Descriptive and Comparative Osteology of the Oldest Fossil Squirrel, *Protosciurus* (Rodentia: Sciuridae)

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ABSTRACT

Emry, Robert J., and Richard W. Thorington, Jr. Descriptive and Comparative Osteology of the Oldest Fossil Squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithsonian Contributions to Paleobiology*, number 47, 35 pages, 16 figures, 3 tables, 1982.—The early history of the Sciuridae is not well known, squirrels being generally poorly represented in the Tertiary fossil record. A nearly complete skeleton, recently discovered in early Oligocene deposits of Wyoming, represents what may be the oldest fossil squirrel known. For the first time, this early squirrel can be compared fully with its extant relatives. The specimen, assigned to *Protosciurus jeffersoni*, retains the primitive protrogomorphous zygomasseteric structure, as in other known *Protosciurus*, but the masseteric fossa of the mandible is farther forward than in most nonsciurid protrogomorphs. The auditory region of the skull has derived squirrel characters, but it is in the postcranial skeleton where similarities to extant squirrels are most apparent. Except for minor differences in joint construction, the skeleton is strikingly similar to that of *Sciurus niger*, the living fox squirrel. It differs from extant ground squirrels in the more gracile proportions of its long bones and asymmetry of foot construction. This early member of the squirrel family was clearly an arboreal squirrel, with morphology, and presumably habits, very similar to those of extant Sciurinae.

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Contents

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Introduction

The stimulus for this report was the discovery in 1975 of a nearly complete skeleton of what was apparently a fossil squirrel in the Oligocene White River Formation of Wyoming. Fossil remains of squirrels are relatively uncommon in the North American Tertiary record. Postcranial remains are even less common, and were completely unknown for the Oligocene members of the family. Thus, the specimen, with excellently preserved postcranial material, is particularly important; it gives us the first opportunity to determine how squirrel-like the early members of the family were. It also provides the evidence needed to place early Oligocene taxa confidently in the family Sciuridae, where they were placed only tentatively on the basis of dental and cranial morphology.

ACKNOWLEDGMENTS.—Our first expression of appreciation is to Jennifer Emry, who found the critical fossil, without which this study could not have begun. The specimen was skillfully prepared in the laboratory by Leroy Glenn and Frederick Grady. The pencil drawings are by Lloyd Logan. For access to collections in their care, or loans of fossil material, we thank Donald Savage and Barbara Waters of the Museum of Paleontology, University of California, Berkeley, and Richard Tedford and Malcolm McKenna of the American Museum of Natural History. For improvements in the manuscript as a result of their careful critical reviews we thank the following: Dr. Craig C. Black, Director, Carnegie Museum of Natural History, Pittsburgh; Dr. Lawrence R. Heaney, Museum of Zoology, the University of Michigan, Ann Arbor; and Dr. John H. Wahlert, North Museum, Franklin and Marshall College, Lancaster, Pa. We thank John Wahlert also for sharing his knowledge of incisor enamel microstructure.

Material

The specimen that is the focus of this report is USNM 243981 (USNM = the former United States National Museum collections in the National Museum of Natural History, Smithsonian Institution), provisionally referred to *Protosciurus jeffersoni*. It consists of the palate with complete maxillary dentition, both auditory bullae with petrosals attached, and numerous other skull fragments, both mandibular rami with complete dentition, and most of the postcranial skeleton, partly

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articulated or closely associated (Figure 1). The skeleton represents a young individual, with the complete mature dentition in place but practically unworn, and with the epiphyses still unfused; the gray squirrel, *Sciurus carolinensis*, reaches this stage of ontogenetic development at about eight months of age (240 days, USNM 528003). The specimen was found in the White River Formation in the head of Little Lone Tree Gulch, in the Flagstaff Rim area of Natrona County, Wyoming, at about 13.5 meters (45 feet) below ash B on the generalized zonation section (Emry, 1973:29). The White River Formation here is Chadronian in age, and the part of the section where USNM 243981 occurred is believed to represent, on the basis of much other faunal evidence, the early part of the Chadronian. It is probably slightly older than the well-known Pipestone Springs localities of Montana and probably younger than early Chadronian localities such as the Yoder of eastern Wyoming and the Porvenir of west Texas. Several other specimens of *Protosciurus jeffersoni* (maxillae, jaws, or teeth) have been found in the same stratigraphic sequence, but this specimen occurred lower in the section than any other. If we are correct in its being slightly older than the Pipestone Springs occurrences of *P. jeffersoni*, then it is probably the oldest known fossil squirrel specimen.

The cranial and dental parts of the fossil were

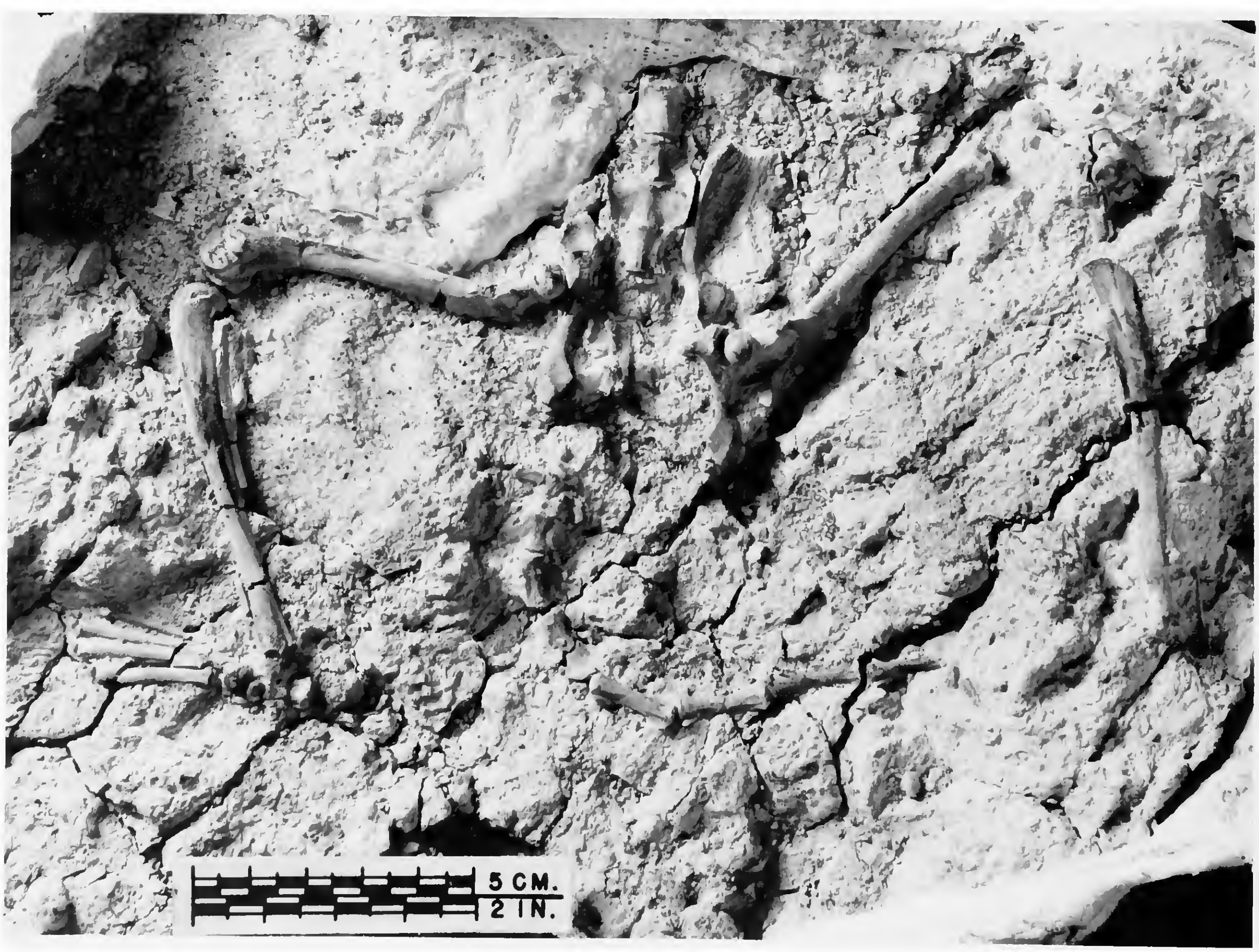

FIGURE 1.—Posterior part of skeleton of *Protosciurus*, USNM 243981, still in the original matrix as it occurred. (Approximately × .75.)

compared with other *Protosciurus* specimens, and other fossil rodents, as cited in the text. The postcranial skeleton was compared principally with specimens of recent squirrels of North America. It was compared most carefully with the following specimens in the collections of the Smithsonian's Division of Mammals: *Sciurus niger*, 261765, 251574, 257984; *Sciurus carolinensis*, 500977; *Spermophilus beecheyi*, 484951 and 21241; and *Cynomys ludovicianus*, 35012. The taxa were selected to match the fossil approximately in size. *Sciurus niger* 261765 and 21241 were chosen to match closely the ontogenetic stage of the fossil specimen. The variation of characters used in the comparisons was checked against a collection of approximately 200 *Sciurus* of 10 species, 90 *Spermophilus* of 12 species, and 40 *Cynomys* of three species. A number of characters were checked against specimens of *Marmota*, *Ammospermophilus*, *Tamias*, *Eutamias*, *Xerus*, *Protoxerus*, *Heliosciurus*, *Funisciurus*, *Callosciurus*, *Ratufa*, *Petaurista*, *Eoglaucomys*, and *Glaucomys*, particularly when the anatomy of the fossil did not closely resemble that of either *Sciurus* or *Spermophilus*. Generally, however, the comparisons of the fossil with *Sciurus* were most apt, those with *Spermophilus* and other Marmotinae were less so, and those with flying squirrels (i.e., *Glaucomys*, *Eoglaucomys*, and *Petaurista*) least appropriate.

Comparisons of the postcranial material of USNM 243981 with other fossil rodents was limited by the amount and quality of appropriate fossil material. Adequate material of *Paramys delicatus* is available, most major elements of the appendicular skeleton being represented by USNM 13254, 17162, 18062, and 23556. *Ischyromys* is also represented by abundant material in the Smithsonian's paleobiology collections. As cited in the text, specific comparisons were made with certain other fossil rodents in which the appropriate parts are known and where comparisons were likely to be meaningful. We use the term paramyid in the sense of the Paramyidae of Wood (1962) or Wahlert (1974), i.e., we do not include *Ischyromys* and its close relatives.

Taxonomic Identity of USNM 243981

In the following section, on the descriptive and comparative osteology of USNM 243981, it is pointed out that its dental features most closely resemble those of *?Protosciurus jeffersoni*, even though here there are distinctions to be made. *Protosciurus* was erected by Black (1963), who included in the genus what he then regarded as the geologically oldest sciurids. He later (1965) tentatively assigned to *Protosciurus* another species, which is even older geologically, and which has had a long and complex taxonomic history. This was *Sciurus jeffersoni* Douglass (1901), from the medial Chadronian (approximately early Oligocene) Pipestone Springs locality of southwestern Montana. The species had been transferred to *Prosciurus* by Matthew (1909), to *?Prosciurus* by Wood (1937), and to *Cedromus* by Wood (1962). Wood has since (1980) reiterated his belief that it belongs in *Cedromus*.

Black's reluctance to place *?Protosciurus jeffersoni* unequivocally in *Protosciurus* was apparently because certain dental features did not allow it to be placed confidently in the Sciuridae, whereas *Protosciurus condoni* (the genotypic species) and other referred species are more clearly members of the squirrel family.

The same dental features (e.g., more distinct and multiple conules, more distinct hypolophids) that distinguish *?P. jeffersoni* from *P. condoni* and *P. mengi* are present, but even more distinct, in USNM 243981. That is to say, both *?P. jeffersoni* and USNM 243981 diverge from typical *Protosciurus* in the same way, with USNM 243981 being somewhat more divergent.

In the following description and comparison it is shown that USNM 243981 has several derived features that are found elsewhere only in members of the Sciuridae. On this basis, and in spite of its being protrogomorphous and having dental differences, USNM 243981 is placed in the Sciuridae. Its similarities to *?P. jeffersoni* suggest that, for the present, it is best to place them together in *Protosciurus jeffersoni* and to place this taxon firmly in the Sciuridae. This is done with the expectation that more and better material might show that *P. jeffersoni* is generically distinct from *Protosciurus*, and that USNM 243981 is specifically distinct from *P. jeffersoni.*

For the purposes of this report, it is not necessary to resolve these questions. It is sufficient to conclude that USNM 243981 is certainly a sciurid, closest to *Protosciurus jeffersoni*, which is by inference also clearly a sciurid.

In the following sections, a reference to *Protosciurus* is to USNM 243981, unless it is otherwise qualified.

Anatomy

Skull, Mandibles, and Dentition

The anterior part of the skeleton, including the skull and mandibles, of USNM 243981 had been weathered out of the sediments when discovered, and, judging from the parts preserved, the skull had been crushed and broken before and during the burial process. The palate, with well-preserved teeth, is intact (Figure 2), and both tympanic bullae with attached periotics are preserved, along with numerous smaller skull fragments. The mandibles are both present; each is broken posteriorly, but all cheek teeth are intact.

Skull.—Enough remains of the inferior zygomatic root of the maxillary to show that this specimen, like the others known of *Protosciurus*, is protrogomorphous, with the masseter limited to the ventral root of the zygoma. This is the primitive condition for rodents (found, for example, in most paramyids, ischyromyids, and sciuravids) and is not the condition found in modern sciurids, which lend their name to the sciuromorphous condition. As will be shown below, USNM 243981 has derived features found only in sciurids and is placed in the Sciuridae on the basis of these derived characters. It is clear then that the sciuromorphous condition is not primitive for the family Sciuridae. This had been suspected previously. Black (1963), for example, mentioned that in *Protosciurus condoni* (the genotypic species, of late Oligocene age) there is no indication that the masseter had expanded anterior to the infraorbital foramen. That sciuromorphy was not the primitive condition in Sciuridae should not be surprising. The condition was independently derived at least three times, in the castorids and geomyoids in addition to sciurids, and is developed to some degree in glirids and in the advanced ischyromyid *Titanotheriomys.*

A fragment of parietal shows that USNM 243981 lacked the sagittal crest that is found invariably in the paramyids and most other protrogomorphs, and has instead the low, apparently lyre-shaped, temporal crests typical of modern squirrels but found in other advanced rodent groups too.

In USNM 243981, the anterior border of the internal nares is even with the posterior end of M_3 (Figure 2), very much as in *Protosciurus condoni* and other fossil sciurids such as *Protospermophilus* (see Black, 1963, pls. 3, 14, 15). In modern sciurids (at least in *Sciurus*, *Tamiasciurus*, *Tamias*, *Spermophilus*, and *Marmota*) the palate is slightly longer, with the anterior edge of the internal nares somewhat behind M^3. This contrasts with the situation in paramyids, in which the anterior border of the internal nares is usually between the more posterior cheek teeth; e.g., in *Leptotomus* it is usually at the anterior edge of M^3, in *Paramys* from the anterior to middle part of M^3, and in *Reithroparamys* at the anterior edge of M^3. In other protrogomorphous contemporaries of *Protosciurus*, the internal nares are also more anteriorly placed; at the anterior edge of M^3 in *Ischyromys*, opposite the middle of M^2 in *Cylindrodon*, and opposite the middle part of M^3 in *Ardynomys.*

Auditory Region.—USNM 243981 has large tympanic bullae, completely fused to the periotics, as in modern sciurids, so that each bulla and periotic separates from the skull as a single unit. Both are detached from the skull in the fossil specimen, and except for part of the basioccipital adhering to the right bulla, neither is in place relative to other bones of the skull. In shape and size (e.g., relative to length of P^4-M^3), the bullae of *Protosciurus* are very similar to those of *Sciurus niger*, even in details of the mastoid process, the

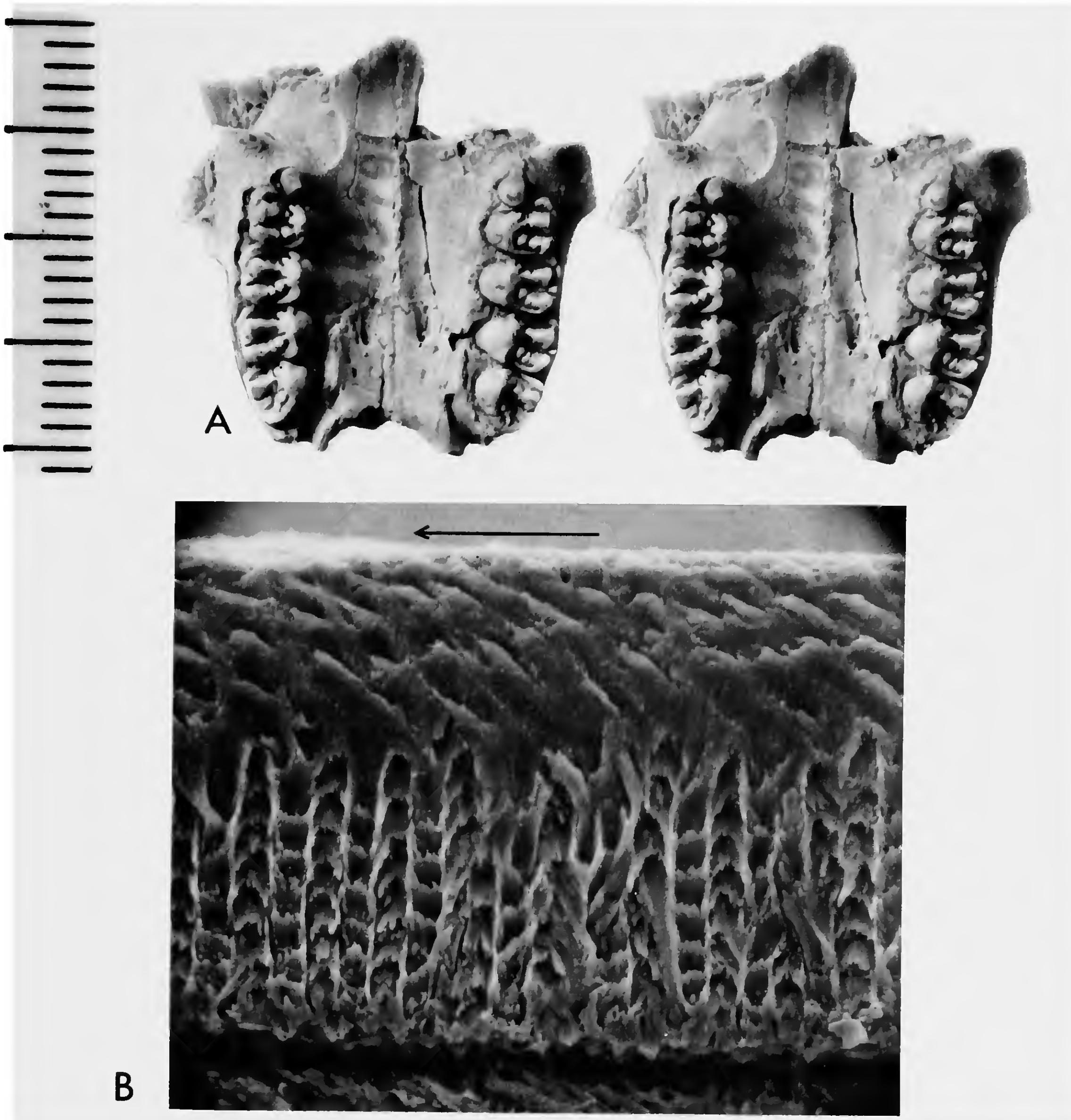

FIGURE 2.—A, stereogram of palate and complete maxillary dentition of *Protosciurus*, USNM 243981 (approximately × 3, scale in mm); B, scanning electron micrograph showing enamel microstructure of I^1, in sagittal section (arrow points in direction of tip; approximately × 1000).

shape of the external meatus and the morphology of its lip, and in the position of the various foramina.

Because the ventral surface of the periotic of modern Sciuridae has significant derived features, part of one bulla of *Protosciurus* was sacrificed to allow access to the periotic. The right bulla was chosen because it was not so well preserved as the left, the thinner bone being cracked and somewhat displaced due to crushing. During removal of this thin tympanic bone, it could be determined that, as in modern sciurids, transbullar septae were present, but because of the displacement of the bone, the number and orientation of the septae could not be determined.

In modern Sciuridae, the stapedial artery penetrates the medial wall of the bulla, near its contact with the basioccipital, and enters a bony tube, apparently developed from the periotic, though probably also with some tympanic contribution. In many modern squirrels the artery is enclosed in this bony conduit until it leaves the periotic near the anterior margin. In some there is a short gap in the bony tube at the position of the stapes, but in others the artery is enclosed even where it passes through the stapes, so that in a dried specimen, the stapes surrounds, and is suspended by, this conduit of bone. In USNM 243981, enough of the bulla was prepared away to determine that the stapedial artery is enclosed in the bony tube at least from the medial wall of the bulla across the promontorium and in the parts that can be seen is very similar to *Sciurus*.

The malleus is in place in each bulla of *Protosciurus*; at least the face that can be observed through the external auditory meatus has no apparent differences from the malleus of *Sciurus*.

The dorsomedian face of the periotic of *Protosciurus* is very similar to that of *Sciurus*, comparing more closely, in position of features, to *S. niger* than it does in *S. carolinensis*, *Tamiasciurus*, *Marmota*, and *Tamias*. This surface is divided into two faces by a ridge that is a continuation of the tentorium. The internal auditory meatus, appendicular fossa, and cochlear duct are all seen on the part facing the cerebellar fossa, and their relative positions are as in *Sciurus*. The internal auditory meatus is divided into dorsal and ventral parts by a thin partition of bone; the upper part, the beginning of the facial canal (7th cranial nerve), opens as a flattened foramen into the dorsal surface of the internal auditory meatus, and the ventral part is divided into several smaller foramina for the fibers of the acoustic (8th cranial) nerve. The opening into the appendicular fossa is circular, and, as in *Sciurus*, the appendicular fossa is nearly spherical, with its maximum diameter somewhat larger than the opening. This is in contrast to *Ischyromys*, which has a circular opening, but a fossa that is nearly cylindrical, with the opening larger in diameter than any part of the fossa.

The auditory region of this early squirrel already contains the derived features of modern sciurids: periotic and tympanic bulla fused into a single unit, bulla enlarged, transbullar septae present, and stapedial artery enclosed in a bony conduit through the middle ear. This contrasts with paramyids, in which the bulla is not coossified with any other skull bones and is usually not found with the skull. The bulla is completely unknown in *Paramys*, and may never have been ossified. *Leptotomus* has bullae that are at least partially ossified (Wood, 1962:66), but they are not fused to any other bones. Both *Paramys* and *Leptotomus* have a shallow channel on the surface of the petrosal indicating the presence, and course, of the stapedial artery (Wahlert, 1974). *Reithroparamys* has a well-formed, completely ossified bulla, not fused to other bones of the skull, and a stapedial artery indicated by a foramen between the tympanic and periotic (Wahlert, 1974). The enlarged, ossified bulla of *Ischyromys* and *Cylindrodon* are like those mentioned above in not being fused to other skull bones but differ in lacking the foramen for the stapedial artery. In spite of the similarities in zygomasseteric structure between *Protosciurus* and these geologically older and contemporary protrogomorphs, *Protosciurus* is very different in its auditory region. The combination of derived features seen in USNM 243981 is characteristic of, and apparently limited to, the Sciuridae.

MANDIBLE.—The lower jaw of USNM 243981 is generally like that described for other species of *Protosciurus* (Black, 1963, 1965), comparing best with *?P. jeffersoni* (Black, 1965). The anterior limit of the masseteric fossa is beneath the posterior part of M_1 (Figure 3) as in other known *Protosciurus*. This is somewhat further forward than in most protrogomorphs; in paramyids for example, it is usually at least as far back as the posterior

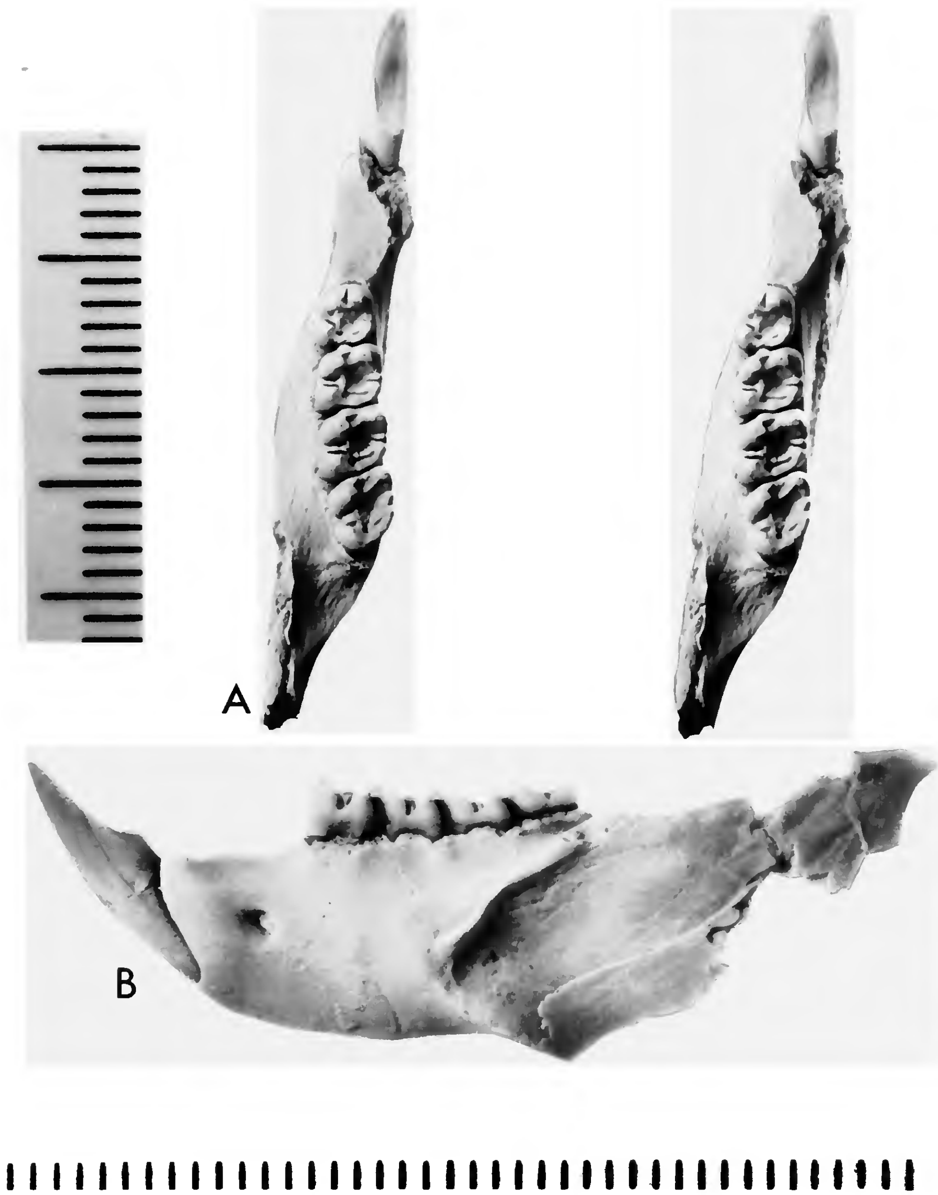

FIGURE 3.—Left mandible of *Protosciurus*, USNM 243981: A, occlusal view, stereogram; B, lateral view. (Approximately × 3, scale in mm.)

part of M_2. On the other hand, most modern sciurids are somewhat more advanced, with the masseteric fossa extending forward beneath P_4. In USNM 243981 the anterior edge of the ascending ramus passes the alveolar border at the posterior edge of M_3, somewhat more posterior than in *P. mengi* and *P. condoni* and somewhat more anterior than in paramyids, where it is invariably somewhat behind M_3. The diastema between I_1 and P_4 is short and very little depressed, as is the case in the described specimens of *?P. jeffersoni* (Black, 1965:18). This differs from *P. condoni*, in which the diastema is short but very much depressed, more like the condition in modern squirrels.

DENTITION.—The dentition of USNM 243981 is similar in most features to that of *?Protosciurus* *jeffersoni* described by Black (1965), differing mainly in having a slightly more complicated cusp pattern. It differs from geologically younger species of the genus (i.e., the genotypic species *P. condoni* and also *P. mengi*) in the same way, but to a greater degree than, the Chadronian material assigned by Black (1965) to ?*P. jeffersoni* differs from the later species.

The incisors in USNM 243981 are transversely compressed to about the same degree as in other described *Protosciurus.* The cross section of the upper incisor measures 2.0 mm transversely by 3.4 mm anteroposteriorly, for a ratio of .59 for width to length. The lower incisor is 1.7 by 3.3 mm, and the ratio about .52. In *Sciurus niger* (N=5) the same ratios are, respectively, about .52 and .46, and in *S. carolinensis* (N=4), the same ratios are .46 and .36. The incisors of *Protosciurus* are therefore less transversely compressed than in these two modern *Sciurus* species but are much closer to these squirrels than to most of the paramyids, which have incisors that are about as broad as long in cross section. The enamel on the *Protosciurus* incisors is finely wrinkled, covering the anterior face and reaching about a quarter of the way back on the lateral face on the upper incisor and about a third of the way back on the lateral face of the lower incisor.

Wood (1980:19) considered uniserial incisor enamel diagnostic of the Sciuridae (and of the infraorder Sciuromorpha). Wood believed it probable that the change in enamel microstructure from pauciserial in Ischyromyoidea to uniserial in Sciuromorpha accompanied the shift from protrogomorphous to sciuromorphous jaw muscles. Wilson (1972:221) suggested that the change from pauciserial to uniserial enamel may have preceded the development of the more powerful sciuromorphous jaw muscles and may have been a necessary prerequisite. Wilson's interpretation is supported best by the present evidence.

USNM 243981 is protrogomorphous, and a scanning electron micrograph (Figure 2B) shows that it has uniserial enamel. The lamellae of the inner lamellar part are oriented approximately perpendicular to the enamel surface. This differs from the more derived uniserial enamels, in which the lamellae are inclined toward the tip of the tooth, as the prisms of the outer homogeneous layer are in this specimen. John Wahlert (pers. comm.) has observed that enamel like this, with lamellae not inclined, occurs in *Eutypomys thomsoni* and *Prosciurus relictus*, and that in *Mesogaulus novellus* it is but slightly inclined. Korvenkontio (1934) lists this condition in four species of *Sciurus* and also in *Arctomys*, although Wahlert (pers. comm.) observed considerable superimposed complexity in the latter genus. In the other sciurids studied, the lamellae are inclined toward the tip of the tooth. The distribution of these enamel microstructure patterns suggests that the most primitive uniserial enamel has uninclined lamellae, the condition seen in *Protosciurus* and retained in *Sciurus.* The inclined lamellae of the other sciurids may be more derived.

USNM 243981 is primitive (like paramyids, for example, and like many sciurids) in retaining P^3, in this case a relatively simple peg with a small posterior shelf. The other maxillary teeth, P^4-M^3, are each broader than long (see Figure 2). On P^4 the anterior cingulum is swollen, anterior to the paracone, into a distinct parastyle. The same feature is present on the molars, but becomes progressively less prominent from M^1 to M^3. The first two molars have distinct mesostyles, which are also present but smaller on P^4 and M^3 The posterior cingula are swollen near their lingual ends, most noticeably on M^1 and M^2, into small hypocones. These are near the protocones and are connected to them but are distinct from them. On the lingual faces of M^{1-2} small pits mark the constriction separating protocones from hypocones. The teeth of USNM 243981 are very similar in size to those of the type and topotypic specimens of *Protosciurus jeffersoni* (see Table 1).

In P^4 to M^3 the protolophs connect to the protocone, and the metalophs do likewise except in M^3, where the metaloph is imperfectly formed, consisting only of small conules in the posterior basin (see Figure 2). M^3 has a triangular outline. The lophs are much more complex than in *P. condoni* and *P. mengi* and are somewhat more

TABLE 1.—Measurements, in mm, of teeth of *Protosciurus jeffersoni* (AP = anteroposterior, TR = transverse, CM = Carnegie Museum of Natural History; data for CM specimens from Black, 1965)

Measurement	USNM 243981		Type CM 736		CM 10112	
	AP	TR	AP	TR	AP	TR
I^1	2.0	3.4	--	--	--	--
P^3-M^3	12.1	--	--	--	--	--
P^4-M^3	11.4	--	--	--	--	--
P^4	2.8	3.5	--	--	2.7	3.6
M^1	2.9	3.7	--	--	2.9	3.9
M^2	2.9	3.7	--	--	2.9	3.8
M^3	3.0	3.1	--	--	--	--
I_1	1.7	3.2	--	--	--	--
P_4-M_3	12.1	--	12.7	--	--	--
P_4	3.0	2.6	2.7	2.7	--	--
M_1	2.9	3.0	2.7	3.1	--	--
M_2	3.2	3.1	2.8	3.2	--	--
M_3	4.0	2.9	3.6	3.3	--	--

complex than in the Pipestone Springs specimen referred to ?*P. jeffersoni* by Black (1965, fig. 1b). Each loph is divided into several small conules. Black (1965:20) stated that in the Pipestone Springs specimen assigned to ?*P. jeffersoni*, neither protoconules nor metaconules can be distinguished with certainty in the lophs, but Black's illustration (1965, fig. 1b) shows what appears to be distinct metaconules on M^{1-2}. The lower dentition of USNM 243981 is like the upper dentition in being somewhat more complex than that of ?*P. jeffersoni* described by Black and considerably more complex than in the later species of *Protosciurus*. P_4 is the smallest of the lower cheek teeth, and M_3 is the largest, with M_1 being slightly smaller than M_2 (Figure 3). The trigonid basin of P_4 is like that of ?*P. jeffersoni* in being a narrow anteroposteriorly directed slit between the closely spaced metaconid and protoconid. The trigonid basins are completely enclosed on M_{1-3} by metalophids. The anterior cingulids of M_{1-3} are quite thick and, on M_{1-2}, are so swollen that they appear cusplike, a characteristic noted by Black (1965:20) in the M_1 of ?*P. jeffersoni*. Each lower cheek tooth has a distinct mesostylid in the valley between metaconid and entoconid. Entoconids are not distinctly separated from the posterior cingula (posterolophids). A distinct, transversely elongated mesoconid fills the valley between protoconid and hypoconid of each tooth; these seem to be more buccally elongated than in later *Protosciurus* species.

Low but distinct hypolophids (least distinct on M_3) extend from the entoconids nearly all the way across the basins toward the hypoconids but do not quite join them. These hypolophids are slightly more distinct than in the specimen of *?P. jeffersoni* described by Black (1965), who noted that hypolophids are not present in the later species of *Protosciurus* nor in modern Sciurinae.

In dental characters, USNM 243981 is most like *?P. jeffersoni* (Black, 1965). It differs from later species of *Protosciurus*, and from Sciurinae in general, in the same way that *?P. jeffersoni* does, but the differences are slightly more pronounced. One trend in sciurid evolution seems to be toward simplification of tooth crown pattern. USNM 243981 represents the beginning of this trend, most nearly retaining the dental characteristics of its presumed ancestral group. Most paramyids, for example, have conules in the protoloph and metaloph, complete metalophids, and, in *Leptotomus*, some development of a hypolophid. These are characters not seen in modern sciurinae, nor in the geologically younger species of *Protosciurus*, but do appear in *?P. jeffersoni* and in USNM 243981.

The multiple conules in the protolophs and metalophs of USNM 243981 are reminiscent of the teeth of some flying squirrels. They are similar in this way, for example, to the several species from the Barstovian and Clarendonian of California referred by James (1963) and Lindsay (1972) to *Sciuropterus* and recently placed by Engesser (1979) in a new genus, *Petauristodon.* James (1963) and Lindsay (1972) believed the California taxa were congeneric with fossils from the European Neogene (for example, see Mein, 1970), but Engesser (1979) pointed out, as Lindsay had also mentioned, that certain North American paramyids have subdivided lophs, accessory lophules, hypocones, and other characters seen in the California material. Engesser concluded that the California material, which he called *Petauristodon*, has nothing to do with the European fossil "*Sciuropterus*" and instead was probably derived from a North American ancestor. USNM 243981 is temporally intermediate between the paramyids and the *Petauristodon* species, and this, in conjunction with the morphologic similarities, provides support for Engesser's hypothesis.

Vertebral Column

The vertebral column is remarkably well preserved for a fossil specimen. The anterior part of the skeleton was weathered and eroded, but at least parts of all the presacral vertebrae were nevertheless recovered, along with much of the tail.

The atlas is comparable in detail to that of *Sciurus.* It has no spine. The transverse processes are incomplete but appear to have been identical to those of the modern squirrel. The vertebrarterial and atlantal foramina are small as in modern Sciuridae, rather than large as in *Paramys* and *Ischyromys.* The facets for the axis are not as widely separated as in *Paramys.*

Little is preserved of the axis except for the centrum, which does not differ detectably from that of *Sciurus.* The atlantal articular facets are continuous with the articular surface of the odontoid process, as in squirrels, and unlike the condition seen in *Paramys*, where the atlantal facets are widely separated and isolated from the odontoid. The ventral surface is excavated on either side of a low median ridge, just as in *Sciurus*, whereas *Paramys* has a heavy median keel.

The posterior five cervicals are still tightly articulated, along with the first thoracic, in cemented matrix. Some of the processes are broken, but, as far as can be determined from the outer surfaces, they are very much like the neck vertebrae of *Sciurus.*

If *Protosciurus* had 12 thoracic vertebrae, as modern squirrels do, and as Wood (1937:179) pointed out is probably the primitive number for rodents, then parts of all are preserved in the fossil specimen. Parts of the second and third thoracics can be identified by their distinctive transverse processes. The next five (fourth through eighth) consist mostly of centra, though parts of the neural arch are preserved in two of them; these five are too poorly preserved to allow them to be put confidently into sequence. The ninth thoracic through first lumbar are associated as a unit. The anticlinal vertebra is the antepenultimate thoracic as in *Sciurus*. Of the second lumbar, only the left half of the centrum was recovered. The third lumbar through twelfth caudal are all preserved in articulation, or so nearly so that there can be no doubt about the correct sequence. The third through seventh (last) lumbar still remain as a unit, not completely freed from the matrix. None of the lumbars have all of the processes preserved, but all have most of them; they differ in no significant ways from those of *Sciurus*. As in most mammals, but particularly so in rodents and emphatically so in squirrels, the vertebrae increase progressively in size from the anterior thoracics through the lumbar series. The posterior lumbars are twice the dimensions of the anterior thoracics in *Protosciurus*, as they are in *Sciurus*.

Protosciurus (USNM 243981) has one sacral and one fused pseudosacral. The following free vertebra, however, has the morphology of the second pseudosacral of squirrels, and very likely would have been fused into the sacrum had the individual been fully mature; it is considered a second pseudosacral.

The first 12 caudals were articulated, or nearly so (see Figure 1), and broken parts of most of the more posterior caudals were scattered through the matrix. The original number of caudals cannot be determined, but there were clearly about as many as in modern squirrels. The 12 anterior ones are like those of *Sciurus* in most details. Seven have complete neural arches, compared to nine in *Sciurus* (at least in *S. niger*, USNM 251574 and 257984), and, according to Wood (1962:23), six in *Paramys* and 10 in *Ischyromys*. There is some doubt about the associations in the latter two genera, however, and so the numbers should not be taken too confidently.

In *Protosciurus* the centra are very short in the anterior caudals and rapidly increase in length posteriorly. The second caudal is shortest, and the 11th is longest (Figure 4). This is comparable to the pattern seen in *Sciurus*, where the second or third is the shortest, and the 11th to 13th the longest (Thorington, 1966:21). In *Protosciurus* the longest caudal is slightly more than three times the length of the shortest. This is more nearly comparable to the ratio seen in *Glaucomys* and only slightly greater than that seen in *Eutamias*. These have a somewhat higher ratio than in *Tamiasciurus* and *Sciurus*, in which the longest is about two-and-a-half times the length of the shortest. However, in all these modern genera except *Sciurus*, the longest caudal is usually more proximal than in *Protosciurus*; in *Tamiasciurus* the longest is eighth to tenth, *Glaucomys* the eighth to ninth, and *Eutamias* the ninth to eleventh (Thorington, 1966:16–21).

There seems to be little doubt that *Protosciurus* could have flexed its tail abruptly over its back as squirrels do. The pattern of caudal vertebrae is very different in *Paramys* (Wood, 1962:23), which has a much more massive tail, with the longest vertebrae (the 13th and 14th) being barely twice the length of the shortest, which is the third (see Figure 4). Wood is probably justified in saying that *Paramys* could not have exhibited the extreme dorsiflexion of the tail seen in the squirrels, as it was restored by Matthew (1910:53).

Pectoral Limb

Scapula.—The glenoid ends of both scapulae of USNM 243981 were recovered. These show the proximal ends of the subscapular spine, the suprascapular spine, and the coracoid process (Figure 5). In every feature that can be examined, the scapulae of *Protosciurus* clearly resemble those of *Sciurus*. The subscapular spine terminated approximately 7 mm from the glenoid articular surface. The coracoid was stout, as in *Sciurus*, and although broken, it was clearly larger than in *Spermophilus*. The glenoid surface has a prominent superior beak, shaped like that of *Sciurus*, perhaps

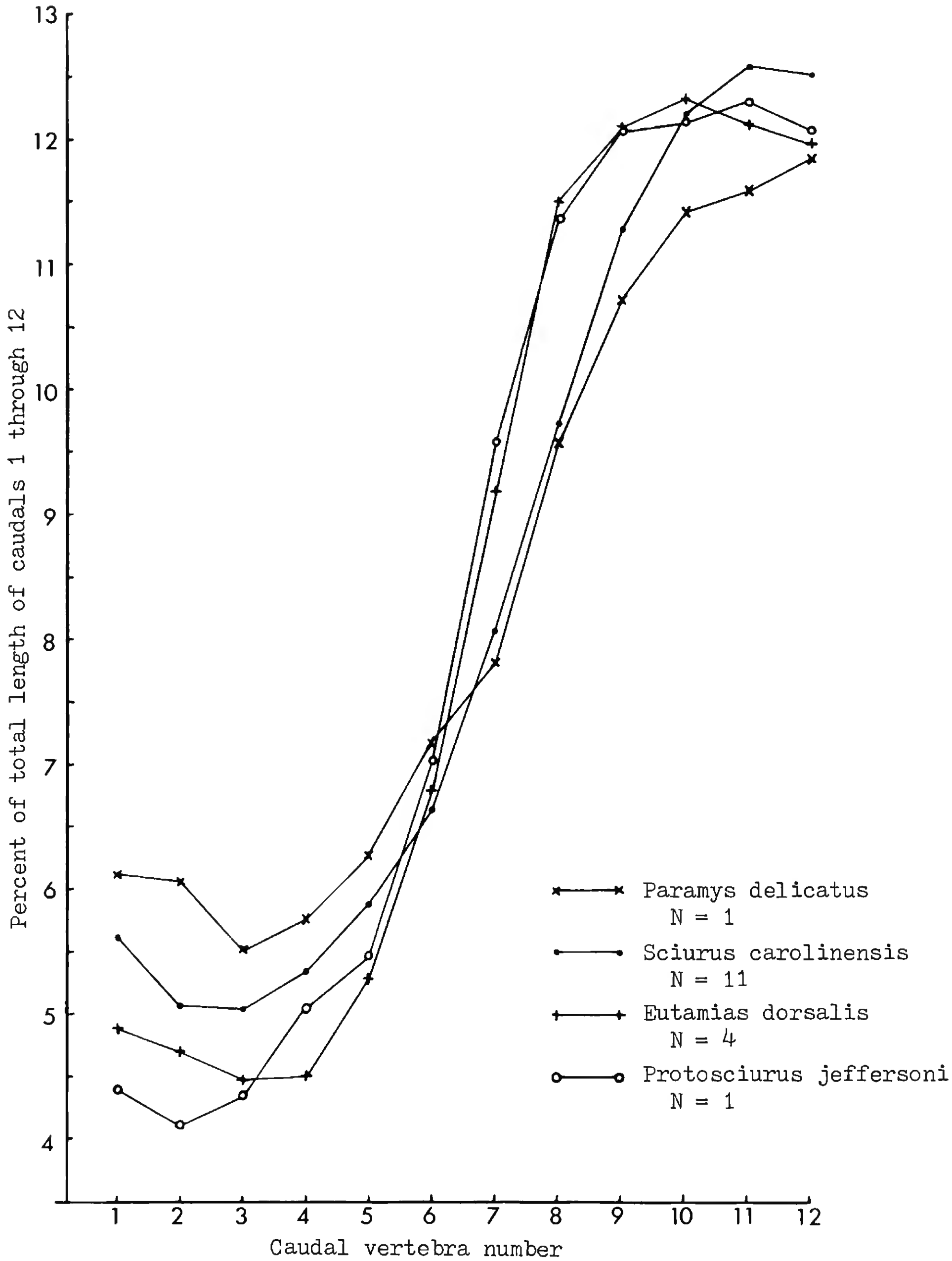

FIGURE 4.—Relative lengths of centra of first 12 caudal vertebrae of four rodent species, in terms of percent each centrum represents of total length of all 12 in its respective tail. *Protosciurus* is closest to *Eutamias dorsalis* in relative flexibility of its tail. Data for *Sciurus carolinensis* and *Eutamias dorsalis* from Thorington, 1966.

indicating that the origin of the long head of the biceps was oriented as in *Sciurus*, and differing slightly from that of *Spermophilus*. Similarly, the origin of the long head of the triceps, deep to the axillary border of the scapula, is like that in *Sciurus* and dissimilar to the strong origin in *Sper-*

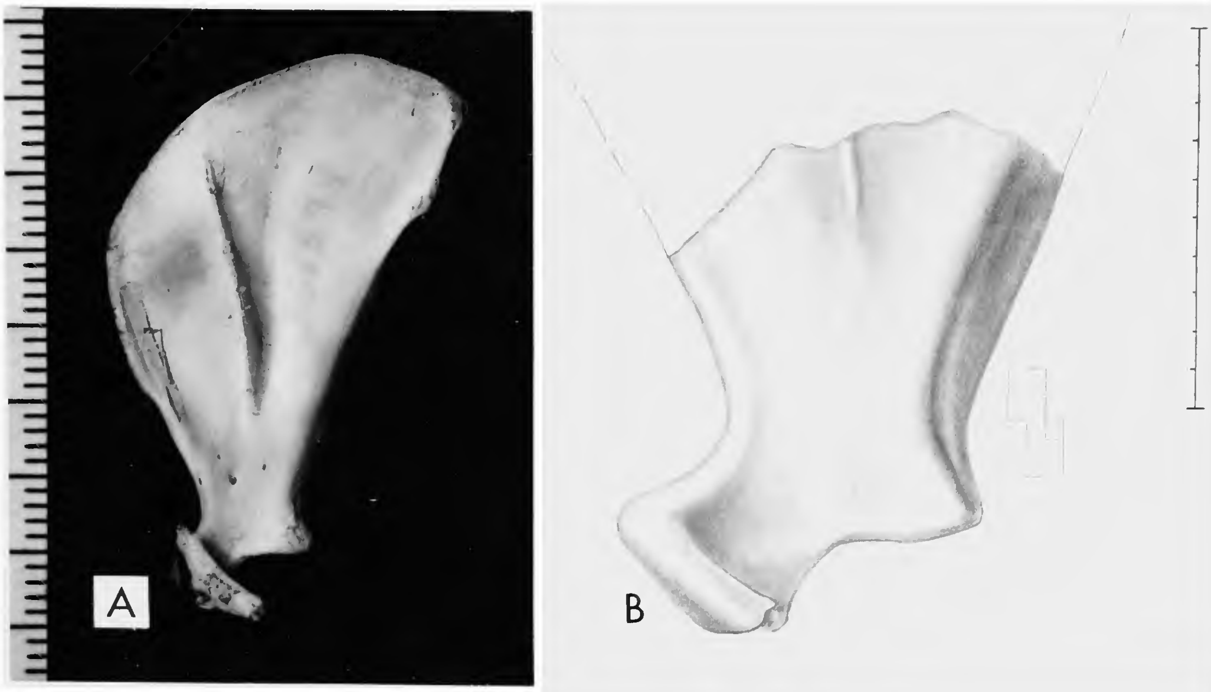

FIGURE 5.—Comparison of right scapulae of two squirrel species in medial view: A, *Sciurus niger*, USNM 251574 (approximately × 2); B, glenoid end only, *Protosciurus*, USNM 243981 (approximately × 5). Note particularly the subscapular spine. (Scales in mm.)

mophilus, which is not overlapped by the axillary border.

A character of particular taxonomic importance in *Protosciurus* is the presence of the subscapular spine. So far as we can determine, a subscapular spine is characteristic of the family Sciuridae, being present in all members of the family, regardless of size or habit of the animal, i.e., from small chipmunks to large marmots and from ground squirrels, to tree squirrels, to flying squirrels. Also, so far as we can determine, the only nonsciurid rodent with a subscapular spine is *Anomalurus* (it may occur in other anomalurid genera as well, but appropriate material is not available in the USNM collections). This feature therefore seems to be an important derived character, with taxonomic significance at the family level.

HUMERUS.—The humeri of ground squirrels appear more robust than do those of tree squirrels of similar body size. In part, this is due less to the stoutness than to the fact that ground squirrels have relatively shorter limbs. The humerus of *Protosciurus* is long and gracile, striking in its overall similarity to that of *Sciurus* (Figures 6, 7).

In ground squirrels, and in *Tamias*, the infraspinatus muscle inserts into a pit on the greater tuberosity, whereas in *Sciurus*, the posterior edge of the insertion is flush with the articular surface of the head. This is perhaps a function of the strength of the infraspinatus. In this characteristic, *Protosciurus* resembles *Sciurus*.

The deltoid ridge of adult tree squirrels differs greatly in appearance from that of ground squirrels (Figure 7A–C). In *Sciurus* it is narrow, with the deltoid and pectoralis insertions parallel to one another. In *Protosciurus* it is clearly very similar to *Sciurus*, rather than broad proximally as it is even in young *Spermophilus*. *Paramys* is much like the ground squirrels in this respect, with the deltoid

FIGURE 6.—Left humerus of *Protosciurus*, USNM 243981: A, anterior view; B, posterior view. (Approximately × 1.5.)

crest broad proximally, perhaps somewhat broader, relatively, than in *Spermophilus* but less so than in *Marmota. Tamias* is like the ground squirrels in this character.

The posterior and medial surfaces of the shaft of the humerus of *Protosciurus* have two ridges, which probably bounded the origin of the medial head of the triceps, indicating that this muscle had a strong fascial origin. The medial ridge extends from the lesser tuberosity over the proximal third of the shaft, ending immediately distal to the level of insertions of the teres major and latissimus dorsi muscles. The posterior ridge is a continuation of the lateral ridge of the humerus and extends proximally to within five millimeters of the head. These ridges are not so sharply defined on any recent sciurid we have examined. They are present but faint on the humeri of *Sciurus*, *Spermophilus*, and *Cynomys* and slightly more distinct on adult *Marmota. Paramys* is more like *Protosciurus* in having the posterior of these two ridges quite distinct, though the medial ridge is less distinct, as in the sciurids mentioned.

The medial epicondyle tends to be more robust in ground squirrels and prairie dogs than in tree squirrels, because of the stronger flexor musculature of the former. In *Paramys*, the median epicondyle is also quite robust. It is robust in some *Sciurus* species, but in *Protosciurus* it is much less

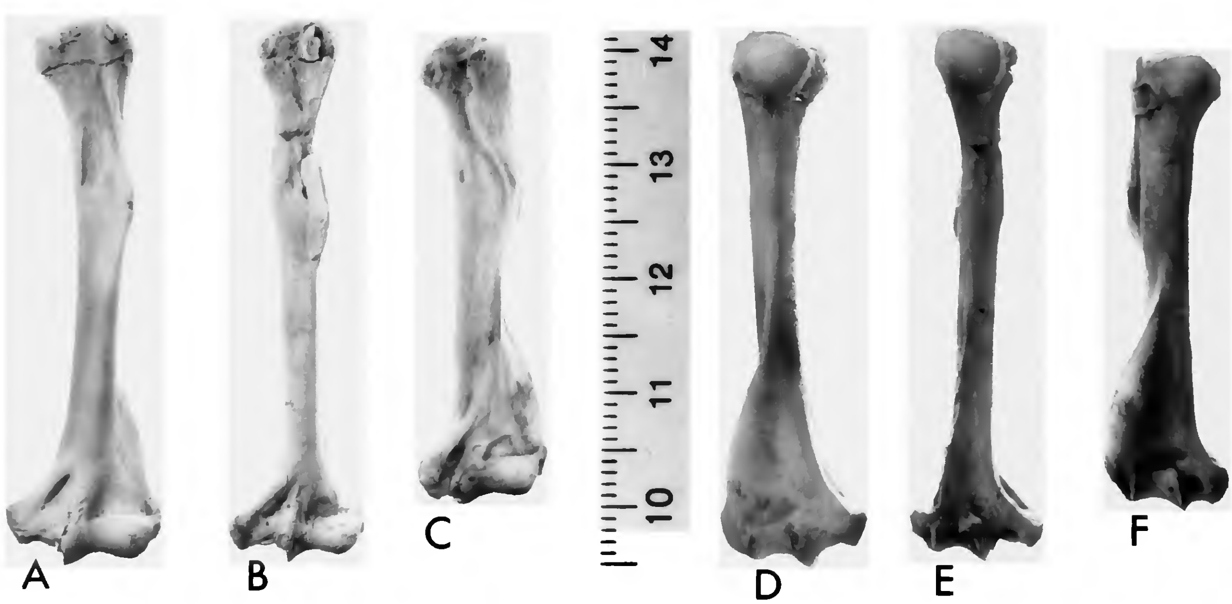

FIGURE 7.—Comparison of left humeri of three squirrel species: A, D, *Sciurus niger*, 251574; B, E, *Protosciurus*, USNM 243981; C, F, *Spermophilus beecheyi*, USNM 484951. (A–C, anterior views; D–F, posterior views; all to same scale, approximately × 1.5; scale in mm.)

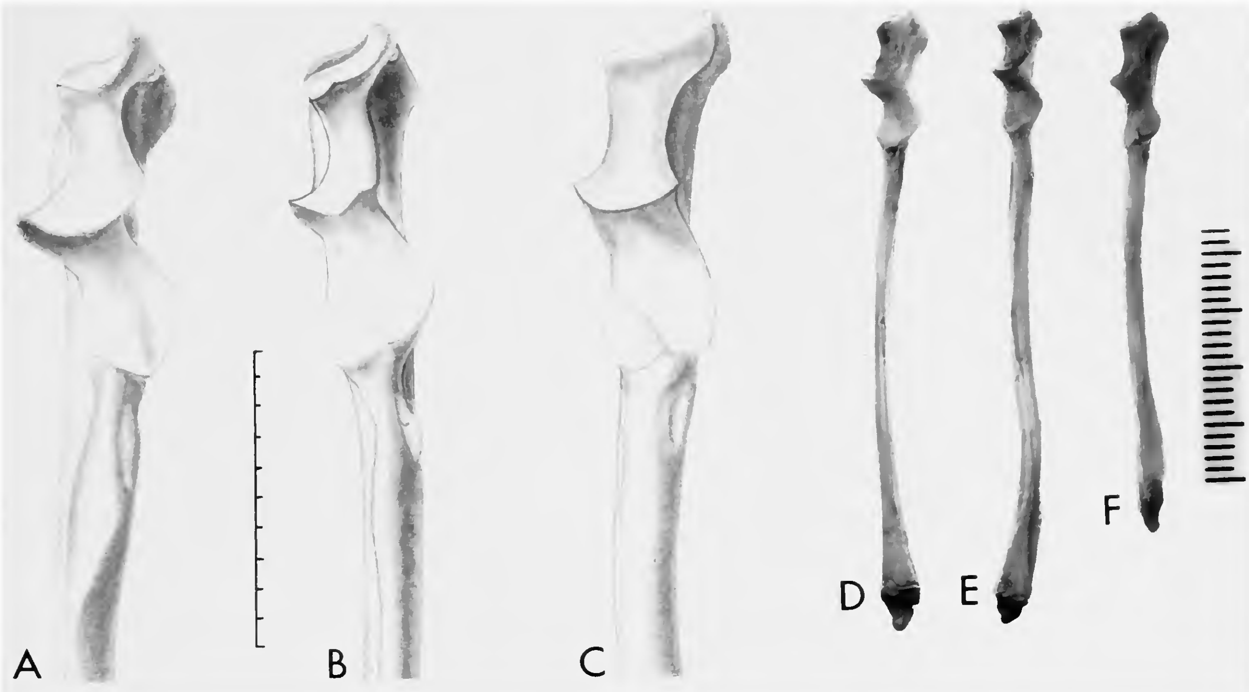

FIGURE 8.—Comparison of right ulnae of three squirrel species in anterior view: A, *Sciurus niger*; B, *Protosciurus*; C, *Spermophilus beecheyi*, showing different relationships between humeral and radial facets; D, *Sciurus niger*, USNM 251574; E, *Protosciurus*, USNM 243981; F, *Spermophilus beecheyi*, USNM 484951. The outward flexure of the distal part of the *Protosciurus* ulna is probably a preservational artifact. (A–C all at same scale, approximately × 4; D–F all at same scale, approximately × 1.5; scales in mm.)

so, closely resembling in this respect the gray squirrel *Sciurus carolinensis*.

The humero-ulnar ligaments appear to have differed in *Protosciurus* from those of recent squirrels. Posteriorly, between the medial edge of the trochlea and the median epicondyle, *Protosciurus* has a deep, transversely oriented, groove of insertion, where recent squirrels examined have only a pit, which is usually shallow. The deep pit on the medial surface of the trochlea of recent squirrels, a point of insertion of ligaments, is shallower in *Protosciurus*. *Paramys* shows yet another variation, having a shallow depression posteriorly, a moderately developed pit on the median surface of the trochlea, and a small but deep pit anteriorly, between the trochlea and median epicondyle.

ULNA.—The ulnas of tree squirrels differ from those of ground squirrels in proportions and in the appearance of the shaft. The general appearance of the ulna of *Protosciurus* is like that of tree squirrels of the genus *Sciurus* (Figure 8). In detail, however, there are several characteristics in which the fossil is either unique or more like the ground squirrels.

The proximal end of the ulna differs subtly between tree and ground squirrels. In tree squirrels the proximal end of the olecranon is drawn out into a thin medial ridge, which is thinner and directed more in the axis of the ulna, whereas it is broader and more medially directed in ground squirrels. *Protosciurus* is intermediate in this character, which probably reflects some difference in the manner of insertion of the triceps tendon.

Protosciurus resembles the tree squirrels in the shape and orientation of the proximal radial articular facet. In *Sciurus* it is more nearly continuous with the articular surface of the trochlear notch, whereas in *Spermophilus* and especially in *Cynomys* the plane of the radial notch is more nearly parallel to the main axis of the ulna and hence at a greater angle with the trochlear notch (see Figure 8A–C). *Paramys* is like the ground squirrels in this character, perhaps having the radial surface deflected at an even greater angle away from the trochlear notch.

The insertion of the brachialis in *Protosciurus* appears to have been more distal to the coronoid process than is usual in recent squirrels. We estimate the distance from the coronoid process to the middle of the brachialis insertion to be 4.3 mm in a *Protosciurus*, 2.9 mm in a *Sciurus niger*, 2.1 mm in a *S. carolinensis*, and 2.0 mm in a *Spermophilus beecheyi*; homologous points are difficult to define, but certainly this length is greatest in *Protosciurus* and least in *Spermophilus*. The more distal insertion of the brachialis could have enabled *Protosciurus* to flex its forearm more powerfully.

In both tree and ground squirrels, the shaft of the ulna has a laterally flattened interosseous crest, forming a blade off the main part of the shaft, as if the interosseous membrane had become partially ossified. The crest is concave on the extensor side. In *Sciurus* and *Protosciurus* the crest is quite thin at midshaft, whereas in *Spermophilus* it is thicker. In *Sciurus* it disappears on the distal third of the ulna, whereas it tapers more gradually and extends further toward the distal end of the bone on *Spermophilus* and *Protosciurus*. It may thus provide a more substantial origin for distal fibers of the flexor and extensor muscles, which take origin in this interosseous area. The ridge of origin of the muscle extensor indicus, which lies distal to the extensor fossa of the ulna of ground squirrels, is not found on the ulna of *Sciurus* or *Protosciurus*. Particularly in Recent tree squirrels, but also to a lesser degree in *Protosciurus*, the shaft of the ulna bows outward (Figure 8). In *Spermophilus* it is very indistinctly curved, and in *Paramys* it is quite straight. The shaft of the bone in *Paramys* is proportionately heavier than in *Spermophilus* and much heavier than in *Sciurus*. In *Paramys* the interosseous crest has a distinct thickened area of insertion and is not produced into a blade as in *Protosciurus* and the modern sciurids.

The distal end of the diaphysis of the ulna is triangular in cross-section in young squirrels. In adult *Sciurus* it becomes laterally flattened. In adult *Spermophilus* it retains a triangular cross-section because of the prominent ridge for origin of the pronator quadratus muscle, which is never as strongly developed in *Sciurus*. In *Protosciurus*, the distal end of the shaft is triangular in cross-section, like that of *Sciurus* and *Spermophilus* of similar developmental age, and the ridge of the pronator quadratus is very prominent. Therefore it is likely that the pronator quadratus muscle of *Protosciurus* was more like that found in *Spermophilus* than in *Sciurus*. In *Paramys*, the pronator quadratus ridge is very prominent, perhaps even more so than in the ground squirrels and in *Protosciurus*.

The distal articular surfaces of the ulna of *Protosciurus* resemble those of *Sciurus*, more than those of *Spermophilus*, because the carpal articular surface is elongate and approaches the radial articulation. In the ground squirrels, the carpal articular surface is hemispheroidal and well separated from the radial articulation. *Protosciurus* also shares with *Sciurus* a deep pit for insertion of the ulno-carpal ligament. This pit is much shallower in *Spermophilus*. *Protosciurus* is dissimilar to both *Sciurus* and *Spermophilus* in having a broader dorsal tunnel for the tendon of extensor carpi ulnaris.

Radius.—The radius of *Protosciurus* is long and gracile as in tree squirrels and agrees in most details with those of *Sciurus* (Figure 9). The right distal epiphysis is missing; the length of the right radius given in Table 3 is an estimate made by adding the thickness of the left epiphysis to the length of the part preserved.

The proximal articular surface appears slightly more concave in *Sciurus* and *Protosciurus* than in *Spermophilus*. The neck of the radius of *Protosciurus* is also like that of the tree squirrels, in that there is a ridge on the ulnar surface, between the head

FIGURE 9.—Comparison of left radii of three squirrel species: A, D, *Sciurus niger*, USNM 251574; B, E, *Protosciurus*, USNM 243981; C, F, *Spermophilus beecheyi*, USNM 484951. (A–C, anterior views; D–F, lateral views; all to same scale, approximately × 1.5; scale in mm.)

and the abductor pollicis prominence, which is present in *Sciurus* and not in *Spermophilus*. Proximal to the bicipital tuberosity there is a pit for the insertion of the quadrate ligament connecting the radius and the ulna. This is prominent in *Sciurus*, less prominent in *Spermophilus* and *Cynomys*, and very prominent in *Protosciurus*.

At the midshaft on the ulnar side of the radius there is a groove for the interosseous membrane. This groove seems slightly more prominent in *Spermophilus* than in *Sciurus*, and it is much more prominent than either in *Protosciurus*. The supinator ridge on the lateral edge of the extensor surface of the radius is faint in *Sciurus*, more prominent in *Spermophilus*, and intermediate between the two in *Protosciurus*.

The distal end of the radius is more closely bound to the ulna in tree squirrels than it is in ground squirrels, but when the bones are separated, the extent of the synovial joint and the extent of the distal radio-ulnar ligaments seem similar. *Protosciurus* has a similar extent of origin of the radio-ulnar ligaments and joint.

The distal volar surface of the radius is notably flattened, perhaps even slightly concave, in ground squirrels, presumably associated with the strong origin of the pronator quadratus. In *Protosciurus* it is convex, as it is in *Sciurus niger* of the same developmental age. This seems somewhat surprising in view of the evidence of the ulna suggesting that *Protosciurus* had a strong pronator quadratus like that of ground squirrels. On the extensor surface, the radius of a ground squirrel shows many more features associated with extensor tendons than does the radius of a tree squirrel. The radius of *Protosciurus* is like that of *Sciurus* in being almost featureless in comparison with *Spermophilus* and *Cynomys;* however, the one distal epiphysis closely matches the left distal epiphysis of *Spermophilus beecheyi*. It shows a distinct groove for the abductor pollicis tendon, which is not prominent on the epiphysis of *Sciurus*.

A radius of *Paramys* has not been described, and no complete one was found in the USNM collection. The proximal part of a right radius is preserved in USNM 13254 (*Paramys delicatus*) and radii are known for other paramyids (Wood, 1962). All of those known are relatively stouter than in *Sciurus*, and most are even relatively shorter and thicker than in *Marmota.*

CARPUS.—The following wrist bones were found and identified (Figure 10): left and right pisiform, left and incomplete right triquetrum (cuneiform), right scaphoid, and left and right hamate (unciform).

Scaphoid: The scaphoid and lunate were not fused in *Protosciurus.* An unbroken right scaphoid exists, but the lunate was not found. The existence of the lunate as a separate bone was inferred from the following evidence: (1) the scaphoid of *Protosciurus* is smaller than that of *Sciurus* and appears to be lacking the ulnar 1/3 to 1/4 of the bone, in comparison to the scapholunate of *Sciurus*; (2) the articular surface of the scaphoid is narrower than the articular surface of the distal end of the radius, whereas the opposite is true in *Sciurus* and other modern squirrels; (3) the ulnar side of the scaphoid has an articular surface that does not articulate with the triquetrum; (4) the scaphoid does not articulate with the hamate in *Protosciurus*, although there is a facet on the hamate, which in Recent squirrels articulates with the scapholunate. Therefore, there must have been another bone, the lunate, between the scaphoid bone and the triquetral and hamate bones of *Protosciurus.*

In *Protosciurus*, the radial articular surface of the scaphoid is broadly convex as in Recent squirrels, and it extends ventrally as in *Spermophilus*, further than in *Sciurus.* On the radial side of the scapholunate of modern squirrels, there is an articular surface for the falciform bone. In *Sciurus* and in *Spermophilus* there is a groove distal to this articular surface in which ligaments insert. In *Protosciurus* the medial surface is similar in shape to that of *Sciurus*, presumably for the articulation of the falciform, but there is no groove; therefore, the ligaments must have been differently arranged, perhaps more like those in *Protoxerus*, which also lacks the groove. On the medial side of the palmar surface of the scaphoid there is a groove for ligament insertion. This is similar to a groove in the scapholunate of *Sciurus.* The homologous groove in the scapholunate of *Spermophilus* is deeper. The scaphoid of *Protosciurus* has a planar lateral surface, which is tilted ventrolaterally and slightly distally. This is similar to the corresponding articular surface in other rodents that have unfused scaphoid and lunate bones (e.g., *Bathyergus* and *Ctenodactylus*). The distal surface of the scaphoid of *Protosciurus* is slightly concave. In *Sciurus* and *Spermophilus*, the distal surface of the scapholunate is not only concave but has a deep pit in the middle. The homologue of the pit seems to have lain between the scaphoid and lunate in *Protosciurus.*

Triquetrum (cuneiform): The triquetrum forms the lateral border of the carpal arch. The shape and orientation of the bone is thus a reflection of the shape of the arch, which differs between tree squirrels and ground squirrels. This makes comparison difficult. The ulnar articular surface is planar concave and appears to have the same general orientation to the whole wrist in tree and ground squirrels. Relative to the main axis of this facet, the main axis of the bone is at approximately 45° or less in *Spermophilus*, whereas it is at approximately 75° in *Sciurus.* In *Protosciurus* the orientation appears to be more like that of *Sciurus* but is estimated to be an intermediate 60°. The ulnar articular surface is most concave in *Sciurus*, less so in *Spermophilus*, and least in *Protosciurus.* The articular surface for the pisiform is broad and planar-convex in *Sciurus*, elongate and concave in *Spermophilus*, and elongate and planar in *Protosciurus.* On its medial surface, the triquetrum articulates with the scapholunate in *Sciurus* and *Spermophilus* and with the lunate in *Protosciurus.* In *Spermophilus* this facet is approximately perpendicular to the planes of the proximal and distal surfaces of the bone. In *Sciurus* it is more proximally directed. In *Protosciurus* it is shaped more like that of *Spermophilus* and is directed slightly distally. Distally, the triquetrum articulates with the hamate. This articulation is a broad and concave facet in all three genera.

Pisiform: The pisiform of *Protosciurus* is generally intermediate in shape between those of *Sciurus* and *Spermophilus.* At their proximal ends, where they articulate with the triquetrum and the ulna, they are proximo-distally compressed. The body tends to be laterally compressed. The distal end is laterally compressed in *Sciurus*, knoblike in *Spermophilus*, and intermediate in *Protosciurus*.

Hamate (unciform): The dorsal surface of the hamate is similar in shape in *Protosciurus*, *Sciurus*, and *Spermophilus*. The proximal surface articulates with the triquetral bone. In *Spermophilus* the lateral surface of the triquetral facet is deeply grooved, much more so than in *Sciurus*, so that part of the articular surface faces laterally. *Protosciurus* is similar to *Sciurus* in this orientation of the triquetral-hamate articulation. This covers a bit more than half of the proximal articular surface in *Protosciurus*. The more medial part is presumed to be the lunate-hamate articular surface.

The distal surface of the hamate is roughly triangular in both *Sciurus* and *Protosciurus*. The broader palmar surface makes the hamate of *Spermophilus* appear more trapezoidal. The articular surfaces for the 4th and 5th metacarpals are very similar in *Sciurus* and *Protosciurus*. In *Spermophilus* the articular surface for the 4th metacarpal is more square (rather than rectangular), and for the 5th it is more rectangular (rather than triangular).

The medial surface of the hamate is similarly

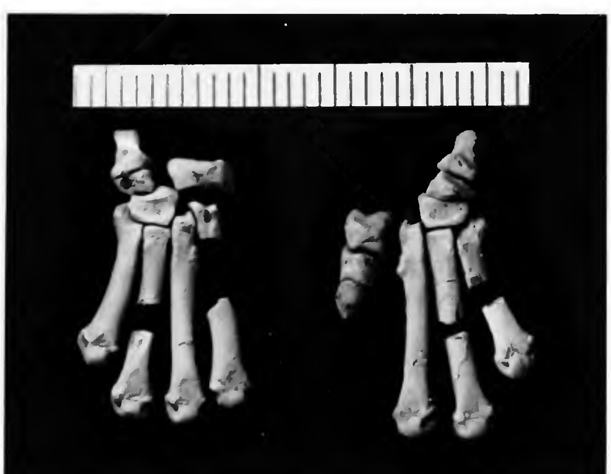

FIGURE 10.—Dorsal view of preserved parts of right and left carpus and metacarpus of *Protosciurus*, USNM 243981. (Approximately × 2; scale in mm.)

shaped in *Spermophilus* and *Protosciurus*. In *Sciurus* there is a strong lip on the proximal edge, not found in the other two; however, the pit at the distal edge is much deeper in *Spermophilus*, suggesting a stronger ligament than found in *Sciurus* and *Protosciurus*. On the palmar surface the groove for ligaments is smaller in *Sciurus* than in *Spermophilus* or *Protosciurus*. In *Protosciurus* it is a broader trough than in the other two.

MANUS.—Neither hand of USNM 243981 is complete, but the following material was recovered (Figure 10): metacarpal and phalanges of left first digit, proximal end and distal half of right second metacarpal, right and left third metacarpals, most of right and left fourth metacarpals (each missing a short section of midshaft), complete right and incomplete left fifth metacarpals, and numerous phalanges, which probably cannot be definitely referred to their respective digits.

Metacarpals: The metacarpals of tree squirrels are long and gracile compared to the shorter, stubbier metacarpals of ground squirrels. The metacarpals of *Protosciurus* resemble those of the tree squirrels, *Sciurus*, in their proportions. In *Sciurus*, metacarpal four is longer than three, whereas the reverse is true in the ground squirrels, *Spermophilus*. Unfortunately, in *Protosciurus*, each of the fourth metacarpals is broken, and a short section of shaft missing, making it impossible to determine their length, and hence the length relative to the third metacarpal. A single complete manus is apparently not known for *Paramys*, and so any interpretation of relative length of metacarpals would have to be based on a composite hand and therefore would not be reliable. The manus is known in other paramyids, however. In *Pseudotomus robustus* and *Ischyrotomus petersoni*, both members of the subfamily Manitshinae, the third metacarpal slightly exceeds the fourth in length, as in modern ground squirrels.

The first metacarpal of *Protosciurus* is short (2.1 mm), as are the phalanges of this digit. The ungual phalanx is very short and broad, virtually identical in morphology to that of *Sciurus*. This similarity, and the similarity in other morphologic details of this digit, leaves little doubt that *Protosciurus* had a very short thumb tipped by a nail as in Recent squirrels. The reduction of the first digit is a characteristic of the order Rodentia, and so it is the extreme similarity in morphologic details between *Protosciurus* and *Sciurus* that is significant here, rather than the reduced size of the first digit.

The proximal articular surface of the second metacarpal differs only slightly from that of *Sciurus*. On the lateral side, the palmar portion of the articular surface is slightly expanded in *Sciurus*, and in *Spermophilus* it is further expanded in comparison with *Protosciurus*. Consequently, the lateral edge of the articular surface is slightly notched in *Sciurus* and markedly notched in *Spermophilus* for passage of a ligament, whereas it is unnotched in *Protosciurus*.

The proximal articular surfaces of the third metacarpals are virtually identical in *Protosciurus* and *Sciurus*, both being laterally compressed. This is in contrast to the broader articular surface in *Spermophilus*, in which the palmar and especially the dorsal edges are expanded laterally toward the fourth metacarpal.

The fourth metacarpal is also similar in *Protosciurus* and *Sciurus*. The proximal articular surface is almost triangular in shape, broader dorsally and coming to a rounded point at the palmar end. In *Spermophilus* it is broader on the palmar surface, so that the overall shape of the articulation is more trapezoidal. *Spermophilus* has a rounded facet on the dorso-medial surface of the articular surface, where it articulates with the dorsal expansion of the third metacarpal. This facet is dissimilar to the relatively flat articulation between the metacarpals in *Protosciurus* and *Sciurus*.

Similarly, the articulation between the fourth and fifth metacarpals is flat and dorso-ventrally oriented in *Sciurus*, whereas in *Spermophilus* the facet on the fifth metacarpal is more convex and fits into a concave facet on the fourth. *Protosciurus* seems to have been intermediate but most similar to *Sciurus*. The articular surface for the hamate is more triangular on the fifth metacarpals of *Protosciurus* and *Sciurus* and more rectangular in *Spermophilus*.

Phalanges: A number of proximal, medial, and distal phalanges were recovered. These cannot be assigned with any certainty to their respective digits (some are slightly assymetrical, but it is virtually impossible to distinguish the proximal phalanx of the left third digit from that of the right fourth digit, for example). Each can be closely matched, however, to one of the phalanges of *Sciurus niger*. The insertions of the long flexor muscles on the proximal phalanges appear identical in *Protosciurus* and *Sciurus*. The proximal and medial phalanges of *Spermophilus* are relatively much shorter. The distal phalanges of *Protosciurus* are like those of *Sciurus*: dorsoventrally deep, laterally compressed, curving blades. The distal phalanges of ground squirrels are straighter, not so deep dorsoventrally and broader transversely.

INTERPRETATION OF THE HAND.—Perhaps the most striking, and unexpected, feature of the wrist of *Protosciurus* is the lack of fusion of the scaphoid and lunate bones. A fused scapholunate is characteristic of almost all living rodents. Rather vague and contradictory references in the literature regarding this feature in modern rodents have caused us to check its distribution as far as possible in modern rodents. Within the Bathyergidae, which have been cited as having separate scaphoid and lunate, we were able to check four of the five genera (three specimens of *Cryptomys*, one of *Heliophobius*, four of *Bathyergus*, and two of *Heterocephalus*; appropriate material of *Georychus* is not available in the USNM collections). Of these the scaphoid and lunate are separate in all except *Heterocephalus*, which has a fused scapholunate. Within the Ctenodactylidae, which also have been mentioned as having separate scaphoid and lunate bones, we were able to check only *Ctenodactylus* (three specimens), and confirm that the bones are in fact separate. Appropriate material of the other ctenodactylids (*Pectinator*, *Massoutiera*, and *Felovia*) was not available, but they are all so similar to *Ctenodactylus* in other features that it would be surprising if the scaphoid and lunate were not separate in all of them.

Matthew (1910) noted the presence of separate scaphoid and lunate in *Bathyergus* when stating that among modern rodents only, it shares this character state with the ischyromyoids. Matthew (1910) described separate scaphoid and lunate in *Pseudotomus robustus*, *Ischyrotomus petersoni*, and *Leptotomus grangeri*. Inasmuch as the two carpals were separate in all three of the paramyids in which material was sufficiently complete to allow a determination to be made, Matthew considered this condition to be characteristic of the family. It has since been determined that *Reithroparamys* has a fused scapholunate, and that in the type of *Leptotomus grangeri* (= *L. leptodus*), the left carpus has a fused scapholunate, and the right has two separate bones (Wood, 1962). It also has been determined (Wood, 1976) that the European paramyid *Ailuravus* has separate scaphoid and lunate bones. So, while the scaphoid and lunate are separate in some paramyids, they are fused in others, and the primitive state is not diagnostic of the family. The distribution of the primitive (unfused) and derived (fused) states of this character among fossil rodents is so incompletely known that it is not useful taxonomically. The retention of the primitive state in *Protosciurus* says nothing of the relationships of the Sciuridae. It does suggest, however, that the co-ossified scapholunate of recent squirrels was probably acquired independently from the same derived character in other rodents.

Tree squirrels have longer, thinner hands than ground squirrels. The broader hands of the ground squirrels, with the axis strongly centered around the third digit, are presumably better adapted for digging. The different shapes of the articular surfaces between the metacarpals probably also reflect different ways that the hands are used by tree and ground squirrels. The tree squirrel morphology would seem to allow mostly dorsal and ventral movement of the metacarpals relative to one another, whereas the articular surfaces between the metacarpals of ground squirrels may allow more rotation, as when the hand is cupped, or may restrict motion and thus increase the strength of the hand for digging. In these characteristics, *Protosciurus* is much like the tree squirrels and dissimilar in morphology to the ground squirrels. Thus we conclude by analogy that it was not well adapted to digging.

Pelvic Limb

Inominate Bone.—Both inominates of *Protosciurus* are present but damaged. Each has the ilium, acetabulum, and dorsal ramus of the ischium relatively complete, but ventral rami of ischium and pubis are represented only by fragments.

The ilium is shaped much like that of *Sciurus* (Figure 11). The iliac wings diverge slightly, not widely as in the ground squirrels and prairie dogs. The iliac ridge is more pronounced than in most Recent squirrels, forming a sharp division between the superior and inferior gluteal fossae. This condition is approached in some specimens of *Sciurus griseus*. The superior gluteal fossa is larger than the inferior, similar to the condition in *Sciurus* and unlike the condition in flying squirrels. There is a prominent ridge in the inferior gluteal fossa, presumably the origin of gluteus minimus, similar to that seen in *Spermophilus* and in some specimens of *Sciurus carolinensis*. The femoral tubercle is large and rounded, and it is separated by only a shallow groove from the acetabular lip, as seems characteristic of sciurids generally.

In the acetabulum, the unfused sutures between the ilium, ischium, and pubis are seen to be normally located for sciurids, but it seems surprising that they are not completely fused in an animal of its developmental stage. In *Sciurus carolinensis*, for example, the acetabular sutures fuse at about four months of age, long before the long bone epiphyses fuse. As previously mentioned, the dental wear and stage of epiphyseal fusion of long bones in the *Protosciurus* specimen correspond to those of an eight-month-old *Sciurus carolinensis*. Compared to modern squirrels, the fusion of the acetabular sutures in *Protosciurus* was therefore apparently retarded relative to that of the long bones.

The dorsal ramus of the ischium of *Protosciurus*

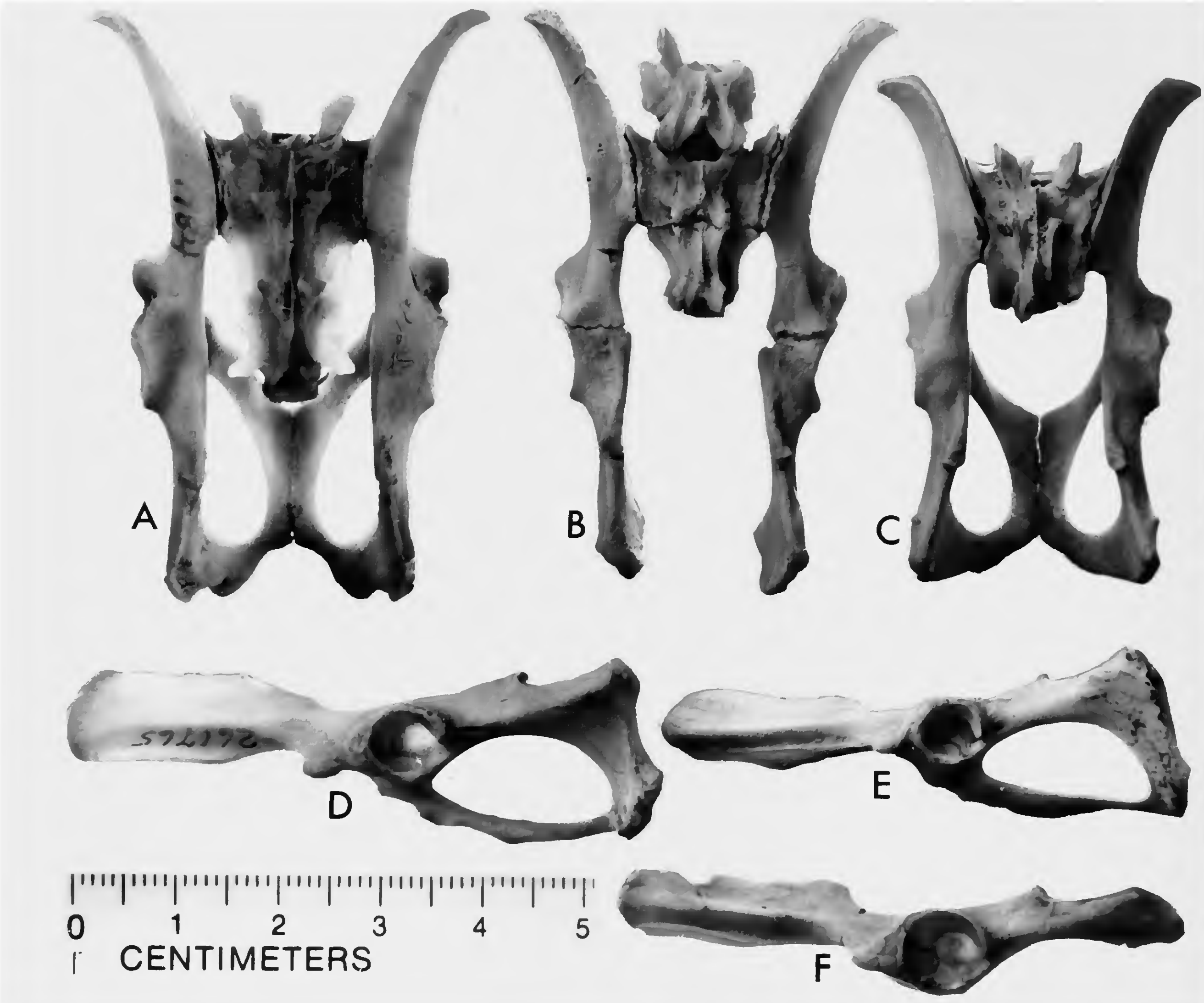

FIGURE 11.—Comparison of pelvis and sacrum of three squirrel species: A, D, *Sciurus niger*, USNM 257984; B, F, *Protosciurus*, USNM 243981; C, E, *Spermophilus beecheyi*, USNM 484951. (A–C, dorsal views; D–F, lateral views; all to same scale, approximately × 1.5; scale in mm.)

is not easily distinguished from that of *Sciurus*. The ischial spine of the dorsal border is prominent. This is more characteristic of tree squirrels and flying squirrels than of ground squirrels, presumably reflecting a different function of the obturator internus muscle.

FEMUR.—The femur of *Protosciurus* is striking in its similarity to that of the fox squirrel *Sciurus niger* (Figure 12).

A sharp distinction is seen between the tree squirrels and *Spermophilus* in the orientation of the lesser trochanter; in tree squirrels it is directed medially, and in ground squirrels it is directed posteromedially. In this character, *Protosciurus* is unambiguously similar to a tree squirrel like *Sciurus* (Figure 12). The lesser trochanter in *Cynomys* projects more medially, as in *Sciurus*, but is distinctive in other ways, such as the strong, elongated distal edge. In these respects, *Protosciurus* is like *Sciurus* and not like *Cynomys*. In *Tamias*, the lesser trochanter is directed posteromedially, much as in *Spermophilus*.

The condylar width of *Protosciurus* is greater than that of *Spermophilus* and like that of *Sciurus*, but the intercondylar fossa is narrow as in ground squirrels and unlike the broad shallow intercondylar fossa of *Sciurus*. The facets for insertion of ligaments and tendons on the external surfaces of the condyles can be very prominent in adult *Spermophilus*. They are less prominent and very similar in *Sciurus* and *Protosciurus*. The medial condyle is only indistinctly larger than the lateral in *Sciurus* and *Protosciurus* (Figure 12), whereas it is distinctly larger in *Spermophilus* and *Cynomys*.

The third trochanter is similarly positioned, high on the shaft, in *Protosciurus*, *Sciurus*, and *Spermophilus*, but is less prominent and laterally expanded in *Spermophilus* (Figure 12). The shaft of the bone is quite straight in all three genera. In *Protosciurus* and *Sciurus* the sides of the shaft are nearly parallel, whereas in *Spermophilus* the shaft is narrowest just below the trochanters and increases progressively in width from there distally to the condyles.

When the femur of *Protosciurus* is compared to that of *Paramys*, differences are immediately apparent. The femur of *Paramys* (and most other paramyids and ischyromyids as well) is consider-

FIGURE 12.—Comparison of left femora of three squirrel species: A, D, *Sciurus niger*, USNM 251574; B, E, *Protosciurus*, USNM 243981; C, F, *Spermophilus beecheyi*, USNM 484951. (A–C, posterior views; D–F, anterior views; all to same scale, approximately × 1.5; scales in mm.)

ably more robust, the neck relatively longer, the third trochanter much more distally positioned, and the shaft usually bowed outward slightly and anteroposteriorly compressed. In *Reithroparamys* the femur is quite straight, has a relatively proximally placed third trochanter, and is relatively gracile for a paramyid; but even in this paramyid genus, the femur is no more gracile than that of *Marmota* (which is quite robust by sciurid standards), has a relatively longer neck, and the third trochanter is lower on the shaft than in *Marmota*.

TIBIA.—The tibia of *Protosciurus* is, as a whole, very similar to that of *Sciurus* but in a few features is intermediate between tibiae of *Sciurus* and *Spermophilus* (Figure 13).

The tibial crest extends more distally in *Protosciurus* than it does in *Sciurus*, suggesting a more distal insertion of the semitendinosus muscle. The hamstring muscles of the ground squirrels insert more distally than do those of tree squirrels, especially if the shorter tibia is taken into account. Thus *Protosciurus* may have been somewhat intermediate in this set of characters.

In ground squirrels the popliteal fossa is deep and bounded by a lateral ridge and an especially distinct medial ridge, on which the popliteus inserts. The popliteal fossa of *Sciurus* is shallower, and the bounding ridges less sharply defined. This region in *Protosciurus* approaches the condition in ground squirrels, *Spermophilus* (Figure 13). In the middle of the popliteal fossa of *Protosciurus* there is a distinct ridge, like that seen in *Spermophilus* (Figure 13) but oriented a bit differently. This ridge is absent in modern *Sciurus* of similar developmental age (i.e., those in which the proximal epiphysis is not yet fused) and is lacking or very indistinct even in mature *S. niger*, though it is fairly distinct in some *S. carolinensis*. This ridge, and the prominent lateral ridge, probably indicate that *Protosciurus* had a strong muscle flexor digitorum fibularis.

The distal ends of the tibiae of *Sciurus*, *Spermophilus*, *Cynomys*, and *Protosciurus* do not differ greatly. The median malleolus in *Protosciurus* is somewhat larger than in the other genera and the tibia participates slightly more in the lateral surface of the astragular joint. The tibio-fibular joint of *Protosciurus* is apparently like that of *Sciurus*; the tibia is not ridged at this articulation as it is in *Cynomys* and *Spermophilus*.

The tibiae of paramyids, where known, are similar in general to those of sciurids but are much stouter. The muscular crests are even more strongly developed than in the ground squirrels. In *Paramys*, for example (USNM 23556), the cnemial crest is distinct more than halfway down the shaft, and the popliteal fossa is quite deep with a sharp medial ridge and a distinct lesser ridge within the fossa as mentioned above for *Protosciurus*. In *Paramys* the medial malleolus is large and contributes to the tibio-astragular joint to about the same extent as in *Protosciurus*, which is somewhat more than in living sciurids.

FIBULA.—The fragmented fibula of *Protosciurus* is somewhat stouter than that of *Sciurus*, particularly in its proximal half. Distally it is very similar to a *Sciurus* fibula. *Protosciurus* has an extensive flexor fibularis fossa, and the shaft does not seem to spiral as in *Sciurus*. The lateral protuberance at the distal end of the shaft is more distal in *Spermophilus* and *Cynomys* than in *Sciurus* and *Protosciurus*. *Protosciurus* has a deep pit for insertion of the talofibular ligaments, but this is seen in some *Sciurus* as well. The known paramyid fibulae are relatively even stouter than in *Protosciurus*. Wood's comment (1962:27) that the head of the fibula of *Paramys* is "larger than in any nonparamyid rodents with which it has been compared" is not negated by *Protosciurus*.

TARSUS.—The right tarsus of *Protosciurus* (USNM 243981) was found intact, articulated with the tibia and metatarsals (Figure 1), and is virtually complete. The left tarsus had been disarticulated before burial, and the only bones found were the calcaneus (broken), astragalus, navicular, and third cuneiform (ectocuneiform).

Calcaneus: The posterior tuberosity of the calcaneus is more laterally compressed in *Sciurus* than in *Spermophilus*, and the medial surface is more curved. In *Protosciurus*, the tuberosity is stouter and less compressed laterally than in *Sciurus*, but the medial surface is more curved than in

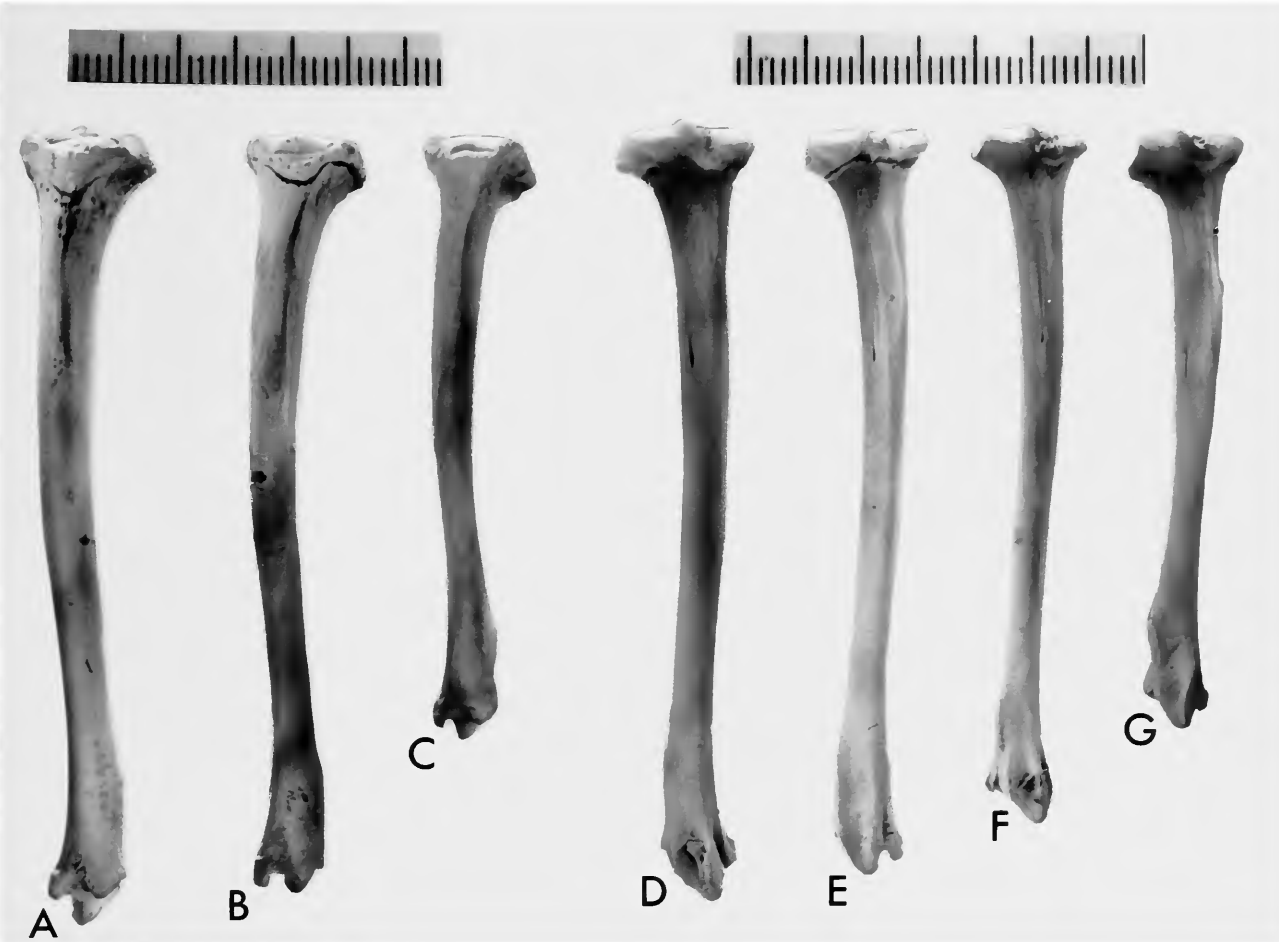

FIGURE 13.—Comparison of left tibiae of four squirrel species: A, D, *Sciurus niger*, USNM 251574; B, E, *Protosciurus*, USNM 243981; C, G, *Spermophilus beecheyi*, USNM 484951; F, *Sciurus carolinensis*, uncataloged specimen. (A–C, anterior views; D–G, posterior views; all to same scale, approximately × 1.5; scales in mm.)

Spermophilus (Figure 14). The lateral ridge of the tuberosity is more prominent than in *Sciurus*, forming a more prominent shelf for attachment of the calcaneo-fibular ligament.

The medial articular facet of the calcaneus is discrete and circular in *Protosciurus*, as it is also in *Spermophilus*. There is a very distinct groove between the medial and posterior articular facets, which is also like that seen in *Spermophilus*. In *Sciurus*, the groove between the facets is less distinctive, and the medial facet is less discrete and less circular.

In *Spermophilus* and *Protosciurus* the transverse part of the calcaneus is more nearly perpendicular to the main axis than it is in *Sciurus*, causing the medial articular facet to be only slightly more distal than the peroneal process. As in *Spermophilus*, the medial process of *Protosciurus* lacks the broad connection with the distal end of the bone that is seen in *Sciurus*.

Protosciurus must have had a strong interosseous ligament, because the groove distal to the posterior facet is as deep as that seen in *Sciurus*, and the lateral distal groove is as distinct as that in *Spermophilus*. The peroneal groove is more prominent in *Sciurus* than in *Spermophilus* and *Protosciurus*. In the latter two, it does not extend onto the body of the calcaneus the way it does in *Sciurus*.

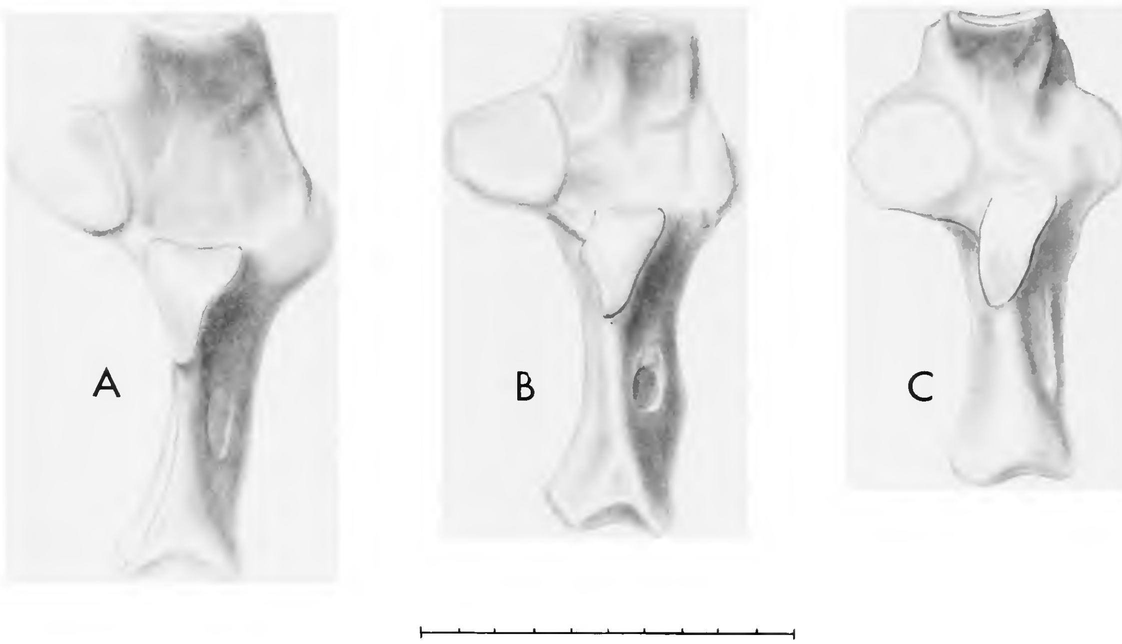

FIGURE 14.—Dorsal views of right calcanea of three squirrel species: A, *Sciurus niger*, USNM 261765; B, *Protosciurus*, USNM 243981; C, *Spermophilus beecheyi*, USNM 484951. (All to same scale, approximately × 5; scale in mm.)

The plantar surface of the medial process or sustentaculum of *Protosciurus* differs from both *Sciurus* and *Spermophilus.* Among the ground squirrels, the medial process is broadly concave, forming a groove for the tendon of the muscle flexor digitorum fibularis. In tree squirrels and in *Protosciurus* the plantar surface is more planar; but in *Protosciurus* there are two ridges, with a groove between them, rather like those seen in some *Cynomys.*

Astragalus: In the astragalus of *Sciurus*, the lateral ridge of the trochlea is much larger than the medial ridge, and there is a strong groove between them. *Protosciurus* is more like *Spermophilus* in that the lateral ridge and medial ridges are more similar in size, but in *Protosciurus* the groove between the ridges is deeper than in either *Sciurus* or *Spermophilus* (Figure 15). In *Sciurus*, the groove of the trochlea and the articular surface extend into a pit distally, at the base of the neck. This pit is not present in *Spermophilus* or *Protosciurus.*

The posterior medial surface of the trochlea is more extensive in *Sciurus* than *Spermophilus.* It forms a hook behind the medial articular facet of the calcaneus. Therefore the plantar surface of the astragalus has a groove for the medial calcaneo-astragalar articulation in *Sciurus.* This is not present in *Spermophilus*, so that the astragalus lies more on top of the calcaneus and does not hook around it. In *Protosciurus* the morphology is intermediate. The posterior surface forms a slight hook, not as extreme as in *Sciurus*, thereby forming a shallow plantar groove. The calcaneal surface of this hook does not appear to have an articular surface, as it does in *Sciurus.*

Because of the hook, the medial surface of the trochlea is larger in *Sciurus* than it is in *Spermophilus.* The larger proportion of the medial surface seems to be for the insertion of the deltoid ligament in *Sciurus*, whereas the larger proportion in *Spermophilus* seems to be the articular surface for the medial malleolus of the tibia. *Protosciurus* appears intermediate, with a strong deltoid insertion but also a large articular surface.

Protosciurus has a very distinct deep groove on the plantar surface of the astragalus, separating the posterior and medial calcaneal facets. There is only a faint suggestion of such a groove in *Sciurus* and even less in *Spermophilus*. The groove separating the facets is also found in the Asiatic giant squirrels, *Ratufa*, in which it is as prominent as in *Protosciurus*, and to a lesser extent in *Protoxerus*, the largest tree squirrels of Africa.

The head of the astragalus is concavo-convex in *Sciurus* and planar convex in *Spermophilus*. This navicular articular surface is planar convex in *Protosciurus* and does not exhibit the saddle shape common to tree squirrels like *Sciurus*.

Navicular: The navicular of *Protosciurus* is similar to that of *Spermophilus* in having an astragalar-navicular joint that is almost planar concave. It has only the suggestion of a convexity at the plantar edge, like that in *Spermophilus* and in contrast to the distinct convexity seen in *Sciurus*. The dorsal lip of the joint is almost as prominent in *Protosciurus* as it is in *Sciurus*, more so than in *Spermophilus*. The plantar lip is more distinct than in the Recent squirrels. The medial side of the astragalar-navicular joint is expanded in *Sciurus*, so that it lies dorsal to the whole of the proximal end of the medial cuneiform. In *Spermophilus* it is not so expanded, and the joint lies dorsal to only about two-thirds of the proximal end of the medial cuneiform. *Protosciurus* is similar to *Spermophilus* in lacking the medial expansion of the navicular.

The articular surface for the third cuneiform is triangular in shape in *Protosciurus*, similar to that of *Spermophilus* and dissimilar to the thinner more elongate facet in *Sciurus*. The articular surface for the second cuneiform is shaped like a broad

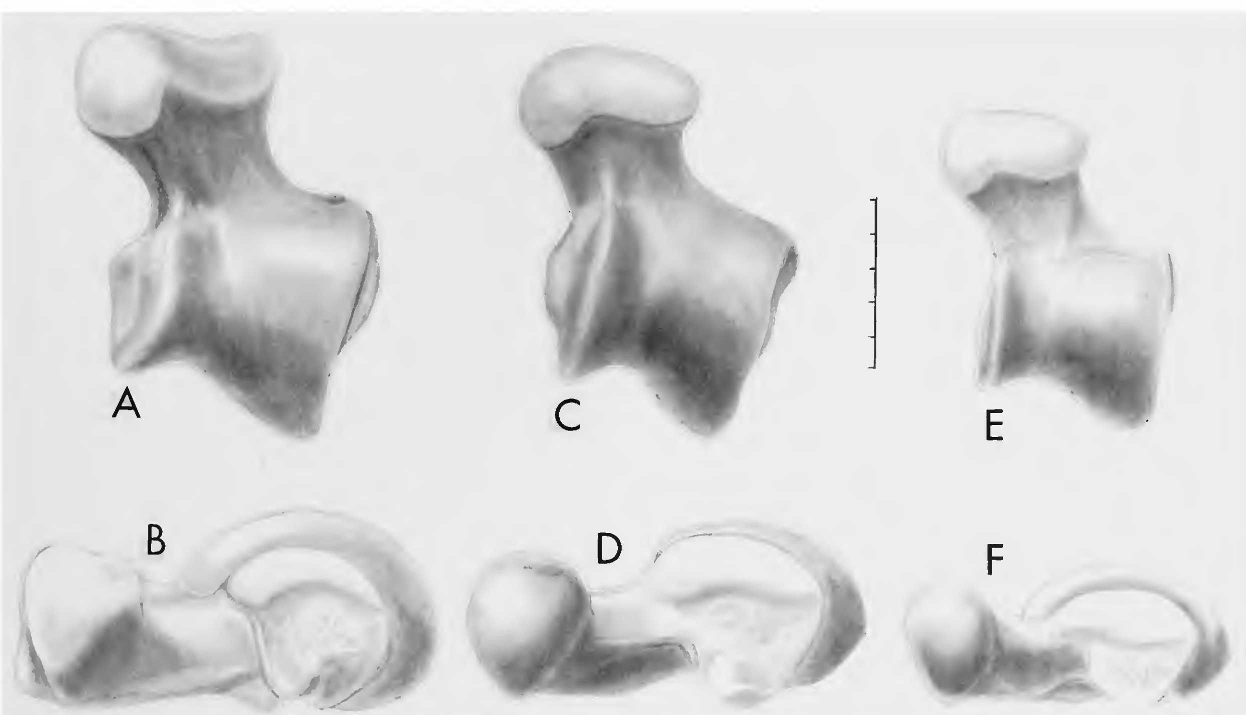

FIGURE 15.—Comparison of right astragali of three squirrel species in dorsal (above) and medial (below) views: A, B, *Sciurus niger*, USNM 261765; C, D, *Protosciurus*, USNM 243981; E, F, *Spermophilus beecheyi*, USNM 484951. (All to same scale, approximately × 5; scale in mm.)

comma in all three genera. *Sciurus* has a prominent distal facet for articulation with the first cuneiform, in addition to the ventromedial facet found in *Spermophilus*. *Protosciurus* is like *Spermophilus* in lacking the distal facet.

There is a prominent lateral facet for articulation with the cuboid in *Protosciurus*. Between this facet and the plantar process there is a broad groove, as in *Spermophilus*. This groove is very narrow in *Sciurus*. The plantar process is cylindrical like that of *Sciurus* (contrary to the description for *Sciurus* given by Bryant, 1945:304).

First Cuneiform (entocuneiform): In *Protosciurus*, as in other sciurids, this is a laterally compressed, proximodistally elongate bone. It has a proximal facet for the small supplemental medial tarsal bone, which is missing but was apparently present as in modern sciurids. We cannot determine if a medial sesamoid was present. The first cuneiform of *Protosciurus* did not articulate proximally with the astragalus. On the dorsolateral surface of the proximal end are articular surfaces for the navicular and second cuneiform. The distal end has an elongate articular surface for the first metacarpal. In most of these characters, the first cuneiform is like that of *Spermophilus*. In some individuals of *Sciurus carolinensis* and *Tamiasciurus hudsonicus*, the first cuneiform has a small articular surface for the astragalus and the articular surface for the navicular is more dorsal on the first cuneiform. In *Sciurus niger*, the first cuneiform does not contact the astragalus, and the navicular articulation faces proximally, at nearly right angles to the long axis of the bone, rather than facing proximolaterally as it does in *Protosciurus*.

Second Cuneiform (mesocuneiform): The second cuneiform of *Protosciurus* is roughly a half cylinder (bisected through its axis) or a three-dimensional comma. The plantar part of the distal end is missing. The proximal articular surface is planar. The distal surface has a ridge aligned dorsoventrally, which fits into a groove on the second metatarsal. The second cuneiform of *Sciurus* is quite distinct from that of *Spermophilus*, especially when viewed from the medial side, but the missing fragment of this bone of *Protosciurus* makes comparison difficult. In general shape the bones of *Protosciurus* and *Sciurus* seem most similar, but in some details, such as the shape of the facet for the first cuneiform, *Protosciurus* is more similar to *Spermophilus*.

Third Cuneiform (ectocuneiform): This bone of *Protosciurus* is narrow and proximodistally elongate like that of *Sciurus*, rather than short and broad as in *Spermophilus*. It is dissimilar to that of *Sciurus* in having a more wedge-shaped proximal articular surface, as in *Spermophilus*, rather than the more elaborate rectangular facet of *Sciurus*. This bone also lacks the distinct ventral groove found in *Sciurus*. Otherwise it is very similar to the homologous bone of *Sciurus*. The distal articular surface is bilobate, like a figure eight with a narrow ventral loop, as it is in *Sciurus*, and dissimilar to the wedge-shaped facet of *Spermophilus*.

Cuboid: There are no differences that we can discover between the cuboid of *Protosciurus* and the same bone of *Sciurus*. The deep groove of the plantar surface, through which passes the tendon of the peroneus longus muscle, has a strong proximal margin as in *Sciurus*. In *Spermophilus* this lip is not so prominent.

PES.—The right metatarsals of *Protosciurus* were intact, articulated with the tarsus (Figure 1). The first and third left metatarsals, and parts of the other three, were found individually in the matrix. None of the phalanges were articulated but most were found.

Metatarsals: The metatarsals of tree squirrels are long and gracile in comparison with those of ground squirrels. The metatarsals of *Protosciurus* are intermediate, though closer to the proportions of those of *Sciurus* than to those of *Spermophilus*. The first metatarsal of *Protosciurus* is shorter and relatively stouter than that of *S. carolinensis* and *S. niger* (Figure 16). The proximal process is less keeled than in those modern squirrels and has a less concave proximal articular surface. The first metacarpal of *Spermophilus beecheyi* is relatively shorter, but the proximal process relatively longer, than in *Sciurus* and *Protosciurus*. *Sciurus* differs from both *Protosciurus* and *Spermophilus* in having the first metatarsal more twisted, so that the ventral process is directed more laterally relative to the distal head of the bone. The other four metatarsals have articular surfaces similar to those of *Sciurus* and *Spermophilus*. In both *Sciurus* and *Protosciurus* the fourth metatarsal is longer than the third (Figure 16), whereas in *Spermophilus* the third is slightly longer than the fourth. The metatarsals of *Spermophilus* are all relatively shorter and stouter than in either *Sciurus* or *Protosciurus*.

Phalanges: As mentioned above, none of the phalanges were articulated with any of the metatarsals or with each other. A few phalanges (such as the first phalanx of the first digit, which is distinctive in having the processes for the digital flexors more proximally placed) can be definitely assigned to the correct position. Most are so similar, except for slight size differences, that we cannot be sure to which digit they belong. Each phalanx can be matched very closely with a phalanx of *Sciurus niger;* some of the toes of the foot seen in Figure 16 are assembled by use of this modern analogue. We want to stress, however, that there is no reasonable alternate way of assembling these toes that would significantly change the morphology of the foot.

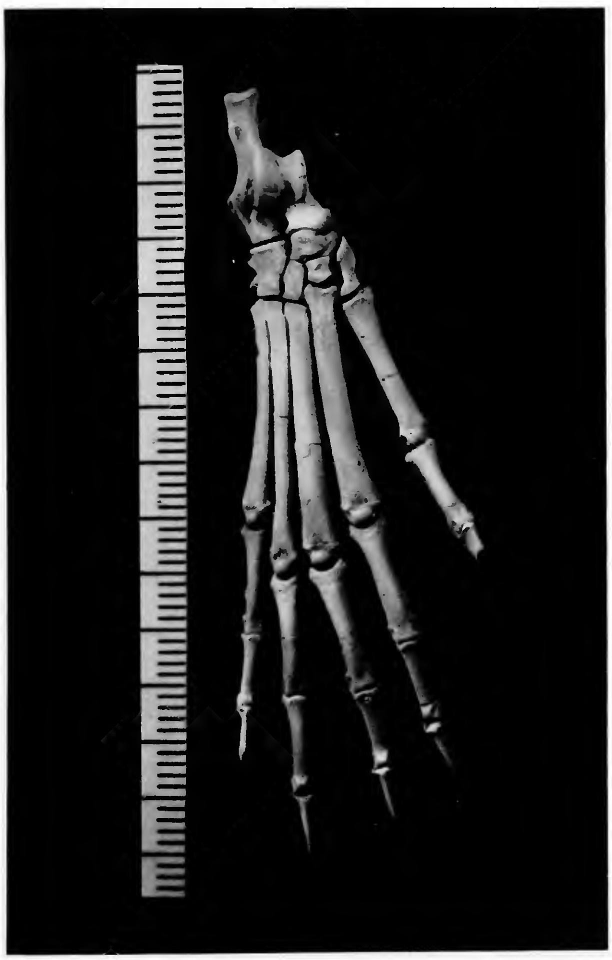

FIGURE 16.—Right rear foot of *Protosciurus*, USNM 243981, in dorsal view. (Approximately × 1.5; scale in mm.)

The phalanges of *Protosciurus* are virtually identical in proportions and details of construction (such as the position and strength of the ventral processes for insertion of tendons of the digital flexors) to the same bones of *Sciurus*. The distal phalanges (claws) of *Protosciurus* are sickle shaped, transversely compressed, deep dorsoventrally, and quite curved. The phalanges of *Spermophilus* are significantly shorter and stouter, the distal ones being straighter and broader in cross section.

INTERPRETATION OF THE FOOT.—In the bones of the foot, *Protosciurus* exhibits an interesting constellation of characters, some like those of North American tree squirrels and others like those of North American ground squirrels. When a tree squirrel descends a tree head first, it extends and inverts its foot so that the toes point back up the tree. This involves extreme extension at the tibio-astragalar joint and "rotation" at the subastragalar joints. The shapes of these articular surfaces in *Protosciurus* are more similar to those of ground squirrels than to those of the tree squirrels of the tribe Sciurini. In these characters, however, it would appear that the Sciurini exhibit highly derived tree-squirrel characteristics, which are not shared by all tree squirrels. For example, the Asiatic giant squirrels, *Ratufa*, retain the groove of the plantar surface of the astragalus, between the medial and posterior calcaneal facets, as seen in *Protosciurus*. This groove contains loose connective tissue except at its posterior end, where there is a strong astragalo-calcaneal ligament. Separated by this groove, each facet appears to be part of an independent synovial joint. The loss of the groove appears to result from the coalescence of the two facets into one continuous synovial joint, probably associated with increased mobility between the astragalus and the calcaneus, but as *Ratufa* demonstrates, this is not an obligatory characteristic for tree squirrels. Similarly, the tree squirrels of Africa (*Protoxerus*, *Heliosciurus*, and *Funisciurus*) and *Callosciurus* of Asia are not as extreme as the Sciurini in their specializations in these joints. Members of the Sciurini exhibit the most extreme saddle joints between the astragalus and the navicular bones and the greatest posterior extension on the astragalus at the tibio-astragalar joint. Therefore we interpret the similarity of the joint morphology between *Protosciurus* and the Marmotini as retention of primitive characters in the latter, not as a demonstration that *Protosciurus* was a terrestrial squirrel.

The proportions of the foot bones, like the proportions of the limb bones, are quite similar between *Protosciurus* and tree squirrels. Relatively shorter metatarsals seem to be characteristic of ground squirrels—both Holarctic and African—and shorter feet tend to be characteristic of terrestrial vs. arboreal rodents generally. Thus, it seems most likely that *Protosciurus* was a tree squirrel, that it was remarkably like modern tree squirrels in its proportions and long bone morphology, but that it was clearly primitive in details of its foot morphology, and that many recent tree squirrels are more specialized in these characters for arboreal locomotion than was *Protosciurus*.

The relative lengths of the calcaneus and cuboid to the fourth metatarsal are similar in *Sciurus* and *Protosciurus* and different from *Spermophilus* and *Cynomys* as shown in Table 2. Compared with the length of the fourth metatarsal, the first two metatarsals are short in *Protosciurus*. The first phalanges of the first four toes are similar in proportion to the length of the fourth metatarsal in *Sciurus* and *Protosciurus*. Because the metatarsals are short in *Spermophilus*, the first phalanges are long in proportion. In *Cynomys* the first phalanges are proportioned to the fourth metatarsal as in the tree squirrels, even though the metatarsals are short. Thus *Protosciurus* had a foot proportioned very much like that of *Sciurus*, except that it had shorter metatarsals on the first and second digits.

The foot of *Protosciurus* differs in many respects from that of *Paramys* and the other paramyids in which feet are known. The paramyid foot is considerably more robust than in *Protosciurus* and modern *Sciurus*. In *Paramys* the astragalus is much blockier, with a shorter neck and a broad relatively flat head with uniformly convex navicular articulation facet. The navicular of *Paramys* is

TABLE 2.—Ratios showing relative lengths of foot bones in various sciurids and *Paramys* (boxed numbers indicate important differences)

Ratio	Sciurus niger N = 5	Sciurus carolinensis N = 3	Sciurus griseus N = 3	Protosciurus jeffersoni N = 1	Spermophilus beecheyi N = 3	Cynomys ludovicianus N = 3	Paramys delicatus N = 1
Metatarsal 1/ metatarsal 4	.70	.71	.69	.61	.68	.62	.66
Metatarsal 2/ metatarsal 4	.94	.97	.94	.89	.97	1.02	1.03
Metatarsal 3/ metatarsal 4	.97	.98	.97	.96	1.00	1.04	1.00
Proximal phalanx 1/ metatarsal 4	.36	.36	.37	.35	.46	.39	.45
Proximal phalanx 2/ metatarsal 4	.47	.48	.48	.45	.56	.48	----
Proximal phalanx 3/ metatarsal 4	.46	.47	.46	.46	.55	.47	.56
Proximal phalanx 4/ metatarsal 4	.47	.49	.47	.47	.57	.47	.47
Calcaneus + cuboid/ metatarsal 4	.75	.73	.72	.73	.94	.92	1.01

narrower transversely, so that the first cuneiform defines the whole medial edge of the tarsus between the astragalus and first metatarsal. The contact of the astragalus and first cuneiform is much more extensive than in any modern squirrel (many of which do not have an astragalar facet at all on the first cuneiform). In *Paramys* the foot is quite symmetrical, centered around the third digit which is longest, as in the ground squirrels, and unlike *Protosciurus* and *Sciurus* which have a longer fourth toe. The foot of *Paramys* is broader not only because of the heavier proportions of the individual bones but in their orientation as well—the metatarsals diverge much more in *Paramys*, compared to the more nearly parallel arrangement of metatarsals two to five in *Protosciurus* (Figure 16) and *Sciurus*. The proportions of the phalanges of *Paramys* are more nearly like, perhaps even slightly stouter than, those of *Spermophilus*, compared to the slender gracile toes of *Protosciurus* and the sciurines. The distal phalanges (claws) of *Paramys* are broadly triangular in cross section and quite straight compared to the thin sickle-shaped claws of *Protosciurus* and the living tree squirrels.

Summary of Characteristics of the Limbs of *Protosciurus*

Viewed as a squirrel, *Protosciurus* was clearly more advanced in its postcranial skeleton than in its dental and some of its cranial features. The long bones of the forelimb closely resemble those of *Sciurus* in proportions and details of shape. The minor differences in muscle origins and insertions suggest that the forelimb of *Protosciurus* was slightly more powerful than that of *Sciurus* of the same size. The more prominent origin of the triceps, the more distal insertion of the brachialis, and the stronger insertion of ligaments at the elbow suggest that *Protosciurus* had stronger flexion and extension. It also probably had stronger pronation and supination, to judge from the more prominent supinator ridge and the distinct ulnar insertion of the pronator quadratus. *Protosciurus* was less robust in the forelimb than *Spermophilus beecheyi*, which perhaps indicates it was not a burrow-digging animal. It lacked the strong insertion of the infraspinatus, the broad insertion of the deltoid, and the strong medial humeral epicondyle, which characterize the recent North American ground squirrels and prairie dogs.

In the carpus the separate scaphoid and lunate represent the primitive rodent condition and have little significance except to suggest that fusion of these two bones in the Sciuridae was independent from that in other rodent groups. The metacarpals and phalanges most clearly resemble those of *Sciurus* but do have some features seen in the hand of *Spermophilus*. As a whole the hand was thin as in *Sciurus*, differing significantly from the shorter, broader hand of *Spermophilus*. The incompleteness of both fourth metacarpals precludes determining whether the fourth digit was longer than the third, as in arboreal squirrels, or the converse, as in ground squirrels.

In general, the hind limb of *Protosciurus* is remarkably similar to that of Recent *Sciurus*. In the hip, the shape of the ilium suggests that the gluteal musculature was much more like that of *Sciurus* than that of *Spermophilus*, and the orientation of the lesser trochanter suggests the same for the iliopsoas musculature. At the knee, the more distal insertion of the semitendinosus and the deeper popliteal fossa suggest that *Protosciurus* had stronger flexion at the knee and ankle than does *Sciurus*.

Except for the relatively shorter first metatarsal, and minor differences in the tarsus, the foot of *Protosciurus* is virtually that of *Sciurus* in all features, including proportions of the individual bones and their orientation. The astragalonavicular joint is not the concavo-convex saddle joint of the Sciurini, which are the most derived in this feature. It is similar to that of other (callosciurine and paraxerine) tree squirrels, however, and differs slightly from that of ground squirrels. The fourth digit of the foot of *Protosciurus* is longer than the third, as in the modern arboreal squirrels, and unlike the ground squirrels in which the third is longer.

Table 3 illustrates the similarity of *Protosciurus*

TABLE 3.—Lengths and ratios of lengths of the long bones of *Protosciurus* compared with those of the extant fox squirrel *Sciurus niger*

Bone/Ratio	Sciurus niger	Protosciurus	Significance
Bone			
Humerus	51.2 ± 3.4	48.8	n.s.
Radius	48.4 ± 3.7	45.6	n.s
Femur	65.2 ± 4.9	63.8	n.s.
Tibia	73.4 ± 6.0	67.8	n.s.
Ratio			
Radius/ Humerus	.936 ± .021	.934	n.s.
Tibia/ Femur	1.122 ± .018	1.063	p<.01
Humerus/ Femur	.791 ± .015	.765	n.s.
Radius/ Tibia	.655 ± .017	.673	n.s.
Intermembral*	.722 ± .010	.717	n.s.

*Radius + Humerus / Femur + Tibia

to *Sciurus niger* in size, in the relative proportions of upper and lower limb elements, and in forelimb versus hind limb lengths. When these statistics are compared to similar ones for *Paramys*, and other rodents, given by Wood (1962:28), the similarity between *Protosciurus* and *Sciurus* is further emphasized. In *Paramys*, for example, the tibia is shorter than the femur, whereas the converse is true of *Protosciurus* and *Sciurus*. The hind limb of *Paramys* is significantly longer, relative to the forelimb, than it is in the squirrels.

Summary

Wood (1980:29) doubts that there are any certain North American Oligocene sciurids. This position is probably unassailable, given his definition of the Sciuridae, which states, among other conditions to be met, that the masseter lateralis anticus must have spread up along the side of the snout (i.e., that it must have achieved sciuromorphy). Wood (1980) regarded any protrogomorphous ancestor of the Sciuridae as belonging in the Ischyromyoidea. He continued to follow his 1962 assignment of *jeffersoni* to the genus *Cedromus*; but, whereas he placed *Cedromus* in the Paramyidae in 1962, he placed it in the family Aplodontidae of the superfamily Aplodontoidea in 1980. In this scenario, the species is not even a member of the superfamily that Wood believes includes the ancestors of the Sciuridae. Wood (1980:30) left the genus *Protosciurus* tentatively in the Sciuridae, though he believed it should be placed in the Paramyidae.

USNM 243981 is, quite clearly, closely related to, if not conspecific with, *Protosciurus jeffersoni*. It is protrogomorphous, which would exclude it from the Sciuridae as defined by Wood (1980), but it also has a number of derived characters that would make it a very unusual paramyid. For example, the incisors are more laterally compressed, the masseteric fossa of the mandible more anteriorly placed, and the fourth digit of the foot longer than the third. These nonparamyid features are characteristic of sciurids, although not unique to sciurids. There are, however, other nonparamyid characters of *Protosciurus* that do seem to be diagnostic of Sciuridae. These include the enlarged, septate, tympanic bulla tightly fused to the periotic; stapedial artery enclosed in a bony tube through the middle ear cavity; and the presence of a subscapular spine. Other unreported specimens of *Protosciurus jeffersoni* show that the skull is very broad interorbitally and that the frontals have relatively large postorbital processes like those of extant squirrels. These derived characters, occurring in a specimen with a postcranial skeleton that is virtually that of a modern arboreal squirrel, seem to us sufficient reason for placing it in the Sciuridae, in spite of its not having achieved sciuromorphy.

This specimen of *Protosciurus* suggests that, at least postcranially, some tree squirrels have changed very little since early Oligocene time. The postcranial skeletons of *Protosciurus* and *Sciurus* are so similar that *Protosciurus* tells us little more about the ancestry of squirrels than *Sciurus* does. The apparent lack of change since early Oligocene time is partly explained by the fact that squirrels are basically conservative rodents. They still retain the primitive rodent dental formula and show none of the loss or fusion of skeletal elements that characterize so many of the fossorial and saltatorial rodents, for example. The differences between *Protosciurus* and *Paramys* are many, but except for the few derived features of *Protosciurus* mentioned, the differences are quite subtle, being mainly in proportions. The limb elements of *Paramys*, and what we know of most other paramyids, are distinctly more robust than those of *Protosciurus*. Even the modern ground squirrels, which tend to have shorter and stouter limbs than arboreal squirrels, are more gracile than most of the paramyids. The differences that do exist between *Paramys* and *Protosciurus* are essentially the differences between *Paramys* and living squirrels and perhaps serve best to emphasize the extreme similarity between *Protosciurus* and living sciurines, particularly *S. niger*.

Black (1963), while noting that postcranial material was not known for any of the early squirrels, visualized the ancestral squirrels as being chipmunk-like. He noted that chipmunks are intermediate, both in their morphology and in their ecology, between the tree squirrels and the ground squirrels. In the postcranial characters observed during the course of the present study, we find that *Tamias* is intermediate not so much in the sense of having individual characters that are intermediate, but in having some ground squirrel characters and some tree squirrel characters. In the details of joint morphology and of muscle origins and insertions, for example, *Tamias* seems to be more like the ground squirrels; but in the proportions of its limbs and feet, *Tamias* is more gracile than the ground squirrels, or more nearly comparable to the tree squirrels. In its postcranial osteology, *Tamias* might be viewed as a ground squirrel that has acquired, or perhaps retained, the slender proportions most compatible with its semiarboreal habit. The slenderness of its limbs and feet may be due in part to its small size; the largest chipmunk is still smaller than most ground squirrels. In the few details of joint morphology in which *Protosciurus* is more like the ground squirrels than the tree squirrels, it also is more like *Tamias*, but as we have mentioned above, these characters are most likely primitive ones retained in all forms that have them and therefore of little value in phylogenetic reconstruction. The postcranial skeleton of *Protosciurus* is, in our view, more nearly comparable to that of the Sciurini than of the Tamiini.

Our comparisons would not support the view of Matthew (1910:52) that *Paramys* was "unmistakably adapted to an arboreal habitat." If *Par-*

amys was an arboreal rodent it was certainly not so specialized for arboreal locomotion as *Protosciurus* and the sciurines are. Our view would more nearly coincide with that of Wood (1962:27), who did not "feel quite so confident of there being any special arboreal adaptations, but it would seem probable that *Paramys* spent considerable periods of time on the ground as well as in the trees."

Leptotomus sciuroides is exceptional among the paramyids in having relatively slender limbs, tibia proportionately long compared to the humerus, and inflated auditory bullae, all characteristics which make it more squirrel-like (Wood, 1962:100). *Leptotomus sciuroides* has no particular dental similarities to *Protosciurus*, however, and also is characteristically primitive in its very pinched, narrow postorbital region and in having the anterior edge of the masseteric fossa beneath the posterior edge of M_2. Wood (1962) was probably correct in concluding that *L. sciuroides*, in spite of its slender limb proportions, is not so close to the ancestry of the Sciuridae as some of the other paramyids may be.

There seem to be no features of *Protosciurus* to suggest that it could not have been derived from within the Paramyidae, but the derivation of squirrels from the Paramyidae has long been accepted with little dissension. There has been disagreement, as Wood (1980:29) pointed out, as to the precise source within the Paramyidae (Black, 1963:229, 230; Bryant, 1945:264, 265; Wilson, 1960:64; Wood, 1962:116, 117). USNM 243981 sheds very little additional light on the problem.

To sum up, USNM 243981 is closely related to, or is, *Protosciurus jeffersoni.* Whether this species should be placed in a different genus, perhaps in *Cedromus* or perhaps in a new genus, is a question that is not answered herein and is incidental to this report. Of more importance here is that it can be clearly recognized as a squirrel, that it was almost certainly a tree squirrel, with postcranial morphology, and presumably habits, very similar to those of the extant arboreal squirrels of the tribe Sciurini. We place it in the Sciuridae on the basis of several derived characters that appear to be diagnostic of the family. Its protrogomorphy is a primitive rodent feature, saying nothing of relationships, and should not exclude it from the family Sciuridae. The retention of this primitive character state in an early member of the family does suggest, however, that, of the several groups of rodents that independently attained complete sciuromorphy (sciurids, geomyoids, and castorids), the last to do so may have been the group from which the condition derives its name.

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