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THE SKULL OF *SCIURAVUS NITIDUS*, A MIDDLE EOCENE RODENT

MARY R. DAWSON
SMITH COLLEGE, NORTHAMPTON, MASS.

Primitive rodents of the family Sciuravidae are known primarily from the Eocene of western North America, with the genus *Sciuravus* itself ranging from late early Eocene (Gazin, in press) through the late Eocene (Wilson, 1949b, pp. 81-82). The type specimen of *Sciuravus nitidus* Marsh, 1871, the type species, is an incomplete maxilla with M^{1-3} from the middle Eocene Bridger formation of Wyoming. The type specimen is from the lower Bridger, but specimens referred to *S. nitidus* occur throughout the Bridger formation (Wilson, 1938, pp. 130-132). The skull of *S. nitidus* was described briefly by Matthew (1910, pp. 59-60). More recent collections from the Bridger have yielded more complete specimens of this species than were available to Matthew. These specimens allow an amplified description to be made of the skull of *S. nitidus*, the only Bridger sciuravid whose essentially complete skull is known.

ACKNOWLEDGEMENTS

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Sciuravus nitidus; to Drs. J. T. Gregory and E. L. Simons for access to the collections and for facilities for study in the Yale Peabody Museum (Y.P.M.); to Drs. C. C. Black of the Carnegie Museum (C.M.) and M. C. McKenna of the American Museum of Natural History (A.M.N.H.) for the loan of specimens. Plates I, III, IV, and V, figure 1 are prepared from photographs furnished by courtesy of the Smithsonian Institution, and plate V, figure 2 is from a photograph by J. Howard, Yale Peabody Museum. This study, supported by National Science Foundation Grant G14254, was completed while the author was a Research Associate of the Division of Vertebrate Paleontology, Yale Peabody Museum.

DESCRIPTION

The following description of the skull and lower jaw of *Sciuravus nitidus* is based in large part on U.S.N.M. No. 22477, a nearly complete skull with associated lower jaw and postcranial fragments from near Millersville, Wyoming. The specimen was collected by C. L. Gazin and F. L. Pearce in 1946. The skull is distorted by some anteroposterior compression and the left side is pushed forward relative to the right. Tooth wear indicates that the individual was adult. Other specimens used are: U.S.N.M. No. 18100, partial skull and jaws of a young individual having dP^4; A.M.N.H. No. 12551, skull flattened dorsoventrally and jaws figured by Matthew (1910, figs. 13-15); A.M.N.H. Nos. 12531 and 13101, partial skulls. Less complete specimens include Y.P.M. No. 13458, C.M. No. 9683, U.S.N.M. Nos. 17697 and 17700. All specimens are from the lower Bridger.

Skull. The overall appearance of the skull is that of a rather generalized, primitive rodent. Postmortem distortion of the specimens prevents an entirely clear picture of the skull shape. Thus, the doming of the parietals in U.S.N.M. No. 22477 is due at least in part to anteroposterior compression, A.M.N.H. No. 12551 is flattened dorsoventrally, U.S.N.M. No. 18100 and A.M.N.H. No. 13101 are compressed transversely.

Viewed dorsally (pl. I) the skull widens from the anterior tips of the nasals to the anterior zygomatic roots, has its greatest width across the zygomatic arches, which essentially parallel one another, and is narrower posterior to the arches. The nasals are slightly convex dorsally, especially anterodorsally, and extend farther forward than the anterior surface of the incisors. The nasals terminate posteriorly about on a line with the anterior orbital border. The frontals exhibit a distinct interorbital constriction, anterior to which there is a protrusion on each side possibly similar to the "rudiments of processes" in *Pseudocylindrodon* (Burke, 1938, p. 260). The protrusion is less in evidence in A.M.N.H. No. 12551 and U.S.N.M. No. 18100 than in U.S.N.M. No. 22477. The large interparietal, shown in Nos. 12551 and 18100, has a convex anterior margin and widens posteriorly. Lateral to it the parietal extends to the occipital bone. There is no sagittal crest. The squamosal is incomplete in all specimens but seems to have had a narrow dorsal exposure. The occipital bone extends onto the dorsal skull surface for a very short distance, and the nuchal crest on that bone forms the posterodorsal margin of the skull.

Maxillary, jugal, and squamosal components form the zygoma. The jugal contacts the maxilla and lacrimal anteriorly, tapers posteriorly, and terminates bluntly below the posterior edge of the zygomatic process of the squamosal.

The anterior surface of the anterior zygomatic root is essentially vertical and is in a line anterior to P^3 (pls. III, IV). The root is farther forward relative to the cheek teeth than in *Paramys delicatus* (Matthew, 1910, fig. 2). The rounded infraorbital foramen, which is situated in the maxilla medial to the anterior zygomatic root, is relatively a little larger than in *Aplodontia*. From a ventromedial knob of bone on the anterior root a ridge passes laterad, curves backward and upward onto the lateral surface of the jugal, and continues toward the posterior end of that bone, diminishing posteriorly. As preserved in U.S.N.M. No. 22477, the outer surface of the zygoma faces laterally above and ventrolaterally below the ridge. The origin of the masseter muscle seems to be limited to the zygoma, the "primitive sciuromorph" or "protrogomorph" condition. There is no indication that any of the masseter muscle originated on the rostrum anterior to the anterior zygomatic root. The ridge on the zygoma probably marks the dorsal edge of the origin of the masseter lateralis muscle. That the anterior part of the masseter may have been strengthened is suggested by the ventromedial knob and the ridge, which is more distinct anteriorly.

The orbit is moderately good-sized, about comparable in proportions to that in *Cavia* but relatively smaller than in *Cynomys*. The lacrimal bone forms part of the anteromedial orbital border. The surface of this bone is lightly pitted where it extends onto the face anterior to the orbit. The most complete orbital wall occurs in U.S.N.M. No. 18100, although cracking obscures details. The frontal forms most of the anteromedial orbital wall. Near the dorsal rim of the orbit and posterior to the supraorbital protrusion is a small foramen. The sphenopalatine foramen (terminology of foramina follows Hill, 1935) is ventromedian in the orbit, approximately in line with M^2, and is bounded anteriorly, dorsally, and ventrally by the maxilla. Boundaries of the palatine bone are not clear, and either this bone or the maxilla borders the sphenopalatine foramen posteriorly. Several foramina are present in the maxilla posterolateral to the sphenopalatine foramen. A plate of bone posterior to the maxilla and frontal in the orbit seems to be the orbitosphenoid. More posteriorly, in a line behind M^3, the posteromedial orbital wall is depressed and overhung by more dorsal parts. A dorsoventrally elongated slit in the depression may be the sphenoidal fissure. The alisphenoid borders the slit posterolaterally. Anterodorsal to the slit and partly separated from it by a bony bar is a rounded gap. It is suggested tentatively that the optic foramen may be in the gap. Parietal and squamosal form part of the posterior wall of the orbit.

On the palate (pls. II, III) the elongate incisive foramina are separated from one another by a median septum and are within the premaxilla except posteriorly, where they are bounded by the maxilla. A slight concavity of the maxilla occurs anterior to P^3. The two rows of teeth essentially parallel one another. Between them the palate is nearly flat.

The palatine extends forward about to a line with the anterior or middle of M^1, where the jagged maxilla-palatine suture crosses the palate transversely. The foramen for the palatine artery is present approximately in line with the anterior half of M^2. The posterior margin of the palate, about opposite the middle of M^3, has a posteriorly directed median projection, on each side of which a small flange of bone projects anteroventrally below the palatal surface.

The region of the pterygoid plates is incompletely preserved in all specimens but can be reconstructed in part. A ridge extends posterad from behind M^3, becomes thicker, and leads into entopterygoid and ectopterygoid plates. A shallow pterygoid fossa is enclosed by the plates. The specimens suggest that the entopterygoid plate lacked a contact with the bulla, but the ectopterygoid plate continues posteriorly and contacts the lateral side of the bulla. In *Paramys delicatus* (Matthew, 1910, fig. 2) the ectopterygoid plate is absent, and the pterygoid fossa is less distinct than in *S. nitidus.* A small foramen between the plates in A.M.N.H. No. 12551 may represent the posterior opening of the sphenopterygoid canal. Posterolateral to this foramen is a second foramen, probably the foramen ovale. The ectopterygoid plate forms a bridge across this foramen, which resembles the foramen ovale in *Paradjidaumo* (Wilson, 1949a, pp. 38-39 and fig. 1C) and in *Cynomys.* The position of another foramen is indicated by a notch in the basisphenoid at the anteromedial edge of the tympanic bulla.

The tympanic bulla in *Sciuravus nitidus* is ossified but seems to have been loosely attached. Out of seven otic regions, in U.S.N.M. Nos. 22477 and 18100 and A.M.N.H. Nos. 12531 and 12551, the bulla is in place in two cases, on one side in Nos. 22477 and 12531. A suture seems to be traceable between bulla and periotic, and where the bulla is missing there is no clear broken area on the periotic. The rounded bulla is not dissimilar in general appearance to that in *Neotoma.* The bulla has a large opening but lacks an elongated bony meatus. The anterodorsal lip of the opening is thickened. The bulla in A.M.N.H. No. 12531 may have been incomplete dorsally, and a process of the squamosal curves down over this possibly incomplete closure. Viewed ventrally, the bulla has a short anteromedial protrusion. The bulla does not completely cover the petrosal, which is exposed medial to the bulla. A somewhat similar exposure of the petrosal has been reported in *Paradjidaumo* (Wilson, 1949a, p. 39). Where absence of the bulla exposes the periotic, the auditory prominence appears as a distinct, raised structure. The fenestra vestibuli faces dorsolaterally and the fenestra cochleae posterolaterally. The mastoid process is short and blunt, and the stylomastoid foramen seems to be represented by a notch medioventral to the process.

Between the bullae the basioccipital exhibits a distinct longitudinal ridge. The elongate jugular foramen is between basioccipital and periotic, posteromedial to the bulla. The hypoglossal foramen pierces the condyle posterior and medial to the jugular foramen.

The occipital surface (pl. V, fig. 1) is convex dorsally. The nuchal crest leads into two ridges, one on the lateral surface of the mastoid and the other along the mastoid-exoccipital contact. The mastoid is exposed on the occipital surface near the dorsal part of the latter ridge. The short paroccipital process does not contact the bulla.

Lower jaw. On the lateral surface of the horizontal ramus (pl. IV) a large mental foramen is present about in line with the anterior wall of P_4. A smaller foramen or foramina occur slightly farther posteriorly. The masseteric fossa is bounded by dorsal and ventral ridges that meet in a line approximately between M_1 and M_2. The masseteric fossa in *Paramys delicatus* does not extend so far anteriorly (Matthew, 1910, fig. 1). The nearly complete lower jaw of C.M. No. 9683 shows that the coronoid process rises steeply and hooks backward toward the lower condyloid process. The lateral surface of the coronoid process is slightly concave for the insertion of the temporalis muscle. On the medial surface of the jaw (pl. V, fig. 2) a ridge extends posterodorsad from the posterior end of the row of cheek teeth toward the condyle. The dental foramen is in the dorsal side of the ridge, approximately in a line below the posterior edge of the coronoid process. Ventral to the ridge is the concavity for insertion of the internal pterygoid muscle; unfortunately, the area for pterygoid insertion is not completely preserved in any of the specimens. A slight concavity dorsal to the ridge on the condyloid process probably marks the insertion of the external pterygoid muscle.

Measurements (in millimeters) of U.S.N.M. No. 22477:

Greatest length of skull	39.4
Anterior width across zygomatic arches	21.5
Posterior width across zygomatic arches	22.2
Height occiput	12.8
Length diastema, posterior of I to P^3	8.1
Length right P^3-M^3	9.6
Length left P_4-M_3	9.5
Outside depth of lower jaw at M_1	6.2

DISCUSSION

Sciuravids have been suggested, mostly on the basis of dental characters, as possible ancestors for various later rodent groups including muroids and geomyoids (Wilson, 1949a, p. 47, 1949b, pp. 97-98; Wood, 1959, p. 358). As described here the skull of *Sciuravus nitidus* does not seem to add much in the way of positive evidence on relationships. Primitive features include the large jugal, zygomasseteric structure, seemingly shallow pterygoid fossa, ossified but loosely attached bulla, short paroccipital processes. The incomplete medial covering of the petrosal by the bulla may also be primitive, a feature that *S. nitidus* shares with *Paradjidaumo*, an eomyid. The masseter muscles may have been somewhat better developed for gnawing than in some contemporary paramyids, such as *Paramys delicatus*. This is suggested by the more anterior position of the anterior zygomatic root and of the mandibular masseteric fossa, and by the distinct anterior knob and ridge on the zygoma. A more distinct pterygoid fossa than in *P. delicatus* suggests some strengthening of the pterygoid muscles as well. The zygomasseteric structure is still, however, that of a primitive sciuromorph. Whether the indications of muscle strengthening show that the sciuravids were experimenting along lines leading toward more advanced zygomasseteric conditions remains a matter of speculation. At any rate, the skull of *S. nitidus* seems to lack any specializations countering the suggestions that sciuravids gave rise to some of the advanced rodent groups.

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Plate I

Dorsal view of skull of *Sciuravus nitidus*, U.S.N.M. No. 22477, approx. x 3.

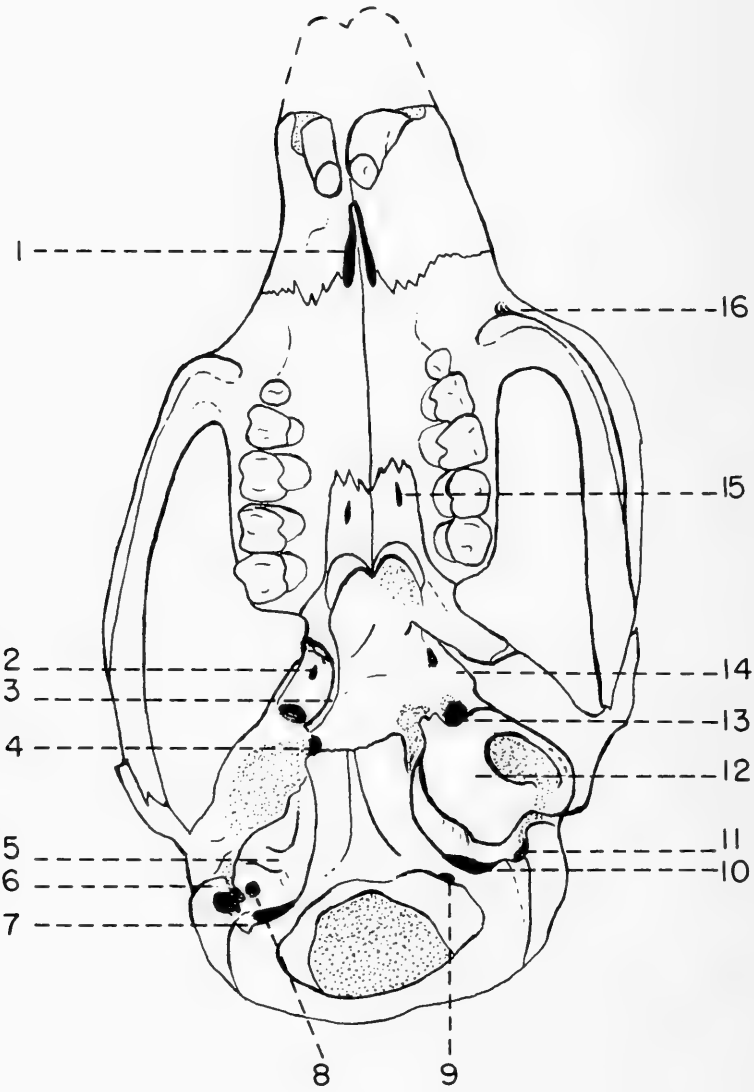


Plate II

Ventral view of skull of *Sciuravus nitidus,* approx. x 3. Based on U.S.N.M. No. 22477; restored in part from A.M.N.H. Nos. 12551 and 12531. 1, incisive foramen; 2, sphenopterygoid foramen; 3, entopterygoid plate; 4, foramen in basisphenoid; 5, auditory prominence; 6, mastoid process; 7, paroccipital process; 8, fenestra cochleae; 9, hypoglossal foramen; 10, jugular foramen; 11, stylomastoid foramen; 12, tympanic bulla; 13, foramen ovale; 14, ectopterygoid plate; 15, foramen for palatine artery; 16, infraorbital foramen.

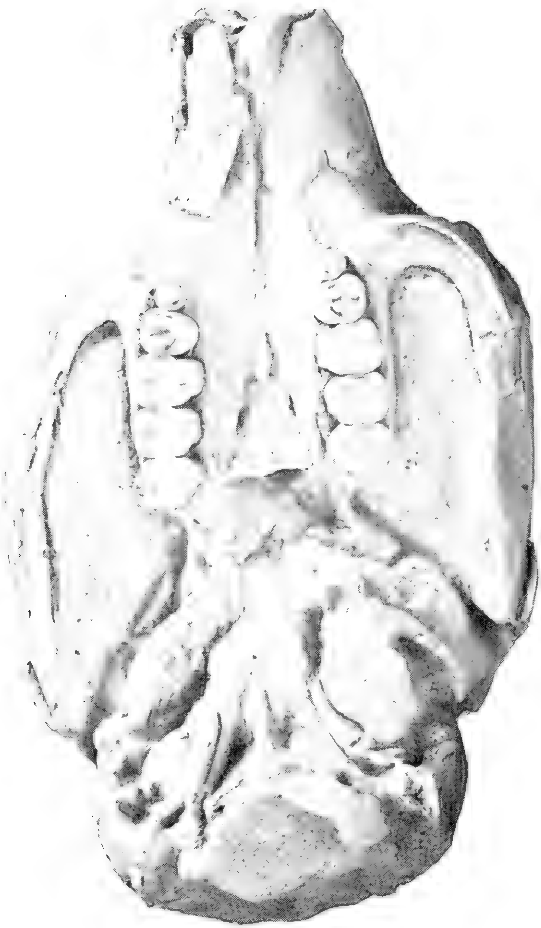
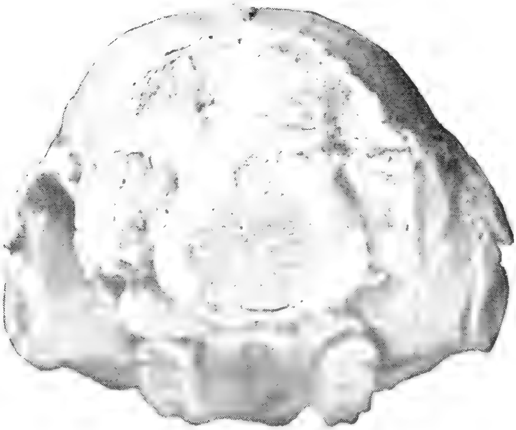


Plate III

Ventral view of skull of *Sciuravus nitidus,* U.S.N.M. No. 22477, approx. x 3.



1

2

Plate IV

Lateral view of skull and lower jaw of *Sciuravus nitidus,* U.S.N.M. No. 22477, approx. x 3.

Plate V

Sciuravus nitidus, approx. x 3. Figure 1. Occipital view of skull, U.S.N.M. No. 22477. Figure 2. Medial view of right lower jaw, C.M. No. 9683.

Date Due