HYSTRICOMORPH RODENTS
FROM THE LATE MIOCENE OF
COLOMBIA, SOUTH AMERICA

BY

ROBERT W. FIELDS

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ROBERT W. FIELDS

(A contribution from the University of California Museum of Paleontology)

ABSTRACT

The stage of evolution of *Scleromys schürmanni*, *S. colombianus*, n. sp., *Olenopsis aequatorialis*, *Neoreomys huilensis*, n. sp., and *Prodolichotis pridiana*, n. sp. indicates that the La Venta fauna is late Miocene in age. It is correlated with the Carmen de Apicalá fauna on the presence of *Scleromys schürmanni* and *S. colombianus* in both faunas, and with the Friasian fauna of Argentina on the stage of evolution of the mammals.

The fauna combines aquatic, amphibious, arboreal, and riparian elements with a dominant group of savanna-type animals. The climate was probably similar to that of the present llanos of Colombia.

Statistical and morphologic evidence indicates that *Scleromys schürmanni* and *S. colombianus* are genetically stable, homogeneous species, and that *Olenopsis aequatorialis* is possibly a chronocline species.

Critical study of the cheek teeth in *Olenopsis* and *Dinomys* indicates possible diametric growth of the teeth in the latter genus. *Olenopsis*, however, has closed fossettes and roots, features which seem to negate any possibility of diametric growth of the teeth.

Relationship of *Scleromys* and *Olenopsis* to the family Dinomyidae seems certain. It is suggested that several other genera are closely related to *Dinomys* and should be assigned to the Dinomyidae. A partial reclassification is given.

Investigation of the middle ear and auditory ossicles in *Olenopsis* and in several living genera indicates that the Dinomyidae are closely related to the Erethizontidae. Further critical study of the auditory region may furnish the key to a better understanding of the group.

The presence of *Prodolichotis pridiana* in the fauna extends the range of the Dolichotinae back into the Miocene. Occurrence of *Neoreomys* in the La Venta and Friasian faunas extends its range into late Miocene. *Neoreomys* is probably ancestral to *Isomyopotamus* and *Myocastor*. *Olenopsis* is probably ancestral to *Tetrastylus*, and a species of *Tetrastylus* is the ancestor of *Dinomys*.

INTRODUCTION

THE FIRST PART of this discussion is a description of the hystricomorph rodents in the large collection of fossil mammals from the La Venta badlands[1] in the upper Magdalena River Basin, Department of Huila, Colombia, South America. This collection is now housed in the University of California Museum of Paleontology.

There are several nearly complete skeletons, skulls, numerous lower jaws, and many isolated teeth of these rodents. The family Dinomyidae is represented by two genera and three species, one of which is new. There is a new species for each of the families Caviidae and Capromyidae. An upper tooth has been assigned questionably to the family Erethizontidae, and a small jaw without teeth has been placed tentatively in the Echimyidae. The relationships of these forms to previously described fossils and recent South American hystricomorphs are of utmost importance because they substantiate certain taxonomic affinities that Miller and Gidley (1918) and Stirton (1947A) have suggested but could not prove because of inadequate materials. The La Venta hystricomorphs offer a key to certain of these affinities.

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[1] Stirton (1951A) introduced the term "La Venta" as a faunal name and designated the fossil assemblage from the "Monkey Unit" as type of the fauna. He also proposed most of the terminology for the stratigraphic units that was adopted by Royo y Gómez (1946) and is used in this paper.
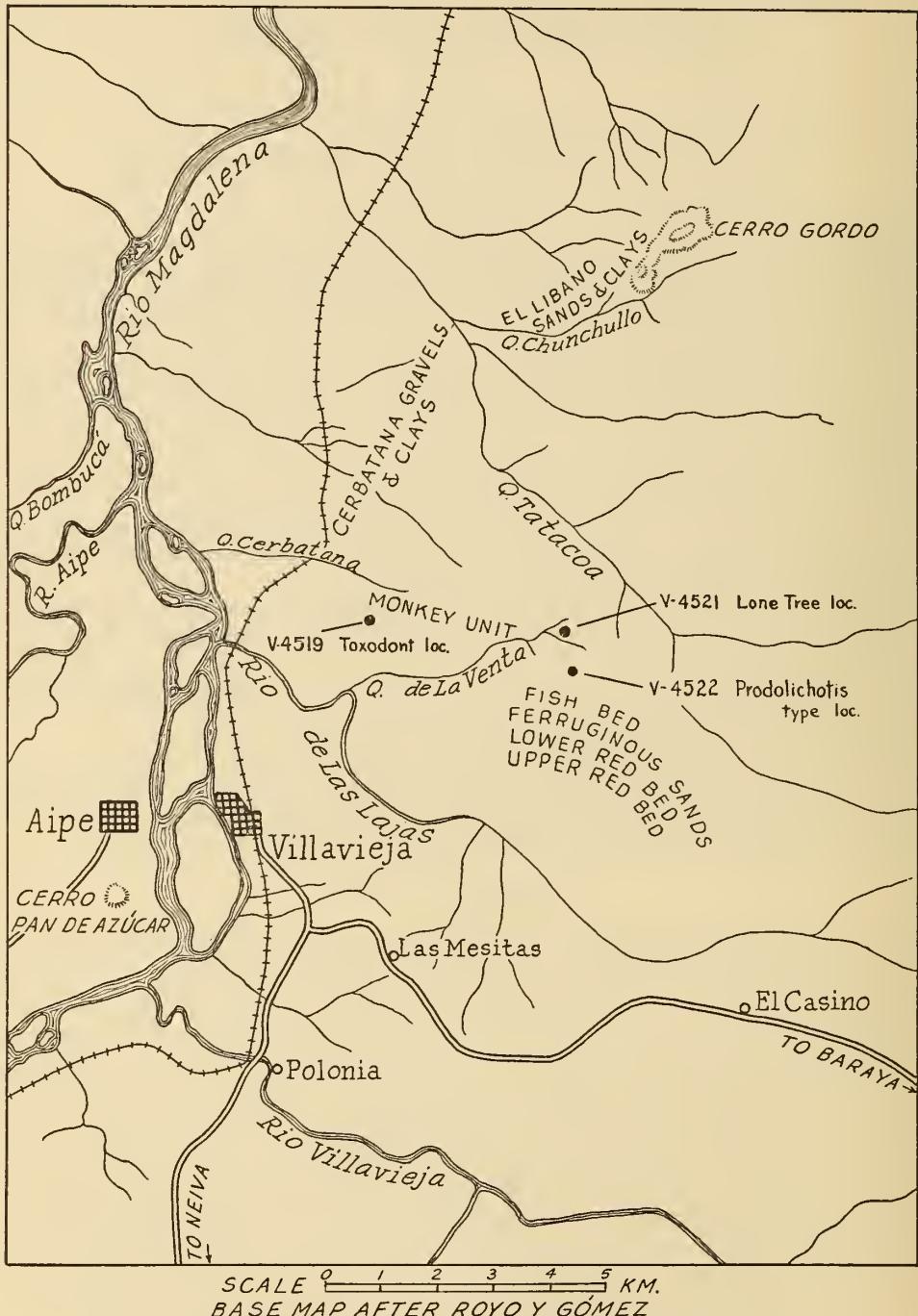
Fig. 1. Index map of the Villavieja region in Huila, Colombia, showing type
localities and geographic position of La Venta exposures.

The second part of this study is my interpretation of: environmental conditions in the upper Magdalena Valley as they existed during La Venta time; evolutionary trends in the La Venta fauna as expressed in the rodents; and correlation and age of the La Venta fauna.

A preliminary faunal list has been made by D. E. Savage (1951B). Other studies of the fauna are being worked out and published as time allows. Groups on which studies have been published are the Sirenia (Reinhart, 1951), Chiroptera (Savage, 1951A), Primates (Stirton, 1951A; Stirton and Savage, 1951), and Interatheriidae (Stirton, 1953A). My detailed study of the stratigraphy of the La Venta area is in preparation.

As a result of the industrious efforts of Florentino Ameghino, the fossil mammals of Argentina have been well known for many years, but until recently the continental Tertiary stratigraphy and vertebrate paleontology of northern South America, especially Colombia, has been neglected. Attention was first drawn to the fossil mammals in the upper Magdalena River Basin of Colombia when, in 1939, Dr. Stirton received a leontiniid upper premolar and a juvenile astrapothere mandible from William Effinger of the Richmond Petroleum Company. They had been collected on the west side of the Magdalena River near Guacirco, between Neiva and Aipe, Department of Huila, by George R. Hyle, in 1938.

In 1944, Dr. Stirton was granted a John Simon Guggenheim Fellowship to seek evidence of intercontinental dispersal of terrestrial vertebrates between North and South America. Because of the 1938 discovery and the country's ideal geographic position as a pathway for dispersal between the Americas, Colombia was selected as the most promising area for investigation. The Colombian government, through its Servicio Geológico Nacional, coöperated by organizing a commission for six months of exploration in the area selected by Stirton. Dr. José Royo y Gómez was assigned as geologist and Dr. Manual I. Varón as topographer. On this first expedition into the La Venta badlands, many significant and interesting fossil vertebrates were found, including many of the excellently preserved hystricomorph rodents described in this paper.

The second expedition, January to July, 1949, on which I served as paleontologist, was jointly sponsored by the University of California Associates in Tropical Biogeography and the Servicio Geológico Nacional de Colombia. The Servicio again organized a six-months' commission and assigned Sr. Diego Henao-Londoño as geologist and Sr. Isreal Osario as topographer. Dr. Alden H. Miller, ornithologist, Dr. Herbert L. Mason, botanist, and Dr. R. A. Stirton, all from the University of California, spent one month in the field with the expedition in the La Venta area. The efforts of the second expedition augmented the earlier collection with many more specimens, including many of the best-preserved hystricomorphs yet found in the La Venta area. During this period of exploration, Henao and I mapped the area between Cerro Gordo and the Upper Red Beds. The mapping was done in order to establish the stratigraphic relationships of the many fossil localities.

The third expedition, May to July, 1950, was also sponsored by the University of California Associates in Tropical Biogeography and the Servicio Geológico Nacional. Dr. D. E. Savage, leader of the party, added further significant discoveries to the collection from La Venta. During this expedition, Savage attempted to find fossil mammals in the so-called Gigante group, a sequence of tuffaceous beds strati-

graphically above the La Venta section and exposed along the Villavieja–Neiva Road. These beds, however, are apparently barren of fossil vertebrates although they contain much fossil wood.

METHODS AND PRINCIPLES

Mensuration.—All measurements in this paper are in the metric system. Millimeters are used exclusively in the systematic descriptions. All measurements have been made with the same metric vernier calipers, reading to 0.1 mm.

Statistical analyses have been made wherever available samples were of sufficient size to permit evaluation. No species has been recognized on the quantitative values alone. Evaluation of all qualitative and quantitative values determinable have been utilized in recognizing new species. All calculations were made with a K & E Log-Log Duplex Slide Rule.

Terminology, symbols, and abbreviations.—Assemblages of fossils from different localities are herein recognized as one fauna when the genera and species are identical (Stirton, 1936A, p. 164). Thus the assemblages from Carmen de Apicalá and La Venta both represent the La Venta fauna (Stirton, 1953B).

Standard deviation is defined by Simpson and Roe (1939) as: "An essential parameter of the normal curve, symbolized by σ, (or S.D.), determining its dispersion,
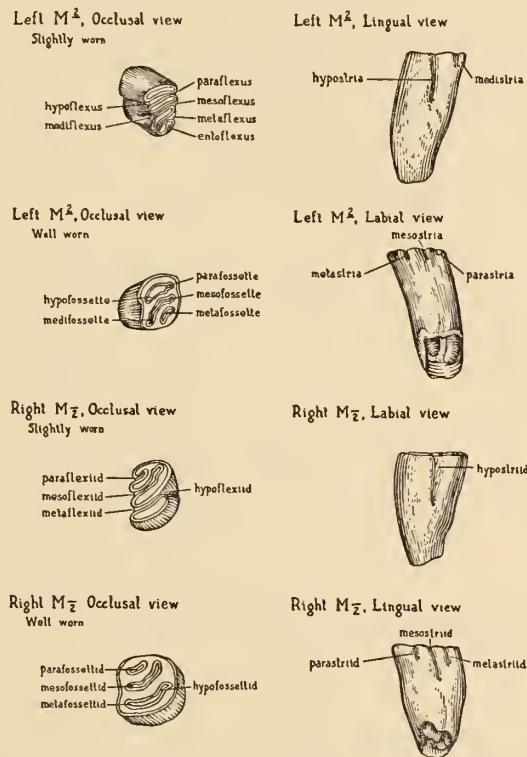
Fig. 2. Dental terminology used in description of *Scleromys, Olenopsis,* and *Neoreomys.* Examples are from *Olenopsis aequatorialis.* (Entofosette and entostria, not shown, are associated with entoflexus.) $\times$ 1.

and hence the most important estimate of dispersion that can be made from a sample."

Simpson and Roe (1939) define coefficient of variation as: "A conventional calculated numerical representation of the intensity of variation." See Simpson and Roe (1939, p. 397) for a definition of variation.

Symbols pertaining to statistical analyses are described in text. They follow Simpson and Roe (1939) and Cazier and Bacon (1949).

The University of California Museum of Paleontology will be abbreviated U.C.M.P.; the American Museum of Natural History will be abbreviated A.M.N.H. and the Chicago Natural History Museum will be abbreviated C.N.H.M.

The only taxonomic abbreviation used is ?, which means that the particular category is of questionable affinity. The abbreviation is placed before the name to which the reference is made.

References cited are alphabetized according to the listing in the bibliographies of fossil vertebrates, Hay (1902a, 1930a); Camp and VanderHoof (1940); Camp, Taylor, and Welles (1942); and Camp, Welles, and Green (1949, 1953).

Dental Terminology.—The cheek teeth of rodents belonging to the families Dinomyidae and Capromyidae show strong parallelism to those of the beavers in the development of prominent fossettes and inflections. Stirton's (1935) dental nomenclature of beaver teeth was used in naming the fossettes and inflections on these South American hystricomorphs. The application of these terms does not necessarily imply homology but has been used as a matter of convenience. The lateral grooves, occlusal inflections, and fossettes have been given names in accordance with their topographic proximity to the same characters on the beaver teeth. The presence of two additional flexii, fossettes, and strii on the upper teeth has made it necessary to introduce new names for these features. The terms **entoflexus, entofossette, entostria, mediflexus, medifossette,** and **medistria** are used (see Fig. 2).

Technique used in studying isolated cheek teeth.—Original attempts to segregate isolated cheek teeth of *Scleromys colombianus* proved unsuccessful. It became apparent that tooth appearance at various stages of wear must be understood before any of these teeth would be of value, and that serial sections must be made from known cheek-teeth series if any of the isolated teeth were to be properly identified. The usual sectioning methods were attempted but proved unsatisfactory. The sections could not be cut thin enough, and too much of the tooth height was lost by the cutting and polishing. If stages of wear were to be understood, sections had to be thin, the amount of tooth lost by cutting reduced to a minimum. Besides these requirements, upper teeth which are curved, would have to be cut at increasing angles toward the base of the tooth in order to approximate, at the point of each cut, the appearance of a naturally worn tooth. No commercially made diamond or steel saw could fulfill these requirements.

This prompted me to build a cutting device incorporating all of the required adjustments and capabilities (see Pl. 36, *a-b*). The result was a saw using one-inch (diameter) jeweler's blades and powered by a Dremel, Model 2, Moto-Tool, which operates at a speed of 27,000 revolutions per minute. The remainder of the apparatus was constructed after the plan of a turret lathe. A slide bar was mounted to the right of the motor assembly and at a right angle to the motor shaft. This allowed the specimen to be fed into the overhead blade by means of a machine screw feed. Above the slide bar were mounted a vertical post and turret with a lock screw and calibrated angle scale to allow angle adjustment for cutting the upper cheek teeth. A box chuck with cinching plate and screws, to hold the specimen in place, was mounted on a slide bar above the turret. This chuck was backed by a screw feed and lock, that allowed the specimen to be moved ahead into the cutting line of the saw after each successive cut. A calibrated (millimeter) scale and traveling needle were attached to the side of the box chuck in order to keep close record of the thickness of each section. While testing the device, one of the blades was accidentally mounted backward. It was found that the blade in this reversed position cut much more rapidly and with less vibration, and the surface of the cut was as smooth as though it had been polished. All the serial sections were cut in this manner with a loss of only 0.2 mm. (thickness of set on saw) between sections.

The isolated teeth were found to be brittle, but after some experimentation, it was discovered that if each tooth was immersed in liquid plastic and placed in a vacuum chamber for about one-half hour the tooth, upon drying, was completely impregnated and sufficiently durable for cutting. Each tooth was then embedded in dental plaster, but with one side exposed for orientation during the cutting process. The plaster blocks, after drying, were also impregnated with liquid plastic. This was necessary because the high speed of the saw created so much heat that a water bath was required. The plastic waterproofed the plaster and kept it from losing strength. Each cut required about two minutes. Sections as thin as 0.3 mm. were obtained with this apparatus. The serial sections provided an index of stage of wear for each cheek tooth and made it possible to apply accurate statistical methods in the study of each sample.

Mode of Accumulation of the Fossils

Many of the specimens found in the La Venta deposits were preserved as complete or nearly complete skeletons. Others were dismembered before burial and their remains scattered at random in the deposits. Many of the animals preserved as complete skeletons must have become mired in mud flats or swamps, where they either sank into the muds immediately or were later buried by additional mud or silt during the next period of flooding.

Concentrations of complete or nearly complete skeletons occur in certain parts of the area. These accumulations probably indicate transportation by running water. Eddies no doubt allowed animal remains to sink to the bottom where they were later buried.

The great number of skulls with lower jaws still attached and articulating limb elements suggest that some of the animals died near streams, where their skeletons were washed about until they became partly dismembered. Ligaments may have held the bones together during transportation and allowed them to be buried as oriented parts.

Broken bones and teeth from many animals were concentrated in particular beds or in pockets along stream channels. These remains show the effects of abrasion from water transportation.

Many of the animals found, especially among the rodents and interatheres, are immature. This indicates a high mortality rate among the younger animals. Some of these juvenile animals were, no doubt, mired while attempting to cross mud flats and died of starvation. Others may have been killed by predators, their remains being left near streams where they would have an excellent chance for burial by the next flood.

The death and burial of many of the terrestrial animals were probably caused by floods that submerged great expanses of the flood plain habitat.

Most of the bone found in the La Venta deposits is well preserved and hard. Replacement by mineral matter is common but not always present. Some specimens, especially those from the bentonitic red beds, are excessively soft, swollen, and badly distorted. It is probable that some specimens macerated under water, and that the bone became soft because of the loss of organic matter. Other specimens show the effects of aerial dessication and sun-checking from long exposure before burial.

FAUNAL LIST

Savage (1951B), Stirton (1953B), and I list the following mammals from the La Venta fauna.

Class Mammalia
  Order Marsupialia
    Family Didelphidae
    Family Borhyaenidae
  Order Chiroptera
    Family Phyllostomatidae. *Notonycteris magdalensis* Savage, 1951.
  Order Primates
    Family Cebidae
      Subfamily Pithecinae. *Cebupithecia sarmientoi* Stirton and Savage, 1951.
      Subfamily Alouattinae. *Homunculus tatacoensis* Stirton, 1951A.
      Subfamily Cebinae. *Neosaimiri fieldsi* Stirton, 1951A.
  Order Edentata
    Family Megalonychidae
    Family Megatheriidae
    Family Mylodontidae
    Family Myrmecophagidae
    Family Dasypodidae
    Family Glyptodontidae
  Order Rodentia
    Family Erethizontidae. ?*Steiromys*
    Family Caviidae
      Subfamily Dolichotinae. *Prodolichotis pridiana* Fields, n. sp.
    Family Dinomyidae
      Subfamily Potamarchinae. *Scleromys schürmanni* Stehlin, 1940B. *Scleromys colombianus* Fields, n. sp. *Olenopsis aequatorialis* (Anthony), 1922.
    Family Capromyidae. *Neoreomys huilensis* Fields, n. sp.
    Family Echimyidae
  Order Condylarthra
    Family Didolodontiadae
  Order Litopterna
    Family Macraucheniidae
    Family Proterotheriidae
  Order Notoungulata
    Family Henricosborniidae
    Family Leontiniidae
    Family Toxodontidae
    Family Interatheriidae. *Miocochilius anomopodus* Stirton (1953B).
    Family Hegetotheriidae
  Order Astrapotheria
    Family Astrapotheriidae. *Xenoastrapotherium kraglievichi* Cabrera; *Astrapotherium.*

Order Sirenia

Family Trichechidae. *Potamosiren magdalenensis* Reinhart, 1951.

This list includes collections from all horizons and localities in the La Venta badlands.[2] In this study only the rodents are considered.

DESCRIPTION OF MATERIALS
Order RODENTIA
Family Dinomyidae

Scleromys schürmanni Stehlin
(Figs. 3-6)

Holotype.—Stehlin (1940B, p. 179); part of left maxillary with P⁴-M³ in place; no number.

Topotypes.—Isolated right $P_{\overline{4}}$, U.C.M.P. no. 40557, loc. V-4421. Right M², U.C.M.P. no. 40556, loc. V-4421. Right M³, U.C.M.P. no. 40555, loc. V-4421.

Type locality.—Area of Finca Llano Redondo, 2.5 kilometers from Carmen de Apicalá, Melgar Basin, Colombia, South America.

Referred specimens.—Partially crushed skull and mandible; skull lacking zygomatic archesl occipital region crushed; mandible lacking angular processes and condyloid processes, U.C.M.P. no. 38987, loc. V-4522. Slightly distorted skull lacking nasals, zygomatic arches, and occipita, condyles, U.C.M.P. no. 38988, loc. V-4536. Right mandible with $DP_{\overline{4}}$, U.C.M.P. no. 39902, loc. V-4536. Fragmentary skeletal parts of young individual, U.C.M.P. no. 39916, loc. V-4523. Proximal part of adult femur, U.C.M.P. no. 40514, loc. V-4520.

Revised diagnosis.—Skull elongate, low; parietal region broad, flat, frontals extremely flattened; nasals long, straight, extending anterior to incisors; rostral masseteric fossa shallow, ovoid anteroposteriorly; infraorbital foramen fairly large with basilar furrow for transmission of nerves; lacrymal large; no accessory opening on rostrum for lacrymal duct; palate long, narrow, incisive foramen elongate, bounded by bony ridges continuing posteriorly to P⁴s; posterior palatine foramen small; palatal margin of internal nares between M³s smooth, ovoid; basicranial axis elongate, narrow; interorbital region open as orbital fissure; auditory bullae moderately enlarged, elongate anteroposteriorly; external auditory meatus rounded with circular opening ventral to tubular part; stylomastoid foramen posterior and between double opening; foramen magnum wide, low; incisors somewhat flattened, enamel extending halfway onto lateral face; cheek teeth semi-rooted, with three weak inflections on labial side, one deep inflection on lingual side; tooth rows somewhat converging anteriorly; mandible heavy; posterior end of incisor extending into ascending ramus; diastema short; coronoid process low, distorted outward, masseteric fossa shallow, masseteric crest small; angular process slightly inflected.

SUPPLEMENTARY DESCRIPTION

Stehlin (1940B, pp. 179-181) refers to characters displayed in *S. schürmanni*, but does not designate a type specimen; furthermore his description does not agree with the published figure. Since this species is common in the La Venta fauna, it seems desirable to describe the new material and compare it, when possible, with the specimen described and figured by Stehlin. The referred specimens, U.C.M.P. nos. 38987, 38988, and the topotypes, nos. 40555, 40556, 40557, are augmented in the University of California collection by numerous rami, one right maxilla with teeth, and a number of isolated teeth.

Cranium (Fig. 3, *a-c*).—Parietals short, laterally expanded, no development of sagittal crest, similar to *Dinomys*; frontals nearly rectangular, ending posteriorly in transverse coronal suture above glenoid fossa, ending anteriorly in transverse suture

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[2] For complete reference to stratigraphic horizons and vertebrate localities, see Stirton (1951A, pp. 316–317) and Fields, "The Geology of the La Venta badlands, Colombia, South America," in preparation.

opposite dorsal root of infraorbital foramen; postorbital process blunt, much as in *Dinomys*, nasals long, narrow; premaxillary large, dorsal spur extending back between maxillary and nasal, as in *Capromys*, suture on lateral face of rostrum smooth, ventral part of maxillo-premaxillary suture serrate, meeting at posterior border of incisive foramen; maxillary expanded, extending onto dorsal and ventral roots of zygoma; ventral surface of infraorbital foramen deeply furrowed anteroposteriorly for nerve transmission as in *Cuniculus*; lacrymal large, extending dorsally onto
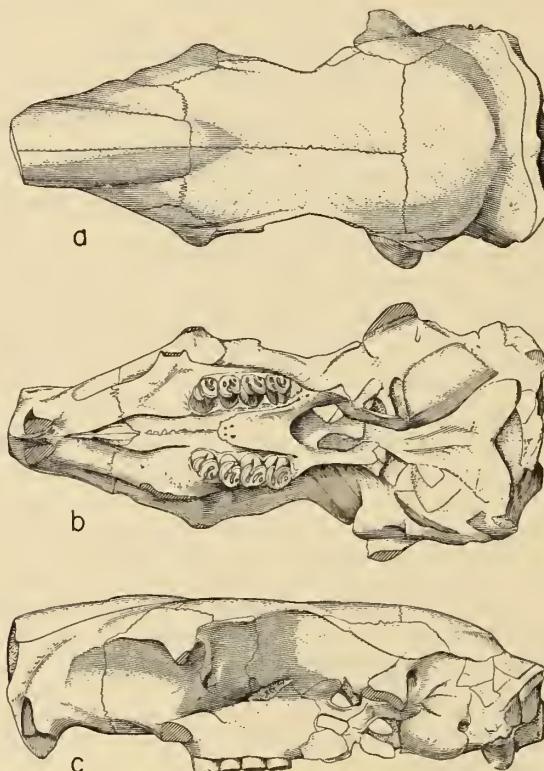
Fig. 3. *Scleromys schürmanni* Stehlin, U.C.M.P. no. 38987, loc. V-4522, Unit Below Fish Bed: *a*, dorsal view of skull; *b*, palatal view of skull; *c*, left lateral view of skull; × 1.

anterodorsal orbital rim, similar to *Dinomys*, lacrymal duct small, on medial face of infraorbital foramen, no accessory opening on rostrum in contrast to *Dasyprocta* and *Neoreomys*; orbital region relatively large, much more elongate than in *Neoreomys*, much as in *Proechimys*; orbitosphenoid small, bounding optic foramen; palatine extends forward to posterior margin of P^4 alveolus, posterior palatine foramen fairly large, entirely within palatine, continuing forward onto maxillaries as shallow furrow; palate somewhat constricted anteriorly; internal nares rounded, wide, smooth, much as in *Dasyprocta*, anterior border of internal nares between M^2; palatine extends posteriorly to point directly below optic foramen; palatopterygoid suture serrate; pterygoid long, thin, extending back to bullae; spenopalatine foramen large as in *Dasyprocta*; alisphenoid fairly large, perforated deep under pterygoid wing by combined foramen lacerum medius and foramen rotundum; alisphenoid

bar connecting with lateroposterior wing of palatine, underlain anteroposteriorly by alisphenoid canal, perforated laterally by foramen ovale; median lacerate foramen large, much as in *Dinomys*; posterior lacerate foramen elongate, probably including carotid canal and anterior condyloid foramen; basicranial axis long, narrow; presphenoid small, narrow; basisphenoid long, wedge-shaped, forming floor of optic foramen; basioccipital wide posteriorly; auditory bullae moderately inflated; external auditory meatus directed posterolaterally and slightly upward, rounded; accessory rounded ventral opening present as in *Dinomys*; stylomastoid foramen between and posterior to openings to external auditory meatus and anterior to mastoid

MEASUREMENTS OF CRANIUM

Measurements	U.C.M.P. No. 38987	U.C.M.P. No. 38988
Greatest anteroposterior length	70.3+	75.7±
Basilar length (inferior margin of foramen magnum to posterior border of incisive alevoli)	56.8	....
Palatal length (palatal margin of internal nares to posterior border of incisive alveoli)	30.4	33.7
Postpalatal length (posterior margin of palate to inferior border of foramen magnum)	26.4	....
Depth of rostrum at zygomatic root	19.4	21.8±
Depth, floor of basisphenoid to dorsum	11.3±	16.4±
Length of bullae	12.5±	11.8±
Width of bullae	11.1	11.6
Width of cranium (narrowest point between dorsal rim of orbits)	18.3	19.3
Height of infraorbital foramen	9.4	....
Palatal breadth (between P^4)	4.2	4.4
Palatal breadth (between M^3)	6.9	7.6
Greatest width between maxillary ridges (posterolateral to incisive foramen)	5.2	5.1

process of periotic; squamosal small, stout; glenoid fossa transversely narrow, elongate anteroposteriorly; postglenoid foramen small as in *Dinomys* and *Neoreomys*; paraoccipital process compressed to posterior margin of bullae, not lengthened, similar to *Dinomys*; occipital region wide, fairly flat; occipital condyles wide, flat; foramen magnum wide, low.

Dental formula.—$I\frac{1}{1}$; $C\frac{0}{0}$; $P\frac{1}{1}$; $M\frac{3}{3}$.

Upper dentition (Fig. 3b.—Cheek-tooth series directed posterolaterally, right and left occlusal surfaces at approximately 160 degree angle to one another; teeth remain open-rooted until late in life, subhypsodont; enamel fairly thick, no cement in fossettes; M^2 largest tooth in series; teeth with small oppressed area on upper border indicating contact surface where teeth meet; incisors extremely curved, base above zygomaxillary fossa of palate, anterior to cheek-tooth series, similar to *Proechimys*; enamel face nearly flat, somewhat velvety as a result of discontinuous, minute, linear striations; enamel band extending halfway onto rounded lateral face, one-third of flat internal face covered; general appearance and wear pattern similar to *Dasyprocta*.

P^4 ovoid in cross-section, slightly longer than wide, erupts after M^3; hypoflexus

deep, on anterolingual part of crown, hypostria extending to basal one-fourth of tooth, hypoflexus continuous with paraflexus in unworn tooth; paraflexus isolated as parafossette in early stage of wear; labial moiety of crown with crescent-shaped mesoflexus and simple, rounded metaflexus; stria shallow; parastria longer than mesostria; mesostria longer than metastria; metaflexus isolated as metafossette when mesoflexus still remains open to labial side; only hypoflexus remains open in half-worn tooth, other flexi retained as fossettes; hypoflexus isolated as hypofossette and metafossette lost in advanced stage of wear.

M^1 and M^2 differ from P^4 in shape; anterolingual moiety rounded; posterior and labial faces somewhat flattened; mesostria longer than parastria or metastria; meta-

MEASUREMENTS OF UPPER DENTITION

Measurements	U.C.M.P. No. 38987	U.C.M.P. No. 38988
Upper dentition (length from anterior face I to posterior margin M^3)	35.5	39.0
Length of diastema (posterior border of incisive alveoli to anterior border P^4 alveoli)	17.7	19.8
P^4-M^3, alveolar length	13.6	14.8
P^4-M^3, occlusal length	13.1	13.6
I, anteroposterior diameter	4.1	4.2
I, transverse diameter	2.2	2.4
P^4, anteroposterior diameter	3.4	3.5
P^4, transverse diameter	3.2	3.4
M^1, anteroposterior diameter	3.0	3.2
M^1, transverse diameter	3.6	3.7
M^2, anteroposterior diameter	3.3	3.4
M^2, transverse diameter	3.3	3.7
M^3, anteroposterior diameter	3.4	3.5
M^3, transverse diameter	3.2	3.4

stria shorter than parastria; parafossette slightly ovoid transversely; mesofossette persistent, lingual part curved posteriorly, not crenulated; metafossette weak, rounded, lost before hypoflexus becomes isolated; hypoflexus directed anterolabially, hypofossette with similar orientation; M^2 slightly larger than M^1; hypostria situated more posteriorly on M^1 than on M^2.

M^3 more elongate than M^{1-2}, more ovoid in outline; hypostria on anterolingual angle of tooth in contrast to M^{1-2}; hypoflexus comparatively straight transversely; paraflexus isolated early; mesoflexus more persistent than paraflexus or metaflexus; metaflexus extremely weak, metafossette lost in initial stage of wear; mesofossette deep, strongly curved posteriorly, sometimes connecting with metafossette in slightly worn teeth.

Mandible (Fig. 4, *a-g*).—Heavy, deep, short, and wide, much as in *Dinomys*; symphysis long, broad, level of anterior margin above alveolar border of cheek teeth, posteroventral end with transverse sulcus for reception of transversus mandibularis muscle; diastema short, dorsal surface gently curved back to $P_{\overline{4}}$, labial face rounded, medial face concave; mental foramen small, round to ovoid, usually single, occasionally double; anteroventral margin of rami with distinct digastric crest as in *Dasyprocta*; mylohyoid line not distinct, lingual surface slightly rugose for reception

of mylohyoideus; ventral margin of rami follow line of incisors; alveolar surfaces of rami slope ventrolingually; alveolar border wide, much as in *Dinomys*, teeth firmly set; angle originates below P^4; masseteric crest elongate, sloping, larger than in *Dasyprocta*, smaller than in *Neoreomys*; angular process distorted outward, posterior part deflected somewhat lingual; masseteric fossa shallow, smooth, extends for-
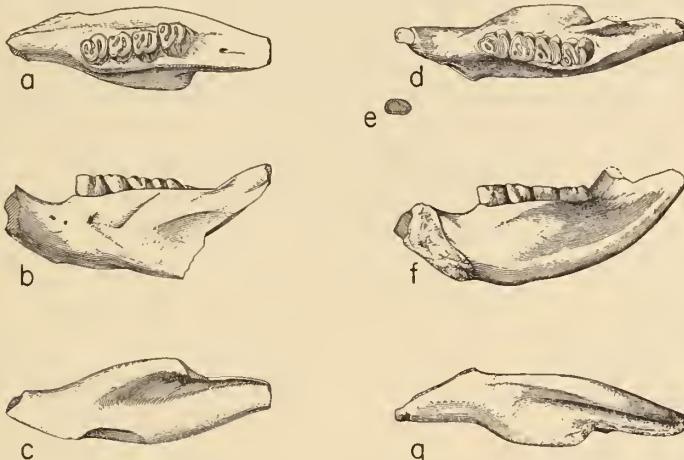
Fig. 4. *Scleromys schürmanni* Stehlin, La Venta area: *a-c*, left mandibular ramus, U.C.M.P. no. 38987, loc. V-4522, Unit Below Fish Bed; *a*, occlusal view; *b*, labial view; *c*, ventral view: *d-g*, right mandibular ramus, U.C.M.P. no. 37931, loc. V-4534, Quebrada Tatacoa locality; *d*, occlusal view; *e*, cross-section of incisor; *f*, lingual view; *g*, ventral view; all drawings × 1.
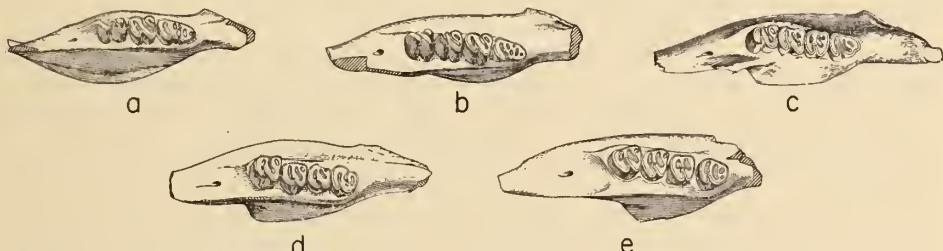
Fig. 5. *Scleromys schürmanni* Stehlin, La Venta area: series of mandibular rami showing eruption of $M_{\bar{3}}$, progressive wear in dental series, and posterior shift of inferior dental foramen; *a*, juvenile with $DP_{\bar{4}}$, $M_{\bar{1}}$, and newly erupted $M_{\bar{2}}$, U.C.M.P. no. 39902, loc. V-4536; *b*, juvenile with $DP_{\bar{4}}$, $M_{\bar{1}}$, $M_{\bar{2}}$, and newly erupted $M_{\bar{3}}$, U.C.M.P. no. 38974, loc. V-4521; *c*, young adult with $P_{\bar{4}}$, $M_{\bar{1}}$, $M_{\bar{2}}$, and slightly worn $M_{\bar{3}}$, U.C.M.P. no. 37931, loc. V-4534; *d*, adult with moderately worn $M_{\bar{3}}$, U.C.M.P. no. 38987, loc. V-4522 (specimen drawn in reverse for clarity of purpose in this figure); *e*, old adult with well-worn $M_{\bar{3}}$, U.C.M.P. no. 40585, loc. V-4529; all drawings × 1.

ward to anterior face of $M_{\bar{1}}$, ventral crest distinct, dorsal crest insignificant; coronoid process low, triangular, slightly distorted outward; inferior dental foramen posterior to $M_{\bar{3}}$, lingual to coronoid process, labial to inferior pterygoid crest, continued onto condyloid process as groove; inferior pterygoid crest small; inferior pterygoid fossa extremely large, deep, extending anteriorly to area ventral to M^1, delimited ventrally by strong medial crest of angular inflection, narrow posteriorly.

Lower dentition (Fig. 5, *a-e*).—Cheek-tooth series slope anterolingually; tooth pattern as in uppers but reversed; $M_{\bar{3}}$ largest tooth in series.

Incisor extremely long, base in conyloid process, somewhat similar to *Dasyprocta*;

enamel face essentially flat, extends more than halfway onto slightly convex lateral surface, and one-fourth way onto flat internal face.

$P_{\overline{4}}$ erupts after $M_{\overline{3}}$; anterior moiety elongate, ovoid, posterolingual part more angulate; hypoflexid on posterolabial part of crown, slightly curved transversely, hypostriid extends to basal one-fourth of tooth; paraflexid, metaflexid, and corresponding striids distinguishable only in unworn teeth; mesoflexid long, curved anterolabially, tooth half worn before development of mesofossettid; parafossettid small, usually transversely ovoid, sometimes connected to labial part of mesofossettid; metafossettid develops only in advanced stages of wear; hypofossettid forms in extreme stage of wear.

MEASUREMENTS OF LOWER DENTITION

Measurements	U.C.M.P. No. 38987
$P_{\overline{4}}$-$M_{\overline{3}}$, alveolar length	14.6
$P_{\overline{4}}$-$M_{\overline{3}}$, occlusal length	13.5
$P_{\overline{4}}$, anteroposterior diameter	3.4
$P_{\overline{4}}$, transverse diameter	3.4
$M_{\overline{1}}$, anteroposterior diameter	3.1
$M_{\overline{1}}$, transverse diameter	3.3
$M_{\overline{2}}$, anteroposterior diameter	3.3
$M_{\overline{2}}$, transverse diameter	3.4
$M_{\overline{3}}$, anteroposterior diameter	3.7
$M_{\overline{3}}$, transverse diameter	3.5
Depth of mandible below $P_{\overline{4}}$ (lingual portion)	9.1±
Depth of mandible below $M_{\overline{3}}$ (lingual portion)	7.6±

$M_{\overline{1}}$ and $M_{\overline{2}}$ differ from $P_{\overline{4}}$ in proportions and general outline; anterolingual moiety angulate, posterolabial moiety curved; parastriid not developed; mesostriid of $M_{\overline{1}}$ longer than metastriid; mesostriid and metastriid of $M_{\overline{2}}$ subequal; parafossettid of $M_{\overline{1}}$ and $M_{\overline{2}}$ small, ovoid, disappears in heavily worn teeth; mesofossettid persistent, directed anterolabially with slight S curve; metafossettid isolated soon after mesofossettid; hypoflexid directed posterolingually isolated as hypofossettid in advanced stages of wear; $M_{\overline{2}}$ slightly larger than $M_{\overline{1}}$; hypoflexid of $M_{\overline{1}}$ situated more anteriorly than on $M_{\overline{2}}$.

$M_{\overline{3}}$ with anterolingual border nearly square; anterior moiety triangular, posterior moiety crescentic; length of metastriid and mesostriid variable, mesostriid usually longer than metastriid, occasionally metastriid longer; hypoflexid as in $M_{\overline{2}}$; other characters as in $M_{\overline{1}}$ and $M_{\overline{2}}$.

Deciduous dentition.—$DP_{\overline{4}}^{4}$ only deciduous teeth; $DP_{\overline{4}}$ shorter crowned than permanent premolar, distinctly rooted, base somewhat constricted anteroposteriorly, occlusal pattern distinct, hypostriid long, extends to basal one-third of tooth; metastriid equal to, or shorter than, mesostriid, mesoflexid persistent, carries across crown, continues on labial side of tooth as accessory striid; parastriid shorter than mesostriid or metastriid; parafossettid continues as short accessory striid on anterolabial angle of tooth; hypoflexid directed sharply posterolingually, anteroposterior diameter of $DP_{\overline{4}}$, at base of hypostriid, 4.4 mm., transverse diameter, 2.5 mm.

Postcranial skeleton.—Only fragmentary parts of one young individual (U.C.M.P. no. 39916) preserved, with exception of proximal part of adult femur (U.C.M.P. no. 40514).

Pelvis.—Acetabular part of right ischium; acetabulum deep, incisura acetabuli open as in *Dinomys*; ischial spine greatly reduced, evident as slight elevation of dorsal ischial border; lesser ischial notch shallow; ischial obturator border smooth; obturator foramen more elongate anteroposteriorly than in *Echimys*; inner surface flattened, no inflection of dorsal margin above acetabulum. Acetabular part of left ilium; acetabular border with elevated rim; lateral face of ilium with moderately developed tuberosity anterior to acetabulum; auricular border with well-developed posterior-inferior spine; great sciatic notch prominent, much as in *Dinomys*.

Femur.—General appearance somewhat similar to that of *Lagidium*; greater trochanter extends above head; posterior intertrochanteric ridge smooth, slightly

MEASUREMENTS OF FEMUR

Measurements	U.C.M.P. No. 40514
Anteroposterior diameter of neck...	2.5
Dorsoventral diameter of neck...	3.4
Diameter of head...	5.4
Transverse diameter of shaft at lesser trochanter............................	4.9
Anteroposterior diameter of shaft at lesser trochanter........................	5.2

curved anteriorly; trochanteric fossa deep, narrow, bounded laterally by overlapping posterior intertrochanteric ridge; neck rounded ventrally, dorsal margin with small ridge extending from greater trochanter to head, much as in *Echimys*; head well-rounded, pit for ligamentum teres well-rounded, deeper than in *Echmiys*, more as in *Lagidium*; lesser trochanter prominent, but small, rounded; lateroproximal surface of shaft marked by distinct linea aspera and elongate fossa extending distally from outer surface of greater trochanter, much as in *Cuniculus* and *Echimys*; shaft apparently straight; internal condyle more prominent than in *Echimys*, articular surface flattened laterally, internal tuberosity smooth; intercondyloid fossa much wider than in *Echimys*, margins not definitely outlined, patellar groove not as elongate anteroposteriorly as in *Echimys* or *Cuniculus*; external condyle similar to that in *Lagidium* but not extending as far ventrally; laterodistal surface of shaft marked by small, shallow pit for tendon of gastrocnemius muscle, pit more prominent than in *Echimys* or *Chinchilla*, not so distinct as in *Lagidium*.

Tibia.—Left tibia lacking articular epiphyseal ends; shaft straight, subtriangular in cross-section, anterior proximal surface produced into sharp crest, internal side of crest flattened, external face strongly concave; area distal to external tuberosity developed as sharply defined crest extending to surface for fibula below; posterior surface of proximal end deeply concave; distal end more rounded than shaft, much as in *Lagidium*, anterior and internal faces flattened, external surface rounded. Total length not known.

Calcaneum (Fig. 6, *a-c*).—Similar to *Lagidium*; elongate distally to astragalar face, compressed transversely; astragalar facet as wide as high, oblique, convexo-

TABLE 1
Comparative Measurements of Scleromys Species

Dentition	U.C.M.P. No. 39987	U.C.M.P. No. 38988	Scleromys schürmanni[a]	A.M.N.H. No. 9304 S. angustus[b]	Scleromys angustus[c]	Scleromys osbornianus[d]	U.C.M.P. No. 39931
Upper							
Upper dentition length	35.5	39.0	....	44.0	....	....	....
Palatal breadth (between P^4)	4.2	4.4	....	6.0	....	....	....
Palatal breadth (between M^3)	6.9	7.6	....	12.0	....	....	....
P^4-M^3 occlusal length	13.1	13.6	13.7±	18.0	16.5±	18.0±	13.2
I, anteroposterior diameter	4.1	4.2	....	4.3±	....	....	....
I, transverse diameter	2.2	2.4	....	4.0±	....	4.0±	....
P^4, anteroposterior diameter	3.4	3.5	3.5±	5.0±	....	....	3.5
P^4, transverse diameter	3.2	3.4	3.8±	4.3±	....	....	3.4
M^1, anteroposterior diameter	3.0	3.2	3.0±	4.8±	5.0±	....	2.9
M^1, transverse diameter	3.6	3.7	4.0±	4.5±	6.0±	....	3.6
M^2, anteroposterior diameter	3.3	3.4	3.4±	4.3±	....	....	3.2
M^2, transverse diameter	3.3	3.7	4.4±	4.7±	....	....	3.8
M^3, anteroposterior diameter	3.4	3.5	3.8±	4.2±	....	....	3.6
M^3, transverse diameter	3.2	3.4	3.5±	4.1±	....	....	3.2
Lower							
P_4-M_3, occlusal length	14.6	....	....	20.0	....	22.0±	....

[a] Taken from Stehlin (1940b).
[b] Taken from Scott (1950b).
[c] Taken from Ameghino; *Enumeracion sistemat.*, etc., 1887, p. 11.
[d] Taken from Ameghino; *Enum. Synopt. des mamm. Foss. de Patagonia*, 1894, p. 69.

concave dorsoventrally, convex obliquely; sustentacular facet prominent, wide, slightly concave dorsoventrally; distal face rugose, pierced by large nutrient foramen; peroneal tubercle small, not grooved; distomedial cuboidal facet with obliquely convex face, anterior part wide, pinched posteriorly; lateral face of bone smooth; flattened, posterior border straight; internal face above astragalar facet concave dorsoventrally, flat anteroposteriorly; posterodistal surface with sharply defined groove for tendon of flexor digitalis longus muscle; anterior face above astragalar facet concave, dorsoventrally straight distally to astragalar facet.

Astragalus (Fig. 6, *d-f*).—General appearance as in *Lagidium*; calcanear facet wide, triangular, obliquely concave, dorsoventrally concavo-convex; sustentacular facet separated from calcanear facet by deep, oblique groove for tendon of flexor hallucis longus muscle; sustentacular facet long, slightly convex, extends from in-
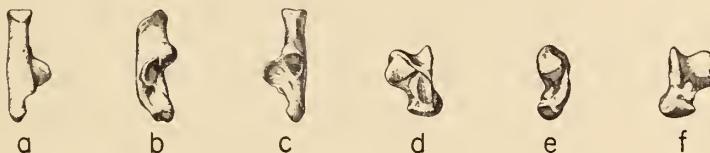
Fig. 6. *Scleromys schürmanni* Stehlin, U.C.M.P. no. 39916, loc. V-4523, Fish Bed: *a-c*, left calcaneum; *a*, posterior view, *b*, medial view, *c*, anterior view: *d-f*, left astragalus; *d*, posterior view, *e*, lateral view, anterior view; all drawings × 1.

ternal condyle to head, internal margin of facet straight, lateral border convex, widened distally; internal condyle with sharp rim and steep wall; external condyle spread laterally; anterior face with deep concavity at base of trochlea for origin of extensor brevis digitorum muscle; head and neck sharply divergent (15 degrees) from axis of condyles; transverse axis of head parallel with transverse axis of condyles; navicular facet well-rounded, broad internally, continued onto internal face of neck as facet for accessory sesmoid bone.

Comparisons.—Certain rodent specimens in the La Venta fauna and from Carmen de Apicalá compare closely with *Scleromys schürmanni* described by Stehlin (1940в). Specific measurements of the dental series are not given in his description; however, the published figure is to scale, and approximate measurements were obtained (see table 1).

Two species from Argentina and one from Colombia are referable to Ameghino's genus *Scleromys*, and another is described in this report. The importance of the criteria for generic and specific distinctions in this group is probably overrated when one considers the inadequacy of the samples of each species. The Santa Cruz species, *S. angustus* Ameghino and *S. osbornianus* Ameghino, are not common in that fauna. *S. schürmanni* from Carmen de Apicalá was described from a fragmentary left maxillary with P⁴ and M³ in place. In view of the fact that the affinities of the genus and its species are rather obscure, an attempt has been made to evaluate the genus. The type materials were not available to me. From appraisal of the published descriptions (Ameghino, 1887, 1894; Scott, 1905в; Stehlin, 1940в; Stehlin and Schaub, 1951), the following conclusions seem significant.

Scleromys angustus and *S. osbornianus* are distinct from *S. schürmanni* in: size (25 and 30 per cent larger), more anterior position of internal nares.

S. angustus and *S. osbornianus* resemble *S. schürmanni* as follows: broad, flattened parietal region with no development of a sagittal crest; wide, regularly curved internal nares, without median spine; convex "crepe-like" enamel surface on incisors; similar dental pattern on cheek teeth, ovoid P$\frac{4}{}$ and M$\frac{2}{}$, increasing size from P$\frac{4}{}$ to M$\frac{2}{}$ with M$\frac{3}{}$ equal to P$\frac{4}{}$ in size, isolation of paraflexus from hypoflexus in early stage of wear, elongate hypostria, relatively superficial parastria and mesostria, and minute metastria; ovoid P$_{\overline{4}}$, increasing size from M$_{\overline{1}}$ to M$_{\overline{3}}$, angular outline on lower molars; early isolation of metaflexid from hypoflexid with development of metafossettid.

Neoreomys from the Lower Miocene, Santa Cruz beds of Argentina has been considered by Ameghino (1887) and Scott (1905B) to be closely allied to *Scleromys*. *Neoreomys* shows the following distinctions: much larger size; less flattened cranial roof; posteriorly restricted parietals with development of distinct sagittal crest; larger, more rounded bullae; larger, more lengthened paraoccipital processes; shorter frontals with distinct superior orbital notch; wider, more convex nasal; shorter rostrum; much deeper rostral masseteric fossa; greatly expanded lacrymal that meets jugal on zygomatic plate; presence of large accessory opening of lacrymal duct anterior to infraorbital foramen; absence of special canal in infraorbital foramen for transmission of nerves; shorter, more rounded orbital region; prominently developed postorbital process; more angular internal nares with median spine and more anteriorly placed palatal border (between posterior moieties of M^2); greater anterior convergence of palate; larger posterior palatine foramen; distinct dental pattern, broader hypoflexus; more gently curved upper incisor (base above M^2); slightly grooved, more flattened enamel face; shorter lower incisor (base below M^3); higher-crested coronoid process; shorter, less excavated inferior pterygoid fossa.

Generic similarities between these two genera are difficult to find. Apparently both Ameghino and Scott were influenced by the superficial similarity of the teeth. The materials known are fragmentary. Scott (1950B, p. 401) states: "not even a well preserved skull has yet been found and the skeleton is entirely unknown." With such poor material, no broad conclusions can be drawn on the relationships of this form. Nevertheless, Scott (1905B, p. 402) writes: "From all the known material, it seems evident that *Scleromys* is closely allied to *Neoreomys*."

Dinomys differs from *Scleromys schürmanni* in: much larger size; relatively shorter diastema; broader, more flattened incisors; more posterior base on upper incisor (above M^1); more rectangular rostral masseteric fossa; more convergent tooth rows; relatively larger posterior palatine foramen; more distinct palatine grooves separated by high median ridge; more triangular internal nares with median notch; extreme hypsodonty and lophodonty in cheek teeth; greater reduction of coronoid process; relatively shorter, wider inferior pterygoid fossa; presence of M$_{\overline{2}}$ as largest tooth in lower series.

Dinomys resembles *S. schürmanni* in the following: broad, heavy skull; depressed parietals; distinct temporal crest but no sagittal crest; long frontals; long, anteriorly expanding nasals; rectangular premaxillary spur extending back to frontal between maxillary and nasal; enlarged incisive foramen with lateral ridges extending back to P$\frac{4}{}$ alveoli; furrow in infraorbital foramen for transmission of nerves; large lacrymal; no accessory lacrymal opening on rostrum; elongate orbital region; blunt postorbital process; expanded squamosal with dorsal margin extending over tem-

poral crest, posterior spur extending back to mastoid between periotic and parietal; combined foramen lacerum anterius and foramen rotundum; greatly enlarged alisphenoid canal; broad mesopterygoid fossa; large pterygoid wings extending to bullae; moderately expanded auditory bullae; presence of enlarged ventral opening to external auditory meatus; short, blunt paraoccipital process; low, ovoid foramen magnum; wide, flat occipital condyles; wide supraoccipitals extending onto dorsal surface of skull; heavy lamboidal crest; short massive mandible with heavy symphysis; small masseteric crest; flattened masseteric fossa; no dorsal crest; extremely long lower incisor (base well behind $M_{\bar{3}}$).

Echimys from Neotropical America is different from *Scleromys* in: much smaller size; greatly inflated auditory bullae; larger, more rounded external auditory meatus; enlarged mastoid and paraoccipital processes; more rounded foramen magnum with dorsoventrally oriented occipital condyles; distinctly V-shaped internal nares; smaller lacrymal; absence of special canal in infraorbital foramen for transmission of nerves; complete loss of postorbital process; shorter diastema; narrower, more convex upper incisors with more posteriorly situated base (above P^4); parallel cheek-tooth rows; less hypsodont cheek teeth; deeply recessed mandibular masseteric fossa; relatively large, crested coronoid process; presence of distinct spur on lingual face of angular process; proportionally shorter lower incisors (base below $M_{\bar{3}}$).

Echimys shows resemblance to *Scleromys* in: elongate orbital region, lack of accessory opening for lacrymal on lateral face of rostrum; broadly flattened parietal region with no development of sagittal crest; depressed, long, broad frontals with relatively little interorbital constriction; no development of superior orbital notch; narrow, elongate nasals extending beyond anterior face of incisors; moderately elongated incisive foramen with premaxillo-maxillary suture meeting at posterior border.

Cercomys from Brazil differs as follows: larger auditory bullae; larger, more rounded, tubular external auditory meatus; lengthened paraoccipital process; quadrilaterally shaped foramen magnum with vertically oriented occipital condyles; V-shaped internal nares; much smaller lacrymal that forms distinct but small spur on anterodorsal margin of orbit; proportionally shorter diastema; expression of incisor on lateral face of rostrum as distinct ridge; parallel tooth rows; comparatively narrow palate with median ridge; excessively enlarged incisive foramen with premaxillo-maxillary suture meeting near anterior border; brachyodont cheek teeth with simple ovoid crown; excessively recessed mandibular masseteric fossa; narrow, high, spined coronoid process; shorter lower incisor (base below $M_{\bar{3}}$); development of ventral, flat plate on angular process.

Cercomys displays similarity in: development of distinct canal in infraorbital foramen for passage of nerves; lack of accessory opening for lacrymal canal on rostrum; flattened cranial roof with depressed frontals, flattened parietals, no development of sagittal crest, presence of small, blunt postorbital process; proportionally long orbital region; anterior position of dorsal zygomatic root.

Capromys from Cuba and the Isle of Pines is distinguished by: prominent bullae, no accessory opening below external auditory meatus; usually lengthened paraoccipital processes; longer, well-ridged parietals with tendency toward development of sagittal crest; relatively shorter, more rounded orbital area; no development of canal for nerve transmission in infraorbital foramen; more arched rostrum; rela-

tively longer, wider, transversely more convex nasals that do not extend beyond anterior face of incisors; more posterior ventral and dorsal zygomatic roots (ventral over P^4, dorsal over M^1); large posterior palatine foramen with anterior continuation as distinct furrows; more convergent tooth rows, distinctly narrower, less curved upper incisors (base over M^1); evergrowing cheek teeth with two outer and one inner flexi; stria extending to base of teeth; presence of cement in flexi; distinctly expanded ventral angular crest on mandible, presence of lingual spur on inflection of angular process; more distinct inferior pterygoid crest; smaller, less excavated inferior pterygoid fossa; larger, wider sulcus for reception of transversus mandibularis muscle, noticeably shorter lower incisor (base below $M_{\bar{3}}$).

Capromys agrees with *Scleromys* in: size and position of lacrymal; lack of accessory opening for lacrymal duct on rostrum; widened, smooth internal nares, presence of small, rather blunt postorbital process.

Dasyprocta is particularly distinct from *Scleromys* in the following: relatively narrower skull; longer, more distinctly ridged parietals with well-developed sagittal crest; comparatively shorter frontals with constricted interorbital surface; development of sharp superior orbital notch; noticeably longer, anteriorly wider, transversely convex nasals; smaller rostral masseteric fossa; greatly enlarged lacrymal that extends onto zygomatic plate and nearly contacts with jugal; more posteriorly placed dorsal zygomatic root (above M^1); presence of large accessory lacrymal opening above ventral zygomatic root; absence of special canal in infraorbital foramen for transmission of nerves; markedly smaller incisive foramen; absence of bony ridges running from incisive foramen to P^4; lack of anterior constriction of palate; more anterior position of internal nares (between posterior moieties of M^2); distinctly smaller, shorter orbital region; enlarged, sharp, ventrally projected postorbital process; somewhat lengthened paraoccipital processes; relatively narrower upper incisors; presence of bulbous area on maxillaries over base of incisors; parallel tooth rows; more complicated tooth pattern; greater degree of hypsodonty; slightly more anteriorly situated coronoid process.

Dasyprocta has the following characters in common with *Scleromys*: rounded, wide internal nares; similar configuration and size of auditory bullae; ventrally notched external auditory meatus; similar development of mastoid process; backward extension of lower incisors (base well behind $M_{\bar{3}}$); moderately developed coronoid process with flattened dorsal crest; similar degree of excavation of inferior pterygoid fossa; comparable development of inferior pterygoid crest; shallow, comparatively smooth mandibular masseteric fossa; relatively small, narrow inferior angular crest.

Myocastor is distinguished by: relatively narrower skull; longer, narrower parietals, with distinct parasagittal ridges; shorter, relatively narrower frontals; comparatively longer, straighter nasals with greater transverse convexity; no projection of nasals anterior to enamel face of incisors; higher, shorter, narrower rostrum; enlarged incisive foramen with premaxillo-maxillary suture meeting at midpoint of labial rim of foramen; lack of bony ridges lateral to incisive foramen; more posterior position of dorsal zygomatic root (above M^2); extremely small lacrymal; lack of special canal in infraorbital foramen for transmission of nerves; shorter, more rounded orbital region; distinctly smaller auditory bullae; somewhat tubular external auditory meatus with no ventral opening; extremely shortened basicranial axis;

greatly enlarged mastoid and paraoccipital processes; distinctly V-shaped internal nares with excessive lateral pinching of opening; relatively narrower palate with deeply furrowed midline; strongly convergent tooth rows (premolars almost meet along midline); greater degree of hyposodonty; proportionally larger teeth with more complicated occlusal pattern, more open flexi, presence of cement in flexi and fossettes; progressively larger size from P^4 to M^3; larger, more gently curved upper incisors (base above M^1) with external projection on lateral face of rostrum marking course of incisor; more massive lower jaw with distinctly shorter incisors (base below $M_{\overline{3}}$); smaller size and more anterior position of coronoid process (opposite anterior moiety of $M_{\overline{3}}$); shorter, less excavated inferior pterygoid fossa; greatly expanded inferior crest below masseteric fossa.

Myocaster is similar to *Scleromys* in: absence of accessory opening for lacrymal duct on rostrum; presence of small, blunt postorbital process.

Isolobodon from the Pleistocene of the West Indies displays the following distinctions: more curved cranial roof; posteriorly constricted parietal region; relatively smaller bullae without accessory opening below main body of external auditory meatus; comparatively shorter, wider frontals; longer, relatively larger nasal with greater transverse convexity; proportionally wider, more curved, shorter rostrum; greatly enlarged incisive foramen; more posteriorly placed dorsal zygomatic root (above M^1); smaller lacrymal; shorter, more rounded orbital region; greater constriction of palate between P^4; more anteriorly placed internal nares (anterior margin between posterior moieties of M^2); presence of median spine on rim of internal nares; enlarged mastoid and paraoccipital processes; less arched upper incisor with bulblike expansion on maxillary lateral to base (over M^1); strongly hypsodont cheek teeth, presence of cement in flexi; greater expansion of ventral crest of mandible; very slender, proportionally higher coronoid process; more distinct inferior pterygoid crest; shorter, less excavated inferior pterygoid fossa; shorter lower incisor (base under $M_{\overline{3}}$); relatively longer mandible.

Isolobodon is like *Scleromys* in: presence of incipient canal in infraorbital foramen for transmission of nerves; presence of small, blunt postorbital processes.

STATISTICAL ANALYSIS

I have referred the small *Scleromys* material from the La Venta fauna and Carmen de Apicalá to Ameghino's genus because of the marked similarity in shape of the cheek teeth and their enamel patterns. Assignment to Stehlin's species *S. schürmanni* is based on similarity in size and shape of the teeth and on the dental patterns. The most significant characters are in the ovoid outline of P^4 and M^3; in the slightly larger, more angular appearance of M^2; and in the pattern developed as the inflections isolate and become expressed as fossettes. Stehlin's (1940B) figure and the topotypes show that the specimens from La Venta and Carmen de Apicalá are within the same size range (see table 1).

It is unfortunate that the U.C.M.P. materials are represented by only three measurable upper cheek-tooth series. Nevertheless, greater statistical validity and a cross check have been possible because of the large number of mandibles with complete dentition in the La Venta fauna.

Before presenting the statistical data the sampling method will be explained. *S. schürmanni* is represented from near the base of the La Venta section, V-4530,
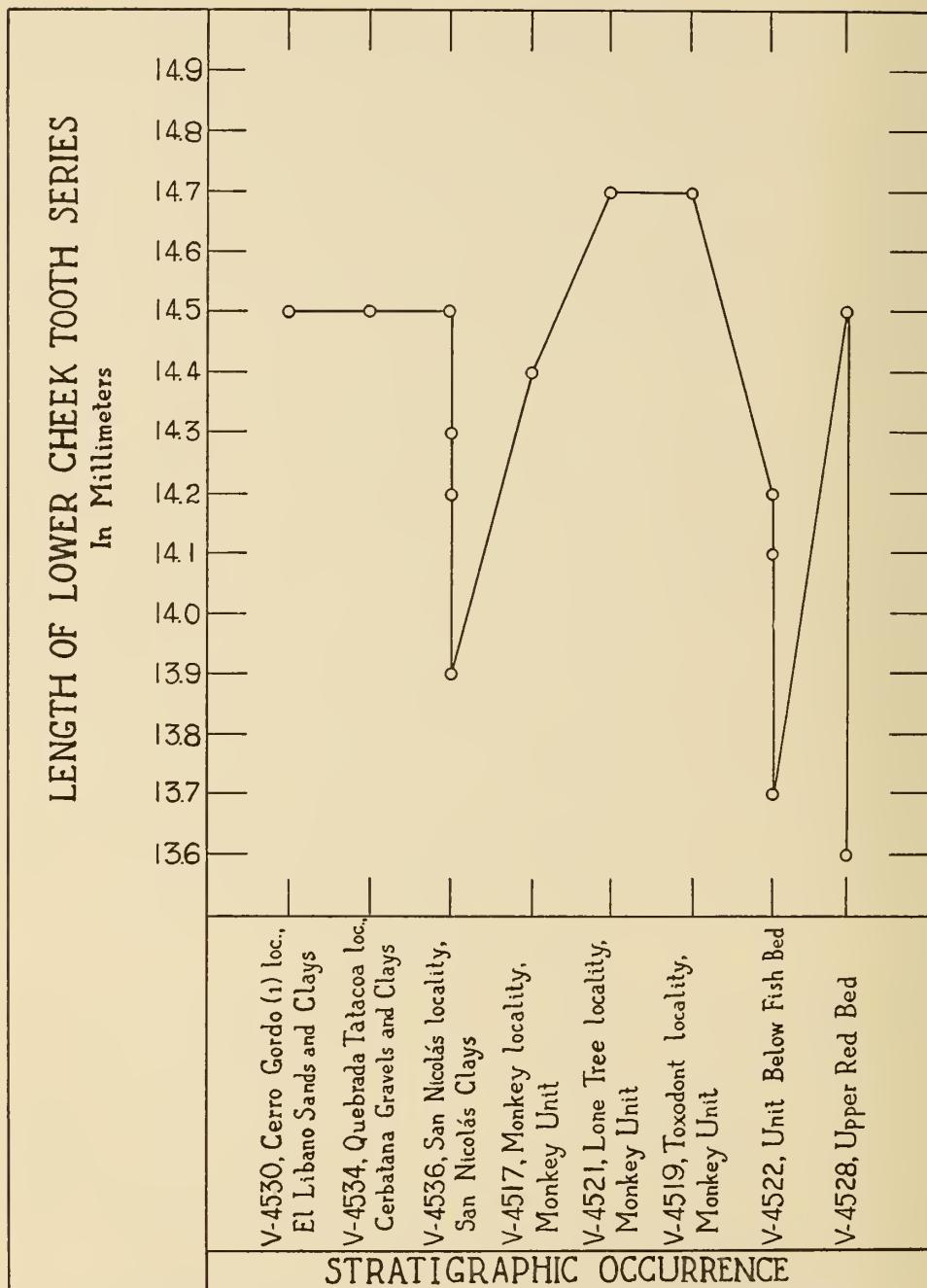
Fig. 7. *Scleromys schürmanni* Stehlin: scatter diagram of 14 mandibles showing that there is no correlation of size with stratigraphic occurrence.

within the El Libano Sands and Clays, to the top of the sequence, V-4529, the Las Mesitas locality. This includes a stratigraphic thickness of more than 705 meters. Specimens from the lower part of the section and those from the uppermost levels are morphologically indistinguishable.

As a preliminary test, a scatter diagram was made using all available mandibles upon which the length $P_{\bar{4}}$ to $M_{\bar{3}}$ could be determined. This measurement was plotted against stratigraphic occurrence (Fig. 7). The result indicates that there is no correlation between the length of $P_{\bar{4}}$ to $M_{\bar{3}}$ and position in the stratigraphic column. Specimens ranging from large to small occur at any stratigraphic level. As examples: in the San Nicolás locality, V-4536, there is a range from 13.9 mm. to 14.5 mm., and in the Upper Red Beds, V-4528, specimens range from 13.6 mm. to 14.5 mm. Stratigraphically these two localities are some 250 meters apart. If the measurements and stratigraphic occurrence of the three available upper cheek-tooth series are observed, it can be seen that—although a thickness of 100 meters separates the materials—no. 38987 from the Unit Below the Fish Bed, V-4522, and no. 39931 from the San Nicolás locality, V-4536, are essentially alike in P^4 to M^3 length, whereas no. 38988, also from V-4536, is of larger size. It is probable that there is no evidence for correlation of size to stratigraphic occurrence. What, then, should constitute a sample? If specimens from each locality were to be dealt with as single samples, would any significant differences be seen? Several tests of arithmetic means, standard deviations, and coefficients of variation were run, using the small-sample standard deviation formula (Simpson and Roe, 1939, p. 205) because of the small number of specimens. Measurement taken was the length of $P_{\bar{4}}$ to $M_{\bar{3}}$, measured on the longest occlusal length (see table 2).

These formulas were used:

$$M = \frac{\Sigma(X)}{N}$$ (Simpson and Roe, 1939, p. 86): where M = the mean (arithmetic only); Σ = result of adding all measurements; X = any given value of variate; N = number of observations made.

$$\sigma \text{ or S.D.} = \sqrt{\frac{\Sigma d^2}{N-1}}$$ (*Ibid.*, 1939, p. 205): where σ or S.D. = sigma or standard deviation; d^2 = deviations (from the mean) squared; N − 1 = number of observations minus one (1), a corrective factor for small samples.

C.V. = 100 S.D./M (Cazier and Bacon, 1949, p. 371): where C.V. = coefficient of variation.

These results were obtained:

STATISTICAL RESULTS

Sample	Locality	Number of specimens	Mean	S.D.	C.V.
1............	V-4536	4	14.20 ± .12	.245 ± .08	1.72 ± .61
2............	V-4522	3	14.00 ± .15	.265 ± .08	1.83 ± .74
3............	V-4528	2	14.05 ± .15	.205 ± .10	1.46 ± .73

It can readily be seen that in a quantitative analysis of this character *S. schürmanni* does not vary appreciably over the stratigraphic separation of 250 meters between V-4536 and V-4528. It may be assumed that no significant differences

TABLE 2

Tabulation of All Available Lower Jaws of Scleromys schürmanni in the U.C.M.P.

No. of specimen	Loc. no.	Description of spec.	Total length P_4-M_3	Ant.-post. dia. of incisor	Trans. dia. of incisor	Depth of mand. below P_4	Trans. dia. of P_4	Ant.-post. dia. of P_4
37931	V-4534	R. Mand.	14.5	3.5	1.9	10.0	3.2	4.0
39917	V-4517	R. Mand.	14.4	3.6	2.4	11.1	3.5	....
40491	V-4536	L. Mand.	14.3	3.5	2.1	8.9	3.2	3.9
39894	V-4519	R. Mand.	14.7	3.7	2.4	8.8	3.5	4.7
38356	......	R. Mand.	13.9	3.6	2.1	8.4	3.2	3.9
37929	V-4530	L. Mand.	14.5	3.5	2.1	9.4	2.9	4.0
40488	V-4536	R. Mand.	Young	3.5	2.2	9.3	D.P.*	D.P.
40493	V-4536	R. Mand.	14.5	....	....	....	3.5	4.3
39913	V-4527	L. Mand.	Young	2.7	1.6	7.3	D.P.	D.P.
40495	V-4522	R. Mand.	Young	3.1	1.8	9.1	D.P.	D.P.
40489	V-4536	R. Mand.	13.9	3.7	2.1	10.2	3.4	3.9
40490	V-4536	L. Mand.	Young	3.6	2.0	9.9	D.P.	D.P.
38974	V-4521	R. Mand.	14.7	3.5	2.0	11.2	3.7	4.2
40496	V-4522	R. Mand.	14.1	4.0	2.3	....	3.5	4.2
39902	V-4536	R. Mand.	Young	2.8	1.8	7.6	....	....
38986	V-4522	L. Mand.	14.2	3.8	2.3	10.3	3.5	4.2
38901	V-4528	R. Mand.	13.6	....	....	....	3.2	3.8
38902	V-4528	R. Mand.	14.5	3.4	2.1	....	2.9	3.8
40492	V-4536	L. Mand.	14.2	3.6	2.1	10.2	2.9	3.6
38987	V-4522	L. Mand.	13.7	3.6	2.0	9.6	3.2	3.2

* D.P.—deciduous premolar.

would be found by treating each locality as a separate sample. Single locality samples would contain no more than four individuals, and in most cases one. In the use of very small samples, i.e., two, three, or four specimens, the degree of error multiplies, and in single-specimen samples the resultant values may lead to extremes of error in systematic designations; thus, samples based on one or few specimens are used only when there is no other alternative.

The following statistical analysis of *S. schürmanni* has been drawn from all available materials, regardless of stratigraphic position in the La Venta section. The analysis is not intended as a population study, and the samples used do not meet the definition of the term "population" as defined by Simpson and Roe (1939, p. 166). The object of this work is to determine variation in the species in the La Venta fauna, and to determine the probability of species relationship between the La Venta materials and the specimen described by Stehlin (1940b) from Carmen de Apicalá.

As has been mentioned before, there are only three upper dental series represented in the fauna. Values for these are given in table 1. By following the methods outlined these values were obtained: ($\pm$ = standard error: Cazier and Bacon, 1949, p. 372)

Sample A. Occlusal length of P^4 to M^3.

$$M. = 13.30 \pm .15$$
$$S.D. = .265 \pm .108$$
$$C.V. = 1.99 \pm .81$$

It is significant that even with the expected high standard error for mean, standard deviation, and coefficient of variation in small samples, the modified results are still exceptionally low.

In an analysis of mandibular tooth row length, fifteen specimens were available.[3] A complete analysis of measurements is given in table 2. Values obtained for the length $P_{\bar{4}}$ to $M_{\bar{3}}$ are:

Sample B. Occlusal length of $P_{\bar{4}}$ to $M_{\bar{3}}$.

$$M. = 14.27 \pm .09$$
$$S.D. = .35 \pm .06$$
$$C.V. = 2.45 \pm .44$$

If these analyses are valid, *S. schürmanni* is exceptional. Of the three values obtained in samples A and B, the coefficient of variation is most significant. The values 1.99 $\pm$ .81 and 2.45 $\pm$ .44 are considered very low. Simpson and Roe (1939, p. 123) state: "-5 or 6 are good average values. Much lower values usually indicate that the sample was not adequate to show the variability." In paleontological studies, samples of 15 specimens are the exception, and are usually considered adequate. Simpson and Roe state further (1939, p. 123) that: "Much higher values usually indicate that the sample was not pure, for instance, that it included animals of decidedly different age or of different minor taxonomic divisions." The values in both samples A and B are low, even though the animals included are stratigraphically as much as 540 meters apart. In addition, the individuals are morphologically indistinguishable. The statistical data are probably adequate and reasonably uni-

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[3] It may again be noted that these fifteen individuals represent all the available material from the La Venta section and are dealt with as one sample.
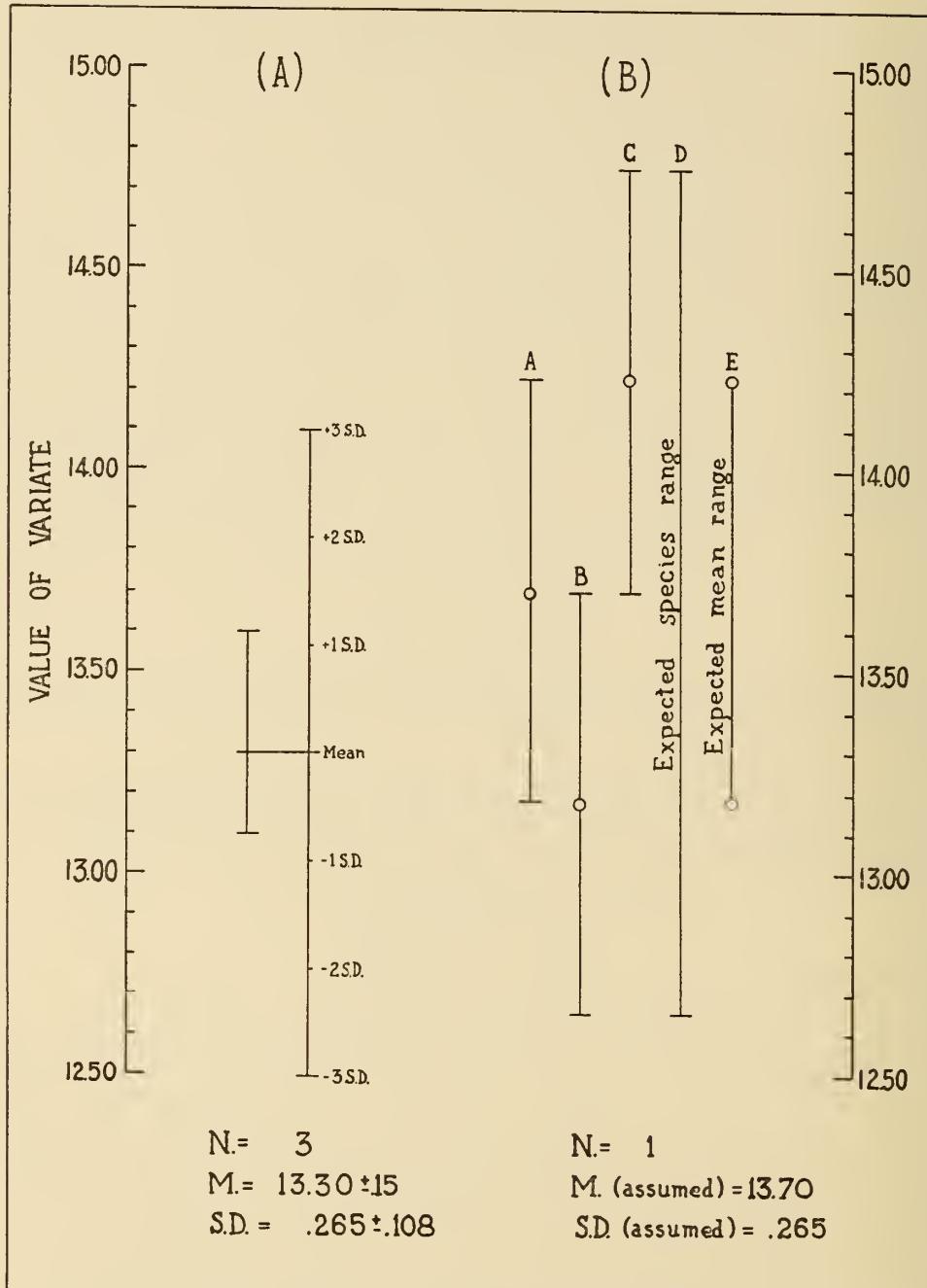
Fig. 8. *Scleromys schürmanni* Stehlin: graphic comparison of the holotype with a three-specimen sample from the La Venta area: (A) the observed range and expected range of the species based on data from three-specimen sample and Table II; (B) the expected range and mean range of the holotype of *Scleromys schürmanni* Stehlin.

fied. The low values of standard deviation from the mean and coefficient of variation represent in a clear and useful way the inherent low variability of *S. schürmanni*.

Figures 8 and 9 are graphic analyses of data obtained in samples A and B. Figure 8 is a graph of the data obtained from sample A. Although they represent a small sample, the data are the only quantitative values that can be compared directly
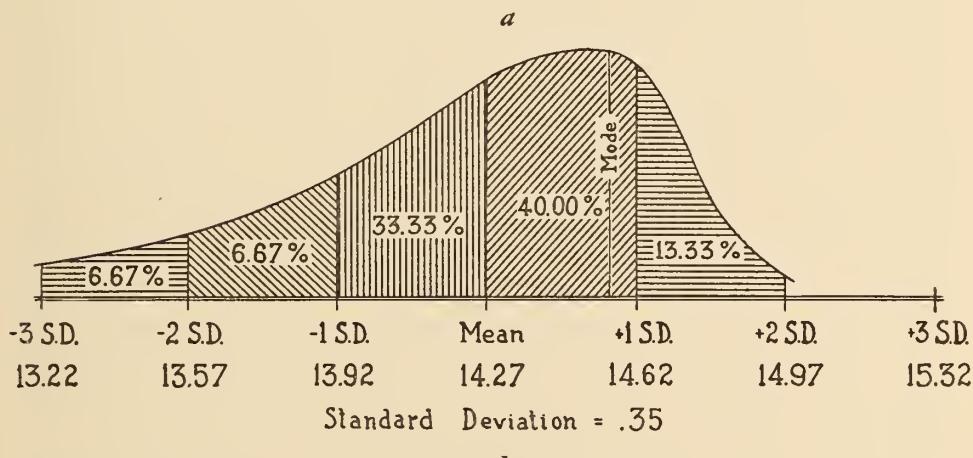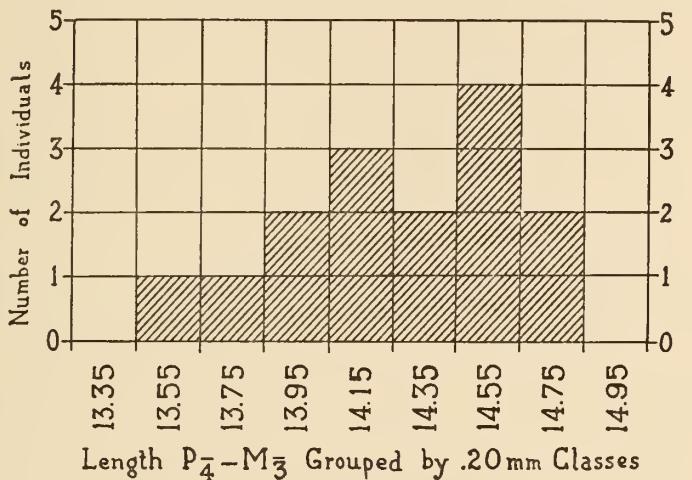
Fig. 9. *Scleromys schürmanni* Stehlin: *a*, histogram of length $P_{\overline{4}}$-$M_{\overline{3}}$. The mean is 14.27 ± .09; *b*, combination normal probability curve and area of normal curve based on data from sample B showing negative skewness of curve and percentage of individuals in areas of curve.

to the type of *S. schürmanni*. The calibrated vertical line in the figure is the expected range of ±3 S.D. from the mean of the length P^4 to M^3, wherein at least 95 out of every 100 specimens of the species would be found. The solid vertical line shows the observed range, and the short horizontal line identifies the mean for sample A.

Figure 8(B) is a graphic analysis of the type specimen of *S. schürmanni* (Cazier and Bacon, 1949, pp. 366–367). The unit value for P^4 to M^3 in the type is 13.70 mm. In vertical line A, this value is assumed to be the mean, and -2 S.D. and $+2$ S.D.

from the mean give an estimated range from 13.17 to 14.23 mm. If the type specimen is moved to a point -2 S.D. from the original assumed mean (line B), the range then becomes 12.64 to 13.70 mm. If the same is done for $+2$ S.D. (line C), the minimum expected range would be 13.70 mm. and the maximum 14.76 mm. The expected species range limits of from 12.64 to 14.76 mm., or ± 4 S.D., are derived and shown in line D. It would then be expected that 95 out of every 100 specimens observed would fall in these limits. Line E represents the expected mean range if additional specimens were found.

If the plotted ranges of D (the expected species range) and E (the expected mean range) are compared with the expected range in sample A, it can be seen that there is considerable overlap. The ± 3 S.D. range in sample A lies almost completely within the range of D, and the calculated mean in sample A lies within the expected mean range as plotted on E.

The histogram (Fig. 9, a) shows the length and frequency of lower tooth rows in sample B. Figure 9, b, presents the same results plotted on a combination normal probability curve and area of normal curve. The result is a negatively skewed curve. Nevertheless the mode lies within one standard deviation of the mean, indicating that the distribution is probably valid and usable in estimating the variability of tooth-row length in the species. By plotting of areas of ± 1 S.D., ± 2 S.D., and ± 3 S.D. on the curve, it becomes the expression of the species from which the sample was taken. Usually (see Cazier and Bacon, 1949, p. 370) 68.27 per cent of the total observations are expected to fall within the limits of ± 1 S.D. from the mean. In sample B, 73.33 per cent of the individuals fall in that limit. For the ± 2 S.D. area, 95.45 per cent of the observations are expected. In the present sample, 93.33 per cent are in that limit. In ± 3 S.D. from the mean, 99.73 per cent are expected. The present materials show 100.00 per cent represented. The skewness of the curve and the empty area between $+2$ S.D. and $+3$ S.D. may indicate that the species has an actual range, in the length $P_{\overline{4}}$ to $M_{\overline{3}}$, greater than is represented in sample B.

From these data a fairly accurate estimate can be made of the actual limits of dental series variability in the species. From figure 8, it may be estimated that the maximum limit in the length of P^4 to M^2 is about 14.76 mm. and the minimum around 12.64 mm. Since sample A falls well within these limits, it may be concluded that the *Scleromys* material from La Venta is statistically assignable to *S. schürmanni*. The maximum limit of $P_{\overline{4}}$ to $M_{\overline{3}}$ length is about 15.32 mm. and the minimum limit around 13.22 mm. From the maximum and minimum limits of range, it can be seen that in the upper cheek-tooth series length there is a variability of only 2.10 mm. and in the lowers only 2.12 mm. Thus it may be concluded, both from the statistical results and from morphological evidence, that *Scleromys schürmanni* is a genetically stable, homogeneous species.

DISCUSSION

Ameghino (1887 and 1894), Scott (1905B), Stehlin (1940B), and Stehlin and Schaub (1951) have presented certain erroneous conclusions concerning the dental characters of *Scleromys*. Some of the confusion has been due to a lack of good material from which an understanding of stages of cheek-tooth wear could be gained. In the La Venta materials almost all stages of wear are represented, and a critical analysis of the changing pattern could be made.

In Ameghino's (1887, p. 11) description of *S. angustus*, the upper molars are said to have one deep internal inflection and two shallow external inflections. To the lowers he attributes one deep external fold and one internal fold that soon isolates as a fossette.

Scott (1905B, p. 401) states that the upper cheek teeth are divided into two prisms by a deep lingual fold extending obliquely across the crown, the outer part of which, in advanced stages of wear, divides to form an external fossette. On the posterior prism he identifies only one labial fold that in early stages of wear becomes separated as a fossette. To the lower series he attributes one deep labial inflection and one smaller lingual inflection.

The materials referred to the genus *Scleromys* in this paper agree fairly well with Ameghino's original characterization of the upper molars in *S. angustus*, except that he does not account for a third labial inflection, the metaflexus. In plate LXV, figure 13, Scott (1905B) indicates only a hypoflexus and mesoflexus plus a parafossette on M^1; there are no metafossettes on the teeth as drawn. Scott apparently did not realize that the paraflexus and hypoflexus were continuous in unworn teeth. The presence of a parafossette on M^1 tends to indicate the existence of the paraflexus in unworn teeth.

The metafossette is apparently more persistent in *S. schürmanni*. In M^1 and M^2 it is not lost until the teeth are worn down to the base of the hypostria. In P^4 and M^3 it is lost somewhat earlier. If a metafossette was present in *S. angustus*, it was lost much earlier. Scott's figure indicates that the teeth are not excessively worn; nevertheless, no metafossette is shown on M^1 and M^2. Once the hypoflexus isolates in *S. schürmanni*, the teeth show only the hypofossette and parafossette anteriorly and the mesofossette posteriorly, a condition which agrees with Scott's observatious on *S. angustus* and *S. osbornianus*.

The description of *S. schürmanni* (Stehlin, 1940B) and the general description of the genus *Scleromys* (Stehlin and Schaub, 1951) are indeed incongruous. There is little agreement between Ameghino's and Scott's work concerning *S. angustus* and *S. osbornianus*, and Stehlin's characterization of the upper cheek teeth of *S. schürmanni* contradicts his published figure. By Stehlin's description, these teeth have one lingual inflection directed obliquely forward and four transversely directed labial inflections; however, his figure shows the same characteristic pattern seen in the La Venta materials. In their descriptions, Stehlin (1940B) and Stehlin and Schaub (1951) apparently used more inference than fact in a rather obvious effort to show relationship to the European theridomyids.

Ameghino and Scott characterize the lower teeth as having one external deep inflection and one smaller internal inflection. Here again, a lack of material showing various stages of wear probably led to erroneous conclusions. Scott figures the lower dentition of both *S. angustus* and *S. osbornianus* (1905B, p. 1, pl. LXV, Figs. 14, 15). In M_3 the hypoflexid carries across and is continuous with the metaflexid. The mesofossettid is large, and in beginning stages of wear would, no doubt, appear as a distinct mesoflexid, as it does in the late-erupting P_4 shown in the figure. The parafossettid seems to be linked with the mesofossettid, a condition occasionally seen in *S. schürmanni*; however, it seems that the parafossettid of *S. angustus* and *S. osbornianus* are somewhat weaker and wear away earlier than in *S. schürmanni*. Thus it can be seen that, in the lowers, the number of lingual inflections in *Scleromys*

is two, rather than one, or possibly three if the parafossettid began as an inflection in the unworn teeth. It may be concluded that the lower teeth are essentially like the uppers except that the pattern is reversed.

Distinction between primitive and advanced characters in *S. schürmanni* is difficult, as comparisons with *S. angustus* and *S. osbornianus* are meager. One character that could be primitive is the smaller size. This, however, is a rather weak point and not considered significant, as both large and small species are common in many genera of rodents. Other comparisons are restricted to the dentition, but here again most of them are questionable. From published data it cannot be estimated whether *S. schürmanni* shows a greater or lesser degree of hyposodonty. However, several characters of the dental pattern seem more advanced in *S. schürmanni*. The fossettes seem to extend farther into the body of the teeth; this is especially conspicuous in the metafossette of the upper teeth and the parafossettid on the lower teeth. Actual comparison with the Santa Cruz species is impossible, but the persistent fossettes of *S. schürmanni* are probably represented by somewhat longer stria on the sides of the teeth, particularly the hypoflexi and mesoflexi. This would seem to indicate a somewhat later age than Santacrucian for *S. schürmanni*.

Skeletal parts reveal little concerning the adaptive characters of *S. schürmanni*. There seem to be few specialized characters. The limbs are evidently normal in length, but rather slender. Unfortunately, neither hind nor front feet are known, but the cuboidal facet on the calcaneum and the navicular facet of the astragalus show similarity to living forms like *Lagidium*, in which there is a reduction of metatarsals I and V. Presence of this character would indicate adaptive specialization toward a digitigrade cursorial body form. It may be noted that none of the amphibious adaptations in the skeleton of *Myocastor* or of the fossorial specializations of *Ctenomys* is present in the limb of *S. schürmanni*.

Scleromys colombianus Fields, n. sp.
(Figs. 10–14)

Holotype.—Incomplete right lower jaw with broken incisor, P_4 to M_3 in place; U.C.M.P. no. 37927.

Paratype.—Fragment of left ventral zygomatic root of maxillary with unerupted P^4, M^1 to M^3 in place and right M^1, U.C.M.P. no. 40549.

Referred specimens.—Crushed rostral part of skull with upper incisors, U.C.M.P. no. 40497, loc. V-4522. Fragmentary palate with waterworn right P^4 and M^1, left P^4 to M^2, U.C.M.P. no. 38900, loc. V-4528. Incomplete right lower jaw with unerupted P_4, slightly worn M_1 and M_3, U.C.M.P. no. 39654, loc. V-4517. Incomplete left mandible with P_4 to M_3, U.C.M.P. no. 37994, loc. V-4522. Left mandible with M_1 to M_3 and isolated M^3 apparently from one individual, U.C.M.P. no. 38960, loc. V-4528. Fragment of both lower jaws with DP_4s, left maxillary fragment with DP^4, U.C.M.P. no. 40550, loc. V-4519. Nearly complete right tibia, left femur, and metatarsal III, fragment of metatarsal IV, glenoid part of right scapula, and other miscellaneous limb elements, U.C.M.P. no. 40487, loc. V-4536. Proximal end of right femur without head, U.C.M.P. no. 37918, loc. V-4518. Left calcaneum, U.C.M.P. no. 37951, loc. V-4520. Right astragalus and distal ends of right and left tibia, U.C.M.P. no. 40563, loc. V-4517. Left M_3, U.C.M.P. no. 40213, loc. V-4421. Left M_3, U.C.M.P. no. 37980, loc. V-4421.

Type locality.—Toxodont locality, Monkey Unit, vicinity of Villavieja, Department of Huila, Colombia, South America, U.C.M.P. loc. V-4519. (See note 2.)

Fauna.—La Venta.

Age.—Late Miocene.

Diagnosis.—Rostral part of skull elongate; rostral masseteric fossa shallow, anterior part some-

what squared, bounded by anterior and dorsal ridge; no accessory opening on maxillary for lacrymal duct; nasals straight, narrow; infraorbital foramen with ventral furrow for transmission of nerves; ventral root of zygomatic arch anterior to P^4; upper incisors strongly curved, not expressed on outer surface of maxillary, anterior face crepe-like, slightly convex; incisive foramen somewhat enlarged, evidently with bony ridges extending back to P^{4}s; tooth rows convergent anteriorly; posterior palatine foramen between M^{1}s, elongate, continued forward as shallow furrow; cheek teeth hypsodont, semi-rooted with three superficial inflections on labial side, one long anterior and one shorter posterior inflection on lingual side; M^2 largest in series; mandible heavy; angle distorted outward; inferior pterygoid fossa deep, narrow, elongate; mandibular masseteric fossa shallow, smooth; ventral mandibular crest smooth, rounded; masseteric crest not prominent; diastema short; coronoid process low, distorted outward; lower incisor extends into condyloid process; lower cheek teeth with one long labial inflection, three superficial lingual inflections with middle inflection longer than anterior, posterior inflection shorter than middle inflection on P$_{\overline{4}}$ to M$_{\overline{2}}$, equal to or longer than middle inflection on M$_{\overline{3}}$; M$_{\overline{3}}$ largest of lower molars; P$_{\overline{4}}$ with greatest anteroposterior diameter.
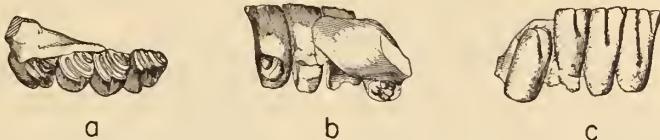
Fig. 10. *Scleromys colombianus* Fields, n. sp.; paratype, U.C.M.P. no. 40549, loc. V-4519, Toxodont locality: left upper cheek tooth series; *a*, occlusal view; *b*, labial view; *c*, lingual view; × 1.

DESCRIPTION

Cranium.—Not well represented; rostrum evidently shorter than in *Dasyprocta*; nasals long, narrow, slightly expanded anteriorly; premaxillary expanded dorsoventrally, dorsal spur extending back between nasal and maxillary as in *Dinomys*; lateral part of premaxillo-maxillary suture slightly serrate, directed slightly dorsoposteriorly, ventral part serrate with anteriorly bowed lobe to side of incisive foramen meeting lateral border of incisive foramen 3.0 mm. from anterior margin; maxillary wide, comparatively flat on lateral face of rostrum, forms broad ventral root of zygomatic plate; ventral surface of infraorbital foramen slightly furrowed for transmission of nerves, not as deep as in *Scleromys schürmanni*; rostral masseteric fossa shallow, somewhat squared anteriorly as in *Dinomys*, nearly flat anteroposteriorly, anterior and dorsal margins with elevated rim; no external expression of incisors on lateral face of rostrum; palatine extends forward to anterior margin of M^1; posterior palatine foramen relatively larger than in *S. schürmanni*, elongate, on anterior margin of palatine, continuing forward onto maxillary as shallow furrow; palate constricted anteriorly, 3.8 mm. wide between P^{4}s, 5.0 mm. wide between M^{1}s.

Dental formula.—I$_{\overline{1}}^1$; C$_{\overline{0}}^0$; P$_{\overline{1}}^1$; M$_{\overline{3}}^3$.

Upper dentition (Fig. 10, *a-c*).—Cheek teeth directed posterolaterally, opposite occlusal surfaces at approximately 165 degree angle to one another; hypsodont, evidently evergrowing for at least part of individual's lifetime; old teeth with one small posterolateral root and one small anterolateral root, lingual roots apparently fail to develop; enamel laminae fairly thick, not crenulated; no cement in fossettes; anterior fossette extends to base of root area; M^2 largest tooth in series, DP^4 retained until after M^3 erupts and begins wear.

Incisors strongly curved, base above zygomaxillary fossa anterior to P^4, much as in *S. schürmanni*; enamel face with crepe-like texture, more convex than in *S.*

schürmanni; lateral and medial faces slightly convex; tooth with rounded triangular cross-section.

P⁴ slightly longer than wide in unworn state, width equal to length in advanced stages of wear, anterior and lingual faces rounded; labial and posterior faces flat; anterolingual part of crown marked by prominent hypoflexus, corresponding hypostria extends halfway down lingual side of tooth; hypoflexus continuous with paraflexus in unworn tooth; posterolingual moiety of crown marked by second inflection, **mediflexus** (new term, Fig. 2) entering from lingual side posterior to hypoflexus, mediflexus continuous with mesoflexus in unworn tooth; corresponding **medistria** (new term, Fig. 2) on posterolingual side half as long as hypostria, line of medistria

MEASUREMENTS OF UPPER DENTITION

Measurements	U.C.M.P. No. 40549 (Paratype)
P⁴-M³, alveolar length..	18.0
P⁴-M³, occlusal length..	18.2
I, anteroposterior diameter...	4.9[a]
I, transverse diameter..	3.4[a]
P⁴, anteroposterior diameter..	4.3
P⁴, transverse diameter...	4.2
M¹, anteroposterior diameter..	4.6
M¹, transverse diameter...	4.0
M², anteroposterior diameter..	4.7
M², transverse diameter...	4.2
M³, anteroposterior diameter..	4.6
M³, transverse diameter...	3.4

[a] Taken from U.C.M.P. no. 40497.

not parallel with hypostria, base deflected posteriorly; labial moiety of crown with paraflexus, mesoflexus, metaflexus and corresponding stria; parastria longer than mesostria, metastria lost in initial stages of wear with formation of narrow, elongate, oblique metafossette; parastria, mesostria, and medistria lost at approximately same time; mesofossette oblique, crescentic, enamel border not crenulated; parafossette not formed until hypoflexus isolates; hypofossette, parafossette, mesofossette, and metafossette persist to base of tooth; **medifossette** (new term, Fig. 2) does not develop.

M¹ and M² differ from P⁴ in cross-section, anterior outline convexly curved dorsoventrally and transversely; lingual face convex dorsoventrally and anteroposteriorly, deeply infolded toward crown by hypostria; posterior face concave dorsoventrally, flattened transversely; posterolingual margin marked by deep medistria; labial surface concave dorsoventrally, rounded anteroposteriorly; hypoflexus slightly curved, directed anterolabially oblique, enamel walls continuous with paraflexus in unworn teeth, mediflexus and mesoflexus continuous in beginning stages of wear, more curved and oblique than hypoflexus; metaflexus strongly oblique, nearly straight, open to posterior margin in unworn teeth; parastria, mesostria, and metastria superficial, subequal in length, lost in beginning stages of wear; hypostria of varying length, usually extends to within 4.0 mm. of base, usually somewhat deeper on M² than on M¹; medistria short, approximately 5.0 to 7.0 mm. shorter than

hypostria but 70 per cent longer than external stria; metafossette divides in advanced stages of wear, lost before hypoflexus isolates as hypofossette; parafossette formed before hypoflexus is lost; hypofossette and mesofossette persist to base of tooth; anterolingual lamina of hypoflexus on M^1 deflected more posteriorly than on M^2; posterolingual lamina of hypoflexus on M^2 diverted more posteriorly than on M^1; hypostria of M^1 placed more posteriorly than on M^2.

M^3 more elongate, more compressed laterally than M^{1-2}; anterior face less oblique than on M^{1-2}; lingual face deeply incised by long hypostria that extends to within 3.0 mm. of base; medistria deep with sharp anterior border, more rounded posterior border; posterior face rounded with wavy surface, concave dorsoventrally; labial side somewhat flattened anterposteriorly; concave dorsoventrally; parastria, mesostria, and metastria shallow, subequal in length; fossettes less oblique, not so curved
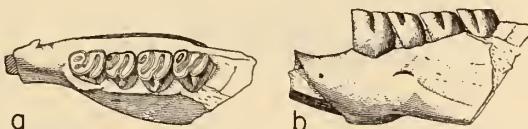
Fig. 11. *Scleromys colombianus* Fields, n. sp., U.C.M.P. no. 39253, loc. V-4534, Quebrada Tatacoa locality: left mandibular ramus; *a*, occlusal view; *b*, labial view; $\times$ 1.

as in M^{1-2} in beginning stages of wear, more oblique in advanced stages of wear; other characters as in M^{1-2}.

Mandible (Figs. 11, *a*, *b*; 12, *a-c*).—Massive, short, wide, much as in *S. schürmanni*; symphysis long, heavy, anterior border above alveolar line of cheek teeth; geniohyoid pit deep, elongate anteroposteriorly; diastema fairly short (approximately 15 mm.); dorsal surface forming gentle curve from incisor alveolus to P_4, labial face rounded, lingual surface concave; mental foramen small, usually single; distinct digastric crest posterior to symphysis; mylohyoid line smooth, rounded; ventrolingual border of ramus follows line of incisor; alveolar border wide, sloping ventrolingually as in *S. schürmanni*; teeth firmly set; anterior origin of angle below M_I; masseteric crest ovoid, not so prominent as in *Neoreomys* and *Capromys*; anterior part of angle distorted outward, posterior extension deflected somewhat lingually; masseteric fossa not so shallow as in *Dasyprocta*, smooth, extends forward to area below M_I; ventral mandibular crest prominent, forms distinct lateral ridge posteriorly; dorsal crest fails to develop; coronoid process low, triangular, distorted outward, situated posterior to $M_{\bar{3}}$; inferior dental foramen 6.0 mm. behind $M_{\bar{3}}$ on alveolar border, lingual to posterior part of coronoid process; inferior pterygoid crest insignificant; inferior pterygoid fossa extremely deep as in *Dasyprocta*, extends forward to area below M_I as in *S. schürmanni*; inferior margin of angle with well-developed lingual crest forming laterally flattened ventral plate.

Lower dentition (Figs. 11, *a*, *b*; 12, *a-c*).—Cheek teeth hypsodont, semi-rooted occlusal surfaces with anterolingual slope; enamel pattern somewhat different from upper cheek teeth; $P_{\bar{4}}$ largest tooth in series; no cement in fossettids; posterior fossettid extends to base of root area.

Incisors extremely long as in *S. schürmanni*; anterior face more convex than in *S. schürmanni*; slightly oblique; labial surface moderately convex, enamel band covering half of surface; lingual face flat, enamel covering anterior one-third of surface.

$P_{\overline{4}}$ erupts after $M_{\overline{3}}$; tooth somewhat wedge-shaped, point of wedge anterior; more elongate than molars; labial side of tooth rounded; anterior surface nearly flat; lingual face flat; posterior side moderately rounded, meets lingual face at acute angle; hypostriid extends to basal one-fourth of tooth, basal part bent slightly anterior; parastriid not developed; mesostriid relatively prominent, perpendicular, retained until tooth 40 per cent worn; metastriid superficial, lost in beginning stages of wear; hypoflexid directed sharply posterolingually, slightly curved, sometimes with distinct transverse twist of lingual part in well-worn tooth; laminae usually smooth, sometimes with slightly wavy outline; metafossettid forms only in extremely worn teeth; mesoflexid directed anterolabially, usually straight, sometimes slightly crescentic in beginning stages of wear and strongly crescentic in advanced
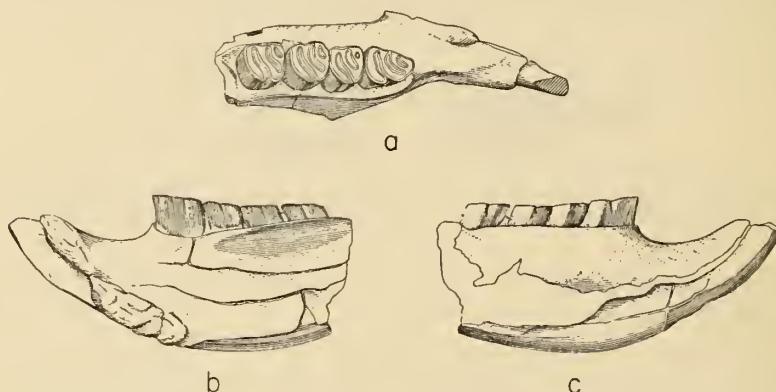
Fig. 12. *Scleromys colombianus* Fields, n. sp.; holotype, U.C.M.P. no. 37927, loc. V-4519, Toxodont locality: right mandibular ramus; *a*, occlusal view; *b*, lingual view; *c*, labial view; × 1.

stages, sometimes with transverse warping of lingual part in extremely worn teeth; laminae usually smooth, occasionally wavy; mesofossettid persists to base of tooth; area of parafossettid variable, sometimes remains single to near base of tooth, but may break up into two or even three ovoid fossettids in advanced stages of wear.

$M_{\overline{1}}$ and $M_{\overline{2}}$ distinct from $P_{\overline{4}}$ in proportions and outline; anteroposterior diameter greater than transverse diameter in unworn teeth, equal to or less than transverse diameter in extremely worn teeth; labial face strongly rounded anteroposteriorly; anterior side transversely flattened; lingual surface slightly concave anteroposteriorly; posterior face slightly oblique, convex, meets lingual face in acute angle; labial side marked by long hypostriid oriented almost perpendicular to occlusal surface but at angle to anterior wall of tooth; lingual wall with parastriid, mesostriid, and metastriid, also marked by dorsoventral groove posterior to base of mesostriid that carries to base of tooth; metastriid half as long as mesostriid, lost in early stage of wear; parastriid superficial, lost in initial stage of wear; hypoflexid continuous with metaflexid in unworn tooth; posterior lophid with individual cuspule on labial part in unworn teeth, lost before metaflexid loses connection with lingual wall; hypoflexid straight in little-worn teeth, becoming crescentic, finally acquiring distinct transverse warp in advanced stages of wear; hypofossettid with gentle S shape; metafossettid forms only in extreme stage of wear; mesoflexid strongly oblique, open through anterior wall of unworn tooth, connection lost soon

after wear begins, outline nearly straight in little-worn tooth becoming crescentic as tooth wears to base of mesostriid, mesofossettid strongly curved, sometimes with S curve, retained to base of tooth; paraflexid like mesoflexid, connection to anterior wall and parastriid lost in initial stage of wear; parafossettid elongate in little-worn teeth, never crescentic, becoming ovoid, rarely dividing as wear progresses, finally becomes rounded at level of hypostriid base, lost soon after formation of hypofossettid; $M_{\bar{2}}$ slightly larger than $M_{\bar{1}}$; flexids not so strongly oblique on $M_{\bar{2}}$; hypostriid placed more posteriorly on $M_{\bar{2}}$.

$M_{\bar{3}}$ largest of molars; not as elongate as $M_{\bar{1}\text{-}\bar{2}}$ in unworn teeth; sides much as in anterior molars; anteroposterior and transverse diameters remain more constant

MEASUREMENTS OF LOWER DENTITION

Measurements	U.C.M.P. No. 37927 (Holotype)
$P_{\bar{4}}$-$M_{\bar{3}}$, alveolar length	22.1
$P_{\bar{4}}$-$M_{\bar{3}}$, occlusal length	21.6
I, anteroposterior diameter	5.3
I, transverse diameter	3.5
$P_{\bar{4}}$, anteroposterior diameter	6.4
$P_{\bar{4}}$, transverse diameter	4.9
$M_{\bar{1}}$, anteroposterior diameter	4.5
$M_{\bar{1}}$, transverse diameter	4.7
$M_{\bar{2}}$, anteroposterior diameter	5.3
$M_{\bar{2}}$, transverse diameter	5.5
$M_{\bar{3}}$, anteroposterior diameter	5.4
$M_{\bar{3}}$, transverse diameter	5.2
Depth of mandible below $P_{\bar{4}}$ (lingual)	14.7

to base of tooth; length of hypostriid more variable than in $M_{\bar{1}\text{-}\bar{2}}$; metastriid usually as long or longer than mesostriid; parastriid superficial; hypostriid more parallel to anterior wall, thus at slight angle to occlusal surface; posterior lophid not as wide as in $M_{\bar{2}}$ but with accessory labial cuspule; posterior wall of tooth with longitudinal furrow owing to slight constriction lingual to cuspule; hypoflexid and hypofossettid oblique, labial warp usually somewhat greater than in $M_{\bar{2}}$, S pattern usually more pronounced; mesoflexid and mesofossettid as in $M_{\bar{2}}$; other characters as in $M_{\bar{2}}$.

Deciduous dentition.—Only $DP_{\bar{4}}^{4}$ are deciduous; milk teeth much shorter crowned than permanent premolars; rooted base constricted anteroposteriorly; occlusal pattern unique; external moiety of upper and internal moiety of lower with four inflections; hypoflexus of upper and hypoflexiid of lower strongly oblique, hypostria and hypostriid extend almost to base; lower DP with short external striid anterior to hypostriid; anterior moiety with two (sometimes three) isolated or united fossettids; upper DP with one accessory fossette on posterior moiety.

Postcranial skeleton.—Only parts of the skeleton are known.

Femur.—Proportions almost same as those in *S. schürmanni*; greater trochanter extends well above head; intertrochanteric ridge subparallel to axis of shaft, edge smooth, rounded, slightly curled toward head; trochanteric fossa deep, narrow, ends in ovoid pit that almost penetrates to external surface of femur; neck ovoid in

MEASUREMENTS OF DP⁴

Measurements	U.C.M.P. No. 40550
Anteroposterior diameter at base of external stria............................	5.7
Transverse diameter at base of external stria..................................	3.6
Anteroposterior diameter at base of hypostria..............................	4.6
Transverse diameter at base of hypostria.....................................	3.5

MEASUREMENTS OF DP₄

Measurements	U.C.M.P. No. 40550	U.C.M.P. No. 40510
Anteroposterior diameter at base of internal striids................	7.2	7.7
Transverse diameter at base of internal striids....................	3.3	3.5
Anteroposterior diameter at base of hypostriid....................	6.1	6.5
Transverse diameter at base of hypostriid........................	3.5	3.3

MEASUREMENTS OF FEMUR

Measurements	U.C.M.P. No. 40487	U.C.M.P. No. 37918
Anteroposterior diameter of neck.................................	3.2	....
Dorsoventral diameter of neck....................................	4.1	....
Anteroposterior diameter of shaft at lesser trochanter.............	9.5	9.3
Transverse diameter of shaft at lesser trochanter.................	7.6	7.5
Anteroposterior diameter of shaft halfway between distal condyles and lesser trochanter..	5.8	....
Transverse diameter of shaft halfway between distal condyles and lesser trochanter..	7.8	....
Length of shaft from distal margin of external condyle to nob of lesser trochanter...	53.2	....
Length from lesser trochanter to proximal surface of greater trochanter...	....	16.3
Estimated total length of femur.................................	69.5±	....

MEASUREMENTS OF TIBIA

Measurements	U.C.M.P. No. 40487	U.C.M.P. No. 40563
Length from anterior tuberosity to descending process.............	79.5	....
Estimated total length of tibia...................................	90.0±	....
Anteroposterior diameter 10.0 mm. below tuberosity...............	7.8	....
Transverse diameter 10.0 mm. below tuberosity..................	7.2	....
Anteroposterior diameter from internal malleolus to descending process...	6.9	6.8
Transverse diameter across astragalar condyles..................	7.8	7.7

cross-section, dorsoanterior surface with slight ridge running from greater trochanter to head; head not preserved; lesser trochanter as avoid nob, lateral surface flattened, internal surface more concave than in *S. schürmanni*; dorsolateral area of greater trochanter developed as enlarged tubercle, anterior part overhangs anteroproximal face of shaft; linea aspera prominent, proximal part deflected anteriorly meeting dorsolateral tubercle of greater trochanter, distal part deflected toward posterior surface of shaft, accompanying elongate furrow discontinuous, not as well developed as in *S. schürmanni*; shaft straight, slightly flattened anteroposteriorly; internal condyle large; internal tuberosity not enlarged; intercondyloid fossa wide, patellar groove more elongate than in *S. schürmanni*; continuous with anterior profile of shaft, not expanded forward as in *Cuniculus* or *Cercomys*; external condyle not preserved; pit for ligament of gastrocnemius muscle on laterodistal surface of shaft not as prominent as in *S. schürmanni*.
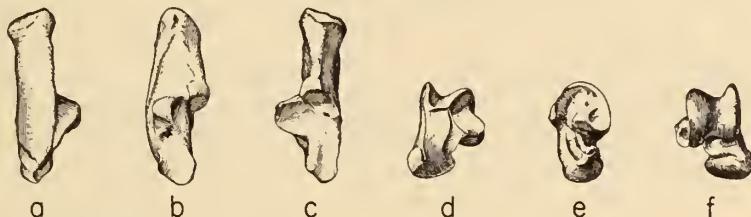
Fig. 13. *Scleromys colombianus* Fields, n. sp.; left calcaneum, U.C.M.P. no. 37951, loc. V-4520, Interathere locality: *a*, posterior view; *b*, medial view; *c*, anterior view: right astragalus, U.C.M.P. no. 40563, loc. V-4517, Monkey locality; *d*, posterior view; *e*, lateral view; *f*, anterior view; × 1.

Tibia.—Right tibia lacking proximal epiphysis; shaft essentially straight; distal part bent forward and outward, semiovoid in cross-section; proximal part subtriangular in cross-section; anterior tuberosity extended as crest much as in *S. schürmanni*; proximointernal part of shaft slightly convex; proximolateral face concave, not as much as in *S. schürmanni*; external tuberosity continued distally as sharp crest to surface for articulation of fibula; fibular notch not well developed; popliteal line concave; distal part of shaft with slightly concave anterior surface; internal, external, and posterior surfaces more rounded; astragalar condyles slightly oblique anterolaterally; descending process smooth, shorter than internal malleolus.

Calcaneum (Fig. 13, *a-c*).—Proportions as in *S. schürmanni*; astragalar facet approximately at midpoint of proximodistal length, oblique to anteroposterior axis, concave distally, strongly convex proximally, not obliquely convex as in *S. schürmanni*, facet one-third longer than wide; sustentacular facet widely expanded medially, slightly concave proximodistally, distal face pierced by nutrient foramen as in *S. schürmanni*, posterior surface of facet grooved for tendon of flexor digitalis longus muscle, furrow more pronounced than in *S. schürmanni*; peroneal tubercle developed as obliquely grooved proximodistal ridge; cuboidal facet flattened dorsoventrally, concave anteroposteriorly in contrast to that in *S. schürmanni*, anterior part wide, posterior margin constricted proximodistally; medial surface of bone proximal to astragalar facet flattened anteroposteriorly, concave proximodistally; anterior and lateral surfaces continuous as oblique flattened surface; posterior length of bone straight, slightly convex transversely, wider than in *S. schürmanni*.

MEASUREMENTS OF CALCANEUM

Measurements	U.C.M.P. No. 37951
Total length of calcaneum	21.2
Anteroposterior diameter of proximal end	5.2
Transverse diameter of proximal end	6.4
Proximodistal length of astragalar facet	5.2
Transverse width of astragalar facet	3.6
Proximodistal diameter of sustentacular facet	4.7
Transverse diameter of sustentacular facet	4.0

MEASUREMENTS OF ASTRAGALUS

Measurements	U.C.M.P. No. 40563
Total length of astragalus	12.3
Width of condyles at widest point	7.0
Length from medial surface of head to lateral extremity of sustentacular facet	6.7
Anteroposterior diameter of head at widest point	5.2
Transverse diameter of head	5.8

MEASUREMENTS OF SCAPULA

Measurements	U.C.M.P. No. 40487
Anteroposterior diameter of glenoid fossa	6.1
Transverse diameter of glenoid fossa	4.3
Smallest anteroposterior diameter of neck	5.0
Transverse diameter of neck at same level	2.4

Astragalus (Fig. 13, *d-f*).—Much as in *S. schürmanni*; calcanear facet oriented obliquely, one-third longer than wide, proximal part cup-like, distal part convex proximodistally and transversely; sustentacular facet long, convex proximodistally, essentially flat transversely, extends from posterior lip of trochlea and internal condyle to head, internal border straight proximally, distal part deflected laterally, external border convex, proximal part contacts with calcanear facet distal to lip of external condyle; sustentacular facet and calcanear facet separated by deep median groove for tendon of flexor hallucis longus muscle, groove not as wide as in *S. schürmanni*; external condyle wide; internal condyle with sharp rim and steep wall; trochlea deep, carries forward to deep concavity for origin of extensor brevis digitorium muscle; neck 15 degrees divergent from proximodistal axis of condyles; anterior surface of neck with transverse ridge halfway between concavity for extensor brevis digitorium muscle and head; navicular facet strongly convex, broad internally, extends onto anterior face, continues onto posteromedial surface of neck as rounded facet for accessory sesmoid bone, lateral part narrow, posterior part continuous with calcanear facet.

Scapula.—Glenoid angle, fossa and distal part of neck preserved; glenoid fossa shallow, elongate anteroposteriorly, one-third longer than wide, borders rounded but distinct; glenoid angle not so extended as in *Lagidium* or *Cercomys*; supraglenoid tubercle small, separated from corocoid process by shallow, broad furrow, placed more laterally than in *Lagidium*, corocoid process missing but evidently much as in *Lagidium*, no ligamental groove on medial surface as in *Cercomys* or *Myocastor*; incisura scapulae relatively deep, not so deep as in *Lagidium*, not so shallow as in *Myocastor*; neck extremely flattened laterally; glenoid border sharp; corocoid border more rounded.

Right Metatarsal IV.—Proximal end of mt. IV preserved; cuboidal facet oblique to longitudinal axis of bone, wide anteriorly, constricted posteriorly, medial margin with distinct notch; proximomedial surface convex, with small, rounded convex facet for articulation with mt. III; proximolateral surface concave with elongate facet for articulation of mt. V, facet wide anteriorly, constricted posteriorly, distal border with shallow notch; proximal part of shaft triangular, transversely ovoid more distally.

Right Metatarsal III.—Proximal surface not well preserved; proximolateral surface with concave pit for reception of facet on mt. IV; medial surface flattened, surface rugose; anterior surface more flattened than in *Lagidium*, *Myocastor*, or *Cercomys*; shaft compressed anteroposteriorly, straight; head perpendicular to shaft; facets flattened, keel on posterior half of facet, more prominent than in *Lagidium*. Total length of mt. III, 33.7 mm.

Comparisons.—*Scleromys colombianus* is the fourth species referable to the genus *Scleromys* Ameghino. Characters that seem to place the new species in the genus *Scleromys* are as follows:

1. Parietal region broad and flattened with no development of sagittal crest.
2. Similarity of dental pattern on upper and lower cheek teeth.
3. M^2 largest tooth in upper series, $M_{\overline{3}}$ largest of lower molars; $P_{\overline{4}}$ more elongate than lower molars.
4. Extremely curved upper incisors, anterior face with crepe-like surface.
5. Excessively lengthened lower incisors (base extending to condyloid process).
6. Upper diastema longer than cheek-tooth series (length of tooth row equal to length from anterior rim of P^4 alveolus to anterior margin of incisive foramen).
7. Enlarged incisive foramen with lateral bony ridges extending to P^4 alveoli.
8. Ventral zygomatic root anterior to P^4.
9. Small, elongate, anteriorly situated posterior palatine foramen.
10. Smooth, wide, and rounded internal nares.

Scleromys angustus Ameghino and *S. osbornianus* Ameghino differ from *S. colombianus* in: more parallel cheek-tooth rows; less persistent metafossette in upper cheek teeth; less persistent parafossettid in lower premolar and molars; absence of mediflexus and medistria; smaller, less wedge-shaped P^4; less curved fossettes.

S. angustus and *S. osbornianus* resemble *S. colombianus* in: nearly equal size and proportions; identical length of premolar-molar series (see table 1); convex, crepe-like enamel surface on incisors; similar dental pattern; presence of ovid P^4 and M^2; enlarged M^2; increasing size from $P_{\overline{4}}$ to $M_{\overline{3}}$; subangular cross-section of lower molars; elongate hypostria and hypostriid.

Scleromys schürmanni is distinct from *S. colombianus* as follows: smaller size (25 per cent smaller); less convex upper incisors; less hypsodont, more completely rooted, more rounded cheek teeth; more simplified dental pattern; absence of medistria and mediflexus; earlier isolation of parafossette; less persistent metafossette; less rounded incisive foramen; more ovoid anterior margin of rostral masseteric fossa; deeper, longer nerve canal on ventral margin of infraorbital foramen; wider palate with less anterior convergence of tooth rows; wider, less rugose palatines; smaller, less furrowed posterior palatine foramen; presence of longer, narrower inferior pterygoid fossa; more anteriorly situated masseteric crest; relatively more concave lingual mandibular face; more ovoid $P_{\bar{4}}$; weaker development of parafossettid and earlier isolation of metafossettid; more superficial mesostriid and metastriid; less elongate patellar groove on femur; transversely narrower calcaneum with less pronounced groove for tendon of flexor digitalis longus muscle; wider groove for tendon of flexor hallucis longus muscle on astragalus.

S. schürmanni agrees in: long upper diastema; anterior position of ventral zygomatic root (anterior to P^4); extremely curved upper incisors; flattened, shallow rostral masseteric fossa; presence of wide rectangular dorsal spur of premaxillary extending back to frontal between nasal and maxillary; enlarged incisive foramen with lateral bony ridges extending back to P^4; position of posterior palatine foramen between first molars; presence of superficial external stria and elongate hypostria; persistence of mesofossette; increasing tooth size from P^4 to M^2 with more ovoid M^3; proportions and massiveness of lower jaw; extremely long lower incisor; low, outwardly distorted coronoid process; elongate hypostriid; increasing size from $M_{\bar{1}}$ to $M_{\bar{3}}$; similar proportions and characters in postcranial skeleton except for differences listed above.

Differences between *Neoreomys* from the Santa Cruz fauna and *Scleromys colombianus* are the same as those discussed in the comparison with *S. schürmanni* except that the new species more nearly approaches the size of *Neoreomys*.

Dinomys seems to be distinct from *S. colombianus* primarily in size and in the following dental characters: relatively larger, broader incisors with flattened enamel face; more posteriorly placed base on upper incisor (above M^1); extremely hypsodont, open-rooted cheek teeth with development of nearly complete lophodont pattern; presence of distinct parastria, mesostria, metastria, hypostria, and medistria on upper cheek teeth, all of which extend to base of teeth; hypostriid and additional anterior striid on labial face; parastriid, mesostriid, and metastriid on lingual surface of lower cheek teeth also extend to base of teeth; development of $M_{\bar{3}}$ as largest tooth in series, other differences are seen in: nearly complete loss of coronoid process; slightly shorter, wider inferior pterygoid fossa; presence of third trochanter on femur with less expanded internal and external condyles; more shortened distal part on calcaneum; relatively more expanded calcanear facet on astragalus.

Dinomys is remarkably like *S. colombianus* in having: long, anteriorly expanded nasals; enlarged premaxillary with rectangular dorsal spur extending back to frontal between nasal and maxillary; slightly serrate lateral part of premaxillo-maxillary suture directed dorsoposteriorly; enlarged incisive foramen with lateral bony ridges extending back to P^4; enlarged maxillary that forms broad ventral root on anteriorly placed zygomatic arch; ventral furrow in infraorbital foramen for transmission of nerves; shallow rostral masseteric fossa with somewhat squared anterior part, ridged

anterior and dorsal rims, and anteroventral depression; no accessory opening for lacrymal duct on lateral face of rostrum; anterior margin of palatines between M¹s; elongate posterior palatine foramen situated on anterior border of palatine with anterior continuation onto maxillary as palatine canal; anteriorly converging tooth rows; increasing size from P⁴ to M² with M³ more ovoid than M¹ and M²; retention of DP₄⁴ until after M₃³ begins wear; massive, short mandible with long, heavy symphysis; deeply incised geniohyoid pit; short diastema; small mental foramen; distinct digastric crest; smooth mylohyoid line; wide alveolar border with gentle ventrolingual slope; firmly implanted teeth; anterior limit of angle below M₁; small masseteric crest below posterior moiety of P₄; outwardly deflected anterior part of angle with slight lingual flexure on posterior part; smooth, flattened masseteric fossa extending to area below M₁; development of distinct ridge on posterior part of ventral mandibular crest; no development of inferior pterygoid crest; ventrolingual crest on posterior extension of angle with laterally flattened ventral plate; extremely long lower incisors (root area well behind M₃); presence of wedge-shaped P₄.

Any further comparisons of *Scleromys colombianus* with *Echimys, Cercomys, Capromys, Dasyprocta, Myocastor,* and *Isolobodon* would be repetitious since the differences and similarities noted between *S. schürmanni* and these genera are essentially the same as those of *S. colombianus.* The only comparative character that would be altered is size. The size difference between *Echimys, Cercomys,* and *S. colombianus* is greater than in *S. schürmanni*; in contrast, *Capromys, Dasyprocta, Myocastor,* and *Isolobodon* seem closer to *S. colombianus* in size than does *S. schürmanni.*

STATISTICAL ANALYSIS

Scleromys colombianus is represented by only one complete upper dental series. However, many lower jaws were collected, and isolated teeth form perhaps 40 per cent of all rodent materials in the La Venta fauna.

The species occurs from the base of the section, V-4531, Cerro Gordo (2), El Libano Sands and Clays, to the uppermost level, V-4529, Las Mesitas. The morphological characters in specimens from the lower and upper part of the section are as uniform as they were in *S. schürmanni*; thus samples in the following statistical analysis have been drawn from all available materials within the La Venta section regardless of stratigraphic position.

Analysis of the length P₄ to M₃ has not been attempted in *S. colombianus* since only three specimens in the University of California collection have all four teeth preserved; however, six specimens were found in which the length M₁ to M₃ could be determined (see table 3). This measurement is probably as significant as the P₄ to M₃ length, and since it offered a larger sample, it was chosen for analysis. With the methods previously outlined, values for occlusal length of M₁ to M₃ were obtained.

$$\text{Occlusal length of } M_{\bar{1}} \text{ to } M_{\bar{3}}.$$
$$\text{M.} = 14.3 \pm .23$$
$$\text{S.D.} = .577 \pm .166$$
$$\text{C.V.} = 4.03 \pm 1.16$$

The value C.V. = 4.03 ± 1.16 is considered a good average value (Simpson and Roe, 1939, p. 123), which indicates that *S. colombianus* is a normal species with average variability. The holotype represents an individual somewhat larger than

TABLE 3

Comparative Measurements of Scleromys colombianus—Lower Dentition

U.C.M.P. spec. no.	U.C.M.P. loc. no.	Length $P_{\overline{4}}$-$M_{\overline{3}}$	$I_{\overline{1}}$		$P_{\overline{4}}$		$M_{\overline{1}}$		$M_{\overline{2}}$		$M_{\overline{3}}$	
			Ant.-post. diam.	Trans. diam.	Ant.-post. diam.	Trans. diam.	Ant.-post. diam.	Trans. diam.	Ant.-post. diam.	Trans. diam.	Ant.-post. diam.	Trans. diam.
39253..........	V-4534	18.7	4.2	3.0	4.9	3.9	3.9	3.8	4.6	4.3	5.3	4.1
39888..........	V-4536	...	...	...	...	...	3.9	4.0	4.8	4.7	5.5	4.6
39654..........	V-4517	...	4.1	2.9	...	...	4.6	4.1	5.6	4.8	...	...
40551..........	V-4519	...	...	...	6.2	4.3	3.8	4.1	4.7	4.5	...	...
37927[a].......	V-4519	21.6	5.3	3.5	6.4	4.9	4.5	4.7	5.3	5.5	5.4	5.2
37994..........	V-4522	20.8	...	...	6.2	4.5	4.0	4.5	4.9	4.8	5.7	4.7
38034..........	V-4523	...	4.2	3.0	...	...	3.8	3.9	4.5	4.7	5.3	4.7
38960..........	V-4528	...	4.4	3.1	...	...	4.2	4.1	4.8	4.6	5.4	4.6

[a] Holotype.

TABLE 4

Tabulation of Measurements on Sectioned Scleromys Colombianus Teeth
(Index numbers correspond to numbers on sections Fig. 14)

Tooth	Index	Above base of longest fossette	Ant.-post. diameter	Trans. dia. ant. moiety	Trans. dia. post. moiety	Tooth	Index	Above base of longest fossette	Ant.-post. diameter	Trans. dia. ant. moiety	Trans. dia. post. moiety
P⁴	1	8.6	3.9	3.2	3.7	M²	1	10.4	5.2	3.2	3.5
	2	7.7	4.2	3.4	4.0		2	9.6	5.3	3.4	3.8
	3	6.9	4.5	3.9	4.2		3	9.0	5.4	3.7	3.9
	4	6.3	4.6	4.1	4.3		4	8.1	5.3	3.8	4.1
	5	5.6	4.7	4.3	4.3		5	7.7	5.2	3.9	4.2
	6	4.9	4.7	4.5	4.4		6	7.1	5.1	4.0	4.2
	7	4.1	4.6	4.6	4.5		7	6.3	4.8	4.1	4.2
	8	3.2	4.5	4.5	4.5		8	5.7	4.7	4.1	4.2
	..	...	...	...	...		9	5.1	4.6	4.2	4.2
	..	...	...	...	...		10	4.7	4.5	4.2	4.2
	..	...	...	...	...		11	4.1	4.4	4.3	4.2
	..	...	...	...	...		12	3.5	4.3	4.3	4.3
P₄	1	8.2	5.5	3.3	3.6	M₂	1	9.3	...	4.3	...
	2	7.4	6.0	3.6	3.9		2	9.0	5.6	4.5	4.7
	3	6.5	6.3	3.8	4.3		3	8.3	6.1	4.6	4.7
	4	5.9	6.3	3.8	4.4		4	7.6	6.0	4.7	4.8
	5	5.2	6.3	3.8	4.3		5	7.0	6.0	4.8	4.9
	6	4.5	6.3	3.7	4.2		6	6.2	5.7	4.9	5.0
	7	3.8	6.2	3.5	4.2		7	5.5	5.6	4.9	5.1
	8	2.9	6.2	3.4	4.2		8	4.8	5.5	4.8	5.1
	9	2.1	6.2	3.3	4.3		9	4.0	5.2	4.8	5.0
	10	1.4	6.1	3.2	4.4		10	3.3	4.9	4.8	5.0
	..	...	...	...	...		11	2.7	4.5	4.8	4.9
	..	...	...	...	...		12	2.1	4.2	4.7	4.8
M₁	1	7.1	5.0	3.5	3.3	M₃	1	8.3	4.6	3.8	3.6
	2	6.4	5.7	3.7	3.4		2	7.5	4.6	4.0	3.8
	3	5.7	5.7	3.8	3.7		3	7.0	4.6	4.2	4.1
	4	5.1	5.6	4.0	4.2		4	6.4	4.8	4.3	4.3
	5	4.4	5.5	4.2	4.3		5	5.7	4.9	4.4	4.4
	6	3.9	5.3	4.2	4.4		6	5.1	4.9	4.5	4.6
	7	3.3	4.9	4.2	4.4		7	4.3	5.0	4.6	4.6
	8	2.7	4.6	4.1	4.3		8	3.6	5.0	4.7	4.6
	..	...	...	...	...		9	3.0	4.9	4.6	4.6
	..	...	...	...	...		10	2.3	4.8	4.5	4.5

TABLE 5

QUANTITATIVE ANALYSIS OF SCLEROMYS COLOMBIANUS TEETH

(Index of stage of wear based on sectioned teeth—Fig. 14)

Tooth	No. spec.	Index	M S.E.$_m$	S.D. S.E.	C.V. S.E.$_v$
P$_{\overline{4}}$	5	1	5.32 ± .09	.217 ± .068	4.07 ± 1.28
	5	3	5.12 ± .07	.172 ± .054	3.36 ± 1.06
	4	4	5.82 ± .15	.320 ± .113	5.49 ± 1.94
	3	7	6.03 ± .08	.153 ± .062	2.54 ± 1.04
M$_{\overline{1}}$	12	1	4.74 ± .06	.218 ± .046	4.59 ± .93
	5	2	4.96 ± .08	.195 ± .061	3.93 ± 1.24
	4	3	5.20 ± .12	.245 ± .087	4.71 ± 1.66
	3	8	4.26 ± .14	.252 ± .102	5.91 ± 2.41
M$_{\overline{2}}$	11	3	4.97 ± .07	.245 ± .052	4.74 ± 1.01
	8	4	5.04 ± .09	.280 ± .070	5.55 ± 1.38
	5	6	4.92 ± .12	.277 ± .087	5.63 ± 1.46
	5	9	4.76 ± .05	.114 ± .035	2.99 ± .75
M$_{\overline{3}}$	7	1	4.65 ± .08	.233 ± .062	5.00 ± 1.34
	5	4	5.46 ± .09	.208 ± .065	3.81 ± 1.20
	9	5	5.36 ± .08	.268 ± .062	4.99 ± 1.17
	4	7	5.32 ± .09	.189 ± .067	3.55 ± 1.25
P^4	3	2	4.37 ± .06	.115 ± .047	2.63 ± 1.07
M^3	14	1	4.86 ± .06	.257 ± .048	5.28 ± .98
	6	2	5.23 ± .05	.137 ± .039	2.62 ± .75

the mean. The length M$_{\overline{1}}$ to M$_{\overline{3}}$ is 15.20 mm.; nevertheless, it fits well into the species range and is within the area ±2 S.D. from the mean, or within a linear range from 13.14 to 15.45 mm. in which 95.45 per cent of the total observations would be expected to fall.

The serial sections (obtained by the process outlined in the introduction of this paper) made it possible to establish a number index for stage of wear in the numerous, isolated upper and lower cheek teeth of *Scleromys colombianus*, and allowed an accurate grouping of isolated teeth representing the same stage of wear, thus giving, for P^4, M^3, P$_{\overline{4}}$, M$_{\overline{1}}$, M$_{\overline{2}}$, and M$_{\overline{3}}$,[4] a series of samples containing specimens segregated by stage of wear. Each of these teeth was measured for anteroposterior diameter (table 4), and the results were subjected to statistical analysis (table 5). Index 8 of M$_{\overline{1}}$ has the highest coefficient of variation, 5.91 ± 2.41. The lowest coefficient of variation is in index 7 of P$_{\overline{4}}$ where the value is 2.54 ± 1.04. These values were obtained from very small samples, and thus the degree of error is expected to be high (Simpson and Roe, 1939, p. 123). In larger samples (five or more specimens), the highest value is in index 4 of M$_{\overline{2}}$ with a coefficient of variation of 5.55 ± 1.38,

---

[4] Very few isolated M¹s and M²s were found. It is interesting to note that in both *S. schürmanni* and *S. colombianus* there is a deficiency of upper cheek teeth, whereas lowers are abundant. This peculiarity is, no doubt, due to accidents of collecting.

and the lowest value, 2.62 ± .75, is found in index 2 of $M^{\underline{3}}$. Neither of these values is extreme, but they possibly indicate greater variation in certain teeth. $P_{\overline{4}}$ with a coefficient of variation difference, from highest to lowest, of 2.95 and $M_{\overline{2}}$ with 2.64 seem to be the most variable in the lower series, whereas $M_{\overline{3}}$ with a difference of 1.45 seems to be the least variable. The quantitative factors agree with qualitative observations of these teeth.

In the paratype of *S. colombianus*, $P^{\underline{4}}$ measures 4.3 mm. compared to a mean of 4.35 ± .06 as established by analysis of isolated teeth. $M^{\underline{3}}$ is 4.6 mm. in anteroposterior diameter, which is somewhat smaller than the mean of 4.86 ± .06. Thus the paratype is slightly smaller than the mean for the species.

VARIABILITY IN DENTAL PATTERN OF THE CHEEK TEETH

Certain isolated teeth show variability in dental pattern. There is a tendency for the anterior moiety of lowers and the posterior moiety of uppers to break up into additional inflections; the resultant patterns are somewhat erratic (see Fig. 14, a-f). These variations probably represent random mutations that are either non-adaptive or have not become conspicuously oriented.

Several interesting characters were found concerning gross form in the serial sections of the cheek teeth. The relative lengths and widths of each tooth at numbered stages of wear are shown in table 4.

The lower premolar in unworn condition presents a strongly triangular cross-section with the most acute angle on the anterior part. By the time the tooth is half worn, the anterior moiety becomes squared. As wear progresses, the outline again becomes strongly triangular. As may be seen from the values obtained from $P_{\overline{4}}$, the tooth, at its apex, is constricted in occlusal measurements, expanded at the midpoint of crown height, and at the base the anterior moiety constricts to a measure smaller than that at the apex.

In $M_{\overline{1}}$ and $M_{\overline{2}}$ the gross form is different from $P_{\overline{4}}$. The relationship between length and width is indeed interesting, as the tooth wears from an unworn to an extremely worn state. The anteroposterior diameter decreases steadily toward the base, and in extremely worn teeth is less than the transverse diameter.

$M_{\overline{3}}$ shows still further differences. The anteroposterior diameter increases toward the base and only slightly decreases at the extreme base of the tooth. The transverse diameters also increase toward the base; thus the $M_{\overline{3}}$ is always longer than wide, even in extremely worn teeth.

In the upper cheek teeth, $M^{\underline{1}}$ and $M^{\underline{2}}$ show the same characters as their counterparts in the lower jaw, but $P^{\underline{4}}$ and $M^{\underline{3}}$ are somewhat different.

$P^{\underline{4}}$ is much rounder in outline than $P_{\overline{4}}$. In contrast to the lower tooth, $P^{\underline{4}}$ maintains nearly the same proportions throughout its height. At no stage of wear is it much longer than wide. At the base it tends to become equilateral.

$M^{\underline{3}}$ stands in strong contrast to its lower counterpart. The anterior transverse diameter in the unworn tooth is somewhat narrower than the posterior, but in advanced stages of wear they tend to become equal. The anteroposterior diameter in the unworn tooth is greater than the width, but in contrast to $M_{\overline{3}}$ it decreases considerably and in extremely worn teeth equals the transverse diameter.
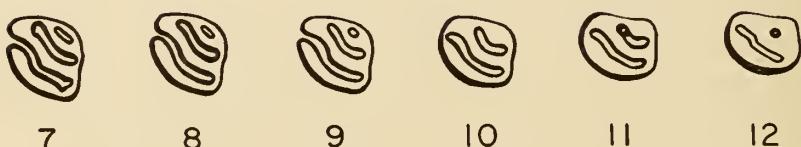
Fig. 14. *Scleromys colombianus* Fields, n. sp.: serial sections obtained from use of sectioning device. Numbers below each cut indicate index of stage of wear for each tooth (see tables 4 and 5). *a*, left P$\overline{4}$, U.C.M.P. no. 39909, loc. V-4936; *b*, left M$\overline{1}$, U.C.M.P. no. 40550, loc. V-4519; *c*, left M$\overline{2}$, U.C.M.P. no. 40755, loc. V-4525; *d*, left M$\overline{3}$, U.C.M.P. no. 40541, loc. V-4523; *e*, right P$\overline{4}$, U.C.M.P. no. 40549, loc. V-4519; *f*, right M$\overline{3}$, U.C.M.P. no. 40662, loc. V-4523: × 2.

1 2 3 4 5

6 7 8 9 10

d.　　　　　Left　M$\frac{}{3}$

1 2 3 4

5 6 7 8

e.　　　　　Right　P$\frac{4}{}$

1 2 3 4 5 6

7 8 9 10 11 12

f.　　　　　Right　M$\frac{3}{}$

Fig. 14 (*Continued*)

<div align="center">DISCUSSION</div>

Scleromys colombianus seems more specialized in dental character than *S. schür-manni*, *S. angustus*, or *S. osbornianus*. The teeth of the new species are actually and relatively higher crowned than the teeth in *S. schürmanni*. In tooth size *S. colombianus* is very similar to the Argentine species, but in other respects is distinct. All the fossettes in the teeth, except the metafossette and parafossettid, extend into the root area. The metafossette and parafossettid extend farther into the teeth than do those of *S. schürmanni*. These characters are seen in the much longer hypostria and hypostriid and the prominent medistria on the upper teeth. This latter character is evidently lacking in all other species of *Scleromys*. Apparently *S. colombianus* has reached a stage of evolution well above that of the Santacrucian species and foreshadows some of the specializations seen in the Pliocene genera of South America.

The fragmentary skeletal remains indicate nothing significant concerning adaptive radiation of body form. The limb bones are relatively more massive than those in *S. schürmanni*, but aside from being somewhat larger, *S. colombianus* was probably very similar to *S. schürmanni* in appearance.

<div align="center">RELATIONSHIPS OF SCLEROMYS</div>

The foregoing observations on S. *schürmanni* and *S. colombianus* have led to the conclusion that *Scleromys* is more closely related to *Dinomys* than to other recent South American hystricomorph rodents. *Dinomys* has usually been regarded as an isolated type among the Hystricomorpha. Thomas (1896) placed *Dinomys* in a separate family, the Dinomyidae. Tullberg (1899) questionably assigned the genus to a separate family, Dinomyidae. Miller and Gidley (1918) also placed the genus in a separate family but included several fossil genera. Ellerman (1940) assigns *Dinomys* to a monotypic family within his superfamily Hystricoidea. Simpson (1945I, pp. 95, 212) followed other authorities and placed the genus in a monotypic family under his superfamily Cavioidea. Winge (1924), on the other hand, assigned *Dinomys* to his group, Dinomyes, under part Dasyproctini of his Hystricidae. Weber (1928) proposed the subfamilies Dasyproctinae, Caviinae, and Hydrochoerinae.

Dinomys is sufficiently distinct from other Recent South American hystricomorphs to warrant retention of separate family rank. A definition of the family Dinomyidae is given by Miller and Gidley (1918, p. 446) and Ellerman (1940, p. 170). Ellerman gives the best characterization of *Dinomys*, but it is unfortunate that he did not have a better sample. His description and figure are based upon an immature individual in which $P_{\overline{4}}^4$ have just begun wear.

At this point it might be well to clarify the definition of the skull and mandible. My evaluation is based on materials made available by the American Museum of Natural History and the Chicago Natural History Museum. The A.M.N.H. specimens include one complete skeleton, A.M.N.H. no. 70345, and the skull and mandible of half-grown individual with $DP_{\overline{4}}^4$ and $M_{\overline{1}-\overline{2}}^{1-2}$ in place, A.M.N.H. no. 110001. The C.N.H.M. specimens include two complete adult skeletons, C.N.H.M. nos. 66891 and 57186; skull and mandible of a juvenile, C.N.H.M. no. 34405; skulls and mandibles of three adult animals, C.N.H.M. nos. 24234, 34702, and 65793.

Revised description of Dinomys.—Skull massive, broad, long; parietal region broad, marked by distinct temporal crests, no sagittal crest; frontals flattened, somewhat longer than parietals; nasals long, flattened, broadened anteriorly; premaxillary large, forming prominent buttress anterior to incisors, dorsal rectangular spur extending back between nasal and maxillary, meeting frontal on transverse line with nasal; maxillary expanded, forms major part of zygomatic plate; external nares broad, low; rostral masseteric fossa shallow, square, anterior and dorsal rim with distinct ridge; upper incisor slightly expressed on lateral surface of rostrum; infraorbital foramen large, broad ventrally, ventral margin with shallow furrow for transmission of nerves; lacrymal canal closed in front of orbit; lacrymal large, extends onto anterodorsal rim of orbit, otherwise excluded from zygomatic plate, lacrymal duct large, ovoid, directly below dorsal zygomatic root; orbital region elongate; postorbital process blunt; orbitosphenoid small, surrounding optic foramen; alisphenoid large, perforated by combined foramen lacerum anterius and foramen rotundum, extended laterally to margin of glenoid fossa, posteriorly to bulla, extended medially as bar connecting with wing of palatine, bar underlain by greatly enlarged alisphenoid canal, base of bar perforated by foramen ovale; diastema short; incisive foramen enlarged, bounded laterally by bony ridges extending to P^4 alveoli; tooth rows converging anteriorly; posterior palatine foramen between anterior moieties of M^2s, extended anteriorly as deep palatine grooves, separated along midline by prominent ridge; palatine large, extends anteriorly to M^2, expanded posteriorly; internal nares posterior to M^3, smooth, marked by small median notch; basicranial axis long, narrow; pterygoid prominent, thick, extends to auditory bulla; foramen lacerum medius large, somewhat ovoid, includes Eustachian tube and anterior part of carotid canal; foramen lacerum posterius elongate, includes posterior part of carotid canal and anterior condyloid foramen; jugal long, anteriorly broad, meets maxillary in vertical interdigitating suture on zygomatic plate, extends back to glenoid fossa; squamosal large, forms body of wide, elongate glenoid fossa; zygomatic part short, broad, overlaps jugal; dorsal part extends onto parietal surface over temporal crest, posterior part extends back to mastoid part of periotic as long narrow spur between auditory bulla and parietal; auditory bullae medium in size; external auditory meatus with incomplete ventral rim, continuous with large accessory canal, margin of canal infolded and crenulated; stylomastoid foramen small, posterior to constriction between external auditory meatus and accessory canal; mastoid part of periotic widely exposed, surface rugose; supraoccipital extends onto dorsal surface of skull over wide, prominent lamboidal crest; midline of occipital surface with prominent dorsoventral crest; exoccipitals subtriangular in shape; paraoccipital processes massive, closely oppressed to mastoid, not lengthened; foramen magnum low, ovoid; occipital condyles broad, flat, extend broadly onto ventral surface of basioccipital.

Dental formula.—I^1_1; C^0_0; P^1_1; M^3_3.

Upper Dentition.—Cheek teeth strongly hypsodont, open-rooted, cement in fossettes and on walls of teeth, M^2 largest in series, M^3 most elongate.

Upper incisors broad, flat, heavy, strongly curved, base above M^1; enamel with crepe-like texture.

P^4 with two anterior transverse lophs, posterior moiety usually with isolated labial enamel column and two continuous lophs; internal wall with two stria and ex-

ternal wall with four stria (if isolated column is lacking, three external stria) all continuous to base of tooth.

M^1 with two anterior lophs, posterior moiety marked by labial inflection developing V-shaped loph; two internal stria and three external stria, all of which continue to base.

M^2 with two anterior lophs; posterior moiety with or without isolated column and with continuous posterior loph, anterior lamina of which usually folds into loph; two internal and three external stria, all continuous to base.

M^3 with two anterior lophs and posterior V-shaped loph; isolated external column occasionally present as in P^4 and M^2; posterior lamina of posterior external inflection usually folded double into posterior part of loph.

Mandible.—Heavy, nearly as broad as long; symphysis long, massive, anterior margin level with alveolar border, posteroventral border with massive buttress; diastema short; mental foramen small; digastric crest distinct; mylohyoid line indistinct; ventral border of rami flattened, reflects shape of incisors; alveolar border wide; angle originates below $M_{\bar{1}}$; masseteric crest ovoid, below $M_{\bar{1}}$; angle distorted outward; masseteric fossa shallow, smooth, extends forward to area below $M_{\bar{3}}$; ventral crest distinct; dorsal crest not developed; coronoid process almost lost, remnant opposite $M_{\bar{3}}$; inferior dental foramen posterior to $M_{\bar{3}}$, continues onto condyloid process as groove; inferior pterygoid crest insignificant; inferior pterygoid fossa deep, elongate, ventrolingual border with distinct crest; condyles ovoid, heavy, drawn lingually from dorsoventral line of angle.

Lower dentition.—Cheek teeth hypsodont, open-rooted, cement present, $M_{\bar{2}}$ largest in series.

Lower incisor broad, flat, sometimes faintly grooved, base extends well behind $M_{\bar{3}}$.

Lower premolar and molars less variable than uppers; two continuous posterior lophs and V-shaped anterior loph; two external and three internal striids, all of which extend to base of teeth; anterolingual inflection sometimes isolates as fossettid, in such case anterolingual striid disappears in early stage of wear.

Relationship of Scleromys to Dinomys.—As stated previously *Scleromys* is clearly related to *Dinomys*. Characters that seem to place *Scleromys* in the family Dinomyidae as represented by *Dinomys* are:

1. Skull broad, flat, with depressed parietals, long frontals, long flattened, anteriorly expanded nasals.
2. Sagittal crest not developed but with distinct temporal crests.
3. Rostrum broad, with squared rostral masseteric fossa bounded by distinct dorsal, anterior, and ventral rims.
4. Infraorbital foramen greatly enlarged, with ventromedial groove for transmission of nerves.
5. Dorsal and ventral zygomatic roots anteriorly placed.
6. Lacrymal enlarged, situated on anterodorsal rim of orbit with distinct posterior spur, ventral margin does not meet jugal.
7. Internal nares posteriorly placed.
8. Alisphenoid canal greatly enlarged.
9. Auditory bullae moderately enlarged.

10. External auditory meatus large, anteriorly tubular with greatly enlarged and connected accessory ventral opening.
11. Mastoid process heavy, blunt, closely oppressed to bulla.
12. Paraoccipital process massive, oppressed to mastoid, not lengthened.
13. Occipital condyles low, wide.
14. Upper incisors strongly curved, enamel band thick.
15. Mandible nearly as wide as long.
16. Symphysis long, heavy, with strong posterior buttress.
17. Angle strongly distorted outward.
18. Condyles wide, heavy.
19. Coronoid process reduced.
20. Lower incisor extremely long, enamel band thick, flat.

Olenopsis aequatorialis (Anthony)

(Figs. 15–24)

1922. *Drytomomys aequatorialis* Anthony, Amer. Mus. Novit., no. 35, 1-4, 2 figs.

Holotype.—To quote from Anthony (1922), "The type is a fragmentary skull, only the anterior portion of the cranium, carrying four molar teeth, and the anterior portion of the mandible, all of the teeth present. Accompanying these parts of the skull are a few fragments of limb bones. A.M. no. 13219."

Type locality.—Near the hacienda of Señor Carrasco, near Nabon, Provincia del Azuay, Equador, South America.

Referred specimens.—Nearly complete juvenile skeleton with right auditory bulla, mandible with complete dentition, U.C.M.P. no. 41636, loc. V-4519. Fragmentary juvenile skeleton, palatal part of skull with right P^4, M^1, and M^3 and left P^4, M^1, parieto-occipital region of skull with well-preserved auditory bullae, mandible with complete dentition, U.C.M.P. no. 39969, loc. V-4519. Mandible with complete left dental series and right I, $P_{\overline{4}}$, and $M_{\overline{1}}$, fragmentary skeletal elements, U.C.M.P. no. 40055, loc. V-4519. Left lower jaw with complete dentition, U.C.M.P. no. 37928, loc. V-4525. Part of left lower jaw with $M_{\overline{1}}$ in place, proximal part of right humerus, U.C.M.P. no. 39898, loc. V-4519. Fragmentary mandible with right and left incisors, left $P_{\overline{4}}$ and $M_{\overline{3}}$, U.C.M.P. no. 39843, loc. V-4936. Right and left $DP_{\overline{4}}$, $M_{\overline{1}}$, and $M_{\overline{2}}$, U.C.M.P. no. 39928, loc. V-4521. Right and left I, $P_{\overline{4}}$, $M_{\overline{1}}$, and $M_{\overline{2}}$, U.C.M.P. no. 40623, loc. V-4528. Fragments of right maxillary with P^4 to M^2, U.C.M.P. no. 38044, loc. V-4524. Fragment of right maxillary with P^4 to M^2, fragments of left tarsus, U.C.M.P. no. 39653, loc. V-4519.

Revised diagnosis.—General proportions robust; skull elongate, low; parietals wide, flat; no sagittal crest; nasals evidently long, broad, expanding anteriorly; rostrum wide, high; premaxillary enlarged with buttress anterior to incisor; rostral masseteric fossa deep ventrally, anterior border somewhat squared, ventral margin bounded by ridge leading back to ventral zygomatic root; infraorbital foramen with slight ventral furrow; ventral zygomatic root opposite anterior margin of P^4; upper incisors greatly curved, expressed on side of rostrum, enamel face slightly convex; palate long; cheek-tooth series slightly longer than diastema; incisive foramen greatly enlarged, bounded by bony ridges continuing back to P^4s; tooth rows convergent anteriorly; posterior palatine foramen continued forward as canal; basicranial axis elongate; interorbital region open as orbital fissure; auditory bullae moderately enlarged; external auditory meatus prominent, ventral opening below tubular part; stylomastoid foramen posterior to meatus; mastoid part of periotic oppressed to bulla; paraoccipital process oppressed to mastoid; foramen magnum low, wide; upper cheek teeth hypsodont, semi-rooted, labial surface with four superficial inflections, lingual surface with one long and one shorter inflection; M^2 largest of upper molars; mandible massive; symphysis long, heavy; angle distorted outward; inferior pterygoid fossa deep posteriorly; mandibular masseteric fossa shallow; ventral mandibular crest with prominent anterior ridge; masseteric crest ovoid, depressed, below posterior moiety of $P_{\overline{4}}$; coronoid process reduced, distorted outward, opposite pos-

terior moiety of M$\overline{3}$; lower incisor extends into condyloid process, enamel face essentially flat; diastema short, approximately half as long as cheek-tooth series; lower cheek teeth with one labial inflection, three, or rarely four, more superficial lingual inflections; M$\overline{1}$-$\overline{2}$ with middle inflection longer than anterior or posterior, M$\overline{3}$ with posterior inflection longer than, or equal to, middle inflection. Other characters will be mentioned in the description, some of which may prove equally or more diagnostic than some of those above.

SUPPLEMENTARY DESCRIPTION

Anthony (1922, pp. 2-3) described the type of *Olenopsis aequatorialis* on a partial skull with right P$\underline{4}$, M$\underline{1}$, left P$\underline{4}$, M$\underline{2}$, and a nearly complete mandible with complete dentition, but he considered it a new genus, *Drytomomys*. In this paper *Drytonomys* is synonymized with *Olenopsis* Ameghino; however, the species is retained as valid.[5] Specimens from the La Venta fauna offer an opportunity to redescribe this species on more complete materials. Referred materials are supplemented in the University of California collection by many isolated teeth that afford a means for statistical analysis.

Cranium (Fig. 15, *a*, *b*).—Parietals extremely flattened, laterally expanded as rounded temporal crests anterior to bullae, no development of sagittal crest, antero-posterior length proportionately longer than in *Scleromys*, general appearance similar to *Dinomys*; frontals and nasals not preserved, nasals evidently long, expanded anteriorly; rostrum somewhat widened as in *Dinomys*; premaxillary short ventrally, much expanded dorsally; lateral part of premaxillo-maxillary suture smooth, directed dorsoposteriorly, ventral part serrate, meets lateral border of incisive foramen anterior to widest diameter; maxillary enlarged, forms broad ventral root of zygomatic plate; incisive foramen enlarged, wider than in *Myocastor*, bounded by distinct ridges continuing to P$\underline{4}$s; ventral margin of infraorbital foramen marked by slight furrow for nerve transmission, somewhat variable as in *Dinomys*; rostral masseteric fossa deep ventrally, shallow dorsally, anteriorly squared; palatine evidently elongate, extends to anterior moiety of M$\underline{1}$; palatine foramen extended into incisive foramen as palatine canal, separated along midline by distinct ridge; tooth rows more convergent anteriorly than in *Dasyprocta* or *Cercomys*, not as extreme as in *Myocastor* or *Lagidium*; basicranial area relatively longer and wider than in *Myocastor*; presphenoid relatively long, somewhat wedge-shaped; basisphenoid evidently long; basioccipital relatively wider than in *Myocastor*, much as in *Dinomys*; auditory bullae moderately inflated; external auditory meatus directed dorsally with smooth, slightly elevated rim; accessory ventral opening present as in *Dinomys*; stylomastoid

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[5] Anthony (1922, p. 1) states: "Mr. A. M. Tweedy . . . gave [to the American Museum of Natural History] . . . parts of a skull and skeleton of a large hystricomorph rodent related, among fossil genera, to *Neoreomys* of the Santa Cruz beds, and among living forms to *Myocastor*." In figure 1, which shows the nature of the locality, Anthony's caption reads: "Diagram based upon a sketch made by Mr. A. M. Tweedy, who was given the data by Señor Carrasco, the original collector of the fossil bones." Anthony further states (p. 2): "There is little doubt that this hystricomorph lived in the Pleistocene." This animal seems to be referable to the same species found in the La Venta fauna, where, on the basis of stratigraphic and evolutionary data, we can assign a late Miocene age to the beds. Anthony's Pleistocene age is highly debatable since he never visited the locality, and his data concerning the locality and occurrence are thirdhand. Furthermore, he mentions only *Neoreomys*, *Myocastor*, and *Hydrochoerus* in his comparisons. It is my opinion that, since Anthony's type specimen and those from the La Venta fauna are morphologically indistinguishable and since our means of dating the La Venta beds are more reliable, we should discard his Pleistocene date. Furthermore, if Anthony had compared his specimen with more genera from the Santa Cruz, I believe that he would have discovered the generic affinity between his specimen and *Olenopsis*.

foramen between and posterior to external openings of bullae; mastoid process closely oppressed to bulla; paraoccipital process short as in *Dinomys*; squamosal large, proportions as in *Dinomys*; glenoid fossa smooth, shallow, elongate, broad transversely; occipital region wide with rounded lambdoidal crest; supraoccipital marked by median ridge; suture between supraoccipital and exoccipital raised as diagonal ridge; foramen magnum wide, low, ovoid in outline; occipital condyles diagonal as in *Dinomys*, not perpendicular as in *Myocastor* and *Dasyprocta*.
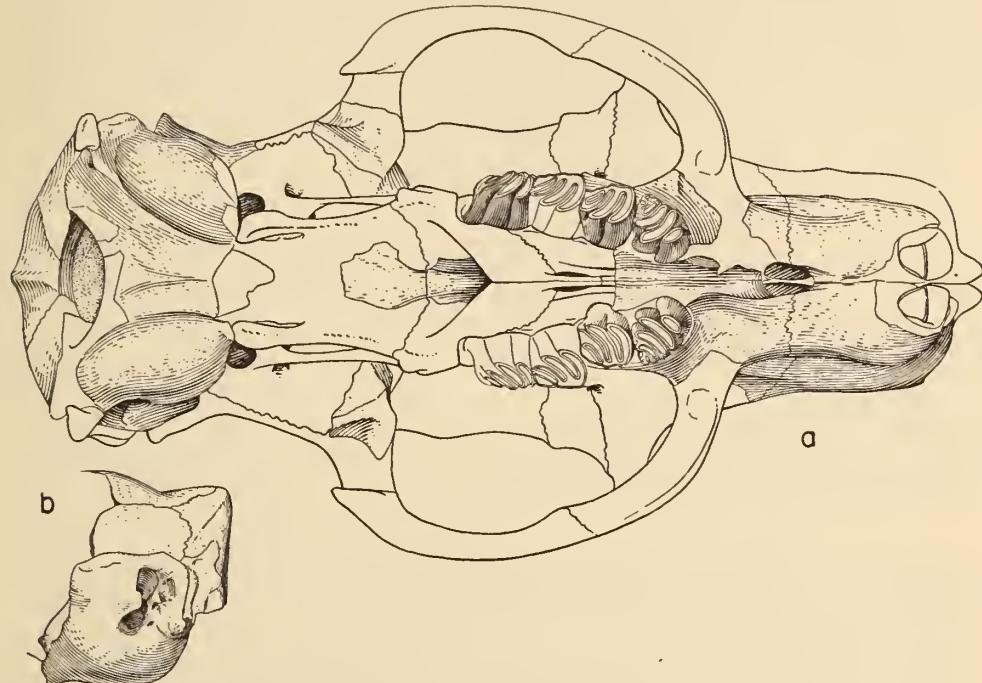
Fig. 15. *Olenopsis aequatorialis* (Anthony), U.C.M.P. no. 39969, loc. V-4519, Toxodont locality: *a*, palatal view of skull partially restored from C.M.N.H. no. 57186, *Dinomys* (restored parts not shaded); *b*, left auditory bulla showing enlarged ventral opening of external auditory meatus; both drawings × 1.

Cranial measurements were taken from the only available specimen, a two-thirds-grown individual. Total length of the skull can only be estimated, as the parts between the posterior margin of M^1 and glenoid fossa are lacking.

Dental formula.—I$\frac{1}{1}$; C$\frac{0}{0}$; P$\frac{1}{1}$; M$\frac{3}{3}$.

Upper dentition (Fig. 15, *a*).—Cheek teeth hypsodont, open-rooted until late in life, semi-rooted in advanced stage of wear, one small posterolateral and one antero-lateral root; basal anterolingual part with band of thickened enamel; enamel laminae thick; no evidence of cement in fossettes; anterior fossette extends to base of tooth; DP^4 lost after M^3 erupts.

Incisor robust with thick enamel cutting edge; extremely curved; root over alveolus of P^4; enamel face slightly convex; medial surface essentially flat; lateral face slightly concave.

P^4 somewhat oblique to molars, subtriangular in cross-section, longer than wide in unworn state, width equal to, or greater than, length in advanced stages of wear;

posterior wall flattened; labial surface nearly flat anteroposteriorly, concave dorso-ventrally; anterior and lingual faces continuous as rounded, convex surface; anterior moiety of crown with prominent hypoflexus, hypostria extends to basal fourth of tooth, hypoflexus continuous with paraflexus in unworn tooth; postero-lingual moiety with more superficial mediflexus; medistria, half as long as hypostria, relatively longer than in *Scleromys*; mediflexus and mesoflexus continuous in un-worn tooth; hypostria and medistria oblique to long axis of tooth; labial moiety with paraflexus, mesoflexus, metaflexus, and **entoflexus** (new term, Fig. 2); **entostria** (new term, Fig. 2) lost in initial stage of wear with formation of variously shaped **entofossette** (new term, Fig. 2), lost after mediflexus isolates; metastria lost soon after entofossette forms; metafossette oblique, strongly crescentic, lost soon after hypoflexus isolates; mesostria and parastria lost at approximately same time; tooth

MEASUREMENTS OF CRANIUM

Measurements	U.C.M.P. No. 39969
Length of diastema (posterior border of incisive alveoli to anterior margin of P⁴)	26.0
Palatal breadth (between P⁴)	4.3
Palatal breadth (between posterior moiety of M¹)	9.2
Length of bullae	19.2±
Width of bullae	14.6
Width of occiput (across mastoid processes)	41.5
Height of occiput (basioccipital to dorsum)	26.8
Width of basioccipital (across anterior margin)	9.6

half-worn before medistria disappears; parafossette continuous with hypofossette; mesofossette continuous with medifossette; hypofossette, parafossette, and medi-fossette persist to base of tooth.

M^1 and M^2 differ from P^4 in several respects; unworn teeth subrectangular, anteroposterior diameter greater than transverse, becoming equal to, then less than, transverse diameter as wear progresses; anterior face convex; labial wall essentially flat anteroposteriorly, concave dorsoventrally; posterior surface concave; lingual wall convex; hypostria and medistria more curved than on P^4, more or less parallel to anterior wall; medistria relatively longer than on P^4, extends to basal three-fifths of tooth; parastria and entostria shorter than mesostria and metastria; mesostria equal to or longer than metastria, lost in early stage of wear; entofossette lost as medifossette isolates; parafossette continuous with hypofossette, mesofossette con-tinuous with medifossette, all extend to base of tooth; metafossette slightly shorter, base level with end of hypostria; sometimes divides at base; posterior lamina of hypoflexus on M^2 with posteriorly directed notch; fossettes of M^2 more crescentic than on M^1.

M^3 more elongate, more compressed laterally than M^{1-2}; anteroposterior diameter consistent to base of tooth, transverse diameter increases slightly toward base of tooth, never equal to anteroposterior diameter; anterior face less convex dorsoven-trally than M^{1-2}; posterior surface flattened dorsoventrally, slightly convex trans-versely; labial and posterior walls at acute angle to each other; hypostria and medi-stria longer than on M^{1-2}, not so curved as on M^{1-2}; mesostria and metastria longer

than parastria or entostria; metastria usually longer than mesostria, sometimes equal to or shorter; flexi progressively more oblique, more crescentic from hypoflexus to metaflexus; other characters as in M^{1-2}.

Mandible (Figs. 16, *a-d*; 17, *a-c*).—Robust, heavy, short, much as in *Dinomys*; symphysis long, thickened, anterior border at level of alveolar surface of cheek-tooth series; geniohyoid pit extremely deep; diastema shorter than in *Myocastor*, equal to length in *Dinomys*, dorsal surface somewhat convex anteriorly, posteriorly raised as prominent shoulder at $P_{\bar{4}}$ alveolus, labial surface bulbous, lingual surface flat dorsally, inflected ventrally; mental foramen single, small, not as small as in *Dasyprocta*, nor as large as in *Cuniculus*; digastric crest low but distinct, not so

MEASUREMENTS OF UPPER DENTITION

Measurements	U.C.M.P. No. 39969 (juvenile)	U.C.M.P. No. 38044 (adult)
P^4-M^3, alveolar length (estimated)	28.7±	32.3±
P^4-M^2, alveolar length	....	23.0
I, anteroposterior diameter	6.9	....
I, transverse diameter	5.2	....
P^4, anteroposterior diameter	6.6	7.8
P^4, transverse diameter	6.3	8.3
M^1, anteroposterior diameter	6.9	7.3
M^1, transverse diameter	5.5	7.3
M^2, anteroposterior diameter	....	8.1
M^2, transverse diameter	....	8.3
M^3, anteroposterior diameter	7.3	....
M^3, transverse diameter	5.2	....

prominent as in *Myocastor*; mylohoid line indistinct; ventrolingual line of ramus follows line of incisor; alveolar border wide with more ventrolingual slope than on *Dinomys*, less than on *Cuniculus*; origin of angle below $M_{\bar{1}}$; masseteric crest small, ovoid, dorsal rim depressed into face of ramus; anterior part of angle distorted outward, extension directed posteriorly; masseteric fossa not as deep as it is on *Myocastor*, not as shallow as it is on *Dasyprocta*, surface smooth, extends forward to masseteric crest; ventral mandibular crest prominent anteriorly; no development of dorsal crest; coronoid process reduced, distorted outward, opposite posterior moiety of $M_{\bar{3}}$; inferior dental foramen posterolateral to inferior pterygoid crest on dorso-lingual surface of alveolar border; inferior pterygoid fossa not as deep or narrow as it is in *Scleromys* or *Dasyprocta*, not as wide or shallow as it is in *Myocastor* and *Lagidium*; inferior margin of angle with posterior crest on lingual side forming flattened ventral plate as in *Dinomys*.

Lower dentition (Figs. 16, *a-d*; 17, *a-c*; 18, *a-c*).—Cheek teeth much the same as in uppers, but enamel pattern reversed and more variable; fossettids progressively longer from parafossettid to hypofossettid; teeth progressively larger from $P_{\bar{4}}$ to $M_{\bar{3}}$; $P_{\bar{4}}$ subequal to $M_{\bar{3}}$.

Incisor robust, extremely long as in *Scleromys* and *Dinomys*; enamel face flat, wide, thick; labial side slightly concave; lingual face flat.

$P_{\bar{4}}$ erupts after $M_{\bar{3}}$; tooth wedge-shaped in cross-section, broad posteriorly, more

elongate anteroposteriorly than molars; lingual face flat; labial wall slightly convex with median cleft below base of hypostriid; posterior surface convex, meets lingual face at acute angle; anterior face narrow, flat dorsoventrally, rounded transversely; hypostriid variable, usually extends to basal third of tooth, slightly curved; lingual
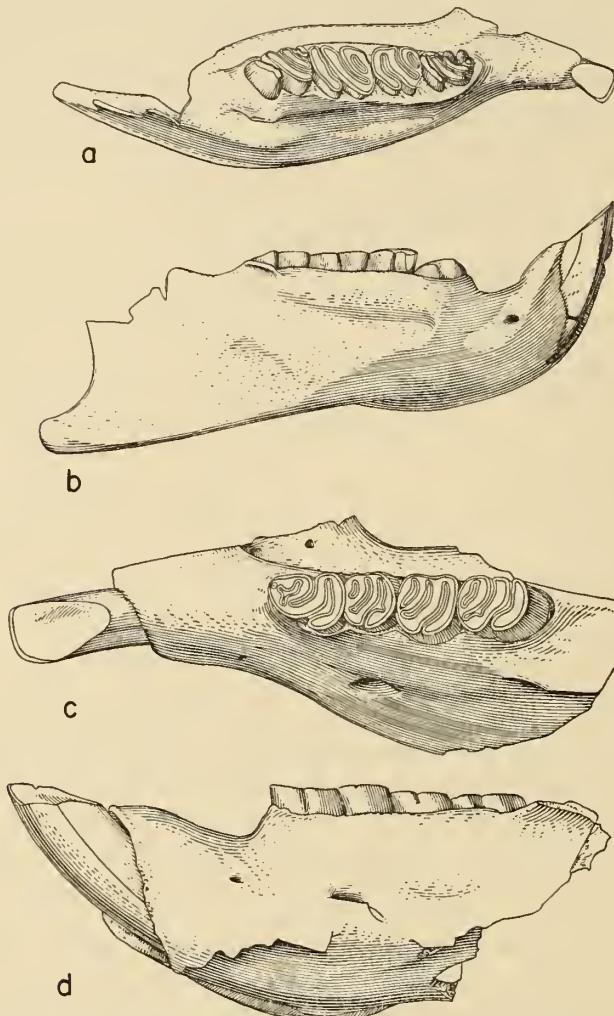
Fig. 16. *Olenopsis aequatorialis* (Anthony), La Venta area: *a*, *b*, right ramus of young animal, U.C.M.P. no. 41636, loc. V-4519; *a*, occlusal view, *b*, labial view; left ramus of adult, U.C.M.P. no. 40055, loc. V-4519; *c*, occlusal view; *d*, labial view; all drawings × 1.

face with parastriid, mesostriid, metastriid, rarely with additional anterior superficial striid; mesostriid usually extends to basal three-fifths of tooth; parastriid usually shorter, rarely as long as mesostriid; metastriid shorter than parastriid; metaflexid and hypoflexid continuous in unworn tooth, laminae usually smooth; hypoflexid crescentic in early stage of wear, becoming notched as wear proceeds; metafossettid forms to lingual side of notch and hypofossettid to labial side in extreme state of wear; mesoflexid oblique, strongly crescentic, labial part warped,

then notched as wear progresses; mesofossettid persists to base of tooth; base sometimes divides, laminae crenulated in advanced stage of wear; paraflexid variously formed, usually crescentic with wavy laminae, occasionally connected to superficial anterior fossettid, sometimes forming Y-shaped or reverse S-shaped fossettid in moderate stages of wear; fourth fossettid lost before mesofossettid isolates; parafossettid divides into two or three isolated lakes in well-worn tooth.
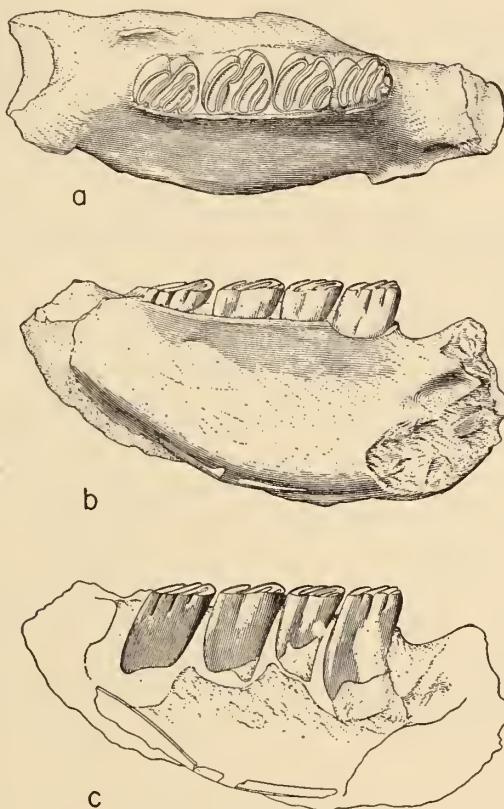
Fig. 17. *Olenopsis aequatorialis* (Anthony), U.C.M.P. no. 37928, loc. V-4525, Unit Between Ferruginous Sands and Lower Red Beds: left mandibular ramus; *a*, occlusal view; *b*, lingual view; *c*, labial view with bone removed to expose bases of teeth; × 1.

$M_{\overline{1}}$ and $M_{\overline{2}}$ differ from $P_{\overline{4}}$ in proportions and outline; anteroposterior diameter greater than transverse diameter in unworn teeth, becoming wider than long in advanced stage of wear; anterior moiety as broad as posterior in worn tooth; anterior face concave dorsoventrally, flat transversely; lingual wall flat with cleft posterior to mesostriid; labial face convex; posterior wall convex, meeting lingual surface at acute angle; hypostriid perpendicular to occlusal surface, relatively longer than on $P_{\overline{4}}$; parastriid slightly longer than metastriid on $M_{\overline{1}}$, shorter than metastriid on $M_{\overline{2}}$; mesostriid half as long as hypostriid; hypoflexid and mesoflexid more oblique than on $P_{\overline{4}}$, laminae slightly wavy in little-worn tooth, becoming notched and crescentic as wear proceeds; half-worn tooth with distinct labial notch on posterior laminae of hypoflexid and mesoflexid; paraflexid simple, slightly crescentic, para-

fossettid lost soon after hypoflexid isolates; superficial anterior fossettid rarely forms, lost in early stage of wear; mesofossettid divides to form enamel lakes, one labial, one lingual to position of notch in extremely worn tooth; metafossettid and hypofossettid separate in same manner.

$M_{\bar{3}}$ subequal to $P_{\bar{4}}$ in size; anteroposterior and transverse diameters more constant to base of tooth than in $M_{\bar{1}\text{-}\bar{2}}$; anterior face slightly convex; lingual wall flat
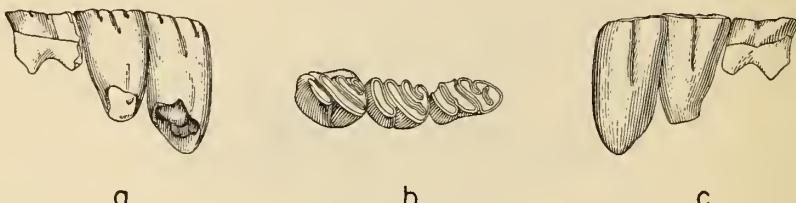
Fig. 18. *Olenopsis aequatorialis* (Anthony), U.C.M.P. no. 39928, loc. V-4521, Lone Tree locality: right $DP_{\bar{4}}$, $M_{\bar{1}\text{-}\bar{2}}$; *a*, lingual view; *b*, occlusal view; *c*, labial view; $\times$ 1.

dorsoventrally, slightly concave anteroposteriorly; posterior surface convex, meeting lingual wall at more acute angle than on $M_{\bar{1}\text{-}\bar{2}}$; anterior moiety wider than posterior throughout length of tooth; length of hypostriid more variable than on $M_{\bar{1}\text{-}\bar{2}}$, usually as short as in $P_{\bar{4}}$; metastriid usually longer than mesostriid, occasionally as short or shorter than mesostriid; parastriid shorter than mesostriid or metastriid;

MEASUREMENTS OF LOWER DENTITION

Measurements	U.C.M.P. No. 39969 (juvenile)	U.C.M.P. No. 37928 (adult)	U.C.M.P. No. 40055 (old animal)
$P_{\bar{4}}$-$M_{\bar{3}}$, alveolar length	30.0	32.2	35.2
$P_{\bar{4}}$-$M_{\bar{3}}$, occlusal length	28.7	31.8	32.8
I, anteroposterior diameter	5.5	6.4	9.8
I, transverse diameter	4.7	5.2	7.6
$P_{\bar{4}}$, anteroposterior diameter	6.9	7.4	9.6
$P_{\bar{4}}$, transverse diameter	5.0	5.5	7.3
$M_{\bar{1}}$, anteroposterior diameter	6.4	7.6	6.5
$M_{\bar{1}}$, transverse diameter	5.6	6.9	6.8
$M_{\bar{2}}$, anteroposterior diameter	8.0	8.3	7.5
$M_{\bar{2}}$, transverse diameter	5.9	7.8	7.8
$M_{\bar{3}}$, anteroposterior diameter	7.4	8.5	9.2
$M_{\bar{3}}$, transverse diameter	4.9	6.8	7.2
Depth of mandible below $P_{\bar{4}}$	19.0	25.5±	29.8

flexids strongly oblique, not crescentic in little-worn tooth, laminae with wavy outline; hypoflexid more warped than on $M_{\bar{3}}$; posterior lamina of mesoflexid develops posterolaterally directed notch at base of mesostriid; paraflexid isolates in beginning stage of wear; parafossettid, mesofossettid, and hypofossettid extend to base of tooth; metafossettid fails to isolate from hypofossettid.

Deciduous dentition.—Much as in *Scleromys colombianus*; DP^4 with long hypostria, medistria, and short posterior stria on lingual face; labial wall with superficial parastria, mesostria, metastria, and entostria; metafossette sometimes connected posteriorly to one, two, or three small superficial fossettes; $DP_{\bar{4}}$ with long hypostriid

and shorter anterior striid on labial wall; lingual face with metastriid, mesostriid, parastriid, and superficial anterior striid; mesostriid longer than other lingual striids; anterior moiety with small parafossettid and one, two, or three small superficial fossettids anterior to it.

Postcranial skeleton.—One nearly complete skeleton and two partial skeletons of this species are known from the La Venta fauna. Unfortunately, the best specimen,

MEASUREMENTS OF DP⁴

Measurements	U.C.M.P. No. 40727
Anteroposterior diameter at base of internal stria..............................	10.8
Transverse diameter at base of external stria...................................	4.7
Anteroposterior diameter at base of hypostria................................	8.3
Transverse diameter at base of hypostria.....................................	5.3

MEASUREMENTS OF DP₄

Measurements	U.C.M.P. No. 39928
Anteroposterior diameter at base of internal striids...........................	9.5
Transverse diameter at base of internal striids...............................	4.5
Anteroposterior diameter at base of hypostriid...............................	8.8
Transverse diameter at base of hypostriid....................................	4.6

U.C.M.P. no. 41636, is a juvenile individual on which nearly all epiphyses are loose or missing; of the other two, one is another young animal, U.C.M.P. no. 39969, and the other is a fragmentary adult skeleton, U.C.M.P. no. 40055.

Scapula.—Glenoid, fossa, neck, postscapular fossa, distal part of spine, and proximal part of acromion preserved; glenoid fossa ovoid, concave; glenoid angle not

MEASUREMENTS OF SCAPULA

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 40055
Anteroposterior diameter of glenoid fossa.........................	11.8	19.3
Transverse diameter of glenoid fossa..............................	8.6	13.4
Smallest anteroposterior diameter of neck.........................	10.7	18,5
Transverse diameter of neck at same level........................	4.4	8.7

prolonged as in *Myocastor*; coracoid process broken, evidently blunt, no ligamental groove on medial surface as in *Lagidium* or *Myocastor*; incisura scapulae not as deep as in *Lagidium*, nor as shallow as in *Myocastor*; neck relatively shorter than in *Cuniculus*; glenoid border convex proximodistally, thickened transversely; postscapular fossa shallow, not so concave as in *Cuniculus*; spine thickened; metacromion enlarged, deflected posteriorly; scapula seems closer to *Dinomys* than to any of the genera available for comparison.

Humerus.—Shaft straight; head simple, large; bicipital groove short, wide, shallow; greater tuberosity low, bulbous, not elevated above head as in *Cuniculus*; pectoral ridge extends nearly one-half length of shaft, not as long as in *Cuniculus*, longer than in *Myocastor*, distal part elevated as laterally curved crest, more prominent than in *Lagidium* and *Cuniculus*, not as rugose or twisted as in *Myocastor*; deltoid ridge insignificant; entepicondylar foramen absent; distant end transversely

MEASUREMENTS OF HUMERUS

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 40055	U.C.M.P. No. 39898
Length from head to distal keel.....................	80.0±	....	....
Width across tuberosities..........................	....	....	26.1
Diameter across head (bicipital groove to lower border)	13.4	....	26.8
Width across epicondyles..........................	18.7	28.4	....

expanded; capitulum flattened; trochlea saddle-shaped; median keel more sharply defined than in living genera except *Lagidium*; radial fossa deeper than coronoid fossa; olecranon fossa deeper, broader than in *Myocastor*; medial epicondyle expanded; lateral epicondyle small, with low tubercle; proportions and morphologic characters more like those in *Dinomys* than in other genera compared.

Ulna.—Olecranon slightly arched forward; sigmoid notch somewhat oblique, upper border deflected laterally, transversely convex, moderately deep, lower

MEASUREMENTS OF ULNA

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 40055
Greatest length...	85.0±	....
Width across styloid process......................................	6.5	....
Length across styloid process.....................................	8.3	....
Width across upper border of sigmoid notch.......................	8.1	11.9

medial lip directed distally; radial notch small, subtriangular; bicipital fossa shallow, elongate; shaft essentially straight, lateral face concave proximally, rounded distally; medial face slightly convex; midpart of shaft with anteroposterior diameter twice transverse diameter; styloid process deflected posteriorly; proportions as in *Dinomys*.

Radius.—Articular circumference flattened; facet for radial fossa of humerus more flattened than in *Cuniculus*, not as flat as in *Myocastor*; neck transversely ovoid; bicipital tuberosity narrow, elongate, more pronounced than in *Cuniculus*; interosseous membrane attachment as linear groove on posterior surface of shaft; distal end subtriangular, posterior part excavated for reception of styloid process of ulna; shaft slightly bowed anteriorly; most characters similar to those in *Dinomys*.

Scapholunar.—Scaphoid and lunar fused; proximal surface transversely crescentic, convex anteroposteriorly; distal surface concave anteroposteriorly, flattened transversely, evidently articulates with trapezium, trapezoid, magnum, and unciform; lateral face with crescentic facet for cuneiform; general configuration like that

in *Dinomys*, not so rugose or angulate as in *Myocastor*; greatest width 11.0 mm., as measured on U.C.M.P. no. 41636.

Unciform.—Medial half of proximal surface as knoblike facet for scapholunar, lateral half with sloping facet for cuneiform; anterior face flat proximodistally, convex transversely; medial surface with subtriangular facet for magnum; distal facet concave anteroposteriorly; lateral part transversely convex, articulates with mc. V; medial part transversely concave, articulates with mc. IV; proportions as in *Dinomys*; transverse width of U.C.M.P. no. 41636, 7.7 mm.

MEASUREMENTS OF RADIUS

Measurements	U.C.M.P. No. 41536
Length from head to styloid process..	68.0±
Transverse diameter of head...	10.6

Pisiform.—Longer than broad, with enlarged ends, much as in *Dinomys*, not rectangular as in *Lagidium*; distally more bulbous than in *Myocastor*.

Metacarpals and *phalanges.*—Digits five in number; mc. I vestigal; mc. III and IV longer than II and V; distal ends of metacarpals bulbous; proximal ends convex anteroposteriorly; proximal phalanx III slightly longer and heavier than IV; proximal phalanx IV somewhat larger than II or V; proximal phalanx I reduced to short conical element; median phalanges half as long as proximal counterparts, subtriangular in cross-section, less curved than in *Myocastor*; general appearance as in *Dinomys* but metacarpals more slender and elongate.

MEASUREMENTS OF PELVIS

Measurements	U.C.M.P. No. 39969	U.C.M.P. No. 40055
Length from crest of ilium to anterior rim of acetabulum..........	64.4	....
Diameter of acetabulum..	13.4	17.4

Pelvis.—Acetabulum moderately deep; incisura acetabuli open; ischial spine more reduced than in *Cuniculus*, expressed as knob with rugose surface; ischial obturator border slightly notched anteriorly but not as deeply as in *Cuniculus*, not smooth as in *Cercomys*; obturator foramen evidently not as elongate as in *Lagidium*; tuberosity of ischium not expanded as in *Cuniculus*; pubis not preserved; acetabular part of ilium moderately elevated; lateral surface of ilium with enlarged tubercle anterior to acetabulum, not as prominent as in *Lagidium*; great sciatic notch deeper and closer to acetabulum than in *Cuniculus*; auricular border straight; posterior inferior spine well developed; iliopectineal line smooth, rounded; iliopectineal eminence blunt, crest not as sharp as in *Lagidium*; crest of ilium thickened, not expanded or deflected as much as in *Lagidium* or *Cuniculus*; iliac fossa shallow, wide; second sacral vertebra contacts with ilium at posterior-inferior spine, elements of pelvis more like those in *Dinomys* than in other living genera observed.

Femur.—Proportions very similar to those in *Scleromys*; greater trochanter ex-

tends above capitulum, not as massive as in *Cuniculus*, not as low as in *Myocastor* nor as high as in *Lagidium*; intertrochanteric ridge more curved than in all genera compared except *Dinomys* and *Cercomys*, edge smooth, rounded, curled toward head; trochanteric fossa deep, ovoid, less rounded than in *Cuniculus*; neck thick, broadly ovoid; head well-rounded, relatively larger than in *Cuniculus* or *Lagidium*; pit for ligamentum teres rounded, small, not as prominent as in *Myocastor*; lesser

MEASUREMENTS OF FEMUR

Measurements	U.C.M.P. No. 39969	U.C.M.P. No. 40055	U.C.M.P. No. 39599
Greatest length	99.2	....	132.0±
Proximodistal diameter of neck	8.0	12.3	10.7
Anteroposterior diameter of neck	6.8	10.1	8.6
Diameter of head	13.2	17.4	15.7
Diameter across lesser trochanter	15.5	22.6	17.7
Width across distal condyles	23.8	35.9	....
Length of internal condyle	24.5	....	....

trochanter prominent, ovoid, lateral surface flattened, medial surface concave; lateral part of greater trochanter as enlarged tubercle overhanging anteroproximal face of shaft, distally continuous as distinct, posterodistally deflected linea aspera; shaft robust, straight, ovoid distally; medial condyle larger than lateral condyle; medial and lateral tuberosities not expanded as in *Myocastor*; intercondyloid fossa wider than in *Myocastor*; patellar groove not as elongate as in *Cuniculus*, longer than

MEASUREMENTS OF TIBIA

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 39969	U.C.M.P. No. 40055
Length from spine to malleolus	125.3	....	....
Transverse diameter of head	25.0	24.7	....
Anteroposterior diameter of head	19.2	18.9	....
Width across astragalar facet	17.4	16.6	20.0
Diameter from medial malleolus to descending process	15.5	15.1	18.2

in *Lagidium*, not expanded anteriorly as in *Cuniculus*; pit for ligament of gastrocnemius muscle shallow, elongate, not deep as in *Lagidium*.

Patella.—Elongate, wedge-shaped; proximal part broad, thickened, anteriorly convex; distal anterior face concave, rugose, elongate with subrounded distal apex; posterior face with proximodistally and transversely concave medial facet and proximodistally concave, transversely flattened lateral facet; medial facet narrower and more oblique than lateral facet; proximal width, 9.5 mm.; length, 19.7 mm.; as measured on U.C.M.P. no. 39969.

Tibia.—Shaft essentially straight, 23 per cent longer than in *Dinomys*; proximal end expanded transversely and posteriorly, subtriangular in cross-section; tubercle for attachment of patellar ligament ovoid with transverse ridge; external tuberosity higher than internal tuberosity; tibial spine shorter than in *Myocastor* and *Cunicu-*

lus; papliteal notch wider and longer than in *Myocastor* and *Lagidium*, expanded anteriorly; cnemial ridge straight, not as long as in *Cuniculus*, more clearly defined than in *Myocastor*; distal part subtriangular; medial malleolus shorter and wider than in *Lagidium*, relatively longer and narrower than in *Myocastor*; distal fibular facet oblique, small, ovoid, not elongate or extended toward malleolus as in *Lagidium* or *Myocastor*, nor as small and rectangular as in *Cuniculus*; descending process short, astragalar facet deep, oblique.

MEASUREMENTS OF CALCANEUM

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 39969	U.C.M.P. No. 40055
Greatest length	....	34.6	....
Length from nutrient foramen to olecranon	....	26.8	39.2
Anteroposterior diameter of olecranon	9.8	10.8	13.2
Transverse diameter of olecranon	11.1	11.8	15.5
Proximodistal length of astragalar facet	10.8	11.4	12.8
Transverse width of astragalar facet	7.6	7.8	8.2

Calcaneum (Fig. 19, *a-c*).—Proportions very similar to those in *Dinomys*; astragalar facet oblique, convex proximally, concave distally, flattened transversely, subrectangular in outline; sustentacular facet widely expanded, crescentic in shape, concave, distal rim pierced by large foramen as in *Dinomys* and *Scleromys*; posterior surface of sustentacular expansion grooved for tendon of flexor digitalis longus muscle; peroneal tubercle with oblique groove, not as prominent as in *Lagidium*;

MEASUREMENTS OF ASTRAGALUS

Measurements	U.C.M.P. No. 41636	U.C.M.P. No. 39969
Total length	20.7	20.9
Width of condyles at widest point	12.5	12.7
Length from head to proximal end of sustentacular facet	14.1	14.5
Anteroposterior diameter of head	7.0	7.3
Transverse diameter of head	9.8	10.0

cuboidal facet oblique, broadly ovoid in shape, concave anteroposteriorly, convex transversely; medial surface of bone flattened proximodistally, slightly convex transversely; lateral face concave above astragalar facet; proximal part of bone longer than distal part, triangular in cross-section, not as ovoid as in *Lagidium*; olecranon larger, more rugose than in *Myocastor* and *Lagidium*; groove for tendon of Achilles not distinct.

Astragalus (Fig. 19, *d-f*).—Essentially as in *Dinomys*; calcanear facet oblique, broadly wedge-shaped, proximal half strongly concave proximodistally, distal half flattened becoming convex at apex; sustentacular facet long, extends from posterior lip of trochlea to head, surface as squared oval, convex; separated from calcanear facet by deep, distally broadened median groove for tendon of flexor hallucis longus muscle; median groove wider than in all recent genera observed except *Dinomys*;

external condyle wide, transversely convex; internal condyle with sharp rim and steep wall; trochlea deep, smooth, continues forward to pit for origin of extensor brevis digitorium muscle; condyles broader distally; neck more elongate than in *Myocastor*, relatively shorter than in *Lagidium*, broad transversely, 15 degrees oblique to proximodistal axis of condyles, transverse ridge on anterior face as in *Dinomys*; navicular facet well rounded, twice as wide as long, medial half broader than lateral part, continuous with sustentacular facet; medial side of head with
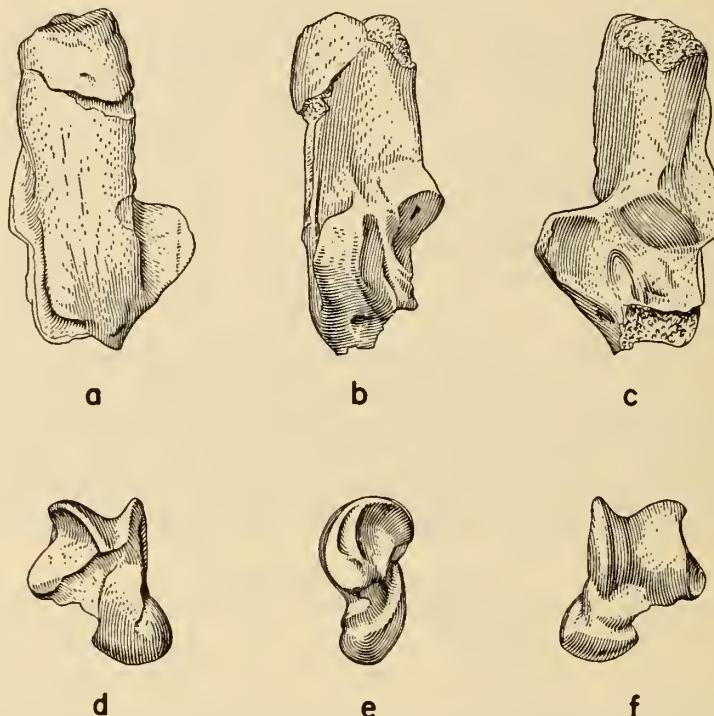
Fig. 19. *Olenopsis aequatorialis* (Anthony), La Venta area: *a-c,* left calcaneum, U.C.M.P. no. 40055, loc. V-4519; *a,* posterior view; *b,* medial view; *c,* anterior view: *d-f,* left astragalus, U.C.M.P. no. 39969, loc. V-4519; *d,* posterior view; *e,* lateral view; *f,* anterior view; × 1.

convex face for sesmoid bone; proximolateral face with facet for malleolus of fibula, facet "comma-shaped," flag part parallels rim of external condyle.

Navicular.—Proximal outline as rounded triangle; astragalar facet large, deeper than in *Myocastor*; posterior part of proximal surface excavated for attachment of ligament, sesmoid facet medial to excavation oblique; cuboidal facet oblique, sub-rounded, concave, on anterior half of lateral face; ectocuneiform facet triangular, half as long as cuboidal facet, surface flattened, anterior rim slightly rounded; mesocuneiform facet broadly crescentic; entocuneiform facet small, rectangular, oblique to mesocuneiform facet; body of navicular one-third deeper over ecto-cuneiform facet than over mesocuneiform facet; posterior surface as broad, flat tubercle extending below level of mesocuneiform facet; anteroposterior diameter, 12.2 mm.; greatest width of face, 10.1 mm.; greatest depth of face, 5.9 mm.; all measured on U.C.M.P. no. 39969.

Cuboid.—Calcanear facet more elongate, less convex anteroposteriorly, more concave obliquely than in *Dinomys*; navicular facet triangular in outline, slightly convex; ectocuneiform facet concave, higher than broad; facet for mt. IV antero-posteriorly oblique; facet for mt. V as two obliquely oriented pits on lateral surface; posterior face with enlarged tubercle that overhangs mt. V; greatest height, 11.8 mm.; greatest anteroposterior diameter, 10.2 mm.; all measurements from U.C.M.P. no. 39969.

Ectocuneiform.—Relatively larger than in *Dinomys*; body as subtriangular prism; anterior face square, convex transversely; cuboidal facet convex, on proximal half of lateral face, distal half of face excavated; medial face with narrow proximal mesocuneiform facet, distal part with flat, oblique facet for articulation with mt. II; greatest depth of anterior face, 6.1 mm.; greatest width of anterior face, 7.7 mm.; measured on U.C.M.P. no. 39969.

MEASUREMENTS OF PES

Measurements	U.C.M.P. No. 39969
Length of mt. II	44.7
Length of proximal phalanx III	23.2±
Length of proximal phalanx V	16.2
Length of median phalanx III	10.8
Length of distal phalanx III	12.6

Mesocuneiform.—Half as large as ectocuneiform; body flattened transversely; navicular facet subovoid; ectocuneiform facet convex, occupies entire lateral face; medial face with facet for entocuneiform, facet for mt. II concave anteroposteriorly, flat transversely; depth of anterior face, 3.6 mm.; width of anterior face, 4.1 mm.; measured on U.C.M.P. no. 39969.

Entocuneiform.—Essentially as in *Dinomys*; elongate proximodistally; proximo-lateral surface with small ovoid navicular facet; lateral face with small facet for mesocuneiform; distal face with facet for vestigial mt. I; proximodistal length, 11.1 mm. anteroposterior diameter, 4.8 mm.; transverse diameter, 2.8 mm.; U.C.M.P. no. 39969.

Metatarsals and Phalanges.—Only left mt. II complete; digits five in number; mt. I vestigial; mt. III and IV subequal in length, heavier and slightly longer than II and V; distal ends bulbous; mt. II extended proximally one-half the height of ectocuneiform; mt. II and V with proximal posterior projections; metatarsals relatively (44 per cent) longer than those in *Dinomys* but otherwise very similar; proximal phalanges III and IV longer and heavier than II and V; distal ends of II and V not as bulbous as those of III and IV; median phalanges half as long as proximal counterparts; distal phalanges as in manus; pes twice as large as manus.

Cervical vertebrae.—Neural arch of axis; entire third, fourth, and fifth; centrum and part of neural arch of sixth and seventh preserved; vertebrae closely oppressed, showing tendency toward fusion of anterior part of series, as in *Dinomys*; transverse process of sixth not developed into anteroposterior rodlike process as in *Lagidium* and *Cuniculus*; general proportions and morphologic characters as in *Dinomys*.

TABLE 6

Comparative Measurements of Olenopsis Species

Measurements	Olenopsis uncinus[a]	Olenopsis typicus[b]	Olenopsis aequatorialis[c]	U.C.M.P. No. 39969	U.C.M.P. No. 37928	U.C.M.P. No. 40055	U.C.M.P. No. 39928
Occlusal length from $P_{\overline{4}}$ to $M_{\overline{3}}$	....	....	31.5	28.7	31.8	32.8	....
I, anteroposterior diameter	....	5.0	10.2	5.5	6.4	9.8	....
I, transverse diameter	4.0	3.8	8.4	4.7	5.2	7.6	....
$DP_{\overline{4}}$, anteroposterior diameter	8.0	9.5	....	....	....	....	9.5
$DP_{\overline{4}}$, transverse diameter	6.0	4.5	....	....	....	....	4.5
$P_{\overline{4}}$, anteroposterior diameter	....	....	9.5	6.9	7.4	9.6	....
$P_{\overline{4}}$, transverse diameter	....	....	6.7	5.0	5.5	7.3	....
$M_{\overline{1}}$, anteroposterior diameter	6.0	8.0	6.2	6.4	7.6	6.5	7.7
$M_{\overline{1}}$, transverse diameter	6.0	8.0	7.0	5.6	6.9	6.8	5.8
$M_{\overline{2}}$, anteroposterior diameter	....	8.0	7.5	8.0	8.3	7.5	8.0
$M_{\overline{2}}$, transverse diameter	....	8.0	7.4	5.9	7.8	7.8	6.2
$M_{\overline{3}}$, anteroposterior diameter	....	....	8.8	7.4	8.5	9.2	....
$M_{\overline{3}}$, transverse diameter	....	....	7.5	4.9	6.8	7.2	....
Depth of mandible below $P_{\overline{4}}$	13.0	19.0	29.7±	19.0	25.5±	29.8±	....
Depth of mandible below $M_{\overline{2}}$	....	18.0	28.2±	18.3	23.6±	27.8±	....
Length of diastema	....	19.0	17.0±	16.5	....	18.0	....

[a] From published figure (Ameghino, 1889B).
[b] From published figure (Ameghino, 1891E).
[c] From published figure (Anthony, 1922).

Thoracic vertebrae.—Entire series of fourteen vertebrae preserved but many processes missing; centrum of fourteenth twice as large as that of fourth; neural spines long, thin, sloping posteriorly from first to eight; ninth nearly vertical, short; eleventh to fourteenth progressively shorter, stouter, sloped anteriorly; gross relationships as in *Dinomys*.

Lumbar vertebrae.—Complete series of five preserved; transverse processes becoming wider posteriorly; fifth nearly as wide as sacrum; neural spines sloped anteriorly, longer than in *Dinomys*; centra become progressively larger toward sacrum.

Sacrum.—Much as in *Dinomys*; not completely preserved; specimen young; vertebrae not fully fused; first and second fused; fragments indicate four vertebrae involved in sacrum; first sacral with greatly expanded transverse processes that articulate firmly with iliac fossa; transverse processes of second sacral one-half as large as those on first, articulate with ilium on area of posterior inferior spine; posterior sacrals not articulated with ilium; width across first sacral, 38.6 mm.; length of transverse process of first sacral, 26.0+ mm.; measured on U.C.M.P. no. 41636.

Caudal vertebrae.—Five vertebrae preserved, from two individuals, essentially as in *Dinomys*; chevron bones small, not as long as in *Lagidium*.

Comparisons.—Characters that seem to place *Olenopsis aequatorialis* in the genus *Olenopsis* are:

1. Massive, heavy mandible.
2. Similarity of dental pattern on cheek teeth.
3. $M_{\bar{2}}$ largest of lower series.
4. Subequal size of $P_{\bar{4}}$ and $M_{\bar{3}}$.
5. Extremely long lower incisors (base well behind $M_{\bar{3}}$), with excessively thick, broad, flattened enamel face.
6. Exceptionally short lower diastema (half as long as cheek-tooth series).
7. Reduced coronoid process opposite posterior moiety of $M_{\bar{3}}$.

Olenopsis uncinus Ameghino, from the Santa Cruz fauna, and *Olenopsis typicus* Scalabrini, from the Paraná beds, are the only other species known. Type materials of the three species were not seen; thus it was necessary to rely on the published descriptions (Ameghino, 1889ʙ and 1891ᴇ; Anthony, 1922). Unfortunately, *O. uncinus* is known from only a left DP⁴; part of a left ramus with incisor, $DP_{\bar{4}}$, and slightly worn $M_{\bar{1}}$; right $DP_{\bar{4}}$ of another young individual. *O. typicus*, by coincidence, is represented by a left ramus of an immature animal with incisor, $DP_{\bar{4}}$, and $M_{\bar{1}}$ and $M_{\bar{2}}$ in place. For comparative purposes, only the mandible is available in the three species. Good comparison with the Argentine species is difficult as the specimens are much less mature than the type of *O. aequatorialis* or any of the specimens from La Venta; thus size comparisons can not be definitely established (see table 6).

O. uncinus and *O. typicus* differ from *O. aequatorialis* in: relatively less robust appearance; proportionally longer diastema; slightly less complicated cheek-tooth pattern; less robust incisors.

O. uncinus and *O. typicus* resemble *O. aequatorialis* in: similarity of dental pattern; gross shape of cheek teeth; flattened, broad incisors with base posterior to $M_{\bar{3}}$; reduced coronoid process situated opposite posterior moiety of $M_{\bar{3}}$; massive, elongate symphysis; prolonged retention of $DP_{\bar{4}}$.

Scleromys differs from *Olenopsis* in: smaller size; less robust incisors with more

convex enamel face; less hypsodont, more completely rooted, more rounded cheek teeth; more simplified dental pattern with less persistent stria and fossettes; absence of entoflexus; weaker development of parafossettid and shorter, less curved mesoflexid on lower teeth; relatively smaller incisive foramen; longer upper and lower diastems; less convergent dental rows; less complex sutural pattern between palatines and maxillaries; lack of pronounced median ridge anterior to posterior palatine foramina; shallower rostral masseteric fossa; deeper, more sharply defined nerve channel on ventral margin of infraorbital foramen; straighter nasals; more rounded parietals; shallower, less robust mandible; deeper, longer inferior pterygoid fossa; relatively larger, higher, more posteriorly situated coronoid process; less robust postcranial skeleton; narrower calcaneum with more elongate distal part and shallower groove for flexor digitalis longus tendon; narrower, less excavated groove for tendon of flexor hallucis longus muscle on astragalus; relatively shorter, more curved tibia.

Scleromys agrees with *Olenopsis* in: long, flattened cranial roof; absence of sagittal crest; enlarged premaxillary with strong buttress anterior to incisors; squared rostral crest; enlarged premaxillary with strong buttress anterior to incisors; square masseteric fossa; absence of accessory rostral opening for lacrymal duct; lateral bony ridges passing backward from incisive foramen to alveoli of P4s; elongate basicranial axis; prominent orbital fissure; moderately enlarged auditory bullae; enlarged accessory ventral opening below tubular part of external auditory meatus; closely oppressed mastoid process; short, blunt paraoccipital process; low, wide foramen magnum; strongly curved upper incisors; extremely long lower incisors; elongate, massive mandibular symphysis; laterally distorted angle; shallow mandibular masseteric fossa; ovoid, depressed masseteric crest.

Olenopsis has been compared to *Myopotamus* and *Neoreomys* by Ameghino (1889в) and to *Myocastor* and *Neoreomys* by Anthony (1922). All these genera differ from *Oleonopsis* in having: less flattened cranial roof; development of distinct sagittal crest; larger, extremely lengthened paraoccipital process; more convex, relatively longer nasals; longer rostrum with more rounded masseteric fossa; absence of nerve canal in infraorbital foramen; shorter, more rounded orbit with distinct orbital notch and prominently developed postorbital process; relatively shorter basicranial axis; less robust incisors with convex enamel face; less curved upper incisor (base above M^2); shorter lower incisor (base below anterior moiety of $M_{\bar{3}}$); distinct dental pattern with wide flexi; increasing size from $P_{\bar{4}}^4$ to $M_{\bar{3}}^3$; proportionally larger cheek teeth; less robust mandible; shallower geniohyoid pit; more posteriorly placed masseteric crest (below $M_{\bar{1}}$); deeper, more elongate masseteric fossa; more prominent, laterally expanded ventral masseteric crest; wider, extremely shallow inferior pterygoid fossa.

Detailed similarities between these genera and *Olenopsis* are difficult to find. Superficial similarities of dental pattern have evidently led to erroneous conclusions concerning relationships of *Olenopsis* and *Scleromys*.

Dinomys differs from *Olenopsis* primarily in having: extremely hypsodont, completely rootless cheek teeth with more complete, lophodont enamel columns; parastria, mesostria, metastria, hypostria, and lower counterparts distinct to base of teeth; additional labial striid anterior to hypostriid also extending to base of tooth; relatively shorter tibia and metatarsals.

Dinomys resembles *Olenopsis* in having: robust general form and similar size; extremely flattened cranial roof; no development of sagittal crest; absence of postorbital process; elongate orbital region; anteriorly expanded nasals; greatly enlarged incisive foramen with lateral bony ridges extending back to P^{4}s; shallow nerve canal on ventrolingual margin of infraorbital foramen; shallow, anteriorly squared rostral masseteric fossa; no accessory lacrymal opening on side of rostrum; elongate posterior palatine foramen with distinct canals continuing forward into incisive foramen; enlarged ventral accessory opening on external auditory meatus; short, massive mastoid process; short paraoccipital process closely oppressed to mastoid; low, broad foramen magnum; elongate basicranial axis; robust, flattened, extremely broad incisors; strongly curved, externally expressed upper incisors; anteriorly converging tooth rows; increasing size from P$^4_{\overline{4}}$ to M$^2_{\overline{2}}$ with M$^3_{\overline{3}}$ subequal to P$^4_{\overline{4}}$ in size; heavy, broad mandible with long massive symphysis; reduction of coronoid process; deeply excavated geniohyoid pit; extremely short lower diastema; small mental foramen; distinct digastric crest; small, ovoid, depressed masseteric crest situated below P$_{\overline{4}}$; shallow, flat masseteric fossa; extremely long lower incisor (base well behind M$_{\overline{3}}$), with external expression as wide, flattened surface along ventrolingual line of incisor. Other similarities are seen in: tendency toward fusion of anterior cervical vertebrae; presence of fourteen thoracic vertebrae; extreme anteroposterior expansion of transverse process on first sacral vertebra; development of heavy, flattened ribs; short, robust pelvis; massive, straight femur and tibia; shortening of distal part of calcaneum with development of large nutrient foramen on ventral surface of sustentacular facet and deeply excavated groove for tendon of flexor digitalis longus muscle; widening of calcanear facet and deepening of groove for tendon of flexor hallucis longus muscle on astragalus; presence of four functional digits on manus and pes with mt. I and mc. I retained as short vestigial elements.

Further comparisons of *Olenopsis* with available living forms would be of no further significance in establishing relationships. Most of the differences noted between *Scleromys* and these genera are even more pronounced when these genera are compared with *Olenopsis*.

DESCRIPTION OF THE AUDITORY REGION IN OLENOPSIS
(Figs. 20-24)

The structure of the auditory region in hystricomorph rodents has attracted the attention of some earlier investigators, and several accounts have been written. The internal structure of the bulla, however, has not received adequate attention. Van der Klaauw (1931b) published a general account of the auditory region in fossil mammals and compared them to certain recent forms. The present investigation came as a result of finding a right bulla of *Olenopsis* in which the internal structure of the bulla and the auditory ossicles were perfectly preserved. Such a rare find could not be neglected. Comparative materials available at the University of California permitted a comparison with *Erethizon, Cavia, Dinomys, Dasyprocta,* and *Isolobodon.* The auditory bullae of these genera were removed from the skull so that the cerebral and nasal faces could be studied. Each bulla was sectioned on an oblique anteroposterior plane through the external auditory meatus and mastoid region and passing ventral to the styliform process (see Fig. 20). By opening the
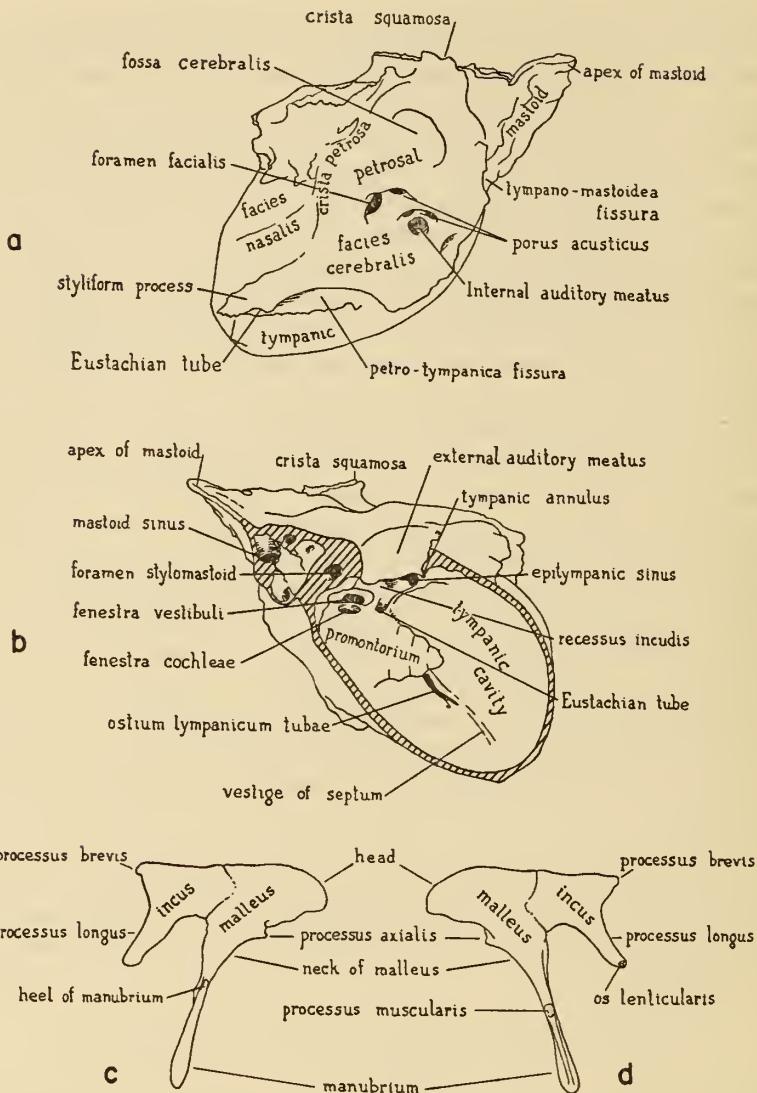
Fig. 20. Terminology of the auditory bulla, incus and malleus: *a*, cerebral view of bulla; *b*, internal view of bulla (cross-hachuring indicates plane of section exposing middle ear); *c*, ventral view of incus and malleus; *d*, dorsal view of incus and malleus. Example is from *Dasyprocta*: *a, b*, × 2; *c, d*, approx. × 7.5.

bulla in this manner the features of the middle ear could be readily observed and compared. Figure 20, *a, b, c*, and *d* shows the topography of structures and the terminology used in the following description and comparisons.[6]

Cerebral surface.—Facies cerebralis divided into dorsal and ventral, slightly concave parts by rounded anteroposterior ridge; fossa cerebralis large, deeply excavated; foramen facialis small, situated deep under anteroposterior ridge of facies cerebralis; internal auditory meatus slightly larger and somewhat more ventral than foramen facialis; porus acusticus compound, anterior pore penetrates dorsal

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[6] The terms used are from C. J. Van der Klaauw (1931B) and B. Patterson (1936A).

wall of foramen facialis, median pore pierces dorsal wall of internal auditory meatus, posterior pore penetrates posterior wall of internal auditory meatus; crista petrosa prominent, broad dorsally; crista squamosa fairly smooth, not greatly expanded; mastoid not greatly enlarged, apex of mastoid rounded; tympano-mastoidea fissura moderately deep; petrotympanica fissura not well preserved but evidently shallow; facies nasalis meets facies cerebralis at sharp angle along crista petrosa, surface slightly concave, pierced by several venous foramena; styliform process robust, short; anterior opening for Eustachian tube enlarged.

Internal structure.—Tubular part of external auditory meatus moderately elongate; epitympanic sinus enlarged, situated anterior to external auditory meatus, partially divided by septum; tympanic cavity ovoid anteroposteriorly, relatively shallow, surface with ridges representing vestigial septa; ostium tympanicum tubae broad, bounded by lateral ridge; promontorium simple, small, broadly pear-shaped, coil of cochleae only slightly evident on surface, apex connected to floor of tympanic cavity by thin laminae that continues anteriorly along medial side of ostium tympanicum tubae; fenestra cochleae moderately large, opens laterally into vestibule, margin irregular; fenestra vestibule ovoid, situated deep in floor of vestibule; mastoid region moderately recessed as mastoid sinus, continuous with tympanic cavity, area of separation marked by several spines extending into cavity; tympanic annulus indistinct; recessus incudis broad, deep, situated above dorsal rim of tympanic annulus; stylomastoid foramen situated in posterior wall of external auditory meatus; internal opening for Eustachian tube moderately large, situated anterior to vestibule and medial to recessus incudis.

Malleus.—Malleus twice as large as incus; head robust, subtriangular in cross-section; processus axialis moderately developed, accompanied by medial sulcus; neck broad, rounded distally; processus muscularis moderately enlarged and raised; manubrium broad distally, spatulate; heal opposite and lateral to processus muscularis, not raised from neck. Malleus not separable from incus.

Incus.—Body short, stout; processus brevis broadly rounded, apex developed as short, rounded knob; processus longus stout, relatively long with slight posteromedial spur leading to os lenticularis, which is broadly ovoid in outline and relatively small.

COMPARISON WITH OTHER GENERA[7]
(Figs. 21-24)

Cerebral surface.—The cerebral face of the bulla in *Olenopsis* is more like that in *Dinomys* than in other genera compared, except that in *Dinomys* the fossa cerebralis is extremely shallow and represented by a double concave area. In this respect *Dinomys* resembles *Erethizon*, and *Olenopsis* seems more like *Dasyprocta*. *Olenopsis* closely resembles *Dinomys* and *Erethizon* in the character of the foramen facialis, internal auditory meatus, and porus acusticus. In these features *Cavia* and *Dasyprocta* show much greater excavation, and *Isolobodon* is greatly divergent. The tympanomastoidea fissura and petrotympanica fissura are deeply incised on *Erethizon*, *Dasyprocta*, and *Isolobodon*, but are poorly developed on *Dinomys*, *Cavia*, and *Olenopsis*. The configuration of the facies nasalis in *Olenopsis* is most like that in *Dinomys*. It is comparatively flat, rectangular in outline, subequal to the facies cerebralis in surface area, and pierced by several venous foramena. The ventral

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[7] *Erethizon, Cavia, Dinomys, Dasyprocta,* and *Isolobodon.*
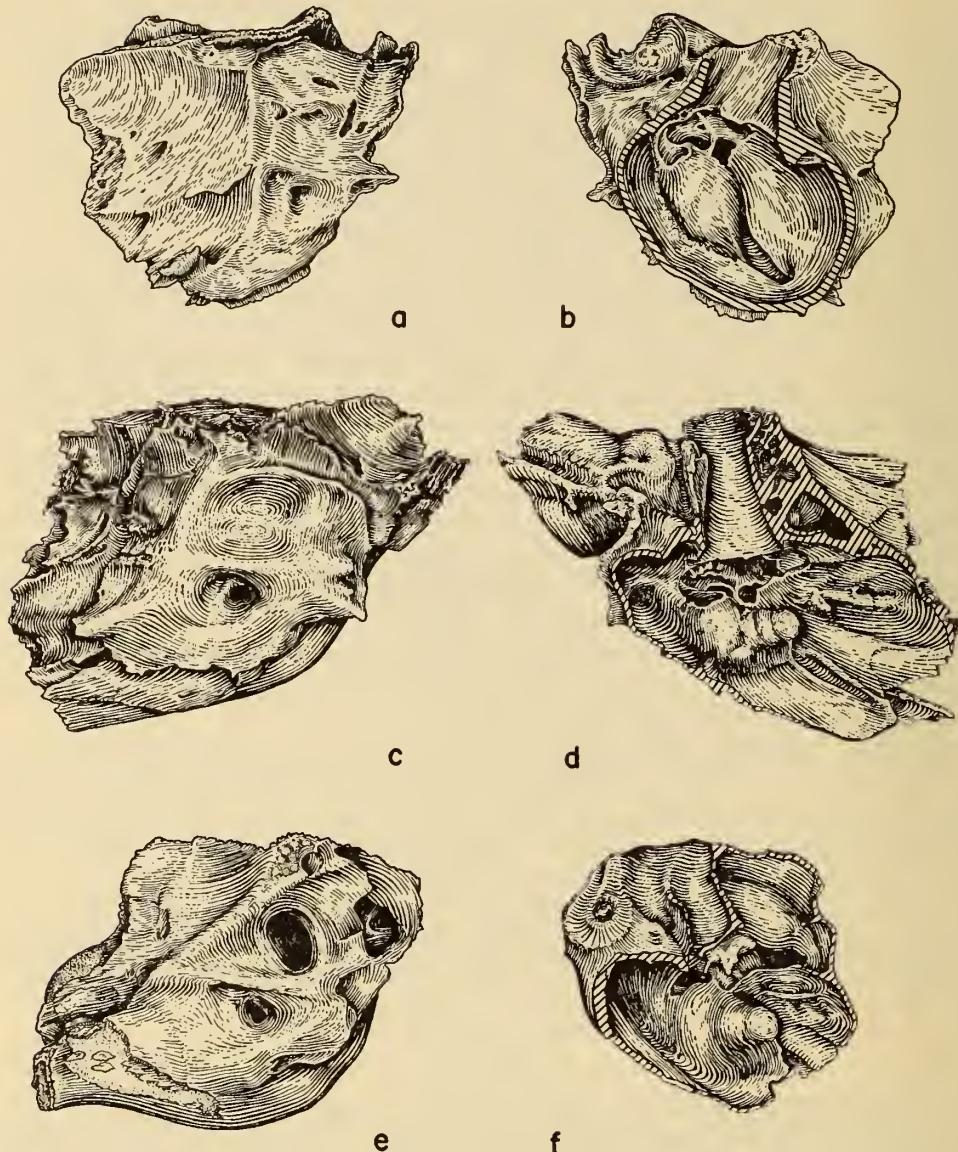
Fig. 21. The auditory bullae of hystricomorph rodents: *a, b, Erethizon; a,* cerebral view; *b,* internal view: *c, d, Dinomys; c,* cerebral view; *d,* internal view: *e, f, Olenopsis aequatorialis* (Anthony); *e,* cerebral view, U.C.M.P. no. 39969, loc. V-4519; *f,* internal view, U.C.M.P. no. 41636, loc. V-4519; all drawings × 2.

part is slightly furrowed anteroposteriorly. The facies nasalis in *Erethizon* is larger and broadly triangular in outline. The dorsal part is slightly concave, and the ventral part is traversed by a prominent furrow. In *Cavia* the facies nasalis is triangular and ventrally furrowed as in *Erethizon,* but the surface is anteroposteriorly convex. In *Dasyprocta* and *Isolobodon* the facies nasalis is small, smooth, more continuous with the tympanic, and shows only slight development of a ventral furrow. In *Olenopsis* the crista petrosa is dorsally prominent as in *Dasyprocta,* but is depressed ventrally as in *Dinomys.* In *Cavia* it is dorsally developed as a double ridge, and the
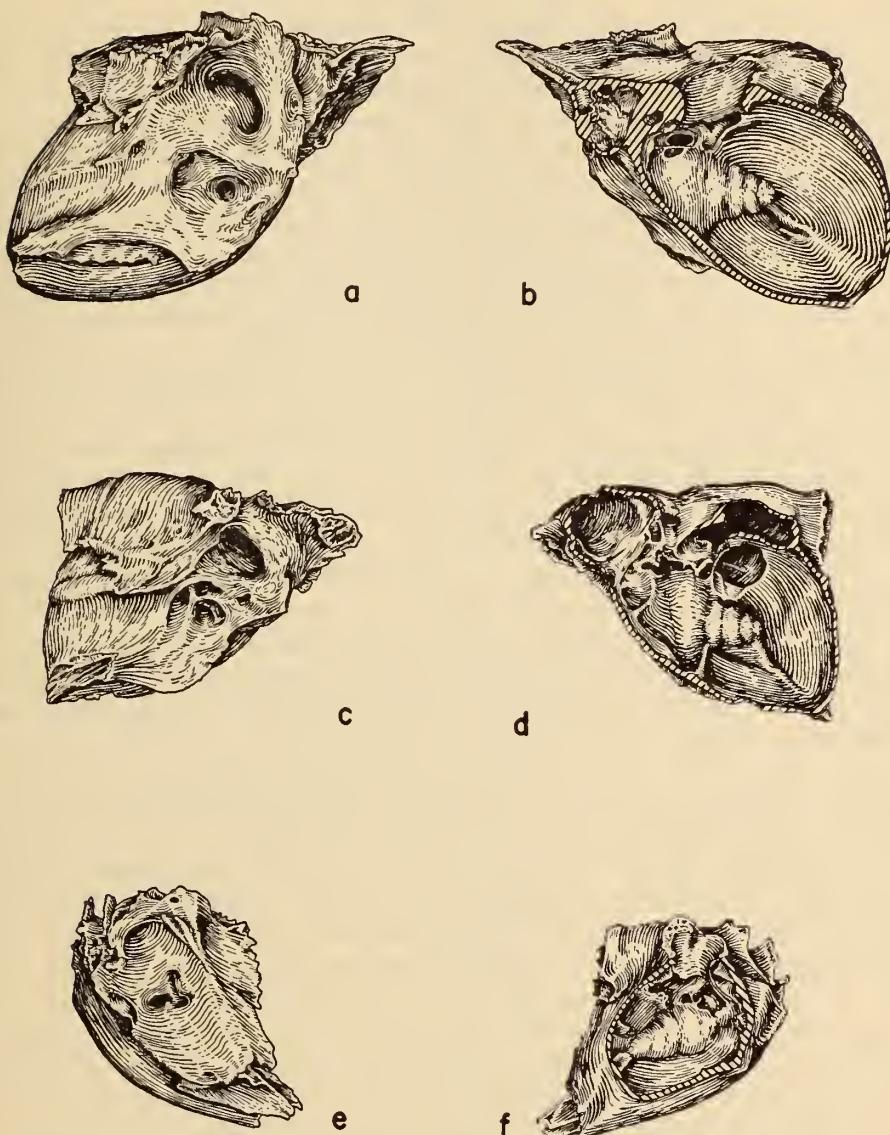
Fig. 22. The auditory bullae of hystricomorph rodents: *a, b, Dasyprocta; a,* cerebral view; *b,* internal view: *c, d, Cavia; c,* cerebral view; *d,* internal view: *e, f, Isolobodon; e,* cerebral view; *f,* internal view: all drawings × 2.

ventral part is missing. In *Isolobodon* the crista petrosa forms a continuous line from the dorsal limit to the styliform process. The styliform process of *Olenopsis* and *Dinomys* is short and stout, whereas in *Dasyprocta, Cavia,* and *Isolobodon* it is lengthened and slender. In *Erethizon* the styliform process is short as in *Dinomys* but is developed as a high spur. The mastoid area of *Olenopsis, Dinomys,* and *Erethizon* is not greatly expanded, and the mastoid apex is not drawn out as in *Dasyprocta* and *Cavia.* In *Isolobodon* the mastoid process showed less expansion than in any of the other genera.

Internal structure.—The external auditory meatus of *Olenopsis* is like that of *Dinomys*, and is more lengthened than in the other genera compared. *Olenopsis* shows further resemblance to *Dinomys* in the position and size of the epitympanic sinus and in the presence of a partial epitympanic septum. In *Dasyprocta* and *Cavia* the epitympanic sinus is greatly enlarged and shows no development of septa. In *Erethizon* and *Isolobodon* it is small and situated dorsal to the external auditory meatus. The tympanic cavity of *Olenopsis* shows greatest resemblance to *Dinomys*. The floor of the cavity is ridged and uneven. In *Dasyprocta* the cavity is deep and the walls are smooth. *Cavia* presents a tympanic cavity with triangular outline; the floor is flattened and shows several ridges. In *Cavia* further divergence is seen in the presence of an excessory sinus with vestigial septa situated medial to the epitympanic sinus and lateral to the promontorium. *Erethizon* shows the smallest, most simplified tympanic cavity, and it has thicker walls than the other genera. There are no evident ridges, and the external auditory meatus opens broadly into the cavity. In *Isolobodon* the tympanic cavity is deeper and more elongated than in any of the genera compared. The walls are rough and partial septa are present. The promontorium of *Olenopsis*, as in *Dinomys*, is simple and broadly pear-shaped with only slight external expression of the cochleaer coil. In *Erethizon* the promontorium is a simple "wheat-grain-shaped" chamber embedded in the floor of the tympanic cavity. In *Cavia*, *Dasyprocta*, and *Isolobodon* it is more elongate, and the coil of the cochleae is prominent. In *Cavia* and *Isolobodon* the apex of the promontorium lies closer to the floor of the tympanic cavity than it does in *Dasyprocta*, *Dinomys*, and *Olenopsis*. In *Erethizon*, *Dinomys*, and *Olenopsis* the ostium tympanicum tubae is broad and not roofed over as in the other genera. The fenestra cochleae of *Olenopsis* opens laterally into the vestibule, is moderately large, and has an irregular border as in *Dinomys*. In *Erethizon* the fenestra cochleae opens posterolaterally as a round, smooth-bordered opening on the ventral rim of the vestibule. In *Cavia* the fenestra cochleae is hidden from view by the arch of the promontorium and is situated deep in the vestibule. *Dasyprocta* has a comparatively small, round, smooth-margined fenestra cochleae opening laterally and slightly posteriorly onto the ventral rim of the vestibule. In *Isolobodon* this fenestra opens posterolaterally as in *Erethizon*, but is relatively larger with an undulating margin. The vestibule in *Olenopsis* is relatively smaller and deeper than in *Erethizon* and *Isolobodon*, but not as small or as deep as in *Dasyprocta* and *Cavia*. It is more nearly the size and depth of the vestibule in *Dinomys*. The fenestra vestibuli in *Olenopsis* is moderately large, ovoid, and situated dorsal and somewhat anterior to the fenestra cochleae as in *Dinomys*, *Cavia*, and *Dasyprocta*. *Cavia* differs in having a minute bar of bone passing from the lateral wall, through the stapideal foramen, to the medial wall. In *Erethizon* and *Isolobodon* the fenestra vestibuli is completely anterior to the fenestra cochleae. *Isolobodon* resembles *Cavia* in having a transverse bar across the fenestra. In *Olenopsis* and *Dinomys* there is a moderately large mastoid sinus, the ventral wall of which has several spines projecting into the cavity, probably representing vestiges of a septum. In *Erethizon* there is no mastoid sinus. In *Dasyprocta* this area is cancellous and separated by a heavy wall from the tympanic cavity. In *Isolobodon* there is a small septate mastoid sinus, and in *Cavia* the mastoid process is excavated to its apex as a very large sinus that is continuous with the tympanic cavity, there being no vestige of a septum. The recessus incudis of *Olenopsis* is somewhat more

shallow and smaller than it is in *Dinomys*, but not as small or shallow as in *Erethizon* or as large and deep as in *Cavia*, *Dasyprocta*, or *Isolobodon*.

Auditory ossicles.—The incus and malleus in *Olenopsis* have the same general form as in *Dinomys* and *Erethizon*. In *Dasyprocta* and *Cavia* they are more slender and elongate. The stapes of *Olenopsis* could not be removed from the matrix. The ossicles of *Isolobodon* were not preserved.

Malleus (Figs. 23, 24).—In *Olenopsis* the head is very similar to that in *Dinomys*, except that in *Dinomys* it is somewhat more robust, with a more rounded cross-section. The head in *Erethizon* is also more robust and shorter than it is in *Olenopsis*. In *Dasyprocta* it is more elongate and slender. The head in *Cavia* is extremely lengthened, slender, and has a ventrally bent end. The processus axialis in *Olenopsis* and *Dinomys* is prominent, slightly notched, and accompanied by a medial sulcus of variable size that extends onto the neck. In *Erethizon* the processus axialis is large with an irregular edge, and the accompanying medial sulcus is greatly enlarged and extends from the tip of the head back onto the neck. In *Dasyprocta* the processus axialis ends abruptly at the side of a small medial sulcus. This process, in *Cavia*, is greatly reduced, but the medial sulcus is greatly enlarged, extending to near the tip of the elongate head. The neck in *Olenopsis* is not as robust as it is in *Dinomys* or *Erethizon* nor as thin as in *Dasyprocta* and *Cavia*. In *Olenopsis* and *Dinomys* the processus muscularis is moderately enlarged and elevated. In *Erethizon* it is greatly enlarged and strongly elevated. In *Dasyprocta* and *Cavia* the processus muscularis is small and not greatly elevated. The manubrium in *Olenopsis*, *Dinomys*, and *Erethizon* is not greatly elongate, but distally forms a broad, shallow spatula-shaped articulation for the tympanic membrane. The heel of the manubrium is opposite the processus muscularis. In *Dasyprocta* the manubrium is more elongate and narrow, and the heel is elevated, enlarged, and situated proximal to the processus muscularis. In *Cavia* the manubrium reaches an extreme development. Distally it is somewhat expanded and deeply spatulate; proximally it is elevated from the neck and terminates on the extremely high heel at the base of the head. The incus and malleus are inseparable in all genera. In *Erethizon* and *Dasyprocta* the line of demarcation is more indistinct than it is in *Olenopsis*, *Dinomys*, and *Cavia*, where this line is marked by raised edges on both incus and malleus.

Incus (Figs. 23, 24).—The processus brevis in *Olenopsis* is most like that in *Erethizon* and *Dinomys* where the apex is drawn into a short, rounded point. This process in *Dasyprocta* is of equal size, but the tip is drawn medially into a short hook. In *Cavia* the processus brevis is cone shaped and relatively larger than in the other genera. The head of the incus is longer in *Dasyprocta* and *Cavia* than it is in *Dinomys* and *Olenopsis*. In *Erethizon* it is extremely short. The processus longus in *Olenopsis*, *Dinomys*, and *Erethizon* is stout and relatively long, with a distal flexure at the os lenticularis. In *Dasyprocta* the processus longus is more slender and straighter. This process in *Cavia* is short and conical with a distinct distal spur. The os lenticularis in *Erethizon* is large and ovoid. In *Dinomys*, *Dasyprocta*, and *Olenopsis* it is relatively small and usually more rounded, and in *Cavia* it is exceedingly small and rounded.

Remarks.—In order to establish familial characters in the auditory region it would be necessary to study and compare a larger number of genera than has been examined in this study. With the small sample available, only generic differences
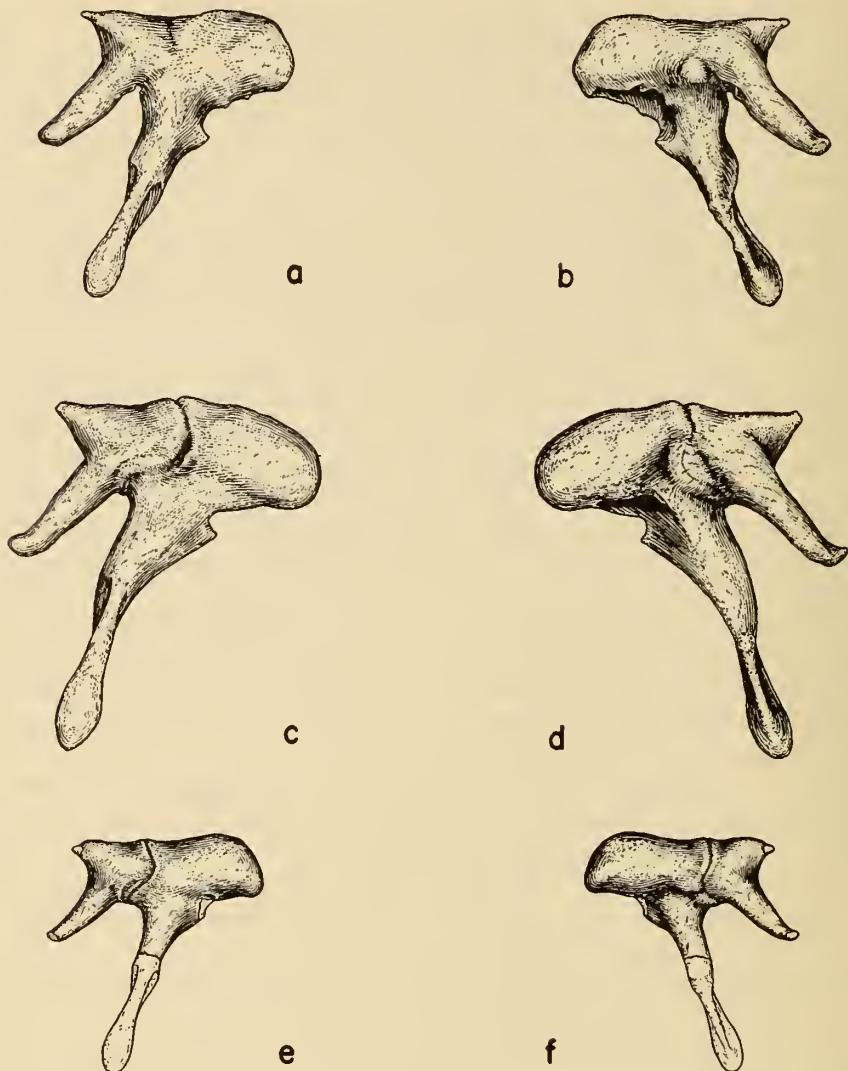
Fig. 23. Incus and malleus of hystricomorph rodents: *a, b, Erethizon; a,* ventral view; *b,* dorsal view: *c, d, Dinomys; c,* ventral view; *d,* dorsal view: *e, f, Olenopsis aequatorialis* (Anthony), U.C. M.P. no. 41636, loc. V-4519; *e,* ventral view; *f,* dorsal view; (light part restored from impression in matrix); all drawings × 8.

could be observed, and even at this level, specific and individual variation might tend to lessen the importance of characters that seem significant. Individual differences are present in the incus and malleus of *Dinomys* (Figs. 23, *b,* and 24, *a*). Conclusions must therefore remain tentative.

In a general appraisal *Dinomys, Olenopsis,* and *Erethizon* seem to show the greatest similarity of structure, and *Dasyprocta* and, especially, *Cavia* seem to be much more specialized. *Isolobodon* seems more primitive in retaining partial septa in the tympanic and epitympanic cavities, but the tympanic cavity is proportionally as large as that in *Dasyprocta.* When the auditory structure and ossicles are com-
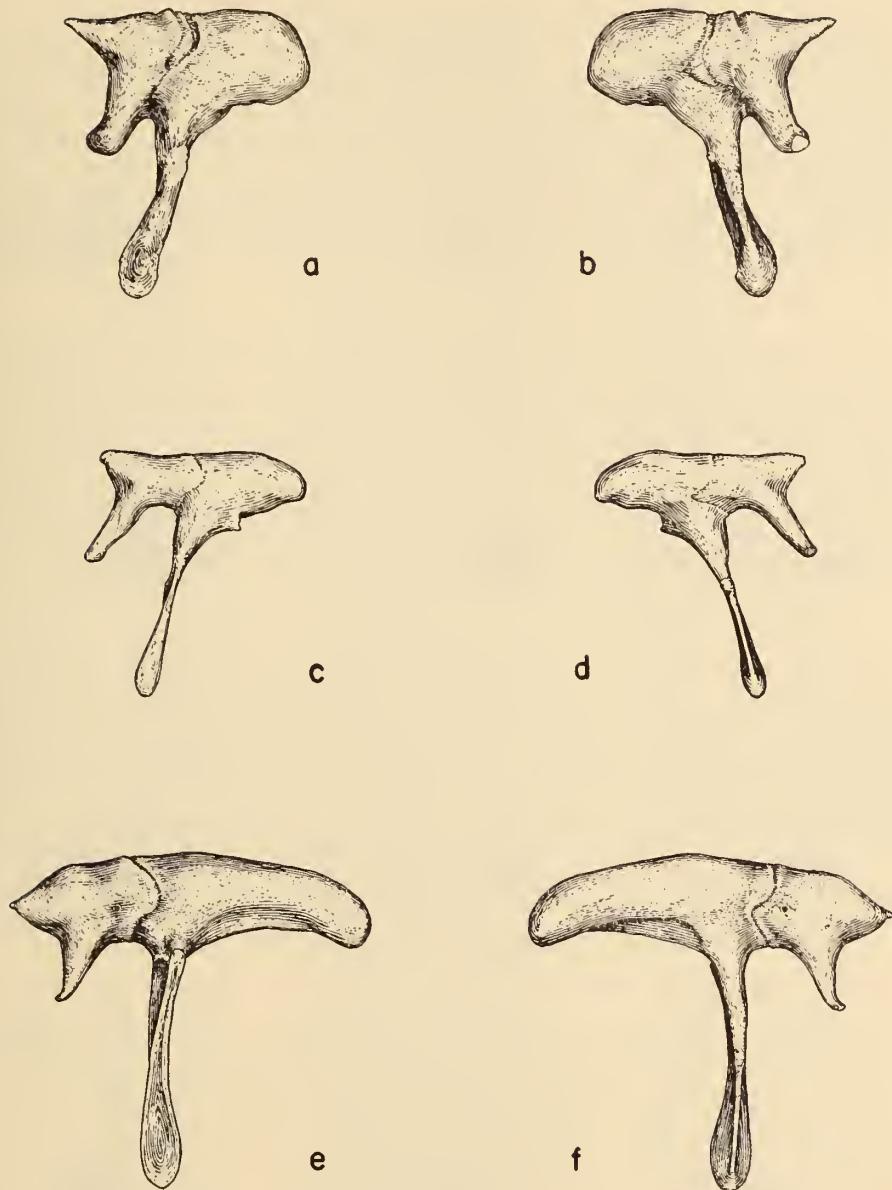
Fig. 24. Incus and malleus of hystricomorph rodents: *a, b, Dinomys; a,* ventral view; *b,* dorsal view: *c, d, Dasyprocta; c,* ventral view; *d,* dorsal view: *e, f, Cavia; e,* ventral view; *f,* dorsal view; all drawings × 8.

pared, there seems to be little doubt that *Olenopsis* is related to *Dinomys*. The internal structures of the auditory regions in these two forms are much more similar to each other than to other forms studied, and differences between *Olenopsis* and *Dinomys* in the incus and malleus are not significant. The characters of the malleus, especially the proportions of the head and manubrium, are major reasons for separating these genera from *Dasyprocta* and *Cavia*.
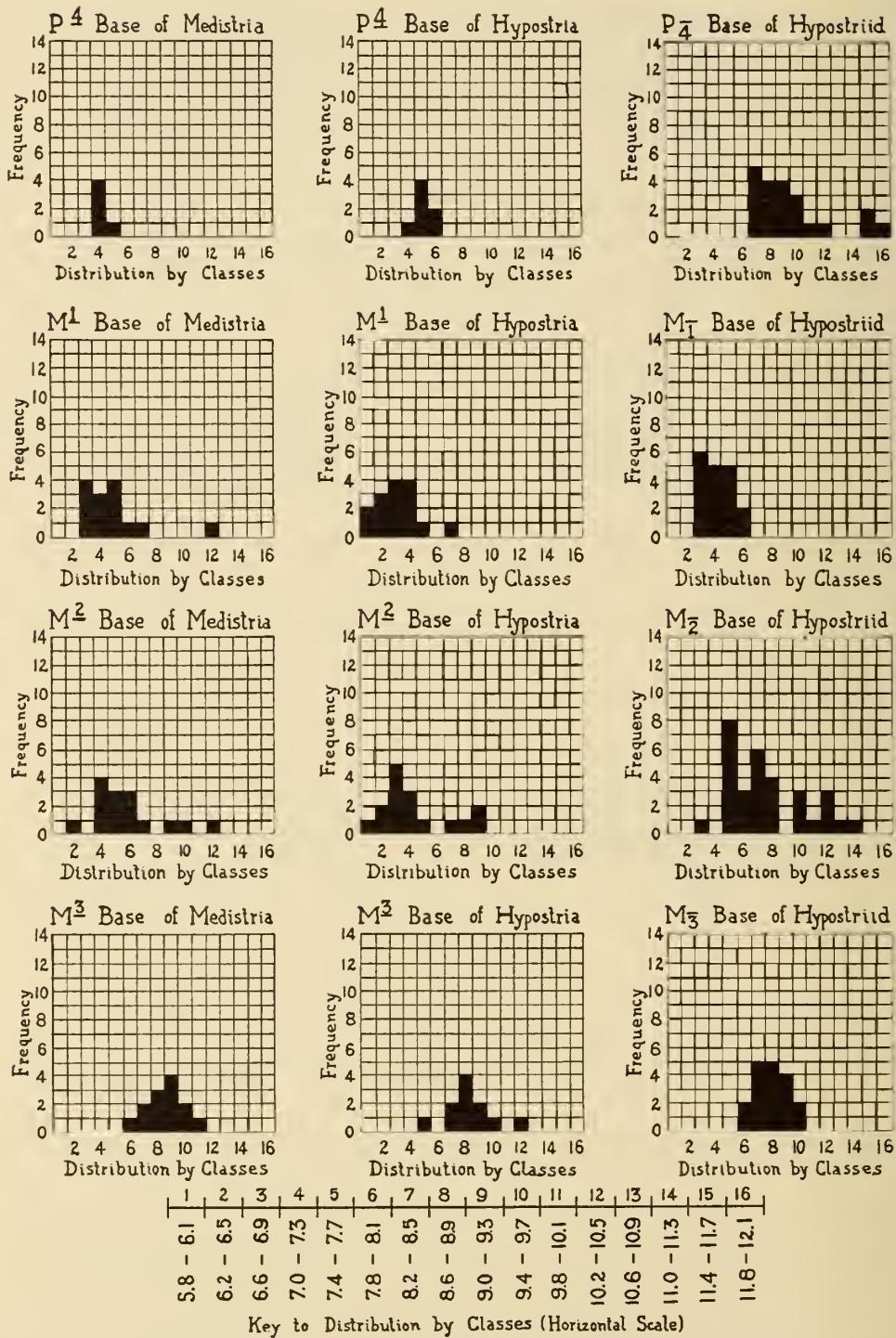
Fig. 25. *Olenopsis aequatorialis* (Anthony): histograms of anteroposterior diameter of upper and lower cheek teeth. Measurements taken parallel to occlusal surface. Note skewness and secondary grouping in M², P₄, and M₃.

Apparently the family Dinomyidae, at least in the detailed character of the auditory region, shows closer relationship to the generalized Erethizontidae than was hitherto suspected. It is unfortunate that material was so limited.

Future study, based on a large series of specimens, of the auditory region in recent and fossil forms may eventually supply an independent series of characters to be used as a check on classification by the generally used teeth, skull, and skeleton. The auditory region may possibly provide the solution to some of the confusion that parallelism and convergence have brought about in the systematic position and relations of different genera and families among the Hystricomorpha.

STATISTICAL ANALYSIS

Olenopsis aequatorialis has been recovered from near the base of the section, V-4531, Cerro Gordo (2), to the uppermost unit, V-4529, Las Mesitas, but it is most abundant in the upper levels. The specimen from V-4531 is a questionably identified incisor. The lowest stratigraphic unit in which material of certain identification was found is V-4536, San Nicolás locality. From that level upward the species is increasingly abundant, thus differing from *Scleromys*, which is found in relatively equal abundance throughout the section. It is impossible to distinguish individuals from the uppermost levels of the section from those of the lower stratigraphic units by dental patterns, but there seems to be a great variation in size.

Samples for the following statistical analysis were drawn from all available materials in the entire stratigraphic section. In the analysis of the length $P_{\overline{4}}$ to $M_{\overline{3}}$, there were only six specimens upon which this measure could be determined; of these specimens, four are adults and two are individuals in which $M_{\overline{3}}$ is in initial stage of wear, thus representing younger animals. With these facts in mind, two calculations were made: the first using all six individuals, the second using the four adult specimens.

Sample 1. Occlusal length of $P_{\overline{4}}$ to $M_{\overline{3}}$.

(6 specimens)

M. = 32.01 ± .82

S.D. = 2.03 ± .58

C.V. = 6.34 ± 1.83

Sample 2. Occlusal length of $P_{\overline{4}}$ to $M_{\overline{3}}$.

(4 adults)

M. = 33.07 ± .77

S.D. = 1.54 ± .54

C.V. = 4.66 ± 1.63

These samples include animals stratigraphically as much as 100 meters apart. Nevertheless, the value C.V. = 4.66 ± 1.63, as based on known adult specimens, is a good average value (Simpson and Roe, 1939, p. 123); and even when the two young animals are included in the sample, the coefficient of variation is within the usual scope of a species. The type specimen as described by Anthony is slightly smaller than the La Venta adults, but, nevertheless, fits well within −2 S.D. from the mean of the University of California materials. From these samples it seems that *Olenopsis aequatorialis* is a species with normal variability. The picture is not so definite, however, when isolated teeth are subjected to statistical analysis.

TABLE 7

QUANTITATIVE ANALYSIS OF OLENOPSIS AEQUATORIALIS TEETH

Tooth	Ant.-post. Diam. at	Sample	No. spec.	Mean	S.D.	C.V.
P^4	Base of medistria	All spec.	5	7.20 ± .06	.14 ± .05	1.94 ± .61
	Base of hypostria	All spec.	7	7.63 ± .11	.298 ± .079	3.91 ± 1.04
M^1	Base of medistria	All spec.	14	7.53 ± .22	.854 ± .161	11.34 ± 2.14
	Base of hypostria	All spec.	15	6.80 ± .11	.429 ± .178	6.31 ± 1.15
M^2	Base of medistria	All spec.	15	7.90 ± .26	1.01 ± .18	12.78 ± 2.33
	Base of medistria	Small spec.	12	7.46 ± .13	.449 ± .092	6.02 ± 1.23
	Base of medistria	Large spec.	3	9.66 ± .29	.503 ± .205	5.21 ± 2.13
	Base of hypostria	All spec.	16	7.30 ± .25	1.01 ± .18	13.76 ± 2.43
	Base of hypostria	Small spec.	12	6.76 ± .13	.439 ± .089	6.49 ± 1.32
	Base of hypostria	Large spec.	3	8.8 ± .26	.453 ± .185	5.14 ± 2.09
M^3	Base of medistria	All spec.	13	9.03 ± .15	.559 ± .109	6.19 ± 1.21
	Base of hypostria	All spec.	11	8.89 ± .21	.688 ± .146	7.75 ± 1.63
$P_{\bar{4}}$	Base of mesostriid	All spec.	21	9.40 ± .23	1.068 ± .165	11.34 ± 1.74
	Base of mesostriid	Small spec.	17	8.95 ± .12	.475 ± .083	5.31 ± .90
	Base of mesostriid	Large spec.	4	11.35 ± .34	.675 ± .139	5.94 ± 1.23
$M_{\bar{1}}$	Base of mesostriid	All spec.	18	7.20 ± .10	.409 ± .068	5.68 ± .95
$M_{\bar{2}}$	Base of mesostriid	All spec.	31	8.66 ± .19	1.08 ± .136	12.47 ± 1.57
	Base of mesostriid	Small spec.	22	8.04 ± .11	.497 ± .075	6.19 ± .92
	Base of mesostriid	Large spec.	9	10.17 ± .16	.474 ± .111	4.66 ± 1.09
$M_{\bar{3}}$	Base of mesostriid	All spec.	18	8.74 ± .11	.466 ± .077	5.33 ± .89

The anteroposterior diameter of all teeth, measured parallel to the occlusal surface and at the base of the mesostriid, was used as an index point in order to standardize measurement of the lower premolar and molars. In the upper premolar and molars, two measurements were obtained: the first was the anteroposterior diameter of the teeth at the base of the medistria and the second was the anteroposterior diameter at the base of the hypostria. Both measurements were taken parallel to the occlusal surface.

As a preliminary step these quantities were plotted against stratigraphic occurrence on scatter diagrams. Here, as in *Scleromys schürmanni* and *S. colombianus*, there was no correlation between size and stratigraphic occurrence. Specimens from any stratigraphic level might range from small to large.

As a second step, the quantities obtained for each group of teeth were classed and plotted on histograms (Fig. 25). It can be seen that the mode lies to the left of the mean, thus favoring the smaller measurements. If distribution curves were to be drawn, they would be negatively skewed. The histograms also show, for M^1 and M^2 and for $P_{\overline{4}}$ and $M_{\overline{2}}$, that there is a definite break at the right or larger value side, with a bimodal curve developing. These individuals stand apart on the histograms (note histograms of M^1, M^2, $P_{\overline{4}}$, and $M_{\overline{2}}$). However, these same teeth have dental patterns indistinguishable from the smaller materials; thus size is the only distinguishing character.

When the measurements are subjected to statistical analysis, the results are interesting (table 7). In $P^{\underline{4}}$ the coefficient of variation is low. In M^1 the value C.V. = 11.34 ± 2.14 is high. Here there is only one tooth that is excessively large (see histograms for M^1, Fig. 25). When all specimens of M^2 are analyzed, the resultant coefficients of variation are excessive: 12.78 ± 2.33 and 13.76 ± 2.43 (table 7). When specimens falling to the right and to the left of the break in the M^2 histograms are separated and both elements of the distribution analyzed separately, good average values are seen in each case (table 7). The sample for M^3 has a coefficient of variation only slightly above average. The collecting failed to produce any M^3 lying outside the expected normal variation. In $P_{\overline{4}}$, where sampling was good, the analysis of all materials again revealed a coefficient of variation beyond the usual limits. Segregating the specimens into two groups on the basis of size, as in M^2, the results show the segregated samples to have good average values for the coefficient of variation. The $M_{\overline{2}}$s also display this splitting into two size groups. $M_{\overline{1}}$ and $M_{\overline{3}}$ show acceptable values as bulk samples.

From the data it might be concluded: either that *Olenopsis aequatorialis* shows an extreme range of variation in tooth size, or that the genus is represented by two, rather than one, species in the La Venta fauna. If the materials were to be split into two species, the type of the larger species would be a single isolated tooth, and the only character by which this separation could be made is size. As has been stated before, the occlusal pattern of these large teeth is indistinguishable from the smaller. Until better materials are discovered, wherein further distinctions may be found (if they exist), it is preferable to include these larger teeth within the species *O. aequatorialis*.

DISCUSSION

Ameghino's original description of *Olenopsis uncinus* (1889B) is based upon juvenile material in which only $DP_{\overline{4}}^{4}$, $M_{\overline{1}}$, and $M_{\overline{2}}$ are present; his description of *O. typicus* (1891E) is again based on the left ramus of a young individual with $DP_{\overline{4}}$, $M_{\overline{1}-\overline{2}}$, and with $P_{\overline{4}}$ showing beneath $DP_{\overline{4}}$. Although Ameghino realized that his materials were juvenile, he typified the genus as being unique in having only two molars ($M_{\overline{1}}$ and $M_{\overline{2}}$), which, according to present evidence, is erroneous. Scott (1905B) did not detect this discrepency and follows Ameghino by stating that "the dental formula is $P_{\overline{1}}\ M_{\overline{2}}$." Ameghino's error is, in part, due to his failure to consider growth stages. His conclusions were probably based on the position of the inferior dental foramen in respect to $M_{\overline{2}}$. In the growth stage represented by the Santa Cruz and Paraná materials, the inferior dental foramen has the same space relationship to $M_{\overline{2}}$ as it has to the $M_{\overline{3}}$ in fully grown individuals. Specimens of *Olenopsis* in the University of California collection fail to show the intermediate stages of growth, but specimens of *Scleromys schürmanni* can be used to substantiate conclusions concerning the dental series in *Olenopsis*. In figure 5, *a-e*, it can be seen that as the proportions of the mandible increase and as $M_{\overline{2}}$ and then $M_{\overline{3}}$ erupt from the jaw, the inferior dental foramen is drawn progressively backward and finally comes to lie behind $M_{\overline{3}}$, and has the same space relationship to $M_{\overline{3}}$ that it had to $M_{\overline{2}}$ in the younger animal. From this evidence it seems that *Olenopsis* has a normal hystricomorph dental formula.

There is one perplexing problem. In the fossil materials and in *Dinomys* there is an apparent difference of molar tooth size in young and adult individuals. In the fossil materials, U.C.M.P. no. 39969 and U.C.M.P. no. 41636 are juveniles; U.C.M.P. no. 40055 is a full-grown adult. The anteroposterior diameter of the premolars and molars in the younger animals is definitely less than in the adult. This difference is, in part, due to stage of wear, but is too great to be entirely the result of wear, and it cannot be attributed to the increasing size of each tooth toward its base, as this is not characteristic of these materials. This is especially true of $M_{\overline{1}}^{1}$ and $M_{\overline{2}}^{2}$, the anteroposterior diameters of which decreased considerably toward the bases. In $P_{\overline{4}}^{4}$ and $M_{\overline{3}}^{3}$ the anteroposterior diameter is more constant. In $P_{\overline{4}}^{4}$ it may increase slightly in some individuals, but usually remains the same throughout. In $M_{\overline{3}}^{3}$ there is sometimes a slight decrease in anteroposterior diameter, but here again most of these teeth have a constant anteroposterior diameter.

A similar, but slightly different, situation is seen in *Dinomys*. There is a definite difference in size of teeth in juvenile and adult animals. Wear would have no effect on diameter of the teeth since they are columnar and of constant anteroposterior diameter throughout their length. Two questions arise at this point. Is diametric growth possible in erupted teeth? If so, does it account for the difference in size of teeth in juvenile and adult animals?

In the teeth of *Dinomys*, which are entirely rootless, the process of diametric growth is possible, as the enamel organ supplies new enamel to the base of the column throughout at least part of the life of the individual. Since the enamel organ remains active, expansion of the teeth is possible as the gross proportions of the skull increase. This factor could account for the difference in size of teeth in juvenile and adult *Dinomys*.

Complications arise when *Olenopsis aequatorialis* is considered. One character—the tendency of the cheek teeth to decrease in diameter toward their base—contrasts with the condition in *Dinomys*. A second characteristic difference is that the cheek teeth of *O. aequatorialis* are not completely open-rooted. The fossettes are closed at the base of the teeth, and small roots are acquired in later life. Nevertheless, the enamel organ remains active for a part of each individual's lifetime. Proof of this fact is seen in the presence of thickened enamel on the basal anterolingual margin of upper teeth and the basal posterolateral margin of lower teeth. The explanation given for cheek-teeth growth in *Dinomys* cannot be used here because of the presence of closed fossettes in the fossil materials. If these fossettes were open at the base, diametric growth would be possible, but the fact that they are closed seems to negate any possibility for diametric growth in *O. aequatorialis*, and thus it cannot account for the difference in size of young and adult specimens.

Donaldson and French (1927) gave evidence of diametric growth in rat molars. Donaldson (1929) found similar results in cat skulls, and Beust (1930) obtained evidence similar to that of Donaldson and French in pig mandibles. H. E. Wood and F. D. Wood (1931) refute the diametric-growth hypothesis of Donaldson and French, and consider the results fortuitous. Their conclusions are substantiated by experiment, but neither the original works of Donaldson and French and Beust nor the refutation by Wood and Wood will stand much critical examination. Data are far from complete and neither prove nor disprove the possibility of diametric growth.

It may be argued that the difference in size of juvenile and adult teeth is evidence for two distinct species, and that the results of the statistical analysis of isolated teeth is proof of the presence of two species. The possibility of two species was considered but disregarded after examination of mandibular tooth rows in the University of California collection. By using a number of successively older animals, beginning with half-grown individuals in which $M_{\overline{3}}$ is just erupting and ending with older individuals in which $M_{\overline{1}}$ is completely worn away, one could assemble a graded series of dental rows. In this series there would be a progressive increase in tooth size from the young to the older individuals. If these animals were to be divided into two species, where would the division be made? Since the occlusal pattern is indistinguishable and morphologic characters in the mandible are identical, size would be the only criterion of division, and in the graded series the division would, of necessity, be at an arbitrary point and would lead to a confusion of relationships.

O. aequatorialis seems more advanced than *O. uncinus* from the Santa Cruz fauna in having a broader, more flattened incisor and a somewhat more complicated dental pattern on the cheek teeth. The parastriid of *O. uncinus* is evidently very weak. Ameghino's description and figure indicate the presence of a well-developed hypostriid, a relatively short metastriid and mesostriid, with the parastriid represented by a superficial groove on the occlusal surface of the tooth. Since the Argentine specimen is a juvenile, it is difficult to establish size relationship, but the figured specimen represents an animal about the same size as *O. aequatorialis*. The Paraná species, *O. typicus*, has an incisor with an enamel face about as flat as the one in *O. aequatorialis*. In the cheek teeth, distinctions are difficult to discern, primarily owing to the poor quality of the published figures and to Ameghino's inadequate description of dental characters. It seems, however, that the paraflexid is larger and

more completely developed and that the flexids are less crescentic and less oblique than in the La Venta species. The striids also seem to be relatively longer than those in *O. aequatorialis*. If the figures are to be trusted, the coronoid process in *O. typicus* is more reduced than it is in *O. aequatorialis*.

From the meager evidence available, *O. aequatorialis* seems to represent an evolutionary stage intermediate between the Santacrucian and Mesopotamian species.

Olenopsis is well represented by postcranial remains in which there is some evidence of adaptive radiation of body form. The body of *Olenopsis* is very much like that of *Dinomys* except that the tibia is 23 per cent longer and the metatarsals are 44 per cent longer. The lengthening of the distal parts of the limb is usually evidence
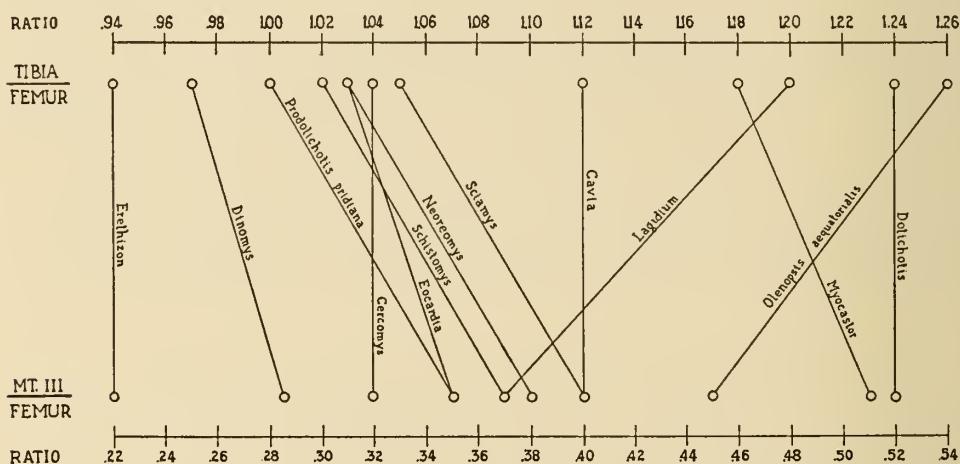
Fig. 26. Ratio between the length of the tibia and femur compared to the ratio between the length of mt. III and the femur in various fossil and recent South American hystricomorph rodents.

of digitigrade, cursorial types. If the ratio between the length of the femur and metatarsal III and the ratio between the length of the tibia and the femur are calculated—for genera such as: *Myocastor*, an amphibious form; *Dolichotis*, a digitigrade, cursorial animal; *Lagidium*, a digitigrade form with possible saltatorial adaptations; *Cavia*, the guinea pig; several extinct cavies of generalized form; *Erethizon*, the arboreal procupine; *Sciamys*, a fossil erethizontid; *Cercomys*, an echimyid of general form with probable scansorial adaptations; *Dinomys*, a plantigrade, terrestrial form—and then compared with ratios found in *Olenopsis*, some interesting results appear. In the graph of these ratios (Fig. 26), *Olenopsis* seems to resemble *Lagidium* in the adaptive character of the hind limb. *Dinomys* seems more generalized, and shows relationships of limb proportion much like those in *Myocastor*, *Erethizon*, and some of the more generalized fossil forms. The fore limbs of *Olenopsis* are small in comparison to the hind, and the vertebral column seems rather rigid. These characters are seen in *Lagidium* but are not generally found in amphibious rodents. Although the evidence is scanty it seems to indicate that *Olenopsis* was a digitigrade, cursorial form that was able to take to water as a means of retreat.

RELATIONSHIPS OF OLENOPSIS

Consideration of characters of *Olenopsis* clearly indicates a close relationship to *Dinomys* and an even closer affinity to *Scleromys*. Most earlier writers did not see the similarities between these fossil genera and the living *Dinomys*. *Olenopsis* and *Scleromys* have been compared to forms like *Neoreomys*, *Myopotamus*, and *Myocastor* in which there is a superficial resemblance in the dental pattern. It is not surprising that relationships to these genera were suspected since both *Olenopsis* and *Scleromys* are poorly known in the Santa Cruz fauna. Anthony, however, had a good cranium, mandible, and skeletal elements of *O. aequatorialis* upon which several key characters were preserved, but apparently he was not impressed with these features as no mention is made of *Dinomys*.

Characters that seem to relate *Olenopsis* to *Scleromys* are: broad, flattened skull with depressed parietals, long, anteriorly expanded nasals; no development of sagittal crest but with distinct temporal crests; broad rostrum with squared rostral masseteric fossa bounded by anterior and ventral rims; enlarged infraorbital foramen with depressed groove for transmission of nerves; anteriorly situated ventral zygomatic root; absence of accessory lacrymal opening on rostrum; moderately enlarged auditory bullae; enlarged external auditory meatus with greatly enlarged and connected accessory ventral opening; heavy, blunt mastoid process oppressed to bulla; short, massive paraoccipital process oppressed to mastoid; low, wide occipital condyles; strongly curved upper incisors with thick enamel band; extremely long lower incisors; similar dental pattern on cheek teeth; short, wide mandible with long, massive symphysis, short diastema, reduced coronoid process, laterally distorted angle and flattened shallow masseteric fossa.

Characters that seem significant in establishing the relationship of *Olenopsis* and *Dinomys* are much the same as those showing the relationship between *Scleromys* and *Dinomys* (see pp. 322-323) and those given above for the affinities between *Scleromys* and *Olenopsis*. Additional relationship can be seen in: robust postcranial skeleton; compressed cervical vertebrae with evidence of fusion in anterior part of series; presence of fourteen thoracic vertebrae; broad, flattened ribs and sternum; identical appearance of calcaneum and astragalus; robust incisors with broad, flat enamel faces. Detailed similarities can be found in: similar development of mastoid process; long, tubular external auditory meatus; simple promontorium; prominent mastoid and epitympanic sinuses; well-developed crista petrosa; broad, flattened, somewhat rugose facies nasalis; anteroposteriorly ridged facies cerebralis with prominent foramen facilais and internal auditory meatus; compound development of porus acusticus; moderately excavated tympano-mastoidea fissura; absence of osseous bar running through stapideal foramen; presence of vestigial septa in tympanic cavity; wide ostium tympanicum tubae; enlarged Eustachian tube; reduced styliform process.

DEFINITION OF THE FAMILY DINOMYIDAE

The morphologic relationship of *Scleromys* and *Olenopsis* to *Dinomys* and to the family Dinomyidae seems certain. As has been stated earlier, *Dinomys* is sufficiently distinct from other groups of South American hystricomorphs to warrant retention of separate family rank. It seems advisable, at this time, to clarify the

definition of the family Dinomyidae as based on the fossil forms and *Dinomys*. Miller and Gidley (1918), Anthony (1916, 1917, 1926), Kraglievich (1934), and Stirton (1947A) have directed attention to the close similarity between certain fossil genera and *Dinomys*. Most of these genera have extremely hypsodont, open-rooted cheek teeth and are from Pliocene beds. The present work, dealing with late Miocene forms, allows for a broader vertical classification in which phylogenetic relationships may be ascertained. The following definition of the family Dinomyidae is modified after Miller and Gidley (1918) and Ellerman (1940).

Body form robust. Semicursorial to cursorial. Manus and pes with four functional digits; pes longer than manus, claws long, flattened; hind limb sometimes lengthened; anterior cervical vertebrae tend to fuse; thoracic and lumbar vertebrae closely articulated; back stiffened; first sacral vertebra greatly expanded; caudal series long; ribs broad, flattened; skull massive, long, low, with depressed parietals; no development of sagittal crest but with temporal crests well developed; tendency for reduction of postorbital process; orbital region elongate; absence of accessory lacrymal opening on rostrum; shallow, anteriorly squared rostral masseteric fossa; zygomatic region not abnormal, without bony cheekplates; shallow to prominent canal for transmission of nerves in infraorbital foramen; anteriorly placed ventral zygomatic root; palate constricted anteriorly; internal nares smooth; basicranial axis elongate; no tendency toward excessive enlargment of bullae; external auditory meatus with accessory ventral and continuous opening; short, massive mastoid and paraoccipital process; low, wide foramen magnum; mandible with angular process strongly distorted outwards; symphysis elongate, massive; coronoid process reduced or lost; incisors, upper and lower, proportionally large, with thick enamel band tending to become broad and flat; upper incisor strongly arched; lower incisor extremely long, extends into condyloid process; cheek teeth subhypsodont to extremely hypsodont, semi-rooted to completely open-rooted; pattern as series of transverse lophs; lingual moiety of uppers, labial moiety of lowers with one to three inflections; labial moiety of uppers, lingual moiety of lowers with two to five inflections; sides of teeth with stria and striids, strii reaching to base of tooth where they are extremely hypsodont and completely open-rooted.

Remarks.—This definition of the family Dinomyidae includes part of a group of hypsodont rodents that have been given varied family assignments depending on the author and the date of publication. Simpson (1945I, pp. 95-97, 212), in his classification, includes most of these genera in the Heptaxodontidae, and he follows Kraglievich in using his Potamarchidae, Eumegamyidae, and Neopiblemidae as subfamilies under the family Heptaxodontidae. Stirton (1947A) gives a brief résumé of this group: "The evidence from these fossil forms [Mesopotamian], however, strengthens rather than detracts from the idea of including these genera in the Dinomyidae." I agree with Stirton except that some of the genera mentioned by him, when studied in the light of present information, show characters that suggest greater relationship to other groups.

In the opinion of Kraglievich (1926) the number of lophs on the cheek teeth is not a diagnostic character in recognizing different genera. This conclusion is based on evidence in the type mandible of *Eumegamys paranensis*. On $P_{\overline{4}}$ there are six laminae, $M_{\overline{1}}$ has four, and $M_{\overline{2}}$ and $M_{\overline{3}}$ have five. Kraglievich's conclusion is, in part, correct, but this difference in number of lophs can be explained by stage of wear.

$M_{\bar{1}}^{1}$ erupt early and are considerably worn by the time $DP_{\bar{4}}^{4}$ are replaced by $P_{\bar{4}}^{4}$. $M_{\bar{2}}^{2}$ erupt sometime after $M_{\bar{1}}^{1}$, and $M_{\bar{3}}^{3}$ come into use at about the same time as $P_{\bar{4}}^{4}$. Thus $M_{\bar{1}}^{1}$ always show more wear than any of the other permanent teeth. This is the condition in the type specimen of *Eumegamys paranensis*, in which $M_{\bar{1}}$ is worn to a point where the anterior inflection is no longer evident. Wear, then, would account for the seeming variation in the number of inflections on the individual cheek teeth. These apparent differences are also affected by the comparative length of strii on the sides of the teeth. Unfortunately, earlier authors were unaware of the significance of the strii, the lengths of which provide a diagnostic character upon which specific, as well as generic, distinctions can be made. On a broader scale, the strii afford a means of determining phylogenetic lines and of understanding more completely the evolution of this group.

It is difficult, if not impossible, to determine the length of each stria and striid on the teeth of the numerous genera and species described by Ameghino, Kraglievich, Rusconi, and Rovereto. Certain conclusions, nevertheless, can be drawn in regard to the validity of proposed genera.[8] *Scleromys, Olenopsis, Simplimus, Potamarchus, Gyriabrus, Tetrastylus, Telicomys,* and *Eumegamys* should be included in the family Dinomyidae as valid genera. All these genera display dental characters and patterns similar to *Dinomys.* There is further similarity in the excessively long lower incisors, which tend to have extremely broad, flattened enamel faces, and in the extreme reduction of the coronoid process.

Simpson followed Scott (1905B) in placing *Scleromys* and *Olenopsis* in the family Capromyidae along with the genus *Lomomys* Ameghino, 1891, which is here synonymized with *Scleromys.* The dental pattern is that of *Scleromys,* but was originally distinguished from that genus on the presence of only three cheek teeth, another example of misidentification of a juvenile specimen.

From a perusal of other proposed genera it seems likely that *Isostylomys* Kraglievich, 1926; *Carlisia* Kraglievich, 1926; *Rusconia* Kraglievich, 1931; *Diaphoromys* Kraglievich, 1931; and *Protomegamys* Kraglievich, 1932, are synonyms of *Eumegamys* Kraglievich, 1926. It is also probable that *Tetrastylopsis* Kraglievich, 1931, is a synonym of *Tetrastylus* Ameghino, 1886. *Simplimus* Ameghino, 1904, may be a synonym of *Olenopsis* Ameghino, 1889, but I would hesitate to make a definite decision without first seeing the type of *Simplimus. Proberomys* Kraglievich, 1926, and *Pseudosigmomys* Kraglievich, 1931, have been placed in the family Heptaxodontidae under the subfamily Eumegamyinae by Simpson (1945I). These two genera may be congeneric with *Euphilus* Ameghino, 1889, which is a questionable chinchillid. The poorly known genera *Neoepiblema* Ameghino, 1889, and *Dabbenea* Kraglievich, 1926, were originally put in the family Neoepiblemidae by Kraglievich (1926B) and later placed in the Heptaxodontidae under subfamily Neoepibleminae by Simpson (1945I). These genera show close similarity to *Heptaxodon* Anthony and probably are correctly referred to the Heptaxodontidae. *Tetrastylomys* Kraglievich, 1926, and *Pentastylomys* Kraglievich, 1926, were placed as Heptaxodontinae *incertae sedis* by Simpson (1945I). These forms show some resemblance to *Clidomys* and may be related to that form. The genus *Telodontomys* Kraglievich, 1931, is based on a single molar tooth of unknown significance.

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[8] It would be impossible to evaluate the validity of proposed species without seeing the type specimens. Sometimes specific distinctions are based on characters that probably represent individual variation.

If a reassignment of genera to the family Dinomyidae is to be made, what status do the subfamilies Potamarchinae and Eumegamyinae have under the new classification? These two subfamilies, as near as can be determined, were established to separate forms with semi-rooted, less hypsodont teeth from forms with open-rooted, extremely hypsodont teeth. The subfamily Potamarchinae, then, includes those forms with semi-rooted, less hypsodont teeth from Miocene and Pliocene beds, and the subfamily Eumegamyinae encompasses those forms with open-rooted, extremely hypsodont teeth from Pliocene beds. This separation seems valid and is retained. The classification of the family Dinomyidae, based on present evidence, will then include the subfamily Potamarchinae and Eumegamyinae, plus the subfamily Dinomyinae with the living *Dinomys* as type genus. My classification is as follows:

Superfamily Cavioidea Kraglievich, 1930c, p. 60
    Family Dinomyidae Alston, 1876, p. 96 (= *Dinomyina* Troschel, 1874, p. 132).
        Mioc.–R.; S.A.
        Subfamily Potamarchinae Simpson, 1945, p. 96 (= Potamarchidae Kraglievich, 1926ʙ, p. 129). Mioc.-Plioc.; S.A.
            Scleromys Ameghino, 1887 (= *Lomomys* Ameghino, 1891). Mioc.; S.A.
            Olenopsis Ameghino, 1889 (= *Drytomomys* Anthony 1922). Mioc.-Plioc.; S.A.
            Simplimus Ameghino, 1904. Mioc.–Plioc.; S.A.
            Potamarchus Burmeister, 1885. Plioc.; S.A.
        Subfamily Eumegamyinae Kraglievich, 1932ʙ, p. 318. [Including Tetrastylinae Kraglievich, 1931, p. 255; Gyriabrinae Kraglievich, 1930ʙ, p. 220.] Plioc.; S.A.
            Eumegamys Kraglievich, 1926 (= *Megamys* of almost all authors but not *Megamys* D'Orbigney and Laurillard, 1842; *Isostylomys* Kraglievich, 1926; *Carlesia* Kraglievich, 1926; *Rusconia* Kraglievich 1931; *Diaphoromys* Kraglievich, 1931; *Protomegamys* Kraglievich, 1932). Plioc.; S.A.
            Tetrastylus Ameghino, 1886 (= *Tetrastylopsis* Kraglievich, 1931). Plioc.; S.A.
            Gyriabrus Ameghino, 1891. Plioc.; S.A.
            Telicomys Kraglievich, 1926. Plioc.; S.A.
        Subfamily Dinomyinae Kraglievich, 1931c, p. 262.
            Dinomys Peters, 1873. R.; S.A.
            ?Dinomyidae *incertae sedis*
            Teledontomys Kraglievich, 1931. Plioc.; S.A.

Family Caviidae

Prodolichotis pridiana Fields, n. sp.
(Fig. 27)

Holotype.—Nearly complete skeleton, U.C.M.P. no. 38761. *Cranium*: complete but laterally distorted by crushing, dental series intact. *Mandible*: right ramus complete except for posterior part of angle; incisor and cheek teeth in place. *Scapula*: complete left scapula; basal part of right scapula showing glenoid fossa; coracoid process and incisura scapulae. *Humerus*: complete right and left humeri. *Radius*: both right and left radii. *Ulna*: complete right and left ulnae. *Carpals*: complete left carpal series; right scapholunar, cuneiform, pisiform, unciform, and trapezium. *Metacarpals*: complete left series; right mc. II, III, IV, V. *Phalanges*: left proximal and medial series complete, distal phalanges II and V; right proximal III and IV, medial phalanx III, and distal III preserved. *Femur:* head of right femur. *Tibia:* complete right tibia; astragalar facet of left tibia.

Tarsals: complete right tarsal series; left calcaneum lacking sustentacular facet, navicular lacking heel, broken ectocuneiform and cuboid. *Metatarsals:* complete right series. *Phalanges:* complete right proximal, medial, and distal series. *Vertebrae:* atlas, axis, seven thoracic and two lumbar.

Paratype.—Fragmentary skeleton, U.C.M.P. no. 41669. *Cranium:* complete but crushed. *Mandible:* right and left rami with dentition. *Scapula:* distal part of right scapula with coracoid process, glenoid fossa, and incisura scapulae. *Ulna:* proximal two-thirds of left ulna. *Radius:* badly crushed left radius. *Carpals:* left scapholunar, unciform, and magnum. *Metacarpals:* left mc. IV and V. *Innominate:* complete left and right ilium, ischium, acetabular part of left and right pubis. *Femur:* complete but crushed left femur; shaft and head of right femur. *Tibia:* complete but crushed right tibia. *Tarsals:* complete right calcaneum, astragalus, navicular, ectocuneiform, and broken cuboid; badly crushed left calcaneum, astragalus, complete cuboid, and broken ectocunei. form. *Metatarsals:* crushed left mt. II, III, and IV. *Vertebrae:* cervicals III, IV, V, VI, and VII-thoracics I, II, III; parts of several lumbars and nearly complete sixth lumbar, several caudals; *Miscellaneous:* fragments of many ribs, unidentified phalanges and sesmoids.

Referred specimens.—Skeletal parts and isolated teeth, U.C.M.P. no. 39922, loc. V-4936. Skeletal parts, U.C.M.P. no. 39885, loc. V-4521. Left maxillary with P^4-M^3, U.C.M.P. no. 39899, loc. V-4521. Left mandibular ramus with P_4-M_3, U.C.M.P. no. 37930, loc. V-4522. Right mandibular ramus with P_4-M_3, U.C.M.P. no. 39930, loc. V-4536. Left mandibular ramus with P_4-M_3, U.C.M.P. no. 41671, loc. V-4521. Right mandibular ramus with P_4-M_3, U.C.M.P. no. 41672, loc. V-4521. Right mandibular ramus with P_4-M_3, U.C.M.P. no. 41673, loc. V-4521.

Type locality.—Between Fish Bed and Monkey Unit, vicinity of Villavieja, Department of Huila, Colombia, South America, V-4522. (See note 2.)

Fauna.—La Venta.

Age.—Late Miocene.

Diagnosis.—Skull long, narrow, with well-developed sagittal crest; orbit deep, rounded; rostrum long, narrow; masseteric fossa ovoid, deep; lacrymal large, contacts with frontal and maxillary; lacrymal duct large, deep in anterior rim of orbit, with accessory rostral opening above ventral zygomatic root; jugal forms small zygomatic plate with broad, deep notch anterior to squamosal suture; squamosal with posterior projection extending back to exoccipital and mastoid above bulla; auditory bullae not greatly enlarged, ovoid, deep; external auditory meatus with extended anterior wall, open below with enlarged accessory opening; paraoccipital process considerably elongated; incisive foramen narrow, elongate; palate short; internal nares V-shaped, anterior border opposite posterior margin of M^2; palatines greatly expanded, nearly meeting anterior expansion of squamosal on alisphenoid bar; pterygoid thin, extends to bulla; tooth rows nearly meet anteriorly. Mandible with deep masseteric ridge; masseteric crest greatly expanded; symphysis long, slender; coronoid process large, high; inferior dental foramen elongate, placed below inferior pterygoid crest. Incisors slender, enamel face rounded, smooth; lower incisor somewhat procumbent, short, base lingual to M_2; upper incisor tightly arched, base well ahead of P^4. Cheek teeth evergrowing, unilaterally hypsodont, with small deposit of cement between lobes, enamel limited to sides of lobes and area of constriction opposite deep reëntrant plication; P^4-M^2 with two lobes separated by deep reëntrant fold; M^3 with additional posterior flange; M_1-M_3 with two lobes separated by deep reëntrant fold; P_4 with additional, shallow, anterior reëntrant plication resulting in one normal posterior lobe and two smaller anterior lobes.

DESCRIPTION

Cranium (Fig. 27, *a*).—Elongate, comparatively narrower than in *Cavia* or *Dolichotis*; nasal long, straight, pointed anteriorly, not extended as far forward as premaxillary; frontal relatively broad, orbit roofed in by expansion of frontal, supraorbital notch present as in *Dolichotis*; postorbital process prominent, overhangs squamosal; parietal narrow, not as long as frontal, posterior part depressed; sagittal crest short, broad posteriorly; temporal crest low, posteriorly deflected toward sagittal crest; occipital region high, narrow, as in *Dolichotis*; supraoccipital extends onto dorsal surface of cranium, contacts with parietal, squamosal, and mastoid; foramen magnum dorsoventrally ovoid; occipital condyles oriented vertically as in
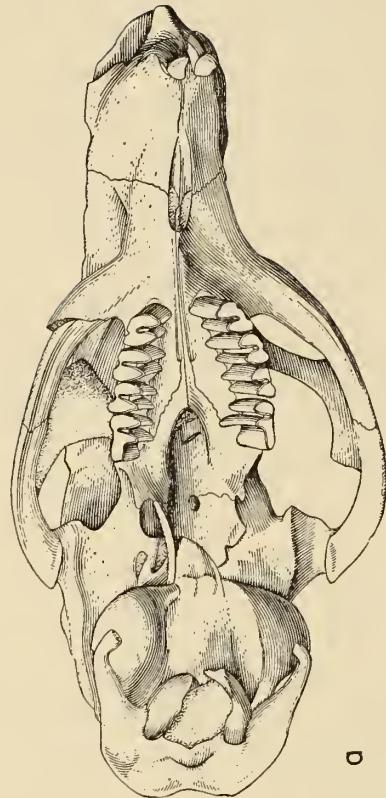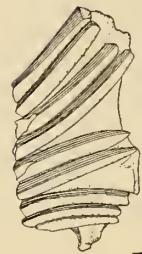
Fig. 27. *Prodolichotis pridiana* Fields, n. sp., La Venta type area: *a, b*, holotype, U.C.M.P. no. 38761, loc. V-4519, Toxodont locality; *a*, palatal view of skull; *b*, occlusal view of right mandibular ramus; *c*, U.C.M.P. no. 39899, loc. V-4521, Lone Tree locality; lingual view of left P⁴ M¹⁻³ showing angle of teeth in maxillary: *d*, U.C.M.P. no. 37930, loc. V-4520, Interathere locality; lingual view of left P₄, M₁₋₃ showing angle of teeth in mandible; all drawings × 1.

Dolichotis; paraoccipital process elongate, much as in *Dolichotis*, but not comparable to structure in *Hydrochoerus*, distal part deflected lingually; basicranial axis elongate; basioccipital comparatively wide, thick; basisphenoid broad posteriorly, tapers rapidly to slender rod anteriorly; presphenoid rodlike, narrow; auditory bullae deep, broadly ovoid, styliform process blunt; external auditory meatus much as in *Dolichotis*, bounded by incomplete elevated rim, ventral part open into moderately large ventral, accessory opening; stylomastoid foramen large, posterior to external auditory meatus, anterior to extremely small mastoid process; mastoid enlarged, articulates with exoccipital, parietal, and squamosal; epitympanic sinus of petrosal greatly inflated, expressed externally as in *Dolichotis*, forms dorsal rim of external auditory meatus; squamosal with posterior projection as thin lamina over petrosal, flared posteriorly to meet mastoid and supraoccipital; dorsal projection meets frontal at postorbital process, medial projection meets petrosal, and extends onto alisphenoid bar; lateral projection overlaps jugal on side of narrow glenoid fossa; pterygoid small, crest extends to bulla; alisphenoid restricted to posterior wall of orbit medially, posterior part extends to bulla, anterior parts extend over greatly enlarged alisphenoid canal to palatine; optic foramen deep, directly dorsal to enlarged sphenorbital foramen; anterior lacerate foramen and foramen rotundum form single enlarged foramen above alisphenoid bar; carotid canal, median lacerate foramen and Eustachian tube open from cranium as enlarged fissure; foramen ovale remains separate; posterior lacerate foramen and anterior condyloid foramen much as in *Dolichotis*; palatine enlarged, extends into medial wall of orbit; internal nares wide, anterior margin smooth, V-shaped; palate short, surface pitted; tooth rows nearly meet anteriorly; posterior palatine foramen elongate, continued forward as deep grooves; jugal prominent, developed as small zygomatic plate, extends posteriorly to glenoid fossa, marked by deep, rounded notch above suture with squamosal; lacrymal large, contacts with frontal above and posteriorly, and maxillary on side of infraorbital foramen; lacrymal duct deep under dorsal root of zygomatic arch, opens anteriorly on side of rostrum; orbit short, round, extremely deep as in *Dolichotis*; dorsal root of zygomatic arch over M^2, ventral root anterior to P^4; maxillary forms ventral root of zygomatic arch, extends along underside of jugal to level of M^3; rostral masseteric fossa deep, ovoid anteriorly, almost completely restricted to maxillary, posterodorsal margin as sharp ridge; infraorbital foramen with no separate canal for nerve transmission; premaxillary high, extends back between nasal and maxillary to frontal, anterior part developed as sharp ridge anterior to incisor; incisive foramen elongate, narrow, with median septum.

Dental formula.—I_1^1; C_0^0; P_1^1; M_3^3.

Upper dentition (Fig. 27, *a*, *c*).—Cheek teeth extremely hypsodont, evergrowing, with small deposit of cement in inflections; enamel limited to sides of lobes and constricted area on labial face; P^4 to M^2 with two lobes; M^3 with accessory posterior flange; pulp cavities evident as slight fissures on occlusal surface of each lobe.

Incisor tightly arched, base above anterior margin of ventral zygomatic root, one-third deeper than wide; enamel face rounded, surface smooth; labial and posterior faces rounded; medial face flat.

P^4 with pronounced posterior tilt, anterior and labial walls dorsoventrally concave; anterior lobe more bulbous than on M^{1-2}; anterior enamel wall slightly striated parallel to length of tooth; deep part of inflection deflected more posteriorly than

on M^{1-2}; enamel laminae somewhat undulated; point of posterior lobe pinched, forms sharp ridge on lingual wall; posterior wall of posterior lobe essentially flat; labial groove oriented slightly posterior to lingual inflection; labial wall lacking enamel except along line of labial groove.

M^1 and M^2 essentially alike; M^2 slightly smaller than M^1 in occlusal measurements; anterior and posterior lobes subequal in size; M^1 tilted slightly posteriorly; M^2 essentially vertical; anterior wall of M^2 slightly convex dorsoventrally; labial wall slightly concave; anterior wall of M^1 more convex than on M^2, labial wall more concave than on M^2; inflection on M^2 wider than on M^1; labial groove on M^1 and M^2 opposite inflection. Other characters as in P^4.

MEASUREMENTS OF CRANIUM
(Cranium partly crushed, measurements approximate)

Measurements	U.C.M.P. No. 38761
Greatest anteroposterior length	109.0
Basilar length (inferior margin of foramen magnun to posterior border of incisive foramen)	80.2
Palatal length (palatal margin of internal nares to posterior border of incisive alveoli)	44.0
Postpalatal length (posterior of palate to inferior border of foramen magnum)	36.2
Depth of rostrum at ventral zygomatic root	27.4
Depth, floor of basisphenoid to dorsum	19.8
Length of bullae	15.5
Width of bullae	11.0
Width of cranium (narrowest point between dorsal rum of orbits)	21.7
Height of infraorbital foramen	11.0
Palatal breadth (between P^4)	1.7
Palatal breadth (between posterior flange of M^3)	12.5
Length of incisive foramen	13.7
Greatest width of incisive foramen	3.5

M^3 differs from P^4-M^2 in presence of elongate posterior flange developed from posterolabial side of second lobe; pulp cavity of posterior lobe continuous into flange; anterior lobe more bulbous than on M^2; lateral groove opposite reëntrant fold; labial wall of flange convex; lingual face slightly convex; posterior wall flattened; enamel continuous on walls except on labial face of anterior lobe; anterior wall strongly convex; labial wall moderately concave as in M^2.

Mandible (Fig. 27, *b*).—Symphysis long, slender, anterior margin above level of alveolar border, posterior limit with elongate sulcus for transversus mandibularis muscle; diastema elongate (equal to length of cheek-tooth series), straight, convex on all surfaces; mental foramen much as in *Dolichotis*, moderately large, elongate; masseteric crest greatly enlarged and prominent, extends from below $M_{\overline{1}}$ back to area below $M_{\overline{2}}$; angular process drawn far backward, not distorted outward; coronoid process high, prominent, posterior to $M_{\overline{3}}$; condyloid process low; dorsal crest extends from condyle to masseteric crest below $M_{\overline{2}}$; area between coronoid process and dorsal crest deeply excavated for reception of masseter medialis muscle; ventral crest not prominent; inferior pterygoid crest small; inferior dental foramen greatly

enlarged, enters ramus below inferior pterygoid crest; inferior pterygoid fossa shallow, elongate, deepest part posterior to inferior dental foramen and below condyle.

Lower dentition (Fig. 27, *b, d*).—Tooth pattern as in uppers but reversed; $P_{\overline{4}}$ with distinct pattern.

Incisor somewhat procumbent as in *Dolichotis*, base lingual to $M_{\overline{2}}$, subrounded in cross-section; enamel face rounded, smooth; enamel extends well onto side of tooth.

$P_{\overline{4}}$ essentially vertical in jaw; labial and anterior walls slightly concave; differs from molars in presence of additional anterior lobe; posterior lobe normal, median

MEASUREMENTS OF UPPER DENTITION

Measurements	U.C.M.P. No. 38761
Upper dentition length (from anterior face of I to posterior margin of $M^{\underline{3}}$)	53.4
Length of diastema (posterior border of incisive alveoli to anterior border $P^{\underline{4}}$ alveoli)	29.6
$P^{\underline{4}}$-$M^{\underline{3}}$, alveolar length	20.8
$P^{\underline{4}}$-$M^{\underline{3}}$, occlusal length	19.3
I, anteroposterior diameter	4.6
I, transverse diameter	3.0
$P^{\underline{4}}$, anteroposterior diameter	4.7
$P^{\underline{4}}$, transverse diameter (anterior lobe)	4.5
$P^{\underline{4}}$, transverse diameter (posterior lobe)	4.4
$M^{\underline{1}}$, anteroposterior diameter	4.2
$M^{\underline{1}}$, transverse diameter (anterior lobe)	4.3
$M^{\underline{1}}$, transverse diameter (posterior lobe)	4.3
$M^{\underline{2}}$, anteroposterior diameter	4.3
$M^{\underline{2}}$, transverse diameter (anterior lobe)	4.1
$M^{\underline{2}}$, transverse diameter (posterior lobe)	4.1
$M^{\underline{3}}$, anteroposterior diameter	6.3
$M^{\underline{3}}$, transverse diameter (anterior lobe)	4.0
$M^{\underline{3}}$, transverse diameter (posterior lobe)	3.4
$M^{\underline{3}}$, transverse diameter of flange	2.0

lobe smaller than posterior, and anterior lobe smaller, less attenuated than median lobe; inflection between median and posterior lobes narrow, not deflected; anterior inflection shallow, broad; posterior and labial walls with complete enamel; anterior face with enamel restricted to labial part; lingual wall with enamel limited to band along line of groove opposite posterior inflection; $P_{\overline{4}}$ differs from $M^{\underline{3}}$ in presence of lobe rather than smooth flange.

$M_{\overline{1}}$ and $M_{\overline{2}}$; essentially alike in occlusal pattern, larger than $P_{\overline{4}}$; two lobes present, subequal in size; labial margins of lobes drawn into point with resultant sharp ridges on labial wall; inflection wider than posterior inflection on $P_{\overline{4}}$; labial groove slightly posterior to loop of lingual inflection; loop of inflection deflected slightly anteriorly; enamel on labial wall restricted to band along line of groove; enamel walls complete on other faces; $M_{\overline{1}}$ tilted slightly forward in jaw, anterior wall essentially flat, lingual wall slightly concave; $M_{\overline{2}}$ tilted forward at greater angle than $M_{\overline{1}}$; anterior wall convex in contrast to $M_{\overline{1}}$; lingual wall as in $M_{\overline{1}}$.

$M_{\overline{3}}$ with posterior lobe more rounded than on anterior cheek teeth; loop of inflec-

tion deflected more anteriorly than on $M_{\overline{1}\text{-}\overline{2}}$; lingual groove placed more posteriorly than on $M_{\overline{1}\text{-}\overline{2}}$; lingual wall with enamel, except along posterior side of lingual groove, thus differing from all other teeth; forward tilt of $M_{\overline{3}}$ greater than on $M_{\overline{2}}$, otherwise as in $M_{\overline{2}}$.

MEASUREMENTS OF LOWER DENTITION

Measurements	U.C.M.P. No. 38761
$P_{\overline{4}}$-$M_{\overline{3}}$, alveolar length	20.2
$P_{\overline{4}}$-$M_{\overline{3}}$, occlusal length	19.3
I, anteroposterior diameter	3.9
I, transverse diameter	2.8
$P_{\overline{4}}$, anteroposterior diameter	4.7
$P_{\overline{4}}$, transverse diameter (anterior lobe)	2.5
$P_{\overline{4}}$, transverse diameter (median lobe)	2.8
$P_{\overline{4}}$, transverse diameter (posterior lobe)	3.9
$M_{\overline{1}}$, anteroposterior diameter	4.6
$M_{\overline{1}}$, transverse diameter (anterior lobe)	4.1
$M_{\overline{1}}$, transverse diameter (posterior lobe)	4.0
$M_{\overline{2}}$, anteroposterior diameter	4.7
$M_{\overline{2}}$, transverse diameter (anterior lobe)	4.1
$M_{\overline{2}}$, transverse diameter (posterior lobe)	3.9
$M_{\overline{3}}$, anteroposterior diameter	5.3
$M_{\overline{3}}$, transverse diameter (anterior lobe)	3.8
$M_{\overline{3}}$, transverse diameter (posterior lobe)	3.4
Depth of mandible below $P_{\overline{4}}$	13.3
Depth of mandible below $M_{\overline{3}}$	16.1

Postcranial skeleton.—Described from elements preserved in holotype, U.C.M.P. no. 38761, and paratype, U.C.M.P. no. 41669.

Scapula.—Prescapular fossa large, shallow; coracoid border rounded, not as straight as in *Cavia*; postscapular fossa in form of acute triangle; axillary border

MEASUREMENTS OF SCAPULA

Measurements	U.C.M.P. No. 38761
Length of scapula (vertebral border to acromion)	67.5±
Smallest anteroposterior diameter of neck	8.2
Transverse diameter of neck at same level	4.1
Length from point of acromion to posterior margin of metacromion	19.8
Anteroposterior diameter of glenoid fossa	10.7
Transverse diameter of glenoid fossa	8.2

straight as in *Lagidium*; vertebral border moderately rounded; spine large, extends from axillary border to area lateral to prescapular notch; spine deflected posteriorly over postscapular fossa; acromion broad, extends below glenoid fossa; metacromion greatly enlarged, broad, posterior margin somewhat squared, gives appearance of "flag"; infrascapular fossa with longitudinal furrow along line of spine; neck small, incisura scapulae deeper than it is in *Cavia*, as in *Lagidium*, glenoid fossa broadly ovoid, fairly deep; coracoid process enlarged as in *Lagidium*.

Humerus.—Essentially as in *Dolichotis*; head broad, prominent, overhangs posterior surface of shaft; lesser tuberosity prominent, greater tuberosity greatly enlarged, forms high ridge above head, surface for infra-spinatus as concave pit on lateroposterior surface of greater tuberosity; bicipital groove deep, elongate; shaft essentially straight, much deeper than broad; deltoid ridge greatly elongated, extends to basal one-fourth of shaft, massive, proximal part distorted laterally; distal end not greatly expanded; supinator ridge low, not distinct; olecranon fossa large, deep, open to anterior; external condyle small; not expanded; internal condyle

MEASUREMENTS OF HUMERUS

Measurements	U.C.M.P. No. 38761
Length from greater tuberosity to trochlea	74.5
Width across tuberosities	13.3
Width across epicondyles	12.8

enlarged, developed as rounded rugose knob; trochlea broad, deep, internal and external margin raised into sharp keel, internal keel continuous onto capitulum; external keel not extended onto capitulum.

Ulna.—Much as in *Dolichotis*; olecranon enlarged with prominent lateral ridge extending down to proximal lip of sigmoid notch; sigmoid notch deep, transversely narrow, not broad as in *Cavia*, dorsal lip extended; coronoid process of distal lip small; radial notch small; posterior face of shaft with concave outline; distal part of shaft deflected laterally, distal facet for articulation of radius elongate, narrow; styloid process, elongate, much as in *Cavia*, not as in *Dolichotis*.

MEASUREMENTS OF ULNA

Measurements	U.C.M.P. No. 38761
Greatest length	75.6
Anteroposterior diameter of olecranon	7.9
Transverse diameter of olecranon	6.3
Width of dorsal lip of signoid notch	5.7

Radius.—Articular circumference proximodistally narrow, elongate, transversely convex; proximal facet for articulation with humerus with raised crest on anteromedial edge; interosseous membrane attachment as linear groove on posterior surface of shaft; shaft with concave posterior outline; distal end transversely expanded; surface for ulna broadly concave; styloid process deflected posteriorly, not greatly extended.

Scapholunar.—Scaphoid and lunar fused; much as in *Cavia*; radial facet laterally convex, medially concave; posteromedial surface with bulbous, proximally directed node as in *Cavia*; magnum facet anteroposteriorly concave, posterior end terminates in distally directed node; facets for trapezoid and trapezium concave; lateral face with small rounded facet for articulation with cuneiform; greatest width, 7.4 mm.; measured on U.C.M.P. no. 38761.

Cuneiform.—Not much different from *Cavia*; proximal surface constricted, with small, square, concave facet for styloid process of ulna; posterolateral face with flat, triangular facet for pisiform; distal face with comma-shaped unciform facet, transversely concave and slightly convex anteroposteriorly; lateral part of bone drawn to posterodistally directed point; transverse width, 6.2 mm.; measured on U.C.M.P. no. 38761.

MEASUREMENTS OF RADIUS

Measurements	U.C.M.P. No. 38761
Greatest length (crest of head to styloid process)	57.3
Transverse diameter of head	8.2
Transverse diameter of distal end	8.8

Pisiform.—Cuneiform facet triangular; proximoanterior face with concave facet for styloid process of tibia; posterior end of bone transversely and proximodistally enlarged; medial side concave; length, 8.6 mm.; U.C.M.P. no 38761.

Unciform.—Relatively large; proximal surface with broad, crescentic, and convex facet for cuneiform; distal face with medial concave, subrectangular facet for mc. IV, lateral facet for mc. V smaller, more triangular, transversely convex, and oriented at an angle to medial facet; greatest width, 5.6 mm.; U.C.M.P. no. 38761.

MEASUREMENTS OF MANUS

Measurements	U.C.M.P. No. 38761
Length of metacarpal I	3.7
Length of metacarpal II	19.3
Length of metacarpal III	23.6
Length of metacarpal IV	20.5
Length of metacarpal V	15.0
Length of proximal phalanx III	9.2
Length of proximal phalanx IV	8.5
Length of proximal phalanx V	6.8
Length of median phalanx IV	4.7
Length of median phalanx V	3.8
Length of distal phalanx V	5.0

Magnum.—Proximal surface articulates with scapholunar; medial face with elongate facet for mc. II and small ovoid facet for trapezoid; lateral surface with ovoid, slightly convex unciform facet; distal surface oblique, transversely concave, articulates with enlarged mc. III.

Trapezoid.—Small; articulates with magnum, scapholunar, trapezium, and lateroproximal edge of mc. II.

Trapezium.—Small, rectangular; distomedial surface with facet for vestigial mc. I.

Metacarpals and phalanges.—Digits four in number; mc. III largest; mc. II and IV subequal in size; mc. V small; mc. I reduced to minute ovoid bone; proximal phalanges broad proximally, not expanded distally, size relationships as in metacarpals; proximal phalanx I completely lost; median phalanges short, flattened,

relatively broad; distal phalanges longer than median counterparts, broad with anterior cleft; size of median and distal phalanges with same relationship as in metacarpals.

Pelvis.—Acetabulum deep; incisura acetabuli wide, deep; acetabular rim elevated, prominent; ischial spine small; obturator foramen elongate, ovoid, with smooth ischial and pubic borders; ischial tuberosity not expanded; lateral surface of ilium with rounded, elongate ridge anterior to acetabulum, more prominent than in *Cavia*; great sciatic notch shallow, elongate, smooth; posterior-inferior spine not

MEASUREMENTS OF PELVIS

Measurements	U.C.M.P. No. 41669
Length from crest of ilium to anterior rim of acetabulum......................	49.5±
Diameter of acetabulum...	10.0±
Length from tuberosity of ischium to posterior rim of acetabulum..............	29.0±

prominent, smooth; auricular border straight, smooth; crest of ilium flared outward, not greatly enlarged; anterior-superior process not prominent.

Femur.—Much as in *Cavia* but with relatively long, slender shaft; head relatively small as compared to general proportions, prominently defined; pit for ligamentum teres ovoid, deep, placed posterior to apex of head; neck slender, short; greater trochanter bulbous, extends above level of head, not as long as in *Lagidium* nor as short as in *Cavia*; intertrochanteric ridge straight, thick with smooth edge; trochanteric fossa broadly ovoid, deep; lesser trochanter small, developed as low,

MEASUREMENTS OF FEMUR

Measurements	U.C.M.P. No. 41668	U.C.M.P. No. 39885
Greatest length..	82.5±	....
Proximodistal diameter of neck..................................	5.6	....
Anteroposterior diameter of neck................................	4.5	....
Diameter of head..	9.5	....
Diameter across distal condyles.................................	....	14.4
Length of internal condyle......................................	....	14.6

rounded knob, relatively smaller than in *Cavia*; shaft straight, slender as compared to *Cavia*, transversely ovoid in cross-section; linea aspera straight, developed as slender ridge extending halfway down lateral face of shaft; distal end not expanded as much as in *Cavia*; internal condyle wider than external condyle; internal and external tuberosities indistinct, developed as shallow pits; intercondyloid fossa rectangular in outline, deeper and narrower than in *Cavia*, not so deep as in *Lagidium*; patellar groove broad and shallow, much as in *Dolichotis*.

Tibia.—Relatively more slender and much longer than in *Cavia*; proportions as in *Dolichotis*; shaft essentially straight from anterior aspect; head bent posteriorly; distal part of shaft straight, subtriangular in cross-section; internal tuberosity of head not expanded as much as external tuberosity; proximal fibular facet as

rounded, distally extended node; tuberosity for patellar ligament broad, ovoid; papliteal notch deep, narrow, more sharply defined than in *Cavia*; cnemial ridge prominent, more sharply ridged and longer than in *Cavia*, essentially as in *Dolichotis*; distal end of bone not expanded as much as in *Cavia*; descending process short, broad, rounded; medial malleolus not greatly lengthened, broad; fibular articulation as distinct ridge, extended proximally along distal two-thirds of shaft.

MEASUREMENTS OF TIBIA

Measurements	U.C.M.P. No. 41669
Greatest length (spine of papliteal groove to medial malleolus)	82.7
Transverse diameter of head	18.2
Width across astragalar facet	9.5
Diameter from medial malleolus to descending process	9.0

Calcaneum.—Astragalar facet not as oblique as in *Cavia* or *Lagidium*, convex proximodistally, ovoid in outline; sustentacular facet expanded; triangular in outline, not as concave as in *Lagidium*, distal and medial rim with distinct groove, pierced distally by small foramen; posterior surface of sustentacular facet proximodistally convex, transversely flat; groove for tendon of flexor digitalis longus muscle not as prominent as in *Lagidium*; olecranon more broadened than in *Cavia*,

MEASUREMENTS OF CALCANEUM

Measurements	U.C.M.P. No. 38761
Greatest length	26.7
Length from nutrient foramen to olecranon	19.8
Anteroposterior diameter of olecranon	8.5
Transverse diameter of olecranon	6.6
Proximodistal length of astragalar facet	8.4
Transverse width of astragalar facet	4.3

triangular in outline, with transverse groove; cuboidal facet more oblique and more deeply concave than in *Lagidium*, anterior rim with prominent, medially directed spur; medial surface of bone above sustentacular facet concave; posterior surface slightly convex proximodistally; lateral surface concave above astragalar facet; distolateral extremity with small, deeply grooved peroneal tubercle.

Astragalus.—More as in *Lagidium* than in *Cavia*; calcanear facet not as oblique nor as short as in *Cavia*, deeply concave proximodistally, distal part drawn laterally as in *Lagidium*; sustentacular facet long, extends from lip of trochlea onto head, facet widest opposite distal margin of calcanear facet; groove for flexor hallucis longus muscle as in *Lagidium*, proximally wider than in *Cavia*; external condyle broad, with shallow wall; internal condyle with rounded rim and steep wall, trochlea broad, not as deep as in *Lagidium* nor as shallow as in *Cavia*, distal part ends in deep pit for origin of extensor brevis digitorium muscle, pit delimited distally by prominent transverse ridge running across neck below condyles; neck relatively shorter,

less deflected than in *Cavia*, transversely broader and flatter than in *Lagidium*; head wider than deep; navicular facet roughly triangular in outline, convex, continuous with sustentacular facet; medial side of head developed as prominent knob with facet for articulation of sesmoid bone; proximolateral face of calcanear facet with concave facet for malleolus of fibula.

Navicular.—Extremely specialized; astragalar facet subrounded, deeply concave, posterolateral rim elevated as crest; lateral face with broadly ovoid, flat facet for cuboid, medial surface with ovoid, convex facet for proximal end of vestigial mt. V, facet meets posteromedial rim of astragalar facet; dorsal face excavated lateral to facet for mt. V and posterior to astragalar facet; distal face with two facets, medial facet for mesocuneiform, smaller than ectocuneiform facet; mesocuneiform facet ovoid, flat anteriorly, posterior part extended distally; ectocuneiform facet cres-

MEASUREMENTS OF ASTRAGALUS

Measurements	U.C.M.P. No. 38761
Total length	13.6
Width of condyles	9.0
Length from head to proximal end of sustentacular facet	11.2
Anteroposterior diameter of head	5.4
Transverse diameter of head	7.5

centic, transversely convex, anteroposteriorly concave; posterior face developed as much enlarged, distally long clawlike, plantar spur; greatest anterposterior diameter, 9.1 mm.; transverse diameter of astragalar facet, 5.6 mm.; length of plantar process, 10.3 mm.; anteroposterior diameter of plantar process (from posterior rim of mesocuneiform facet to posterior surface), 5.2 mm.; measured on U.C.M.P. no. 38761.

Cuboid.—Much as in *Cavia*; calcanear facet extends onto anterior face, facet strongly oblique to proximodistal axis, surface transversely flat, extremely convex anteroposteriorly; proximoanterior part of medial face with rounded, flat navicular facet; medial face excavated below navicular facet; lateral face with grooved facet for vestigial mt. V on anterodistal part; posterior surface traversed distally by deep groove for tendon of peroneus lungus muscle, surface of posterior face developed as large prominence for attachment of ligament as in *Lagidium*; distal facet for mt. IV subtriangular, slightly concave; greatest height, 6.5 mm.; greatest anteroposterior diameter, 7.5 mm.; as measured on U.C.M.P. no. 38761.

Ectocuneiform.—Body as subtriangular prism; anterior face nearly square; medial navicular facet somewhat pear-shaped in outline, transversely concave, anteroposteriorly convex; lateral face with small crescentic navicular facet on proximal rim, surface excavated distally, medial surface with four facets; proximal part with two anteroposteriorly elongated, lenselike mesocuneiform facets; distal part with anterior and posterior rounded facets for reception of mt. II; distal face with pear-shaped facet for mt. III; greatest height, 5.4 mm.; measured on U.C.M.P. no. 38761.

Mesocuneiform.—Much as in *Lagidium*, navicular facet lozenge-shaped; lateral face with two small facets for articulation with ectocuneiform; distal surface with

rectangular facet for mt. II, facet concave anteroposteriorly, convex transversely; medial surface with rugose ligamental attachment for entocuneiform.

Entocuneiform.—Essentially as in *Cavia*; elongate, extends down onto medial side of mt. II, transversely flattened; proximolateral surface with small, ovoid navicular facet; lateral face with ligamental area for attachment to mesocuneiform below navicular facet; distal half of lateral face with elongate facet and ligamental area for reception of mt. II; vestigial mt. I evidently fused to distal end of entocuneiform; length, 9.8 mm.; measured on U.C.M.P. no. 38761.

Metatarsals and phalanges.—Pes greatly enlarged, with same size relationship to manus as seen in *Cavia* and *Lagidium*; pes one-third longer than manus; mt. III

MEASUREMENTS OF PES

Measurements	U.C.M.P. No. 38761
Length of metatarsal II.	29.3
Length of metatarsal III.	31.4
Length of metatarsal IV.	28.9
Length of metatarsal V.	7.0
Length of proximal phalanx II.	12.5
Length of proximal phalanx III.	14.2
Length of proximal phalanx IV.	11.5
Length of median phalanx II.	6.9
Length of median phalanx III.	8.3
Length of median phalanx IV.	5.7
Length of distal phalanx II.	9.3
Length of distal phalanx III.	12.5
Length of distal phalanx IV.	8.5±

largest, evidently supports most of weight; shaft broad, anteroposteriorly flattened; ectocuneiform facet large, triangular; distal condyle not expanded, surface of condyle flat, keel present on posterior half of condyle; metatarsals II and IV shorter and less robust than mt. III; mt. II with medially bowed shaft; proximal end transversely compressed, proximal facet articulates with mesocuneiform, lateral facet meets ectocuneiform and proximolateral surface of mt. III; proximomedial surface excavated for articulation of entocuneiform; proximoposterior surface with distinct tubercle; shaft subtriangular in cross-section; distal end relatively more expanded than in mt. III, condyle smaller than on mt. III, face convex, medially oblique, posterior keel at angle to line of shaft; mt. IV subequal to mt. II in length, proximal end not compressed, proximomedial surface with tubercle for articulation with mt. III, cuboidal facet triangular, drawn posterior into small tubercle; proximolateral face excavated, with L-shaped facet for articulation of vestigial mt. V; shaft bowed laterally, subtriangular in cross-section; distal condyle a mirror image of mt. II; mt. V vestigial, medial surface with small facet for mt. IV; proximal end with oblique, concave cuboidal facet; distal end as tapered node.

Proximal phalanx III much larger than phalanx II or IV; proximal end transversely expanded; shaft broad, plantar surface excavated with lateral and medial ridgelike tubercles, distal condyle transversely flat, not expanded; phalanx II slightly larger than phalanx IV, proximal ends not as greatly expanded as on

phalanx III; medial phalanges half as long as proximal counterparts; distal phalanges nearly as long as proximal counterparts, plantar surface distally flat, wedge-shaped, proximal part with broad, ovoid tubercle, appearance almost hooflike.

Cervical vertebrae.—Entire series preserved: atlas as in *Cavia*; neural arch smooth; neural spine as small tubercle, transverse processes short, edges rounded; cranial articular facets large, crescentic; posterior facets round, vertical, flat; vertebrar-terial canal small; hypophysial tubercle smaller than in *Cavia*: axis with higher, stronger neural spine than in *Cavia*; odontoid process shorter than in *Cavia*: third to seventh cervicals essentially as in *Cavia*.

Thoracic vertebrae.—Neural spines generally longer than in *Cavia*; transverse processes wider, more complicated than in *Cavia*, more as in *Lagidium*; numbers four, five, eight, nine, ten, twelve, and thirteen preserved in type specimen; centra enlarged greatly from front to rear; centrum of number thirteen twice as large as in number four; neural spines directed posteriorly in anterior thoracics, anteriorly on number thirteen.

Lumbar vertebrae.—Much as in *Cavia* but neural spines longer, more massive; numbers one and six preserved, transverse processes on number six larger, more wing-shaped than in *Cavia*.

Sacrum.—Consists of three solidly fused vertebrae; essentially as in *Cavia*, but neural spines thin, evidently more elongate; rudiments of zygapophyses not so reduced as in *Cavia*, much as in *Lagidium*; major articulation with pelvis on first sacral vertebra; length of sacrum, 30.0± mm.; transverse width across first sacral, 23.0± mm. measured on U.C.M.P. no. 39885.

Caudal vertebrae.—Tail evidently longer than in *Cavia* or *Dolichotis*; neural spines longer than in *Cavia*; only three caudals preserved; nearly equal in size.

Comparisons.—*Prodolichotis pridiana* is the sixth species referable to the genus *Prodolichotis* Kraglievich, 1932, and is the first-known occurrence of the genus in rocks of pre-Pliocene age. Of the previously described species, *P. molfinoi* Kraglievich from beds of Mesopotamian age is the oldest. *P. prisca* (Rovereto) and *P. mendocina* (Rovereto) are from beds assigned to the Huayquerian stage. *P. lacunosa* (Ameghino) has been described from beds of Montehermosan age, and the fifth species, *P. perfecta* (Ameghino), is from beds assigned to the Chapadmalalan stage.[9]

Kraglievich (1932B), in his original generic diagnosis, characterizes *Prodolichotis* as having a cranium similar to *Dolichotis*, but with a shorter rostrum, narrower frontals; M³ more as in *Orthomyctera*, with the posterior lobe not well developed and the internal furrow, which defines it, wide and superficial, instead of being compressed and deep as in *Dolichotis*. In the description of the genotype, *P. prisca* (Rovereto), Kraglievich mentions several other characters that seem to be of generic validity. These are: lacrymal not completely intersecting the maxillary on the face of the infraorbital foramen and lower incisor extending back as far as in *Dolichotis*. *Prodolichotis pridiana* agrees with the genotypic species in all these characters.

Prodolichotis prisca differs from *P. pridiana* in: slightly smaller size; somewhat larger auditory bullae; more anteriorly placed internal nares (opposite inflection of M²).

Prodolichotis mendocina is distinct from *P. pridiana* in having: smaller size; diastema shorter than cheek-tooth series; smaller, more rounded anterior lobe on P₄.

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[9] The stage names used here are those proposed by Simpson (1940).

Prodolichotis molfinoi differs from *P. pridiana* in having: relatively shallower, more slender mandible; but seems similar to *P. pridiana* in: size; position and size of masseteric crest; width and depth of inflection between anterior and median lobe of $P_{\bar{4}}$.

Prodolichotis lacunosa and *P. perfecta* are indeterminate and without known significance; thus these species are regarded as *nomina vana*.

Orthomyctera differs from *Prodolichotis* in: much smaller size; relatively smaller occipital region; shorter, lower sagittal crest; more wedgelike posterior flange on M^3; less developed anterior lobe on $P_{\bar{4}}$; shorter lower incisor; shorter diastema.

Orthomyctera resembles *Prodolichotis* in: similar development of auditory region; presence of narrower frontals than those in *Dolichotis*; absence of enamel on lateral face of lobes in upper teeth; and lingual face of lobes in lower teeth.

Pliodolichotis is primarily distinguished from *Prodolichotis* by the presence of an additional lobe on last upper molar, in which it differs from all genera in the subfamily Dolichotinae.

Dolicavia is distinguished from *Prodolichotis* in having: narrower rostrum and palate; wider infraorbital foramen with more vertically oriented dorsal and ventral zygomatic roots; more dorsally placed lacrymal that does not reach anterior rim of the infraorbital bar; no notch on jugal; less procumbent lower incisors; anterior and posterior lobes of P^4 equal in size; shorter, broader flange on M^3; smaller anterior lobe on $P_{\bar{4}}$ with no inflection separating it from the median lobe; deeper, more posteriorly oriented labial furrow on upper and lingual furrow on lower cheek teeth.

Dolicavia agrees with *Prodolichotis* in: length and size of lower incisors; position of masseteric crest.

Dolichotis differs from *Prodolichotis* in having: larger size, relatively longer rostrum; broader frontals and parietals; depressed occipital region; presence of sagittal furrow rather than sagittal crest; relatively shorter, more rounded orbit; more expanded zygomatic arch with larger maxillary and smaller jugal parts; smaller, more posteriorly placed jugal notch; larger, more inflated auditory bullae; larger, more inflated mastoid; narrower basicranial axis; more anteriorly placed internal nares; longer, relatively narrower incisive foramen; relatively smaller, less arched upper incisors; more clearly defined third lobe on M^3 with deep, narrow reëntrant angle between median and posterior lobe; relatively longer lower diastema; more widely expanded masseteric crest; presence of ventral expansion of ramus below $P_{\bar{4}}$ and $M_{\bar{1}}$; relatively lower, narrower mandibular condyles; more simplified, flange-like anterior lobe on $P_{\bar{4}}$ with no indication of inflection between anterior and median lobes.

Dolichotis resembles *Prodolichotis* in: enlarged lacrymal that nearly intersects maxillary on infraorbital bar; absence of special canal in infraorbital foramen; expanded squamosal meeting alisphenoid and palatine on alisphenoid bar, posterior part extending over epitympanic sinus of bulla and contacting with mastoid, supraoccipital, and parietal; united cranial foramina; similar development of petrosal with greatly enlarged epitympanic sinus; enlarged external auditory meatus with continuous ventral opening; similar position and size of stylomastoid foramen; lengthened, lingually arched paraoccipital process; high and relatively narrow occiput; large, vertically oriented occipital condyles; short, heavily pitted palate; convergent tooth rows (P^4s almost meet); similar curvature to each upper cheek

tooth; absence of enamel on labial face of lobes in upper teeth and on lingual face of lobes in lower teeth; procumbent lower incisors with base below $M_{\bar{3}}$; similar position and size of inferior dental foramen; posteriorly extended mandibular angle with little lateral distortion; similar position and size of dorsal mandibular crest and accompanying fossa; high, crested coronoid process; similar orientation and curvature to each lower cheek tooth.

<div align="center">STATISTICAL ANALYSIS</div>

P. pridiana has been recovered from V-4536 in the San Nicolás Clays; V-4517, V-4936, V-4521, and V-4519 in the Monkey Unit; V-4522 in the Unit Below Fish Bed, and V-4523 in the Fish Bed. The stratigraphic thickness is only 125 meters. This seems unique when compared to the previously described forms in the La Venta fauna. Although *Olenopsis* and, especially *Scleromys* occur in nearly every locality from the base of the section through the uppermost levels, only thirteen individuals of *P. pridiana* are represented in the La Venta assemblage. Possibly, this meager representation is due to the fortunes of collecting, but in a well-exposed area where small forms have been collected in abundance this seems unlikely. It seems more probable that this scarcity is of greater significance (see pages 000-000).

The poor representation of *P. pridiana* in the La Venta fauna limits the application of statistical analysis to the materials. The only analysis possible is on the alveolar length of $P_{\bar{4}}$-$M_{\bar{3}}$. Six specimens were available for this analysis. By applying small-sample methods, the following values were obtained:

<div align="center">

Alveolar length of $P_{\bar{4}}$-$M_{\bar{3}}$.

M. = 19.76 ± .63

S.D. = 1.55 ± .45

C.V. = 7.84 ± 2.28

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The sample is admittedly small, but *P. pridiana* is probably a species with average variability. The holotype, U.C.M.P. no. 38761, represents an individual larger than the mean by only .34 mm. and is within ±1 S.D. from the mean, wherein 68.27 per cent of all observations are expected to fall. In the usual concept of variation in a species, the calculated range of variability in the length $P_{\bar{4}}$-$M_{\bar{3}}$ of *P. pridiana* would be from 15.11 ± 1.35 mm. to 24.41 ± 1.35 mm. This requirement is met by all available specimens, and all animals in the University of California collection fall within ±2 S.D. from the mean, or a linear range from 16.66 ± .90 to 22.86 ± .90 mm.

<div align="center">DISCUSSION</div>

Prodolichotis pridiana has been placed in Kraglievich's genus because of the marked similarity in: shape, character, and position of the lacrymal bone; size and shape of the parietal and occipital regions; relative size and position of the coronoid process and inferior dental foramen; size and complexity of the supplementary lobes on $M^{\underline{3}}$ and $P_{\bar{4}}$; position and character of the inflections and grooves on the cheek teeth.

With the postcranial skeletons of the holotype and paratype, some interesting observations can be made concerning adaptive radiation of body form. In general body proportions *P. pridiana* seems similar to *Cavia* except in certain details. In the vertebral column, *P. pridiana* has greater expansion of the neural arches, only three vertebrae fused into the sacrum, and a longer caudal series. In these charac-

ters *P. pridiana* is more like *Dolichotis*. In the hind limb the ratio between the length of the tibia and the length of the femur shows a generalized condition similar to that of *Eocardia* from the Santa Cruz fauna. The ratio of length of tibia to length of femur is 1.00 for *P. pridiana* and 1.03 for *Eocardia*. In *Cavia* this ratio is 1.12 and in *Dolichotis* 1.24 (see Fig. 26). The same relationships are seen in the fore limbs. The ratio of length of humerus in *P. pridiana* is 0.77 and in *Eocardia* 0.78. In *Cavia* this ratio is 0.87, and in *Dolichotis* it reaches the extreme, 1.29. In relative size of the hind foot, *P. pridiana* again agrees with *Eocardia*. The ratio between length of mt. III and the femur in *P. pridiana* and in *Eocardia* is 0.35. In *Cavia* this ratio is 0.40, and in *Dolichotis* 0.52 (see Fig. 26). When the ratio between length of hind limb (femur + tibia) and length of the fore limb (Humerus + radius) is calculated, somewhat different relationships are seen. In *Eocardia* this ratio is 0.65 and thus the fore limb is much shorter than the hind. In *Cavia* the limbs come nearer to being equal in length, the ratio being 0.78. *P. pridiana* is beyond *Cavia* in this character, with a ratio of 0.80, and indicates a tendency toward lengthening of the fore limb as in *Dolichotis*, where the ratio is 0.92. If the ratio between the length of mc. III and mt. III is calculated, *Dolichotis* shows the greatest difference, 0.60. *Cavia* follows with 0.72, and *P. pridiana* displays the least size difference between mc. III and mt. III with a ratio of 0.75.

In a summary, the following characters seem evident. In the lengthening of the distal part of the hind limb, *Dolichotis* is the most extreme and *Prodolichotis* the least. In the trend to lengthen the distal part of the front limb, *Dolichotis* is again most extreme and *Prodolichotis* the least. In the tendency to enlarge the elements of the pes, *Dolichotis* shows the greatest specialization and *Prodolichotis* the least. In comparative size of front and hind feet, *Dolichotis* again exhibits the greatest difference and *Prodolichotis* the least. In all these characters, *P. pridiana* is most like *Eocardia* from the Santa Cruz fauna. A comparison of the over-all length of hind and fore limbs, *P. pridiana* is more like *Cavia* and possibly foreshadows the specialization seen in *Dolichotis*. Morphologically the pes of *P. pridiana*, with its complete loss of metatarsals I and V and greatly enlarged third metatarsal, indicates a digitigrade adaptation.

The foregoing observations, together with those mentioned under comparisons, have led to the conclusion that *P. pridiana* is related to *Dolichotis*, but is probably not ancestral to the living genus. It, nevertheless, is a form of great interest and importance, for it brings to light one step in the development and phylogeny of the Dolichotinae and furnishes substantial evidence that caviid specializations that had their beginnings in the late Oligocene were clearly defined and close to reaching stability by late Miocene time.

Family Capromyidae

Neoreomys huilensis Fields, n. sp.
(Fig. 28)

Holotype.—Incomplete left lower jaw with $P_{\overline{4}}$ to $M_{\overline{3}}$ in place; base of incisor; U.C.M.P. no. 37973.

Type locality.—Lone Tree Locality, Monkey Unit, vicinity of Villavieja, Department of Huila, Colombia, South America, V-4521. (See note 2.)

Fauna.—La Venta.

Age.—Late Miocene.

Diagnosis.—Mandible heavy; angle distorted outward; inferior pterygoid fossa broad, shallow, elongate; masseteric crest small, oblique, ovoid, below anterior moiety of $M_{\overline{1}}$; mandibular masse-

teric fossa shallow; ventral mandibular crest smooth, extends forward to masseteric crest; incisor small, base posterior to M$\overline{3}$, enamel face convex, smooth; cheek teeth subhypsodont with broad hypoflexid; hypostriid not continuous to base of tooth; mesostriid of P$\overline{4}$ longer than metastriid, metastriid longer than parastriid; metastriid on M$\overline{2}$ and M$\overline{3}$ longer than mesostriid; parastriid longer than mesostriid; metastriid on M$\overline{3}$ longer than on M$\overline{1-2}$; M$\overline{1}$ to M$\overline{3}$ progressively larger; P$\overline{4}$ equal to M$\overline{3}$ in anteroposterior diameter.

DESCRIPTION

Mandible.—Shallow, much as in *Neoreomys australis*, but much smaller, about as large as *Scleromys colombianus*; symphysis apparently long, not as massive as in *Scleromys*; inferior pterygoid fossa shallow, not nearly so deep as in *Scleromys*; angle distorted outward, not as extreme as in *Scleromys*; masseteric crest small, as oblique,
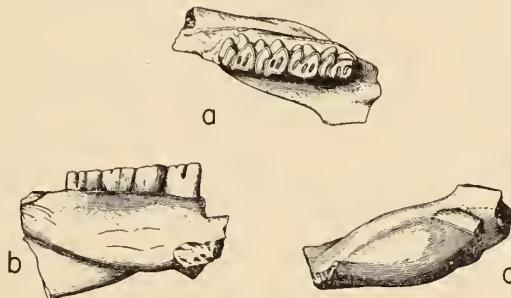

Fig. 28. *Neoreomys huilensis* Fields, n. sp.; holotype, U.C.M.P. no. 37973, loc. V-4521, Lone Tree locality; *a*, occlusal view of left mandibular ramus; *b*, lingual view; *c*, ventral view; × 1.

ovoid shelf below anterior moiety of M$\overline{1}$ as in *N. australis*; mandibular masseteric fossa shallow, extends forward to masseteric crest, dorsal part somewhat excavated below coronoid process, separated from ventral part by median ridge; coronoid process not present but evidently large, anterior margin arises opposite M$\overline{3}$; inferior dental foramen elongate, below inferior pterygoid crest; alveolar border narrow, elevated more than in *N. australis* and *Scleromys*, constricted posterior to M$\overline{3}$.

Dental formula.—I$\frac{1}{1}$; C$\frac{0}{0}$; P$\frac{1}{1}$; M$\frac{3}{3}$.

Dentition.—Incisor relatively smaller than it is in *N. australis*, base slightly behind M$\overline{3}$; tooth not strongly curved as in *Scleromys*; enamel face strongly convex.

P$\overline{4}$ erupts late; anteroposterior diameter much greater than transverse diameter in unworn state; transverse diameter increases with wear, never equal to anteroposterior diameter; hypoflexid wide, continuous with metaflexid in unworn tooth; metaflexid narrow, isolates from hypoflexid in early stage of wear; mesoflexid wider than metaflexid; paraflexid small, isolates as parafossettid in initial stage of wear, labial wall of tooth dorsoventrally convex; hypostriid wide, forms V-shaped plication, anterior limb of V shallow, tapers to anterolabial angle of tooth, posterior limb of V sharp, narrow; anterior face of tooth dorsoventrally concave, transversely convex; lingual wall dorsoventrally concave, slightly convex anteroposteriorly, mesostriid long compared to metastriid; parastriid superficial, metastriid longer than parastriid; posterior face of tooth convex, parafossettid and metafossettid transversely elongate, slightly oblique and crescentic; mesofossettid forms close to lingual wall of tooth, oriented transversely, lenselike in outline; fossettids extend below base of hypoflexid.

$M_{\bar{1}}$ and $M_{\bar{2}}$ differ considerably from $P_{\bar{4}}$; anterior outline strongly concave dorsoventrally, transversely more convex than on $P_{\bar{4}}$; labial face essentially as in $P_{\bar{4}}$; lingual face concave dorsoventrally, anteroposteriorly less convex than in $P_{\bar{4}}$; posterior face more flattened dorsoventrally, more convex transversely than in $P_{\bar{4}}$; anteroposterior diameter greater than transverse diameter in unworn tooth; equal to, then less than, transverse diameter in greatly worn tooth; hypoflexid wider and deeper than in $P_{\bar{4}}$; metaflexid deeper than paraflexid or mesoflexid, retains connection with hypoflexid after paraflexid and mesoflexid isolate as fossettids, connection of metaflexid to hypoflexid lost at same time; metastriid longer than mesostriid and parastriid; mesostriid of $M_{\bar{2}}$ longer than on $M_{\bar{1}}$; hypoflexid isolates as hypo-

MEASUREMENTS OF LOWER DENTITION

Measurements	U.C.M.P. No. 37973 (Holotype)
$P_{\bar{4}}$-$M_{\bar{3}}$, alveolar length..	17.9
$P_{\bar{4}}$-$M_{\bar{3}}$, occlusal length...	17.4
I, anteroposterior diameter..	3.1
I, transverse diameter...	2.5
$P_{\bar{4}}$, anteroposterior diameter...	4.4
$P_{\bar{4}}$, transverse diameter...	3.5
$M_{\bar{1}}$, anteroposterior diameter...	4.3
$M_{\bar{1}}$, transverse diameter...	3.8
$M_{\bar{2}}$, anteroposterior diameter...	4.2
$M_{\bar{2}}$, transverse diameter...	4.3
$M_{\bar{3}}$, anteroposterior diameter...	4.5
$M_{\bar{3}}$, transverse diameter...	3.9

fossettid in extreme stage of wear; parafossettid, mesofossettid, and metafossettid of $M_{\bar{1}}$ usually subequal in size, mesofossettid of $M_{\bar{2}}$ smaller than that of $M_{\bar{1}}$, more transverse and lense-shaped than on $P_{\bar{4}}$; metafossettid situated posterior to hypoflexid in worn tooth.

$M_{\bar{3}}$ with greater anteroposterior diameter than $M_{\bar{1}}$ or $M_{\bar{2}}$; anterior face less concave dorsoventrally and posterior face less convex dorsoventrally than on $M_{\bar{1}}$ or $M_{\bar{2}}$; posterior face flattened transversely with median dorsoventral furrow; anteroposterior diameter always greater than transverse diameter; anterior moiety of tooth much wider than posterior moiety; hypoflexid much as in $M_{\bar{1}\text{-}\bar{2}}$ but anterior limb concave; metastriid much longer than on $M_{\bar{1}}$ or $M_{\bar{2}}$, extends to basal one-half of tooth; other characters as in $M_{\bar{1}\text{-}\bar{2}}$.

Comparisons.—Characters that seem to place *Neoreomys huilensis* in Ameghino's genus are:

1. Similarity of dental pattern in lower cheek teeth.
2. Decrease in anteroposterior diameter toward base in $M_{\bar{1}\text{-}\bar{2}}$.
3. Increasing size from $M_{\bar{1}}$ to $M_{\bar{3}}$ with $P_{\bar{4}}$ subequal to $M_{\bar{3}}$.
4. Relatively shallow, broad mandible.
5. Enlarged coronoid process.
6. Narrow alveolar border with constriction posterior to $M_{\bar{3}}$.

Neoreomys australis differs from *N. huilensis* in: larger size; relatively shallower,

more elongate mandible; less elevated alveolar border; somewhat larger masseteric crest; more convergent tooth rows; relatively larger, shorter incisor with flattened enamel face.

Myocastor differs from *Neoreomys huilensis* in: much larger size; relatively more massive; deeper mandible, more elevated alveolar border; smaller masseteric crest; reduced coronoid process; greatly enlarged, laterally expanded ventral mandibular crest; relatively larger, shorter incisor; more flattened enamel surface; increasing size from $P_{\overline{4}}$ to $M_{\overline{3}}$; longer parastriid, mesostriid, and metastriid; presence of cement in inflections.

Myocastor resembles *N. huilensis* in: shallow, broad inferior pterygoid fossa; narrow alveolar border with constriction posterior to $M_{\overline{3}}$; placement of inferior dental foramen below inferior pterygoid crest; similar dental pattern on cheek teeth.

DISCUSSION

Only two specimens of *Neoreomys huilensis* have been found in the La Venta fauna. They are both from the Lone Tree Locality in the Monkey Unit. It seems probable that this form was quite rare in the fauna, especially since so much is known of the small rodents through most of the section. Although the lack of specimens could be attributed to the fortunes of collecting, this apparent rarity implies some greater significance (see page 391).

Scott (1905B) referred Ameghino's species *N. indivisus*, *Pseudoneoreomys leptorhynchus*, and *Pseudoneoreomys mesorhynchus* to *Neoreomys australis* Ameghino 1887. He also placed *Pseudoneoreomys pachyrhynchus* as a synonym of *Neoreomys*, but retained the species as valid. Two other species, *N. dicisus* and *N. variegatus*, are retained by Scott as valid. The two latter species are known from the type specimens only. *N. decisus* is distinguished from *N. australis* by having a flat, rather than convex, incisor. *N. variegatus* is distinguished from *N. australis* by the presence of a groove on the anterolabial wall of $P_{\overline{4}}$. In *N. pachyrhynchus* the rostrum is described as being broad and heavy, and Scott (1950B, p. 400) states that this species seems to be larger than *N. australis*: "The type specimen appears to be rather smaller than the somewhat crushed and distorted skull in the collection of the American Museum of Natural History (No. 9,130)." The length of $P_{\overline{4}}$-$M_{\overline{3}}$ is given as 24 mm. Scott (1950B, p. 399) tabulates several specimens of *N. australis*. In the length of $P^{\underline{4}}$-$M^{\underline{3}}$, the following measures are given: A.M.N.H. no. 15,222—25 mm.; A.M.N.H. no. 15,572—24 mm.; A.M.N.H. no. 15,266—23 mm. In the University of California collection, two specimens of *N. australis* are available for measurement of the length $P^{\underline{4}}$-$M^{\underline{3}}$: U.C.M.P. no. 15964—24 mm. U.C.M.P. no. 15435—23 mm. Obviously, there is little difference in the length of the dental series in any of these specimens. It is my opinion that *N. pachyrhynchus* is also a synonyn of *N. australis* and that the broader rostrum is an example of individual variation.

In *N. decisus* and *N. variegatus* the problem is much the same. In *N. decisus* the length of $P_{\overline{4}}$-$M_{\overline{3}}$ is given by Ameghino (1887, p. 11) as 29 mm. For *N. variegatus* the length of $P_{\overline{4}}$-$M_{\overline{3}}$, as given by Ameghino (1894, p. 68), is 30 mm. To refer once again to Scott's (1905B, p. 399) tabulations of *N. australis*, the lengths of $P_{\overline{4}}$-$M_{\overline{3}}$ are: A.M.N.H. no. 15,396—25 mm.; A.M.N.H. no. 15,365—25 mm.; and A.M.N.H. no. 15,266—27 mm. One specimen in the University of California collection, U.C.M.P. no. 15150, measures 27 mm.

STATISTICAL ANALYSIS

If all the above mentioned measurements are subjected to quantitative analysis, the following results are obtained:

Occlusal length of $P_{\bar{4}}$-$M_{\bar{3}}$.

$$M. = 27.00 \pm .86$$
$$S.D. = 2.15 \pm .61$$
$$C.V. = 7.96 \pm 2.27$$

The coefficient of variation of 7.96 ± 2.27 indicates, even in this heterogeneous sample, that all of these specimens probably belong to the same species. Here again, the evidence seems to prove that *N. decisus* and *N. variegatus* are synonyms of *N. australis*.

If these species are synonymous, then *N. australis* is the only species of *Neoreomys* n the Santa Cruz fauna, and *N. huilensis* from the La Venta fauna is the only other species known.

Fig. 29. ?*Steiromys* Ameghino, U.C.M.P. no. 40853, loc. V-4536, San Nicolás locality; occlusal view of ? left $M_{\bar{2}}$; $\times$ 3.

RELATIONSHIPS OF NEOREOMYS

It does not seem probable that *N. australis* could give rise to *N. huilensis*, but it is possible that *Neoreomys* is directly ancestral to *Isomyopotamus* from the Montehermosan fauna. These forms show many resemblances to *Myocastor* in the character of the lower dentition. With more information it may be possible to verify that *N. huilensis* is closely related to, and indeed ancestral to, both *Isomyopotamus* and the existing genus *Myocastor*.

Family ERETHIZONTIDAE

?*Steiromys* sp.

(Fig. 29)

A completely unworn upper molar—tentatively identified as left M^2, with the labial enamel wall and roots missing—and a broken fragment of another molar—evidently from the same individual, U.C.M.P. no. 40853, loc. V-4536, the San Nicolás locality—indicate the presence of a "porcupine" in the La Venta fauna. The occlusal pattern of this tooth is much the same as that in *Erethizon* and perhaps even more like the pattern in *Steiromys intermedius*, described and figured by Scott (1905B) in his monograph on the Santa Cruz fauna. The tooth is somewhat rectangular in occlusal outline. The masticating surface is marked by an anterior, crescent-shaped enamel lake and a smaller, more ovoid, posterior enamel lake. Between these lakes, and entering from the labial side, are two valleys: the posterior of these is deflected posteriorly around the lingual border of the posterior lake, the anterior valley traverses the labial moiety of the crown and abuts against the enamel rim of an oblique valley entering the occlusal surface from the lingual side. The crown is low and the enamel thick. Measurements: anteroposterior diameter, 4.5 mm.; transverse diameter 3.5+ mm.; height of crown, 2.6 mm.

Family ECHIMYIDAE
(Fig. 30)

An incomplete left mandibular ramus with incisor but no cheek teeth, U.C.M.P. no. 40852, from V-4536, the San Nicolás locality, may be referred to the family Echimyidae. It most closely resembles the left mandibular ramus of *Cercomys* among modern mammals available for comparison, but is somewhat shallower below the tooth row. The diastema is relatively shorter and the tooth row somewhat
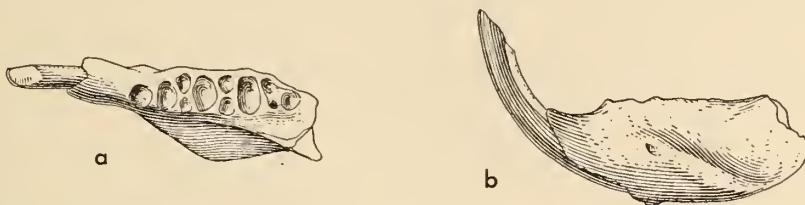

Fig. 30. Echimyidae, U.C.M.P. no. 40852, loc. V-4536, San Nicolás locality; left mandibular ramus; *a*, occlusal view; *b*, labial view; × 2.

longer, as evidenced by the well-preserved root sockets. In character and number of roots present on each tooth, the fossil specimen is identical to *Cercomys*. $P_{\overline{4}}$ was evidently narrower than the molars and had one rounded anterior root and a larger, transversely ovoid posterior root. $M_{\overline{1}}$ and $M_{\overline{2}}$ had two, small, transversely oriented anterior roots and a large, transverse, broadly ovoid posterior root. The crowns of $M_{\overline{1}\text{-}\overline{2}}$ were probably of subequal anteroposterior and transverse diameters. The

MEASUREMENTS OF LOWER JAW

Measurements	U.C.M.P. No. 40852
$P_{\overline{4}}$-$M_{\overline{3}}$, length of alveoli	11.4
I, anteroposterior diameter	1.9
I, transverse diameter	1.5
Length of diastema	3.8
Depth of mandible below $M_{\overline{1}}$ alveolus	6.0

anterior moiety of $M_{\overline{3}}$ had a fairly large, rounded lingual root and a small, ovoid labial root. The posterior moiety had a single, triangular root that was somewhat smaller than the posterior root on $M_{\overline{1}\text{-}\overline{2}}$. The incisor is relatively smaller than in *Cercomys* but of the same proportions. The ventral mandibular crest is laterally expanded, but not as strongly as it is in *Cercomys*, and the masseteric fossa is not as deep as in the living forms. The coronoid process and angle are missing, but evidently they were much the same as in *Cercomys*.

Among the fossil genera from the Santa Cruz fauna, the La Venta specimen seems most like *Adelphomys* in: size; lateral expansion of the ventral mandibular crest; length of the diastema; and height of the alveolar border. The La Venta specimen bears certain resemblances to *Heteropsomys* and *Homopsomys* from the Pleistocene of the West Indies.

The echimyid affinities of this La Venta form seem certain, but without the cheek teeth, generic and specific identification is impossible.

EVOLUTION OF THE LA VENTA RODENTS

Characters have been mentioned in the description and discussion of the La Venta rodents that suggest evolutionary trends in the families Dinomyidae, Caviidae, and Capromyidae, but intergradational evolutionary series in these South American hystricomorphs are not clearly demonstrable. Phyletic sequences, no doubt, are present, but have been obscured by paleontologists who neglected the stratigraphy

| STRATIGRAPHIC OCCURRENCE OF LA VENTA FAUNA RODENT SPECIES	*Scleromy schürmanni*	*Scleromy colombianus*	*Olenopsis aequatorialis*	*Prodolichotis pridiana*	*Neoreomy huilensis*	*?Steiromys* sp.	Echimyidae sp.
Las Mesitas	▌	▌	▌				
Upper Red Beds	▌	▌	▌				
Unit Between Upper & Lower Red Beds	▌	▌	▌				
Lower Red Beds	▌	▌	▌				
Unit Between Ferruginous Ss. & L. Red Beds	▌	▌	▌				
Ferruginous Sands	▌	▌	▌				
Unit Above Fish Bed	▌	▌	▌	▌			
Fish Bed	▌	▌	▌	▌			
Unit Below Fish Bed	▌	▌	▌	▌	▌		
Monkey Unit	▌	▌	▌	▌	▌		
Cerbatana Gravels & Clays - San Nicolás Clays	▌	▌	▌	▌		▌	▌
El Libano Sands & Clays	▌	▌	▌				

Fig. 31. Stratigraphic occurrences of La Venta fauna rodent species within the La Venta badlands section.

or who, perhaps, never saw the site from which their assemblages were collected. Materials from the La Venta fauna, when compared with forms from other ages in South America, bring to light certain probable relationships and lineages.

Stratigraphic relationships (Fig. 31).—The Honda group, as represented in the La Venta badlands, is a sequence of strata over 700 meters thick. Deposition of these beds seems to have been rapid as no evolutionary faunal sequence can be demonstrated.[10] The three best represented species—*Scleromys schürmanni, Scleromys colombianus*, and *Olenopsis aequatorialis*—extend, without visible change,

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[10] It is interesting to note that the Santa Cruz fauna has a similar aspect. Simpson (1940) states that the Santa Cruz formation may reach a thickness of 500 meters in places, but that no faunal sequence has been demonstrated.

from the lowest unit, El Libano Sands and Clays, throughout the section to the Las Mesitas unit.[11] *Prodolichotis pridiana, Neoreomys huilensis, ?Steiromys*, and the echimyid species, however, have limited stratigraphic range (Fig. 31). These apparent stratigraphic limits might be interpreted as significant evidence of an evolutionary sequence within the La Venta fauna, but if this were true it might be expected that other related forms would be found in higher or lower parts of the section, which the present search does not reveal. The limited stratigraphic occurrence of *Prodolichotis* and *Neoreomys* more likely indicates rare elements in the fauna and probably some facies differences between the beds in which they occur and those in which they are absent. *?Steiromys* and the echimyid species are represented by one specimen each from the same locality. It is possible that these two forms were actually more common in the fauna, but here again a facies difference possibly accounts for the small number of specimens collected.

It is incredible that the faunas of the Santa Cruz and La Venta beds demonstrate no evolutionary advances. Simpson (1940), in speaking of the Santa Cruz fauna, states: "Doubtless evolutionary advance will be more clearly demonstrable by the application of more refined field and laboratory methods." This is admittedly possible, but for the La Venta fauna more refined field and laboratory methods have been applied without establishing any evolutionary sequence. It must then be concluded, on our present information, that the observed uniformity of the La Venta fauna is a natural phenomenon and not a factor resulting from inadequate field or research techniques.

Speciation in the La Venta Rodents.—In studying each of the La Venta rodents, special attention was given to characters that might give evidence for speciation. Such evidence is lacking in all the forms studied, with the possible exception of *Olenopsis*, where certain isolated teeth seem to be larger than the average. These teeth, however, have occlusal patterns whose variability is well within the valid limits of a species. One of the largest of these teeth was found in the San Nicolás Clays, near the midpoint of the stratigraphic section. Most of the larger teeth, however, occur in the upper one-third of the section. It is therefore possible that two species of *Olenopsis* are present in the La Venta fauna, but a second species has not been recognized (for reasons mentioned on page 000). After careful consideration of all data on the teeth of *Olenopsis*, it seems that the larger forms are correctly referred to *Olenopsis aequatorialis*. If any differences do exist, they are on a subspecific level and indicative of a chronocline species (Simpson, 1943c).

Evolutionary trends.—The only possible evolutionary trend in the La Venta fauna is displayed in *Olenopsis aequatorialis*, which may be a chronocline species. The evolutionary trend, then, would be a tendency toward greater size.

Broader considerations on the generic and family levels, with their greater time range, offer better evidence of evolutionary trends.

The Dinomyidae, as defined in this paper, seems to represent an important unit in a poorly understood complex of Tertiary rodents, one of which gave rise to the single living genus *Dinomys*. Evolutionary trends suggested by the structural diversity among dinomyids are:

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[11] Stirton's studies (1953a) on the abundant interatheres of the La Venta fauna disclose a similar situation.

1. A general broadening and flattening of the cranial roof with resultant loss of the sagittal crest and its functional replacement by distinct temporal crests.
2. A vertical and transverse expansion of the rostrum and development of a large, squarely outlined masseteric fossa.
3. An expansion of the alisphenoid canal.
4. Development of an enlarged ventral accessory opening connecting with the tubular part of the external auditory meatus.
5. A reduction of the mastoid and paraoccipital processes.
6. A shortening of both the upper and lower diastems.
7. Development of exceedingly large upper and lower incisors with broad, flattened, and thickened enamel faces.
8. Development of extremely long, lower incisors, the bases of which lie well behind $M_{\bar{3}}$.
9. A change from cheek teeth with two inflections on one side and one on the other to five inflections on one side and four on the other.
10. Associated with item 9 is a tendency toward strong hypsodonty accompanied by a trend to lengthen the strii on the sides of the teeth until in extremely hypsodont forms they reach to the base of the teeth.
11. Also associated with item 9 is a trend toward loss of cheek-tooth roots.
12. A divergent, but perhaps significant, trend toward complete loss of the coronoid process, as in *Tetrastylus* and *Dinomys*.
13. Fusion in the anterior cervical vertebrae and a general stiffening of the vertebral column.
14. A trend toward larger size and robust body form.
15. A reduction to four functional digits on manus and pes.
16. A relative lengthening of the hind limb.

A Phylogeny of the Dinomyidae (Figs. 32, 33).—The Dinomyidae apparently originated in pre-Colhuehuapian time (late Oligocene) from an erethizontid, possibly something similar to *Asteromys* or *Ascaremys*, which showed a trend toward hypsodonty and deepening of the tooth inflections.

The oldest recognizable record of a dinomyid is in the late Oligocene Coyaima fauna of Colombia (Stirton, 1953ʙ). Unfortunately this fauna is poorly represented; only an incisor and a badly waterworn upper molar (U.C.M.P. no. 38390) and the proximal part of a calcaneum (U.C.M.P. no. 38887) are known of this early dinomyid. These remains indicate relationship to *Scleromys*, and it is possible that a species of that genus is represented. At present, however, no near relationship to later forms can be shown because of the scant and poorly preserved materials.

By Santacrucian time radiation within this family is shown by the occurrence of two species of *Scleromys* and one species of the larger, more robust *Olenopsis*. The species of *Scleromys* show early stages in the evolutionary trends mentioned in characters 2, 6, 9, 10, 11, and 12 listed above. The Santa Cruz species of *Olenopsis* shows additional early advances in characters 7, 8, and 14.

The smaller species of *Scleromys* present in the La Venta fauna seems more generalized than the larger, and shows no great differences from the Santa Cruz species except that it is smaller. The larger species, *S. colombianus*, shows consider-

able advance, especially in characters 2, 6, 9, 10, 11, and 12. The La Venta species of *Olenopsis* is more advanced than the Santacrucian species in characters 6, 7, 8, and 12.

It seems probable that one of the Santacrucian species of *Scleromys*, possibly *S. angustus*, gave rise to both *S. schürmanni* and *S. colombianus*. Species of this genus are not known from later faunas and seem to have died out before Mesopotamian time (early Pliocene). *Olenopsis* most certainly was derived from *Scleromys*, but their coexistence in the Santa Cruz fauna indicates that the split occurred in pre-Santacrucian time, probably in Colhuehuapian or even earlier.

Simplimus, known only from isolated teeth and several bones, has been reported from beds of Friasian (late Miocene) and Mesopotamian ages. It is possibly a synonym of *Olenopsis*, but if not, it probably descended from that genus. From what can be seen, the Friasian form is much like *O. aequatorialis*. The Mesopotamian species of *Simplimus* is known from only one molar tooth, which is like the Mesopotamian species of *Olenopsis* in being higher crowned than the La Venta and Friasian forms.

Potamarchus, another poorly known Mesopotamian form, is probably a dinomyid, but is distinct from any of its contemporaries. It may be a divergent form derived from *Olenopsis*.

By the beginning of Pliocene time, evolutionary trends in the Dinomyidae had become well established. *Olenopsis* carried over into the Mesopotamian, but died out at the close of that faunal "stage." It gave rise to possibly three of the genera that were to become dominant elements in the South American Pliocene faunas. These forms were probably descendants of some one or more unknown Chasicoan (late Miocene) species of *Olenopsis*.

The genus *Tetrastylus* is closely related to *Olenopsis*, but has gone beyond *Olenopsis* in characters 1, 2, 4, 5, 7, 10, 11, 12, and 14. Although it is like *Olenopsis* in retaining three lingual inflections on the lower and three labial inflections on the upper cheek teeth, it has developed a second labial inflection on the lower teeth. Further specialization is seen in pronounced hypsodonty and presence of strii that carry to the base of the teeth.

Telicomys retains a similar dental arrangement, and is believed to be descended from a species of *Tetrastylus*. It represents an advanced stage in the evolution of the dinomyids as seen in characters 2, 7, 10, 11, 12, and 14, but shows a secondary development of a small sagittal crest and lateral expansion of the occipital region. This late Tertiary genus became extinct at the close of Chapadmalalan time (early late Pliocene) and apparently left no descendants. It was probably a divergent and highly specialized line that was either unable to adjust to changing climatic conditions or could not compete with the influx of North American forms at the close of Pliocene time.

Gyriabrus, from early and middle Pliocene faunas, is another divergent line probably derived from *Olenopsis*. This genus is not as well known as most Pliocene dinomyids, but shows certain advanced dental characters. An additional inflection on both upper and lower cheek teeth indicates an advanced stage in the evolutionary trends of characters 9, 10, and 11. The lower incisor shows a stage of evolution equal to that of *Tetrastylus*, but is not greatly advanced beyond the La Venta species of
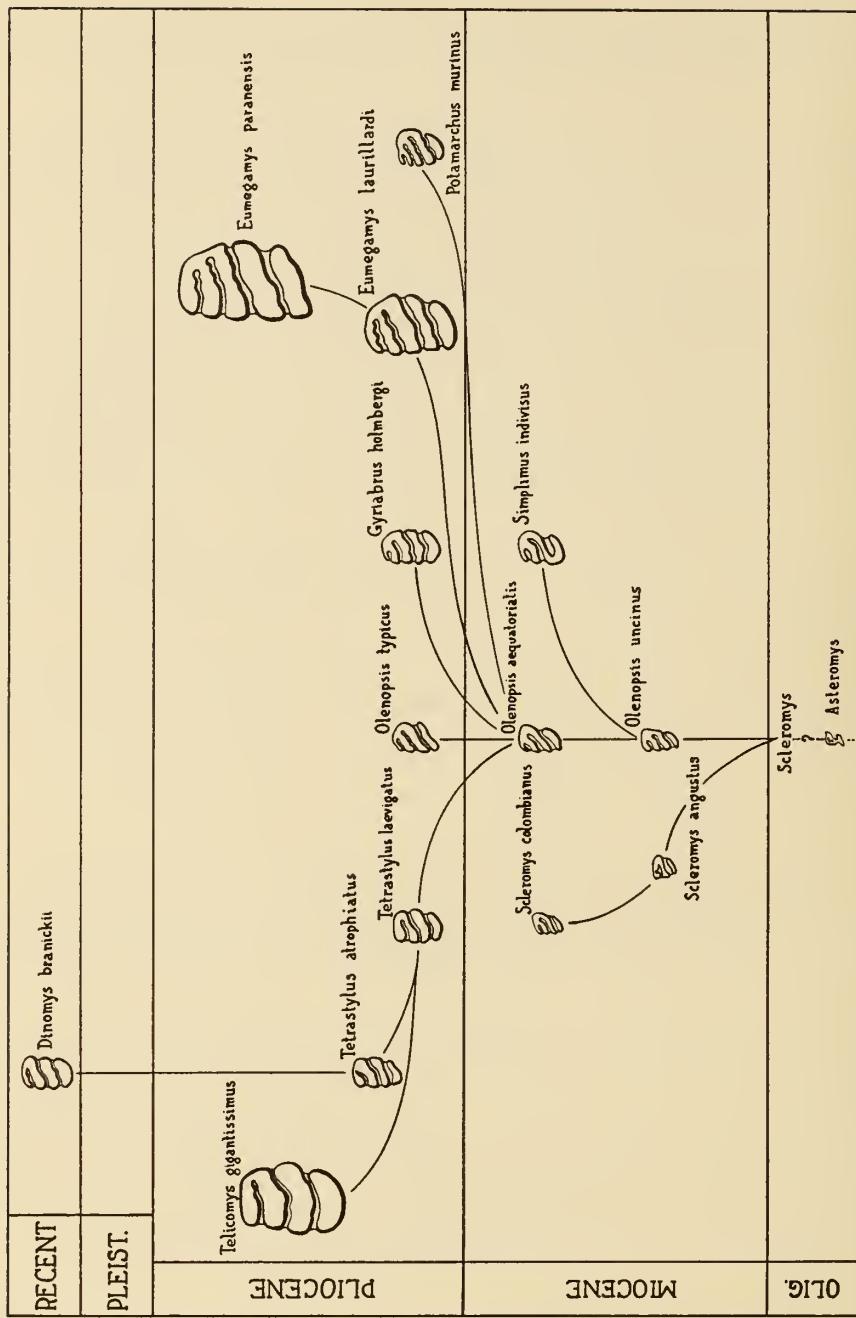
Fig. 32. Phylogeny of the dinomyid M_3: *Scleromys angustus* after Scott; *Olenopsis uncinus, O. typicus, Asteromys,* and *Potamarchus* after Ameghino; *Gyriabrus holmbergi, Eumegamys laurillardi, E. paranensis,* and *Tetrastylus laevigatus* after Kraglievich; *Tetrastylus atrophiatus, Simplimus indivisus,* and *Telicomys gigantissimus* after Rovereto. All drawings × ¾.
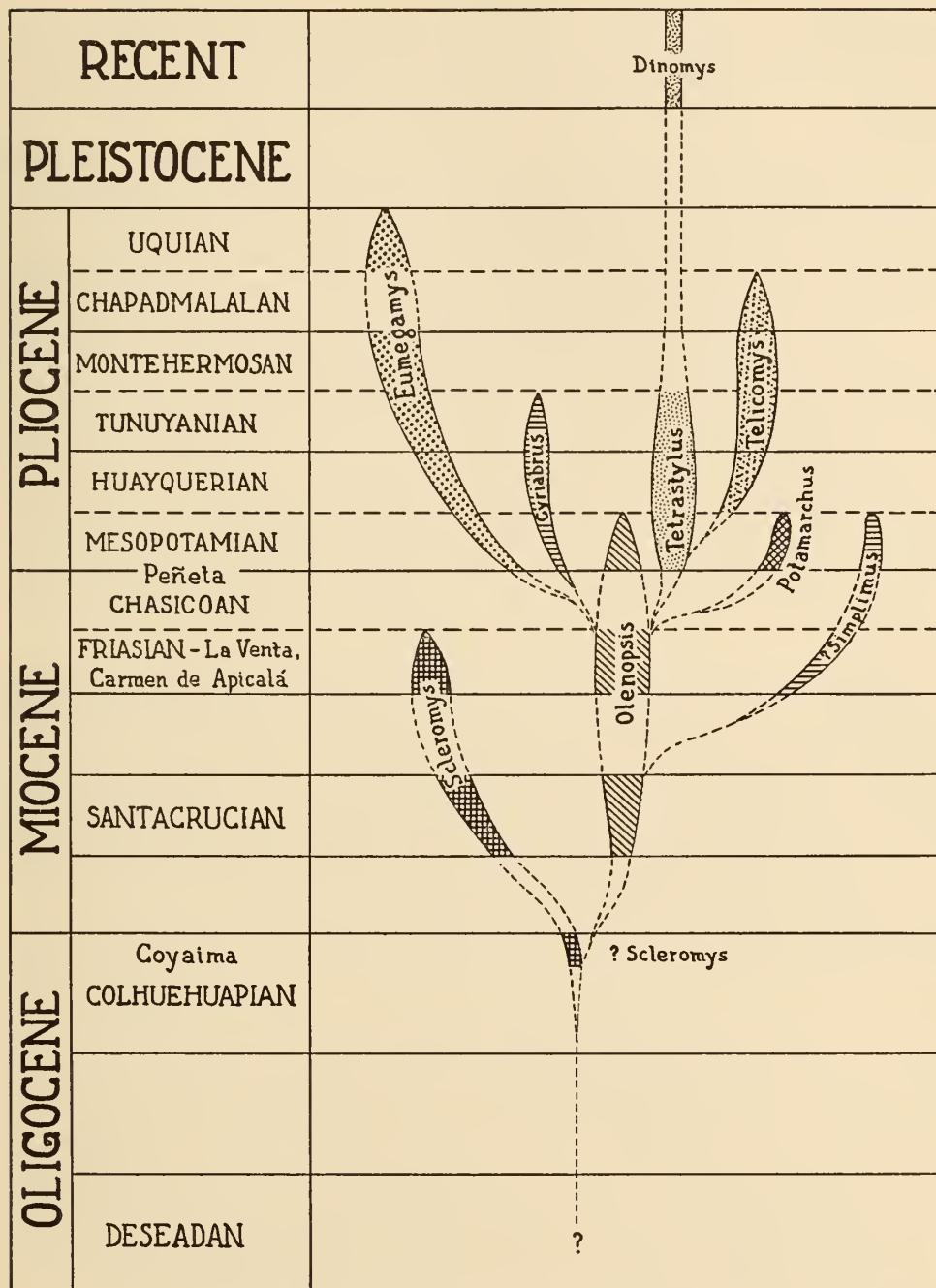
Fig. 33. Phylogeny of the family Dinomyidae.

Olenopsis. The coronoid process is completely missing in *Gyriabrus.* In size, the species of this genus are equal to some of the late species of *Olenopsis,* but apparently did not become as large as the later species of *Tetrastylus. Gyriabrus* apparently died out at the close of Tunuyanian time (early middle Pliocene) without leaving descendants.

Eumegamys is a divergent and highly specialized genus that probably represents the culmination of maximum dinomyid evolution. It was either derived from *Olenopsis* or from an unknown species of *Gyriabrus,* possibly during Chasicoan time. In dental pattern it is like *Gyriabrus* but far exceeds that genus in size. The incisors reach a size far in excess of any of the other Pliocene dinomyids. In *Eumegamys burmeisteri,* the number of inflections on the upper teeth increased to 5, and the height of crown measured 88 mm. According to Ameghino (1889A) this species was as large as a hippopotamus. It thus seems evident that through the processes of specialization the dinomyids, like so many other mammalian groups, have shown a development of gigantism in at least one line. *Eumegamys* has a longer geologic range than any other Pliocene dinomyid and is relatively abundant in all Pliocene faunas, indicating that the genus was quite successful. The great size of this rodent probably allowed it to fill a highly specialized ecologic niche in which a smaller rodent could not survive. Its extinction at the close of Uquian (latest Pliocene) time was probably brought about by the same factors that contributed to the annihilation of *Telicomys.*

Dinomys is the only living survivor of this once diversified and highly successful group of rodents. It is known from only one species and has no fossil record. However, *Tetrastylus ?atropheatus* Rovereto, 1914, is so much like *Dinomys* in tooth character that it may be a species of that genus. It is equal to *Dinomys* in size and has a somewhat reduced $M_{\overline{3}}$, a character also present in *Dinomys.* There seems to be little doubt that *Tetrastylus* is ancestral to *Dinomys,* as the two genera show the same trends in structural diversity in the teeth; in fact, there is little difference between them in observable morphological characters.

Dinomys never reached the high degree of specialization seen in forms like *Telicomys, Gyriabrus,* and *Eumegamys.* In limb structure it is more generalized than *Olenopsis,* in which interesting and important evolutionary trends are seen—trends carried on into some of the later forms, but evidently not inherited by *Dinomys.* It is unfortunate that so little is known of the limbs in those forms with a high degree of specialization in cheek teeth. If such information were available, the fossil dinomyids would probably have the same usefulness in South American continental Tertiary correlation that the beaver and horse have in North America.

The position of Prodolichotis in the Phylogeny of the Caviidae.—Probably the three most significant evolutionary trends in the Dolichotinae are the development of accessory lobes on $P_{\overline{4}}$ and $M^{\underline{3}}$ and the tendency to develop extremely elongated hind limbs. *Prodolichotis* follows these trends, but indicates that the evolutionary tempo of each trend differs.

A critical analysis of limb proportions has been undertaken in the discussion of *Prodolichotis pridiana* (pp. 375-376). Here it is only necessary to state that the stage of evolution shown in the limb structure of *Prodolichotis* is much the same as that seen in *Eocardia* from the Santa Cruz fauna. It is probable that the extremely elongated hind limbs seen in *Dolichotis* are the result of a slow but persistent evolu-

tionary trend, and that *Eocardia* and *Prodolichotis pridiana* represent two early steps in that trend.

It is interesting to note that in the trend toward development of accessory lobes on $P_{\overline{4}}$, *Prodolichotis* has gone beyond *Dolichotis*. M^2 in *Prodolichotis*, however, has not reached the point of complexity seen in *Dolichotis*, but rather seems to be near the same stage of evolution as *Orthomyctera*.

The stage of evolution of these characters in *Prodolichotis* indicates that the rate of evolution has differed from that in *Dolichotis*. Nevertheless, from comparison of other characters, it seems certain that *Prodolichotis* and *Dolichotis* are closely related and probably evolved from the same ancestral stock. *Prodolichotis* represents a divergent line that was successful for a time, but became extinct at the close of Montehermosan (late middle Pliocene) time.

Orthomyctera, a relatively small dolichotine from the Pliocene, is perhaps closer to *Dolichotis* than any of the known fossil genera and is probably ancestral to the living genus. Much more work is necessary before a clear phylogenetic sequence can be demonstrated. Most of the work on the dolichotines has been done by Ameghino and Kraglievich, both extreme splitters. A critical revision would, no doubt, uncover considerable synonymy, and it would probably be found that some of the late Pliocene genera and species named by Ameghino and Kraglievich are referrable to *Dolichotis*.

ENVIRONMENT

A restoration of the environment in the area of the La Venta badlands in late Miocene time is based on both paleontologic and ecologic information. Careful consideration has been given to the sediments with the purpose of learning the conditions under which they were deposited. The La Venta area was a broad flood plain through which the ancestral Magdalena River and many tributaries meandered, and stream conditions varied from place to place and from time to time. Vast amounts of sediment were deposited over the flood plain during periods of flooding. The rivers and streams retreated to their channels in the dry seasons. Across wide stretches of the flood plain the retreating waters left broad mud flats and swamps. Occasionally the meanders of the rivers were cut off and developed into oxbow lakes.

No identifiable plant remains have been found in the La Venta area, but Butler (1942) reports a fossil flora from beds of upper Honda age near Falán, about ten kilometers southwest of Mariquita near the village of Honda, Department of Tolima, in which *Bambusium, Heliconia, Ficus, Persia, Nectandra, Goeppertia, Citharexylon, Tecoma, Chrysophyllum, Styrax, Buettneria, Gouania, Condaminae, Vochysia, Trigonia, Moquillea, Inga,* and *Pithecolobium* have been found. This flora is wet-tropical in character and is closely related to the existing flora of the upper Amazon Basin, where the average annual rainfall is more than seventy-five inches.

A similar flora probably lived in the La Venta area. There must have been heavy stream-border and swamp forests in the lowlands and broad expanses of llanos on the slightly higher ground stretching back from the swamp and mud-flat areas.

The abundance of crocodilians and chelonians in the La Venta fauna supports the geologic evidence for lowland swamps and broad rivers. Other aquatic and amphibious animals were fresh-water gastropods, crustaceans, lungfish, catfish, perch,

frogs, and the sirenian *Potamosiren magdalenensis* Reinhart, 1951. The presence of lungfish may lend support to the geologic evidence of seasonal drying and retreat of the streams to their channels.

The wide range in kinds of terrestrial mammals in the La Venta fauna is evidence of numerous and varied ecological conditions. Among the notoungulates the inter-atheriids, hegetotheriids, and toxodontids, with their high-crowned, rootless teeth, indicate a rather harsh diet that would be common in savanna habitats. In the in-teratheres and hegetotheres, the limb structure has become modified to that of cursorial animals. Similar modifications are seen in the limbs of the proterotheres and macraucheniids, but the teeth in these animals are more brachyodont and probably indicate a browsing habit. It is probable that the edentates, with their insectivorous to frugivorous adaptations, invaded nearly every environmental situation present. The astrapotheres were probably semiamphibious animals that fed on soft vegetation along the streams and in the swamp areas.

The occurrence of primates in the La Venta fauna (Stirton, 1951), along with some of the smaller sloths and the opossums that were probably arboreal or scan-sorial, is good evidence of forested areas. Occurrence of galliform birds is indicated by one poorly preserved specimen. This bird may have been a denizen of the dense woods and thickets along the lowlands.

Wide range in size and structure among the La Venta rodents indicates a success-ful invasion of a number of environments. ?*Steiromys* and the echimyid were prob-ably arboreal forms living in the stream-border forests. The two species of *Scleromys* were terrestrial and probably lived along the banks of the rivers and around the swamps. It is possible that they ventured into the swamps and rivers, but probably only as a retreat from predators like the borhyaenids. Proof that these marsupial carnivores preyed on small rodents was found when a well-preserved skeleton of a ''*Lycopsis*-like'' borhyaenid was prepared. Preserved in the body cavity were several broken rodent bones and an upper molar tooth of *Scleromys colombianus*. Occasionally these small rodents fell prey to one of the crocodilians or even one of the larger turtles. Evidence for this was preserved in a large coprolite, most likely belonging to a crocodilian, in which two molar teeth, claws, and several bones of *Scleromys schürmanni* were found.

Olenopsis probably lived in the lowland areas, but morphological evidence indi-cates that this large form was more cursorial than its relative, *Scleromys*. It seems most logical to assume that *Olenopsis* inhabited the transitional or more savanna-like fringes of the forested areas, and made its home in some fallen tree or dug a den under the roots of large trees.

Prodolichotis most likely had habits similar to its living relative, *Dolichotis*. Its habitat was probably on the llanos where it lived side by side with the interatheres, hegetotheres, and proterotheres. This habitat preference may account for its rarity as a fossil in the La Venta fauna. The question then arises why the interatheres are so numerous in the deposits? This, as Stirton (1953a) suggests, may be due, in part, to the fact that they became bogged in mud flats (possibly when the animals flocked to the rivers and swamps in search of water). *Prodolichotis* probably ventured into the swamp and river areas less frequently, and even when it did, its lighter body weight would have kept it from becoming mired.

It is curious that a form like *Neoreomys*, which was so dominant in the Santa Cruz fauna, is poorly represented in the La Venta fauna. Conditions of deposition and probable environmental niches in these two faunas seem to be very similar. Either some ecologic factor essential to the survival of *Neoreomys* was lacking during most of the time of deposition of the La Venta beds, or the few specimens repre-

Genera Represented	OLIG. DESEADAN	MIOCENE COLHUEHUAPIAN	MIOCENE SANTACRUCIAN	MIOCENE FRIASIAN – LA VENTA	CHASICOAN	PLIOCENE MESOPOTAMIAN	PLIOCENE HUAYQUERIAN	PLIOCENE TUNUYANIAN	PLIOCENE MONTEHERMOSAN	PLIOCENE CHAPADMALALAN	PLIOCENE UQUIAN	PLEISTOCENE
Erethizontidae												
Steiromys		██	██	██		██						
Caviidae												
Prodolichotis				██			██	██	██			
Dinomyidae												
Scleromys		██	██	██								
Olenopsis			██	██								
Simplimus				██								
Potamarchus						██						
Eumegamys						██	██	██	██	██	██	
Tetrastylus						██	██	██				
Gyriabrus						██						
Telicomys							██	██	██			
Capromyidae												
Neoreomys			██	██								

Fig. 34. Geologic range of hystricomorph genera represented in the La Venta Friasian fauna. It is to be noted that *Prodolichotis* and *Simplimus* do not occur in faunas older than Friasian, and that *Scleromys* and *Neoreomys* are not known in faunas later than Friasian.

sented in the La Venta fauna are holdovers of a formerly dominant rodent group that was crowded out by a more successful line like *Scleromys*.

Environmental conditions were diverse and changeable in the La Venta area during late Miocene time, but the number and kinds of individual animals occurring in the fauna indicate that competition for survival was keen. Coupled with the biological competition was the struggle, on the part of all these forms, to survive the conditions of physical environment. Needless to say, few, if any, of the terrestrial forms inhabited the mud flats left after a period of flooding; nevertheless, some of the animals became mired in these mud flats and died there. Several of the

TENTATIVE CORRELATION OF TERRESTRIAL PROVINCIAL AGES AND FAUNAS.

	COLOMBIA FAUNAS	ARGENTINA "STAGES"	UNITED STATES PROVINCIAL AGES	EUROPE STAGES
PLEISTOCENE	Cátedras	Pampean / Ensenadan	Rancholabrean / Irvingtonian	Astian-Villafranchian
PLIOCENE	Cocha Verde? / Peñata	Uquian / Chapadmalalan / Montehermosan / Tunuyanian / Huayquerian Mesopotamian	Blancan / Hemphillian / Clarendonian	Pontian / Sarmatian
MIOCENE	La Venta, Carmen de Apicalá	Chasicoan Friasian / Santacrucian	Barstovian / Hemingfordian / Arikareean	Vindobonian / Burdigalian / Aquitanian
OLIGOCENE	Coyaima / Chaparral, Peneyita	Colhuehuapian / Deseadan	Whitneyan / Orellan / Chadronian	Chattian / Stampian / Sannoisian
EOCENE	Tama	Mustersan / Casamayoran	Duchesnian / Uintan / Bridgerian / Wasatchian	Ludian / Aversian / Lutetian / Cuisian / Sparnacian
PALEOCENE		Riochican	Clarkforkian / Tiffanian / Torrejonian / Dragonian / Puercan	Thanetian

Fig. 35. Tentative correlation of terrestrial provincial ages and faunas, after Stirton, 1953B.

interatheres and glyptodonts found in the La Venta badlands show that they died in this way. The feet of one of the glyptodonts were in a position which indicated that the animal died while attempting to free itself from the mud. In this same individual, the top of the carapace shows the effects of dessication and sun-checking. Doubtless hundreds of animals lost their lives in a similar way.

CORRELATION AND AGE OF THE LA VENTA FAUNA
(Based on evidence from the rodents)

Accurate conclusions on the chronological significance of this large and varied faunal assemblage cannot be attained until each group has been thoroughly studied. There is, however, sufficient evidence on the rodents and the interatheres to establish a late Miocene age for the fauna.

If the stratigraphic range of the genera in the La Venta fauna are plotted on a graph (Fig. 34), certain relationships are immediately seen. ?*Steiromys* is of little value in establishing a chronology of South American rodents, but it is worth noting that the known range of the genus is from Colhuehuapian to Mesopotamian. *Neoreomys* was formerly known only from the Santa Cruz fauna and the Río Senquer, a Friasian fauna. The occurrence of *Prodolichotis* in other faunas is restricted to beds of Huayquerian to Montehermosan age. Before its discovery in the La Venta and Carmen de Apicalá faunas, *Scleromys* was known only from beds of Santacrucian age. *Olenopsis* is known from Santacrucian through Mesopotamian time.

The other genera of the family Dinomyidae, except *Simplimus* from Friasian and Mesopotamian faunas, are restricted to the Pliocene. Thus it may be assumed that the La Venta fauna is post-Santacrucian and pre-Mesopotamian in age.

Stirton (1953B) states that the group to which the La Venta interatheres belongs is not represented in the Santa Cruz formation, but its stage of evolution—when compared with *Cochilius* from the Colhuehuapian—is too advanced for an early Miocene form.

The La Venta species of *Scleromys* are clearly more advanced than the species in the Santa Cruz fauna. It has also been noted that the genus is not known from beds of Pliocene age. The La Venta *Olenopsis* shows an advance over its Santacrucian ancestor, but is not as progressive as its Mesopotamian descendant. Attention has already been drawn to the possibility of *Simplimus* being a synonym of *Olenopsis*. If not, the Friasian *Simplimus* has paralleled *O. aequatorialis* and represents an animal in the same stage of evolution.

The rodents from La Venta seem to represent a transitional fauna falling between the Santacrucian and Mesopotamian "stages" as designated by Simpson (1940). The La Venta species of *Scleromys*, *Neoreomys*, and ?*Steiromys* are reminiscent of Santa Cruz forms. *Olenopsis aequatorialis* shows affinities to both Santacrucian and Mesopotamian species. *Prodolichotis pridiana* suggests relationship to the Santa Cruz Eocardiidae, but its stage of evolution indicates a closer affinity to the Mesopotamian Dolichotinae.

The animals found in the Friasian faunas indicate a similar stage of evolution. Unfortunately, only *Neoreomys* is common to the Friasian and La Venta faunas; nevertheless, from the stage of evolution of these two faunas it seems probable that

the La Venta fauna is nearer in age to the Friasian "stage" than to any of the other South American "stages" designated by Simpson (1940). It is unfortunate that the fossils from the Río Frías, Río Fénex, Laguna Blanca, Río Huemules, Río Senquer, and Río Guenquel are so meager and, as admitted by Kraglievich (1930), so poorly allocated stratigraphically. If more were known of the Friasian fossils and of stratigraphic relationships, it would probably be seen that the La Venta fauna is contemporaneous with at least part of the Friasian fauna in Argentina.

No further refinement can be obtained by an examination of geological data. Honda deposition, as defined by Butler (1942), came to a close at the end of Miocene time and is separated from later deposits by local disconformities. In Argentina, at approximately this same time, there was a period of submergence and marine inundation represented by the Mayan "stage" (Simpson, 1940).

Stirton (1953b) has drawn up a correlation chart of the Argentinian and Colombian faunal assemblages. He also suggests possible correlations with North American provincial ages and European stages. Stirton correlated the La Venta and Carmen de Apicalá assemblages with the Friasian "stage" of Argentina primarily on the basis of evidence gained in his study of the La Venta interatheres and on information from this study of the La Venta rodents. His correlation chart is reproduced here (Fig. 35).

SUMMARY

1. The La Venta fauna is one of the largest and most complete late Miocene faunas known, and is the only well-known fauna in northern South America. Fossil rodents have been collected from nearly all stratigraphic levels in the La Venta section, but no obvious progressive changes or other evidence of difference in age could be found. Thus, it is concluded that each rodent species ranged through the entire 700 meters of the beds.

2. The beds in which the La Venta fauna occurs are apparently part of the series of strata called Honda by Hettner (1892). The sequence exposed in the La Venta badlands consists of gravels, sands, and clays, the uppermost levels of which contain decomposed volcanic ash. They were deposited over a vast flood plain during late Miocene time. Field evidence indicates that conditions of deposition were variable, and that alternating periods of flooding and drying caused the formation of red-bed deposits and peculiar torpedo-shaped sandstone concretions. Lithologic contents of the sediments indicate that they were derived from mountainous areas to the south and west of the La Venta region, and suggest that the source area was not far from the site of deposition. Lithologically these beds correlate with Butler's (1942) upper Honda. (See Fields, "The Geology of the La Venta Badlands, Colombia, South America," in preparation.)

3. The age of the Honda group was formerly considered to be Miocene. Paleontological data from Honda beds at Coyaima indicate that the deposition of Honda sediments began in late Oligocene time. Stratigraphic associations at Carmen de Apicalá indicate that Honda deposition did not begin at the same time in all areas.

4. The La Venta fauna is of late Miocene age, as indicated by the stage of evolution of *Scleromys schürmanni*, *S. colombianus*, *Olenopsis aequatorialis*, and *Neoreomys huilensis*, and the presence of *Prodolichotis pridiana* showing intermediate evolutionary conditions between early Micoene eocardids and Pliocene dolichotids. The

La Venta assemblage is correlated with the Carmen de Apicalá fauna on the presence of *Scleromys schürmanni* and *S. colombianus* in both faunas, and with the Río Frías fauna of Argentina on the stage of evolution of the mammals. It is younger than Santacrucian and older than Mesopotamian.

5. Ecologically the fauna combines aquatic, amphibious, arboreal, and riparian elements with a dominant group of savanna-type animals. The riparian forests supported *Neoreomys huilensis*, *Scleromys schürmanni*, and *S. colombianus*. *Olenopsis aequatorialis* occupied the outer fringes of the forests, and *Prodolichotis pridiana* inhabited the savanna.

6. The climate was probably wet-tropical (i.e., similar to the present llanos of Colombia), as evidenced by the plants found at Falán. The region was subjected to periodic and extensive floods. During dry seasons, the rivers retreated to their channels, leaving vast swamps and mud flats in the lowlands. Many animals became mired in the mud and died. These mud flats provided favorable burial conditions for preservation of many of the complete skeletons found in the La Venta badlands.

7. Statistical and morphologic evidence indicates that *Scleromys schürmanni* and *S. colombianus* are genetically stable, homogeneous species.

8. The rodent described by Anthony (1922) as *Drytomomys* is a synonym of *Olenopsis* Ameghino and belongs to the same species found in the La Venta fauna.

9. *Olenopsis* was erroneously described by Ameghino (1889в) as having a premolar and only two molars. Present information indicates that this characterization was based on an immature individual in which $M_{\overline{3}}$ had not yet erupted from the jaw.

10. *Olenopsis aequatorialis* shows more than average variability in size, and possibly represents a chronocline species.

11. A critical study of the teeth in *Olenopsis aequatorialis* and *Dinomys* indicates possible diametric growth in the cheek teeth of the latter genus. *Olenopsis*, however, has closed fossettes and late-appearing roots, features which seem to negate any chance of diametric growth.

12. Relationship of *Scleromys* and *Olenopsis* to *Dinomys* and to the family Dinomyidae seems certain. It is suggested that several other genera, placed by Simpson (1945ı) in the family Heptaxodontidae, are closely related to *Dinomys* and should be assigned to the Dinomyidae.

13. Much synonymy is apparent among the described genera of Tertiary hystricomorphs from South America. A partial revision and reclassification has been attempted.

14. Critical investigation of the middle ear and auditory ossicles in *Olenopsis* and several living hystricomorphs indicates that the Dinomyidae are more closely related to the Erethizontidae than previously suspected.

15. Future study of the auditory region in recent and fossil hystricomorphs may offer the key to a more detailed understanding of the evolution and classification of this complex group.

16. The presence of *Prodolichotis pridiana* in the La Venta fauna extends the lower range of the subfamily Dolichotinae into the Miocene and furnishes substantial evidence that caviid specializations were clearly defined and close to reaching stability by late Miocene time.

17. Occurrence of *Neoreomys* in the La Venta and Friasian faunas extends its range into late Miocene.

18. *Neoreomys* is probably ancestral to *Isomyopotamus* and *Myocastor*.

19. *Olenopsis* is probably ancestral to the diverse array of Pliocene dinomyids, and some species of *Tetrastylus* is the ancestor of *Dinomys*.

20. The height of crown, number of inflections, and length of strii on the cheek teeth of dinomyids are the most useful criteria for close correlation in the Miocene and early Pliocene.

In conclusion, it may be stated that, with further use of refined field and laboratory techniques, the dinomyid rodents may become as important in South American continental correlation as the beavers and horses have in North America. Evolutionary trends in this group are already clearly defined and well oriented. Further collecting will no doubt uncover additional detailed information concerning origins and diversity of the various lines. The series already known will be refined, and further detailed correlation of widely separated areas will be possible.

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PLATE

PLATE 36

a. Sectioning device. Complete assembly: to left, motor mounted on adjustable shaft; center, turret on sliding mount, feed screw and knob in foreground; to right, water jet, tank, and control bulb used to cool overhead blade.

b. Sectioning device. Detailed view of turret and slide bar, note degree scale and lock screw on turret, millimeter scale, traveling needle, feed screw, and lock nut on box chuck.

a

b