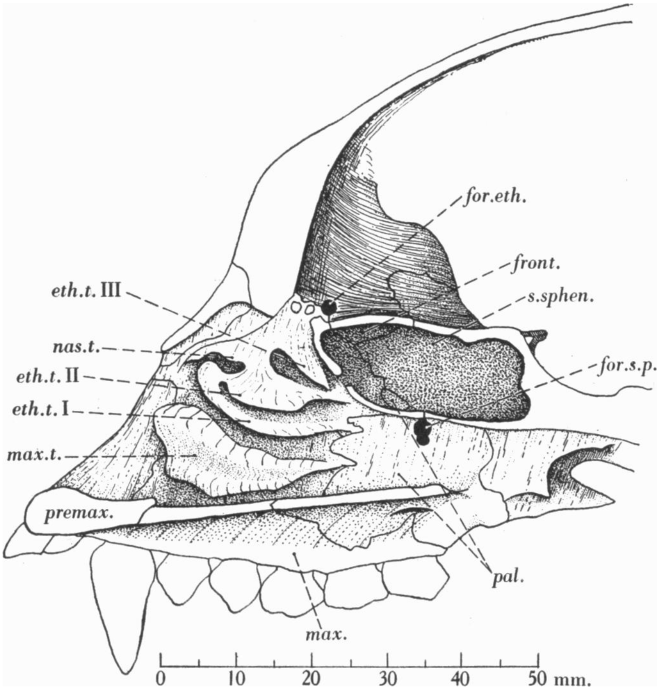


Fig. 3. Lateral nasal fossa wall of *Hylobates hoolock* (R.C.S. D 1), macerated specimen, undissected.

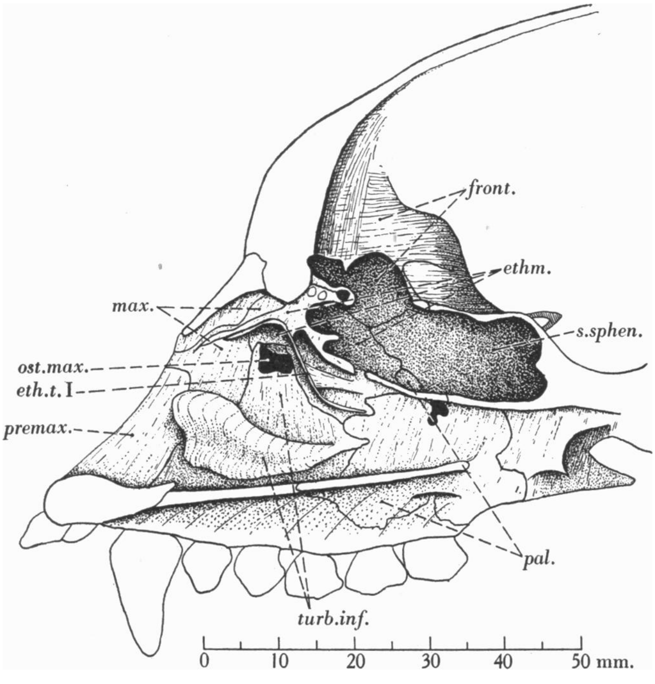


Fig. 4. Same specimen as preceding, with ethmoturbinal I removed and sphenoidal sinus fully opened.

cavity, and that the extra conchae sometimes found in human embryos (Schaeffer, 1910 *b*) are of phylogenetic significance.

Again, in its possession of but two sinuses, sphenoidal and maxillary, the gibbon is a primitive type among anthropoid apes. Paulli (1900) has shown the maxillary sinus to be a primitive eutherian possession, it being the only paranasal sinus found in Insectivora and Chiroptera, and its occurrence being constant in other mammalian orders, save in very small or aquatic forms. The sphenoidal sinus also, although not so ancient an acquisition nor so widely distributed as the maxillary sinus, is, nevertheless, a primitive primate possession (Seydel, 1891). On the other hand the true frontal (*vide infra*) and ethmoidal sinuses are confined to the African anthropoid apes and man. Thus the sole specialization of importance in the nasal apparatus of the gibbon lies in the relatively large size of the sphenoidal sinus and in the invasion thereby of the frontal, ethmoid and palatine bones. Though it is possible, as Pocock (1927) has suggested, that the gibbons represent a secondarily dwarfed type of ape, such consideration need not detract from the conclusion here drawn that, in respect of their paranasal sinuses, they have preserved, with but little change, the primitive anthropoid ape inheritance.

SINUSES OF THE ORANG

In a wet specimen (R.C.S. 990) of a young orang, wherein all the maxillary milk teeth, save the canine, have erupted, the nasal fossa displays but two well-developed conchae, viz. the maxilloturbinal and ethmoturbinal I, although an ill-developed nasoturbinal and ethmoturbinal II are also recognizable. The sphenoidal sinus is represented by a small dimple only in the posterior nasal fossa wall, but the capacious maxillary sinus seems already to have attained its adult disposition. No trace exists of any plica semilunaris, nor, consequently, of either hiatus or sulcus semilunaris; the maxillary sinus therefore opens by an ostium directly (though relatively far back) into the middle meatus. Conditions are essentially similar in a second, somewhat larger and older specimen (R.C.S. E 166) wherein almost the entire permanent dentition has been acquired, and an identical type of maxillary ostium is present in an adult male specimen (R.C.S. E 167 *a*).

A skull of a young adult male orang (St. Thos. 3) has the paranasal sinuses already fully developed, although the cranial sutures, save only the maxillo-premaxillary, persist with perfect distinctness. The sphenoidal sinuses are relatively very small, occupying merely the most inferior part of the sphenoidal body: right and left sinuses, separated by an osseous septum, are equally developed, and each opens in the customary primate site on the posterior wall of the nasal fossa. The maxillary sinus, on the contrary, is enormous, and has secondarily invaded every bone (save the premaxilla) which it may ever invade in any mammal (cf. Paulli, 1900). Its opening, again direct into the middle meatus without trace of any uncinate process, is bounded above and anteriorly

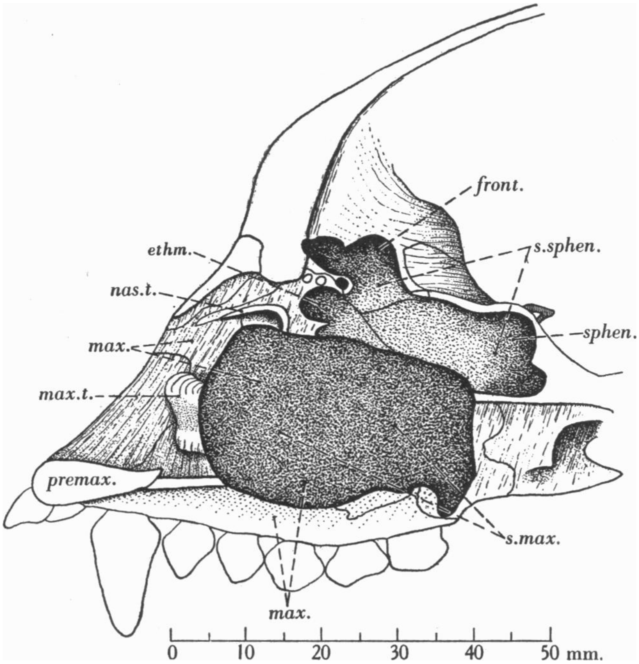


Fig. 5. Same specimen as in Fig. 4 with maxillary sinus fully opened.

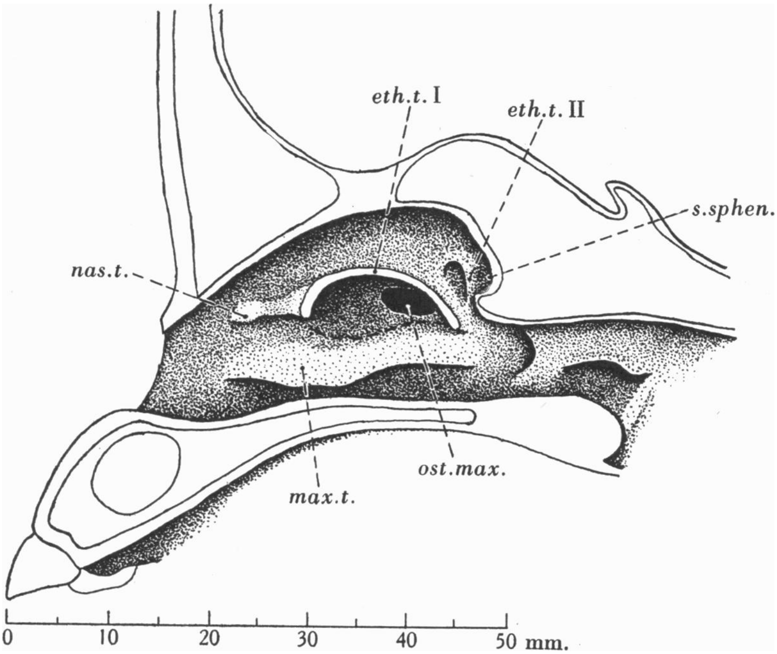


Fig. 6. Lateral nasal fossa wall of young orang (R.C.S. 990), wet specimen, with ethmoturbinal I cut to expose ostium maxillare.

by the ethmoid, inferiorly by the vertical plate of the inferior turbinate, whilst posteriorly it is completed by the vertical plate of the palatine.

The sinus not only occupies the entire maxilla but also invades the lachrymal, frontal, ethmoid, zygomatic, palatine and sphenoid bones. Its sphenoidal extension, situated dorsal to the true sphenoidal sinus, invades both the pterygoid process and the zygomatic process of the temporal. The canals for the infra-orbital and ethmoidal neuro-vascular structures project into the sinus, as does the nasolachrymal duct, whilst the optic nerve and the internal carotid artery encroach upon its sphenoidal extension.

These orang specimens would appear to be typical in respect of the constitution of their nasal fossae. Ethmoturbinal II may be altogether absent (Zuckerkandl, 1887; Seydel, 1891), whilst one or other sphenoidal sinus may be suppressed or represented by a shallow sphenoidal depression only (Paulli, 1900). The third specimen described above appears to be the first recorded showing equal development of right and left sphenoidal sinuses.

The true nature of the sphenoidal extension of the orang's maxillary sinus was first recognized by Seydel (1891) who corrected the earlier and mistaken impression that this cavity represented the sphenoidal sinus proper. Later, Paulli (1900) confirmed Seydel's observations and conclusions, but the work of both these authorities appears to have been forgotten, as Underwood (1910) again misunderstood the precise anatomy of these sinuses. More curious still is the statement by Wegner (1936) that in the young orang of milk dentition age a group of ethmoidal cells lies anterior to the sphenoidal sinus, and that a subsequent breaking down of these cells puts the sphenoidal and maxillary sinuses into secondary but direct communication. Wegner, however, provided no detailed description nor any figure of these supposed ethmoidal sinuses, but as in Seydel's (1891) animal and in our young specimens no trace of such was found, and as, moreover, the anatomy of the true sphenoidal sinuses is now adequately known in the orang, Wegner's explanatory notion may be finally dismissed. It is evident from Seydel's figures that his specimen resembled ours in the constitution of the orifice of the maxillary sinus, but he interpreted as a processus uncinatus that margin of the ethmoid which meets the inferior turbinate. Such an interpretation, however, appears untenable, since the typical uncinate process invariably stands well away from the lateral meatal wall, raising a distinct ridge of mucous membrane (the plica semilunaris) and thus causing the ostium maxillare to lie buried in the sulcus semilunaris. In the orang, on the contrary, the ostium maxillare lies flush with the lateral meatal wall, and in view of this, as well as of the known variability of the gibbon uncinate process, it is not unreasonable to infer, as is here done, the complete absence of an uncinate process from the orang skull. Again Weinert (1926) has described both anterior and posterior ethmoidal cells in the orang skull, but it is clear from his figures that these supposed ethmoidal cells are merely outlying parts of the maxillary sinus.

The frontal extension of the maxillary sinus, first described by Seydel (1891)

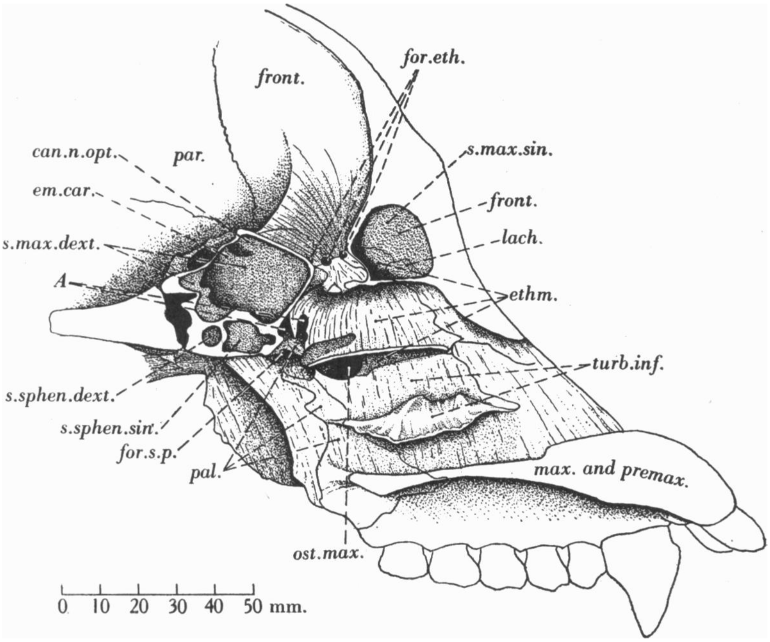


Fig. 7. Lateral nasal fossa wall of adult orang (St Thos. 3) with ethmoturbinal I cut to expose ostium maxillare. A = hiatus between ethmoid and palatine, filled in life by mucous membrane, separating maxillary sinus from nasal cavity.

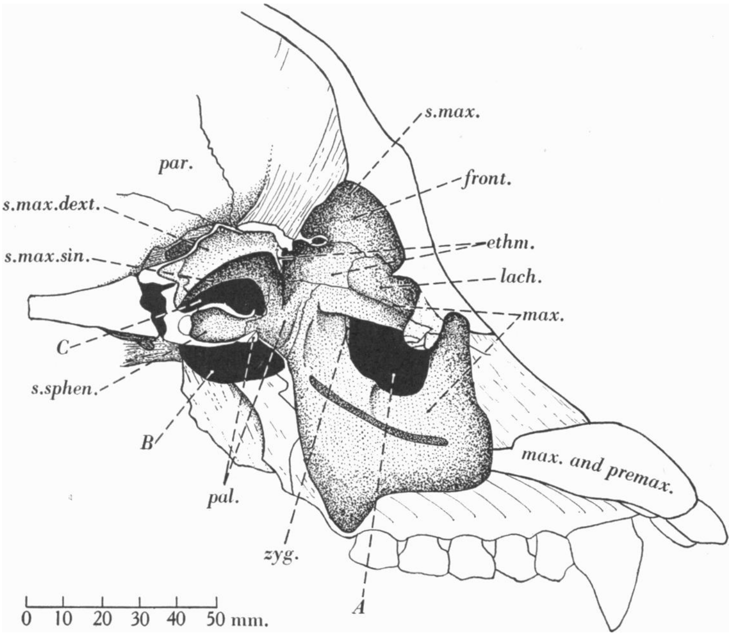


Fig. 8. Same specimen as in Fig. 7 with maxillary and sphenoidal sinuses fully opened. A = extension of maxillary sinus into zygomatic, B = extension into pterygoid process, C = extension into sphenoidal great wing and into temporal.

and recently discussed by Bauermeister (1939), is unusual, yet it may assist understanding of apparently similar frontal cavities in other Primates. As Selenka (1899) pointed out, absence of a true frontal sinus is a primitive feature among Primates. This indeed is only to be expected, since the true frontal sinus is of ethmoidal derivation, and ethmoidal sinuses are, amongst Primates, confined strictly to the African anthropoid apes and man. Yet "frontal sinuses" have been described in several genera, including *Lemur*, *Nycticebus*, *Alouatta* (Seydel, 1891), *Cebus* (Weidenreich, 1924) and *Daubentonia*, *Hapalemur*, *Propithecus*, *Indris* (Weinert, 1926). But as Paulli (1900) suggested, a critical examination shows that in each instance the so-called "frontal" sinus is atypical in its connexion with the nasal cavity, never opening into the antero-superior part of the middle meatus as the true frontal sinus should, and therefore not homologous with that structure.

From the primitive anthropoid ape type already outlined, the orang differs in the absence of any processus uncinatus and therefore of a semilunar groove, as well as in the enormous expansion of its maxillary sinus. Whilst in the other large anthropoid apes the pneumatization of the facial skeleton has been partly effected by the elaboration of neomorphic ethmoidal cells, in the orang it has been achieved by an expansion of the maxillary sinus so exuberant as to reduce the sphenoidal sinuses to insignificance.

It seems therefore most probable that the orang diverged from the anthropoid phylogenetic stem before the appearance therein of ethmoidal sinuses, and that it met the functional demands for a lightening of the skull by a structural specialization of its primitive primate sinus inheritance.

SINUSES OF THE CHIMPANZEE

As, apart from the gibbons, the chimpanzee manifests the most primitive disposition of paranasal sinuses seen in any anthropoid ape, it is here considered in some detail.

A wet specimen (R.C.S. 898) shows a maxilloturbinal doubly-rolled as in the gibbon and orang, and overhanging a deep inferior meatus which receives a non-dilated naso-lachrymal duct. A small nasoturbinal is continuous with ethmoturbinal I. In the middle meatal wall a slightly everted plica semilunaris, separated by a distinct hiatus semilunaris from a narrow but prominent bulla, leads to a deep sulcus semilunaris, in the antero-inferior part of which appears the constricted ostium maxillare. From the anterior part of the sulcus another opening leads into a small, spherical anterior ethmoidal sinus, which bulges into the interior of the frontal sinus. The frontal sinus itself opens into the angle between the bulla ethmoidalis inferiorly and the attachment of ethmoturbinal superiorly. A small ethmoturbinal II overhangs a narrow superior meatus, whence opens a posterior ethmoidal cell which reaches the wall of the orbit. A distinct ethmoturbinal III occurs. Posteriorly a narrow orifice leads into the sphenoidal sinus. The maxillary sinus invades the hard palate to become contiguous with its fellow of the opposite side though separated therefrom by a com-

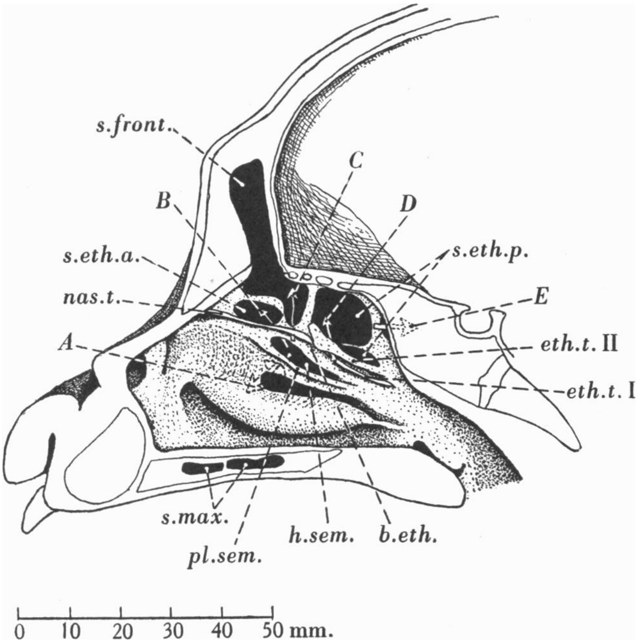


Fig. 9. Lateral nasal fossa wall of chimpanzee (R.C.S. 898), wet specimen, with ethmoturbinal I removed and with frontal and ethmoidal sinuses opened. Arrow A passes from sulcus semilunaris through ostium maxillare (broken line) into maxillary sinus; B from sulcus semilunaris into anterior ethmoidal sinus; C from suprabullar groove into frontal sinus; D from superior meatus into posterior ethmoidal sinus; E enters sphenoidal sinus.

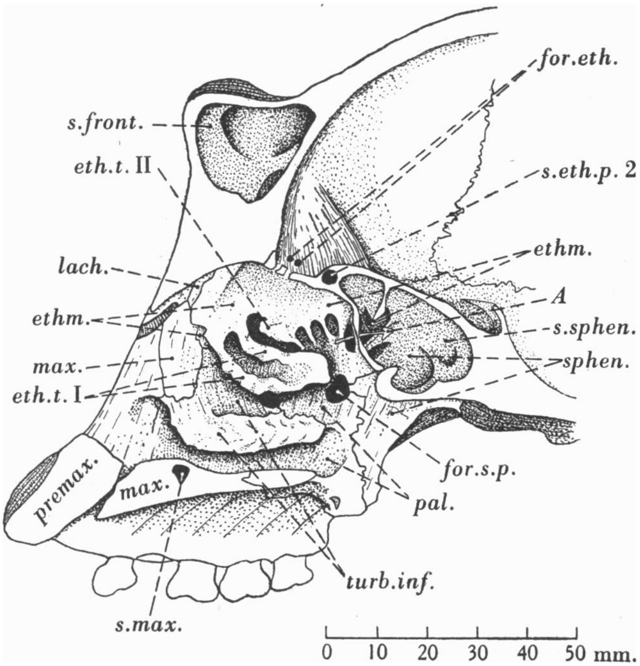


Fig. 10. Lateral nasal fossa wall of chimpanzee (R.C.S. 12.53), macerated specimen: arrow A enters sphenoidal sinus.

plete bony septum. (Such an intrapalatal extension of the chimpanzee antrum was by Underwood (1910) rather unhappily termed "supra-palatine".)

The correspondence between these several features and the constitution of the underlying osseous nasal fossa wall is well exemplified by the skull of an adult chimpanzee (R.C.S. 12.53). Herein a doubly-rolled maxilloturbinal is again encountered, while the uncinate process present has that everted disposition and form which characterizes the plica semilunaris of the wet specimen. Except where attached at its anterior extremity to the ethmoidal lateral mass, the processus uncinatus remains free from articulation with other bones, so that, although when viewed medially it overlaps both the ethmoid and the palatine vertical plate, actually it stands well away from both these structures. Thus in the macerated preparation, between the inferior border of the processus uncinatus and the superior margin of the inferior turbinate, there appears a gap or fontanelle, closed, in life, by the soft tissues forming the medial wall of the sulcus semilunaris. As the processus uncinatus terminates freely, the hiatus semilunaris in the macerated skull remains unclosed posteriorly. A bulla ethmoidalis being indistinguishable in this particular skull, the superior boundary of the hiatus semilunaris is formed instead by the attachment of ethmoturbinal I. A frontal sinus opens into the angle between ethmoturbinal I and the middle meatal lateral wall, immediately antero-superior to the hiatus; in the absence of an ethmoidal bulla its precise morphological position is indefinable, although probably identical with that of the frontal sinus in the wet specimen (No. 898). The sinus itself extends from the ethmoid into the frontal and lachrymal. An anterior ethmoidal sinus, opening into the sulcus semilunaris, lies chiefly within the lachrymal, but is roofed to a small extent by the frontal. In the floor of the sulcus semilunaris the maxillary orifice (ostium maxillare) is completely circumscribed—by the ethmoid superiorly, by the inferior turbinate anteriorly and inferiorly, and by the palatine posteriorly. The sinus extends considerably into the hard palate, including its premaxillary element. Posteriorly it invades the ethmoid so as to effect apposition with the sphenoidal sinus. Two posterior ethmoidal sinuses open into the superior meatus and each attains the orbital wall: the sphenoidal sinus, occupying partly the sphenoid and partly the ethmoid, has extensions into both the alisphenoid and pterygoid processes.

In a second macerated specimen (C 5) the uncinate process effects a minute articulation (1 mm. in extent) with a narrow ascending process from the inferior turbinate: otherwise the nasal fossa wall agrees in osseous constitution with that seen in specimen R.C.S. 12.53 and in other crania examined.

Accounts of the structure of the chimpanzee nasal fossa are so scarce and so incomplete that it is impossible to determine whether the present specimens agree with examples previously recorded in the literature. Sonntag (1923), dissecting the nasal fossa of a young female chimpanzee, encountered, but did not identify, "a movable mucosa-covered bony crest"—clearly, from his description, the uncinate process underlying the plica semilunaris. Selenka

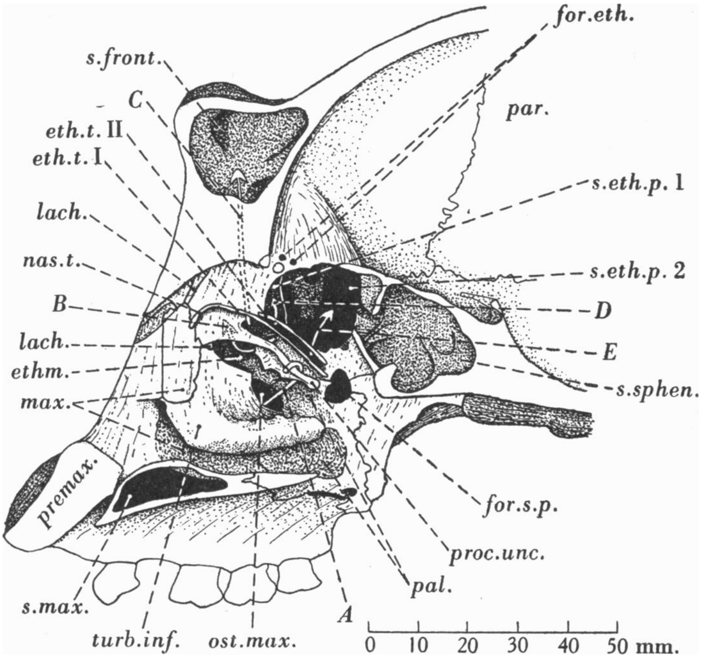


Fig. 11. Same specimen as preceding with ethmoturbinals I and II removed, intrapalatal extension of maxillary sinus and posterior ethmoidal sinuses opened. Arrow A curves over uncinate process and enters ostium maxillare; B passes from sulcus semilunaris into anterior ethmoidal sinus; C enters frontal sinus; D and E pass from superior meatus into posterior ethmoidal sinuses.

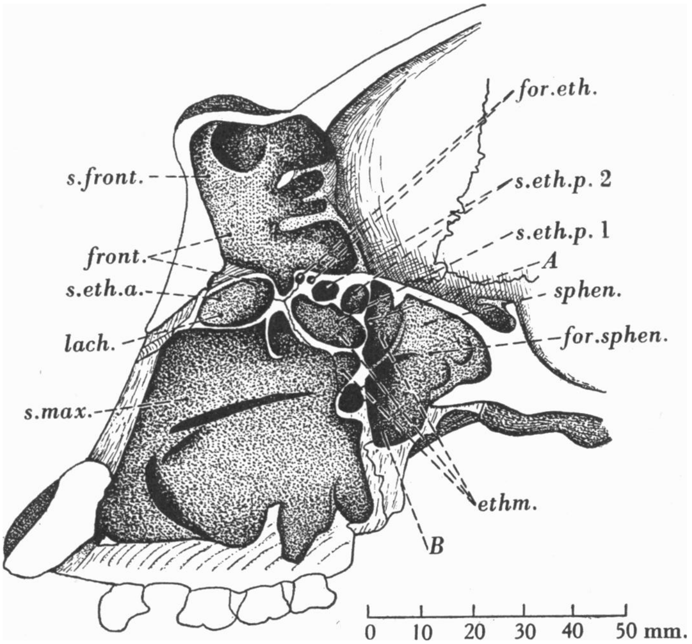


Fig. 12. Same specimen as preceding, dissected to plane of medial orbital wall and with maxillary, frontal and sphenoidal sinuses opened. A = extension of sphenoidal sinus into great wing; B = extension into pterygoid process.

(1898), from a study of the skull as a whole, suggested that the chimpanzee is the least specialized of the great anthropoid apes; he considered the orang to have diverged from the primitive anthropoid ape stem-form and to have become therefore less man-like in structure than the chimpanzee, whose pronounced supraorbital ridges, wide interorbital septum and development of frontal sinuses he regarded as generic specializations.

Wegner (1936) considered the chimpanzee as the most man-like of anthropoid apes in respect of its nasal fossa constitution, instancing its well-developed ethmoidal sinuses and its long sulcus semilunaris. As, however, he erroneously supposed ethmoidal sinuses to be present in young orangs, he failed to appreciate the significance of the first appearance of such structures in the anthropoid group. Further, he over-estimated the profusion of ethmoidal sinuses in the chimpanzee, wherein (as also commonly in the gorilla) no more than three such cells appear.

The chimpanzee resembles the more primitive gibbon type in the number and arrangement of its conchae, and in the anatomical relations of its plica and sulcus semilunaris, and (when this structure is developed) of its ethmoidal bulla. It differs, however, in the possession of ethmoidal and frontal sinuses, and possibly also in a certain incompleteness of ossification of the medial wall of the sulcus semilunaris which is responsible for fontanelle formation. Though such characters represent a specialization and an advance upon the gibbon type, they obtain also in the gorilla and in man, and hence would appear to be relatively primitive anthropoid features. The sole specific specialization encountered in the chimpanzee nasal fossa is the intra-palatal extension of the maxillary sinus, apart from which this animal appears to have retained that structural nasal equipment characteristic of the common anthropoid ape stock after the phylogenetic deviation therefrom of the gibbons and the orang.

SINUSES OF THE GORILLA

In a wet specimen of a four years old gorilla (L.G.A.) all four permanent first molars have erupted, and the permanent central incisors are in process of eruption; the nasal mucosa is intact and the paranasal sinuses appear already to have attained maturity of arrangement and extent. The inferior meatus receives the lower end of the dilated nasolachrymal duct. In the middle meatal wall a plica semilunaris appears as an everted ridge, and a bulla ethmoidalis as a short elevation above it, the two being separated by an intervening hiatus semilunaris. This last extends posteriorly beyond the relatively short plica and bulla, so that its hinder part is bounded by two structures only, the attachment of ethmoturbinal I above and the middle meatal lateral wall behind and below. In the absence of any distinct sulcus semilunaris, the hiatus semilunaris leads directly into the maxillary sinus and into the anterior ethmoidal sinus. A well-developed frontal sinus, with floor invaginated by the anterior ethmoidal sinus, opens inferiorly between the attachment of ethmoturbinal I and the ethmoidal bulla. Of the two posterior ethmoidal sinuses opening into the superior meatus,

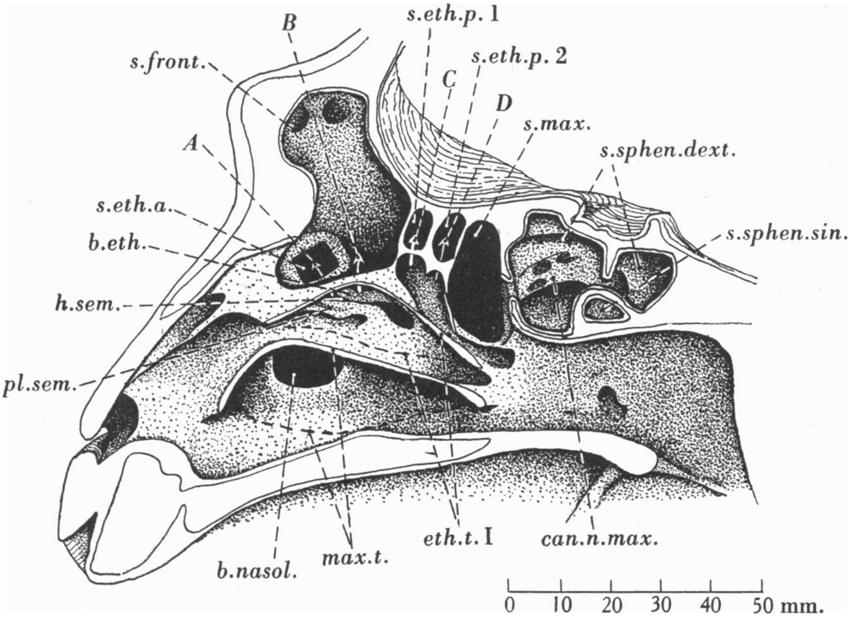


Fig. 13. Lateral nasal fossa wall of young gorilla (L.G.A.), wet specimen, with maxillo-turbinal and ethmoturbinal I removed and with frontal and ethmoidal sinuses opened. Arrow A passes from hiatus semilunaris to anterior ethmoidal sinus; B from suprabullar groove to frontal sinus; C and D from superior meatus to posterior ethmoidal sinuses.

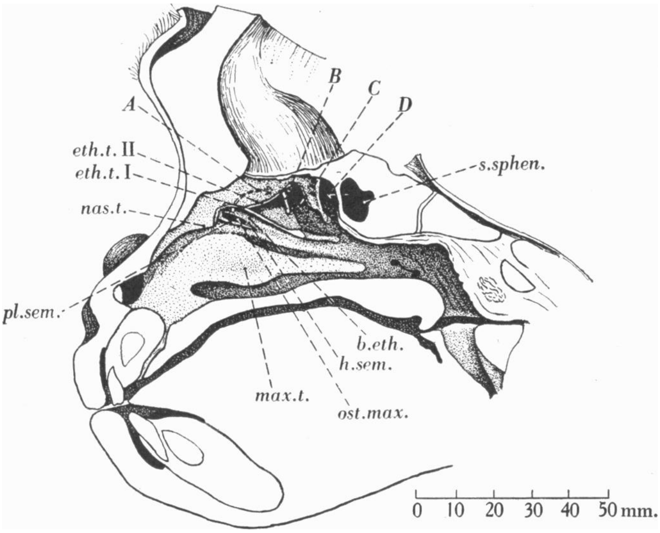


Fig. 14. Lateral nasal fossa wall of young gorilla (T.C.D.), wet specimen, with ethmoturbinals I and II removed. Arrow A passes from suprabullar groove to frontal sinus; B and C from superior meatus to posterior ethmoidal sinuses; D through ostium of sphenoidal sinus.

the anterior is shallow but the posterior is deeper and extends to the orbital wall. The maxillary sinus is large and attains the anterior cranial fossa floor in two places—first, between frontal and posterior ethmoidal sinuses, second, between the posterior ethmoidal and sphenoidal sinuses. The last named sinus is capacious.

In a younger wet specimen (T.C.D.), wherein the first molars alone of the permanent dentition have erupted, the nasal mucosa is intact and the general anatomy of the nasal fossa is much the same, save that the plica semilunaris is relatively longer. The plica extends posterior to the hiatus as a distinct ridge which ends by fusing with the main mass of the ethmoid. The frontal sinus, which superiorly has not yet gained the supraorbital region, opens below (as in the previous specimen) between ethmoturbinal I and the ethmoidal bulla, and extends posteriorly into the ethmoidal region. Two posterior ethmoidal cells, of unequal size, are recognizable, opening into the superior meatus. A half-grown sphenoidal sinus occupies the anterior portion of the sphenoidal body and opens into the spheno-ethmoidal recess. A well-dilated nasolachrymal duct is received into the inferior meatus.

In a third, and still younger, intact wet gorilla specimen (L.G.B.) none of the permanent teeth have as yet begun their eruption. Of the paranasal sinuses there are present the maxillary, a rudiment of the sphenoidal, a single, large, posterior ethmoidal, and an immature frontal which has not yet invaded the frontal bone. The nasoturbinal, maxilloturbinal and ethmoturbinals I, II and III are all characteristically developed. The inferior meatus receives the already dilated nasolachrymal duct. The middle meatus presents on its lateral wall a long and prominent plica semilunaris, separated from the bulla ethmoidalis above by a relatively deep sulcus semilunaris, in the anterior part of which appears the oval ostium maxillare. Posteriorly the plica semilunaris fuses with the main mass of the ethmoid. No distinct fronto-nasal duct is detectable.

A condition of parts essentially similar to that obtaining in the foregoing wet specimens, particularly in the matter of number and appearance of ethmoidal cells, is displayed by an infant gorilla skull (R.C.S. 30 A) which has its milk dentition *in situ*, and its first permanent molars far from eruption. The inferior meatus receives an already well-dilated nasolachrymal duct; the maxillary sinus occupies the entire maxilla behind the bulla ossea nasolachrymalis, and opens into the sulcus semilunaris above a (now broken) processus uncinatus. The sphenoidal sinus occupies the whole of the presphenoid and extends into the alisphenoid and pterygoid processes. A moderate sized frontal air-cell extends forwards to gain the frontal bone, and opens below into the sulcus semilunaris anterior to the ostium maxillare. Two posterior ethmoidal cells, one small, one large, constitute the bulk of the ethmoidal lateral mass.

A second young gorilla cranium (R.C.S. 34.31) with milk dentition *in situ* and about the same size and age as specimen 30 A, shows an incipient frontal

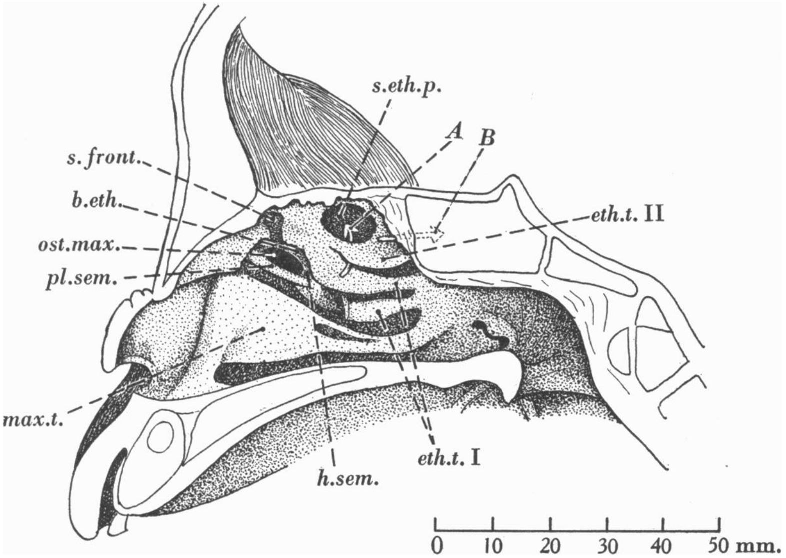


Fig. 15. Lateral nasal fossa wall of young gorilla (L.G.B.), wet specimen, with ethmoturbinal I partly removed, and frontal and posterior ethmoidal sinuses opened. Arrow A enters posterior ethmoidal sinus; B enters the sphenoidal sinus.

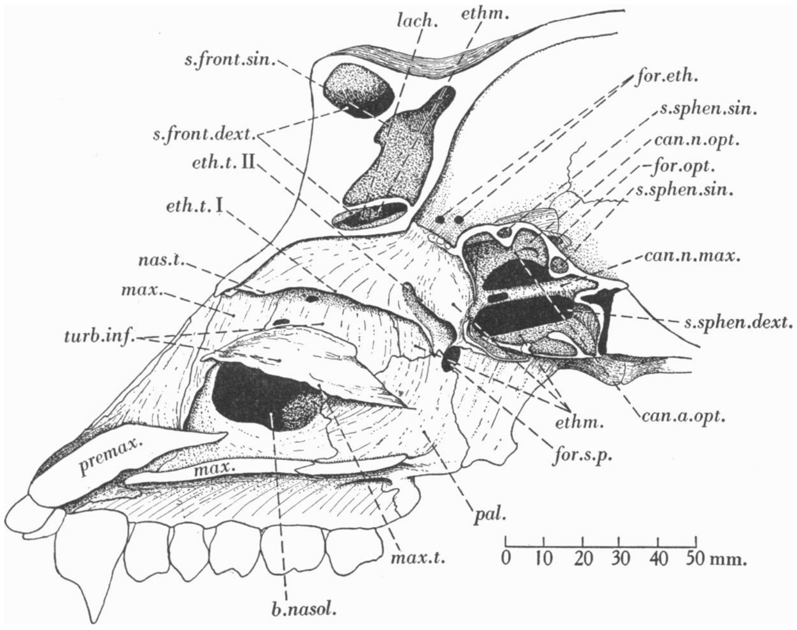


Fig. 16. Lateral nasal fossa wall of adult gorilla (St Thos. 1), macerated specimen, undissected.

sinus which has already reached the frontal bone. The sphenoidal sinus not only occupies the anterior moiety of the sphenoidal body but invades the ethmoid also; the maxillary sinus occupies the maxilla behind the dilated bulla nasolachrymalis. A large posterior ethmoidal cell is present.

An adult female gorilla cranium (R.C.S. 26.5) likewise presents capacious frontal and sphenoidal sinuses, and a maxillary sinus which occupies by extension the whole of the ethmoidal lateral mass. A single posterior ethmoidal cell, reduced by antral encroachment, occurs on the right side only.

In an adult male gorilla (R.C.S. 25) the frontal sinus is enormous and complicated; the sphenoidal sinus extends into the alisphenoid and pterygoid processes; the maxillary sinus invades the zygomatic bone laterally and the ethmoidal lateral mass superiorly, becoming thus contiguous with the frontal and sphenoidal cavities. On the right the true sphenoidal sinus is exceptionally small and the ipsilateral maxillary sinus has invaded the sphenoid by way of functional replacement. A single posterior ethmoidal cell is present bilaterally. A mature gorilla skull (C 1), of uncertain sex, presents a multilocular and somewhat complicated frontal sinus, a sphenoidal sinus extending into the alisphenoid and pterygoid processes, and a maxillary sinus which involves the greater part of the ethmoidal lateral mass. A single large posterior ethmoidal sinus opens into the superior meatus. In a huge mature male gorilla (B.M. unregistered) the frontal and sphenoidal sinuses are maximally developed. The antrum, which opens into the sulcus semilunaris above a well-developed uncinate process, fills not only the body of the maxilla behind the nasolachrymal bulla, but also the greater part of the ethmoidal lateral mass, becoming thus contiguous with the frontal and sphenoidal sinuses. A relatively large and still discrete posterior ethmoidal sinus opens into the superior meatus.

The macerated skull of a subadult animal (St. Thos. 1) exhibits a complete dentition and a full complement of unobliterated cranial sutures. The nasolachrymal duct presents a short uninflated upper portion continuous at the lachrymo-maxillary articulation with an enormously dilated lower portion (bulla ossea nasolachrymalis): the lateral wall of this bulla is formed chiefly by the maxilla, the medial wall by the inferior turbinate's vertical plate plus a small part of the palatine, whilst the bulla is closed above by the lachrymal. In the lateral bullar wall runs the infraorbital canal, the bony wall of which is partially deficient. In the middle meatus the processus uncinatus is attached at both its extremities, viz. anteriorly to the attachment of ethmoturbinal I and posteriorly to the lateral mass of the ethmoid. Thus in the recent state this specimen must have resembled specimen T.C.D. in possessing the type of plica semilunaris which extends backwards beyond the hiatus semilunaris, in contradistinction to the type of plica (seen in specimen L.G.A.) which stops short of the hinder end of the hiatus. Between its attached extremities the processus uncinatus is free, being separated by the hiatus semilunaris from the bulla ethmoidalis above, and by a fontanelle (closed in life by soft tissue) from the extensive vertical plate of the inferior turbinate below.

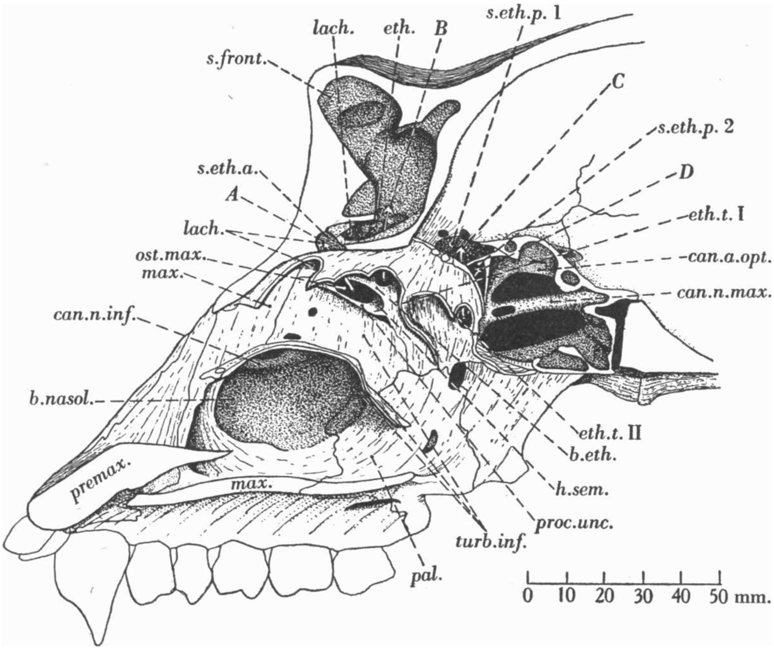


Fig. 17. Same specimen as preceding with maxillo-turbinal and ethmoturbinals I and II removed, and with frontal and ethmoidal sinuses opened. Arrow A enters anterior ethmoidal sinus; B enters frontal sinus.

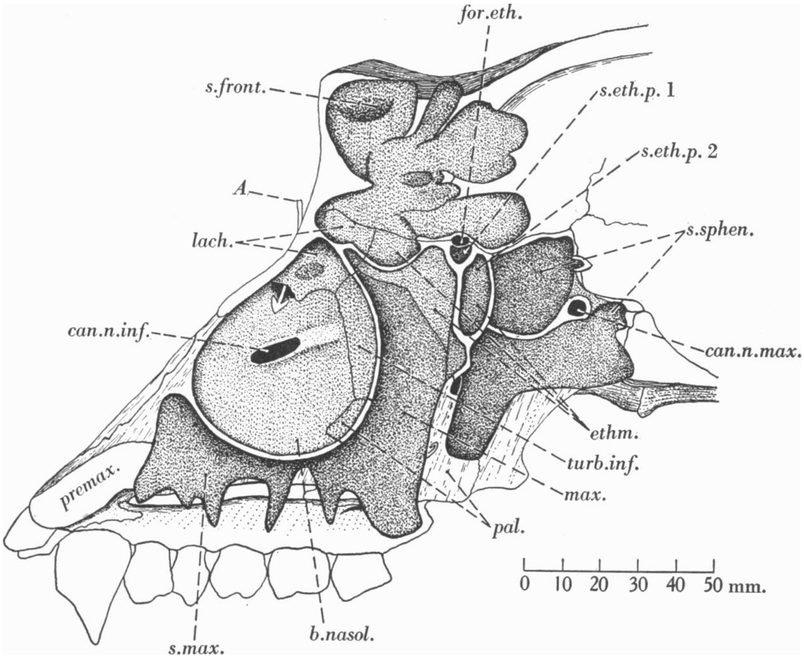


Fig. 18. Same specimen as preceding, dissected to plane of medial wall of orbit, showing sinuses and nasolachrymal bulla. Arrow A passes through the undilated portion of nasolachrymal duct to bulla nasolachrymalis.

The bulla ethmoidalis is a short ridge situated above and parallel to the uncinate process. At the anterior end of the hiatus semilunaris lies the entrance to the anterior ethmoidal sinus, an excavation into the lachrymal bone. The ostium maxillare presents a distinct margin inferiorly (where bounded by the superior margin of the vertical plate of the inferior turbinate) but elsewhere its margins are not demarcated from the floor of the sulcus semilunaris. The frontal sinus, occupying chiefly the frontal, but circumscribed in some part by both lachrymal and ethmoid, opens below between ethmoturbinal I and the bulla ethmoidalis. The maxillary sinus, occupied anteriorly by the bulla nasolachrymalis, is extremely large, occupying not only the maxilla but portions of the ethmoid and the palatine also. Each of the two posterior ethmoidal sinuses present reaches the orbital wall, and each is contiguous with the sphenoidal sinus. This last structure attains its maximal anthropoid ape development in the gorilla. In the present specimen it occupies entirely the large sphenoidal body and extends deeply into both the alisphenoid and pterygoid processes, effecting pneumatization of all parts of the sphenoid save only the orbito-sphenoid element, and establishing contiguity with the frontal, maxillary and posterior ethmoidal sinuses. The sinus is traversed by the bony canal containing the maxillary nerve, and the upper part of its lateral wall is depressed by the structures (optic nerve and ophthalmic artery) grooving the superficial aspect of the sphenoidal body.

Examination of other gorilla skulls reveals an identical type of nasal fossa structure. The uncinate process shows much variability, some skulls presenting the short, freely ending type of process responsible for the short plica semilunaris noted in specimen L.G.A., and others the long, doubly attached type of process, described in specimen St. Thos. 1 (see Fig. 19).

The suture between ethmoid and inferior turbinate may, and often does, become obliterated at a relatively early post-natal age—indeed its persistence in an animal so mature as the St. Thos. 1 specimen is unusual. That the intranasal sutures of this particular specimen have however been correctly identified, and that such sutures suffer but little change of position during the later stages of post-natal growth, is amply confirmed by a study of infant gorilla skulls, in particular by one (R.C.S. 34.4) wherein the deciduous incisors alone have erupted and the deciduous canines and first molars are but in process of eruption. (In this infant gorilla, the bulla nasolachrymalis is already characteristically distinct.)

A wet specimen of an adult (11 years old) female lowland gorilla ("Moina"), whose skeleton still retains traces of immaturity, presents nasoturbinal, maxilloturbinal and ethmoturbinals I and II. The inferior meatus receives the dilated nasolachrymal duct. The middle meatus presents a long, large and prominent plica semilunaris, bounded superiorly by a deep and co-extensive sulcus semilunaris, in the hinder moiety of which appears the narrowly oval ostium of the maxillary sinus. The plica semilunaris terminates postero-inferiorly by fusing with the ethmoidal portion of the lateral nasal fossa wall. Above the sulcus

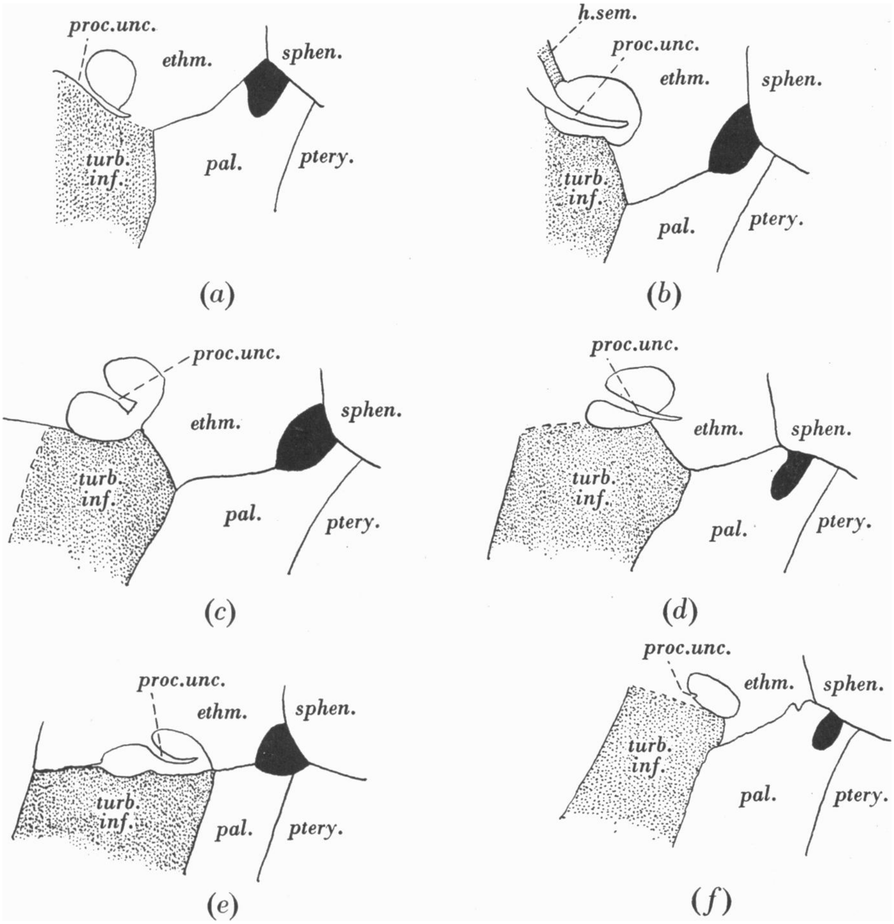


Fig. 19. Scheme showing variations of uncinate process in the gorilla: (*a*) adult male (B.M. unreg.); (*b*) adult (private coll.); (*c*) adult (St Thos. 1); (*d*) young (R.C.S. 30 A); (*e*) subadult (B.M. 3 K); (*f*) subadult female (R.C.S. 27).

semilunaris, between it and the ethmoidal bulla, the fronto-nasal duct opens into the middle meatus close to the attachment of ethmoturbinal I. The sphenoidal sinus, reduced by reason of the encroachment thereupon of the antrum, is divided by a median septum; each moiety opens by a small circular aperture into the spheno-ethmoidal recess. The maxillary sinus is enormous: not confined to the maxilla it invades the frontal, the ethmoid and the sphenoid. It is separated from the frontal sinus by a thin bony lamina only: it occupies the entire lateral mass of the ethmoid from nasal to orbital extremities and thence extends backwards to occupy almost the whole of the sphenoidal body, being separated from the reduced sphenoidal sinus proper by a thin curved bony lamina. No individual ethmoidal cells are anywhere recognizable, nor is there even suggestive evidence of their former presence.

The absence of distinct ethmoidal cells noted in "Moina" is paralleled by the condition of parts obtaining in certain macerated gorilla crania. Thus an adolescent female gorilla (R.C.S. 27) exhibits extensive frontal, maxillary and sphenoidal sinuses: the maxillary sinus invades the entire ethmoidal lateral mass and is contiguous with the other two sinuses. No traces of individual ethmoidal cells, past or present, are discernible.

A heavily crested adult gorilla skull (R.C.S. 22.2) presents a complex multilocular frontal sinus which invades almost the whole orbital roof: a large, irregularly septate sphenoidal sinus exhibits the usual alisphenoid and pterygoid extensions. The maxillary sinus, lying lateral and posterior to the naso-lachrymal bulla and opening into the middle meatus above a distinct uncinate process, occupies by extension the whole of the ethmoidal lateral mass; it extends along the entire medial orbital wall, and is separated by thin osseous laminae only from the frontal and sphenoidal sinuses. No trace whatever of ethmoidal cells is detectable.

Another adult male gorilla (R.C.S. 20) presents essentially similar features. Frontal, sphenoidal and maxillary sinuses are characteristically developed: the antrum extends into the whole lateral mass of the ethmoid, thus becoming contiguous with the frontal sinus antero-superiorly and the sphenoidal sinus postero-superiorly. No ethmoidal cells occur nor is there even a suggestion of their former presence.

Broadly speaking, in the gorilla ethmoidal cells (which never exceed three in number in young skulls) may disappear, possibly with advancing age, and their place may be taken by a progressively enlarging maxillary antrum, whereas in man on the contrary, these cells maintain a persistent, life-long elaboration and extension. The very constancy of the gorilline frontal sinus (itself essentially an ethmoidal derivative) presupposes the general occurrence of at least one anterior ethmoidal cell, and all young specimens, wet or dry, examined by us present clearly established ethmoidal cells.

It is however equally possible that, in some gorilla specimens at least, middle and posterior ethmoidal cells do not appear at any stage of development, and that in such cases the antrum early attains its maximal extra-

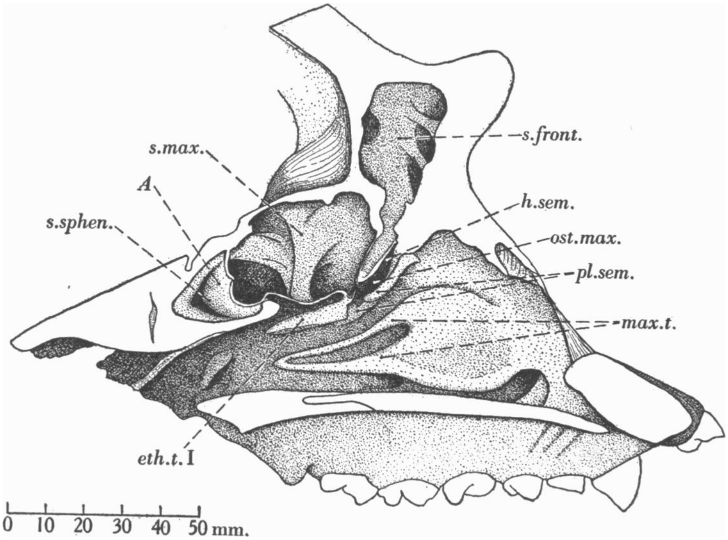


Fig. 20. Lateral nasal fossa wall of eleven years old female gorilla ("Moina"), wet specimen, as exposed by paramedian section. A = septum separating maxillary and sphenoidal sinuses.

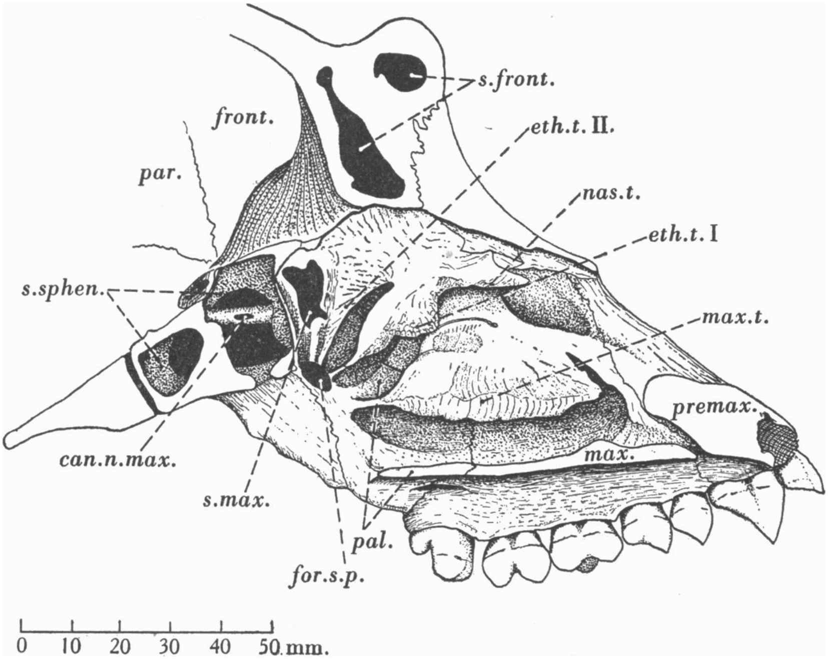
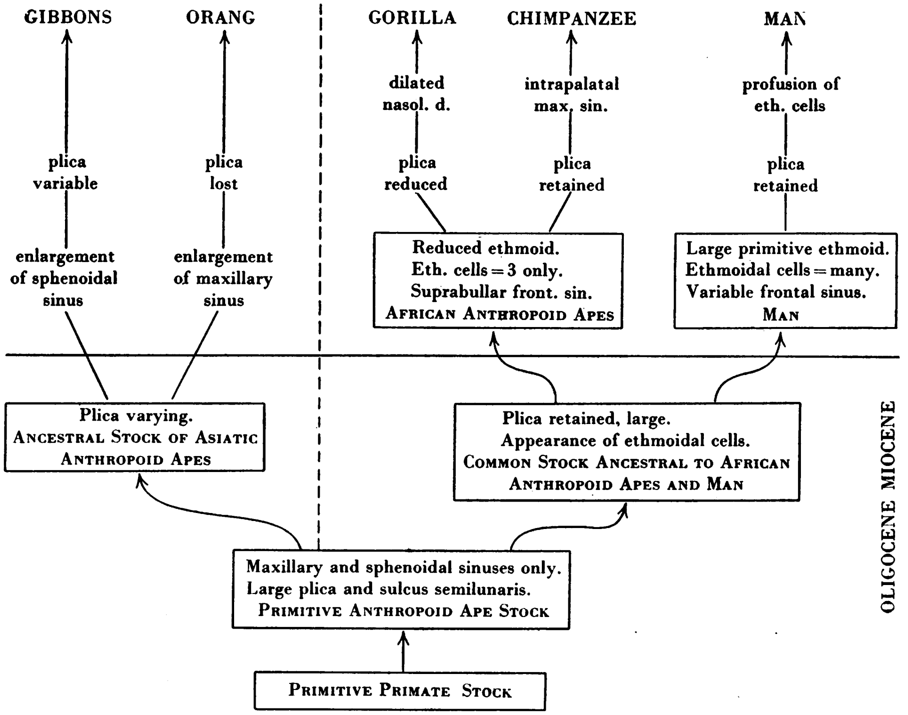


Fig. 21. Lateral nasal fossa wall of subadult female gorilla (R.C.S. 27), macerated specimen.

maxillary extension. Bauermeister (1939) failed to find ethmoidal cells in his gorilla material.

In most details our present findings in the gorilla agree well with those of earlier observers. Seydel's (1891) young animal is the only other specimen with an intact nasal mucosa to have been so far described and figured: this beast possessed a plica semilunaris of the long type, and Seydel called particular attention to the very hominoid arrangement of the structures surrounding its ostium maxillare. (Actually, the chimpanzee is even more man-like in this regard, but Seydel lacked chimpanzee material at the time he wrote.)

Table I. *Tentative phylogenetic scheme based on present findings*



Keith (1902) gave the first illustration of the gorilline nasolachrymal bulla, previously described by Seydel, but unfortunately stated that a similar bulla characterized the chimpanzee also. Bolk (1917) has carefully described the successive stages of the bullous transformation of the gorilla's nasolachrymal duct, indicating, in old animals, its attainment to the orbital floor and the consequent direct opening into it of the lachrymal sac. Observations made during the present enquiry, however, do not support Bolk's supposition, but rather that of Aichel (1934) who correlates variations in size of the bulla with racial rather than with age differences. Certainly, in quite young specimens, the bulla is already established, and may attain the floor of the orbit. The only authors to study in any detail the constitution of the osseous walls of both nasolachrymal duct and paranasal sinuses in the gorilla are Wegner (1936) and Wood Jones (1938); corresponding studies in other anthropoid apes appear to have been made for the first time during the present investigation. Unhappily, both these authors interpret as an intrinsic portion of the ethmoid that part of the inferior turbinate which forms the posterior wall of the nasolachrymal bulla, Wegner indeed specifically identifying it as the processus uncinatus. Now from a study of the specimens described above (particularly St. Thos. 1 and R.C.S. 34.4) such an interpretation appears plainly erroneous, for there can be no doubt as to the real nature of the bone in question. It is emphatically not the uncinate process, which is herein correctly identified for the first time since Seydel's (1891) paper.

If that portion of the inferior turbinate which participates in the formation of the wall of the nasolachrymal bulla were truly part of the ethmoid, then the ostium maxillare would indeed be entirely surrounded by ethmoid. It is upon such an hypothesis that Wood Jones (1938) has suggested (*a*) that the gorilline maxillary sinus is really an enlarged ethmoidal sinus, (*b*) that in this genus a true maxillary sinus is not developed. His conception of an ostium maxillare surrounded by ethmoid in the gorilla, but by maxilla in man, is untenable, for actually the ostium maxillare of the gorilla—like that of all other anthropoid apes and of man—lies between the ethmoid superiorly and the inferior turbinate inferiorly.

SINUSES OF MAN

Under this heading are discussed those points only which are relevant to an intelligible comparison of the paranasal sinuses in man and anthropoid apes. The human condition of affairs is most closely matched by the African anthropoid apes, and by the chimpanzee more particularly, since the gorilla lacks the well-developed plica and sulcus semilunaris of man and in addition manifests a peculiarly distinctive dilatation of its nasolachrymal duct—the well-known bulla ossea nasolachrymalis. The principal (often sole) opening of the human maxillary sinus into the sulcus semilunaris—the only opening to appear in the human embryo (Schaeffer, 1910*a*)—corresponds exactly to the anthropoid ape ostium maxillare; the human antrum, however, not infrequently displays one or more accessory ostia situated in the soft tissues which close the fontanelles in the lateral nasal fossa wall behind and below the uncinate process. Certain other deficiencies of the walls of neighbouring sinuses (e.g. maxillary and frontal) which occur occasionally in man are unknown in anthropoid apes.

Ethmoidal sinuses are much more profuse and elaborate in man than in the African anthropoid apes, wherein indeed their number probably never exceeds three. The human ethmoidal sinuses develop not only from the lateral walls of both the middle and the superior meatus, but frequently from the supreme meatus also (Paulli, 1900; Schaeffer, 1910*b*). The human frontal sinus shows considerable variability in its precise site of outgrowth from, and its communication with, the nasal fossa. It arises sometimes from a frontal recess of the middle meatus, or from a groove within that recess, sometimes from the anterior terminal recess of the sulcus semilunaris, and occasionally at least from a groove situated above the ethmoidal bulla but below the middle concha (Grünwald, 1912, types I, II and III). In every gorilla and chimpanzee specimen examined during this investigation the frontal sinus was found to arise as a diverticulum from this supra-bullar groove, and although present anthropoid ape material is too scanty to permit of certain pronouncement on the matter, it appears at least highly probable that such a suprabullar type of frontal sinus (the rarest form encountered in man) occurs most frequently, if not constantly, in the African anthropoid apes.

The understanding of the morphology of the human paranasal sinuses has been illuminated by detailed studies of their ontogenetic history (Killian, 1896; Mihalkovics, 1898; Kallius, 1905; Schaeffer, 1910 *a*, *b*; van Gilse, 1927). Soon after the appearance of the nasal conchae as eminences upon the ectodermal wall of the primitive nasal capsule a sulcus and a plica semilunaris are found (50–60 days stage), modelled at first in epithelium and soft tissues only and lacking any skeletal basis. Later (about the 65–70 days stage) the maxillary sinus appears as a localized outpouching of the wall of the sulcus semilunaris. In the mesenchymal tissues surrounding both sulcus and sinus cartilage is then deposited, so that the sulcus comes to lie between the processus uncinatus medially and the cartilaginous nasal fossa wall laterally, whilst the sinus comes to occupy the angle between this wall and the inturned margin thereof forming the cartilaginous framework of the inferior concha. (Such relationships are of course of a secondary nature, as ontogenetically the appearance of the cartilage is entirely subsequent to the primary modelling of the non-skeletal tissues.) Still later (4th month stage) the mucosa above the sulcus semilunaris bulges medialwards as the bulla ethmoidalis, and cartilage is developed beneath it. Meantime the maxilla itself (ossified in the 2nd month) remains separated from the developing maxillary sinus by the dense mesenchymal stratum wherein the cartilage of the lateral nasal wall afterwards develops; it is only by the subsequent resorption of this cartilage and the continued expansion of the sinus that the latter attains its first direct contact with the maxilla. With the ossification of the cartilaginous lateral nasal wall (in the 6th month) the maxillary sinus comes to lie between the ethmoid above and the inferior turbinate below, a secondary relationship dependent upon the mode of ossification of the preexistent cartilaginous anlagen. (The remaining paranasal sinuses also make their initial appearance prior to ossification of the nasal fossa walls, but their history requires no discussion here.)

The early appearance of the sulcus semilunaris in the human embryo—paralleled by a corresponding precocity in other mammalian embryos (Peter, 1902)—suggests its primitive nature, and supports the thesis that both its absence in the orang and certain gibbons, and its reduction in the gorilla, are in the nature of secondary degenerative modifications.

A review of nasal fossa embryology emphasizes the importance of the correct identification of mucosal folds, elevations, depressions and the like, as these early structures are surer criteria of sinus homologies than are the sutures between the tardily-appearing osseous elements of the lateral nasal wall.

Moreover, Paulli (1900) has shown that the maxillary sinus may establish contact with but a small part of the maxilla (as in *Hyrax* (*Procavia*), *Equus*, *Rhinoceros*, *Coelogenys*) or may fail entirely to establish any relationship with the maxilla (as in *Dicotyles*, *Hippopotamus*, *Cynaelurus* (*Acinonyx*), *Hystrix*), though in all these genera, the opening of the sinus, the sole reliable guide to its identity, occupies an essentially identical morphological position.

PHYLOGENETIC CONCLUSIONS

Certain conclusions concerning human and anthropoid ape phylogeny, derived from a study of the evidence presented in this paper, are indicated in Table I (*q.v.*). Admittedly such a table, based solely upon considerations of nasal sinus anatomy, must possess but limited intrinsic value: nevertheless, once constructed, a table of even this restricted nature is at least available for detailed comparison with others based upon wholly different lines of anatomical reasoning, and is therefore perhaps not unjustified.

An interpretation of paranasal sinus morphology alone yields strongly suggestive evidence that the primitive anthropoid ape stock gave rise to three divergent lines, leading respectively to the relatively primitive gibbons, to the highly specialized orang, and to the African anthropoid apes and man. Of the last group, the chimpanzee remains a relatively unspecialized member, the gorilla is distinguished particularly by an inflated nasolachrymal duct, whilst man is characterized by a remarkably complex ethmoidal labyrinth. The evidence of paranasal sinus structure, considered alone, is inadequate for the demonstration of the mutual relationships of these three forms, yet it does suggest the derivation of both chimpanzee and gorilla from an anthropoid ape common stock distinct from that leading to man. On the other hand, the common possession of ethmoidal sinuses suggests a close affinity between man and the African anthropoid apes to the exclusion of all other Primates.

The only comparable table based upon the evidence of nasal anatomy is that of Zuckerkandl (1887), who, erroneously believing ethmoidal sinuses to occur in *Mycetes*, suggested the derivation of the anthropoid apes from a common ancestor already equipped with such structures, and related possibly to *Anaptomorphus*. Zuckerkandl recognized the aberrant nasal structure of the orang and the specializations peculiar to man, but, from want of African material, could not, in his table, separate gorilla, chimpanzee and gibbon.

Selenka (1899), working on the skull as a whole, gave carefully compiled lists of both the primitive and the specialized characters exhibited by each anthropoid ape. He recognized clearly the relatively primitive nasal structure of the gibbon and (apart from its innovation of frontal sinus development) of the chimpanzee: he suggested the possibility of a common origin of the chimpanzee and man from a dryopithecine ancestor.

The conclusions suggested in our table agree closely with those of most students of anthropoid ape structure, in particular those of Morton (1927), whose views were based upon comprehensive studies of the anthropoid ape foot, arm-body ratio, posture, dentition, skull and endocranial cast. His proto-anthropoid ape stage of the Oligocene corresponds to our "primitive anthropoid ape stock", and his dryopithecine stage of the Miocene to our "common stock ancestral to the African anthropoid apes and man".

Similar conclusions, emphasizing the close relationship between man and the African anthropoid apes through a Miocene dryopithecine stock, are set forth in Abel's table (1934), compiled on a strictly palaeontological basis.

On the other hand, our conclusions differ from those of certain other anatomists who have made particular studies of paranasal sinus anatomy. Thus both Weinert (1926) and Wegner (1936), mistakenly believing that orangs possess ethmoidal sinuses, failed to recognize these structures as a specialized neomorphic development linking man with the gorilla and chimpanzee. Wood Jones (1929) has denied any close relationship between man and the African anthropoid apes, and has argued against their derivation from any recent common ancestral stock. He stresses, for instance, the specialized cynomorphic reduction of the ethmoid in the anterior cranial fossa of the gorilla and chimpanzee, so marked a contrast to the human retention of a primitively large ethmoid. His later conclusion (1938) that the gorilline maxillary sinus is not homologous with that of man would, if correct, tend to separate these two forms, but reasons are given above for the rejection of this conclusion as untenable.

It is not denied that in their elaboration of ethmoidal sinuses and other structural details man and the African anthropoid apes may have pursued parallel evolutionary trends from a remote period. It is equally likely, however, if not indeed more probable, that the possession of such anatomical features indicates a real relationship through the medium of a common ancestral stock. The points emphasized by Wood Jones (1929) do indeed proclaim the close structural affinity between chimpanzee and gorilla, but the evidence of nasal anatomy compels the association of man with these forms.

On the functional side we have nothing to add to the suggestion made by Weidenreich (1924) and others that the paranasal sinuses are "dead" spaces in the skull, situated where but weak mechanical forces traverse the bones, and, for the sake of lightness, filled with air rather than with marrow.

SUMMARY

1. Wet and dry preparations from forty-eight juvenile and adult anthropoid ape specimens, representing all extant forms, have been examined.

2. All anthropoid apes tend to preserve the primitive primate heritage of paranasal sinus structure, viz. maxillary and sphenoidal sinuses only. The maxillary sinus opens always between the ethmoidal lateral mass superiorly and the inferior turbinate inferiorly: its ostium is primitively situated in a semilunar groove (sulcus semilunaris) guarded by a mucosal ridge (plica semilunaris) overlying the processus uncinatus, and thus opens indirectly into the middle meatus by means of this groove.

3. Some gibbons retain the primitive primate structural arrangement, others exhibit a reduction of the plica semilunaris so that the maxillary sinus opens directly into the middle meatus.

4. The orang skull is characterized by an enormous extension of the maxillary sinus which reduces or obliterates the sphenoidal sinus, and by a complete loss of the plica semilunaris.

5. The African anthropoid apes and man have acquired neomorphic ethmoidal sinuses, including a frontal sinus.

6. The chimpanzee presents a distinctive intrapalatal extension of the maxillary sinus; otherwise it preserves a type of paranasal sinus structure from which that of the gorilla and man may well have been derived.

7. The gorilla presents a dilated nasolachrymal duct, which encroaches upon the maxillary sinus, together with great variability in the degree of development of the plica semilunaris. The ostium of the maxillary sinus is disposed in typical anthropoid ape fashion.

8. Man is characterized by an extreme development and variability of the ethmoidal sinuses.

To Profs. A. B. Appleton, J. K. Jamieson and W. E. Le Gros Clark, we accord grateful acknowledgement of their generous loan of preserved gorilla material.

MATERIAL EXAMINED

Gibbons, wet		Text reference
(i) *Hylobates* sp.	Roy. Coll. Surg. Mus., Phys. Ser. E 165	R.C.S. E 165
(ii) *H. lar leuciscus*, ad. ♂	Roy. Coll. Surg. Mus., Phys. Store 30 A	R.C.S. 30 A
(iii) *H. lar leuciscus*, ad.	Roy. Coll. Surg. Mus., Phys. Store 30 B	R.C.S. 30 B
(iv) *H. lar lar*, juv.	Roy. Coll. Surg. Mus., Phys. Store 30	R.C.S. 30
Gibbons, macerated		
(i) *Hylobates hoolock*, ad. ♀	Roy. Coll. Surg. Mus., uncatalogued	D 1
(ii) *Hylobates hoolock*, ad. ♂	Private coll.	D 2
(iii) *Symphalangus syndactylus*, juv.	Roy. Coll. Surg. Mus., Comp. Ost. 60	R.C.S. 60

Orang, wet			
(i)	juv., incomp. milk dent.	Roy. Coll. Surg. Mus., Phys. Store 990	R.C.S. 990
(ii)	juv., perm. can. erupted	Roy. Coll. Surg. Mus., Phys. Ser. E 166	R.C.S. E 166
(iii)	juv., milk dentition	Roy. Coll. Surg. Mus., Phys. Ser. E 167	R.C.S. E 167
(iv)	ad. ♂	Roy. Coll. Surg. Mus., Phys. Ser. E 167*a*	R.C.S. E 167*a*
Orang, macerated			
(i)	juv., milk dentition	Roy. Coll. Surg. Mus., Comp. Ost. 54	R.C.S. 54
(ii)	ad. ♀	Roy. Coll. Surg. Mus., Comp. Ost. 44.6	R.C.S. 44.6
(iii)	ad. ♂	Roy. Coll. Surg. Mus., Comp. Ost. 45	R.C.S. 45
(iv)	ad. ♂	Roy. Coll. Surg. Mus., Comp. Ost. 39	R.C.S. 39
(v)	subad. ♀	Roy. Coll. Surg. Mus., Comp. Ost. 40 B	R.C.S. 40 B
(vi)	ad. ♂	St Thomas's Hospital, Anat. Mus.	St Thos. 3
Chimpanzee, wet			
(i)	ad.	Roy. Coll. Surg. Mus., Phys. Store 898	R.C.S. 898
(ii)	juv.	Roy. Coll. Surg. Mus., Phys. Ser. E 168 (1st perm. molars *in situ*)	R.C.S. E 168
(iii)	subad. ♀	Roy. Coll. Surg. Mus., Phys. Ser. E 168.2	R.C.S. E 168.2
Chimpanzee, macerated			
(i)	juv., milk dentition + 1st perm. molars	Private coll.	C 2
(ii)	juv., milk dentition	Private coll.	C 3
(iii)	immat. ♀	Private coll.	C 4
(iv)	ad. ♂, old	Private coll.	C 5
(v)	immat., ♀	Roy. Coll. Surg. Mus., Comp. Ost. 10.4	R.C.S. 10.4
(vi)	immat.	Roy. Coll. Surg. Mus., Comp. Ost. 12.55	R.C.S. 12.55
(vii)	ad. ♀	Roy. Coll. Surg. Mus., Comp. Ost. 6	R.C.S. 6
(viii)	ad. ♂	Roy. Coll. Surg. Mus., Comp. Ost. 8	R.C.S. 8
(ix)	ad. ♂	Roy. Coll. Surg. Mus., Comp. Ost. 9	R.C.S. 9
(x)	ad. ♂	Roy. Coll. Surg. Mus., Comp. Ost. 10.5	R.C.S. 10.5
(xi)	ad. (? sex)	Roy. Coll. Surg. Mus., Comp. Ost. 12.53	R.C.S. 12.53
Gorilla, wet			
(i)	Infant, milk dentition		L.G.B.
(ii)	juv., milk dentition + 1st perm. molars,	Trinity College, Dublin	T.C.D.
(iii)	juv. (*c.* 4 years) first perm. molars fully erupted		L.G.A.
(iv)	immat.	Roy. Coll. Surg. Mus., Phys. Ser. E 168.5	R.C.S. 168.5
(v)	ad., ♀, 11 years	Roy. Coll. Surg. Mus., uncatalogued	"Moina"
Gorilla, macerated			
(i)	baby, milk incisors only	Roy. Coll. Surg. Mus., Comp. Ost. 34.4	R.C.S. 34.4
(ii)	juv., milk dentition	Roy. Coll. Surg. Mus., Comp. Ost. 30 A	R.C.S. 30 A
(iii)	juv., milk dentition	Roy. Coll. Surg. Mus., Comp. Ost. 30.31	R.C.S. 30.31
(iv)	immat., ♀, Gaboon	Roy. Coll. Surg. Mus., Comp. Ost. 27	R.C.S. 27
(v)	ad., ♀	Roy. Coll. Surg. Mus., Comp. Ost. 26.5	R.C.S. 26.5
(vi)	ad., ♂	Roy. Coll. Surg. Mus., Comp. Ost. 25	R.C.S. 25
(vii)	ad., ♂	Roy. Coll. Surg. Mus., Comp. Ost. 20	R.C.S. 20
(viii)	ad., ♂, Kivu	Roy. Coll. Surg. Mus., Comp. Ost. 22.2	R.C.S. 22.2
(ix)	ad. (? sex)	Private coll.	C 1
(x)	ad., ♂	St Thomas's Hospital Anat. Mus.	St Thos. 1
(xi)	immat.	Brit. Mus. (N.H.) Ost. Room, 3 K	B.M. 3 K
(xii)	ad. ♂	Brit. Mus. (N.H.) Mammal Gallery, uncat.	B.M. unreg.

KEY TO FIGURES

b.eth.	bulla ethmoidalis	*nas.t.*	nasoturbinal
b.nasol.	bulla nasolachrymalis	*ost.max.*	ostium of maxillary sinus
can.a.opt.	canal for ophthalmic artery	*pal.*	palatine
can.n.inf.	canal for infraorbital nerve	*par.*	parietal
can.n.max.	canal for maxillary nerve	*pl.sem.*	plica semilunaris
can.n.opt.	canal for optic nerve	*premax.*	premaxilla
dext.	right	*proc.unc.*	uncinate process
ethm.	ethmoid	*ptery.*	pterygoid
em.car.	carotid eminence	*sin.*	left
eth.t. I	ethmoturbinal I	*s.eth.a.*	anterior ethmoidal sinus (cell)
eth.t. II	ethmoturbinal II	*s.eth.p.*	posterior ethmoidal sinus
eth.t. III	ethmoturbinal III	*s.eth.p.* 1	posterior ethmoidal sinus 1
for.eth.	ethmoidal foramen	*s.eth.p.* 2	posterior ethmoidal sinus 2
for.opt.	optic foramen	*s.front.*	frontal sinus
for.s.p.	sphenopalatine foramen	*s.max.*	maxillary sinus (antrum)
front.	frontal	*s.sphen.*	sphenoidal sinus
h.sem.	hiatus semilunaris	*sphen.*	sphenoid
lach.	lachrymal	*temp.*	temporal
max.	maxilla	*turb.inf.*	inferior turbinate
max.t.	maxillo-turbinal	*zyg.*	zygomatic

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