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The Cranial Anatomy of *Cricetops dormitor*, an Oligocene Fossil Rodent from Mongolia

MARC A. CARRASCO[1] AND JOHN H. WAHLERT[2]

ABSTRACT

A description of the cranial, mandibular, and dental morphology of *Cricetops dormitor*, an Oligocene muroid rodent, is presented. *Cricetops* exhibits a unique combination of primitive muroid characters (e.g., the presence of a large hystricomorphous infraorbital foramen) and derived muroid characters (e.g., a prominent metacone in the upper third molar) that cloud its taxonomic affiliations. In addition, *Cricetops dormitor* lacks many characters, including a highly inclined zygomatic plate, that have been used to unite members of the family Muridae. Overall, these results suggest that the phylogenetic position of *Cricetops* within the Muroidea needs to be reevaluated.

INTRODUCTION

The 1922 and 1925 expeditions to Mongolia of the American Museum of Natural History revealed an extremely diverse and large mammalian fauna in the Hsanda Gol Formation (Mellett, 1966, 1968). The dominant species of this fauna, accounting for more than one-third of the recovered specimens, was the muroid rodent *Cricetops dormitor*. Most *Cricetops* specimens were isolated upper and lower jaws, but several partial and complete skulls were also found (Matthew and Granger, 1923; Mellett, 1966). The more recent 1991–1997 American Museum Expeditions to Mongolia recovered not only several hundred upper and lower jaws, but more importantly, more than ten partial and complete skulls of *C. dormitor*.

Despite the wealth of specimens from the 1922 and 1925 expeditions, no detailed study

[1] Ph.D. Candidate, Division of Paleontology, American Museum of Natural History.
[2] Research Associate, Division of Paleontology, American Museum of Natural History; Professor of Biology, Baruch College, City University of New York; member of doctoral faculty, CUNY Ph.D. program in biology: ecology, evolutionary biology, and behavior subprogram.

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of *C. dormitor* has been done. The original description and diagnosis (Matthew and Granger, 1923) included an illustration of a dentition and partial skull of the species (redrawn in fig. 1), but lacked any detailed description. For his doctoral dissertation, Mellett (1966) described the fauna from the Hsanda Gol Formation, emphasizing *Cricetops*, but his study did not include clear illustrations of the genus. In addition, his results remain unpublished. Other brief dental (Schaub, 1925; Kowalski, 1974; Wahlert, 1984), mandibular (Repenning, 1968), cranial (Lindsay, 1977; Flynn et al., 1985), and general (Vorontsov, 1982) descriptions have been published on *Cricetops*. Only Wahlert's work (1984) on dentition provided detailed illustrations and descriptions of this species. Given the wealth of old as well as new cranial specimens of *C. dormitor*, an amplified description of its skull and mandible can be made.

The taxonomic history of *Cricetops* was summarized in Wahlert (1984). Traditionally, the genus has been placed in the Muroidea and associated with the Cricetidae. McKenna and Bell (1997) placed *Cricetops* and *Enginia* (Bruijn and Koenigswald) in its own murid subfamily, Cricetopinae. On the basis of dental similarities, Wahlert (1984) proposed that *Cricetops* and the living African rodent *Lophiomys* were sister taxa. This hypothesis was disproved by Aguilar and Thaler (1987) who described *Protolophiomys* from the Upper Miocene of Spain. The skull has a broadened, pebble-textured roof as in *Lophiomys*. However, the buccal and lingual cusps of the upper molars do not form transverse, bicusped ridges with enclosed basins, and the anteroloph in M1 is not as strongly developed as in *Cricetops* and living *Lophiomys*. Thus the similarities of the dentitions in these genera were acquired independently. Subsequently, Aguilar and Michaux (1989–1990) described a Pliocene *Lophiomys* from Morocco; it, too, does not have the strongly bicusped lophs of the living species.

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TABLE 1
Cranial Dimensions of *Cricetops dormitor* MAE 91-1965 (millimeters)[a]

LENGTH	
Condylobasilar (est)[b]	46.7 (AMNH 21660)[c]
Diastemal	14.1
Incisive foramen	10.6
Palatal	23.3
Pterygoid (est)	6.8 (AMNH 21660)
WIDTH	
Anterior palatal	5.6
Posterior palatal	6.2
Interorbital	6.5
Mid-frontal	7.1
Zygomatic (est)	29.9 (MAE 91-70)
Posterior cranial (est)	19.3

[a] See Measurements section for definitions of dimensions.
[b] Estimated measurements.
[c] Alternative specimen used.

MATERIALS AND METHODS

Illustrations were drawn using a Nikon microscope with a camera lucida. Alignment of specimens (both cranial and mandibular) was done with the occlusal plane parallel to the plane of the page in ventral and dorsal views and perpendicular to this plane in side view. The mandible was drawn in life position and not flat on the microscope stage.

Terminology for muscles follows that of Klingener (1964) and Repenning (1968). Names for the bones and cranial foramina were taken from Wahlert (1985) and Wahlert et al. (1993) except for some terms of the auditory region, which were taken from MacPhee (1981). The dental terminology follows that of Reig (1977) with the modifications proposed by Wahlert (1984).

Measurements

Cranial and dental dimensions of *Cricetops dormitor* are presented in tables 1 and 2. All measurements were taken to the nearest 0.1 mm with a Nikon SMZ-U stereoscope (cranial dimensions) or Helios dial calipers (dental dimensions). Because no specimen

TABLE 2
Dental Dimensions of Type Specimens of *Cricetops dormitor* AMNH 19054 (millimeters)

	Upper Right	Lower Right
LENGTHS		
Incisor (depth)	2.8	2.8
Molar toothrow	9.7	9.6
First molar	4.2	3.5
Second molar	2.9	3.0
Third molar	2.6	3.1
%Toothrow Length		
First molar	43%	36%
Second molar	30%	31%
Third molar	27%	32%
WIDTHS		
Incisor	2.3	2.0
First molar		
anteroloph	2.3	—
protoloph/metalophid	2.6	2.1
metaloph/hypolophid	2.6	2.3
Second molar		
protoloph/metalophid	2.6	2.5
metaloph/hypolophid	2.5	2.5
Third molar		
protoloph/metalophid	2.4	2.6
metaloph/hypolophid	2.1	2.4

was completely preserved, some measurements in table 1 were taken from additional specimens, as noted. All dental measurements in table 2 were taken using the type specimen, AMNH 19054.

In table 1, condylobasilar length is the distance between lines tangent to the posterior edges of both the incisor alveoli and the occipital condyles. Diastemal length is the shortest line between the posterior margin of the incisor alveolus and the anterior margin of the upper first molar. Palatal length is measured from a line tangent to the back of the incisor alveoli to the most posterior point of the palatine bones along their midline. The shortest distance between the posterior edge of upper third molar and the anterior rim of the foramen ovale is the pterygoid length.

Anterior and posterior palatal widths are the shortest distance between the alveoli of upper first and third molars, respectively. Interorbital width is the minimum expanse between the two orbits. Midfrontal width is the distance across the dorsal roof of the frontals at their anteroposterior midpoint. The maximum breadth across the zygomatic arches is the zygomatic width. The posterior cranial width is the distance between the most medial portions of the posterior zygomatic roots of the squamosal.

Specimens Examined

All specimens examined are from the Department of Vertebrate Paleontology of the American Museum of Natural History (AMNH) or the Mongolian–American Expeditions (MAE).

Cricetops dormitor: Skull material: MAE 91-70, 91-397, 91-441, 91-1965, below lava, Tatal Gol; MAE 91-174, 91-312, 91-471, below lava, West of Camp Hill #1, Tatal Gol; MAE 91-221, E of camp, below lava, Tatal Gol; MAE 95-60, NE of camp, Below lava, Tatal Gol; MAE 93-5, Dike Loc., Tatal Gol; AMNH 19046, 21660, 85325, 85324, Loh; AMNH 19049, 19054 (holotype), 19055, 107650 (an isolated petrosal), Tatal Gol (= "Grand Canyon" or 10 mi W of Loh). Lower dentitions: MAE 91-221, E of camp, below lava, Tatal Gol; MAE 91-441, 91-731, 91-735, below lava, Tatal Gol; AMNH 19054 (holotype), 84356, 84588, 84698, 84727, Tatal Gol; 19051, 19059, 81307, 85324, Loh; AMNH 82195, 15 mi E of Loh. All specimens are from the early Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia.

CRANIAL ANATOMY

Figures 1, 2

Dorsal View

The nasals narrow posteriorly until they meet the frontal in a W-shaped suture that is medial to the posterior edge of the anterior zygomatic root and a little farther back than the premaxillae; anteriorly, they overhang the front of the snout. An internasal element is present in two specimens, the type and MAE 91-1965. Lateral to the premaxilla/nasal suture, a ridge on the premaxillary bones runs anteroposteriorly along the laterodorsal edge of the rostrum. It appears to mark the upper boundary of the masseter medialis pars anterior that passed through the large infraorbital foramen. Dorsomedial to the zygomatic

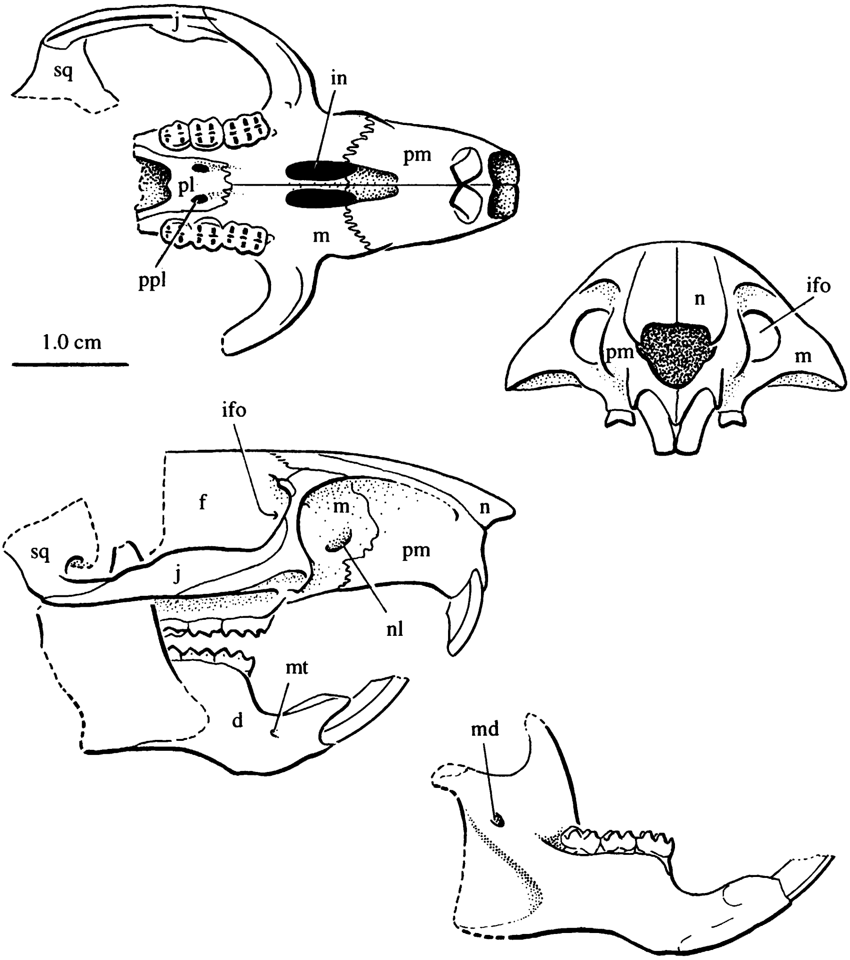

Fig. 1. Type specimen of *Cricetops dormitor* (AMNH 19054). AMNH 85324 was used to restore processes of the lower jaw.

Abbreviations for bones: **as** alisphenoid; **bo** basioccipital; **bs** basisphenoid; **d** dentary; **f** frontal; **ip** interparietal; **itn** internasal; **j** jugal; **l** lacrimal; **m** maxilla; **mst** mastoid; **n** nasal; **oc** occipital; **os** orbitosphenoid (not labeled); **p** parietal; **pl** palatine; **pm** premaxilla; **sq** squamosal.

Abbreviations for foramina: **aaf** anterior alar fissure (not labeled); **ac** alisphenoid canal; **bu** buccinator; **dpl** dorsal palatine; **dr** dorsal rostral; **eth** ethmoid; **fo** foramen ovale; **hy** hypoglossal; **ifo** infraorbital; **in** incisive; **ito** interorbital; **md** mandibular; **mlf** middle lacerate; **msc** masticatory; **mt** mental; **nl** nasolacrimal; **op** optic; **pgl** postglenoid; **plf** posterior lacerate; **ppl** posterior palatine; **sf** sphenofrontal; **spl** sphenopalatine; **t** temporal; **trc** transverse canal.

root, the premaxilla forms an anterolaterally directed, zigzag suture with the frontal; after the suture meets the maxilla at the anterior edge of the zygomatic root, it turns ventrally and runs down the lateral side of the rostrum anterior to the infraorbital foramen. A small projecting piece of the lacrimal bone can be seen at the posterodorsal edge of the anterior root of the zygomatic arch.

The frontals extend from a suture with the parietal at the back of the orbit anteriorly to the posterior ends of the nasals, where they curve laterally along the posterior edge of the premaxillae and terminate dorsal to the middle of the anterior zygomatic root. The pronounced interorbital constriction is greatest posterior to the middle of the frontals. A sagittal crest occurs along the posterior half of

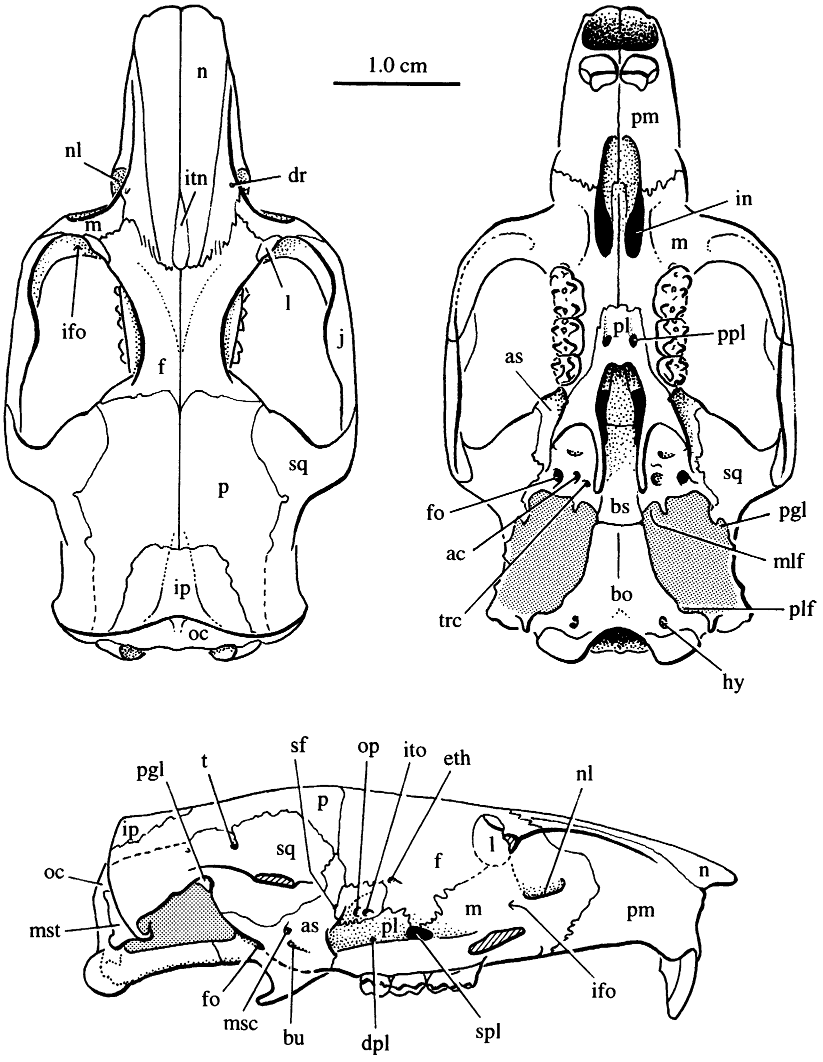

Fig. 2. Composite skull of *Cricetops dormitor* based on AMNH 19054, AMNH 21660, and MAE 91-1965. In lateral view, the zygomatic arch has been removed to expose the orbit. See the caption of figure 1 for abbreviations.

the frontals; the crest bifurcates anteriorly about mid-orbit into two orbital ridges that continue anterolaterally and end at the posterior edge of the anterior zygomatic root. Posteriorly the sagittal crest runs to the interparietal, where it diminishes and splits into two small ridges that continue across the interparietal and terminate at the nuchal crest (in one specimen [MAE 91-471] the sagittal crest does not split and is still prominent across the interparietal). The presence of a median crest indicates that the temporalis muscles were large.

The parietals overlap the posterior edges of the frontals; the suture of each runs anterolaterally from a point on the sagittal crest medial to the anterior edge of the posterior zygomatic root. The suture curves sharply ventrally at the back edge of the orbit. The parietals are bordered laterally by the squamosal bones, posteromedially by the interparietal, and posterolaterally by the occipital at the nuchal crest. The interparietal meets the occipital along the nuchal crest and extends laterally only about halfway along the crest.

Lateral View

The rostrum tapers anteriorly. The diastema is relatively flat until it curves sharply ventrally at the posterior edge of the upper incisors. A bulge, produced by the incisor root, extends across the lateral side of the premaxilla and terminates behind the anterior edge of the maxilla, medial to the nasolacrimal foramen. The premaxilla occupies more than half of the lateral surface area of the rostrum.

The maxilla extends from about the middle of the rostrum to an area posterior to M3. It forms the anterior zygomatic root and most of the anterior portion of the zygomatic arch. The orbital edge of the maxilla is a suture between the maxilla and frontal that starts at the lacrimal bone, descends posteriorly, and begins to zigzag as it approaches the sphenopalatine foramen; posterior to the foramen, the suture continues in a straight line between the maxilla and the more medial palatine to a point behind M3.

The lacrimal bone is in the most posterodorsal portion of the anterior zygomatic root; because of its fragile nature, the lacrimal is only partially preserved in some specimens. Somewhat oblong in shape, the lacrimal appears to extend from the dorsomedial wall of the infraorbital foramen to the posterodorsal tip of the zygomatic root. Anterior to the infraorbital foramen, a bulge and foramen in the maxilla mark the beginning of the lacrimal canal.

The frontal, which occupies most of the orbital wall, touches the sphenopalatine foramen. The frontal is bordered anteriorly by the lacrimal and maxillary bones; posteriorly by the parietal and alisphenoid; and ventrally by the orbitosphenoid, palatine, and maxillary bones. The orbitosphenoid is a small bone situated in the posteroventral portion of the orbit; its dorsal suture with the frontal is jagged, in contrast to its straighter posterior and ventral sutures in contact with the alisphenoid and palatine, respectively. The palatine bone is unusually well exposed in the floor of the orbit, where it extends like a narrow finger between the orbitosphenoid and the maxilla; it extends anterodorsally along the anteroventral part of the orbitosphenoid and reaches the posterior edge of the sphenopalatine foramen. The alisphenoid, at the back of the orbit, appears boot-shaped with almost its entire dorsal edge bordered by the squamosal; its dorsal tip makes contact with the descending tip of the parietal. The squamosal occupies a large region of the posterolateral portion of the cranium, and its lateral margin arches over the auditory bulla. The parietal bounds the squamosal dorsally. The interparietal is also visible in lateral view.

The zygomatic arch is composed of the maxilla, jugal, and squamosal bones. The jugal is a vertically flat bone that forms the medial part of the arch. It extends anterodorsally above the zygomatic wedge of the maxillary root and terminates just before reaching the infraorbital foramen; it does not reach the lacrimal bone. The jugal is thickest and tallest in its center where its dorsal extension accommodated the origin of the M. masseter medialis, pars anterior on its medial side. The jugal thins posteriorly in contact with the widening squamosal root. The arch is proportionally more robust than those of most extant muroid rodents probably because of more extensive use of the M. masseter lateralis profundus and medialis during mastication.

Ventral View

The premaxillae terminate in a zigzag suture with the maxilla; the suture intersects the incisive foramina about one-third of the way from their anterior tips. The ventral maxillary root of the zygoma is not expanded into a plate, and the muscle origin of the anterior part of the M. masseter lateralis profundus is horizontal and slightly indented. The M. masseter superficialis attached to a shallow depression anterior to the toothrow at the origin of the zygomatic root.

Anteriorly, the palatines meet the maxillae medial to the posterior half of M1. They terminate along the midline at a point medial to the middle of M3, but flare posterolaterally behind the toothrows. Just posterior to the M3s, cup-shaped posterior extensions of the palatines form the anterior portion of the pterygoid fossae. The pterygoid region, which is best preserved in MAE 91-1965, has prominent medial and lateral pterygoid flanges. The triangular anterior part accommodated the origin of the internal pterygoid muscle. At the back there is a change of inclination, and the bone, which contains three major foramina, slopes dorsally toward the auditory bulla. The medial basisphenoid extends posteriorly between the auditory bullae where it abuts the basioccipital. The basioccipital widens posteriorly around the back of the bullae and laps onto their medial edges. A prominent anteroposterior ridge is present along the middle of the basioccipital.

Portions of the alisphenoid, squamosal, jugal, and mastoid region can be seen along the lateral edges of the skull in ventral view. Only the dorsal rims of the bullae were preserved because of their fragile nature. However, it does appear that the bullae were not greatly inflated, relative to modern muroids, and had no medial extensions.

Posterior View

The back of the skull is composed of the occipital bone medially and dorsolaterally, and the mastoid region ventrolaterally. The dorsal region of the occipital has crenulations that run down from a strong nuchal crest toward the foramen magnum. In addition to the crenulations, a low ridge runs along the medial portion of the occipital from the foramen magnum to the dorsal tip of the nuchal crest. The two occipital condyles protrude ventrally next to the mastoid regions, which occupy the posteroventral corners of the skull. The mastoid regions appear to be somewhat vesicular in texture and slightly inflated dorsally. Paroccipital processes were present, but they are broken.

CRANIAL FORAMINA

The size of the infraorbital foramen and the muscles it transmits have been significant historically in rodent systematics. In *Cricetops*, the foramen is rather broad and dorsoventrally tall. A large anterior portion of the M. masseter medialis traversed the foramen and clearly originated dorsally on the side of the rostrum, the hystricomorphous condition. The enlarged foramen also transmitted the infraorbital branch of the maxillary division of the trigeminal nerve and blood vessels to the rostrum. Just anterior to the infraorbital foramen, there are small perforations in the dorsal surface of the premaxilla.

The incisive foramina are oval and intersected by the premaxillary/maxillary suture about two-thirds of the distance from their posterior tips. They are long, extending as far back as the anterior edge of M1 and occupying up to 75% of the diastemal length.

The posterior palatine foramina lie entirely within the palatine bone medial to the upper second molar. Grooves run from these foramina anteriorly and gradually diminish toward the posterior border of the incisive foramina. The posterior palatine foramina are also quite long (about 1.5 mm).

The nasolacrimal foramen is entirely within the maxilla anterior to the middle of the infraorbital foramen and anteroventral to the lacrimal bone. A dorsal rostral foramen lies on the dorsolateral edge of the premaxilla above the nasolacrimal foramen. No maxillary or other foramina were found on the rostrum.

The sphenopalatine foramen lies dorsal to M2 and is about the length of M2; it is bordered by the frontal dorsally, the palatine posteriorly, and the maxilla ventrally and anteriorly. The dorsal palatine foramen is posterior to the sphenopalatine foramen and within the maxillary/palatine suture dorsal to the middle of M3. Anterodorsal to this foramen is the ethmoid foramen (dorsal to the anterior portion of M3). It opens ventrally from a small arc-shaped groove within the frontal bone. Posteroventral to the ethmoid are the large interorbital and optic foramina in the orbitosphenoid; they are separated from each other by only a thin sheet of bone that runs posteromedially into the cranium. The interorbital is the more anterior and smaller foramen; it opens laterally into the orbit. Just behind M3, the optic foramen opens anterolaterally and has a maximum diameter of about 0.8 mm. At the back of the orbit, the sphenofrontal foramen opens anteriorly from within the alisphenoid/orbitosphenoid suture. In one specimen (MAE 91-397), the foramen is W-shaped and appears to be a combination of two small foramina.

The anterior alar fissure at the back of the orbit is formed by the anterior edge of the alisphenoid bone. The palatine bone floors the fissure and the orbitosphenoid forms its medial wall. The fissure varies from 1–2 mm posterior to M3. The masticatory and buccinator foramina perforate the lateral surface of the alisphenoid; both are very large and separated from each other. The buccinator, the more anterior foramen, opens anteriorly and the masticatory foramen opens dorsally. Together they form an L-shape. The canals have a common origin at the anterior end of the foramen ovale.

The foramen ovale opens within the alisphenoid bone at the posterior end of the lateral pterygoid flange and faces ventrally. There are two apertures medial to the foramen ovale. We interpret the more lateral of the two, which lies in the center of the pterygoid region, to be the entrance to the alisphenoid canal. The second, the transverse canal, perforates the lateral side of the medial pterygoid flange. One specimen, MAE 91-1965, is asymmetrical: the alisphenoid and transverse canals share a common large entrance on the left side, whereas they are separate on the right. The middle lacerate foramen is present along the anterior border of the bulla posterior to the transverse canal. It is difficult to tell if a posterior alar fissure, a feature common in muroids, was present because most of the bulla is absent.

The posterior lacerate (jugular) foramen is lenticular and located posterior to the auditory bulla between the bulla and the basioccipital. The hypoglossal foramen, posteromedial to the posterior lacerate foramen, is sometimes double. Although the bulla is not preserved, it appears that a stapedial foramen was present on the medial side of the bulla just anterior to the posterior lacerate foramen because a groove on the promontorium for the stapedial artery (as will be discussed in more detail later) is present. Unfortunately, because of the poor preservation of the bulla and the area along its medial border, it is difficult to reconstruct the carotid canal. A stylomastoid foramen opens at the posteroventral corner of the skull between the tympanic bulla and the mastoid region.

On the lateral side of the skull, both postglenoid and squamosomastoid foramina (not figured) are present. The postglenoid foramen is a large opening between the posterior part of the squamosal and the auditory bulla. A temporal foramen can be found anterodorsal to the postglenoid foramen near the suture between the squamosal and parietal. The squamosomastoid foramen is dorsal to the squamosal flange and is surrounded by the parietal and squamosal. The external auditory meatus opens laterally; it is round and lacks any large bony extension.

The mastoid foramen and foramen magnum can be seen on the back of the skull. The mastoid foramen lies between the occipital and the dorsomedial border of the mastoid region. The foramen magnum is somewhat oval with its longest dimension horizontal.

MANDIBULAR MORPHOLOGY

Figure 1

In lateral view, the diastema of the mandible curves gently backward from the incisor alveolus to an area slightly anterior to the lower first molar where it curves sharply dorsally to meet the anterior edge of m1. The mental foramen is anterior to m1 below the middle of the diastema. The superior and inferior masseteric crests meet ventral to the middle of the lower second molar and at about the same level as the mental foramen. The inferior crest forms a slight ridge along the ventral border of the mandible. A small extension of this crest past the anterior limit of the superior masseteric crest allows for an elongated insertion of the M. masseter lateralis profundus, pars anterior. The superior masseteric crest runs posterodorsally in a straight line toward the coronoid process in parallel with its anterior edge.

The coronoid process originates lateral to the anterior portion of the lower third molar and ascends steeply so that the posterior portion of this tooth is obscured. Using the occlusal plane as horizontal, the process rises in a straight line, bends a little anteriorly as it nears the tip, and then curves slightly posteriorly at the tip to form a hook. It is separated from the condyloid process by a shallow superior sigmoid notch. The condyloid process lies immediately posterior to the end of the coronoid process. The condyloid process also terminates in a posterior hooklike

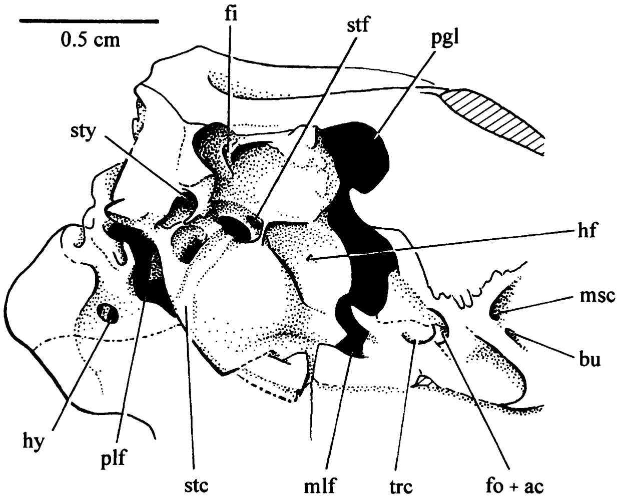

Fig. 3. Ventral view of the right auditory region of *Cricetops dormitor* (AMNH 21660). Anterior is to the right.

Abbreviations: **ac** alisphenoid canal; **bu** buccinator foramen; **fi** fossa incudis; **fo** foramen ovale; **hf** hiatus falopii; **hy** hypoglossal foramen; **mlf** middle lacerate foramen; **msc** masticatory foramen; **pgl** postglenoid foramen; **plf** posterior lacerate foramen; **stc** stapedial channel; **stf** stapedial foramen; **sty** stylomastoid foramen; **trc** transverse canal.

protrusion, but extends farther posteriorly and less high dorsally than the coronoid process. The inferior sigmoid notch is hardly noticeable because the posterior border of the mandible curves gently between the condyloid process and the angular process. The angular process is not well preserved in any of the specimens, but it appears to have been blunt and somewhat rounded. The steep angle of the ascending ramus relative to the toothrow and the weak inferior sigmoid notch make the posterior portion of the mandible very broad and high. The masseteric fossa is essentially flat except for a slight bulge ventral to the coronoid process, where the incisor alveolus terminates.

In medial view, the mandibular symphysis ends posteriorly below the anterior portion of m1. The mandibular foramen lies behind the posterior limit of the incisor alveolus. It is a diagonally oriented slit that opens at the same level as the toothrow. A triangular indentation occurs in the posteroventral portion of the mandible; its dorsal ridge is for the insertion of the M. masseter superficialis and its ventral ridge for that of the M. pterygoideus internus.

Dorsally, one can see the pit for the insertion of the internal part of the temporal muscle between the ascending ramus and the posterior portion of the toothrow. The dental row runs parallel to the ascending ramus, but is angled anterolaterally with respect to the body of the mandible. The coronoid, condyloid, and angular processes lie approximately in the same vertical plane. The coronoid flexes a little laterally and the condyloid slightly medially.

AUDITORY REGION

Figure 3

In ventral view, only the most posterior portion of the mastoid region of the petrosal can be seen behind the auditory region. Because of their fragile nature, the bullae are not well preserved in any specimen. However, the petrosal bone of the inner ear is intact in several specimens and allows a thorough description of the auditory region and the soft parts that marked it. Medially the petrosal is bordered by the basioccipital and basisphenoid and is separated from them by a thin space. The middle lacerate foramen and postglenoid foramen are anterior to the petrosal. The basisphenoid and parts of the pterygoid, alisphenoid, and squamosal form the bony portion anterior to the periotic. Laterodorsally the squamosal meets the auditory region. The posterior border of the petrosal is formed by the posterior lacerate foramen whereas its mastoid region occupies the posterolateral corner of the skull.

The auditory region is preserved best in AMNH 21660, a skull that is flattened in the posterior part and obliquely distorted. In ventral view, the petrosal is divided into distinct areas: the promontorium; three anterior basins, the carotid sulcus medially, the fossa for the tensor tympani muscle centrally, and the epitympanic recess laterally; and, posteriorly, the descending mastoid bone. The promontorium, formed by the bulge of the first turn of the cochlea, is the largest surface in the auditory region. The fenestra cochlearis and the fenestra vestibuli are at the posterior and lateral sides of the promontorium, respectively. The fenestra cochlearis is a round, vertical aperture that opens posteriorly within the cochlear fossula. The fenestra vestibuli, which accommodated the footplate of the stapes, opens laterally with its long axis almost horizontal. In another specimen, MAE 91-471, the internal cast of the cochlea is exposed; the canal makes about 2.5 turns from the fenestra vestibuli. The posteroventral surface of the promontory is excavated by a transverse channel for the stapedial artery. The artery appears to have crossed the opening of the fenestra cochlearis in AMNH 21660, but damage has removed the fragile lip of bone beneath the fenestra (visible in MAE 91-471), and this appearance is an artifact; the artery did not cross any part of the fenestra. After passing through the stapes, the artery entered the fallopian canal within the ridge that separates the two lateral basins. The canal is open ventrally in this specimen. However, its crystalline mineral filling suggests that the canal was completely enclosed, otherwise it would be filled with the same fine-grained, tawny matrix that encased the specimen.

A swell that runs anteriorly from the center of the promontorium separates the carotid sulcus medially from the fossa for the tensor tympani muscle laterally. This fossa is parabola-shaped with its vertex near the fenestra vestibuli, lateral to the promontorium. A tiny, anteriorly facing foramen, the hiatus falopii, opens in the middle of the fossa; it transmitted the greater petrosal nerve. The anterior end of the epitympanic recess is lateral to the posterior part of the fossa for the tensor tympani muscle. The two basins are separated by the ridge housing the stapedial artery. A small, roughly transverse pocket near the back of the recess may be the fossa incudis where the incus was moored. A broad curving pad of bone at the anterior end of the recess may have supported the bulla.

The mastoid part of the petrosal terminates the auditory region posteriorly. It descends as an anteriorly curved hook that probably wrapped around the external auditory meatus. From the tip of the mastoid hook, a bridge of bone ascends medially; it forms the anterior curvature of the stylomastoid foramen where the facial nerve emerged. Part of the internal course of the facial nerve is exposed in MAE 91-471 because the bone is damaged. The stapedius fossa for origin of the stapedius muscle forms a small basin dorsal to the stylomastoid foramen. A tiny foramen of unknown function is present in its anteromedial curvature. The channel of the facial nerve is on the lateral side of the stapedius fossa. The nerve's path can be followed to the entrance of the fallopian canal opposite the fenestra vestibuli from which it ran anteriorly together with the stapedial artery below it. The nerve bent medially away from the artery at the genu of the fallopian canal. The mastoid eminence, which was outside the bulla, is lateral to the stapedius fossa.

DENTITION

Figure 4, table 2

The dentition was described in detail by Wahlert (1984); the following is a simplified reexamination of its structure. The lower molars are narrower than the upper molars; each set of teeth is of nearly uniform width; the two ends of the toothrows taper slightly. Two bicusped ridges cross each tooth: uppers, the protoloph and metaloph; lowers, the metalophid and hypolophid. The first molars are elongated and have a third ridge at the front: uppers, the anteroloph, which consists of lingual and buccal anterocones; lowers, a single

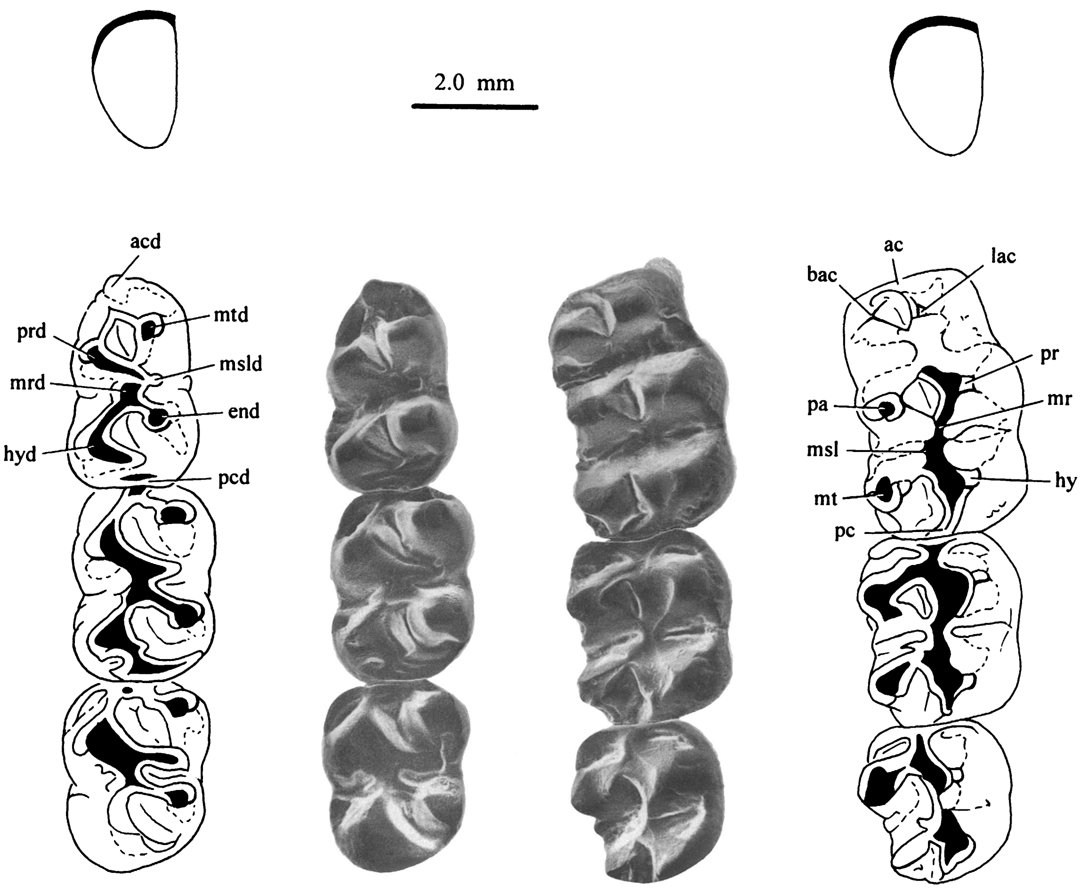

Fig. 4. Lower right reversed (left side of fig.) and upper right (right side of fig.) dentitions of *Cricetops dormitor* (AMNH 19054). Anterior is to the top.

Abbreviations: **acd** anteroconid; **ac** anterior cingulum; **bac** buccal anterocone; **end** entoconid; **hy** hypocone; **hyd** hypoconid; **lac** lingual anterocone; **msl** mesoloph; **msld** mesolophid; **mt** metacone; **mtd** metaconid; **mr** mure = endoloph; **mrd** murid = ectolophid; **pa** paracone; **pc** posterior cingulum; **pcd** posterior cingulid; **pr** protocone; **prd** protoconid.

cusp, the anteroconid. Each bicusped ridge is interrupted by a more or less anteroposterior valley. A low, posterior cingulum/id completes the back of each tooth; in M1/m1 and M2/m2 they are adjacent to the anterior cingulum/id of the next tooth. The transverse lophs are interconnected by a low, median crest that runs anteroposteriorly; in the upper teeth this mure is homologous to the endoloph and, in the lowers, the murid, to the ectolophid. In the lower teeth, the anterior arm from the protoconid and metaconid join at the anterior cingulid.

The teeth bear wear facets on the anterior, top, and posterior sides of the major lophs/ids with the exception of the metaloph in M3, which has no posterior facet, and the anteroconid in m1, which has no anterior facet. This agrees with the fact that lower teeth occlude half a tooth anterior to the corresponding upper. The anterior crests (metalophids) of m2 and m3 occlude with the low cingula between M1 and M2 and between M2 and M3, respectively. The posterior crests (hypolophids) of m1, m2, and m3 occlude in the transverse median valleys of the corresponding upper teeth. In *Cricetops*, the first molar is the longest tooth in both the upper and lower dentition; M1 accounts for 43% of the toothrow length and m1 for 36%. M1 is the widest tooth, and m1, which traversed it, is narrower. The second molars of upper and lower dentitions are of nearly equal dimensions. The third molars are the shortest, and m3 is wider than M3. That the width of the upper teeth decreases posteriorly suggests that the lowers were drawn anteromedially across the them with the condyle serving as a pivot; the posterior lower molar, which is close to the pivot, traversed a smaller arc than the anteriormost lower molar.

In M2 and M3 a tiny spurlike mesoloph extends buccally from the metaloph-endoloph junction. The lower molars bear a short mesolophid that extends lingually from the posterior arm of the protoconid to behind the metaconid. It is most extensive in m3; the mesolophid does not sit in the deepest part of the valley between the major lophs but is a part of the lower slope of the metalophid.

If one counts the transverse features of the teeth (counting adjacent cingula/ids between teeth as a single feature and including the single anteroconid of m1), the number in upper teeth is 9 (mesolophs are tiny) and in lowers 12 (mesolophids are big). One expects features to correspond in similarly designed upper and lower teeth because there should be corresponding functions for cuspate lophs traveling across transverse valleys. The difference observed here could be a solution to a possible difference in rates of wear.

DISCUSSION AND CONCLUSIONS

Cricetops dormitor has a variety of characters that clearly ally it with the Muroidea. These include a rough depression or tubercle for attachment of the superficial masseter, the absence of upper premolars, and an M1 whose length is greater than its width. However, *Cricetops* possesses a unique suite of primitive and derived cranial and dental characters that make its phylogenetic placement relative to other muroids difficult.

While other Oligocene muroid rodents such as *Eumys*, *Eucricetodon*, and *Leidymys* show the early signs of myomorphy in their possession of an inclined zygomatic plate (the anterodorsal tilt of the ventral side of the anterior zygomatic root), *Cricetops* retains the more primitive condition of lacking this plate and showing no signs of myomorphy. *Cricetops* also retains a variety of other primitive characters including a large hystricomorphous infraorbital foramen, an inferior masseteric crest that meets the superior masseteric crest ventral to m2, and a large entoconid on m3. These characters would suggest that *Cricetops* is a primitive muroid rodent. However, a number of other characters indicate that *Cricetops* is more derived than many other Oligocene muroid rodents. These include a more anterior intersection of the incisive foramina by the premaxilla/maxilla suture, a prominent M3 metacone, the presence of an ectolophid in m1, opposite rather than alternate molar cusps, and enclosure of the stapedial artery in a canal where it passes alongside the fossa for the tensor tympani. These conflicting signals indicate that a number of characters found within *Cricetops* are homoplastic and have been secondarily derived.

Cricetops also lacks characters that would unite it with species of the extant family Muridae (sensu Musser and Carleton, 1993). For example, *Cricetops*, as well as other Oligocene muroid rodents such as *Eumys* and *Eucricetodon*, lacks a highly inclined zygomatic plate (greater than 60°), an ethmoid foramen dorsal to M1 or the anterior half of M2, and an anterior connection between the protoconid and metaconid on m1. These characters suggest that *Cricetops*, as well as other Oligocene muroid rodents, should not be placed within extant murid subfamilies, such as the Cricetinae, as suggested by Flynn et al. (1985).

This brief survey of the morphological characters of *Cricetops dormitor* indicates that there is a need to reevaluate its phylogenetic position within the Muroidea as well as the phylogenetic position of other fossil muroids. The new specimens of *Cricetops* described in this paper, the numerous new specimens of Asian and European muroids recently discovered (e.g., Lindsay, 1994; Shevyreva, 1994; Carrasco, 1997; Emry et al., 1998; Dawson and Tong, 1998), and the well-documented collections of North American muroids (e.g., Wood, 1936, 1937, 1980; Martin, 1980; Korth, 1981, 1984) should provide a good foundation for such an analysis.

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