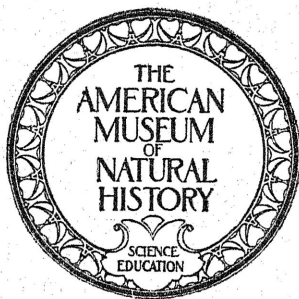


THE OSTEOLOGY AND RELATIONSHIPS OF THE ELEPHANT SHREWS (MACROSCOLIDIDAE)

BY FRANCIS GAYNOR EVANS



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Article IV.—THE OSTEOLOGY AND RELATIONSHIPS OF THE ELEPHANT SHREWS (MACROSCOLIDIDAE)

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INTRODUCTION

The Macroscolididae are a small family of insectivorous mammals confined to Africa but widespread on that continent. The family is divided into two subfamilies: the Rhynchocyoninae, containing the single genus *Rhynchocyon*, and the Macroscolidinae, containing the genera *Petrodromus*, *Elephantulus*, *Nasilio* and *Macroscelides*. All members of the family have rather long slender legs, a long rat-like tail and an elongated proboscis-like snout, in allusion to which they are commonly called elephant shrews.

In size these animals vary from *Rhynchocyon*, adult males of which, according to Allen (1922, p. 22), average about 515 mm. in total length, to *Elephantulus*, *Nasilio* and *Macroscelides* which are all about the size of a small rat.

In all these forms the hind legs are longer than the front ones as in saltatorial types; hence they are frequently referred to as jumping shrews. However, according to Lang and to Loveridge they run on all four feet instead of hopping.

These interesting mammals are usually

grouped with the Tupaiidae in the suborder Menotyphla, order Insectivora, in opposition to all the other insectivores which are placed in the suborder Lipotyphla. This division of the Insectivora into two suborders is based chiefly on the presence of a well-developed auditory bulla and of a caecum in the Menotyphla and their absence in the Lipotyphla, although there are also other differences between the two groups.

Carlsson (1909, p. 394) believes, however, this separation of the Insectivora into the above two suborders is completely untenable and that the Macroscolididae are more closely related to the Erinaceidae than to the Tupaiidae.

Students of vertebrate evolution have long held that the Primates have evolved from the insectivores or insectivore-like ancestors and that of the living insectivores the Tupaiidae are the closest to the primate stem. In recent years the latter belief has been extended, and Carlsson (1922, p. 268) states "that the Tupaiidae cannot be counted in the Insectivora but form a proper suborder of the Prosimiae." In the

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same paper (p. 267) she again says that the Macroscelididae are more closely related to the Erinaceidae than to the Tupaiidae.

Le Gros Clark, in his book "Early Forerunners of Man" as well as in several separate papers on the anatomy of *Tupaia*, also removes the Tupaiidae from the Insectivora and puts them in the suborder Lemuroidea, order Primates, a conclusion accepted by Simpson (1935, p. 29).

If the above conclusions concerning the

Tupaiidae are true then the Macroscelididae are left as the only members of the Menotyphla, and if the latter suborder is invalid, as Carlsson believes, their true systematic position is left in doubt.

In view of the above conditions a restudy of the relationships of the Macroscelididae to the other Insectivora, especially the Erinaceidae, and to the Tupaiidae seems justified. The Lemuroidea were also included in the study.

MATERIALS AND METHODS

As alcoholic specimens of the Macroscelididae are quite rare in the museum collections of this country the present study has been limited to the osteology, although I was unable to secure a complete skeleton of *Elephantulus*. The skull and skeleton of the various genera have been compared with those of members of the Erinaceidae and the Tupaiidae, the only two families to which they have been considered to be related. They were also compared with several species of Malagasy and non-Malagasy lemurs. *Gymnura* was used as a representative of the Erinaceidae and of a generalized primitive insectivore.

The skulls and skeletons of the following species were studied, for the loan of which I am indebted to the kindness and generosity of Dr. Glover M. Allen, late Curator of Mammals, Museum of Comparative Zoölogy, Harvard University; Dr. John Eric Hill, Department of Mammalogy, The American Museum of Natural History; and Dr. G. S. Miller, Curator of Mammals, United States National Museum.

<i>Rhynchocyon stuhlmanni claudi</i>	No. 51216	A.M.N.H.
<i>Rhynchocyon claudi</i>	49429	" " " "
" "	49444	" " " "
" "	49445	" " " "
" "	49517	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86551	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86555	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86557	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86559	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86564	" " " "

<i>Nasilio brachyrhyncha brachyura</i>	" 86570	A.M.N.H.
<i>Nasilio brachyrhyncha brachyura</i>	" 86576	" " " "
<i>Nasilio brachyrhyncha brachyura</i>	" 86596	" " " "
<i>Macroscelides rozeti</i>	31795	" " " "
<i>Elephantulus revolti</i>	54013	" " " "
" <i>renatus</i>	25674	M.C.Z.
" "	25663	" " " "
" <i>ocularis</i>	22842	" " " "
<i>Petrodromus tordayi</i>	55373	A.M.N.H.
" "	55374	" " " "
<i>Petrodromus</i> sp. (labeled <i>Elephantulus ocularis</i>)	241593	U.S.N.M.
<i>Tupaia belangeri chinensis</i>	35830	M.C.Z.
" "	35841	" " " "
" <i>ferruginea</i>	6276	" " " "
" sp.	106506	A.M.N.H.
" "	106507	" " " "
<i>Gymnura alba</i>	103737	" " " "
" "	103886	" " " "
" <i>rafflesii</i>	3052	" " " "
" <i>alba</i>	7104	M.C.Z.
<i>Lemur fulvus</i>	19159	A.M.N.H.
" "	42760	" " " "
" <i>rufifrons</i>	41262	" " " "
" "	41264	" " " "
" "	41268	" " " "
" <i>variegatus</i>	77828	" " " "
" <i>nigrifrons</i>	18696	" " " "
<i>Perodicticus potto faustus</i>	52696	" " " "
" "	52708	" " " "
" "	52714	" " " "
" "	72716	" " " "

I also want to thank Dr. G. G. Simpson of The American Museum of Natural History for allowing me to study the valuable fossil, *Anagale gobiensis*, No. 62079 A.M.N.H., from the Oligocene of Mongolia.

In addition measurements of the limb bones were made of the following species of mammals in the collections of the American Museum and of the Museum of Comparative Zoölogy.

<i>Dipodomys phillipsi</i>	No. 6310	M.C.Z.	<i>Macropus rufus</i>	No. 14153	A.M.N.H.
" "	" 6311	" " "	" "	" 35186	" " " "
" "	" 6312	" " "	" "	" 35231	" " " "
<i>Pedetes caffer salinae</i>	" 42025	A.M.N.H.	" "	" 35735	" " " "
" " (no manus or pes)	" 42057	" " " "	" "	" 35761	" " " "
<i>Pedetes caffer</i>	" 70392	" " " "			
" <i>surdaster surdaster</i>	" 54219	" " " "			
" <i>caffer orangiae</i>	" 81747	" " " "			
<i>Jaculus orientalis</i>	" 70096	" " " "			
" "	" 70004	" " " "			
<i>Napaeozapus insignis</i>	" 67797	" " " "			
<i>insignis</i>	" 55980	" " " "			
<i>Allactaga mongolica</i>	" 5029	" " " "			
<i>Macropus rufus</i>					

I also want to express my great appreciation for the interest and helpful criticism shown by Dr. W. K. Gregory of the American Museum during the writing of this paper while I was a member of the Department of Zoölogy at the University of New Hampshire.

OSTEOLOGY OF THE MACROSCOLIDIDAE

SKULL

Figures 1 and 2

The skull of the Macroscelididae when seen from above (Fig. 1) is roughly triangular in shape with a fairly long tapering snout, a broad interorbital region and a swollen brain case. *Petrodromus* has the proportionally longest and narrowest skull, in which respect it is nearer to the primitive insectivore condition as represented by *Gymnura*. In the remaining Macroscelididae (Table I, Index I) the skull undergoes a progressive shortening and widening which culminates in *Macroscelides*. *Petrodromus* is also the most primitive in having the narrowest muzzle and the relatively smallest interlacrima width (Table I, Index III) while *Rhynchocyon* is the most specialized in these features. In the Macroscelidinae (Table I, Index II) there is a progressive reduction in the size of the olfactory chamber, beginning with *Petrodromus* and culminating in *Elephantulus*, while in *Rhynchocyon* it is secondarily lengthened.

Rhynchocyon exhibits the best development of the supraorbital shelf and differs from the other genera in having a supraorbital notch and a short postorbital process. The latter, as earlier noted by Wortman (1920, p. 3) and by Weber (1928, p. 114), is borne on the parietal, a condition which, whenever it occurs (as in *Hyrax*) is plainly a specialized one. However, I was unable to find the alleged reptilian elements which Wortman (1921, pp. 5, 7) described in members of this family with the exception

of the one he questionably calls the "septomaxillary." This element was present on both sides in only one of the specimens and just on the right side in another. Homologizing this element with the septomaxillary of reptiles seems to be erroneous as the septomaxillary of reptiles is associated with the external nares whereas the element in question in *Rhynchocyon* is associated with the lacrimal and is far removed from the nares. These elements more probably correspond to such rare and secondary bones of human anatomy as the os japonicum of the malar tract.

The brain case is swollen in all genera but increases progressively in size (Table I, Index VI) from the smallest in *Petrodromus* to the proportionally largest in *Rhynchocyon* and *Macroscelides*. The temporal fossae are well defined in *Rhynchocyon* and *Petrodromus*, and in these genera there are distinct and quite well-developed sagittal and lambdoidal crests. In the other genera the fossae are ill defined, and the crests are vestigial.

In all genera except *Rhynchocyon* the occiput is swollen, so that a considerable amount of the nuchal surface is visible in dorsal view. This condition increases progressively from *Petrodromus* to *Macroscelides*, although it is said to be absent in some species of the latter.

The zygoma is uniformly well developed throughout the family, but in *Rhynchocyon* (Fig. 1, A) it is flatter dorso-ventrally and more laterally arched than is the case in the Macroscelidinae. *Rhynchocyon* also

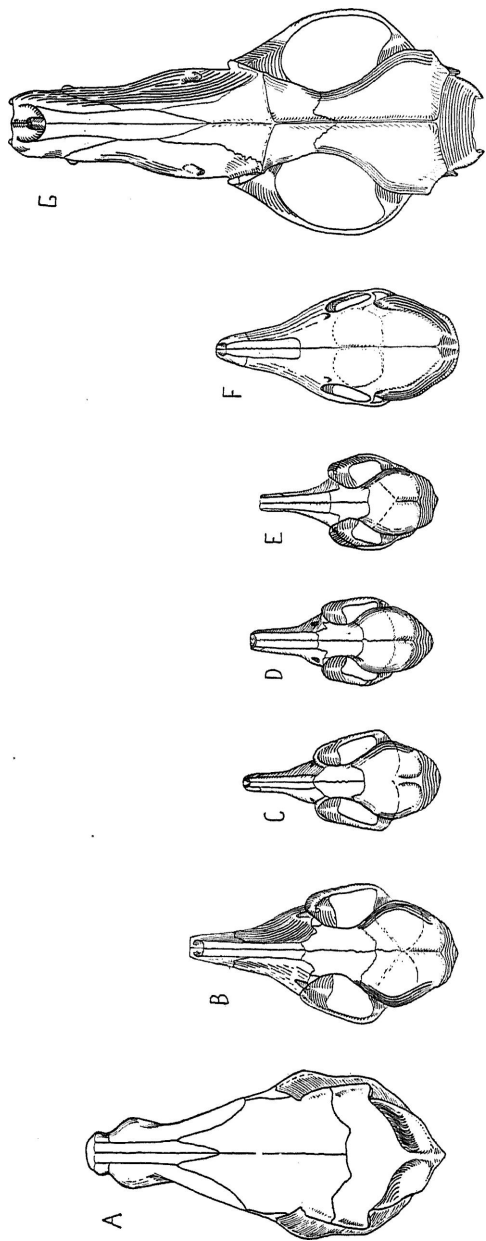


Fig. 1. Dorsal view of the skulls of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*). $\times \frac{2}{3}$. A, *Rhynchocyon*; B, *Pterodromus*; C, *Elephantulus*; D, *Nasillo*; E, *Macroscelides*; F, *Tupaia*; G, *Echinosorex*.

TABLE I.—SKULL MEASUREMENTS (MM.) AND INDICES (PER CENT)

Measurements and Indices	<i>Rhynchocyon claudi</i>	<i>Petrodromus tordayi</i>	<i>Nasilio brachyrhyncha</i>	<i>Elephantulus renatus</i>	<i>Macroscelides rozeti</i>	<i>Tupaia belangeri</i>	<i>Gymnura alba</i>
(1) Skull, total length pmx.-condyle	62.1	48.6	31.3	33.0	30.8	44.5	91.9
(2) Skull, max. bizygomatic width	35.7	25.3	18.3	19.3	19.4	23.1	46.6
Index I—Rel. bizyg. width (2) \times 100	57.5	52.3	58.4	58.5	62.9	51.9	50.7
(1)							
(3) Face, preorb. length (ant. rim of orbit to pmx. tip)	36.8	24.6	15.2	14.3	15.2	20.6	42.0
Index II—Face length (3) \times 100	59.3	50.6	48.5	43.4	49.3	46.2	45.7
(1)							
(4) Preorb. breadth (across lac. tubercle)	30.6	14.9	13.0	13.4	14.0	15.7	28.4
(4) \times 100	49.3	30.6	41.6	40.5	45.4	35.2	30.9
Index III—							
(1)							
(5) Cranium = (1) - (3) Cranial length	25.3	24.0	16.6	18.7	15.6	23.9	49.9
(5) \times 100	40.7	49.4	51.5	56.6	50.6	53.7	54.2
Index IV—							
(1)							
(6) Least parietal width	18.3	9.6	7.8	8.3	7.0	14.8	14.5
(6) \times 100	29.5	19.8	24.8	24.9	22.7	33.2	15.7
Index V—							
(1)							
(7) Greatest parietal width	30.8	18.7	13.9	15.1	14.7	18.0	22.2
(7) \times 100	49.6	38.5	44.4	45.7	47.7	40.4	24.1
Index VI—							
(1)							
(8) Tymp. bulla, max. length	10.6	6.9	5.7	6.6	5.9	8.4	No bulla
(8) \times 100	17.0	14.2	18.2	20.0	19.1	18.8	
Index VII—							
(1)							

differs from the latter in having a prominent masseteric ridge on the zygoma.

The maxillae are large in all and form most of the side of the muzzle. The nasals are long and slender and in *Rhynchocyon* (Fig. 1, A) differ from those in the *Macroscelidinae* by ending in long sharp points which push in between the frontals. The premaxillae in all except *Rhynchocyon* are quite large and on the dorsum of the muzzle extend a considerable distance posteriorly along the nasals.

The lacrimals are large and divided by the anterior rim of the orbit into a facial and an orbital part, the former being the larger in *Rhynchocyon*. The single foramen is located in the orbital part. A small lacrimal tubercle is present.

All the genera have a proboscis-like snout which is not seen in the prepared skull. According to Parker (1885, p. 245) that of *Rhynchocyon* consists of thirty double rings of cartilage.

In the orbito-temporal region (Fig. 14) the large orbital plate of the frontal forms most of the median wall of the orbit and articulates with the lacrimal anteriorly, the palatine and orbitosphenoid ventrally, and the parietal posteriorly.

The palatine also has a large orbital wing which forms the antero-ventral part of the median wall of the orbit and articulates with the lacrimal and frontal dorsally, the maxilla anteriorly and ventrally and with the orbitosphenoid and alisphenoid posteriorly.

Most of the ventro-posterior part of the orbital wall is formed by the large orbitosphenoid articulating dorsally with the frontal and parietal, anteriorly with the palatine and ventrally and posteriorly with the alisphenoid. On the ventral surface of the skull it also articulates with the basisphenoid.

The large orbital part of the lacrimal forms the anterior wall of the orbit and articulates with the frontal, palatine and maxilla within the orbit. Laterally it articulates with the jugal which forms the antero-ventral rim of the orbit.

The small alisphenoid is located at the extreme caudo-ventral corner of the orbit and articulates with the orbitosphenoid, parietal and squamosal at a common meeting place of the four bones. Antero-ventrally it articulates with the posterior extension of the palatine.

In ventral view (Fig. 2) the outstanding features are the enormous auditory bullae and, except in *Rhynchocyon*, the high degree of palatal fenestration. In *Rhynchocyon* the palate is approximately the same width throughout and, except for the anterior and tiny posterior palatine foramina, there are no vacuities. In the Macroscelidinae the palate narrows anteriorly and becomes highly fenestrated. The general shape of the palate in *Macroscelides* approaches that of *Rhynchocyon*. The posterior margin of the palate is emarginate in all, but less so in *Macroscelides* and *Rhynchocyon*.

The external pterygoid fossae are small in *Rhynchocyon*, but in the Macroscelidinae they are very large and extend forward to the posterior margin of the palate.

The jugals are well developed and extend back to the glenoid region although they do not reach the articular area for the mandibular condyle.

The auditory bullae are large and progressively approach each other in the midline, culminating in *Macroscelides* (Fig. 2, E) where the opposite bullae almost touch. The main portion of the bulla (Fig. 15, A) is formed by the greatly inflated entotympanic, while the ectotympanic forms a tubular external auditory meatus, the medial

end of which fits inside the former. In the adult the two are fused.

In *Rhynchocyon* (Fig. 2, A) the external auditory meatus, which lies between the postglenoid and the mastoid processes, is quite long and runs in a lateral and slightly caudal direction. In the Macroscelidinae (Fig. 2) it progressively becomes shorter and wider, culminating in *Macroscelides*. The meatus in *Nasilio* faces slightly posteriorly as in *Rhynchocyon*, but in the other genera it faces more laterally and anteriorly.

The tympanic wing of the alisphenoid is also inflated and forms the antero-internal corner of the bulla. According to Van der Klaauw (1931, pp. 232, 249, 268) there are two different entotympanics: a rostral and a caudal one. The important part of the alisphenoid bulla in the Macroscelididae, i.e., the part on the medial side of the eustachian tube, is, according to him, the rostral entotympanic, while the main part of the bulla is formed by the caudal one.

The mastoid portion of the periotic, the squamosal and the exoccipital are also swollen but less so in *Rhynchocyon* than in the other genera. In some species of *Macroscelides*, according to Van Kampen (1905, p. 447), the squamosal, the parietal and the mastoid have large accessory cavities communicating with the tympanic cavity. Van der Klaauw (1931, p. 83) also records the presence of epitympanic sinuses in *Macroscelides*.

The insectivores are the only mammals in which the basisphenoid lies in the wall of the tympanic cavity, but this is not true of all of them and, according to Van Kampen (1905, p. 445), the tympanic wing of the basisphenoid is absent or nearly so in the Macroscelididae.

The periotic or petrosal forms the posterior part of the base of the bulla and is visible on the ventral surface of the skull (Fig. 15, A) as a triangular area bounded medially by the basioccipital, anteriorly by the bulla and laterally by the mastoid region. The latter is inflated, triangular in shape and placed on the latero-occipital aspect of the skull.

The shape of the bullae (Fig. 2) varies in the different genera, and Carlsson (1909, p. 353) states that the bullae of *Rhyncho-*

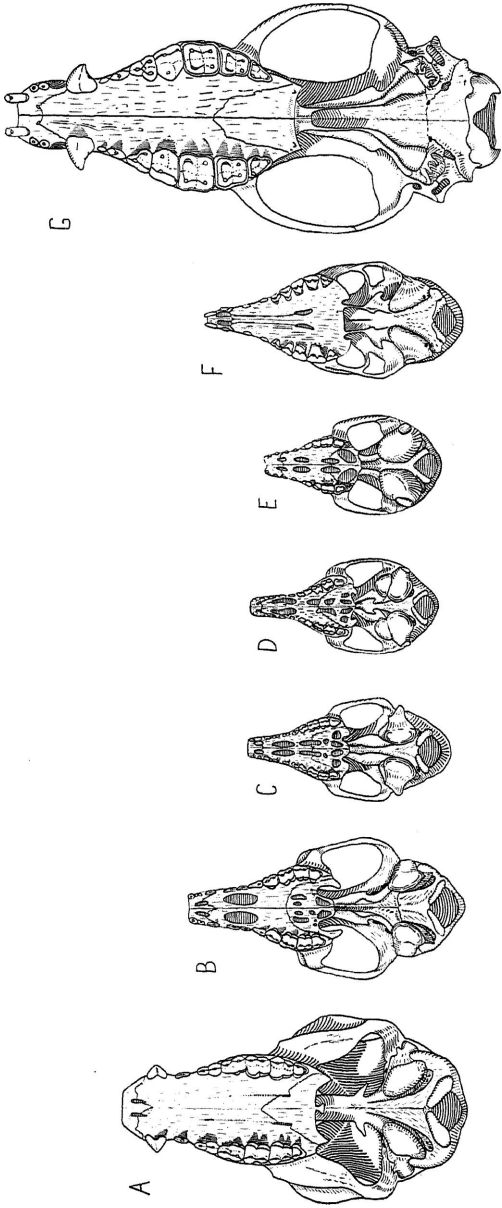


Fig. 2. Ventral view of the skulls of the Macroscelididae, *Tupaia* and *Echinorex* (*Gymnura*). $\times \frac{2}{3}$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Elephantulus*; D, *Nasua*; E, *Macroscelides*; F, *Tupaia*; G, *Echinorex*.

cyon and *Macroscelides* are greatly inflated, while those in *Elephantulus* and *Nasilio* are small. Actual measurements of the bullae (Table I, 8), however, do not completely support this statement. In regard to the length of the bullae in proportion to the skull length (Table I, Index VII) those of both *Nasilio* and *Elephantulus* are larger than in *Rhynchocyon*. The bullae of *Elephantulus* are the largest in the family while *Petrodromus* has the smallest bullae of all. Index VII (Table I) shows that with respect to the size of the bullae *Nasilio* and *Rhynchocyon* occupy an intermediate position in the family.

With regard to the auditory ossicles (Fig. 16) Doran (1879, p. 444) says, "The Macroscelididae have a more specialized malleus than can be seen in any other insectivore except *Chrysochloris*; the extremely constricted neck and the narrow lamina and process gracilis running straight forwards to the Glasserian fissure are highly characteristic. The process muscularis is well developed. The head is better developed in *Rhynchocyon* than in *Macroscelides*. In *Petrodromus* the malleus is far more like that in *Sorex* than in the other two genera but the incus is not in any sense shrew-like." The stapes, according to Gregory (1910, p. 282), has straight crura and a bony canal for the stapedial artery.

The occiput (Fig. 1), except in *Rhynchocyon*, exhibits a progressive degree of inflation and consequent reduction in size of the lambdoidal crests in passing from *Petrodromus* to *Macroscelides*. The condyles have a convex posterior face and are extended vertically so that their articular surfaces almost meet anterior to the foramen magnum. The paroccipital processes are very slight.

SKULL FORAMINA

In the Macroscelididae the skull foramina are very complete in number and essentially the same in their location and arrangement throughout the family.

The infraorbital foramen is conspicuous and is located above P^3 in *Rhynchocyon* which has a long infraorbital canal. In the Macroscelidinae the infraorbital canal is short, and the foramen is placed further

back, opening above P^3 - P^4 in *Petrodromus* and *Macroscelides* and above M^1 in *Elephantulus* and *Nasilio*.

As previously noted the lacrimal foramen lies within the orbit in the orbital part of the lacrimal. The optic foramen is large, and a prominent suboptic foramen lies immediately beneath it. By means of these two foramina the opposite orbits communicate with each other. As in most insectivores the sphenoidal fissure and the foramen rotundum are united.

The alisphenoid canal, according to my observations and to Weber (1928, p. 114), is absent, but Muller (1935, p. 243) records it as present. The foramen ovale has its usual position but in ventral view of the skull is almost obscured by the large size of the bulla.

The large jugular foramen lies between the bulla and the occipital condyle, with the conspicuous carotid foramen located immediately anterior to it. In *Rhynchocyon* the latter foramen is in the suture between the entotympanic bulla and the petrosal, but in the Macroscelidinae it is in the petrosal. In *Macroscelides typicus*, according to Carlsson (1909, pp. 353, 389) it has the same position as in *Rhynchocyon*.

The postglenoid foramen is conspicuous and lies antero-dorsal to the external auditory meatus. The stylomastoid foramen is present as are also the sphenopalatine, the anterior and posterior palatine, and ethmoid. The condylar foramina are small and distinct from the jugular.

There is no malar nor supraorbital foramen.

MANDIBLE

Figure 3

The mandible has a rather long slender corpus and a high ascending ramus so that the condyle is far above the level of the cheek teeth. The coronoid process is usually quite short and level with or only slightly above the level of the condyle; in *Nasilio* (Fig. 3, D) it is longer and very slender. The angle of the jaw ends in a sharp upturned point. The mental foramina are usually double and located below P_1 and P_4 . In *Elephantulus* one of them is below the canine, and *Nasilio* has just one foramen which is located below P_1 .

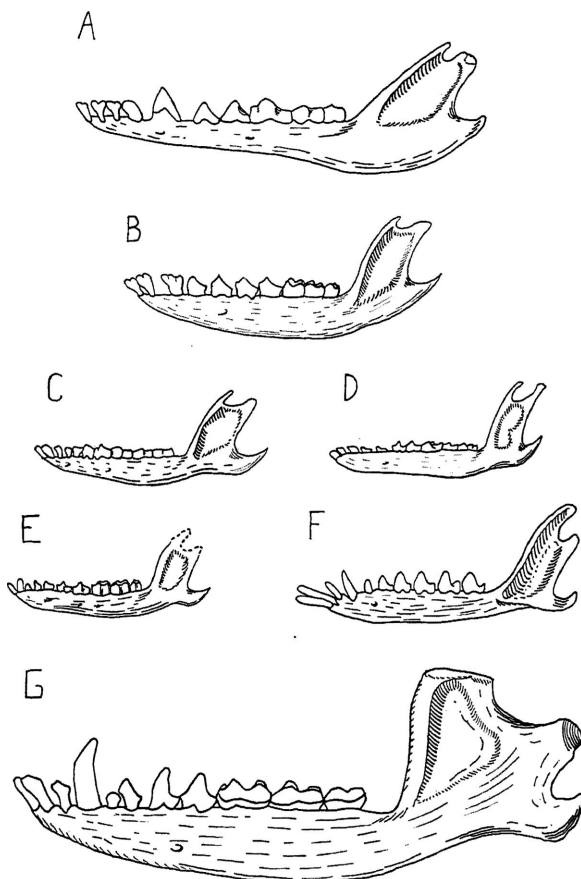


Fig. 3. Lateral view of the left mandibles of the Macroscelididae, *Tupaia* and *Echinorex* (*Gymnura*). $\times 1$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Elephantulus*; D, *Nasilio*; E, *Macroscelides*; F, *Tupaia*; G, *Echinorex*.

In *Rhynchocyon* the ascending ramus of the mandible is much more posteriorly inclined than in the Macroscelidinae due to the posterior expansion and migration of the orbit and postorbital process.

DENTITION

The permanent dental formula is not the same throughout the family. In *Rhynchocyon* it is $I \frac{1}{3} - \frac{0}{3} C \frac{1}{1} - \frac{1}{1} P \frac{4}{4} - \frac{4}{4} M \frac{2}{2} - \frac{2}{2} = 34$ or 36, while in all the Macroscelidinae, except *Nasilio* which has three lower molars, the formula is $I \frac{3}{3} - \frac{3}{3} C \frac{1}{1} - \frac{1}{1} P \frac{4}{4} - \frac{4}{4} M \frac{2}{2} - \frac{2}{2} = 40$. According to Gregory (1910, p. 281) the

Macroscelididae are among the few insectivores retaining $P \frac{1}{1}$.

Upper Dentition

Figures 2 and 4

The incisors are peg-like with a single cusp and are slightly enlarged, a typical insectivore modification. *Rhynchocyon* (Fig. 2, A) differs from other members of the family in that old individuals sometimes completely lose the upper incisors.

The upper canine is small, two rooted and premolariform in the Macroscelidinae,

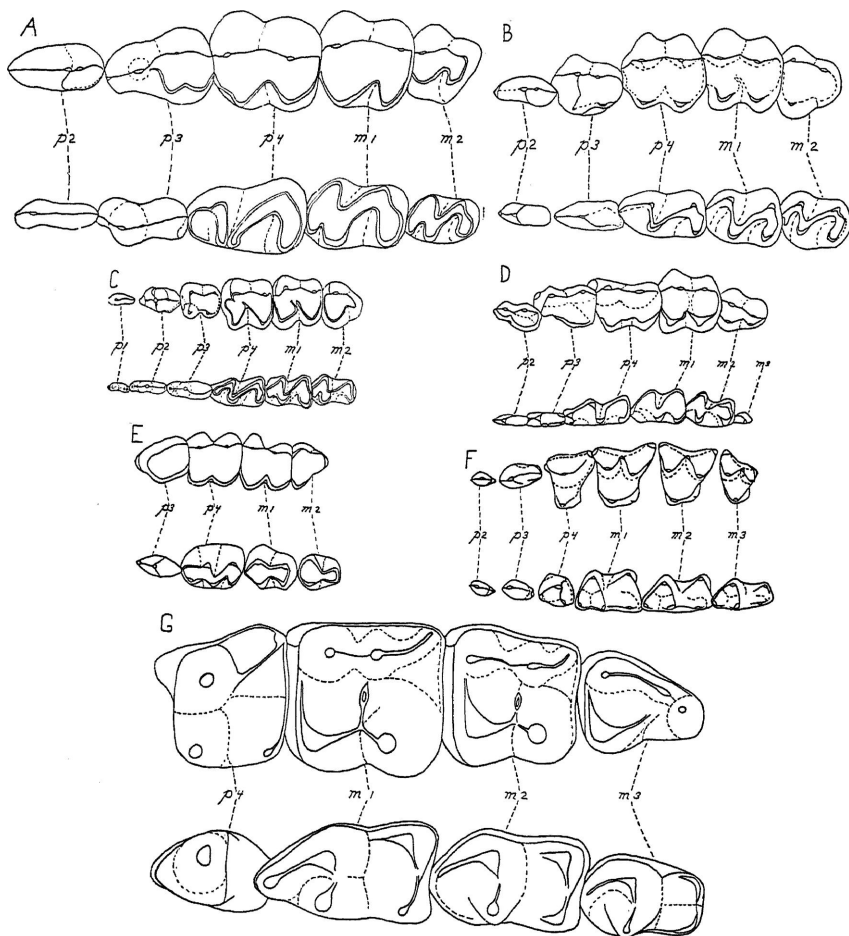


Fig. 4. Cheek teeth (upper left and lower right) of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*). Circa $\times 10/3$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Elephantulus*; D, *Nasilio*; E, *Macroscelides*; F, *Tupaia*; G, *Echinosorex*.

but in *Rhynchocyon* it is larger and has the typical canine shape.

P¹ is much smaller than the canine in *Rhynchocyon*, but in the Macroscelidinae the two are subequal. In all the genera it is a laterally compressed tooth with a single well-developed cusp. P² (Fig. 4) is larger and has both a paracone and a metacone, the former being the larger. In *Elephantulus* (Fig. 4, C) there is in addition a small anterior cusp, while in *Nasilio* the protocone also appears on P².

P³, in *Petrodromus*, *Elephantulus* and *Macroscelides*, is submolariform with a well-defined protocone, paracone and metacone, plus a small hypocone. In *Rhynchocyon* and *Nasilio* (Fig. 4, A and D) it is less molariform in shape, although the same cusps are present, with the addition in the latter genus of a well-defined anterior accessory cusp.

Throughout the family the cheek teeth (P⁴-M³) are quadritubercular, subhypodont and without cingula. P⁴ is completely

molariform, and in all the cheek teeth the paracone and metacone are definite cusps, while the protocone and hypocone are rather crescentic or V-shaped. However, the condition of the latter is due to wear, as all my specimens were fully mature individuals. In *Rhynchocyon* it has been shown by Allen (1922, p. 33) that this tooth (P^4) belongs to the permanent set and is not merely a retained deciduous tooth. In *Elephantulus* and *Macroscelides* M^2 shows a tendency to have the hypocone reduced.

Lower Dentition

Figures 3 and 4

The incisors (Fig. 3) in *Elephantulus*, *Nasilio* and *Macroscelides* are short peg-like teeth. In *Rhynchocyon* (Fig. 3, A) the incisors are expanded distally and have distinctly bilobed tips, while those of *Petrodromus* are incipiently lobed.

The canine is small and two-rooted.

In the Macroscelidinae P_1 is small, with a single large protoconid, but in *Rhynchocyon* it is caniniform and is the tallest tooth in the mandible. P_2 is elongated, laterally compressed and larger than P_1 . There is a large protoconid, and accessory anterior and posterior cusps may also be present (Figs. 3, 4). P_3 is larger than P_2 but with the same number and arrangement of the cusps.

The cheek teeth are subhypsodont, without cingula, and show clearly defined traces of the tuberculosectorial pattern, in which the paraconid has been generally reduced, leaving the well-developed protoconid, metaconid, hypoconid and entoconid (Fig. 4). This is particularly true of P_4 which is submolariform in shape and in *Nasilio* and *Macroscelides* (Fig. 4, D and E) has a small paraconid. The trigonid and talonid are equal in height, and in P_4 , which is longer antero-posteriorly than any of the molars, the talonid is the wider of the two. In *Rhynchocyon* (Fig. 4, A) P_4 has a well-developed metastylid.

The molars are quadritubercular, and among my specimens only *Nasilio* (Fig. 4, D) had a definite paraconid on M_1 . In *Petrodromus* (Fig. 4, B) the talonid of M_1 is a trifle wider than the trigonid, but in

the other genera the two are subequal in width. M_2 is essentially the same as M_1 , except that the talonid has become narrower than the trigonid. *Nasilio* (Fig. 4, D) differs from the other genera in having a small M_3 .

In *Rhynchocyon*, according to Allen (1922, p. 32), the deciduous dental formula is $I \frac{1-1}{3-3} C \frac{1-1}{1-1} P \frac{3-3}{3-3} = \frac{10}{14} = 24$. $P \frac{1-1}{1-1}$, which has no successor, does not appear until later.

The single upper incisor (I^3) is small, has no successor and frequently persists throughout life. The deciduous upper canine is a small tooth with a pointed central cusp and a small posterior cusp. It is lost at the same time as the deciduous premolars, but the permanent canine is slow in maturing.

The three milk premolars erupt simultaneously. DP^2 , like P^2 , is laterally compressed, slightly longer than high, and with two main cusps: a larger anterior one and a smaller posterior one. Small anterior and posterior accessory cusps are also present.

DP^3 is an elongated subtriangular tooth with the posterior half the broader. There are three buccal cusps (a small anterior cusp, a large paracone and a small metacone) and two lingual cusps (a low broad protocone and an incipient hypocone). There is no W-shaped crest connecting the lingual cusps as in P^3 , but in other respects the two teeth are quite similar.

DP^4 is very similar to P^4 in being quadrate in shape, submolariform and with four well-developed cusps, the buccal ones the higher. According to Allen's figure (1922, p. 34, Fig. 3) they differ slightly from P^4 in having a small anterior and a posterior cingulum cusp, in the absence of a W-shaped crest connecting the lingual cusps, and in being more distinctly divided into an anterior and a posterior moiety.

As described by Allen (1922, p. 32) the deciduous lower incisors and canine differ from the permanent ones only in details, the canine being bilobed and DI_2 and DI_3 being trilobed at the tip. In the adult the canine ends in a single point, and the incisors are all bilobed. The deciduous lower canine is separated from DP_2 by a

long diastema which is occupied by P_1 in the adult.

The milk premolars (DP_2 - DP_4) increase successively in size, culminating in DP_4 . DP_2 is very similar to P_2 , differing chiefly in having better developed anterior and posterior cusps. DP_3 is larger than DP_2 but otherwise is essentially the same as it and P_3 . DP_4 is a large molariform tooth with subequal trigonid and talonid but with, according to Allen's figure (p. 31, Fig. 3), some accessory cusps absent on P_4 . The permanent P_4 is a little more completely molariform than DP_4 , but otherwise the two teeth are very similar.

Among the Macroscelidinae the deciduous dentition of *Nasilio* has recently been described by Hill (1938, p. 465). According to him the complete deciduous formula is $DI \frac{1-2}{1-2-3}$ $DC \frac{1-1}{1-1}$ $DP \frac{2-2-4}{2-2-4}$ plus $P \frac{1}{1}$ which, as in *Rhynchocyon*, has no predecessor.

The milk teeth differ from the permanent ones in the following respects. Deciduous I^1 is smaller than I^1 and has a small posterior cusp which is lacking in I^1 . The second milk incisor is smaller, relatively, than I^2 and has a hook-shaped anterior cusp. The deciduous canine is essentially the same as the permanent canine but smaller. Deciduous P^2 is much narrower than P^2 and has more cusps. Deciduous P^3 has three main cusps (*pr*, *pa*, *me*) plus two smaller anterior cusps and a postero-medial cusp (*hy*) while DP^4 is essentially the same but larger and with a better developed hypocone. According to Hill (1938, p. 465) P^2 - P^4 have a quadritubercular pattern like M^1 , but in my specimens only P^4 is molariform.

The deciduous lower incisors differ from the permanent ones chiefly in having more lobate and elongated tips. The canines are essentially the same except that the deciduous one is smaller. Hill was unable to differentiate DP_2 from P_2 , but DP_{3-4} are larger and more complex than their successors.

The order of tooth replacement, according to Hill (1938, p. 467), shows several differences from that in *Rhynchocyon*. Deciduous C_1 appears later than the incisors in *Nasilio*, and $DP \frac{2}{2-3}$ and $DP \frac{2-4}{2-4}$

develop together instead of $DP \frac{2}{2}$ and $DP \frac{3-4}{3-4}$ developing together. Permanent $P \frac{1}{1}$ is the first of the premolars to develop and erupts some time before I^3 . The permanent lower incisors are irregular in appearance, DI_2 being one of the last teeth replaced, while in *Rhynchocyon* the lower incisors and the lower canine are replaced simultaneously. Both upper and lower canines mature rapidly and at about the same time. Permanent $M \frac{1}{1}$ develops early, but $P \frac{2}{2}$, as in *Rhynchocyon*, are among the last teeth to develop.

POSTCRANIAL SKELETON

In the following description *Elephantulus* is omitted, as I was unable to secure any skeletal material.

Pectoral Girdle and Foreleg

Figures 5 and 6

The scapula (Fig. 5) is roughly triangular in shape, with a slightly convex vertebral border and concave coracoid and glenoid borders. In *Rhynchocyon*, *Petrodromus* and *Nasilio* the coraco-vertebral angle is obtuse and rounded, while the gleno-vertebral angle, especially in the first two genera, is pulled out into a prominent spur. The supraspinatus and the infraspinatus fossae are subequal in size. The spine is well developed and bears a prominent acromion and a long, slender, slightly hooked meta-acromion process. The coracoid process is well developed.

A well-formed but not large clavicle is present.

The humerus (Fig. 6) has an ovoid head, well-defined greater and lesser tuberosities and a distinct bicippital groove. Prominent entepicondylar and supratrochlea foramina are present. The capitulum is large, and the trochlea, which is continuous with it, is quite wide. In *Rhynchocyon* the humerus is more bent than in the Macroscelidinae.

In the Macroscelidinae (Fig. 6) the radius and ulna are fused distally, but in *Rhynchocyon* (Fig. 6, A) they remain separate although they are closely appressed. The radius in the former articulates with the scaphoid, lunar and cuneiform but only with the first two in *Rhynchocyon*.

The carpus (Fig. 6) consists of nine bones. The scaphoid and lunar are separate. In the Macroscelidinae there is a very narrow contact between the lunar and the unciform, but in *Rhynchocyon* (Fig. 6, A) this contact is absent. The centrale is free and has no contact with the unciform. The magnum in the Macroscelidinae is very slightly compressed laterally. I was unable to find the "three other small bones" reported by Peters (1852, p. 96) in the carpus of *Petrodromus*, but according to his figure one of them is the centrale.

The metacarpals and phalanges are elongated, and all the digits bear long, sharp, slightly curved claws. *Rhynchocyon* differs from the Macroscelidinae in lacking

(Table II, Index II) is longer in *Rhynchocyon* than in the Macroscelidinae in which, starting with *Petrodromus*, it exhibits the same manner of decrease as the forearm.

Pelvic Girdle and Hind Leg

Figures 7-9

The ilium (Fig. 7) is long and slender throughout the family and in *Petrodromus* and *Nasilio* (Fig. 7, B, D) has a tubercle on the lateral side immediately anterior to the acetabulum. The latter is circular in shape, deep, and has a prominent cotyloid notch except in *Macroscelides* where the notch seems to be absent. The ischium is well developed and deep dorso-ventrally, especially in *Rhynchocyon* and *Petrodromus*.

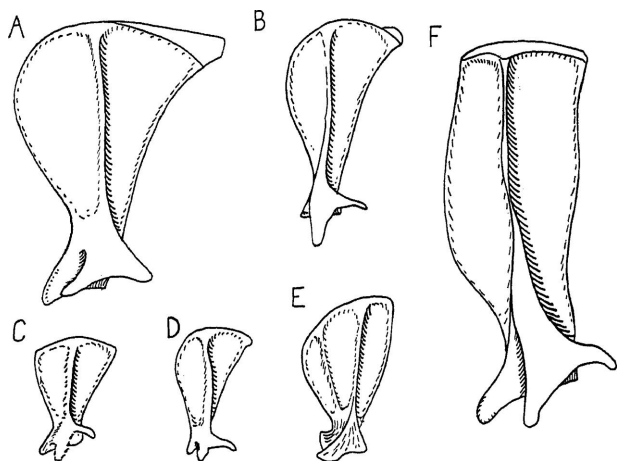


Fig. 5. Left scapula of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*). $\times 1$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Macroscelides*; D, *Nasilio*; E, *Tupaia*; F, *Echinosorex*.

the pollex and first metacarpal and in having only two phalanges in the fifth digit which is, as far as I know, unique among mammals. In the Macroscelidinae the pollex appears to be slightly opposable. The third digit is the longest throughout the family.

The proportionate lengths of the different segments of the foreleg vary in the different genera and are indicated by the indices in Table II. In *Rhynchocyon* (Index I) the forearm and the upper arm are the same length, but in the Macroscelidinae the former is the longer and shows a secondary progressive decrease in length from *Petrodromus* to *Nasilio*. Metacarpal III

The pelvic symphysis is long and formed jointly by the pubis and the ischium. The obturator foramen is large and triangular in shape in *Rhynchocyon* and *Macroscelides*. In *Petrodromus* it is rhomboidal in shape, while in *Nasilio* it is an elongated oval. There is a prominent foramen between the obturator foramen and the acetabulum in *Petrodromus*.

The femur (Fig. 8) has a globular head with a deep foveal pit and is set at about a fifty-five degree angle to the shaft in all except *Macroscelides* in which the angle is about seventy degrees. The greater and the lesser trochanters are well developed, while further down the shaft is a prominent

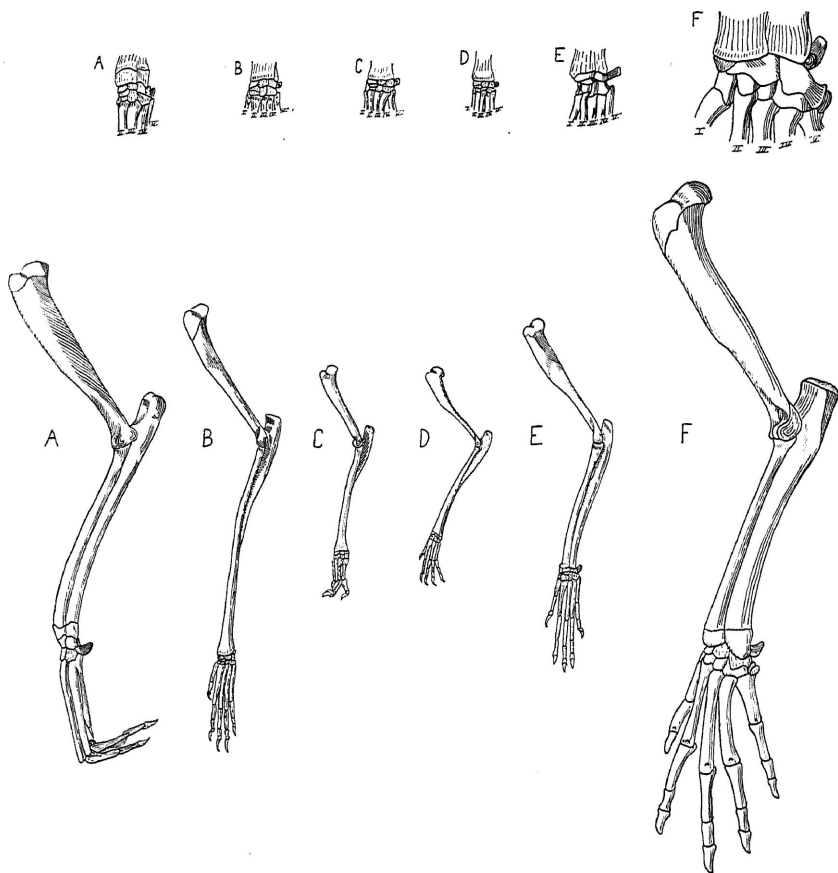


Fig. 6. Left foreleg ($\times \frac{2}{3}$) and carpus ($\times \frac{1}{3}$) of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*). A, *Rhynchocyon*; B, *Petrodromus*; C, *Macroscelides*; D, *Nasilio*; E, *Tupaia*; F, *Echinosorex*.

third trochanter. Sesamoid bones are present behind the condyles.

The patella is an elongated, flattened, oval bone. The tibia and fibula (Fig. 8) are fused distally and articulate with both the astragalus and the calcaneum. The malleoli are well developed.

The astragalus (Fig. 9) is rather long and narrow with a blunt rounded head bearing a broad navicular and a small cuboid facet. The neck is rather long and only slightly constricted in *Rhynchocyon* and *Petrodromus* but more so in *Nasilio* and *Macroscelides*. The trochlea is high and

pulley-like with well-developed keels, the fibular one being distinctly the higher. The ectal facet is obliquely placed, while the sustentacular is more vertical. The latter is the smaller and is not quite continuous with the navicular facet. There is no astragalar foramen.

The cuboid and the cuneiforms are elongated. In *Macroscelides* (Fig. 9, C) the three cuneiforms are subequal in length, but in *Rhynchocyon* and *Petrodromus* (Fig. 9, A and B) the third is markedly the longest. In *Nasilio* (Fig. 9, D), however, the first is a trifle longer than the

TABLE II.—LIMB MEASUREMENTS (MM.) AND INDICES (PER CENT)

Measurements and Indices	<i>Rhynchocyon claudi</i>	<i>Petrodromus torquatus</i>	<i>Nasilio brachyrhyncha</i>	<i>Macroscelides rozeti</i>	<i>Tupaia belangeri</i>
(1) Humerus, max. length	41.6	29.0	17.9	18.1	27.8
(2) Radius, max. length	41.6	41.2	18.9	21.8	24.6
Index I—Radio-humeral (2) \times 100					
(1)	100.0	142.1	105.6	120.4	88.5
(3) Metacarpal III, max. length	21.3	10.5	5.5	5.4	9.7
Index II—Mtcp. III- (3) \times 100					
humeral (1)	51.2	36.2	30.7	29.8	34.9
(4) Femur, max. length (gr. trochanter to medial condyle)	59.8	41.0	24.5	24.0	34.4
(5) Tibia, length (surf. of condyle to artic. surf. for astragalus)	73.5	52.6	31.7	34.7	35.3
Index III—Tibio-femoral (5) \times 100					
(4)	122.9	128.3	129.4	144.6	102.6
(6) Metatarsal III, max. length	32.9	24.9	13.0	17.0	16.1
Index IV—Metatars. III- (6) \times 100					
femoral (4)	55.0	60.7	53.6	70.8	46.8
Index V—Humero-femoral (1) \times 100					
(4)	69.6	70.7	73.1	75.5	80.8
Index VI—Intermembral (1) + (2) \times 100					
(4) + (5)	62.4	75.0	65.5	68.0	75.2

third, although both are a good deal longer than the second.

The metatarsals and phalanges (Fig. 9) are elongated in all genera, and all the digits end in long, sharp, curved claws. The hallux is lacking in *Rhynchocyon* and *Petrodromus* (Fig. 9, A and B). Digit III is the longest in all except *Petrodromus* and *Nasilio*, in which the fourth is the longest.

All members of the family have very long hind legs and feet with the shank of the leg longer than the thigh. In this respect *Rhynchocyon* (Table II, Index III) has proportionately a shorter lower leg than any of the Macroscelidinae which show a progressive increase in length from *Petrodromus* to *Macroscelides*. *Rhynchocyon* (Index IV) also has a proportionately shorter foot than any of the Macroscelidinae except *Nasilio*. The humerus is

shorter, proportionately, in *Rhynchocyon* than in any of the Macroscelidinae (Index V) in which it progressively lengthens, culminating in *Macroscelides*. The forelegs are longest in proportion to the hind legs in *Petrodromus* (Index VI) and shortest in *Rhynchocyon*.

Vertebral Column

The vertebral formula is not the same in the two subfamilies. In the Rhynchocyoninae there are seven cervicals, thirteen thoracics, eight lumbar, three sacral and twenty-eight caudals, while the Macroscelidinae differ in having only seven lumbar and twenty-five or twenty-six caudals.

The atlas is normal, and the axis has the usual large and expanded transverse and spinous processes characteristic of mammals. In the post-axial cervicals the spi-

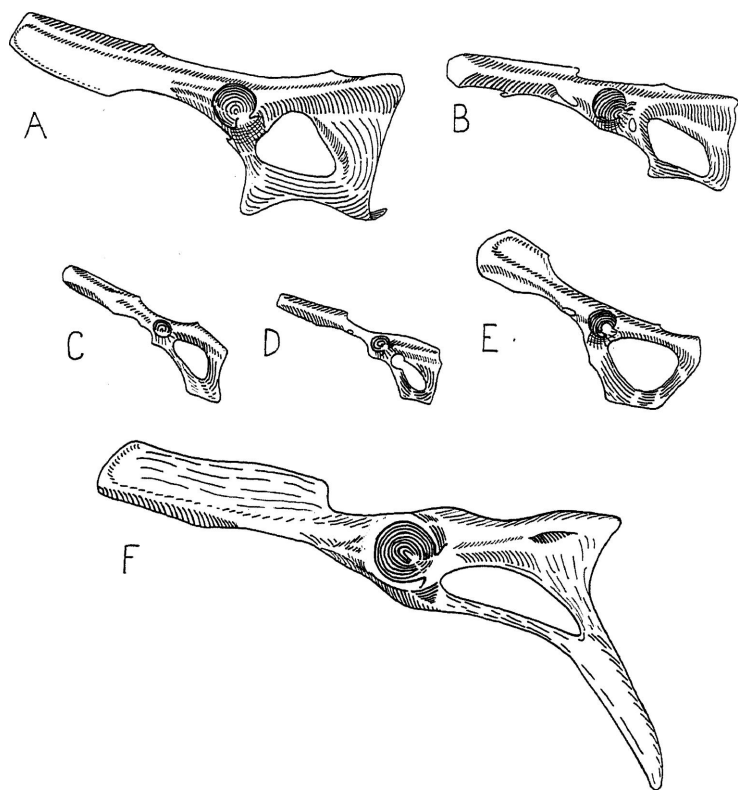


Fig. 7. Pelvic girdle of the Macroscelididae, *Tupaia* and *Echinorex* (*Gymnura*). $\times 1$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Macroscelides*; D, *Nasūio*; E, *Tupaia*; F, *Echinorex*.

nous processes are reduced, while the transverse processes of the sixth and seventh cervicals are bifurcated distally. The spinous processes of the first ten anterior thoracic vertebrae are posteriorly inclined, while the eleventh thoracic is anticlinal. Correlated with the pseudo-hopping habitus the spinous and transverse processes of the four posterior lumbar vertebrae are elongated for the attachment of the pelvic musculature. The caudals, as in several insectivores, are elongated and in *Rhynchocyon* bear "chevron bones" which are absent in the other genera.

Ribs and Sternum

There are thirteen pairs of ribs, of which the first pair in the Macroscelidinae and the first several pairs in *Rhynchocyon* are widened. The ribs are long, curved, double-headed, and the first seven pairs are attached to the sternum by long and slender costal cartilages. The manubrium is somewhat triangular with the broad end anterior and bearing a cartilaginous episternum. The body of the sternum consists of four pieces in *Rhynchocyon* and three in the Macroscelidinae. The xiphoid process is elongated and may be forked distally.

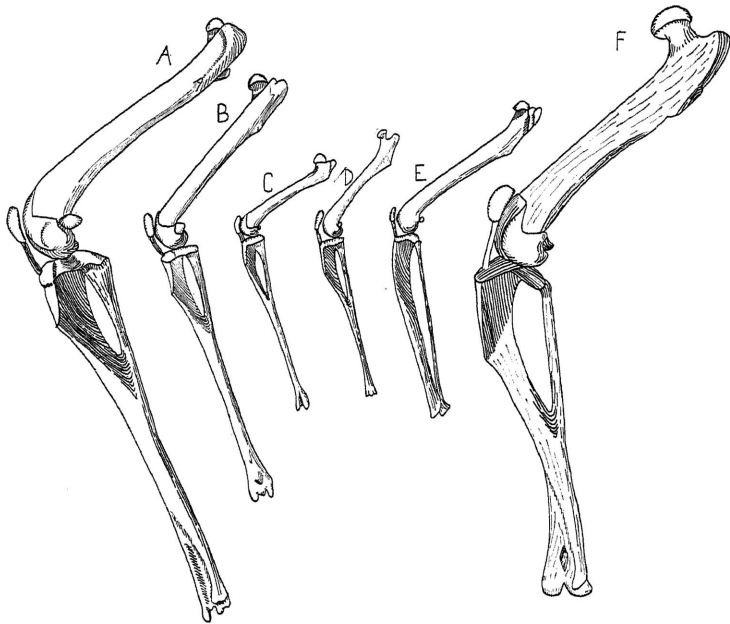


Fig. 8. Left hind leg of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*). $\times \frac{2}{3}$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Macroscelides*; D, *Nasilio*; E, *Tupaia*; F, *Echinosorex*.

RELATIONSHIPS WITHIN THE MACROSCELIDIDAE

From the above description of the osteology the Macroscelididae are seen to be a highly specialized family of insectivores which, although clearly divided into two subfamilies, exhibit a remarkable degree of uniformity of structure.

Petrodromus (see Table I) is the most primitive member of the family, having the proportionally narrowest skull (Index I), the most constricted interorbital region (Index V) and the smallest brain case and bullae (Indices VI and VII). It also represents the most primitive form in the proportional size of the olfactory chamber (Indices II and III) which is secondarily shortened and widened in the other Macroscelidinae. In *Rhynchocyon*, however, the olfactory region of the skull has been secondarily lengthened and widened.

Nasilio, *Elephantulus* and *Macroscelides*, in spite of slight differences among them-

selves, may be placed in a single group, as they are all very similar and more highly specialized than is *Petrodromus*. *Rhynchocyon* is also highly specialized and is rightfully placed in its own subfamily.

When the limb measurements and proportions (Table II) are analyzed *Petrodromus* is again seen to be the most primitive member of the family in having the proportionally longest forelegs in relation to the hind legs (Index VI). Furthermore, each segment of its foreleg is proportionally longer (Indices I and II) than the corresponding segments in all the other members of the family except *Rhynchocyon* which has a proportionally longer metacarpal III (Index II). In *Rhynchocyon* this secondary elongation of metacarpal III is probably associated with its pseudoungulate habitus. In *Nasilio* and *Macroscelides* the shortening of the various seg-

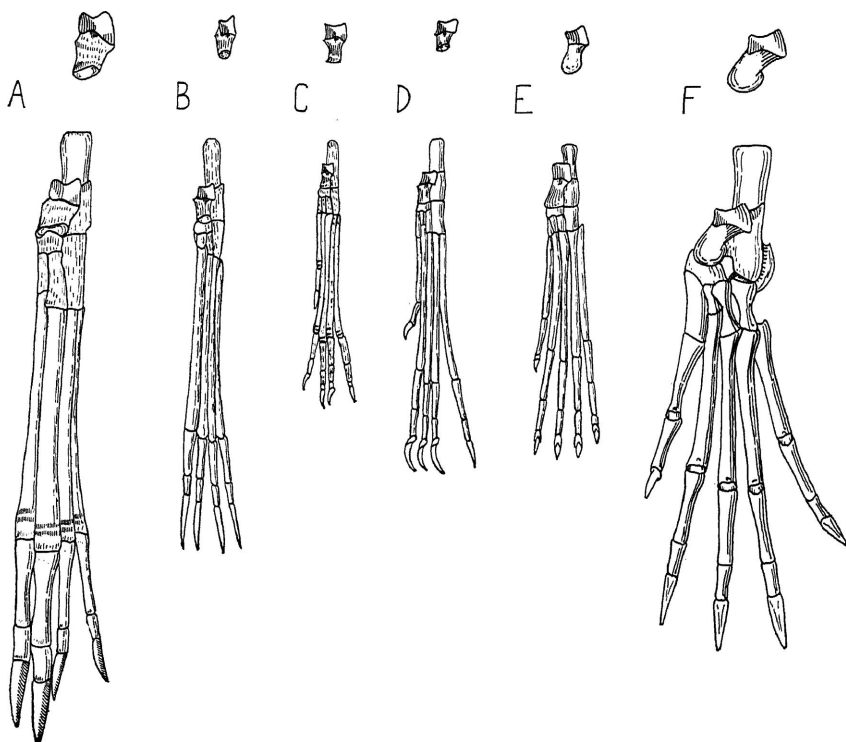


Fig. 9. Left pes and astragalus of the Macroscelididae, *Tupaia* and *Echinosorex* (*Gymnura*) $\times 1$. A, *Rhynchocyon*; B, *Petrodromus*; C, *Macroscelides*; D, *Nasilio*; E, *Tupaia*; F, *Echinosorex*.

ments of the forelegs is a secondary feature, indicating a higher degree of specialization.

Petrodromus is also the most primitive member of the family in having the proportionally shortest shank (Index III) of any member of the family except *Rhynchocyon*. In *Nasilio* and *Macroscelides*, especially the latter, the shank has been secondarily elongated. In this respect, plus the proportionally longest metatarsal III (Index IV) *Macroscelides* is the most highly specialized.

Both *Nasilio* and *Macroscelides* are more specialized than *Petrodromus* and have proportionally shorter forelegs and longer hind legs (Indices VI and III), although *Nasilio* is very close to *Petrodromus* in the latter feature.

The conclusion from a study of both the skull and the limb measurements and proportions is that *Petrodromus* is the most primitive member of the family while *Rhynchocyon* and the *Elephantulus-Nasilio-Macroscelides* group are the most specialized.

TABLE III.—LIMB INDICES OF THE MACROSCOLIDIDAE AND RICOCHETAL MAMMALS (PER CENT)

Measurements and Indices	<i>Rhynchoeyon claudi</i>	<i>Petrodromus tordayi</i>	<i>Nasitio brachyhyncha</i>	<i>Macroscelides rozeti</i>	<i>Macropus rufus</i>	<i>Dipodomys phillipsi</i>	<i>Pedetes caffer</i>	<i>Jaculus orientalis</i>	<i>Napaeozapus insignis</i>	<i>Alladaga mongolica</i>
(1) Humerus, max. length	41.6	29.0	17.9	18.1	110.2	17.3	49.0	14.6	11.4	14.1
(2) Radius, max. length	41.6	41.2	18.9	21.8	165.4	20.6	42.8	16.4	12.3	18.3
Index I—Radio-humeral (2) × 100	100.0	142.1	105.6	120.4	145.6	119.0	87.3	112.7	107.8	129.8
(1)										
(3) Metacarpal III, max. length	21.3	10.5	5.5	5.4	25.3	3.9	7.6	2.8	2.4	3.3
Index II—Mtcp. III-humeral (3) × 100	51.2	36.2	30.7	29.8	23.0	22.5	15.4	19.2	21.1	23.4
(1)										
(4) Femur, max. length (gr. trochanter to medial condyle)	59.8	41.0	24.5	24.0	220.8	34.4	106.6	39.4	17.3	36.2
(5) Tibia, length (surf. of condyle to artic. surf. for astragalus)	73.5	52.6	31.7	34.7	395.3	46.8	127.6	55.3	23.0	54.6
Index III—Tibio-femoral (5) × 100	122.9	128.3	129.4	144.6	179.0	136.0	120.0	140.4	132.9	150.8
(4)										
(6) Metatarsal III, max. length	32.9	24.9	13.0	17.0	135.8	21.8	45.2	41.2	12.3	34.3
Index IV—Metatars. III-femoral					61.5					
(6) × 100	55.0	60.7	53.6	70.8	(IV)	61.3	42.4	104.6	71.1	94.6
(4)										
Index V—Humero-femoral (1) × 100	69.6	70.7	73.1	75.5	50.0	50.2	46.0	37.1	66.0	39.0
(4)										
Index VI—Intermembral (1) + (2) × 100	62.4	75.0	65.5	68.0	44.7	46.6	39.2	32.7	58.8	35.7
(4) + (5)										

COMPARISON WITH RICOCHETAL MAMMALS

In the Macroscelididae, as in ricochetral forms, there has been a secondary shortening of the various segments of the forelegs coupled with a lengthening of the different segments of the hind legs.

Ricochetral forms of mammals are only found among the Marsupialia and the Rodentia. In the following table (Table III) the limb proportions of the various genera of Macroscelididae have been compared with those of hopping forms of mammals. In *Macropus* the proportion for

metatarsal IV was used as it is the longest in the pes.

From Table III it is seen that the length of the forearm (Index I) of the Macroscelididae, due to secondary shortening, compares very favorably with that of leaping forms. None of the former has a forearm shorter than the humerus, as does *Pedetes*, or as long as in *Macropus*, although the latter is the only genus of those considered that surpasses *Petrodromus* in this respect. However, with respect to the

secondary shortening of metacarpal III (Index II) the Macroscelididae are less specialized than all the other genera, in which this process has been carried much further.

The Macroscelididae also compare favorably with ricochet forms in the secondary lengthening of the lower leg (Index III). None of them has so short a shank as *Pedetes*, and that of *Macroscelides* is exceeded in length only by *Allactaga* and *Macropus*. The secondary lengthening of metatarsal III (Index IV) in the Macroscelididae more closely approaches that of some ricochet forms. In none of them is it so short as in *Pedetes* or so long as in *Allactaga* and *Jaculus*. In *Petrodromus*, however, it is very close to that of *Macropus* and *Dipo-*

domys, while in *Macroscelides* it is only a little shorter than in *Napaeozapus*. All the Macroscelididae are less specialized than the ricochet forms in having a longer humerus (Index V) and foreleg (Index VI).¹

The Macroscelididae, in spite of their apparent adaptation for hopping, do not do so. Mr. Arthur Loveridge, who during his many years in Africa has observed them in the wild state as well as in captivity, tells me that they run on all four feet and use their long hind legs for kicking back the leaves, etc., in their search for termites. He also says that if a light is suddenly flashed on them at night they thump the ground with their hind feet in much the same way as a rabbit.

ANCESTRY OF THE MACROSCELIDIDAE

Except for a jaw fragment from the Oligocene of Europe, described by Filhol (1892, p. 134) as *Pseudorhynchocyon*, and a fossil *Elephantulus* of unknown age that Broom (1938, p. 251) found in a Transvaal limestone cave the Macroscelididae are unknown as fossils. Consequently nothing is known of their ancestry and early evolution, but several years ago Simpson (1931) described a form from the Oligocene of Mongolia which seems to me to throw some light on this question.

The form referred to is *Anagale gobiensis* which Simpson (1931, p. 2) originally described as a new genus and species of insectivore which is (p. 21) "closely related to the Tupaiidae but referable to an extinct and non-ancestral family Anagalidae." Earlier, on page 18 of the same paper, he states that "*Anagale* already possessed all the characters shared by Tupaiidae and Macroscelididae" but that "as regards *Anagale* itself, it is seen that it is much closer to the Tupaiidae than to the Macroscelididae and that it is in no sense intermediate between the two." In a later paper (Simpson, 1935, p. 29) he removes both the Anagalidae and the Tupaiidae from the Insectivora and puts them in the suborder Lemuroidea, order Primates.

Therefore in view of the importance of

Anagale I undertook a restudy of its structure and possible relationship to the Macroscelididae.

The skull when viewed from above (Fig. 10, B) resembles that of *Rhynchocyon* in general size and shape more than it does that of *Tupaia*. It exhibits the same broad flat interorbital region, short postorbital processes, large open orbits, low sagittal crest and shallow but well-defined temporal fossae as are seen in *Rhynchocyon*. The nasals are slightly expanded posteriorly and push in between the frontals to some extent. The frontals, as in *Rhynchocyon*, are broad, flat, unfused and form a well-developed supraorbital shelf which has neither foramen nor notch. A further resemblance is seen in the fusion of the opposite parietals and the absence of an interparietal. The brain case is a little less swollen, the temporal fossae larger and the lambdoidal crests higher than in *Rhynchocyon*, but these differences are probably due to the generally more primitive character of *Anagale*.

A conspicuous difference between the two is that in *Anagale* the postorbital processes are much further forward which

¹ Some of the above measurements were taken on zoo animals and are probably different from those that would be obtained from wild animals.

may imply a backward displacement of the orbits in *Rhynchocyon*.

The well-developed, dorso-ventrally flattened zygoma is essentially the same as in *Rhynchocyon*. The jugal, which forms an essential part of the zygoma, is well developed and extends back to the glenoid region but lacks the facial expansion it exhibits in *Rhynchocyon*. The jugular foramen and the postorbital ring of bone seen in *Tupaia* are also absent. In the presence of a jugal-lacrima contact and the absence of one between the maxilla and the squa-

mosal is essentially the same as in *Rhynchocyon*, but the zygomatic process is not so long nor so flattened dorso-ventrally. In shape and position the mastoid region and process are intermediate between the *Tupaia* and the *Rhynchocyon* condition, resembling one as much as the other.

In the important orbitotemporal region the sutures are obliterated by crushing, but Simpson (1931, p. 6) believes that within the orbit the palatine and lacrimal are in contact so as to exclude the maxilla from the frontal, a characteristic feature for

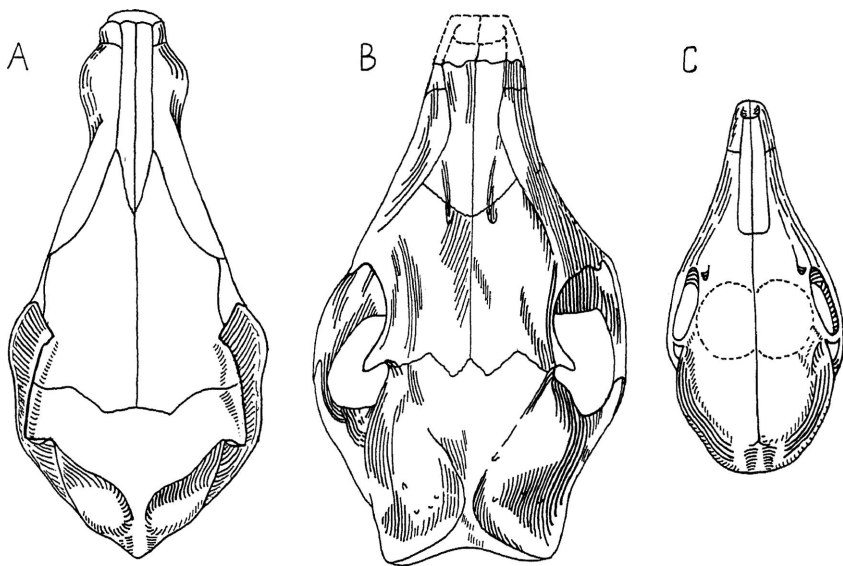


Fig. 10. Dorsal view of skulls of *Rhynchocyon*, *Anagale* (redrawn from Simpson, tip of snout restored) and *Tupaia*. $\times 1$. A, *Rhynchocyon*; B, *Anagale*; C, *Tupaia*.

mosal *Anagale* resembles both *Rhynchocyon* and *Tupaia*.

In the small facial expansion of the lacrimal *Anagale* approaches the Macroscelidinae and *Tupaia* more than *Rhynchocyon* in which it is large. A further resemblance to *Tupaia* is seen in the large size of the lacrimal tubercle and the presence and position of the two lacrimal foramina which are in notches, one above and one below the tubercle and slightly on the facial part of the lacrimal.

The small squamous portion of the squa-

both the Macroscelididae and the Tupaiidae.

The occiput is not swollen as in *Tupaia* and, although it lacks the curved superior border and has higher lambdoidal crests, is in general more like that of *Rhynchocyon*. The foramen magnum is a little more circular than in *Rhynchocyon*, but the occipital condyles, paroccipital processes and other features of the two are essentially the same.

In general shape the palate (Fig. 11, B) is a little closer to that of *Rhynchocyon* but resembles the other Macroscelididae and

Tupaia in the presence of definite palatal vacuities. The presence of a sharp crest formed by the palatine and the pterygoid and running back almost to the bulla is a feature which *Anagale* shares with both *Rhynchocyon* and *Tupaia*. The three genera also resemble each other in the small size of the external pterygoid fossae.

In the actual size of the bullae (Table IV, 8) *Anagale* closely approaches *Rhynchocyon*, but its almost perfect spherical shape is unique. Simpson (1931, p. 5) believes that a small fragment of bone found within

the base of the skull *Anagale* differs from both *Tupaia* and *Rhynchocyon*. The alisphenoid region in front of the bulla is not inflated as in the Macroscelididae.

Most of the skull indices (Table IV) are closer to those of *Rhynchocyon* than to those of *Tupaia*, the exceptions being Index V (least parietal width), in which *Anagale* is intermediate between *Rhynchocyon* and *Tupaia*, and Index VI (greatest parietal width), in which it is closer to *Tupaia*. In the proportional size of the bullae (Index VII) *Anagale* is practically identical with

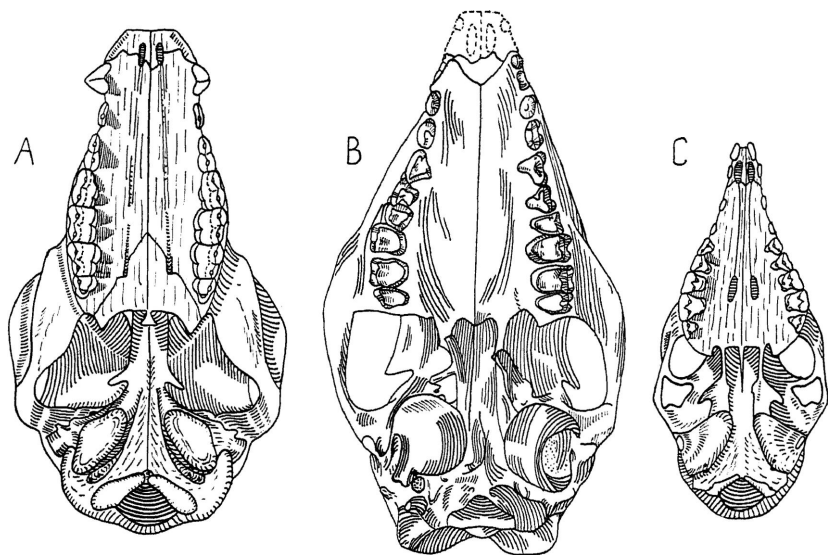


Fig. 11. Ventral view of skulls of *Rhynchocyon*, *Anagale* (redrawn from Simpson, with tip of snout restored) and *Tupaia*. $\times 1$. A, *Rhynchocyon*; B, *Anagale*; C, *Tupaia*.

the left bulla was the tympanic ring, in which case the entire bulla would be formed from the entotympanic as in *Tupaia*.

If this is true then perhaps a large entotympanic bulla enclosing a ring-shaped ectotympanic, as in *Tupaia*, is the primitive Menotyphlan condition, and the Macroscelid condition, in which the ectotympanic forms an external auditory canal fused with the entotympanic at its inner end, is a secondary condition derived from the first by differential growth.

In the absence of a petrosal exposure on

Petrodromus but is smaller than the rest of the Macroscelididae and than *Tupaia*. In the relative bizygomatic width (Index I) *Anagale* is closer to all the Macroscelidinae except *Petrodromus* than it is to *Tupaia*, being the same as *Nasilio* and *Elephantulus*. *Anagale* is more primitive in the length of the snout (Index II) than *Tupaia* or any of the Macroscelidinae, in all of which there has been a secondary shortening of the olfactory region, while in *Rhynchocyon* it has been secondarily lengthened.

The number and arrangement of the de-

TABLE IV.—SKULL MEASUREMENTS AND INDICES OF *Anagale*, *Tupaia* AND THE MACROSCELIDIDAE

Measurements and Indices	<i>Tupaia</i> <i>bel-</i> <i>angeri</i>	<i>Anagale</i> <i>gobien-</i> <i>sis</i>	<i>Rhyn-</i> <i>chocyon</i> <i>claudi</i>	<i>Petro-</i> <i>dromus</i> <i>tordayi</i>	<i>Nasilio</i> <i>brachy-</i> <i>rhyncha</i>	<i>Elephan-</i> <i>tulus</i> <i>renatus</i>	<i>Macro-</i> <i>scelides</i> <i>rozeti</i>
(1) Skull, total length pmx.-condyle	44.5	69.3c*	62.1	48.6	31.3	33.0	30.8
(2) Skull, max. bizygomatic width	23.1	40.8	35.7	25.3	18.3	19.3	19.4
Index I—Rel. bizyg. width (2) × 100	51.9	58.8e	57.5	52.3	58.4	58.5	62.9
(1)							
(3) Face, preorb. length (ant. orbital rim to pmx. tip)	20.6	38.0e	36.8	24.6	15.2	14.3	15.2
Index II—Face length (3) × 100	46.2	54.8e	59.3	50.6	48.5	43.4	49.3
(1)							
(4) Preorb. breadth (across lac. tubercle)	15.7	32.3	30.6	14.9	13.0	13.4	14.0
(4) × 100	35.2	46.5	49.3	30.6	41.6	40.5	45.4
Index III—							
(1)							
(5) Cranium = (1) - (3) Cranial length	23.9	31.3e	25.3	24.0	16.6	18.7	15.6
(5) × 100	53.7	45.1e	40.7	49.4	51.5	56.6	50.6
Index IV—							
(1)							
(6) Least parietal width	14.8	21.6	18.3	9.6	7.8	8.3	7.0
(6) × 100	33.2	31.1	29.5	19.8	24.8	24.9	22.7
Index V—							
(1)							
(7) Greatest parietal width	18.0	28.8	30.8	18.7	13.9	15.1	14.7
(7) × 100	40.4	41.5	49.6	38.5	44.4	45.7	47.7
Index VI—							
(1)							
(8) Tymp. bulla, max. length	8.4	10.0	10.6	6.9	5.7	6.6	5.9
(8) × 100	18.8	14.4	17.0	14.2	18.2	20.0	19.1
Index VII—							
(1)							

* c = estimate.

terminable skull foramina are essentially similar to those of *Rhynchocyon* except for the presence of an alisphenoid canal and the probable absence of the suboptic foramen. The latter may be present, although Simpson does not record it. *Anagale* agrees with *Rhynchocyon* and *Tupaia* in having a long infraorbital canal and a prominent foramen above P³. The optic, sphenopalatine, ovale, postglenoid, stylo-mastoid, eustachian jugular, carotid and condylar foramina are all present and essentially the same in the three genera. *Anagale* is closer to *Tupaia* in the position of the lacrimal foramina, the possession of an alisphenoid canal and the probable absence of a suboptic foramen. It is closer to

Rhynchocyon in having the sphenoidal fissure and foramen rotundum combined and in lacking the malar and supraorbital foramina.

The teeth (Fig. 12), like the skull, combine features of *Rhynchocyon* and *Tupaia* but on the whole are nearer the latter. The dental formula, which according to Simpson (1931, p. 2) is $? \frac{3 \frac{1}{2} 4 \frac{3}{2}}{3 \frac{1}{2} 4 \frac{3}{2}} = 44$, is closer to that of *Tupaia* ($\frac{2 \frac{1}{2} 3 \frac{3}{2}}{3 \frac{1}{2} 3 \frac{3}{2}} = 38$) than to that of *Rhynchocyon* ($\frac{2 \frac{1}{2} 4 \frac{2}{2}}{3 \frac{1}{2} 4 \frac{2}{2}} = 36$). *Anagale* is thus seen to have the complete primitive placental formula.

According to Simpson (1931, p. 2) I¹, if present, was probably small and well separated from the corresponding tooth on the other side. I² is small, styliiform, single-rooted, with an unexpanded crown and es-

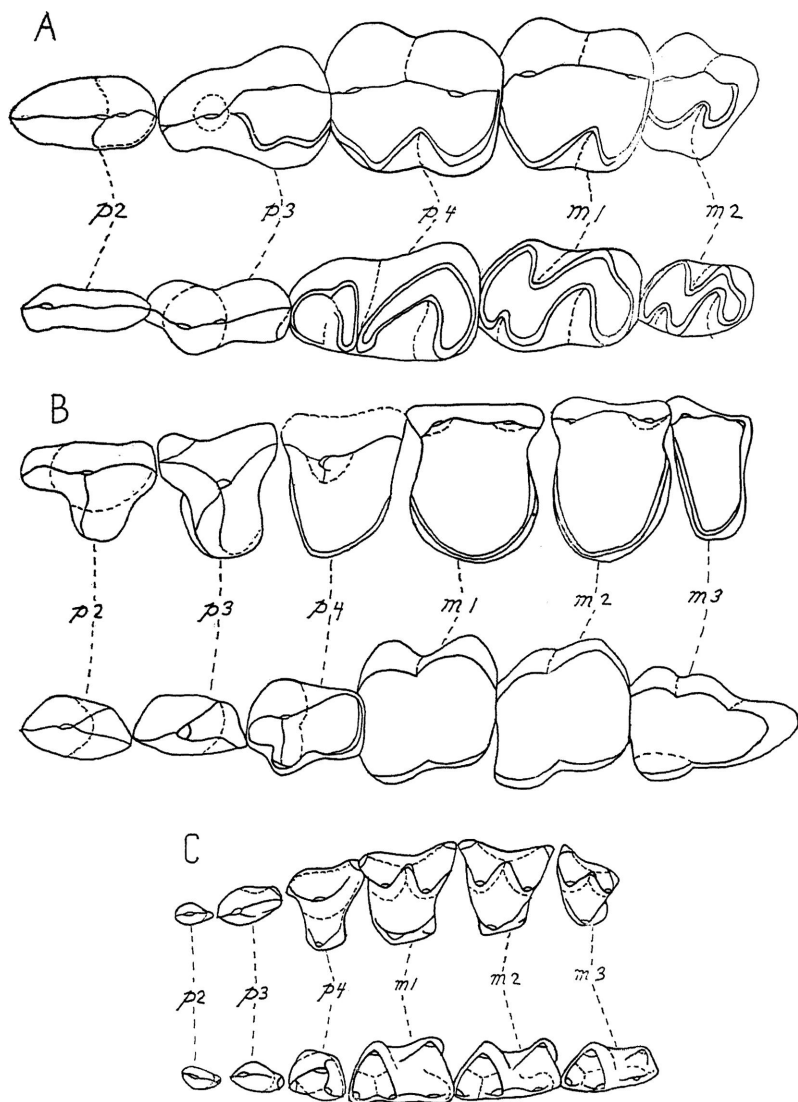


Fig. 12. Cheek teeth (upper left and lower right) of *Rhynchocyon*, *Anagale* and *Tupaia*. $\times 5$. A, *Rhynchocyon*; B, *Anagale*; C, *Tupaia*.

essentially the same as its homologue in *Tupaia*. Judging from the alevoli for I^3 it was slightly larger than I^2 but otherwise the same. Thus, with respect to the number of incisors, *Anagale* is more primitive than either *Tupaia* or *Rhynchocyon*, but with

respect to the character of the individual teeth it is closer to the former.

The upper canine is essentially similar to that of *Tupaia*, being but little taller than I^2 , although it is stouter.

Another primitive feature of the denti-

tion in which *Anagale* differs from both *Tupaia* and *Rhynchocyon* is the complete absence of a diastema in the cheek teeth (Fig. 4). With respect to the shape of the premolars *Anagale* approaches *Rhynchocyon* more closely than *Tupaia*, as incipient molarization extends to P^2 in the two former genera and only to P^3 in *Tupaia*. However, with regard to the number and arrangement of the cusps none of the premolars is so completely molariform as P^4 in *Rhynchocyon*. Each has a large paracone, preceded and followed by slight basal cusps, and a small protocone. Simpson

to subdivide the inner half of M^{1-2} into two moieties, nor is there a trace of a cingulum hypocone.

The paracone and metacone are external in position, non-crescentic and connected by a crest which is but slightly W-shaped. In these features *Anagale* approaches *Rhynchocyon*. A further resemblance to the latter is seen in the slight development of the external cingulum and the absence of the mesostyle and anterior cusp, both of which are present in *Tupaia*. In the possession of an upper third molar *Anagale* agrees with *Tupaia*, but this is simply a

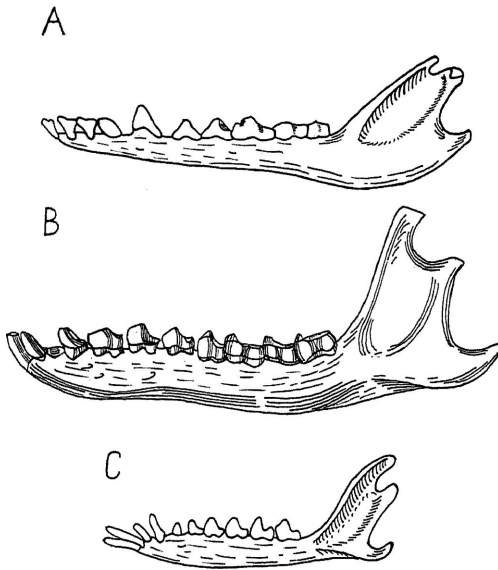


Fig. 13. Lateral view of left mandible of *Rhynchocyon*, *Anagale* (redrawn from Simpson) and *Tupaia*. $\times 1$. A, *Rhynchocyon*; B, *Anagale*; C, *Tupaia*.

(1931, p. 2) also found evidence of a fourth cusp, an incipient hypocone or a prominent metaconule, on P^4 . The premolars are thus closer in some respects to the *Rhynchocyon* condition than to *Tupaia*, in which only P^4 shows any evidence of molarization in shape, although it has only a paracone and protocone with no evidence of a hypocone.

The molars are closer to those of *Tupaia* in being mainly tritubercular, transversely widened and, according to Simpson (1931, p. 2), with three main cusps and an incipient hypocone. There is no tendency

primitive placental character to be expected in an Oligocene form.

Comparison of the upper molars of many families of mammals leads us to suspect that the anteroposterior elongation of M^1 , M^2 in *Rhynchocyon* is secondary, and that its remote ancestors would have relatively wider upper molars with little or no hypocones. Thus the molars of *Anagale* are far more primitive than those of *Rhynchocyon*.

The lower teeth of *Anagale* also show a mixture of Macroscelid and Tupaoid characters, the incisors, canines and first three premolars exhibiting the latter. P_4 ,

however, is more like the deciduous P_4 of *Tupaia*, as figured by Butler (1939, p. 27), in showing marked traces of the tuberculo-sectorial pattern, than it is like the permanent P_4 . In this respect it is more like P_4 of *Rhynchocyon* which has a well-developed tuberculo-sectorial pattern. M_1 and M_2 differ from those of both *Rhynchocyon* and *Tupaia* in being relatively wider and more nearly square in shape, due to the marked anteroposterior compression of the trigonid. The more quadrate form of the crown of M_1 , M_2 , as compared with the more compressed or elongated crowns in *Rhynchocyon* conforms with the greater anteroposterior extension of the corresponding upper molars in the latter genus.

The molars show a definite derivation from the tuberculo-sectorial pattern, although the size and position of the paraconid cannot be determined with certainty. In this respect M_1 and M_2 differ from those in *Tupaia*, which exhibit a completely developed tuberculo-sectorial pattern and approach the *Rhynchocyon* condition in which there is a tendency, particularly on M_2 , to have the paraconid reduced or absent. In the presence of an M_3 *Anagale* resembles *Tupaia* and is more primitive in retaining a well-developed hypoconulid.

The mandible of *Anagale* (Fig. 13, B) is far more primitive than that of *Tupaia* and still more so than that of *Rhynchocyon*. The condyle is less elevated above the plane of the cheek teeth than in either of the above, and the ascending ramus as a whole is more vertical in position. The angular process is more like that of a primitive placental, and the coronoid process is less reduced. In the last two features *Anagale* approaches *Pseudorhynchocyon* from the Oligocene of Europe, although the latter is more specialized in having the ascending ramus of the mandible posteriorly inclined as in *Rhynchocyon*.

What remains of the post-cranial skeleton shows the same mixture of *Rhynchocyon*-like and *Tupaia*-like characters as the skull and dentition.

The atlas, except for the absence of the ventral tubercle and a less antero-posteriorly expanded transverse process, is almost identical with that of *Rhynchocyon*.

The remaining cervicals are also very close to the latter.

The general shape of the scapula is closer to that of *Tupaia*. Most of the arm and carpus is lost, but the phalanges and claws of the manus are close to those of *Rhynchocyon*.

In the free and unfused condition of the tibia and fibula *Anagale* agrees with *Tupaia*. The astragalus also resembles that of *Tupaia* in having a broad and fairly shallow trochlea but agrees with *Rhynchocyon* in having the fibular margin of the trochlea decidedly the more prominent. A further agreement with the *Rhynchocyon* astragalus is the condition of the sustentacular facet which is almost but not quite continuous with the navicular facet. In the possession of an astragalar foramen *Anagale* is far more primitive than the other genera.

From the above comparison *Anagale* is seen to have both *Tupaia*-like and *Rhynchocyon*-like characters in the skull, skeleton and dentition and thus does not completely agree with Simpson's statement (1931, p. 18) that "it is much closer to the *Tupaia*idae than to the *Macroscelididae* and that it is in no sense intermediate between the two."

These characters are presented in tabular form below.

CHARACTERS IN WHICH *Anagale* RESEMBLES *Rhynchocyon*

- 1.—General size and shape of skull.
- 2.—Short postorbital process.
- 3.—Open orbits, no postorbital ring.
- 4.—Low sagittal crest and moderate lambdoidal crests.
- 5.—Shallow but well-defined temporal fossae.
- 6.—Nasals push in between the frontals.
- 7.—Opposite parietals fused.
- 8.—Zygoma well developed and dorso-ventrally flattened.
- 9.—Small squamous portion of the squamosal.
- 10.—General character of the occiput.
- 11.—Actual size of bullae.
- 12.—The majority of the skull indices approach those of *Rhynchocyon*.
- 13.—Sphenoidal fissure and foramen rotundum combined.
- 14.—Malar and supraorbital foramina absent.
- 15.—Fossa on side of snout (not so well defined as in *Rhynchocyon*).
- 16.—Incipient molarization in shape of upper premolars extends to P^2 .

- 17.— P^4 closer to *Rhynchocyon* as, according to Simpson, it has an incipient fourth cusp.
- 18.—Shape, size and position of paracone and metacone on upper molars.
- 19.—Slight development of the external cingulum on the upper molars; absence of mesostyle and anterior cusp.
- 20.— P_4 more like that of *Rhynchocyon*.
- 21.— M_{1-2} approach the *Rhynchocyon* condition in having the paraconid reduced or absent.
- 22.—Character of the atlas and remaining cervicals.
- 23.—Phalanges and claws of manus close to those of *Rhynchocyon*.
- 24.—Fibular margin of astragalar trochlea decidedly more prominent.
- 25.—Sustentacular facet of the astragalus is almost but not quite continuous with the navicular facet.

CHARACTERS IN WHICH *Anagale* RESEMBLES *Tupaia*

- 1.—No facial expansion of the jugal.
- 2.—Large lacrimal tubercle.
- 3.—Presence and position of the two lacrimal foramina.
- 4.—Structure of the bulla.
- 5.—Alisphenoid not inflated in front of bulla.
- 6.—Presence of alisphenoid canal.
- 7.—Dental formula closer to *Tupaia*.
- 8.—Character of the upper incisors and canines.
- 9.—General shape of upper molars.
- 10.—Presence of M_3^3 .
- 11.—Lower incisors, canines and first three premolars resemble those of *Tupaia*.
- 12.— P_4 more like DP_4 than P_4 of *Tupaia*.
- 13.—General shape of scapula.
- 14.—Tibia and fibula free.
- 15.—Trochlea of astragalus broad and fairly shallow.

CHARACTERS IN WHICH *Anagale* RESEMBLES BOTH THE MACROSCOLIDIDAE AND THE TUPAIIDAE

- 1.—Brain case swollen (not so much as in the Macroscelididae and the Tupaiidae).

- 2.—Broad flat interorbital region.
- 3.—Large orbits.
- 4.—Large auditory bullae.
- 5.—Small facial expansion of the lacrimal (as in the Macroscelidinae and *Tupaia*).
- 6.—Presence of a contact between the lacrimal and the jugal.
- 7.—No contact between the maxilla and the squamosal.
- 8.—Presence of a contact between the palatine and lacrimal within the orbit, thus excluding the maxilla from the frontal.
- 9.—Lacrimal divided by a ridge into a facial and an orbital portion.
- 10.—Jugal extends back to the glenoid region but not to the actual articular area for the condyle.
- 11.—Position and character of the mastoid region and process.
- 12.—Presence of palatine vacuities as in the Macroscelidinae and *Tupaia*.
- 13.—Palatines and pterygoids form a sharp ridge running back almost to the bulla.
- 14.—Small external pterygoid fossae as in *Rhynchocyon* and *Tupaia*.
- 15.—Long infraorbital canal as in *Rhynchocyon* and *Tupaia*.
- 16.—The optic, sphenopalatine, ovale, postglenoid, stylomastoid, eustachian, carotid and condylar foramina are all present and essentially the same in position.
- 17.—The foramen magnum faces slightly downward.
- 18.—The articular surface of the occipital condyles is nearly continuous anterior to the foramen magnum.
- 19.—Small paroccipital process.
- 20.—Small triangular alisphenoid shelf at the angle between the pterygoid crest and the bulla.

My conclusion from the above is that *Anagale* is in many features intermediate in character between the Macroscelididae and the Tupaiidae and that it is not very distant from the common ancestral stock of the two families.

AFFINITIES OF THE MACROSCOLIDIDAE WITH *GYMNURA* AND *TUPAIA*

As stated in the introduction, the Macroscelididae and the Tupaiidae are commonly grouped together in the suborder Menotyphla, in opposition to the Lipotyphla which includes all the remaining insectivores. Carlsson (1909) believes, however, this separation is invalid and that the Macroscelididae are more closely related to the Erinaceidae than to the Tupaiidae, while some other workers have completely removed the latter from the In-

sectivora and placed them in the Lemuroidea.

These conclusions, however, seem open to question, so a restudy of the relationships of the Macroscelididae to the Erinaceidae and the Tupaiidae was undertaken. *Gymnura* was used as a representative of the Erinaceidae and of a primitive insectivore, while *Tupaia* represented the Tupaiidae.

When skulls of members of the three families are viewed dorsally (Fig. 1) those

of the Macroscelididae and the Tupaiidae are seen to resemble each other more closely in shape than either resembles that of *Gymnura*. Both have a tapering snout, large orbits, a broad flat interorbital region and a swollen brain case with a short slight sagittal crest and low lambdoidal crests. A further resemblance is the inflation of the occiput in *Tupaia* and the Macroscelidinae, while the frontal in all genera of both families forms a broad supraorbital shelf. This is perforated by supraorbital foramina in *Tupaia* and notched in *Rhynchocyon*.

Gymnura (Fig. 1, G) has, however, a less tapering snout, small orbits, a marked interorbital constriction and a small uninflated brain case with a long prominent sagittal crest and high lambdoidal crests. As in *Rhynchocyon* there is no inflation of the occiput. The frontal does not form a supraorbital shelf.

In all three families the orbital and the temporal fossae are continuous, but in *Tupaia* there is a complete postorbital ring of bone, while the Macroscelididae show the beginnings of one in the postorbital processes of *Rhynchocyon*. Neither of the two latter features is present in *Gymnura*.

In ventral view of the skulls (Fig. 2) the outstanding feature is the presence of large auditory bullae in the Macroscelididae and the Tupaiidae and their absence in *Gymnura*. With the exception of *Rhynchocyon* the Macroscelididae also resemble *Tupaia* in having a palate which narrows anteriorly and is fenestrated. *Rhynchocyon*, however, resembles *Gymnura* in having a palate approximately the same width throughout and with no vacuities except the anterior and posterior palatine foramina. *Gymnura* differs from *Tupaia* and the Macroscelididae in having the posterior margin of the palate regular and raised to form a ridge. In both *Gymnura* and the Macroscelidinae the pterygoid fossae are large and extend forward to the posterior margin of the palate, while they are very small in *Tupaia* and *Rhynchocyon*.

With the exception of *Rhynchocyon* the Macroscelididae and *Tupaia* agree with *Gymnura* in having a slender zygomatic

arch, but its structure is different. In *Tupaia* and the Macroscelididae the jugal is well developed and extends back to the glenoid region, although it does not reach the articular surface for the jaw condyle, while in *Gymnura* it is reduced to a tiny element in the center of the zygoma. The jugal foramen of *Tupaia* is lacking in *Gymnura* and in my specimens of the Macroscelididae, although, according to Muller (1935, p. 251), Weber reports its presence in the latter.

Tupaia and the Macroscelididae also agree in the possession of a large lacrimal which is divided by a prominent ridge into a well-defined facial and a large orbital portion. A distinct tubercle is also present. In *Gymnura* the facial portion is lacking, and the orbital part is small. The Macroscelididae and *Gymnura* agree, however, in having a single lacrimal foramen, but its position is not the same in both, being well within the orbit in the former and in the orbital rim of the latter. *Tupaia* differs from both by having two lacrimal foramina, one above and one below the tubercle. One of them is more on the facial side, while the other may be within the orbit. According to Muller (1935, p. 194) most of the Tupaiidae have only one foramen which is located in the facial part of the lacrimal.

In the important orbito-temporal region (Fig. 14, A, B) the Macroscelididae and *Tupaia* also exhibit a high degree of resemblance. In both the palatine has a large extension in the rostral and medial wall of the orbit and meets the lacrimal so as to exclude a contact between the maxilla and frontal within the orbit. A second diagnostic feature for the two is the contact between the lacrimal and the jugal. The frontal in both has a large orbital wing which forms a large part of the median orbital wall and makes contact with the palatine. The orbitosphenoid is large but the alisphenoid fairly small and does not have any contact with the frontal. Muller (1935, p. 228) states that in most Tupaiinae the orbitosphenoid and the squamosal are in contact, but this is not true in my specimens, and the contact in the Macroscelididae is very slight. According to him (1935, p. 251) the orbito-temporal region in

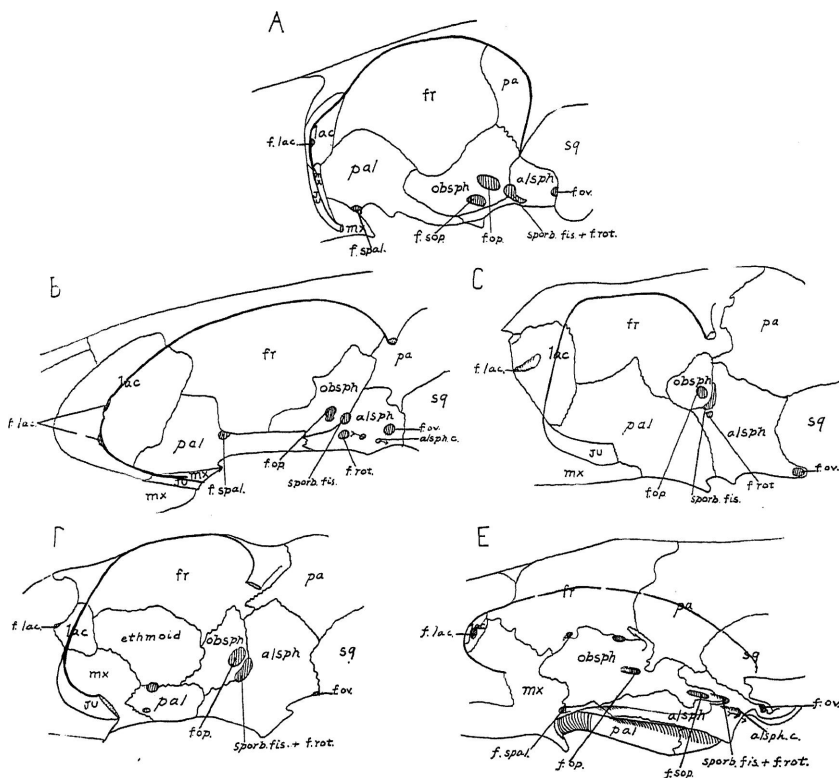


Fig. 14. Orbito-temporal region. A, *Petrodromus*; B, *Tupaia* (modified from Le Gros Clark and J. Muller); C, *Lemur*; D, *Perodicticus*; E, *Echinorex* (*Gymnura*). Alsph., alisphenoid; alsph. c., alisphenoid canal; f. lac., lacrimal foramen; f. op., optic foramen; f. ov., foramen ovale; f. sop., suboptic foramen; f. spal., sphenopalatine foramen; sporb. fis. + f. rot., sphenorbital fissure + foramen rotundum; fr., frontal; ju., jugal; lac., lacrimal; mx., maxilla; pa., parietal; pal., palatine; sq., squamosal.

Tupaia and the Macroscelididae represents the ancestral or primitive condition for mammals, but for various reasons this is decidedly open to question.

In *Gymnura* (Fig. 14, E) the orbital part of the palatine is small, and the contact with the lacrimal is absent, thus allowing the maxilla and frontal to be in contact within the orbit. The contact between the palatine and the frontal and between the lacrimal and the jugal is also absent. A further difference from *Tupaia* and the Macroscelididae is the presence of a contact between the maxilla and the orbitosphenoid.

Gymnura, *Tupaia* and the Macroscelididae all agree in the absence of a contact

between the frontal and the alisphenoid, while, according to Muller (1935, p. 219), one is present in all other Insectivora. A further agreement is the communication of the opposite orbits through the optic foramen and the contact between the orbitosphenoid and the parietal. *Gymnura* agrees with my specimens of *Tupaia* in the absence of a contact between the orbitosphenoid and the squamosal, although Muller (1935, p. 228) says it is present in most Tupaiinae. In all the genera considered the alisphenoid plays only a small part in forming the wall of the orbit.

The orbitosphenoid of *Gymnura* differs from that of *Tupaia* and the Macroscelididae in forming a larger part of the me-

dian orbital wall. According to Muller (1935, p. 223) *Gymnura* differs from the others in having a separate interorbital septum lying in the cerebral cavity. The contribution of the frontal to the wall of the orbit is smaller than in *Tupaia* and the Macroscelididae, while that of the parietal is larger.

With regard to the size of the alisphenoid in the Erinaceidae Muller (1935) contradicts himself, stating on page 233 that it is small and located chiefly in the basal part of the orbit, while on page 234 he says it is

The alisphenoid lies in the tympanic chamber in the Erinaceidae, the Macroscelididae and the Tupaiidae, but the development of the part within the chamber varies. In *Erinaceus*, according to Van der Klaauw (1931, p. 250), it is a low transverse ridge, while in other genera of the family it may be well developed and inflated. In the Macroscelididae and the Tupaiidae it is in the anterior or cranial wall of the tympanic cavity and is inflated in the former but very small in the latter.

The ectotympanic is also variously de-

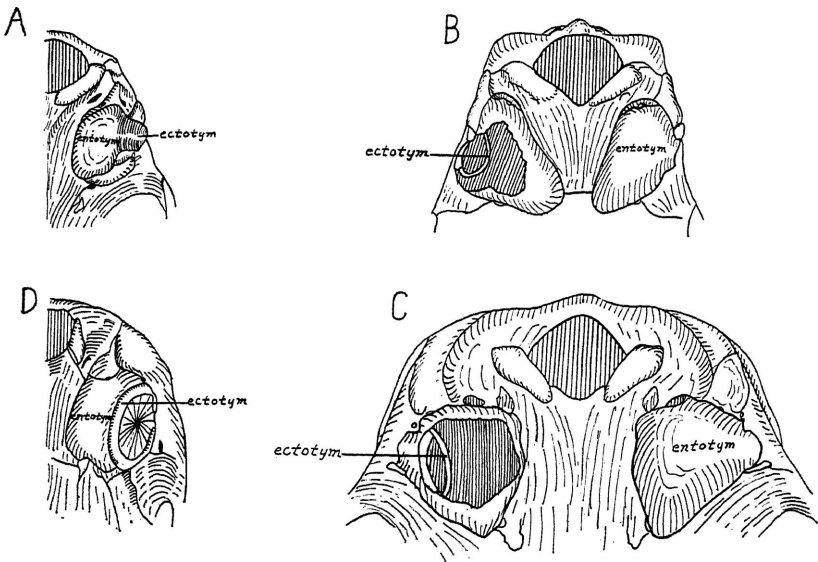


Fig. 15. Auditory region. A, *Petrodromus*; B, *Tupaia* (modified from Van Kampen); C, *Lemur* (modified from Van Kampen); D, *Perodicticus* (modified from Van Kampen). Ectotym., ectotympanic; entotym., entotympanic.

larger than the orbitosphenoid. My own observations on *Gymnura* are in accordance with the first statement.

As previously noted one of the most conspicuous differences between *Gymnura* on the one hand and *Tupaia* and the Macroscelididae on the other (Fig. 2) is the presence of auditory bulla in the latter and their absence in *Gymnura*. The bullae are formed largely (Macroscelididae) or entirely (*Tupaia*) by the entotympanic, an element completely absent in *Gymnura* and other Lipotyphla.

veloped in the three families. It is not expanded to any extent in the ventral wall of the tympanic cavity in any insectivores, but Van der Klaauw (1931, p. 254) states that in *Erinaceus* it forms a bony recessus meatus acustici externus. In the Macroscelididae it forms both a bony recessus and a cylindrical meatus, but in *Tupaia* it is ring-shaped and located within the bulla, having nothing to do with its formation.

In most insectivores the posterior wall of the tympanic chamber is formed by the tympanic wing of the petrosal, but its de-

velopment varies in the different families. Van der Klaauw (1931, p. 287) states that it is well developed in *Gymnura*, while in *Macroscelides*, according to Carlsson (1909, p. 352), it is a ridge. Van der Klaauw (1931, p. 287) also says the tympanic wing of *Rhynchocyon* is like that of *Erinaceus* in being divided into two processes on the petrosal. In *Tupaia*, according to Van Kampen (1905, p. 449) and Carlsson (1909, p. 352), the tympanic process of the petrosal is absent.

each other more closely than either resembles *Gymnura*. As Van Kampen (1905, p. 452) says, "A distinct os bullae only occurs in the Macroscelididae and the Tupaiidae which together form the suborder Menotyphla." Further on he states that the difference between the Menotyphla and the Lipotyphla is not so much in the presence or absence of a bulla as of an entotympanic. In conclusion he says, "The composition of the tympanic cavity is accordingly in agreement with the division of

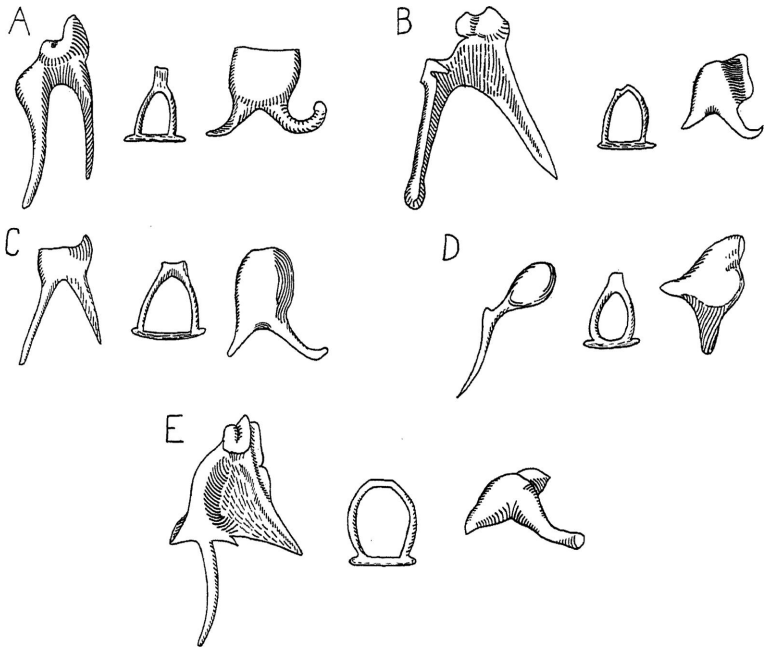


Fig. 16. Auditory ossicles (redrawn from Doran). A, *Rhynchocyon*; B, *Macroscelides*; C, *Tupaia*; D, *Lemur*; E, *Echinosorex* (*Gymnura*).

The insectivores are the only mammals having the basisphenoid in the wall of the tympanic cavity, but this is not true of all families of them. In *Gymnura*, according to Van der Klaauw (1931, p. 246), the basisphenoid has a large expanded tympanic wing, while it is absent in *Tupaia* (Van Kampen, 1905, p. 449) and either the same or nearly so in the Macroscelididae (Van Kampen, 1905, pp. 445, 447).

Thus in the auditory region the Tupaiidae and the Macroscelididae resemble

the Insectivora into Menotyphla and Lipotyphla . . ."

In general shape the auditory ossicles (Fig. 16) of *Tupaia* and the Macroscelididae resemble each other more than either does the ossicles of *Gymnura*. Doran (1878, p. 440) states that the malleus of the Macroscelididae is very different from the type of *Erinaceus*, while that of *Tupaia* much resembles the malleus of some lower primates, especially *Midas*, *Hapale* or certain lemurs. He (pp. 440-442) also found that

the stapes of the Macroscelididae and of *Tupaia* had the aperture between the crura filled by a bony canal in the recent skeleton, while this was not the case in *Gymnura*. In *Petrodromus* he found that the incus is unlike that of *Erinaceus* but also diverges from that of *Macroscelides* and *Rhynchocyon* and tends toward *Tupaia*.

All the genera under consideration exhibit the usual number and distribution of skull foramina with the following differences among themselves. In *Tupaia* and *Rhynchocyon* the infraorbital canal is long, but *Gymnura* agrees with the Macroscelidinae in having a short one. *Gymnura* and the Macroscelididae agree in having the sphenoidal fissure and the foramen rotundum combined, while they are separate in *Tupaia*. The former two also have a prominent suboptic foramen, an insectivore character, while in *Tupaia* it is either absent or perhaps combined with the optic foramen. According to Muller (1935, p. 242) the alisphenoid canal is present in the Tupaiinae, the Macroscelidinae and the Gymnurinae, but I did not find it in the Macroscelidinae.

The supraorbital and malar (jugal) foramina of *Tupaia* are absent in both the Macroscelididae and *Gymnura*. *Rhynchocyon*, however, has an indication of a supraorbital foramen in the supraorbital notch.

The mandible in all the genera (Fig. 3) has a well-developed ascending ramus which raises the condyle, especially in the Macroscelididae, high above the level of the cheek teeth. *Tupaia* resembles the Macroscelidinae in having a slender curved coronoid process. This process is broad and truncate in *Gymnura* and reduced to a small spine in *Rhynchocyon*. In *Tupaia* and *Gymnura* the coronoid process extends well above the condyle, while in the other genera the two are approximately equal in height. The angular process is much reduced in *Rhynchocyon* but is well developed and more or less hook-like in the other genera. *Gymnura* has a single large mental foramen below P_3 , while the others usually have two rather small ones, the first below the canine or P_1 and the second below P_3 or P_4 .

With regard to the number of permanent

teeth *Gymnura* is the most primitive and retains the complete placental formula ($I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{3}{3}$) with 44 teeth. The other genera, however, exhibit various degrees of reduction in the number of permanent teeth. All the Macroscelidinae, except *Nasilio* which retains M_3 , have 40 teeth ($I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{2}{2}$), while *Tupaia* has 38 ($I \frac{3}{3} C \frac{1}{1} P \frac{3}{3} M \frac{2}{2}$). *Rhynchocyon* is the most specialized of all, having only 36 or 34 ($I \frac{1-0}{2} C \frac{1}{1} P \frac{4}{4} M \frac{2}{2}$) depending on whether or not the upper incisors are retained in old individuals. Thus in regard to the total number of teeth *Tupaia* and the Macroscelididae, particularly the Macroscelidinae approach each other more closely than either one approaches *Gymnura*.

The Macroscelididae (Fig. 4) are more specialized than either *Tupaia* or *Gymnura* in having a molariform P_4 and in the loss, except in *Nasilio*, of M_3 . *Nasilio* thus has 42 teeth in all and in this respect is the closest of all the Macroscelididae to *Gymnura*. According to Gregory (1910, p. 281) the Macroscelididae are among the few insectivores retaining $P \frac{1}{1}$, a primitive feature they share with *Gymnura*.

A further agreement between the Macroscelididae and *Gymnura* is the general shape of the quadritubercular upper molars. This is, however, a superficial resemblance, and in the development and arrangement of the molar cusps *Gymnura* more closely approaches the *Tupaia* condition in having low, blunt cusps with the primary triangle still plainly visible. The hypocone is only indirectly connected to the protocone, but the latter is connected with both the paracone and the metacone by crests.

In all these features *Gymnura* is more primitive than the Macroscelididae and resembles *Tupaia*. The latter, however, has less quadrangular upper molars, and the hypocone is incipient and not connected with the protocone at all. The primitive triangle is thus fully developed. *Tupaia* differs from both *Gymnura* and the Macroscelididae in having an anterior cusp and well-developed styles. In these features the molars of *Tupaia* and *Gymnura* are thus seen to resemble each other more closely than they do those of the Macroscelididae. They are also more primitive

and closer to the ancestral tritubercular type than is the case in the Macroscelididae.

In the remaining upper teeth the Macroscelidinae, *Tupaia* and *Gymnura* agree in having the first upper incisor enlarged, but *Rhynchocyon* has very small upper incisors which may be lost in old age. In both *Gymnura* and *Rhynchocyon* the upper canine is large. A long diastema is present between the incisors and the canine in both *Gymnura* and *Tupaia* but not in the Macroscelididae.

The lower molars of *Gymnura* and *Tupaia* (Fig. 4) also approach each other and are more primitive than those of the Macroscelididae in exhibiting the fully developed tuberculo-sectorial pattern. This pattern is not so evident in the Macroscelididae, as there is a tendency to have the paraconid reduced. The Macroscelididae also have a more or less molariform P_4 , while *Tupaia* and *Gymnura* do not. *Tupaia* differs from the others in the loss of P_1 and in having quite procumbent lower incisors. *Gymnura* is the only one having a large lower canine. *Rhynchocyon* is the most specialized in having the distal end of the lower incisors bilobed, although they are incipiently so in *Petrodromus*. It also has a small, incisiform lower canine and a large caniniform P_1 .

The lower cheek teeth of *Gymnura* and *Tupaia* thus resemble each other more than they do those of the Macroscelididae and are also more primitive. The most specialized condition of the lower incisors, canines and premolars is seen in *Rhynchocyon*.

The skull indices (Table I) of the genera being considered also throw some light on their relationships. Thus *Gymnura* (Index I) has a narrower skull than any of the Macroscelididae or than *Tupaia*, although it is closer to the latter. The muzzle (Index II) of *Gymnura* is also narrower than that of *Tupaia* or any of the Macroscelididae except *Petrodromus* and *Elephantulus*. In the size of the olfactory chamber (Indices III, IV) *Gymnura* is by far the most primitive and still has a long narrow olfactory chamber associated with a small brain case. This would indicate that smell is probably the dominate sense in *Gymnura*, and that in all probability the olfactory

lobes of the brain are still large and well developed, a primitive mammalian condition. In *Tupaia* and the Macroscelididae the olfactory chamber is much reduced in size, while the brain case is enlarged. A further resemblance is the large size of the orbits, signifying that sight is the dominant sense with the reduction in the size of the olfactory lobes of the brain and increase in the size of the cerebrum. In all these indices *Tupaia* and the Macroscelididae agree with each other and differ from *Gymnura*.

The Macroscelididae and *Tupaia* also resemble each other more closely in the majority of the post-cranial skeletal features than either one does *Gymnura*.

In general shape the scapula of *Gymnura* (Fig. 5, F) is closest to that of *Nasilio*, although it differs from all the Macroscelididae in being more narrow with the anterior and axillary borders nearly parallel. It agrees with the Macroscelididae in having a long slender metacromion process.

The clavicle and an entepicondylar foramen are present in all, but the latter is not so prominent in *Gymnura* as in *Tupaia* and the Macroscelididae. In all of them the capitellum of the humerus is large and more or less continuous with a fairly wide trochlea. As in *Rhynchocyon* (Fig. 6) the radius and ulna of *Gymnura* and *Tupaia* are free and unfused.

In the number of adult carpals (Fig. 6) the Macroscelididae and *Tupaia* agree closely, there being nine in the former and eight or nine in the latter, depending on whether or not the scaphoid and lunar are separate. They also have the centrale free. *Gymnura*, however, lacks the centrale, and the scaphoid and lunar are fused in the adult, thus making seven carpals in all.

The centrale has no contact with the unciform in either the Macroscelididae or in *Tupaia*, but its size varies, being subequal with or larger than the trapezium in the former and the smallest bone of the carpus in the latter. The magnum of both is slightly compressed laterally. All the genera considered exhibit a contact between the lunar and the unciform, but it is very narrow in the Macroscelididae and *Gymnura*.

Rhynchocyon differs from the others in lacking the pollex which in *Tupaia* and the Macroscelidinae, but not in *Gymnura*, is slightly to moderately opposable. The third digit is the longest in all.

The outstanding feature in the pelvic girdle (Fig. 7) of the Macroscelididae and of *Tupaia* is the long symphysis formed by both the pubis and the ischium. In *Gymnura* there is no symphysis, and the opposite pubic bones are connected only by a narrow band of cartilage while the ischia are widely separated.

The tibia and fibula of *Gymnura* (Fig. 8, F) are fused distally as in the Macroscelididae, but they remain free in *Tupaia*. The third trochanter of the Macroscelididae and *Tupaia* is represented in *Gymnura* only by a ridge.

In both *Tupaia* and the Macroscelididae the astragalus (Fig. 9) is long and narrow with a high narrow trochlea having well-developed keels, the fibular one being distinctly the higher. In *Gymnura* the astragalus has a very short neck and a low broad trochlea with the tibial keel the higher. In both *Gymnura* and *Tupaia* the tibia and fibula articulate with the astragalus alone. In *Gymnura* the head of the astragalus is rounded and has a very broad contact for the navicular but none for the cuboid. The cuboid is not elongated and the cuneiforms are well developed, the first being distinctly the longest and the second the shortest. Except for the rounded head of the astragalus *Gymnura* differs in all these features from the Macroscelididae and *Tupaia*. The rounded head of the astragalus is also found in *Tupaia*.

With respect to the vertebral formula *Gymnura* has fifteen dorsal vertebrae, while *Tupaia* and the Macroscelididae have only thirteen. The last two also approach each other in the number of lumbar vertebrae, the Macroscelididae having seven-eight and *Tupaia* six-seven, although Mivart (1867, p. 294) found some specimens of *Tupaia* with five-six. *Gymnura* has four sacral vertebrae, the first two articulating with the ilium. *Tupaia* and the Macroscelididae have three sacral vertebrae, but only the first one articulates with the ilium in *Tupaia* and *Rhynchocyon*, al-

though all of them do in the Macroscelididae. All the genera are very similar in the number of dorso-lumbar vertebrae, *Gymnura* having twenty, *Tupaia* nineteen-twenty and the Macroscelididae twenty-twenty-one.

Thirteen pairs of ribs are present in *Tupaia* and the Macroscelididae, but there are fifteen in *Gymnura*. The sternum of the latter agrees with that of *Tupaia* in being composed of a manubrium, a five piece corpus and a xiphoid process. The Macroscelididae differ from this in having only three-four pieces in the body.

The conclusions from the above osteological study are that the Macroscelididae are much more closely related to the Tupaiidae than to the Erinaceidae, as represented by *Gymnura*, and hence do not support Carlsson's views.

The osteological features in which the Macroscelididae resemble *Tupaia* and *Gymnura* are tabulated below.

RESEMBLANCES OF THE MACROSCELIDIDAE TO *Tupaia*

- 1.—General shape of skull.
- 2.—Large brain case.
- 3.—Large orbits.
- 4.—Broad flat interorbital region.
- 5.—Low lambdoidal and sagittal crests.
- 6.—Inflation of occiput (Macroscelidinae).
- 7.—Large auditory bullae.
- 8.—Presence of entotympanic.
- 9.—Absence of tympanic wing on basisphenoid.
- 10.—Aperture between crura of stapes filled by bony canal.
- 11.—Lacrimal large and divided by prominent ridge into facial and orbital part; touches jugal.
- 12.—Large distinct lacrimal tubercle.
- 13.—Structure of the orbito-temporal region.
- 14.—Jugal well developed and extends back to the glenoid region.
- 15.—Palate narrows anteriorly and is fenestrated (Macroscelidinae).
- 16.—Pterygoid fossae small (*Rhynchocyoninae*).
- 17.—Long infraorbital canal (*Rhynchocyoninae*).
- 18.—Coronoid process of jaw is slender.
- 19.—Number of dorsal, lumbar and sacral vertebrae.
- 20.—Large entepicondylar foramen in humerus.
- 21.—Nine carpals (some *Tupaia*).
- 22.—Scaphoid and lunar separate (some *Tupaia*).
- 23.—Centrale free and has no contact with the unciform.
- 24.—Magnum slightly compressed laterally.
- 25.—Long pelvic symphysis formed by both pubis and ischium.
- 26.—Prominent third trochanter on femur.

- 27.—Astragalus long and narrow with a high trochlea.
- 28.—Fibular keel of trochlea distinctly higher than tibial keel.
- 29.—Astragalus articulates with both the navicular by a broad facet and the cuboid by a narrow one.
- 30.—The cuneiforms are subequal in length.

RESEMBLANCES OF THE MACROSCOLIDIDAE TO *Gymnura*

- 1.—No inflation of the occiput (*Rhynchocyon*).
- 2.—No postorbital ring.
- 3.—Palate approximately the same width throughout and unfenestrated (*Rhynchocyon*).

- 4.—Pterygoid fossae large and extend forward to the posterior margin of the palate (Macroscelidinae).
- 5.—Slender zygoma (Macroscelidinae).
- 6.—Prominent suboptic foramen.
- 7.—Sphenoidal fissure and foramen rotundum combined.
- 8.—Short infraorbital canal (Macroscelidinae).
- 9.—Presence of a tympanic process of the petrosal.
- 10.—Retention of $P \frac{1}{1}$.
- 11.—Large canines (*Rhynchocyon*).
- 12.—General shape of the upper molars.
- 13.—Long slender metacromion process of scapula.

POSSIBLE LEMUROID AFFINITIES OF THE MACROSCOLIDIDAE

As noted in the introduction, it is generally accepted by zoologists that the Tupaiidae are the closest to the Primates of all the insectivores. Others, however, want to remove the Tupaiidae completely from the Insectivora and place them in the suborder Lemuroidea.

The latter conclusion, however, is not generally accepted and, in view of the close relationship between the Tupaiidae and the Macroscelididae shown above, it is

instructive to check the lemuroid osteological features of *Tupaia* with the skeleton of the Macroscelididae.

According to Gregory (1910, pp. 278-279; 1913, p. 248) and Carlsson (1922, pp. 233-238) the following are lemuroid features of the skeleton of *Tupaia*. These features have been checked with the skeleton of the Macroscelididae and for comparative purposes are presented in tabular form below.

LEMUROID FEATURES OF *Tupaia* COMPARED WITH THE MACROSCOLIDIDAE

<i>Tupaia</i>	Macroscelididae
1.—Lemuroid shape of skull	Skull shape very similar to <i>Tupaia</i>
2.—Large brain case	Large brain case
3.—Large orbits	Large orbits
4.—Orbits open widely into temporal fossae	Orbits open widely into temporal fossae
5.—Wide interorbital region	Wide interorbital region
6.—Postorbital bar	No postorbital bar; postorbital process in <i>Rhynchocyon</i>
7.—Olfactory region of skull more or less reduced	Olfactory region of skull more or less reduced
8.—Large auditory bullae	Large auditory bullae
9.—Ectotympanic enclosed within bulla forming a ring	Ectotympanic enlarged forming outer wall of bulla and tubular external auditory meatus
10.—Lacrima divided into facial and orbital part	Lacrima divided into facial and orbital part
11.—Lacrimal foramen in orbital part or in orbital rim; occasionally in facial part	Lacrimal foramen in orbital part
12.—Lacrimal and jugal in contact	Lacrimal and jugal in contact
13.—Jugal (malar) foramen present	Jugal foramen absent (present according to Weber)
14.—Supraorbital foramen present	Supraorbital foramen absent; represented by notch in <i>Rhynchocyon</i>
15.—Lemur-like structure of the orbit	Lemur-like structure of the orbit
16.—Pterygoid fossae approach the lemuroid condition	Pterygoid fossae approach the lemuroid condition
17.—Postglenoid process high	Postglenoid process high (Macroscelidinae)
18.—Foramen ovale largely hidden by bulla	Foramen ovale largely hidden by the bulla
19.—Jaw condyle high above level of the cheek teeth	Jaw condyle high above level of the cheek teeth
20.—Masseteric fossa shallow	Masseteric fossa shallow
21.—Mandibular symphysis extends back to first P	Mandibular symphysis extends back to C-P ₁

- | | |
|---|---|
| <p>22.—Mental foramen below first P
 23.—Entepicondylar foramen present
 24.—Centrale free
 25.—Lunar and unciform in contact
 26.—Magnum compressed laterally
 27.—Pollex divergent
 28.—Metacarpals and phalanges elongated
 29.—12–13 dorsal vertebrae
 30.—6–7 lumbar vertebrae

 31.—3 sacral vertebrae
 32.—Greater trochanter more proximal in position than the head of the femur
 33.—Third trochanter present
 34.—Malleoli powerfully developed
 35.—Hallux divergent

 36.—Fibular crest of trochlea higher than tibial crest
 37.—Trochlea narrow above, broad below; concavity slight
 38.—Ectal facet smaller than sustentacular
 39.—Sustentacular and navicular facets are continuous
 40.—Trochlea extends back dorsal to the ectal facet</p> | <p>Mental foramen below C–P₁
 Entepicondylar foramen present
 Centrale free
 Lunar and unciform in contact
 Magnum slightly compressed laterally
 Pollex slightly divergent (<i>Macroscelidinae</i>)
 Metacarpals and phalanges elongated
 13 dorsal vertebrae
 7 lumbar vertebrae (<i>Macroscelidinae</i>)
 8 lumbar vertebrae (<i>Rhynchocyon</i>)
 3 sacral vertebrae
 Greater trochanter more proximal in position than the head of the femur
 Third trochanter present
 Malleoli powerfully developed
 Hallux not divergent; absent in <i>Rhynchocyon</i> and <i>Petrodromus</i>
 Fibular crest of trochlea higher than tibial crest

 Trochlea narrow above, broad below; concavity deep
 Ectal facet larger than sustentacular
 Sustentacular and navicular facets are continuous (<i>Macroscelidinae</i>)
 Trochlea extends back dorsal to the ectal facet</p> |
|---|---|

From the above table it is seen that the Macroscelididae are practically identical with *Tupaia* in thirty-two of the forty lemuroid characters of the latter. In two other characters, the extent of the mandibular symphysis (21) and the position of the mental foramen (22), they are only very slightly different from *Tupaia*.

The Macroscelididae lack the supra-orbital foramen and the postorbital ring of *Tupaia*, but *Rhynchocyon* approaches these features in having a distinct supraorbital notch and a postorbital process. If the jugal foramen is present in the Macroscelididae, as Weber, according to Muller (1935, p. 251), has reported, it would increase the number of lemuroid features they share with *Tupaia* to thirty-three.

The large size of the ectal facet on the astragalus and the absence of the hallux in *Rhynchocyon* and *Petrodromus* are probably adaptive features correlated with their habits.

In the structure of the orbit-otemporal region (Fig. 14) the Macroscelididae agree with *Tupaia* and the Malagasy lemurs (Fig. 14, C) but not with the non-Malagasy lemurs (Fig. 14, D). The Macroscelididae, *Tupaia* and Malagasy lemurs all have a large orbital process on the palatine which

is in contact with the lacrimal, thus separating the maxilla from the frontal within the orbit. They also do not have the ethmoid showing in the orbital wall. In the non-Malagasy lemurs (Fig. 14, D) the orbital process of the palatine is small and does not meet the lacrimal. There is also a large os planum of the ethmoid visible within the orbit.

In the composition of the orbit the Malagasy lemurs differ from all the rest of the Primates and show, as Wood Jones (1917, p. 329) says, "a very common mammalian, but definitely non-primate, arrangement of the bony elements present in this region."

Perhaps this condition could be interpreted as the retention of a Menotyphloid character by the Malagasy lemurs, as it differs from that in *Gymnura* (Fig. 14, E) which lacks the os planum of the ethmoid but shows a broad orbital contact between the maxilla and the frontal.

A great deal of importance has been attached to the lemuroid structure of the bulla of *Tupaia*, but a comparative study of the structure of the bulla in both the Malagasy and the non-Malagasy lemurs indicates that the significance of this resemblance has been overemphasized.

The auditory bulla of *Tupaia* does re-

semble that of lemurs but so does the bulla of the Macroscelididae. The point in question is that the bulla of *Tupaia* (Fig. 15, B) is similar to that of the Malagasy lemurs (Fig. 15, C), while that of the Macroscelididae (Fig. 15, A) resembles the bulla of the non-Malagasy lemurs (Fig. 15, D).

The essential difference is that in *Tupaia* and the Malagasy lemurs the bulla is formed entirely by the entotympanic, while the ectotympanic forms a ring within the bulla. In the Macroscelididae and the non-Malagasy lemurs the entotympanic is also large and forms most of the bulla, but the ectotympanic, instead of being ring-shaped and located within the bulla, forms the outer wall of the bulla and a more or less tubular external auditory meatus. In these

respects the Macroscelididae and the non-Malagasy lemurs approach the human condition.

The conclusion from the above comparison of the Macroscelididae and *Tupaia*, with respect to their lemuroid osteological features, is that if *Tupaia*, on this basis, is placed with the lemurs the Macroscelididae should be also. This is indicated by the great resemblance between the Macroscelididae and *Tupaia*, since the features tabulated above, in which the Macroscelididae differ from the lemuroid characters of *Tupaia*, are of little significance, due to the different habitus of the former or to features in which the Macroscelididae resemble the non-Malagasy lemurs; while *Tupaia* agrees with the Malagasy lemurs.

POSSIBLE PERISSODACTYL AND ARTIODACTYL AFFINITIES OF THE MACROSCELIDIDAE

Frechkop (1931) has also wanted to separate the Macroscelididae from the Tupaiidae and believes that they show marked Ungulate affinities. He apparently uses Ungulate in its older sense and does not seem to distinguish between the Perissodactyla and the Artiodactyla.

According to him the molars of the Macroscelididae represent a specialized type found only among the Ungulates and do not show any resemblance to those of *Tupaia* as they seem to lack the double V's.

Stehlin (1906, p. 1135) believes that the quadrangular pattern in Artiodactyla molars has arisen from an original triangular pattern in an entirely different way in each of the three sections into which he divides the order. These three sections are the Hypoconifera (Dichobunidae and Elotheridae), the Cainotherids and the "Euartiodactyla."

In the hypothetical original pattern there were three main cusps (protocone, paracone and metacone) arranged in a triangle. The inner cusp was connected with each outer cusp by a crest having a small accessory cusp. According to him (1906, p. 1137) the quadritubercular molar in the "Euartiodactyla" (e.g., *Dichodon*) arose from the original pattern by the forward

migration of the inner cusp and the enlargement of the accessory cusp in the crest originally connecting the protocone with the metacone. Accordingly this fourth main cusp would really be an enlarged metaconule and not the hypocone.

If the Macroscelididae are related to the Artiodactyla their molars must be derived from the above original pattern. If this is true there must have been a loss of some of the cusps originally present. Furthermore, if we assume that the Macroscelid molar pattern is derived from the original pattern the question at once arises as to which of the three ways was followed in their case. Unfortunately, the Macroscelididae are so poorly known as fossils that at present there is no way of checking this.

Other features that Frechkop believes show Ungulate affinities are the molariform P⁴ and the orientation of the teeth in the jaw. According to him, "If we pass straight lines, following the posterior border of the teeth, to the sides of the upper jaw we see that this line forms, with the median line of the palate, an angle directed forward in *Tupaia* and backward in *Rhynchocyon* and *Elephantulus*. . . This last orientation, which accompanies bunodont molars, is found in the Ungulates."

When the above procedure was tried on my specimens the results did not agree with those of Frechkop. In *Tupaia* I found the angle formed with the mid-line of the palate was directed backward for all the teeth from P^4 - M^3 . In *Rhynchocyon* the angle varied from markedly forward in P^3 , through approximately a right angle for M^1 , to backward for M^2 . The orientation in *Elephantulus* was essentially similar.

Also, a comparison of the upper molars of *Rhynchocyon* with those of *Tapirus indicus*, as figured by Hatcher (1894, Pl. IV, fig. 3), does not support Frechkop's statements of their close resemblance, as *Rhynchocyon* completely lacks the proto-loph and metaloph characteristic of *Tapirus*. The lower molars also lack the metalophid and hypolophid and appear more like those of *Lambdaotherium*, as figured by Osborn (1907, p. 179, Fig. 168).

The Macroscelididae resemble the Perissodactyla in having molariform posterior premolars and bilobed lower molars. They differ from the Artiodactyla in not having the last lower molar trilobed.

The conclusion from the above is that the dentition of the Macroscelididae does not seem to show very marked resemblances to either the Perissodactyla or the Artiodactyla, as their teeth, particularly the upper molars, do not exhibit the lophodont or selenodont structure so characteristic of these orders. However, they do show quite close similarities to those of *Tupaia* and could easily have arisen from the *Tupaia* condition by an increase in the buccal side of the tooth and the development of a hypocone. The lower molars also are quite similar to those of *Tupaia*.

The structure of the orbito-temporal region and of the auditory bulla of the Perissodactyla and the Artiodactyla is also different from that in the Macroscelididae.

In the Perissodactyla, as represented by the horse, the orbital part of the palatine is small and forms just a minor part of the ventral orbital wall. Typically there is a small orbital contact between the frontal and the maxilla and none between the palatine and the lacrimal. However, according to Sisson (1917, p. 67), the palatine

and lacrimal are sometimes in contact as in the Macroscelididae, but such a contact would be narrow and not broad as in the latter group.

The arrangement of the foramina in this region is also different from that in the Macroscelididae. The foramen rotundum is separate from the sphenoidal fissure, and the foramen ovale, according to Sisson (1917, p. 63), is confluent with the foramen lacerum (foramen lacerum medium of Flower).

The auditory bulla of the horse is also quite different from that of the Macroscelididae and, according to Van der Klaauw (1931, p. 264), is formed entirely from the ectotympanic in the modern Equidae. In *Tapirus* and *Rhinoceros*, however, the ectotympanic forms a recessus meatus, a cylindrical external auditory meatus and (in *Rhinoceros*) the lateral wall of the bulla. In these respects they approach the Macroscelididae.

The orbito-temporal region of the Artiodactyla, as represented by the cow, also differs from that in the Macroscelididae, although it is closer to them than is the case in the horse. The lacrimal and palatine are apparently in contact, as in the Macroscelididae, so as to prevent the frontal and maxilla from meeting within the orbit. However, the cow differs from both the Macroscelididae and the horse in having the orbitosphenoid separate the frontal from contact with the palatine. The sphenoidal fissure and the foramen rotundum are combined, and the foramen ovale is separate as in the Macroscelididae.

The auditory bulla of the cow and, according to Van der Klaauw (1931, p. 265), of all modern Artiodactyla with the possible exception of the Suidae, is apparently formed entirely from the ectotympanic, a marked difference from the Macroscelididae.

The presence of an entotympanic in the Perissodactyla and in the Artiodactyla is questionable. According to Van der Klaauw (1931, pp. 283-284), a separate entotympanic is not visible in *Equus*, although it may be present, but a bony one is found in the modern *Rhinoceros* where it forms the median wall of the bulla.

The same author quotes Parker as finding a rudimentary entotympanic in *Tapirus indicus*. However, Van Kampen, according to Van der Klaauw, did not know about Parker's observation and considered it more probable that the entotympanic was fused with the petrosal and represented by the crest on its under surface.

Van der Klaauw (p. 284) also says that Parker described a few entotympanics in *Sus*, but that Van Kampen could not find them. He also states that an entotympanic has been very doubtfully reported in the foetal *Hippotamus*.

An entotympanic is thus seen to be very rare in both the Perissodactyla and the Artiodactyla, and as a consequence their auditory bulla is quite different from that of the Macroscelididae.

In lacking the posterior expansion of the nasals the Macroscelididae resemble the Artiodactyla. The absence of the alisphenoid canal is another Artiodactyla feature, but if this is present, as Muller (1935, p. 243) reports, it would be a Perissodactyla feature.

Frechkop also considers the large size of the facial part of the skull of *Rhynchocyon* as evidence of Ungulate affinities, since it is close to that of the horse. However, in the Macroscelidinae (Table V) the facial part of the skull is proportionately much shorter and quite close to that of *Tupaia*.

TABLE V

	Facial, Skull Length Index
Cow	67.5
Horse	63.7
Rhynchoconinae:	
<i>Rhynchocyon</i>	63.2
Macroscelidinae:	
<i>Petrodromus</i>	53.4
<i>Nasilio</i>	52.7
<i>Elephantulus</i>	49.0
<i>Macroscelides</i>	53.7
Tupaiaidae:	
<i>Tupaia</i>	51.3

According to Frechkop the interorbital width of the skull in the Macroscelididae attains the value of that in the Ungulates, but the interorbital width-skull length index (Table VI) shows that *Rhynchocyon* greatly exceeds both the horse and the cow

in this respect, while the Macroscelidinae are much less and close to *Tupaia*.

TABLE VI

	Interorbital Width, Skull Length Index
Cow	32.5
Horse	29.8
Rhynchoconinae:	
<i>Rhynchocyon</i>	41.0
Macroscelidinae:	
<i>Petrodromus</i>	18.6
<i>Nasilio</i>	20.9
<i>Elephantulus</i>	20.3
<i>Macroscelides</i>	22.8
Tupaiaidae:	
<i>Tupaia</i>	33.2

In the post-cranial skeleton the Macroscelididae also exhibit both Perissodactyla and Artiodactyla features. The Perissodactyla features are the presence of a third trochanter, the fact that the navicular facet on the astragalus is much larger than the cuboid facet and that the third digit is the longest in the manus and pes (except in *Petrodromus* and *Nasilio*).

The Artiodactyla features are: dorsal vertebrae thirteen (twelve-fifteen in Artiodactyla); lunar-unciform contact (Macroscelidinae); tibia and fibula fused and both articulated with the astragalus and calcaneum; pes tetradactyl in *Rhynchocyon* and *Petrodromus*.

In the possession of a caecum and the contact of the astragalus with both the navicular and the cuboid the Macroscelididae agree with both the Perissodactyla and the Artiodactyla but differ from them in having a free centrale in the carpus.

The carpus also differs from that in the Perissodactyla in having the scaphoid resting equally on the centrale and the trapezium, while the lunar rests mostly on the magnum in place of the unciform. In *Rhynchocyon* the carpus differs from that in the Artiodactyla in having no contact between the lunar and the unciform, while only a narrow one is present in the Macroscelidinae.

The astragalus of the Macroscelididae lacks the double trochlea and the large sustentacular facet characteristic of the Artiodactyla.

The conclusion from the foregoing is that

the Macroscelididae do not show any significant Perissodactyla or Artiodactyla affinities in spite of a few resemblances between them. The molar pattern, the structure of the orbito-temporal region, the for-

mation of the auditory bulla, the skull proportions, the carpus and the character of the astragalus all show important diagnostic differences from the Perissodactyla and the Artiodactyla.

SUMMARY AND CONCLUSIONS

1.—The Macroscelididae is a small family of insectivores confined to the continent of Africa. The family is divided into two subfamilies: the Rhynchocyoninae, containing the single genus *Rhynchocyon*, and the Macroscelidinae, containing the genera *Petrodromus*, *Nasilio*, *Elephantulus* and *Macroscelides*.

2.—The Macroscelididae are shown to be quite highly specialized insectivores.

3.—*Petrodromus* is the most primitive member of the family, while *Macroscelides* and *Rhynchocyon* are the most specialized, with *Nasilio* and *Elephantulus* occupying an intermediate position.

4.—In their limb proportions the Macroscelididae are intermediate in position when compared with ricochet mammals.

5.—The Macroscelididae are very poorly known as fossils but *Anagale gobiensis* Simpson from the Oligocene of Mongolia is, in many osteological features, intermediate between the Macroscelididae and the Tupaiidae and is either the common ancestor of the two families or quite close to it.

6.—Comparative osteological studies show that the Macroscelididae are much more closely related to the Tupaiidae than

to the Erinaceidae, and that the division of the Insectivora into the suborder Menotyphla, including the Macroscelididae and the Tupaiidae, in opposition to the suborder Lipotyphla, including all the remaining insectivores, is valid. This is contrary to the opinion of Carlsson.

7.—In view of the great similarity and close relationship between them the Macroscelididae and Tupaiidae should not be separated.

8.—The Macroscelididae are shown to have almost all of the lemuroid features found in *Tupaia*, the differences between them being due either to their different habitus or to features in which the Macroscelididae agree with the non-Malagasy lemurs, while *Tupaia* agrees with the Malagasy lemurs.

9.—On the basis of their lemuroid osteological characters the Macroscelididae show about as much justification for placing them with the lemurs as does *Tupaia*, and if the latter is placed with the Lemuroidea the former should be also.

10.—Comparative osteological studies do not support Frechkop's view that the Macroscelididae show significant Ungulate affinities.¹

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¹ After this paper was finished the late Dr. Glover M. Allen informed me that the genus *Gymnura* had been changed to *Echinorex*.

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