

SEWELL, R. B. (1920). On *Mesocoelium sociale* (Lühe). *Rec. Indian Mus.* 19 : 81-95.  
 SMYTH, J. D. (1962). *Introduction to animal parasitology*. London : The English Universities Press.  
 SOULSBY, E. J. L. (1958). Immunity to helminths. *Vet. Rev.* 4 : 1-16.  
 SZIDAT, L. (1932). Parasiten aus Liberia und Französisch-Guinea. II. Teil : Trematoden. *Z. Parasitenk.* 4 : 506-521.  
 TALIAFERRO, W. H. (1940). The mechanism of acquired immunity in infections with parasitic worms. *Physiol. Rev.* 20 : 469-492.  
 THOMAS, J. D. (1958 a). Studies on the structure, life history and ecology of the trematode *Phyllodistomum simile* Nybelin, 1926 (Gorgoderidae : Gorgoderinae) from the urinary bladder of brown trout *Salmo trutta* L. *Proc. zool. Soc. Lond.* 130 : 397-435.  
 THOMAS, J. D. (1958 b). Studies on *Crepidostomum metoecus* (Braun) and *C. farionis* (Müller), parasitic in *Salmo trutta* L. and *S. salar* L. in Britain. *Parasitology* 48 : 338-352.  
 THOMAS, J. D. (1964 a). Studies on the growth of brown trout (*Salmo trutta* L.) from four contrasting habitats. *Proc. zool. Soc. Lond.* 142 : 1-51.  
 THOMAS, J. D. (1964 b). Studies on populations of helminth parasites in brown trout (*Salmo trutta* L.). *J. Anim. Ecol.* 33 : 83-95.  
 THOMAS, J. D. (1964 c). A comparison between the helminth burdens of male and female brown trout, *Salmo trutta* L., from a natural population in the River Teify, West Wales. *J. Parasit.* 54 : 1-10.  
 THOMAS, J. D. (1965). Studies on the anatomy, life history and allometry of *Mesocoelium monodi* Dollfus. *J. Zool.*, in press.  
 WALKER, H. O. (1962). Weather and climate. In *Agriculture and land use in Ghana*. Ed. J. B. Wills. London and Accra : Oxford University Press.

1) choroid  
 2) aged det.  
 5) pallid  
 4) traction epiphyses  
 of sacch. leg → int. morphology of tapir skulls

V.M. Zup  
 P1-P2 P1-P3  
 P1-P4  
 P1-P5  
 P1-P6

TRACTION EPIPHYSES IN THE MAMMALIAN SKULL

BY

A. J. E. CAVE \*

University of London

[Accepted 13th October 1964]

(With 2 plates and 7 figures in the text)

Traction epiphyses in the mammalian skull are described for the first time, an account being given of the mastoid epiphysis of the otariid pinnipeds and of the lacrimal (antorbital) epiphysis in tapirs, elephants and rhinoceroses.

CONTENTS

	Page
Introduction .. .. .	495
Material and methods .. .. .	496
The otariid mastoid epiphysis .. .. .	496
The lacrimal antorbital epiphysis .. .. .	498
In Tapiridae .. .. .	498
In Elephantidae .. .. .	499
In Rhinocerotidae .. .. .	500
Discussion .. .. .	507
Acknowledgments .. .. .	508
References .. .. .	508

INTRODUCTION

Epiphyses play an important role in the postnatal development of the mammalian skeleton yet they are accorded the scantiest attention in most authoritative treatises on vertebrate structure and development. This is perhaps understandable since the embryologist is necessarily concerned with the prenatal stages of skeletal development and the taxonomist with the fully mature skeleton, while all save a minority of mammals complete their postnatal skeletal growth within so relatively short a time that only in domesticated forms is the ordered study of epiphyses generally practicable. Thus it is that such authors as Reynolds (1913), Kingsley (1925), Goodrich (1930), de Beer (1937), Romer (1949) and Grassé (1955) are uninformative as to the nature and topographical distribution of epiphyses, being content at best with a casual definition of, or reference to, a long bone epiphysis. (Lancaster (1902) indeed employed the etymologically apt term 'epiphysis' for the 'ossicones' capping the cranial 'ossicuspis' in *Giraffa* and *Okapia*, but this particular usage of the word never gained general adoption.) It has been left largely to the human anatomist to devote consistent attention to postnatal skeletal development in the most continuously and intensively studied of all mammals—man—whose extended

\* Morrison Watson Research Fellow, Victoria University of Manchester.

period of postnatal growth, covering some twenty-five years, affords more adequate opportunity for repeated and detailed observation upon the maturation of individual bones.

Thus it was Parsons (1904, 1908) who first classified the mammalian epiphyses into pressure, traction and atavistic varieties, since when a considerable literature has accumulated concerning the distribution of the traction epiphyses and their probable ontogenetic and phylogenetic modes of origin.

The traction epiphyses fall into two classes, viz. (1) those which develop in response to the ordinary dynamics of musculo-osseous attachment, (2) those which, as Parsons postulated, and as Barnett & Lewis (1958) clearly demonstrated, are functionally biphasic formations, acting as sesamoids in the young animal but as traction epiphyses in the adult (sesamepiphyses).

But, of whatever class, all the traction epiphyses recognized to date pertain to the bones of the appendicular skeleton and vertebral column: none has been recorded hitherto for any cranial bone, and indeed epiphyses of any variety are omitted from consideration of the postnatal development of the individual cranial components, whether these be cartilage bones or membrane bones. This may well be because such consideration has principally concerned the human or primate cranium wherein epiphyses do not occur.

Nevertheless, cranial epiphyses may occur in the postnatal development of the mammalian cranium, and attention is directed herein to the presence of two such undoubted epiphyses, one associated with the temporal bone in the otariid pinnipeds, the other associated with the antorbital process of the lacrimal bone in (at least) the tapirs, elephants and rhinoceroses.

#### MATERIAL AND METHODS

The occurrence of these hitherto undescribed traction epiphyses was established in the mammalian forms indicated by examination of the extensive series of crania (representing in each instance successive growth stages from infancy to old age) in the osteological collections of the British Museum (Natural History), supplemented by specimens in the author's private collection, and by a single specimen in Ghar Dalam Museum, Malta.

The selected specimens described below are readily identifiable by their respective catalogue numbers which are provided as references.

#### THE OTARIID MASTOID EPIPHYSIS

The descriptive mastoid process of the otariid cranium (Fig. 1 (e)) is a relatively massive prominence of characteristic configuration wholly unlike that of its phocid counterpart: into it, by stout tendon, are inserted the powerful sternomastoid and other muscles. It is associated with an epiphysis (ossiculum mastoideum) first observed by Cave & King (1964) in the genera *Arctocephalus*, *Eumetopias*, *Otaria* and *Neophoca* and by them studied in detail in *Arctocephalus* material (Pl. 1, fig. 1). This epiphysis is probably present also in the otariid *Callorhinus* and *Phocartos*, but is notably wanting in the phocid cranium. The mastoid ossicle (Fig. 1 (c),(d)) is a constant cranial feature in *Arctocephalus*, wherein it attains an average adult size of 16 × 10 mm in the male and of 8 × 5 mm in the female.

In the young *Arctocephalus* cranium the squamosal and petromastoid elements of the composite mastoid process develop, as secondary markings, ridges which bound a sulcus containing the squamomastoidean suture. Older pup crania (Fig. 1 (a)) manifest a facet on the mastoidean lip of this sulcus,

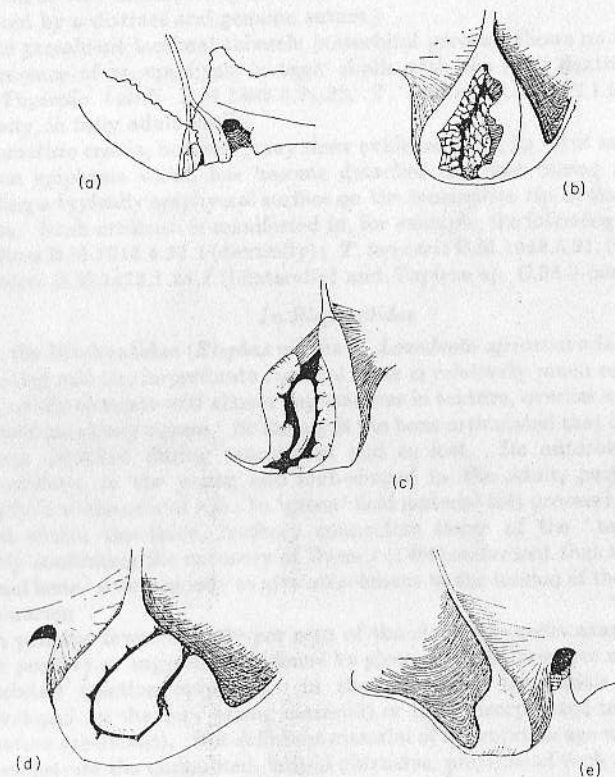


Fig. 1—*Arctocephalus tropicalis gazella*, mastoid region. (a) Young skull, showing mastoid sulcus; (b) immature skull, showing mastoid (epiphyseal) vallecule; (c) immature epiphysis *in situ*; (d) mature epiphysis *in situ*; (e) adult skull (epiphysis synostosed).

within the area of attachment of the future ossicle (epiphysis). With later skeletal growth the sulcal lips increase in size and prominence and come finally to enclose an oval or triangular vallecule, with which they form a bed for the mastoid ossicle: the surface of this bed, like the cranial aspect of the ossicle, is typically epiphyseal in configuration (Fig. 1 (b)).

In the sub-adult cranium an immature mastoid ossicle (Fig. 1 (d)) is present, attached to this bed by cartilage and constituting an obvious traction epiphysis to the mastoid process. From the beginning of early adult life onwards it



continues to enlarge, demarcated from the mastoid process by an epiphyseal line and very gradually effecting synostosis with that process. It tends, however, to remain discrete, and detachable by maceration, until late adult life, when it loses its identity and becomes unrecognizably incorporated into the mastoid process. This delayed synostosis accounts for its loss, on one side or on both, from many museum specimens, with a consequent exposure of its obtrusively epiphyseal bed (Fig. 1 (b)). In Table 1 are listed selected specimens which display either the mastoid traction epiphysis *in situ* or its epiphyseal bed exposed by its post-mortem loss.

Table 1—Specimens showing evidence of mastoid traction epiphyses

<i>Arctocephalus tropicalis gazella</i>	<i>Arctocephalus tropicalis tropicalis</i>
B.M. 1960.8.10.55	B.M. 1955.3.4.5
B.M. 1960.8.10.48	B.M. 1955.3.14.4
B.M. 1960.8.10.47	B.M. 1957.8.1.1
B.M. 1960.8.10.45	B.M. 1957.8.1.2
B.M. 1960.8.10.21	B.M. 1957.4.23.11
B.M. 1960.8.10.28	
B.M. 1960.8.10.50	
B.M. 1962.6.14.5	
B.M. 1958.7.8.1	<i>Eumetopias</i>
B.M. 1958.4.24.4	B.M. 1950.7.21.2
B.M. 1957.7.11.12	B.M. 1950.7.21.3
B.M. 1960.8.4.3	
B.M. 1960.8.4.4	
B.M. 1958.4.24.3	
B.M. 1957.7.11.1	<i>Otaria</i>
B.M. 1958.7.8.7	B.M. 1939.1.21.116
B.M. 1960.8.10.44	B.M. 1939.1.21.117
B.M. 1960.8.10.45	B.M. 1959.12.4.7
B.M. 1960.8.10.57	
B.M. 1962.6.14.7	
<i>Arctocephalus forsteri</i>	<i>Neophoca</i>
B.M. 1959.12.22.1	B.M. 1925.10.8.32

## THE LACRIMAL ANTORBITAL EPIPHYSIS

This epiphysis is present in tapirs, elephants and rhinoceroses, forms possessing not only extremely thick palpebral plates, attached medially by the densest and toughest of ligamentous tissues, but also a very well developed, functionally active, cartilago nictitans.

*In Tapiridae*

In the Tapiridae the lacrimal foramen is 'double' since the lacrimal fossa is bridged posteriorly by a thin, flat osseous lamina whose lateral free extremity (antorbital process) forms a somewhat rectangular tubercle projecting laterally from the orbital rim. (This bridge develops as a medial osseous ingrowth from the antorbital process into the ligamentous tissue passing posterior to the lacrimal sac, which is ultimately circumscribed by bone much as the vertebral

artery is encompassed by the developing cervical transverse process. The stages of such bridge formation are traceable in the following specimens: *Tapirus roulini* B.M.1872.1.24.12, *Tapirus terrestris* B.M.1948.12.20.3, and *Tapirus indicus* B.M.1912.4.27.1: in the last two specimens the antorbital medial ingrowth is still incompletely fused with the rest of the lacrimal bone as is indicated by a distinct and genuine suture.)

The prominent lacrimal tubercle (antorbital process) shows no evidence of the presence of an epiphysis in tapir skulls with the milk dentition *in situ* (e.g. *Tapirella bairdi* B.M.1868.3.21.22, *T. roulini* B.M.1872.1.24.12), nor, naturally, in fully adult skulls.

Immature crania, however, may show evidence (Pl. 1, fig. 2) of an antorbital traction epiphysis which has become detached and lost during maceration, revealing a typically epiphyseal surface on the incomplete tip of the antorbital process. Such evidence is manifested in, for example, the following specimens: *T. indicus* B.M.1912.4.27.1 (dextrally); *T. terrestris* B.M.1948.5.21 (bilaterally); *T. roulini* B.M.1872.1.24.2 (bilaterally) and *Tapirus* sp. C.58.3 (sinistrally).

*In Elephantidae*

In the Elephantidae (*Elephas maximus*, *Loxodonta africana*) a lacrimal fossa is wanting and the imperforate lacrimal bone is relatively much reduced. Its body, ovally elongate and almost papyraceous in texture, overlies and obscures the frontomaxillary suture. So loosely is the bone articulated that it commonly becomes detached during maceration and so lost. Its antorbital process, mammilliform in the young and club-shaped in the adult, projects infero-laterally from the orbital rim. In 'green' field material this process is completely buried within the thick, leathery connective tissue of the 'tendo oculi', forcibly confirming the accuracy of Owen's (1886) statement that the elephant lacrimal bone 'serves chiefly to give attachment to the tendon of the orbicularis palpebrarum'.

In perhaps fewer than 30 per cent of the elephant crania examined could either positive or suggestive evidence be gleaned of the presence of a lacrimal (antorbital) traction epiphysis: in the remainder the ossicle was either undeveloped (in the very young material) or fully incorporated into the skull (in mature specimens). But sufficient material of appropriate age was available to demonstrate the undoubted, indeed obtrusive, presence of such a structure: frequently the epiphysis had become detached with the cranial soft parts and thus lost, but, in these instances, its former presence was witnessed by the typically epiphyseal nature of the articular area for its reception on the antorbital process, an area cup-shaped in the younger immature specimens but convex in the older (Pl. 1, fig. 3; Fig. 2 (a)).

The lacrimal traction epiphysis is present in such *Elephas maximus* specimens as B.M.1879.11.21.693 and in the mounted skeleton at Ghar Dalam, Malta. It is present in such *Loxodonta africana* specimens as B.M.10410, B.M.1929.1.1.36 and B.M.49.697 (wherein its synostosis with the antorbital process has begun). In B.M.49.695 and B.M.1937.5.20.2 an unmistakable epiphyseal line demarcates the epiphysis: in B.M.1928.11.13.1 the epiphysis has been largely lost, but a fragment remains *in situ* and is passively movable

upon its articulation. The epiphysis was formerly present in the articulated skeleton (B.M. unregistered) of a sub-adult African elephant.

The elephant lacrimal epiphysis, when fully developed, has the form of a roughly hemispherical cap upon the antorbital process: in the material examined it is invariably a single entity (Fig. 2 (b), (c), (d)).

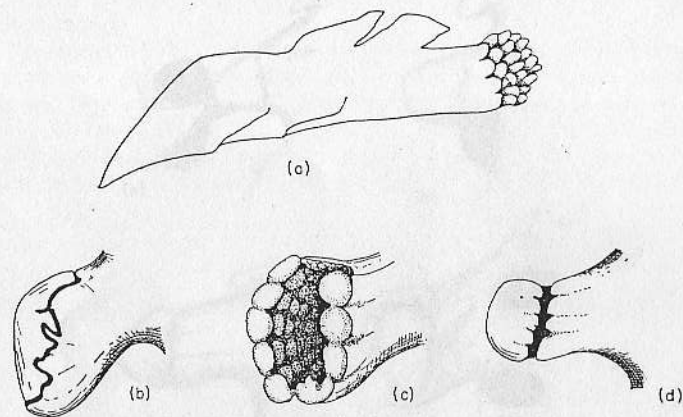


Fig. 2—Elephant lacrimal epiphysis. (a) *Loxodonta* (B.M. unreg.) lacrimal bone showing epiphyseal extremity; (b) *Loxodonta* (B.M.1929.1.1.36) showing right lacrimal epiphysis *in situ*; (c) *Loxodonta*, showing epiphyseal area on antorbital process; (d) *Elephas maximus* (Ghar Dalam, Malta).

#### In Rhinocerotidae

In the Rhinocerotidae the orbital rim divides the lacrimal bone into facial and orbital regions and upon this rim the antorbital process appears as a relatively large tubercle, ovate in *Rhinoceros*, mastoid in *Didermocerus* and *Diceros*, quadrangular in *Ceratotherium*. The lacrimal fossa is usually bridged posteriorly by ligament in the more primitive members of the family, by bone in the more specialized members. Thus in the material examined the lacrimal bridge was ligamentous in 93 per cent of *Rhinoceros unicornis* crania and in 83 per cent of *Rhinoceros sondaicus* crania, being otherwise osseous: the bridge was invariably osseous in *Didermocerus* and *Ceratotherium* crania (even in the *Ceratotherium neonatus*). In *Diceros* the bridge was osseous in some 77 per cent of specimens.

This lacrimal bridge represents an ossification of the dense ligamentous tissue passing posterior to the lacrimal sac from the medial canthic region. Its incidence is an indirect measure of the stresses and strains affecting that part (antorbital process) of the lacrimal bone which receives the major attachment of the palpebral structures, and it almost predicates the appearance of a traction epiphysis thereupon. Where an osseous lacrimal bridge is the general generic rule, such an antorbital traction epiphysis is the more frequently detectable. (This does not imply that a lacrimal traction epiphysis is consequent upon the

presence of an osseous lacrimal bridge, for the traction epiphysis may co-exist with the ligamentous type of bridge (e.g. specimen B.M.1902.12.18.1) and is present in forms such as *Loxodonta* in which not only a lacrimal bridge but even a lacrimal fossa is wanting.) The lacrimal bony bridge represents the replacement of dense ligamentous tissue by bone in response to functional requirements, the antorbital traction epiphysis the response of the lacrimal bone to the pull of the 'tendo oculi'. Descriptively, the osseous lacrimal bridge comprises anterior and posterior arms meeting at a lateral apex.

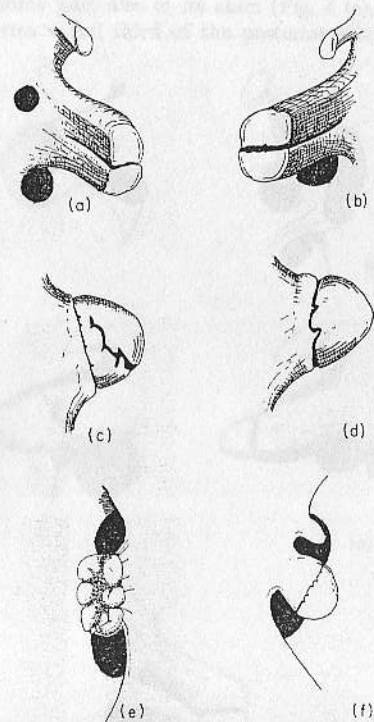


Fig. 3—Lacrimal epiphysis in *Rhinoceros unicornis* and *R. sondaicus*. (a) *Rhinoceros unicornis* (B.M.1962.7.6.7), posterior aspect of right antorbital process; (b) ditto, anterior aspect of same process; (c) *Rhinoceros unicornis* (B.M.3.2.13.1), right antorbital process; (d) *Rhinoceros unicornis* (B.M.1951.11.30.2), antorbital process; (e) *Rhinoceros sondaicus* (B.M.1902.12.18.1), epiphyseal area on right antorbital process; (f) ditto, left antorbital epiphysis *in situ*.

In *Rhinoceros unicornis* specimen B.M.1950.10.18.4 remnants of an epiphyseal line appear upon each lacrimal antorbital process and exactly comparable remnants are visible in B.M.1950.10.18.5 (a male animal some eighteen years of age). Specimen B.M.1951.11.30.2 shows an epiphysis *in situ* on the left



antorbital process: in B.M.3.2.13.1 an epiphysis is present dextrally but its contralateral fellow has been lost since death (Fig. 3 (c)). A typically tuberculated articular surface for a now lost antorbital epiphysis is present dextrally in specimens B.M.1952.4.1.1 and B.M.70.3.10.18. In specimen B.M.1962.7.6.7

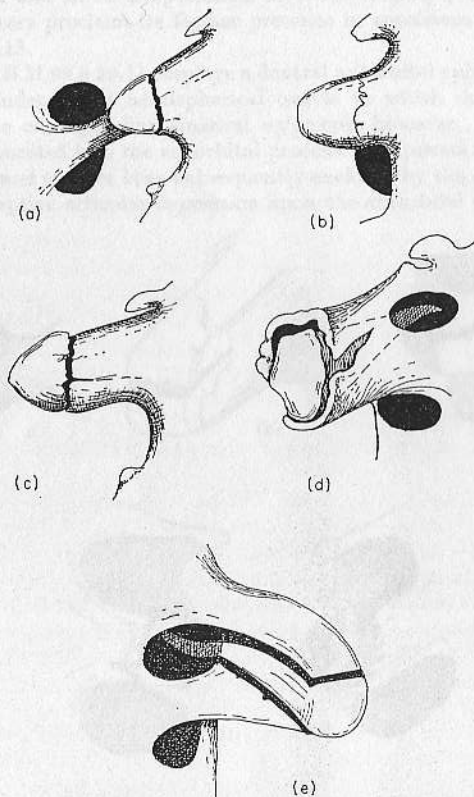


Fig. 4—Lacrimal epiphysis in *Didermocerus sumatrensis*. (a) right antorbital process in B.M.1461b; (b) right antorbital process in B.M.79.3.11.1; (c) B.M.1948.1.14.1, anterior aspect of right antorbital process; (d) ditto, posterior aspect of left antorbital process; (e) ditto, posterior aspect of right antorbital process.

a variant condition obtains, the antorbital process showing division into dorsal and ventral moieties (Fig. 3 (a), (b)): the evidence of similar variant conditions in other genera would suggest that the lacrimal epiphysis is already enclosed by these moieties.

In *Rhinoceros sondaicus* specimen B.M.1902.12.18.1 the left lacrimal antorbital epiphysis remains *in situ* (Fig. 3 (e), (f)), but the right epiphysis has been lost since death.

In *Didermocerus sumatrensis* (Fig. 4) a discrete antorbital epiphysis is present bilaterally in specimens B.M.1948.1.14.1 and B.M.1461b, and unilaterally in specimens B.M.1949.2.1.1, B.M.79.3.11.1, B.M.86.12.20.8 and B.M.1952.4.1.2. The epiphysis is the usual hemispherical cap upon the tip of the antorbital process save in B.M.1948.1.14.1, where arrangements are otherwise. Therein the lacrimal epiphysis would appear anteriorly to be the customary cap, but posteriorly it is seen to be produced medialwards and to form (bilaterally) an unusually large portion of the antorbital process, i.e. not merely its tip, but some part also of its stem (Fig. 4 (c), (d), (e)). Thus the dextral epiphysis forms a full third of the posterior thickness of the process

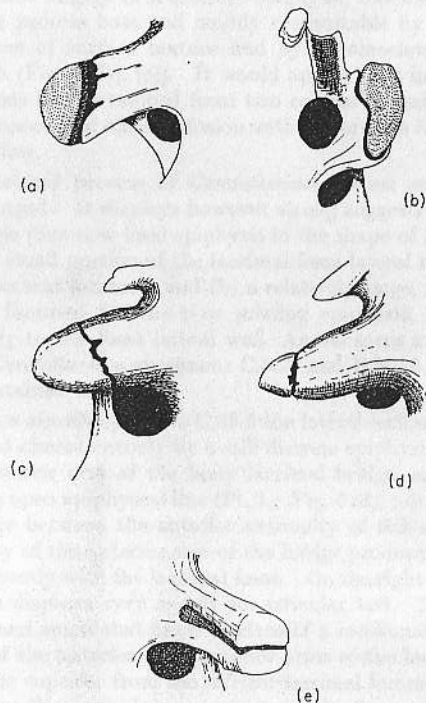


Fig. 5—Lacrimal epiphysis in *Dicerus bicornis*. (a) B.M.99.6.29.11, anterior aspect of right antorbital process; (b) posterior aspect of same process; (c) C.58.11, anterior aspect of right antorbital process; (d) U.70, anterior aspect of right antorbital process; (e) B.M.99.6.29.11, left antorbital process.

and extends deeply into the lacrimal fossa parietes. The sinistral epiphysis is embraced by the still ununited dorsal and ventral moieties of its antorbital process and likewise extends into the lacrimal fossa wall. On either side, therefore, the lacrimal epiphysis makes an unusually substantial contribution

to the antorbital process, an arrangement representative perhaps of nothing more than a minor variation in epiphyseal development.

In *Diceros bicornis* material (Fig. 5) a lacrimal antorbital epiphysis is observable *in situ* in such specimens as B.M.99.6.29.11, U.70 and C.58.11. Epiphyseal scars proclaim its former presence in specimens B.M.33.5.5.1 and B.M.23.10.20.18.

Specimen B.M.99.6.29.11 displays a dextral antorbital epiphysis in the usual form of an independent hemispherical ossicle to which dried cartilage still adheres. The corresponding sinistral epiphysis, however, is already almost wholly incorporated into the antorbital process: it appears to have elongated medialwards and to have been subsequently enclosed by the dorsal and ventral lips of its receptive articular depression upon the antorbital process.

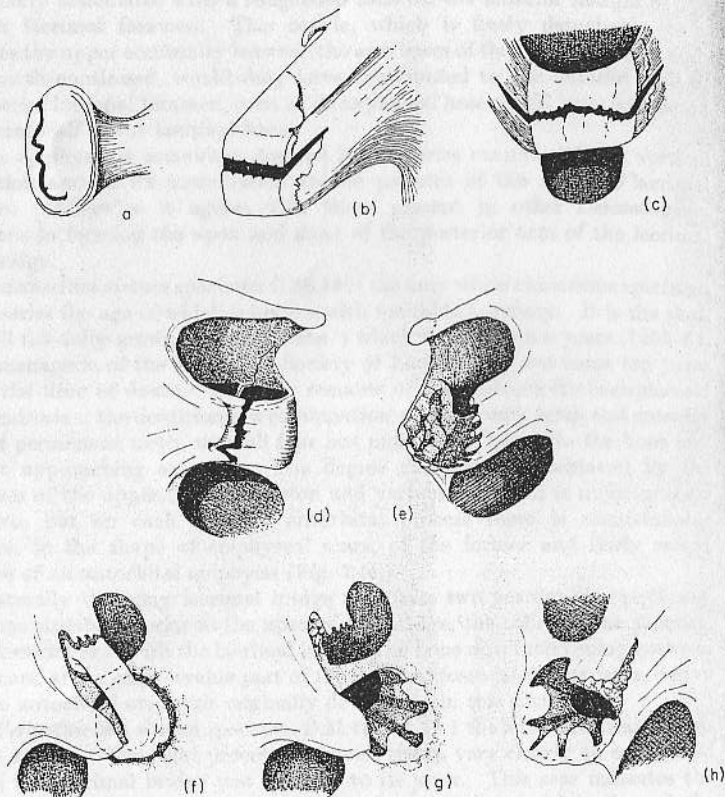


Fig. 6—Lacrimal epiphysis in *Ceratotherium simum*. (a) C.58.5, partly synostosed epiphysis; (b) C.58.7, anterior aspect of right antorbital process; (c) C.58.7, lateral aspect of same process; (d) C.58.8, left lacrimal epiphysis *in situ*; (e) C.58.8, bed of right lacrimal epiphysis; (f) C.58.9, left lacrimal epiphysis *in situ*; (g) bed of same; (h) C.58.9, bed of right lacrimal epiphysis.

In *Ceratotherium simum* specimen C.58.5 the free extremity of the right antorbital process displays the remains of an epiphyseal line (Fig. 6 (a)), but the contralateral antorbital process is skeletally mature.

In specimen C.58.7 there is evidence of the bilateral presence of an antorbital epiphysis. The right antorbital process is horizontally incised apically by a wedge-shaped fissure, having epiphyseal walls and being cartilage-filled in life. The inferior lip of this cleft process is composed largely of an epiphysis which has begun synostosis with the base of the process but is still demarcated therefrom peripherally by an epiphyseal line. The superior lip of the antorbital process is likewise composed largely of a discrete epiphysis, but one more intimately synostosed to the process base and readily recognizable by its scar of union, i.e. by a difference of surface texture and by an associated series of small vascular foramina (Fig. 6 (b), (c)). It would appear that in this instance the antorbital epiphysis had developed from two centres of ossification, and that each ossific component had effected fusion with the process itself in advance of fusion with its fellow.

The left antorbital process of *Ceratotherium simum* specimen C.58.7 is considerably damaged. It displays however strong suggestive evidence of the presence of a single (but now lost) epiphysis in the shape of (a) a slender bony process forming a small portion of the lacrimal fossa lateral wall as the margin of the superior lacrimal foramen, and (b) a relatively large, rough, epiphyseal area below that foramen for the now missing epiphysis, which must have contributed largely to the fossa lateral wall. Appearances are very similar to those present in *Ceratotherium* specimens C.58.9 and B.M.1948.1.28.2, wherein the epiphysis is retained *in situ*.

In *Ceratotherium simum* specimen C.58.8 the lateral wall of the left lacrimal fossa is constituted almost entirely by a still discrete epiphysis which forms the apex and the posterior arm of the bony lacrimal bridge, and is demarcated peripherally by an open epiphyseal line (Pl. 2; Fig. 6 (d), (e)). Removal of the remaining cartilage between the anterior extremity of this epiphysis and the posterior extremity of the anterior arm of the bridge produces an irregular gap communicating directly with the lacrimal fossa. On the right—side loss of this lacrimal epiphysis displays very clearly its articular bed. This is formed by the tuberculated and spiculated upper surface of a semilunar bony bar which unites the bases of the anterior and posterior arms of the lacrimal bridge and which separates the superior from the inferior lacrimal foramen. The lacrimal epiphysis thus contributes in large measure to the formation of the lateral parietes of the lacrimal fossa and constitutes the apex and most of the posterior arm of the lacrimal bridge.

In *Ceratotherium simum* specimen C.58.9 at the time of death a single lacrimal epiphysis was present bilaterally, since when the left epiphysis remains loosely *in situ* while the right has been lost.

Dextrally the bony bridge across the lacrimal fossa has a well-developed anterior and an extremely short posterior arm, continuous superiorly and inferiorly so as to form the inferior and superior margins, respectively, of the superior and inferior lacrimal foramina.



Immediately below the superior lacrimal foramen the bridge apex is excavated down to the lumen of the lacrimal fossa by an obtrusively epiphyseal area (Pl. 1, fig. 4; Fig. 6 (f), (g), (h)) occupied in life by a discrete epiphysis whose deepest portion constituted part of the fossa lateral wall.

Sinistrally, the well-developed anterior arm and the extremely short posterior arm of the lacrimal bridge are united at their bases by bone so as to form the inferior and superior margins, respectively, of the superior and inferior lacrimal foramina. Between these margins lies a deeply excavated epiphyseal articular area, extending deeply to the lacrimal fossa. This area is loosely occupied by the irregularly expanded base of a single unciform epiphysis which additionally articulates with a roughened area on the anterior margin of the superior lacrimal foramen. This ossicle, which is freely detachable, thus straddles the upper continuity between the arm bases of the lacrimal bridge and, had growth continued, would duly have contributed to the anterior wall of the superior lacrimal foramen, even as its expanded base would have completed the lateral wall of the lacrimal fossa.

This epiphysis is somewhat unusual in the series examined in its vertical disposition and in its contribution to the parietes of the superior lacrimal foramen. Otherwise it agrees with those present in other *Ceratotherium* specimens in forming the apex and most of the posterior arm of the lacrimal bony bridge.

*Ceratotherium simum* specimen C.58.18 is the only white rhinoceros specimen in this series the age of which is known with tolerable accuracy. It is the skull of a still not fully grown animal ('Bebe') which lived for nine years (1955-64) in the menagerie of the Zoological Society of London and was some ten years old at the time of death. No trace remains of the basioccipito-basisphenoid synchondrosis: the dentition is a combination of worn milk teeth and recently erupted permanent teeth, with all four last molars still buried in the bone and not yet approaching eruption. The degree of synostosis achieved by the epiphyses of the appendicular skeleton and vertebral column is unfortunately unknown, but on each lacrimal antorbital process there is unmistakable evidence, in the shape of epiphyseal scars, of the former and fairly recent presence of an antorbital epiphysis (Fig. 7 (c)).

Bilaterally the bony lacrimal bridge manifests two perceptible epiphyseal scars, one situate anterior to the apex of the bridge, the other at the junction of its posterior arm with the lacrimal bone. The bone now intervening between these scars, and a considerable part of the lacrimal fossa lateral parietes, derive from an antorbital epiphysis originally developing in this situation.

In *Ceratotherium simum* specimen B.M.1948.1.28.1 the left antorbital process is fully mature. The right process, however, shows very clearly an epiphyseal scar on the lacrimal bridge just anterior to its apex. This scar indicates the junction between the anterior extremity of an antorbital epiphysis and the antorbital process proper. The epiphysis in question has been responsible for the formation of the arch apex and most of its posterior arm (Fig. 7 (a)).

In *Ceratotherium simum* specimen B.M.1948.1.28.2 the right lacrimal bridge shows an epiphyseal scar just anterior to its apex, evidence of the former presence here of an epiphysis extending forward to that scar.

The left lacrimal bridge recalls exactly conditions present in specimen C.58.9, for a relatively large, passively movable but undetachable epiphysis

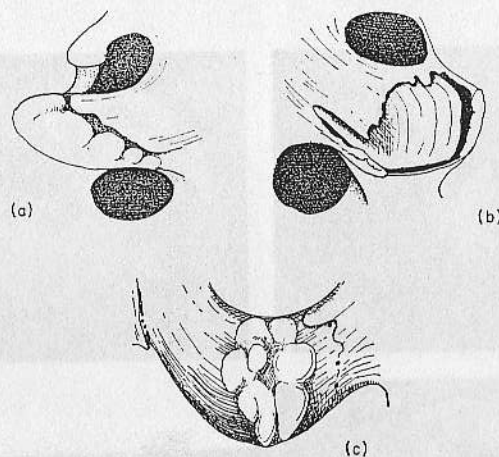


Fig. 7.—Lacrimal epiphysis in *Ceratotherium simum*. (a) B.M.1948.1.28.1, epiphyseal area, right antorbital process; (b) B.M.1948.1.28.2, left epiphysis *in situ*; (c) C.58.18, traces of right epiphysis.

remains *in situ* (Fig. 7 (b)). The bases of the long anterior, and the extremely short posterior, arms of the bridge establish mutual continuity above and below this epiphyseal ossicle, and so form a trough-like bed for its reception. The deep surface of this ossicle completes the lateral wall of the lacrimal fossa and the epiphysis itself would ultimately have been responsible for the formation of most of the posterior arm and of the apex of the lacrimal bridge.

#### DISCUSSION

The mastoid epiphysis of the otariid skull requires little comment. It is invariably single and cannot be mistaken for a Wormian (sutural) bone since none such ever develops at the petro-squamous junction. The possibility was considered that this particular epiphysis might be a sesame epiphysis, i.e. a biphasic formation functioning as a sesamoid within the sternomastoid tendon during early immaturity but later assuming an epiphyseal role. But there is no direct evidence favouring such interpretation and all the available osteological evidence indicates that the ossiculum mastoideum is nothing other than an uncomplicated traction epiphysis.

The lacrimal antorbital traction epiphysis develops as a single structure, a hemispherical cap upon the tip of that process. Exceptionally, however (in rhinoceros skulls at least), the epiphysis may develop from two centres of ossification or contrariwise it may develop somewhat precociously. In the former event, the free extremity of the antorbital process manifests a horizontal

cleavage (e.g. *Rhinoceros unicornis* B.M.1962.7.6.7 : *Diceros bicornis* B.M.99.6.29.11 : *Ceratotherium simum* C.58.7). In the latter event, the epiphysis extends medialwards and comes to form an unusually large proportion of the antorbital process as well as some part of the lacrimal fossa parietes (e.g. *Didermocerus sumatrensis* B.M.1948.1.14.1).

It is not unusual to encounter curiously different stages of antorbital epiphysis development on the two sides of the same skull while the considerable variation in the rate of epiphysis growth manifested by individuals of a given genus precludes all satisfactory correlation of the stages of such growth with the known or estimated age of the individual. (In this connexion the desirability of preserving the skeletons of immature animals dying in zoological menageries is obvious, for only in such material can age be estimated with any tolerable degree of accuracy.)

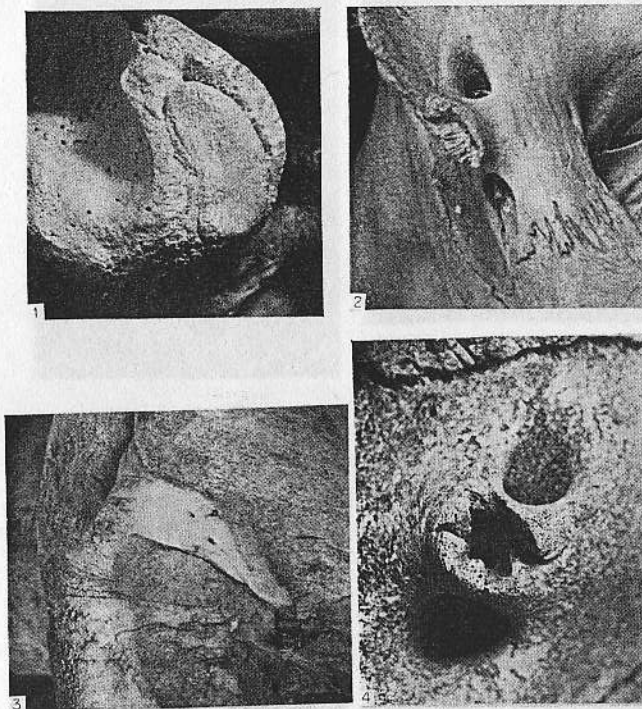
The evidence thus briefly submitted herein establishes the undoubted occurrence of traction epiphyses in the mammalian skull. Such structures can therefore no longer implicitly be regarded as confined to the non-cranial skeleton. This novel morphological finding is in no sense surprising inasmuch as epiphyses are developed in subservience to the functional requirements of the growth and maturation of individual bones and their precise topographical incidence is wholly incidental thereto.

#### ACKNOWLEDGMENTS

Grateful acknowledgment is tendered to Dr F. C. Fraser, Keeper of Zoology, British Museum (Natural History), for generously permitting examination of the osteological material in his care, to Miss Judith E. King and Mr M. C. Sheldrick for repeated assistance during that examination, and to Professor V. G. Griffiths for access to material in Malta. The photographs are the work of Mr Brian Biles, by kind permission of Dr P. J. Lawther.

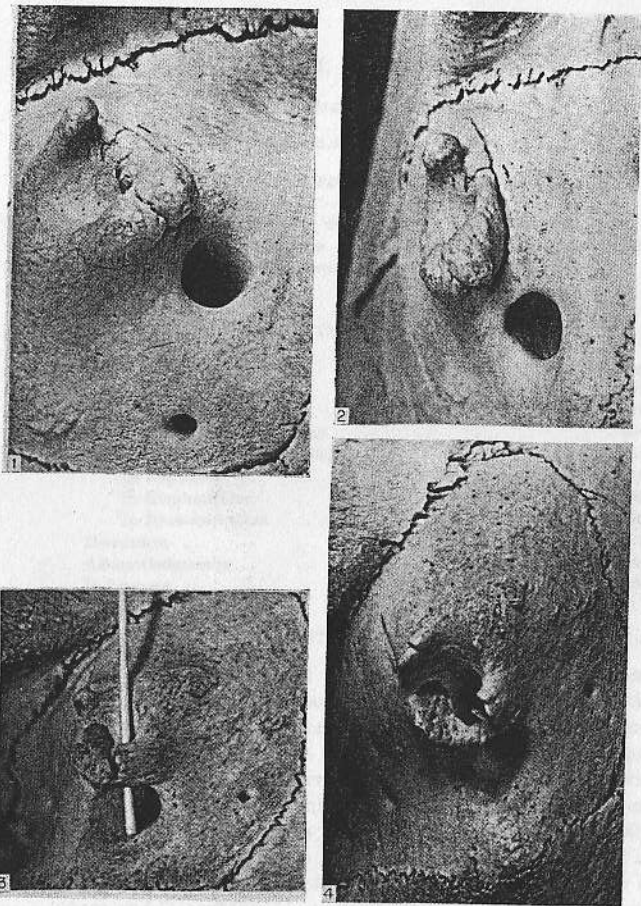
#### REFERENCES

- BARNETT, C. H. & LEWIS, O. J. (1958). The evolution of some traction epiphyses in birds and mammals. *J. Anat., Lond.* **92** : 593-601.
- CAVE, A. J. E. & KING, J. E. (1964). The mastoid ossicle of the otariid skull. *Ann. Mag. nat. Hist.* (13) **7** : 235-240.
- DE BEER, G. R. (1937). *The development of the vertebrate skull*. Oxford : Oxford University Press.
- GOODRICH, E. S. (1930). *Studies on the structure and development of vertebrates*. London : Macmillan.
- GRASSÉ, P.-P. (1955). *Traité de Zoologie*. **17**. Mammifères. Paris : Masson.
- KINGSLEY, J. S. (1925). *The vertebrate skeleton*. London : John Murray.
- LANCASTER, E. R. (1902). On *Okapia*, a new genus of Giraffidae from Central Africa. *Trans. zool. Soc. Lond.* **16** : 279-314.
- OWEN, R. (1886). *The anatomy of vertebrates*. **2** : 441. London : Longmans Green & Co.
- PARSONS, F. G. (1904). Observations on traction epiphyses. *J. Anat., Lond.* **38** : 248-258.
- PARSONS, F. G. (1908). Further remarks on traction epiphyses. *J. Anat., Lond.* **42** : 388-396.
- REYNOLDS, S. H. (1913). *The vertebrate skeleton*. Cambridge : Cambridge University Press.
- ROMER, A. S. (1949). *The vertebrate body*. London & Philadelphia : Saunders Company.



1. *Arctocepalus tropicalis gazella* (B.M. 1960.8.10.28) showing mastoid epiphysis.
2. *Tapirus* sp. (C. 58.3) showing epiphyseal area on left antorbital process.
3. *Loxodonta africana* (C. 58.1.2) showing epiphyseal area on lacrimal antorbital process.
4. *Ceratotherium simum* (C. 58.9) showing articular area for right lacrimal epiphysis.





1. *Ceratotherium simum* (C. 58.8) showing lateral aspect of left lacrimal epiphysis.
2. *Ceratotherium simum* (C. 58.8) showing posterior aspect of left lacrimal epiphysis.
3. *Ceratotherium simum* (C. 58.8) showing loss of epiphysis from right lacrimal bridge (white rod occupies lacrimal fossa).
4. *Ceratotherium simum* (C. 58.8) showing details of epiphyseal area on right lacrimal bridge.