

A COMPARISON OF THE OSTEOLOGY OF THE JERBOAS AND JUMPING MICE.

By MARCUS W. LYON JR.,

Aid, Division of Mammals.

The forms considered in the present paper are those that have usually been classed, especially recently, as a family of rodents under the name *Dipodidae*, as has been done by Mr. Thomas in his paper "On the Genera of Rodents." While there may be strong grounds for such a classification and for the association of the six genera, *Sminthus*, *Zapus*,¹ *Dipus*, *Alactaga*, *Platysercomys*, and *Euchoreutes*, of which the first two are each usually put in a separate subfamily; yet the limited material at hand is sufficient to show strong osteological affinities between *Zapus* and *Sminthus* which has not usually been recognized and which places them in contrast to the rest of the group.

The writer has had for comparison complete skeletons of *Zapus* and an Egyptian *Dipus* in the United States National Museum, two skeletons of different species of *Alactaga* in the American Museum of Natural History, kindly placed at his disposal by Dr. J. A. Allen, and several odd skulls of *Zapus*, *Dipus*, and *Alactaga*, as well as the skin and skull of the type of *Sminthus flavus* in the National Museum.

Zapus and *Dipus* represent pronounced types, and for that reason, and because of the more complete material available, are compared at some length.

The vertebral column, with the exception of the cervical region, is essentially the same in each genus: the neck is short and weak; the dorsal vertebrae (twelve) present no peculiarities; the lumbar vertebrae (seven), especially the posterior ones, are built on a heavy plan with largely developed neural and anteriorly directed transverse proc-

¹This genus has been separated into three subgenera by Mr. Preble, North American Fauna No. 15, and recently Mr. Gerrit S. Miller, jr., Preliminary List of New York Mammals, Bulletin New York State Museum, VI, 1899, pp. 275, 330-331, has raised the subgenus *Napaeozapus* to generic rank. It differs from true *Zapus* only in the absence of the minute upper premolars. Doubtless in time many of the subgenera in the other genera will be thus raised to generic rank.

esses. Four vertebræ form the sacrum, which is of the same form in each, and like that of the *Muridae*. The caudal series is much longer than all the preceding portions of the column taken together; *Zapus* has the greater number of vertebræ—about thirty-six (there is some variation in different skeletons)—and the skeleton of *Dipus* shows twenty-eight.

The atlas is a large ring, essentially the same in each genus, but the second cervical or axis shows considerable differences in the two genera.

In *Zapus* it is well developed and entirely free from the remaining five distinct vertebræ behind, as well as from the axis in front.

In *Zapus* atlas and axis are entirely free and articulate in the usual manner.

In *Dipus* the axis and the four succeeding vertebræ are completely fused into one large compound "axis," with a large compound neural spine which shows no signs of segmentation. The fused centrum does show signs of segmentation, however.

In *Dipus* atlas and axis, free dorsally and laterally only, below they are fused into one piece.

The seventh cervical is free from the rest of the series in each case. The pectoral arch presents a few differences.

In *Zapus* the clavicle is longer, slenderer, and uniformly curved, convex outwardly.

Scapula with the vertebral border curving into the anterior border, a shape usually seen in the *Muridae*. The suprascapular and infrascapular fossæ are about equal in size.

In *Dipus*, clavicle stouter and heavier and somewhat in the shape of an italic *f*.

Scapula with an almost straight vertebral border, which does not slope gradually into the anterior border. The suprascapular is much smaller than the infrascapular fossa.

The anterior limbs present no noticeable differences aside from relative proportions.

The fore limb of *Zapus* is about one-half the hind limb, or about three-quarters the dorso-lumbar series of vertebræ.

The fore limb of *Dipus* is about one-quarter the hind limb, or about two-thirds of the dorso-lumbar series of vertebræ.

The pelvis shows no differences.

The hind limbs show marked differences, both as regards relative size and the number of elements in them. The ratio of the lengths of the different segments of the limbs to the total length of the leg is practically the same in each, but—

Zapus has shorter legs, the dorso-lumbar series of vertebræ being about two-thirds the length of the hind limb.

Dipus has longer legs, the dorso-lumbar series of vertebræ being about one-third the total length of the limb.

The femur is similar in each, but *Zapus* has a triangular projection (third trochanter) on the upper outer side, which, commonly found in the *Muridae*, is lacking in *Dipus*.

The tibia is essentially the same in each, though *Dipus* has a larger crest in front.

The fibula is slender, long and distinct above, as usual in the Myomorphs, but fuses firmly with the tibia below, a little above its middle in *Dipus* and about as far below the middle in *Zapus*.

The tarsus is composed of the same elements in each genus, but is differently arranged in each, as—

Zapus has the anterior nonarticular part of the astragalus rather elongated, thus pushing the navicular forward, so that the outer side is in contact with the cuboid.

In *Zapus* the internal cuneiform is not much elongated and ends in an articular surface for the first metatarsal.

Dipus has the corresponding part of the astragalus shortened, so that the navicular appears somewhat shut off from the cuboid.

In *Dipus* the internal cuneiform is disproportionately long and lies close against the second metatarsal, ending in a thinned extremity.

The metatarsal bones show striking differences.

In *Zapus* they are five in number, elongated and separate, the lateral ones being subequal, but decidedly shorter than the three central ones. Each metatarsal bears a digit.

All the digits have three phalanges except the innermost, which bears but two as usual.

The three middle digits have the relative proportions seen in *Dipus*, a slightly longer median one and two subequal lateral ones. The innermost or first digit, hallux, reaches only as far as the metatarsophalangeal articulation of the middle toes, and the first phalanx of the outer or fifth toe reaches the same point.

In *Dipus* there is but one long rounded bone, "cannon" bone, trifid at its distal extremity, where it presents three articulating surfaces for the three digits. It is to be regarded as a compound bone composed of three fused metatarsals.

The two lateral digits are subequal and but little shorter than the middle one. Each is composed of three phalanges. There is just a trace of metatarsal five, on the outer posterior part of the "cannon" bone.

The skulls, as a whole, show very little resemblance to one another, points of community being found in the maxillo-zygomatic region only. The skulls of the *Dipodidae* (*Dipus*, *Alactaga*, *Platysercomys*, *Euchoreutes*, *Sminthus*, and *Zapus*) are characterized chiefly by the great development of the antorbital foramen, large and rounded and with a more or less separate canal for the transmission of the superior maxillary division of the trigeminal nerve. The malar consists of a more or less horizontal portion articulating with the squamosal posteriorly and with the maxilla anteriorly, and a large more or less vertical portion, the anterior edge of which is in contact with the maxilla, the posterior edge free and forming the anterior boundary of the orbit, while the superior end of the vertical part is in contact with the lachrymal. But these common characters present several important differences in the two genera.

In *Zapus* the skull has a decided murine aspect, long and slender, with an unexpanded brain-case, no mastoid bullæ, and the zygoma sloping downward and backward from the maxilla.

The palatal and pterygoid regions are quite different in the two genera.

In *Zapus* the palate bones are much shortened posteriorly, the free edge concave and ending on a line with the last molar teeth. It shows exactly the same condition as is found in *Mus*.

The pterygoids have the usual form and proportions seen in *Mus*.

In *Zapus* the external pterygoid plate assumes a more horizontal position and longitudinal direction, as in *Mus*.

Between the external plate (a process of the alisphenoid) and the internal pterygoid plate (the true pterygoid bone) is a shallow fossa, entirely destitute of a floor and of the same form as is found in *Mus*.

The tympanic bones are of similar form and position in each genus, triangular in outline and placed more transversely than longitudinally, as against the position in the *Muridae*. They are each inflated to form bullæ, which are—

smaller in *Zapus*, not approaching the median line, with the apices free from the basisphenoid. The inner edges abut closely against the basioccipital, so that no vacuities are formed.

The mastoid portion of the petrotic is not abnormally enlarged in *Zapus*, does not overcrowd any of the other bones, and has a form and position very similar to *Mus*.

The squamosal in *Zapus* is a thin and expanded bone, with its antero-posterior

In *Dipus* the skull has no murine aspect whatever; it is broad and heavy, much expanded behind, with the mastoid bones inflated as large as the true bullæ and the outer border of the antorbital foramen standing out in wing-like projections and sloping downward and slightly forward.

In *Dipus* the palate is much more elongated and produced posteriorly to a considerable distance behind the last molars and ends in a blunted projecting spine.

The greater posterior length of the bony palate makes the pterygoids correspondingly shorter.

In *Dipus* the external pterygoid plate is more vertical and more transversely placed.

Between the external and internal pterygoid plates is a deep and conspicuous fossa, running forward and being floored by the posterior lateral portions of the bony palate and having for its roof the alisphenoid. It is a fossa on the order of that seen in *Microtus*.

larger in *Dipus*, nearer the median line, and the apex of each is definitely fused to the basisphenoid. Between their inner edges and the basioccipital are large vacuities.

The mastoid portion of the petrotic is greatly inflated in *Dipus* and presents almost as much surface on the posterior part of the skull as the tympanic bulla does on the ventral surface. The two portions push inward to such an extent as to encroach upon the supraoccipital and render that bone correspondingly narrow. They swell out laterally and superiorly, so that a portion is seen above the tympanic and between a posterior process of the squamosal and the parietal and supraoccipital.

The squamosal in *Dipus* is a compact and much contracted bone, with its dorso-

diameter greater than its dorso-ventral, and is of the same type as is found in the *Murida*.

The zygomatic process of the squamosal much expanded at its origin *curves* decidedly downward. This is in accordance with its higher origin from the bone.

The zygomatic region shows several differences. That of *Dipus* is apparently an extreme type, between which and *Mus*, *Zapus* seems to be somewhat intermediate. In *Mus* and other murines, both roots of the zygomatic process of the maxilla (saying that there is an upper root above the antorbital foramen and a lower root below it) arise one directly above the other. This condition holds—

in *Zapus*, where the lower root arises just in front of the premolar and the upper root about on a line directly above. This condition causes the anterior part of the zygomatic arch to slope from above downward and backward.

Zapus has an almost triangular malar, which fits into the obtuse angle in the zygomatic process of the maxilla. The lower posterior angle of the malar is attenuated into a slender process going backward to the squamosal.

The antorbital foramen in *Zapus* is more nearly elliptical, the major axis of the ellipse inclining outward from above downward.

At the lower inner corner of this foramen is a separate canal for the transmission of the second division of the fifth nerve, formed by a thin plate of bone arising from the lower root of the zygomatic process and abutting against the outer surface of the maxilla.

In *Zapus* the line of contact of this thin plate with the maxilla is always evident, and very often the plate fails to meet the side of the maxilla.

The wall of the orbito-temporal fossa in *Zapus* shows a condition such as is found in *Mus* and the *Murida* generally, with all the bones ossified and in close approximation to one another.

The incisor teeth in both genera are short and curved backward after the manner of the *Murida*. Each tooth is traversed by a groove

ventral diameter much greater than its antero-posterior. Its shape and position are difficult to describe, and are best seen in the figure.

The zygomatic process of the squamosal comes out almost horizontally, *sloping* a little downward. This is in accordance with its lower origin from the bone.

but in *Dipus* the upper root comes off at a considerable distance posterior to a point directly above the lower root. This condition causes the anterior part of the zygomatic arch to slope downward and forward.

Dipus has a biradiate malar, the vertical part of which is much expanded laterally and fits into a right angle in the maxilla. The horizontal part is slender and runs backward to meet the squamosal.

The antorbital foramen in *Dipus* is more nearly ovoid, and the long axis inclines slightly inward from above downward.

In *Dipus* this plate is completely ankylosed and the line of fusion obliterated.

In *Dipus* the wall of this fossa shows quite a deficiency in ossification. The optic foramina are unusually large. Just behind the orbito-sphenoid is a large crescent-shaped vacuity bounded in front by the orbito-sphenoid and the orbital plate of the frontal; above and behind, by the squamosal; and below, by the alisphenoid.

in its anterior face. Each genus has three upper molars on a side and as many below, with the enamel thrown into folds, which are more complex in *Zapus*. *Zapus* has a small upper premolar, but in the genus *Nyctezapus* this tooth is entirely wanting. The premolar is lacking in *Dipus*.

The lower jaw of *Zapus* is much deeper behind and has a well developed coronoid process almost equaling in size the condyloid process. The sigmoid notch is correspondingly deep and pronounced.

Scarcely any prominence can be seen in *Zapus* corresponding to the covering of the root of the lower incisor.

The angle of the lower jaw in *Zapus* is deepened, with the lower border turned inward, and is not perforated by a foramen.

The lower jaw of *Dipus* is shallow behind and with the coronoid process scarcely at all developed, with a corresponding diminution of the sigmoid notch.

The cap covering the root of the lower incisor forms a prominent projection beneath the condyloid process in *Dipus*.

The angle of the lower jaw in *Dipus* is shallow and perforated by a large foramen.

Alactaga very closely resembles *Dipus* and differs from *Zapus* in essentially the same points that *Dipus* does. Its chief differences from *Dipus* are the scarcely inflated mastoid bullæ and the incomplete foramen for the nerve at the lower inner angle of the antorbital foramen. The vertical part of the malar is not so greatly expanded laterally and the audital bullæ are less inflated. *Alactaga* has the "cannon" bone of *Dipus*, but on either side of it is a small non-functional toe, consisting of a metatarsal and a digit. The cervical vertebræ show a tendency toward consolidation, but not that complete fusion found in *Dipus*.

In *Alactaga* the incisors are ungrooved and are not recurved as in *Dipus*, but project more forward, presenting an appearance seen in the Hares. A small premolar is present. The molars have a more complex enamel pattern.

In nearly all these respects *Dipus* is seen to be a much more specialized type. Both *Dipus* and *Alactaga* share nearly everything in common, aside from greater specialization, and are placed in strong contrast to *Zapus*.

*Euchoreutes*¹ is an animal with the foot structure of *Alactaga* and a skull on the *Dipus-Alactaga* type, but appearing more slender and with greatly enlarged bullæ. In the structure of its zygomatic arch, as well as in its narrower proportions, it approaches slightly the type of skull seen in *Zapus* and *Sminthus*. "The zygoma is very weak and thin, and the vertical portion, which separates the optic from the antorbital foramen, is also very thin and slopes from above downward posteriorly (as in *Zapus*, *Sminthus*, and the *Muridae*), while in *Alactaga* the corresponding part of the zygoma is either vertical or anteriorly

¹ From the description and figures, Selater, Proc. Zool. Soc., London, 1890, pp. 610-613.

directed. * * * There is, as in *Dipus*, a separate canal at the base of the foramen for the exit of the nerve."¹

The skull of *Sminthus* very closely approaches that of *Zapus*, and it is hard to see how Alston, in his arrangement of the Rodents, could have considered it as an aberrant member of the family *Muridae*, and *Zapus*, *Dipus*, etc., as forming the *Dipodidae*.

The structure of the zygomatic arch and the shape of antorbital foramen is almost precisely the same as are these structures in *Zapus*. The latter has a slightly wider malar and the separate passage for the nerve is a little more marked. The palates are of the same style, but the posterior free edge has a median spine in *Sminthus*. The only really striking differences are in the teeth. The upper incisors of *Sminthus* are plain, and the molars (there is also a small premolar) do not have the enamel in the same pattern, but raised up into cusp-like prominences arranged in pairs. While no skeleton is available, a careful examination of the skin reveals the fact that the hind feet are of similar form to those of *Zapus*—at least with respect to freedom of metatarsals, number of digits and phalanges.

Pedetes has often been classed with the *Dipodidae*, but recently² it has been shown to possess many hystricomorph affinities, and Thomas has placed it in that group of Rodents under the family *Pedetidae*.

Dr. Coues, in *Monographs of North American Rodentia*, and Dr. Gill, in the *Arrangement of the Families of Mammalia*, put *Zapus* in a separate family from that of *Dipus* and *Alactaga*. It is inferred that *Sminthus* went to the *Muridae*. It would be in strict accordance with the facts, however, to associate *Zapus* and *Sminthus* in one group, following Winge, as the family *Zapodidae*; and *Dipus*, *Alactaga*, *Platysercomys*, and *Euchoreutes* in an equivalent group as the family *Dipodidae*.

The only pronounced common feature of the two families is the structure of the zygomatic arch and antorbital foramen. They all present the rare condition of a lachrymo-malar articulation. The arch has the most murine shape in *Sminthus*; *Zapus* is a shade further away; *Euchoreutes* shows a condition further removed, but on a skull of otherwise *Dipus* structure; *Alactaga* is much further removed, and *Dipus* still more so from the murine form.

The variations from a murine type of skull are entirely correlated with variations from a murine type of metatarsus. The *Zapus-Sminthus* group with the most generalized skull has the most generalized foot with the free metatarsals. We pass from generalization to specialization by both the foot and the skull and teeth from *Alactaga* to *Dipus*. Similar observations hold good in the case of the cervical vertebrae.

¹Slater, Proc. Zool. Soc., 1890, pp. 610-613.

²Thomas, Proc. Zool. Soc., 1896, pp. 1012-1028, and Parsons, Proc. Zool. Soc., 1898, pp. 858-890.

In summing up, the old family *Dipodidae* is seen to be composed of two clearly defined though somewhat related families, of which *Zapus* is typical of the one and *Dipus* of the other. The antorbital foramen and its subdivision for the nerve and lachrymo-malar articulation are the only striking points of similarity between the two families, but otherwise the skulls are widely different and each homogeneous in its own family.

The *Zapodidae* are at once recognized by the five separate metatarsals, free cervical vertebrae, and general murine aspect of the skull. It is composed of two easily separable subfamilies.

Zapodinae, with the enamel of the molar teeth thrown into folds and the crowns presenting a generally smooth surface; upper incisors grooved; skull less murine; zygoma heavier and less oblique palate concave posteriorly. It contains the three genera, *Zapus*, *Napaeozapus*, and *Eozapus*.

Sminthinae, with the enamel of the molar teeth in an entirely different pattern, and above folded in opposite loops so that there seems to be four cusp-like processes on each tooth; the upper incisors without grooves; and slenderer skull and zygoma. It contains the genus *Sminthus* and possibly the fossil genus *Eomys*, which is usually referred to this group.

The *Dipodidae* are to be recognized by the fusion of the three middle metatarsals into a "cannon" bone, longer hind limbs, a tendency toward consolidation of the cervical vertebrae, as well as a totally different form of skull, much laterally expanded. It seems to be readily separable into the three following groups, of which the first two should take subfamily rank, the *Dipodinae* in contrast to the third group containing *Euchorentes*.

Dipus group with *Dipus* and its subgenera, hind foot with three digits; cervical vertebrae ankylosed; mastoid considerably inflated; upper incisors grooved; no small premolar; antorbital canal for nerve complete.

Alactaga group, with *Alactaga* and its subgenera, hind foot with more than three digits, but lateral ones much shortened; cervical vertebrae not completely fused; mastoids not much inflated; upper incisors without grooves; and a small premolar present above; antorbital canal for nerve not fully complete. *Platysercomys* without the small premolar probably belongs to this group.

Euchorentinae is at once told from the preceding by the posterior slope of the zygoma and more elongated skull and interorbital constriction; no root-cap for incisor on side of mandible; posterior palatine foramina very large; hind foot with five digits; upper incisors not grooved; upper premolar present.

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EXPLANATION OF PLATES.

All figures one and a half times natural size. The letters on the plates have the following significance:

<i>Sq</i> , squamosal.	<i>N</i> , navicular.
<i>m</i> , mastoid.	<i>Cu</i> , cuboid.
<i>So</i> , supraoccipital.	<i>Ec</i> , <i>Mc</i> , and <i>Ic</i> , external, middle, and internal cuneiform.
<i>C</i> , calcaneum or os calcis.	
<i>A</i> , astragalus.	

PLATE XXV.

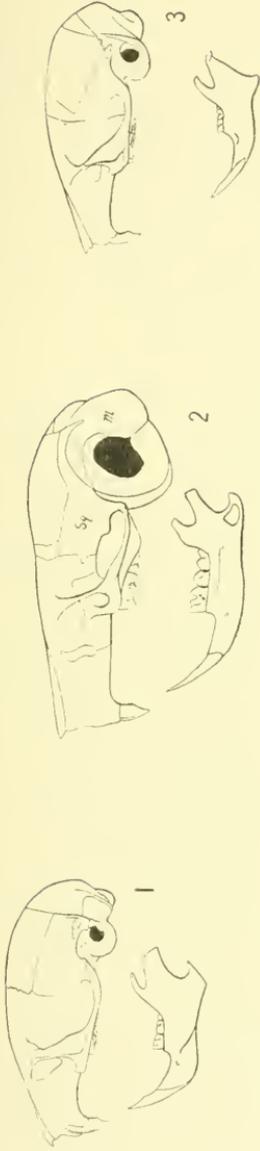
- Fig. 1, lateral view of skull of *Zapus*.
- 2, lateral view of skull of *Euchoreutes*, redrawn to scale from Selater's figures in Proc. Zool. Soc. Lond., 1890, p. 611. Compare with *Zapus* and *Sminthus* and note similarity of the zygomata.
- 3, lateral view of skull of *Sminthus*.
- 4, lateral view of skull of *Dipus*.
- 5, lateral view of skull of *Alactaga*.

PLATE XXVI.

- Fig. 1, ventral view of skull of *Zapus*.
- 2, ventral view of skull of *Euchoreutes*, redrawn to scale from Selater's figures in Proc. Zool. Soc. Lond., 1890, p. 611. Note the similarity of the ventral view with the same aspects of *Dipus* and *Alactaga*.
- 3, ventral view of skull of *Sminthus*.
- 4, ventral view of skull of *Dipus*.
- 5, ventral view of skull of *Alactaga*.

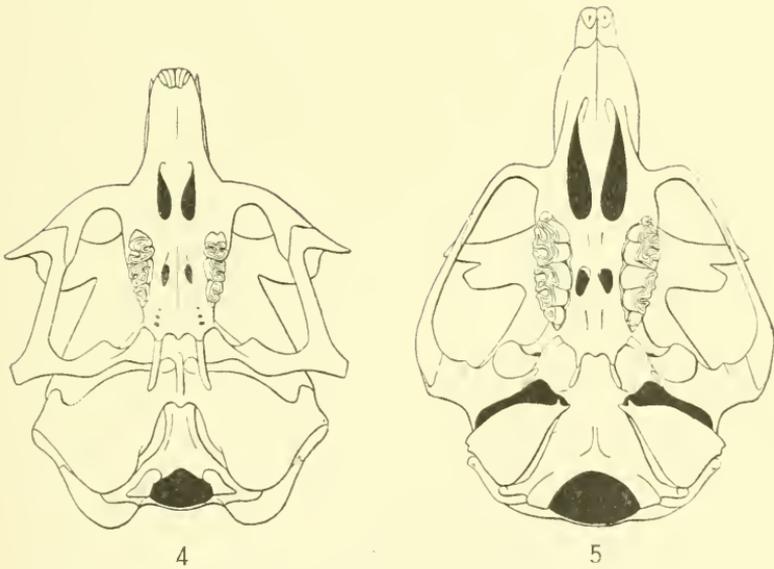
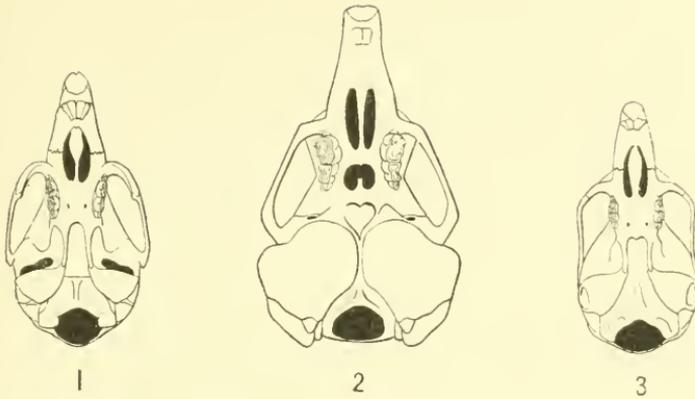
PLATE XXVII.

- Fig. 1, left hind foot of *Zapus*, dorsal view and internal lateral view of the tarsal bones.
- 2, left hind foot of *Alactaga*, dorsal view and internal lateral view of the tarsal bones. The pre-tarsal part is drawn from a specimen in the American Museum of Natural History; the tarsal bones are filled in from a dissected tarsus taken from a skin in the U. S. National Museum.
- 3, left hind foot of *Dipus*, dorsal view and internal lateral view of the tarsal bones. Rudiment of the fifth metatarsal may be seen.



SKULLS OF ZAPUS, EUCHOREUTES, SMINTHUS, DIPUS, AND ALACTAGA

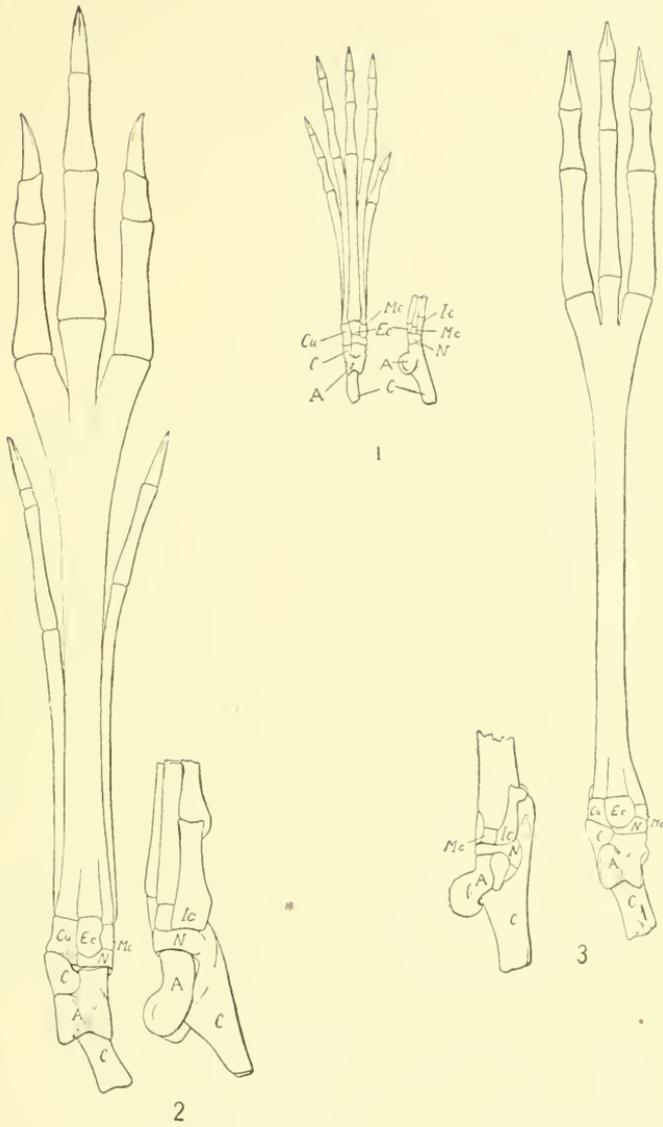
FOR EXPLANATION OF PLATE NET PAGE 602.



SKULLS OF ZAPUS, EUCHOREUTES, SMINTHUS, DIPUS, AND ALACTAGA.

FOR EXPLANATION OF PLATE SEE PAGE 668.





LEFT HIND FEET OF ZAPUS, ALACTAGA, AND DIPUS.

FOR EXPLANATION OF PLATE SEE PAGE 668.