

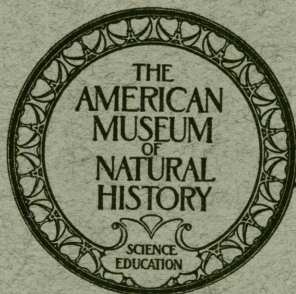
THE VERTEBRAL COLUMNS OF RICOCHETAL RODENTS

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Article VI.—THE VERTEBRAL COLUMNS OF RICOCHETAL RODENTS

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INTRODUCTION

The herbivorous animals are constantly preyed upon by a host of carnivorous enemies, and they survive chiefly because of such protective specializations as unusual fecundity, defensive armor, and speed.

Among land mammals speed is usually dependent on the propulsive force of the hind legs more than on the fore legs. An extreme development of this principle of locomotion has led to the differentiation of a number of groups that for speed depend completely on simultaneous propulsive strokes of the rear legs, the fore feet touching the ground only in slow progression.

Coupled with this change of habit there have been a number of profound morphological changes. The chief of these has been the elongation of the rear limbs, particularly the distal sections, by which means the length of extension for their catapultic function is increased, and their efficiency in absorbing landing shock multiplied. To obtain the powerful lifting component of a leap, the muscles of these limbs are also tremendously enlarged in the transverse direction. The lateral digits are reduced or lost, and fusion of the metatarsal bones to form a birdlike cannon bone occasionally takes place. The ankle joint becomes ginglymoid, and movement here is confined to flexion and extension, though the angle of movement is increased. The rear feet are widely separated for the sake of stability, and the animal becomes digitigrade or even unguligrade. The toes commonly bear strong hoof-like claws or are protected by heavy fleshy pads or a stiff brush of hairs. The nature of the protecting device appears to be correlated with habitat, for the species with the greatest amount of hair on the feet are those living in the most sandy districts. The fore limbs of the greater number of these animals are considerably reduced. The neck in some is strikingly shortened; occasionally the head is enlarged. The tail is usually considerably lengthened and sometimes bears a terminal tuft. When the tail is not elongated it is enlarged.

The occurrence of a number of groups of bipedal leaping rodents, whose origins were independent within the order, offered a good field for study of the essential modifications of the vertebral column for this locomotor habit. Such a study of the products of parallel evolution promised to shed some light on the relative influences of the habitus and of the phyletic heritage on the structure of a species. It seemed probable that the data obtained would in some instances allow a weighing of the effect which size differences impose on bone architecture. It was with the hope that the available materials would be suited to the analysis of these problems that the studies of which the present paper is a product were undertaken.

PREVIOUS STUDIES

Such a striking locomotor specialization as bipedalism in the Rodentia has naturally not escaped the attention of previous investigators. Few of these studies, however, have given much attention to the vertebral column. Giebel (1865) wrote on the osteology of *Zapus* but neglected to give adequate treatment to the spine. Parsons (1898) studied the anatomy of *Pedetes* which he compared in many points with the anatomy of *Jaculus*. Lyon (1901) compared the osteological characters of *Zapus*, *Jaculus*, and *Allactaga*. A few striking points concerning the differences in their columns, such as fusion of cervical vertebræ, length of tail, etc., were noted, but details of columnar structure were not given. Lull (1904) reviewed the skeletal characters of saltatory mammals in general and in his paper mentioned the fusion of cervical vertebræ, increase in size of lumbar vertebræ, and increase in tail length occurring in ricochetors. Apparently no studies of the vertebræ of leaping rodents other than these have as yet been published, though one other investigator in the United States, one in the Union of Socialistic Soviet Republics, and one in Germany have such investigations under way at the present moment.

The broader principles of mechanical adaptations in skeletons have been dealt with in many papers. Among the more important of these are: Gregory's (1912) 'Principles of Quadrupedal Locomotion,' Fick's (1904-1911) three-volume treatise on 'Anatomy and Mechanics of Joints,' Borelli's (1710) treatment of lever principles, Cope's (1889) 'Mechanical Causes of the Development of Hard Parts of the Mammalia,' Haycraft's (1900) chapter on animal mechanics which appeared in Schäfer's 'Physiology,' two papers of le Hello (1908, 1914) which were concerned chiefly with the locomotion of the horse, Jansen's (1920) book on bone formation, and Koch's (1917) treatise on the structure of the femur. Chabry's (1883, 1885) studies of the mechanics of the leap, while important to the correct interpretation of the function of limbs, have no direct bearing on vertebral column mechanics. The recent report by Hirsch (1931) on the mechanics of the frog's leap is a contribution of great value in the interpretation of the relation between the body and its trajectory.

DEFINITIONS

The word "saltation" is commonly applied to the form of locomotion produced by synchronous striking of the hind feet without recourse to the use of the fore limbs. Muybridge (1899, p. 205) recognized the

ambiguity of this word and applied the military term "ricochet" to the type of locomotion characteristic of the kangaroo to distinguish it from the "rotary gallop" used by the rabbit and others. He did not, however, distinguish between the gallop of the horse and that of the rabbit, though the two differ in that the latter is composed of a series of leaps in which both fore feet tend to touch the ground at the same moment, as do the rear feet shortly afterwards; whereas in the gallop of the horse there is a more evenly distributed striking order. Such a difference in any study of locomotion must be recognized.

Other terms, too, applying to locomotion are variously used by different authors, while for some aspects of bipedalism suitable words have never been coined. Because of this it seems advisable to define at this point such terms as I shall use in the sense that I shall apply them.

SALTATION.—Progression by leaping that is of two types: quadrupedal (the Spring) and bipedal (the Ricochet and the Hop), which are defined below.

BIPEDALISM.—Two-footed progression which may be **ALTERNATE** (the Bipodal Run which is rapid and involves a moment of suspension, or Walk, which is slow and requires continuous support) or **PAIRED** (the Ricochet which is rapid, or Hop which is slow).

SPRING (Quadrupedal Saltation) (Figs. 1 C, 2 C).—Progression composed of a series of leaps in which the hind legs supply the chief propulsive force, lifting the body completely from the ground and forward. The fore feet touch the ground simultaneously or in close sequence; the body rolls forward over these as in a vault; the hind feet, overstepping the fore feet, at least in greatest speed, come down next and again lift the body forward. This is a modified form of rotary gallop. The Spring is sometimes used by hares, squirrels, white-footed mice, frogs, and toads.

RICOCHET (Bipedal Saltation) (Figs. 1 D, 2 D).—Forward progression by a series of rebounds in which the two hind feet strike the ground at the same moment or practically synchronously, and the fore feet not at all. This is rapid, sustained hopping. The Ricochet is employed by jerboas, kangaroos, and certain other animals.

The word "ricochet" is recognized by Webster's Dictionary as both a noun and a verb. I propose, and shall use, the following derivatives of this word:

RICOCHETOR.—A body which ricochets

RICOCHETAL.—Relating to the ricochet.

THE BIPEDAL RUN OR WALK.—Progression on the two rear feet alone, in which the feet strike the ground in alternation. This gait is employed by men, birds, and bipedal lizards. It is also used at times by some jerboas.

ORIGIN AND DEVELOPMENT OF THE RICOCHET

The ricochet is a type of locomotion which, because it is wasteful of energy, is not well adapted to long sustained rapid progress. This theoretical statement is borne out by the observation of Boehme and

Krasovsky (1931, p. 426) that the jerboa *Dipus* ("Dipodipus") *sagitta nogai* fleeing by great leaps is soon seriously exhausted, and that at the first opportunity it hides itself in some vegetation where it lies curled up and breathing heavily. Locomotion is efficient in the sense of covering the maximum distance with the minimum effort, to the degree with which the trajectory of the center of gravity remains near the horizontal. Vertical movements involve lifting, and where the vertical components of progression are great there is consequent expenditure of energy in a direction perpendicular to that of progress. The energy of momentum is also lost in the landing shock of the ricocheting animal instead of being carried over into the next stride. Mechanical efficiency is not, however, always biological efficiency, and for many species high speed sustained for a short period is of greater importance in the escape from enemies than conservation of energy. The ricochet is above all a means of producing high speed by the attainment of the greatest range for each thrust, and this involves a very large lifting component accompanying the forward movement. It is a mode of locomotion too wasteful for heavy-bodied animals which require a relatively flat trajectory and maximum saving of inertia.

If air friction were not encountered, a body projected forward and into space would attain the maximum horizontal range for any given force of projection, provided that the angle of projection is 45 degrees. In air, however, the maximum range is attained with an angle of projection between about 40 and 44 degrees. As air retardation increases with increased velocity, a given body attains the greatest range at an angle of projection closest to 45 degrees when the initial velocity is lowest, and closest to 40 degrees when velocity is highest (American Expeditionary Forces, 1918). Range decreases toward zero for angles of projection from 45 degrees to 90 degrees. The jerboa (*Jaculus orientalis*) and the kangaroo rat (*Dipodomys merriami*) both occasionally leave the ground at angles between 45 and 90 degrees, but this is in play, and not when speed is the aim, as I have observed.

The evolution of the ricochet may be traced to the rotary gallop of quadrupeds. In the gallop of the horse or the racing dog, the fore limbs, which are relatively powerful, come down first and shove off again before the hind feet touch the ground (Figs. 1 A, 2 A). The fore limbs are powerful elements of propulsion and in some cases may be of greater importance than the rear feet. In such animals as the deer or pronghorn, however, where the fore limbs are relatively weak and the rear legs strong, succession of footfall is the same as in the horse, but the

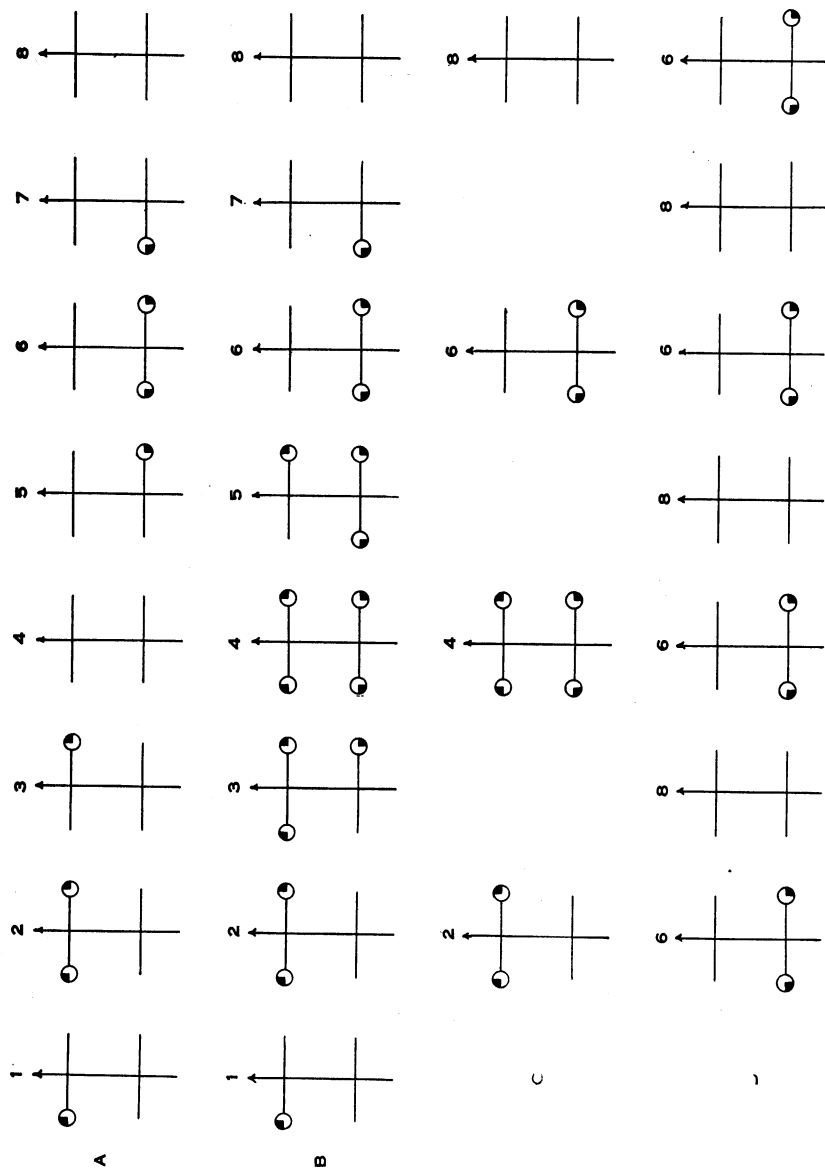


Fig. 1. The sequence of footfall in the riocchet and its antecedent locomotor types.

A.—The type of rotary gallop characteristic of animals with powerful fore limbs. There is a moment of suspension (A 4) between the instant that the last fore foot leaves the ground (A 3) and that at which the hind foot of the same side touches the ground (A 5). A second moment of suspension (A 8) follows the propulsive thrust of the rear legs.

B.—The type of rotary gallop characteristic of animals with weak fore limbs. No interval of suspension occurs between the times of propulsive thrusts of the fore limbs and the rear limbs, but there is an instant in which all four feet are in contact with the ground (B 4). As in the previously described type, the rear feet project the animal entirely above the ground (B 8).

C.—The Spring: Through synchronization of the movements of the fore legs and the hind legs a modified form of the second type of rotary gallop is produced. Here phases B 1, 3, 5, 7 disappear. As in the rotary gallop, from which the leap was derived, the rear limbs function as the chief propulsive members and total suspension of the body occurs only following the thrust of the rear limbs.

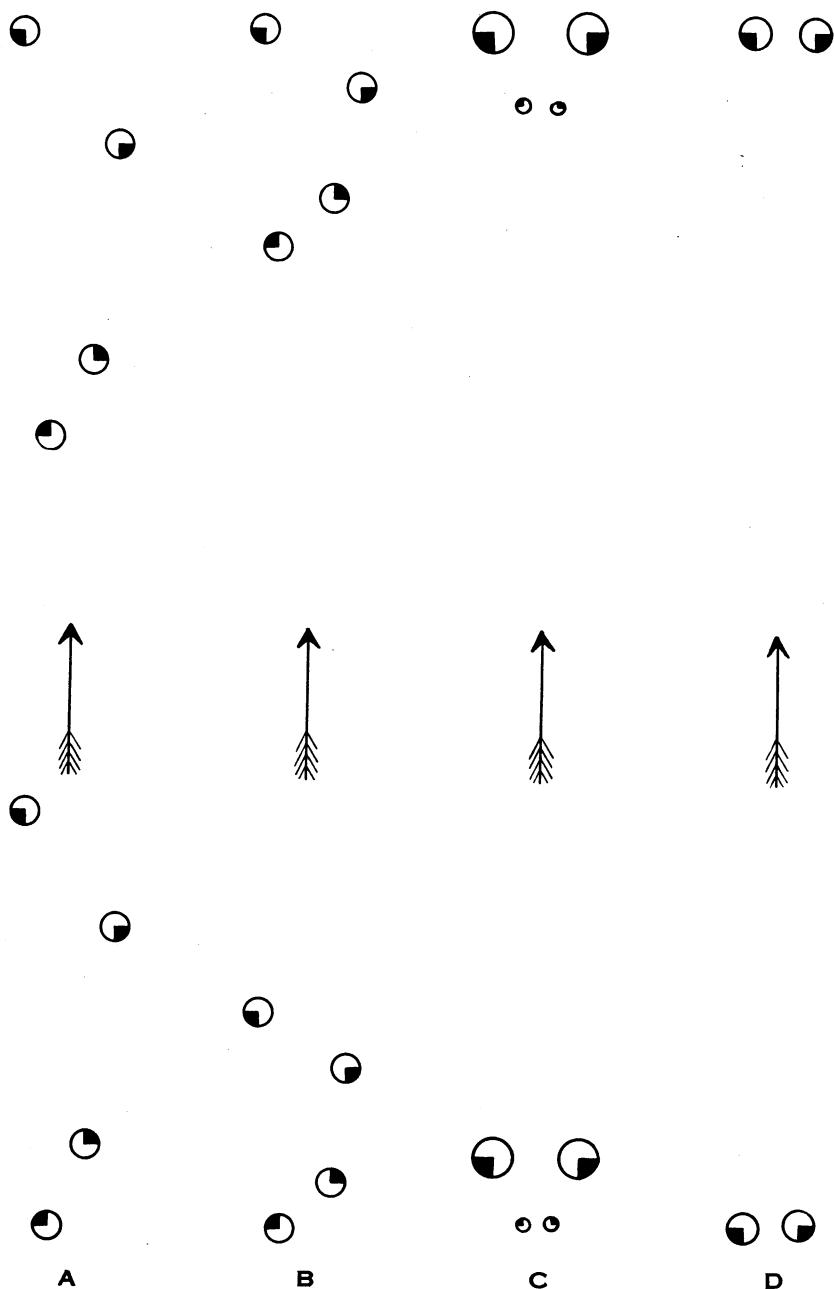


Fig. 2. Idealized track patterns of the four types of locomotion defined by figure 1. The blackened sector of each circle indicates which foot of the four the track represents. Thus a circle with the lower right quarter blackened represents the track of the right hind foot.

- A.—Track pattern of the type of rotary gallop characteristic of animals with strong fore limbs.
- B.—Track pattern of the type of rotary gallop characteristic of animals with weak fore limbs.
- C.—Track pattern of the spring.
- D.—Track pattern of the ricochet.

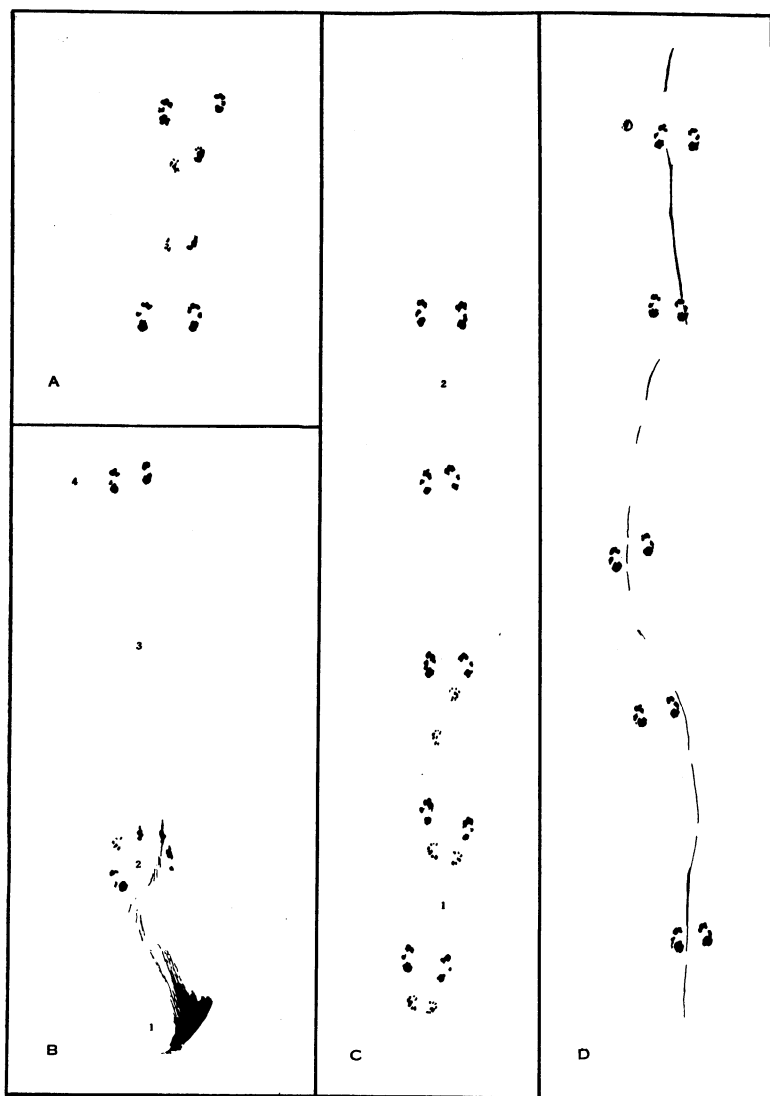


Fig. 3. Track records of *Dipodomys merriami* obtained by allowing the animal to move over a strip of paper after walking over an area of inked cotton.

A.—Initiation of locomotion when undisturbed. The first four tracks were made by the four feet of the crouching animal. From this position the kangaroo rat raised its fore feet from the paper, and by extending its body brought the fore feet down again in advance of their former position. Just before or immediately after this the rear feet left the paper and next came in contact with it in advance of the fore feet.

B.—Initiation of locomotion when disturbed. The tracks bunched around B 2 are made by the crouching kangaroo rat. The animal was startled by a noise and leapt with enough force to cover a nine and one-half inch interval (B 3) landing on its rear feet alone (B 4) and ricocheting away with the tail held clear of the paper. Though at the initial catapult the inked tail brush left a strong mark, this does not indicate that the tail was used as an aid to propulsion.

C.—Transition from the spring (C 1) to the ricochet (C 2). It can be seen that a greater distance is covered by a single cycle of the ricochet than by a cycle of the leap.

D.—The Ricochet: The tail tuft was heavily weighted by the ink and it may be only for this reason that the tail came in contact with the paper. The course of the tail drag in relation to the tracks suggests that the tail is an aid in the maintenance of lateral balance.

fore feet do not shove off from the ground until the rear feet have come down, overstepped the fore feet, and absorbed some of the shock imparted by the descending body (Figs. 1 B, 2 B). In an animal of this latter type the function of the fore limbs is on the way of becoming the same as in the hare in which these appendages are little more than vaulting poles that support the body during the moment before the rear feet reach the ground.

In the evolution of the ricochet there are successive stages of synchronization of the hind feet in which they tend more and more to strike the ground at the same moment. Likewise the fore feet come to act in unison so that the tracks of the animal show strict pairing of the footprints. However, where such an animal as the rabbit uses this quad-

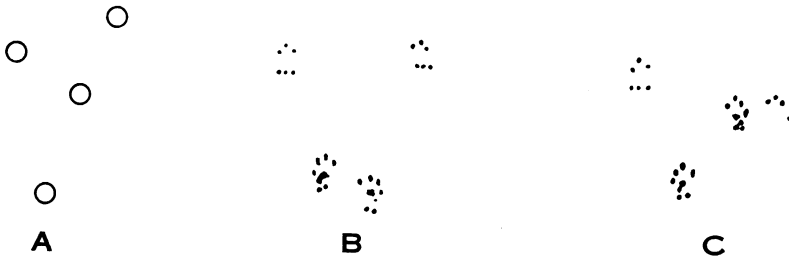


Fig. 4. Track records of an adult female pocket mouse (*Perognathus penicillatus eremicus*) obtained by inking the feet.

A.—Transverse gallop: Stride three and one-half inches. Details of the tracks indistinct.

B.—Practically a spring. Stride three and seven-eighths inches.

C.—Rotary gallop, (counter clockwise). Stride three and five-eighths inches.

rupedal saltation at high speeds the fore feet are commonly not synchronized, but one oversteps the other by a short distance. In some other animals (well illustrated by the action of a squirrel on snow) tracks are found perfectly paired (Figs. 1 C, 2 C).

The ricochet evolved from quadrupedal saltation at a time when the overstep of the rear feet became so great that the contact of the fore feet impeded the advance of the mass as a whole.

The studies of Fuld (1901) and Regnault (1911) on bipedal dogs, and those of Colton (1929, 1930) on bipedal white rats suggest that ricochetal forms originated from digitigrade quadrupeds and not, except remotely, from plantigrade stock. On the other hand, species with short fore limbs have probably not originated from highly developed cursorial types which are usually moderately large animals with four long limbs and a long neck. It seems to me that in the case of the Heteromyidæ,

Perognathus (Pl. XVIII) represents well the locomotor development that would precede the origin of a ricochetal species.

THE ROLE OF THE VERTEBRAL COLUMN, ITS ASSOCIATED LIGAMENTS AND MUSCLES

The vertebral column of mammals is fundamentally a rod extending the length of the body, the function of which is to furnish a partial rigidity within the body that may meet compression, tension, and torsion stresses originating from the action of external natural forces, from the interaction of animal and environment, and from muscle pull. The column is segmented to allow motion. Its possible motions are by adaptation variously restricted regionally and variously limited as to latitude. Some of this restriction is imposed by the architecture of the bone, some by the ligaments, and some by opposing muscular action. The restrictions of movement act to furnish resistance to muscle pull and to protect the spinal cord against strangulation and shock due to rotation, flexion and extension of the column, and the dislocational movements of the pelvis.

The vertebral column as a whole is subject to stresses in four principal directions: antero-posterior (compression stresses), dorso-ventral (flexion and extension stresses), dextral-sinistral (abduction stresses), diagonal (torsion or rotation stresses).

The antero-posterior stresses are induced by propulsive strokes of the hind legs acting against inertia. In the animal standing partially erect these stresses are brought about by the action of gravity. Contraction of any of the longitudinal muscles also invokes such stresses. Resisting compression are the bony centra, the inter-vertebral fibro-cartilages, and the articular capsules.

Dorso-ventral stresses arise from the flexion and extension movements; from the antero-posterior rocking motions of locomotion, particularly the spring and the ricochet; by action of gravity on the viscera and other structures suspended from the horizontal column; and from the pull of the scapular muscles. The forces exerted by the extensor group are the most important. It is these muscles which serve to counteract gravity, to raise and hold the fore part of the body more or less upright when the fore legs are not in use. It is they that must maintain the posture of the head even when the fore feet are on the ground. These muscles fill the great troughs on either side of the vertebral spines. Some are in short bundles connecting adjacent vertebræ; others run in long systems which may pass several joints.

The flexors of the vertebral column occur in part on the column and in part external to it. On the under side of the neck there is a small weak group which serves three functions. These are lateral flexion, elimination of head bobbing during bounding—which the interaction of gravity and the spinal extensors alone could not counteract—and lastly, the anchoring of the elements in relation to each other (particularly the atlas and the axis) so that the extensors of the head may act. Another group of flexors (the psoas) occurs in the posterior lumbar section. The psoas major has as its chief function the flexing of the thigh on the recovery movement of the propulsive cycle, though it is also of importance to flexion of the column in such acts as digging where strong flexion forces are required. The psoas minor, on the other hand, acts directly as a flexor of the column, and though typically weak, obtains good leverage on the innominate bone and is well adapted to relatively rapid action. The most important flexors of the column are, however, not the muscles on the column, but *Mm. recti abdomini* and the transverse abdominal muscles. In the caudal region the flexors are strongly developed. They are of added importance in such forms as jerboas where they are called into play in bracing the tail when the animal uses this member as a prop, when using it to steady or correct position at the moment of projection (Fig. 3 B), and when stiffening the tail as a means of sustaining trajectory in unsupported passage through the air. The flexion and extension stresses are resisted by the dorsal and ventral longitudinal ligaments, supra-spinous and inter-spinous ligaments, the ligamenta flava, the contact of vertebral arches and spines, the resistance of the bony thoracic complex, and the muscles opposing those producing the stress.

Almost all abduction stresses are produced by muscular pull in such actions as turning, cleaning movements, and lashing of the tail. Muscles which are essentially abductors (lateral flexors) are confined to the caudal region. Any flexor or extensor contracting on one side more than the other naturally produces lateral flexion. Abduction stresses are met by inter-transverse ligaments and muscles, the ligamenta flava, contact of the vertebral arches and processes, resistance of the thorax, and action by opposing muscles.

Rotational stresses accompany diagonal rocking induced by alternate use of the limbs. They also arise in response to certain non-locomotor activities. The muscles of rotation are of somewhat less importance in the ricochetors than in animals using the transverse gallop, for there is not the need to brace against the rocking strain

present during the latter form of locomotion. The ricochet forms do, however, retain all the primitive needs for the muscles of rotation, such as their use in cleaning movements, feeding activities, and the localized movements within a burrow. At the same time it may be expected that there is some reduction in the possibility of rotation movements due to adaptation in the bone against excess play in movement during the ricochet. In the cervical region of those forms with fused cervical vertebræ all rotation is of course eliminated, except for that between atlas and axis. Muscles which check wrenching of the pelvis by lateral motion are, in some cases (as *Mm. ilio-spinalis*), also those which aid in maintaining the upright posture in bipeds, and hence are retained in these animals, though the leverage may be changed. Rotation stresses (except in the atlas-axis articulation) are resisted chiefly by the inter-transverse and inter-spinous ligaments, the ligamenta flava, the thorax, the contact of zygapophyses, and by muscle action.

The stresses to be resisted, and hence the rôle of the vertebral column during the ricochet, differ from those during the gallop, the spring, and the bipedal run.

The gallop subjects the column to strong rotational stresses and to large flexion and extension movements. It does not require that the extensors of the back give any great amount of support to the fore end of the body.

The spring greatly increases the flexion and extension movements of the column over those of the gallop, but minimizes the rotational strain. This change is due to the synchronization of the propelling thrusts of the pairs of limbs, and to the increased overstep of the fore feet by the hind feet. Here, as in the gallop, the front limbs are sufficiently powerful to impart an upward momentum to the anterior part of the body, by which means the work of supporting that end of the body is partially withheld from the *spinalis dorsi* muscles.

During the bipedal run as practiced by the jerboas, the body is held nearly horizontal during rapid progress. In this manner wind resistance is lessened, and the center of gravity is thrown forward over the forwardly moving center of support. Here also there is a rotational strain on the column induced by the alternate action of the rear feet. Unlike the condition occurring in the gallop or in the spring, a great load is thrown on the spinal extensor muscles which must support the fore end of the body. Their work, however, is lessened in all bipedal rodents by the balancing action of the neck and the increased cervical flexure which shift the center of gravity backward.

During the ricochet the functions of the column are the same as they are during the bipedal run, with the exceptions that rotational stresses are removed by synchronization of the movements of the hind feet, and the supportive strains greatly multiplied during the period of projection.

The vertebral column of the moving bipedal rodent may be considered a balanced beam in which the fulcrum is the line joining the two femur heads. This beam is not, however, straight, but deviates dorso-ventrally from a straight line in order that there may be better muscle leverage, that shock absorption may be more efficient, and that the weight of the head and viscera may be most economically carried. The presence of the dorsally concave cervical flexure cares for the balance of the head, while the ventrally concave lumbar flexure is in adaptation to the support of the abdominal viscera.

These curves of the column are essentially elastic arches which are trussed with muscles and ligaments. The cervical flexure is trussed chiefly by the ligamentum nuchæ, but also by certain lesser ligaments and the extensor muscles. Most of these short ligaments and muscles truss but portions of the arch. The thoraco-lumbar curve, which is convex dorsally, is trussed by the thorax and by the abdominal muscles. The ventral longitudinal ligament aids in supporting the arch. The tail may be thrown into a single arch concave dorsally or ventrally, or into a multimodal, sinusoidal curve in which the caudal flexors and extensors play their appropriate rôle of trusses in the region needed. Here, of course, the muscles, their tendons, and the ligaments do not form a single tie beam extending directly across the base of the arch, but constitute in effect an infinite number of small trusses, the component of which is a single greater truss.

Between the ricochetors and their quadrupedal antecedents there are no differences in principle of arch construction. No curves have been added; none have been lost. The cervical flexures of ricochetors are more pronounced than those of quadrupeds, as illustrated in the X-ray photographs of *Notomys* and *Rattus* (Pl. XII). No difference in the lumbar flexure has been demonstrated.

Stresses met by major regional development and configuration are composed of many smaller stresses imparted by particular muscles. These are frequently transmitted by tendons to the bone affected. The architecture of the individual vertebra is, then, adapted not only to its position in a vertebral region, but also to the stresses of the forces working upon it. The vertebra serves as the fulcrum for the entire series of

vertebræ in front of and behind it, and also as a lever for the movement of the region in which it is located. Where there are strong forces to be met the bone is more massive or more prominently modified. Thus in the lumbar region of ricochetors the centra are large and the processes long and strong. In the proximal caudal region where caudal muscles take origin and where leverage for most muscle insertions is not good, the configuration of vertebræ is far stronger than in the distal caudal segments where there are but weak tendon insertions and a small amount of weight to be moved.

THE USE OF TAILS

Tails of ricochetal animals may serve as counterbalances, guides, accessory propulsive organs, props, marks for recognition, and as a means of distracting enemies. They appear to be variously adapted to these several uses through modified length, weight, musculature, hair distribution, and coloration.

COUNTERBALANCE (Pl. XI).—For the purpose of counterbalance tails may be relatively short and heavy as in the kangaroo (*Macropus*), the jumping shrews (*Macroscelididæ*), the spring haas (*Pedetes*, Pl. XVII, fig. 2), and the club-tailed jerboa (*Cardiocranius*, Pl. XI); greatly lengthened, but aided by a heavy terminate brush as in the five-toed jerboa (*Alactagulus*, Pl. XI) and the kangaroo rat (*Dipodomys*, Pl. XIX); or greatly attenuated without the resource of a heavy brush as in the jumping mice (*Zapodinae*, Pls. XI, XIV) and the dwarf jerboa (*Salpingotus*, Pl. XVII, fig. 1). These relations are more fully discussed under the heading of CAUDAL VERTEBRAL LENGTH (page 639).

That the tail is important to correct leaping in ricochetal rodents is shown by several observations, among which is the following. Miller (1899, p. 330) writes of a young *Zapus hudsonius* whose tail was cut off by the knife of a mowing machine. The injured mouse did not have its leaping powers impaired, but lost all control of its movements. The body, launched into the air deprived of its balancing tail, turned end over end and would sometimes strike the ground facing the opposite direction from that it had first taken. The next frantic leap would carry it back to the starting point. Though I have watched a similar tailless jumping mouse it was at all periods of activity confined to a small cage where it had no opportunity to display its leaping ability.

The balancing rôle of the terminal brush such as is seen in *Alactagulus* (Pl. XI) is obvious. The animal may thus dispense with a longer tail on the principle that an ounce at the end of a sixteen-inch

lever will give the same leverage as a pound at the end of a one-inch beam. The tuft must act not only through its weight, but also through its resistance to the wind.

Amputations, which are occasionally autonomous (Sumner and Collins, 1918), of the tails of the heteromyid genera *Perognathus* and *Dipodomys* are by no means infrequent, and these injuries are often followed by abnormal hairy growths on the stumps. This may be interpreted, regardless of the mechanism involved, as a replacement of the brush or pencil that was on the original tip, and perhaps even as a counterbalance to serve instead of the original terminal part of the tail. Inasmuch as these abnormal hairy growths may occur at any point of caudal injury, even without amputation, Howell (1923, p. 57) concludes that the tails, in harmony with the rear legs, are in a state of "genetic unrest" due to a great "evolutionary velocity," so that they are easily affected by stimuli of all kinds, including those of a pathological nature. I have shown in this study (p. 688 and Fig. 27) that there is a well-marked osteological adaptation for caudal autotomy in *Perognathus*.

Similar bushy tails due to tail amputations are known in the climbing dormice *Eliomys*, *Graphiurus*, *Claviglis* (Thomas, 1905). These cases were correlated with the presence of a long terminal rod of bone, supposed by Thomas to represent a regeneration similar to that occurring in lizard tails, but interpreted by Henneberg (1909) as being probably due to ankylosis of several vertebræ. The mechanism of tail separation in the dormice has recently been shown by Gögl (1930) to occur only by the easy breaking of the skin at definite loci of young connective tissue in the tail sheath. "Autotomy" of tails is described in *Apodemus* and *Tatera* by Cuénot (1907) and Henneberg (1909), but in these cases no hairy tufts appeared. In these two genera it seems safe to assume that the need of a tail is less than in the pocket mice, kangaroo rats, and dormice.

SUPPORT.—Strongly distichous tails serve to distribute the weight thrown on to the tail when this member is used as the third leg of a tripod. Many species live on areas of loose sand, and the tail fan keeps the tail from sinking below the surface level. A captive *Jaculus*, which I have observed, invariably used its tail for a prop whenever it stopped running, but unless the stop was protracted, remained up on its toes. Many photographs of living jerboas (see Pl. XV, XVI) standing erect show the tail similarly used, and numerous authors attest this function of the tail. The tails of *Dipodomys* (Pl. XIX) are also used for props. A photograph of a *Pedetes* (Pl. XVII) shows the tail in such a position,

though here the photograph does not show conclusively whether the tail is but resting or whether the weight is thrown upon it.

Various illustrations, some of which were drawn from life, showing leaping species of Gerbillinæ resting with their fore feet off the ground, also show the tail used for support. As with the kangaroos, *Pedetes*, etc., the tail is shown in contact with the soil for as much of its length as could reach the ground with the animal in this position. In the jerboas and kangaroo rats the first section of the tail is held parallel to the ground and then bent down to furnish contact only in the region of the distichous terminal tuft (Pl. XV, fig. 1; Pl. XIX, fig. 3).

PROPULSION.—It is commonly said that the kangaroos add impetus to their leaps by using the tail as a third leg in initiating the spring. With *Pedetes* it is possible that similar use is made of the tail, but where data are available on the more lightly built leapers there is little indication of such habits. Boehme and Krasovsky (1931, p. 425) conclude, however, that in *Dipus sagitta nogai* the tail acts as an accessory propulsive agent in great leaps. In some, if not all, species of small ricochetel rodents the tail may sometimes touch the ground between leaps. My records on *Dipodomys* show that the tail makes the touches when the animal travels at moderate speed (Fig. 3 D), not when moving at top speed. This indicates the probability that within this genus the tail's function is one of balance checking and not one of propulsion.

Of *Microdipodops megacephalus dickeyi*, Hall and Linsdale (1929, p. 300) note, "The tail mark is faint or absent when the consecutive tracks of the hind feet are far apart and the tracks of the fore feet absent." Here too then, it appears that when there would be greatest call for accessory propulsive force the tail is not called into play.

Examination of the tracks of *Perognathus lordi* shows that the tail may sometimes be held completely clear of the ground when the mouse is traveling, touch the ground at each jump, or be allowed to drag constantly (Dice, 1919, p. 17).

DIRECTION CONTROL.—The vertical arrangement of hair on the upper surfaces of the tail tips of some ricochetel rodents leads one to believe that these serve the animal the same purpose as do vertical vanes on the shaft of an arrow. It is likely that these vanes on the animal aid in the elimination of lateral swerving much in the manner that the horizontal vanes act in sustaining elevation. Similar arrangements occur in several widely separated species. In *Dipodomys* the large brush is often crested anteriorly and horizontally distichous terminally. In *D. obscurus* there is sometimes even a distinct ventral keel. Bailey

(1931, p. 249) states that captive *D. spectabilis* exercising on a revolving wheel keep the tail curved TO THE INSIDE of the circle in which they are running and thus are able to spin the wheel without being thrown off. Traces of a dorsal crest are occasionally discernible in the small Egyptian jerboa (*Jaculus jaculus*).

TRAJECTORY CONTROL.—It is possible that a ricochetor, equipped with a tail tuft that is horizontally distichous, may purposely alter its trajectory after the feet are off the ground. This would be accomplished in one direction by action of the caudal extensors, in the other by the caudal flexors. Such functioning of the tail tuft would make possible some choice of landing-site which on uneven or stony ground would be of importance.

Well marked horizontal vanes which would serve this purpose of trajectory control are present on the tails of the Euchoreutinae, Allactaginae, most of the Dipodidae, and *Dipodomys*. In all of the other forms considered the tails whether naked, lightly haired, or bearing a brush, have the end terete. This is true of the ricochetal Insectivora and Marsupialia. None of the larger ricochetors (Pedetidae, Marsupialia, Insectivora) have developed caudal guiding vanes, for to be effective these vanes would need to be so immense as, for obvious reasons, to be impractical.

PROTECTION.—Lataste (1882, p. 246) states that the tail of *Jaculus orientalis* is kept constantly in right and left motion, and this suggests that against a natural background it would be the only point visible, and thus serve to distract an enemy's attention from the body. No trace of such motion was observable in the *Jaculus* which I have watched. In this case, however, the animal had long been captive, was then confined to a small room and was not particularly nervous. These circumstances might be expected to affect the behavior.

One of the most striking parallelisms between the ricochetal animals is the presence of a prominent marking, usually of black and white, at the tip of a long tail. This color pattern by focusing the attention of the enemy on a markedly fragile appendage far removed from vital organs, probably serves as an important means of prolonging the life of the individual. An enemy seizing such an easily parted structure as the tail of a pocket mouse would be little the better off for its capture. The function of recognition may also be assigned to the conspicuous markings of the tail tips.

A review of the coloration of the tail tip in the animals under consideration shows how constant the feature is. In the genus *Notomys*,

N. longicaudus has the tail apically black preceded by white, while *N. alexis* and *N. macrotis* have tails contrastingly black and white horizontally. Similar contrasting dark brown over white is seen in *N. fuscus* and *N. gouldi*. *N. mitchelli* has a solid black end. Some related forms such as *Mesembriomys hirsutus* and *Conilurus hemileucurus*, which do not appear to be ricochetal, have the tail terminally white, but then so do other types of rodents such as the aquatic *Hydromys* of Australia.

Hallomys of Madagascar has the tail tip white, but in its relative *Macrotarsomys* the hairs of the terminal brush are brown. Among the Pedetidae the tail tip is consistently black, which contrasts with the general brown of the body and tail base.

Among the Dipodidae tail tips ending in bands of white-black-white or merely black and white are common. This pattern is the general rule in the Euchoreutinae, Allactaginae (Pls. XI, XV, fig. 2) and Dipodinae (Pl. XV, fig. 1; and Pl. XVI, fig. 1). The tail tips of the Cardiocraninae (Pls. XI and XVII, fig. 1) are self-colored. Of the Zapodinae, *Napæozapus* (Pl. XI) possesses a white tail tip, but the other subgenera are not so marked.

Of the Heteromyidae some species of *Dipodomys* present strikingly marked tail tips ending in white preceded by a band of black. The shaft of the tail is typically black or dark brown above and below with a white band along each side (Pl. XIX). The species of *Microdipodops* (Pl. XVIII) have the tip of the tail blackish and the under side lighter than the upper. The tails of *Perognathus* (Pl. XVIII) are not conspicuously marked.

Many species of gerbilles are marked with black or dark brown on the tail tip, but such markings seem unrelated to tail length or leaping habits.

STRUCTURES AND NON-RICOCHETAL ACTIVITIES WHICH MAY AFFECT VERTEBRAL FORM

It cannot be supposed that bipedal rodents are skeletally adapted only to ricochetal movements, nor that all ricochetal rodents have the same environment to which their skeletons must be adapted.

SKULL SHAPE.—In some species the skull is generally primitive in shape and size (Zapodinae, *Perognathus*, some Gerbillinae, and the Madagascan, Australian, and New Guinean leaping rodents). In others (Dipodidae, except Zapodinae, *Dipodomys*, and *Microdipodops*, some gerbilles, and Pedetidae) the skull is highly altered by the strikingly inflated auditory and mastoid bullae, a modification which carries the

center of gravity of the skull backward. This inflation of these bullæ is not in itself a response to upright posture or ricochetal progress, for it is found in varying degrees among many desert-living, strictly quadrupedal mammals. Changes in skull weight and balance cannot but affect the cervical and the thoracic vertebræ.

CHEEK POUCHES.—All members of the Heteromyidæ are equipped with external fur-lined cheek pouches in which they carry great loads of food. In *Dipodomys* these pouches are occasionally so distended by food that their combined bulk equals that of the head. It is to be expected that this weight added to the fore end of a bipedal animal needs to be compensated for by an equalizing balance from the rear.

FOOD AND WATER REQUIREMENTS.—The food and water requirements of rodents are reflected in the size of the abdomen. For example Howell (1925) has shown that the differences in the food habits of two types of squirrels are strongly reflected in their digestive tracts. One, a tree squirrel, whose diet was varied and highly nutritious had a relatively small, unspecialized small intestine. The other, a ground squirrel which fed chiefly on grasses of low nutritional value, had a large and specialized small intestine and cæcum. Howell has elsewhere (1926) demonstrated similar adaptations in the wood rats.

A hasty survey of the literature has not revealed any specialized food habits among the species treated in this paper that I can correlate with gross abdominal form, nor does an examination of a series of alcoholics reveal quantitative differences of value to such a correlation.

The fact that the kangaroo rats (*Dipodomys*) use very little water is well known. They are said never to drink and to obtain all their necessary water from their food. I have myself kept a kangaroo rat for eight months without water and with no other food than sunflower seed, flax seed, and rolled oats to which would be added about once a month a single pod of a green pea or a string bean. Celery and lettuce though offered were not eaten. It is at least possible that other desert living bipedal rodents are equally conservative of water. The scanty amount of liquid consumed does not, however, mean that volume for volume the kangaroo rats carry less water in their systems than other heavier drinkers, but only that the intake and outgo are proportionately reduced. An increased visceral load imposes greater gravitational strain on the column, and if increased visceral load could be demonstrated the effect could be studied.

REPRODUCTION.—The total volume of the young born in one litter should be reflected in the anatomical adaptations, but there is not

sufficient data on this subject to use in considering the young as a factor in vertebral form.

In the Dipodidæ, for example, I find records of the young of *Zapus* numbering from four to eight; in *Allactaga* litters of five or six; in *Jaculus* a litter of seven. These records show no significant difference. Until there are data on series of each genus correlated with weight of young at birth and weight of mother, the factor of weight and size of young must be considered constant.

The number of young in *Pedetes* has apparently been reduced. Litters of one and two are recorded, whereas the number of young born to generalized rodents is usually very high.

BURROWING.—All of the Dipodidæ are probably good diggers since there are published accounts of the burrows or digging operations of *Sicista*, *Zapus*, *Allactaga*, *Dipus*, *Scirtopoda*, and *Jaculus*. All of the Heteromyidæ burrow, and some species of the genus *Dipodomys* are known to dig very extensive labyrinths. Caged *Perognathus* and *Dipodomys* which I have had, spent a large part of their active hours in moving the sand about the cage. This was done by synchronous strokes of the fore feet throwing the sand back to within reach of the hind feet which carried it back farther still. When the sand was roughly banked in the corner or against the wall by this action, the animal would turn around and push the sand into the desired spot with the fore feet. *Pedetes* and *Notomys* are said to excavate burrows. The habits of the Madagascar and New Guinea forms are unrecorded.

The fore limbs of the ricochetel rodents, though always reduced both in proportion to hind legs and body length, are important structures in dressing the fur, in feeding, and in digging. Burrowing necessitates the retention of well-developed fore limbs, but for efficiency these must be short, and it is conceivable that burrowing, not disuse, has been responsible for their reduced length. The degree of reduction however, is, exceeded in the most specialized and gigantic of bipedal dinosaurs and by some of the kangaroos which do not burrow. The observation of Serebrennikov (1930) that *Allactaga jaculus* does all of the actual excavating of its burrows with the incisor teeth (which protrude forward in this genus) may be considered further evidence that the fore limbs are not shortened in accommodation to burrowing habits. The ricochetel Insectivora have not had the fore limbs strikingly shortened in relation to body length, which may be considered evidence that they resort to quadrupedal progress with some frequency. It is not thought that they use the hands a great deal for manipulating their food, or that they burrow extensively.

There is little uniformity in the vertebral adaptation of burrowing animals. Some, such as the marsupial mole (*Notoryctes*) have shortened necks with fused vertebræ; others, as the pocket gopher (*Heterogeomys*) have shortened necks with broad but unfused vertebræ; still others, as Brewer's mole (*Parascalops*) retain necks of primitive length and show no tendency to broaden or coalesce the vertebræ. All forms examined, however, even such partially fossorial forms as the prairie dog (*Cynomys*), as contrasted to a tree squirrel (*Sciurus*), show a strengthening of the sacrum and the pelvic attachments. Furthermore all show a tendency toward linear uniformity in length of neural spines, and all have the lumbar spines short, flat-topped, and broad. There is among them a strong trend toward reduction of the lumbar diapophyses.

In all of these features, except the parallel development in some forms of short necks, the ricochetal rodents differ widely from burrowing animals. In determining structure of the column, the ricochetal habits in these animals are dominant to their fossorial activities.

THE RICOCHETAL TYPES OF MAMMALIA

Of the eighteen generally recognized living orders of mammals several are so specialized in their locomotor apparatus that there is no possibility of their becoming adapted either to quadrupedal saltation or to the ricochet. Two of these orders, the Cetacea and the Sirenia, are exclusively aquatic. A third, the Pinnipedia, is practically so. The Chiroptera have diverged widely from other mammals through their life in the air. The Dermoptera have become so specialized for gliding that they are unable to run in the manner of more generalized mammals. The Proboscidea are far too large for leaping to be possible. It is true that the Reptilia developed bipedal giants in *Tyrannosaurus* and its relatives, but fossil footprints show that the great bipedal dinosaurs ran by using alternate strides.

Seven of the remaining twelve orders in their primitive stages, it would seem, might have developed some ricochetal species, yet have specialized in other types of locomotion. These are the Monotremata, Carnivora, Xenarthra, Tubulidentata, Artiodactyla, Perissodactyla, and Hyracoidea. The Primates as a group have developed for tree life. Six at least of the living genera are, however, occasionally or commonly bipedal: man, the two genera of gibbons, the spider monkey, *Propithecus*, and the aberrant *Tarsius*. *Propithecus* and *Tarsius* are, in a sense, ricochetal, yet their life is largely confined to the trees, and their feet are profoundly different from all other ricochetal types in their prehensile ability.

The Lagomorpha, though quadrupedally saltatorial, have never developed true ricochetel types. Some species will rise on their hind legs and take short hops on these, but when speed is paramount all four feet are used. It has been said that the Greenland hare (*Lepus groenlandicus*) travels far at high speed on its hind legs, but these observations need confirmation.

Three large and primitive orders remain, each of which has invaded several realms of locomotion. The Marsupialia, the Insectivora, and the Rodentia have developed arboreal, natatorial, fossorial, and ricochetel types.

Among the marsupials there have been, apparently, two independent developments of ricochetel habits. One of the three families of the Polyprotodontia, the Dasyuridæ, has developed a ricochetel representative. The ricochetel species of the Diprotodontia are all placed in one family, the Macropodidæ, a group containing no other locomotor types.

The Macroscelididæ are the only ricochetel Insectivora, and they are confined to Africa.

The Rodentia have more successfully developed divergent locomotor types than any other group. A statement of the number of independent origins of bipedal groups will vary, however, according to whose classification one accepts.

The classification of the Rodentia is in a chaotic state. The only recent reviewers of the whole group are Miller and Gidley (1918), but these authors have not yet published more than a synopsis of their researches, with the result that some other workers are hesitant about accepting their classification. Simpson (1931) has recently published his views on the classification of all the Mammalia, and for the Rodentia has compiled a generally conservative system that follows most closely that of Weber.

For this report I have adopted a classification of the ricochetel rodents that seems in accord with the best recent researches. In the main it follows Miller and Gidley (1918), but is different in some features. A summary of the classification outlined below is given in figure 5.

DIPODIDÆ.—A natural group of ancient origin in which all the members, with the possible exception of the genus *Sicista*, are ricochetel. Their range is holarctic.

Affinities with the Myomorpha are suggested by Simpson (1931) and other authors. Miller and Gidley (1918), however, erect a new sub-order, the Dipodoidæ, in which they place the Dipodidæ and a number of other families, such as the Paramyidæ, Aplodontiidæ, Anomaluridæ, and Pedetidæ.

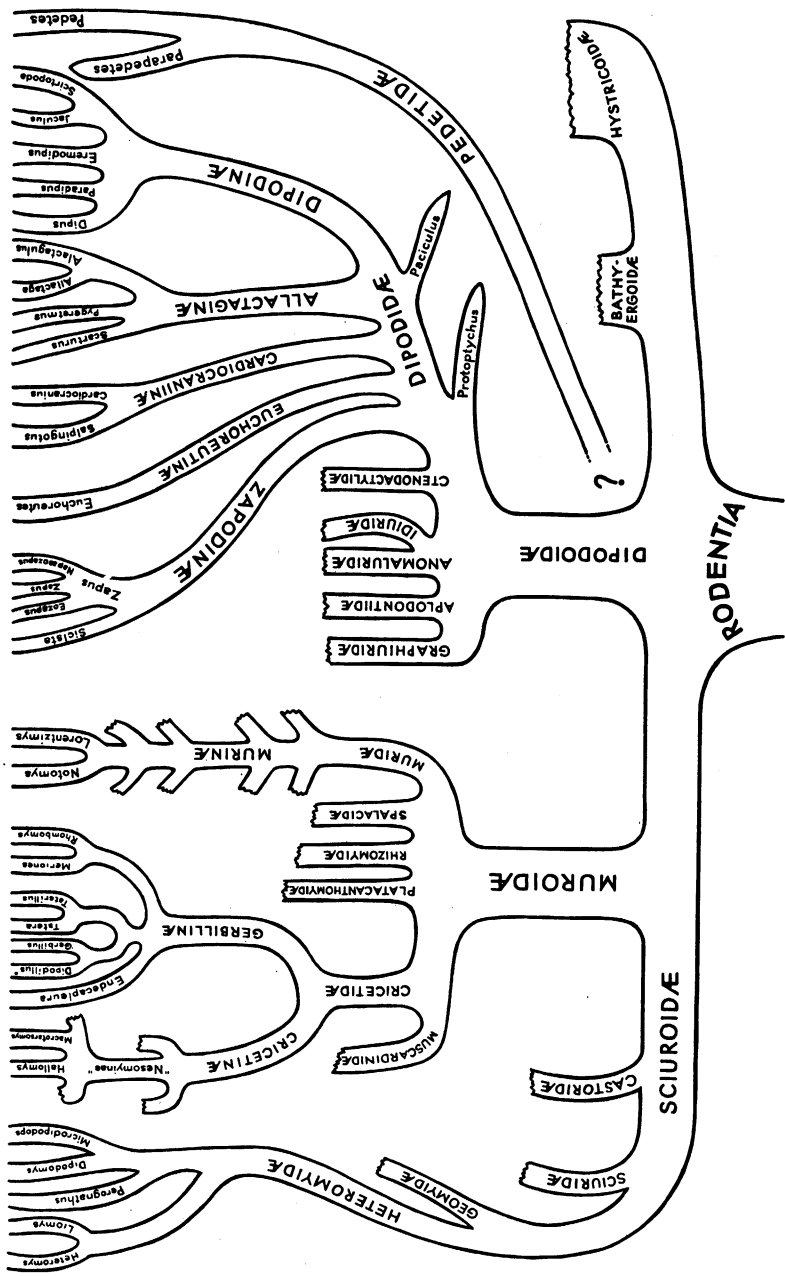


Fig. 5. The supposed interrelationships of the ricochet rodents and their allies. Groups which have not produced ricochet types are shown as broken branches. Fossil genera are placed in closed branches. The characters of the genera named are given in the text.

Vinogradov has recently revised the living Dipodidæ. The first sections of this revision (1925, 1930), the only ones which have so far appeared, concern genital, skull, and mandibular characters, respectively. Though others, among them Brandt (1844), Howell (1920), Lichtenstein (1828), Lyon (1901), Méhely (1913), Pocock (1922), Preble (1899), and Thomas (1908) had done much work on these rodents, their classifications concerned but sections of the family, were based on scanty material, or were not sufficiently documented. Vinogradov, considering the whole group, has had abundant material (that of the Museum of the Academy of Sciences of the Union of Socialistic Soviet Republics, the Berlin Museum, and the British Museum). His review is highly original and, in my opinion, very satisfactory. Vinogradov's revision, however, has to date extended only to generic and super-generic groups. For the specific arrangements, with the exception of that of the Zapodinae, I have been dependent on a scattered literature and assume responsibility for my generic associations. My species of *Sicista* are based in part on Méhely's revision of the European members of the genus but are individually of little significance when one considers the present chaotic state of the classification of this genus. For the members of the genus *Zapus* (and the subgenera *Napæozapus* and *Eozapus*) I have used Preble's Monograph.

The genera of the Dipodidæ are the following:

Sicista, GRAY.—Bush mouse (Pl. XIII). Europe and Asia from Norway to Lake Baikal. A small aberrant dipodid with the hind feet and the tail modified for scansorial existence. It is, however, an active leaper and probably employs the ricochet.

Zapus, COUES.—Jumping mouse (Pls. XI, XIV). North America and Szechwan. The American species inhabit meadows and woodlands near water. The jumping mice are long-tailed rodents with greatly elongate hind legs. Though capable leapers, they often progress on all fours.

Euchoreutes, W. L. SCLATER.—Long-snouted jerboa. Chinese Turkestan and Inner Mongolia. This is a genus of five-toed jerboas, externally somewhat similar to *Allactaga*. It is certainly bipedal in habits.

Cardiocranius, SATUNIN.—Club-tailed dwarf jerboa (Pl. XI). Gobi Desert. This diminutive jerboa is noteworthy for its short, heavy tail. To judge from external appearances it is strictly bipedal.

Salpingotus, VINOGRADOV.—Long-tailed dwarf jerboa (Pl. XVII, fig. 1). Western Gobi Desert, (?) Afghanistan. This genus possesses the most highly inflated auditory and mastoid bullæ of any mammal, and one of the species (*S. kozlovi*) the longest tail. It is probably strictly bipedal.

Allactaga, F. CUVIER.—Five-toed jerboa. From the Dnieper River in Ukraina to eastern Mongolia. A jerboa with long feet, a long, tufted tail, long ears and protruding incisors. It is bipedal.

Alactagulus, NEHRING.—Small five-toed jerboa (Pl. XI). Central Asia. External appearance of a small species of *Allactaga*.

Pygeretmus, GLOGER.—Feather-tailed jerboa. Central Asia. A jerboa with a long tail, well-haired its entire length and variously described as distichous and as dorsally rounded.

Scarturus, GLOGER.—Four-toed jerboa (Pl. XV, fig. 2). Northeast Africa. A jerboa whose principal external characteristic is the presence of but four toes on the hind feet.

Dipus, ZIMMERMAN. Three-toed jerboa. Central Asia, Mongolia. This and the following four genera of three-toed jerboas are similar in proportions. They have greatly elongated rear feet in which the metatarsals are fused into a cannon bone. The toes bear well-developed brushes on their under surfaces. The tail is always haired distally and sometimes along its entire length. All are ricochetors.

Scirtopoda, BRANDT.—Three-toed jerboa. Southeastern Europe and western Asia.

Paradipus, VINOGRADOV.—Comb-footed jerboa. Turkmenia. The feet bear thickened, horny bristles on the outer edges.

Eremodipus, VINOGRADOV. Three-toed jerboa. Turkmenia.

Jaculus, ERXLEBEN.—African three-toed jerboa (Pls. XV, XVI, fig. 1). North Africa, Arabia, Iraq, and Persia.

PEDETIDÆ.—A family possibly remotely related to the Dipodidæ. Contains but one living genus. Parsons (1898) concluded from myological studies that *Pedetes* was allied to the Dipodidæ, but that it was structurally nearer the Hystricomorphs than is the latter group. Miller and Gidley (1918) appear to have adopted a similar view of its affinities.

Pedetes, ILLIGER.—Spring Haas or jumping hare (Pl. XVII, fig. 2). Southern and eastern Africa. The largest of ricochetal rodents. The tail which is muscular and hairy is about as long as the head and body. The toes are capped with heavy, hoof-like claws.

Parapedetes, STROMER.—A *Pedetes*-like rodent from the Miocene of southwest Africa. It was different from the modern genus in its smaller size, less specialized skull, and shorter hind legs.

HETEROMYIDÆ.—A well-defined family of small rodents characterized in part by the presence of external fur-lined cheek pouches. The group is confined to the western United States, Mexico, Central America, and northern South America. The family is universally conceded to be a branch of the Sciuroidæ (Sciuromorpha). The only modern genera are the following:

Heteromys, DESMAREST.—Spiny pocket mouse. Tropical or subtropical continental America from Mexico to Ecuador. Trinidad and the West Indies. A rat-like quadrupedal rodent with a pelage of grooved spines and a tail usually longer than the head and body.

Liomys, MERRIAM.—Spiny pocket mouse. Tropical and Sonoran Zones from southern Texas and Sonora to Panama. Externally similar to *Heteromys*.

Perognathus, WIED.—Pocket mouse (Pl. XVIII, figs. 1–3). North America west of the Mississippi, from British Columbia to the Valley of Mexico. Usually in desert and semidesert country. These are small rodents of murine form whose tail,

which is often highly tufted or penciled, usually about equals head and body length. The rear legs are slightly elongated. The locomotion is typically quadrupedal, but there is a tendency toward saltation. It is suspected that some members of the genus may occasionally employ the ricochet.

Microdipodops, MERRIAM.—Pygmy kangaroo rat, or kangaroo mouse (Pl. XVIII, fig. 4). Arid parts of the Great Basin district in Nevada, California, and Oregon. Probably limited to areas of vegetated fine sand. A small, large-headed, jumping rodent with heavy untufted tail longer than the head and body. The rear legs are elongated. The soles of the five-toed hind feet are densely haired.

Dipodomys, GRAY.—Kangaroo rat (Pl. XIX). Warmer arid sections of the western United States and northern Mexico. The tail, which is usually half longer than the head and body, bears a tuft. The hind legs are greatly elongated. The soles of the feet are more or less hairy.

For the specific names of the kangaroo rats of the genus *Dipodomys* I have adopted the list of Grinnell (1921). Miller's (1924) list has been of great service in reference to the other Heteromyidæ.

MURIDÆ.—A family of rodents which is cosmopolitan in distribution. Most of the species are generalized quadrupedal types, but some are modified for specialized modes of life.

Rattus, G. FISCHER.—Rat (Pl. XII, fig. 1). Originally confined to the Old World. Now cosmopolitan. The members of the genus are terrestrial or slightly scansorial quadrupeds. The only species considered here are the Norway or wharf rat (*R. norvegicus*) and a smaller Chinese species (*R. confucianus*).

Notomys, LESSON.—Jerboa mouse (Pl. XII, fig. 2; Pl. XX, fig. 1). Australia. A lightly built mouse whose external proportions parallel those of a jerboa to a remarkable degree.

Lorentzimys, JENTINK.—Jerboa mouse. New Guinea. A little-known animal whose proportions are those of a ricochetor.

CRICETIDÆ.—A highly diversified family represented on all continents of the world. It has given rise to saltatory rodents two or more times. Simpson has without comment relegated the family to the synonymy of the Muridæ. A group of Madagascar genera, including two which may be ricochetors (*Hallomys* and *Macrotarsomys*), has been made a subfamily, the Nesomyinæ, by Forsyth-Major (1897). He considered the group the most primitive of cricetine rodents and concluded that it was near to the Cricetinae and the Microtinae. Miller and Gidley (1918) have not recognized the Nesomyinæ but have placed them among the Cricetinae.

The Gerbillinæ, some of which are apparently bipedal, are considered a subfamily of the Cricetidæ by Miller and Gidley and others.

The genera of Cricetidæ referred to in this paper are the following:

Tatera, LATASTE.—Gerbilline. Asia and Africa.

Taterillus, THOMAS.—Gerbilline. Africa.

Endecapleura, LATASTE.—Gerbilline. Africa.

Dipodillus, LATASTE.—Pygmy Gerbilline. Asia and Africa.

Gerbillus, DESMAREST.—Gerbilline (Pl. XX, fig. 2). Africa.

Members of all of these five genera of lightly built gerbilles may occasionally ricochet, but it is improbable that any of them are primarily ricochetors. It is suspected that species of *Dipodillus* and *Gerbillus* are more likely to ricochet than those of the preceding three genera.

Hallomys, JENTINK.—Madagascar.

Macrotarsomys, MILNE-EDWARDS AND GRANDIDIER.—Madagascar.

These two genera of "Nesomyinæ" are the nearest approach to ricochetors found in Madagascar. The first may possibly ricochet, the second probably does so.

GEOGRAPHICAL OCCURRENCE OF RICOCHETAL TYPES

Ricochetal rodents occur in every continent but South America. The greatest number of forms occur, however, in the steppes and deserts of Eurasia. In Europe, due to the lack of suitable habitat, there are few species. The most primitive of the Dipodidæ, *Sicista*, spreads through the boreal sections of Europe and Asia from Norway to Lake Baikal. Species of *Allactaga*, of *Dipus*, and of *Scirtopoda* occur in the southern European steppes east of the thirtieth meridian.

In Asia a rich fauna of the Dipodidæ is found, particularly in the Gobi and the deserts of Turkestan, Persia, and Arabia. In fact every genus of this family is to be found in some part of the continent, unless one assigns full generic rank to *Eozapus* and *Napæozapus*. In this latter case the North American genera *Napæozapus* and *Zapus* would prove the exceptions. It is probable that Central Asia is the center of origin and dispersal for the Dipodidæ. In Asia, too, are found many of the Gerbillinæ, some of which appear to be partially adapted to ricochetal progress.

In Africa the jerboas occur only in the arid North, but the Pedetidæ occupy much of the southern and eastern sections of the continent. Some species of jumping rats of the genera *Gerbillus* and *Dipodillus* closely approach ricochetal habits, if they do not in fact attain them, and these genera occur in much of the territory between the ranges of the Dipodidæ and the Pedetidæ.

Madagascar has produced at least two rodents from cricetid stock that probably employ the ricochet. One of these (*Hallomys*) occurs in the southeastern section of the island, whereas the other (*Macrotarsomys*) lives in the open central-western district.

Australasia has produced not only its ricochetal marsupials, but also two genera of bipedal mice. One of these (*Notomys*) attains its highest development in the central arid plateau. The other (*Lorentzimys*) occurs in Dutch New Guinea, though its habitat seems not to have been recorded. There appear to be other forms of jumping mice in the grassy plains of Papua and in the forests of northeast New Guinea, but I am unable to learn their identity.

In North America there are the dipodid genus *Zapus* and the sub-genus *Napæozapus*. These occur chiefly in the meadows, fields, and woodlands of the North. In the arid districts of the southwestern United States and northern Mexico the heteromyid kangaroo rats (*Dipodomys*) and kangaroo mice (*Microdipodops*) have specialized to a point exceeded only by the jerboas, while some of the related pocket mice are nearly, if not actually, bipedal at times.

It is more than a coincidence that the ricochetal rodents of Asia, Africa, Australasia, and North America have reached their greatest specialization in the arid desert countries. This type of locomotion is obviously adapted to a milieu in which the animal could see well ahead where it was to land, and where vegetation would not interfere unduly with its passage. In desert countries there is also less opportunity of concealment from enemies than in well-vegetated country, and fewer avenues of escape than in a land where the development of arboreal or natatorial habits may offer additional protection. In the desert the possible necessity of going further from the burrow for food would give advantage to the animal able to travel most rapidly, and thus better able to escape its enemies when pursued away from home than a quadrupedal type. Numerous descriptions of the rapid dodging of ricocheting jerboas and jumping mice attest the added advantage of this type of locomotion to an animal attempting to escape in an open region.

The geographical distribution and habitat preferences of the meadow jumping mouse and the woodland jumping mouse, as well as certain other species, demonstrate that ricochetal progress is not confined to desert country nor is it of advantage there only. In these cases though, adaptation has not been so radical as in the desert-living genera. It is also believed that the jumping mice resort to the ricochet less frequently than do jerboas and kangaroo rats.

OBSERVED LOCOMOTION IN THE RICOCHETAL RODENTS

Ricochetal locomotion is well established by published observations for *Zapus*, *Napæozapus*, *Allactaga*, *Dipus*, *Jaculus*, *Pedetes*, *Dipodomys*,

and *Microdipodops*. I myself have observed such progress in *Zapus hudsonius*, *Zapus (Napæozapus) insignis*, *Jaculus orientalis*, and *Dipodomys merriami*. The limb proportions of the jerboas show clearly that these animals could not move comfortably any other way than by ricocheting or bipedal running.

The primitive zapodid *Sicista* is not usually described as a leaping rodent in the sense that *Zapus* is such, and its foot length does not indicate that it is as specialized for leaping, but I am led to believe by a photograph and a note by Argyropulo (1930, pp. 258-261, reproduced here as Pl. XIII, fig. 1) that it is quite possible that this species (*Sicista ?tianshanica*) at least may be ricochetal. Argyropulo writes of this species progressing by long shallow leaps, with its body drawn up and its tail stretched almost straight out behind. That the *Sicista* of Scandinavia is well adapted to climbing is shown by the notes and photographs of Arwidsson (1930) (Pl. XIII, figs. 2, 3).

Observations published by Cerva (1929, p. 393) state that *Sicistæ* which he had captive jumped around on the sand floor of their cages like fleas, and that they were able to leap out from a glass aquarium with sides 15 cm. high. Cerva also states that this kind of mouse if held by the fore feet will wrap its tail around one's free finger, which bears out the deduction that they are prehensile-tailed.

Zapus creeps along on all four feet a good part of the time, particularly when feeding. I have observed such progression on several occasions. Living in well-vegetated habitats—as do those species which I know—they must be forced to resort to quadrupedal habits much of the time. *Zapus hudsonius* frequently travels in the low, arched runways of the meadow mouse (*Microtus pennsylvanicus*), where it could not travel erect even if it chose to do so.

The jerboas occasionally, or often, move along on all fours. This is quite awkward for them, and a captive *Jaculus* which I have watched used the fore feet only when it wished to move but a few inches, or when crawling under a very low piece of furniture. This individual in its ordinary progress about the room moved by bipedal running and not by hopping, which seems to be a common method of progression with jerboas that are not pursued.

The pocket mice of the genus *Perognathus* (Heteromyidæ) show strong bipedal potentialities, but the data at hand suggest that few species, and these but rarely, resort to the ricochet. The only pocket mouse which I have observed moving rapidly is *P. penicillatus eremicus*, a desert-living species. On no occasion did any of the three specimens

which I had as captives ricochet over the floor, though they had ample space and were occasionally frightened by kangaroo rats which were liberated with them. The smooth, hard nature of the floor and their lack of familiarity with it may have inhibited their moving in this manner. Three of their types of locomotion are illustrated with actual track records (Fig. 4).

My most informative data have been generously supplied by Dr. Seth B. Benson of the Museum of Vertebrate Zoölogy, Berkeley, who sent to me copies of his notes very shortly after they were taken. Rather than mar the accuracy of Dr. Benson's observations by rewording or condensing them, I shall quote him in full on the several specimens which he had observed. The silky pocket mice (subgenus *Perognathus*) are less saltatorial than the coarse-haired pocket mice (subgenus *Chætodipus*), according to Dr. Benson, and can hardly be classed as ricochetors. His observations on this group are:

Perognathus l. longimembris at Rose Station, 1300 feet, Kern Co., Calif., March 27, 1930.

We investigated the problem of progression in pocket mice using the thin layer of fine dirt over the floors and tables inside the Station to record the tracks. I found that even when the mouse was moving rapidly all four foot marks were present. The mark of the tail was also present. When the mouse moved slowly the hind feet were used alternately. Mice we have chased at night appeared to use all four feet. A *Peromyscus* we chased seemed more saltatorial than the pocket mice.

Perognathus p. bangsi at 1 mi., S. Peck's Butte, 2250 ft., Los Angeles Co., California. (About 12 mi. E. Palmdale.) April 5, 1930.

We took one out to the sand dunes to find out whether or not the creatures are ever bipedal. The mouse protested vocally when we turned him out on the sand and whenever we approached him. . . . The mouse showed great reluctance to run anywhere save to the nearest bush, the light and heat apparently bothering him. But we finally did get him to run very well. His gait was not so markedly bobbing as in the *penicillatus*, neither did his tail move about so much.

In his first dash, in a six foot stretch after the mouse had attained high speed, the tracks were apart 12, 7, 17, 14, 12, 12 inches, the irregularity being due to the uneven ground. In all of these the marks of all four feet were present. The marks of the hind feet were 20 mm. apart, the fore feet, 10 mm. apart, and 18 mm. behind the marks of the hind feet. The marks were side by side.

I do not believe that this pocket mouse very often leaps without using the front feet. It probably does so occasionally. Certainly it did not while running at what was probably the limit of its speed. And certainly at ordinary speeds, as shown by tracks over the sand, all four feet are normally used.

I might add that the sand at this place was very fine, tracks of ground beetles being easily preserved. I did not see any bipedal tracks save those made by kangaroo rats. The rodent population was overwhelmingly of *Perognathus p. bangsi*, *Perognathus penicillatus stephensi*, *Dipodomys m. merriami*, and *Dipodomys deserti*. I caught no *Peromyscus* and but one *Onychomys*. For these reasons I referred all small

tracks to pocket mice and in no case did I see anything save four-footed tracks, which were plentiful.

Perognathus xanthonotus, 1 mi. S. Walker Pass, 5300 feet. Kern County, California. April 12, 1930.

After digging a little more the mouse came out and escaped from the excavation, running down the hill with great speed. It ran on all fours. But we captured it.

The *parvus* group of pocket mice do not appear to be much adapted for the saltatorial mode of progression. My notes are limited to the following observation.

Perognathus xanthonotus. August 7, 1929, Freemont Canyon, 4900 feet, Kern Co., California.

When I had almost reached the end of the burrow a *Perognathus* ran out swiftly and took refuge in a thick bush. I chased the *Perognathus* from bush to bush for five minutes before I captured it. . . . It ran very swiftly on all fours like an "ordinary" mouse, or it appeared to run so. It was very wary of me and seemed quite terrified.

I have observed *Perognathus l. bangsi* and *Perognathus i. inornatus* in the field and have had them and also *Perognathus f. flavus* in captivity. When moving slowly they certainly use all four feet. Those I have observed in the wild at night also used all four feet or certainly appeared to do so. I have also seen them make rather long jumps.

The notes on the coarse-haired pocket mice are:

I have had specimens of *Perognathus c. californicus* in captivity for the past seven months. This mouse is apparently as highly specialized for leaping as any member of the genus. When crawling along slowly, when the footing is insecure, this mouse uses all four feet alternately, catlike, but usually the hind feet are moved together. When running fairly rapidly all four feet are placed on the ground. Only when running very rapidly does the truly saltatorial habit come into play. Mice I have frightened have leaped six feet in distance and have leaped up to a height of about two feet when jumping directly upwards. These leaps were taken blindly, without regard to consequences, and probably represent the maximum. I have been impressed throughout by the lack of saltatorial progression even when plenty of space has been provided. However, they would probably be able to handle themselves better on rough ground, where I have not yet watched them. I might add that I have seen my mice walk erect in their cages, using their tails as props.

I have had specimens of *Perognathus intermedius* in captivity and I have yet to see them use the saltatorial mode of running, although I do not doubt that they may use it. But I have seen them make long, sudden leaps.

Perognathus penicillatus stephensi, at 1 mi. So. Peck's Butte, 2250 ft., Los Angeles County. April 5, 1930.

The first mouse released ran with a distinct bobbing or hopping motion. But this motion was not more marked than that which takes place when *Peromyscus* runs. The mouse dashed from bush to bush seeking shelter until driven out. And it was quite difficult to drive the mouse into the open. The dashes averaged 25 feet in length, and presumably, while making the dashes, the mice reached their highest speed. The tail was waved up and down vigorously, kangaroo rat fashion. In the first dash the tracks were 14 inches apart for 15 feet. The tracks were represented by two dots $\frac{3}{4}$ inches apart. The dots were deep, indicating that the feet struck the

sand vigorously and that the mouse was running on its toes. In the next seventeen feet, after the mouse had rested awhile, there were 17 sets of tracks. The distance between tracks varied from 10 to 14 inches depending upon the irregularities in the surface of the sand. In this series, marks of all four feet were present. The marks of the hind feet were now 1 inch apart and preceded the marks of the front feet by about 1 inch. The right front foot mark was slightly in advance of the left. Subsequent tracks, made over a period of five minutes contained marks of all four feet. In making these the mouse appeared to run as swiftly as before. It may be true that the fore feet touched the ground lightly during the first dash but that the marks were obscured by sand kicked backwards by the hind feet. But this is not likely.

The other mouse ran on only two feet for a distance of six feet, after which it used all four feet. The marks of the front feet were opposite and varied from 20 to 55 mm. behind the hind foot marks. The longest leap on the level was 22 inches.

Perognathus penicillatus does have the power of saltatorial movement but doubtless uses it only occasionally, otherwise we would have found their tracks on the sand showing it. The experiments we tried were not conclusive because of the heat and light. I judge that the temperature was about 80 degrees F. The mice were distressed from their exertions after a few minutes. But the experiments did show that under these conditions the mice used all four feet most of the time, a thing which kangaroo rats would not do. I have released many of the latter from live traps when rather cold and even then, when not capable of moving swiftly, they used only the hind feet.

Of *Dipodomys spectabilis* Bailey (1905, p. 148) wrote:

"I have never seen a print of the tiny hands which apparently are never used in locomotion." Warren (1910, p. 75) noted, however, a *Dipodomys montanus* which ran on all fours without leaping. As the discrepancy between the lengths of the fore legs and rear legs is not so great in the kangaroo rats as in jerboas, it is probable that among some of the species of *Dipodomys* quadrupedal locomotion is not a rare occurrence.

Tracks of *D. deserti* show that it may jump a distance of eight feet, according to Seton (1929, p. 434).

I have recorded a number of short runs of specimens of *D. merriami*. When hopping less than 75 mm., the fore feet came into contact with the floor (Fig. 3 C). Only once did the fore feet make track marks on a longer leap, and this on one of 130 mm., which was the average length of hops made. The longest leap recorded was of 240 mm. (nine and one-half inches) (Fig. 3 B). It was, however, impossible to frighten these animals into truly long leaps, nor did they have an opportunity to do their best, for the floor was of smooth brown wrapping paper. The tracks of fore and hind feet were always strictly paired, except at a turn. At times the feet would touch medially, at other times would be separated as much as 22 mm. This was not correlated with the length of the jump. In no case was there alternate moving of the hind feet as in the jerboas. The tracks showed completely digitigrade progress. The tail marks showed

only when the animal slowed down at the end of a run or through the run when the tail was heavily burdened with ink (Fig. 3 D).

The Australian kangaroo mice *Notomys* (Muridæ) are listed as ricochetal chiefly on inference from an examination of photographs of living specimens. Though I find no specific statement to the effect that they do bound along on their hind feet, it is practically certain that they do so.

The Malagasy Nesomyinæ, *Hallomys* and *Macrotarsomys*, are considered ricochetal solely on the basis of their foot lengths.

It has been stated by Büttikofer (according to Allen and Coolidge, 1931, p. 597) that the giant African rat (*Cricetomys gambianus liberix*) "will sit up on its haunches using its tail for a support like a miniature kangaroo. Like the latter it will sometimes leap forward on its hind feet alone." Since the paper in which this quotation appears was not published until after my manuscript was completed, I have not given consideration to the vertebral structure of this animal. There is nothing about the external character of *Cricetomys* to suggest that it is a ricochetor.

It may be that a few other rodents of several groups that to me appear to be on the threshold of ricochetal development will some time be known to advance occasionally in this specialized manner. This might be looked for among the Murinæ, Gerbillinæ, Cricetinæ, Nesomyinæ, Chinchillidæ, and perhaps elsewhere.

The number of records showing the actual distance covered in leaps of these animals are so few that they are of no value for comparative purposes. The leap which is the longest in terms of comparative length which I have encountered, is a twelve-foot spring by *Zapus* (*Napæozapus*) *insignis*, which is about forty times the length of its head and body (Snyder, 1924, p. 234). It is probable that this can be exceeded by some of the jerboas. Leaps of *Dipus sagitta nogai* 140 cm. in length are recorded by Boehme and Krasovsky (1931, p. 426), and it is said that such leaps seriously exhausted the animal.

MATERIALS

The selection of a primitive type of rodent with which to compare ricochetal forms is not simple, for few animals are not specialized one way or another in their locomotor habits. Among the Heteromyidæ we are fortunate in having the living primitively quadrupedal types of *Heteromys* and *Liomys*. Within the Dipodidæ there is the more or less primitive genus *Sicista* which, however, as elsewhere noted, is somewhat

arboreal in its habits and which has the vertebral column, at least of the tail, adapted to scansorial existence. The relationships of *Pedetes* are obscure so that we cannot compare it with any quadrupedal type that may be considered closely related. Among the Muridæ there are many primitive forms and all transitional phases between these and good ricochetal species. Since, however, for lack of specimens, this study does not adequately embrace the ricochetal Muridæ, the careful selection of a genetically related type is of no major importance. The primitive Eocene rodent *Paramys* is for reasons of antiquity and recognized generalization (Matthew, 1910) a good type to use for comparison as to certain features. The species of *Paramys* which I have for comparison, however, are all animals larger than *Pedetes* and not easily comparable to the small rodents. Furthermore, though the specimens are in good condition for fossils, there is no one specimen that is perfect. Only the basic features may then be considered. For practical purposes of contrast in all characters and groups, I have taken as a generalized type a murid rodent, the common house rat, *Rattus norvegicus*, and included in the study the more generalized genera of each group under consideration.

I do not compare extensively the ricochetal rodents with ricochetal insectivores or marsupials as the heritage of these groups is different. Such a comparison, though interesting, belongs within a realm beyond the scope of this paper and is at the present time included in the researches of another investigator.

I had available for study over sixty skeletons of rodents belonging to ricochetal groups. Some of these were complete, others no more than half so; some were mounted, some unmounted though largely articulated. A few were completely disarticulated. Some were so perfectly cleaned (the finest examples coming from the United States Biological Survey) that no possible detail was obscured or lost. Others were not well done and had to be partially recleaned.

The majority of the skeletons were misidentified or had such antiquated nomenclature applied to them that it was a major problem to name accurately the material with which I worked.

The most serious lack of specimens was that of the Australian *Notomys*, the New Guinea and Madagascar jumping rats, a good series of gerbilles, and specimens of the following genera of Dipodidæ: *Euchoreutes*, *Cardiocranius*, *Salpingotus*, *Alactagulus*, *Pygeretmus*, *Scarturus*, *Paradipus*, and *Eremodipus*. This is an imposing list, but unfortunately, of most of these there are either no skeletons in any collection, or the few that are known are now in use by another investigator.

The specimens available to me are itemized in the following list. The names of the museums whose catalogue numbers are given are abbreviated as follows:

AMNH—American Museum of Natural History
 DRD—Donald R. Dickey, California Institute of Technology
 MVZ—Museum of Vertebrate Zoölogy
 RTH—Private collection of the author
 USBS—United States Biological Survey
 USNM—United States National Museum
 WN—Württemberg Naturaliensammlung

SKELETONS USED IN THE STUDY

DIPODIDÆ	TOTAL NUMBER
<i>Sicista loriger</i> (USNM 122117)	1
<i>Zapus hudsonius</i> (AMNH 5403, 90655; DRD 13584)	3
<i>Zapus princeps</i> (RTH 40)	1
<i>Zapus (Napæozapus) insignis</i> (AMNH 74851, 74849)	2
<i>Allactaga mongolica</i> (AMNH 55978, 55980)	2
<i>Allactaga jaculus</i> (AMNH 227; WN 397, 1039)	3
<i>Dipus sowerbyi</i> (AMNH 55979)	1
<i>Jaculus jaculus</i> (WM 1145 a, 1145 b)	2
<i>Jaculus orientalis</i> (AMNH 35914, 70004, 70096; USNM 14606)	4
<i>Scirtopoda telum</i> (WN 1321)	1
PEDETIDÆ	
<i>Pedetes cafer</i> (AMNH 70392)	1
<i>Pedetes cafer orangizæ</i> (AMNH 81747)	1
<i>Pedetes cafer ?salinzæ</i> (AMNH 42057, 42025)	2
<i>Pedetes surdaster</i> (AMNH 52419)	1
HETEROMYIDÆ	
<i>Liomys species</i> (AMNH 16780)	1
<i>Liomys pictus</i> (AMNH 8347)	1
<i>Heteromys anomalus</i> (AMNH 7524)	1
<i>Heteromys longicaudus</i> (AMNH 3645)	1
<i>Perognathus apache</i> (AMNH 5556)	1
<i>Perognathus (Chætodipus) fallax</i> (AMNH 310; USBS 43061, 43062)	3
<i>Perognathus (Chætodipus) penicillatus eremicus</i> (AMNH 100022, 100023)	2
<i>Microdipodops megacephalus</i> (USBS 54579, 54815)	2
<i>Microdipodops m. dickeyi</i> (MVZ 38797, 38798, 38801)	3
<i>Microdipodops polionotus</i> (MVZ 17031, 24101, 27097)	3
<i>Dipodomys deserti</i> (DRD 15457)	1
<i>Dipodomys heermanni goldmani</i> (DRD 13207)	1
<i>Dipodomys heermanni tularensis</i> (DRD 13242, 13243, 13263)	3
<i>Dipodomys merriami</i> (AMNH 100021, 100057)	2
<i>Dipodomys m. simiolus</i> (DRD 9674)	1
<i>Dipodomys nitratooides</i> (DRD 13292, 13262, 13270, 13296, 13294)	5

SKELETONS USED IN THE STUDY (Continued)

HETEROMYIDÆ	TOTAL NUMBER
<i>Dipodomys ordii luteolus</i> (AMNH 184, 14983)	2
<i>Dipodomys phillipsii</i> (USBS 132763)	1
<i>Dipodomys spectabilis</i> (AMNH 35035, 68327)	2
GERBILLINÆ	
<i>Meriones auceps</i> (AMNH 55977)	1
<i>Tatera afra</i> (AMNH 210)	1
<i>Tatera robusta</i> (WN 2146)	1
<i>Gerbillus</i> species (AMNH 215)	1
CRICETINÆ ("NESOMYINÆ")	
<i>Eliurus penicillatus</i> (AMNH 31801)	1
MURINÆ	
<i>Rattus norvegicus</i> (AMNH 148, 181, 69551, 77725, 100084, 100085, 100086)	7
PARAMYIDÆ	
<i>Paramys delicatus</i> (AMNH 12506)	1
<i>Paramys robustus</i> (AMNH 19205, 13091)	2
<i>Paramys</i> species (AMNH 12561, 17031)	2

Notes concerning *Parapedetes namaquensis* from the Miocene of southwest Africa are taken from the description of Stromer (1926).

Besides these there was a large collection of skeletons of other rodents, and of ricochetal Insectivora and Marsupialia which were used for comparison. A number of additional specimens of *Dipodomys* arrived too late for inclusion in this report.

There were also available, preserved in alcohol, specimens of the following genera:

DIPODIDÆ

Zapus (*Napæozapus*), *Allactaga*, *Alactagulus*, *Jaculus*.

PEDETIDÆ

Pedetes.

HETEROMYIDÆ

Liomys, *Heteromys*, *Perognathus*, *Microdipodops*, *Dipodomys*.

GERBILLINÆ

Gerbillus

MURINÆ

Rattus, *Notomys*.

As skins and skulls, for study of external tail characters, etc. there were at hand specimens of the following:

DIPODIDÆ

Sicista, *Zapus*, *Zapus* (*Napæozapus*), *Zapus* (*Eozapus*), *Allactaga*, *Alactagulus*, *Cardiocranius*, *Dipus*, *Scirtopoda*, "*Stylodipus*," *Jaculus*.

PEDETIDÆ

Pedetes.

HETEROMYIDÆ

Liomys, Heteromys, Perognathus, Dipodomys.

GERBILLINÆ

Meriones, Rhombomys, Gerbillus, Dipodillus, Tatera, Taterillus.

Living specimens of the following species were observed during locomotion.

DIPODIDÆ

Zapus hudsonius, Z. (Napæozapus) insignis, Jaculus orientalis.

HETEROMYIDÆ

Perognathus penicillatus eremicus, Dipodomys merriami.

METHODS

It was my object to compare every skeleton in the series listed for all but a few of the points considered. Because of the imperfection of many skeletons, however, this object could not be fully realized. For some features, such as regional changes in volume of the centra, observations were limited to a small number of representative specimens, as it did not seem probable that a fuller series would demonstrate important differences. For the sake of contrast, any particular feature was studied not only among the rodents, but also in less detail in many skeletons of mammals of other groups. Where measurements were required or practical, these were made with calipers registering accurately to a tenth of a millimeter. Where angles were measured, this was done in one of two ways. Either the angle was read directly from a projection of the skeleton against a calibrated background, or by taking a series of measurements at perpendiculars to the plane of reference and then plotting these on graph paper. It was standard practice to measure one feature at a time through the entire series, in order that variation in technique would be minimized. Small asymmetries were not considered.

The particular points of measurement are those defined by Duerst (1926).

A binocular microscope was regularly used in the study of all small material.

Where it was convenient to express a measurement in percentage of body length, which is here usually referred to as precaudal length, the comparison made was to the total of the length of the skull between its most anterior point and the occipital condyles plus the length of the vertebral column along the curves between the anterior face of the atlas and the caudal end of the pseudosacrum (dried composite column height). It is believed that this measurement expresses body size more accurately than any other linear measurement possible on dried skeletons.

Lengths of particular bones of limbs, or of regions of the body are often expressed as ratios of precaudal vertebral length (Mollison, 1911, Howell, 1926). Whereas this system may be considered as advantageous in that it eliminates the variable length of the skull, it seems to me desirable to include skull length, in that the body proportions are determined in large part in relation to the functioning of the body mass as a whole. In such short-necked forms as the ricochetal rodents the head is an integral part of the body mass. If one were dealing with animals in which the neck were greatly elongated and the head small, as for example a swan, it might prove desirable to use the thoraco-lumbar-sacro-pseudosacral length as a unit of comparison, but with bipedal rodents which are so compacted as to be popularly described as looking like potatoes on toothpicks, I believe that the over-all length, exclusive of the caudal vertebræ, should be used.

The proportional lengths of any given region in a series of animals are most accurately expressed in terms of some factor external to them. Thus in comparing neck lengths, by expressing the measurements as proportions of head and body length, of precaudal, or presacral column lengths, diluting factors which mask some proportions are introduced, while by using such an external factor as thoraco-lumbar length the ratios stand out in true relation. Unfortunately this technique is not applicable to the column as a whole, inasmuch as there is no common unit to which all bear relation that is not itself an independent variable, or which, if considered stable, is not itself one of the units to be compared.

The shrinkage in length of the spinal column on drying is of so small a magnitude that it need not be considered as a serious source of error in any of the conclusions which I have drawn. Todd and Pyle (1928, p. 318) have found that in human material this shrinkage amounts to only 1.5 per cent of the dried ventral body height.

Though the work was done chiefly on cleaned skeletons, regional dissections were made when without them observed differences in skeletons could not be understood. Limited dissections were made of *Zapus*, *Jaculus*, *Pedetes*, *Heteromys*, *Dipodomys*, and *Rattus*.

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THE NUMBERS OF VERTEBRÆ

Cervical Region

Though the normal mammalian quota of seven cervical vertebræ is not reduced in any of the ricochetal species, these elements are in some cases fused to an extent equaled only among the Cetacea and certain burrowing mammals where also strong, short necks are better adapted to the mode of life.

With ricochetal development and its usually concomitant, though probably unrelated, increase in head size, there is a shortening of the neck. This is probably an adaptation toward making the body more compact and, hence, easier to manage as a unit. A short neck virtually eliminates bobbing of the head and thus lessens the work of the dorsal neck muscles. Fusion of cervical elements carries the same mechanical principle to a point of greater efficiency, simplifying and strengthening the region. This shortening of the neck and fusion of elements necessarily minimizes movement in this region, but some of the necessity for flexibility is eliminated by the extreme shortening of the fore limbs which

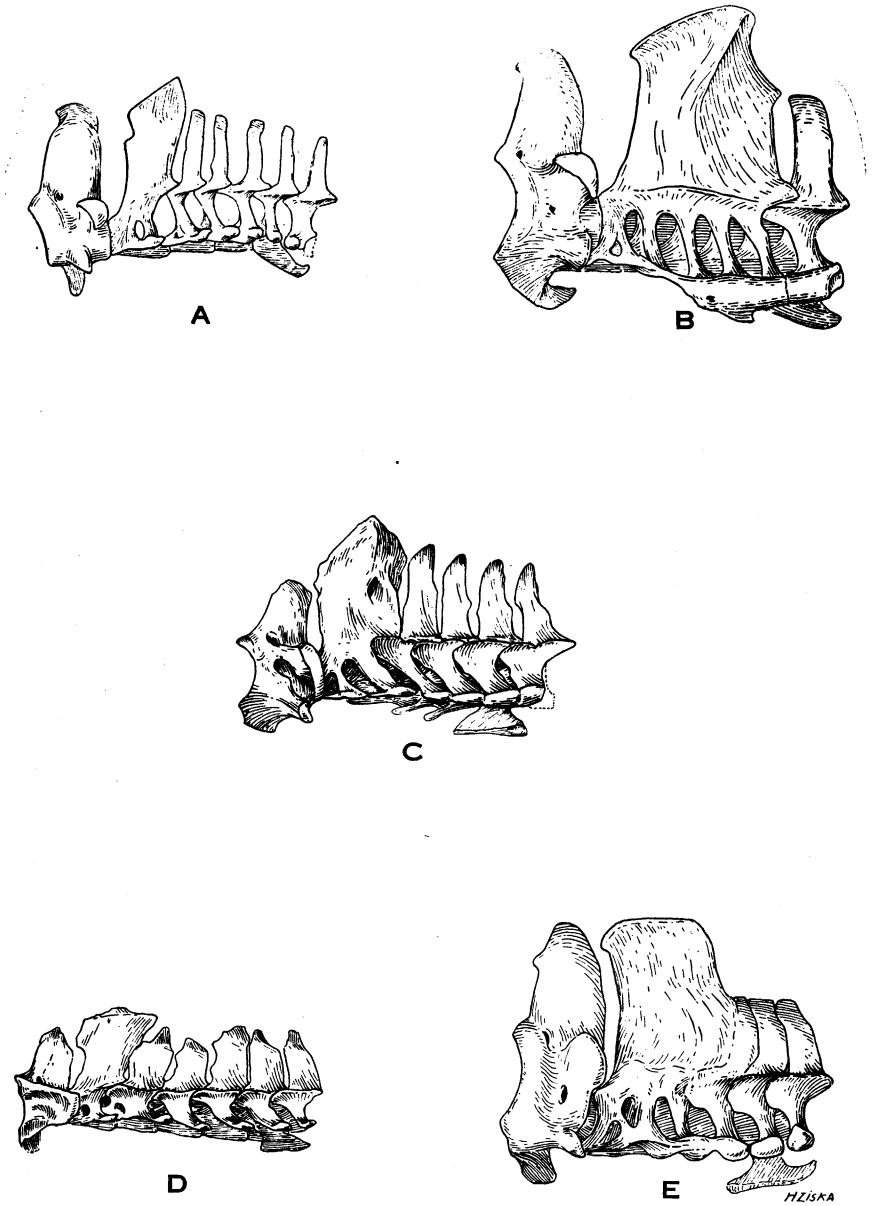


Fig. 6. Types of cervical vertebræ in norma lateralis;

- A.—*Zapus insignis* (74851) $\times 6.8$.
 B.—*Jaculus orientalis* (14606) $\times 5.2$.
 C.—*Pedetes surdaster* (54219) $\times 1.3$.
 D.—*Rattus norvegicus* (148) $\times 1.6$.
 E.—*Dipodomys heermanni tularensis* (13243) $\times 5.3$.

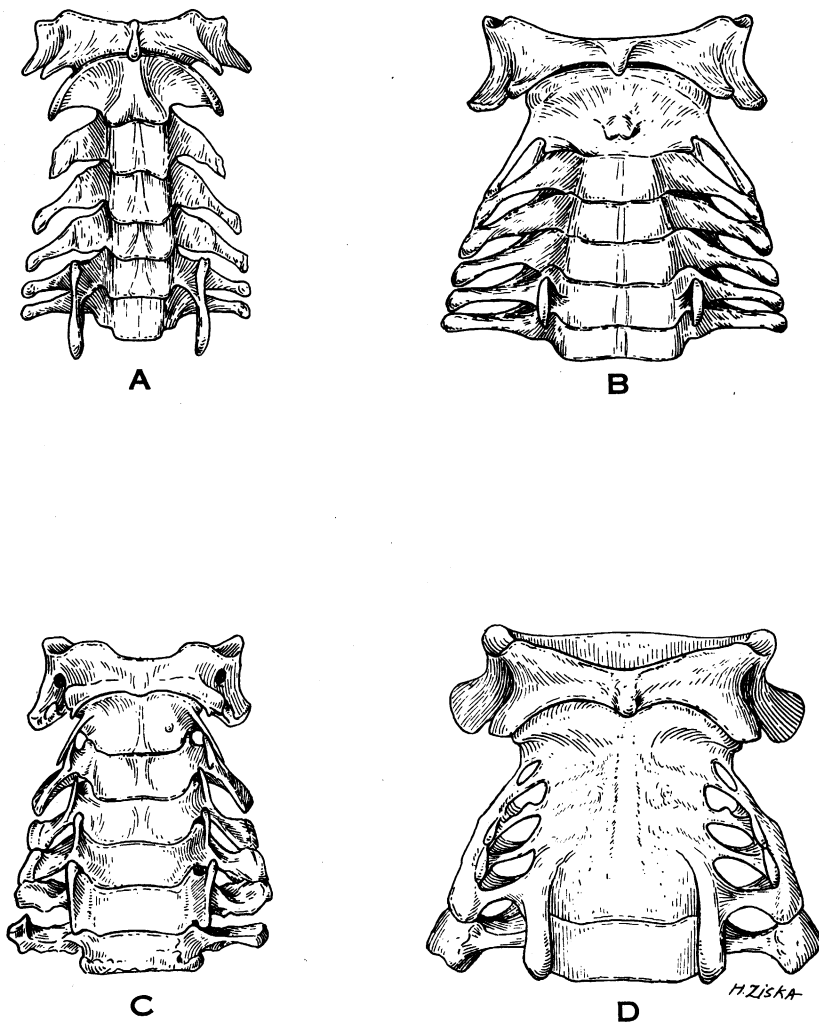


Fig. 7. Types of cervical vertebræ in norma ventralis.

- A.—*Heteromys anomalus* (7524) $\times 3.6$.
 B.—*Dipodomys phillipsii* (132763) $\times 6.4$.
 C.—*Pedetes cafer* (psalinæ) (42025) $\times 1.4$.
 D.—*Jaculus orientalis* (14606) $\times 5.3$.

brings the mouth within reach of the ground when the animal is standing on all four feet. The habitual use of the hands for conveying food to the mouth also detracts from the demand for cervical flexibility.

The extent of fusion of the cervical elements as found in the specimens studied, is given in Table I. It is seen that the atlas never fuses with the axis, the first fusion to take place both ontogenetically and phyletically being practically always between the axis and the third cervical vertebra. Other units may be added in caudal sequence. The only specimen encountered not following this rule is a *Microdipodops* (54815) in which there is fusion only between the left sides of the fourth and fifth elements. The sixth and seventh vertebræ appear to fuse with the cervical block only within the Dipodinæ, though this of course may occur also in other groups of which I have no representatives.

Fusion between the units first becomes apparent in the neural arches. It extends on to the tips of the transverse processes and eventually to the centra, though the segmental character of the latter is always evident.

The most conspicuous feature of such a compound cervical vertebra as is found in *Dipus* is the formation of one strikingly large neural spine, composed chiefly of the original spine of the axis, but including also the neural arches of the other fused units.

The degree of neck shortening that is critical for the fusion of two or more elements appears to be reduction to about fifteen per cent of the thoraco-lumbar length (or seven per cent of the combined head and body length). It is probable that necks may be shorter without showing vertebral fusion, or longer and demonstrating fusion, as in *Dipodomys*, but the average is near that stated.

Of five *Pedetes* skeletons available four were the South African *P. cafer*, and one the East African *P. surdaster*. In the latter the axis and the third cervical vertebra were completely fused in their arches and centra. Parsons (1898, p. 861) describes the second and third vertebræ as being so close together that very little motion between them is possible. Without further material it is impossible to say whether this is an individual variation or a specific character. In any case a phyletic tendency toward neck shortening is suggested.

It is of interest to note that *Allactaga*, a genus which retains several primitive characters, such as the first and fifth toes and the brushless feet, also retains a relatively long neck with no fusion of vertebræ. Even the long-skulled *Zapus* has shortened its neck as much as *Allactaga*. *Dipus*, which is a little less specialized in skull characters than are

Sciropoda and *Jaculus*, has the seventh cervical vertebra fused with numbers two to six, which alone are definitely fused in *Jaculus*.

Among the Heteromyidæ coössification is found in *Dipodomys* and *Microdipodops*. In the latter genus I found but one specimen in which fusion occurred, and this was restricted to the left side of the fourth and fifth elements.

In *Dipodomys* the number of cervical elements involved in fusion seems dependent in part upon age, in part upon specific tendencies. The one specimen showing the fifth vertebra fused with the fourth was a male whose teeth showed it to be an old individual.

The suggestion might be advanced that the burrowing activities of these rodents account for the fused vertebræ, but this does not seem tenable because of the rarity of such phenomena in the strictly fossorial rodents.

Ricochetal modification has not, then, affected the numbers of cervical vertebræ, but where there has been reduction of neck length to less than, approximately, fifteen per cent of the thoraco-lumbar length, fusion of from two to six of the post-atlantal elements has taken place.

Thoraco-Lumbar Region

The primitive rodent quota of dorsal vertebræ appears to be nineteen, twelve of which are thoracic and seven lumbar. This combination of numbers is prevalent in living rodents and is that of the oldest known fossil genus, *Paramys* of the Eocene epoch. This quota has been considerably increased in some rodents, such as *Capromys*, where twenty-three units are usually present, seventeen of which are thoracic and six lumbar. Only one symmetrical specimen of the rodents considered in this paper exceeded the primitive quota of nineteen. This was an *Eliurus* in which there was an additional thoracic vertebra which brought the total of the combined thoraco-lumbars to twenty.

In specimens with nineteen dorsal vertebræ all but a few of the symmetrical individuals had the usual combination of twelve thoracic and seven lumbar units. The exceptions were the seven specimens of *Rattus*, the specimen of *Sicista*, one of six specimens of *Perognathus*, and one of sixteen specimens of *Dipodomys*. Taken alone these figures might be construed as suggestive that the primitive combination was thirteen thoracic and six lumbar vertebræ, *Sicista* and *Rattus* representing primitive, or normally quadrupedal types; the exceptions for *Perognathus* and *Dipodomys* representing reversions to an ancestral condition. Consideration of a large series of other quadrupedal rodents, however,

leads me to conclude that this explanation is untenable, for the prevalent combination as stated above is of twelve and seven.

Two asymmetrical specimens of *Microdipodops* represent divergence from type in opposite directions. In one of these (38801) (Fig. 8) the sacral attachment is displaced posteriorly on the left side to the twenty-first post-cervical vertebra, while in another (38798) the attachment is displaced anteriorly on the right side to the nineteenth post-cervical. As these two cases balance each other they point to no tendency to shift the sacral attachments anteriorly or posteriorly.

The evidence shows that ricochet habits have not occasioned alteration of the primitive quota of nineteen dorsal vertebræ, and that in the bipeds, as in most rodents, these vertebræ are usually divided into twelve thoracic and seven lumbar elements.

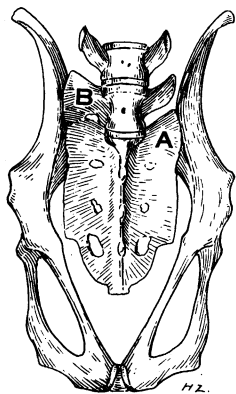


Fig. 8. An asymmetrical sacro-iliac attachment in *Microdipodops megacephalus dickeyi* (38801). Norma ventralis. The first unit fused on the left side (A) is the homologue of the second sacral vertebra, while on the right side the first unit fused. (B) is the true first sacral. $\times 3.1$.

Sacral-Pseudosacral Region

Among living generalized rodents the wings of two vertebræ normally unite with the ilium to form the sacral attachment. It is these which, following Flower (1870), I designate as the sacral vertebræ in contradistinction to the vertebræ ankylosed to them, but which do not come into direct contact with the innominate bone. The true criterion for the distinction between sacral and pseudosacral vertebræ, the presence or absence of a costal element, cannot be used since embryological material is lacking. In every specimen considered the first unit assumed the greatest share in the formation of the sacro-iliac joint. In this respect the ricochetal rodents present no trend of divergence from the condition common to generalized mammals of equal size. Occasionally (in the series given here, *Meriones*, one; *Tatera*, one of two; and *Paramys*, one) but one vertebra is in union with the ilium.

Two of seven *Microdipodops* sacra which I have examined were asymmetrical in attachments. In each of these there were three vertebral wings forming contact with the ilium on the right side, and but two on the left side. In one case the first vertebra entering this complex was the

nineteenth post-cervical of which the right wing was fused with the ilium; in the other individual the right wing of the twentieth post-cervical unit and the left wing of the twenty-first were united to the ilium. As previously stated, since these two cases display shifting in opposite directions they do not indicate any phyletic tendency toward increasing or decreasing the length of the thoraco-lumbar series, but should probably be interpreted as ontogenetic variations of no phyletic significance.

Within any group of ricochetal rodents or their relatives, the number of vertebræ entering into the formation of the pseudo-sacrum appears to be determined chiefly by the age of the individual.

The only dipodid skeleton seen with a variation from the usual number of two pseudosacral vertebræ for the group was the specimen of *Sicista* where but one element was found.

Among the Heteromyidæ the usual number of pseudosacrals is three, but some individuals have only two. From the consideration of other characters it is evident that such individuals, though mature, are not aged.

The four sacra of *Pedetes* examined had but a single pseudo-sacral vertebra, though Parsons (1898, p. 861) has reported the presence of two in one specimen. The presence of but a single unit is in harmony with conditions found in other large-tailed ricochetors. Thus in the leaping shrew (*Rhyncocyon*) there is but a single pseudosacral vertebra, while in the kangaroos and wallabies there are none.

The contrast between the short pseudosacra of large-tailed animals and the long pseudosacra of thin-tailed animals seems to be due to the spreading out of the area of origin of the caudal musculature in the former, and to its restriction in the latter. In *Pedetes* caudal muscles continue to take origin from the diapophyses far to the rear of the pseudo-sacrum. In the thin-tailed ricochetors such muscular origins are confined to the dorsal and ventral surfaces of the sacrum and pseudosacrum and to the diapophyses lying within the limits of the pelvis. It is probable that in the case of *Sicista* the presence of but a single pseudosacral vertebra is similarly correlated with the origin of the caudal musculature beyond the limits of the pelvis.

It is concluded that although age may add caudal units to the sacral-pseudosacral complex, the normal number found in any one species is determined by the musculature of the tail, the muscular-tailed species having fewer vertebral units coössified than the tendinous-tailed species.

Caudal Region

The exact number of caudal vertebræ can be determined on but a very few specimens because of the rarity with which the terminal segments are preserved. From such complete specimens as are available, however, it is clear that increase in tail length is due not alone to the lengthening of a definite number of vertebræ, but is furthered by the multiplication of units. Even within one species of mammal there is likely to be a great variation in the number of vertebræ, as is illustrated in the house cat where Jayne found variation from eighteen to twenty-six.

The Zapodinæ have attained extreme tail length by increasing the number of caudal vertebræ. In this direction the subgenus *Napæozapus* has gone further than *Zapus hudsonius* representing the subgenus *Zapus*, as may be seen by comparing the figures of Table IV. The specimen of *Sicista* at hand, though having a greater number of caudal vertebræ than any of the Dipodinæ or Allactaginæ, does not have as many elements as the specimens of *Zapus*, yet has a longer tail than any individual of the latter genus. This is somewhat surprising in view of the fact that the tail of *Sicista* is prehensile, a condition one might expect to find associated with short units rather than long ones.

Within the jerboas, *Scirtopoda* and *Jaculus* have more units than *Dipus* and less than *Allactaga*, while all of these have less than the Zapodinæ.

Among the Heteromyidæ it is found that there are fewer caudal units in *Microdipodops* than in *Heteromys*, *Liomys*, and *Perognathus*, whereas in *Dipodomys* there are always more than in these three genera. *Microdipodops* then, has achieved a fairly long tail through lengthening of the units, while *Dipodomys* has its long tail, at least in part, by virtue of units added.

One of the five *Pedetes* skeletons examined was equipped with its original complement of caudal vertebræ which numbered thirty-one. This is the same number reported by Parsons (1898, p. 862) for a specimen which he examined.

It is of course impossible to determine whether addition of caudal units is proximal, intermediate, or distal, as there are no characters of these vertebræ which mark any particular unit as being homologous with any similar one in another series. It seems probable, however, that addition of vertebræ would be terminal.

Summary of Conclusions Concerning Vertebral Numbers

There is an axial gradient in the variability in numbers of vertebræ of the ricochetal rodents and their relatives. The cervical region shows no deviation. In the thoraco-lumbar section there is variation in total number of only one, and variation in either of the divisions of only one element. In the sacral vertebræ there is a range of variation of one; in the pseudosacral of two; and in the combined sacral-pseudosacral of three. The number of caudal units varies as much as fifteen.

Though the primitive number of cervical vertebræ is always found, these elements are subject to fusion with the shortening of the neck. Fusion between atlas and axis never takes place, but the cervical vertebræ caudal to the axis may ankylose to form a single bone. Such synostosis always takes place in caudal sequence. Cases of fusion are usually found in cervical vertebral series which constitute less than fifteen per cent of thoraco-lumbar length or seven per cent of the head and body length, but are rarely found in series which constitute more than this percentage. The ankylosis of cervical vertebræ is, then, an outcome of neck shortening.

Reduction in neck length has the effect of eliminating motion of the head during ricochetal progress. The subsequent formation of a compound cervical vertebra further eliminates neck motion and also furnishes a broad strong surface for the attachment of certain cervical ligaments and muscles.

The primitive rodent combination of twelve thoracic and seven lumbar vertebræ is practically constant in the ricochetal rodents. There is rare variation due to the development of vestigial extra ribs, or to anomalous attachments of the innominate bone.

The sacrum is composed of two vertebræ as is the case in the majority of generalized rodents. The first of these always forms by far the greater portion of the attachment surface.

The pseudosacrum is typically composed of two elements within the Dipodidæ and of three in the Heteromyidæ. Variation of these numbers is usually, or always, due to age variation. The presence of but one pseudosacral vertebra in *Pedetes* is attributed to the extension of the area of origins for the caudal muscles on to the post-pelvic caudal diapophyses (Fig. 23). The presence of two or three pseudosacral vertebræ in thin-tailed forms is associated with the localization of origins of caudal muscles to the sacrum-pseudosacrum and the intra-pelvic caudal diapophyses.

The numbers of caudal vertebræ might be expected to vary in response to demands for flexibility or for elongation. Since unusual flexibility is not required of the tails of leaping animals, the increases in vertebral numbers that do take place are attributed to the response to demands for tail length.

A direct ratio between increase in caudal vertebral numbers and caudal vertebral length is best marked in *Zapus* (Table IV) in which genus a specimen with thirty-three caudal vertebræ equaling 163.6 per cent of head-body length is in contrast with a specimen with thirty-nine caudal vertebræ whose combined length is 176.8 per cent of head-body length. In *Allactaga* and among the *Dipodinae* the increase in caudal elements is also in direct ratio with increase in caudal length, but is not proportionate to this increase. Thus there are only four more vertebræ in the tail of an *Allactaga* 175.3 per cent of head-body length than in a *Dipus* with a tail 159.6 per cent of head-body length.

The differences of proportionate tail lengths of the specimens of *Dipodomys* listed in Table IV are greater than would be expected from a consideration of the small number of added elements alone. Specimens of *Microdipodops* bear tails which average longer than those of *Heteromys*, *Liomys*, or *Perognathus*, yet the *Microdipodops* have fewer caudal vertebræ than individuals of these other genera. In this case it is apparent that length has been gained by the extension of a small number of elements, a course which results in the development of a tail relatively less flexible than its antecedent. The tail of *Microdipodops* is thicker than that of *Dipodomys* or of *Perognathus*, and, if one may judge by specimens preserved in alcohol, less flexible as well.

The numbers of vertebræ show greatest adaptation to ricochetel habits in the pseudosacral and caudal regions. Functionally the cervical vertebræ show numerical adaptation through the coalescence of the primitive numbers.

DIFFERENCES IN RELATIVE LENGTH OF THE SKULL AND REGIONS OF THE VERTEBRAL COLUMN

The Skull

When the skull lengths (condylo-nasal) are correlated with data on ricochetel specialization, the *Dipodidæ* and *Heteromyidæ* appear to show divergent tendencies as to head length. As may be seen by the data in Table V, there is a reduction in relative skull length from the primitive *Sicista* through *Zapus* to the jerboas. In the *Heteromyidæ*, on the contrary, there is an increase in proportionate skull length from

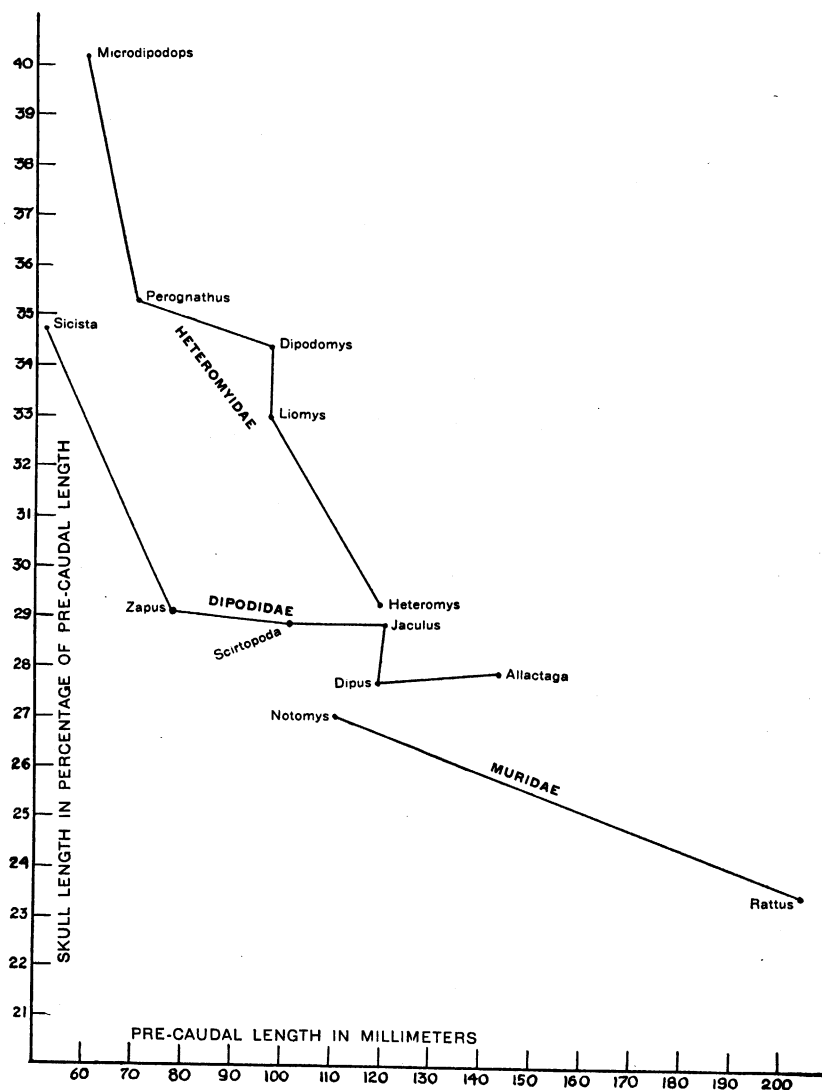


Fig. 9. The relation of proportionate skull length to actual precaudal length. The names of the genera of each family are connected with solid lines so that these groups will be more easily recognized. These lines merely connect nearest points and are themselves of no significance. It is indicated by these plottings that within one family the skulls of the smaller animals are usually proportionately larger than those of the larger animals. It is also evident that the skulls of the Dipodidae are for equal body size shorter than those of the Heteromyidae.

Heteromys to *Liomys*, to *Perognathus* and *Microdipodops*. *Dipodomys*, however, has a skull relatively shorter than that of *Perognathus*.

If skull length is plotted against absolute body size, a correlation immediately becomes apparent (Fig. 9). There is a distinct tendency for the skulls of the smaller forms of one family to be proportionately larger than those of the larger animals in the same family. If family associations are disregarded, the correlation between all genera for skull to head and body length is low and follows that of the families only in a general broad tendency between extremes. The highest ratio of skull to head and body length encountered is that of *Microdipodops* with an average head and body length for five specimens of 60.1 mm., and a skull 40.2 per cent of the head and body length. The lowest ratio is that of a specimen of *Paramys* where the skull length is about 19 per cent of the approximate head and body length (470 mm.). Of recent rodents measured, the lowest ratio is that of *Rattus*, in which the skull in three specimens averages 23.4 per cent of the 204.3 mm. average head and body length. Were the skull measurements based on greatest skull length, the contrast between these three would be even more striking, for the inflated auditory and mastoid bullæ of *Microdipodops* project far caudad of the occipital condyles and increase the greatest length by a high margin. It is probable that the large heads of small forms are a disadvantage which is compensated for by the high ratio of leaping power to size.

Cervical Region

Among the rodents the cervical series of vertebræ is shortened in ratio to the degree of ricochetal specialization. As previously stated, the shortening of the series is commonly accompanied by fusion of elements.

The extent of reduction in neck length as expressed by the relation to head and body length and thoraco-lumbar length is given in Table VI and demonstrated in figure 10. The relation to thoraco-lumbar length best demonstrates the true relation. Where the head length is included, a factor at least partly dependent upon actual size of the animal, the ratio of neck length is disturbed by a factor to which it has little relation. Thus *Allactaga* appears to have a neck relatively longer than that of *Zapus* when the standard is head and body length. This, however, is erroneous, as shown by the comparison to thoraco-lumbar length; it is due to the larger actual size and hence proportionately shorter skull of *Allactaga*, which, in contradistinction to *Zapus*, gives a relatively shorter head plus body length with which to compare neck length.

On the basis of ratio of neck length to thoraco-lumbar length, *Sicista* has a far longer neck than *Zapus*. Between *Zapus* and *Allactaga* there is no significant difference, but the three-toed jerboas all have distinctly shorter necks than the five-toed *Allactaga*. *Scirtopoda* has a shorter neck than *Jaculus*, and *Jaculus* a shorter neck than *Dipus*.

Among the Heteromyidæ, *Heteromys* and *Liomys* have neck vertebrae approximately the length of those of *Sicista*, *Rattus*, and *Tatera*,

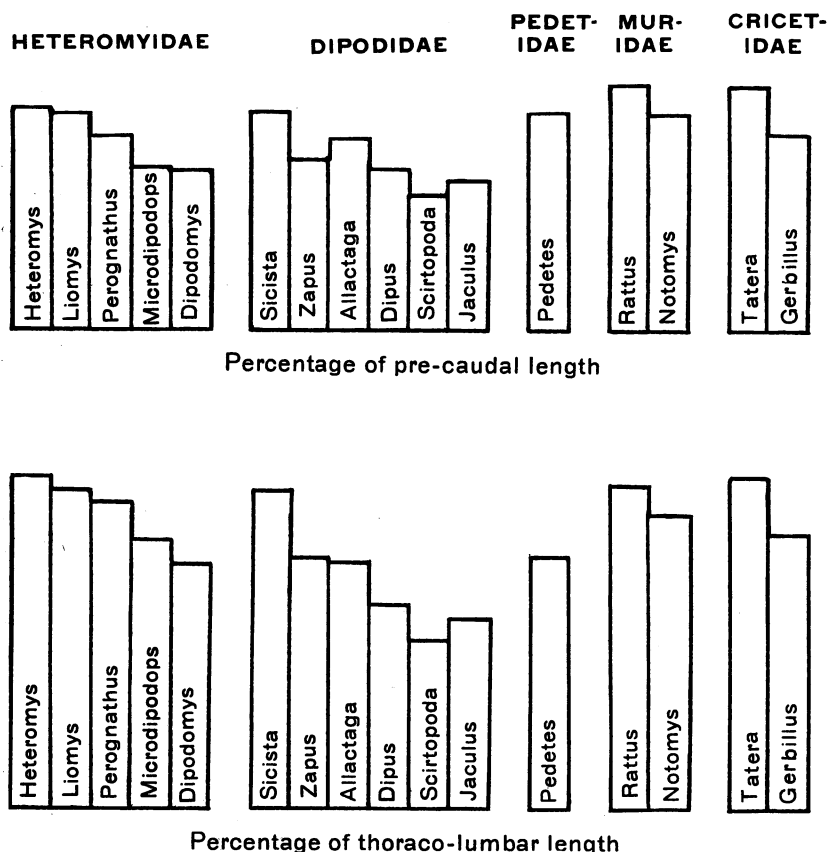


Fig. 10. The lengths of cervical vertebral series in relation to head and body length and in relation to thoraco-lumbar length. The interrelationships of these vertebral lengths as expressed in percentages of pre-caudal lengths are misleading largely because of the independent variable of the included skull length. Thus in comparison to pre-caudal length *Allactaga* has a longer cervical vertebral series than has *Zapus* simply because *Zapus* is a small animal with a long skull and *Allactaga* is a comparatively large animal with a short skull.

quadrupedal forms of other families. *Perognathus*, in many ways transitional between the ratlike *Heteromys* and *Liomys* and the bipedal *Microdipodops* and *Dipodomys*, has a neck intermediate in length between these extremes, though it is nearer that of the quadrupedal members of its group than the bipedal. The necks of *Dipodomys* average shorter than those of the other Heteromyidæ, but are only about as short as those of the dipodid *Allactaga*.

Pedetes retains a relatively long neck in which it resembles the ricochetors of the marsupial family Macropodidæ, and the insectivorous family Macroscelididæ. It should be recalled that large mammals have small heads and the strain imposed on the neck by the head weight is relatively less than in small mammals.

Notomys has a somewhat shorter neck than *Rattus*, but a neck relatively longer than any other small ricochetor.

The neck of *Gerbillus* is proportionately shorter than that of the ratlike *Tatera*.

As stated in the previous section of this paper, I interpret this shortening of the neck to be an adaptation to the elimination of head bobbing during the ricochet and as a means of shifting the center of gravity backward, an obvious advantage where propulsion is from the rear.

It is a commonplace observation that neck length among the mammals is correlated with length of the fore limbs, and it is not impossible that the neck shortening detailed above is simply the outcome of limb shortening. But since the bipedal rodents are hand feeders, it is easier to believe that in ricochetal rodents the neck length is adaptational to locomotion, and the length of the fore limbs adaptational to neck length, or as neck length, is adapted to reduction of weight far forward. Everything considered, it seems that necks are shortened in relation to the degree of ricochetal specialization.

Thoraco-Lumbar Region

There is no clearly demonstrable change in relative proportions of the thoracic and lumbar regions (Table VII) other than that due to the presence of a vestigial thirteenth pair of ribs, in contrast to the usual twelve pairs in the compared material.

The combined thoraco-lumbar length as expressed in percentage of head and body length varies to some extent between primitive and specialized types, but the only way of explaining this apparent difference is in the alterations of proportion of skull, cervical, and pseudosacral regions. There is no reason to suppose that the thoraco-lumbar region

is not as much subject to change as are the other regions, but as the thoraco-lumbar region must serve largely as the unit of measurement, one cannot well measure it in terms of the units measured. The percentage of the combined skull and precaudal vertebral length occupied by the thoracic and the lumbar vertebræ of the various genera is given in Table XI.

Sacral-Pseudosacral Region

In the discussion of the changes in number of pseudosacral elements the conclusion was drawn that the linear extent of the sacral-pseudosacral fusion was in inverse relation to the posterior extent of the caudal musculature.

This conclusion is somewhat strengthened by the comparison of the measurements of linear extent of the sacrum-pseudosacrum in the various forms considered, as shown by their ratios to head and body length. Thus thin-tailed *Zapus* has a long sacrum-pseudosacrum, 14.2 per cent of the head and body length. The larger jerboas, whose tails are all more or less similar, have sacra-pseudosacra of similar proportions. *Sicista*, with a prehensile tail which is probably muscled well past the level of the ischia, has a sacrum-pseudosacrum but 9.6 per cent of the head and body length. A similar, though less striking, change occurs in the Heteromyidæ, with *Dipodomys* as the nearest approach to a thin-tailed form at one extreme, and *Microdipodops* with its thick tail near the other. *Liomys*, represented by but a single complete specimen, presents a yet lower ratio, diverging sharply in this respect from its genetic and locomotor counterpart *Heteromys*. This inconsistency is attributed to the fact that the fourth and fifth post-sacral vertebræ of *Liomys* have not fused.

Pedetes, an animal with the most muscular tail of any ricochetal rodent, has a lower ratio of sacrum-pseudosacrum to pre-caudal length than that of any other form measured.

It appears then, as was concluded in a review of the numbers of sacral-pseudosacral vertebræ, that the length of the compound bone formed by these units is, in the main, determined by the distribution the origins of caudal musculature.

Caudal Region

The tails of ricochetal animals are notably longer than those of their non-ricochetal relatives. The reasons for this increase are considered elsewhere. It will be noted that among the forms considered there is a

marked variation in tail length, and that this variation is related to: (a) degree of bipedality; (b) tail diameter; (c) degree of terminal hairing.

The tail length of white rats has been found to be dependent upon temperature (Przibram, 1922), at least within the narrow limits imposed by the genetic constitution. Low temperature decreases growth of

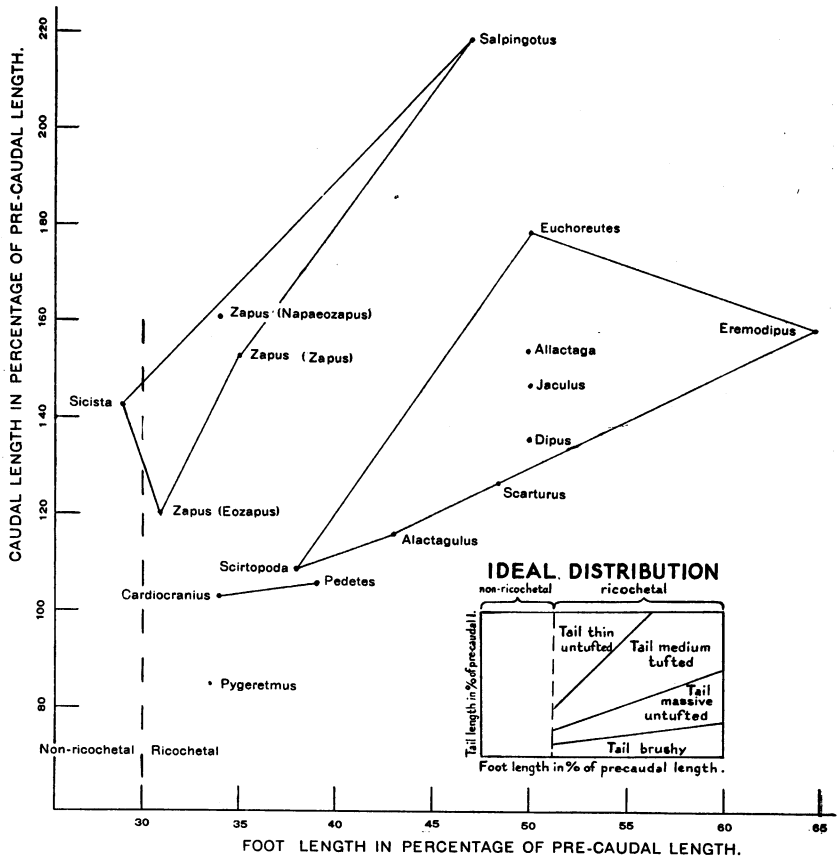


Fig. 11. The relation of tail length to mass and to hairy covering. Dipodidæ and Pedetidæ. Lines connect the extreme variants of genera with similar tails and enclose within the polygons so formed the intermediate types. The tail types are indicated in the key chart in the corner showing the ideal distribution. It is indicated by these plottings that in relation to comparative elongation of the hind feet that thin untufted tails are longer than those which bear tufts; that these latter are longer than heavy uniformly haired tails, and that probably, the shortest tails of ricochetors are those which are heavily haired.

tail length, while high temperature increases it. Though individually significant, these ontogenetic variations are not comparable in magnitude with the variation in the mean specific or generic tail lengths. These latter are most certainly adaptational.

Two sets of measurements are available for tail length studies: the first taken from the same skeletons as my other data; the second based on published field records.

These two sets of figures are not directly comparable, for they are expressions of different units. In field measurements the caudal vertebrae occurring within the limits of the pelvis are included in the head and body length. This tends to produce lower tail ratios for field measurements than for those based on skeletons. External measurements also include a slight additional amount of flesh anterior to the skull. This too lowers the tail ratio. A difference seemingly of greater magnitude than either of the above, is that in the skeletal measurements the head and body length is taken along the curves of the column, whereas these curves are not entirely eliminated in head and body measurements of an animal in the flesh. The fact, however, that the average tail-body ratios obtained from my measurements of skeletons are in most cases much higher (Table X) than the average ratios for field measurements of corresponding genera, suggests that the first two mentioned factors are productive of greater discrepancies than the last.

The exact interrelations between tail diameter and tail length cannot be accurately determined, for weight would be a factor dependent on proportion of bone, degree of hairiness, etc. Even more impossible to measure is the weight to be counterbalanced. The almost indeterminable body size anterior to the acetabula, and the weight of the body posterior to the acetabula, as well as shifting relations due to change in posture, would make such a determination, however accurate, quite meaningless. There is no doubt a correlation between posture and weight distribution posterior to the acetabula, but these factors are beyond the means of mensuration by available methods.

The principle of the relation between tail length, mass, and tufting has been considered in the introduction to this paper. It remains to compare with the theoretical expectation the actual conditions found among the animals studied. Even with the relatively crude methods of evaluation of the factors concerned, it is clear that at least within any one family of ricochetal rodents the conditions closely approximate the theoretical relations. The series of *Dipodidae*, richer in genera than any other ricochetal rodent family, furnishes the best example of the inter-

relations of the factors enumerated. The conclusions may be advanced: firstly, that ricochetral rodents with terminal tail tufts have relatively shorter tails for equal relative foot length than do those with thin, untufted tails, and that they have relatively longer tails than ricochetral rodents with untufted, massive tails; secondly, that among animals with tails similar in their conditions of mass and terminal hairing, increased foot length is generally accompanied by increased tail length. The evidence for these conclusions is given in Tables IX and X, and figure 11. Examples of the three types are illustrated in Plate XI.

The cases among the Dipodidæ as compiled from the generic averages given in Table IX, are plotted in figure 11. Here the extreme forms with a similar combination of tail hairing and mass are connected with lines and the other's enclosed in the polygons so formed.

Among those with untufted, thin tails, the dwarf jerboa *Salpingotus* has by far the greatest tail length and longest foot. The Chinese jumping mouse *Zapus (Eozapus) setchuanus* has the shortest foot and tail, except for the bush mouse *Sicista* which, though long-tailed, has a short foot adapted for climbing.

The eight genera of jerboas with well-tufted tails are, with two exceptions, animals with foot length from 48 to 50 per cent of head and body length. These eight present a rather wide latitude of tail development that is probably correlated with some unmeasured factors of body or tail size or shape. Of the two exceptions *Eremodipus* has a particularly long foot, *Scirtopoda* a particularly short one.

The dwarf jerboa *Cardiocranius* has, in the one specimen available to me, a tail best described as uniformly haired and massive (Pl. XI). Its foot is shorter than that of any other jerboa except *Pygeretmus* with which it is equal. Moreover, its tail is shorter than that of any except *Pygeretmus*, which latter, though not massive, is equipped with long hairs throughout, a unique condition that has allowed the greatest tail shortening found among the Dipodidæ.

Pedetes has been placed on the chart with the Dipodidæ to show that its heavy tail is accompanied by a low ratio of foot length to tail length.

The two genera of ricochetral Heteromyidæ (*Dipodomys* and *Microdipodops*) have the same arithmetical relationships between their foot length, tail length, mass, and tufting as is found in the Dipodidæ. These two, though having approximately equal proportionate foot lengths, differ clearly in proportionate tail length. *Dipodomys* has a long tail of moderate diameter, tufted, though not as strikingly so as that of many jerboas. *Microdipodops* has a shorter, untufted tail of

comparatively massive proportions. The coarse-haired pocket mice *Perognathus* (*Chaetodipus*), are less strictly quadrupedal than the silky pocket mice, *P.* (*Perognathus*), and, though having an average foot length the same as the latter, differ in having, on the average, longer tails with more of a terminal pencil. Similar relationships are found among the subricochetal gerbilles (contrast *Tatera* and *Gerbillus*).

In summary, it is found that tails of ricochetors are modified as balancing organs either by extension, by tufting, by increased thickness, or by two or more of these. Tail length, if the character of the tail remains unchanged, increases with increase of foot length. For similar foot length of ricochetors, the tails that are unhaired, or lightly haired, are longer than those that bear a well-developed tuft, whereas those in the latter class are longer than those that are massive.

Summary of Conclusions Concerning the Lengths of the Skull and Regions of the Vertebral Column

It is concluded that within families there is a tendency for the skulls of the larger members of the group to be relatively shorter than those of the smaller members. The Heteromyidæ have skulls longer in comparison to body size than do the Dipodidæ. If there is any relation between skull length and bipedality I have not been able to discover it.

The cervical vertebrae of ricochetal rodents are shortened in proportion to the degree of ricochetal specialization. The relation of the length of the cervical series to the thoraco-lumbar series is a better index to neck shortening than that of relation to head and body length, for the latter is diluted by the largely independent factor of skull length. The shortest neck encountered was in the jerboa *Scirtopoda*, where one specimen had a neck length but 10.4 per cent of the thoraco-lumbar length. Among the Heteromyidæ, *Dipodomys* attains the shortest neck, sixteen specimens averaging but 15.5 per cent of thoraco-lumbar length. The mean corresponding percentage for quadrupedal rodents is about 20 per cent. *Pedetes*, *Notomys*, and *Gerbillus* have departed very slightly from the primitive proportion. Neck shortening among bipeds is interpreted as an adaptation to the elimination of head bobbing.

There is no clearly demonstrable change in the ratio of thoracic to lumbar regions other than that due to the presence of a vestigial thirteenth pair of ribs which by adding a vertebra to the thoracic series and taking one from the lumbar, increases the proportionate length of the former.

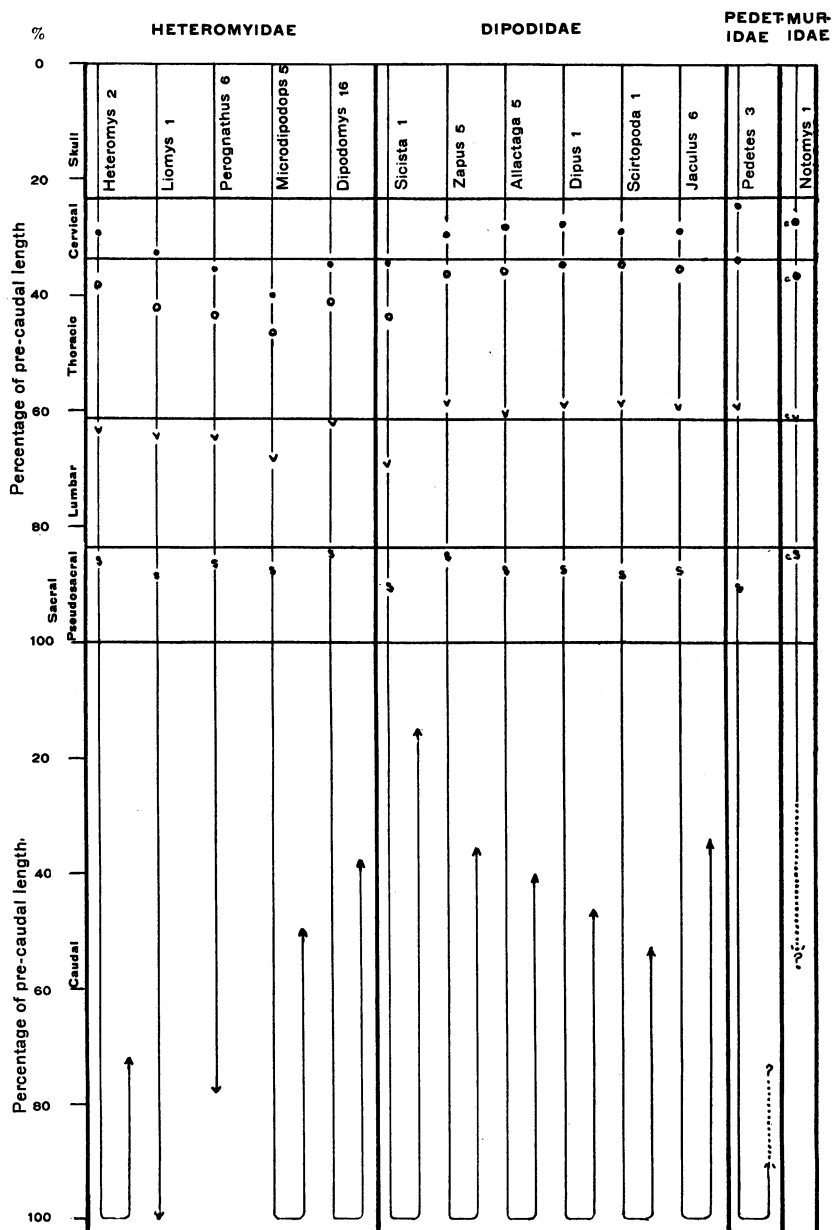


Fig. 12. Relative lengths of skulls and regions of the vertebral column in percentage of precaudal length. The solid horizontal lines represent the lengths of the skull and vertebral regions in *Rattus* arranged in their natural sequence. This arrangement shows that in general the Dipodidae are shorter skulled, shorter necked, longer tailed animals than are the Heteromyidae.

As the dorsal region is that around which the other regions fluctuate, there is no unit with which to measure any change occurring in the proportions of the region itself.

The relative length of the sacrum-pseudosacrum, after the elongation due to age increment is eliminated, is found to be correlated with the type and extent of caudal musculature. Thin-tailed forms such as *Jaculus* have the origins of the caudal muscles confined to the sacral region and the first few caudal elements (Fig. 23 B). In consequence, the combined sacrum-pseudosacrum is long. *Pedetes*, a type with a heavy tail in which caudal muscular origin extends well along the length of the tail (Fig. 23 C), has a very short sacrum-pseudosacrum. *Sicista*, whose sacrum-pseudosacrum is the shortest among the Dipodidæ, presumably has muscular origins extending far beyond the level of the ischia, for it has a prehensile tail. Unfortunately its caudal musculature has never been described, and I have had no specimen available for dissection.

Caudal length is determined by the interaction of three factors: degree of ricochetal specialization, nature and extent of caudal hairing, and tail diameter. Within one group of ricochetors the relatively longest tails are thin tails, neither tufted nor luxuriantly haired. The relatively next longest tails are terminally tufted; the third massive; and the shortest, if one may judge by a single case, luxuriantly haired throughout the greater part of the tail length. Within the Dipodidæ the first group is represented by *Zapus* and *Salpingotus*; the second by *Allactaga*, *Alactagulus*, *Scarturus*, and the Dipodinæ. The thick-tailed group is represented only by *Cardiocranius*, though *Pedetes* forms a parallel case. *Pygeretmus* is the only genus with a relatively well-haired tail. Other groups of ricochetors follow the same trend shown in the Dipodidæ, but are not so rich in illustrative material.

With certain exceptions, longer tails accompany longer rear feet within any one of the four groups listed above.

The tail lengths of the non-ricochetal rodents bear little or no relation to the foot lengths.

CHANGES IN LENGTHS OF CENTRA

Changes occurring in the proportional lengths of the various regions of the vertebral column between primitive and specialized types are merely summations of the changes occurring among the units within such regions. The regional changes themselves are informative and yet they obscure such independent changes as occur within the limits of the region. The intermediate vertebræ do not in all cases form a uniformly

graded series increasing or decreasing from one extreme to the other, but show differential increment or loss. This intraregional specialization is most extreme in the caudal series.

Presacral Centra Lengths

The centrum of the atlas is represented by the odontoid process of the axis. This process is, in the rodents studied, about as long as the antero-posterior length of the vertebral arch of the atlas. Since the atlas is very short in all of the ricochet forms, the odontoid process is correspondingly short. The functions and proportions of the latter do not seem to be otherwise altered. The ring of the atlas is shortened in proportion to the length reduction of the entire cervical region.

The axis vertebra is the longest of the cervical series in all rodent specimens examined. In generalized forms such as *Rattus*, *Heteromys*, *Liomys*, and *Tatera*, the third to the seventh cervical vertebræ are practically equal in length. In such ricochet rodents as *Dipodomys*, *Pedetes*, *Dipus*, and *Gerbillus*, the vertebræ decrease in length from the third to the fifth, but increase in length from the sixth into the lumbar region. For other genera it was impossible to obtain sufficiently accurate measurements. Where elements are fused individual vertebral length ceases to be of significance. It appears that the position of the shortest post-atlantal cervical vertebra, where there is a shortest one, corresponds to the cervical center of motion, or lies immediately in front of it. If examination of a sufficient number of X-rays of these rodents would substantiate this conclusion, it would be possible to say that this localization of length reduction is correlated with the demand for greatest flexibility at the principal angles in the axis of the column.

Caudad to the fifth or sixth cervical vertebra, the vertebræ increase in length from the fourth to the sixth lumbar unit. This is usually the fourth in the *Dipodidæ*, the fifth in the *Heteromyidæ*. Between this point and the sacrum a reduction invariably occurs. Inasmuch as a small number of long units are better adapted to rigidity, and hence to transmission of the thrust, than are a larger number of short units, and inasmuch as the thrust transmitted decreases anteriorly, the increase in length caudad or the decrease cephalad might be interpreted as a response to the factor of thrust. The presence of one to three vertebræ, at the caudal end of the lumbar series, that are shorter than those immediately preceding may be made possible by the additional bracing furnished in the pelvic region where there is firm anchorage of ligaments and muscles. It is difficult, however, to see any advantage in the shortening of the units in this area.

As the vertebrae of the sacrum and pseudosacrum are fused, and in consequence act as a unit, the proportions and significance of which are dealt with in the preceding section, the matter is not again considered here.

By plotting the proportionate lengths of selected vertebrae in ratio to the longest presacral unit of the individual specimen, one difference

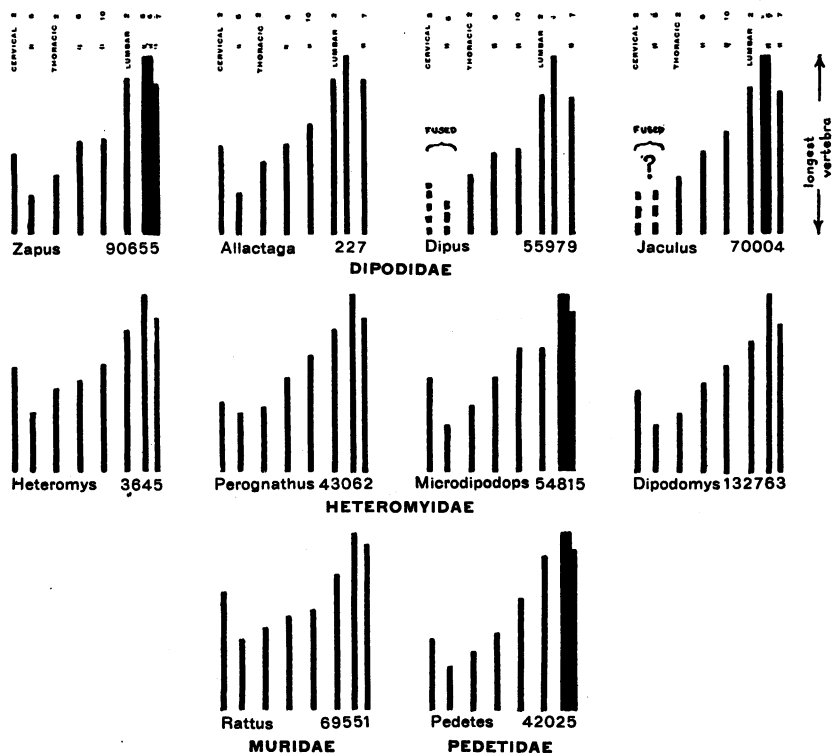


Fig. 13. The length of selected presacral centra reduced to the unit length of the longest centrum in the selected specimen. The measurements here plotted show that there is a lower range of variation in the lengths of the centra of quadrupedal than of ricochetal species.

between the quadrupedal and ricochetal species is seen. This difference, evident from an examination of figure 13 where the computations are graphically recorded, is that there is greater disproportion between the units of ricochetors than between those of quadrupeds. *Rattus*, *Heteromys*, and *Perognathus* are clearly in contrast to the others as regards proportion of the shortest unit of the series to the longest.

The Lengths of Caudal Centra

In most rodent tails which I have examined, the caudal centra are progressively shortened from the first to the second and third. In short-tailed jumpers such as *Lepus*, *Lagostomus*, and *Viscacia*, this progressive

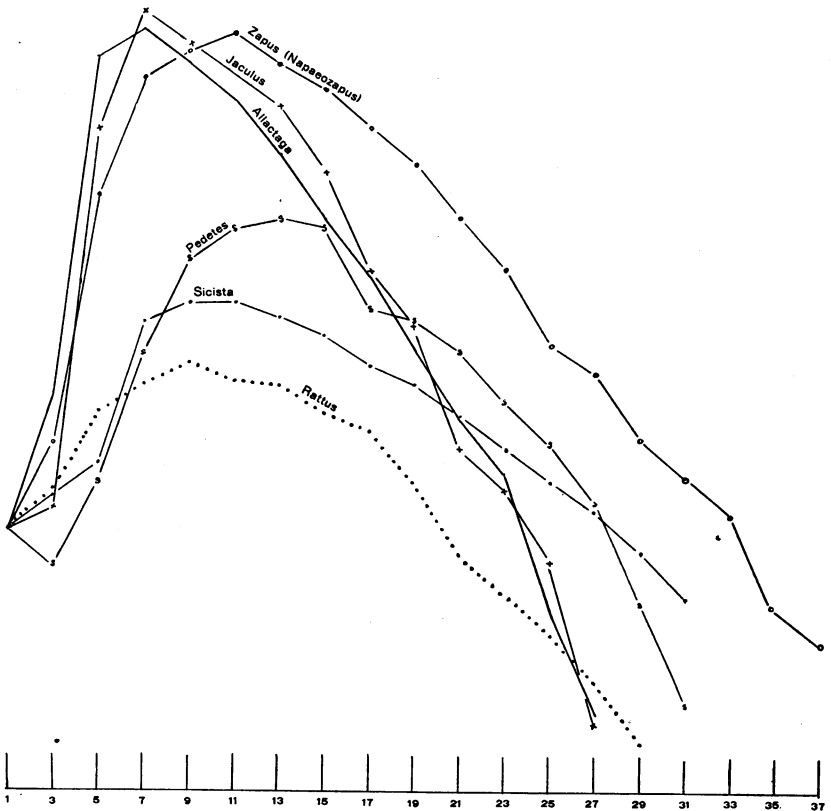


Fig. 14. The length of caudal centra of *Dipodidæ*, *Pedetes*, and *Rattus*. The initial shortening or increase in length of centra, the position of the longest vertebrae and the relation of unit lengthening and number of units to tail length is indicated in this pattern. The length of units are plotted in relation to common length for the first unit.

shortening continues as far as the sixth or seventh caudal vertebra. Certain other rodents (*Castor*, *Anomalurus*) show neither decrease nor increase in the first three segments, while in *Microdipodops* and the *Dipodidæ* there is an increase in length from the first.

The significance of shortening of proximal caudal vertebræ lies in the resultant adaptation to dorsal tail flexion. Shorter elements permit a smaller radius of tail curvature in this region. This type of caudal modification is exemplified by such creatures as rabbits and squirrels, where the tail may be laid flat against the back. The jerboas, on the other hand, cannot curl the tail over the back, and in relation to this,

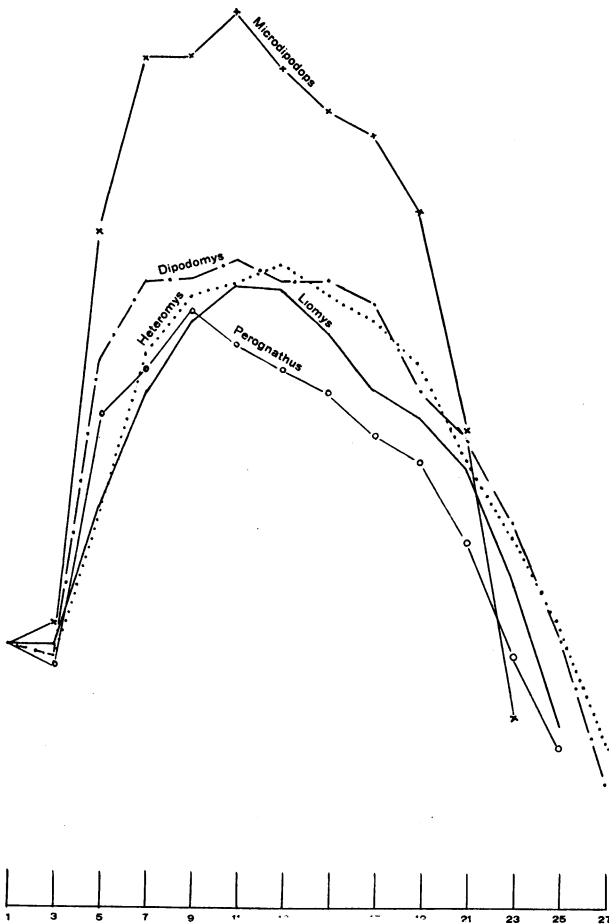


Fig. 15. The lengths of caudal centra of Heteromyidae. It is evident by comparison of this figure with figure 14 that the Heteromyidae have tails with fewer vertebræ than have the Dipodidae.

one finds no shortened vertebræ at the base of the tail. Of the Pedetidæ, Dipodidæ, and Heteromyidæ, *Pedetes* alone shows well-marked modification for dorsal flexing in the proximal caudal region (Fig. 14). Its first to fifth caudal vertebræ are all relatively short, the third being the shortest. In all other genera of these three families no great shortening occurs, and increase in length is rapid after the fourth caudal vertebra.

The decrease in length of the proximal caudal centra, where it occurs, is a continuation of that in the sacral-pseudosacral series, and extends about as far distally as do the "pseudo-sacraform" vertebræ at the anterior end of the tail—the section bearing strong diapophyses. When no actual decrease in length occurs, the centra remain practically constant in length until the diapophyses disappear; that is, until they are beyond the sphere of influence of the origins of mm. extensor caudæ lateralis, pyriformis, agitator caudæ, abductor caudæ externus, and flexor caudæ longus et brevis. This point of demarcation also corresponds, roughly, to the posterior end of the body, or the level of the caudal border of the ischium. Beyond this point the tail of thin-tailed forms is equipped with tendons but not with muscles.

Following the progressive decrease in centra lengths there is an increase which is usually rapid and which extends about to the middle of the tail where the longest segments are found.

In natatorial rodents (*Castor*, *Ondatra*, *Hydromys*) the middle segments are fairly uniform in length, an arrangement suited to the formation of sinuous curves.

The extent of increase in length relative to the shortest anterior caudal centrum is, among measured Dipodidæ, Heteromyidæ, and Pedetidæ, greatest in *Microdipodops*, where the longest caudal vertebra is over 3.4 times as long as the first caudal vertebra. In *Pedetes*, where the tail is thick and muscular and where the great contrast between tail base and body is lacking, the increase is less pronounced—but 2.4 times. However, the difference is not truly great, as will be seen in figure 14.

In short-tailed jumping rodents (*Lepus*, *Lagostomus*, *Viscacia*) there is even greater contrast between the lengths of caudal elements, and the change from one extreme to the other is most abrupt.

Distal to the region of maximal length the vertebræ fall off in length with less abruptness than that with which they increased. The final segment is often a mere button.

In review, it is evident that the ricochetral rodents show little or none of the shortening of the proximal caudal centra which occurs in rodents that flex the tail sharply upwards or over the back. The centra

increase in length to the middle of the tail, beyond which they fall off in length.

REGIONAL CHANGES IN SIZE AND SHAPE OF CENTRA

At various levels the vertebral centra of any animal differ in length, breadth, and volume. Thus the shape of the centrum varies from one element to the next. Between different species of mammals these regional differences in volume and in shape of vertebræ are not the same.

To determine accurately all these differences on such small articulated skeletons as were available to me is quite impossible, yet because the results, if comparable data could be secured, promised to be interesting, certain measurements were arbitrarily selected which would, in a measure, be indicative of the changes occurring. The differences between the length of centra having already been considered, the area of the transverse section was used as indicative of volume. Transverse section was arbitrarily established at the anterior face of the selected centrum, and the height and breadth of these surfaces were measured. The centra chosen for types were those at or near the foci of obvious changes in the column, with a few intermediate elements measured to establish continuity of trend. No calibrations were made on the first vertebra since it possesses no centrum. The measurements of the second centrum were made just posterior to the dens epistrophei. The most posterior element measured was the tenth caudal vertebra. But one specimen of a genus was measured, the specimen selected being determined by its suitability to accurate mensuration by the calipers.

The differences in the shape of the transverse sections seem to be correlated with the size and shape of the spinal cord which they underlie, with the chief direction of motion between the elements of the region, and with the nature of associated structures, such as ribs, etc. The area of transverse section is probably influenced by all of these factors and, as well, is in all likelihood related to the amount of compressive strain imposed upon these bodies in the direction of the longitudinal axis.

Certain major regional changes in size and shape of centra as expressed by the area of the section and by the index obtained from dividing height by width, occur in all the ricochetal rodents examined. Some of these are also common to the quadrupedal relatives of these forms. Inasmuch as ricochetal adaptation is in many respects only an exaggeration of a primary tendency of these more primitive members of the same stocks to use the hind limbs as the chief propulsive agents, the major regional differences between quadrupeds and ricochetors are primarily quantitative.

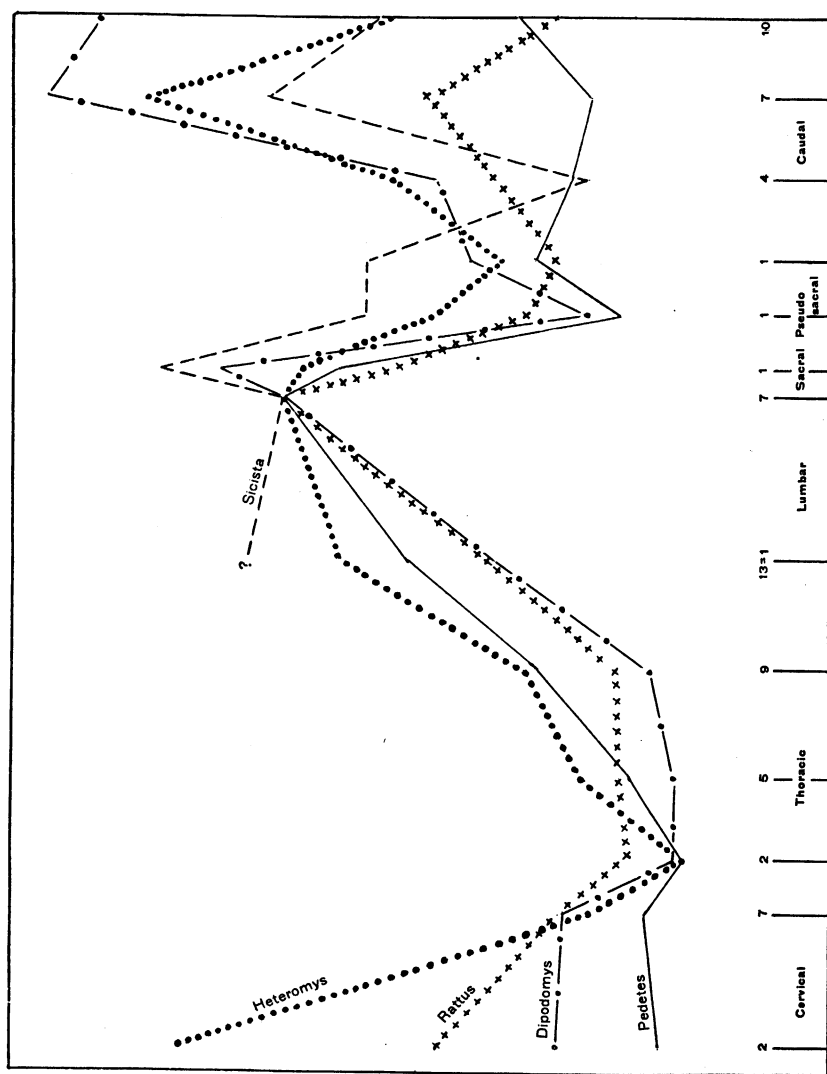


Fig. 16. The products of the heights times the widths of the anterior articular surfaces of the vertebral centra of selected types of rodents are all reduced to relationship to the seventh lumbar unit which in turn is reduced to a common size in each specimen.

The usual characters of these differences, with exceptions as noted, are:

1.—DECREASE IN AREA OF THE ANTERIOR ARTICULAR SURFACE OF THE CENTRA FROM THE SECOND CERVICAL CENTRUM TO THE SECOND THORACIC CENTRUM. In this region the centra are broad and shallow, and, as elsewhere noted, short. This condition among primates, Gregory (1920, p. 113) correlates with the habit of holding the head at right angles to the column. There appears to be a similar correlation among the rodents studied, for those which ricochet carry the head more flexed upon the cervicals and also have broader, shallower cervical centra than do their quadrupedal relatives that move with neck extended. This modified shape of the centra appears to me, however, to be in all probability a result of neck shortening, which I interpret as an adaptation to leaping in rodents. Neck shortening necessitates an exaggeration of the cervical enlargement of the spinal cord, which in turn, it seems, requires broader vertebræ to house the enlargement. Depth of centra is, then, lessened because of the added support furnished by increased width and by the usual accompanying ankylosis of the cervical elements.

The reduction in caudal sequence of the area of transverse section is much more marked in the quadrupedal *Rattus* and *Heteromys* than in any of thericochetors. In *Perognathus*, whose locomotor development is transitional, the decrease is intermediate between that of the quadrupeds and ricochetors.

The axis has the widest centrum in all compared forms except *Pedetes* where the entire lumbar series as well as the first sacral vertebra are broader.

2.—INCREASE IN AREA OF THE TRANSVERSE SECTION OF THE CENTRA FROM NEAR THE MIDDLE OF THE THORACIC REGION TO THE LAST LUMBAR VERTEBRA. BOTH THE HORIZONTAL AND VERTICAL DIAMETERS OF THE CENTRA INCREASE, THE LATTER ALWAYS INCREASING MORE RAPIDLY THAN THE FORMER FROM THE SECOND TO THE FIFTH THORACIC CENTRUM.

The increment in sectional area is relatively uniform from the ninth thoracic to the last lumbar. In some forms (*Pedetes*, *Heteromys*) the increase is uniform from the second thoracic centrum. In others (*Allactaga*, *Dipodomys*, *Rattus*) there is little increment between the second and ninth thoracic units. In *Microdipodops* the area actually decreases to the fifth thoracic unit, beyond which there is the usual increase.

The ratio of height to width varies in this region, but in all, the vertical diameter increases relatively more rapidly than the width, from

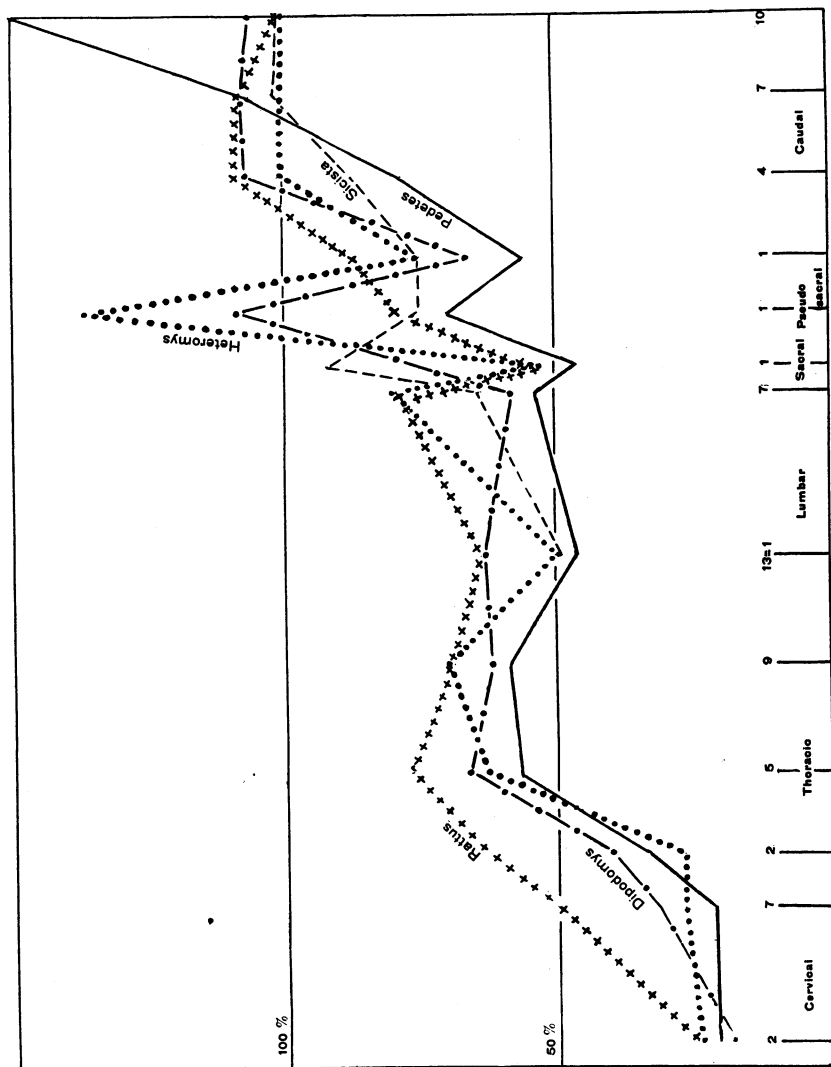


Fig. 17. The ratio of height to width of the anterior articular surfaces of vertebral centra.

the second to the fifth thoracic centrum, the region of maximum thoracic solidity. Caudad to the fifth element the breadth of the centra increases rapidly. In *Heteromys*, *Perognathus*, *Microdipodops*, *Sicista*, and *Zapus* the maximum breadth is attained at about the end of the thoracic region, the point of minimum accessory bracing.

In *Rattus*, *Dipodomys*, *Allactaga*, *Jaculus*, and *Pedetes* the increase in diameter continues to the sacrum though the increase is not nearly so rapid in the lumbar region as in the thoracic. This is a character common to many generalized rodents.

It would thus appear that the tendency to have the greatest diameter at about the first lumbar vertebra is a characteristic of small mammals with leaping tendencies (pronounced in *Peromyscus*), while the last of the lumbar series is most fully widened in more quadrupedal types (e. g., *Rattus*, *Tamias*) and in larger leaping rodents that are not strictly bipedal. This condition of great width at the posterior end of the lumbar region is found in the rabbits and also in the kangaroos. The vertical diameter of the centra increases with fair uniformity from the mid-thoracic region through the lumbar region. As a result the ratio of height to width usually decreases in the posterior part of the thoracic region and increases through the lumbar region (Fig. 17).

The width of the thoracic centra appears to be correlated with the rigidity of the thorax. Where the thorax is least flexible the centra are narrow, where most flexible the centra are broad. The mid-thoracic region contains the narrowest centra of any of the presacral series.

The breadth of lumbar vertebræ of primates has been correlated (Gregory, 1920, p. 114) with the position of the body at rest. In the lemur where the body is horizontal at rest, the centra are narrow. In the macaque the vertebræ are broad, a condition which Gregory associates with its habit of sitting up. The lemur-like condition of relatively narrow lumbar centra is found in *Heteromys*, *Perognathus*, *Rattus*, and *Zapus*. Relatively broader than the lumbar vertebræ of the animals listed above are those of *Microdipodops*, *Dipodomys*, *Allactaga*, *Jaculus*, and *Pedetes*, animals which on the average may hold their bodies nearer the vertical than those in the group of narrower lumbar vertebræ.

3.—AREA OF THE ANTERIOR FACE OF THE FIRST SACRAL CENTRUM IN MOST MEASURED GENERA LESS THAN THAT OF THE LAST LUMBAR. The specimens of *Dipodomys*, *Sicista*, and *Zapus* that were measured are not like the other genera in this respect, but have increased area from the last lumbar to the first sacral centrum.

The decreased area and a lowered ratio of width to height are due to an increase in breadth from the last lumbar to the first sacral centrum,

with either no increase in depth or a meager one. In the cases of the three exceptions named above, the width decreases in each while the height increases. The specimen of *Pedetes* selected at random, so far as trend of measurements was concerned, falls into the category of most of the other animals considered. There is variation, however, for sacral vertebræ both narrower and broader than the last lumbar are represented.

4.—AREA OF THE ANTERIOR FACE OF THE FIRST PSEUDOSACRAL CENTRUM IS IN ALL CASES LESS THAN THAT OF THE FIRST SACRAL. THERE IS A NARROWING OF THE PSEUDOSACRAL CENTRA IN ALL FORMS (except *Sicista*). This narrowing is most marked in the *Heteromyidæ*.

5.—THE AREA OF THE ANTERIOR SURFACE OF THE FIRST CAUDAL CENTRUM IS LESS THAN THAT OF THE FIRST SACRAL IN ALL FORMS, BUT IS LESS THAN THAT OF THE FIRST PSEUDOSACRAL ONLY IN THE QUADRUPEDAL *Heteromys* AND *Rattus*, AND IN *Zapus*. In *Sicista* the areas of the first pseudosacral and the first caudal centra are equal, while in the jerboas, *Perognathus*, *Microdipodops*, and *Dipodomys*, the area is greater. Typically the vertebræ increase in width between the last pseudosacral and the first caudal centra.

6.—DISTAL TO THE FIRST CAUDAL CENTRUM, WITH THE EXCEPTIONS OF *Sicista* AND *Pedetes*, THE AREAS INCREASE TO A MAXIMUM AT ABOUT THE SEVENTH ELEMENT AND THEN DECREASE TO THE END OF THE TAIL. In *Sicista* the same increment occurs, except that it does not commence until about the fourth caudal centrum. In *Pedetes* the increase of area is even further postponed because of the greater backward extension of the region of the diapophyses.

Distal to the first caudal vertebra the depth of the centrum in relation to its breadth increases sharply until about the fourth to seventh caudal element where the centra become practically circular in section. *Pedetes* is different from the other measured genera in this respect, the centra becoming taller than wide at about the fifth element. This lateral compression continues to the end of the tail. The terminal caudal segments of *Sicista* are not depressed as are the corresponding elements of some larger, prehensile-tailed animals.

To summarize, it is found that the differences between the shapes and relative sizes of the centra of quadrupedal and of ricochetal mammals are chiefly quantitative. The width, height, and area of section seem to be in part determined by the width of the spinal cord, in part by the degree of bracing which they receive from other bone structures or from muscles, and in part by the habits of the animal. The position of the

widest lumbar vertebra is probably related to the average position of the vertebral column.

VERTEBRAL PROCESSES

NEURAL SPINES

I have found that the neural spines as they vary in their height, length, inclination, and strength, usually reflect both the animal's habits and phylogenetic heritage. Thus between *Rattus* and *Heteromys* there is great similarity of lumbar spines, but a striking difference in the spines of the interscapular region even though there appears to be no dissimilarity between the locomotor habits nor the proportions of the fore limbs of these two genera that would sufficiently account for this difference in structure. It must then reflect heritage. The murine and cricetine rodents, when they are of generalized quadrupedal types, usually have the interscapular spines of a pattern similar to that of *Rattus*, while the two genera of quadrupedal Heteromyidæ, originating from different stock than *Rattus*, have spines of a different type.

There is a tendency for only one large spine to be present on the cervical vertebræ of ricochetors, and for this to be confined to the axis. Where cervical vertebræ two to six are fused the spine is limited to the anterior end of the block. The spine of the axis extends more or less directly upward and usually is narrow antero-posteriorly. There is no tendency for it to become terminally elongated in this plane, a configuration common among long-necked rodents.

The atlas never bears a strong spine, though in *Dipodomys* a small tubercle is sometimes present on the summit of the neural arch. Among the more ratlike gerbilles the spines on cervical vertebræ three to seven are present, though light and rudimentary. In *Perognathus* there is a light spine on cervical vertebra three. In long-necked *Pedetes* low spines are present on all of the cervical vertebræ, and are lowest on five and six.

The usual disappearance among ricochetal rodents of spines from the cervical vertebræ caudad to the second may be attributed to one or both of the following factors.

Among ricochetors the neck usually becomes shortened and sharply flexed upon the thoracic region. This sharp flexion necessitates the elimination of long spines on the last few cervical vertebræ as such spines would by terminal contact interfere with each other.

There is less necessity for strong spines on the posterior cervical elements because of the removal of some strain of head pull accompanying neck shortening, neck flexion, and semi-upright posture.

The loss of spines is probably somewhat compensated for by increased strength of the median fibrous septum which gives rise to some muscle fibers.

The chief differences between the neural spines of the trunk vertebrae of ricochetel rodents and more generalized types occur, as will be shown, (1) in the posterior displacement of the region of the highest thoracic spines from the interscapular region (often Thoracic 2) to the region of the center of motion (the summit of the dorso-lumbar curve) (the quadrupedal Heteromyidæ are exceptions to this generality, their interscapular spines resembling those of ricochetors); (2) in the extreme lengthening of the posterior lumbar spines; (3) in the great reduction of the spines over the sacrum, except in *Pedetes* where, on the contrary, these are excessively developed.

The spines in the first part of the thoracic region are low or altogether wanting in ricochetel rodents. In the majority of quadrupedal species, however, the thoracic spines are elongated in the shoulder region for the dual purpose of (1) increasing the area of attachment for *M. rhomboideus* and raising this anchorage above the level of the surrounding axial muscles, and (2) giving increased area for origin to the large neck muscles found in these animals whose necks are long and usually held nearly horizontal.

In all the ricochetel rodents seen there is a gradual increase from front to rear in the height of the thoracic spines above the dorsum of the neural arch. The length of the spines does not increase, for, to the contrary, the spines become shorter though more nearly vertical. This increase in height continues to the center of motion. The jumping shrew (*Rhyncocyon*) offers a marked contrast to the ricochetel rodents in this respect, for its interscapular spines are high, indicating extensive use of the fore limbs.

The thoracic spinous processes are strongly inclined backward at the point of their first appearance on the columns of ricochetel rodents and some quadrupedal species, but in caudal sequence are progressively raised to the vertical at the center of motion. The strong initial recumbency of these thoracic spines, which is in contrast with the vertical anterior thoracic spines of such a quadrupedal form as *Rattus*, seems to be associated with sharp cervical flexure. The recumbency of spines is not attributed to the possibility of mechanical interference by contact between tall vertical thoracic spines and the flexed cervical vertebrae, but rather to a response to the direction of pull by the epaxial muscles which are attached to these spines.

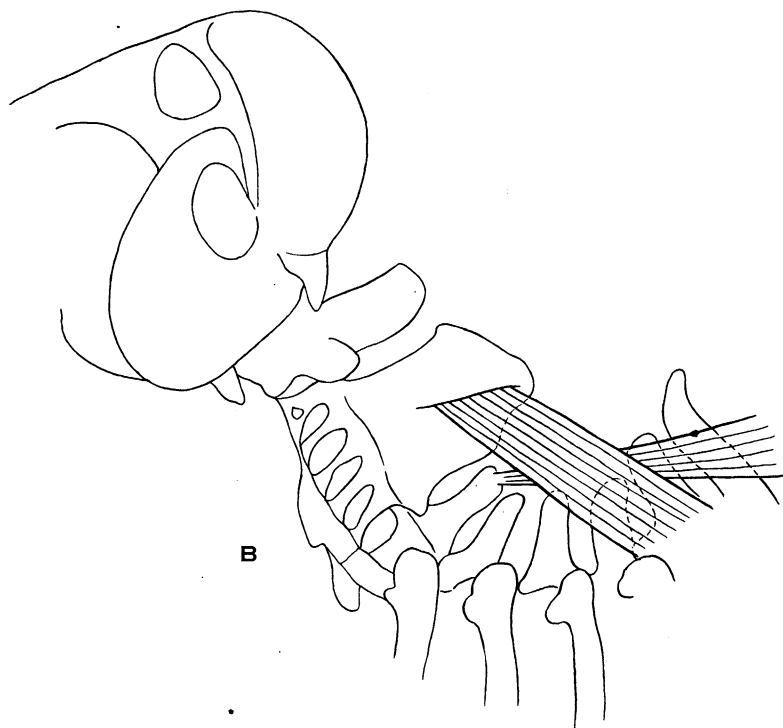
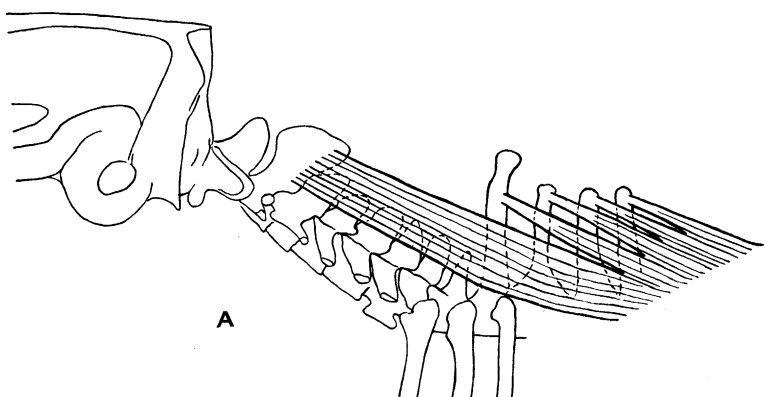


Fig. 18. Cervical insertions of the spinalis dorsi.

A.—Rat type (*Rattus norvegicus*).

B.—Jerboa type (*Jaculus orientalis*).

The latter type differs from the former chiefly in the complete separation of the most cranial lateral slip spinalis cervicis from the main belly of this muscle. This is apparently due to the differences in cervical length and flexure in the two types.

The marked difference between the interscapular spines of the *Rattus* type and those of the *Jaculus* type is distinctly associated with the contrasting musculature of the two types (Fig. 18).

In *Jaculus*, representative of the group in which the spines on the first two or three thoracic vertebræ are low or wanting, *M. spinalis dorsi* extends forward as a strong muscle from about the level of the center of motion and inserts by a strong tendon on the neural arch of the seventh cervical vertebra. Because of the strong cervical flexion this tendon of insertion meets the neural arch at an angle of about sixty degrees. In *Rattus*, on the other hand, *M. spinalis dorsi* inserts by a very strong tendon on to the enlarged spine of the second thoracic vertebra as well as by smaller tendons on to the spines of several vertebræ to the rear. Since the neck of *Rattus* is held more nearly horizontal than the neck of *Jaculus*, the insertion of the tendons on these raised lever-arms is more effective than insertions directly on the neural arches would be, for this latter course would necessitate extremely acute angles of insertion and result in weakness. One other marked difference between the *spinalis dorsi* muscle of *Jaculus* and that of *Rattus* contrasts the two types of cervical length and cervical flexion. In *Rattus* the most lateral and cranial slip (*M. spinalis cervicus*) inserts on the spine of the axis. It is continuous with the belly of the muscle from which arise the tendons of insertion which attach on to the second thoracic spine and others caudad to it. The homologous slip in *Jaculus* has entirely separated from the main belly of the muscle. It originates on the transverse processes of the first to the fifth thoracic vertebræ and inserts on the spine of the axis. I interpret this difference as due to the necessity of staggering the direction of muscle slips along a sharp concavity. In *Rattus* the muscle fibers of the *spinalis cervicus* may continue from those in the thoracic region, because in passing from one vertebra to the next there is little change in the alignment of the sites of insertion of the successive tendons.

There seems to be a slight tendency for the position of the center of motion which represents the modal point of the thoraco-lumbar arc to shift caudally with bipedal specialization in the Dipodidæ, but such a tendency cannot be demonstrated in the Heteromyidæ. The position of the center of motion in the Dipodidæ is given in Table XII.

A similar caudal shifting may occur within the gerbilles, though my few specimens can only suggest this. In the ratlike *Meriones* the center of motion lies at thoracic vertebra ten, as it does in *Rattus*. In the somewhat bipedal *Gerbillus* the single specimen had the center of motion

between the tenth and eleventh thoracic units. In *Tatera*, whose proportions are similar to those of *Gerbillus* the center of motion was at the eleventh thoracic unit.

In *Pedetes* the center of motion is between the eleventh and twelfth thoracic vertebræ in four specimens, at the twelfth in one.

In this connection it is interesting to note that with bipedalism and the development of upright posture in Primates, the center of motion moves caudally.

Posterior to the center of motion the height of the spines may or may not decrease slightly for one or two units, but within the lumbar series the rise in height is strikingly rapid and uniform to the last lumbar vertebræ. The increase in length of these spines is correlated with the necessity of increasing leverage for the action of the Mm. multifidus spinæ which support the fore end of the body during bipedal progression.

Though the factor of thinning of spines has not lent itself well to quantitative treatment, it is clear from examining a series of skeletons that there is a marked reduction in the antero-posterior diameters of the spines of the lumbar vertebræ of ricochetal rodents. Among the Heteromyidæ, *Heteromys* and *Liomys* have broad spines, while in *Pero-gnathus* and the more advanced genera the thinning is extreme. All of the Dipodidæ available have the spines well thinned, as has *Pedetes*. The gerbilles, *Meriones*, *Gerbillus*, and *Tatera* all have broad lumbar spines like those of *Rattus* and other rodents of generalized locomotor habits. In *Paramys* the lumbar spines are of moderate breadth.

It would seem that the functional difference between the two types of spines is that the broad-spined quadrupedal animals require strength to guard against too great lateral strain, for which short broad spines are adapted. The ricochetal animals need efficient leverage in the spines to aid in support of the fore part of the body, but dispense with lateral bracing in these structures. It is for this reason that they bear long slender processes.

The figure (19) representing the height of spines above the neural arch is not an index to the comparative LENGTHS of spines, particularly in the lumbar regions. For example in *Rattus*, the lumbar increase in spinal height is proportionately equal to that in *Pedetes*, whereas in spinal length there is great contrast. The spines of *Pedetes* and other ricochetors are strongly inclined forward, for which reason their "height" is not indicative of their length.

Pedetes and *Parapedetes* differ strikingly from the Dipodidæ and the Heteromyidæ in that over the sacrum is a long heavy spine formed by

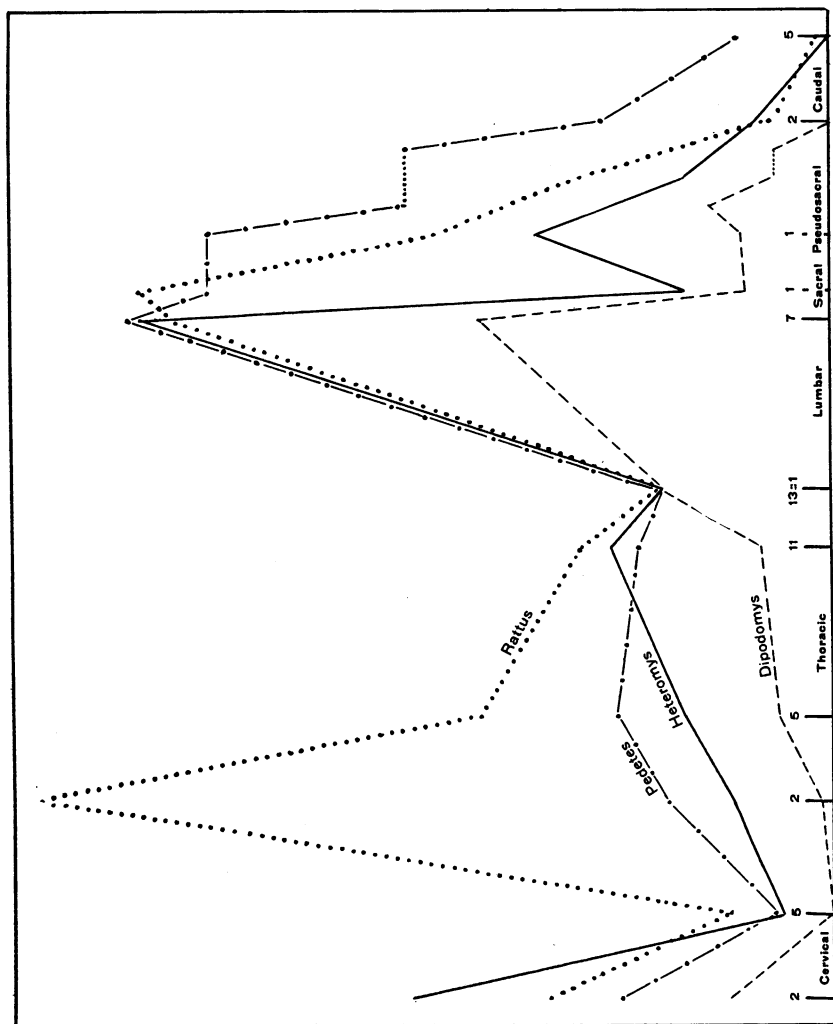


Fig. 19. The height of neural spines of selected vertebrae on the vertebral columns of four representative types of rodents. The height of spines is shown in relation to the spine on the thirteenth post-cervical vertebra which is considered constant for each of the genera.

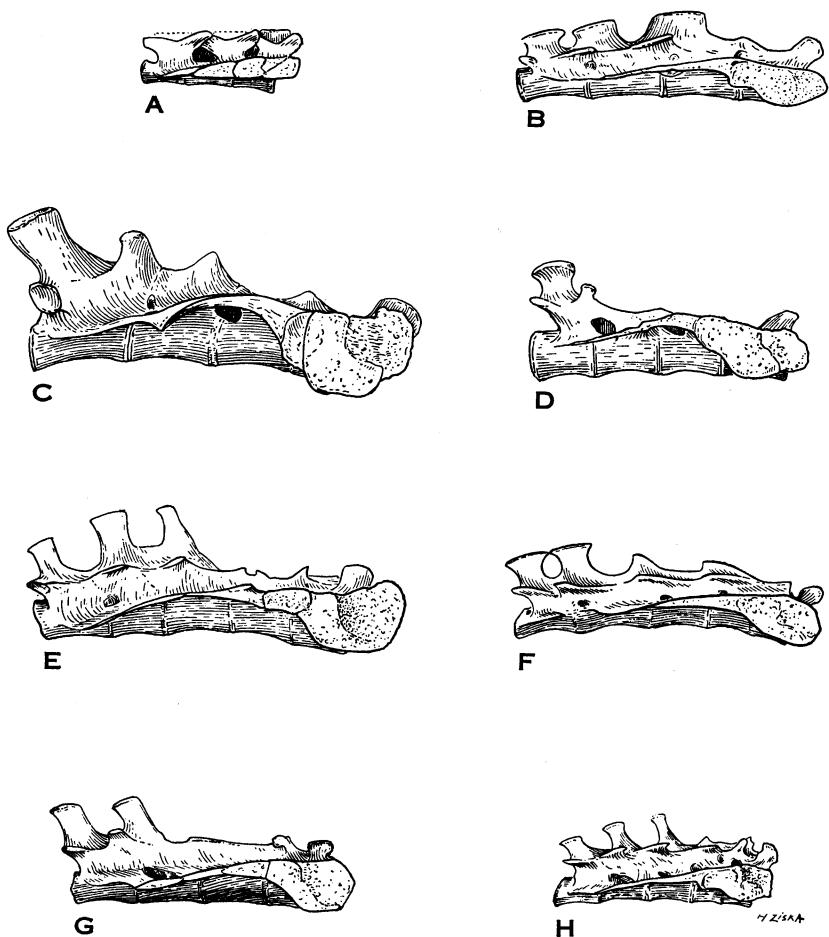


Fig. 20. The sacra-pseudosacra of selected Dipodidæ and Heteromyidæ. Anterior end to the right.

- A.—*Sicista loriger* (122117) $\times 3.2$.
 B.—*Zapus hudsonius* (13584) $\times 3.2$.
 C.—*Allactaga jaculus* (227) $\times 2.1$.
 D.—*Jaculus orientalis* (70004) $\times 2.1$.
 E.—*Liomys* species (16780) $\times 2.1$.
 F.—*Perognathus fallax* (43061) $\times 3.2$.
 G.—*Dipodomys heermanni goldmani* (13207) $\times 2.1$.
 H.—*Microdipodops polionotus* (24101) $\times 3.2$.

the distal union of two to three spines, while caudad to this level the spines are sharply reduced. The *Dipodidæ* and *Heteromyidæ* have reduced spines or no spines directly over the sacrum, but have a moderately high and strong spine over the last, and sometimes next to the last

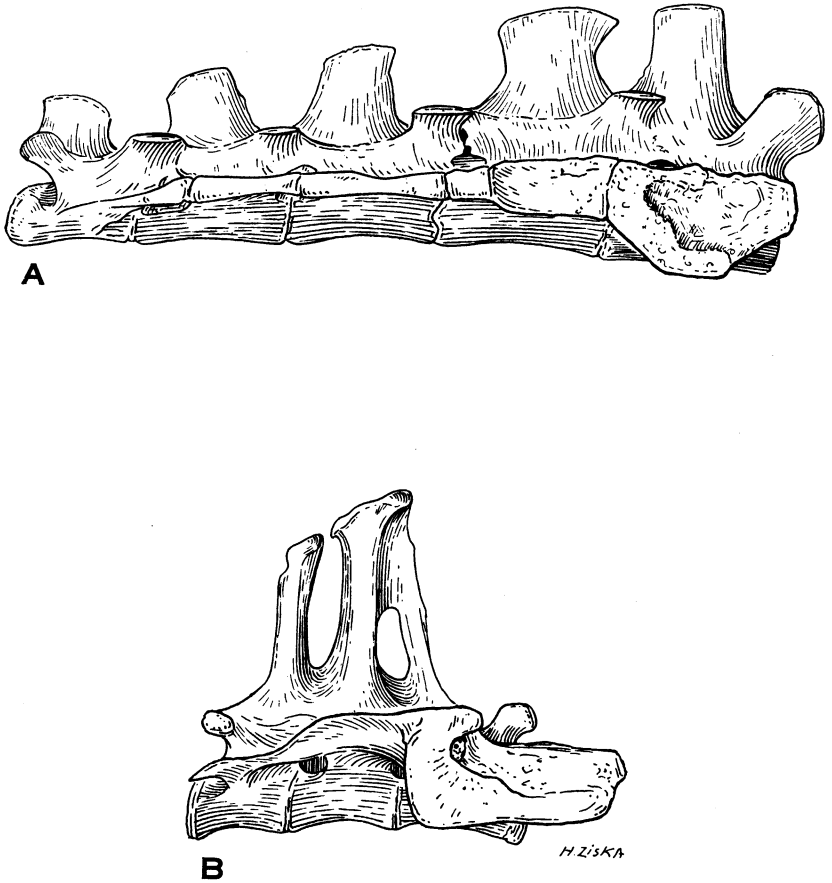


Fig. 21. The sacra-pseudosacra of *Rattus* and *Pedetes*.

A.—*Rattus norvegicus* (148) $\times 3.0$.

B.—*Pedetes cafer fealinx* (42025) $\times 1.5$.

pseudosacral vertebra. (See Figs. 19, 20.) Correlated with this osteological difference is a well-marked difference in the muscles. To take *Jaculus orientalis* as a type for the jerboas, it is found that as the tail musculature is largely confined to the body region, the caudal extensors

are proportionately more enlarged in the sacral region than they are in *Pedetes*. From the spines of the fifth, sixth, and seventh lumbar vertebræ and the intervening ligaments, originates a large-bellied muscle, *M. extensor caudæ lateralis*, which fills the trough alongside of the median line over the sacral and first pseudosacral vertebræ to the local exclusion of the multifidus muscles and the very spines themselves. At the level of the enlarged spines of the last (second) pseudosacral vertebra (Fig. 20 D) this great muscle narrows to tendons which pass along the side of the tail.

Anterior to the origin of this muscle is a well-developed multifidus uniting the spines of the vertebræ.

Posterior to the last pseudosacral there is also a well-developed multifidus mass, *M. extensor caudæ medialis*. This takes origin from the strong spine of the last pseudosacral unit. As this spine is not reinforced by muscle pull from the front, it is enlarged to care for the uncompensated strain from the rear.

In *Pedetes* the last lumbar spine is united to the compound sacral spine by a strong band of muscle which is part of the multifidus system; other slips of the multifidus composing the extensor caudæ medialis arise from the seventh lumbar spine, the sacral spine, and the first few caudal spines and unite to pass into the tail region. The chief muscle that imposes strain on the sacral spine in a longitudinal direction is the band uniting this spine and that of the seventh lumbar. The force exerted by this muscle would not seem ample to explain the great development of the sacral spine (Fig. 21 B), which is non-existent in jerboas and the *Heteromyidæ* (Fig. 20). Some strain comes from *M. extensor caudæ medialis*, but I believe that the main reason for the height of the sacral spine of *Pedetes* lies in the necessity for the skeleton to rise above the muscle mass that it may furnish anchorage to the strong leg muscles that attach to the lumbo-dorsal fascia.

Beyond the last pseudosacral unit the spines taper away, becoming totally lost as the caudal vertebræ assume the cylindriform character of the middle and terminal units.

It is concluded that the configuration of the neural spines may reflect either the habitus or the heritage of a species. The usual absence of spines of the third to seventh cervical vertebræ of ricochetal species is attributed to the sharp cervical flexure occurring in the column of these types. This curvature has produced changes in angles of muscle insertion that call for the loss of these spines, and the curvature itself often places the neural arches of the cervical series in such close proximity to

those of the anterior thoracic series that the presence of spines would result in their mutual contact. The loss or reduction of the interscapular spines in ricochetors is attributed to the reduction in size of the fore limbs and their muscles of attachment to the spines, and to the reduction in strain imposed upon them by the neck muscles. This latter is brought about by the frequent assumption of the upright posture, by sharp cervical flexion, and neck shortening. The recumbency of the anterior thoracic spines of ricochetors appears to be due to the change in direction of muscle pull brought about by cervical flexion.

The neural spines of the lumbar region of ricochetors are unusually long in accommodation to the necessity of increasing leverage and area of origin to the multifidus muscles whose rôle in raising and holding up the fore part of the body is of increased importance in bipedal species. These same spines are thin, probably because they do not need a great deal of lateral bracing.

The marked differences of the spines over the sacra of *Pedetes* and the smaller ricochetal rodents are correlated with muscular differences, but can not be adequately interpreted in terms of mechanics. The presence of a heavy spine on the last pseudosacral vertebra of the smaller ricochetal rodents is probably due to the pull of the median caudal extensor uncompensated by any pull in front.

TRANSVERSE PROCESSES

The Transverse Process of the Atlas

The evolution of the ricochetors, involving shortening of the atlas, shortening and fusion of other cervical elements, and change in shape of the skull with associated reduction in neck movements, has also produced modifications in the transverse process of the atlas.

In passing from primitive to specialized types the chief changes occurring in the transverse process are a reduction and simplification in muscle attachment areas and a shift in the relations of the main planes of muscle attachment from the horizontal to the vertical.

With the simplification of this atlantal architecture, reduction of bone volume and reduction of area of attachment, there is an opening up of the foramina that transmit the first and second spinal nerves and the vertebral artery. As is to be expected in such minute features, there is some variation of these characters within a genus. There are not sufficient specimens at hand to determine which of these variations are due to age or specific differences, but as a number of specimens are bilaterally asymmetrical in these anatomical characters little importance

can be attached to individual cases. Five atlases in a series of fifty-three (Dipodidæ, Heteromyidæ, Pedetidæ) show such asymmetry.

The vertebro-arterial foramen of the atlas is converted into a canal through lack of fusion at the outer end of the upper and lower limbs of the transverse process in the following:

DIPODIDÆ: *Zapus*, *Napæozapus*, *Allactaga*, *Dipus*, *Scirtopoda*, *Jaculus*. HETEROMYIDÆ: *Heteromys*; seven out of twelve possible cases in *Perognathus*; three out of twelve possible cases in *Microdipodops*. The two limbs of the process meet and fuse in all but two of the ten hemi-vertebræ of *Pedetes*; in *Tatera*, *Meriones*, *Gerbillus*, *Eliurus*, *Liomys*; five out of twelve cases of *Perognathus*; nine of twelve cases of *Microdipodops*; and all *Dipodomys*. Lack of fusion is then apparently a character of the Dipodidæ, while among the Heteromyidæ the condition occurs with increasing frequency as necks grow shorter.

The atlantal foramen occurs in every specimen, though there are three cases of bilateral asymmetry (one *Dipodomys*, one *Perognathus*, one *Dipus*) in which, on one side, the foramen is represented by a notch through failure of bone development on the anterior edge. Through the atlantal foramen pass the first spinal nerve and the vestige of the vertebral artery.

The first spinal nerve and vertebral artery parallel each other between the atlantal foramen and the vertebro-arterial canal. Where they pass the anterior edge of the transverse process they typically pass through a notch in this border (Fig. 6 A, B, E). In some animals, however, the winglike transverse process expands anteriorly, passing lateral to the nerve and artery to meet and fuse with the arch of the atlas at its anterior border, thus making a foramen through which the nerve and artery pass. Such a condition occurs in *Pedetes* (Fig. 6 C), one side of one *Dipodomys*, *Eliurus*, and *Meriones*. This is, it seems, a change that is subject to occur in vertebræ where neck shortening is not great. It is, I believe, a method of increasing surface area of the upper limb of the transverse process, and not of protecting the nerve and artery.

The second spinal nerve passes out through a groove in the caudal border of the atlantal arch, dorsal to the posterior articular facets. In none of these rodents is the groove converted into a foramen, as it is in the rodents *Ondatra* and *Hydrochærus*.

The changes concerned with the areas of muscle insertion on the dorsal surface of the transverse process are intimately associated with the changes directly attendant to neck shortening. The most simple form of atlantal transverse process found in rodents is that in which the

upper and lower limbs of the process unite to form a horizontal plate of which the upper and lower surfaces are the principal planes of muscle attachment. In such processes there is no marked posterior surface. The transverse foramen usually pierces the lower surface nearer the posterior border than the anterior. This simple type of process occurs in such diverse types of rodents as *Cynomys*, *Anomalurus*, *Castor*, and *Cavia*.

A modification of the type described above presents prominent anterior and posterior muscle attachment areas, chiefly on the lower limbs of the process. Viewed laterally, the edge of such a process is like an inverted "L" (T). This form of process is, perhaps, that most commonly occurring in rodents. It is found in *Rattus* (Fig. 6 D), *Hydromys*, *Peromyscus*, *Tatera*, *Eliurus*, *Ondatra*, *Lagostomus*, *Thomomys*, and, usually *Pedetes*, though the specimen shown in figure 6 happens not to be of this type.

In certain other rodents the anterior and posterior planes are of greater surface area than the dorso-ventral planes (Fig. 6 E), a change in relationship accompanying shortening of the atlas. This type of process occurs occasionally in *Perognathus* and *Microdipodops*, and usually in *Dipodomys*.

The most extremely modified type of process is characterized by the lack of fusion of the upper and lower limbs of the transverse process (Fig. 6 A, B, C), so that there are actually two processes. The upper of these (diapophysis) bears two principal planes. One of these faces dorsad-caudad-mediad, or caudad-mediad, and is analogous to the dorsal surface of the first type of process described. The other plane faces ventrad-craniad-laterad, or craniad-laterad, and is partially analogous to the ventral surface of the first type of process. The lower process (parapophysis) bears anterior and posterior faces. This condition of a divided process occurs in *Zapus*, *Allactaga*, *Dipus*, *Sciurtopoda*, *Jaculus*, *Heteromys*, most *Perognathus*, and three out of twelve *Microdipodops*. It also occurs in the fossorial *Heterogeomys*.

There is, as mentioned above, a shifting in angulation of the chief planes of insertion on the dorsal limb, in general, from a horizontal (Fig. 6 D) to a vertical plane (Fig. 6 E). Though several systems of measuring this were tried, no system based on any two points gave a consistent representation of the whole. For example, measurements of angle in relation to the vertical axis of the atlas were taken on the imaginary plane between the antero-dorsal external angle of the upper limb and the caudo-ventral external angle of the lower limb (Fig. 6 D, E). This is in every case, however, a composite of from two to four planes and has no apparent

significance. It was found that the most consistent change was the most prominent one—a change in the angle between the horizontal axis of the neural canal and the plane of insertion of *M. obliquus capitis inferior*, which is nearly paralleled by an opposite plane, chiefly occupied by *M. rectus capitis lateralis*.

A review of the specimens indicated that the angle taken by the plane of insertion of *M. obliquus capitis inferior* was in large measure determined by the space available on the side of the atlas. Where vertebrae were long, the deviation from the horizontal was small (Fig. 6 D). Where vertebrae were short and compressed, the plane approached the vertical (Fig. 6 E). The best way of expressing the degree of compression of the atlas seems to be the ratio obtained by dividing the greatest height of the atlas by the length at the level of the transverse process. The figures obtained from these two sets of measurements are given in Table XIII.

The figures appear more harmonious when the sizes of the individuals are considered. They tend to show that a large mammal with a short neck may have the same angulation of this plane as a small mammal with a long neck.

As cases in point selected from Table XIII the following two groups may be given:

CASE I

	ANGLE OF PLANE	CERVICAL VERTEBRÆ IN PERCENTAGE OF THORACO-LUMBAR LENGTH	TOTAL HEAD AND BODY LENGTH
<i>Jaculus orientalis</i> (70004)	70°	10.6 per cent	125 mm.
<i>Dipus sowerbyi</i> (55979)	70°	12.7 "	119 mm.
<i>Zapus hudsonius</i> (5403)	70°	15.7 "	71.5 mm.

CASE II

<i>Dipodomys phillipsii</i> (132763)	80°	14.6 "	94 mm.
<i>Zapus insignis</i> (74849)	80°	15.0 "	82 mm.
<i>Perognathus fallax</i> (43061)	80°	19.7 "	71 mm.

To demonstrate the same point another way we may consider the case by grouping together three specimens of about the same proportionate neck length.

CASE III

<i>Pedetes cafer ?salinæ</i> (42057)	40°	15.1 "	339 mm.
<i>Allactaga jaculus</i> (227)	50°	15.3 "	162 mm.
<i>Zapus insignis</i> (74849)	80°	15.0 "	82 mm.

The factors actually determining the planes discussed are, I believe, the pull of *Mm. obliquus capitis inferior* and *rectus capitis lateralis*. This latter muscle commonly inserts on the paroccipital process, which in *Jaculus* lies almost exactly parallel to this muscle's plane of origin on the wing of the atlantal transverse process when the head is in its average or most usual resting position—as determined by the articular surfaces of the occipital condyles and the receptive fossæ on the atlas.

The Transverse Processes of the Second to Seventh Cervical Vertebrae

The transverse processes of the cervical vertebrae from the second to the seventh are not greatly expanded antero-posteriorly in any of these forms. In all forms listed, both ricochetal and quadrupedal, the process of the second vertebra is weak (Fig. 6, 7), caudally directed, and not greatly extended laterally. The seventh, on the contrary, is strong, perpendicular to the antero-posterior axis, and extended farther laterally than any other, with the exception in some specimens of that of the atlas. The processes of the vertebrae from the third to the sixth are strictly transitional in nature except for the development of inferior lamellæ elsewhere considered.

The process of the seventh cervical vertebrae is imperforate in the few specimens on which this feature could be seen.

The degree of serial increase in lateral extension of these processes varies greatly within the group of rodents studied (Fig. 7). Those sets of cervical vertebrae in which the increase is apparently most rapid are generally those with proportionately short necks. The case with the most extreme degree of flare is that of a *Jaculus orientalis* (70004), in which there is fusion of five of the elements, and the neck is but 10.6 per cent of thoraco-lumbar length. An opposite case is that of *Heteromys longicaudus* (3645), in which there is no fusion of cervical vertebrae, and the neck is 18.6 per cent of thoraco-lumbar length (Figs. 10, 12).

The Transverse Processes of the First Thoracic Vertebrae and All Those Posterior to It

The extreme extension of the seventh cervical transverse process is followed by an abrupt shortening of the first thoracic process. Caudally up to the point at which they disappear, the processes decrease in length very gradually.

Measurements of the series of rodents show that the angle formed between the median plane and a line connecting the tips of the transverse processes of the seventh cervical and the first thoracic vertebrae is

approximately the same as the angle formed between the median plane and the line connecting the tips of the processes of the second and seventh cervical vertebræ. One may then say that the greater the proportionate increase in length of the seventh transverse process, the greater the proportionate decrease in length of the first thoracic transverse process.

In the case of *Jaculus orientalis* (70004), the decrease in lateral extent of the first thoracic process from the seventh cervical is so abrupt that the outer side of the tuberculum of the first rib is the same distance from the mid-line as is the tip of the seventh cervical transverse process.

The thoracic transverse processes are proportionately longer in the larger than in the smaller rodents studied, though I can see no reason for this. There is no apparent correlation between process length and other structures.

The transverse processes disappear, resolving themselves into the superimposed metapophyses and anapophyses which can first be discerned somewhere between the seventh and eleventh thoracic vertebræ. The transverse processes lose their identity as such at the eleventh or twelfth thoracic vertebræ.

In review, it has been found that the transverse process of the atlas in ricochetors differs from that of quadrupedal types chiefly in the restrictions imposed upon it by neck shortening. Thus there is a simplification and reduction in the areas for muscle attachment and a shift in these planes from the horizontal to the vertical. In most *Dipodidæ* the transverse processes of the atlas are divided into diapophyses and parapophyses, whereas in almost all *Heteromyidæ*, *Pedetidæ*, *Gerbillinæ*, and quadrupedal rodents in general the transverse process is complete. The transverse processes of the second to seventh cervical vertebræ are much the same in ricochetal and quadrupedal species. The transverse processes of the thoracic region are closely similar among all the species studied with the exception that those of the larger species are proportionately, as well as actually longer.

DIAPOPHYSES

The diapophyses extend from the first lumbar vertebræ to the sacrum where they are functionally replaced by the wings of the sacral vertebræ that are, by analogy with other animals, named transverse processes. It has, however, yet to be demonstrated, I believe, that any rodent has separate ossification centers between the sacral vertebræ and the ilia. The diapophyses continue posteriorly beyond the sacral vertebræ into

the tail region. In thin-tailed animals these caudal diapophyses disappear at about the sixth caudal vertebra, while in animals with muscular tails the diapophyses may be recognizable practically to the tip of the tail.

Cursorial, leaping, and ricochetal mammals have the diapophyses produced sharply downward and forward. This is in greatest contrast to the horizontal diapophyses both of aquatic mammals (where emphasis is thrown on lateral motion) and of fossorial mammals (in which muscular action is required to control motion in the horizontal plane more than in the vertical plane).

The diapophyses of a leaping animal do not all lie in one plane, nor does a single process always follow a single plane. The processes sometimes curve inward at their tips, while the first few diapophyses are usually inclined more vertically than those to the rear.

The length of the lumbar diapophyses of leaping animals increases sharply from the first to the sixth or seventh. The first pair is always very short. The sixth lumbar vertebra usually bears the longest diapophyses. These processes on the seventh lumbar vertebra are apt to be shortened due to the proximity of the ilia. The comparative lengths of the lumbar diapophyses of *Neotoma* are said by Howell (1926, p. 130) to depend on the age of the individual. Observations on a series of *Dipodomys* led me to conclude that in this genus also the length of the processes increases with age.

The muscles chiefly concerned with the modification of the lumbar diapophyses are probably those which are anatomically most intimately associated with them, *Mm. longissimus dorsi*, *quadratus lumborum*, and *psoas magnus*. The *longissimus* functions to extend the vertebral column and to support the forward part of the body in bipedal progress. The *quadratus*, in forms where the diapophyses project forward and down, assists in flexing the column, an act accompanying leaping. This is of lesser importance in ricochetors than in quadrupedal leapers, such as the hare, where a wide overstep is accompanied by strong arching of the back. The *psoas*, arising in part from the posterior edge of the diapophyses, is important in drawing the femur forward.

It has proved impossible to measure accurately the angle of divergence from the horizontal taken by the lumbar diapophyses on any series of articulated skeletons of small animals. In the few specimens where accurate measurements were obtainable there appeared to be great variation within the members of one genus. In the sixth lumbar vertebra of *Dipodomys*, for example, the angle in one

specimen was 40° below the horizontal and in another 60° . The angle may be determined by the size and strength of the epaxial muscles or by the traction of muscles whose origins or insertions lie on the processes.

The antero-posterior breadth of the lumbar diapophyses varies in the same direction as the antero-posterior diameter of the spinous processes. When the spinous processes are broad in the median plane the diapophyses are broad also; when the spinous processes are narrow, so too are the diapophyses.

The caudal diapophyses of leaping rodents are co-extensive with the areas of origin of the caudal flexors and extensors. Thus in most forms, they extend little beyond the posterior limits of the pelvis. In *Pedetes*, however, whose tail is almost kangaroo-like in its mass, the diapophyses extend far to the rear. The processes in *Microdipodops* extend slightly farther posteriorly than do those of thinner tailed *Dipodomys* or *Perognathus*.

The extent and strength of the caudal diapophyses of *Pedetes* are likely further influenced by extrinsic tail muscles. In this animal the tail is unusually well braced at the base by muscles from the innominate bone. *M. pyriformis* originates only from the lateral margin of the diapophyses of the pseudosacrum and cannot be considered a part of the mechanism which reinforces the tail for the strain imposed upon it when used as the third leg of a tripod, or, as is possible, as an accessory propulsive organ. Immediately caudad to the *pyriformis* lies a well-developed flat muscle originating along the superior border of the ischium over *M. gemellus inferior* and from a ligament over *M. obturator internus*. This muscle, *M. ischio-coccygeus*, inserts on the lateral margins of the first, second, and third caudal diapophyses. From the superior border of the ischium, immediately caudad to the *ischio-coccygeus*, arises another strong muscle, *M. ischio-caudalis*, and this continues farther caudad to aid in flexing the tail. This muscle is greatly enlarged in the kangaroos where its function is the same as in *Pedetes*. A third muscle, *M. pubo-caudalis*, arises from the pubis and inserts on the tip of the diapophyses of the fourth caudal vertebra. This muscle also is a powerful flexor, and together with the *ischio-coccygeus* and the *ischio-caudalis* provides an ample bracing action for the tail when it is used as a prop.

These caudal diapophyses of various individuals lie at varying angles in relation to the transverse plane. Though there is some individual variation in specimens, the specimens of a given species or genus show similar amounts of divergence. Measurements of these processes on the

third caudal unit reveal a striking dissimilarity in angle between various genera, reaching extremes in *Pedetes* with a divergence of 16° from the transverse axis backward toward the median plane. In *Zapus* and in *Perognathus* one encounters a forward divergence of 55° . The difference between these extremes is then 71° . The backward trend of the processes in *Pedetes* is clearly associated with the extreme posterior extent of the

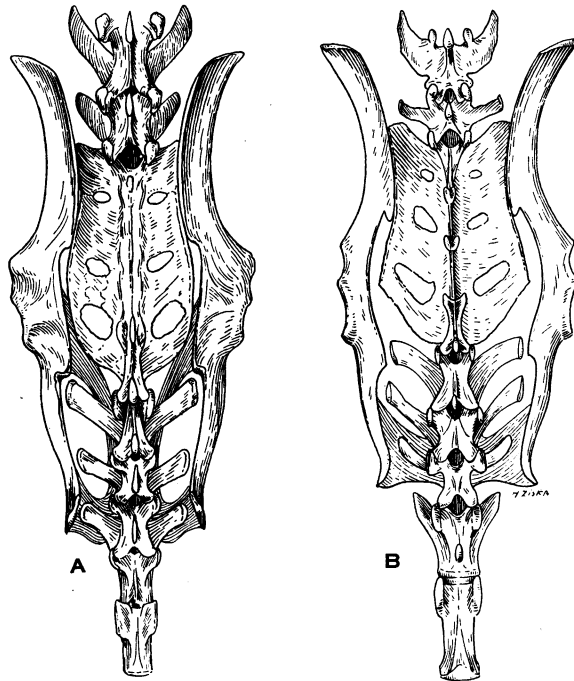


Fig. 22. The vertebræ of the pelvic region.

A.—*Liomys pictus* (8347) $\times 2.8$.

B.—*Dipodomys phillipsii* (132763) $\times 2.3$.

origins of the caudal muscles. In this genus the first caudal diapophyses are produced both forward and backward at their lateral angles and in the posterior series are bifid. In none of the other animals considered in this paper does the backward direction of the caudal diapophyses occur, though it is found also in muscular-tailed ricochetors of other orders, such as the jumping shrew (*Rhyncocyon*) and the kangaroo (*Macropus*).

Neglecting, then, the unusual case of *Pedetes*, we yet find variation in angulation among species, the muscular anatomy of whose tails is

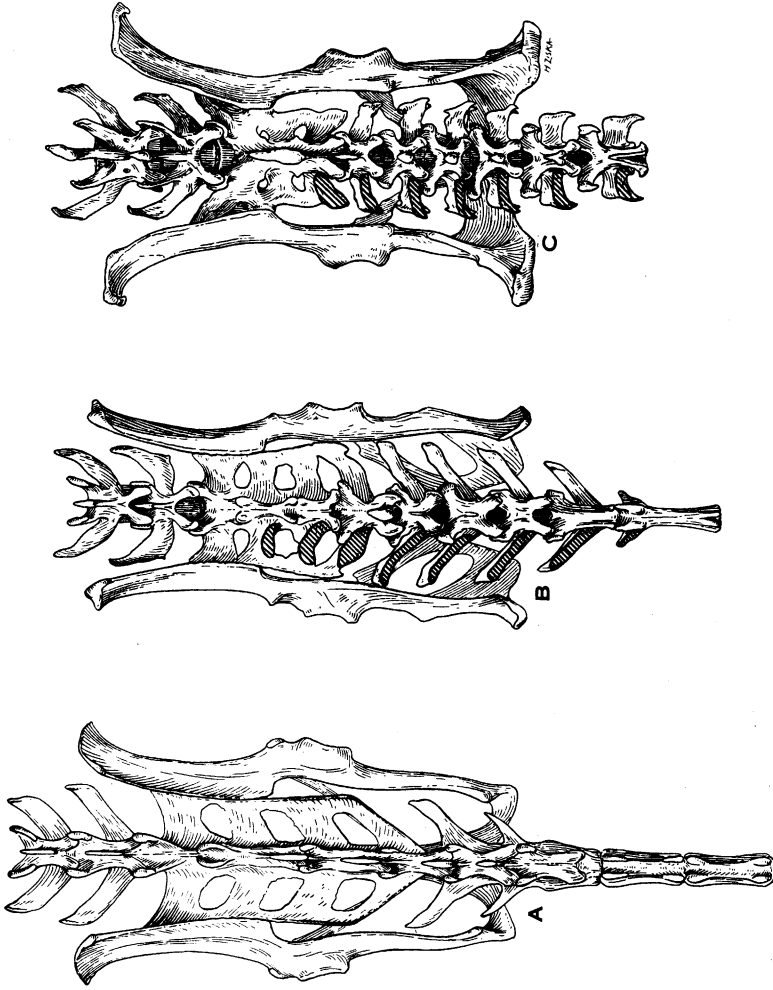


Fig. 23. The vertebrae of the pelvic region.

A.—*Zapus insignis* (74851) $\times 3.3$.

B.—*Jaculus orientalis* (70004) $\times 1.6$.

C.—*Pedetes cafer* (70392) $\times 5.3$.

The hatched areas on the vertebrae of *Jaculus* and *Pedetes* indicate the surfaces of origin of the extensor caudae lateralis.

apparently fundamentally the same. Within available Dipodidæ I find variation ranging from forward deviation of 55° in a *Zapus (Napæozapus) insignis* to forward deviation of but 25° in a *Jaculus orientalis*. Within the Heteromyidæ there is variation from 35° in a *Dipodomys phillipsii* to 55° in a *Perognathus fallax*.

Between these extremes are a good number of intermediates that in general follow the tendency indicated in the extremes; namely, that there is greater forward direction of caudal diapophyses in the smaller forms. I cannot account for this unless it is due to a higher ratio of tail weight to body size in small ricochetors than in large, which would necessitate stronger musculature in the smaller forms than in the larger. Forward divergence of caudal diapophyses increases area for muscular insertion and is a stronger construction for resisting muscular pull from the rear than is a strictly transverse process.

In summary, it has been impossible to establish any definite relation between the length, shape, position, size, or distribution of lumbar diapophyses and leaping habits. It is found that the diapophyses of the seventh lumbar vertebra are frequently shorter than those of the sixth. This is due to the proximity of the ilia to the seventh vertebra. Lumbar diapophyses in *Dipodomys* appear to increase in length with age.

The caudal diapophyses of ricochetors are linearly coextensive with the areas of origin of caudal flexors and extensors on the tail. In *Pedetes* where muscle origins and insertions both occur on a single diapophyses, both antero-external and postero-external angles are produced into processes, and terminally these processes become bifid. The caudal diapophyses of small thin-tailed mammals have a greater forward divergence than corresponding processes of larger tailed species, but the reason for this has not been found. The unusual development in *Pedetes* of certain extrinsic caudal flexors which insert on the proximal diapophyses, in all probability accounts for the size and configuration of the diapophyses of this animal.

METAPOPHYSES

The differences between the metapophyses of ricochetal rodents and those of generalized quadrupedal rodents are quantitative and not qualitative. Characters such as regional elongation, breadth and constriction, that are incipient in quadrupedal types are found exaggerated in bipedal types. This is due in the main, it seems, to the increased anterior load carried by the epaxial muscles of the ricochetors.

The condition of the metapophyses as found in all forms is this: The metapophyses first appear in the mid-thoracic region but are not prominent anterior to the "center of motion." The first three or four pairs of metapophyses posterior to this level are particularly long, especially in the ricochetors. Caudad to this region of long processes, the processes become shorter in serial order to the sacrum. The width of the processes remains practically uniform from the center of motion to the sacrum. Behind the pseudosacrum the metapophyses again appear as strong, prominent features which may continue in diminishing magnitude to the tip of the tail.

The lengthened metapophyses directly caudad to the center of motion serve to give greater area and better leverage to the insertion of those slips of the longissimus dorsi whose origin is from the spinous processes to the rear. There is here a good correlation between structure and demand, for in the bipedal rodents there is need for greater strength of these muscles in supporting the fore end of the body, and in these same rodents the processes of insertion, as well as those of origin, are lengthened from the primitive condition.

The first few caudal prezygapophyses bear metapophyses which are chiefly concerned with the insertions of the extensor caudæ medialis and are developed proportionately to the development of this muscle. A short distance behind the pelvis the zygapophyses no longer articulate with each other and the prezygapophyses function only as metapophyses on which are inserted other tendons of the extensor caudæ medialis.

In summary, it is found that the metapophyses of the bipedal rodents are slightly longer and heavier just behind the center of motion than are the corresponding processes of quadrupedal species. This difference is probably due to the greater pull of the extensors which support the fore end of the body.

ANAPOPHYSES

The anapophyses are the tubercles for attachment of the tendons of insertion of the longissimus dorsi and of the tendons of origin of the extensor caudæ lateralis. Between quadrupedal types and ricochetal types in the series of skeletons studied there is not a striking difference in anapophyses. Among the quadrupedal forms (*Rattus*, *Heteromys*, *Liomys*) these processes appear farther forward than they do in the ricochetors (*Jaculus*, *Scirtopoda*, *Dipus*, *Allactaga*, *Zapus*, *Dipodomys*, *Microdipodops*). Moreover, among the latter group, the anapophyses

at the anterior end of the lumbar series are proportionately longer and stronger than the corresponding processes of the quadrupedal types.

Vallois (1922, p. 319) states that among mammals in which the "longissimus caudæ" (*M. extensor caudæ lateralis*) is large, the anapophyses are long and placed very low on the vertebra, and that animals with a weak "longissimus caudæ" have weak anapophyses, placed high on the lumbar vertebræ. In *Pedetes* where this muscle is very well developed, the anapophyses are long and strong but are situated high on the neural arch up to the fifth lumbar vertebra. On the sixth and seventh vertebræ these processes are weak or non-existent, and where present are lower than those anterior to them. It is at this level that the extensor caudæ lateralis takes origin.

The anapophyses of ricochetors, except for being longer and stronger anteriorly than those of quadrupedal species, are not different from the latter.

ZYGAPOPHYSES

There are several mechanisms for restraining rotational movements of the column induced by the use of the limbs on alternate sides. These are the interaction of the muscles, the limitations imposed by ligaments, the binding of the intercentral capsules, the rigidity imparted by the thorax, and the apposition of vertebral processes. In most mammals the cervical region is practically free of opposing processes since it is usually advantageous to retain flexibility here, and few external strains are put upon it. The thoracic region is similarly free because the ribs alone give sufficient guarantee that there will be no undue torsion in the column. Caudal to the region of the first floating rib, however, the zygapophyses are perhaps the most important structures adapted to elimination of rotational movements. There is also a tendency for the metapophyses to overlap dorsally the gliding surfaces of the zygapophyses. The greater regional divergence of these surfaces also gives better leverage to the bracing action, but this divergence is traceable to a corresponding increase in diameter of the spinal cord and centra. Convergence of these articular surfaces in the inter-iliac region seems to be in accommodation to the epaxial muscles enlarged in this area.

In quadrupedal animals, particularly those which employ such rocking gaits as the transverse gallop, the rotational strain is greater than in ricochetors. This strain is greatest between the sacrum and the last lumbar vertebra and diminishes through absorption as it is transmitted forward. At the thorax it is virtually eliminated. For this reason it

might be expected that the mechanism for resisting shock would be greatest in the posterior part of the lumbar region, and that animals whose normal gait did not produce great rotational stresses would show less of a mechanism for such resistance.

The ricochetors do show much of the difference from quadrupeds that is suggested above. Instead of the zygapophysial contact surface being most widely separated at the sacrum, one finds that the point of greatest separation lies at about the second lumbar vertebra, posterior to which (best marked in the jerboas) the surfaces come much closer together. This is obviously not due to any lack of necessity for maintained breadth, but is in accommodation to the increased size of the muscles which are enlarged to help carry the load of the fore part of the body that is supported only through the acetabula in the bipedal animals.

The contact surfaces of the zygapophyses are most nearly vertical in the posterior lumbar region of the quadrupeds. (In this study's series, *Rattus*, *Eliurus*, *Tatera*, *Gerbillus*, *Meriones*.) In all of the Heteromyidæ they are at approximately the same angle throughout their extent. The same condition occurs in many of the Dipodidæ (*Zapus*, *Allactaga*, *Dipus*, *Scirtopoda*). This is also true in the "jerboa marsupial" *Antechinomys*. In *Jaculus* and *Pedetes* the surfaces most closely approach the vertical in the mid-lumbar region. The significance of this has not been determined.

Greatest bony envelopment of the zygapophysial surfaces, as a means of restricting vertebral motions to flexion and extension movements, thus eliminating rotation, is most pronounced in the posterior lumbar region of the quadrupedal rodents, *Rattus*, *Eliurus*, *Meriones*, *Tatera*, *Gerbillus*, and *Sicista*. Such envelopment is pronounced but equally distributed in the lumbar region of *Zapus* and *Napæozapus*. The envelopment is greatest at about the first lumbar vertebra in *Allactaga*, *Dipus*, *Scirtopoda*, and *Jaculus*. In *Pedetes* the degree of envelopment is poor, but occurs slightly in the mid-lumbar region. It would seem that the occurrence of the greatest degree of bony envelopment in the posterior lumbar region of quadrupeds is due to the presence of greater rotational stresses at this point. These stresses arise from alternate use of limbs and are greatest near the sacrum. Forward to the center of motion the stresses decrease from absorption. Other than this, no constant differences between the zygapophyses of ricochetors and quadrupedal types are found.

VENTRAL PROCESSES AND RIDGES

In all mammals the system of the axial flexors associated with skeletal parts ventral to the precaudal vertebræ is extensive, strong, and equipped with good leverages. In consequence the flexor musculature directly associated with the column is comparatively insignificant. The lightness of this musculature is reflected in the absence of striking bony configuration of the under side of the column.

Cervical Region

In the cervical region the vertebral muscles associated with flexion are *Mm. longus colli*, *longus capitis*, and *scalenus*. Among rodents the

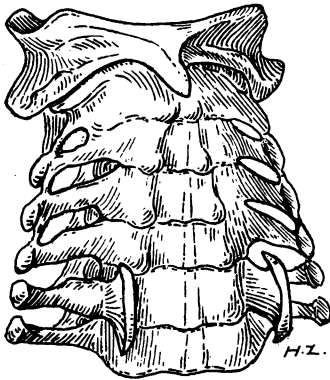


Fig. 24. Ventral oblique aspect of the cervical vertebræ of *Dipodomys deserti* (15457) showing the inferior spine of the atlas, the inferior lamellæ of the sixth cervical vertebra, and the two backwardly diverging lines of low processes on the intermediate vertebræ.

first of these muscles is functionally divisible into two main parts. One of these takes origin by fleshy fibers from the ventral surface of the centra of the anterior thoracic region, and inserts upon the caudal border of the inferior lamella of the sixth cervical vertebra (Fig. 24). The other part originates in slips from the anterior border of this lamella and from the bases of the transverse processes. In *Pedetes* the slips of origin anterior to the sixth cervical vertebra arise from forwardly directed processes that are serially homologous to the inferior lamella of the sixth vertebra (Fig. 7 C) and resemble those of other medium-sized mammals such as the house cat and Virginia opossum. These slips insert on to the median inferior spine of the atlas and a series of points or low processes (Fig. 24), which typically form a wedge, the apex of which is the prominent and backwardly directed ventral spine of the atlas, and the base of which lies on the fifth cervical centrum.

The inferior lamellæ may be anvil-shaped (*Dipodomys*, Figs. 6 E, 7 B; *Rattus*, Fig. 6 D; *Pedetes*, Figs. 6 C, 7 C) with processes directed forward and backward, or may be directed wholly to the rear. The latter type is constant in all available specimens of *Dipodidae* (Figs. 6 A, B, 7 D), whereas the anvil type occurs with an occasional individual exception in

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the Heteromyidæ, Gerbillinæ, and Pedetidæ. The anvil-shaped lamellæ are so formed in response to muscular traction from in front and behind. The backwardly pointing lamellæ of the Dipodidæ are probably all associated with the small size of the muscular slip of the longus colli originating on the forward part of this lamella. In *Pedetes*, (Figs. 6 C, 7 C) the lamellæ are relatively smaller than in any of the other genera of leaping rodents which I have seen.

The relative size of the inferior median atlantal processes appears to be influenced or determined by two opposing factors. One of these is the actual size of the neck, the longer necked forms bearing relatively shorter processes. Thus in a *Pedetes* (42025) with a 30 mm. neck (15.5 per cent thoraco-lumbar length) there is no trace of a process. In an *Allactaga* (227) with a 13 mm. neck (15.3 per cent thoraco-lumbar length) the process is 3.1 per cent of the neck length. In a *Zapus* (90655) with a 7 mm. neck (17.2 per cent thoraco-lumbar length) the process is 11.4 per cent of the neck length.

The second factor operating to control length of the median inferior atlantal process is fusion of cervical vertebræ. In *Jaculus* and *Dipus*, for example, in the series examined, the inferior process of the atlas is shorter than would be expected considering the simple factor of absolute neck length as founded on specimens with free vertebræ. Thus a *Jaculus* (70004) with a 7 mm. neck (10.6 per cent thoraco-lumbar length) has the inferior process of the atlas but 7.1 per cent of cervical length, while a *Zapus* (90655) with a 7 mm. neck (17.2 per cent thoraco-lumbar length) has a process 11.4 per cent of the cervical length.

The divergent tubercles posterior to the atlas are found well-marked or prominent on cervical vertebræ two to five of all the genera studied, except *Jaculus*, *Dipus*, and *Pedetes*. In the first two of the excepted genera this absence is associated with the fusion of elements which eliminates need for muscle action, and, in the first of which at least, the muscular slips are reduced. In *Pedetes* the inferior spine of the atlas is weak, too, though Mm. flexor colli longi, as revealed by dissection, are well developed.

The Median Inferior Lumbar Ridge

The pull of the psoas muscles has produced a prominent, sharp ridge in the mid-ventral line of the centra over which they take origin, in some of the ricochetal rodents. These ridges are best developed in animals with large psoas muscles. Inasmuch as the psoas muscles are chiefly flexors of the thigh, they are important parts of the leaping

mechanism. It is improbable, however, that ricochet mammals make heavy demands upon the second function of the psoas—namely, flexion of the column, which is of great importance among quadrupedal leapers.

These median inferior lumbar ridges extend through the entire lumbar series of *Zapus* and are more prominently developed in this genus than in any of the other Dipodidæ at hand. In *Jaculus orientalis*, the large Egyptian jerboa, there are weak ridges on the third to fifth lumbar vertebræ, but in *Jaculus jaculus*, the small Egyptian jerboa, in *Scirtopoda*, *Dipus*, and *Allactaga* no specimens with these ridges were seen. By dissection of *Zapus* and *Allactaga* I have found the psoas muscles of the former to be proportionately about twice as large as those of *Allactaga*, and it seems probable that this difference in proportionate muscular development explains the differences observed in the topography of the ventral surfaces of the lumbar vertebræ.

In *Pedetes* there are weak ridges on the lumbar centra.

The conditions found among the Heteromyidæ seem disharmonious. Two specimens of *Liomys* show no ridges, while two specimens of the somewhat similar animal *Heteromys* have ridges on the lumbar vertebræ. Weak ridges occur in most specimens of *Perognathus*. No ridges were found in *Microdipodops*. In the heavier bodied species of *Dipodomys* ridges are developed, but on the smaller species they are not.

It is probable that aging of an individual increases the prominence of these ridges as it does of most others of the body. It may well be that the reason that ridges have not been found in my limited series of specimens of some genera, is that the specimens at hand, though those of adults, were not those of old individuals.

The Median Inferior Ridge of the Sacral-pseudosacral Region

Presaging the appearance of the chevron bones, there is found in certain skeletons a marked ventral ridging, constriction or lateral compression of the sacral-pseudosacral centra. This would seem to be in accommodation to the origins of the sub-axial tail musculature. It does not follow that the degree of ridging is in direct proportion with the size of chevron bones, for there are probably differences in the levels of origin of the hypaxial caudal muscles in the different species.

The observed differences do not seem correlated with tail length or strength as might be anticipated, but are seemingly related to size, the smaller animals being the better ridged. *Pedetes*, for example, has flat-bottomed sacral vertebræ. *Allactaga* has a less developed ridge than have the smaller jerboas, and all the jerboas examined have less well-marked ridges than have the Zapodinae.

As was the case with the psoas muscles, the caudal extensors are found to be far larger in proportion to the animal's size in *Zapus* than in *Allactaga*. It is assumed that here too the differences in configuration of the centra are due to the variation in strength of the muscles originating upon them.

To summarize, it is found that the inferior lamellæ of the sixth cervical vertebræ are anvil-shaped except in the Dipodidæ, in which family these lamellæ are produced into a process only at their rear edge. This condition among the Dipodidæ is attributed to the very small size of the longus colli in these animals, possibly an association of neck reduction. The length of the median inferior atlantal process is effected by the size of the animal, for this process is very short in such a large animal as *Pedetes*. The fusion of cervical elements tends farther to reduce the length of this process. The development of a sharp median inferior lumbar ridge is traceable to the development of large psoas muscles. The marked variation in the ridging of the sacral-pseudosacral centra may be associated with tail musculature.

CHEVRON BONES

The chevron bones of the small-tailed ricochetal rodents are low throughout their extent. In *Pedetes*, on the contrary, though the linear distribution of chevrons is much the same as in the thin-tailed species, these bones are high and prominent.

In all species listed the chevrons first appear as paired bony nodules or plates between the first and second to second and third caudal vertebræ. They increase in height, uniting medially to form a true chevron, and reach their greatest height at the level of the caudal border of the pelvis (between caudal vertebræ two to three, three to four, or four to five, Fig. 25). They decrease in length distally at approximately the same rate as that of increase from the opposite end, soon becoming either flat-topped arches (Fig. 26, B, C) (Dipodidæ and Heteromyidæ) which extend almost to the tip of the tail, or paired sesamoidal nodules lying on the faces of corresponding low processes on either side of the mid-ventral line at the cephalic end of each vertebra (*Pedetes*, Fig. 26 A).

The function of the chevrons is to furnish greater attachment and better leverage for certain ventral tail muscles (Mm. flexor caudæ brevis) which do not extend far beyond the body limits, nor far within the body. The chevrons are best developed where one would expect so to find them. Because *Pedetes* is heavy tailed the chevrons are better developed in this animal than in the jerboas, jumping mice, and kangaroo rats. The great

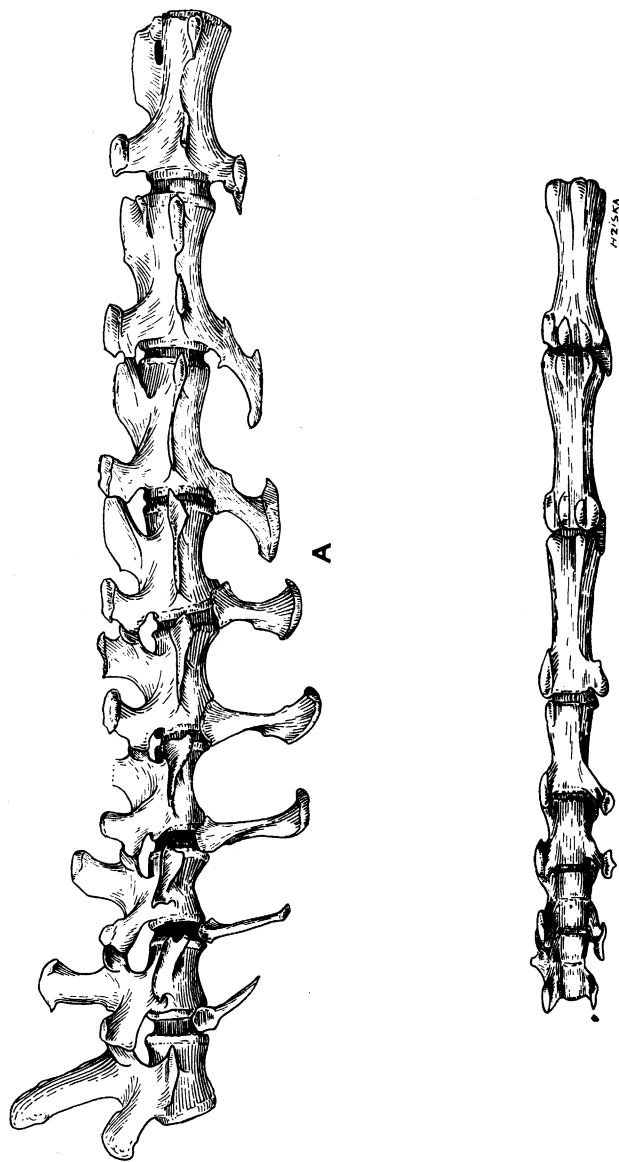


Fig. 25. The anterior caudal vertebrae and chevron bones of (A) *Pedetes cafer* (70392) ($\times 6$) and (B) *Jaculus orientalis* (70096) ($\times 1.1$) showing the enormous difference between the heights of the chevron bones of a muscular-tailed type and a tendinous-tailed type.

development of chevrons in *Pedetes* is paralleled among the heavy-tailed ricochetal marsupials. Distally in the *Dipodidæ* and *Heteromyidæ* the flat-topped arches that are vestiges of the chevron bones serve to protect the caudal blood vessels. In *Pedetes* the nodules found beyond the chev-

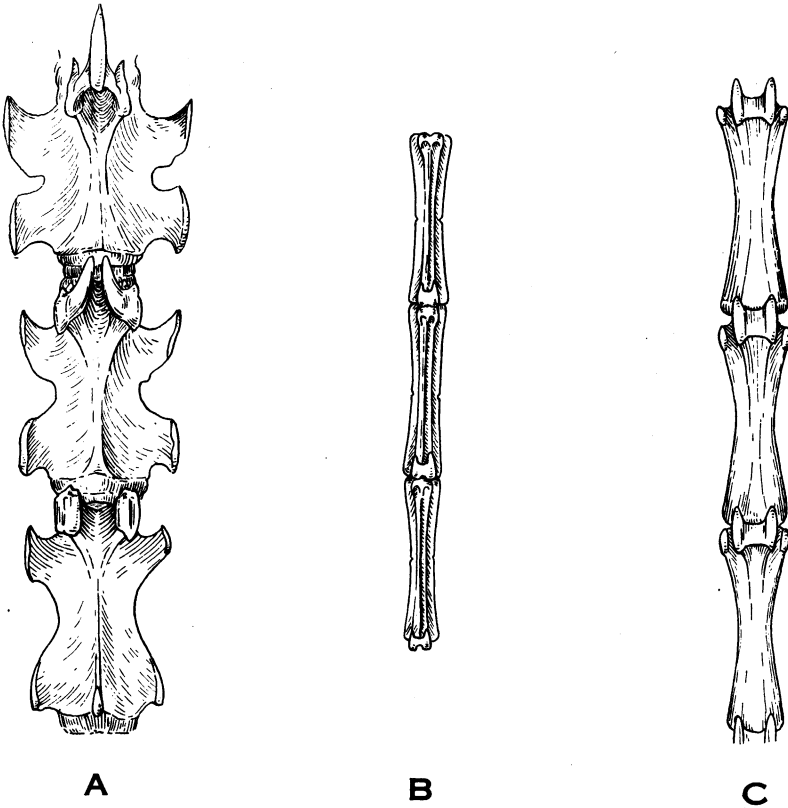


Fig. 26. Chevron bones.

A.—*Pedetes cafer* (70392) ($\times 1.5$). Showing the transition from a true chevron bone between the eighth and the ninth vertebrae and the sesamoidal nodules between the ninth and the tenth vertebrae. The chevrons of this region are borne on pedicles at the anterior end of each vertebra.

B.—*Perognathus fallax* (43061) ($\times 4.5$). Showing the presence of low flat-topped chevron bones lying over the distal end of each vertebra.

C.—*Jaculus orientalis* (70096) ($\times 2.3$). Showing the flat-topped chevrons lying over the intercentral discs.

rons are at the insertions of the tendons of *M. flexor caudæ longus* and may be considered sesamoidal.

In the *Heteromyidæ* the chevron bones are relatively higher than in the *Dipodidæ* though there is little difference in the external appearance of their tails. Because of the difficulties of measuring such small features

as the chevron bones of mice, the percentages given below are but roughly indicative of the trends. Thus the differences shown between the three families, *Dipodidæ*, *Heteromyidæ*, and *Pedetidæ*, are probably approximately correct, while within the families the differences between the genera could all be surpassed by possibilities of variation.

It is found then, that the chevron bones of small-tailed ricochetals rodents are weakly developed. In *Pedetes*, on the contrary, as in the heavy-tailed ricochetals marsupials, the chevrons are highly developed. The chevrons of the *Heteromyidæ* are higher than those of the *Dipodidæ*.

SACRO-ILIAC CONNECTION

The sacro-iliac connection is in part synchondral and in part ligamentous. The most important ligamentary binding is furnished by the great Lig. sacro-iliacum inter-osseum which is inserted laterally over a well-marked area of the ilium contiguous and usually cranio-dorsal to the synchondral area. Its attachment surface on the sacrum is deeply pitted and clearly defined. In addition to this strong mass another ligament, the tubero-sacro-caudale connects the tuberosity of the ischium with the tips of the diapophyses of the first few caudal vertebræ and those of the pseudosacrum. Between these two ligaments, connecting the sacrum and the crest of the ilium, are two groups of fibers named Lig. sacro-iliaca dorsalia longum et breve. The cartilage layer between the wings of the sacrum and the blade of the ilium is extremely thin in most specimens. This synchondral sacro-iliac joint is formed between from one (*Meriones*, *Tatera*, *Paramys*) to two sacral vertebræ. The usual number is two. (See under "Vertebral Numbers.") It is difficult to assign any ancestral or primitive significance to any particular number of sacral vertebræ, as the number in all except a few mammals of certain specialized habits (*e.g.*, fossorial) appears to be determined in large part by the size of the animal. Most large rodents have but a single vertebra forming a true sacrum. Examination of the accompanying figures (Fig. 20) of dipodid sacra reveals that there is in ascending order of size from *Sicista* to *Allactaga* an increase in the importance of the connection between the ilium and sacral vertebra one, and a decrease in the attachment between the ilium and the second sacral vertebra. This same tendency for larger rodents to concentrate the ilio-sacral connection more and more on the first of two or more sacral vertebræ is reflected in the reduced length of the sacral joint in relation to its height. This change in proportion is conveniently expressed by a sacral index formed by dividing the length of the sacro-iliac joint into its height, multiplied

by 100. As I have used this index (which must not be confused with the "symphysis index," $\frac{\text{symphysis length}}{\text{sacral length}} \times 100$, of Mijsberg, 1920), the

length has been taken to include the distance between the most caudal point of synchondral union between sacrum and ilium to the most anterior point of the insertion of Lig. sacro-iliacum inter-osseum as it is measured on the ilium.

That size alone determines this index is doubtful, as certain of the figures indicate other influences. Thus *Jaculus jaculus* is an animal about one half the size of *Jaculus orientalis*, yet its index (70.0) is much higher than that of *Jaculus orientalis* (55.8). Degree of bipedal specialization may be a factor increasing the index, though this factor alone does not harmonize with many of the figures obtained. Dealing with such small numbers of specimens as are available to me, some correlations are apt to be obscured by such differences as those of age. Three specimens of *Dipodomys heermanni tularensis* appear to indicate a change taking place with age. One specimen, a juvenile male, gives an index of 44.4; another, a medium-sized female, has an index of 41.2. The last specimen, a large male, has an index of 35.0.

The series of Dipodidæ is the only one which gives usable results. The Heteromyidæ show no change of the sacro-iliac joint in accommodation to size or locomotor habits, whether this is due to a particularly stable heritage, an evolution too recent to have shown adaptation in this binding or a lack of sufficient specialization to obtain a marked response in sacral concentration, I cannot guess.

Pedetes, the largest ricochetal rodent has an index (53.3) which is exceeded by all of the average indexes of Jerboas measured.

Too few gerbille skeletons are available to furnish data that would be informative when considered alone, though it may be noted that their indexes chance to fall in ascending order in relation to their degree of bipedal specialization. (*Meriones* 42.1, *Tatera* 44.4, and *Gerbillus* 56.6.)

The average indices, their ranges and the number of specimens upon which each was based are given in Table XV.

It is probable that with increased assumption of bipedal habits there is an increase of the strength, and hence the area of the ilio-sacral joint as the total weight of the body must be borne by this union. Further, this binding should increase with increasing use of the hind limbs for propulsion. It seems likely then that ricochetal animals have stronger, larger bindings between sacrum and ilium. Unfortunately the small size and irregular area of the surface to be measured and the small

number of available specimens on which such measurements could be made, make the study of this subject impracticable with the series of rodents at hand.

In review, it is seen that the sacro-iliac connection is usually diarthrose among small rodents, but that with increased size the connection is sometimes confined to a single element of the sacrum-pseudo-sacrum. The ratio of length to height increases with size among ricochetals rodents.

FRACTURE LINES IN CAUDAL VERTEBRÆ

Caudal autotomy involving the vertebræ appears to be known among mammals only in some pocket mice of the genus *Perognathus* and mice of the genus *Proechimys*. The means by which the pocket mice will

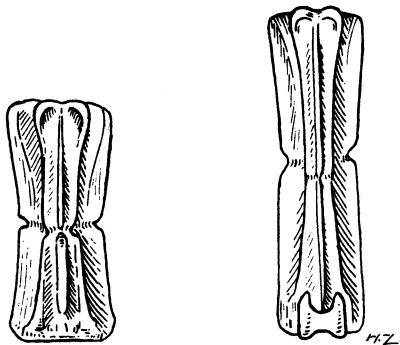


Fig. 27. Fracture lines across the sixth and fourteenth caudal vertebræ of *Perognathus fallax* (43061). Norma ~~caudalis~~ **dorsalis ventralis**

themselves break the tail if lifted by this member is described by Sumner and Collins (1918). These authors show that the break always occurs across a vertebra, usually near its center. No mention is made of any structural peculiarity in the caudal vertebræ which appears adapted to this easy breaking, although it is well known that across the caudal vertebræ of most lizards there is an unossified transverse septum along which the tail readily breaks.

The phenomenon of autotomy was observed by Sumner and Collins only in *Perognathus fallax* and *Perognathus panamintinus bangsi*.

Three skeletons of *Perognathus fallax* at hand all show, across vertebræ distal to the fourth caudal, a marked notching of the diapophyseal and zygapophyseal ridges (Fig. 27), the cristæ connecting the paired

antero-ventral and postero-ventral tubercles, the mid-ventral keel and, to a lesser degree, the mid-dorsal keel. Connecting these notches a distinct furrow marks the surface of the centra. If pressure is applied the vertebra breaks along the line of this furrow. I have no material that would show any internal weakening of the bone in this plane.

Specimens at hand of *Perognathus apache*, *Perognathus intermedius*, and *Perognathus penicillatus eremicus* do not show similar fracture lines in the caudal vertebræ, though the specimens of these are poorly cleaned, and it may be for this reason that the structures are not apparent. cursory examination of the caudal vertebræ of other rodents reveals no parallel construction, except in the tails of the spiny pocket mouse (*Heteromys anomalus*) and the house rat (*Rattus norvegicus*), where, contrary to the condition in *Perognathus*, the vertebræ are strong and do not break under any pressure likely to be exerted upon them.

The caudal vertebræ of small long-tailed rodents are small in diameter near the central plane and are fragile enough to break at this point under slight pressure, but probably not delicate enough to allow autotomy. Among the species studied, only *Perognathus* appears to have an anatomical basis for facilitating the breaking of the caudal centra.

IN CONCLUSION

The independent evolution of four or five groups of rodents to ricochetel locomotor habits has furnished the basis for the analysis of the factors which have controlled some features of the form of the vertebral column in these animals. In some cases the factor has proved to be that of remote hereditary background; in others it has been the actual size of the animal, while many differences between the columns of the ricochetors and their quadrupedal relatives have been due to changes in the stresses accompanying the changed locomotor habits.

The groups of rodents which have developed bipedal habits are named, and their apparent relationships summarized in figure 5. The Dipodidæ are richest in numbers of genera and in diversity of types employing the ricochet. The Heteromyidæ, though not presenting so many types of ricochetors, have within the family a well-graded set of genera ranging from strictly quadrupedal to ricochetel species. *Pedetes*, though without any very near relatives, is of exceptional interest because it has attained a size many times as great as that of any other ricochetel rodent, and differs in vertebral characters from the smaller ricochetors by several factors that are probably due entirely to its greater size. The other groups of ricochetel rodents were poorly represented among the

specimens available, or in the literature on anatomy. In consequence they were of little service to the study.

The ricochetal rodents have their vertebral columns modified from the primitive quadrupedal type more for the changed mechanical conditions consequent to bipedalism and the ricochet than for other activities. In contrast to the quadrupedal mammals, the ricochetors, a large part of the time, have the body weight practically entirely supported by the rear legs, with the line of resistance carried through the sacro-iliac union. Because this union is so strong that it permits of no motion between the elements, the innominate bone functions as part of the sacrum. A line connecting the acetabula is the fulcrum on which the body is balanced. At rest in the bipedal position, the center of gravity is thrown to the rear of this fulcrum by raising the fore end of the body toward the vertical. The tail is then called into use to serve as a prop in balancing the animal. During the ricochet the fore part of the body is lowered, and the center of gravity thrown far forward of the acetabula. The tail acts to balance the anterior part of the body, but this alone is insufficient to maintain equilibrium, and it is necessary that the center of support, represented by a point between the toes of the right and left feet, be thrown far forward of a perpendicular intercepting the horizontal line of the acetabula, and even forward of the perpendicular to the center of gravity, at the moment the feet first strike the ground.

As far as the column is concerned, however, balance is maintained through the acetabula, and the head and body weight is transmitted to this fulcrum through the sacro-iliac union.

Because of this single transverse plane of balance, it is advantageous to the ricochetor for the balancing function of the tail to be increased, and for the center of gravity to be moved backward toward the sacro-iliac union. Because the fore part of the body must be supported by the spinalis dorsi muscles, these muscles must be strengthened and their bony areas of origin so conformed as to give the best leverages. Because the tail is often an organ of support, and because it plays a major rôle in lateral balancing, it is to be expected that the tail is modified for these functions.

Among the bipedal rodents the fore limbs are invariably reduced in size and this reduction should be reflected in the interscapular region of the spinal column. These various conditions have been met as follows:

Moving the center of gravity backward the ricochetors have increased the cervical flexure and shortened the neck, changes which have occasioned other differences. Increased cervical flexure apparently in-

fluences the posterior recumbency of the anterior thoracic neural spines as a means of meeting the changed direction of pull of the spinalis dorsi muscles at a more effective angle. It also may be responsible for the absence of neural spines on the last few cervical and the first thoracic vertebræ.

Neck shortening, when excessive, is accompanied by fusion, in caudal sequence, of post-atlantal cervical vertebræ. This coalescence involves the centra, the neural arches and spines and the tips of the transverse processes. The process may be considered advantageous to cervical strength and rigidity. Neck shortening affects the atlas as well as those elements posterior to this. Shortening of the atlas makes necessary a shift of the main planes of muscle insertion on the transverse process of this vertebra from the horizontal to the vertical, and because of space limitations these surfaces are reduced and simplified. The cervical vertebræ become wide and shallow, a shape incompatible with abduction of the neck, but consistent with vertical movements in the median plane. It is quite possible that this widening of the vertebræ is influenced by the linear restrictions imposed upon the cervical enlargement of the spinal cord enclosed by the neural arches.

The support of the fore end of the body is traceable to the dorsal extensor muscles and the quadratus lumborum, both of which are of exceptional bulk in the ricochetors. The characters of the vertebræ which reflect this increased load are: the increased height of the neural spines of the lumbar region, the increased length and strength of metapophyses just caudad of the center of motion, the longer and stronger anapophyses, and the increased ventral deflection of the lumbar diapophyses. In *Pedetes* there is a strong pair of muscles uniting the neural spine of the last lumbar vertebra and that of the first sacral. This latter spine is exceptionally well developed to care for the strain imposed upon it by this extensor muscle.

Tails function in ricochetors for counterpoise, for the maintenance of lateral balance, for support of the animal standing at rest, and possibly for other locomotor functions involving stresses. For the purpose of counterpoise the tails may be excessively elongated, elongated and tufted, massive or bushy. By the addition of a tuft or brush of hair a certain amount of tail length is dispensed with.

Tail length has been gained by the addition of vertebral units in some ricochetors and by lengthening of a low number of units in others. In contrast to such rodents as squirrels which sometimes lay the tail flat against the back, there is not, except in *Pedetes*, any marked shortening

of the proximal caudal vertebræ, though, as in most mammals, the longest elements are in the center of the tail.

In *Perognathus* an accompaniment of caudal elongation has been the acquisition of a weakened area across the caudal vertebræ along which the tail readily fractures.

The configuration of vertebræ concerned with caudal musculature is very different in ricochetors with long, tendinous tails and those with muscular tails. In the former the number of pseudosacral vertebræ is greater than in the latter, due to the localization of caudal muscular origin, and in consequence, the proportionate length of the pseudosacra of the thin-tailed forms is greater than that in the other type.

The neural spines of the sacrum are weak or absent in the thin-tailed species, because the great belly of the extensor caudæ lateralis, whose origin is on the lumbar neural spines, crowds out the sacral spines. In such forms, however, the last pseudosacral spine is strong and braces against the pull of the extensor caudæ medialis which takes origin here but which in these forms does not extend anterior to the pseudosacrum. The strength of the sacral spine of *Pedetes* was accounted for above. Its great height is probably correlated with the great diameter of the flanking axial muscles, above which it must rise to give anchorage to the lumbo-dorsal fascia on which many muscle fibers take origin.

The linear distribution of the caudal diapophyses is coextensive with the areas of muscular origin. In thin-tailed forms these do not occur far to the rear of the pelvis, but in thick-tailed *Pedetes* the diapophyses are well marked to the middle of the tail. In this genus the proximal diapophyses are unusually strong and deflected slightly downward at their lateral border in response to the pull of the ischio-coccygeus and the ischio- and pubo-caudalis muscles of great importance to flexion of the tail.

The chevron bones are high and strong in the anterior third of the tail of muscular-tailed rodents, but are very low and weak in the thin-tailed species. The chevrons serve to increase the area of muscle origin and to better the leverage of the caudal flexors originating and inserting on them.

The increased amount of weight transmitted through the ilio-sacral joint is probably reflected in increased area of this joint, but the factor proved immeasurable.

A change in the proportions of this union that is well marked in the Dipodidæ, however, is that the height of the articular surface increases in relation to its width, with increasing size of the animal, and cor-

related with this is a tendency for the union to concentrate on a single sacral vertebra.

An examination of end forms (e.g., *Sicista* and *Jaculus* or *Rattus* and *Pedetes*) alone might lead one to adopt the view that a shortening and deepening of the sacro-iliac union accompanies bipedalism, and though there is a possibility that this is true, a consideration of all specimens makes it appear that absolute size and not locomotor habit controls this relation.

The number of like characters which the separately evolved ricochetors have independently acquired in response to similar demands of the locomotion adopted is rather large. The chief of these are:

(1) Short necks in which coalescence of vertebral units has taken place where the cervical series is shorter than about 15 per cent of the thoraco-lumbar length. (Dipodidæ: *Dipus*, *Sciurtopoda*, *Jaculus*. Pedetidæ: *Pedetes*. Heteromyidæ: *Microdipodops*, *Dipodomys*.)

(2) The vertebral centra decrease in length from the third to the fifth cervical units. Caudad to the fifth the units increase in length into the lumbar region. This indicates that where cervical shortening occurs it is most extreme near the end of the cervical series. (Dipodidæ: *Dipus*. Pedetidæ: *Pedetes*. Heteromyidæ: *Dipodomys*. Cricetidæ: *Gerbillus*.)

(3) A greater disproportion between the longest and the shortest centrum in the presacral region than is found in the quadrupedal rodents. (Ricochet Dipodidæ, Heteromyidæ, Pedetidæ.)

(4) Increased tail length which is in the main due to lengthening of units, but which is sometimes also due to the addition of units. (Particularly marked in the following: Dipodidæ: *Zapus*, *Euchoreutes*, *Salpingotus*, *Dipus*, *Eremodipus*, *Jaculus*. Heteromyidæ: *Microdipodops*, *Dipodomys*. Muridæ: *Notomys*. Cricetidæ: *Gerbillus*, *Dipodillus*, *Endecapleura*, *Taterillus*, *Macrotarsomys*.)

(5) Absence of shortening among the anterior caudal vertebrae, which is associated with the absence of sharp dorsal flexion of the tail. (Dipodidæ: *Sicista*, *Zapus*, *Allactaga*, *Jaculus*. Heteromyidæ: *Microdipodops*.)

(6) Wide, shallow cervical vertebrae. (Developed in proportion to the degree of cervical shortening and in consequence with a similar distribution.)

(7) Cervical neural spines confined to the axis. (Dipodidæ: *Sicista*, *Zapus*, *Allactaga*, *Dipus*, *Sciurtopoda*, *Jaculus*. Heteromyidæ: *Perognathus*, *Microdipodops*, *Dipodomys*.)

(8) The neural spine of the axis is directed perpendicularly to the axis of the vertebral column. It is narrow antero-posteriorly. (Dipodidæ: *Sicista*, *Zapus*, *Allactaga*, *Dipus*, *Sciurtopoda*, *Jaculus*. Heteromyidæ: *Perognathus*, *Microdipodops*, *Dipodomys*.)

(9) Anterior thoracic neural spines are short and caudally recumbent. (Dipodidæ: *Zapus*, *Allactaga*, *Dipus*, *Sciurtopoda*, *Jaculus*. Pedetidæ: *Pedetes*. Heteromyidæ: all genera. Muridæ: *Notomys*.)

(10) The spines of the posterior lumbar region are long, narrow antero-posteriorly, and are inclined forward. (Dipodidæ: *Zapus*, *Allactaga*, *Dipus*, *Sciurtopoda*, *Jaculus*. Pedetidæ: *Pedetes*. Heteromyidæ: *Perognathus*, *Microdipodops*, *Dipodomys*.)

(11) The spines over the sacrum are reduced or lost. (Dipodidæ: *Zapus*, *Allactaga*, *Dipus*, *Scirtopoda*, *Jaculus*. Heteromyidæ: all genera.)

(12) The spines of the last or last two pseudosacral vertebræ are very strong in species in which the sacral spine is weak or absent. (See Fig. 20.)

(13) The transverse process of the atlas is reduced and the chief planes of muscle attachment are simplified and shifted from the horizontal toward the vertical. The extent of modification is determined by the degree of compression of the bone. (Dipodidæ: *Zapus*, *Allactaga*, *Dipus*, *Scirtopoda*, *Jaculus*. Pedetidæ: *Pedetes*. Heteromyidæ: all genera.)

(14) The metapophyses are longer than they are in the quadrupeds. (Dipodidæ: *Allactaga*, *Scirtopoda*, *Jaculus*. Pedetidæ: *Pedetes*. Heteromyidæ: *Microdipodops*, *Dipodomys*.)

The effect of absolute size in determining the structure of the skeleton is obvious in several parts of the column. Among the features so controlled are the following:

(1) The condylo-nasal skull length (considered because of its relation to total head and body length) is in inverse proportion to the size of the animal. This is summarized in figure 9 and well illustrated on Plate XVII.

(2) The centra of greatest width are inclined to be at the caudal end of the lumbar series in large leapers, whereas in small leapers these are usually at the anterior end of the lumbar axis. (Contrast *Pedetes* and *Microdipodops*.)

(3) The transverse processes of the larger species are proportionately as well as actually longer than the corresponding processes of the smaller species. The reason for this is not evident. (Contrast *Pedetes* and *Jaculus*.)

(4) The caudal diapophyses of the large species are less forwardly directed than those of small species. (Contrast *Pedetes* and *Microdipodops*.)

(5) The length of the median inferior atlantal process is proportionately less in large mammals than in small. (Contrast *Pedetes* and *Zapus*.)

(6) The first sacral vertebra in large rodents usually assumes a larger share of the ilio-sacral union than it does in small species.

(7) The index obtained by dividing the height of the sacral union by its length is greater in large species than in small. This is another expression of the tendency indicated by the reduction in number of sacral vertebræ, for the sacro-iliac connection to be antero-posteriorly shortened in the larger forms. (Compare *Sicista*, 19 per cent to *Jaculus jaculus*, 70 per cent.)

Among the characters which seem to be attributable to an ancient heritage rather than to present adaptations are:

(1) The constant number of cervical (7) and dorsal (19) vertebræ. (Dipodidæ; Pedetidæ; Heteromyidæ; Muridæ; most Cricetidæ.)

(2) The division of the nineteen dorsal vertebræ into twelve thoracic and seven lumbar vertebræ. (Dipodidæ, except *Sicista*; Pedetidæ; Heteromyidæ, except for occasional individual variants; *Notomys*, *Tatera*, *Gerbillus*, and *Paramys*.)

(3) The usual presence of two sacral vertebræ. (Dipodidæ; Pedetidæ; Heteromyidæ; Muridæ; *Gerbillus*, *Eliurus*.)

(4) The usual presence of two pseudosacral vertebræ in the Dipodidæ and three in the Heteromyidæ.

(5) The presence of fewer caudal vertebræ in the tails of ricochetal Heteromyidæ than in ricochetal Dipodidæ.

(6) The absence of high vertical spines in the interscapular region of *Heteromys* and *Liomys*.

(7) The divided transverse process of the atlas of most Dipodidæ.

(8) The presence of anvil-shaped inferior lamellæ on the sixth cervical vertebra of the Heteromyidæ, Gerbillinæ, and Pedetidæ.

(9) The presence of backwardly directed inferior lamellæ on the sixth cervical vertebra of the Dipodidæ.

Among ricochetal mammals the tail is a very variable structure even within one genus. In general it may be said that the extremes of tail types are tails of great length and small diameter and those which are contrastingly short and thick. These two types of tails differ in numerous skeletal features and exert their influence on the column of the sacro-pseudosacral region. Contrasting features of the types are:

LONG TENDINOUS TAIL

- (1) Numbers of vertebræ high (*Zapus* 39)
- (2) Pseudosacrum long (four vertebræ constitute 14 per cent of the head-body length in *Zapus*)
- (3) Sectional areas of the caudal vertebræ increase to about the seventh caudal vertebra and decrease distal to this (Dipodidæ, Heteromyidæ)
- (4) Spines of the sacrum-pseudosacrum are low and limited to the caudal end (Dipodidæ, Heteromyidæ)
- (5) Caudal diapophyses confined to proximal tail region (well marked only on caudal vertebræ one to five in *Jaculus orientalis*)
- (6) Caudal diapophyses directed sharply forward (Dipodidæ, Heteromyidæ, etc.)
- (7) Chevron bones low and weak (Dipodidæ, Heteromyidæ, etc.)

SHORT MUSCULAR TAIL

- (1) Numbers of vertebræ low (*Pedetes* 31)
- (2) Pseudosacrum short (three vertebræ constitute 9.3 per cent of head-body length in *Pedetes*)
- (3) Sectional areas of the caudal vertebræ increase to about the middle of the tail (*Pedetes*) beyond which decrease occurs.
- (4) Spines of the sacrum-pseudosacrum are high (*Pedetes*)
- (5) Caudal diapophyses occur far to the rear (well marked to about caudal vertebra ten in *Pedetes*)
- (6) Caudal diapophyses perpendicular to axis of the column or produced forward and backward (*Pedetes*)
- (7) Chevron bones high and strong at first third of tail (*Pedetes*)

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TABLE I.—Fusion or Independence of Cervical Vertebral Units in Ricochetal Rodents and Their Non-Ricochetal Relatives Correlated With the Comparative Length of the Cervical Vertebral Series.¹

Rodent	Number of Specimens	Average Cervical Vertebral Length in Percentage of Thoraco-lumbar Length	Location of Fused Units. Cervical Serial Numbers
DIPODIDÆ			
<i>Sicista</i>	1	19.5	None
* <i>Zapus</i>	5	15.6	"
* <i>Allactaga</i>	5	15.5	"
* <i>Dipus</i>	1	12.7	2-7
* <i>Sciurtopoda</i>	1	10.4	2-6 (?)
* <i>Jaculus</i>	6	11.9	2-6
PEDETIDÆ			
* <i>Pedetes cafer</i>	3	15.7	None
* " <i>surdaster</i>	1	?	2-3
HETEROMYIDÆ			
<i>Heteromys</i>	2	20.7	None
<i>Liomys</i>	1	20.0	"
<i>Perognathus</i>	6	19.1	"
* <i>Micropipodops</i>	4	16.3	"
* " "	1	16.6	4-5 part
* <i>Dipodomys</i>	5	14.7	2-3
* " "	10	15.7	2-4
* " "	1	15.5	2-5
MURIDÆ			
<i>Rattus</i>	3	20.2	None
* <i>Notomys</i>	1	c18	?
CRICETIDÆ			
<i>Meriones</i>	1	?	None
<i>Tatera</i>	2	20.7	"
<i>Gerbillus</i>	1	17.2	"
<i>Eliurus</i>	1	?	"
PARAMYIDÆ			
<i>Paramys</i>	1	c22	None

¹An asterisk is placed before the name of each genus, the members of which are primarily ricochetors.

TABLE II.—Numbers of Thoraco-lumbar Vertebrae.¹

Rodent	Number of Specimens	Number of Thoracic Vertebrae	Number of Lumbar Vertebrae	Total Number of Thoraco- Lumbar Vertebrae
DIPODIDÆ				
<i>Sicista</i>	1	13	6	19
* <i>Zapus</i> (<i>Zapus</i>)	3	12	7	19
* " (<i>Napæozapus</i>)	2	12	7	19
* <i>Allactaga</i>	5	12	7	19
* <i>Dipus</i>	1	12	7	19
* <i>Sciurtopoda</i>	1	12	7	19
* <i>Jaculus</i>	6	12	7	19
Maximum		13	7	19
Minimum		12	6	19
Average		12.05	6.95	19
PEDETIDÆ				
* <i>Parapedetes</i>	1 (Stromer) over 10		7	over 17
* <i>Pedetes</i>	4	12	7	19
HETEROMYIDÆ				
<i>Heteromys</i>	2	12	7	19
<i>Liomys</i>	1	12	7	19
<i>Perognathus</i>	5	12	7	19
"	1	13	6	19
* <i>Microdipodops</i>	3	12	7	19
* "	1	12	7 left	19 left
			6 right	18 right
* "	1	12	8 left	20 left
			7 right	19 right
* <i>Dipodomys</i>	15	12	7	19
"	1	13	6	19
Maximum		13	8	20
Minimum		12	6	18
Average		12.06	6.93	19
MURIDÆ				
<i>Rattus</i>	7	13	6	19
* <i>Notomys</i>	1	12	7	19
Maximum		13	7	19
Minimum		12	6	19
Average		12.87	6.13	19

¹An asterisk is prefixed to the name of each group whose members are primarily ricochetors.

TABLE II.—(Continued)

CRICETIDÆ				
<i>Tatera</i>	2	12	7	19
<i>Gerbillus</i>	1	12	7	19
<i>Eliurus</i>	1	13	7	20
Maximum		13	7	20
Minimum		12	7	19
Average		12.25	7	19.25
PARAMYIDÆ				
<i>Paramys</i>	1	12	7	19

TABLE III.—Numbers of Sacral and Pseudosacral Vertebrae.¹

Rodent	Number of Specimens	Number of Sacral Vertebrae	Number of Pseudosacral Vertebrae	Total Number of Sacral- pseudosacral Vertebrae
DIPODIDÆ				
<i>Sicista</i>	1	2	1	3
* <i>Zapus</i>	3	2	2	4
* <i>Zapus (Napæozapus)</i>	2	2	2	4
* <i>Allactaga</i>	5	2	2	4
* <i>Dipus</i>	1	2	2	4
* <i>Scirtopoda</i>	1	2	2	4
* <i>Jaculus</i>	5	2	2	4
Maximum		2	2	4
Minimum		2	1	3
Average		2	1.94	3.94
PEDETIDÆ				
* <i>Parapedetes</i>	1 (Stromer)	?2	?1	3
* <i>Pedetes</i>	4	2	1	3
Maximum		2	1	3
Minimum		2	1	3
Average		2	1	3
HETEROMYIDÆ				
<i>Heteromys</i>	2	2	3	5
<i>Liomys</i>	1	2	3	5
"	1	2	2	4
<i>Perognathus</i>	5	2	3	5
* <i>Microdipodops</i>	4	2	3	5
"	1	2	2	4
"	2	left 2 right 3	2	5
* <i>Dipodomys</i>	14	2	3	5
"	3	2	2	4
Maximum		3	3	5
Minimum		2	2	4
Average		2.03	2.78	4.81
MURIDÆ				
<i>Rattus</i>	2	2	3	5
"	4	2	2	4
* <i>Notomys</i>	1	2	3	5
Maximum		2	3	5
Minimum		2	2	4
Average		2	2.43	4.43

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.

TABLE III.—(Continued)

CRICETIDÆ				
<i>Meriones</i>	1	1	3	4
<i>Tatera</i>	1	1	2	3
"	1	2	2	4
<i>Gerbillus</i>	1	2	3	5
<i>Eliurus</i>	1	2	?	?
Maximum		2	3	5
Minimum		1	2	3
Average		1.6	2.5	4.0
PARAMYIDÆ				
<i>Paramys</i>	1	1	2	3

TABLE IV.—Numbers of Caudal Vertebrae Correlated With the Length of the Caudal Vertebral Series Expressed in Percentage of the Composite Precaudal Vertebral Length Plus Skull Length.¹

Rodent	Caudal Length in Percentage of Precaudal Length	Numbers of Caudal Vertebrae
DIPODIDÆ		
* <i>Dipus</i> (55979)	159.6	25
* <i>Sciropoda</i> (132)	152.3	26
* <i>Jaculus</i> (70004)	164.0	26
* " (70096)	165.4	26
* " (1145a)	187.1	27
* <i>Allactaga</i> (55980)	167.0	28
* " (397)	175.3	29
<i>Sicista</i> (122117)	189.1	31
* <i>Zapus</i> (5403)	163.6	33
* " (90655)	165.0	33
* " (13584)	163.0	35
* " (<i>Napæozapus</i>) (74851)	179.7	37
* " (") (74849)	176.8	39
Maximum	189.1	39
Minimum	152.3	25
Average	169.8	30.4
PEDETIDÆ		
* <i>Pedetes</i> (81747)	123.5	31
HETEROMYIDÆ		
* <i>Microdipodops</i> (54579)	139.9	24
* " (38797)	163.0	24
* " (38798)	163.0	24
<i>Perognathus</i> (100022)	159.9	26
<i>Liomys</i> (8347)	100.0	26
<i>Heteromys</i> (3645)	114.7	27
" (7524)	151.1	28
* <i>Dipodomys</i> (14983)	?	28
* " (9674)	159.9	29
* " (13270)	166.1	29
* " (13294)	168.5	29
* " (13292)	172.2	29
* " (13263)	163.1	30
* " (100057)	?	30
* " (13296)	160.2	31
* " (132763)	180.8	31
* " (13262)	187.8	31

¹An asterisk is prefixed to the name of each specimen of a ricocheter.

TABLE IV.—(Continued)

* <i>Dipodomys</i> (13242)	192.7	31
* " (13207)	196.3	31
Maximum	196.3	31
Minimum	100.0	24
Average	161.1	28.2
MURIDÆ		
<i>Rattus</i> (100084) ¹	132.7	28
" (100085)	138.5	29
" (69551)	121.9	30
" (100086)	151.7	31
Minimum	121.9	28
Maximum	151.7	31
Average	136.2	29.5

¹*Rattus*, Numbers 100084, 100085, 100086, are all males killed the same day at the same place. No. 100084 was the smallest and youngest, No. 100086 the largest and oldest.

TABLE V.—Relation of Proportionate Skull Length to Actual Head Plus Body Length.¹

Rodent	Number of Specimens	Average Length of Skull Plus Precaudal Vertebrae in Millimeters	Average Length of Skull in Percentage of Skull Plus Precaudal Vertebral Length
DIPODIDÆ			
<i>Sicista</i>	1	51.8	34.7
* <i>Zapus</i>	5	77.3	29.1
* <i>Scirtopoda</i>	1	101.1	28.9
* <i>Jaculus</i>	6	120.4	28.9
* <i>Dipus</i>	1	119.0	27.7
* <i>Allactaga</i>	5	143.8	27.9
Maximum		143.8	34.7
Minimum		51.8	27.7
Average		100.5	28.9
PEDETIDÆ			
* <i>Pedetes</i>	3	337.3	24.9
HETEROMYIDÆ			
* <i>Microdipodops</i>	5	60.1	40.2
<i>Perognathus</i>	6	70.4	35.3
* <i>Dipodomys</i>	16	97.9	34.4
<i>Liomys</i>	1	97.0	33.0
<i>Heteromys</i>	2	119.5	29.3
Maximum		119.5	40.2
Minimum		60.1	29.3
Average		87.5	35.1
MURIDÆ			
* <i>Notomys</i>	1	c110	c27
<i>Rattus</i>	3	204.3	23.5
Maximum		204.3	27
Minimum		c110	23.5
Average		c180	c24
PARAMYIDÆ			
<i>Paramys</i>	1	c470	c19

¹An asterisk is prefixed to the name of each group whose members are primarily ricochetors.

TABLE VI.—Proportionate Length of the Cervical Vertebral Series.¹

Rodent	GENERIC AVERAGES		
	Number of Specimens	$\frac{\text{Cerv.}}{\text{H-B}} \times 100$	$\frac{\text{Cerv.}}{\text{T-L}} \times 100$
DIPODIDÆ			
<i>Sicista</i>	1	9.1	19.5
* <i>Zapus</i>	5	7.2	15.6
* <i>Allactaga</i>	5	8.0	15.5
* <i>Dipus</i>	1	6.7	12.7
* <i>Sciurtopoda</i>	1	5.7	10.4
* <i>Jaculus</i>	6	6.3	11.9
Maximum		9.1	19.5
Minimum		5.7	10.4
Average		7.1	14.2
PEDETIDÆ			
* <i>Pedetes</i>	3	9.1	15.7
HETEROMYIDÆ			
<i>Heteromys</i>	2	9.4	20.7
<i>Liomys</i>	1	9.2	20.0
<i>Perognathus</i>	6	8.2	19.1
* <i>Microdipodops</i>	5	6.8	16.8
* <i>Dipodomys</i>	16	6.7	15.5
Maximum		9.4	20.7
Minimum		6.7	15.5
Average		7.3	16.9
MURIDÆ			
<i>Rattus</i>	3	10.3	20.2
* <i>Notomys</i>	1	c9	c18
Maximum		10.3	20.2
Minimum		c9	c18
Average		c9.9	c19.6
CRICETIDÆ			
<i>Tatera</i>	2	10.2	20.7
<i>Gerbillus</i>	1	7.9	17.2
Maximum		10.2	20.7
Minimum		7.9	17.2
Average		9.4	19.5
PARAMYIDÆ			
<i>Paramys</i>	1	c13	c22

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.

TABLE VII.—Proportionate Lengths of the Thoracic and the Lumbar Regions.¹

Rodent	GENERIC AVERAGES			
	Number of Specimens	Number of Vertebrae	$\frac{\text{Th. Length}}{\text{Th. lu. length}} \times 100$	$\frac{\text{Lu. length}}{\text{Th. lu. length}} \times 100$
DIPODIDÆ				
<i>Sicista</i>	1	13	55.6	44.4
* <i>Zapus</i>	5	12	46.8	53.1
* <i>Allactaga</i>	5	12	47.8	52.1
* <i>Dipus</i>	1	12	47.6	52.4
* <i>Sciurtopoda</i>	1	12	45.9	54.1
* <i>Jaculus</i>	6	12	46.6	53.4
Maximum			55.6	54.1
Minimum			45.9	44.4
Average			47.3	52.5
PEDETIDÆ				
* <i>Pedetes</i>	3	12	44.8	55.1
HETEROMYIDÆ				
<i>Heteromys</i>	2	12	51.8	48.1
<i>Liomys</i>	1	12	48.9	51.1
<i>Perognathus</i>	5	12	50.3	49.6
	1	13	50.3	49.6
* <i>Microdipodops</i>	5	12*	53.1	46.8
* <i>Dipodomys</i>	15	12	49.0	50.9
		13	49.0	50.9
Maximum			53.1	51.1
Minimum			48.9	46.8
Average			50.1	49.8
MURIDÆ				
<i>Rattus</i>	3	13	55.5	44.5
* <i>Notomys</i>	1	12	52.1	47.8
Maximum			55.5	47.8
Minimum			52.1	44.5
Average			54.6	45.3
CRICETIDÆ				
<i>Tatera</i>	2	12	48.1	51.8
<i>Gerbillus</i>	1	12	55.2	44.8
Maximum			55.2	51.8
Minimum			48.1	44.8
Average			50.5	49.5
PARAMYIDÆ				
<i>Paramys</i>	1	12	c50	c50

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.

*The two asymmetrical specimens of *Microdipodops* were measured on the medial seven lumbar vertebrae and five sacral-pseudosacral vertebrae.

TABLE VIII.—Proportionate Length of the Sacrum-pseudosacrum.¹

GENERIC AVERAGES				Average No. of Sacral- Pseudosacral Vertebrae
Rodent	Number of Specimens	$\frac{S-Ps}{H-B} \times 100$	$\frac{S-Ps}{Tail} \times 100$	
DIPODIDÆ				
* <i>Zapus</i>	5	14.2	8.2	4
* <i>Jaculus</i>	6	12.7	7.5	4
* <i>Dipus</i>	1	12.6	7.9	4
* <i>Allactaga</i>	5	12.5	7.6	4
* <i>Scirtopoda</i>	1	11.6	7.6	4
<i>Sicista</i>	1	9.6	5.1	3
Maximum		14.2	8.2	
Minimum		9.6	5.1	
Average		12.8	7.6	
PEDETIDÆ				
* <i>Pedetes</i>	3	9.3	?	3
HETEROMYIDÆ				
* <i>Dipodomys</i>	16	15.5	9.3	4.82
<i>Heteromys</i>	2	13.7	10.4	5
<i>Liomys</i>	1	11.3	11.3	4
<i>Perognathus</i>	6	13.5	11.1	5
* <i>Microdipodops</i> ²	5	12.8	8.6	4.86
Maximum		15.5	11.3	
Minimum		11.3	8.6	
Average		14.4	9.7	
MURIDÆ				
<i>Rattus</i>	3	19.2	16.0	4.7
* <i>Notomys</i>	1	c15	?	5
Maximum		19.2	16.0	
Minimum		c15		
Average		c18.1		
CRICETIDÆ				
<i>Gerbillus</i>	1	14.6	13.8	5
<i>Tatera</i>	2	13.2	9.9	3.5
Maximum		14.6	13.8	
Minimum		13.2	9.9	
Average		13.7	11.2	
PARAMYIDÆ				
<i>Paramys</i>	1	c10	?	3

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.²The two asymmetrical specimens of *Microdipodops* were measured on the basis of the modal seven lumbar vertebrae and five sacral-pseudosacral vertebrae.

TABLE IX.—Proportionate Length of the Tail With a Notation as to Foot Length and the Character of the Hairing of the Tail Tip of Ricochetal Rodents and Their Relatives as Recorded in the Literature.¹

Abbreviations: TT = Tip Tufted

TP = Tip Pencilate

UH = Tip hairing approximately uniform with that of the middle part of the tail.

As nearly as one may judge from a perusal of the literature this list includes all forms currently recognized as full species in genera whose locomotor habits certainly or probably include the ricochet. A few selected examples of species in related nonricochetal genera are added for contrast. The data are gathered from published field measurements. Where possible they are averages of large series. Some are the measurements of the type alone. For a few species measurements of the typical race have never been published, but when feasible I have given those of a designated subspecies. Citations are not made for the slight added value of documentation would scarcely justify the additional cost of printing full reference to each original source.

DIPODIDÆ

	Rear Foot in Percentage Head and Body	Tail in Percent- age Head and Body	Terminal Tail Hairing
ZAPODINÆ			
<i>Sicista loriger</i>	26	126	UH
" <i>tianschanica</i>	36	100	?
" <i>caucasica</i>	33	194	?
" <i>montana</i>	29	156	UH
" <i>norvegica</i>	25	134	?
" <i>weigoldi</i>	?	125	?
" <i>napæa</i>	22	114	?
" <i>flava</i>	?	150	?
" <i>caudata</i>	29	182	?
" <i>concolor</i>	c30	127	?
" <i>leathamii</i>	29	170	?
AVERAGE	29	143	?UH
* <i>Zapus (Zapus) hudsonius</i>	36	143	UH
* " " <i>tenellus</i>	38	160	UH
* " " <i>princeps</i>	33	150	UH
* " " <i>major</i>	35	155	UH
* " " <i>nevadensis</i>	36	163	UH
* " " <i>trinotatus</i>	34	161	UH
* " " <i>luteus</i>	36	160	UH
* " " <i>montanus</i>	33	145	UH

¹An asterisk is prefixed to the name of each species which is known to be a ricochetor, or is assumed frequently to employ the ricochet.

TABLE IX.—(Continued)

* <i>Zapus (Zapus) orarius</i>	32	136	UH
* " " <i>pacificus</i>	37	168	UH
* " " <i>saltator</i>	32	145	UH
AVERAGE	35	153	UH
* <i>Zapus (Eozapus) setchuanus</i>	31	120	UH
AVERAGE	31	120	UH
* <i>Zapus (Napæozapus) insignis</i>	34	161	UH
AVERAGE	34	161	UH
EUCHOREUTINÆ			
* <i>Euchoreutes naso</i>	50	179	TT
AVERAGE	50	179	TT
CARDIOCRANIINÆ			
* <i>Cardiocranius paradoxus</i>	34	103	UH
AVERAGE	34	103	UH
* <i>Salpingotus kozlovi</i>	49	247	UH
* " <i>crassicauda</i>	50	227	UH
* " <i>thomasi</i>	41	184	UH
AVERAGE	47	219	UH
ALLACTAGINÆ			
* <i>Allactaga williamsi</i>	47	149	TT
* " <i>elater dzungarizæ</i>	60	188	TT
* " <i>mongolica longior</i>	51	153	TT
* " <i>bulatta</i>	67	179	TT
* " <i>jaculus</i>	47	138	TT
* " <i>ruckbeili</i>	53	147	TT
* " <i>saltator suschkini</i>	49	128	TT
* " <i>grisescens</i>	46	128	TT
* " <i>hotsoni</i>	34	180	TT
* " <i>indica</i>	61	200	TT
* " <i>severtzovi</i>	49	140	TT
* " <i>euphratica</i>	38	120	TT
AVERAGE	50	154	TT
* <i>Alactagulus acontion</i>	49	144	TT
* " <i>shirkovi</i>	36	88	TT
AVERAGE	43	116	TT
* <i>Pygeretmus platyurus</i>	34	84	TT
AVERAGE	34	84	TT
* <i>Scarturus tetradactylus</i>	48	127	TT
AVERAGE	48	127	TT
DIPODINÆ			
* <i>Dipus halli</i>	47	?	TT
* " <i>deaseyi</i>	47	128	TT
* " <i>sagitta nogai</i>	49	130	TT
* " <i>sowerbyi</i>	56	146	TT
* " <i>blanfordi</i>	51	140	TT
AVERAGE	50	136	TT

TABLE IX.—(Continued)

* <i>Scirtopoda andrewsi</i>	43	117	TT
* " <i>haltica</i>	37	102	TT
* " <i>telum</i>	35	107	TT
AVERAGE	38	109	TT
* <i>Paradipus clenodactylus</i>	?	?	TT
AVERAGE	?	?	TT
* <i>Eremodipus lichtensteini</i>	65	159	TT
AVERAGE	65	159	TT
* <i>Jaculus orientalis</i>	52	154	TT
* " <i>darricarrerei</i>	44	138	TT
* " <i>jaculus</i>	53	155	TT
* " <i>microtis</i>	?	?	TT
* " <i>gordoni</i>	55	167	TT
* " <i>florentiæ</i>	48	154	TT
* " <i>macrotarsus</i>	63	?	TT
* " <i>schlüteri</i>	46	150	TT
* " <i>loftusi</i>	37	113	TT
AVERAGE	50	147	TT
PEDETIDÆ			
* <i>Pedetes surdaster</i>	39	105	UH
* " <i>cafer</i>	39	107	UH
* " <i>angolæ</i>	?	?	UH
AVERAGE	39	106	UH
HETEROMYIDÆ			
<i>Heteromys anomalus</i>	27	128	UH
AVERAGE	27	128	UH
<i>Liomys pictus</i>	25	118	UH
AVERAGE	25	118	UH
<i>Perognathus (P.) fasciatus</i>	24	92	UH
" " <i>flavescens</i>	25	90	UH
" " <i>merriami</i>	27	96	UH
" " <i>flavus</i>	27	105	UH
" " <i>apache</i>	26	94	UH
" " <i>gypsi</i>	28	94	UH
" " <i>callistus</i>	26	89	?
" " <i>elibatus</i>	30	112	?
" " <i>longimembris</i>	27	105	TP
" " <i>pericalles</i>	35(!)	137	?
" " <i>bombycinus</i>	34(!)	143	?
" " <i>nevadensis</i>	31	119	?
" " <i>pacificus</i>	26	90	?
" " <i>amplus</i>	27	107	TP
" " <i>inornatus</i>	28	109	?
" " <i>parvus</i>	28	114	TP
" " <i>xanthonotus</i>	26	100	?
" " <i>alticola</i>	27	102	TP
" " <i>lordi</i>	27	116	TP
" " <i>formosus</i>	29	128	TP
AVERAGE	28	107	UH-TP

TABLE IX.—(Continued)

<i>P. (Chaetodipus) baileyi</i>	29	128	TP
" " <i>knekus</i>	27	123	?
" " <i>hispidus</i>	24	97	UH
" " <i>penicillatus</i>	26	113	TP
" " <i>helleri</i>	27	109	TP
" " <i>stephensi</i>	26	118	TP
" " <i>arenarius</i>	30	100	?
" " <i>pernix</i>	28	124	TP
" " <i>intermedius</i>	29	134	TP
" " <i>nelsoni</i>	30	133	TP
" " <i>goldmani</i>	31	124	TP
" " <i>arthus</i>	29	125	TP
" " <i>fallax</i>	30	132	TP
" " <i>anthonyi</i>	31	121	TP
" " <i>femorialis</i>	28	130	TP
" " <i>californicus</i>	27	115	TP
" " <i>spinatus</i>	27	126	TP
" " <i>evermanni</i>	27	105	?
" " <i>bryanti</i>	28	142	TP
" " <i>margaritæ</i>	28	131	TP
AVERAGE	28	121	TP
* <i>Microdipodops polionotus</i>	37	123	UH
* " <i>pallidus</i>	37	148	UH
* " <i>megacephalus</i>	c34	c114	UH
* " <i>californicus</i>	37	135	UH
AVERAGE	36	130	UH
* <i>Dipodomys heermanni</i>	38	159	TT
* " <i>morroensis</i>	35	147	TT
* " <i>gravipes</i>	34	139	TT
* " <i>mohavensis</i>	35	135	TT
* " <i>leucogenys</i>	36	141	TT
* " <i>panamantinus</i>	35	137	TT
* " <i>stephensi</i>	35	145	TT
* " <i>ingens</i>	35	128	TT
* " <i>spectabilis</i>	37	152	TT
* " <i>nelsoni</i>	40	162	TT
* " <i>phillipsii</i>	40	164	TT
* " <i>perotensis</i>	39	163	TT
* " <i>ornatus</i>	36	156	TT
* " <i>elator</i>	29	83(!)	TT
* " <i>merriami</i>	37	140	TT
* " <i>nitratoides</i>	37	148	TT
* " <i>platycephalus</i>	41	156	TT
* " <i>margaritæ</i>	42	160	TT
* " <i>insularis</i>	39	143	TT
* " <i>mitchelli</i>	?	?	TT
* " <i>ordii columbianus</i>	37	126	TT
* " <i>compactus</i>	30	109	TT
* " <i>sennetti</i>	?	?	TT
* " <i>agilis</i>	38	157	TT

TABLE IX.—(Continued)

* <i>Dipodomys venustus</i>	38	159	TT
* " <i>elephantinus</i>	37	155	TT
* " <i>microps</i>	37	135	TT
* " <i>levipes</i>	36	134	TT
* " <i>deserti</i>	37	142	TT
AVERAGE	37	143	TT
MURIDÆ			
<i>Rattus norvegicus</i>	20	120	UH
AVERAGE	20	120	UH
<i>Conilurus albipes</i>	20	107	TP
AVERAGE	20	107	TP
<i>Mesembriomys hirsutus</i>	?	125	TT
AVERAGE	?	125	TT
<i>Leporillus conditor</i>	22	90	TP
AVERAGE	22	90	TP
* <i>Notomys gouldi</i>	30	128	TT
* " <i>sturti</i>	34	151	TT
* " <i>longicaudatus</i>	26	128	TT
* " (<i>"Ascopharynx"</i>) <i>fuscus</i>	31	114	TT
* " " <i>cervinus</i>	33	123	TT
* " <i>alexis</i>	29	124	TT
* " <i>macrotis</i>	34	?	?
* " <i>aquilo</i>	32	?	?
* " <i>mitchelli</i>	27	125	TT
* " <i>mordax</i>	?	?	?
AVERAGE	31	128	TT
* <i>Lorentzimys nouhuysii</i>	26	121	TP
AVERAGE	26	121	TP
CRICETIDÆ			
GERBILLINÆ			
<i>Tatera indica</i>	21	106	TP
" <i>sherrini</i>	23	118	TP
" <i>dunni</i>	23	119	?
" <i>hardwickii</i>	25	115	?
" <i>cuvieri</i>	27	121	TP
" <i>ceylonica</i>	26	94	?
" <i>tæniura</i>	22	101	TP
" <i>persica</i>	22	105	TT
" <i>pitmani</i>	21	95	TP
" <i>bailwardi</i>	25	110	?
" <i>valida</i>	22	100	UH
" <i>benvenuta</i>	20	104	UH
" <i>liodon</i>	?	?	?
" <i>coseni</i>	22	113	UH
" <i>leucogaster</i>	24	98	UH
" <i>joanæ</i>	25	117	?
" <i>robusta</i>	?	?	TP
" <i>swaythlingi</i>	27	128	TP
" <i>lobengulæ</i>	25	119	UH

TABLE IX.—(Continued)

<i>Tatera taboraë</i>	23	93	UH
" <i>phillipsii</i>	27	137	UH
" <i>angolæ</i>	21	105	?
" <i>afra</i>	21	109	UH
" <i>nigricauda</i>	24	103	UH
" <i>brantsi</i>	24	110	TP
" <i>fallax</i>	27	149	?
" <i>flavipes</i>	24	100	UH
" <i>gambiana</i>	22	100	TP
" <i>giffardi</i>	21	111	?
" <i>kempii</i>	24	120	?
" <i>guineæ</i>	23	107	TP
" <i>panja</i>	25	104	?
" <i>hopkinsoni</i>	20	98	?
" <i>iconica</i>	24	125	?
" <i>dichrura</i>	20	105	?
" <i>draco</i>	22	109	?
" <i>dundasi</i>	18(1)	?	?
" <i>ruwenzorii</i>	21	104	?
" <i>smithi</i>	22	94	?
" <i>inclusa</i>	24	113	?
" <i>miliaria</i>	24	116	?
" <i>mombasæ</i>	28	135	?
" <i>neavei</i>	26	98	?
" <i>nigrita</i>	24	104	?
" <i>nyasæ</i>	21	100	?
" <i>pothæ</i>	26	134	?
" <i>ruddi</i>	25	128	UH
" <i>shoana</i>	26	128	TP
" <i>soror</i>	24	112	?
" <i>varia</i>	25	142	TP
" <i>breyeri</i>	24	103	?
" <i>vicinus</i>	c21	c127	TP
" <i>welmanni</i>	?	109	?
" <i>natalensis</i>	27	121	?
AVERAGE	23	112	TP-UH
<i>Taterillus emini</i>	21	111	TP
" <i>lacustris</i>	25	129	TT
" <i>harringtoni</i>	29	137	TT
" <i>gracilis</i>	31	145	TP
" <i>bulleri</i>	24	125	TP
" <i>congius</i>	24	126	TT
" <i>gyas</i>	?	c137	TP
" <i>kadugliensis</i>	27	?	TP
" <i>lowei</i>	26	149	?
" <i>melanops</i>	27	135	TT
" <i>nigeriæ</i>	26	152	TT
" <i>nubilus</i>	26	134	TP
" <i>osgoodi</i>	26	128	TP

TABLE IX.—(Continued)

<i>Taterillus perluteus</i>	28	141	TP
" <i>clivus</i>	18	144	TP
" <i>rufus</i>	22	?	?
" <i>tenebricus</i>	33	138	TT
AVERAGE	26	135	TP-TT
<i>Endecapleura garamantis</i>	28	147	TT
" <i>fumulus</i>	25	142	TP
" <i>quadrinaculatus</i>	26	134	TT
" <i>bottai</i>	24	?	?
AVERAGE	26	141	TP-TT
<i>Dipodillus stigmomyx</i>	24	153	TP
" <i>campestris</i>	27	126	TT
" <i>simoni</i>	23	99	TP
" <i>venustus</i>	?	?	?
" <i>dodsoni</i>	27	141	TP
" <i>mimulus</i>	25	109	TT
" <i>vivax</i>	28	141	TP
" <i>harwoodi</i>	27	125	?
" <i>amoenus</i>	33	155	TP
" <i>poecilops</i>	22	102	UH
" <i>liza</i>	32	115	TP
" <i>calurus</i>	27	127	TP
" <i>watersi</i>	30	160	?
" <i>dasyurus</i>	32	100	UH
" <i>dasyuroides</i>	24	121	?
" <i>grobbei</i>	29	143	UH
" <i>pusillus</i>	31	125	TP
" <i>nanus</i>	35	175	UH
" <i>indus</i>	30	162	TT
" <i>ruberrimus</i>	31	146	TP
" <i>arabium</i>	28	163	TT
" <i>brockmani</i>	27	154	?
" <i>henleyi</i>	29	118	TP
" <i>hilda</i>	?	?	?
" <i>jordani</i>	29	119	?
" <i>marix</i>	30	145	?
" <i>lowei</i>	23	130	TT
" <i>luteus</i>	28	127	?
" <i>mackilligini</i>	?	?	TP
" <i>muriculus</i>	28	126	?
" <i>percivali</i>	26	131	?
" <i>diminutus</i>	30	118	?
" <i>principulus</i>	29	157	TP
" <i>somalicus</i>	29	149	TT
AVERAGE	26	134	TP
<i>Gerbillus (Gerbilliscus) boehmi</i>	?	115	UH
" " <i>fraterculus</i>	27	117	UH
AVERAGE	27	116	UH
<i>Gerbillus (Taterina) lorenzi</i>	31	106	TP
AVERAGE	31	106	TP

TABLE IX.—(Continued)

<i>Gerbillus (Gerbillus) gerbillus</i>	35	149	TP
“ “ <i>eatoni</i>	c26	c137	TP
“ “ <i>andersoni</i>	c32	c147	TP
“ “ <i>cheesmani</i>	27	140	TP
“ “ <i>latastei</i>	28	113	TP
“ “ <i>arduus</i>	34	144	?
“ “ <i>longicaudus</i>	29	133	TP
“ “ <i>calidus</i>	28	116	TP
“ “ <i>imbellis</i>	?	?	UH
“ “ <i>nigariæ</i>	23	110	?
“ “ <i>nancillus</i>	32	146	TP
“ “ <i>dunni</i>	31	133	TP
“ “ <i>acticola</i>	24	122	TP
“ “ <i>pygargus</i>	31	165	TP
“ “ <i>bilensis</i>	26	?	TP
“ “ <i>floweri</i>	c27	?	?
“ “ <i>pæbus</i>	32	146	?
“ “ <i>vallinus</i>	32	?	?
“ “ <i>rosalinda</i>	c28	118	TP
“ “ <i>allenbyi</i>	34	136	TP
“ “ <i>coseni</i>	33	172	?
“ “ <i>pyramidum</i>	32	143	TP
“ “ <i>hirtipes</i>	29	130	TP
“ “ <i>gleadowi</i>	35	151	TP
“ “ <i>peeli</i>	?	?	?
“ “ <i>swalius</i>	28	127	TP
“ “ <i>bonhotei</i>	28	127	?
“ “ <i>dongolanus</i>	22	155	TP
“ “ <i>macropus</i>	23	105(!)	TP
“ “ <i>pulvinatus</i>	25	130	TP
“ “ <i>tristrami</i>	30	128	TP
“ “ <i>riggenbachi</i>	30	137	TP
“ “ <i>agag</i>	27	115	TP
AVERAGE	29	135	TP
“NESOMYINÆ”			
<i>Brachyuromys ramirohitra</i>	21	60	UH
AVERAGE	21	60	UH
<i>Nesomys lambertoni</i>	20	70	UH
“ <i>rufus</i>	21	71	UH
AVERAGE	21	71	UH
<i>Hypogeomys antinema</i>	21	66	UH
AVERAGE	21	66	UH
<i>Gymnuromys roberti</i>	22	107	UH
AVERAGE	22	107	UH
<i>Eliurus tanala</i>	20	125	TP
AVERAGE	20	125	TP
<i>Hallomys audeberti</i>	25	83	UH
AVERAGE	25	83	UH
* <i>Macrotarsomys bastardi</i>	28	c128	TP
AVERAGE	28	c128	TP

TABLE X.—Comparison of Proportionate Length of the Caudal Vertebral Series as Determined by Measurements of Skeletons and Measurements in the Flesh.¹

Rodent	GENERIC AVERAGES		Published Field Measurements From Table IX
	Skeletal Measurements		
	Number of Specimens	Tail Head and Body	
×100			
<hr/>			
DIPODIDÆ			
<i>Sicista</i>	1	189.1	143
* <i>Zapus</i>	5	169.6	154
* <i>Allactaga</i>	2	171.1	154
* <i>Dipus</i>	1	159.6	136
* <i>Scirtopoda</i>	1	152.3	109
* <i>Jaculus</i>	3	172.2	147
Maximum		189.1	154
Minimum		152.3	109
Average		169.8	140.5
<hr/>			
PEDETIDÆ			
* <i>Pedetes</i>	1	123.5	106
<hr/>			
HETEROMYIDÆ			
<i>Heteromys</i>	2	132.9	128 1 sp.
<i>Liomys</i>	1	100.0	118 "
<i>Perognathus</i>	4	159.9	114(!)
* <i>Microdipodops</i>	3	155.3	130
* <i>Dipodomys</i>	10	174.8	143
Maximum		174.8	143
Minimum		100.0	114
Average		160.96	126.5
<hr/>			
MURIDÆ			
<i>Rattus norvegicus</i>	4	136.2	120
* <i>Notomys</i>	1	?	128
Maximum			128
Minimum			120
Average			124.
<hr/>			
CRICETIDÆ			
<i>Tatera</i>	2	132.2	111
<i>Gerbillus</i>	1	105.9	135(!)
Maximum		132.2	135
Minimum		105.9	111
Average		123.4	123

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.

TABLE XI.—Generic Differences in Relative Length of the Skull and Regions of the Vertebral Column.^{1, 2}

Rodent	Number of Specimens Precaudal	Average Percentage of Combined Skull and Precaudal Vertebral Length						No. Spec. Caudal
		Skull	Cerv.	Th.	Lu.	Sacro-Pseudo-Sacral	Caudal	
DIPODIDÆ								
<i>Sicista</i>	1	34.7	9.1	25.9	20.6	9.6	189.1	1
* <i>Zapus</i>	5	29.1	7.2	22.7	26.0	14.2	169.6	5
* <i>Allactaga</i>	5	27.9	8.0	24.7	27.0	12.5	171.1	2
* <i>Dipus</i>	1	27.7	6.7	25.2	27.7	12.6	159.6	1
* <i>Scirtopoda</i>	1	28.9	5.7	24.7	29.1	11.6	152.3	1
* <i>Jaculus</i>	6	28.9	6.3	24.3	27.9	12.7	172.2	3
PEDETIDÆ								
* <i>Pedetes</i>	3	24.9	9.1	25.4	31.2	9.3	123.5	1
HETEROMYIDÆ								
<i>Heteromys</i>	2	29.3	9.4	24.6	22.8	13.7	132.9	2
<i>Liomys</i>	1	33.0	9.2	22.7	23.7	11.3	100.0	1
<i>Perognathus</i>	6	35.3	8.2	21.5	21.3	13.5	159.9	1
* <i>Microdipodops</i> ³	5	40.2	6.8	21.5	18.9	12.8	155.3	3
* <i>Dipodomys</i>	16	34.4	6.7	21.1	22.1	15.5	174.8	10
MURIDÆ								
<i>Rattus</i>	3	23.5	10.3	27.8	22.3	19.2	136.2	4
* <i>Notomys</i>	1	c27	c9	c26	c23	c15	?	
CRICETIDÆ								
<i>Tatera</i>	2	33.1	10.2	22.5	24.2	13.2	132.2	2
<i>Gerbillus</i>	1	31.6	7.9	25.3	20.6	14.6	105.9	1
PARAMYIDÆ								
<i>Paramys</i>	1	c19	c13	c29	c29	c10	?	

¹See also figure 12.

²An asterisk is prefixed to the name of each genus the members of which are primarily ricochetors.

³The two asymmetrical specimens of *Microdipodops* were measured on the basis of the modal seven lumbar vertebrae and five sacro-pseudosacral vertebrae.

TABLE XII¹

Rodent	Position of Center of Motion Thoracic Vertebrae Numbers				
	10	10-11	11	11-12	12
<i>Zapus</i>	2	2	1		
<i>Allactaga</i>	1		4		
<i>Dipus</i>			1		
<i>Scirtopoda</i>			1		
<i>Jaculus</i>			1	4	1

TABLE XIII

Rodent	Atlas Height	Deviation from horizontal of the Plane of Insertion of M. OBL. CAP. INF.
	Length	
<i>Rattus</i> (69551)	1.51	30°
<i>Rattus</i> (100084)	1.72	30°
<i>Pedetes</i> (42057)	1.30	40°
<i>Pedetes</i> (70392)	1.39	45°
<i>Allactaga</i> (397)	1.70	45°
<i>Allactaga</i> (227)	2.33	50°
<i>Jaculus</i> (70096)	1.71	65°
<i>Jaculus</i> (70004)	2.03	70°
<i>Dipus</i> (55979)	1.96	70°
<i>Scirtopoda</i> (1321)	2.04	80°
<i>Zapus</i> (5403)	2.22	70°
<i>Zapus</i> (13584)	2.33	70°
<i>Zapus</i> (74849)	2.33	80°
<i>Heteromys</i> (3645)	2.08	65°
<i>Heteromys</i> (7524)	2.47	65°
<i>Liomys</i> (16780)	2.00	70°
<i>Dipodomys</i> (15457)	2.00	75°
<i>Dipodomys</i> (68327)	2.63	75°
<i>Dipodomys</i> (132763)	2.83	80°
<i>Perognathus</i> (43061)	3.54	80°
<i>Perognathus</i> (43062)	3.29	80°
<i>Microdipodops</i> (54815)	3.08	85°
<i>Microdipodops</i> (54579)	3.16	90°

¹The numbers within the squares indicate the number of specimens.

TABLE XIV.—The Height of Chevron Bones.¹

Rodent	Number of Specimens	Height of Tallest Chevron
DIPODIDÆ		
* <i>Zapus</i>	5	12
* <i>Allactaga</i>	3	15
* <i>Dipus</i>	1	13
* <i>Jaculus</i>	2	24
HETEROMYIDÆ		
<i>Liomys</i>	2	24
<i>Heteromys</i>	2	32
<i>Perognathus</i>	4	24
* <i>Dipodomys</i>	4	34
* <i>Microdipodops</i>	5	26
PEDETIDÆ		
* <i>Pedetes</i>	3	94

¹The average height of the tallest chevron in per cent of the centrum length immediately caudad to it. The figures are reliable only within broad limits because of the difficulties in mensuration of small specimens. Genera whose members are ricochetors are marked with an asterisk.

TABLE XV¹

$$\frac{\text{Height sacro-iliac Joint}}{\text{Length Sacro-iliac Joint}} \times 100$$

Rodent	Number of Specimens	Average Index	Range of Indices
DIPODIDÆ			
<i>Sicista</i>	1	19	19
* <i>Zapus</i>	3	33.6	30.0-37.5
* " (<i>Napæozapus</i>)	2	41.2	40.9-41.5
* <i>Allactaga</i>	3	57.3	50.8-63.0
* <i>Dipus</i>	1	58.1	58.1
* <i>Scirtopoda</i>	1	68.0	68.0
* <i>Jaculus orientalis</i>	3	55.8	52.1-63.1
* " <i>jaculus</i>	2	70.0	68.0-72.1
PEDETIDÆ			
* <i>Pedetes</i>	4	51.9	50.0-56.0
HETEROMYIDÆ			
<i>Liomys</i>	2	44.5	42.0-47.1
<i>Heteromys</i>	2	48.6	41.1-56.1
<i>Perognathus</i>	6	47.6	40.0-54.5
* <i>Microdipodops</i>	7	45.2	40.0-50.0
* <i>Dipodomys</i>	18	41.1	35.0-45.0
GERBILLINÆ			
<i>Meriones</i>	1	42.1	42.1
<i>Tatera</i>	1	44.4	44.4
<i>Gerbillus</i>	1	56.6	56.6
MURIDÆ			
<i>Rattus</i>	3	41.4	32.4-46.4

¹An asterisk is prefixed to the name of each genus whose members are primarily ricochetors.

PLATES XI to XX

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PLATE XI

Three tail types occurring among the Dipodidæ. Left: *Cardiocranius paradoxus*, short heavy tail. Middle: *Alactagulus acontion*, long, tufted tail. Right: *Zapus (Napæozapus) insignis*, long thin tail.

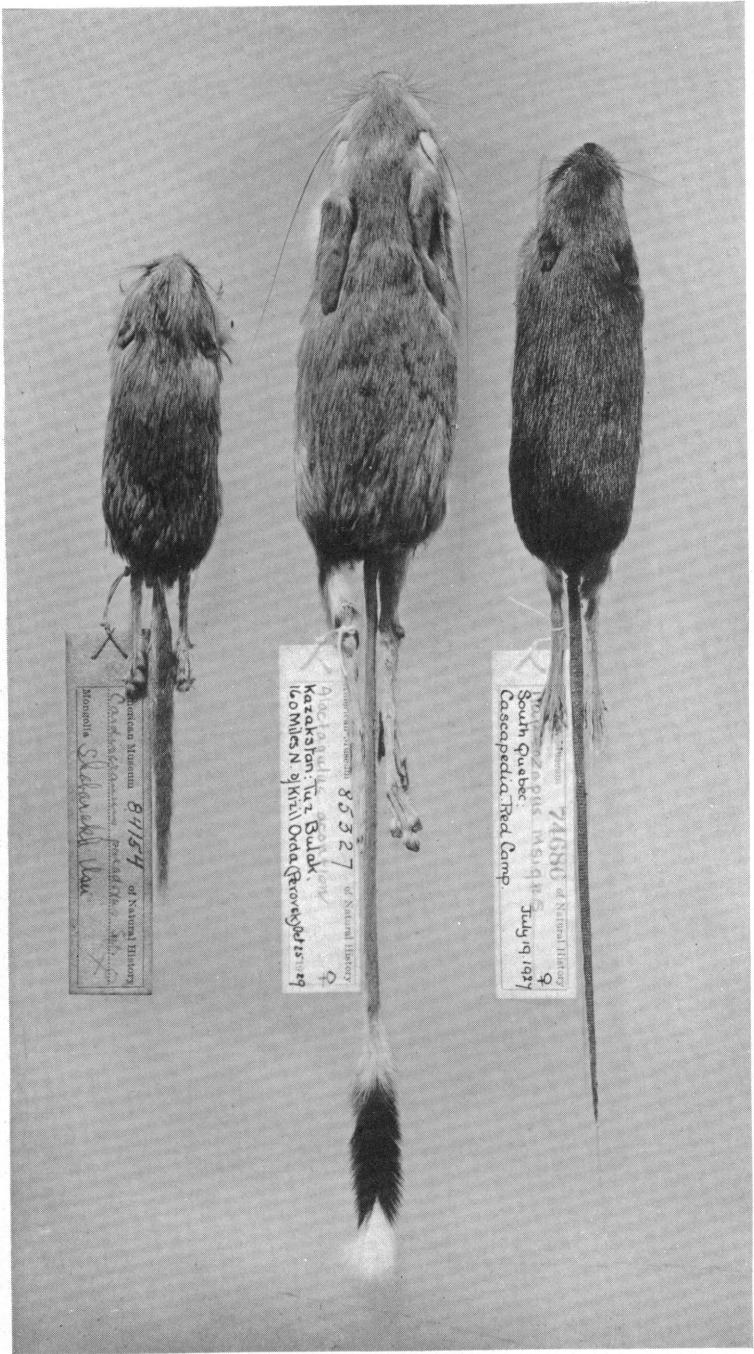
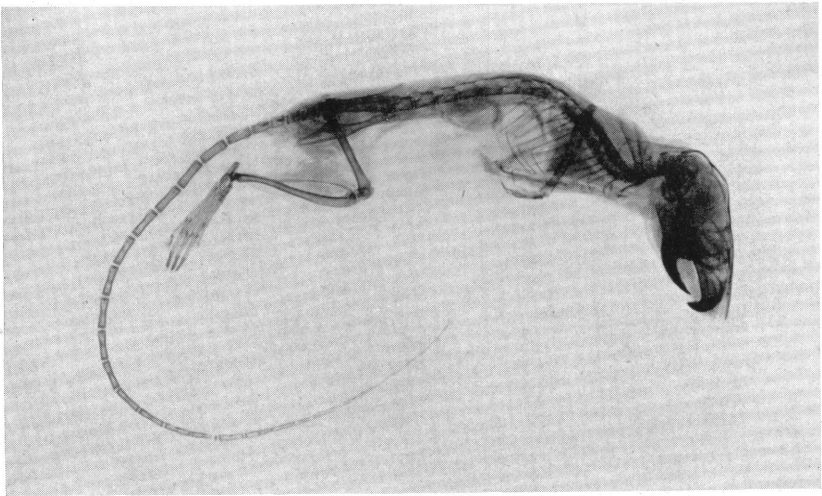


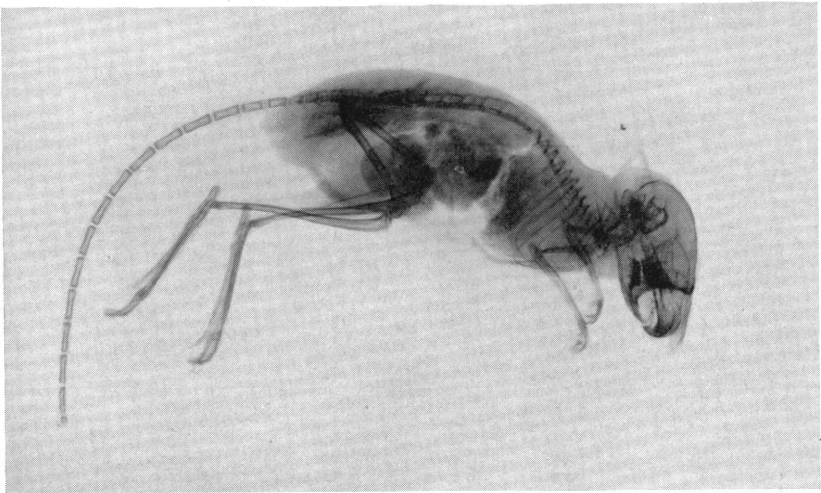
PLATE XII

Fig. 1. X-ray photograph of *Rattus confucianus* (AMNH 44842), showing the open cervical flexure of quadrupedal rodents.

Fig. 2. X-ray photograph of *Notomys mitchelli* (Australian Museum 9909), showing the acute cervical flexure of ricochetal rodents.



1



2

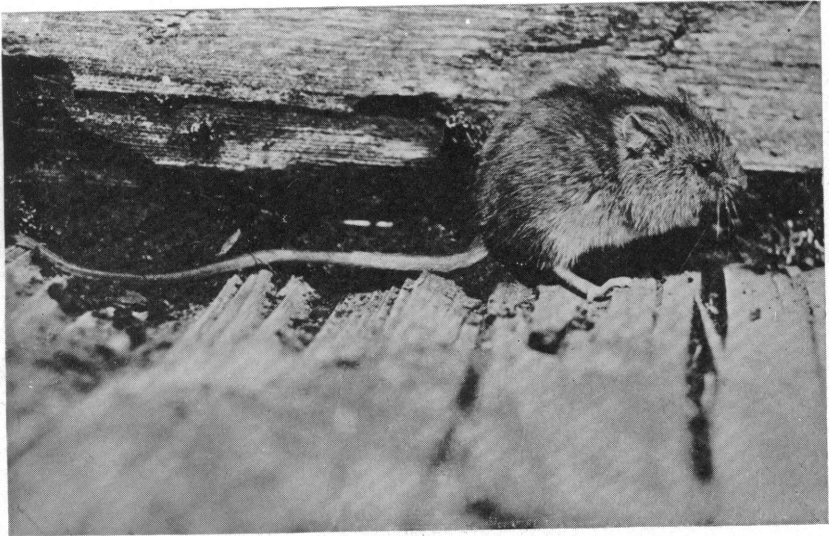
PLATE XIII

Fig. 1. *Sicista tianshanica* in a resting pose strongly suggestive of *Zapus*.

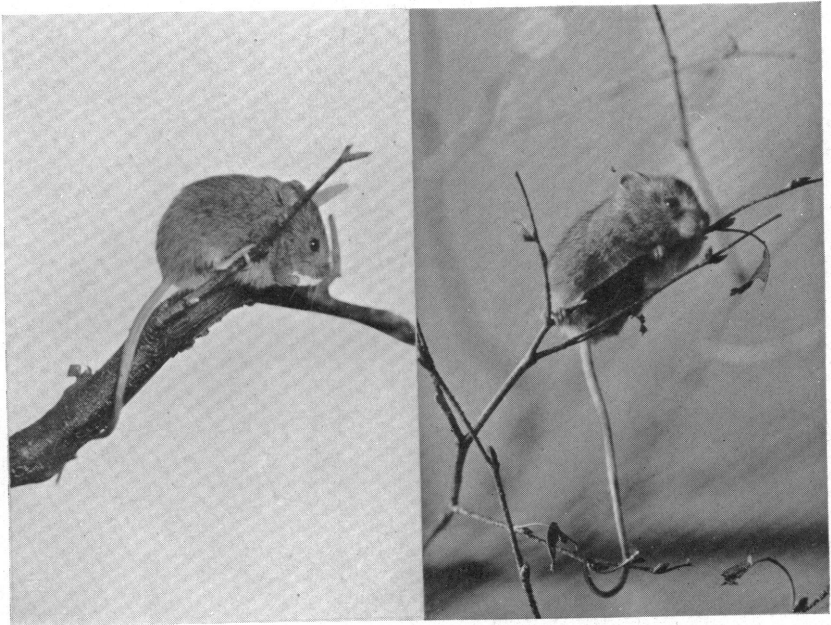
Photograph by courtesy of Anatol J. Argyropulo.

Figs. 2-3. *Sicista montana* climbing. Note the use of the tail, the hands and feet.

Photographs courtesy of Ivar Arwidsson.



1



2

3

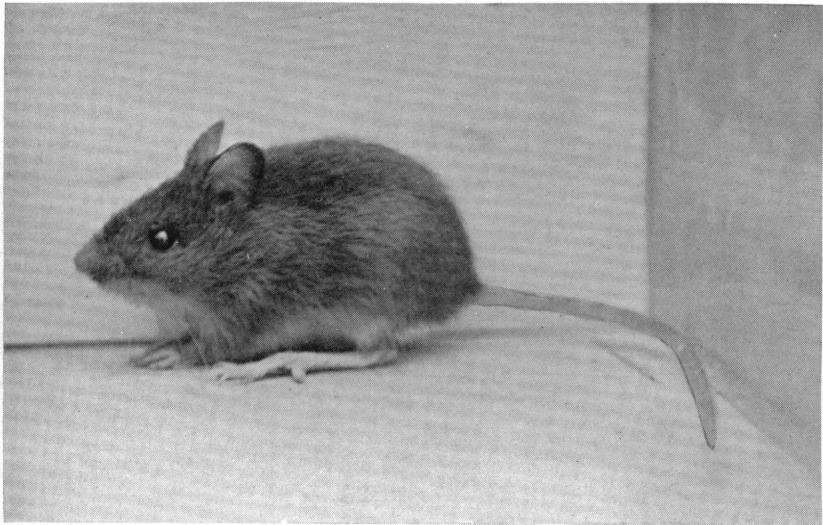
PLATE XIV

Fig. 1. *Zapus hudsonius*.

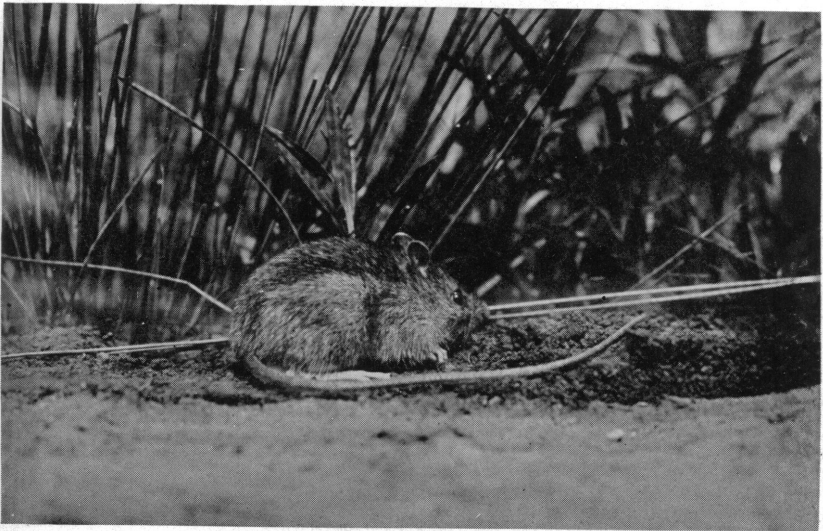
Photograph by W. S. Berridge.

Fig. 2. *Zapus princeps*.

Photograph courtesy of E. R. Warren.



1



2

PLATE XV

Fig. 1. *Jaculus ?orientalis*. Note the bracing action of the tail.

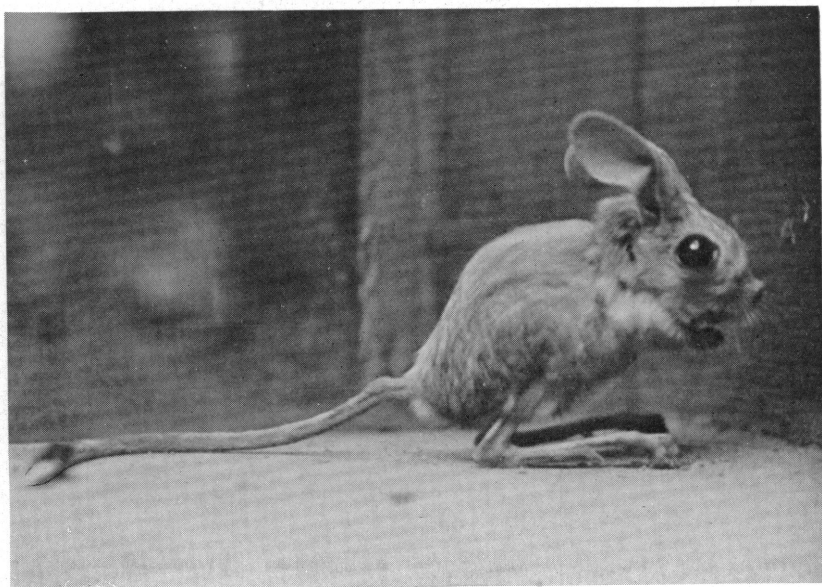
Photograph by W. S. Berridge.

Fig. 2. *Scarturus tetradactylus*. Note the proportions of the fore and hind limbs. The angle near the base of the tail is doubtless due to an injury.

Photograph by W. S. Berridge.



1.



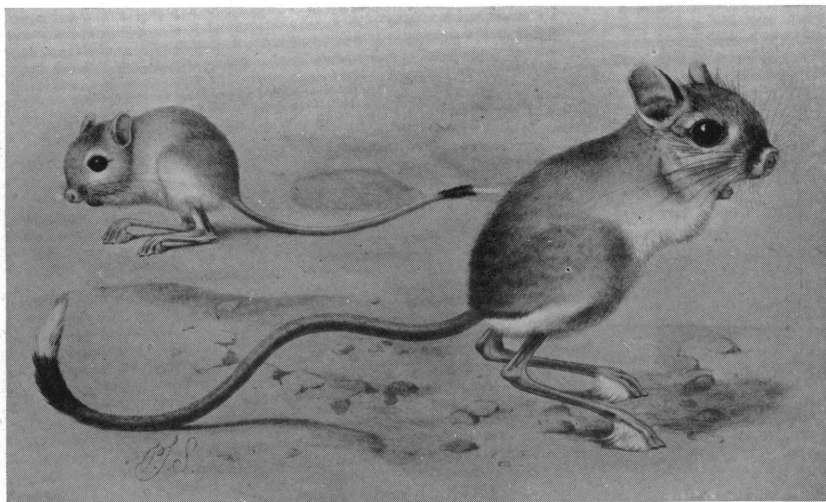
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PLATE XVI

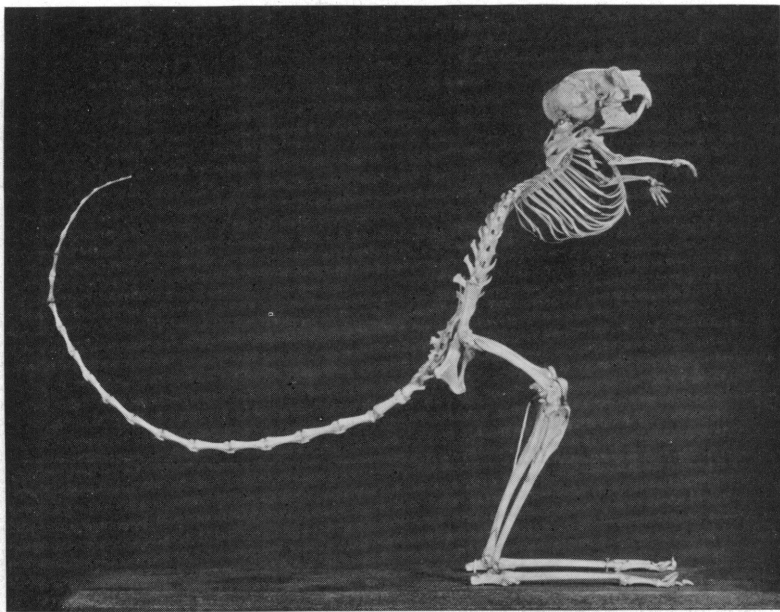
Fig. 1. *Jaculus jaculus*.

From Anderson's 'Zoology of Egypt.'

Fig. 2. *Jaculus orientalis* (35914). The skeleton is mounted in a position probably never assumed by the living animal—that is, with feet fully plantigrade, the tibia extended, and the tail held above the ground and curled upwards.



1



2

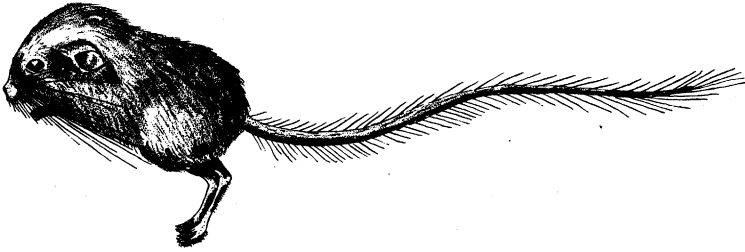
PLATE XVII

Fig. 1. *Salpingotus kozlovi*.

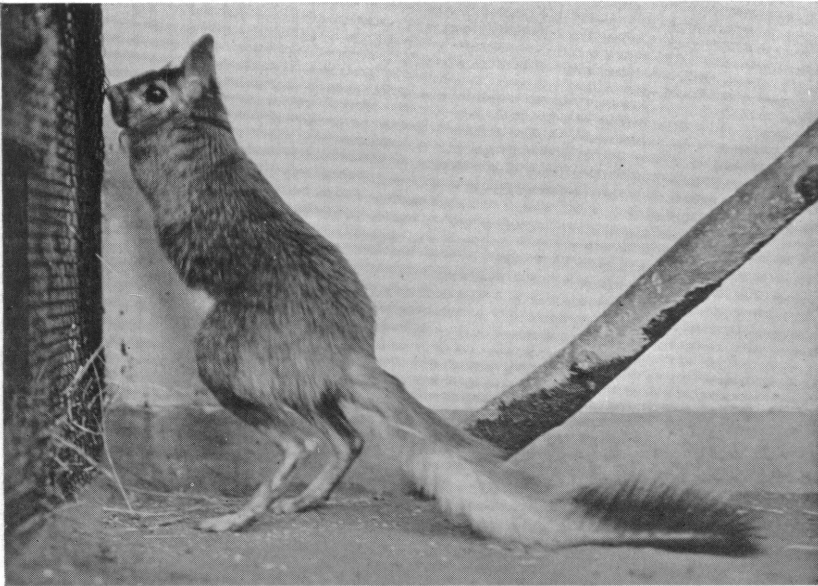
Redrawn from Vinogradov.

Fig. 2. *Pedetes ?cafer*.

Photograph by W. S. Berridge.



1



2

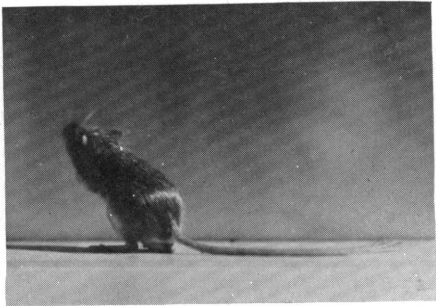
PLATE XVIII

Figs. 1, 2, 3, Poses of *Perognathus penicillatus eremicus*.

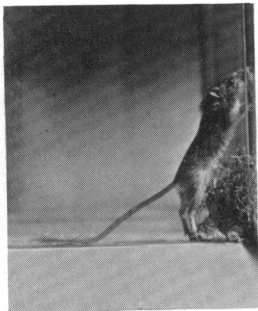
Photographs by the Author.

Fig. 4. *Microdipodops megacephalus dickeyi*.

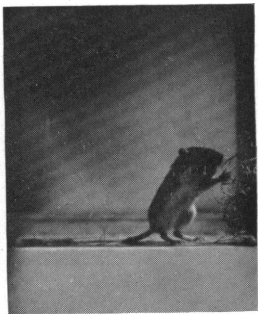
Photograph courtesy of Joseph Dixon.



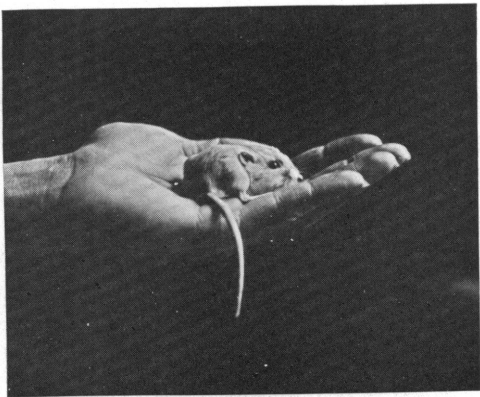
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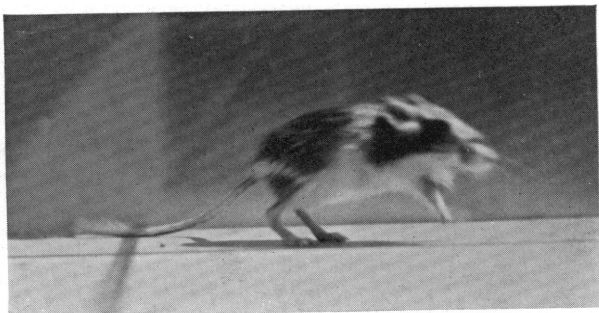


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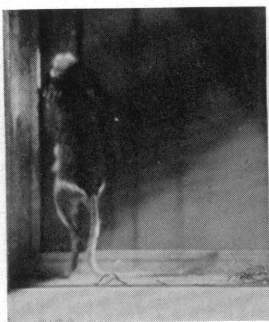
PLATE XIX

Dipodomys merriami. In Fig. 1, the animal is shown in the course of slow quadrupedal progression. In Figs. 3 and 6 the tail is shown used for support. Compare with Plates XV and XVI.

Photographs by the Author.



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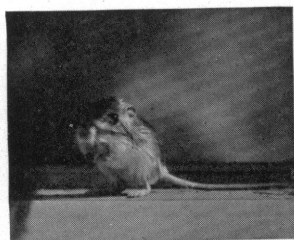
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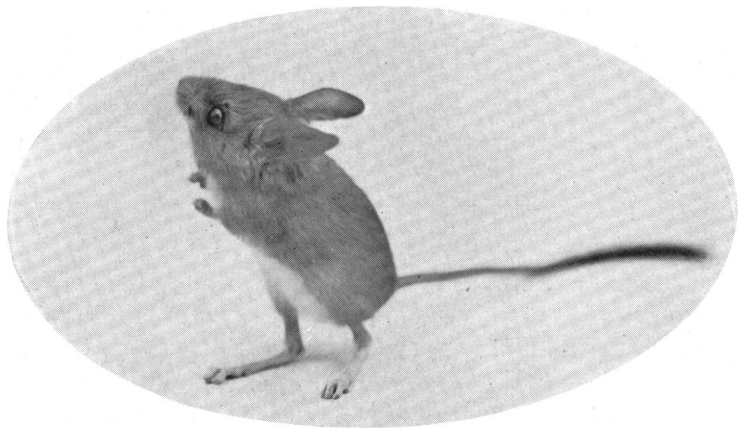
PLATE XX

Fig. 1. *Notomys cervinus*.

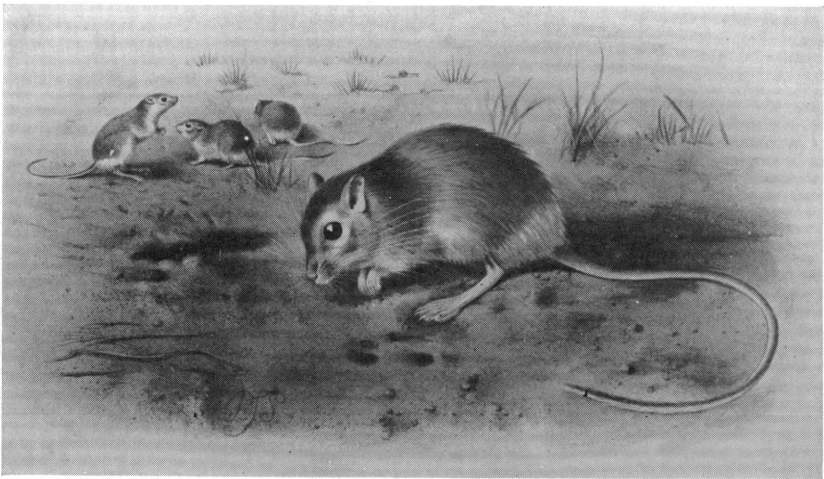
Photograph courtesy of A. S. Le Souef.

Fig. 2. *Gerbillus gerbillus*.

From Anderson's 'Zoology of Egypt.'



1



2

