THE OSTEOLGY AND RELATIONSHIPS OF THE ELEPHANT SHREWS (MACROSCELIDIDAE)

BY FRANCIS GAYNOR EVANS

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

BY FRANCIS GAYNOR EVANS

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INTRODUCTION

The Macroselididae are a small family of insectivorous mammals confined to Africa but widespread on that continent. The family is divided into two subfamilies: the Rhynchoconyinae, containing the single genus Rhynchoconyon, and the Macroselidinae, containing the genera Petrodromus, Elephantulus, Nasilio and Macroselides. 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 Rhynchoconyon, adult males of which, according to Allen (1922, p. 22), average about 515 mm. in total length, to Elephantulus, Nasilio and Macroselides 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 Macroselididae 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
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 Tupai, 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 Zoology, 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.

<table>
<thead>
<tr>
<th>Rhynchocyon stuhlmanni claudi</th>
<th>No. 51216 A.M.N.H.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhynchocyon claudi</td>
<td>&quot; 49429 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 49444 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 49445 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 49517 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>Nasilio brachyrhyncha brachyura</td>
<td>&quot; 86551 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>Nasilio brachyrhyncha brachyura</td>
<td>&quot; 86555 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>Nasilio brachyrhyncha brachyura</td>
<td>&quot; 86557 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>Nasilio brachyrhyncha brachyura</td>
<td>&quot; 86559 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td>Nasilio brachyrhyncha brachyura</td>
<td>&quot; 86564 &quot; &quot; &quot; &quot;</td>
</tr>
</tbody>
</table>

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 Zoology.
**OSTEOLOGY OF THE MACROSCELIDIDAE**

**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 interlacrimal width (Table I, Index III) while *Rhynchocyon* is the most specialized in these features. In the Macroscelididae (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 sphenoidicum 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 Macroscelididae. *Rhynchocyon* also

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**TABLE 1**

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Museum</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dipodomys phillipsi</em></td>
<td>6310 M.C.Z.</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 6311 &quot;</td>
<td>&quot; 6312 &quot;</td>
</tr>
<tr>
<td><em>Pedetes caffer salinae</em></td>
<td>42025 A.M.N.H.</td>
<td></td>
</tr>
<tr>
<td>&quot; (no manus or pes)&quot;</td>
<td>&quot; 42057 &quot;</td>
<td>&quot; 70392 &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 54219 &quot;</td>
<td>&quot; 81747 &quot;</td>
</tr>
<tr>
<td><em>Jaculus orientalis</em></td>
<td>&quot; 70096 &quot;</td>
<td>&quot; 70004 &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 67797 &quot;</td>
<td>&quot; 55880 &quot;</td>
</tr>
<tr>
<td><em>Napaeozapus insignis insignis</em></td>
<td>&quot; 5029 &quot;</td>
<td>&quot; 67797 &quot;</td>
</tr>
<tr>
<td><em>Allactaga mongolica</em></td>
<td>&quot; 67797 &quot;</td>
<td>&quot; 55880 &quot;</td>
</tr>
<tr>
<td><em>Macropus rufus</em></td>
<td>No. 14153 A.M.N.H.</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 35186 &quot;</td>
<td>&quot; 35231 &quot;</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot; 35735 &quot;</td>
<td>&quot; 35761 &quot;</td>
</tr>
</tbody>
</table>

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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 Zoology at the University of New Hampshire.
Fig. 1. Dorsal view of the skulls of the Macroscelididae, Tupaia and Echinosorex (Gymnura). × 1/3. A, Rhynchoeyon; B, Petrodromus; C, Elephantulus; D, Nasilio; E, Macroscelides; F, Tupaia; G, Echinosorex.
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 lacrimal is 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.

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**Table I.**—Skull Measurements (mm.) and Indices (per cent)

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

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 Nasītō 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 Klauuw (1931, pp. 232, 249, 268) there are two different entotympanies: 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 Klauuw (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 Rhynchocyon.
Fig. 2. Ventral view of the skulls of the Macroscelididae, Tupina and Echinopsorix (Gymnura). X 3/4. A, Rhynchocyon; B, Petrodromus; C, Elephantopus; D, Nasito; E, Macroscelides; F, Tupina; G, Echinopsorix.
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 stylar pedicle 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 P³ 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 P₄-P⁴ in Petrodromus and Macroscelides and above M¹ 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 P₁ and P₄. In Elephantulus one of them is below the canine, and Nasilio has just one foramen which is located below P₁.
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 $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{3}{3} = 34$ or 36, while in all the Macroscelidinae, except *Nasilio* which has three lower molars, the formula is $I \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{3}{3} = 40$. According to Gregory (1910, p. 281) the Macroscelidinae are among the few insectivores retaining P $\frac{5}{5}$.

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

P1 is much smaller than the canine in Rhynchoceyon, 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 Rhynchoceyon 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-M2) are quadritubercular, subhypsodont and without cingula. P4 is completely

Fig. 4. Cheek teeth (upper left and lower right) of the Macroscelididae, Tupaia and Echinosorex (Gymnura). Circa X 1/4. A, Rhynchoceyon; B, Petrodromus; C, Elephantulus; D, Nasilio; E, Macroscelides; F, Tupaia; G, Echinosorex.
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 (P₄) belongs to the permanent set and is not merely a retained deciduous tooth. In Elephantulus and Macroscelides M₂ 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 P₁ is small, with a single large protoconid, but in Rhynchocyon it is caniniform and is the tallest tooth in the mandible. P₂ is elongated, laterally compressed and larger than P₁. There is a large protoconid, and accessory anterior and posterior cusps may also be present (Figs. 3, 4). P₃ is larger than P₂ 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 P₁ 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 P₃, which is longer antero-posteriorly than any of the molars, the talonid is the wider of the two. In Rhynchocyon (Fig. 4, A) P₄ has as a well-developed metastylid.

The molars are quadritubercular, and among my specimens only Nasilio (Fig. 4, D) had a definite paraconid on M₁. In Petrodromus (Fig. 4, B) the talonid of M₁ is a trifle wider than the trigonid, but in the other genera the two are subequal in width. M₂ is essentially the same as M₁ except that the talonid has become narrower than the trigonid. Nasilio (Fig. 4, D) differs from the other genera in having a small M₃.

In Rhynchocyon, according to Allen (1922, p. 32), the deciduous dental formula is I ½⁻¹ C ½⁻¹ P ½⁻¹ = 12 = 24. P ½⁻¹, which has no successor, does not appear until later.

The single upper incisor (I₃) 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 (P₃) erupt simultaneously. DP₁, like P₁, 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.

DP₃ 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 P₃, but in other respects the two teeth are quite similar.

DP₄ is very similar to P₄ 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 P₄ 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 DI₂ and DI₃ 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 DP₂ 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 $DP_4$. $DP_3$ is very similar to $P_3$, 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 $DI_{1-1}^{1-1} DC_{1-1}^{1-1} DP_{2-2}^{2-2} DC_{3-3}^{3-3}$ plus $P_1^1$, 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 $P_1$ is much narrower than $P_2$ and has more cusps. Deciduous $P_2$ has three main cusps ($pr, pa, me$) plus two smaller anterior cusps and a posteromedial 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 $DP_3^{3-3}$ and $DP_4^{2-2}$ develop together instead of $DP_2^{3-3}$ and $DP_3^{2-2}$ developing together. Permanent $P_1$ is the first of the premolars to develop and erupts some time before $I_1$. 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 $M_1$ develops early, but $P_2$, 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 metacromion 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 bicipital 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 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 (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). X 1. A, Rhynchocyon; B, Petrodromus; C, Macroscelides; D, Nasilio; E, Tupaia; F, Echinosorex.](image-url)
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 *Rynchocyon* and *Petrodromus* but more so in *Nasitio* 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 *Rynchocyon* and *Petrodromus* (Fig. 9, A and B) the third is markedly the longest. In *Nasitio* (Fig. 9, D), however, the first is a trifle longer than the
### Table II.—Limb Measurements (mm.) and Indices (per cent)

<table>
<thead>
<tr>
<th>Measurements and Indices</th>
<th>Rhynchocyon claudi</th>
<th>Petrodromus lordayi</th>
<th>Nasilio brachyrhyncha</th>
<th>Macroscelides brachyrhyncha</th>
<th>Tupaia belangeri</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Humerus, max. length</td>
<td>41.6</td>
<td>29.0</td>
<td>17.9</td>
<td>18.1</td>
<td>27.8</td>
</tr>
<tr>
<td>(2) Radius, max. length</td>
<td>41.6</td>
<td>41.2</td>
<td>18.9</td>
<td>21.8</td>
<td>24.6</td>
</tr>
<tr>
<td>Index I—Radio-humeral</td>
<td>100.0</td>
<td>142.1</td>
<td>105.6</td>
<td>120.4</td>
<td>88.5</td>
</tr>
<tr>
<td>(3) Metacarpal III, max. length</td>
<td>21.3</td>
<td>10.5</td>
<td>5.5</td>
<td>5.4</td>
<td>9.7</td>
</tr>
<tr>
<td>Index II—Mt. III-humeral</td>
<td>51.2</td>
<td>36.2</td>
<td>30.7</td>
<td>29.8</td>
<td>34.9</td>
</tr>
<tr>
<td>(4) Femur, max. length (gr. trochanter to medial condyle)</td>
<td>59.8</td>
<td>41.0</td>
<td>24.5</td>
<td>24.0</td>
<td>34.4</td>
</tr>
<tr>
<td>Index III—Tibio-femoral</td>
<td>122.9</td>
<td>128.3</td>
<td>129.4</td>
<td>144.6</td>
<td>102.6</td>
</tr>
<tr>
<td>(6) Metatarsal III, max. length</td>
<td>32.9</td>
<td>24.9</td>
<td>13.0</td>
<td>17.0</td>
<td>16.1</td>
</tr>
<tr>
<td>Index IV—Metars. III-femoral</td>
<td>55.0</td>
<td>60.7</td>
<td>53.6</td>
<td>70.8</td>
<td>46.8</td>
</tr>
<tr>
<td>Index V—Humero-fe-moral</td>
<td>60.6</td>
<td>70.7</td>
<td>73.1</td>
<td>75.5</td>
<td>80.8</td>
</tr>
<tr>
<td>Index VI—Intermembral</td>
<td>62.4</td>
<td>75.0</td>
<td>65.5</td>
<td>68.0</td>
<td>75.2</td>
</tr>
</tbody>
</table>

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 lumbars, three sacrals and twenty-eight caudals, while the Macroscelidinae differ in having only seven lumbars 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-
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 antclinal. 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 xiphoïd process is elongated and may be forked distally.
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.

_Nasitio, Elephantulus_ and _Macroscelides_, in spite of slight differences among themselves, 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 pseudo-ungulate habitus. In _Nasitio_ and _Macroscelides_ the shortening of the various seg-
Fig. 9. Left pes and astragalus of the Macroscelididae, Tupaia and Echinosorex (Gymnura) × 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 Macroscelididae and Ricochetal Mammals (per cent)

<table>
<thead>
<tr>
<th>Measurements and Indices</th>
<th>Macropus rufus</th>
<th>Dipodoma philippi</th>
<th>Pedetes caffer</th>
<th>Jaculus orientalis</th>
<th>Nannophractus jacquii</th>
<th>Allactaga mongolica</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Humerus, max. length</td>
<td>41.6</td>
<td>41.2</td>
<td>29.0</td>
<td>21.8</td>
<td>20.6</td>
<td>14.6</td>
</tr>
<tr>
<td>(2) Radius, max. length</td>
<td>17.9</td>
<td>18.1</td>
<td>110.2</td>
<td>165.4</td>
<td>40.6</td>
<td>16.4</td>
</tr>
<tr>
<td>Index I—Radio-humeral</td>
<td>17.3</td>
<td>18.6</td>
<td>49.0</td>
<td>42.8</td>
<td>12.3</td>
<td>18.3</td>
</tr>
<tr>
<td>(1)</td>
<td>100.0</td>
<td>142.1</td>
<td>105.6</td>
<td>120.4</td>
<td>119.0</td>
<td>87.3</td>
</tr>
<tr>
<td>(2) × 100</td>
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<td>112.7</td>
<td>107.8</td>
<td>129.8</td>
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<td></td>
</tr>
<tr>
<td>(3) Metacarpal III, max. length</td>
<td>21.3</td>
<td>10.5</td>
<td>5.5</td>
<td>25.3</td>
<td>3.9</td>
<td>7.6</td>
</tr>
<tr>
<td>Index II—MtCp. III-humeral</td>
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<td>(3) × 100</td>
<td>33.2</td>
<td>15.4</td>
<td>17.3</td>
<td>23.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(4) Femur, max. length (gr. tro-</td>
<td>59.8</td>
<td>41.0</td>
<td>24.5</td>
<td>220.0</td>
<td>34.4</td>
<td>106.6</td>
</tr>
<tr>
<td>chanter to medial condyle)</td>
<td>(4) 36.2</td>
<td>24.0</td>
<td>22.5</td>
<td>15.4</td>
<td>19.2</td>
<td>21.1</td>
</tr>
<tr>
<td>(5) Tibia, length (surf. of condyle to artic. surf. for astragalus)</td>
<td>73.5</td>
<td>52.6</td>
<td>31.7</td>
<td>395.3</td>
<td>46.8</td>
<td>127.6</td>
</tr>
<tr>
<td>Index III—Tibio-femoral</td>
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<td>30.7</td>
<td>29.8</td>
<td>34.7</td>
<td>22.3</td>
<td>23.0</td>
</tr>
<tr>
<td>(5) × 100</td>
<td>54.6</td>
<td>23.0</td>
<td>23.4</td>
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<tr>
<td>(6) Metatarsal III, max. length</td>
<td>32.9</td>
<td>24.9</td>
<td>13.0</td>
<td>17.0</td>
<td>21.8</td>
<td>45.2</td>
</tr>
<tr>
<td>Index IV—Metatars. III-femoral</td>
<td>61.5</td>
<td>60.7</td>
<td>53.6</td>
<td>70.8</td>
<td>61.3</td>
<td>42.4</td>
</tr>
<tr>
<td>(6) × 100</td>
<td>70.8</td>
<td>61.3</td>
<td>71.1</td>
<td>94.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(4)</td>
<td>65.0</td>
<td>60.7</td>
<td>71.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Index V—Humerofemoral</td>
<td>69.6</td>
<td>70.7</td>
<td>73.1</td>
<td>75.5</td>
<td>50.0</td>
<td>46.6</td>
</tr>
<tr>
<td>(1) × 100</td>
<td>75.5</td>
<td>71.1</td>
<td>71.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(4)</td>
<td>75.5</td>
<td>71.1</td>
<td>71.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### COMPARISON WITH RICOCHETAL MAMMALS

In the Macroscelididae, as in ricochetal 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.

Ricochetal 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 Macrocelididae are less specialized than all the other genera, in which this process has been carried much further.

The Macrocelididae also compare favorably with ricochetal forms in the secondary lengthening of the lower leg (Index III). None of them has so short a shank as *Pedetes*, and that of *Macrocelpes* is exceeded in length only by *Allactaga* and *Macropus*. The secondary lengthening of metatarsal III (Index IV) in the Macrocelididae more closely approaches that of some ricochetal 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 *Dipomys*, while in *Macrocelpes* it is only a little shorter than in *Napaeozapus*. All the Macrocelididae are less specialized than the ricochet forms in having a longer humerus (Index V) and foreleg (Index VI).

The Macrocelididae, 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 Macrocelididae 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 Macrocelididae" but that "as regards *Anagale* itself, it is seen that it is much closer to the Tupaiidae than to the Macrocelididae 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 Macrocelididae.

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

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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 fl "
tened zygoma is essentially the same as in
*Rhynchocyon*. The jugal, which forms an
essential part of the zygoma, is well de-
veloped and extends back to the glenoid
region but lacks the facial expansion it ex-
hbits in *Rhynchocyon*. The jugal and
the postorbital ring of bone seen in *Tupaia*
are also absent. In the presence of a jugal-lacrimal contact and the absence
of one between the maxilla and the squa-
mosal *Anagale* resembles both *Rhynchocyon*
and *Tupaia*.

In the small facial expansion of the lacri-
mal *Anagale* approaches the Macroscelid-
inae 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-
momal is essentially the same as in *Rhyn-
chocyon*, 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

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**Fig. 10.** Dorsal view of skulls of *Rhynchocyon, Anagale* (redrawn from Simpson, tip of snout re-

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both the Macroscelididae and the Tup-
aiidae.

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 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 entotympanic 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 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 Macroscelidae.

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 Petrodromus but is smaller than the rest of the Macroscelidae 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 Macrotarsidae

<table>
<thead>
<tr>
<th>Measurements and Indices</th>
<th>Tupaia belangeri</th>
<th>Anagale gobienensis</th>
<th>Rhynchocyon claudi</th>
<th>Petrodromus tordayi</th>
<th>Nasilis brachyrrhyncha</th>
<th>Elephantulus renatus</th>
<th>Macroscelides roezli</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Skull, total length pmx.-condyle</td>
<td>44.5</td>
<td>69.3e*</td>
<td>62.1</td>
<td>48.6</td>
<td>31.3</td>
<td>33.0</td>
<td>30.8</td>
</tr>
<tr>
<td>(2) Skull, max. bizygomatic width</td>
<td>23.1</td>
<td>40.8</td>
<td>35.7</td>
<td>25.3</td>
<td>18.3</td>
<td>19.3</td>
<td>19.4</td>
</tr>
<tr>
<td>Index I—Rel. bizyg. width</td>
<td>51.9</td>
<td>58.8e</td>
<td>57.5</td>
<td>52.3</td>
<td>58.4</td>
<td>58.5</td>
<td>62.9</td>
</tr>
<tr>
<td>(3) Face, preorb. length (ant. orbital rim to pmx. tip)</td>
<td>20.6</td>
<td>38.0e</td>
<td>36.8</td>
<td>24.6</td>
<td>15.2</td>
<td>14.3</td>
<td>15.2</td>
</tr>
<tr>
<td>Index II—Face length</td>
<td>46.2</td>
<td>54.8e</td>
<td>59.3</td>
<td>50.6</td>
<td>48.5</td>
<td>43.4</td>
<td>49.3</td>
</tr>
<tr>
<td>(4) Preorb. breadth (across lac. tuber)</td>
<td>15.7</td>
<td>32.3</td>
<td>30.6</td>
<td>14.9</td>
<td>13.0</td>
<td>13.4</td>
<td>14.0</td>
</tr>
<tr>
<td>(5) Cranium = (1) — (3) Cranial length</td>
<td>35.2</td>
<td>46.5</td>
<td>49.3</td>
<td>30.6</td>
<td>41.6</td>
<td>40.5</td>
<td>45.4</td>
</tr>
<tr>
<td>Index IV—Least parietal width</td>
<td>14.8</td>
<td>21.6</td>
<td>18.3</td>
<td>9.6</td>
<td>7.8</td>
<td>8.3</td>
<td>7.0</td>
</tr>
<tr>
<td>(6) Least parietal width</td>
<td>33.2</td>
<td>51.1</td>
<td>29.5</td>
<td>19.8</td>
<td>24.8</td>
<td>24.9</td>
<td>22.7</td>
</tr>
<tr>
<td>(7) Greatest parietal width</td>
<td>18.0</td>
<td>28.8</td>
<td>30.8</td>
<td>18.7</td>
<td>13.9</td>
<td>15.1</td>
<td>14.7</td>
</tr>
<tr>
<td>Index VI—</td>
<td>40.4</td>
<td>41.5</td>
<td>49.6</td>
<td>38.5</td>
<td>44.4</td>
<td>45.7</td>
<td>47.7</td>
</tr>
<tr>
<td>(8) Tympl. bulla, max. length</td>
<td>8.4</td>
<td>10.0</td>
<td>10.6</td>
<td>6.9</td>
<td>5.7</td>
<td>6.6</td>
<td>5.9</td>
</tr>
<tr>
<td>Index VII—</td>
<td>18.8</td>
<td>14.4</td>
<td>17.0</td>
<td>14.2</td>
<td>18.2</td>
<td>20.0</td>
<td>19.1</td>
</tr>
</tbody>
</table>

* e = 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 P\(^3\). 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 \(2 \times 3^1 \times 4^2 \times 3 = 44\), is closer to that of Tupaia \((2 \times 3^2 = 38)\) than to that of Rhynchocyon \((1^2 \times 3^2 = 36)\). Anagale is thus seen to have the complete primitive placental formula.

According to Simpson (1931, p. 2) \(1^i\), if present, was probably small and well separated from the corresponding tooth on the other side. \(1^3\) is small, styliform, single-rooted, with an unexpanded crown and es-
Fig. 12. Cheek teeth (upper left and lower right) of Rhynchocyon, Anagale and Tupaia. X 5. 
A, Rhynchocyon; B, Anagale; C, Tupaia.

sententially the same as its homologue in Tupaia. Judging from the alevoli for I\(^1\) 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 P2 in the two former genera and only to P3 in Tupaia. However, with regard to the number and arrangement of the cusps none of the premolars is so completely molariform as P4 in Rhynchocyon. Each has a large paracone, preceded and followed by slight basal cusps, and a small protocone. Simpson (1931, p. 2) also found evidence of a fourth cusp, an incipient hypocone or a prominent metaconule, on P4. The premolars are thus closer in some respects to the Rhynchocyon condition than to Tupaia, in which only P4 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 to subdivide the inner half of M1-2 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 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 M1, M2 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 Tupaioid characters, the incisors, canines and first three premolars exhibiting the latter. P4,
however, is more like the deciduous P₄ of *Tupaia*, as figured by Butler (1939, p. 27), in showing marked traces of the tubulo-sectorial pattern, than it is like the permanent P₄. In this respect it is more like P₄ of *Rhynchocyon* which has a well-developed tubulo-sectorial pattern. M₁ and M₃ 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 quadrato form of the crown of M₁, M₂, 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 tubulo-sectorial pattern, although the size and position of the paraconid cannot be determined with certainty. In this respect M₁ and M₂ differ from those in *Tupaia*, which exhibit a completely developed tubulo-sectorial pattern and approach the *Rhynchocyon* condition in which there is a tendency, particularly on M₃, to have the paraconid reduced or absent. In the presence of an M₃ *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 Tupaiidae 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 parietales 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 P₄.
17.—P₄ 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.—P₄ more like that of Rhynchocyon.
21.—M₁-₃ 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 Tupaiidae**

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 Tupaiidae.
8.—Character of the upper incisors and canines.
9.—General shape of upper molars.
10.—Presence of M₂⁻.
11.—Lower incisors, canines and first three premolars resemble those of Tupaiidae.
12.—P₃ more like DP₄ than P₄ of Tupaiidae.
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 Macroscelididae and the Tupaiidae**

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

2.—Broad flat inter orbital region.
3.—Large orbits.
4.—Large auditory bullae.
5.—Small facial expansion of the lacrimal (as in the Macroscelididae and Tupaiidae).
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 Macroscelididae and Tupaiidae.
13.—Palatines and pterygoids form a sharp ridge running back almost to the bulla.
14.—Small external pterygoid fossae as in Rhynchocyon and Tupaiidae.
15.—Long infraorbital canal as in Rhynchocyon and Tupaiidae.
16.—The optic, sphenopalatine, ovale, postglenoid, stylo mastoid, 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 Macroscelididae with Gymnura and Tupaiia**

As stated in the introduction, the Macroscelididae and the Tupaiidae are commonly grouped together in the suborder Menotyphla, in opposition to the Lipo typhla 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 Insectivora 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 Tupaiia 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 palate 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 diagnostically 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 palate. 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, Echinosorex (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-
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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 Tupaiâ 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 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 Tupaiâ 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 (Tupaiâ) by the entotympanic, an element completely absent in Gymnura and other Lipotyphla.

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 entotympanic is also variously de-

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

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 Tupaoidae and the Macroscelididae resemble 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 Tupaoidae 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
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 *Rhinchoceylon* 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 *Rhinchoceylon* the infraorbital canal is long, but *Gymnura* agrees with the Macroscelididae 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 Tupaianae, the Macroscelidinae and the Gymnurinae, but I did not find it in the Macroscelididae.

The supraorbital and malar (jugal) foramina of *Tupaia* are absent in both the Macroscelididae and *Gymnura*. *Rhinchoceylon*, 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 *Rhinchoceylon*. 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 *Rhinchoceylon* but is well developed and more or less hook-like in the other genera. *Gymnura* has a single large mental foramen below P₃, while the others usually have two rather small ones, the first below the canine or P₁ and the second below P₃ or P₄.

With regard to the number of permanent teeth *Gymnura* is the most primitive and retains the complete placental formula (I₂/₃ C₁/₃ P₄/₃ M₃/₃) with 44 teeth. The other genera, however, exhibit various degrees of reduction in the number of permanent teeth. All the Macroscelidinae, except *Nasílio* which retains M₃, have 40 teeth (I₂/₃ C₁/₃ P₄/₃ M₃/₃), while *Tupaia* has 38 (I₂/₃ C₁/₃ P₄/₃ M₃/₃). *Rhinchoceylon* is the most specialized of all, having only 36 or 34 (I₂/₃ C₁/₃ P₄/₃ M₃/₃) 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 P₄ and in the loss, except in *Nasílio*, of M₃. *Nasílio* 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 P₄, 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 Macroscelididae, *Tupaia* and *Gymnura* agree in having the first upper incisor enlarged, but *Rhynchoceyon* has very small upper incisors which may be lost in old age. In both *Gymnura* and *Rhynchoceyon* 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 P₄, while *Tupaia* and *Gymnura* do not. *Tupaia* differs from the others in the loss of P₃ and in having quite procumbent lower incisors. *Gymnura* is the only one having a large lower canine. *Rhynchoceyon* 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 P₁.

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 *Rhynchoceyon*.

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 dominant 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 *Nasitio*, 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 trochea. As in *Rhynchoceyon* (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 sub-equal 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 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, although all of them do in the Macroscelidinae. 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 Tupaia 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.
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.
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.
22. Scaphoid and lunar separate (some Tupaia).
23. Centrale free and has no contact with the uniform.
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 trochea.
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 Macroscelididae to Gymnura
1.—No inflation of the occiput (Rhynchoeyon).
2.—No postorbital ring.
3.—Palate approximately the same width throughout and unfenestrated (Rhynchoeyon).

POSSIBLE LEMUROID AFFINITIES OF THE MACROSCELIDIDAE

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 Carlssen (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 MACROSCELIDIDAE

Tupaia

1.—Lemuroid shape of skull
2.—Large brain case
3.—Large orbits
4.—Orbits open widely into temporal fossae
5.—Wide interorbital region
6.—Postorbital bar
7.—Olfactory region of skull more or less reduced
8.—Large auditory bullae
9.—Ectotympanic enclosed within bulla forming a ring
10.—Lacral divided into facial and orbital part
11.—Lacral foramen in orbital part or in orbital rim; occasionally in facial part
12.—Lacral and jugal in contact
13.—Jugal (malar) foramen present

14.—Supraorbital foramen present
15.—Lemur-like structure of the orbit
16.—Pterygoid fossae approach the lemuroid condition
17.—Postglenoid process high
18.—Foramen ovale largely hidden by bulla
19.—Jaw condyle high above level of the cheek teeth
20.—Masseteric fossa shallow
21.—Mandibular symphysis extends back to first P

Macroscelididae

Skull shape very similar to Tupaia
Large brain case
Large orbits
Orbits open widely into temporal fossae
Wide interorbital region
No postorbital bar; postorbital process in Rhynchoeyon
Olfactory region of skull more or less reduced
Large auditory bullae
Ectotympanic enlarged forming outer wall of bulla and tubular external auditory meatus
Lacral divided into facial and orbital part
Lacral foramen in orbital part

Lacral and jugal in contact
Jugal foramen absent (present according to Weber)
Supraorbital foramen absent; represented by notch in Rhynchoeyon
Lemur-like structure of the orbit
Pterygoid fossae approach the lemuroid condition
Postglenoid process high (Macroscelidinae)
Foramen ovale largely hidden by the bulla
Jaw condyle high above level of the cheek teeth
Masseteric fossa shallow
Mandibular symphysis extends back to C–P.
22.—Mental foramen below first P
23.—Entepicondylar foramen present
24.—Centrale free
25.—Lunar and uniciform 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

Mental foramen below C–P; Entepicondylar foramen present Centrale free Lunar and uniciform in contact Magnum slightly compressed laterally Pollex slightly divergent (Macroscelididae) Metacarpals and phalanges elongated 13 dorsal vertebrae 7 lumbar vertebrae (Macroscelidinae) 8 lumbar vertebrae (Rhynchocyon) 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 Rhynchocyon and Petrodromus 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 (Macroscelidinae) Trochlea extends back dorsal to the ectal facet

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 supraorbital 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 entotympanic 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 entotympanic, 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 lemurioid 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 lemurioid 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 Tupaiaidae 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 Hypoconiferia (Dichobunidae and Elotheridae), the Cainotheriids 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 quadrutubercular 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 Rhynchoceyon 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 P₄–M². In *Rhinchoceyon* the angle varied from markedly forward in P₃, through approximately a right angle for M₁, to backward for M². The orientation in *Elephantulus* was essentially similar.

Also, a comparison of the upper molars of *Rhinchoceyon* 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 *Rhinchoceyon* completely lacks the protoloph and metaloph characteristic of *Tapirus*. The lower molars also lack the metalophid and hypolophid and appear more like those of *Lambdotherium*, 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.

Frecikop 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

<table>
<thead>
<tr>
<th></th>
<th>Facial, Skull Length Index</th>
</tr>
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<tbody>
<tr>
<td>Cow</td>
<td>67.5</td>
</tr>
<tr>
<td>Horse</td>
<td>63.7</td>
</tr>
<tr>
<td>Rhynchocyoninae:</td>
<td></td>
</tr>
<tr>
<td><em>Rhynchocyon</em></td>
<td>63.2</td>
</tr>
<tr>
<td>Macroscelidinae:</td>
<td></td>
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<tr>
<td><em>Petodromus</em></td>
<td>53.4</td>
</tr>
<tr>
<td><em>Nasillo</em></td>
<td>52.7</td>
</tr>
<tr>
<td><em>Elephantulus</em></td>
<td>49.0</td>
</tr>
<tr>
<td><em>Macrocelides</em></td>
<td>53.7</td>
</tr>
<tr>
<td>Tupaíidae:</td>
<td></td>
</tr>
<tr>
<td><em>Tupaia</em></td>
<td>51.3</td>
</tr>
</tbody>
</table>

According to Frecikop 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

<table>
<thead>
<tr>
<th></th>
<th>Interorbital Width, Skull Length Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cow</td>
<td>32.5</td>
</tr>
<tr>
<td>Horse</td>
<td>29.8</td>
</tr>
<tr>
<td>Rhynchocyoninae:</td>
<td></td>
</tr>
<tr>
<td><em>Rhynchocyon</em></td>
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<tr>
<td>Macroscelidinae:</td>
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<tr>
<td><em>Petodromus</em></td>
<td>18.6</td>
</tr>
<tr>
<td><em>Nasillo</em></td>
<td>20.9</td>
</tr>
<tr>
<td><em>Elephantulus</em></td>
<td>20.3</td>
</tr>
<tr>
<td><em>Macrocelides</em></td>
<td>22.8</td>
</tr>
<tr>
<td>Tupaíidae:</td>
<td></td>
</tr>
<tr>
<td><em>Tupaia</em></td>
<td>33.2</td>
</tr>
</tbody>
</table>

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 *Petodromus* and *Nasillo*).

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 *Petodromus*.

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 Macruncelididae 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 formation 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 Macruncelididae 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 Macruncelidinae, containing the genera Petrodromus, Nasitio, Elephasnlus and Macruncelides.

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

3.—Petrodromus is the most primitive member of the family, while Macruncelides and Rhynchocyon are the most specialized, with Nasitio and Elephasnlus occupying an intermediate position.

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

5.—The Macruncelididae are very poorly known as fossils but Anagale gobiensis Simpson from the Oligocene of Mongolia is, in many osteological features, intermediate between the Macruncelididae 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 Macruncelididae are much more closely related to the Tupaiidae than to the Erinaceidae, and that the division of the Insectivora into the suborder Meso-
typhla, including the Macruncelididae and the Tupaiidae, in opposition to the sub-
order 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 Macruncelididae and Tupaiidae should not be separated.

8.—The Macruncelididae 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 Macruncelididae agree with the non-Malagasy lemurs, while Tupaia agrees with the Malagasy lemurs.

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

10.—Comparative osteological studies do not support Frechel's view that the Macruncelididae show significant Ungulate affinities.

BIBLIOGRAPHY

ALLEN, J. A.

BROOM, R.

BUTLER, P. M.
1939. Studies of the mammalian dentition.—Differentiation of the post-canine den-

CARLSSON, ALBERTINA
1909. Die Macruncelididae und ihre Bezie-
400.

1922. Ueber die Tupaiidae und ihre Bezie-

CLARK, W. E. LE GROS

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

Doran, H. G.

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