

**Article II.—STUDIES IN COMPARATIVE MYOLOGY AND
OSTEOLOGY: NO. IV.—A REVIEW OF THE EVOLUTION
OF THE LACRYMAL BONE OF VERTEBRATES WITH
SPECIAL REFERENCE TO THAT OF MAMMALS**

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PLATE XVII

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INTRODUCTION

THE LACRYMAL BONE IN COMPARATIVE ANATOMY AND PALÆONTOLOGY

Cuvier, in the '*Histoire naturelle des Poissons*' (by Cuvier and Valenciennes, 1828), gives a brief résumé (pp. 307–516) of early work on the osteology of the skull of fishes, the subject from which the lacrymal problem later arose. He states that before 1798 very little had been written concerning the bones of the head of fishes. In his '*Leçons d'Anatomie*' (1798) he had said little about the composition of the brain-case but had dealt more in detail with the bones of the face, although still very incompletely. Recognizing the great need for more facts, he had gradually assembled an extensive osteological collection, which had been the basis for his own subsequent researches as well as for those of others.

In 1807 Oken put forth his celebrated theory of the vertebral nature of the skull, which, although exceedingly crude, stimulated a vast amount of comparative anatomical research. Perhaps even more fruitful was the elder Geoffroy's idea of the unity of type in the animal kingdom.

Studies by Geoffroy (1807) and by Cuvier (1812) on the skull of recent and fossil crocodilians furnished, as it were, an intermediate type between man on the one hand and fish on the other, which facilitated the comparison of the two extremes. Cuvier's system of names for the elements of the skull of vertebrates was first published in 1812 and further developed in 1814 and 1817.

In 1815 Spix homologized Cuvier's "*frontaux antérieurs*" of fishes with the lacrymal of man, a view which was also held by Geoffroy. Cuvier (1828, p. 314) in criticising this view remarks: "*Ces os ('frontaux antérieurs') existent dans les crocodiles, dans les tortues, etc., à côté des vrais lacrymaux caractérisés pour tels, et ne peuvent leur être substitués.*"

Thus Cuvier recognized that the lacrymals of crocodiles are homologous with those of man. But, with regard to the "*frontaux antérieurs*," it is now known that these elements (prefrontals) in crocodiles, turtles, etc., are not homologous with the similarly appearing bones in fishes, since the true prefrontals are derm bones while the "*frontaux antérieurs*" of fishes are underlying endocranial elements, ossifications of the lateral, or "*aliethmoid*" wings of the nasal capsules. On this account W. K. Parker (1872) called the "*frontaux antérieurs*" of fishes "*lateral ethmoids*" and T. J. Parker (1893) named them "*parethmoids*."

In 1818 Carus sought to identify the human lacrymal with the first suborbital bone of fishes (Cuvier's "premier sous-orbitaire"). As to this homology Cuvier says (1828, p. 337): "le premier *sous-orbitaire* . . . est articulé à une facette de l'apophyse inférieure externe du frontal antérieur; ce qui pourrait le faire regarder comme analogue de lacrymal." But immediately below in a footnote he says: "C'est l'adorbital ou portion orbitaire du maxillaire de M. Geoffroy. MM. Spix, Bojanus, Bakker et Meckel le rapportent, ainsi que les suivans, au *jugal*. Pour M. Carus, c'est le lacrymal. Ce qui me fait considérer cet appareil comme différent de ceux des autres vertébrés, c'est qu'il recouvre les muscles, au lieu de leur donner attachment." Thus, Cuvier, as well as others of his contemporaries, apparently recognized more or less clearly that the series of suborbital bones in fishes bore some resemblance to the series comprising the bones now called the prefrontal, lacrymal, jugal, and postorbital in reptiles; but, with commendable caution, he doubted the implied homologies. While not sufficiently explicit, his objection probably meant that in the fishes the suborbital series lies altogether outside of the jaw and face muscles, while in mammals the jugal and lacrymal are more or less covered by muscles, the jugal giving attachment to the masseter. He apparently did not take into consideration the probability that in the higher vertebrates, especially the mammals, the dermal bones around the eye have sunk deeply beneath the surface and that the muscles have gained new attachments.

In 1843 Owen, in his table entitled "Synonyms of the Bones of the Head of Fishes according to their Special Homologies," definitely attributes to Cuvier the view that the lacrymal is homologous with the first suborbital of fishes. Owen himself adopted it and so, apparently, did all other authors until quite recent times.

Apparently the first to doubt the correctness of this "Cuvierian concept" was E. Gaupp (1910, p. 535), who in 1898, in describing the development of the lizard skull, raised the question whether the so-called lacrymal of the lizard is really the homologue of the mammalian lacrymal. In 1910 Gaupp developed this idea in an important paper entitled 'Das Lacrimale des Menschen und der Säugetier und seine morphologische Bedeutung.' After reviewing the topographic relations of the so-called prefrontal and lacrymal bones of recent Sauropsida to the nasal capsules and to the ductus naso-lacrymalis, with special reference to conditions in *Lacerta*, he concluded that the evidence pointed to the non-homology of the so-called lacrymal of reptiles with the true lacrymal of mammals,

which appeared to him to be the homologue of the reptilian prefrontal. He therefore proposed to name the reptilian prefrontal "os lacrimale," while for the so-called lacrymal of reptiles he suggested the name "adlacrimale."

Meanwhile (1904–1905) O. Jaekel had reached substantially similar conclusions upon quite different grounds. In describing the skull of *Udenodon pusillus*, a very small anomodont from South Africa, this author applied the name "lacrymalia" to the bones that were located at the anterosuperior quarter of the orbits, and which had by other authors been named prefrontals. He states, however, that certain breaks in this specimen could not be clearly distinguished from zigzag sutures and that there might be two prefrontal elements. However, having recognized the apparent similarity of the dorsal element on the one hand to the lacrymal of mammals, and on the other hand to the prefrontal of reptiles, Jaekel in 1905 ("Ueber den Schädelbau der Nothosauriden") published a series of figures of skulls, including *Trematosaurus*, *Sphenodon*, *Placochelys*, and *Simosaurus*, in which he applied the designation *L* ("lacrymale") to the element formerly called prefrontal, while for the element formerly named "lachrymal," he proposed the name *postnasal*. Thus, Gaupp and Jaekel were in agreement as to the homology of the reptilian prefrontal with the mammalian lacrymal, but they applied different names to the lower element, Jaekel calling it "postnasale" and Gaupp "adlacrimale."

Although adopted without question by von Huene (1911, p. 43) and by Wiman (1917),¹ the Gaupp-Jaekel view of the homology of the lacrymal of mammals with the reptilian prefrontal has not been adopted by Broili, Case, Williston, Broom, Watson,² Houghton, and other authors who have described Permian reptiles in recent years. In opposition to this view in 1912 and '13 I called attention to the fact that Gaupp and Jaekel had neglected to take into consideration the conditions of the preorbital elements of the Cynodontia, the very reptiles which, above all others, might be expected to throw light on this question, and in which, as will be more fully shown below, the lower preorbital element has every appearance of homology with the lacrymal of mammals. In the same papers it was suggested that the resemblance of the prefrontal of *Lacerta* to the lacrymal of mammals was a convergence phenomenon by which Gaupp had been deceived. This topic is further considered on pages 131 and 135 of the present paper.

¹Also by Abel in his 'Die Stämme der Wirbeltiere,' 1919.

²See addendum, p. 263.

In 1864 Nathusius showed that the lacrymal bone had a certain diagnostic value in distinguishing the different races of the genus *Sus*. This side of the subject, with special reference to the ruminants, was developed by Kober (1880) and more fully by Knotternus Meyer (1907).

In 1901 Forsyth Major published a very systematic and minute study of the lacrymal region of primates with important results which are discussed below.

From the viewpoint of anthropotomy, Le Double (1900) has monographed the numerous variations of the lacrymal region of man; while many investigators (e.g., Hoffman, 1882; Born, 1876; Gaupp, 1910; Tüffers, 1913) have worked out the morphology of the naso-lacrymal duct.

ORIGIN AND SCOPE OF THE PRESENT WORK

The present investigation has partly grown out of a difference of opinion between Dr. J. L. Wortman and myself concerning the probable course of evolution of the lacrymal bone in Primates. As will be shown below (page 207), this eminent anatomist and palæontologist assumes certain conditions of the lacrymal region to be primitive in placental mammals which I am compelled to regard as secondary. In seeking collateral evidence on this matter, before finishing the recently published work on the Eocene Primates of the *Notharctus* group, I was led into a somewhat extended review of the morphology and probable history of the lacrymal in all the orders of mammals. This line of study naturally connected itself with the history of the facial bones in recent and extinct reptiles, amphibians, and fishes, a subject to which I had already devoted considerable attention and to which in recent years the labor of those who have described Palæozoic vertebrates of all classes has brought such substantial evidence that most of the skull elements, both dermal and endocranial, can now be clearly followed throughout the Tetrapoda. It thus seemed worth while to bring all these observations and deductions together into a single paper and to prepare a special series of drawings illustrating the general history of the facial bones from fish to man. These drawings have been prepared, very conscientiously and skilfully, by Mr. Erwin S. Christman and Mrs. Elizabeth M. Fulda, under my constant direction.

SYNOPSIS OF THE CLASSIFICATION OF THE VERTEBRATES ADOPTED IN THIS WORK

Phylum CHORDATA

Subphylum VERTEBRATA

Superclass AGNATHA

Class OSTRACODERMI

Ostracoderms

Class ARTHRODIRA

Arthrodirees

Class CYCLOSTOMATA

Cyclostomes

Superclass CHONDRICHTHYES

Class ELASMOBRANCHII

Sharks, chimæroids

Superclass OSTEICHTHYES

Class DIPNOI (DIPNEUSTI)

Lung fishes

Class CROSSOPTERYGII

Crossopterygians

Order Rhipidistia (Osteolepida)

Osteolepidæ, etc.

Order Actinistia

Cœlacanth

Order Cladistia

Polypterus, *Calamoichthys*

Class ACTINOPTERYGII

Actinopterygians

Order Chondrostei

Old ganoids

Suborder Palæoniscoidei

Suborder Acipenseroidei

Order Holostei

New ganoids

Order Isospondyli

Old teleosts

Order Ostariophysi

Order Haplomi

Intermediate teleosts

Order Iniomi, etc.

Order Acanthopterygii

New teleosts

Superclass TETRAPODA

Class AMPHIBIA¹

Subclass STEGOCEPHALIA

Order Phyllospodyli

Branchiosaurs

Order Lepospondyli

Microsaurs, etc.

Order Temnospondyli

Temnospondyls

Suborder Embolomeri

Cricotus, etc.

Suborder Rhachitomi

Eryops, etc.

Suborder Stereospondyli

Mastodonsaurus, etc.

Subclass EUAMPHIBIA (BATRACHIA)

Order Gymnophiona (= Apoda)

Cæcilians

Order Urodela (= Caudata)

Salamanders, etc.

Order Anura (= Salientia)

Frogs and Toads

Class REPTILIA²

Series A ANAPSIDA

Order Cotylosauria

Suborder Seymouriamorpha

Seymouriidae, ?Sauravidae

Suborder Diadectomorpha

Diadectidae, Pariasauridae,

¹For a recent classification of the early Amphibia see Watson, D.M.S., 1917, Proc. Zool. Soc. London, pp. 167-170.

²For recent classifications of the Reptilia, see Williston, 1917, Journ. Geol., XXV, pp. 411-421; Watson, *op. cit.*, pp. 171-183.

Suborder Captorhinomorpha Procolophonidæ
 Limnoscelidæ, Captorhinidæ,
 Pariotichidæ, Gymnarthridæ, Pantyl-
 idæ
 Order Chelonina
 Suborder Eunotosauria
 Suborder Pleurodira
 Suborder Cryptodira
 Suborder Anapsida
 Suborder Trionychia
 Series B SYNAPSIDA
 Order Pelycosauria (= Theromorpha)
 Suborder Caseasauria Caseidæ
 Suborder Pelycosauria (S. S.) Poliosauridæ, Ophiacodontidæ, Sphen-
 codontidæ, Edaphosauridæ
 Order Therapsida
 Suborder Dinocephalia
 Suborder Dromasauria
 Suborder Anomodontia
 Suborder Gorgonopsia
 Suborder Therocephalia
 Suborder Bauriamorpha
 Suborder Cynodontia
 Order Placodontia
 Order Sauropterygia
 Suborder Nothosauria
 Suborder Plesiosauria
 Series C PARAPSIDA
 Order Protorosauria
 Order Squamata
 Order Proganosauria
 Order Ichthyosauria
 Series D RHYNCHOCEPHALIDA
 Order Rhynchocephalia
 Order Choristodera
 ?Order Thalattosauria
 Series E DIAPSIDA (= ARCHOSAURIA in part)
 Order Thecodontia
 Suborder Pseudosuchia
 Suborder Pelycosimia Erythrosuchidæ
 Suborder Phytosauria
 Order Crocodilia
 Order Saurischia (= Dinosauria in part)
 Suborder Theropoda
 Suborder Sauropoda
 Order Ornithischia (= Dinosauria in part)
 Suborder Iguanodontia (= Ornithopoda)
 Suborder Stegosauria
 Suborder Ceratopsia

- Order Pterosauria
- Class AVES
 - Subclass SAURURÆ
 - Order Archæornithes *Archæopteryx*
 - Subclass ORNITHURÆ
 - Order Megistanes Emus, Cassowaries, Kiwis, Moas
 - Order Struthiones, etc.
- Class MAMMALIA¹
 - Subclass A. PROMAMMALIA
 - Order Protodonta
 - Subclass B. PROTOTHERIA
 - Order Monotremata
 - Subclass C. METATHERIA
 - Order Triconodonta
 - Order Multituberculata (Allotheria)
 - Order Marsupialia
 - Subclass D. EUTHERIA Huxley (PLACENTALIA)
 - Order Trituberculata
 - Order Insectivora (Lipotyphla)
 - Suborder Centetioidei (Zalamb-
dodonta) *Zalambdodonts, including Nesophontes*
 - Suborder Soricoidei
 - Suborder Erinaceoidei
 - Suborder Pantolestoidei
 - Order Tillodontia *Esthonyx, Tillotherium.*
 - Order Carnivora²
 - Suborder Procreodi *Oxyclænidæ*
 - Suborder Acreodi *Mesonychidæ*
 - Suborder Pseudocreodi *Hyænodonts, Oxyænids, etc.*
 - Suborder Eucreodi *Miacidæ*
 - Suborder Aeluroidea *Viverridæ, Hyænidæ, Felidæ*
 - Suborder Arctoidea *Canidæ, Procyonidæ, Ursidæ, Mustelidæ*
 - Suborder Pinnipedia
 - Order Cetacea
 - Suborder Archæoceti
 - Suborder Mystacoceti
 - Suborder Odontoceti
 - Order Artiodactyla
 - Order Amblypoda
 - Suborder Taligrada
 - Suborder Pantodonta
 - Suborder Dinocerata

¹The present classification of the mammalia has grown out of the classification adopted in 'The Orders of Mammals' (1910, Bull. Amer. Mus. Nat. Hist., XXVII) and is intended to reflect the chief advances of the last decade in this subject.

²See Matthew, W. D., 1909, Mem. Amer. Mus. Nat. Hist., IX, pp. 321-331; 1915, Bull. Amer. Mus. Nat. Hist., XXXIV, p. 5.

- Order Embrithopoda
- Order Pyrotheria
- Order Proboscidea
- Order Sirenia
- Order Condylarthra
- Order Tubulidentata
- Order Litopterna
- Order Notoungulata
 - Suborder Entelonychia
 - Suborder Astrapotheria
 - Suborder Toxodontia
 - Suborder Typotheria
- Order Hyracoidea
- Order Perissodactyla
- Order Edentata¹
 - Suborder Tæniodonta
 - Suborder Palæanodonta
 - Suborder Xenarthra
 - Suborder Pholidota
- Order Rodentia²
 - Suborder Sciuromorpha
 - Suborder Myomorpha
 - Suborder Dipodomorpha
 - Suborder Hystricomorpha
- Order Lagomorpha
- Order Dermoptera
- Order Chiroptera
- Order Menotyphla
- Order Primates³
 - Suborder Lemuroidea
 - Suborder Tarsioidea
 - Suborder Anthroipoidea

¹For a recent classification of the Edentates see Matthew, W. D., 1918, *Bull. Amer. Mus. Nat. Hist.*, XXXVIII, p. 656.

²For a recent classification of the Rodents see Miller, G. S. and Gidley, J. W., 1918, *Journ. Washington Acad. Sci.*, VIII, pp. 431-448.

³For a recent classification of the Primates see Gregory, W. K., 1915, *Bull. Geol. Soc. Amer.*; XXVI, pp. 426-444; 1916, *Bull. Amer. Mus. Nat. Hist.*, XXXV, pp. 266-267.

CLASSIFICATION, ACCORDING TO FUNCTION AND POSITION, OF THE SKULL
ELEMENTS FIGURED IN THIS WORK, WITH ABBREVIATIONS USED IN
THE ILLUSTRATIONS

A. SKULLS OF FISHES (Figs. 1-7)

1. Mouth and Jaw Bones

pmx.—premaxilla

mx.—maxilla

spm.—supramaxilla

v.—prevomers ("vomeres" of fish)

pa. sp.—parasphenoid (= vomer of mammals)

ect. pt.—ectopterygoid

en. pt.—entopterygoid (pterygoid)

mt. pt.—metapterygoid

pl.—palatine

qu.—quadrate

sym.—symplectic

hm.—hyomandibular

d.—dentary

ang.—angular

2. Circumorbital Series

pf.—prefrontal

l.—lacrymal, l¹, l², subdivisions of lacrymal

j.—jugal, j¹, j², subdivisions of jugal

po.—postorbital, po¹, po², subdivisions of postorbital

pof.—postfrontal

3. Median and Paired Elements on Roof of Endocranium

in.—internasal

"ad.n."—"adnasal"

if.—("eth") interfrontal ("ethmoid")

f.—frontal

pa.—parietal

4. Temporal Region

it.—intertemporal ("sphenotic")

st.—supratemporal ("pterotic")

sq.—squamosal ("cheek plate")

p. op.—preoperculum

qu. j.—quadratojugal

5. Nuchal, Opercular, and Gular Region

dso.—dermosupraoccipital ("supratemporal" of fish)

tb.—tabular ("epiotic")

op.—operculum

s. op.—suboperculum

i. op.—interoperculum

br. st.—branchiostegal

g.—gular

6. Elements of the Endocranium

pa. eth.—parethmoid (ossification of the lateral portion of the olfactory capsule)

sph. eth.—sphenethmoid

B. SKULLS OF TETRAPODA (Figs. 8–196)

1. Mouth and Jaw Bones

pmx.—premaxilla

mx.—maxilla

pl.—palatine

pt.—pterygoid

ecpt.—ectopterygoid

qu.—quadrate

pasp.—parasphenoid (= vomer)

v.—vomer (parasphenoid)

pv.—prevomer

2. Circumorbital Series

pf.—prefrontal

l.—lacrymal

j.—jugal

po.—postorbital

pof.—postfrontal

3. Median and Paired Elements on Roof of Endocranium

n.—nasals

if.—interfrontal

f.—frontal

pa.—parietal

4. Temporal Region

it.—intertemporal

st.—supratemporal

sq.—squamosal

quj.—quadratojugal

5. Nuchal and Occipital Region

dso.—dermosupraoccipital

tb.—tabular

6. Elements of the Endocranium

eth.—ethmoid

lsp.—laterosphenoid

osp.—orbitosphenoid

a.s.—alisphenoid

ANALYSIS AND CLASSIFICATION OF TYPICAL CONDITIONS OF THE LACRYMAL AND SURROUNDING PARTS IN REPTILES, BIRDS, AND MAMMALS

I. Prefrontal present.

1. Lacrymal present.

A¹. Lacrymal extending from orbit to anterior naris. *Cotylosauria** (except *Procolophon*), *Naosaurus*, *Triassochelys*.

A². Lacrymal not extending from orbit to anterior naris.

(1) Lacrymal in contact with nasal.

a¹. Lacrymal extending rostrad beyond prefrontal.

b¹. Maxilla not in contact with prefrontal.

c¹. No antorbital fenestra. *Sphenacodon*, many Therapsida, most Crocodilia.

c². Antorbital fenestra present.

d¹. Premaxilla not in contact with lacrymal. *Euparkeria*, *Mystriosuchus*, *Triceratops*, *Tyrannosaurus*.

d². Premaxilla in contact with lacrymal. *Camplosaurus*, *Gryposaurus*.

b². Maxilla in contact with prefrontal. Some therapsids, *Scylacops*.

a². Lacrymal not extending rostrad beyond prefrontal. *Procolophon*.

(2) Lacrymal not in contact with nasal (separated from it by prefrontal).

a¹. Maxilla barely in contact with prefrontal. *Mycterosaurus*.

a². Maxilla in wide contact with prefrontal.

b¹. Lacrymal not reduced. *Alligator*.

b². Lacrymal reduced. *Aræoscelis*, *Lacerta*, *Cyclura*.

2. Lacrymal absent, its place usurped by prefrontal.

A¹. Maxilla in contact with prefrontal.

(1). Premaxilla in contact with nasal. *Sphenodon*.

(2). Premaxilla not in contact with nasal. *Chelone*.

A². Maxilla not in contact with prefrontal.

(1). Prefrontal in contact with palatine. *Python*, *Boa*.

(2). Prefrontal not in contact with palatine. *Casuarus*.

II. Prefrontal and postorbital bones absent.

1. Lacrymal absent. Monotremes, *Polymastodon*, *Potamogale*, *Manis*, Phocidæ.

2. Lacrymal present.

A¹. A primitive (?) naso-lacrymal contact, lacrymal forming distinct rim on anterosuperior margin of orbit. Lacrymal foramen internal. Lacrymal in contact with jugal. Pars facialis small. Several marsupials, e.g., *Amphiprovivera*, *Borhyaena tuberosa*, *Wynyardia*.

A². A maxillo-frontal contact above lacrymal.

(1) Orbit not closed posteriorly by jugal and frontal.

a¹. Lacrymal in contact with jugal.

b¹. Lacrymal large, extended vertically, often bearing on

the dorso-anterior margin of orbit a prominent rim, which is inclined upward and backward. Pars facialis often extended.

c¹. Jugal not extending in front of orbit.

d¹. Lacrymal foramen internal, pars facialis small. *Palæothentes*.

d². Lacrymal foramen marginal or external. Pars facialis large.

e¹. Tubercle and rim prominent. *Dasyuridæ*, *Peramelidæ*, *Macropus*, *Phalangista*.

e². Tubercle and rim not prominent. *Didelphis*.

c². Jugal extending in front of orbit, pars facialis reduced, tubercle prominent. *Phascolarctos*, *Phascolumys*.

b². Lacrymal large, with large pars facialis; lacrymal rim on anterior border of orbit, if developed, not markedly inclined upward and backward.

c¹. Lacrymal foramen internal, tubercle prominent. Most creodonts, *Perchaerus*, *Dichobune* Archæoceti.

c². Lacrymal foramen external, pars facialis much extended anteroposteriorly. *Orycteropus*, many Suina, Myrmecophagidæ.

c³. As above; jugal meeting frontal behind lacrymal. *Dasypodidæ*.

b³. Pars facialis developed dorsally, tubercle prominent, foramen internal. *Phenacodus*, *Meniscotherium* *Hegetotherium*, *Pachyrhinos*.

b⁴. Lacrymal more or less reduced on anterior rim of orbit, pars facialis slight or wanting. Jugal often extending in front of lacrymal. Lacrymal foramen internal. Most Fissipedia.

b⁵. Pars facialis not large, pars orbitalis in contact with a medial process of the jugal. Sloths, glyptodonts.

b⁶. Pars facialis small or wanting, lacrymal displaced dorsad by upgrowth of jugal and of zygomatic plate of maxilla. Many rodents.

b⁷. Lacrymal flattened beneath widely projecting supra-orbital apophysis of frontals. *Odontoceti*.

b⁸. Lacrymal forming a long sliver of bone between the orbital apophysis of the frontal and the maxilla. *Mystacoceti*.

b⁹. Pars orbitalis extended anteroposteriorly by forward shifting of orbits. Lacrymal forming anterior rim of orbit. *Sirenia*.

a². Lacrymal not in contact with jugal, which, if present, is separated from lacrymal by maxilla.

b¹. Lacrymal vestigial, jugal large, extending to anterior

rim of orbit. *Ursus* sp. div.

- b². Lacrymal a thin, more or less reduced lamina on the wall of the orbit, sometimes bearing a small tubercle. *Lutra*, *Latax*, *Spilogale*, *Eumetopias*.
- b³. Lacrymal with a distinct orbital rim and expanded pars orbitalis, foramen marginal. Jugal more or less reduced. Leptictidæ, Erinaceidæ.
- b⁴. Lacrymal on medial wall of orbit, extended obliquely upward and backward, above enlarged infraorbital tunnel. Lacrymal foramen external; jugal absent. Most zalambdodonts.
- b⁵. Lacrymal expanded in front of orbit, above large tunnel for masseter medialis. *Hydrochaerus*.
- b⁶. Lacrymal very small, on anterosuperior rim of orbit. *Protypotherium*, *Interatherium*.
- b⁷. Lacrymal on anterior margin of orbit, bearing stout tubercle and separated from the palatine by the maxilla. *Mastodon*, *Elephas*.

(2) Jugal meeting frontal behind orbit.

- a¹. Pars facialis expanded dorsally. A double tubercle. Lacrymal in contact with jugal. *Diadiaphorus*.
- a². Pars facialis expanded anteroposteriorly. Tubercle often prominent, lacrymal foramen mostly internal. Lacrymal in contact with jugal. *Megalohyrax*, many Artiodactyla, *Tupaia*, *Rhynchocyon*.
- a³. Pars facialis reduced, tubercle prominent, foramen internal. Lacrymal separated from jugal by maxilla. *Dendrohyrax*.
- a⁴. Pars facialis variable, occasionally extended secondarily. (*Lemur*) or small or absent (*Adapis*, *Archæolemur*). Lacrymal fossa and duct between lacrymal and maxilla. Lacrymal usually in contact with jugal. *Adapis*, *Notharctus*, *Lemur*, *Propithecus*.
- a⁵. Lacrymal forming prominent anterior rim of orbit (crista orbitalis), pars facialis small, a fronto-maxillary contact, lacrymal foramen prominent in front of lacrymal.
 - b¹. Lacrymal in contact with jugal. *Necrolemur*.
 - b². Lacrymal separated from jugal by maxilla. *Perodicticus*, *Galago*, *Tarsius*.
- a⁶. Lacrymal on inner wall of orbit, extended vertically. Lacrymal fossa and duct chiefly anterior to lacrymal. Lacrymal separated from nasal by narrow fronto-maxillary contact. Lacrymal separated from jugal by maxilla. Anthropoid apes, *Homo*.

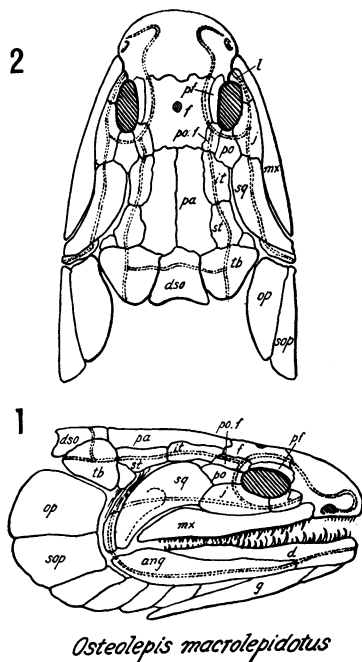
A³. A secondary naso-frontal contact.

- (1) Pars facialis of lacrymal extended. Lacrymal in contact with jugal.
 - a¹. Orbit not closed posteriorly. Many perissodactyls.
 - a². Orbit closed posteriorly by postorbital processes of frontal and jugal. Equidæ.

- (2) Pars facialis reduced, lacrymal separated from jugal by maxilla. Orbit closed posteriorly. Lacrymal fossa and duct between lacrymal and maxilla. Many *Platyrrhinæ*.
- A⁴. Lacrymal in contact with premaxilla. No maxillo-frontal contact. Otherwise much as in *Lemur*. *Chiromys*.

ORIGIN AND EVOLUTION OF THE LACRYMAL IN THE
LOWER VERTEBRATES
Fishes

In the rhipidistian, or osteolepidote fish (Figs. 1 and 2) of the Paleozoic era, there is a ring of dermal bones around the orbit which, as a whole, corresponds to the circumorbital series of contemporary and later Actinopterygii (Figs. 3-6) and to a similar series in the Dipnoi. Of these elements, the one at the antero-inferior corner of the orbit very



Osteolepis macrolepidotus

Figs. 1, 2. Head of a very primitive rhipidistian fish *Osteolepis macrolepidotus* from the Old Red Sandstone, Scotland. Enlarged. After Goodrich.

1. Side view. 2. Dorsal view.

Main lateral line canals indicated by dotted lines.

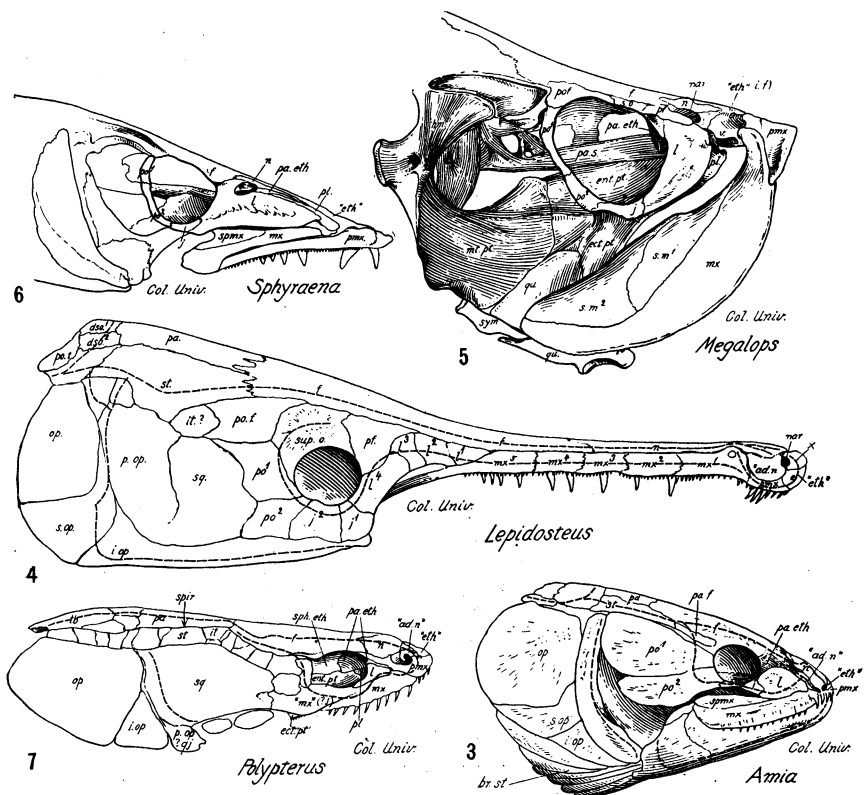
probably represents the mammalian lacrymal, since it has been traced forward from the Rhipidistii¹ through the earliest amphibians and reptiles into the cynodont reptiles, where its homology is clearly established.² The remaining bones of the series in the Rhipidistii, beginning at the anterosuperior border of the orbit, represent the prefrontal,³

¹1915, Ann. N. Y. Acad. Sci., pp. 330-337.

²1913, Journ. Morphol., pp. 3, 4; 1915, Ann. N. Y. Acad. Sci., pp. 330-337.

³Watson and Day, 1916, and Goodrich, 1919.

postfrontal, postorbital, and jugal, respectively, of tetrapod vertebrates. Accordingly, the lacrymal, at its very first appearance in the distant Paleozoic ages, is associated with a set of bones with which, in spite of all the readjustments involved in the evolution of certain fishes into tetrapods, it persistently retains connection.



Figs. 3 to 7. Skulls of Ganoids, Teleosts and *Polypterus*.

3. *Amia calva*. Class Actinopterygii, Order Holostei, family Amiidae. Young specimen. Lateral line canals after Allis.
4. *Lepidosteus tristachus*. Class Actinopterygii, order Holostei, family Lepidosteidae. Lateral line canals adapted from Goodrich, after Allis and Collinge.
5. *Tarpon atlanticus*. Class Actinopterygii, order Ispoondyli, family Elopidae.
6. *Sphyræna barracuta*. Class Actinopterygii, order Acanthopterygii, suborder Percosoces, family Sphyrænidae.
7. *Polypterus bichir*. Class Crossopterygii, order Cladistia, family Polypteridae.

Another bone with which the lacrymal of fishes often gains contact is the palatine. At this stage the lacrymal is separated from the frontal by the prefrontal and the parethmoid.

In *Polypterus* (Fig. 7) the lacrymal is a small wedge-shaped element in the antero-inferior corner of the orbit, which extends toward the nose and begins to resemble the lacrymal of later types. In the dried skull of this fish there is a tunnel beneath the lacrymal which runs forward toward the nostril. At first sight it suggests the naso-lacrymal duct of tetrapods, but Pollard's dissections (1892) show that it transmits the superior maxillary branch of the fifth nerve, which in later types passes through the maxillary.

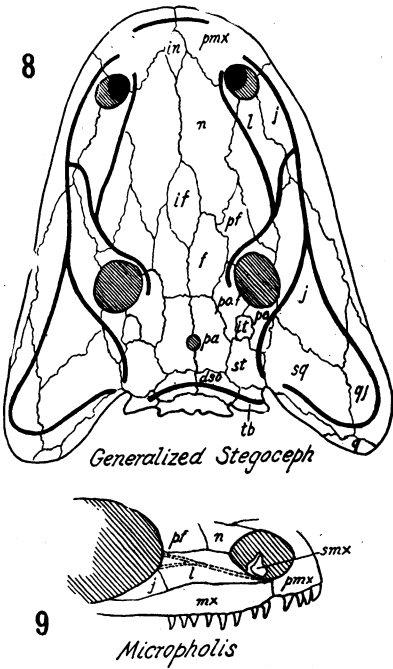


Fig. 8. Generalized stegoceph skull, showing location of sensory grooves. After Moodie.

Fig. 9. Fore part of skull of *Micropholis stowi*, showing course of naso-lacrymal duct. After Watson.

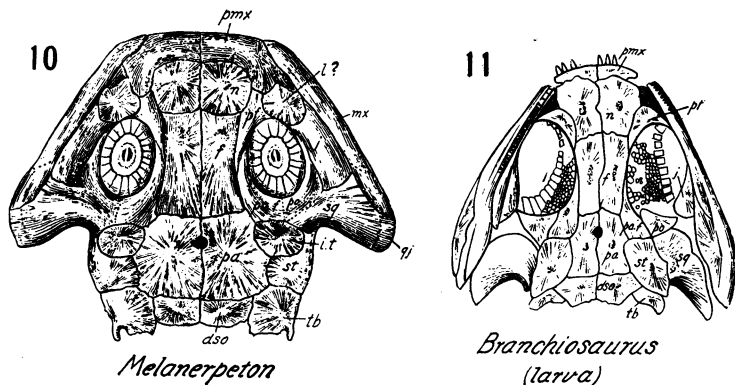
The lacrymal of primitive fishes bears on its outer surface a branch of the "lateral line system," which is supposed by Baur (1896), Allis (1899), Moodie (1908), and others to have given rise to the "sensory grooves" on the surface of the skull of stegocephs (Fig. 8). It has been suggested by Watson (1913) that the naso-lacrymal duct of later tetrapods may be a special derivative of these sensory grooves.

Amphibia

In his description of the skull of *Micropholis stowi* (Fig. 9), a small stegoceph from the Trias of South Africa, Watson refers to the naso-lacrymal duct of this animal in the following passage:

Four of the skulls show very clearly the course of the ductus naso-lacrymalis, which is a narrow canal running in the substance of the lacrymal bone from the orbit, which it leaves by two openings, to the nostril, where it opens behind and below the septomaxilla. This is, I believe, the first recognition of a ductus naso-lacrymalis in the Stegocephalia, and the occurrence is very interesting from several points of view:—

(a) The very superficial position of the duct. In development in recent types this begins merely as an epidermal thickening which grows down into the head and subsequently acquires a lumen; in *Micropholis* we have an early condition where the duct is still in the skin and has not yet sunk at all deeply.

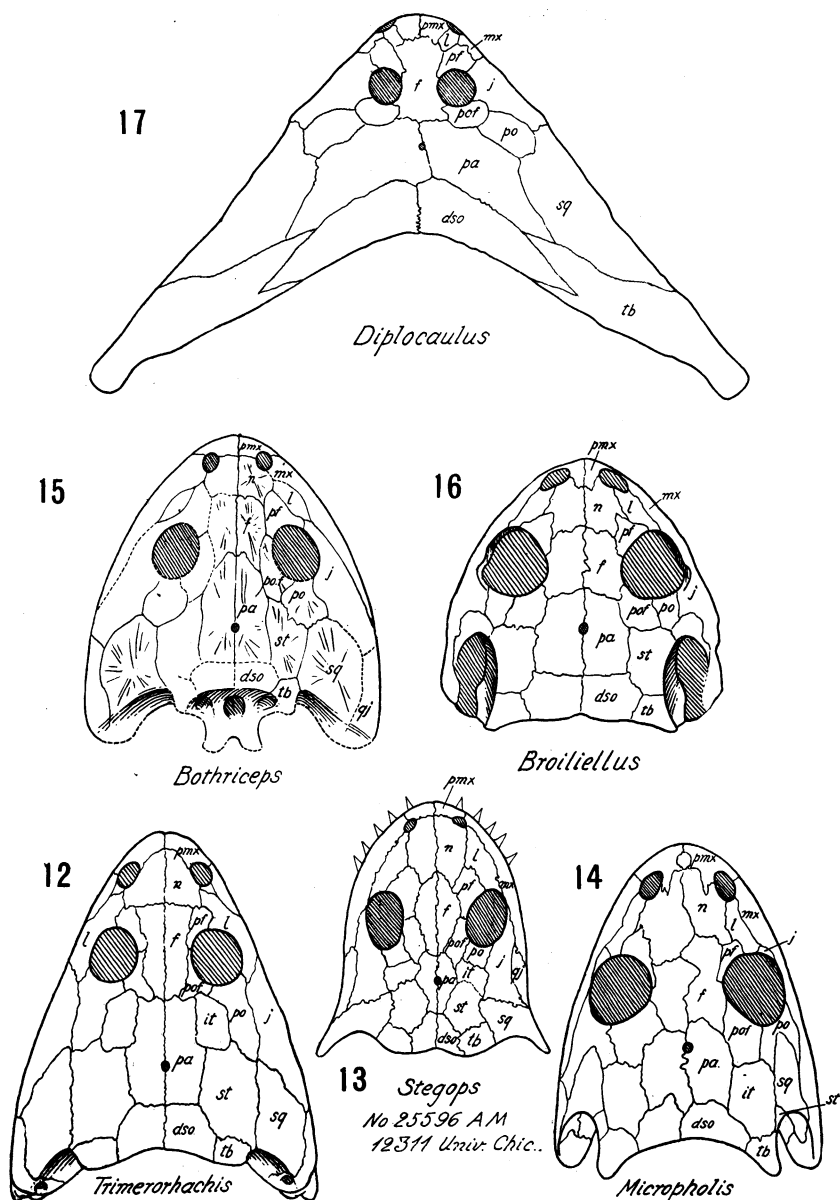


Figs. 10 to 11. Skulls of Branchiosaurs. Class Amphibia, subclass Stegocephalia, order Phyllospondyli.

10. *Melanerpeton folax*. Family Apateonidæ. Permian, Bohemia. After Fritsch. Presence of lacrymal doubtful.
11. *Branchiosaurus amblystoma*. Family Branchiosauridæ. Permian, Saxony. After Credner. Lacrymal absent.

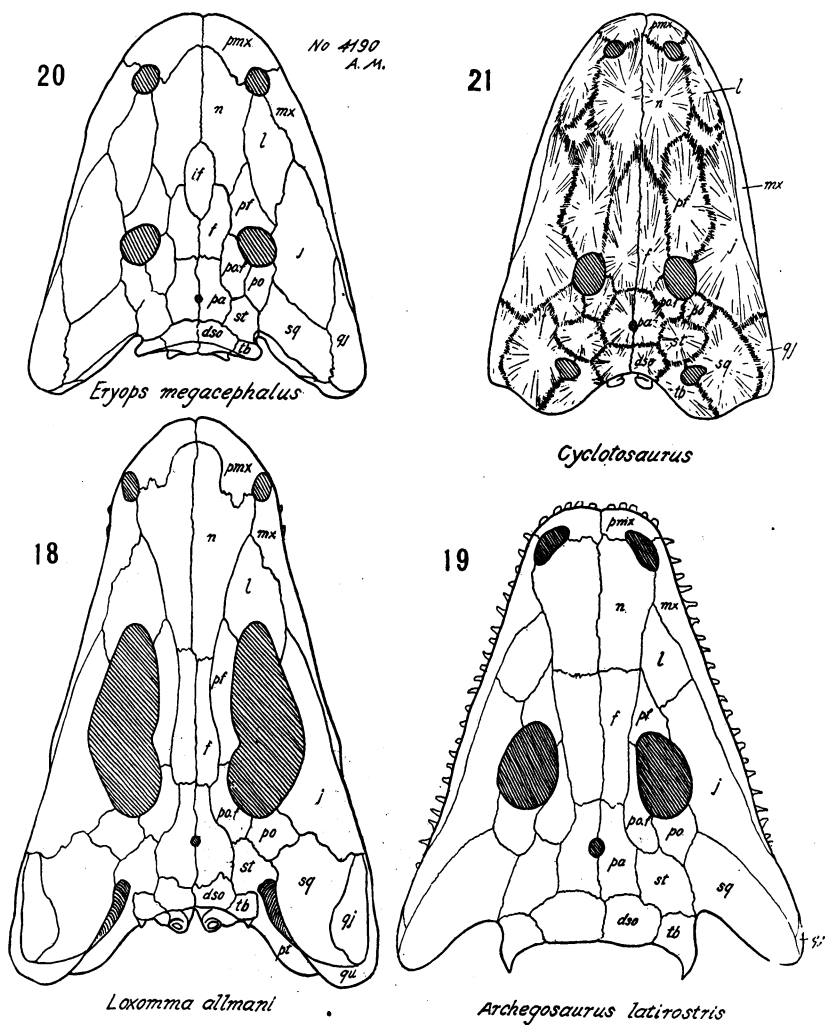
(b) The very great forward extension of the duct and its very unusual exit, practically on the outer surface and just behind the septomaxilla, are of interest. The duct only occurs in Tetrapoda, never in fish, and its origin is obscure; it may be suggested that it is possible that it has been derived from one of the lateral line canals so commonly found in Stegocephalia, of which there is no trace in *Micropholis*. (*Op. cit.*, pp. 342-343.)

In modern urodeles the naso-lacrymal duct, which is continuous with the lacrymal glands, is developed as a solid epithelial cord which follows the cleft leading from the orbit to the nares and lies between the maxillary and lateral nasal processes of the embryonic head. (Keith,



Figs. 12 to 17. Skulls of various Stegocephs. Class Amphibia, subclass Stegocephalia.

12. *Trimerorhachis insignis*. Order Temnospondyli, suborder Rhachitomi, family Trimerorhachidae. Permo-Carboniferous, Clear Fork, Texas. After Williston.
13. *Stegops divaricata*. Order uncertain, family Stegopidae. Coal Measures, Ohio. After Moodie.
14. *Micropholis stowi*. Order Temnospondyli, suborder Rhachitomi, family Micropholidae. Middle Triassic, Procolophon zone, South Africa. After Watson.
15. *Bothriceps australis*. Order Temnospondyli, suborder Rhachitomi, family Brachyopidae. Middle Triassic, Procolophon zone, South Africa. After Broom.
16. *Broiliellus tezensis*. Order Temnospondyli, suborder Rhachitomi, family Dissorhophidae. Permo-Carboniferous, Texas. After Williston.
17. *Diplocaulus megacephalus*. Order Lepospondyli, family Diplocaulidae. Permo-Carboniferous, Texas. After Douthitt.

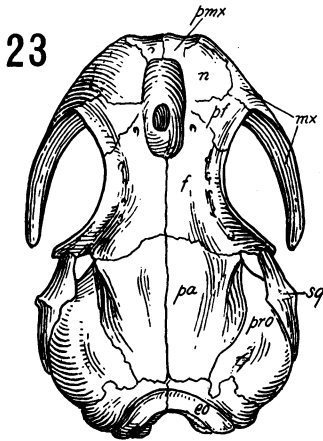


Figs. 18 to 21. Skulls of Stegocephs. Class Amphibia, subclass Stegocephalia, order Temnospondyli.

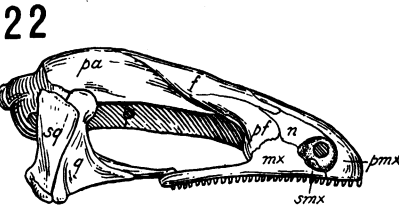
18. "*Loxomma*" *allmani*. Suborder Embolomeri, family Loxomatidae. Upper Carboniferous, Northumberland, England. After Embleton and Atthey.
19. *Archegosaurus latirostris*. Suborder Rhachitomi, family Archegosauridae. Lower Permian, Rhine Province, Germany. After H. von Meyer.
20. *Eryops megacephalus*. Suborder Rhachitomi, family Eryopidae. Permo-Carboniferous, Texas.
21. *Cyclotosaurus robustus*. Suborder Stereospondyli, family Mastodonsauridae. Upper Triassic, Swabia, Germany.

Kingsley.) In urodeles that retain a lacrymal bone (see below, p. 224) it is pierced by the naso-lacrymal duct.

In all really primitive fishes the eyes are located near the front end of the head, not far behind the nostrils, and the same is true of all the more primitive Palæozoic amphibians and reptiles. Hence, it is not surprising that the lacrymal bone at the antero-inferior corner of the orbit often has a wide contact with the nasal bone and extends far toward the nares.



Seironota



Amblystoma

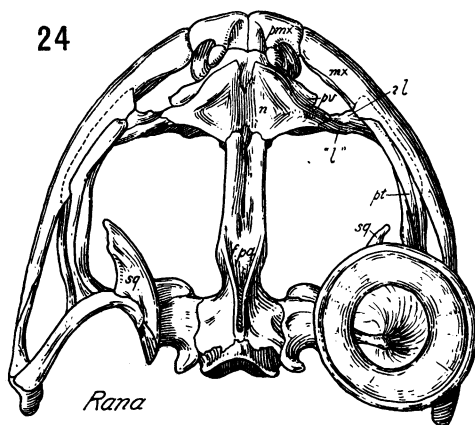
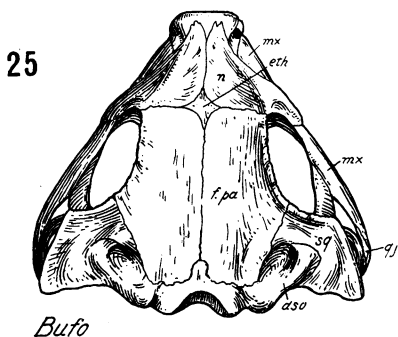
Figs. 22, 23. Skulls of modern Urodeles showing loss of the lacrymal and retention of the prefrontal. Class Amphibia, subclass Euamphibia.

22. *Amblystoma opacum*. Order Urodela, suborder Mycetodera, family Amblystomidae. After W. K. Parker.

23. *Seironota* (= *Salamandrina*) *perspicillata*. Order Urodela, suborder Mycetodera, family Salamandridae. After W. K. Parker.

As a rule, the snout of both Rhipidistii and early Amphibia is wide and depressed, with wide premaxillæ and nasals and laterally placed nares. The maxilla is vertically shallow, never extended dorsad on the face.

In many of the early Amphibia the lacrymal is excluded from the orbital border by the downward growth of the prefrontal which gains contact with the jugal (Figs. 15, 17, 19, 21); but this specialization is avoided by the very ancient stegoceph *Loxomma* (Fig. 18) and by all the primitive reptiles.



Figs. 24, 25. Skulls of modern Anura. Class Amphibia, subclass Euamphibia, order Anura. After W. K. Parker.

24. *Rana pipiens*. Family Ranidae.

Two small bones between the nasals and the maxilla were called by W. K. Parker "pre-orbital" and "anterior suborbital" or lacrymal respectively. By comparison with *Bothriiceps* (Fig. 15) and *Broiliellus* (Fig. 16), the anterior bone (?1) is seen to have the general position of the lacrymal, while the posterior bone ("1") bone, suggests the prefrontal.

25. *Bufo ornatus*. Family Bufonidae. No trace of the prefrontal or of the lacrymal is present. The skull roof is secondarily widened.

At least in *Trematosaurus sobeyi* Houghton the lacrymal was pierced by a large duct and was in contact below with the palatine (cf. Houghton, 1915, Fig. 6, page 51). These conditions thus afford evidence in favor of the Cuvierian view that the bone usually called

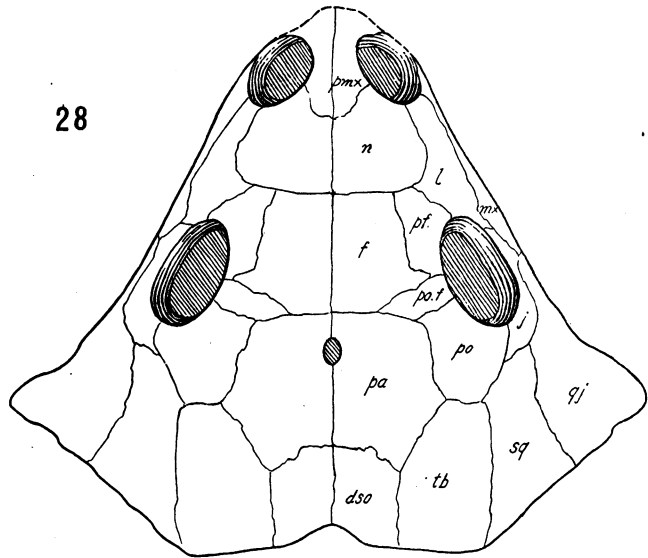
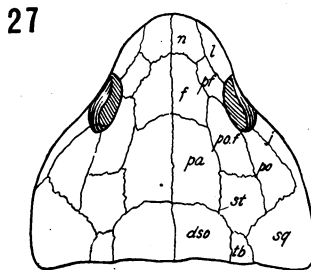
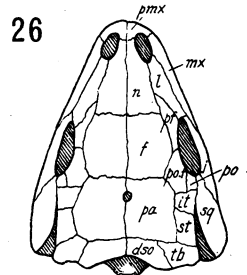
"lacrymal" in the lower vertebrates is rightly identified with that element in the therapsids and mammals. In this stegoceph the lacrymal was extended from the orbit beyond the prefrontal, but was excluded from the nostril and the septomaxilla by the naso-maxillary contact.

Most of the recent Amphibia (Figs. 22-25) have sacrificed the lacrymal, together with many other dermal elements, but a small element in *Ranodon* and *Ellipsoglossa*, which was named Præfrontale II (Pf' of Taf. XXIII, Figs. 64, 69) by Wiedersheim (1877, p. 418), is regarded by the Sarasins as a true lacrymal (1887-1890, p. 157). Wiedersheim (*loc. cit.*) represents the lacrymal at the anterior inferior part of the orbit, articulating with the prefrontal, nasal, and maxilla. Cope (1889, Pl. XXII, fig. 1) shows that the lacrymal is retained by *Gyrinophilus*, which is in many respects the most primitive Plethodontid. In this genus the lacrymal is excluded from contact with the nasal by the broad contact of maxilla and prefrontal. The "nasale laterale" (Wiedersheim) of cæcilians, which has the position of a lacrymal, has been shown by the Sarasins (*op. cit.*, pp. 155-157) to be an exposed flange of the olfactory capsule and is named by them "turbinale."

Primitive Reptiles

In the primitive reptiles of Permo-Carboniferous times (Figs. 26, 29, 30) the skull is deepened by the downward growth of the suspensoria of the jaws, the snout is more or less pointed, the opposite nares being nearer together than was the case in the stegocephs. The lacrymal retains its wide contact with the nasals and is extended longitudinally from the orbit to the nares. The whole circumorbital ring of bones (Figs. 29-35) is intact and little modified and the maxilla is primitively not extended dorsad on the side of face. In the Triassic *Procolophon* (Fig. 33), the last survivor of the cotylosaurs, the enlargement of the orbit and the dorsal growth of the maxilla have contributed to the reduction of the lacrymal, which now parallels that of certain lizards and is becoming smaller than the prefrontal (cf. Watson, 1914).

In the Chelonina (Fig. 36), which doubtless represent a highly specialized offshoot of the Cotylosauria, the true lacrymal has disappeared along with several other elements of the dermal skull, its place being usurped by the prefrontal. Jaekel (1916, Taf. iv, v, and pp. 143-145) figures in *Stegochelys* (*Triassochelys*) *dux* a suture separating the maxilla below from the "postnasale" (lacrymal) above, which is represented as a separate element extending from the anterior nares nearly to the orbit.

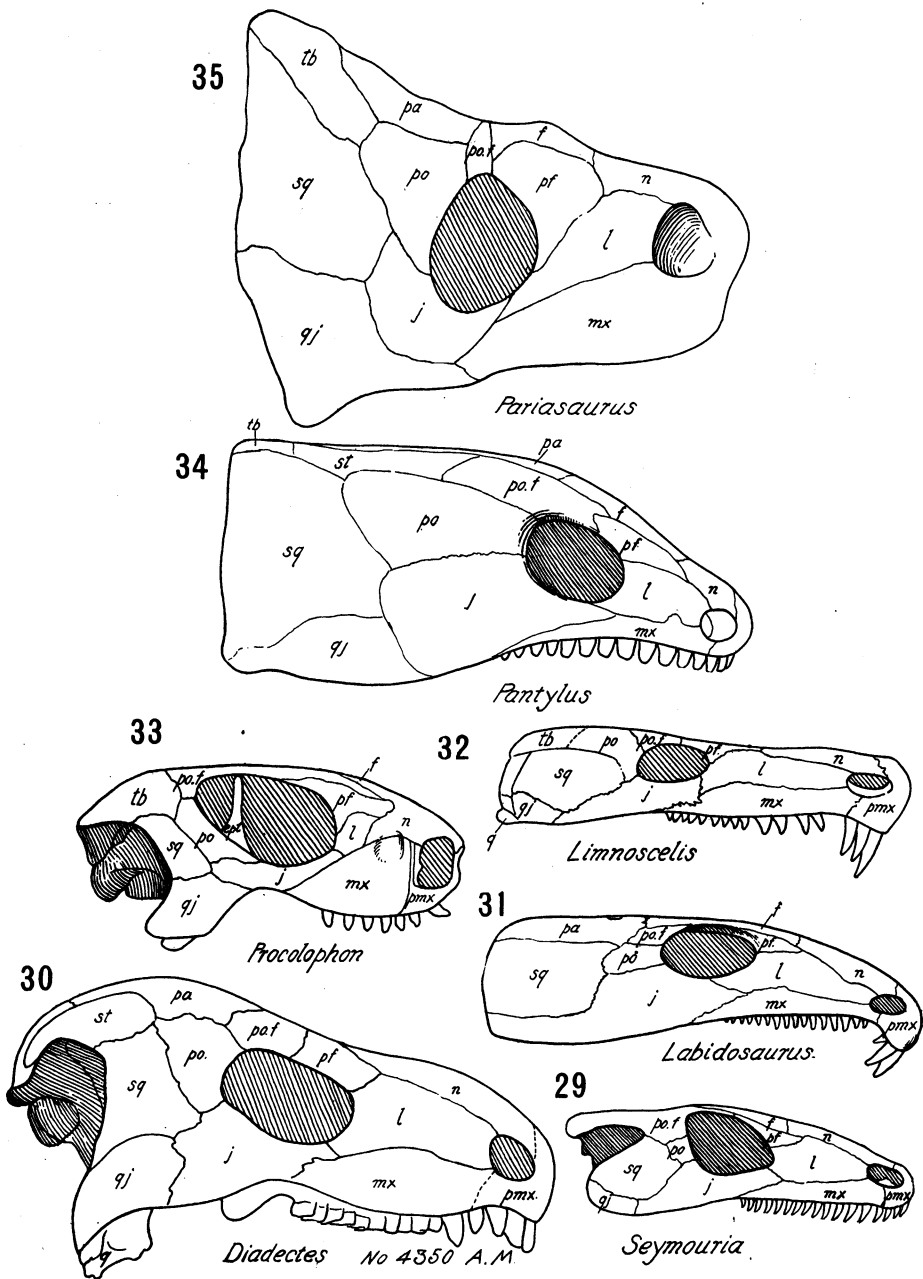
*"Pariasaurus"**Pantylus**Seymouria*

Figs. 26 to 28. Skulls of Cotylosaurs. Class Reptilia, series Anapsida, order Cotylosauria.

26. *Seymouria baylorensis*. Suborder Seymouriamorpha, family Seymouriidae. Permo-Carboniferous, Texas. After Williston.

27. *Pantylus cordatus*. Suborder Captorhinomorpha, family Pantylidae. Permo-Carboniferous, Texas. After Williston.

28. "*Pariasaurus*." Suborder Pariasauria, family Pariasauridae. Middle Permian, Pariasaurus zone, Gouph district, South Africa. After Watson.



Figs. 29 to 35. Skulls of Cotylosaurs. Class Reptilia, series Anapsida, orde Cotylosauria.

29. *Seymouria baylorensis*. Suborder Seymouriamorpha, family Seymouriidae. Permo-Carboniferous, Clear Fork, Texas. After Williston.
30. *Diadectes (Empedias) molaris*. Suborder Diadectomorpha, family Diadectidae. Permo-Carboniferous, Texas. After Broom.
31. *Labidosaurus* sp. Suborder Captorhinomorpha, family Captorhinidae, Uppermost Clear Fork, Texas. After Williston.
32. *Limnoscelis paludis*. Suborder Captorhinomorpha, family Limnoscelidae. Permo-Carboniferous, New Mexico. After Williston.
33. *Procolophon trigoniceps*. Suborder Diadectomorpha, family Procolophonidae, Middle. Triassic, Procolophon zone, Upper Beaufort beds, Dist. Queenstown, Cape Colony, South Africa. After Watson.
34. *Pantylus cordatus*. Suborder Captorhinomorpha, family Pantylidae. Permo-Carboniferous, Lower Clear Fork, Texas. After Williston.
35. "*Pariasaurus*," sp. Suborder Diadectomorpha, family Pariasauridae. Middle Permian, Pariasaurus zone, Gough district, Hottentots River, Cape Colony, South Africa.

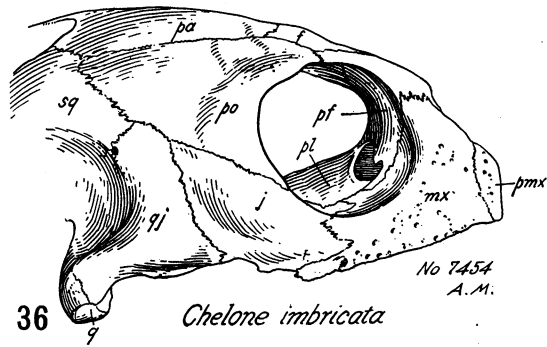
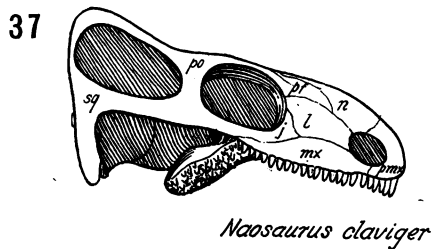
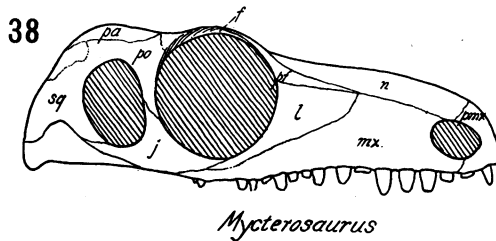
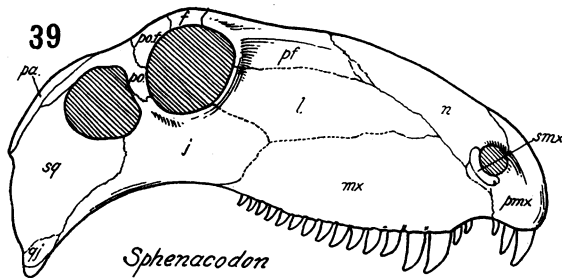


Fig. 36. *Chelone imbricata*. Class Reptilia, series Anapsida, order Testudinata, suborder Cryptodira, family Chelonidae.



Figs. 37 to 39. Skulls of Pelycosaurs. Class Reptilia, series Synapsida, order Pelycosauria.

37. *Naosaurus claviger*. Family Edaphosauridae. Permo-Carboniferous, Wichita beds, Texas. After Williston.
 38. *Mycterosaurus longiceps*. Family Poliosauridae (?). Permo-Carboniferous. Lower Clear Fork, Texas. After Williston.
 39. *Sphenacodon*. Family Sphenacodontidae. Permo-Carboniferous, New Mexico. After Williston.

Among the Pelycosaurs (Figs. 37-39) and their allies, as described by Williston, the lacrymal reaches the nares in *Varanops* and *Naosaurus*; but in *Mycterosaurus*, *Dimetrodon*, and other genera, through the upgrowth of the maxillary and the lengthening of the jaws in front of the orbit, it loses its connection with the nares and retains only a moderate extension on the face in front of the orbit.

Diapsid Reptiles

The next higher grade above the pelycosaurs and allied forms is represented by the group of thecodont reptiles with two temporal fenestræ, including the aëtosauræ, belodonts, crocodilians, dinosaurs, and pterosaurs, in all of which the prefrontals and the lacrymals are both present, and the lacrymal is always excluded from the nares by the upgrowth of the maxilla. A relatively primitive condition of the lacrymal in this series is illustrated in the type skull (Fig. 43) of *Euparkeria capensis* Broom (1913). "Here," writes Broom, "the lachrymal is an unusually large bone. It forms most of the anterior orbital margin. Above, it has a long articulation with the prefrontal, and below a short one with the jugal. Anteriorly it has a large development which forms the upper margin of the antorbital vacuity, meeting the ascending process of the maxilla. Of the anterior process much is below the level of the general surface of the face, suggestive of the antorbital vacuity having lodged a large gland. The prefrontal is a small narrow bone which forms about half of the upper orbital margin. It is bounded above by the frontal and nasal and below by the lachrymal."

The enlargement and fenestration of the lacrymal and the small size of the prefrontal is greatly emphasized in the saurischian dinosaurs, in which the prefrontal is greatly reduced or wanting, and the lacrymal enormously enlarged. In *Tyrannosaurus* (Fig. 42), for example, the lacrymal forms a huge V-shaped brace with its apex directed upward and backward, the anterior limb articulating with the nasals and the ascending process of the maxilla, the posterior limb resting on the jugal. It has been suggested¹ that the antorbital fenestra, which is bounded above and behind by the lacrymal, did not serve for the lodgment of a large gland, as supposed by Broom, but that its inner borders gave insertion to a huge pterygoid muscle, homologous with the pterygoideus anterior of Crocodilia, which extends forward beneath the lacrymal. This suggestion seems to be strengthened by the form and relations of the

¹1915, *Science*, XLI, pp. 763-765; 1919, *Ann. N. Y. Acad. Sci.*, pp. 154, 155.

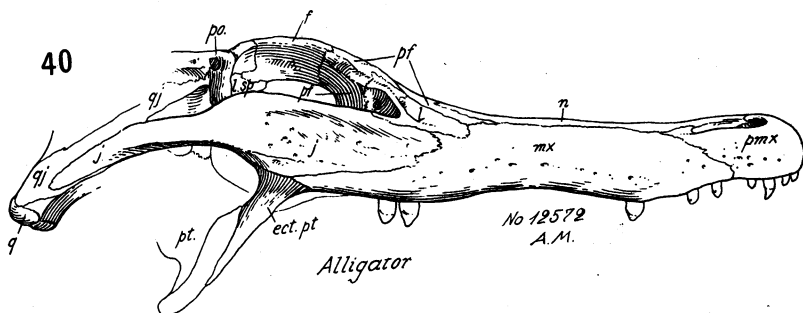
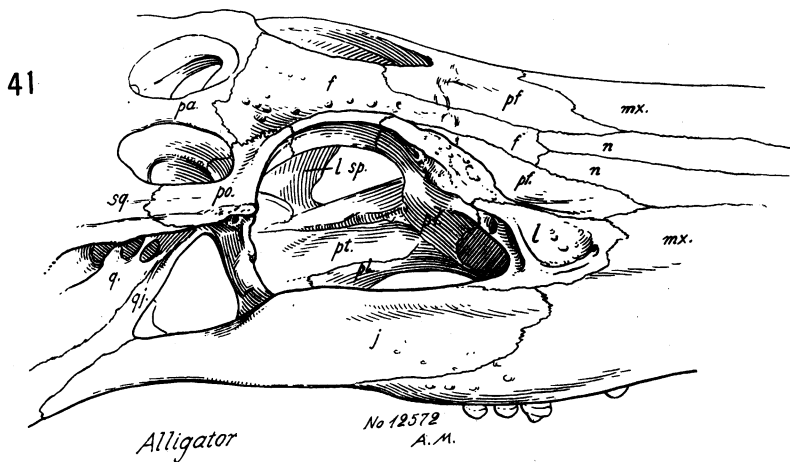
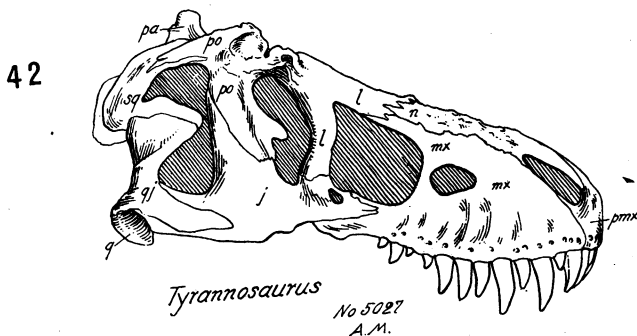


Fig. 40. Skull of *Alligator mississippiensis*. Class Reptilia, series Diapsida, order Crocodilia, suborder Eusuchia, family Alligatoridæ.

Fig. 41. As in Fig. 40, oblique side-top view.

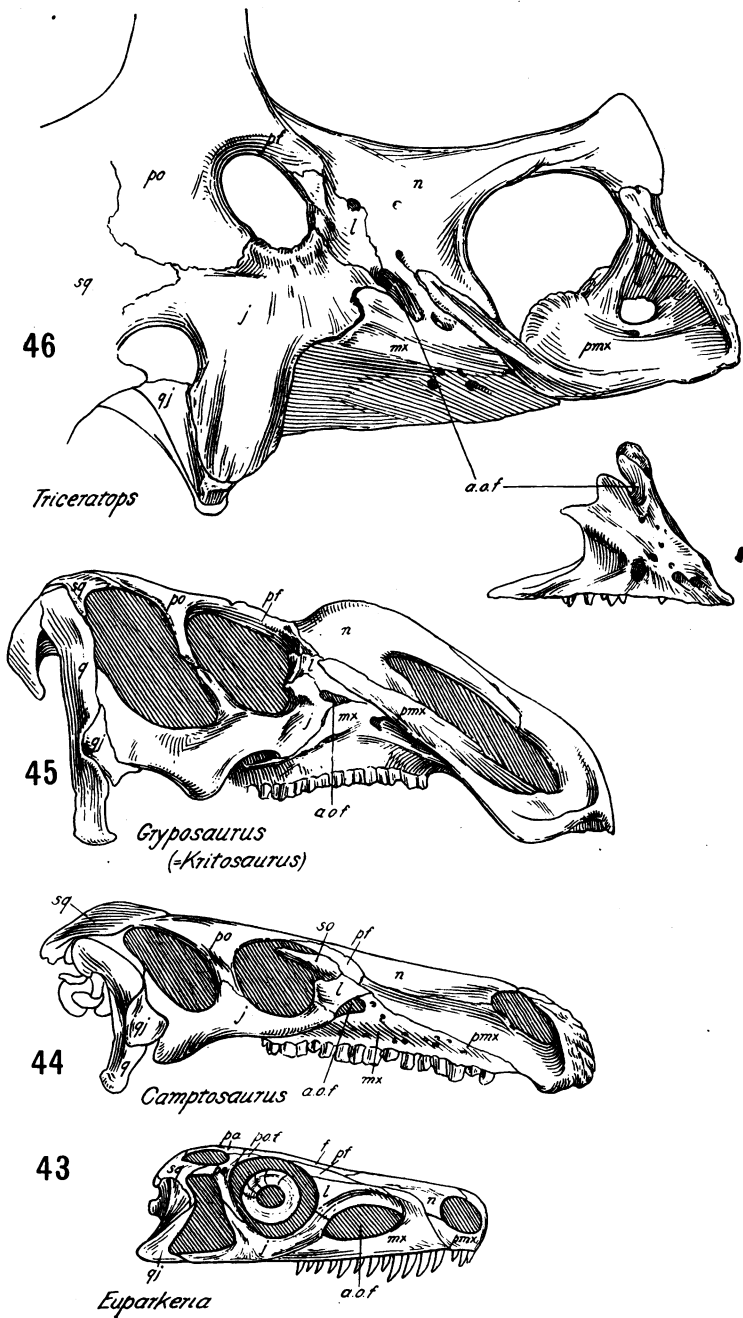
Fig. 42. *Tyrannosaurus rex*. Class Reptilia, series Diapsida, order Saurischia, suborder Theropoda, family Deinodontidæ. Late Cretaceous, Lance Formation, Hell Creek beds, Montana. After Osborn.

antorbital fenestra of *Mystriosuchus*, as figured by McGregor (1906, Pl. VII). Here the general resemblance of the antorbital fenestra to the lateral temporal fenestra, which is known to be a muscle fossa, is very evident. In any case the lacrymal in all the thecodont reptiles plays an important part as a brace between the upper jaw and the frontal region of the skull.

The typical Crocodilia have a well-developed lacrymal bone, which is pierced by the naso-lacrymal duct and usually retains the normal reptilian connections with the nasal, prefrontal, maxilla, and jugal. Owing to the presence of a large tunnel (Fig. 41) in front of the orbits for the pterygoideus anterior muscle, the lacrymal is restricted to the upper part of the face and is widely separated from the palatine bone below. In form, proportions, and other characters the lacrymal differs widely in the different genera and families of this order. Among the thalattosuchians (cf. Fraas, 1902), it is greatly reduced in size and the prefrontal is correspondingly enlarged, while in *Teleosaurus*, *Osteolemus*, *Tomistoma*, and most other Crocodilia it is much larger than the prefrontal. In *Diplocynodon* it is unusually large, in correlation with the widening of the snout. In *Alligator* (Figs. 40, 41) it loses its primitive contact with the nasals. In *Alligatorium meyeri* Jourdan, as figured by Lortet (1892, Pl. x), the lacrymal is essentially similar to that of *Alligator*, save that it retains a slight contact with the nasal.

The whole configuration of the facial elements of the relatively primitive ornithischian dinosaur *Camptosaurus* (Fig. 44), as figured by Gilmore (1909, p. 205), may readily be derived from the pattern in *Euparkeria* (Fig. 43) by a great increase in size of the premaxilla, which in turn was correlated with the development of a beak. This has crowded back the ascending process of the maxilla and greatly reduced the antorbital vacuity. In this way the premaxilla has gained contact with both the lacrymal and the prefrontal and has excluded the nasals from contact with the lacrymal. The reduced lacrymal, however, still borders the vestigial antorbital fenestra posteriorly and retains its primitive contact with the prefrontal above and the jugal below. Above it is a new derm bone, the presupraorbital, which attains a large size in *Stegosaurus*.

The pattern of the facial elements in *Iguanodon* (as figured by Dollo, 1883, Pl. ix) differs from that of *Camptosaurus* in the deepening of the maxilla, which is in wide contact with the nasals, and separates the premaxilla from the prefrontals. The antorbital fossa is almost vestigial and the lacrymal is now very small but retains its normal contacts with



Figs. 43 to 46. Skulls of a pseudosuchian (*Euparkeria*) and of typical ornithischian dinosaurs, showing the retraction of the lacrymal, the reduction of the ant-orbital fenestra, and the backward extension of the premaxilla in the Ornithischia.

43. *Euparkeria capensis*. Class Reptilia, series Diapsida, order Thecodontia, suborder Pseudosuchia, family Aëtosauridæ. Upper Triassic, Cynognathus zone, Burghersdorp beds, Cape Colony, South Africa. Natural size. After Broom.
44. *Camptosaurus*. Order Ornithischia, suborder Iguanodontia, family Camptosauridæ. Upper Jurassic, Morrison Formation, Wyoming. Composite restoration, after Gilmore. $\times \frac{1}{2}$.
45. *Gryposaurus* (= *Kritosaurus*) *notabilis*. Order Ornithischia, suborder Iguanodontia, family Trachodontidæ. Upper Cretaceous, Belly River formation, Alberta, Canada. After Lambe.
46. *Triceratops flabellatus*. Order Ornithischia, suborder Caratopsia, family Ceratopsidæ, Late Cretaceous, Lance Creek beds, Converse Co., Wyoming. After Hatcher.

the prefrontal, maxilla, and jugal (*op. cit.*, p. 234). As in *Camptosaurus*, the lacrymal is surmounted by a divergent presupraorbital bone.

In *Stegosaurus*, as figured by Gilmore (1914, Pl. v), the antorbital fenestra has been obliterated by the secondary spreading of the lacrymal, nasal, and ascending process of the maxilla. In general, the *Stegosaurus* face is closely related in its construction to that of *Iguanodon*.

In *Trachodon* the anterior nares are greatly enlarged, extending back to the lacrymals without, however, disturbing the primitive ornithischian relations of the lacrymal.

In the highly specialized crested trachodonts (figured by Brown and by Lambe) the nasal cavity is enlarged and prolonged backward on to the top of the skull, so that the premaxillæ and nasals extend far backward and upward; to some degree recalling the condition in the odontocetes among mammals. But, in spite of this, the lacrymal retains much of its primitive ornithischian position and connections. *Gryposaurus* (= *Kritosaurus*) *notabilis* Lambe (Fig. 45) shows the initial stage in the dorsal growth of the nasal region. Here the lacrymal is in contact with the prefrontal, premaxilla, maxilla, and jugal, as in the primitive *Camptosaurus*, but the presupraorbital bone appears to be absent. In *Stephanosaurus* (cf. Lambe, April 1914, Pl. 1), and still more in *Corythosaurus* Brown, the extraordinary enlargement and dorsal growth of the nasal chamber has conditioned a great expansion of the prefrontal, which covers the side of this chamber and now separates the lacrymal from the premaxilla.

In the Ceratopsia the lacrymal forms the stout anterior rim of the orbit and, together with the prefrontal bone, it transmits stresses from the postorbital horns downward to the stout jugal, forward to the nasal, and both downward and forward to the maxilla. In front of the wide jugo-lacrymal junction is a narrow fissure, directed forward and downward and located just below the narrow ascending process of the maxilla. On comparing this fissure in *Triceratops* (Fig. 46) with the homologous opening in *Monoclonius* and other ceratopsians and trachodonts, it appears to represent a vestige of the antorbital fenestra, lying between the maxilla and the lacrymal. In the relatively primitive *Brachyceratops montanus* Gilmore (1917, p. 15) the fissure in question is large and lies between the ascending and the jugal processes of the maxilla, exactly as does the small antorbital vacuity of *Camptosaurus*. The fissure is nearly

obliterated in *Stephanosaurus* and *Corythosaurus*, where it has no appearance of transmitting either nerves or blood vessels.¹

In conclusion, the pattern of the facial elements in the whole ornithischian series appears to be derived from the primitive fenestrate type represented by *Aëtosaurus*, *Ornithosuchus*, and *Euparkeria*, a result which is in harmony with the fact that the pelvis of *Euparkeria* distinctly foreshadows the ornithischian type.

In pterosaurs the anterior nares are extended dorsad and the premaxillæ have long ascending processes which articulate with the frontals between the enlarged prefrontals (called "lacrymals" by von Huene, 1914). The lacrymals, as shown in the skull of *Scaphognathus* figured by E. T. Newton (1888, Pls. LXXVII, LXXVIII), bound the large antorbital fenestræ dorsoposteriorly and are in contact below with the jugals. The elements which are interpreted as nasals by both Newton and von Huene are long, narrow strips which are lateral to the prefrontals.

According to von Huene (1913, p. 60) there is a separate supra-orbital, clearly defined by sutures on both sides, on the anterosuperior margin of the orbit. In the more specialized genus *Nyctosaurus*, as figured by Williston (1902) and von Huene (1914), the nares are confluent with the enlarged antorbital fenestræ and the lacrymals are fused with the prefrontals. According to von Huene there is also a supra-orbital bone. The nasals are greatly abbreviated.

As thus described, the circumorbital region of pterosaurs might perhaps be derived from the conditions figured in the aëtosaurian genus *Euparkeria* (Fig. 43), except for the anomalous position of the supposed nasals, which are chiefly lateral to the prefrontal. Newton and von Huene have noted the general resemblance of the orbital region of pterosaurs to that of birds.

Birds

In the whole class of birds the prefrontal is enlarged (Fig. 51) and simulates a mammalian lacrymal, since it transmits the lacrymal duct and is located at the anterosuperior quarter of the orbit. Hence it has often been called "lacrymal." Von Huene (1914, p. 61) regards the

¹For this reason, I would doubt the interpretation of this fissure as either an infraorbital foramen (Hatcher, Marsh, Lull, 1907, pp. 26, 27) or as a "lacrymal foramen" (*op. cit.*, Pls. XXXII, XXXIV, XLIV). The real homologue of the mammalian infraorbital foramen, according to Gaupp (1910), is the longitudinal series of foramina in the maxilla of recent reptiles, opening on the face above the tooth-row. These are named by Gaupp "foramina maxillo-facialia." They serve for the transmission of twigs of the maxillary nerve. A similar row or rows of vessels is present in the maxilla of many dinosaurs of both orders; they are very plain in the *Ceratopsia* and in the *trachodonts*. The fissure in question can hardly be the ductus naso-lacrymalis, which must lead from the orbit to the interior of the nasal chamber at a deep level, instead of opening in front on the side of the face.

upper part of this element as the homologue of the reptilian supraorbital. This identification may eventually be confirmed, especially in view of the general similarity of the dorsal part of the element in question to the true supraorbital of primitive ornithischian dinosaurs (Fig. 44). Nevertheless, in early stages of development, this bone, in struthious and other birds, has more the appearance of a true reptilian prefrontal, as shown in the figures by W. K. Parker (1869), T. J. Parker (1891), and Pycraft (1900). I, therefore, provisionally identify it as prefrontal rather than as lacrymal or as supraorbital.

Rhynchocephalida, Parapsida

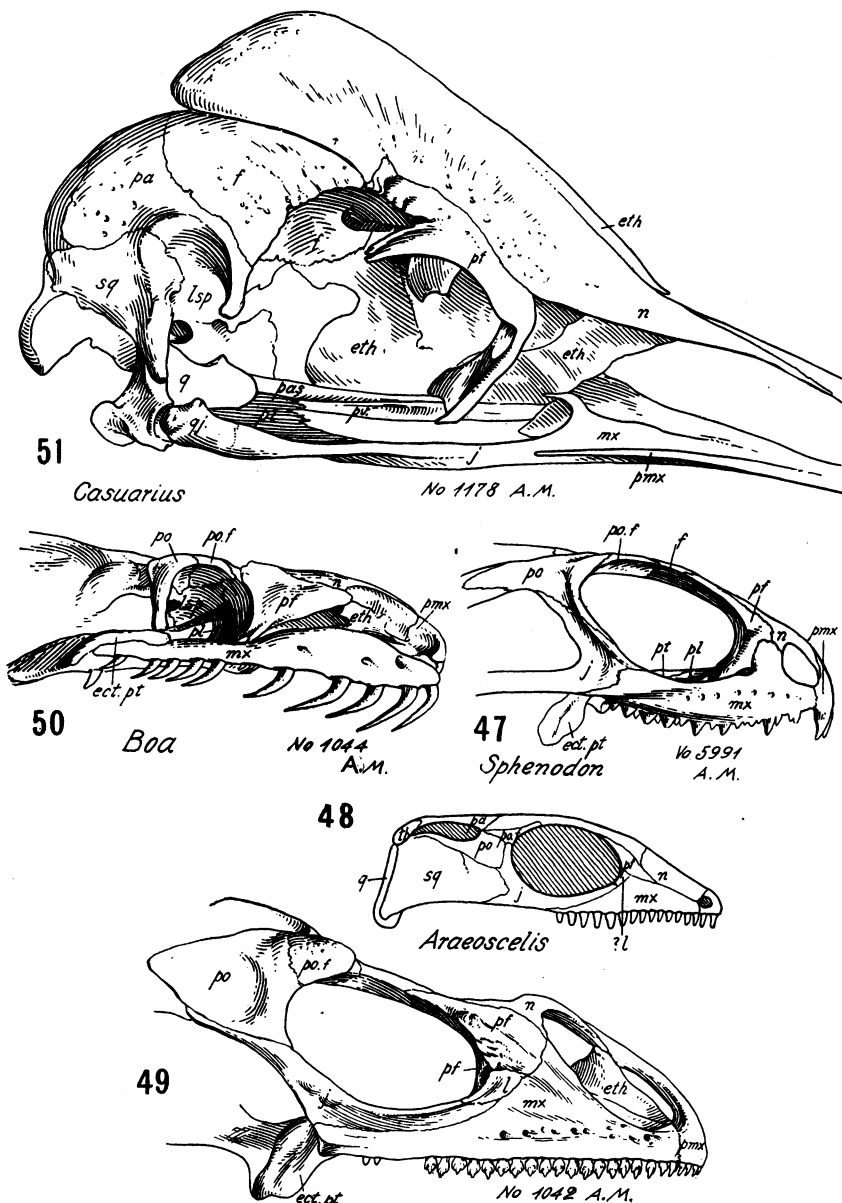
In the Triassic rhynchosaurian genus *Hyperodapedon*, according to Burckhardt (1900), a small lacrymal is present. It is separated from the prefrontal by the posterior tip of the enlarged premaxilla. In the allied *Stenomotopon* Boulenger (1903), the prefrontal alone forms the anterior brace between the enlarged maxilla and the frontals and the lacrymal is absent. Essentially similar conditions appear in the modern *Sphenodon* (Fig. 47). Here, as in so many other reptiles, the prefrontal is enlarged, forms the anterior brace of the orbit, and is in contact below with the palatine. It thus parallels in position and function the parethmoid of fishes. The lacrymal foramen lies between the prefrontal and the maxilla.

In *Champsosaurus*, of the group called Choristodera, the prefrontal shares in the elongation of the snout. A fair sized lacrymal is present, in contact with the prefrontal, maxilla, and jugal (Brown, 1905, Pl. III).

In *Palæohatteria* Credner, which Williston was inclined to relate to the Protorosauria and Squamata, the lacrymal, according to Credner's figures (1888, Pl. xxv), was of fairly primitive type, retaining its normal contacts with the prefrontal, nasal, maxilla, and jugal. According to Credner's Fig. 3, Pl. xxv, the lacrymal was just excluded from the orbital rim by a slight prefrontal-jugal contact.

In *Aræoscelis* Williston (Fig. 48), of the American Permian, enlargement of the orbit is associated with an apparent reduction of the lacrymal, the prefrontal usurping its contact with the nasal.

In *Sauranodon* and *Pleurosaurus* Lortet's plates show that the prefrontal was enlarged and probably the lacrymal was small or wanting. Watson (1914) states that in *Pleurosaurus* the lacrymal is a very small bone forming a part of the orbital boundary and wedged in between the prefrontal and maxilla. These reptiles were formerly referred to the Rhynchocephalia, but Boulenger, Watson and Williston have advanced cogent objections to this view and they are referred by Watson to the suborder Acrosauria von Meyer, of the order Squamata.



Figs. 47 to 51. Skulls of various Sauropsida showing reduction or absence of the lacrymal and its replacement by the prefrontal.

47. *Sphenodon (Hatteria) punctata*. Class Reptilia, series Rhynchocephalia, order Rhynchocephalia, family Sphenodontidae.
48. *Araucoscelis gracilis*. Class Reptilia, series Parapsida, order Squamata (?), suborder Araucoscelidia (?Protorosauria), family Araucoscelidae. Permo-Carboniferous, Clear Fork, Texas.
49. *Cyclura cornuta*. Class Reptilia, series Parapsida, order Squamata, suborder Sauria, family Iguanidae.
50. *Boa constrictor*. Class Reptilia, series Parapsida, order Squamata, suborder Ophidia, section Aglypha, family Boidae.
51. *Casuarus* sp. Class Aves, subclass Ornithura, order Megistanes, family Dromidae. Immature skull with many open sutures.

In many of the recent lizards (Fig. 49) the lacrymal is reduced sometimes to a vestige, while the enlarged prefrontal crowds it away from the nasals and partly appropriates the naso-lacrymal duct. As already noted, Gaupp (1910) emphasized the fact that in *Lacerta* the enlarged prefrontal overlaps the cartilaginous nasal capsule laterally and is medial to the naso-lacrymal duct. In these characters it agrees with the mammalian lacrymal, with which Gaupp homologized it. It also has other topographic relations often seen in mammalian lacrymals, namely, it articulates above with the frontal, below with the palatine, and in front with the enlarged maxilla; in *Lacerta* it is also separated from the nasal by the junction of the maxillary process of the frontal with the frontal process of the maxilla, as is the lacrymal in many mammals. In Iguanids the enlarged prefrontal is in wide contact with the nasals as it is in the anomodonts.

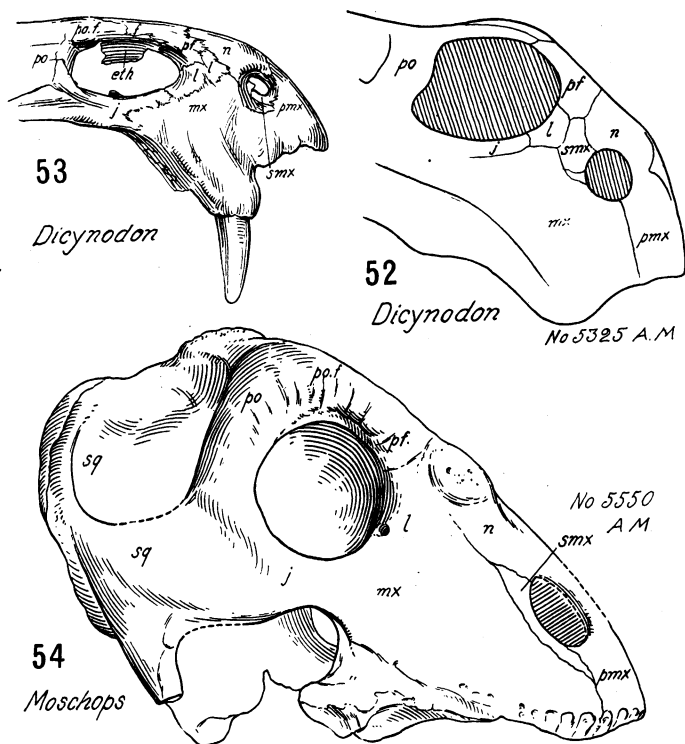
Nevertheless, it is highly probable that these resemblances are largely due to convergence, because a comprehensive review of the whole anatomy of lizards shows that they are genetically very far removed from the ancestors of the mammals, in contrast with the Therapsida, which finally approach the mammals in every part of the skeleton and in which there seems to be no room for doubt that the lacrymal, and not the prefrontal, is homologous with that of mammals.

The predominance of the prefrontals over the lacrymals, which is less marked in the monitors, attains its logical extreme in the snakes (Fig. 49), in which the lacrymal is entirely wanting.

THE LACRYMAL REGION IN THE THERAPSID REPTILES

The Therapsida (Figs. 52 and 57) are sharply distinguished from the more primitive Permian reptiles by the relatively small anterior extension of the lacrymal, which is overgrown anteriorly by a large ascending flange of the maxilla. Originally in this order the skull may have been short and the orbit located nearly half-way between the tip of the nose and the occiput, as it is in the Dromasauria and in the more primitive of the Dinocephalia. In the Dromasauria the lacrymal is crowded between the very large orbit and the enlarged maxilla; it is, however, in contact anteriorly with the septomaxilla and separates the maxilla from the nasals (Broom, 1914). Similar conditions prevail in the anomodont *Dicynodon* (Fig. 52). Here, according to Broom (1912, pp. 342, 343) the "lachrymal has a comparatively small facial portion, though it forms a considerably larger part of the inner wall of the orbit." Broom also notes the presence of a lacrymal foramen which, he states, is rather large and lies inside the orbit.

The most detailed and complete description of the lacrymal region of an anomodont is that by Igerna B. J., and W. J. Sollas (1913-1916) in their accounts of the structure of the skull of *Dicynodon* (Fig. 53), based on serial sections. The lacrymal contributes a vaulted lamina to



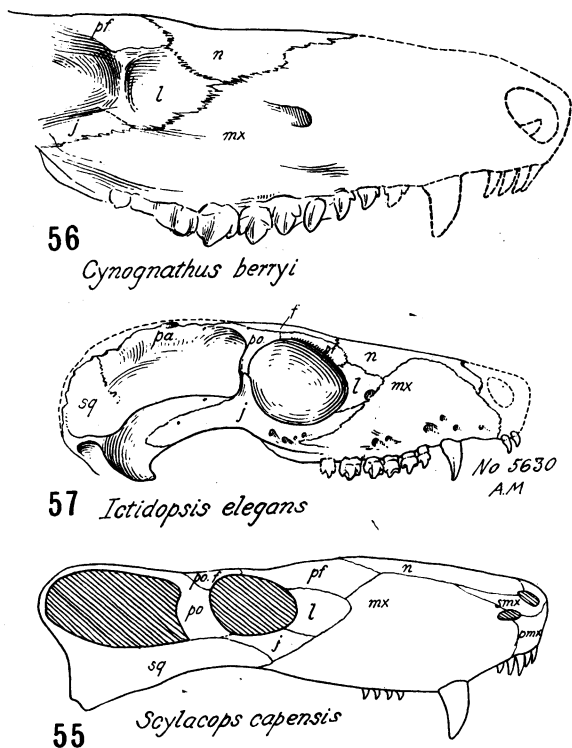
Figs. 52 to 54. Skulls of a Dinocephalian and two Anomodonts. Class Reptilia, series Synapsida, order Therapsida.

52. *Dicynodon moschops*. Suborder Anomodontia, family Dicynodontidae. Endothiodon zone, Beaufort beds of the Karroo system, Graaf Reinet district, Cape Colony, South Africa. After Broom.
53. *Dicynodon leoniceps*. Suborder Anomodontia, family Dicynodontidae. Middle Permian, Pariasaurus zone, Beaufort beds, Karroo system (from the Gough district) Cape Colony, South Africa. After I. B. J. and W. J. Sollas.
54. *Moschops capensis*. Suborder Dinocephalia, family Tapinocephalidae. Lower (?) Permian, "Horizon, not improbably Upper Ecca series." R. Broom. Karroo System, Cape Colony, South Africa.

the outer wall of the chamber surrounding the tusk. This vaulted lamina meets the prefrontal and is overlapped by the nasal, while its thickened outer wall is penetrated by the lacrymal duct, which leads downward and forward, opening into the nasal cavity (*op. cit.*, 1916, Pl. xxxvi,

fig. 7). The facial part of the lacrymal is in contact with the jugal, maxilla, nasal, and prefrontal.

Among the Dinocephalia, as figured by Broom and Watson, the lacrymal is in contact above with the nasal and prefrontal and below



Figs. 55 to 57. Skulls of a Gorgonopsian and two Cynodonts. Class Reptilia, series Synapsida, order Therapsida.

55. *Scylacops capensis*. Suborder Gorgonopsia, family Gorgonopsidae. Upper Permian, Cistecephalus zone, Beaufort beds, Cape Colony, South Africa. After Broom. $\times \frac{3}{4}$.
56. *Cynognathus berryi*. Suborder Cynodontia, family Galesauridae. Upper Triassic, Cynognathus zone, Upper Beaufort beds, Lady Mere, Cape Colony, South Africa. After Seeley, somewhat modified.
57. *Ictidopsis elegans*. Suborder Cynodontia, family Galesauridae. Upper Triassic, Cynognathus zone, Upper Beaufort beds, Harrismith, Orange River Colony, South Africa. Natural size.

with the maxilla and the jugal. The ascending flange of the maxilla is well developed, restricting the facial portion of the lacrymal anteriorly, separating the lacrymal from the extended septomaxilla and gaining contact between these two elements with the nasal. In the type of *Moschops capensis* Broom (Amer. Mus. No. 5550, Fig. 54) the lacrymal

is perforated on both sides of the skull by a large duct which opens on the face immediately in front of the orbit. In another skull of *Moschops*, however, this foramen is not visible.

In the Gorgonopsia (Fig. 55) the face is perhaps secondarily elongated, the vertical flange of the maxillary is greatly enlarged and deepened and the ascending process articulates with the prefrontal and covers the pars facialis of the lacrymal anteriorly. The prefrontal is large and separates the lacrymal from the nasal.

The lacrymal of the therocephalian *Lycosuchus vanderrieti* has been thus described by Broom (1902, p. 198): "The lachrymal is considerably shorter than the prefrontal, and fits in between the prefrontal, the maxillary, and the jugal. It has apparently only a single lachrymal canal, well within the orbit."

The lacrymal region of the Cynodontia has been noticed of late years especially by Broom (1911, 1914), Watson (1911)¹ and Haughton (1918). Broom states that in *Gomphognathus minor* the lacrymal forms the front of the orbit and much of its inner wall. In *G. polyphagus* it is considerably larger, extending to part of the upper margin of the orbit, almost as in primitive marsupials. In this species, also, the prefrontal is smaller than in others. The lacrymal in these forms, as well as in *Cynognathus* (Fig. 56), has a wide contact with the nasal. The lacrymal is especially well shown in the type of *Ictidopsis elegans* Broom (Amer. Mus. No. 5630), as in Fig. 57. The naso-lacrymal contact is wide and the facial part of the lacrymal is overlapped in front by the high ascending flange of the maxilla. A small lacrymal foramen lies immediately behind the lacrymo-maxillary junction. Possibly the latter may be homologous with the lateral lacrymal foramen of *Thylacinus*, the former with the medial lacrymal foramen of the same genus (Fig. 70.)

In *Cynosuchus whaitsi* Haughton, a very primitive cynodont from the Lower Beaufort Beds, structurally ancestral to *Diademodon*, the lacrymal forms most of the anterior border of the orbit and is in contact with the spreading nasal. "It is pierced just behind its suture with the maxilla by the lacrymal foramen, which communicates by a short canal through the bone with a foramen within the orbit. Within the orbit there is also another smaller foramen above the one referred to" (Haughton, 1918, p. 199). Haughton notes that the palatine of this remarkably mammal-like reptile is mainly a vertical bone; but it is not stated whether the palatine was in contact with the lacrymal on the inner wall of the orbit.

¹See addendum, p. 263.

Thus the Therapsida afford strong evidence for the traditional, or "Cuvierian," view that it is the lower of the two preorbital bones and not the upper, which is the homologue of the mammalian lacrymal. In the older and presumably more primitive Therapsida, such as the Therocephalia and the Gorgonopsia, the prefrontal is larger than the lacrymal, but in the cynodonts, which in all other characters approach the mammals, the lacrymal has increased in size, is pierced by the lacrymal canal and, like the lacrymal of primitive mammals, has firm contact with the jugal, the maxilla, and the nasal.

THE TRANSITION FROM REPTILIAN TO MAMMALIAN CONDITIONS

Owing to the imperfection of the palæontological record, the long ages of the Mesozoic yield but little direct palæontologic evidence as to the final emergence of the mammals from the therapsid stem and the subsequent modernization of the mammalian skull. On very sound and abundant morphological and physiological evidence it is believed, however, that the acquirement of a higher body temperature involved improved respiration, improved circulation and glandular activity, improved heat-conserving and heat-regulating structures, and above all a greatly advanced central nervous system—all of which doubtless conditioned the observed differences between cynodonts and mammals. In the facial region the cynodonts differ from the mammals chiefly in the retention of the prefrontal and postorbital bones. These doubtless dwindled and disappeared, along with several other elements of the skull, as the mammalian grade of organization was approached.

When the ascending ramus of the dentary became so large that it began to press down part of the temporal muscle-mass into a bursa or interarticular disc,¹ the diminishing quadrate and articular bones increased their auditory functions and their jaw-suspending function. Soon afterward the prefrontal and the postorbital probably disappeared² and the lacrymal and the maxilla came to form the sole anterior brace for the zygomatic arch.

One of the great advances connected with this general transformation of poecilotheimal reptiles into homœothermal mammals was the differentiation and spreading of the sphincter colli muscles. These,

¹According to B. Petronievics (1919, pp. 200-203) there is an "incipient condylar process" on the dentary of *Gomphognathus*, which possibly articulated with a "flat surface on the squamosal" behind it and thus either closely approximated to, or even fully exemplified, an early stage in the evolution of a "temporo-mandibular" joint like that of mammals.

²Dr. J. L. Wortman (1920, pp. 1-52) records the occurrence of "prefrontal," "postorbital," "quadrato-jugal," "quadrate" and other "reptilian elements" in the skulls of several modern mammals; but, for reasons which will be set forth elsewhere, I doubt the correctness of his identifications.

as Ruge (1897) has shown, invaded the facial region, carrying with them their primitive nerve, the facialis and its branches, and giving rise to the highly characteristic platysma group, or mimetic muscles, around the eyes, nose, and mouth. The lacrymal bone soon came into functional relations with some of these muscles, which henceforth exert considerable influence upon its subsequent evolution. Perhaps even in the therapsids (cynodonts) the ligament of the eyelids (ligamentum tarsale sive palpebrale) at the inner canthus of the eye may have been attached to the lacrymal bone, just above the orbital opening of the lacrymal duct. In primitive mammals the site of this attachment is marked by the lacrymal spine, or tubercle, while the preorbicularis dorsalis and ventralis muscles cover the facial surface of the lacrymal and are more or less connected with it by fascia. The inner surface of the lacrymal, especially the pars orbitalis, takes part with the frontals in separating the eye and its muscles from the ethmoid region. The lower part of the pars orbitalis articulates with the vertical plate of the palatine.

Through the loss of the prefrontal the lacrymal of mammals has acquired a wide contact with the frontal on the inner wall of the orbit and this contact is apparently never lost. In such primitive mammals as the opossum, which have stout zygomatic arches, the lacrymal serves as a keystone between the whole upper jaw and temporal arch on the one hand and the dermal skull roof on the other, as anyone may realize who will try to spring apart an opossum skull along the naso-maxillary junction. The lacrymal of mammals often articulates with the nasals; sometimes this contact appears to be secondary, but in certain marsupials it may well have been inherited from a cynodont ancestor. The lacrymal usually retains its primitive relations with the palatine, jugal, and maxillary, as well as with the naso-lacrymal duct. The latter is usually covered by a bony tube which primitively runs forward from the lacrymal along the inner wall of the maxillary and opens near the front end of the nasal cavity beneath the lower maxillo-turbinal.

Thus it will readily be seen that the lacrymal of mammals has relations with a considerable number of surrounding elements and that the course of its evolution has doubtless been influenced by changes in each one of these elements, as will be made clear on subsequent pages.

THE LACRYMAL REGION IN ALLOTHERIA, MONOTREMES
AND MARSUPIALS

Allotheria

The oldest known mammal of which the lacrymal region is known is *Tritylodon longævus* (Fig. 58) of the Lower Jurassic of South Africa, which Dr. Broom (1910) believes to be a multituberculate.¹ According to Broom, the lacrymal of this animal is a large element forming the anterior rim of the orbit and with a large preorbital extension. It articulates above with the very wide nasal, in front with the ascending lamina of the maxillary, and below with the stout jugal; it also extends widely on the inner wall of the orbit. Thus it resembles the lacrymal of *Gomphognathus* among the cynodonts in all its relations, except that it does not articulate with the prefrontal, which is lacking.

The Paleocene *Polymastodon taoensis* (Figs. 59, 60), as described by Broom (1914), has extremely wide nasals and small frontals, as in cynodonts, *Tritylodon*, *Ornithorhynchus*, and recent marsupials. The anterior orbital rim is formed, not by the lacrymal, which seems to be wanting, but by the enlarged maxilla, which meets the nasal above the orbit. The parietals send forward narrow processes which completely exclude the frontals from the orbit and even meet the nasals and maxillæ above it. These extraordinary conditions, which may readily be verified on the specimen Amer. Mus. No. 16321, are cited by Dr. Broom as evidence of remote relationship with the monotremes, along with the great reduction of the jugal and the supposed disappearance of the lacrymal.

Monotremata

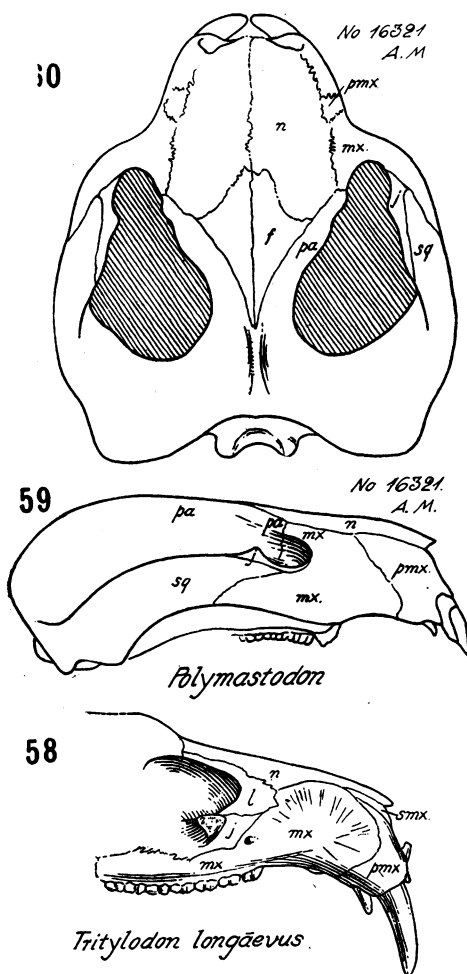
In the living monotremes (Figs. 61, 62) the lacrymal is absent.

Marsupialia

It has long been realized that the existing marsupials probably represent the survivors of an early and pre-placental adaptive radiation, beginning possibly as far back as the Jurassic and extending perhaps in the Cretaceous to Australia.

It has also been held by Huxley, Dollo, Bensley, and others, on morphological grounds, that the opossums represent in many but not all characters the little modified stem forms of the whole group—a conclusion which is further supported by the discovery of primitive

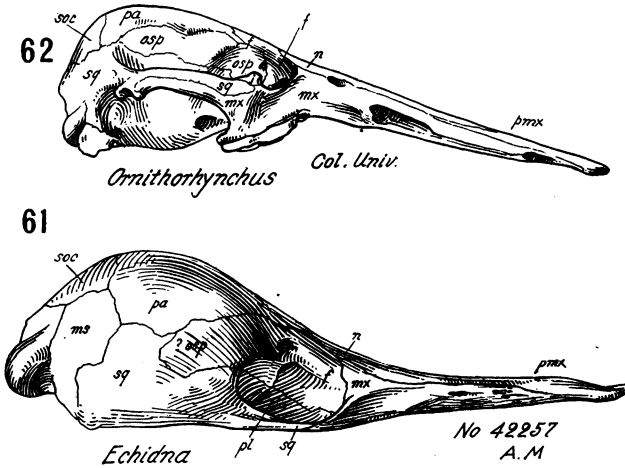
¹At first sight one might feel that there is still some justification for Seeley's view that *Tritylodon* was related to the gomphodont cynodonts. In *Trirachodon kannemeyeri* the lower canines become greatly elongate and pass upward into deep sockets in the upper jaw, the whole suggesting the relation of the enlarged upper and lower front teeth of *Tritylodon*. An important objection to this view, however, is that, according to Broom, the enlarged upper front teeth of *Tritylodon* are borne by the pre-maxillæ, while in *Trirachodon* they are certainly borne by the maxillæ.



Figs. 58 to 60. Skulls of *Tritylodon* and *Polymastodon*. Class Mammalia.

58. *Tritylodon longævus*. Subclass Prototheria, (?), order Multituberculata, family Tritylodontidae. Lower Jurassic, Stormberg beds, Basutoland, South Africa. After Broom.
59. *Polymastodon taoensis*. Subclass Paiotheria (?), order Multituberculata, family Plagiaulacidae. Paleocene, Polymastodon zone, Puerco formation, Ojo Alamo, New Mexico. After Broom.
60. *Polymastodon taoensis*. Dorsal view of skull. After Broom.

opossums in the Upper Cretaceous of North America (Matthew, 1916). Unfortunately, the lacrymal region of the type of *Eodelphis browni* Matthew is not known. The recent opossums are also noteworthy in the present connection because they retain many characters which may well be regarded as a direct heritage from primitive cynodonts. One of these is the wide-spreading nasals (Fig. 63) and another is the form of the



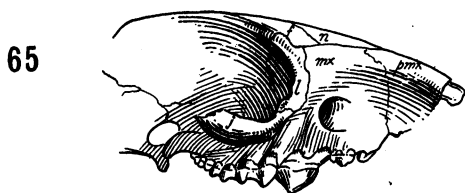
Figs. 61 to 62. Skulls of Monotremes. Class Mammalia, subclass Prototheria, order Monotremata.

61. *Echidna* (= *Tachyglossus*) sp. Family Echidnidae. Young skull showing sutures.

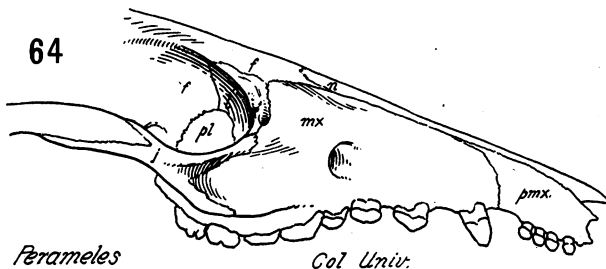
62. *Ornithorhynchus*. Family Ornithorhynchidae. Sutures restored after Watson and van Bemmel.

maxillary bone as seen from the outside, as it curves upward toward the nasals. In *Didelphis*, *Chironectes*, *Marmosa*, and other opossums this ascending blade of the maxilla is not so much developed posteriorly as it is in most mammals, so that it gains only a narrow and rather variable contact with the frontals, in contrast with the wide fronto-maxillary contact of primitive placentals. Beneath the frontal process of the maxilla the lacrymal often nearly or quite reaches the widely spreading nasals, a condition which may be a remnant of the wide lacrymo-nasal contact of the cynodonts. The lacrymal of the opossums is extended dorsally toward the superior border of the orbit but is not so distinctly rimmed above as it is in most marsupials. The pars facialis is rather small and the large lacrymal foramen is marginal, as it is in many marsupials.

Among the Borhyænidae of the Santa Cruz formation perhaps the most primitive conditions are preserved in the genus *Amphiproviverra*



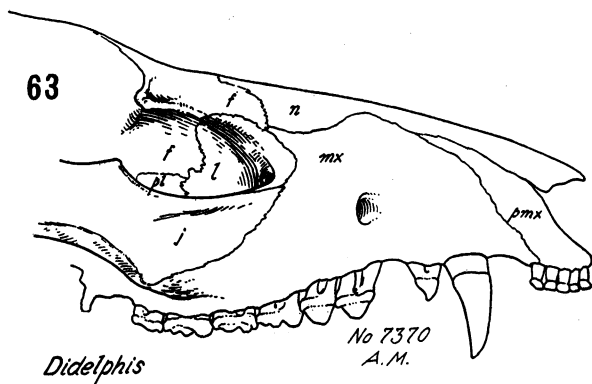
65

Palaeothentes intermedius

64

Perameles

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63

*Didelphis*No 7370
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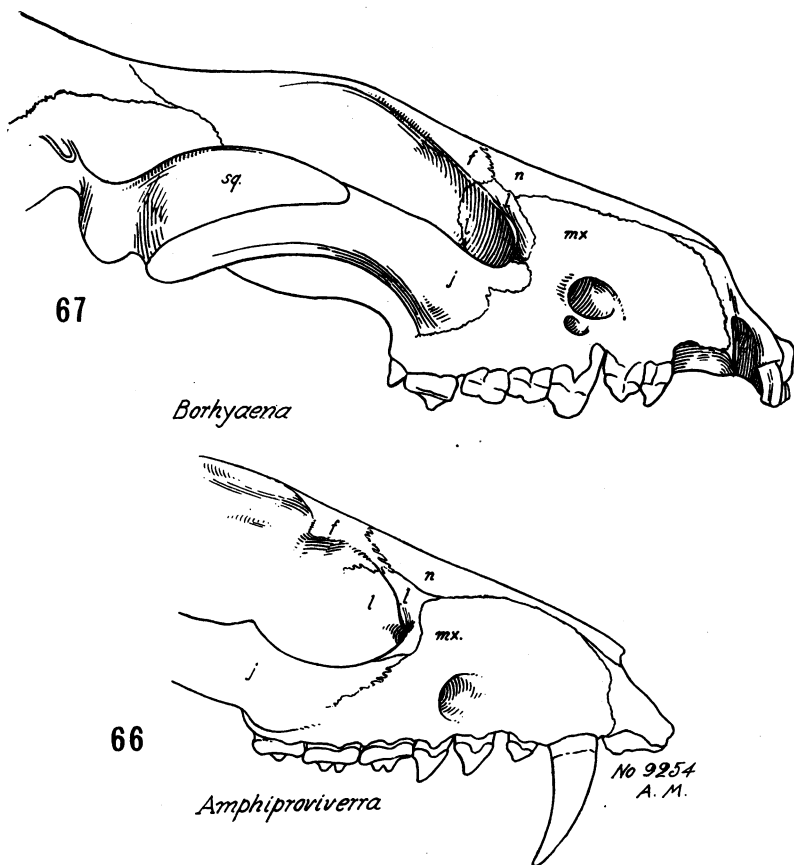
Figs. 63 to 65. Skulls of Polyprotodont Marsupials. Class Mammalia, subclass Metatheria, order Marsupialia, suborder Polyprotodontia.

63. *Didelphis virginiana*. Family Didelphyidae.

64. *Perameles* sp. Family Peramelidae.

65. *Palaeothentes intermedius*. Family Palaeothentidae (Epanorthidae). Middle (?) Miocene, Santa Cruz Formation, Patagonia. After Sinclair.

(Fig. 66); here the lacrymal differs from that of *Dasyurus* in that it has a more prominent orbital rim and a larger pars facialis, which is in wide contact with the spreading nasals. The foramen is within the antorbital border. In *Borhyaena* the pars facialis is of small to moderate size. In *B. tuberata* (Fig. 67) there is a wide naso-lacrymal contact (Sinclair,

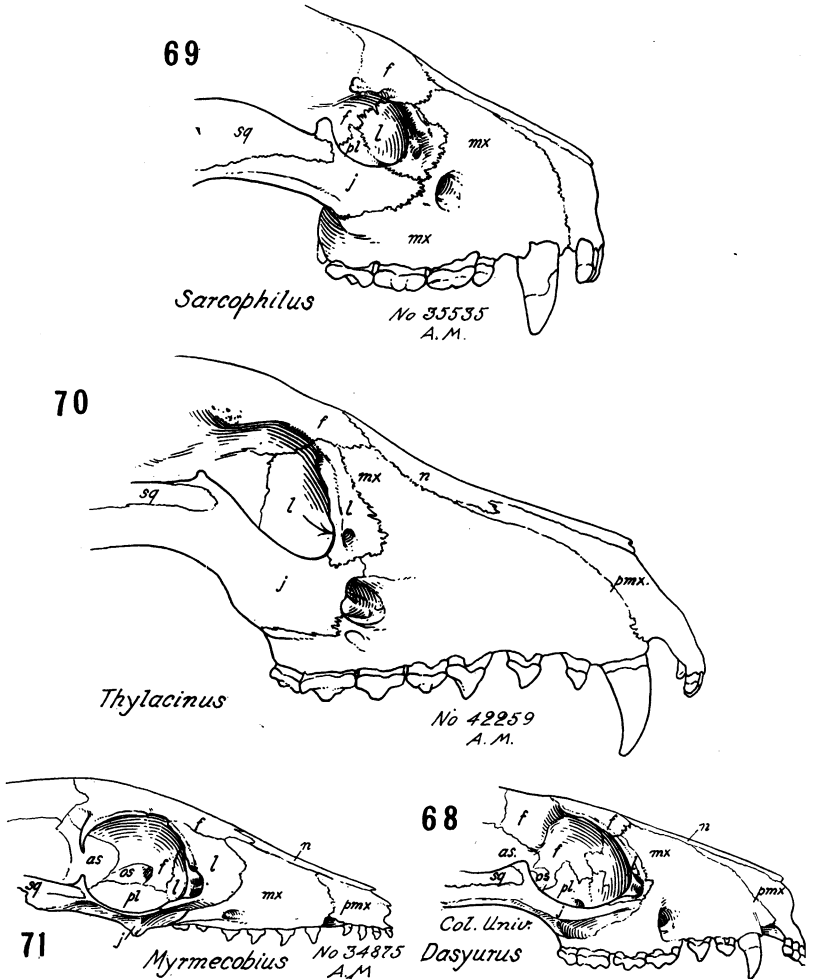


Figs. 66 to 67. Skulls of Polyprotodonts (continued).

66. *Amphiproiverra* sp. Family Borhyænidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.
 67. *Borhyaena tuberata*. Family Borhyænidae. Middle (?) Miocene, Santa Cruz formation, Patagonia. After Sinclair.

1901, Pl. XL) but in *B. excavata* the tip of the maxilla just reaches the frontals and slightly separates the nasals from the lacrymals (idem, Pl. XLV).

In *Dasyurus* (Fig. 68) the lacrymal rim is continuous with the superior border of the orbit. In *Sarcophilus* (Fig. 69), in which the skull is extremely robust and the muzzle very coarse but rather short, the



Figs. 68 to 71. Skulls of Polyprotodont Marsupials (continued).

68. *Dasyurus viverrinus*. Family Dasyuridae, subfamily Dasyurinae.
 69. *Sarcophilus ursinus*. Family Dasyuridae, subfamily Dasyurinae.
 70. *Thylacinus cynocephalus*. Family Dasyuridae, subfamily Dasyurinae.
 71. *Myrmecobius fasciatus*. Family Dasyuridae, subfamily Myrmecobiinae.

lacrymal is of moderate size and has but a moderate extension on the face. The lacrymal foramen is external, on the pars facialis immediately in front of the orbit. In the long-faced *Thylacinus* (Fig. 70) the facial

part of the lacrymal is extended. The lacrymal is expanded superiorly and bears a prominent orbital rim. The main foramen is internal to the rim, but there is another foramen on the pars facialis which leads straight inward to the lacrymal duct. This outer foramen may well be homologous with the single foramen of *Sarcophilus*.

In *Perameles* (Fig. 64) the conformation of the lacrymal region is evidently related to the typical condition of the Dasyuridæ. Although the snout is elongate, the facial part of the lacrymal is very small. The narrow nasals are widely separated from the lacrymals by the wide maxillo-frontal contact. The ethmoid scrolls are expanded and so is the maxillary antrum.

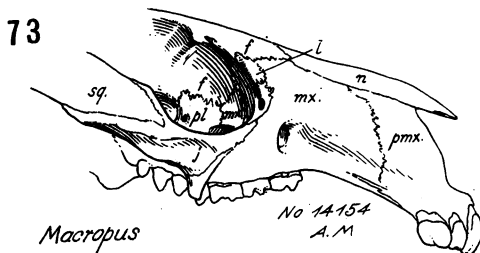
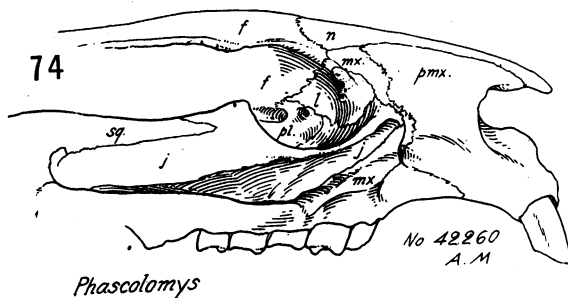
Myrmecobius (Fig. 71) has sometimes been regarded as related in a very special way to the Mesozoic mammals and Wortman (1903, p. 407) assumes that its lacrymal region is primitive. The whole snout is tubular, the ethmoid folds are expanded, and in correlation with this the frontals are widely expanded anteriorly, pushing the lacrymals outward upon the zygomatic arches. The lacrymals are also inflated, as they are in the Menotyphla and other forms with similar construction of the snout and ethmoid region. The pars facialis, as in all such forms, is extended. The dorso-anterior orbital rim of the lacrymal is unusually well developed. The foramen occupies its primitive position behind the antorbital rim. From a study of the basicranial region and other parts of the skull, the writer would endorse the conclusion of Bensley (1903) that *Myrmecobius* is only a specialized dasyurid. Hence its lacrymal region is not as primitive as it is in *Dasyurus*.

Among the diprotodonts perhaps the most primitive construction of the lacrymal region is seen in the early Tertiary genus *Wynyardia* (Fig. 72) of Baldwin Spencer (1900, Pl. L). The lacrymal is extended dorsally over the orbital surface of the frontal and is in contact with the nasal, excluding the maxilla from contact with the frontal. It has a prominent orbital rim and the pars facialis is short. The foramen is located on the pars facialis on the edge of the orbital rim.

Similar types of lacrymal are seen in the modern phalangers and their allies and in the Macropodidæ (Fig. 73). The maxillo-frontal contact varies in extent, but is well developed in the Macropodidæ. In *Halmaturus* the beautiful dissections of Boas and Paulli (1908, Pl. XIII) show that the orbital tubercle, or rim, serves dorsally for the attachment of the fascia covering the temporal mass and ventrally for the attachment of the palpebral ligament. The facial muscles are less differentiated than in placental mammals and clearly suggest their connection with the

platysma muscle. This furnishes additional evidence of primitive conditions in the lacrymal region of marsupials.

In the beaver-like *Phascolomys* (Fig. 74) the great enlargement of the anterior part of the masseter muscle and the consequent outgrowth and dorsal shifting of the anterior part of the zygomatic arch has crowded the lacrymal dorsad and conditioned its reduction in size. The tubercle



Figs. 72 to 74. Skulls of Diprotodont Marsupials. Class Mammalia, subclass Metatheria, order Marsupialia, suborder Diprotodontia.

72. *Wynyardia bassiana*. Family uncertain. Tertiary of Table Cape, Tasmania. After Baldwin Spencer.

73. *Macropus* sp. Family Macropodidæ.

74. *Phascolomys ursinus*. Family Phascolomyidæ.

for the attachment of the palpebral ligament is exceptionally prominent. There is a wide contact with the extremely wide nasals.

The lacrymal region of *Cenolestes* is well shown in two skulls kindly loaned by Dr. W. H. Osgood (Field Mus. Nos. 18602, 18605). In general, the nearest resemblance is with *Perameles*, but the lacrymal is smaller

and has a less well defined orbital crest. The foramen is marginal. The lacrymal is widely separated from the nasals by the maxillo-frontal contact.

In *Palæothentes intermedius* (Fig. 65) of the Santa Cruz formation (Sinclair, 1901, Pl. LXIII, fig. 3) the lacrymal is extended vertically, forming a prominent antorbital rim. It is in contact with the jugal below, with the maxilla in front and with the frontal above; it is separated from the spreading nasal by the fronto-maxillary contact. The lacrymal of *Palæothentes* is thus distinctly more primitive than that of *Cænolestes*, as it is more extended dorsally and forms a more projecting antorbital rim; it also retains a little of the pars facialis near the upper end.

Thus the marsupials as a whole are characterized by the somewhat primitive condition of the lacrymal, which is expanded dorsally, bears a prominent orbital rim and primitively has a small or moderate pre-orbital extension; the foramen is primitively marginal but a second extra-orbital foramen may be present. The fronto-maxillary contact, very small in many opossums, is well developed in many advanced types. The proximal ends of the nasals spread widely and are often in contact with the lacrymals. The primitive contacts with the frontal, maxillary, and jugal are retained; contact with the orbital plate of the palatine, although retained in *Didelphis*, *Sarcophilus*, *Thylacinus*, and *Amphiproviverra*, was replaced by a maxillo-palatine contact in *Phalangista*, *Bettongia*, *Halmaturus*, and *Phascalomys*.

THE LACRYMAL REGION IN THE PLACENTAL ORDERS OF THE PALEOCENE, EOCENE, AND LATER EPOCHS

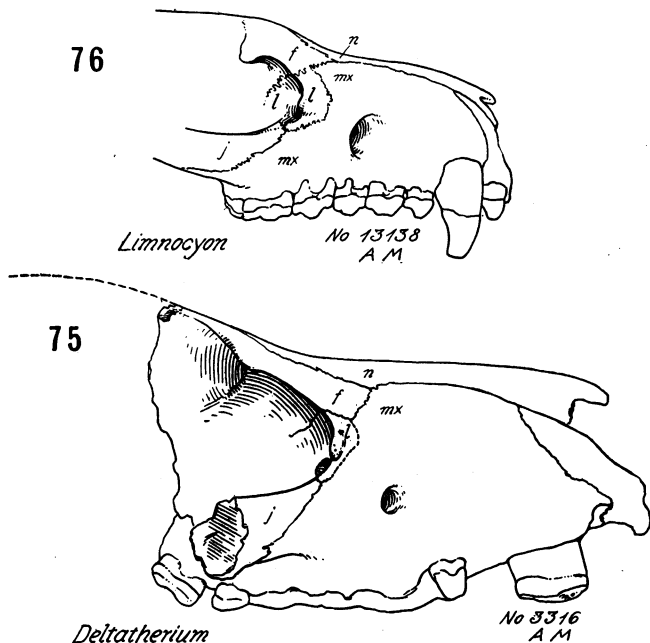
After a long hiatus in our record of the lacrymal during the latter half of the Age of Reptiles, the palæontological record for placental mammals begins in the Paleocene of Europe and North America, by which time most if not all of the placental orders had become well differentiated from each other.

Creodonta

The less specialized creodonts have always been recognized as being very primitive placental mammals, in the construction of the dentition, of the skull, and of the skeleton.

The lacrymal region of various Middle and later Eocene creodonts has been described by Dr. J. L. Wortman (1901, 1902) and by Dr. W. D. Matthew (1907) and is well shown in some exceptionally well preserved skulls in this Museum.

In the very primitive Paleocene *Deltatherium fundaminis* (Fig. 75) the pattern of the lacrymal region is one of the most primitive known among placental mammals. The lacrymal forms part of the distinctly raised anterior rim of the orbit and apparently preserves all its primitive contacts with surrounding elements; it has a moderately developed pars



Figs. 75, 76. Skulls of Creodonts. Class Mammalia, subclass Placentalia, order Carnivora.

75. *Deltatherium fundaminis*. Suborder Procreodi, family Oxyclenidae. Paleocene, Torrejon formation, New Mexico.

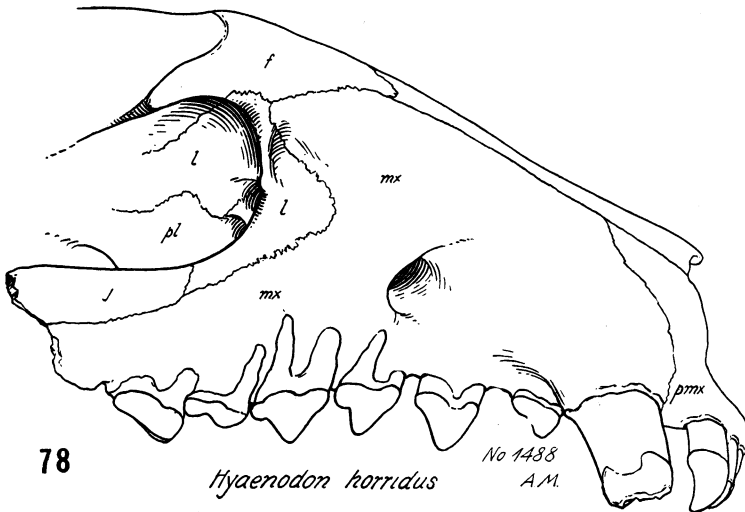
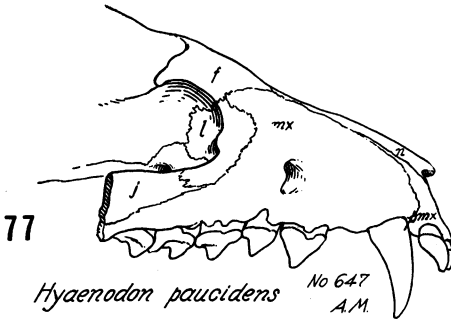
76. *Limnocyon potens*. Suborder Pseudocreodi, family Oxyænidae. Middle Eocene, Lower Bridger, Wyoming.

facialis, a marginal tubercle, with the foramen immediately behind it; there is a good fronto-maxillary contact. The exposed proximal end of the nasals is narrow. The skull was macrosomatic with heavy muzzle, rather small orbits, stout zygomata and unexpanded cranium. The eyes were directed outward and the anterior rims of the orbits were located above m^1 .

In *Limnocyon potens* Matthew (Fig. 76) of the family Oxyænidae essentially identical conditions obtain, except that the pars facialis of the lacrymal is perhaps somewhat larger. *Thinocyon velox* Matthew is a

small member of this family in which the lacrymal region is essentially similar. The maxillary is recessed for the pars facialis and the lacrymal extends well dorsad. The anterior edge of the orbit is above p^4 .

Among the Hyænodontidæ the lacrymal region is perfectly shown in a beautifully preserved skull of *Hyænodon paucidens* Osborn and Wort-



Figs. 77, 78. Skulls of Creodonts (continued).

77. *Hyænodon paucidens*. Suborder Pseudocreodi, family Hyænodontidæ. Middle Oligocene, Oreodon zone, Lower Brule formation. South Dakota.

78. *Hyænodon horridus*. Middle Oligocene, Oreodon zone, Lower Brule formation, South Dakota.

man (Fig. 77); the pars orbitalis is expanded dorsally; the pars facialis is large. The foramen is just medial to the tubercle. The vertical plate of the palatine has the normal carnivore connections with the lacrymal and maxilla. In *Hyænodon horridus* (Fig. 78) the lacrymal region is

similar, save that the pars facialis is somewhat more extended. In *Apterodon*, also, the pars facialis is extended but the orbits are not well rimmed.

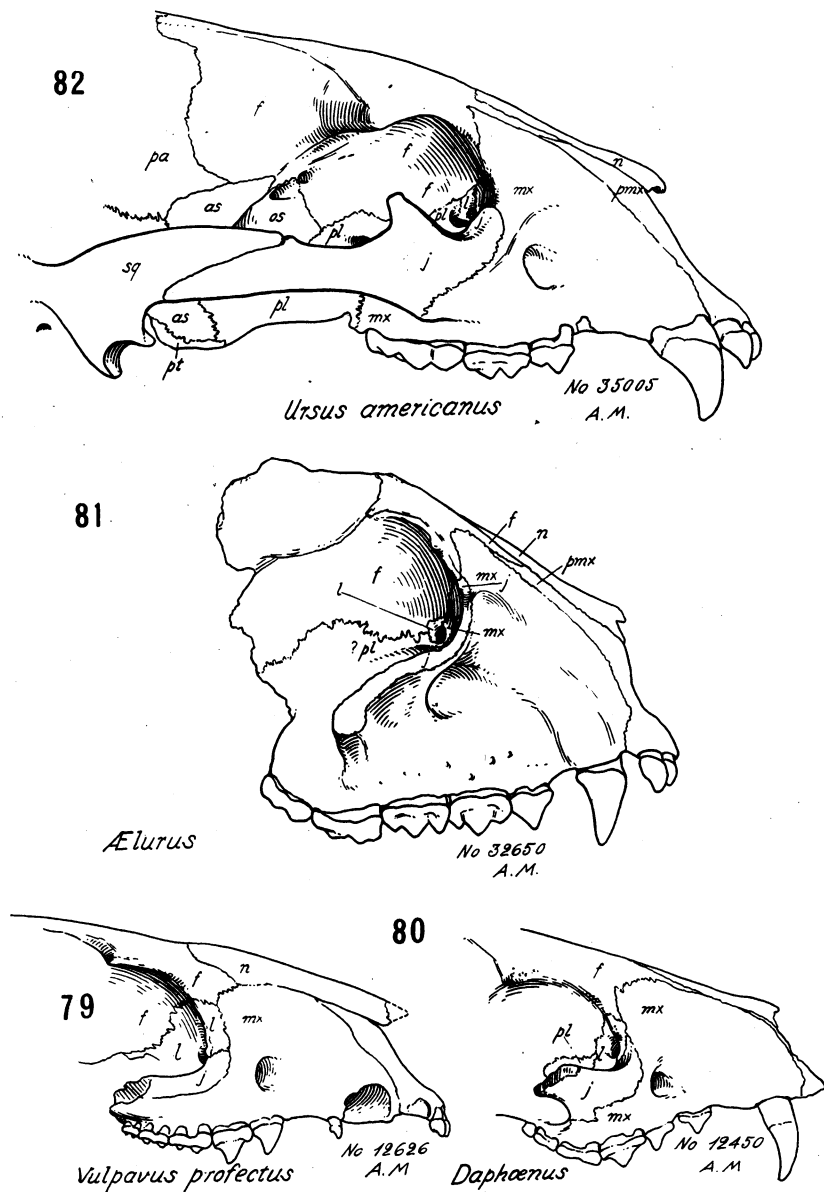
Among the Mesonychidæ the Middle Eocene *Dromocyon* (Wortman, 1901, Pl. IV) shows a very primitive condition of the lacrymal region. Possibly in connection with the backward position of the orbit, the lacrymal is large and bears a well-raised ridge to form the anterior rim of the orbit; the pars facialis is of moderate extent; the foramen is marginal. All the normal contacts with the frontal, maxillary, and jugal are retained. The fronto-maxillary contact is narrow and barely separates the lacrymal from the spreading nasal. The anterior rim of the orbit is quite far back above m^2 . On the whole, this is perhaps the most marsupial-like lacrymal region in all the placentals. In the Upper Eocene *Harpagolestes* the pars facialis is widely extended. Thus the wide extension of the pars facialis, as in the later Mesonychidæ and Hyænodontidæ, is probably a progressive character, while the ancestral creodonts of the Upper Cretaceous may well have had only a moderately developed pars facialis as in *Deltatherium*.

The extension of the pars facialis probably implies in the creodonts, as it does in the artiodactyls, that the inner canthus of the eye was extended forward, together with the orbicularis palpebrarum, preorbicularis dorsalis and p. ventralis muscles. This would cause the eyes to be directed widely outward in contrast with the more forwardly directed eyes of fissipede carnivores.

Fissipedia

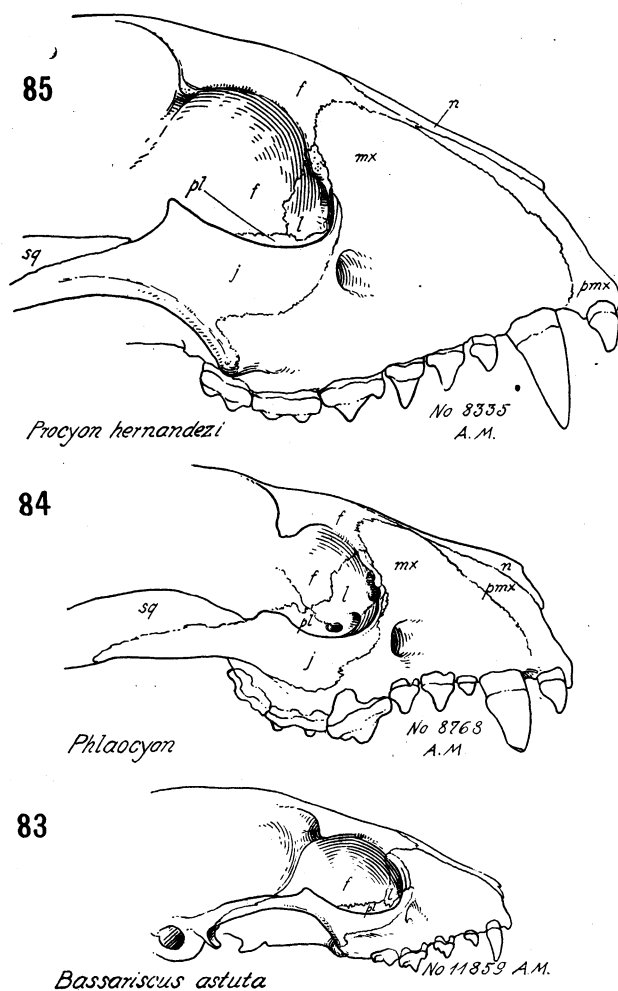
The lacrymal of the typical Fissipedia contrasts widely with the above described conditions in the creodonts, since it has little or no pre-orbital extension, the whole bone is never very large, and sometimes (as in *Ælurus*, Fig. 81) is reduced almost to a vestige, which is crowded into the antero-internal corner of the orbit and lacks its primitive dorsal extension. The lower anterior border of the orbit is often formed chiefly by the jugal and the maxillary. This condition is correlated in part with the forwardly directed position of the eyes in modern carnivores. When the true lacrymal tubercle is reduced or absent as in *Lutra* (Fig. 96), a substitute is developed from the maxilla.

At least the more advanced Miacidæ of the Eocene relate as clearly to the Fissipedia in the lacrymal region as they do in the dentition. In *Vulpavus* (Fig. 79) the lacrymal is much smaller than in the contemporary Creodonta Inadaptiva and has only a small pars facialis which does not



Figs. 79 to 82. Skulls of Carnivora.

79. *Vulpavus profectus*. Suborder Eucreodi, family Miacidæ. Middle Eocene, Orobippus zone, Lower Bridger, Bridger basin, Wyoming.
80. *Daphenus* sp. Suborder Arctoidea, family Canidæ. Middle Oligocene, Oreodon zone, Brule formation, South Dakota.
81. *Elurus fulgens*. Suborder Arctoidea, family Procyonidæ.
82. *Ursus americanus*. Suborder Arctoidea, family Ursidæ.



Figs. 83 to 85. Skulls of Procyonidæ. Subclass Placentalia, order Carnivora, suborder Arctoidea.

83. *Bassariscus astuta*.

84. *Phlaocyon leucosteus*. Lower Miocene, Promerycochærus zone, Martin Cañon beds, Colorado.

85. *Procyon hernandezii*.

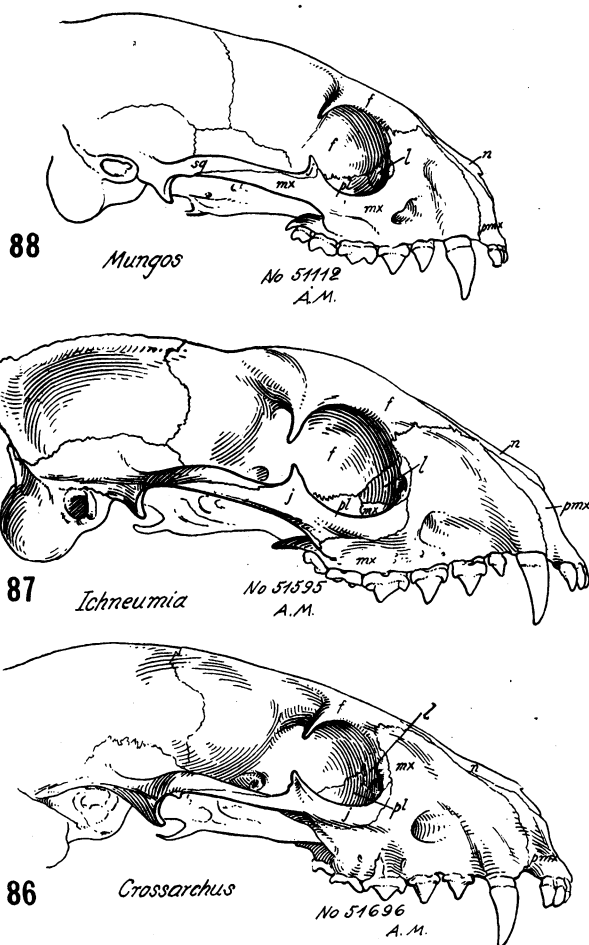
extend beyond the anterior limit of the jugal. The foramen is just behind the low anterior rim of the orbit. The anterior rim of the orbit lies above the fourth upper premolar in *Vulpavus*, as it does also in the creodonts, *Thinocyon*, *Limnocyon*, *Apterodon*, and *Hyænodon*. Hence we cannot ascribe the contrasting condition of the lacrymal in *Vulpavus* and these creodonts to any assumed differences in the position of the orbits with reference to the upper jaw.

Viverravus minutus Matthew is a very small insectivore-like miacid with a long cylindrical skull, very slender zygomata and no orbital ridges. It shows how typical carnivores may give rise to insectivore-like types. The lacrymal region seems to be normal.

In *Cynodictis* of the Canidæ the pars facialis is greatly reduced and the same is true of many other Tertiary and modern fissipeds. In this and other primitive Canidæ, e. g. *Daphænus* (Fig. 80), the lacrymal has a dorsal process which forms part of the orbital rim, and similar conditions are retained in the very primitive genus *Bassariscus* (Fig. 83) of the Procyonidæ. In *Phlaocyon* (Fig. 84), *Procyon* (Fig. 85), and *Nasua* the small orbital rim of the lacrymal bears a small bead-like tubercle. In *Cercoleptes* the lacrymal is very small and in *Ælurus* (Fig. 81) it is vestigial. The last two genera also show similar relations of the jugal and maxilla in this region. In *Æluropus*, according to Lankester's plates (1901), the lacrymal, if present at all, must be very small and confined to the inner wall of the orbit, as it is in *Ælurus* and *Ursus*.

In the Ursidæ (cf. Fig. 82) the lacrymal is much reduced, sometimes almost vestigial, and has usually been withdrawn entirely from the anterior rim of the orbit to the medial surface of the large lacrymal duct. It is thus more or less widely separated from the jugal by the maxilla, which has usurped the place of the lacrymal, and often bears a tubercle for the tarsal ligament. The lacrymal in this family, like other vestigial structures, is more or less variable in form and position. For example, on the left side of a skull of *Ursus malayanus* (Amer. Mus. No. 296) the lacrymal sends a thin flange forward and outward to the anterior margin of the orbit; on the right side it lacks this flange and is restricted to the medial wall of the lacrymal tunnel. In one specimen of *Ursus horribilis alexandræ* (Amer. Mus. No. 16702) the lacrymal on the left side appears to have a considerable dorsal extension on the inner wall of the orbit. In the skull of a Polar Bear (*Ursus maritimus*, Amer. Mus. No. 19259) the very small lacrymal is excluded from contact with the palatine by a process of the maxilla, and the same is true in *U. malayanus* (Amer. Mus. No. 296). But at least in certain skulls of *Ursus americanus* (Fig. 82) and *Ursus horribilis* the lacrymal is in contact with the palatine.

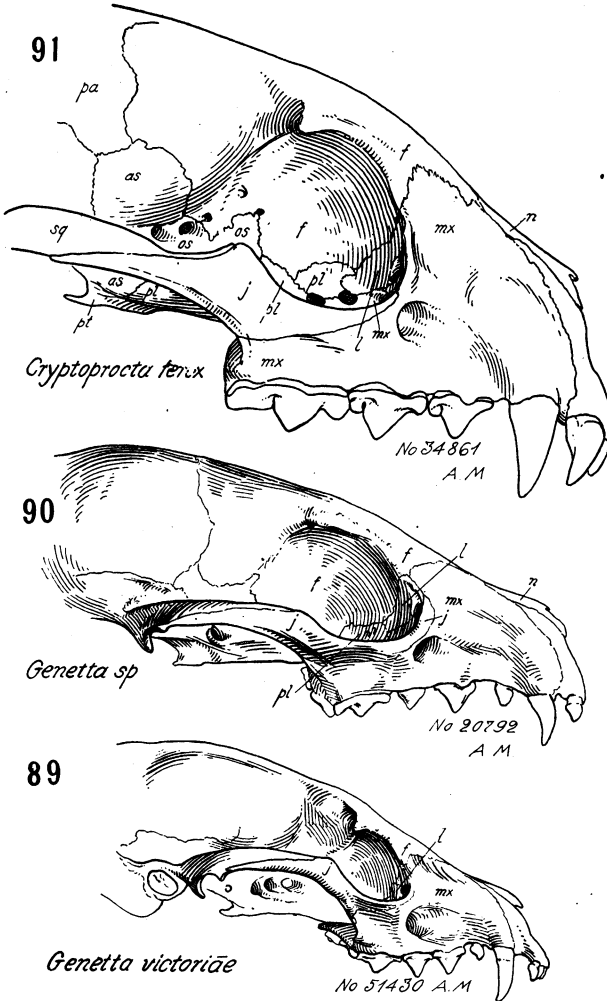
Constant features of the Ursidæ are the great forward extension of the palatine on the inner wall of the orbit and the presence of a large foramen or tunnel, usually between the palatine and the lacrymal and



Figs. 86 to 88. Skulls of Viverridæ. Subclass Placentalia, order Carnivora, sub-order Æluroidæ, family Viverridæ.

immediately behind the lacrymal foramen. This tunnel, like the last-named structure, leads downward into the nasal chamber and at first looks like a second lacrymal foramen, but it is sometimes subdivided (e. g., *U. maritimus*, Amer. Mus. No. 19259) into several openings, which

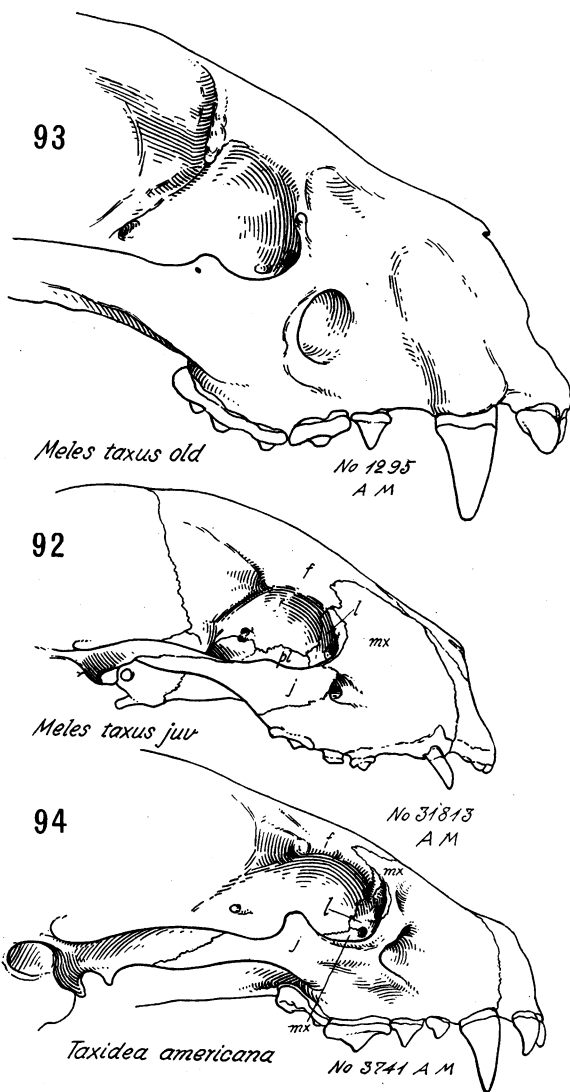
are possibly for branches of the internal maxillary artery. A very similar opening is present in the same location in the Canidæ. Indeed, the whole inner wall of the orbit in the Ursidæ presents several points of



Figs. 89 to 91. Skulls of Viverridæ (continued).

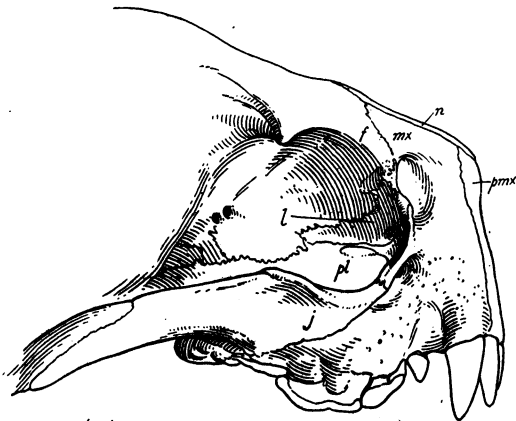
resemblance with the conditions observed in *Canis*, *Mustela*, and *Ælurus*.

In the more primitive genera of the Viverridæ (*Crossarchus*, Fig. 86, *Ichneumia*, Fig. 87), the lacrymal itself bears the tubercle and has a small pars facialis. Remnants of this condition are found in other



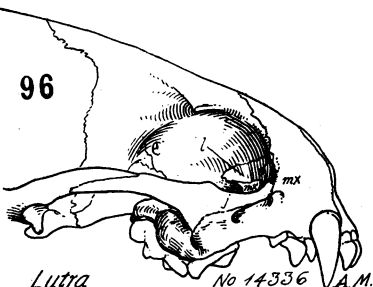
Figs. 92 to 94. Skulls of Mustelidæ. Subclass Placentalia, order Carnivora, sub-order Arctoidea, family Mustelidæ.

98



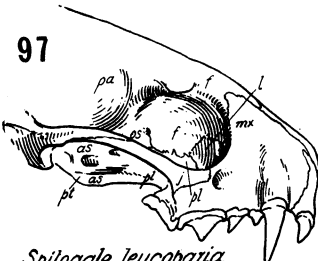
Latax
No 41353 A.M.

96



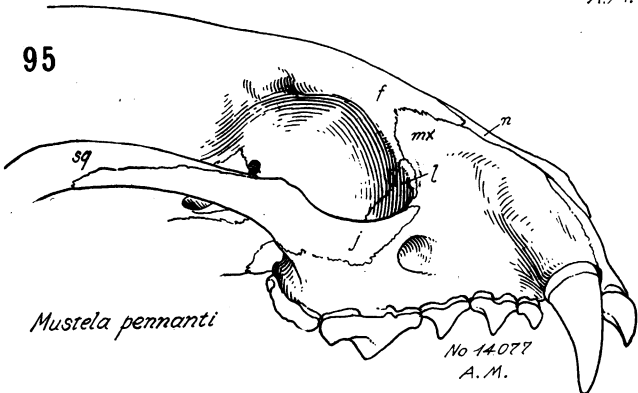
Lutra
No 14336 A.M.

97



Spilogale leucoparia
No 14818
A.M.

95



Mustela pennanti
No 14077
A.M.

Figs. 95 to 98. Skulls of Mustelidæ (continued).

Viverridæ (Fig. 90) and Felidæ and to some extent in the Hyænidæ. In *Genetta victoriae* (Fig. 89) the lacrymal is much reduced and the maxilla usurps its place on the anterior rim of the orbit. *Mongos* (Fig. 88) is remarkable for the vestigial condition of the jugal, which is functionally replaced by the maxilla. In *Cryptoprocta* (Fig. 91) the tubercle is borne by the maxilla.

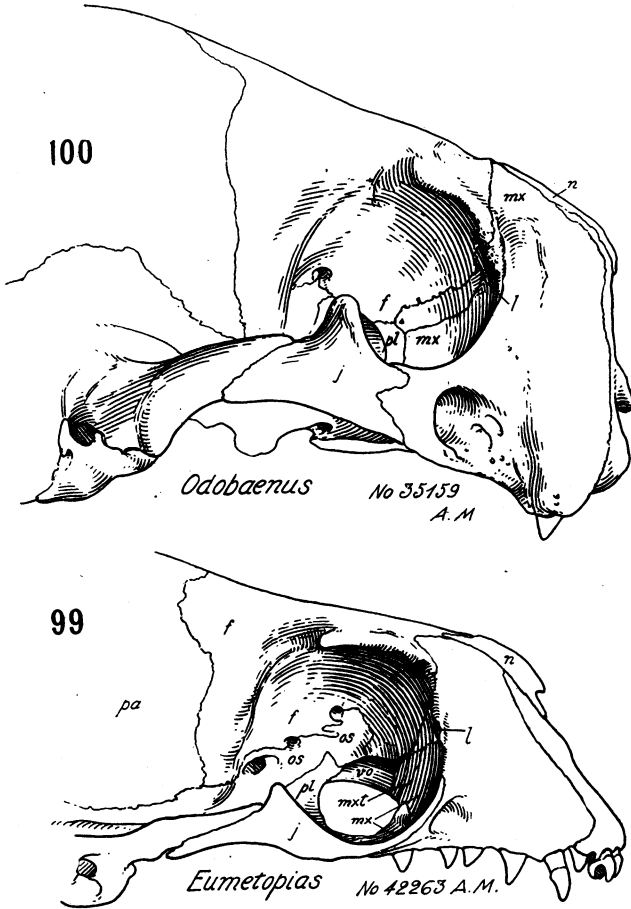
In the Mustelidæ, *Mustela* (Fig. 95) and the young *Meles* (Fig. 92) have a fair-sized lacrymal bearing a small tubercle on the antorbital rim. In *Taxidea* (Fig. 94), which is a very different genus from *Meles*, the antorbital rim is chiefly made from the maxillary; the same is true of most of the other Mustelidæ in which the facial part of the lacrymal is very small. In *Lutra* (Fig. 96) and *Lutax* (Fig. 98) the antorbital rim of the maxillary is sharply ridged for the orbit and the lacrymal is extended anteroposteriorly on the inner wall of the orbit. In these characters, as in many others, the otters relate to the skunks (cf. Fig. 97).

Thus in most modern Fissipedia the lacrymal tends to be reduced and withdrawn from the anterior rim of the orbit to its inner surface, while the maxillary usurps the place of the lacrymal and forms the tubercle. The orbital plate of the palatine is enlarged, often crowding the lacrymal forward to the corner of the orbit.

Pinnipedia

The most primitive known condition of the lacrymal in this group is found in the Otariidæ (cf. Fig. 99); here the lacrymal is a thin sliver of bone, extended more or less transversely on the prominent anterior wall of the orbit and ending laterally in a very projecting tubercle, the front face of which is composed largely of a spur from the maxilla. The latter forms the anterior rim of the orbit below the tubercle and widely separates the lacrymal from the jugal. Possibly the separation of these two elements is due to the great enlargement of the orbit which has dragged the jugal outward and backward. The lacrymal is also widely separated from the palatine, the orbital plate of which is membranous, leaving, in the dried skull, a large vacuity in the side of the brain-case, and exposing the vomer and the maxillo-turbinals. The vacuity in question extends forward between the frontal and the maxilla to the posterior border of the lacrymal. The latter co-operates with the maxilla and the frontal in covering the posterior extension of the greatly enlarged maxillo-turbinals, which appear to have obliterated the maxillary antrum, and to have encroached upon the ethmo-turbinals, which in this group are greatly reduced. The lacrymal itself is imperforate, and apparently the lacrymal duct is absent.

In a very young Atlantic walrus (*Odobænus rosmarus*, Amer. Mus. No. 35159, Fig. 100) an apparent vestige of the lacrymal is represented by an extremely thin sliver of bone covering the maxillo-turbinals on



Figs. 99 to 100. Skulls of Pinnipedia. Subclass Placentalia, order Carnivora, suborder Pinnipedia.

99. *Eumetopias stelleri*. Family Otariidæ.
 100. *Odobænus rosmarus*. Family Odobænidæ.

the inner wall of the orbit between the frontal and the maxilla. The very large projecting tubercle is borne by the maxilla. The whole conformation of the lacrymal and orbital region is fundamentally the same

as in the Otariidæ, and testifies to the relatively close relationship of these two families, which is already established by other evidence.¹

In all the Phocidæ the orbits are very large and the lacrymal is apparently absent, at least as a bony element; but its former site may be indicated by a vacuity on the inner wall of the orbit between the frontal and the maxilla. In the dried skull this vacuity partly exposes the maxillo-turbinals. The whole appearance of this region recalls the above-described conditions in the walrus, in which the orbital plate of the maxillo-turbinal is covered by the vestigial lacrymal. The tubercle, when developed (*Erignathus barbatus*, *Phoca grænlandica*, *Cystophora cristata*, etc.), is borned by the maxilla. The lacrymal duct is absent.

As a whole, the orbital region of the Phocidæ suggests that this family is a specialized offshoot of the walrus-furseal stem, a conclusion which is strongly reinforced by the evidence of other parts of the skull, such as the auditory and olfactory regions.

The reduction and final disappearance of the lacrymal in this sub-order are doubtless more or less correlated with the great enlargement of the maxillo-turbinals, and the loss of the lacrymal duct.

The evidence suggests that the Pinnipedia sprang from some group of Carnivora in which the facial part of the lacrymal had already been lost, but the lacrymal still formed part of the anterior rim of the orbit and bore a normal tubercle as it does in the more primitive Fissipedia.

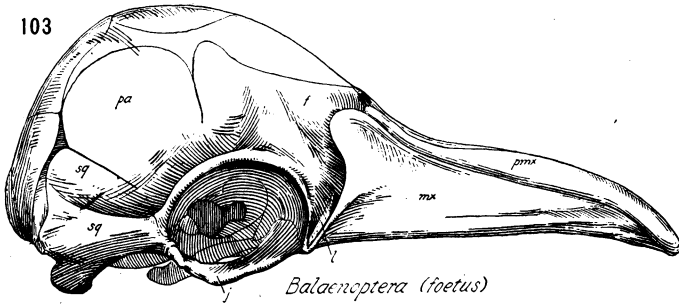
Cetacea

The morphology of the lacrymal of Cetacea will be more intelligible if considered in connection with the general evolution of the facial part of the skull in this order.

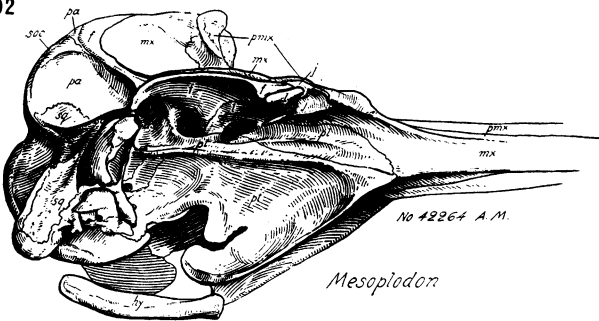
All recent work strengthens the conservative conclusion that the extinct Archæoceti were real cetaceans, and not, as some have held, pseudo-cetaceans, the product of convergent evolution. In the most primitive stage of the Archæoceti, *Protocetus atavus* Fraas from the Lower Tertiary of Egypt, the skull already foreshadows the more typical archæocete type. The rostrum is elongate, the orbital plate of the frontals is widened, and the anterior nares are beginning their shift dorsad. Even *Zeuglodon* itself, though belonging to an extinct side line, shows the following significant skull characters. The skull, as seen from above, is roughly triangular, with widely projecting zygomatic processes of the squamosals and slender jugals. The rostrum is moderately elongate, with the anterior nares dorsal in position, but still well in front of the eyes. The eyes are concealed from above by a broad, rather flat expanse of the frontals. The frontal processes of the maxillæ

¹Amer. Journ. Sci., XXI, pp. 444-450.

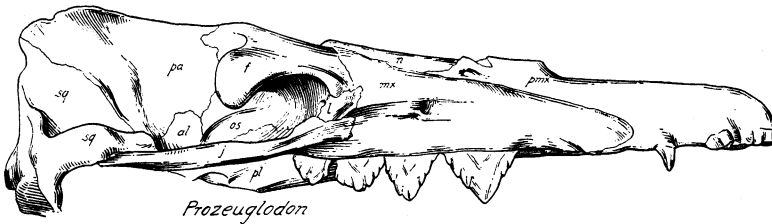
103



102



101



Figs. 101 to 103. Skulls of Cetacea. Subclass Placentalia, order Cetacea.

101. *Prozeuglodon atrox*. Suborder Archæoceti, family Zeuglodontidæ. Upper Eocene, Birket-el-Qurun beds, Fayûm, Egypt. After Andrews.
102. *Mesoplodon grayi*. Suborder Odontoceti, family Ziphiidæ.
103. *Balænoptera borealis*. Suborder Mystacoceti, family Balænopteridæ. After Schulte.

are very wide, but do not yet overlap the orbits. The lacrymal of *Prozeuglodon* (Fig. 101) (as figured by Andrews, 1906, Pl. XXI) recalls the type of the inadapative creodonts, as it has a well-developed pars facialis and retains its normal contacts with the maxilla, jugal, palatine, and frontal. At this stage the lacrymal still forms the anterior rim of the orbit.

In the Upper Oligocene *Patriocetus*, which is regarded by Abel (1914, p. 88) as an ancestral mystacocete, the dentition, as figured in Abel's reconstruction, is of archæocete type, but the wide skull plainly approaches that of the more primitive mystacocetes. The anterior nares are more dorsal, the narial channel between the elongate premaxillæ exposes the vomer in the dorsal view. The orbital plate of the frontal is not far in advance of the stout zygomatic process of the squamosal, and the small orbit is just above the level of the long sloping ascending ramus of the mandible. The maxillo-frontal contact is wide and apparently conceals the lacrymal in the side view of the skull.

The skull of the Miocene *Cetotherium* (Abel, 1914, p. 91), a primitive balænopterid, may readily be derived from the *Patriocetus* type by the great enlargement of the mouth and jaws, the loss of the teeth, the down-growth of baleen plates from the palate, and the subsequent arching of the rostrum. The dorsad shifting of the nares is now virtually complete, as well as the backward and upward growth of the maxillæ and the backward shifting of the orbits, the postorbital process of the frontal being in contact with the massive zygomatic process of the squamosal. In the foetal *Balæna japonica*, as figured by Eschricht (Weber, 1904, p. 555), and in the foetal *Balænoptera borealis* (Fig. 103), as figured by Schulte (1916, Pls. LIV, LV), the imperforate lacrymal is reduced to a long sliver of bone, which is pressed between the frontal process of the maxilla and the orbital apophysis of the frontal. In spite of the downward and outward prolongation of the orbit, the lacrymal retains its primitive contacts at least with the frontal, the maxilla, and the slender jugal.

The relations of the lacrymal with the jugal in the odontocetes have been used as a diagnostic character by Flower (1866), who concluded that among existing cetaceans the lacrymal is a free element only in the Ziphiinæ, while in the Physeterinæ, as well as in the Delphinidæ and the Platanistidæ, it is usually fused with the jugal. Abel (1902, p. 150), however, noted that in *Beluga* of the Delphinidæ, as well as in the Miocene *Eurhinodelphis*, the lacrymal is sometimes distinct from the jugal in young skulls.

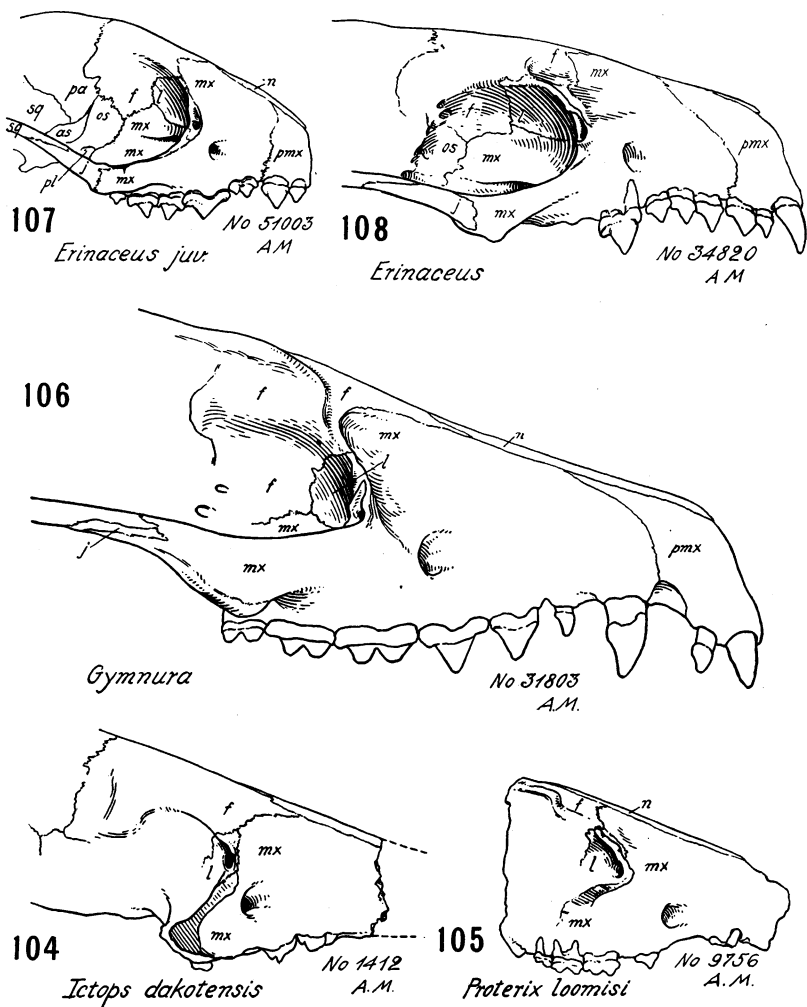
The general relations of the lacrymal in the odontocetes seem to have been foreshadowed in the extinct Squalodontidæ, in which the supraorbital region is fundamentally like that of the Ziphiinæ. In dentition and skull characters the Squalodontidæ tend to connect the physeterid odontocetes with the archæocetes (Abel, 1914, pp. 86, 92-94).

In existing odontocetes the most complete and primitive condition of the lacrymal is seen in the Ziphiinæ. In a young *Mesoplodon grayi* (Amer. Mus. No. 42264, Fig. 102) the lacrymal is a flattened bone lying beneath the expanded orbital plates of the frontal and maxillæ, and forming part of the roof of the orbit; laterally it forms the anterior part of the rim of the orbit and is in contact with the anterior end of the jugal, with the maxilla, the frontal, the palatine, and the pterygoid.

In *Ziphius cavirostris*, according to Kernan (1918, p. 374), the lacrymal is a rather massive disc-like bone on the roof of the orbit, in contact with the maxilla, the jugal, the frontal, the palatine, and the pterygoid. It is pierced by a canal and a fissure which, Dr. Kernan suggests, probably represent the lacrymal canal of other mammals.

In *Kogia breviceps*, of the family Physeteridæ, Schulte (1917, p. 390) states that "it has been open to question whether the jugal might not have disappeared and the element so named be really interpreted as lacrymal, or perhaps as lacrymal and malar, with the zygomatic process of the latter reduced to a ligament. In a dissection of a new-born *Kogia*, a perfectly definite ligamentous arch was present connecting the tip of the malar to the zygomatic process of the squamosal. Very fortunately the skull of the calf on the left side has a separate malar and lacrymal, the latter nasal in position and interposed between the maxilla and the frontal. It is evident, therefore, that the usual elements are present but that the zygomatic process of the malar has been reduced so that it no longer appears as bone." The lacrymal of this animal is overlaid by the frontal and by the maxilla; it also articulates with the malar.

If it be considered remarkable that the lacrymal should persist at all in these excessively specialized skulls, it may be suggested that this element has been sheltered, as it were, by the overlying orbital plates of the frontal and of the maxilla, so that even in *Kogia*, when the rostrum became greatly shortened and the maxillæ and premaxillæ grew even further upward to support the enormous nasal chamber, the lacrymals retained their sheltered place beneath these elements on the roof of the orbits, although in this genus they have been crowded away from the supraorbital margin by the secondary enlargement of the jugal.



Figs. 104 to 108. Skulls of lipotyphlous Insectivores. Subclass Placentalia, order Insectivora, suborder Erinaceoidei.

104. *Ictops dakotensis*. Family Leptictidæ. Middle Oligocene, Oreodon zone, Lower Brule formation, South Dakota.

105. *Proterix loomisi*. Family Erinaceidæ. Middle Oligocene, Oreodon zone, Lower Brule formation, South Dakota.

106. *Gymnura rafflesi*. Family Erinaceidæ.

107. *Erinaceus (Atelerix) langi*. Family Erinaceidæ.

108. *Erinaceus europæus*. Family Erinaceidæ.

Insectivora (Lipotyphla)

The true Insectivora (Lipotyphla) may be conceived either as the rather highly modified descendants of some of the Mesozoic Trituberculata or as merely dwarfed and degenerate Pro-carnivora. Possibly there may be some truth in both views. At any rate, the Zalambdodonta, which are perhaps the most archaic members of the series, are evidently degenerate and retrogressive in the lacrymal region as will be shown below. Very probably the most primitive lacrymal region is preserved in the Eocene and Oligocene Leptictidae (Figs. 104, 105). The skull, as is usual in primitive mammals, is macrosmatic, with expanded ethmoid region; the lacrymal forms parts of the anterior rim of the orbit, with a marginal tubercle and the foramen just medial to it. The lacrymal has a somewhat dorsal position, perhaps as a result of the expansion of the infraorbital canal for the ramus maxillaris of the trigeminal nerve, which is commonly enlarged in animals with a highly sensitive snout. In *Proterix loomisi* Matthew (Fig. 105) the lacrymal begins to resemble that of *Erinaceus* (Figs. 107, 108) as described below. In the existing *Gymnura* (Fig. 106) the ridge on the outer border of the lacrymal that forms the anterior rim of the orbit is sharply defined and separates the eye and its muscles from the area for the naso-labialis and scutularis muscle, which is well defined in front of the eye¹. The marginal foramen opens partly outward. The jugal is a small element in the middle of the zygomatic arch and is widely separated from the lacrymal.

In *Erinaceus* (Figs. 107, 108) that part of the maxilla which forms the bridge over the infraorbital canal becomes further enlarged at the expense of the lacrymal and the jugal, which are widely separated by it from each other. The lower part of the lacrymal fuses with this bridge but the suture is evident in a very young skull of *Erinaceus*. The foramen still perforates the lacrymal, but now opens laterally rather than posteriorly. The dorsally expanded orbital plate of the lacrymal covers the greatly enlarged dorsal ethmo-turbinate. The lacrymal is excluded from contact with the palatine by the maxillary. The fronto-maxillary contact is wide and the exposed proximal ends of the nasals are narrow.

The lacrymal region in *Palaeoryctes puercensis* Matthew (1913), the Paleocene representative of the zalambdodont Insectivora, is not known.

In *Nesophontes*, a primitive zalambdodont of Porto Rico and Cuba recently described by H. E. Anthony (1918), the skull as a whole much resembles that of a young *Solenodon*, except for the more primitive

¹See the dissections in Boas and Paulli (1908, Pl. II).

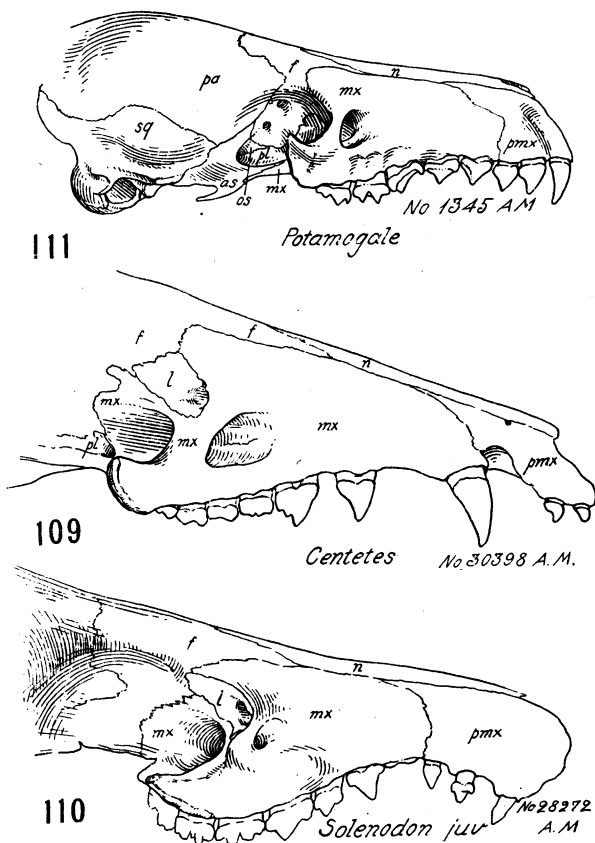
character of the dentition and the greater length of the basicranial region. As in *Solenodon*, the lacrymal is probably fused in the adult with the surrounding elements. The well-developed lacrymal foramen is marginal, immediately above and behind the large infraorbital foramen. In the modern *Centetes* (Fig. 109) the lacrymal region is rather specialized. The animal is highly macrosomatic and the region covering the ethmoturbinals is expanded and cylindrical; the anterior processes of the frontals extend far forward over the maxillæ and widely separate the narrow coössified nasals from the lacrymal. The latter has been displaced dorsad through the marked enlargement of the infraorbital canal of the maxillary, which, as in *Gymnura*, appears to indicate a great development of the superior maxillary nerve. The maxillary has also encroached upon the orbital plate of the palatine which is reduced in size. The lacrymal itself has contact laterally only with the maxillary bridge over the infraorbital canal, which to some extent functionally replaces the absent jugal. The orbital surface of the lacrymal is flatly expanded without spine or crest; the foramen is located at the anterior border of the lacrymal and opens laterally. There is technically little or no pars facialis, since the lacrymal is not extended in front of the orbit. The eyes are very small and face outward.

In *Microgale* and *Echinops* the lacrymal region appears essentially the same as in *Centetes*. In *Hemicentetes* the lacrymal is covered by the ascending process of the maxilla.

In *Solenodon* (Fig. 110) the small, dorsally displaced lacrymal is widely extended on the inner wall of the orbit; the large foramen pierces its anterior end. The region as a whole is essentially like that of *Centetes*. Accordingly, it may be said that the lacrymal region of the Centetidae is especially characterized as follows: (1) by the encroachment of the maxillary, which crowds the lacrymal dorsad above the enlarged infraorbital canal; (2) by the forward growth of the frontals, covering the proximal end of the nasals and widely separating them from the lacrymal; (3) by the reduction of the eyes, causing the loss of an orbital rim and of the lacrymal tubercle; (4) by the expansion and cylindrical form of the ethmoid region, causing the anteroposterior flattening of the lacrymal against the inner wall of the orbit.

In *Potamogale* (Fig. 111) the infraorbital bridge of the maxillary is further enlarged and extends still higher up on the side of the face. The lacrymal foramen is vestigial and the lacrymal itself is vestigial or absent. The orbital plate of the palatine, however, is not reduced.

In *Talpa*, according to W. K. Parker's figures (1885) of a young skull, the small lacrymal is separated from the nasals by the wide fronto-maxillary contact. The lacrymal is closely appressed to the side



Figs. 109 to 111. Skulls of Zalambdodont Insectivores. Subclass Placentalia, order Insectivora, suborder Centetoidea (Zalambdodonta).

109. *Centetes ecaudatus*. Family Centetidae.

110. *Solenodon paradoxus*. Family Solenodontidae.

111. *Potamogale velox*. Family Potamogalidae.

of the face and the lacrymal foramen has shifted forward and lies between the maxilla and the anterior process (pars facialis) of the lacrymal. In an embryo *Sorex* the small lacrymal lies behind the emarginate ascending process of the maxilla (*op. cit.*, Pl. xxxi).

In *Pantolestes natans* Matthew (1907, 1918), which is referred by Dr. Matthew to the Insectivora, the lacrymal itself is not preserved but

the infraorbital is expanded as in many insectivores and the lacrymal was probably small and somewhat displaced dorsad. There is a wide fronto-maxillary contact and the exposed proximal end of the nasals is tapering.

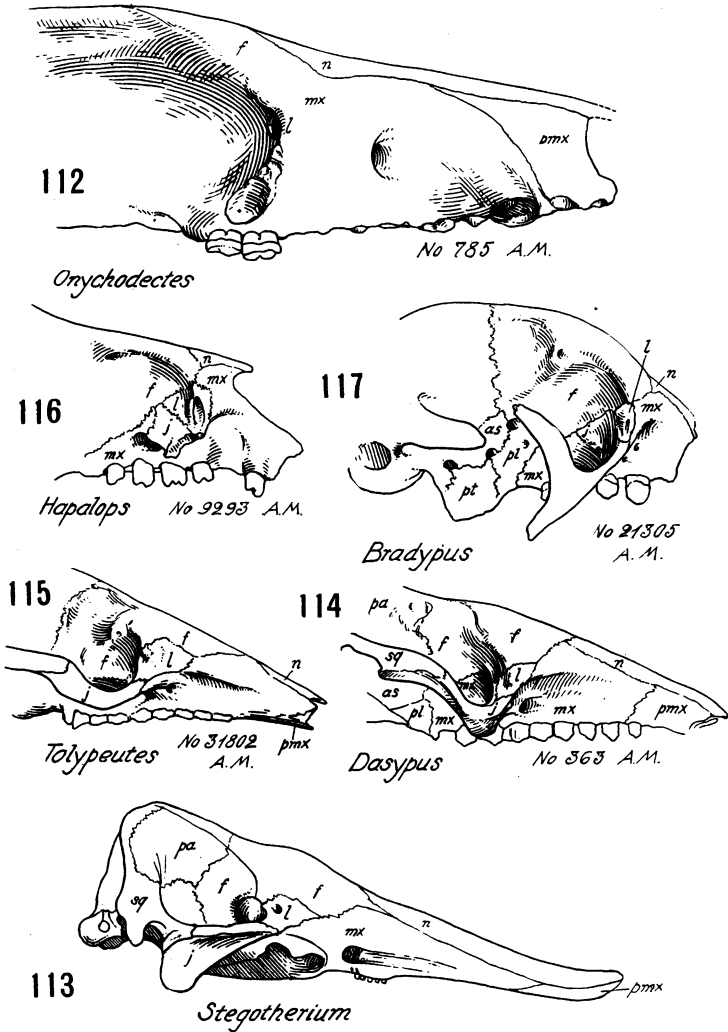
Thus the lacrymal region of the true Insectivora exhibits two principal types. First, and most primitive, is that of the Leptictidæ, in which the lacrymal takes part in the anterior rim of the orbit; it bears a distinct tubercle and has a small pars facialis above the lacrymal foramen, which is marginal in position; the erinaceid type of lacrymal is derived directly from this by the reduction of the pars facialis. The second type is exhibited in the zalambdodonts, including *Nesophontes*, in which the lacrymal is appressed to the inner wall of the orbit and is extended dorso-caudally above the enlarged infraorbital canal; the large lacrymal foramen is marginal; there is no tubercle and the maxilla is deeply notched for the reception of the lacrymal. Similar but more reduced types of lacrymal occur in *Talpa* and *Sorex*. In *Potamogale* (Fig. 111) the lacrymal is wanting.

Tæniodonta (Ganodonta)

Onychodectes (Fig. 112), a very primitive member of the Paleocene Conoryctidæ, has a long, more or less tubular macrosmatic type of skull which recalls that of primitive Insectivora. There are no distinct post-orbital processes on the frontals; the lacrymal was on the anterior rim of the orbit. The sutures are not clear; a double tubercle on the upper part of the anterior rim of the orbit marks the point of attachment of the palpebral ligament and was apparently borne by the lacrymal. The lacrymal foramen was below this ridge and within the margin of the orbit, as in all other primitive placental mammals. On the whole, the lacrymal region recalls that of the Leptictidæ.

In the specialized genus *Psittacotherium* the position and limits of the lacrymal are not clear. The facial portion of the skull has been described by Dr. Wortman (1897, pp. 72, 74) as follows:

In the skull (Fig. 4) the facial portion is seen to be short and deep, the sagittal crest short and inconspicuous, and there is but a faint indication of postorbital processes upon the frontals. The anterior root of the zygoma is situated well forward; it has a considerable vertical depth and projects outwards, downwards, and backwards. In front of and below the zygomatic root is a shallow fossa, at the upper extremity of which is the anterior opening of the infraorbital canal, which is double. Leidy describes two foramina in this situation in *Megalonyx* (Fig. 5), and it is not an infrequent occurrence for this foramen to be double in the modern sloth. In *Psittacotherium* the main canal is below and the smaller one above. Both, however, are placed unusually high on the face. No evidence of a distinct lacrymal is to be seen.



Figs. 112 to 117. Skulls of Edentates. Subclass Placentalia, order Edentata.

112. *Onychodectes tisonensis*. Suborder Tæniodonta, family Conoryctidae. Paleocene, Polymastodon zone, Puerco formation, New Mexico.

113. *Stegotherium tessellatum*. Family Dasypodidae. Middle (?) Miocene, Santa Cruz formation, Patagonia. After Scott.

114. *Dasypus sezcinctus*. Suborder Xenarthra, family Dasypodidae.

115. *Tolypeutes conurus*. Suborder Xenarthra, family Dasypodidae.

116. *Hapalops ruetemeyeri* (?). Suborder Xenarthra, family Megalonychidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.

117. *Bradypus* sp. Suborder Xenarthra, family Bradypodidae.

It may also be noted that the frontals send forward anterior processes for articulation with the maxillæ.

If the tæniodonts are primitive edentates, as held by Dr. Wortman, they show that here, as in other orders, the primitive forms have a well-defined anterior orbital rim, formed in part by the lacrymal, the lacrymal foramen being behind this rim and below the lacrymal tubercle.

Edentata (Xenarthra)

The lacrymal region is not well shown either in the Paleocene *Palæanodon* Matthew (1918) or in the Middle Eocene *Metachiromys*. The skull of the latter, however, approaches the armadillo type, especially in the wide expansion of the frontals anteriorly. The whole region is highly macrostomatic, the ethmo-turbinals being greatly expanded. There is a wide contact between the frontals and the maxilla, due to the marked forward growth of the frontals.

Prodasypus of the Santa Cruz formation, as described by Professor Scott (1906), has a fairly primitive lacrymal with a projecting antorbital rim and a small pars facialis. In *Dasypus* (Fig. 114) the lacrymal is on the face and chiefly in front of the orbit; the foramen is external in position. The orbital part of the lacrymal is limited.

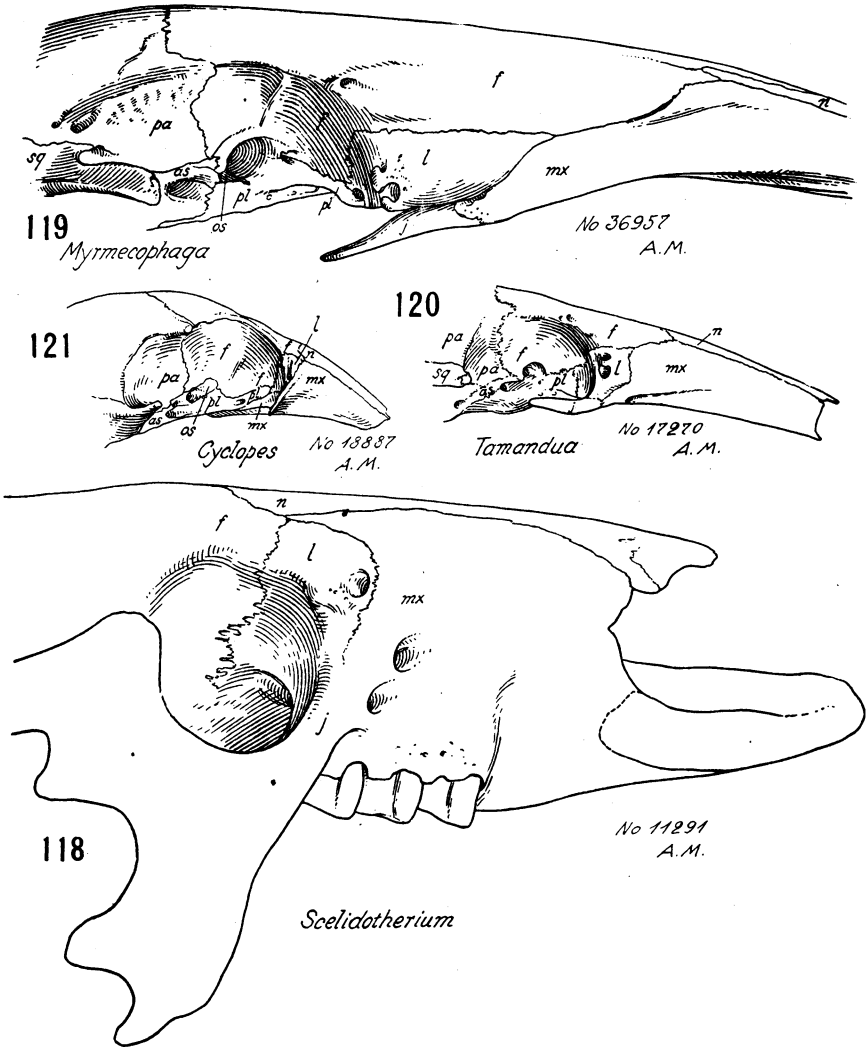
In *Stegotherium* (Fig. 113), a long-faced relative of *Tatusia*, figured by Professor Scott, the lacrymal has an extended pars facialis with a lateral foramen and groove.

In the young *Tatusia hybrida*, as figured by Parker (1885, Pl. vi), the large lacrymal forms the prominent anterior rim of the orbit while the jugal is reduced. The pars facialis is large. The foramen is immediately in front of the orbital rim.

Thus in the armadillos the orbital part of the lacrymal is reduced, the facial part more or less extended, and the foramen is external. The lacrymal is widely separated from the palatine by the maxilla.

In the Santa Cruz glyptodonts the lacrymal has been displaced dorsad through the enlargement of the zygoma.

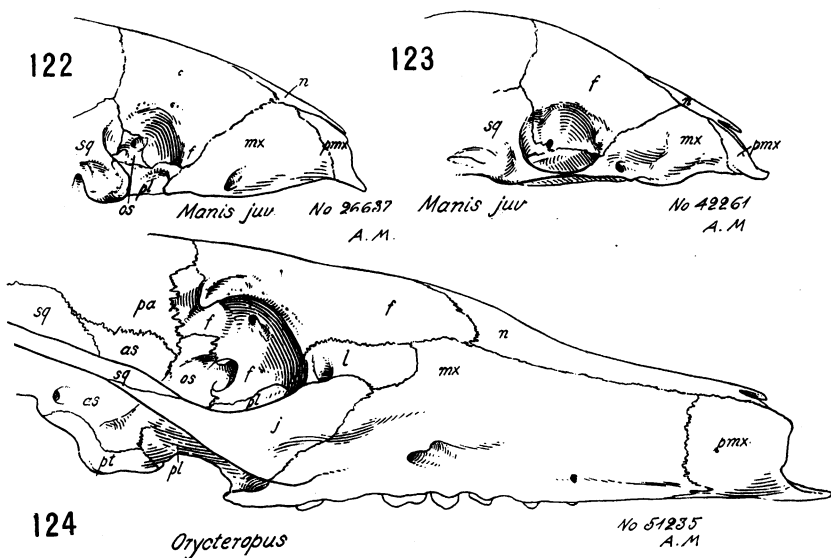
Among the Santa Cruz ground-sloths, *Hapalops* (Fig. 116) has a relatively primitive lacrymal with a moderate-sized pars facialis; the foramen is immediately in front of the orbit. The pars orbitalis is separated from the maxilla by an orbital extension of the jugal. Similar conditions persist in the modern sloths (Fig. 117). Among the Mylodontidæ, *Scelidotherium* (Fig. 118) exhibits a relatively primitive condition of the lacrymal. In *Myrmecophaga* (Fig. 119) the great extension of the facial part of the lacrymal is probably connected with the still



Figs. 118 to 121. Skulls of Edentates (continued). Suborder Xenarthra.
118. *Scelidotherium cuierei*. Family Mylodontidæ. Pleistocene, Pampean formation, Argentina.
119. *Myrmecophaga jubata*. Family Myrmecophagidæ.
120. *Tamandua tetradactyla*. Family Myrmecophagidæ.
121. *Cyclopes dorsalis*. Family Myrmecophagidæ.

greater forward growth of the frontal. Two foramina are present, presumably for the upper and lower palpebral branches of the lacrymal gland. In *Tamandua* (Fig. 120), with its shorter snout, the pars facialis is much less extended. In *Cyclopes* (Fig. 121), in which the snout is secondarily shortened, the lacrymal is crowded between the outwardly spreading maxilla and the frontal, the pars facialis being greatly reduced and the fronto-maxillary contact reduced or absent. In the ant-eaters the lacrymal is in contact with the palatine, but in the sloths it is widely separated from it by the maxilla and the jugal.

Accordingly, we find that the lacrymals of xenarthrous edentates



Figs. 122 to 124. Skulls of *Manis* (subclass Placentalia, order Edentata, sub-order Pholidota) and *Orycteropus* (subclass Placentalia, order Tubulidentata).

122. *Manis* sp. Family Manidae. Young individual.

123. *Manis* sp. Young individual showing secondary zygomatic arch formed by union of processes from the squamosal and maxilla.

124. *Orycteropus* sp. Family Orycteropodidae.

differ widely among themselves; in the armadillos the lacrymal is mostly external to the orbit and widely separated by the maxilla from the palatine. In the sloths, on the other hand, the orbital portion is well defined, but separated from the maxilla by the orbital process of the jugal. In the ant-eaters, with the reduction of the jugal the lacrymal gains a presumably secondary contact with the palatine.

Pholidota

In two very young *Manis* skulls (Amer. Mus. Nos. 26637, 42261, Figs. 122, 123) with sutures all open, there is no trace of a distinct lacrymal, its position being usurped by the vertical plate of the palatine and the descending wall of the frontal. There is a very wide fronto-maxillary contact. A conspicuous foramen at the anterior corner of the orbit, between the frontal and the palatine, at first looks like the lacrymal foramen, but is more probably the spheno-palatine foramen; although Weber (1904, p. 422), after stating that a lacrymal is seldom retained but generally is fused with the maxilla, says that it is always imperforate and that the lacrymal foramen lies between the frontal and the palatine. Possibly the disappearance of the lacrymal in *Manis* may be correlated to some extent with a caudad displacement of the orbits, which have become confluent with the temporal fossa, the preorbital part of the frontal extending downward over the territory of the lacrymal and usurping both its function and position.

Recently Dr. Matthew has shown (1918) that the Pholidota may very well be derived from primitive Xenarthra. In *Manis* the confluence of the orbit with the temporal fossa and the loss of the jugal are conditions that are more or less foreshadowed in *Cyclopes*, while the wide fronto-maxillary contact is seen in *Stegotherium*.

Tubulidentata

In *Orycteropus* (Fig. 124) the lacrymal region recalls the type found in *Myrmecobius*, *Tupaia*, Eocene Artiodactyla, and other genera in which the ethmoid region is widely expanded, the orbit is placed far backward and the lacrymal projects laterally, forming an anterior rim of the orbit and extending well forward on the face. The foramen is external, the pars orbitalis is considerably reduced by the encroachment of the palatine and frontal. The fronto-maxillary contact is well developed. Much of this condition may have resulted from a caudad displacement of the orbits, correlated with a forward growth of the frontal.

The conditions in the lacrymal region of *Orycteropus* could well be derived from those in the Condylarthra to be described below.

Tillodontia

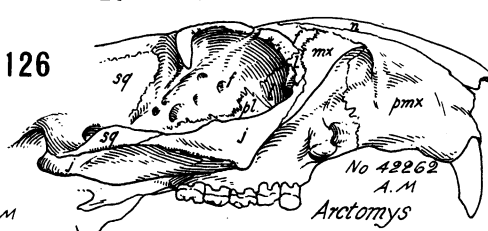
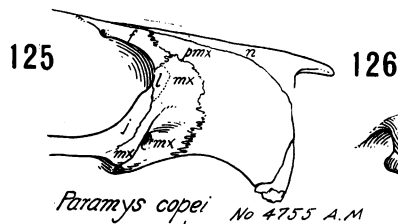
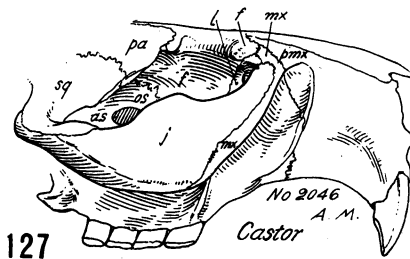
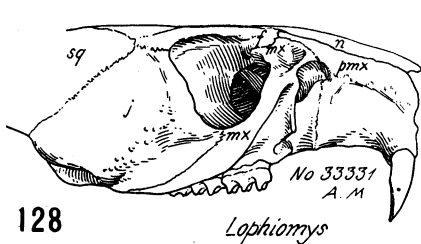
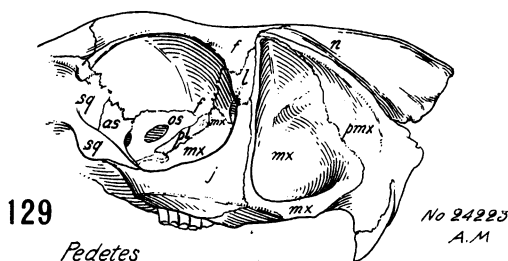
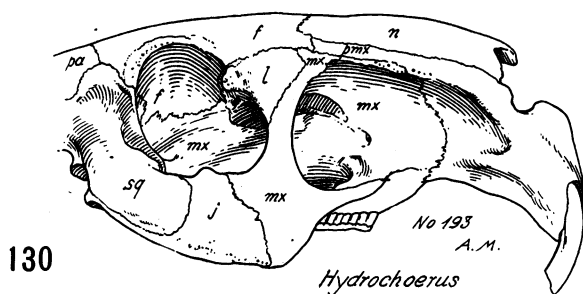
In the Middle Eocene *Tillotherium* the lacrymal region appears to be fairly primitive and creodont-like in spite of the rodent-like modification of the front teeth. The lacrymal forms the anterior border of the orbit; the pars orbitalis is moderately extended dorsally; the pars

facialis is small; the foramen and tubercle are marginal. There is a wide fronto-maxillary contact.

Rodentia

The oldest known rodents, the Ischyromyidæ of the Eocene (cf. Matthew, 1910) already show the chief ordinal characteristics of the skull and dentition. In correlation with the gliriform modification of the incisors (Fig. 125) the premaxillæ are much enlarged and extend up above the maxillæ and lacrymals to gain contact with the frontals; the fronto-maxillary contact and the facial part of the lacrymal are accordingly much restricted; in correlation with the expansion of the masseter the zygomatic arch is typically stout, and the jugal is supported by a more or less well-developed zygomatic process of the maxilla, which bears a tubercle for the anterior end of the masseter lateralis. Post-orbital processes of the frontals are not developed. The modern *Arctomys* (Fig. 126) has advanced beyond this primitive rodent condition by the differentiation of a special slip of the masseter lateralis which has grown forward along the anterior preorbital border of the zygomatic arch so as to invade the lateral surface of the maxilla above the infra-orbital canal, even reaching the premaxilla. The lacrymal, however, which was already reduced in *Paramys*, retains its place in the anterior rim of the orbit, in contact with the maxilla, jugal, palatine, and frontal. It is traversed by the lacrymal duct. The main tubercle is borne by the frontal, but a smaller tubercle below it is developed at the junction of the lacrymal with the jugal. In *Sciurus* this becomes the main tubercle. In *Castor* (Fig. 127) the great development of the anterior slip of the masseter and the correlated growth of the anterior part of the zygoma have displaced the orbit dorsad, so that the very small portion of the lacrymal which remains on the surface faces upward, forward, and outward. The tubercle is borne by the frontal. In the Geomyidæ the maxilla has usurped the place of the jugal in the anterior zygomatic plate and the jugal is limited to the middle of the zygomatic arch, the maxilla has also extended dorsad to the fronto-premaxillary junction, crowding the lacrymal into a more or less reduced condition; it, however, still bears the tubercle.

Similar conditions obtain in *Fiber* and *Mus* where the lacrymal is greatly reduced to a thin plate of bone on the inner wall of the orbit, above the infraorbital fenestra. In *Mus* it ends above in a delicate tubercle. In these and other myomorphs (Fig. 128) the final stages in the reduction of the lacrymal may perhaps be associated with the anterior extension of the medial slip of the masseter, which has worked its



Figs. 125 to 130. Skulls of Rodents. Subclass Placentalia, order Rodentia.

125. *Paramys copei*. Suborder Sciuromorpha, family Iachyromyidae. Lower Eocene, Lambdotherium zone, Wind River basin, Wyoming.
 126. *Arctomys* sp. Suborder Sciuromorpha, family Sciuridae.
 127. *Castor canadensis*. Suborder Sciuromorpha, family Castoridae.
 128. *Lophiomyys imhausi*. Suborder Myomorpha, family Cricetidae.
 129. *Pedetes cafir*. Suborder Dipodomorpha, family Pedetidae.
 130. *Hydrochoerus capybara*. Suborder Hystricomorpha, family Caviidae, subfamily Hydrochoerinae.

way forward above the infraorbital canal, pushing in the medial wall of the nasal chamber and finally appearing on the side of the rostrum in front of the orbit. However, it should be noted that the lacrymal was already reduced in the Oligocene *Ischyromys*, in which the medial extension of the lacrymal may have barely begun.

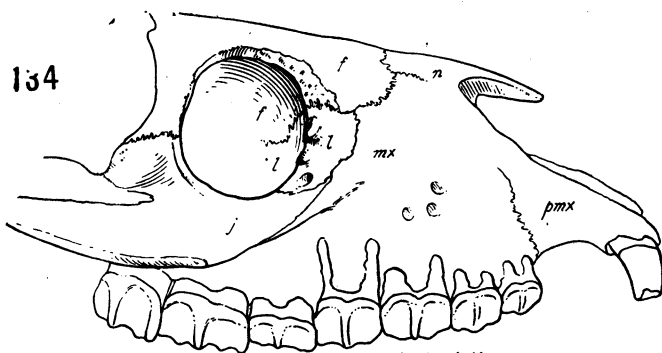
In *Pedetes* (Fig. 129) and allied types this medial slip of the masseter attains enormous dimensions, widely opening up the infraorbital fenestra; but in this group the lacrymal not only retains its place on the anterior rim of the orbit, but, together with the maxilla, plays an important part in transmitting dorsad thrusts from the zygoma to the frontal and to the alveolar process of the maxilla.

Somewhat similar conditions prevail in *Hydrochaerus* (Fig. 130) and allied genera of the Hystricomorpha; but here the lacrymal enjoys a marked secondary expansion, becoming a massive dorsal keystone to the zygomatic arch. The jugal is now restricted to the middle of the arch, and the lacrymal duct is exposed in the dried skull.

Lagomorpha

In *Lepus* and other Lagomorpha the lacrymal is a compressed bone on the anterior wall of the orbit, ending laterally in a large projecting tubercle. It is pierced by the lacrymal duct and is in contact with maxilla, palatine, and frontal. The jugal is fused at an early age with the zygomatic process of the maxilla (Lyon, 1904, p. 345) and is widely separated from the lacrymal (Amer. Mus. No. 9938). The premaxillæ are greatly extended dorsad and gain contact with the frontals as in other rodents. The prominent anterior rim of the orbit is formed exclusively by the maxilla.

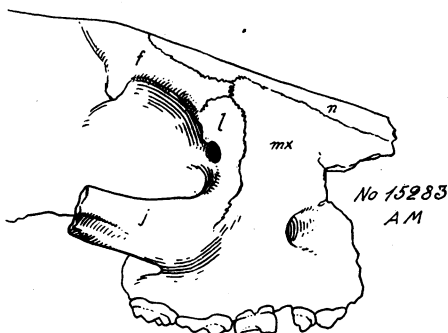
The Lagomorpha date back at least to the Oligocene, and their direct ancestry in the Eocene is unknown. Mr. J. W. Gidley (1912) excludes the Lagomorpha altogether from the Rodentia on the grounds that the two groups were already widely separated in the Oligocene and that they differ in important characters of the jaws, dentition, and limbs. In support of this view one might cite the lagomorph resemblance of *Pachyrukhôs*, of the order Typotheria, which parallels the lagomorphs not only in the general form of the front teeth and jaws but in the adaptive facies of the auditory region. Nevertheless, the peculiar specializations of the lagomorph skull mask, but do not obliterate, a long series of characters which they have probably inherited from some such very primitive rodent as *Paramys*, in which the lacrymal was already reduced to a small bone on the anterior rim of the orbit.



Diadiaphorus

No 9291 A.M.

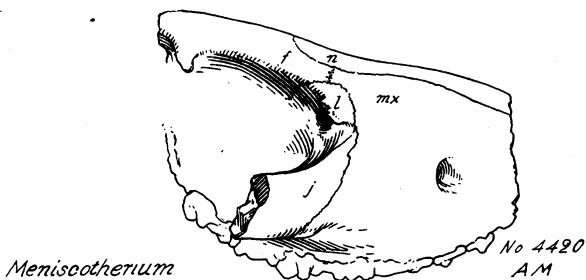
132



Phenacodus primaevus

No 15283
A.M.

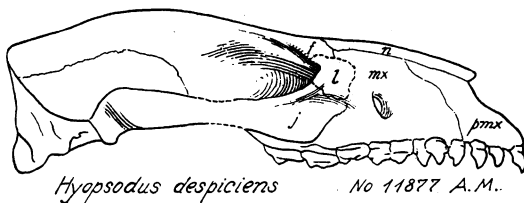
133



Meniscotherium

No 4420
A.M.

131



Hyopsodus despiciens

No 11877 A.M.

Figs. 131 to 134. Skulls of two Condylarths (subclass Placentalia, order Condylarthra) and of a Litoptern (subclass Placentalia, order Litopterna).

131. *Hyopsodus despiciens*. Family Hyopsodontidae. Middle Eocene, Upper Bridger. Uintatherium zone, Bridger Basin, Wyoming. After Matthew.
132. *Phenacodus primaevus*. Family Phenacodontidae. Lower Eocene, Coryphodon zone, Gray Bull beds, Bighorn basin, Wyoming.
133. *Meniscotherium chamense terrarubrae*. Family Meniscotheriidae. Lower Eocene, Meniscotherium zone, Largo beds, San Juan basin, New Mexico.
134. *Diadiaphorus* sp. Order Litopterna, family Proterotheriidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.

Condylarthra

In the members of this order the lacrymal region is very primitive, recalling that of the creodonts, and affording a structurally ancestral stage for the various lines of specialization seen in the different orders of ungulates. In *Phenacodus* and *Meniscotherium* the lacrymal forms a short rim on the anterosuperior margin of the orbit; the tubercle is prominent and is directed downward and backward. The pars facialis is exposed dorsally, the pars orbitalis well developed. Above the lacrymal there is a fronto-maxillary contact of moderate (*Phenacodus*) or slight (*Meniscotherium*) width; the nasals extend well behind this point, as in perissodactyls. The lacrymal foramen is internal and the lacrymal is in contact below with the well-developed jugal.

In *Hyopsodus* (Fig. 131), which has been shown by Matthew (1915) to be a primitive condylarth, the lacrymal has a moderately extended pars facialis and the foramen is within the orbital margin (Matthew, 1909, Figs. 103, 104).

Litopterna

In this order the configuration of the lacrymal region, as well as of the whole skeleton, has probably been derived from the more primitive conditions represented in the Condylarthra. In *Diadiaphorus* (Fig. 134) of the Santa Cruz formation the lacrymal forms a well-marked rim on the anterior margin of the orbit and the pars facialis is extended dorsally. The pars orbitalis is well developed. The main lacrymal foramen is located within the orbit, medial to the orbital rim. Another and external foramen, in the pars facialis above the jugal, leads into a duct which is probably a branch of the main lacrymal duct (? inferior canaliculus). This second, or external, foramen is figured by Professor Scott also in *Licaphrium*, *Thoatherium*, and *Theosodon* (1910, XVII) and may also be seen in skulls in this Museum. In *Diadiaphorus* there are two fairly stout tubercles for the palpebral ligaments on the anterior rim of the orbit, the upper one being the larger. The infraorbital foramen is represented by three foramina, recalling the "foramina maxillo-facialia" of reptiles. The orbit is closed posteriorly by postorbital processes of the jugal and frontal, as it is also in *Licaphrium* and *Thoatherium*, but in *Theosodon* the postorbital projection of the jugal is wanting so that the orbit remains open posteriorly. In this genus the marked retraction of the nasals has not greatly affected the lacrymal. The pars facialis of the lacrymal is moderately developed and the orbital rim is very prominent, bearing a low tubercle.

In its successor, *Macrauchenia*, the anterior nares are entirely dorsal, above the eyes, and the narial passage leads straight downward; at the same time the rostrum is produced forward and the nasals are greatly abbreviated. Notwithstanding these specializations, which suggest the conditions in tapirs and in sea-elephants, the lacrymal region is but little modified. As the orbits are behind the last molar, the pars facialis is somewhat lengthened.

Entelonychia

The older members of this group are probably in many respects the most primitive of the notoungulate series. The lacrymal of *Homalodonto-*

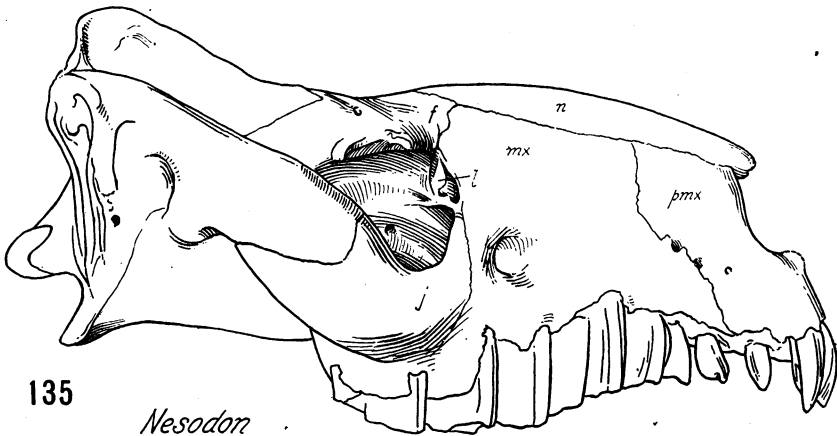


Fig. 135. *Nesodon imbricatus*. Subclass Placentalia, order Notoungulata, sub-order Toxodonta, family Toxodontidæ. After Scott.

therium is thus described by Professor Scott (1912, p. 266): "The lachrymal, the limits of which are not easy to make out in either of the skulls, is, to all appearance, a very small triangular bone, without spine, which is exposed at the superoanterior margin of the orbit; the foramen is not visible from the side." The ascending process of the maxilla overlaps the frontals.

Astrapotheria

In *Astrapotherium*¹ the pars facialis of the lacrymal has been crowded out through the backward and upward retraction of the nasals and the concomitant development of the proboscis. The pars orbitalis bears a prominent swelling.

¹Cf. Fig. 21 of the succeeding paper on the preorbital fossæ of ungulates.

Toxodontia

In *Nesodon* (Fig. 135) the lacrymal is rather small and lies mostly within the orbit, the pars facialis being small. The foramen is marginal and there is a wide fronto-maxillary contact. A contact with the jugal is present. Essentially similar conditions obtain in *Toxodon*. In *Adinotherium*, as figured by Professor Scott (*op. cit.*, Pl. xx, fig. 1) the lacrymal is quite small.

Typotheria

Even among the older typotheres of the Santa Cruz formation the skull is already much specialized and two well-marked types of lacrymal region are presented.

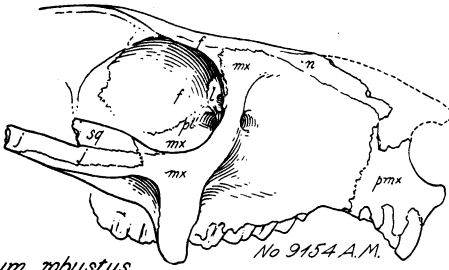
In the first type (*Hegetotherium*, Fig. 136) the lacrymal is comparatively primitive, retaining its normal position and contacts, although the pars facialis is secondarily enlarged, restricting the fronto-maxillary contact; the lacrymal bears the tubercle and the foramen is marginal. In this type the lacrymal forms a keystone which transmits thrusts from the stout zygomatic arch to the frontal and maxilla, the whole series of adaptations probably being connected with the great enlargement and anterodorsad extension of the masseter muscle. The great expansion of the angular region of the mandible, which is the insertion-area of the masseter, also testifies to the enlargement of the masseter, which was conditioned by the somewhat rodent-like modification of the incisors and the hypsodont form of the cheek-teeth.

In *Pachyrhinos* (Fig. 137), a structural derivative of *Hegetotherium*, the anterior end of the masseter must have extended still further dorsad in front of the orbit, carrying the mandible with it and restricting not only the pars facialis of the lacrymal but also the fronto-maxillary contact.

The final stage is attained in *Typotherium*, in which the incisors are of gnawing type. Here the pars facialis of the lacrymal is restricted to the anterior margin of the orbit; but in all these forms the jugal retains contact with the lacrymal.

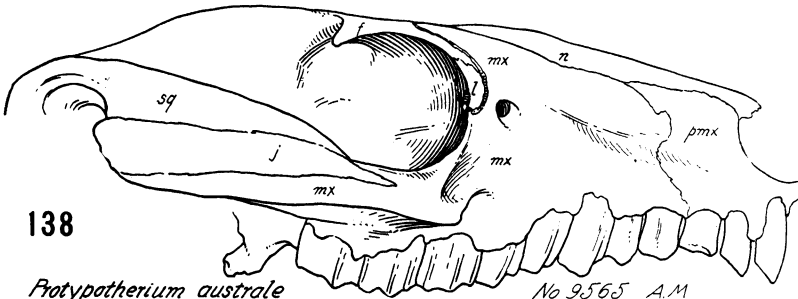
In the second series of typotheres (Figs. 138, 139), of the family Interatheriidae, the jugal is widely separated from the lacrymal and confined to the middle of the zygomatic arch, its place on the anterior border of the orbit being usurped by the maxilla. In this case the anterior end of the masseter fascia was doubtless produced sharply downward, much as in glyptodonts. In this series the lacrymal becomes reduced in size and barely extends to the lateral border of the orbit.

139

*Interatherium robustus*

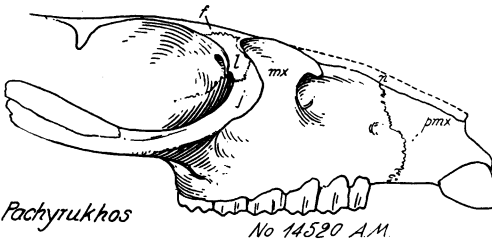
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138

*Protypotherium australe*

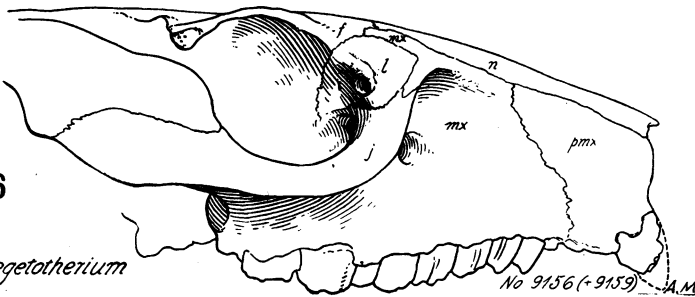
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137

*Pachyrukhos*

No 14520 A.M.

136

*Hegetotherium*

No 9156 (+ 9159) A.M.

Figs. 136 to 139. Skulls of Notoungulata. Subclass Placentalia, order Notoungulata, suborder Typotheria.

136. *Hegetotherium mirabile*. Family Hegetotheriidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.
 137. *Pachyrukhos moyani*. Family Hegetotheriidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.
 138. *Protypotherium australe*. Family Interatheriidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.
 139. *Interatherium robustus*. Family Interatheriidae. Middle (?) Miocene, Santa Cruz formation, Patagonia.

Amblypoda

(Taligrada+ Amblypoda, s. s.)

In *Haploconus* (Fig. 140) the lacrymal is rather small and forms the anterior rim of the orbit; the foramen is marginal and opens backward; there is no preorbital extension of the lacrymal; there is a well-developed fronto-maxillary contact which excludes the lacrymal from the nasals. The lacrymal articulates with the frontal, maxillary, jugal, and probably with the palatine. The whole orbital region is extremely primitive, differing from the condylarth type chiefly in the small size of the pars facialis.

In *Ectoconus* the relations of the lacrymal are the same as in *Haploconus*. In *Pantolambda* the lacrymal is of moderate size and forms the anterior rim of the orbit. There is no pars facialis. The maxillo-frontal contact is wide.

Even in the highly specialized *Uintatherium* (Fig. 141) there is no pars facialis, the lacrymal being entirely within the orbit (Marsh, 1872, Pls. I, II) where it is appressed to the inner wall. The foramen faces externally. The normal contacts with the frontal, maxilla, and jugal are retained.

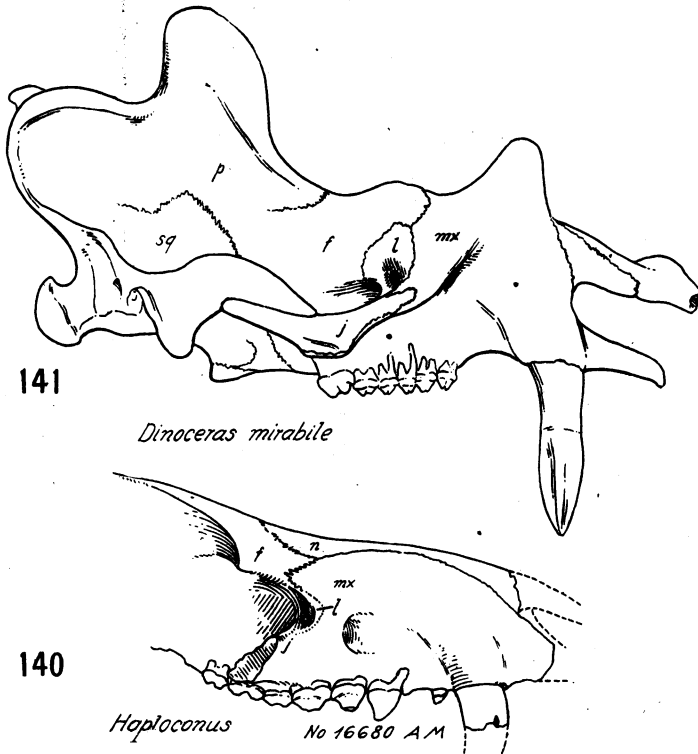
Proboscidea

In the Upper Eocene *Mærittherium* (Fig. 142) the position and limits of the lacrymal are not known. In one specimen "there is on the edge of the orbit a small tubercle presumably borne on the lacrymal, but there is no evidence of a lacrymal foramen" (Andrews, 1906, p. 103). The eyes are very far forward. The jugal is separated from the lacrymal by the maxilla. The orbital region is much more primitive than that of other Proboscidea, and suggests the sirenian type.

In *Palæomastodon* the lacrymal is a "small bone wedged between the frontal and maxilla and grooved below by the upper surface of the antorbital canal. It is perforated by a large foramen which lies within the border of the orbit; above the foramen and on the rim of the orbit there is a small but prominent tubercle" (Andrews, 1906, p. 138). The maxilla usurps the place of the jugal below the orbit and widely separates the lacrymal from the jugal. There is no pars facialis. The lacrymal has perhaps been restricted by the recession of the nares and the crowding back of the trunk muscles.

In *Mastodon americanus* (Fig. 145) the lacrymal is rather widely extended on the inner wall of the orbit. The foramen is on the anterior wall of the orbit near the junction of the lacrymal with the maxilla. The latter widely separates the jugal from the frontal.

In modern elephants (Fig. 146) the lacrymal is rather small and has no pars facialis. It forms the anterior rim of the orbit and has a moderate orbital expansion. The stout tubercle serves for the attachment of the palpebral ligament and the lacrymal is surrounded by the robust orbicularis muscles. (See the dissections in Boas and Paulli, 1908.) The maxillo-frontal contact is wide. The foramen and canal are absent,

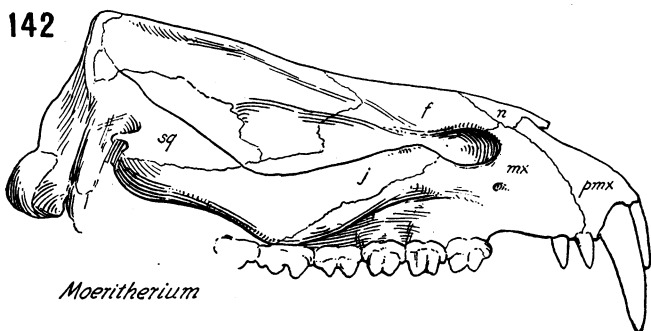
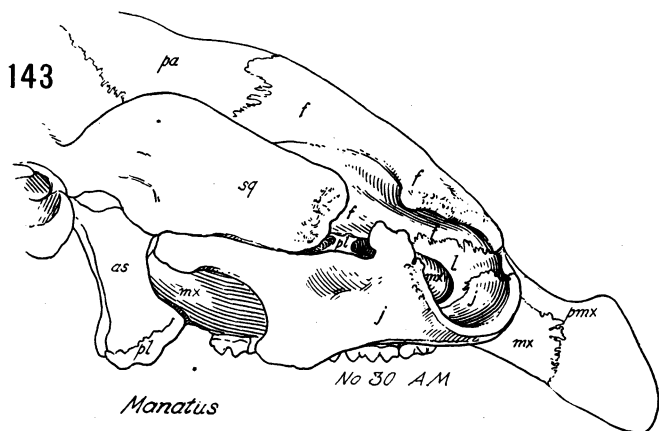
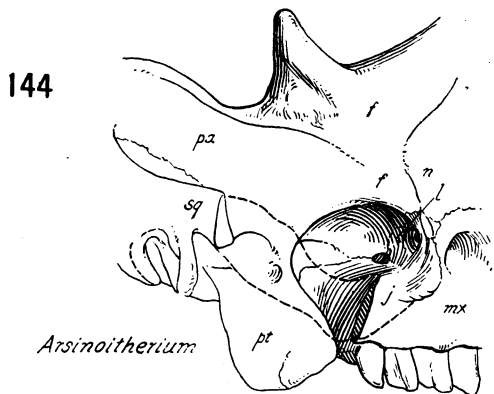


Figs. 140, 141. Skulls of Amblypoda. Subclass Placentalia, order Amblypoda.

140. *Haploconus lineatus*. Suborder Taligrada, family Periptychidae. Paleocene, Polymastodon zone, Puerco formation, San Juan basin, New Mexico.

141. *Dinoceras mirabile*. Suborder Dinocerata, family Uintatheriidae. Middle Eocene, Uintatherium zone, Upper Bridger, Bridger basin, Wyoming. After Marsh.

and likewise the lacrymal gland (Weber, 1904, p. 719). The lacrymal has been less affected by the development of the trunk than have many other elements of the skull.

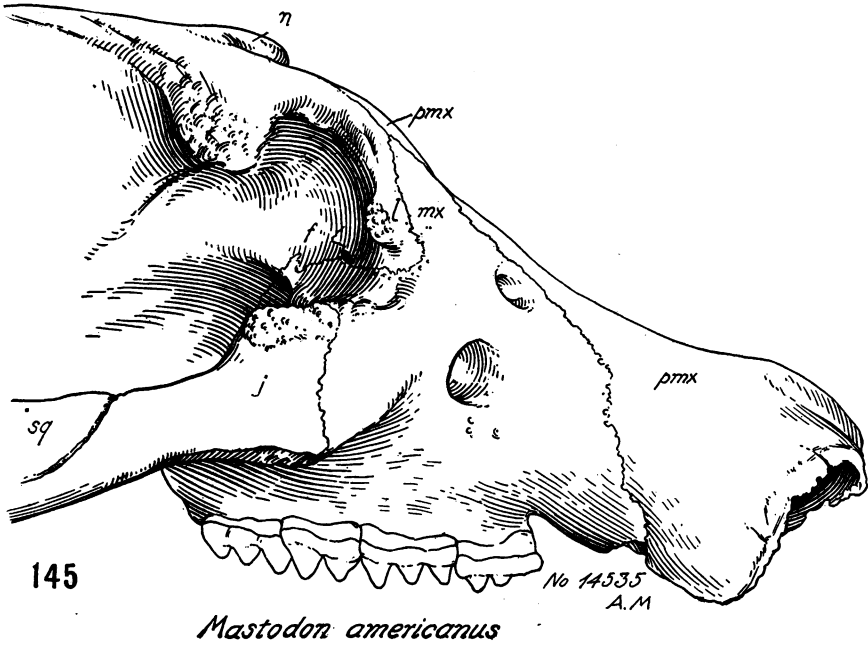
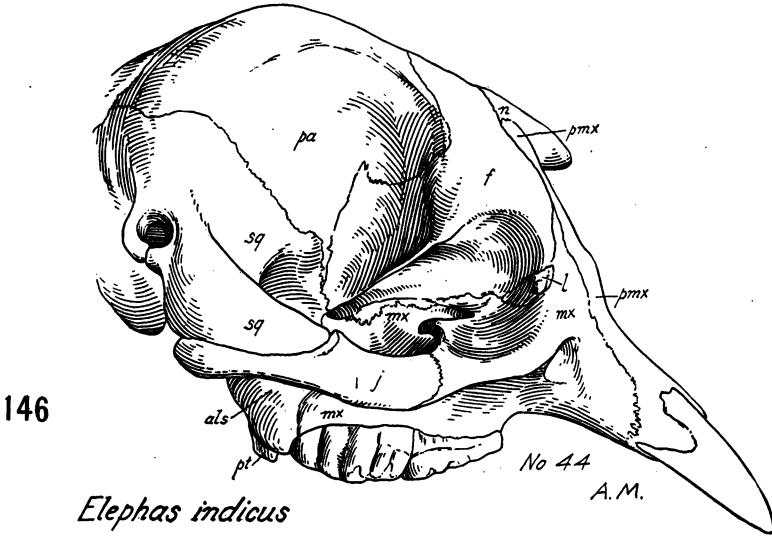


Figs. 142 to 144. Skulls of *Mæritherium*, *Manatus* and *Arsinoitherium*. Sub-class Placentalia, orders Proboscidea, Sirenia, Embrithopoda.

142. *Mæritherium lyonsi*. Order Proboscidea, family Mæritheriidae. Upper (?) Eocene, Quasr-el, Saga beds, Fayûm, Egypt. After Andrews.

143. *Manatus latirostris*. Order Sirenia, family Manatidae.

144. *Arsinoitherium zitteli*. Order Embrithopoda, family Arsinoitheriidae. Lower Oligocene, Fluvio-marine beds, Fayûm, Egypt. After Andrews.



Figs. 145, 146. Skulls of Proboscidea. Subclass Placentalia, order Proboscidea.

145. *Mastodon americanus*. Family Mastodontidae. Pleistocene, Indiana.

146. *Elephas indicus*. Young skull. Family Elephantidae.

Sirenia

The lacrymal of *Eosiren* is not known.

In *Manatus* (Fig. 143) the lacrymal is extended anteroposteriorly on the inner wall of the orbit. No lacrymal duct is visible, and Murie found no lacrymal gland present (Weber, 1904, p. 733). The jugal retains contact with the lacrymal, whereas in the Proboscidea it is widely removed from it.

In the dugong (*Trichechus*) and in *Rhytina* the lacrymal is thickened on the anterior rim of the orbit.

Embrithopoda

The lacrymal of *Arsinoitherium* (Fig. 144) is described by Dr. Andrews (1906, p. 7) as follows:

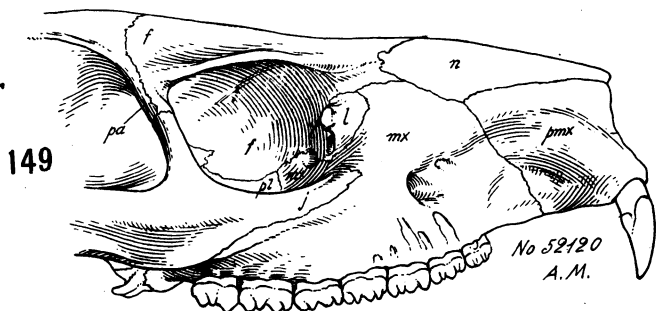
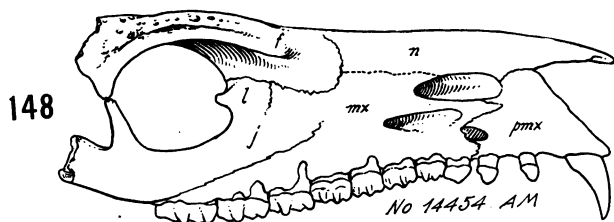
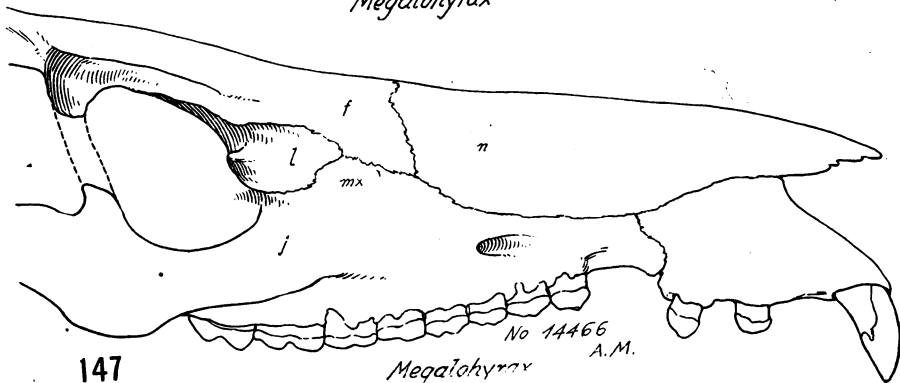
The lacrymal is a small bone occupying the anterior angle of the orbit, wedged in between the frontal above, and the maxilla and jugal below. It bears a vertically-elongated prominence (see Pl. I, l), which forms the actual edge of the orbit and is connected below with a strong crest borne on the front of the maxillary process of the jugal. There seems to be no trace of any lacrymal foramen.

It is rather interesting to find the lacrymal of this animal maintaining so much of its primitive character and position in such highly specialized surroundings.

Hyracoidea

In the Upper Eocene *Megalohyrax* (Figs. 147-148) the face is greatly prolonged in front of the orbits which lie mostly behind the molars. The fronto-maxillary contact is widely extended and with it the pars facialis of the lacrymal. The stout lacrymal spine points backward. Contact with the jugal is retained.

In *Dendrohyrax* (Fig. 149) the lacrymal is a small, more or less quadrilateral bone at the anterior corner of the orbit and with but little orbital expansion. It bears a very prominent spine, which is above the crista anterior of the maxilla. It is separated from the widely spreading nasal by a small to moderate maxillo-frontal contact and from the jugal by the crista anterior of the maxilla. On the inner wall of the orbit it is widely separated from the vertical plate of the palatine by a fronto-maxillary contact. The large foramen is well within the orbit, behind and below the spine. The lacrymal is quite hollow within, its cavity opening anteriorly into the maxillary antrum, lateral to the turbinate bones. The bony naso-lacrymal duct is supported by laminae from the lacrymal and maxilla. Beginning at the lacrymal foramen it turns sharply inward and slightly downward running in toward the ethmoid

*Dendrohyrax**Megalohyrax**Megalohyrax*

Figs. 147 to 149. Skulls of Hyracoidea. Subclass Placentalia, order Hyracoidea, family Hyracidae.

147. *Megalohyrax* sp. Subfamily Saghatheriinae. Lower Oligocene, Fluvio-marine beds, Fayûm, Egypt.
 148. *Megalohyrax* sp. Subfamily Saghatheriinae. Lower Oligocene, Fluvio-marine beds, Fayûm, Egypt.
 149. *Dendrohyrax* sp. Subfamily Hyracinae (Procaviinae).

beneath the ethmo-turbinals. It then turns forward coursing along the inner side of the maxilla and premaxilla and opens below a curved lamina on the inner side of the premaxilla above the enlarged incisor.

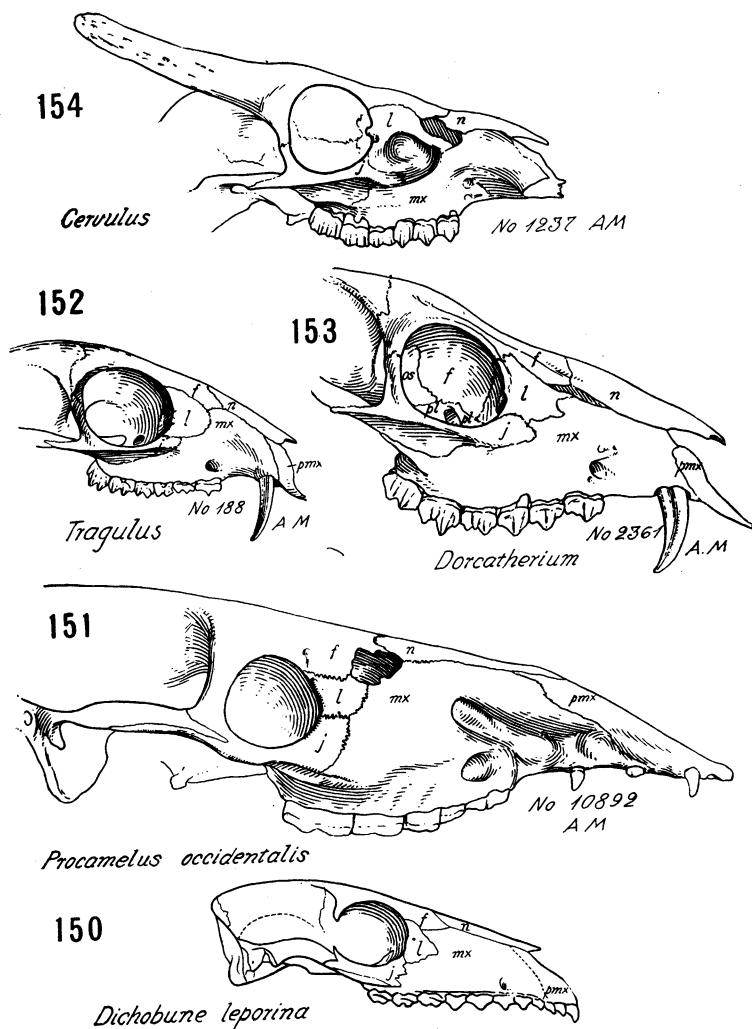
In *Procavia* the lacrymal is less quadrilateral in form, its orbital extension being more covered by the frontal and maxilla. It is set more obliquely, running anterosuperiorly into a point. Its prominent spine is directed downward and backward, rather than outward. It sometimes has contact with the nasal and separates the frontal from the maxilla, but usually it is excluded from the nasals by a small fronto-maxillary contact. It is separated from the jugal by a strip of the maxilla which is of varying width, sometimes very narrow, so that the jugal very nearly reaches the lacrymal. Its ample duct runs sharply downward and forward enlarging in its descent and opening widely below into the nasal tract, behind the anterior palatine foramen. Thus the two living genera of hyracoids exhibit rather wide differences in the lacrymal region.

Artiodactyla

In this order the lacrymal primitively forms the sharp anterior rim of the orbit and the extension of the preorbital part of the lacrymal (pars facialis) early attained an extreme. In modern forms this facial part serves as a base for the orbicular muscles and is correlated with a forward continuation of the inner canthus of the eye and with outwardly directed eyes.¹ The expanded lacrymal also serves in part for the attachment of the maxillo-labialis superior and naso-labialis muscles, and sometimes its external surface is depressed by a large facial gland.

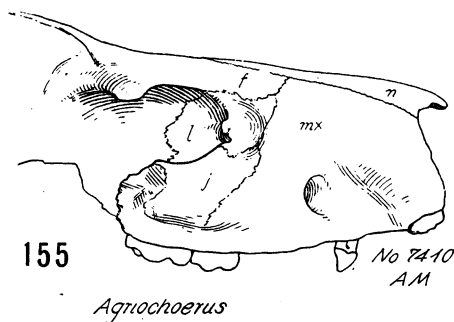
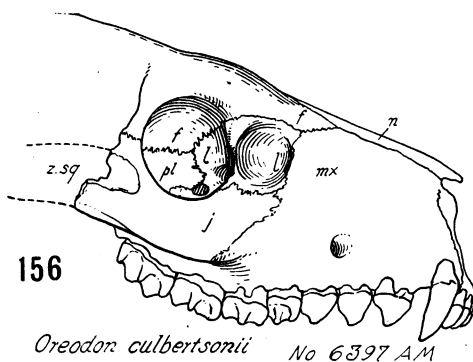
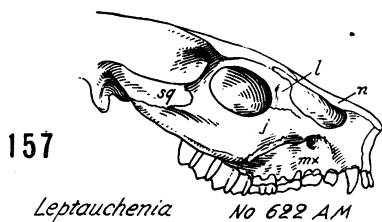
The lacrymal region in the Eocene *Dichobunidae* (Fig. 150) has been carefully figured by Stehlin (1906) and is well shown in an uncrushed skull of *Homacodon vagans* in this museum. These forms suggest *Tupaia* and *Myrmecobius* in the swollen and tubular character of the preorbital part of the face and in the way that the lacrymals form the anterior rim of the orbits and project laterally in the top view. The pars facialis is well developed. The tubercle is marginal and the foramen is medial to it, behind the anterior orbital rim. There is a wide maxillo-frontal contact. The nasals do not spread widely in the top view but are narrowed proximally by the fronto-maxillary contact. Such are the conditions in *Dichobune* and *Tapirulus* according to Stehlin's figures, but in *Mixtotherium* the lacrymal as provisionally restored in Stehlin's figure is much reduced.

¹See the dissections given by Boas and Paulli, Windle and Parsons, Cuvier and Laurillard.



Figs. 150 to 154. Skulls of Artiodactyls. Subclass Placentalia, order Artiodactyla.

150. *Dichobune leporina*. Family Dichobunidae. Upper Eocene (Upper Ludien), Phosphates of Quercy, France, After Stehlin.
 151. *Procamelus occidentalis*. Family Camelidae. Upper Miocene, Procamelus zone, Little White River, South Dakota.
 152. *Tragulus* sp. Family Tragulidae.
 153. *Dorcatherium* sp. Family Tragulidae.
 154. *Cervulus* sp. Family Cervidae.



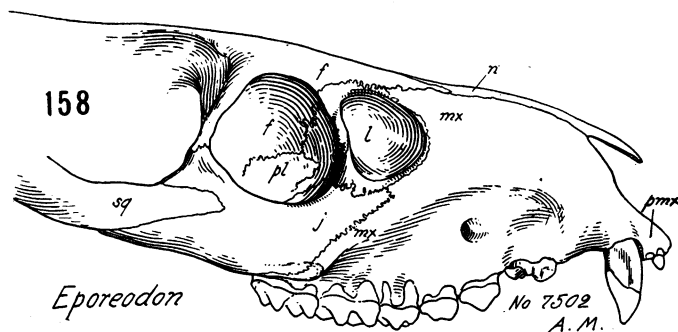
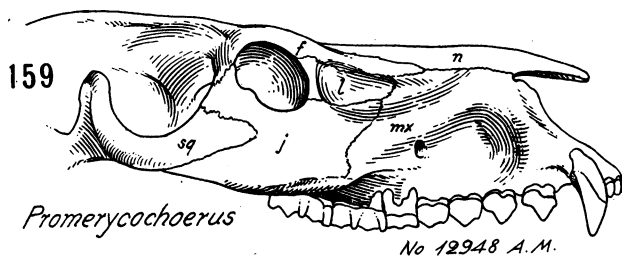
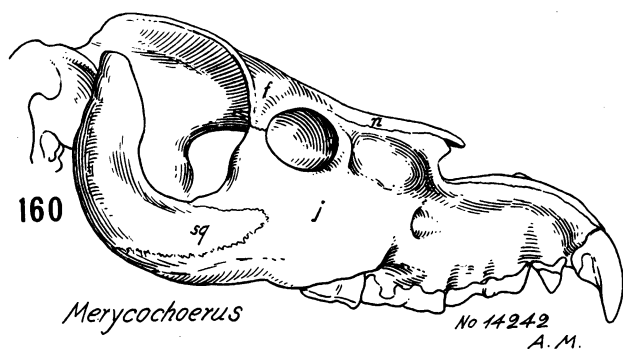
Figs. 155 to 157. Skulls of Oreodonts. Subclass Placentalia, order Artiodactyla, family Oreodontidae.

155. *Agriochoerus trifrons*. Upper Oligocene, John Day formation, Oregon.

156. *Oreodon culbertsonii*, var. *periculatorum*. Middle Oligocene, Oreodon zone, Brule formation Cedar Creek, northeastern Colorado.

157. *Leptauchenia decora*. Upper Oligocene, Protoceras zone, Upper Brule formation, South Dakota.

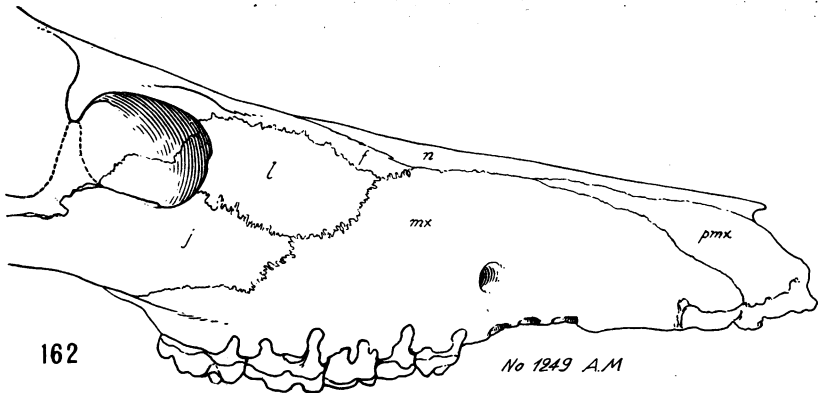
Among the Oreodontidae (Figs. 155–160) the conditions of the lacrymal region might readily be derived from those in the Dichobunidae. The pars facialis now bears a wide depression for a facial gland, the



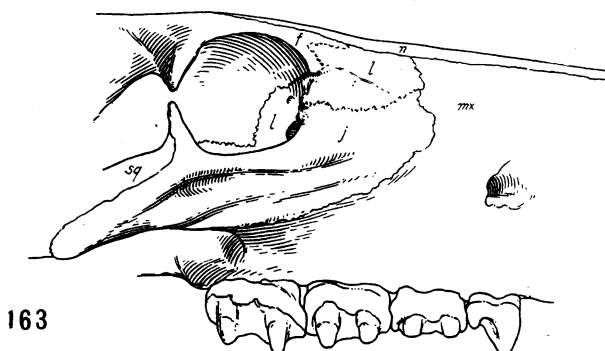
Figs. 158 to 160. Skulls of Oreodonts (continued).

158. *Eporeodon occidentalis* var. *pacificus*. Upper Oligocene, John Day formation, Oregon.
 159. *Promerycochoerus* sp. Lower Miocene, Promerycochoerus zone, Arikaree formation, Lower Rosebud beds, South Dakota.
 160. *Merycochoerus* sp. Lower Miocene, Arikaree formation, Merycochoerus zone, Upper Harrison beds, Nebraska.

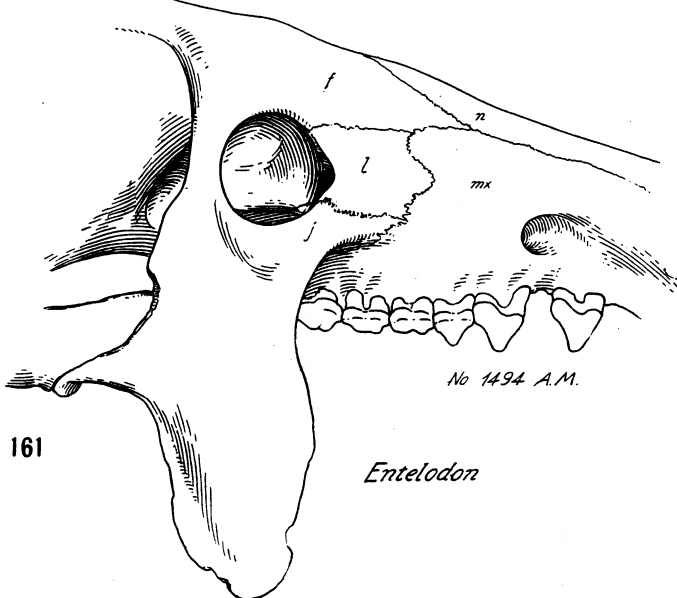
foramen is internal, the nasals narrow proximally, and there is a wide maxillo-frontal contact. In *Agriochærus* similar conditions obtain. In *Merychyus* the anterior apophysis of the frontal is long and thin, lying between the expanded lacrymal and the nasals.



Ancodon brachyrhynchus



Hippopotamus lemerlei



Entelodon

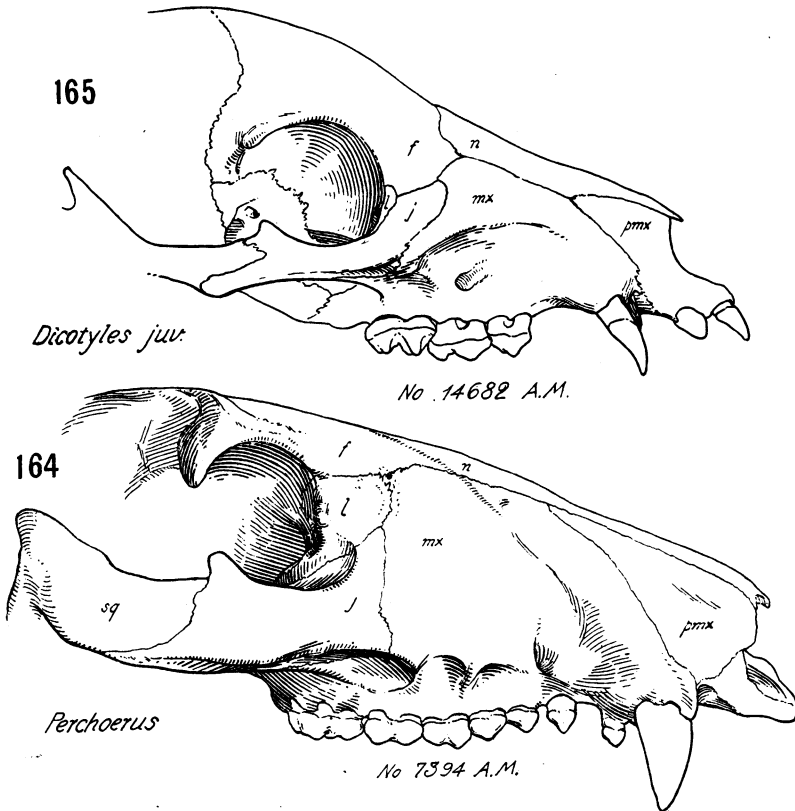
Figs. 161 to 163. Skulls of pig-like Artiodactyls. Subclass Placentalia, order Artiodactyla.

161. *Entelodon* sp. Family Entelodontidae (Elotheriidae). Middle Oligocene, Oreodon zone, Brule formation, South Dakota.

162. *Ancodon brachyrhynchus*. Family Anthracotheriidae. Upper Oligocene, Protocreces zone, Brule formation, South Dakota.

163. *Hippopotamus lemerlei*. Family Hippopotamidae. Pleistocene, Madagascar.

Among the Anthracotheriidae, *Ancodon brachyrhynchus* (Fig. 162) has an extremely long facial extension of the lacrymal, surmounted by even longer anterior apophyses of the frontals. The nasals narrow at the proximal end. In *Heptacodon*, on the contrary, the spreading proximal



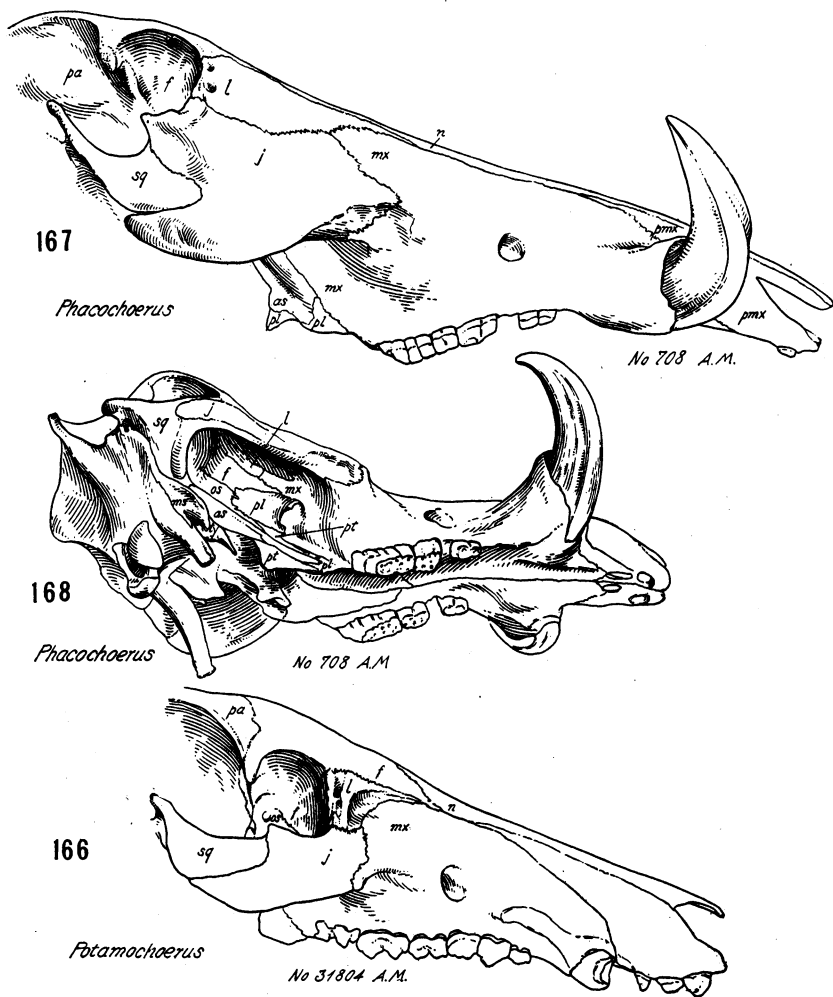
Figs. 164, 165. Skulls of *Perchoerus* and *Dicotyles*. Subclass Placentalia, order Artiodactyla, family Dicotylidae.

164. *Perchoerus pristinus*. Upper Oligocene, Diceratherium zone, John Day formation, Oregon.

165. *Dicotyles* (= *Tayassu*) *pecari*. Young skull with milk teeth.

ends of the nasals are exposed dorsally and extend toward the lacrymals, being perhaps still separated therefrom by a narrow isthmus of the frontal apophysis.

The Hippopotamidae (Fig. 163) are believed by Dr. C. E. Andrews (1906, p. xx) to have been derived from the Anthracotheriidae and their lacrymal region apparently offers nothing inconsistent with this view.



Figs. 166 to 168. Skulls of *Potamochoerus* and *Phacochoerus*. Subclass Placentalia, order Artiodactyla, family Suidæ.

166. *Potamochoerus* sp. Subfamily Suinæ.

167. *Phacochoerus*. Subfamily Phacochoerinae.

168. Same skull as in Fig. 167, oblique lower view to show the relations of the lacrymal to the surrounding elements.

The lacrymal has an extended pars facialis, which has gained wide contact with the nasal and widely separates the frontal from the maxilla.

The lacrymal region of the elotheres (Entelodontidæ, Fig. 161) exhibits little of note. There is a wide fronto-maxillary contact and an extensive pars facialis. Among the Dicotylidæ, *Perchaerus* (Fig. 164) shows a primitive condition of the lacrymal region. In the modern peccaries, however, the lacrymal is much reduced in size and is overlapped by the jugal. The lacrymal still bears the tubercle and is in contact with jugal, maxilla and frontal. There is a prominent foramen, between the lacrymal and the frontal, that leads into the nasal cavity, but it may be the sphenopalatine rather than the lacrymal foramen, as Weber (1904, p. 651) says that the lacrymal foramen of the peccary is absent.

Among the Suidæ (Figs. 166-168), *Phacochoerus* especially has a very widely extended pars facialis. In *Sus* the lacrymal is said to be shorter in domesticated races (Pira, quoted by Hilzheimer, 1918) but the length of the lacrymal is independent of the length of the snout (*idem*).

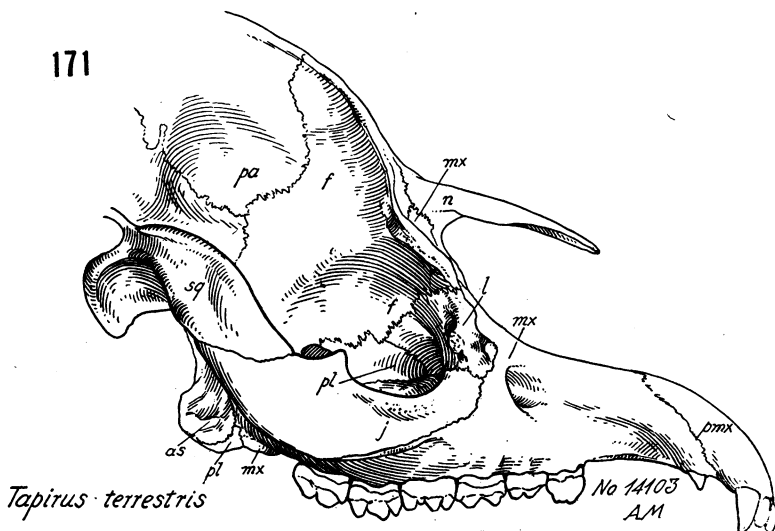
In the earlier Camelidæ (*Protylopus*, Scott, 1913, p. 399, fig. 212A) the pars facialis of the lacrymal is of moderate size, and the lacrymals are separated from the nasals by a fronto-maxillary contact. A slight vacuity is indicated between the nasal, lacrymal, frontal, and maxilla. Somewhat similar conditions obtain in *Procamelus* (Fig. 151). In the modern *Camelus* the proximal ends of the nasals become extraordinarily wide, replacing the fronto-maxillary contact, and are in contact with the lacrymals. The pars facialis is rather reduced and in the dried skull its anterior part is more or less replaced by a vacuity.

In the Pecora (Figs. 153, 154) the pars facialis of the lacrymal sometimes becomes very long as in the ox. It has the oblique position, running forward and inward from the orbit to the snout, which is clearly foreshadowed in *Oreodon*. It usually develops a vacuity at the antero-internal corner and is depressed externally by the facial gland. The maxillaries and frontals are widely separated an obvious specialization. The variations in the details of the lacrymal region in the Pecora have been used for systematic purposes by Dr. Knotternus Meyer (1907).

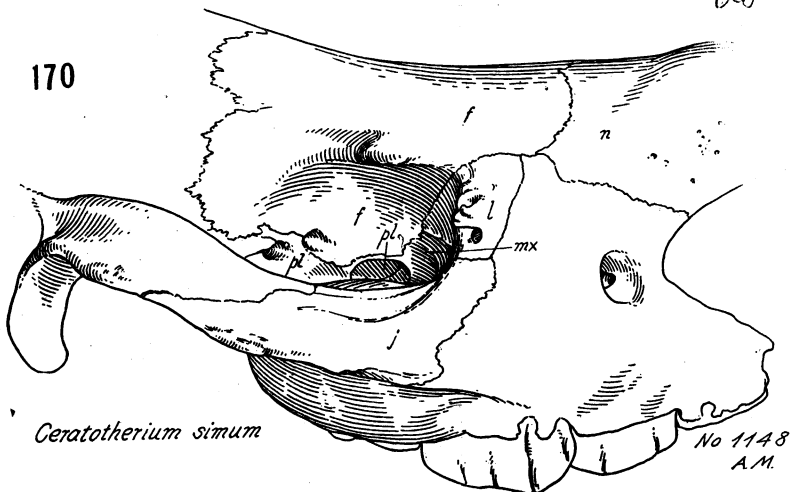
Perissodactyla

In *Mesohippus* the lacrymal is a flat squarish bone of moderate size located at the upper front margin of the orbit; it makes a wide contact with the spreading nasal and widely excludes the frontal from the maxillary. The maxillo-nasal contact does not extend much above the middle of the lacrymal.

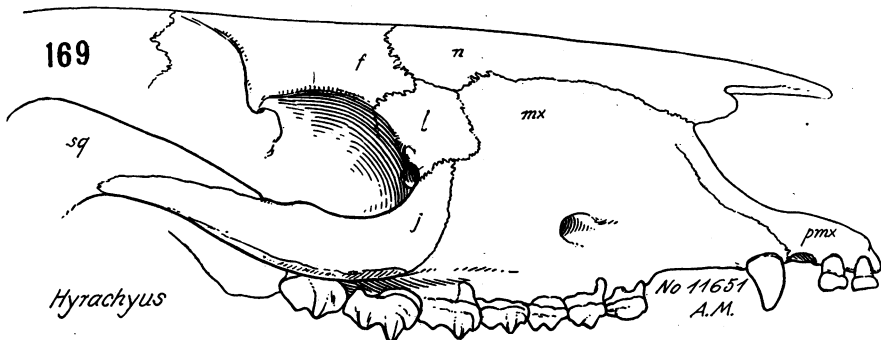
171



170



169



Figs. 169 to 171. Skulls of Perissodactyls. Subclass Placentalia, order Perissodactyla.

169. *Hyrachyus* sp. Superfamily Rhinoceroidea, family Rhinocerotidae, subfamily Hyrachyinae. Middle Eocene, Lower Bridger, Orobippus zone, Bridger basin, Wyoming.
 170. *Ceratotherium simum*. Family Rhinocerotidae. White rhinoceros. Young skull with milk teeth.
 171. *Tapirus terrestris*. Family Tapiridae.

In the later Equidæ *pari passu* with the deepening of the face the lacrymal also expands in size, but the pars facialis always remains more or less square and never much resembles the elongate oblique pars facialis of the Artiodactyla. The foramen lies in the primitive position within the anterior margin of the orbit. The lacrymal and malar fossæ of the Tertiary Equidæ will be discussed in Number V of this series of studies.

As shown in Mr. S. H. Chubb's preparations, the wide nasals of the horse cover the expanded nasal and frontal sinuses. The expanded lacrymals protect the ethmoid region laterally. The lacrymal duct follows its primitive course along the inner side of the maxilla. In a zebra foal the lacrymal is relatively small.

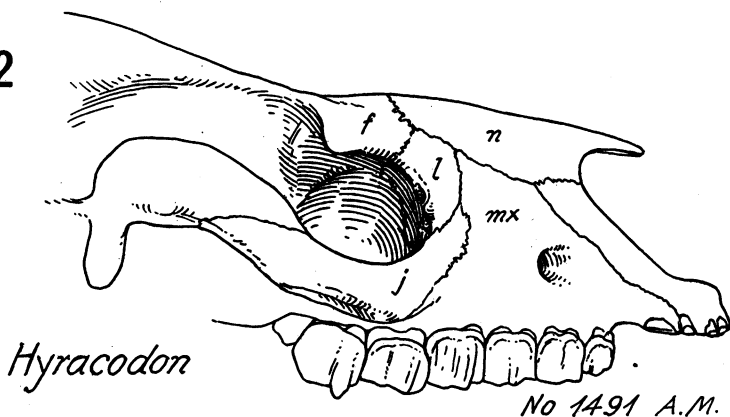
Among those Eocene perissodactyls which are allied both to *Eohippus* and to the ancestors of the Tapiridæ, *Systemodon* and *Isectolophus* have widely spreading nasals, which apparently were in contact and replaced the fronto-maxillary contact. The same was true of the palæotheres, of *Triplopus cubitalis*, which was perhaps allied to the Hyracodontidæ, and of *Hyrachyus* (Fig. 169), a primitive relative of the lophiodonts and rhinoceroses.

The lacrymal region is especially well shown in skulls of *Hyracodon* (Fig. 172). Here the lacrymal has a large contact with the nasals and widely excludes the frontals from the maxilla. The pars facialis is well developed. In *Coloniceros agrestis* Marsh the lacrymal had a well-developed pars facialis and was apparently in contact with the widely spreading nasals, the foramen was internal to the crista anterior of the orbit; a distinct but small tubercle is present just lateral to the foramen. Similar conditions are present in *Cænopus* (Fig. 173), a primitive rhinoceros, and in *Eomoropus* and *Moropus* of the Chalicotheriidæ. Hence it is evident that the early perissodactyls have a very distinctive lacrymal region which differentiates them from other ungulates with an expanded pars facialis.

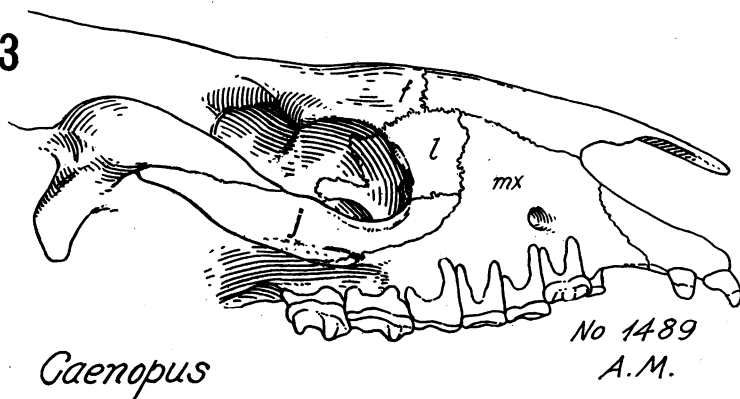
In the tapirs (Fig. 171) the recession of the naso-maxillary fissure backward and upward and the growth of the trunk muscles have conditioned the loss of the pars facialis of the lacrymal and of the lacrymo-nasal contact, the dorsal extension of the ascending process of the maxilla, and the consequent establishment of a new fronto-maxillary contact. These conditions are foreshadowed in the Miocene *Protapirus* but, in view of the apparent constancy of a naso-lacrymal contact in the earlier Perissodactyla, the opposite condition in the tapirs appears to be secondary.

So also the more specialized species of modern rhinoceroses, in spite of the wide naso-lacrymal contact of their early Tertiary predecessors, tend to lose this contact, apparently because the nasals become somewhat drawn forward under the horns, so that in both the Black Rhino-

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173

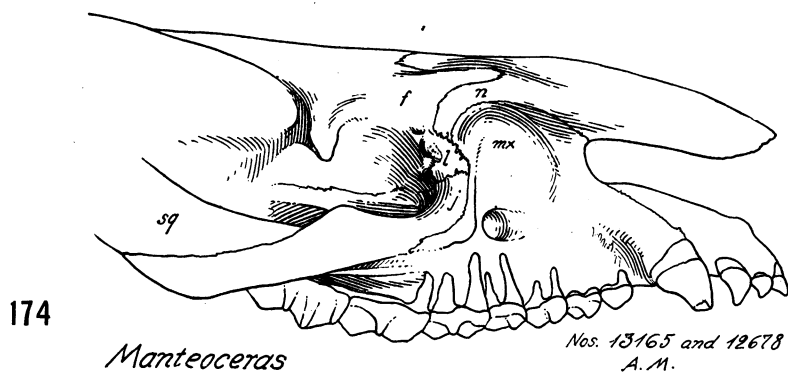
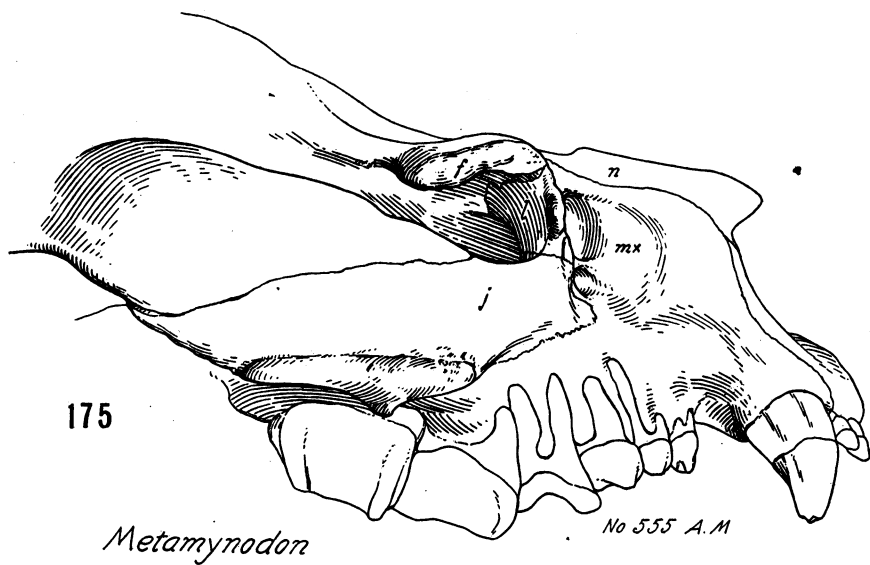


Figs. 172, 173. Skulls of *Hyracodon* and *Caenopus*. Subclass Placentalia, order Perissodactyla, superfamily Rhinocerotidae.

172. *Hyracodon nebrascensis*. Family Hyracodontidae, subfamily Hyracodontinae. Middle Oligocene, Oreodon zone, Brule formation, South Dakota.

173. *Caenopus* (= *Subhyracodon*) *trigonodus*. Family Rhinocerotidae. Middle Oligocene, Oreodon zone, Brule formation, South Dakota.

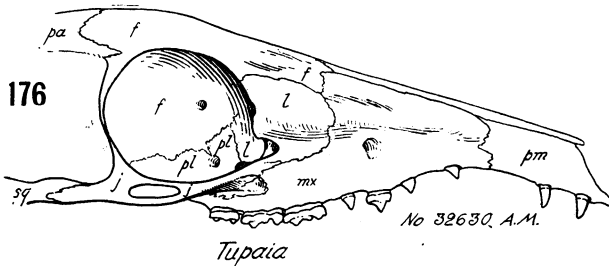
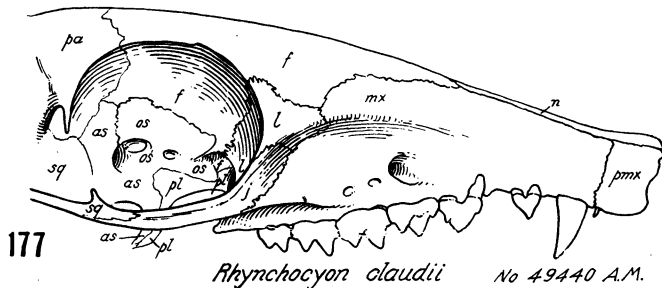
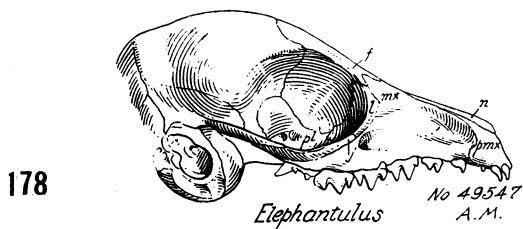
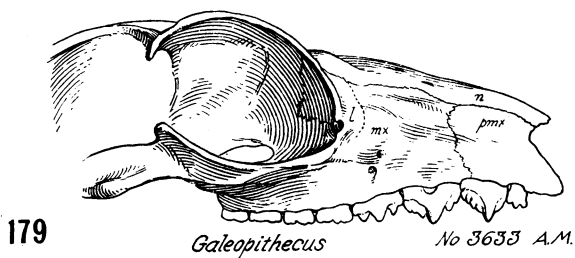
ceros and the White Rhinoceros (Fig. 170) a slight fronto-maxillary contact is established even in very young skulls. The primitive *Rhinoceros sondaicus* retains the naso-lacrymal contact.



Figs. 174, 175. Skulls of *Manteoceras* and *Metamynodon*. Subclass Placentalia, order Perissodactyla.

174. *Manteoceras washakiensis*. Superfamily Brontotheroidea, family Brontotheriidae, subfamily Manteoceratinae. Middle Eocene, Lower Washakie, Uintatherium zone, Wyoming.

175. *Metamynodon planifrons*. Superfamily Rhinocerotioidea, family Amynodontidae. Middle Oligocene, Oreodon zone, Lower Brule formation, South Dakota.



Figs. 176 to 179. Skulls of Tupaoids and *Galeopithecus*. Subclass Placentalia, orders Menotyphla, Dermoptera.

176. *Tupaia* sp. Order Menotyphla, family Tupaiidæ, subfamily Tupainæ.

177. *Rhynchocyon claudii*. Order Menotyphla, family Macroscelididæ.

178. *Elephantulus* (*Macroscelides*) sp. Order Menotyphla, family Macroscelididæ.

179. *Galeopithecus* sp. Order Dermoptera, family Galeopithecidæ.

Among the titanotheres all the numerous Eocene genera which have been investigated by Professor Osborn and the writer have proximally spreading nasals which are in contact with the lacrymals and exclude the frontal from contact with the maxilla. The lacrymal in all these animals forms the anterior rim of the orbit and has no pars facialis. The tubercle is prominent and the large duct is just within the border of the orbit (Fig. 174).

In the later titanotheres the anterior apophyses of the frontals partly overlap the nasals and with them give rise to the rapidly progressive "horns"; but the frontals never gain contact with the maxilla. The extreme development of the "horns" conditions the growth of a lateral supporting pillar in front of the eyes, which is formed from the nasals, frontals, lacrymals, and jugals.

Menotyphla

The tupaoid "insectivores" are widely removed from the true insectivores and are probably survivors of the pre-Tertiary ancestral lemuroid stock.¹ The group appears to be represented in the Lower Eocene by the Plesiadapidae,² which are remotely allied to the Eocene lemuroids.

In the recent *Tupaia* (Fig. 176) the snout is more or less conical, the frontals, maxillæ, and lacrymals widely expanded, to cover the large, highly convoluted ethmoid scrolls. The orbit is deep and sharply rimmed by the jugal, lacrymal, and frontal. The lacrymal, as is usual in such cases, is prominently developed on the well-rimmed projecting margin of the orbit. It has a well-developed pars facialis, the tubercle is marginal and the foramen medial to the tubercle. There is a well-marked fronto-maxillary contact. In *Ptilocercus* the pars facialis bears a depression which is apparently for the preorbicularis muscle. The foramen is marginal, almost in front of the orbit; the lacrymal region as a whole is lemur-like (Gregory, 1910, Fig. 21, p. 273).

Among the Macroscelididae the lacrymal region of *Rhynchocyon* (Fig. 177) agrees in essentials with that of *Tupaia*. The frontal region is even wider. There is a deep fossa for the maxillo-labialis superior on the side of the maxilla in front of the lacrymal. In *Macroscelides* and allied genera (Fig. 178) the anterior rim of the orbit is squeezed between

¹1910, Bull. Amer. Mus. Nat. Hist., XXVII, pp. 279, 280, 321, 322; 1913, Bull. Geol. Soc. Amer., pp. 247-252.

²1920, Mem. Amer. Mus. Nat. Hist., (N. S.) III, part 2. See also Matthew, W. D., 1917, Bull. Amer. Mus. Nat., XXXVIII, pp. 836-838.

the large eye and the facial muscles, and the marginal part of the lacrymal together with the pars facialis is much reduced.

Dermoptera

In *Galeopithecus* (Fig. 179), which may well be remotely related to the Menotyphla, the general conformation of the facial region is somewhat similar to that of *Rhynchocyon*, except that the whole muzzle is now very broad and more or less inflated. The orbits are sharply rimmed above and in front, the lacrymal giving a prominent orbital rim. The pars facialis is extended. The fronto-maxillary contact is reduced. The foramen is within the orbital rim.

Chiroptera

In the Microchiroptera sutures are very hard to make out but in a foetal specimen of *Saccolaimus peli*, kindly placed at my disposal by Mr. Herbert Lang, there is a vacuity on the inner wall of the orbit between the maxilla and the frontal, which may have been filled either by the lacrymal or by the os planum of the ethmoid. In an adult *Saccolaimus* the small lacrymal foramen is on the raised anterior rim of the orbit. There is certainly no pars facialis. The fronto-maxillary contact is large.

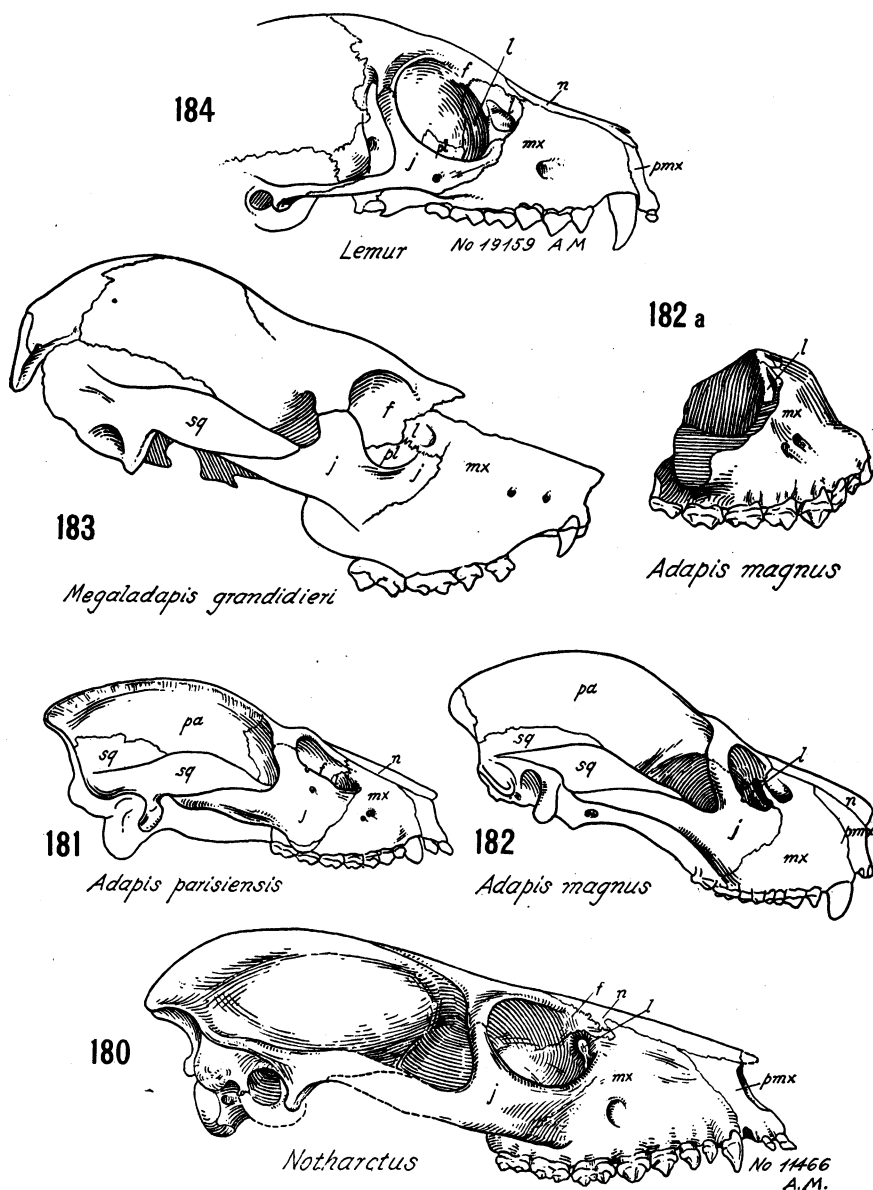
In the Macrochiroptera the lacrymal may readily be seen in young skulls. In *Eidolon helvus* it is a relatively large element crowded well forward so that it has but a small pars orbitalis, which is vertically extended and in contact with the frontal, the palatine, and the maxilla. The pars facialis is moderately extended and is separated from the pars orbitalis by a well-marked crista posterior. The pars facialis bears a large fossa leading into a prominent fissure at the antero-inferior corner of the lacrymal and between the lacrymal and the maxillary. There is also a very small lacrymal foramen on the posterior rim of the crista posterior. The lacrymal is widely separated from the jugal by the maxilla. There is a good fronto-maxillary contact.

Thus the lacrymal region of the Megachiroptera is rather similar to that of a modern *Lemur* and this is very possibly because in both these long-snouted forms the inner canthus of the eye has been shifted forward, extending the pars facialis and lacrymal foramen.

In the secondarily short-snouted *Myonycteris wrightoni*, on the other hand, the pars facialis is short.

Primates

The lacrymal region (Fig. 180) of the Middle Eocene *Notharctus*, a primitive member of the Lemuroidea, has been briefly referred to by



Figs. 180 to 184. Skulls of Lemuroids. Subclass Placentalia, order Primates, suborder Lemuroidea, series Lemuriformes.

180. *Notharctus osborni*. Family Adapidae, subfamily Notharctinae. Middle Eocene, Lower Bridger, Orohippus zone, Bridger basin, Wyoming.
 181. *Adapis parisiensis* var. *bruni*. Family Adapidae, subfamily Adapinae. Upper Eocene, Phosphorites of Quercy, France. After Stehlin.
 182. *Adapis (Leptadapis) magnus*. Family Adapidae, subfamily Adapinae. Upper Eocene, Phosphorites of Quercy, France. After Stehlin.
 182a. *Adapis (Leptadapis) magnus*. After Stehlin.
 183. *Megaladapis grandidieri*. Family Lemuridae, subfamily Megaladapinae. Recent, Madagascar. After Standing.
 184. *Lemur mongoz*. Family Lemuridae, subfamily Lemurinae. Recent, Madagascar.

Dr. Wortman (1903, pp. 172, 174) and has recently been described and figured by the writer (1920, p.155). From imperfect skulls of the ancestral *Pelycodus* it seems probable that this type of lacrymal region even extended back into the Lower Eocene.

As compared with the lacrymal of more primitive Eocene placentals, that of *Notharctus* is characterized by the reduction of the pars facialis and the anomalous position of the lacrymal foramen, which lies in front of the lacrymal at the junction of the lacrymal, maxilla, and jugal.

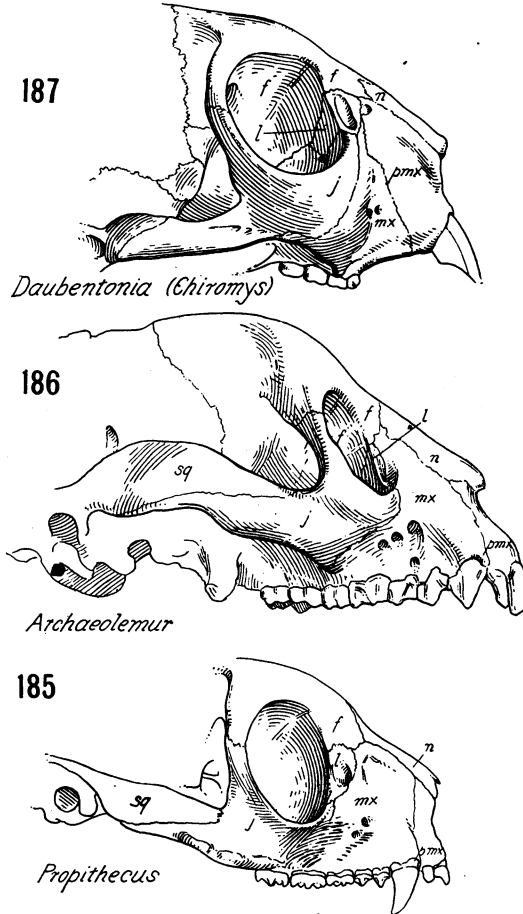
Immediately below the frontal the lacrymal bears a prominent tuberosity, which doubtless served for the attachment of the palpebral ligament. Above the lacrymal and below and in front of the dorsal rim of the orbit there was a shallow groove on the frontal; a similar groove occurs in *Adapis* and in modern lemurs; it may have been the anterior insertion area of the sheet-like orbito-auricularis muscles. The proximal end of the nasals spread widely beneath the overlapping maxillæ. The jugal came very close to or actually touched the lacrymal.

Accordingly, the lacrymal region of *Notharctus* was essentially identical with that of *Adapis*, namely: pars facialis reduced or wanting, antorbital rim represented chiefly by a tuberosity, lacrymal foramen forming a fissure in front of the lacrymal at the junction of the maxilla, lacrymal, and jugal.

The lacrymal region of *Adapis parisiensis* was carefully described by Dr. Forsyth Major in 1901. Dr. Stehlin (1912, pp. 1196-1198, 1251, 1252) has confirmed and extended Major's account and has also described the lacrymal region of *Adapis (Leptadapis) magnus*. In comparison with other Eocene placentals, the three most striking features of the lacrymal in *Adapis* are, first, its small size; second, the preorbital position of the lacrymal foramen, which is a mere fissure in front of the lacrymal and between the lacrymal and maxilla; and, third, the virtual absence of a pars facialis, so that the lacrymal lies almost entirely within the orbit. The dorsal part of the pars facialis, immediately below the frontal, bears a tuberosity which is variously developed in different skulls. This is apparently homologous with the "crista posterior" of the lacrymal of modern lemurs and probably represents a remnant of the primitive antorbital rim. The jugal was sometimes in contact with the lacrymal (Stehlin, 1912, pp. 1251), sometimes separated from it by a narrow strip of the maxilla (Major, 1901, p. 135).

In a young skull of *Megaladapis grandidieri* (Fig. 183) described by Dr. Standing (1908), the jugal is shown in contact with the lacrymal and the lacrymal foramen is marginal, not preorbital. In adult specimens of

all three species of *Megaladapis* the lacrymal foramen is continuous with a large notch in the anterior border of the orbit, recalling the notch between the tuberosity and the lower border of the orbit in *Adapis*. The pars



Figs. 185 to 187. Skulls of Lemuroids (continued). Subclass Placentalia, order Primates, suborder Lemuroidea, series Lemuriformes.

185. *Propithecus coquerelli*. Family Indridae, subfamily Indridinae.

186. *Archaeolemur edwardsi*. Family Indridae, subfamily Archaeolemurinae. Recent, Madagascar.

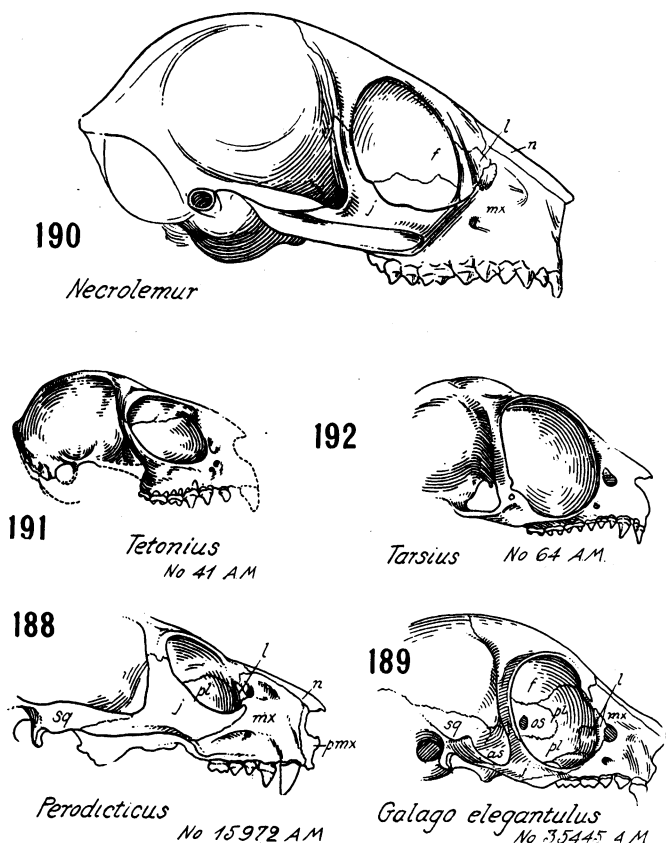
After Standing. $\times 1$.

187. *Chiromys* (= *Daubentonia*) *madagascariensis*. Family Chiromyidae.

facialis of *Adapis* seems to be much less extended anteriorly than it is in the modern *Lemur* (Fig. 184).

In *Lepilemur* (Amer. Mus. No. 31251), which is on the whole one of the most primitive of existing lemurs, the pars facialis is moderately

developed, the crista posterior and its tuberosity are prominent and the lacrymal foramen appears as a fissure between the lacrymal bone and the notched maxilla. Essentially similar conditions recur in other genera



Figs. 188 to 192. Skulls of Loriform Lemuroids, and Tarsioids. Subclass Placentalia, order Primates, suborders Lemuroidea, Tarsioida.

188. *Perodicticus potto*. Series Loriformes, family Lorisidæ, (Nycticebidae), subfamily Lorisinae.
 189. *Galago elegantulus*. Series Loriformes, family Lorisidæ, subfamily Galaginae.
 190. *Necrolemur antiquus*. Family Necrolemuridæ. Middle (?) Eocene? Phosphorites of Quercy, France. After Stehlin. $\times \frac{3}{4}$.
 191. *Tetonius* ("Anaptomorphus") *homunculus*. Family Tarsiidæ. Lower Eocene, Coryphodon zone, Gray Bull beds, Bighorn basin, Wyoming. After Matthew. $\times 1$.
 192. *Tarsius spectrum*. Family Tarsiidæ. Recent, Borneo. $\times 1$.

of modern Lemuridæ, the most variable features being the extent of the pars facialis, which is short in the short-faced *Hapalemur* (*Mioixicebus*) and exceptionally large in adult *Lemur*. In the specimen of *Mioixicebus caniceps* figured by Elliot (1912, I, Pl. xiv) the lacrymal foramen is

represented by a long anteroposterior fissure on the side of the face, corresponding to the direction of the lacrymal canal.

Among the Indrididæ, *Propithecus* (Fig. 185) has a lacrymal which is fundamentally similar to that of *Notharctus* except that the pars facialis is larger as well as the lacrymal canal and foramen. *Meso-propithecus* (Standing, *op. cit.*, Pl. xxii) and *Indris* (Milne Edwards, Pl. xxxiii) show only minor variations of the same type, while in *Lichanotus* (*Avahis* Milne Edwards, Pl. xlv, Major, Text fig. 43), in accordance with the secondary abbreviation of the muzzle, the pars facialis is very short and the foramen is marginal rather than preorbital in position.

As *Palæopropithecus* is clearly a degenerate relative of *Indris*, it is not surprising to find its lacrymal region (Standing, Pls. xi, xii) in the main similar to that of the last-named genus, save that the lower orbital rim (crista anterior) formed by the maxilla is more prominent and projects farther forward and that the foramen in one sense is not preorbital in position, although it is in front of the lacrymal bone.

In *Archæolemur* (Fig. 186) the lacrymal recalls that of *Adapis* and is comparatively primitive. In *Chiromys* (Fig. 187) the enlargement and rodent-like form of the incisors has stimulated an upward and backward growth of the premaxilla, which gains contact with the frontal and even with the lacrymal, crowding the ascending process of the maxilla into a narrow strip and widely separating it from the frontal. But in other respects the lacrymal of this animal is essentially similar to that of *Propithecus* (Fig. 185).

Among the more primitive of the loriform lemuroids (Figs. 188, 189) the lacrymal is essentially similar to that of *Adapis* save that the lacrymal foramen is larger and that the lacrymal itself is usually separated from the jugal by the maxilla. Apparently the jugal has retreated from its primitive contact with the lacrymal while its postorbital branch becomes relatively large. Further enlargement of the eyes merely emphasizes these conditions, as in the smaller Galaginæ (*Hemigalago*, *Galago elegantulus*).

In *Loris* and *Nycticebus*, as observed by Forsyth Major (1901, pp. 140-141), the lacrymal is vestigial or wanting, its place on the inner wall of the orbit being more or less usurped by an element which was identified by Major as the "os planum" or lateral exposure of the ethmoid.¹ The lacrymal foramen in all the Lorisidæ is well developed and is preorbital in position.

¹The observations of Dr. Wood Jones, (1917, Proc. Zool. Soc. London, pp. 323-329) show that the so-called os planum in *Lemur catta* is more probably the anterior plate of the palatine and that it is extremely difficult or impossible to distinguish the sutures on the medial wall of the orbit in many adult lemuroids.

The lacrymal region of *Necrolemur* (Fig. 190) has been described and figured by Stehlin (1916, pp. 1343, 1344) and is well shown in a specimen kindly loaned to the writer by the curators of the Museum of Comparative Zoology at Cambridge, Mass. The lacrymal forms a prominent rim on the anterior border of the enlarged orbit, and has : small pars facialis; the foramen, as in the loriform lemuroids, is preorbital in position. Stehlin says that the lacrymal as a whole recalls that of *Opolemur* (*Atililemur*) *thomasi*, one of the Lemuridæ. In this animal the lower end of the lacrymal touches or nearly touches the jugal and the same may be true of *Necrolemur*. The ascending process of the maxilla bears the usual fossa for the insertion of part of the orbicularis palpebrarum muscle (Stehlin, 1916, p. 1345).

In the Lower Eocene tarsiid *Tetonius* (*Anaptomorphus*) *homunculus* (Fig. 191) the small lacrymal bears a prominent vertical ridge (crista posterior) on the anterior rim of the orbit. To this ridge was doubtless attached the palpebral ligament. In front of the ridge was a depression which may have marked the attachment of the orbicularis palpebrarum muscle. The lacrymal foramen was very probably pre-orbital in position as it is in *Tarsius* and *Necrolemur*. The lacrymal is widely separated from the jugal by the maxillary which forms the greater part of the rim of the orbit anteriorly.

The morphological significance of the above described conditions of the lacrymal region of the lower primates has been interpreted quite differently by Forsyth Major (1901, pp. 150–152) and Wortman (1903, pp. 406). Dr. Forsyth Major's interpretation of the evidence was as follows:

As to the Prosimiæ, if in the future we come upon forms in the Middle or Lower Tertiaries exhibiting a facial expansion of the lacrymal, and a facial fossa l., it will then be the time to ventilate the question whether a similar condition might after all be the primitive one in the Prosimiæ. For the present we have to reckon only with the known facts. In *Adapis parisiensis* we have found the fossa lacrymalis as well as the whole bone to be inside the orbit; the lacrymal is fairly large. From this condition, the form of the lacrymal of recent Lemurs generally can have been arrived at by the development of a crista posterior; that of the non-Malagasy Lemurs, besides, by a gradual reduction of the lacrymal; that of the Malagasy Lemurs, on the contrary, by an increase in size of the pars facialis. The large expansion of the lacrymal on the face and the anterior bordering of the canalis by the latter bone, both characters which among the Prosimiæ occur only in the Malagasy Lemurs, are rather an exception within this group; they go hand in hand with the elongation of the facial cranium generally. As a rule in the Malagasy Lemurs the pars facialis is of moderate size, and the anterior boundary of the fossa is provided by the maxilla. In the Oriental and Ethiopian Lemurs the maxilla *always* borders the fossa to a large extent and chiefly in front; the pars facialis is reduced to a minimum; the pars orbitalis is also

reduced, owing chiefly to the encroachment of the planum. In two genera (*Loris*, *Nycticebus*) the lacrymal disappears entirely from the outer side of the cranium, outside and inside the orbit.

Summing up, and in order to arrive at a generalization, the following points are to be insisted upon:—

β A great facial expansion of the lacrymal, and particularly its extension beyond
r the fossa lacrymalis,—

1. Does not occur, the converse being the case, in the one Tertiary Lemur of which the lacrymal region is known;

2. It is scarcely more frequent in Lemurs than in the higher groups; the greatest reduction of the lacrymal occurs precisely within the Prosimiæ;

3. It is at its minimum in young individuals;

4. The genera of each group in which this character is presented have certainly no closer relationship with those of another group;

5. It can always be traced back to an elongation of the facial cranium, necessitated by a more powerful dentition.

The conclusion is that a great facial expansion of the lacrymal, and particularly its extension beyond the fossa lacrymalis is, in the Lemurs, as well as in the Monkeys, not a primitive condition, but an extreme specialization.

With these conclusions those of the present writer would very largely coincide, especially since the discovery of the lacrymal region of the Middle Eocene *Notharctus* (which in the vast majority of its skeletal characters is in a primitive lemuroid stage of evolution) materially strengthens Dr. Forsyth Major's view that the conditions of the lacrymal region of *Adapis* are essentially ancestral to those in modern lemurs. It is, however, apparently not necessary to assume with Dr. Major that the crista posterior of the lacrymal of modern lemurs represents a new development; to the writer it appears to be merely a remnant of the lacrymal part of the primitive antorbital rim, which has become separated from the lower part of the rim (crista anterior).

Dr. J. L. Wortman (1903, p. 406), citing Dr. Forsyth Major's studies, states that:

From his (Major's) investigations we learn that, with the single exception of *Nesopithecus*, a highly developed extinct type from Madagascar, all the lemurs possess an enlarged lacrymal which reaches beyond the orbit, while the external opening of the lacrymal canal is situated upon the side of the face.

In connection with this passage Dr. Wortman says on page 407:

The large lacrymal with the opening of the canal extraorbital in position is undoubtedly the primitive condition. This is demonstrated by reference to the Marsupials, in some of which, notably *Myrmecobius*, it is unusually large and sends a considerable spur outward upon the zygoma to join the malar. In all Insectivora, Rodentia and primitive Carnivora, the enlarged lacrymal as well as the extraorbital position of the canal is so far as I am aware universal.

The writer, on the contrary, finds it impossible to accept these statements and this conclusion and is, therefore, moved to make the following comments.

1. The condition of the lacrymal region in recent marsupials assuredly does not "demonstrate" that the "large lachrymal with the opening of the canal extraorbital in position" is the primitive condition for lemurs, which are specialized placental mammals very widely removed from the existing marsupials.

2. The conditions in *Myrmecobius* seem, to the writer, obviously not primitive as compared with the conditions in most other polyprotodont marsupials (see page 143 above).

3. The position of the lacrymal foramen in marsupials is essentially different from the "extraorbital position" of this foramen in modern lemurs, since in the former case the foramen, or at least one of the lacrymal foramina, is either behind the antorbital rim or is marginal, while in lemurs it is typically in front of the lacrymal bone, forming a groove or fissure between it and the maxilla.

4. All Insectivora, Rodentia and primitive Carnivora assuredly do not have either the enlarged lacrymal or the extraorbital position of the canal (=posterior opening of the canal?). The facts are indeed quite different. Eocene Carnivora show the pars facialis in various degrees of development. It appears to be only moderately developed in the very primitive *Deltatherium* and widely extended on the face in the relatively highly specialized Mesonychidæ and Hyænodontidæ. The lacrymal foramen in primitive carnivores, so far as the writer has been able to observe, is behind the antorbital rim and never in front of the lacrymal bone, between the lacrymal and the maxilla, as it is in typical lemurs.

The adult erinaceoid insectivores, from the Oligocene onward, have little if any pars facialis and the foramen is marginal. According to W. K. Parker's figures of *Erinaceus* embryos and young (1885, Pls. xvii-xx), the lacrymal foramen in the young stages is behind the crista anterior of the maxilla and therefore fully within the orbit. In the young *Talpa* (Pl. xxvi) and *Sorex* (Pl. xxxi), on the other hand, the foramen is definitely preorbital and (*Talpa*) in front of the lacrymal. In the primitive zalambdodont *Nesophontes* the foramen is marginal; in the specialized *Centetes* and *Solenodon*, on the other hand, the foramen comes to lie in front of the lacrymal. And none of these have a true pars facialis, that portion of the orbit which remains being undoubtedly the pars orbitalis. In the primitive Eocene rodents of the family Ischyromyidæ

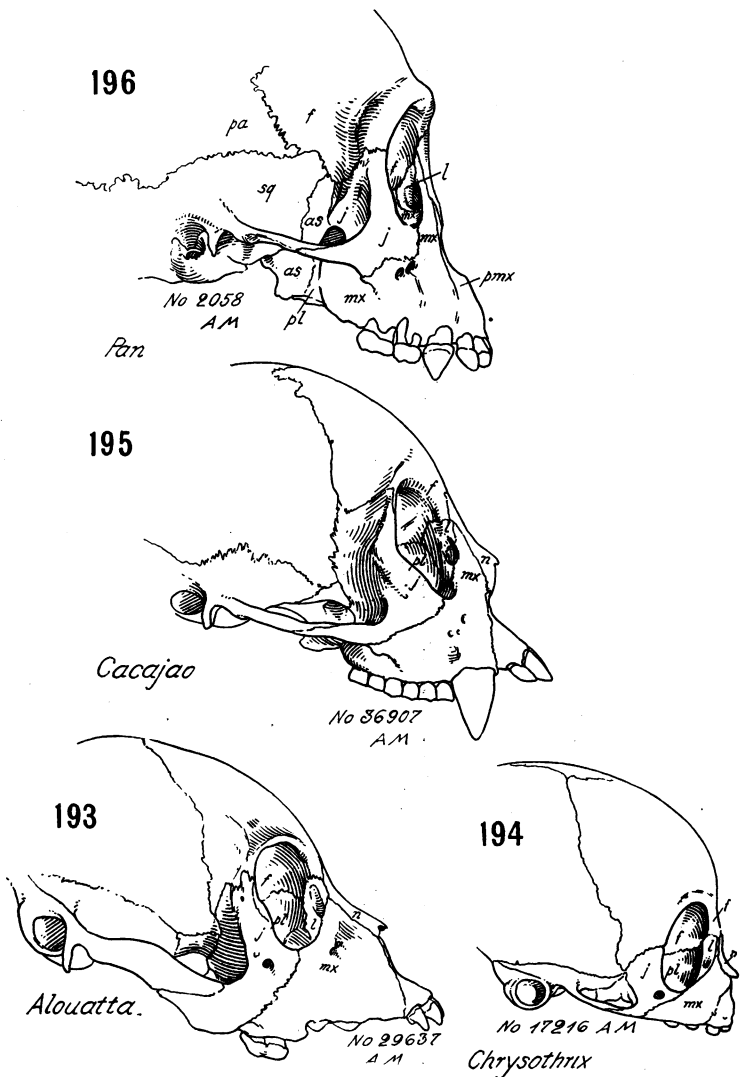
the pars facialis of the lacrymal is small and the foramen is marginal or behind the antorbital rim.

5. In the most primitive Condylarthra, Amblypoda, Rodentia, Tæniodonta, Artiodactyla, Perissodactyla, Menotyphla, etc., the lacrymal foramen is behind the antorbital rim, while in many other placental mammals it is marginal, but it is only in forms which the writer regards as specialized that the foramen shifts forward along the lacrymal duct to a position in front of the lacrymal.

6. As already noted by Forsyth Major, the extent of the pars facialis is variable in recent lemurs, attaining the maximum in adult specimens of the genus *Lemur* and being much less in young specimens and in all the Indrisidæ and Nycticebidæ. Hence it seems reasonable to infer that the extended pars facialis, when it does occur, is a secondary character, the more so as this character is the opposite of what is known in the Eocene lemuroids *Adapis* and *Notharctus*.

Up to the present time apparently no one has attempted to discover the functional significance either of the extended pars facialis of *Lemur* or of the extreme anterior position of the lacrymal foramen in all the Lemuroidea and Tarsioidea. As to the first character, cross-sections of the skull of *Lemur varius* show that the whole nasal cavity (which is of itself unusually large as compared with that of higher primates) is surrounded by a system of greatly inflated sinuses which communicate with the antrum and which have already been noticed in other connections by Forsyth Major (1901, pp. 26). These sinuses are covered externally partly by the lacrymal bone, of which both the pars orbitalis and the pars facialis are in consequence excessively large. Similar but smaller sinuses are present in other Lemuridæ and Indrisidæ. But in the loriform Lemuroidea, and still more in *Tarsius*, the marked reduction of the nasal cavity, and the crowding together of the orbits toward the mid-line, are associated both with a reduced lacrymal and a reduced system of sinuses. Somewhat parallel conditions may be observed in marsupials, the excessively large lacrymal of *Myrmecobius* being associated with an equal development of the lacrymal sinus.

The apparent explanation of the anterior position of the lacrymal duct has been gained by dissection of the orbital region of an ordinary *Lemur*. It was then seen that the eyes bulge from their sockets, that the inner canthus of the eye is carried far forward and with it the lacrymal foramen. This condition becomes very pronounced in the smaller Nycticebidæ and still more in *Tarsius*. From the forward position of the lacrymal foramen in *Notharctus* and *Adapis* as compared with other



Figs. 193 to 196. Skulls of apes and monkeys. Subclass Placentalia, order Primates, suborder Anthropoidea.

193. *Alouatta (Myces) beelzebub*. Series Platyrrhinæ, family Cebidæ. Young skull, pl, os planum.
 194. *Chrysothrix* sp. Series Platyrrhinæ, family Cebidæ. Young skull.
 195. *Cacajao calvus*. Series Platyrrhinæ, family Cebidæ.
 196. *Troglodytes (=Pan)* sp. Series Catarrhinæ, family Simiidæ.

Eocene placentals, it is legitimate to infer that even in these early primates the protrusion of the eyes and the forward shifting of the inner canthus of the eye had already begun. That their eyes were of lemuroid type is also indicated by the whole conformation of the orbital region.

With relatively minor variations and irregularities (described by Major), a single type of lacrymal runs through all the Platyrrhinæ (Figs. 193–195) and Catarrhinæ from *Mycetes* (*Alouatta*, Fig. 193) to the higher apes (Fig. 196) and to man.

This fundamental unity of type is connected with the forward direction of the orbits, with the great increase in depth of the frontal region and with the narrowing and retraction of the muzzle, these changes being in turn partly correlated with the forward growth of the frontal region of the brain and with the change in the normal position of the head on the backbone, connected primarily with sitting and brachiating habits.

Typically, the lacrymal is a small and vertically extended bone appressed to the inner wall of the orbit and having little or no pars facialis. The lacrymal foramen, or fossa, is typically in front of the lacrymal and between the lacrymal and maxilla, but in some cases, (baboons, adult *Mycetes*) in connection with the secondary elongating of the face, the lacrymal foramen is displaced backward so as to pierce the lacrymal bone, the rule being that the position of the foramen is governed in part by the position of the inner canthus of the eye and by the inclination of the lacrymal duct, which, in turn, is correlated with the depth and length of the face.

Among the Platyrrhinæ, the variable development of maxilla, lacrymal, and frontal often brings about a retreat of the maxilla from the frontal, a loss of the fronto-nasal contact, and the establishment of a nasol-acrymal contact; but in many other cases observed by Dr. Forsyth Major (1901, pp. 143–147) the maxillo-frontal contact is retained. The precise position and limits of the lacrymal fossa are usually quite variable. The lacrymal itself varies widely in size, being sometimes very small (*Midas*), sometimes fairly large (adult *Mycetes*), this depending in part on the size of the muzzle. So much of the jugal is devoted to the formation of the postorbital rim and partition that the jugal is widely separated from the lacrymal, leaving the maxilla to form the crista anterior of the orbit. On the inner wall of the orbit the lacrymal (Fig. 193) is in wide contact with the os planum (*pl*) of the ethmoid, as in most of the higher primates.

In the catarrhine division of the Anthropeidea (which division is here understood as including the Old World monkeys, anthropoids and man) the maxilla usually retains its contact with the frontal in spite of the deepening of the face, so that a naso-lacrymal contact is very exceptional. The lacrymal is essentially of the human type with only minor and variable differences. Usually the lacrymal groove or fossa is between the lacrymal and maxilla but in some cases, especially in connection with the secondary elongation of the face in some baboons (Major, Pl. xi, fig. 9), the foramen may be entirely surrounded by the lacrymal. In the gibbon, orang, some chimpanzees, and man the lacrymal is normally in wide contact with the os planum of the ethmoid, but sometimes this contact is replaced by a contact between the orbital walls of the frontal and of the superior maxilla, the latter being thrust up between the lacrymal and the os planum. This is said to be the normal disposition in the gorilla and chimpanzee (Cunningham, 1903, p. 134), and occurs as a variant in man.

Taken in connection with the fundamental unity of construction of the auditory region and indeed of the whole skull throughout the Platyrrhinæ and Catarrhinæ, the lacrymal region offers additional evidence for the traditional view that the suborder Anthropeidea is a natural group. In both the Platyrrhinæ and the Catarrhinæ the retreat of the lacrymal within the orbit is carried to its logical extreme along with the extreme forward turning of the eyes and the consequent inward shifting of the inner canthus of the eyes. From this line of development *Tarsius* and all the modernized lemurs are definitely ruled out through the forward shifting of the lacrymal correlated with bulging eyes directing partly outward; but the lacrymal region of the primitive lemuriform *Notharctus*, as Dr. Wortman well observes (*op. cit.*, p. 410), could readily give rise to that of the Platyrrhinæ and thus to that of all higher primates.

SUMMARY OF THE EVOLUTION OF THE LACRYMAL BONE

The present study, in the writer's judgment, lends strong support to the so-called "Cuvierian concept": namely, that the lacrymal of mammals is the homologue of the lacrymal of the Crocodilia, as named by most authors up to the time of Gaupp and Jaekel, who, on the contrary, held that the Cuvierian concept was erroneous and that the lacrymal of mammals had been derived from the so-called prefrontal of reptiles.¹

Arising as a derm bone, one of the circumorbital series in the rhipidistian fishes, the lacrymal has primary contacts with the prefrontal,

¹ See also Addendum, p. 263.

the jugal, and possibly with the parethmoid, or lateral ossific center of the olfactory capsule, as well as with the palatine. The lacrymal in primitive fish is traversed by the suborbital branch of the lateral line canal; according to Watson this duct may well have given rise to the naso-lacrymal duct, an epithelial derivative with which the lacrymal bone is always typically associated.

In the earliest Tetrapoda the circumorbital series of bones are becoming better differentiated from each other and, in the oldest reptiles, the jugal and squamosal show the beginning of the zygomatic arch. The appearance of the temporal fossa in the early synapsid reptiles was also a significant stage.

As we pass from the lower to the higher classes of vertebrates and from the more primitive to the more specialized members of each class, we observe in general a marked reduction in the number of derm bones covering the skull and attached structures. Thus the teleostomous fishes have by far the highest number. The earliest Amphibia have already lost all the bones of the opercular series, while the modern Amphibia usually have an impoverished skull, lacking the postfrontal,¹ the intertemporal, the supratemporal, postorbital, dermosupraoccipital, tabular, and other elements. The birds lose, among others, the elements of the upper temporal arch, while the mammals sacrifice the pre- and postfrontals, postorbitals, intertemporals, supratemporals, tabulars, quadratojugals, and several elements of the lower jaw. The lacrymal bone often shares the fate of these other elements, especially in many modern Amphibia, and in Chelonia, Ophidia, Rhynchocephalia, and birds; in the last three groups the place of the lacrymal is usurped by the prefrontal. So, too, among the mammals the more primitive types always retain the lacrymal, while in degenerate or highly specialized skulls it is often reduced (e.g., *Ælurus*, many Ursidæ, certain Viverridæ and Mustelidæ) and is sometimes lacking (Monotremes, *Manis*, Phocidæ).

As the orbit was doubtless originally near the anterior end of the head, the lacrymal at first extended from the orbit to the nares, and there it has been found in many of the most ancient and primitive types of Amphibia and reptiles.

In early reptiles the progressive upgrowth of the maxilla covers the anterior part of the lacrymal and is associated with the loss of the lacrymal-parethmoid contact and with the establishment of a lacrymal-

¹This element is doubtfully recorded in some of the Salamandridæ.

maxillary contact. The lacrymal from the first has contact with the spreading nasal and with the jugal. In this stage, which is represented in the Pelycosauria and Therapsida, the lacrymal is pierced by the naso-lacrymal duct, the foramen opening just in front of the orbit, the duct passing downward and forward to open into the nasal cavity.

In the Diapsida or Archosauria, the lacrymal is primitively a large element, often perforated or bordered by the antorbital fenestra, and serving as a brace between the upper jaw and the frontal region of the skull.

In the ancestral mammals the establishment of a dentary-squamosal contact and the forward growth of the temporal muscles conditioned the disruption of the postorbito-jugal contact, the disappearance of the postorbital, and perhaps the forward crowding of the frontal. The prefrontal also disappeared and the only parts of the primitive circum-orbital series remaining are the lacrymal and the jugal. The lacrymal of cynodonts gains contact with the nasal and retains its contact with the jugal. It is pierced by one or two foramina, which are probably connected with the naso-lacrymal duct.

By the loss of the prefrontal the lacrymal gains a wide contact with the frontal, which it never loses. This is the stage apparently represented in the Lower Jurassic mammal *Tritylodon*.

The contact of the lacrymal with the palatine, which we find in mammals, was established in many fishes and was thence transmitted to the Stegocephalia and higher vertebrates.

In cynodont reptiles, as well as in primitive mammals, the lacrymal transmits the strains from the zygomatic arch to the nasals, frontals, maxillæ, and palatines.

With the transformation of cold-blooded reptiles into warm-blooded mammals the stiff mask-like face of reptiles is changed into the mobile face of mammals, through the forward migration of the sphincter colli muscles and the differentiation into the muscles of the lips, cheek, and eyes (Ruge).

Part of the orbicularis muscles (preorbicularis dorsalis, ventralis) become attached to the facial part of the lacrymal and the "tarsal ligament" of the eyelids is attached to the lacrymal on the lacrymal tubercle. All this occurred perhaps during the second half of the Mesozoic Era and is known to us through internal morphological evidence rather than by direct palæontological material.

Among the mammals, the most primitive known types of lacrymal region are found among existing carnivorous marsupials and among such

Paleocene placentals as have more primitive types of dentition. In these forms the skull is macrosmatic, being long and low with a thick muzzle, very narrow brain-case, stout jaws and zygomatic arches, and more or less primitive tritubercular dentition. The eyes are of moderate size with very small postorbital processes. The prominent antorbital rim is formed by the frontals, lacrymals, and jugals, and the eyes are directed outward rather than forward. The dorso-anterior part of the antorbital rim protrudes laterally as seen from above. The lacrymal at this stage has a moderate pars facialis and the foramen is behind the antorbital rim, opening backward. It also has contacts with frontal, nasal, maxillary, jugal, and palatine. Its pars orbitalis covers the lateral extension of the ethmoid scrolls. Its small pars facialis serves for the attachment of the orbicularis, preorbicularis dorsalis and p. ventralis muscles, and its tubercle for the ligament of the palpebral cartilages and, at least sometimes, for the deep fascia of the frontal region.

In general, the marsupials have a more extended dorso-anterior rim on the lacrymal than have the primitive Paleocene placentals and some of them retain the naso-lacrymal contact which in the most primitive placentals was early replaced by a fronto-maxillary contact. Perhaps the most primitive known examples of this stage are *Amphiproviverra* among the marsupials and *Deltatherium* among the Paleocene placentals.

Such animals, although macrosmatic, have a well-balanced condition of the olfactory and visual organs in harmony with their primitively carnivorous or semi-carnivorous habits. But even long before the Paleocene epoch various lines of specialization were initiated which eventually resulted in wide differences in food habits, dentition, sense organs, locomotor organs, etc., so that by Paleocene times we find many specialized placental types such as *Psittacotherium*, *Nothodectes*, *Palæanodon*. Fortunately, however, the "persistent primitive types" of Paleocene and later times such as *Deltatherium*, *Onychodectes*, *Hyopsodus*, *Miocænus*, and many others give us a better idea of what the more generalized Mesozoic precursors of the placental orders were like.

Specialization in food habits, etc., has affected the lacrymal region of mammals in several ways.

(1) Excessive increase in the olfactory scrolls of the ethmoid region and concomitant widening of the frontal region may accompany more or less inflation of the lacrymal region or of the sinuses surrounding the nasal chamber, as in *Myrmecobius*, *Tupaia*, *Galeopithecus*, *Lemur*, and many ungulates.

(2) On the other hand, a great decrease in the olfactory region may condition the dwindling in size of the lacrymal, as in the microsmatic Lorisidæ and Tarsiidæ.

(3) A dorsad displacement of the orbital root of the zygomatic arch through excessive development of the anterior part of the masseter may crowd the lacrymal dorsad and cause its reduction in size, as in *Phascalomys*, rodents, and typotheres.

(4) A backward and upward growth of the nasal tract and surrounding muscles, causing the backward and upward growth of the maxillary, may crowd back the lacrymal and reduce its pars facialis as in the tapir and the elephant.

(5) The encroachment of the maxillary upon the zygomatic arch may separate the lacrymal from the jugal, as in *Erinaceus*.

(6) The encroachment of the maxillary upon the vertical plate of the palatine may separate the lacrymal from the palatine, as in many insectivores.

(7) The development of horns or bony apophyses either in the orbital or in the nasal regions affects the lacrymal in various ways. In the later titanotheres the lacrymal contributes to the bony pillar that supports the "horns" laterally. In the African rhinoceroses the growth of the nasal horns has perhaps conditioned the forward growth of the nasals and their withdrawal from the naso-lacrymal contact. In the Bovidæ the greatly enlarged pars facialis of the lacrymal contributes largely to the strengthening of the face below the horns.

(8) A backward displacement of the orbit, correlated with the forward prolongation of the snout, may condition the elongation of the pars facialis of the lacrymal, as in *Orycteropus*, *Megalohyrax*, *Phaco-chærus*, and many artiodactyls.

(9) An extreme forward displacement of the orbit may condition the elongation of the orbital wall of the lacrymal, as in *Manatus*.

(10) Extreme enlargement and protrusion of the eyes may crowd the lacrymal almost entirely out of the orbit, its place being taken either by the os planum of the ethmoid or by the palatine, as in the Lorisidæ and Tarsiidæ. In such cases the lacrymal foramen is crowded out of the orbit and is located between the lacrymal and the maxilla.

(11) On the other hand, a marked reduction of the eyes causes the subsidence of the antorbital rim, the loss of the lacrymal tubercle, and the close appression of the orbital wall of the lacrymal to the side of the frontal, as in *Myrmecophaga*, zalambdodont insectivores, moles, shrews, etc.

(12) Finally, when the direction of the eyes is shifted, so that they point forward rather than outward, and when, at the same time, the olfactory region is reduced, we have a more or less complete withdrawal of the lacrymal into the orbit, as in all the higher monkeys, apes, and man.

In general, it may be said that the loss of one or more of its primitive contacts tends to release the lacrymal from its hereditary conditions and restrictions and to that extent frees it for new lines of either specialization or reduction.

In some cases it would appear that the lacrymal is not altogether a passive object, which is pushed and moulded by its surroundings, but that it has, so to speak, a certain inherent tendency either to increase, as in the excessively large lacrymal of many artiodactyls, or to diminish, as in the lacrymal of many fissiped Carnivora.

In conclusion, the form and size of the lacrymals of mammals are conditioned, first, by intrinsic hereditary factors which cause the lacrymal to increase or to diminish and, secondly, by several external factors such as the position of the orbits, the length of the snout, the width of the ethmoid region, the degree of inflation of the sinuses around the nasal cavity, special developments of the maxillary and jugal, and diverse modifications of the eyes and circumorbital muscles. In a general way, anteriorly placed orbits, short snouts, and a narrow ethmoid region are found in connection with small lacrymals, with reduced facial exposure, and vice versa, but each case is complicated by special conditions.

THE LACRYMAL PROBLEM IN ITS PHYLETIC AND TAXONOMIC ASPECTS: A PHYLOGENETIC REVIEW OF THE VERTEBRATES

The elements of the lacrymal complex being relatively few in number, it is not surprising to find more or less similar combinations sometimes occurring independently in widely different groups, so that in such cases a similarity in the pattern of the lacrymal region does not denote near relationship. A case in point is the superficial resemblance of the orbital and lacrymal region of the specialized cotylosaurian genus *Procolophon* to those of certain lizards, and another is the general similarity of the whole face, including the lacrymal, of *Myrmecobius*, a marsupial, *Rhynchocyon*, a menotyphlous insectivore, and *Homacodon*, an artiodactyl. Under the category of homoplastic resemblances belong also many of the cases with an extended pars facialis of the lacrymal, such as the following:

<i>Thylacinus</i>	<i>Hyænodon</i>
(Order Marsupialia)	(Order Carnivora)
<i>Orycteropus</i>	<i>Myrmecophaga</i>
(Order Tubulidentata)	(Order Edentata)
<i>Megalohyrax</i>	<i>Phacochærus</i>
(Order Hyracoidea)	(Order Artiodactyla)

On the other hand, the lacrymal region usually bears so peculiar and characteristic a stamp in a series of genera, or even in larger groups, that there can be little doubt of its inheritance from a common ancestor. Good examples of this class are the unity of general type of the lacrymal region throughout the suborder Anthropeidea, the characteristic patterns of the lacrymal in Eocene perissodactyls, artiodactyls, and many other groups.

In fact, when the more detailed patterns of the whole circumorbital region of any two given examples are carefully compared, especially when the functional significance of the given configuration is appreciated, the deceptive resemblances due to convergence or homoplasy are easily recognized and characters of diagnostic value will often be discovered. On the other hand, a classification and a phylogenetic tree of the vertebrates, if based on the characters of the lacrymal region alone, could hardly be expected to yield uniformly reliable results, because at the present time it is generally realized that the whole is greater than any of its parts and that, in order to be durable, a phylogenetic diagram must be based upon as many sources of evidence as possible. Studies by many investigators on special parts and systems, such as the auditory region, the dentition, and the limb structure, together with the far more numerous systematic studies of zoologists and palæontologists, have already provided a general background of knowledge concerning the interrelationships and classification of the vertebrates, so that the attempt may now be made to integrate with the general results already attained from other sources such systematic and phylogenetic evidence as our study of the lacrymal region has yielded.

Dipnoi

The ring of large plates around the eye of Paleozoic dipnoans seems to be, on the whole, homologous with the circumorbital ring of contemporary Crossopterygii, since in both groups this series often bears a more or less complete circumorbital branch of the lateral line canal. This fact, taken in connection with other evidence, points to a common origin of the two great groups, although in view of the form differences

of these elements, both as between the larger groups and as between different genera of the same group, there may be some doubt as to the homology of particular elements in certain cases. In any event, the patterns of the circumorbital series of Devonian Dipnoi and Crossopterygii are sufficiently different to indicate a long pre-Devonian period of divergence of these two stocks from a common ancestral stage.

The circumorbital elements of Arthrodira do not, to the writer, have the appearance of being homologous with those of Dipnoi or of other true fish, from which they differ widely in number and form.

Crossopterygii

The typical Palæozoic crossopterygians have four large circumorbital plates, including the prefrontal, lacrymal, jugal, and postorbital. The so-called supraorbital looks like a true prefrontal, while the "prefrontal" of Watson and Day (1915) appears to be homologous with that bone in *Amia* which was named "antorbital" by Sagemehl and Allis and "preorbital" by Bridges. This dermal preorbital element of *Osteolepis* seems to be homologous with the so-called "anterior frontal"¹ (Traquair, Wellburn) of *Megalichthys* and *Eusthenopteron*. Apparently the most primitive circumorbital pattern in this order is that of *Osteolepis*, from which may have been derived, on the one hand, that of *Glyptopomus* and eventually of *Holoptychius* and, on the other hand, those of *Rhizodopsis* and *Eusthenopteron*.

The coelacanths (order Actinistia) show the preorbital and "supra-orbital" (=prefrontal) broken up into a long tract of squarish ossicles. The lacrymal is a triangular bone in the right position for that element, while the jugal is represented by the enlarged "suborbital" (see Goodrich, 1909, p. 288, Fig. 261). The postorbital remains in place.

Polypterus (of the order Cladistia), as would be expected in a modern survivor of the ancient Crossopterygii, exhibits a specialized and partly degenerate condition of the circumorbital region. Apparently both the dorsal (prefrontal) and the ventral (jugal) members of the circumorbital series have been lost and only the anterior (lacrymal) and posterior (?postorbital) members remain. The lacrymal is a wedge-shaped element that begins to simulate that of the Tetrapoda (see page 113 above).

Dr. Goodrich (1909, pp. 290-300) has cited numerous facts in support of his view that *Polypterus* is very widely removed from the true Crossopterygii and has perhaps a closer affinity with the Actinopterygii. In the present connection it may be said only that the Cladistia appear

¹Not to be confused with the true "anterior frontals" (prefrontals) of tetrapods (see page 97).

rather to be a degraded remnant of the coelacanth (Actinistia), which have lost many primitive crossopterygian characters and in many respects have become more completely ichthyized than their Palæozoic ancestors. The lacrymal region of *Polypterus* could readily be derived from that of the coelacanth chiefly through the loss of the preorbital and suborbital elements and the further specialization of the wedge-shaped lacrymal.

Actinopterygii

In the most primitive Chondrostei (Palæoniscidæ) the eye is enclosed in a narrow dermal ring which appears to be the homologue of the circumorbital series of other fish but is not subdivided into four or five elements. Behind and above this inner ring in primitive Palæoniscidæ is a second series ("postorbitals"), apparently homologous in part with the second ring of the higher ganoids. Behind this series again comes the preoperculum and expanded maxilla, while the true opercular series (operculum, subopercular, and branchiostegals) constitute a fourth and hindmost series. The Platysomidæ exhibit a closely allied pattern, differing in the reduction in number and enlargement of some of the elements of the second ring and in the shortening and deepening of the third and fourth rows. In the modern Spoonbill hardly a trace of this primitive pattern remains, but the sturgeons preserve more of it.

In the primitive Holostei (e. g., *Dapedius*, *Lepidotus*) the inner ring is of large size and well differentiated into from nine to twelve elements, of which two at the lower anterior border of the orbit have the position of the lacrymal. The second row is also subdivided into numerous pieces, behind which comes the preoperculum and next the opercular series. The pattern in *Lepidotus* could readily give rise to that in *Lepidosteus* (Fig. 4) through the elongation of the rostrum and the fragmentation of the maxilla, lacrymal, and other elements.

In *Amia* (Fig. 3) the lacrymal (*l*) and two of the posterior elements (*po*¹, *po*²) of the inner row have become greatly enlarged, the second row has disappeared, leaving the preoperculum more exposed, while the opercular series remains intact. From this amioid pattern that of the more primitive teleosts such as *Elops* has doubtless been derived.

Thus the pattern of the circumorbital region of primitive Actinopterygii affords some evidence for the following phylogenetic and systematic conclusions.

(1) The primitive Actinopterygii are only very remotely related to the primitive Crossopterygii; their respective circumorbital patterns

have probably been derived from an undifferentiated osteichthyan stage, possibly antedating the formation of definite joints in the skin covering the face.

(2) The primitive Chondrostei differ widely from the primitive Holostei in the circumorbital pattern as well as in many other characters, this being evidence of a very early separation of these groups.

(3) The circumorbital pattern of *Lepidosteus* is apparently more readily derived from that of *Lepidotus* than from that of *Eugnathus*, an inference which is in harmony with other evidence cited by Goodrich (pp. 335, 342-344).

(4) The teleosts are closely related to the amioids and show further advances in the specialization of the lacrymal as a large and prominent brace in front of the orbit. This character it retains in very many groups of teleosts, often in spite of high specialization in other parts of the face. This relatively primitive condition of the lacrymal is retained even in the more primitive of the Acanthopterygii, which are the highest of the teleosts. On the other hand, the lacrymal, like other elements, is subject to reduction and loss, especially in degraded families. Some of the other circumorbital bones occasionally afford diagnostic characters, such as the subocular shelf of primitive Acanthopterygii, the "pre-opercular stay" formed by the third suborbital of scorpenoids, etc.

Stegocephalia

The structural and phylogenetic gap between the Stegocephalia and the Crossopterygii, which are their nearest relatives among the fishes, is very great, far greater than that between the Stegocephalia and its contemporaries, the primitive Reptilia. Nevertheless, both these higher classes retain all the elements of the piscine circumorbital series, but so diversely modified in the very numerous and highly specialized families of temnospondyls, branchiosaurs, microsaurs, cotylosaurs, etc., that at first the pattern of the skull roof of Palæozoic Tetrapoda seems like a "shifting mosaic," in which now one and now another element becomes enlarged and pushes itself into new contacts, usurping the place of its diminishing neighbors.

Notwithstanding the labors of Miall, Cope, Fritsch, Moodie, and many others, the family classification of the Palæozoic Amphibia remains in a rather vague and unsatisfactory state,¹ so that it has seemed worth while to examine the patterns of the circumorbital region in the

¹This sentence and, indeed, this whole section on the Amphibia were written a year or more before I received from Dr. Watson a copy of his memoir on "The Evolution of the Amphibia, Part 1". Abel's work on "Die Stämme der Wirbeltiere" was also received too late for me to consider his classification of the Amphibia and Reptilia in this paper.

numerous genera and supposed families in search not only of diagnostic characters but also of evidence concerning the phyletic interrelations of the larger groups.

Eventually this will have to be done by some one like my friend Dr. Watson, who, it is to be hoped, will make another tour of the principal museums of the world and narrowly examine the original material.¹ But the extensive literature of the subject, together with the material at hand, has tempted the writer once more to review the patterns of the skull top of Palæozoic Amphibia, as figured especially in the well-known works of von Meyer, Fritsch, Credner, Thévenin, Broili, Moodie, von Huene, Broom, Watson, and Williston. Owing to the great difficulty in correctly determining the sutural pattern in most specimens of early Tetrapoda, the published figures have been examined critically and with the doubts occasioned by the diverse results reported by different observers of the same or similar materials.

In general, the abundant materials and carefully executed figures published by von Meyer and by Credner seem to withstand the closest inspection and inspire confidence in the accuracy of the sutural limits and patterns as determined by these authors. On the other hand, a critical study of Fritsch's figures of the skull roof of *Branchiosaurus*, *Chelydosaurus*, and of some other types, has raised doubts as to their accuracy in certain particulars which will be noted presently. Williston's final figure of *Trimerorhachis* was based upon a large series of well-preserved specimens, studied with all the caution and intensity for which he was noted. They confirm in the main the figures by Broom, based on less satisfactory material.

In the appended tables are recorded fourteen characters of the lacrymal region, including the presence or absence of the lacrymal itself, and the presence or absence of certain sutural contacts between different elements in its vicinity.

Some of the phylogenetic and systematic conclusions which may be drawn from this study seem to be as follows.

(1) All the more primitive Tetrapoda are characterized by the presence of the lacrymal bone, which is in contact with the prefrontal, nasal, maxilla, jugal, and probably with the palatine.

(2) The early Temnospondyli retain the greatest number of presumably primitive amphibian characters, while the branchiosaurs and microsaurians are more or less aberrant or peculiar—perhaps in correlation with a shortening and broadening of the head.

¹ See footnote on preceding page.

(3) In most Temnospondyli the lacrymal is excluded from the orbit by a prefrontal-jugal contact and from the nares by a naso-maxillary contact. This may well have characterized the primitive temnospondyls, although in some cases the lacrymal retains its piscine location on the anterior border of the orbit.

(4) The numerous genera of rhachitinous temnospondyls which are here provisionally grouped under the family Archegosauridae are distributed under several families by Fritsch, but show a substantial agreement in the pattern of the skull top as well as in the vertebrae.

(5) The Stereospondyli closely agree in the pattern of the lacrymal region with the Eryops group of the Temnospondyli, from which, as Watson has shown, they probably have been derived.

(6) The short-headed temnospondyls belong to two quite distinct families—the Brachyopidae and the Dissorophidae, characterized by differences in the lacrymal region and in development of the otic notch.

(7) *Micropholis* is aberrant in the vestigial condition of the jugal, as well as in other characters.

(8) *Trimerorhachis* is peculiar in the fact that the lacrymal excludes the jugal from the orbital border.

(9) *Chelydosaurus*, as restored by Fritsch, is characterized by the extreme extension of the jugal from the nasal to the squamosal, by the absence of the lacrymal and by the forward extension of the postorbital beneath the orbit so as to gain contact with the prefrontal. Fritsch's plates, however, do not carry conviction on these points.

(10) In Fritsch's figures of *Branchiosaurus* and *Dawsonia* the jugal is represented as extending forward beneath the orbit so as to gain contact with the nasals. But Credner's numerous figures of *Branchiosaurus* in all stages of development give no hint of such an extraordinary condition. Possibly Fritsch's "jugal" is merely the space between the superior maxilla and the bones below the orbit, which are the prefrontal and the jugal. In *Branchiosaurus* the lacrymal is absent even in very young specimens. In the much more primitive *Pelosaurus* the lacrymal is present and the pattern of the whole skull top is clearly allied to the primitive rhachitinous type.

(11) *Stegops*, if it is a microsauro, is apparently very primitive in the extension of the lacrymal from orbit to nares. Its isolated position is noted by Dr. Moodie (1916, p. 112).

(12) *Acanthostoma*, although known from well-preserved skulls figured by Credner, is difficult to place. It resembles *Dasyceps* and *Salamandrina* in the presence of a large intermaxillary fossa. Its lacrymal region is primitive.

(13) Among the microsaur, as figured, the lacrymal is often absent, the prefrontal frequently usurping its place; but when the lacrymal is present the pattern of this region recalls that of the Temnospondyli.

(14) The modern Anura, being degraded and specialized forms, have sacrificed most of the elements of the lacrymal region and seldom retain even doubtful vestiges of the lacrymal itself. But the whole skull pattern of the Anura is reminiscent of the short-faced Rhachitomi¹ rather than of the branchiosaurs, which, as Dr. Moodie has suggested, may well be ancestral to *Cryptobranchus* and its allies.

(15) Notwithstanding the loss of many other skull elements, certain amblystomid salamanders retain a primitive preorbital region, including a well-developed prefrontal and a small lacrymal, pierced by a naso-lacrymal duct (see page 117). Derivation from the conditions seen in *Pelosaurus* and the primitive temnospondyls seems possible.

¹1917, Amer. Nat., pp. 316-317.

Table 1. Characters of the Lacrymal and Contiguous Elements in Temnospondyls, Branchiosaurs, and Microsaurs

	lacrymal present	la extending from orbit to nares	la-na contact	la-mx "	la-ju "	la-orbit "	la-pf "	la-po "	fr-mx "	na-mx "	na-ju "	pf-ju "	ju-sq "	jugal vestigial
Order Temnospondyli														
Loxommatidæ														
<i>Loxomma allmani</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Trimerorhachidæ														
<i>Trimerorhachis insignis</i>	+	+	+	+	+	+	+	+	○	○	○	○	+	○
Archegosauridæ														
<i>Discosaurus permianus</i>	+	?	+	+	?	○	?	+	○	○	?	○	+	○
<i>Archegosaurus latirostris</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
<i>Archegosaurus decheni</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
<i>Actinodon frossardi</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
<i>Sclerocephalus labyrinthicus</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
<i>Osteophorus ræmeri</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
<i>Eryops megacephalus</i>	+	○	+	+	+	○	+	○	○	○	○	+	+	○
<i>Lydekkerina huxleyi</i>	+	○	+	+	+	○	+	○	○	○	○	+	+	○
<i>Nyrانيا trachystoma</i>	+	○	+	+	+	○	+	○	○	○	+	○	+	○
Fam.?														
<i>Cochleosaurus bohemicus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
<i>Melosaurus uralensis</i>	?	○	?	+	?	○	?	+	○	○	+	○	+	○
<i>Chelyosaurus</i>	○?	○	○?	○?	?	○	?	○	○	○	+	+	+	○
<i>Dendrepeton deprivaturn</i>	+	○	+	+	?	○	+	○	○	?	○	+	+	○
Fam.?														
<i>Dasyceps bucklandi</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Fam.?														
<i>Acanthostoma vorax</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Brachyopidæ														
<i>Bothriceps australis</i>	+	○	+	+	+	○	+	○	○	+	○	+	+	○
Dissorophidæ														
<i>Broiliellus</i>	+	+	+	+	○	+	+	○	○	○	○	○	+	○
Micropholidæ														
<i>Micropholis stowi</i>	+	+	+	+	+	+	+	○	○	○	○	○	○	+
Mastodontosauridæ														
<i>Mastodontosaurus</i>	+	○	+	+	+	○	+	○	○	+	○	+	+	○
<i>Capitosaurus</i>	+	○	+	+	+	○	+	○	○	○	+	+	+	○
<i>Cyclotosaurus</i>	+	○	+	+	+	○	?	+	○	○	○	+	+	○
<i>Trematosaurus</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
<i>Metopias</i>	+	○	+	+	+	○	+	○	○	+	○	+	+	○
Order Uncertain														
Stegopidæ	+	+	+	+	○	+	+	○	○	○	○	○	+	○

	lacrymal present	la extending from orbit to nares	la-na contact	la-mx "	la-ju "	la-orbit "	la-pf "	la-po "	fr-mx "	na-mx "	na-ju "	pf-ju "	ju-sq "	jugal vestigial
Order Phyllospondyli														
Apateonidae														
<i>Melanerpeton pusillum</i>	○	○	○	○	○	○	○	○	○	+	+	+	+	○
<i>M. pulcherrimum</i>	○	○	○	○	○	○	○	○	○	+	+	+	+	○
<i>M. fallax</i>	?○	○	○	?+	?+	?+	?+	○	○	○	○	○	+	○
Branchiosauridae														
<i>Protriton petrolei</i>	○	○	○	○	○	○	○	○	○	+	○	+	+	○
<i>Branchiosaurus</i>	○	○	○	○	○	○	○	○	○	+	○	+	+	○
<i>Dawsonia</i>	?	○	?	○	?	?	?	○	○	○	+	+	+	○
<i>Pelosaurus laticeps</i>	+	○	+	+	+	+	+	○	○	+	○	+	+	○
" "	+	{	+	+	+	{	+	○	○	+	○	{	+	○
		○				○						○		
" "	+	{	+	+	+	{	+	○	○	+	○	{	+	○
		○				○						○		
Hylonomidae														
<i>Hylopleosion</i>	?○	○	○	○	○	○	?○	○	○	○	○	?+	?	○
Order Lepospondyli														
Urocordylidae														
<i>Eoserpeton tenuicorne</i>	○	○	○	○	○	○	○	○	?○	○	○	+	+	○
<i>Scincosaurus (Keraterpeton) crassus</i>	?	○	○	?	?	?	?	○	○	○	○	○	+	○
<i>Diceratosaurus punctolineatus</i>	+	○	○	+	○	+	+	○	○	○	○	○	+	○
<i>Diceratosaurus laevis</i>	○	○	○	○	○	○	○	○	○	○	○	○	+	○
Diplocaulidae														
<i>Diplocaulus</i>	+	○	○	+	○	○	+	○	○	○	○	+	+	○
Tutidanidae														
<i>Erpetosaurus minutus</i>	○	○	○	○	○	○	○	○	○	○	○	○	+	○
" <i>tabulatus</i>	○	○	○	○	○	○	○	○	○	○	○	+	+	○
Amphibamidae														
<i>Amphibamus</i>	+	○	+	+	○	○	+	○	○	○	○	+	+	○
Microbrachidae														
<i>Microbrachis pelikani</i>	?	○	?	?	?	?	?	?+	○	+	?+	?+	?	?
Aistopoda														
<i>Dolichosoma longissimum</i>	?○	○	○	○	○	○	?○	○	○	○	○	+	+	○

Table 2.—Characters of the Lacrymal and Contiguous Elements in Palæozoic Reptiles

	lacrymal present	la extending from orbit to nares	la-na contact	la-mx "	la-ju "	la-orbit "	la-pf "	la-po "	fr-mx "	na-mx "	na-ju "	pf-ju "	ju-sq "	jugal vestigial
Cotylosauria														
Seymouriidæ														
<i>Seymouria</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Diadectidæ														
<i>Diadectes</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Pariosauridæ														
<i>Pariasaurus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Limnoscelidæ														
<i>Limnoscelis</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Captorhinidæ														
<i>Labidosaurus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
<i>Captorhinus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Pantylidæ														
<i>Pantylus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
Procolophonidæ														
<i>Procolophon</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Pelycosauria (Theromorphæ)														
Edaphosauridæ														
<i>Naosaurus</i>	+	+	+	+	+	+	+	○	○	○	○	○	+	○
?Poliosauridæ														
<i>Mycterosaurus</i>	+	○	?	+	+	+	+	○	○	+	○	○	+	○
Sphenacodontidæ														
<i>Sphenacodon</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Therapsida														
<i>Scylacops</i>	+	○	○	+	+	+	+	○	○	+	○	○	+	○
Parapsida														
<i>Aræoscelis</i>	+	○	○	+	+	+	+	○	○	+	○	○	+	○

Table 3.—Characters of the Lacrymal and Contiguous Elements in Post-Palæozoic Tetrapoda

	lacrymal present	la extending from orbit to nares	la-na contact	la-mx "	la-ju "	la-orbit "	la-pf "	la-po "	fr-mx "	na-mx "	na-ju "	pf-ju "	ju-sq "	jugal vestigial
Thecodontia														
<i>Euparkeria</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
<i>Mystriosuchus</i>	+	○	+	+	+	+	+	○	○	+	○	○	○	○
Crocodylia														
Crocodylidae														
<i>Alligator</i>	+	○	○	+	+	+	+	○	○	+	○	○	○	○
Rhynchocephalia														
<i>Sphenodon</i>	○	○	○	○	○	○	○	○	○	+	○	○	+	○
Squamata														
<i>Iguana</i>	+	○	○	+	+	+	+	○	○	+	○	○	+	○
<i>Boa</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Aves	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Therapsida														
Cynodontia														
<i>Ictidopsis</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
<i>Cynognathus</i>	+	○	+	+	+	+	+	○	○	+	○	○	+	○
Mammalia														
Primitive Marsupialia	+	○	+	+	+	+	○	○	○	+	○	○	+	○
Primitive Placentalia	+	○	○	+	+	+	○	○	+	+	○	○	+	○

Cotylosauria

Dr. D. M. S. Watson, in his interesting paper (1917) on the classification of the pre-Jurassic Tetrapoda, says that he retains the superorder Cotylosauria "simply because of its use as a dumping-ground for those primitive reptiles which retain a roofed skull," and that even his orders (Seymouriamorpha, Diadectomorpha, Captorhinomorpha) are also "probably somewhat unnatural groups" and that "it would perhaps have been more satisfactory to raise the superfamilies to ordinal rank"—in other words, to expand the old order Cotylosauria into seven orders to include the forms clustering respectively around *Seymouria*, *Diadectes*, *Pariasaurus*, *Procolophon*, *Captorhinus*, *Limnoscelis*, and *Pantylus*. He also states that the real classification, i.e., that into families, is founded as far as possible on the characters of the brain-case. The writer, on the other hand, is impressed not only by the numerous resemblances between

the members of these seven groups, but also by the great changes in skull structure described by Dr. Watson, which take place independently in different families of the group. Some of these changes are the obliteration of the otic notch in the *Pariasauria* and in *Captorhinomorpha*, the turning down on to the nuchal surface of the dermosupraoccipitals and tabulars in *Pantylus* and in the captorhinomorphs, the development of a short, high, *Sphenodon*-like brain-case in *Procolophon*, the independent evolution of vertically placed quadrates in *pariasaurs* and captorhinomorphs, the depression of the inner ear in the captorhinomorphs, the upgrowth of the maxilla to gain contact with the nasals, and the concomitant retraction of the lacrymal in *Procolophon*. But the changes merely disguise, without obliterating, the bonds of affinity between these varied cotylosaurs, so that one may readily sense the relationship of *Limnoscelis* to the captorhinomorphs, of *Procolophon* to the diadectomorphs, and so forth. It seems quite possible that in this very primitive and plastic group of reptiles the level of the internal ear with respect to the floor of the brain-case might change as rapidly as the inclination of the quadrates to the midline of the skull, and that the secondary closing off of the inner ear from the brain-case is after all no great morphological accomplishment in comparison with many other transformations with which we are familiar.

In spite of such internal changes, the *Cotylosauria*, with the exception of *Procolophon*, are characterized by the constancy of the lacrymal region, in which the lacrymal always extends from the orbit to the nares and separates the prefrontal from the jugal and the nasal from the low ascending process of the maxilla. The arrangement of the lacrymal region, like the pattern of the skull as a whole, is closely allied to that of the rhachitomous stegocephs, in so far as the lacrymal is in contact with prefrontal, maxilla, and nasal; but it differs in the extension of the lacrymal from the orbit to the naris, a rare character among the Rhachiotomi. The chief characters of the lacrymal region of the cotylosaurs are recorded in Table 2.

Chelonia

The loss, in this order, of several elements of the skull top, including the lacrymals, the usurpation of the place of the lacrymals by the prefrontal, and the upgrowth of the maxilla so as to gain contact with the prefrontals, are all signs of modernization, which have been paralleled in other groups (e. g., *Sphenodon* and *Ophidia*) and which mask, but do not obliterate, the evidence afforded by the remaining parts of the skull

and mandible of derivation from primitive reptiles, possibly allied to the *Pariasauria* (Jaekel). The reported occurrence in the Upper Triassic chelonian *Stegochelys* (*Triassochelys*) *dux* Jaekel (1916) of a separate lacrymal ("postnasal") extending from the anterior naris to the orbit will, if confirmed, afford further evidence in the same direction; meanwhile, a comparison of all views of the skull of this genus as figured by Jaekel with those of *Diadectes*, *Pantylus*, *Labidosaurus*, *Pariasaurus*, and *Procolophon* has revealed to the writer no decisive evidence in favor of the well-known view that the Chelonians are specially related to the diadectid cotylosaurs. Even less convincing is Boulenger's ingenious argument (1918) for regarding the Chelonians as relatives of *Sphenodon*. His hypothesis that the primitive Chelonians had fenestrated temporal regions and that the roofed-over condition of *Chelone* is entirely secondary must now reckon with the completely roofed condition in the Upper Triassic *Stegochelys* (*Triassochelys*), which, according to Jaekel's figures, is wholly unlike *Sphenodon* except in its primitive reptilian characters.

Pelycosauria (= Theromorpha)

The recent work of Broom, von Huene, Williston, and Watson, has developed the fact that in many characters the pelycosaurs are intermediate between the captorhinomorph cotylosaurs and the Therapsida. This conclusion is supported by the pattern of the lacrymal region. In *Naosaurus* and *Edaphosaurus* the lacrymal extends to the naris and all the relations of the lacrymal and contiguous elements, as recorded in Table 2, agree with the conditions in Cotylosauria. *Sphenacodon* and *Mycterosaurus*, on the other hand, exhibit successive stages in the retraction of the lacrymal and the upgrowth of the maxilla, which gains contact with the nasal as in the therapsid and other higher reptiles. Hence, the group as a whole is characterized by the transitional conditions of the lacrymal from the cotylosaurian to a higher reptilian stage.

Bolosaurus is referred by Broom and Watson to this group rather than to the Cotylosauria; its lacrymal region is of the captorhinid type; but so also is that of *Naosaurus*. The under side of the skull, as observed by Case and von Huene, strongly recalls the captorhinids, but here again *Naosaurus* and even *Dimetrodon* are not far off.

Casea, which was very doubtfully referred to this group by Williston and that only in a distinct suborder, resembles the *Dinocephalia* among the mammal-like series in many curious features of the skull and postcranial skeleton and, indeed, is referred by Watson to the "Anomodontia" or Therapsida. The sutures in the lacrymal region are not visible.

Therapsida

The labors of Owen, Seeley, Broom, Watson, Whaits, and Haughton on the South African mammal-like reptiles of the Permian and Triassic Karroo series, have revealed the wide adaptive radiation of this group.

The oldest known forms, the Dinocephalia, have already taken on some of the specializations of giantism, especially in their excessively short feet, huge thorax, massive skulls, and strong front teeth, fitted perhaps for tearing up tough vegetation. Notwithstanding these specializations, the Dinocephalia retain many ancient characters, such as the large pineal eye, the very primitive lower jaws, the position of the single temporal fenestra below the junction of the postorbital and squamosal, the presence of a small cleithrum and of two coracoid elements, the primitive atlas complex, the plate-like pubis and ischium, and the primitive relations of the tibia and fibula with the tarsus. In another series of characters they have advanced far beyond the crawling bent-kneed pelycosaur stage, and they are evidently heavy-bodied derivatives of a swift-moving type able to extend the knee and raise the body well off the ground. The lacrymal region is fairly primitive and, although the lacrymal is overgrown by the stout maxilla, it is in contact with the enlarged septomaxilla, this probably indicating that the lengthening of the face in this group is secondary.

The Dromasauria, of the Permian, are small lacertiform reptiles with a primitive skeleton, especially in the manus and pes. They have a primitive undifferentiated series of teeth all around the short mouth. The orbit is large and has apparently encroached upon the lacrymal, which is very short and in wide contact with the septomaxilla (Broom). The temporal region is primitive, allied to the dinocephalian type, and structurally ancestral to the specialized anomodont type. The latter is distinguished not only by the beaked jaws, but by the extreme shortening of the lacrymal region and backward prolongation of the zygomatic arch and fossa.

The Permian Gorgonopsia probably stand near the middle of the whole therapsid series. The typical genera retain the primitive position of the temporal fenestra below the postorbital-squamosal bar, and the palate and basiscranii are modified from the primitive pelycosaur type (Watson). The skull is of the predatory, compressed pelycosaur type, often with a festooned row of laniary teeth, but this may be largely a parallel development; that is, it is quite possible that the lengthening of the face is secondary. The lacrymal, as in the higher pelycosaurs, no longer extends to the nares and is overgrown by the enlarged maxilla.

The dentary exhibits a long coronoid process, or ascending ramus, a predatory adaptation, but fundamentally the jaw is allied to the primitive dinocephalian type. The limbs are often of the swift moving type, capable of extending the knees.

The Therocephalia closely resemble the Gorgonopsia in skull form, but the temporal fossa now extends up to the parietals, the postorbital-squamosal contact being lost; the palate develops vacuities near the ectopterygoids (Broom, Watson). The lacrymal region is similar to that of the Gorgonopsia. The Bauriamorpha are another predatory offshoot of the primitive Therapsida, comprising small animals which in some respects foreshadow the cynodonts. Some of them acquired oval-crowned grinding teeth.

The Triassic Cynodontia range in size from *Ictidopsis*, which was about as large as a common dasyure, to *Cynognathus crateronotus* with a skull about fifteen inches long. In *Cynosuchus* the general skull form is like that of the primitive Gorgonopsia, and the simple recurved teeth are arranged in a festoon. The lacrymal region, as described by Houghton, is essentially the same as it is in other members of this suborder. In *Ictidopsis* (Fig. 57) the molars are becoming triconodont. The lacrymal region is very marsupial-like, but the enlarged maxilla has not yet grown backward and upward above the lacrymal. In the higher cynodonts the molars vary from the shearing triconodont type of *Cynognathus* to the oval tuberculate crowns of *Diademodon* and its allies. The incisors and canines are of predatory submammalian type. The upper jaws widely overhang the lower. The mandible is submammalian in so far as the dentary is the predominant element with a wide ascending ramus, while the quadrate and articular are small and seemingly are about to be transformed into the incus and malleus. The palate is distinctly submammalian and the atrophy of the quadrate process of the pterygoid foreshadows the subsequent reduction of that element, which is so large in all other reptiles. The lacrymal region of *Cynognathus* and *Diademodon* is very mammal-like and is in harmony with the view that the cynodonts, as a group, are actually ancestral to the mammals. The expansion and overlap of the lumbar ribs is unique and suggests some radical changes in the musculature, possibly leading to the mammalian diaphragm and eventually to the loss of lumbar ribs and the substitution of apophyses from the centra. The shoulder girdle, humerus, and pelvis foreshadow the monotreme type and in the femur we have the beginnings of the mammalian trochanters.

In brief, the Therapsida range from relatively primitive Permian stages immediately above the pelycosaurs up to highly progressive Triassic types immediately below the mammals. It is customary to regard even the cynodonts as at most very remote relatives of the mammals, but it is now time to call for definite evidence in favor of this a priori assumption.

Parapsida

The most primitive well-known member of this series is perhaps *Palæohatteria*. Here the lacrymal is well developed, although not extending to the naris, and is barely excluded from the orbital border by a slight prefrontal-jugal contact, which recalls the conditions in many temnospondyls. In the relatively primitive Triassic ichthyosaurs and even in their descendants, the normal ichthyosaurs with enlarged orbits, the lacrymal still remains fairly primitive. The Squamata, on the other hand, are characterized by the early reduction of the lacrymal and the concomitant enlargement of the prefrontal—a line of specialization which culminates in the Ophidia in the complete loss of the lacrymal. In the Acrosauria (*Sauranodon*, *Pleurosauros*), also, the lacrymal is reduced and the prefrontal enlarged.

Rhynchocephalida

This series has generally been placed under the Diapsida, but it seems more likely that of its two supratemporal fenestræ the lower one was inherited from primitive pelycosaurs and the upper one was developed independently, just as it was in the true Archosauria, comprising the aëtosauers, phytosaurs, crocodiles, dinosaurs, pterosaurs, and ancestral birds. The more primitive Rhynchocephalida (*Rhynchosaurus*, *Champsosaurus*) retain the lacrymal, with its normal reptilian contacts, but in *Stenométopon* its place is partly usurped by the prefrontal, and in *Sphenodon* the lacrymal has been entirely lost.

Sphenodon presents a curious mixture of characters; the palate recalls both the captorhinid and the primitive lizard types; in the absence of the lacrymal and in the predominance of the prefrontal it parallels especially the Chelonia; while in the loss or fusion of the opisthotic it parallels all recent reptiles except the Chelonia; the skeleton as a whole is distinctly lacertiform, but in some points more primitive.

The derivation of the Rhynchocephalida from some primitive theromorph or pelycosaur is suggested by very many characters of the skull and skeleton in which the former are obviously more advanced than the latter.

Diapsida (Archosauria)

In all the primitive members of this relatively compact natural group (after the exclusion of the Rhynchocephalida, etc.), the skull is already compressed, with a high temporal region and a pointed face; the lacrymal is a large bone on the side of the face and is perforated by a large antorbital fenestra. This condition, with secondary modifications, persists in the earliest phytosaurs, dinosaurs, and pterosaurs, but has probably been lost in the Crocodilia. The birds probably sprang from some very early member of the diapsid series, but parallel the non-diapsid groups in the loss of the true lacrymal and the substitution of an enlarged prefrontal.

Prototheria, etc.

The grouping of the lower mammals into subclasses is in an unsatisfactory state owing to the poverty of the palæontological record and to the degraded and partly specialized conditions of the existing representatives of the Prototheria. The monotremes show strong evidence of remote affinity with the marsupials in the construction of the brain and of very many other parts of the anatomy. On the other hand, their skeleton is totally lacking in any clear marks of a former arboreal stage such as persists even in the most highly modified marsupials, so that it is unlikely that the monotremes ever passed through an arboreal stage. Their orbital region is peculiar not only in the total loss of the lacrymal but in the great expansion of the orbitosphenoid, extremely small frontals, loss or great reduction of the jugal, etc. These and other peculiar skull characters might perhaps have been derived from the conditions in the Multituberculata, as suggested by Broom (1914, p. 3), but, according to Matthew and Granger, the limb structure of *Ptilodus* is clearly against this view. Of the two existing monotremes, *Ornithorhynchus* is apparently the more primitive in many characters.

I have often considered the possibility that the monotremes might be derived directly from some such anomodont as *Lystrosaurus* through the expansion of the box-like cranium, the dwindling of the squamosal and posterior jaw elements, the degeneration of the beak into a leathery "duck-bill," etc. But the retention of marginal teeth in *Ornithorhynchus*, the lack of all positive evidence for direct derivation from either the anomodonts or the dinocephalians, and the evidence of the structural affinity of the monotremes with the marsupials and with the multituberculates are all against such an hypothesis.

Ptilodus, as Mr. Gidley has shown, has numerous skull characters in common with marsupials and, even if Broom's view that the multituberculates are related to the monotremes should be confirmed, it would perhaps only indicate that the monotremes, as well as other multituberculates, have been derived from primitive Metatheria.

The affinities of *Tritylodon* are very puzzling. Its "multituberculate" dentition is very unlike that of *Plagiaulax* and *Ptilodus*, and its resemblances to the typical multituberculates are remote. According to Broom, the lacrymal region is mammalian in type, as it has lost the prefrontal.

In order to discuss effectively the interrelations of the Tertiary groups of mammals in which the lacrymal region is known, it will be necessary to consider briefly the interrelations of the Mesozoic mammals, in which unfortunately the whole skull is unknown, only jaws and teeth being preserved. Among these, the triconodonts are of interest in the present connection only in the fact that they may possibly be allied, on the one hand, to the Protodonta and thus eventually to the cynodonts and, on the other, to the multituberculates and primitive Metatheria. The remarkable diversity in the dentition of the Purbeck (Upper Jurassic) triconodonts and trituberculates, and the sharp differentiation of these two groups even in the Stonesfield Slate (Lower Jurassic) shows that the common ancestral source must be at least of Upper Triassic age, where they were perhaps represented by the Protodonta. The affinities of the Trituberculata are discussed below.

Metatheria

The known Marsupialia, in spite of their wide adaptive radiation, are a rather compact natural group, the more primitive members of the polyprotodont and diprotodont suborders retaining a long series of characters indicating a common origin, possibly in the early Tertiary but not far back in the Mesozoic. The construction of the lacrymal region, while subject to minor variations, reveals several details which are characteristic of the group, especially the tendency for the lacrymal to develop a prominent antorbital rim which is produced dorsoposteriorly. The lacrymal-nasal contact which sometimes occurs may well be a primitive marsupial character. In the more primitive marsupials the lacrymal foramen is behind the antorbital rim, but with advancing specialization it first notches the rim and may even move forward a little in front of it.

The evidence of the lacrymal region is in harmony with the view that the cænolestoids are allied with the Peramelidæ among the Polyprotodontia.

Myrmecobius, in its lacrymal region as well as in the dentition, is merely a specialized dasyurid.

Wynyardia is extremely primitive in the lacrymal region and is probably a primitive diprotodont.

Placentalia

With regard to the Mesozoic Trituberculata, the jaw and dentition indicate that the Lower Jurassic *Amphitherium* was ancestral to *Amblotherium* and other minute insectivorous genera of the Purbeck beds, which are of Wealden age. Owen regarded them all as marsupials but, on account of the form of the angle of the jaw, they may be very primitive placentals. Probably their *Notoryctes*- and *Chrysochloris*-like molars do not indicate any close affinity either with the marsupials or with the zalambdodont placentals. On the other hand, *Amphitherium* itself may stand near the common source of both the Marsupialia and the Placentalia, as suggested by the extremely primitive dentition.

The lacrymal problem in its phyletic and taxonomic bearings is closely connected with the problem of the origin of the placental mammals. Was there ever a single relatively compact natural group of primitive placentals, the source of all the now extremely diversified placental orders? Or have these been derived independently from widely different metatherian groups? If the former is true many at least of the "primitive placental characters" have been derived by inheritance from the ancestral group; if the latter, then these supposedly primitive characters are of convergent derivation.

In the case of the marsupials it is practically certain that we have to do with a natural group for, although extremely diverse in habitus, they are tied together by such a long series of peculiar characters of the dentition, skull, limbs, brain, reproductive organs, etc., that a common origin is practically demonstrated.

The placental radiation, however, is so much older, or at least has progressed so much farther, that among its modern representatives the greater part of the ancestral heritage has been concealed or destroyed by cœnotelic modifications, and we find accordingly that, apart from the presence of a corpus callosum and of an allantoic placenta, there are not many typical characters which hold good of the entire series.

As far back as the Lower Eocene the adaptive radiation of the placentals had gone so far that nearly all the modern orders were well differentiated from each other, and even in the Paleocene there were such highly specialized mammals as bats and stylinodonts. The great

collections of Paleocene and Eocene mammals made by this Museum are constantly increasing the number of Eocene mammals of isolated position and of relatively high specialization, so that the placental radiation must have commenced far back in the Mesozoic.

On the other hand, these collections, which are now being described by Matthew and Granger, are also increasing the number of known forms which unite in themselves characters that were later distributed among different orders, and which multiply the number of apparent connections between diverse placental groups. Here belong many of the genera which Matthew has provisionally referred to the Insectivora, pending the determination of their true positions.

Cope's view of the ultimate unity of origin of the placentals was based partly on his observation that in the Paleocene and Lower Eocene most placental families preserved clear evidence of derivation from primitive stocks with tritubercular upper and tuberculosectorial molars, a conclusion which has been greatly strengthened by subsequent research, especially by Osborn and Matthew. Cope was also impressed by the prevalence in the Paleocene and Lower Eocene of placental mammals with very primitive five-toed hands and feet. It was largely the detailed characters of the limbs and feet which led Matthew (1904) to the generalization that the placentals, as well as the marsupials, had been derived from primitive arboreal ancestors with a "more or less opposable" first digit on both the manus and the pes.¹

The humeri of Paleocene and Eocene mammals seem to give testimony in the same general direction, and after a somewhat extended comparative study (1920, pp. 64-78) I reached the conclusion that in the primitive placentals of the Mesozoic the well-developed forearms were probably capable of a variety of movements as in climbing. It is also highly probable that these primitive unguiculate placentals were quite small, small enough to crawl easily through the underbrush and not so heavy as to make extreme specializations for climbing necessary. Their small size seems a safe inference from the facts that in every case in which the history of the group is well known the phyla run back into small forms with a more or less primitive dentition and skull, and that the varied trituberculate mammals of the Mesozoic were really minute in size.

¹This conclusion is contested by Mr. J. W. Gidley in a brief paper (1919) which was received after the present manuscript was fully written. A criticism of this paper lies beyond the scope of the present work.

Other characters which may provisionally be assigned to these primitive placentals are as follows: manus and pes relatively short, with gently spreading digits and partly divergent pollex and hallux; skull macrosmatic, with brain-case very small, sagittal crest and jaw stout; orbits small, postorbital processes incipient; lacrymal forming part of the prominent antorbital rim, behind which was the lacrymal foramen; lacrymal in contact with jugal, a well-defined fronto-maxillary contact above lacrymal; dental formula of adult—I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$; of young—DI $\frac{3}{3}$, DC $\frac{1}{1}$, DP $\frac{4}{4}$; incisors small, not specially modified, canines of moderate size, subcaniniform, not premolariform; premolars simple, except p^4 , upper molars tritubercular; lower molars tuberculosectorial; diet various, including insects, the nestlings of birds, eggs, fruits, etc.

CARNIVORA.—The classification of the major groups of Carnivora by Matthew (1901, 1909, 1915) is also an expression of the adaptive radiation and phylogeny of the Creodonta and Fissipedia.

At the base of the series are the Oxyclænidæ, which are among the most primitive of all known placental mammals, not only in the dentition but also in the skull, including the lacrymal region (cf. page 146). The skeleton as a whole will shortly be described by Matthew. Meanwhile, it may be noted that the manus of the Lower Eocene *Chriacus gallinæ* (Matthew, 1915, p. 6) is of a very primitive placental type, with short spreading metacarpals, partly divergent pollex and strong claws, the whole being not unlike the climbing manus of the modern *Cercoleptes*. It seems highly probable that this general type of manus, adapted both for climbing and walking, is nearer to the primitive arboreal placental stage than is the compressed and more or less elongate manus of cursorial carnivores.

Closely related to the Oxyclænidæ are the Arctocyoniidæ. In these the dentition is less primitive but the manus and pes of *Clænodon*, as described by Matthew (1901), are even better adapted for grasping and climbing. The Oxyclænidæ and the Arctocyoniidæ are grouped by Matthew as Procreodi because their p_4 and m_1 are not specialized as carnassial teeth. The dental and other characters of *Thryptacodon* (Matthew, 1915, p. 9) of the Oxyclænidæ suggest that there is "probably a near affinity between the less specialized Arctocyoniidæ, and the Cercoleptoid Miacidæ and the Oxyclænidæ, although part of the resemblance is due to parallelism" (Matthew, *op. cit.*, p. 9).

The Miacidæ constitute the division Eucreodi of Matthew, so named because their p_4 and m_1 are specialized as carnassial teeth as in modern

Fissipedia, to which this group is also closely allied in all parts of the skeleton. The pes of *Didymictis* (Matthew, 1915, p. 26) is of semiplanti-grade type, but becoming better adapted for running. The feet of *Vulpavus*, *Miacis*, and *Vassacyon*, according to Matthew, are more "arboreal" in type. The lacrymal region of this family (p. 148) foreshadows the conditions in the modern Carnivora but is more primitive.

The Pseudocreodi of Matthew include the typical and best known creodonts, such as *Hyænodon* and *Patriofelis*, in which the carnassial teeth are behind p_4 and m_1 . In these animals the skeleton is, on the whole, less primitive than that of the Oxyclænidae, being often adapted for running. The muzzle is elongate and with it the pars facialis of the lacrymal. The late members of this group are large and specialized, but the earlier stages are smaller, and the trend is toward the Oxyclænidae as a central type.

The Acreodi of Matthew, including the Triisodontidae, are distinguished by the lack of normal carnassial teeth. The more primitive members (Triisodontidae) have tritubercular molars, which approach the primitive oxyclænid type. The more specialized Acreodi finally attain gigantic size and have various aberrant types of molars. The muzzle becomes long and with it the pars facialis of the lacrymal. The limbs of the late Mesonychidae are of subcursorial type.

The Fissipedia include two rather widely separated groups, the Æluroides and the Arctoidea, which were possibly derived independently from the Eucreodi. Their lacrymal is often reduced and sometimes vestigial. The skeletons show a wide adaptive radiation for climbing, swimming, running, etc.

The Pinnipedia seem to be a very early offshoot of the primitive Arctoidea, which they resemble in the enlargement of the maxilloturbinals and in the auditory and lacrymal regions. That they are not modified Pseudocreodi is indicated by the reduction in number of the true molars, by the consolidation of the scaphoid, lunar, and centrale, and by the detailed characters of the lacrymal region.

INSECTIVORA (Lipotyphla).—The existing lipotyphlous Insectivora are all more or less highly specialized and degraded remnants of primitive Mesozoic placentals, which would perhaps be well represented by *Amphitherium*. Not much is left of the conception of the Insectivora as a primitive order, because most of their purely insectivorous adaptations are rather high specializations which outnumber such primitive placental characters as they still preserve. It is rather from the primitive Paleocene and Eocene representatives of the Creodonta, Tænio-

donta, Taligrada, Condylarthra, etc., that a more accurate concept of the stem placentals is now being derived.

The least specialized insectivores that are known from well-preserved skulls are the early Tertiary Leptictidæ which in the Eocene gave rise to the Erinaceidæ. Their lacrymal region is comparatively primitive, especially in *Ictops dakotensis* (Fig. 104). In the Erinaceidæ the pars facialis becomes further reduced, the foramen becomes marginal and the pars orbitalis expands. Quite characteristic is the peculiar mode of the reduction of the jugal, which finally becomes a vestige embedded in the middle of the zygomatic arch.

The Zalambdodonta are a very ancient stock, only remotely related to the Erinaceoidei. Matthew (1913) has shown that in the Paleocene zalambdodont *Palæoryctes* the molar pattern distantly approached a more normal tritubercular type, while in most of the later zalambdodonts the peculiar V-shaped form is secondary, not primitive. The recently described *Nesophontes* of Anthony, a subfossil insectivore from Porto Rico and Cuba, tends strongly to connect the soricoids as a branch of the primitive zalambdodont stock. The lacrymal region in the zalambdodonts, while more or less degenerate, is quite characteristic in appearance (see page 165).

EDENTATA.—The Edentata have often been regarded as an excessively ancient branch of the mammals, almost deserving of subclass rank, but recent studies of Matthew (1918) give evidence that this order has undergone a very wide adaptive radiation during the second half of the Tertiary, during which the tree sloths were derived from ground sloths allied to *Hapalops*, the ant-eaters from others allied to *Scelidotherrium*. This conclusion is supported by the patterns of the lacrymal region as described on pages 167 and 168 below. The affinity of *Hapalops* to the tree sloths in the lacrymal region is very clear, while *Scelidotherrium* is plainly more primitive than the Myrmecophagidæ. Dr. Matthew shows also that the armadillos and glyptodonts, on the other hand, are the remnants of an older, early Tertiary stock, probably allied to the palæanodonts of Matthew. The lacrymal region of armadillos (pp. 168, 169) is quite distinct from the primitive ground-sloth type.

PHOLIDOTA.—The Pholidota also appear to be derived from this primitive edentate source (Matthew). Their lacrymal is highly degraded and specialized.

TUBULIDENTATA.—The Tubulidentata, on the other hand, have no relations with the edentates and are more probably highly specialized offshoots of the primitive Taligrada or Condylarthra. The great in-

crease in the pars facialis of the lacrymal is associated, as in many other instances, with the elongation of the snout and with the expansion of the olfactory chamber and adjacent sinuses.

TÆNIODONTA.—The more primitive Tæniodonta, such as *Onychodectes*, are now regarded by Matthew as allied to the palæanodonts and primitive edentates. The lacrymal region and, indeed, the whole skull and dentition of the Paleocene *Onychodectes* are very primitive and tend to connect this group with other primitive placentals, especially the Insectivora (Matthew).

LAGOMORPHA.—Mr. Gidley (1912) has emphasized the fact that even the Oligocene Lagomorpha are very highly specialized and widely different in the dentition and limbs from the other rodents. He, therefore, has raised the Lagomorpha to ordinal rank. While accepting this arrangement provisionally, I conclude from a comparison of the auditory, lacrymal, and basicranial regions, dentition, etc., of lagomorphs with those of the Eocene Ischyromyidæ that, on the whole, the latter represent a structural stage through which the lagomorphs must have passed if they were derived from any primitive placentals, as their brain, reproductive organs, etc., clearly indicate. The queer characters of the dentition cited by Mr. Gidley and the cursorial or saltatorial adaptations of the limbs are specializations beyond the more primitive conditions preserved in the Ischyromyidæ, although I do not suggest that they were actually derived from that family.

RODENTIA.—Even Messrs. Miller and Gidley (1918) are at present willing to admit that after the exclusion of the Lagomorpha the remaining rodents form a natural group, and by extending the work of Brandt and of Tullberg they have recently given a remarkably detailed picture of the multitudinous branches and subbranches of the adaptive radiation of this order. They will not admit that the Eocene Ischyromyidæ are ancestral to any of the later superfamilies and families, as held by Matthew (1910), and apparently believe that, since several of the existing families are well established in the Oligocene, the origin of the order must be sought far back in the Mesozoic.

As the evolution and consequent taxonomic characters of the lacrymal of rodents have been conditioned in part by the evolution of the gnawing apparatus, we must consider both together. The least specialized condition is preserved in the Ischyromyidæ, in which the greatly enlarged premaxilla had already extended dorsoposteriorly above the maxilla, gaining a wide contact with the frontal and restricting the maxilla. The lacrymal is consequently reduced to a small element on

the anterior rim of the orbit. The enlarged jugal retains its primitive contact with the lacrymal. The lateral sheet of the masseter probably ended anteriorly in a tubercle borne on the zygomatic branch of the maxilla, beneath the orbit.

In the modern *Arctomys*, representing the Sciuromorpha, the lacrymal is further restricted, but otherwise the lacrymal region is essentially unchanged. A branch of the masseter lateralis now extends in front of the masseteric tubercle, on to the maxilla, in front of the orbit, and this is the sole important difference in this region between *Arctomys* and the Eocene *Paramys*. Now as this preorbital extension of a branch of the masseter is obviously a new adaptation which was not yet developed in the Ischyromyidæ, I can see no good reason for using the primitive condition of that family as evidence for excluding *Paramys* from the ancestry of the Sciuromorpha, especially as the dentition of *Paramys* plainly relates it to that series.

In *Castor* the lacrymal is further restricted and the very powerful preorbital external branch of the masseter has conditioned the great strengthening of the jugal and the deep incision of a groove on the side of the maxilla. Somewhat similar conditions are found in the geomyid series, which, like the castorids, are specialized derivatives of the primitive sciuromorph stock.

In the myomorphs a further reduction of the lacrymal occurs, along with an opening up of the upper part of the infraorbital canal due to the invasion of a medial slip of the masseter.

In the dipodomorph series this medial slip becomes of enormous size, excavating a huge fenestra in the maxilla in place of the infraorbital canal and crowding the masseter lateralis away from the rostrum. The lacrymal in this series forms part of the dorsal brace for the zygomatic arch.

Finally, in the hystricomorphs, the jugal withdraws entirely from this brace, which is formed either chiefly by the maxilla or by the maxilla plus the enlarged lacrymal (Caviidæ); the deep fossa for the masseter medialis now extends far forward on to the premaxilla. In view of the extreme specialization of the molar teeth and of the lower jaw in the hystricomorphs, the conditions above described appear to be equally specialized. Finally, as all this is in complete harmony with the evidence afforded by successive stages of evolution of the jaws and dentition, I believe that the foregoing is a true account, not only of the evolution of the lacrymal and zygomatic region, but of the general evolutionary stages of the groups represented, and therefore accept fully the conclu-

sions of Dr. Matthew that, at least with regard to structural characters, the Ischyromyidæ are ancestral to all the remaining rodents.

TILLODONTIA.—In the Tillodontia the skull pattern, including the lacrymal region, is derived from the primitive placental type and is related to the primitive creodont type.

CETACEA.—The Cetacea are true placental mammals, and I believe that their origin is less excessively remote than the high specialization of existing forms would suggest. As remarked above (p. 158), the various Tertiary cetaceans tend to bridge the gaps between the Odontoceti and Mystacoceti on the one hand and the Archæoceti on the other. The characters of the lacrymal region further strengthen the evidence of relationship. The derivation of the whole order, through *Protocetus*, from the Hyænodontidæ, as suggested by Fraas, has been favorably viewed by Andrews, Abel, and others, but is doubted by Matthew. A review of the dental and cranial characters of *Protocetus* leads to the tentative conclusion that if the archæocetes are related to the hyænodonts it is probably by descent from primitive Pseudocreodi. (Matthew). Other possibilities, such as relationship with the achænodont Artiodactyla, have been considered but do not seem probable.

ARTIODACTYLA.—The Artiodactyla are a group of ancient origin and uncertain affinities. They are, at least, far removed from the Perisodactyla with which they were formerly bracketed under the term Diplarthra of Cope. Even in their Lower Eocene representatives the typical artiodactyl foot structure was already established and, while the dentition runs back to primitive quadri- and tritubercular stages, it shows no special approach to that of any other group. The large size of the lacrymal, especially of the pars facialis, is very characteristic, except in a few cases. The order may possibly be related to the stem of the creodonts, but even the most primitive Eocene Dichobunidæ are already typical artiodactyls. The recently described Eocene genus *Creotarsus* may, when better known, throw some light on the origin of the order (Matthew).

AMBLYPODA.—The Amblypoda, as defined by Osborn, include a wide range of forms from the smaller Paleocene Periptychidæ to the gigantic, excessively short-footed Dinocerata of the Middle Eocene. The smaller, more primitive families, forming the order or suborder Taligrada, are very primitive placental mammals with tritubercular dentition and primitive limbs. Some of them may be allied to the Mioclænidæ among the Condylarthra (Matthew). In *Periptychus* and *Pantolambda* the limbs are very stout, with short hands and feet not far

from the primitive climbing placental type. The lacrymal, known in *Ectoconus* and *Pantolambda*, is very primitive; in the Dinocerata it is spread out on the inner wall of the orbit. This order and other short-footed ungulates, such as the Embrithopoda and Proboscidea, all appear to me to be derived from primitive short-footed procondylarths.

EMBRITHOPODA.—The Embrithopoda differ widely from the Dinocerata, as noted by their describer, Dr. Andrews, who has suggested remote relationship with the Hyracoidea. Their lacrymal region is comparatively primitive, but does not afford much evidence on this point. *Arsinoitherium* may prove to be a graviportal derivative of some condylarth stock, paralleling the rhinoceroses and astrapotheres in molar pattern.

PYROTHERIA AND BARYTHERIA.—The genetic relations of the Pyrotheria and Barytheria with the Proboscidean-Sirenian stem will shortly be discussed by Professor Loomis.

PROBOSCIDEA AND HYRACOIDEA.—The Proboscidea and Hyracoidea were often supposed to be related groups, but they were already very different even in very early Tertiary times and they may rather be quite independent offshoots perhaps from the Condylarthra. Even the oldest known proboscidean, *Mærittherium*, is far more specialized in skull and dentition than any condylarth. While the structural gap between the two groups is too great to permit positive statements, it seems probable that every one of the specialized characters of the dentition of *Mærittherium* has been derived from the far more primitive conditions in some such primitive procondylarth as *Hyopsodus walcottianus* Matthew (1915, p. 322), which has primitive, gently procumbent incisors, small canines, and the right kind of premolars and molars. This conclusion is a natural inference from what is known of the course of evolution of the dentition in parallel cases. The specialized incisors and small canines of *Mærittherium* are surely derived from the far more primitive placental conditions represented in *Hyopsodus walcottianus*; its molars, while still quadrubercular, show the beginnings of the lophodont modification which has masked their primitive placental characters; its upper premolars, however, are relatively primitive derivatives of an *Hyopsodus*-like type; and the same is true of the lower premolars and molars.

Similarly, with regard to foot structure, both the manus and the pes of *Elephas* are simply gigantic and brachypodal modifications of a primitive condylarth type. This conclusion will probably be rejected as too speculative by most palæontologists, and is here recorded rather as a prophecy than as a thesis capable of satisfactory demonstration, but I

suspect that the primitive hyopsodont Condylarthra are a much better starting point than the Taligrada for the line that culminated in the Proboscidea. As to the relations of the Mæritheriidae, while it is quite possible that *Mæritherium* is related to the Sirenia (Osborn, 1909) the numerous detailed and peculiar resemblances to *Palæomastodon* in dentition and skull structure fully support Dr. Andrews in regarding it as the most primitive known member of the Proboscidea.

The lacrymal region of Proboscidea (p. 180) is specialized through the forward shifting of the orbits and thus affords no definite evidence of relationship with more primitive groups. The lacrymal region of *Mæritherium* is far more primitive than that of *Palæomastodon* and, in connection with other evidence, it supports the view that *Palæomastodon* was derived from a *Mæritherium*-like stage.

SIRENIA.—The Sirenia, although very highly specialized for aquatic life, show special resemblances with *Mæritherium* in the skull (including the orbital region) and dentition, and are generally regarded as a derivative of the proboscidean stem.

CONDYLARTHRA.—The Condylarthra, as recently revised by Matthew and Granger (1915, Parts 2 and 3), include, in addition to the Phenacodontidae (Paleocene and Lower Eocene), the families Mioclanidae (Paleocene), Hyopsodontidae (Lower to Upper Eocene), Meniscotheriidae (Lower Eocene), and possibly also the Pleuraspidotheriidae (Paleocene, Europe). The Lower Eocene *Phenacodus* was regarded by Cope as the five-toed atavus of the hoofed mammals and in popular writings has often been referred to as the oldest known stage in the evolution of the Equidae. But Matthew (1897) showed that its "serial" foot structure is not primitive but derived from the more primitive conditions in the Paleocene *Euprotogonia* (*Tetrachodon*), its direct ancestor, and Osborn (in the forthcoming monograph on the Titanotheres) regards it as having no relationship with the contemporary perissodactyla. *Ectocion*, however, of the same family, is regarded by Granger (1915) as "presenting the type of upper molar from which the perissodactyl molars might have been derived" and the same may be said of the lower molars and of the upper and lower premolars. The lacrymal region (p. 176) in this family is known only in *Phenacodus*, where it is fairly primitive but not specially akin to the perissodactyl type. While *Phenacodus* itself is not an ancestor of the Perissodactyla, it retains many characters in the skull and skeleton which tend to support the view that the remote ancestors of the hippoid and other Perissodactyla once passed through a condylarth stage resembling *Ectocion* (Gregory, 1910, pp. 387–397, 450–451).

The fact that *Phenacodus* has a ball and socket lower ankle joint while the known perissodactyls have a hinge joint is not, I think, a valid objection to the foregoing conclusion, since the hinge joint is a progressive character of the perissodactyls, while the ball and socket ankle joint is a primitive placental character. The serial manus of *Phenacodus*, as above noted, is probably a specialized generic character.

The Meniscotheriidae (Granger, 1915) are widely different from the *Phenacodontidae* in dentition and skull as well as in the proportions of the limbs. They have short, spreading hands and feet of primitive placental type, in contrast with the narrower, more tridactyl feet of Phenacodonts. Their lacrymal region is also primitive (p. 175).

Their bunolo-phoselenodont upper molars present a complex crown-pattern which differs from those of the Eocene titanotheres and chalicotheres chiefly in the stronger development of the proto- and metaconules. The lower molars and both the lower and upper premolars also have many points of resemblance with the corresponding parts in chalicotheres and titanotheres. Many other resemblances to these groups, mixed with much more primitive placental characters, are revealed by a study of the skull, vertebræ, humerus, femur, radius and ulna, tibia and fibula, astragalus, manus and pes of *Meniscotherium chamense terrærubræ*. Obviously, however, this Lower Eocene meniscothere is not ancestral to the titanotheres, and probably not to the chalicotheres.

The Phenacodontidae, Hyopsodontidae, and the Mioclenidae run back into very small and extremely primitive species in the Paleocene, which have bunodont tritubercular molars and are not far from the primitive arboreal placental stock. They are, in fact, so primitive that it is only recently that Matthew and Granger have been able to show that they are Condylarthra. Thus, the order Condylarthra is of great phylogenetic interest. Unfortunately, its best and most widely known member, *Phenacodus primævus*, of the Lower Eocene, represents the most specialized stage of its own phylum and never deserved the high place once assigned to it as the "atavus of the hoofed mammals." Nevertheless, the order is probably related, through some of the smallest and oldest members, on the one hand with the primitive arboreal placentals and on the other hand with the Periptychidae, the Perissodactyla, the Proboscidea, the Hyracoidea, and all the orders of extinct South American ungulates.

The Mioclenidae, which are referred to this order, are perhaps even more primitive than any known creodont, and some of the smallest mioclenids may stand near the source of the Primates.

HYRACOIDEA.—The Hyracoidea of the Lower Oligocene of Egypt are already specialized, both in skull structure and in dentition, and afford but little clue as to the origin of the group. The bunoselenodont upper molars and relatively advanced premolars might have been derived, partially by the reduction of the “conules,” from those of a *Meniscotherium*-like condylarth. The Hyracoidea resemble certain Perissodactyla in a number of characters, and may well be a partly parallel offshoot from the pro-Condylarthra. The lacrymal region of the older forms is allied to the primitive condylarth type, but more specialized.

NOTOUNGULATA, ETC.—The extinct South American ungulates, excepting the pyrotheres, exhibit a great adaptive radiation, of which the several branches parallel the Perissodactyla, the Hyracoidea, and in some cases the Rodentia, in body form, dentition, and foot structure. The rodent resemblances of the typotheres are pure analogies, but the perissodactyl and hyracoid characters are probably due to the independent derivation of all these groups from primitive Condylarthra. Thanks to the labors of Burmeister, Ameghino, Lydekker, Roth, Scott, and others, it is established that the South American ungulates include three very distinct orders, the Litopterna, the Notoungulata, and the Pyrotheria. The Litopterna run back into small forms with relatively primitive dentition, which in some cases suggest condylarth types. The Notoungulata have rhinocerotoid molars, but often with an “accessory pillar” in the lower molars and extra folds in the upper.

The lacrymal region of the Litopterna and Notoungulata, so far as known, is readily derivable from the condylarth type.

PYROTHERIA.—The Pyrotheria, according to Professor Loomis, may be related to the Proboscidea and Sirenia.

PERISSODACTYLA.—The very numerous and diversified perissodactyls of the Eocene have been studied and described by many writers, including Cope, Kowalevsky, Osborn, Schlosser, Depéret, Stehlin, Matthew, Granger, and others, who have worked out the systematic relations and evolution of the different families. Professor Osborn (1898) has divided the order into five superfamilies, Hippoidea, Tapiroidea, Rhinoceroidea, Chalicotheroidea, and Titanotheroidea. These superfamilies may be considered under two series, the first, or plagiolophodont series including the horses, palæotheres, tapirs, lophiodonts, rhinoceroses and their allies, and the second, or bunolambdodont series, the chalicotheres, lambdotheres, and titanotheres. The plagiolophodont series tend to have bunolophodont to buno-lophoselenodont molars,

with prominent oblique proto- and metalophs; their premolars are often precociously molarized; the manus and pes are, usually, progressively mesaxonic. Starting with small subcursorial forms like *Eohippus* and *Systemodon*, they give rise to a great adaptive radiation of graviportal and cursorial phyla, with the well-known specialized dentitions of the horses, tapirs, rhinoceroses, and allied families. The related bunolambdodont group, on the other hand, shows a strong tendency to develop bunolambdodont molars with more or less reduced proto- and metalophs, which become vestigial in many titanotheres; the premolars are imperfectly and slowly molarized; and the fore feet pass from the mesaxonic either to the paraxonic or to an asymmetrical arrangement.

In both series the nasals are large and are originally in contact with the lacrymals. All the superfamilies run back to the stem of the Perisodactyla.

MENOTYPHILA.—The Menotyphla are widely removed from the typical Insectivora or Lipotyphla and are probably related to the stem of the Primates, with which they agree in many important characters. But the separation of the two orders probably took place as far back as the Paleocene, since the Paleocene and Lower Eocene Plesiadapidae, which appear to be Menotyphla, were already distinct from, although related to, the Primates.

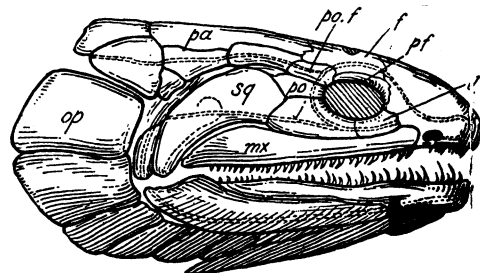
The lacrymal region of the modern Menotyphla is specialized by the inflation of the sinus in its interior, paralleling that of *Lemur* in the great extension of the pars facialis.

DERMOPTERA.—The Dermoptera are at the present time an isolated group apparently related remotely to the Menotyphla and to the Chiroptera. As noted by Matthew (1918), the group was possibly represented in the Lower Eocene by the genus *Plagiomene*.

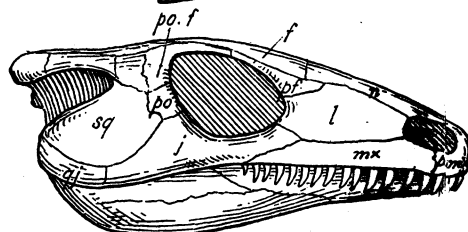
CHIROPTERA.—The Chiroptera date back at least to the Paleocene (Matthew, 1917) and are perhaps remotely related to the Menotyphla-Primate stock. They apparently tend to confirm the theory of the arboreal origin of the placentals and their source must be sought among the primitive bunodont, insectivorous-frugivorous mammals.

PRIMATES.—The premolars and molars of the most ancient and primitive Primates resemble in many characters those of the smallest mioclænid Condylarthra, and it is possible that Cope may eventually be justified in his opinion that the Condylarthra were ancestral to the Primates as well as to many other orders. From the first the dentition is of the bunodont frugivorous-insectivorous type and the primates avoid both the shearing and the advanced lophodont modifications of other orders.

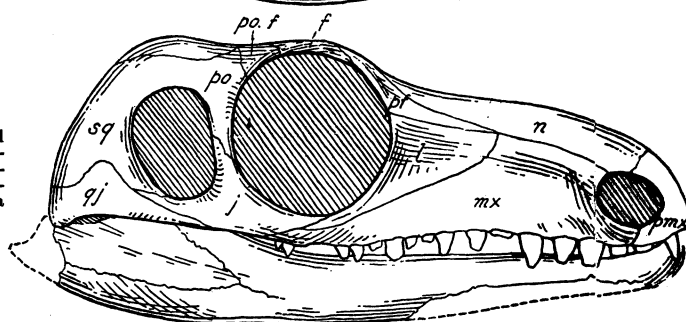
Stage 1. Rhipidistian fish (*Osteolepis*). After Goodrich. Lower Devonian. Lacrymal forming part of the circumorbital series of surface bones; traversed by lateralline canal.



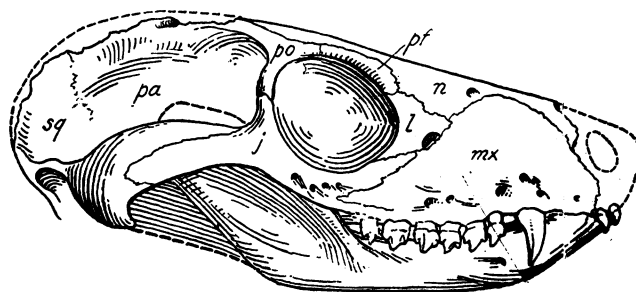
Stage 2. Very primitive cotylosaurian reptile (*Seymouria*). Permian-carboniferous. Elements of the circumorbital series well differentiated from each other. Lacrymal extending from orbit to nares.



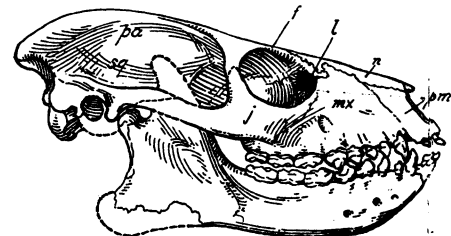
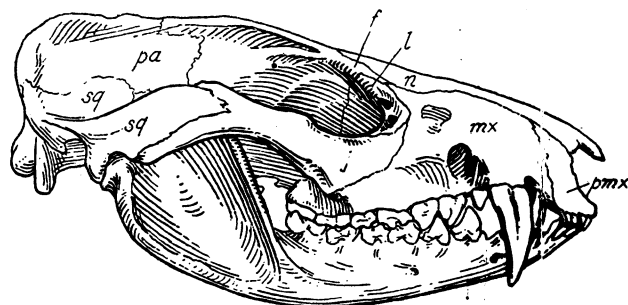
Stage 3. Primitive synapsid reptile (*Mycterosaurus*). Permian-carboniferous. Lacrymal abbreviated anteriorly by upgrowth of maxilla. Beginning of temporal fossa and zygomatic arch.



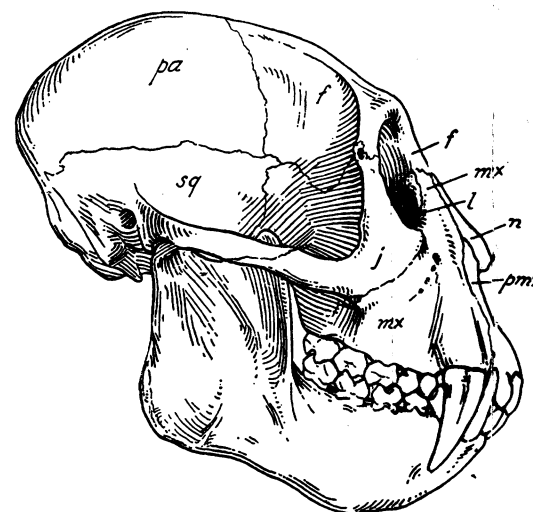
Stage 4. Cynodont reptile (*Ictidops*). Upper Triassic. Lacrymal, temporal fossa, and zygomatic arch of submammalian type. Prefrontal and postorbital still present. Maxilla widely separated from frontals.



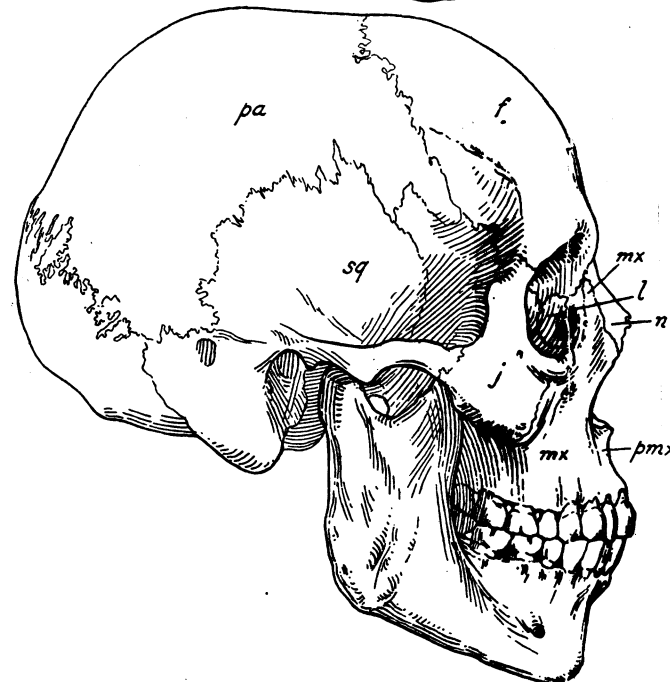
Stage 5. Primitive mammal (*Didelphis*). survivor of Cretaceous Metatheria. Lacrymal with reduced pars facialis. Prefrontal and postorbital absent. Maxilla barely touching frontal.



Stage 6. Primitive primate *Notharctus*. Middle Eocene. Lacrymal chiefly within orbit. Lacrymal foramen shifted in front of the lacrymal. A secondary fronto-jugal contact. Maxilla in contact with frontal.



Stage 7. Old World monkey (*Macacus*), survival of early Tertiary catarrhine stock. Lacrymal wholly within orbit, separated from jugal by maxilla. Face abbreviated. A postorbital partition, eyes directed chiefly forward.



Stage 8. Man. Lacrymal essentially as in Stage 7. Face greatly abbreviated. Eyes directed fully forward.

PLATE XVII

Evolution of the lacrymal bone. Stages 1 to 5, fish to primitive mammal.

Evolution of the lacrymal bone, continued. Stages 6 to 8, primitive primate to man.

The foot structure of the Eocene primates (Adapidæ, Tarsiidæ) is already completely arboreal in type, with elongate phalanges, more or less flattened ungues and sharply divergent hallux. Such hands and feet can never have been derived from specialized terrestrial types and their characters seem to lend support to Dr. Matthew's conclusion (1904) that the stem placentals were more or less arboreal in habit. The pes is literally condylarthrous, as the ankle-joint is of the ball and socket type.

The lacrymal region even of the Eocene primates was already specialized in the reduction of the pars facialis, but is otherwise of primitive placental type, which affords no very definite evidence of the origin of the group.

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ADDENDUM

Watson (1913) on the Naso-lachrymal Duct in *Nyctosaurus* and *Diademodon*.

In his second paper on the skull of *Diademodon* Watson (1913, p. 224) describes the naso-lachrymal duct of *Nyctosaurus* and of *Diademodon* in the following important passage, which I unfortunately overlooked until quite recently:

Another feature extremely clearly shown by these two iron-stone casts is the course of the naso-lachrymal duct. This opens into the orbit by two foramina in the lachrymal bone, leading into canals, which soon unite and then travel forward still in the lachrymal bone until they open into the nasal cavity on the inner side of the maxilla. These relations are so very similar to those existing in *Perameles* between the duct and the lachrymal bone as to leave no doubt that the bone in Cynodonts is homologous with that of the mammal. It is, however, the lower of the two bones usually called lachrymal and prefrontal, and as the Cynodonts are certainly more nearly allied to the mammals than the lizards, it leaves no doubt that Gaupp was not justified in homologizing the reptilian prefrontal with the mammalian lachrymal. Meek, from the conditions in the Crocodile, has already controverted this view, Gaupp having no doubt been misled by the great reduction of the true lachrymal in the types studied by him.

Notwithstanding this decisive evidence in favor of the long established identification of the reptilian lachrymal as homologous with that of mammals, von Huene, Wiman and Abel continue to follow Gaupp's erroneous identification of the reptilian prefrontal with the mammalian lachrymal.

