

EVOLUTION OF THE RHIZOMYINE ZYGOMA

by

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ABSTRACT

Cranial anatomy of a late Miocene rhizomyid, *Brachyrhizomys* cf. *B. pilgrimi*, provides new evidence on the origin of the dorsal, round infraorbital foramen of living rhizomyines. Primitive rhizomyids retain a myomorphous keyhole foramen with a long ventral slit that retracts upward during the evolutionary history of the Rhizomyidae. The primitive condition of the elongated ventral slit is represented by *Kanisamys sivalensis*. Among later burrowers the foramen shows progressive dorsal migration, the ventral slit terminating midway up the snout in *B. tetracharax* and *B. choristos*; well above the midline of the snout in *Brachyrhizomys* cf. *B. pilgrimi*. Apparently this transformation began earlier among Rhizomyinae than among Tachyoryctinae and continued to a more derived stage in rhizomyines. In living *Rhizomys* the ventral slit is absent and only a high round hole remains at the anterior end of the zygomatic arch.

RÉSUMÉ

L'anatomie crânienne d'un Rhizomyinae, *Brachyrhizomys* cf. *B. pilgrimi*, apporte de nouvelles indications relatives à l'évolution du foramen infra-orbitaire des Rhizomyinae actuels. Les formes primitives de Rhizomyinae possèdent un foramen infraorbitaire de type Myomorphe classique, avec une longue fissure ventrale qui se raccourcit vers le haut au cours de l'évolution. La migration vers le haut de cette fissure ventrale est représentée par différents stades illustrés respectivement par *Kanisamys sivalensis*, les formes plus spécialisées (*B. tetracharax* et *B. choristos*) ainsi que par cf. *B. pilgrimi*, chez lequel ce foramen est situé bien au-dessus de la partie moyenne du museau.

Cette évolution a dû commencer plus tôt chez les Rhizomyinae que chez les Tachyoryctinae et a atteint des stades plus évolués chez les Rhizomyinae. Chez les *Rhizomys* actuels, la fissure ventrale est absente, et il ne subsiste qu'un foramen arrondi, en position élevée sur le museau, à l'extrémité antérieure de l'arcade zygomatique.

INTRODUCTION

Rhizomyids are muroid rodents that originated probably during the early Miocene (de Bruijn, Hussain, and Leinders, 1981; Flynn, 1982). Most early Miocene and younger muroids possess an elongated, keyhole shaped infraorbital foramen on the side of the snout. The broad, dorsal part of this foramen transmits the deep portion of the masseter muscle; the ventral slit of the keyhole transmits nerves and blood vessels. Among living rhizomyids, *Tachyoryctes* is derived with respect to this condition: the foramen is dorsal in position and its ventral slit is reduced, descending only to about the midline of the snout. *Rhizomys* is further modified: the foramen is reduced to a round opening that accomodates both muscle and nerve and lies dorsal to the ascending plate of the zygoma; the ascending plate is continuous with the snout and the lateral portion of the masseter, normally confined to the plate, extends onto the muzzle. The snout morphology of *Rhizomys* is superficially squirrel-like, but apparently evolved differently than did true sciuromorphy (Wahlert, 1978). A major difference from sciuromorphy is that the foramen opens anterodorsally and transmits a minor portion of deep masseter muscle. The systematic importance of the modern rhizomyid infraorbital foramen and how it evolved have been unclear up to now.

Since the landmark revision of Siwalik rodents by C.C. Black (1972), many new fossil rhizomyids have been recovered from the Neogene terrestrial deposits of the Indian subcontinent. Major contributions by scientists of Pakistan and of India and by a multinational team co-directed by D. Pilbeam and S.M. Ibrahim Shah have permitted biostratigraphic analysis of the group (Jacobs, 1978; Flynn, 1982; see also Munthe, 1980). Major features of rhizomyid evolution included early diversification of species of *Kanisamys* during the middle Miocene, followed by apparent phyletic evolution of hypsodont species of *Kanisamys*. The tachyoryctine *Rhizomyides* evolved early, probably before 9 Ma (Flynn, 1983). Between 8 and 9 Ma, early members of the genus

Brachyrhizomys had appeared and already acquired burrowing adaptations. Hypsodont *K. sivalensis* and burrowing species of *Brachyrhizomys* were abundant at about 8 Ma. Among the latter, *B. nagrii* is represented by excellent mandibular and cranial material that reflect a fossorial habitus, while other species of *Brachyrhizomys* are known mainly by dentary fragments. *Kanisamys* is placed in the subfamily Tachyoryctinae and *K. sivalensis* shows some derived traits shared by *Tachyoryctes* (see Sabatier, 1982; Flynn 1982). *Rhizomys* evolved probably by the early Pliocene. As advanced Rhizomyinae, *Rhizomys* and *Brachyrhizomys* are linked by many derived conditions of the dentition, skull, and mandible (Flynn, 1982).

In 1967, one of us (M.S.) discovered remains of much of the skull of a large species of *Brachyrhizomys* in the Dhok Pathan Formation of the Potwar Plateau, northern Pakistan. The specimen weathered from yellow fine-grained sediments with siliceous nodules, about 1.5 kilometers southwest of Nila Village, District Jhelum. Associated fauna includes Proboscidea, Rhinocerotidae, Suidae, and the equid cf. *?Hipparion antelopinum* (see comments on hipparionines by Bernor and Hussain, 1985). Description of the rhizomyid material not only adds to our knowledge of the skull and upper dentition of large species of *Brachyrhizomys*, but shines light on the development of the derived infraorbital foramen of its living relatives.

SYSTEMATICS

Family RHIZOMYIDAE MILLER and GIDLEY, 1918

Subfamily RHIZOMYINAE MILLER and GIDLEY, 1918

Genus *BRACHYRHIZOMYS* TEILHARD de CHARDIN, 1942

Brachyrhizomys cf. *B. pilgrimi* HINTON, 1933

Referred material: Specimen 69/681, snout and palate with well preserved incisors and left M1-3/ and right M1-2/, and associated skull fragments and partial left dentary with broken incisor.

Provenance: Dhok Pathan Formation, 1.5 kilometers southwest of Nila, Jhelum District, Pakistan.

Repository: Zoology Department, Punjab University, Lahore, Pakistan.

Description: The snout, palate, and skull fragments are slightly distorted, but well preserved (fig. 1). The long snout is stout and strongly arched, ascending anteriorly as in other species of *Brachyrhizomys*. It is 13.5 mm deep at its shallowest position, which is anterior to the incisive foramen, and 12.5 mm wide at this point. The anterior ascending plate of the zygoma continues laterally as the broad anterior root of the zygomatic arch. The anterior margin of the plate is the maxilla/premaxilla suture, which also approximates the anterior limit of the origin of the lateral portion of the masseter muscle. The ventral slit of the infraorbital foramen terminates about 11 mm above the tooth row, well above the midline of the snout. Dorsolateral to the molars, the maxillary bone forms a nearly vertical wall, reminiscent of, but not as advanced as in *Rhizomys*. This condition is advanced over that of *B. nagrii* in which the maxilla folds inward over the molar roots. The diastema between the incisor and first molar is 25.6 mm. The maxilla/premaxilla suture passes through the anterior part of the incisive

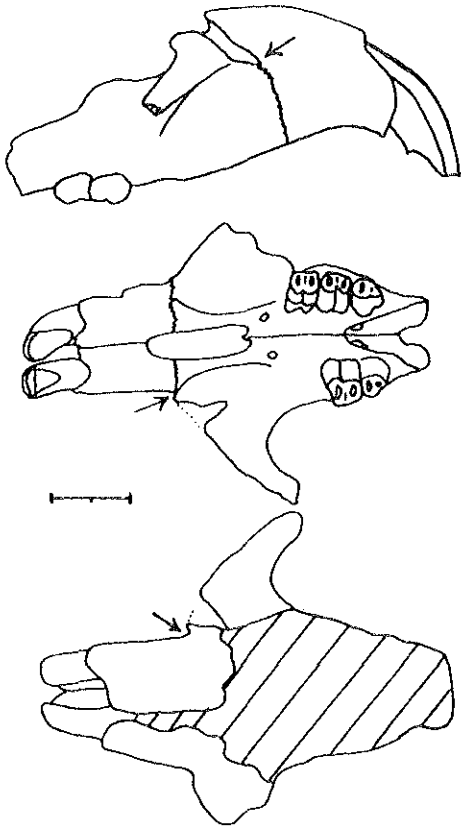


Fig. 1. — Snout and palate of *Brachyrhizomys* cf. *B. pilgrimi* in lateral, ventral, and dorsal view. Arrow indicates ventral slit of the infraorbital foramen. Bar scale equals 10 mm.

Le museau et le palais de *Brachyrhizomys* cf. *B. pilgrimi* en vue latérale, vue ventrale, et vue dorsale. La flèche indique la fente ventrale du foramen infraorbitaire. L'échelle égale 10 mm.

foramen. The incisive foramen, about 14.9 mm long and 5.4 mm wide, ends 8.4 mm behind the incisor. The narrow palate is solid from the incisive foramen, 3.95 mm anterior to M1/, to the posterior emargination, 2.07 mm posterior to M3/. Pterygoid fossae lie far posterior, 4.84 mm behind M3/. The palatine bone extends anteriorly to the front of M3/, where a small fenestra is located. Nutritive foramina lie anteromedial to both M1/. Palatal width decreases slightly posteriorly, from 5.5 mm at M1/ to 5.0 mm at M3/. Skull roof fragments show that temporal ridges converged but did not meet in a sagittal crest.

Molars are moderately and unilaterally high crowned and decrease in wear posteriorly (fig. 2). M1/ (L × W: 3.96, 4.42 mm, approx.) is damaged and worn nearly to the bottom of the lingual reentrant, which terminates 1.43 mm above the base of the enamel. The mesoloph is short. M1/ has four roots as in *B. tetracharax* and *Rhizomys*. M2/ (4.60, 4.79 mm, average of left and right teeth) has a long, continuous mesoloph and the metaloph-posteroloph are fused in this moderately worn tooth. The labial reentrant terminates 1.30 mm above the base of the enamel. The lingual reentrant is short in occlusal view, terminating lingual to the longitudinal midline of M2/.

The left and right M3/ (4.44, 4.24 mm, average) are triangular in outline, with a posteriorly directed apex, and differ in minor details. M3/ is only slightly abraded posteriorly, demonstrating a remarkable gradient in tooth wear from M1/ to M3/.

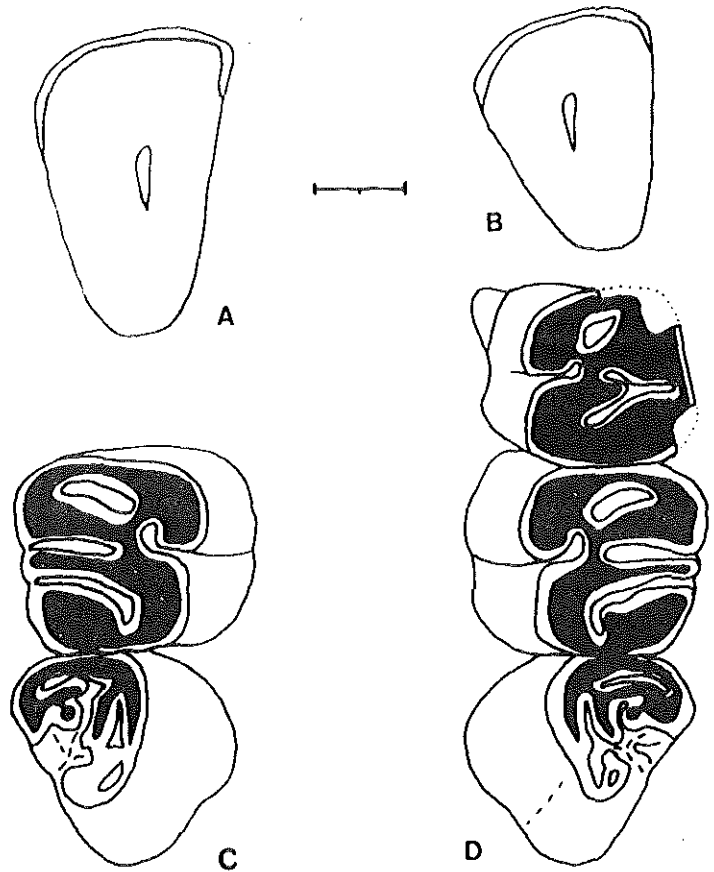


Fig. 2. — Dentition of *Brachyrhizomys* cf. *B. pilgrimi*. A, left I/1; B, right I1/; C, right M2-3/; D, left M1-3/. Bar scale equals 2 mm.

La dentition de *Brachyrhizomys* cf. *B. pilgrimi*. A, I/1 gauche; B, I1/ droite; C, M2-3/ droite; D, M1-3/ gauche. L'échelle égale 2 mm.

There is no lingual reentrant, but an enamel lake labial to the protocone is confluent with a labial reentrant, posterior to the paracone. The large paracone joins the protocone through a protoloph, which is incomplete on the right M3/. The protoloph and narrow anteroloph border a transverse enamel lake (valley on the right M3/). A small cusplule occurs lingual to the paracone in both M3/. Left M3/ has a low mesostyle. The hypocone is absent and the indistinct metacone is lingual relative to the paracone. The lingual wall of M3/ continues posteriorly from the protocone, bends to form a sharp posterior heel, and intersects the metacone.

Upper incisors are more proodont and less strongly curved than in *B. nagrii*. Their cross section (5.35, 3.80 mm) is oval, but more rounded anterolaterally than medially (fig. 2B). The enamel is gently rounded anteriorly and wraps onto about one third of the lateral side of the incisor and bears faint crenulations. The occlusal surface bears two concavities; one on the dentine is gentle, and the other, at the dentine-enamel junction, is more pronounced. The latter results from the fact that the enamel is more resistant to wear than the dentine, thus contributing to a sharp point.

The dentary is massive and while the dorsal border is not preserved, its total depth probably reached 15 mm below M/2. As in other *Brachyrhizomys*, upper and lower ridges of the masseteric crest meet below the middle of M/1, without an anterior

extension (see Flynn, 1982). The mental foramen lies at the mid level of the dentary, just anterior to M/1. The incisor (6.5×4.4 mm in cross section) is heavy and nearly flat anteriorly (fig. 2A). Enamel wraps onto about one fourth of its lateral side and bears fine crenulations. The proodonty of the upper incisor and the chisel shape of the lower incisor suggest that this species used these teeth in borrowing and in cropping vegetation as do living rhizomyids.

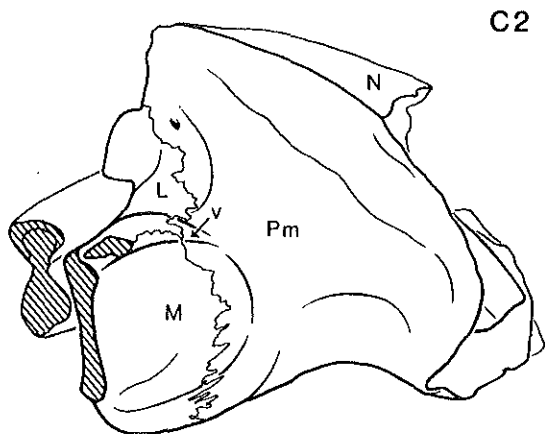
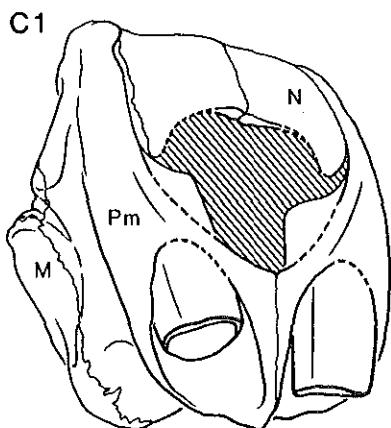
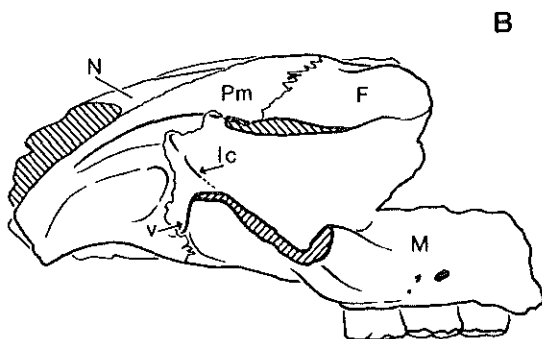
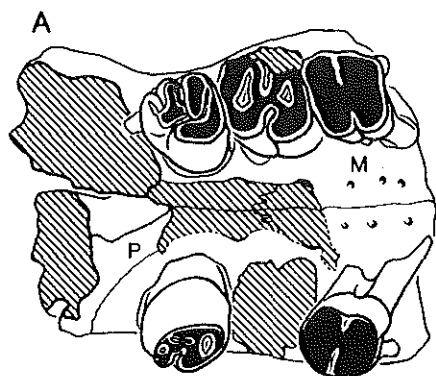
DISCUSSION

Dimensions of specimen 69/681, particularly of its incisor, agree well with sizes for dentary fragments from 8.2 to 7.8 Ma deposits of Pakistan. These were named provisionally *Brachyrhizomys* cf. *B. pilgrimi* by L.J. Flynn (1982). The original hypodigm of *B. pilgrimi*, two jaw fragments from Haritalyangar, India (Hinton, 1933), represents the largest known species of the genus. *B. tetracharax* and *B. choristos* differ in details of the lower molars and are about 20% smaller than the Haritalyangar specimens (Flynn, 1982). Specimens called cf. *B. pilgrimi* are less than 10% smaller than the Haritalyangar material. Furthermore, lower molar morphology, notably isolation of the entoconid, allies them with the holotype of *B. pilgrimi*. In that lower molars of specimen 69/681 are not preserved, its identification is tentative. However, incisor and upper molar dimensions are greater than those of *B. tetracharax*. Also, M3/ of 69/681 is rounded, with a posteriorly elongated heel, unlike M3/ of *B. tetracharax*, which is transversely elongated (fig. 3A and C, Geological Survey of Pakistan specimen GSP-4810). Thus for the present we refer this snout and palate to the same species represented by dentary fragments at other localities in Pakistan. Calling this taxon "cf. *B. pilgrimi*" focuses attention on its close affinity to *B. pilgrimi* and suggests that with better samples, the Pakistani material could be diagnosed as a new species.

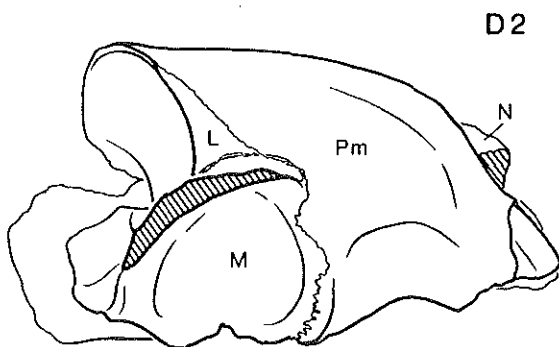
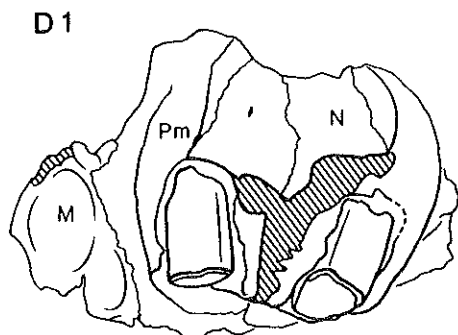
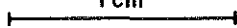
The *B. pilgrimi* lineage appeared before 8 Ma and had no known descendants. Nonetheless, the zygomatic morphology of this and other fossil rhizomyids shows how the derived infraorbital foramen of living rhizomyines evolved. *Kanisamys sivalensis*, a

Fig. 3. — Late Miocene rhizomyid zygomasseteric and palatal morphology. *Brachyrhizomys tetracharax*, GSP specimen 4810; A, palate in occlusal view; C, snout in two views, C1 (right lateral) and C2 (anterior). *Kanisamys sivalensis* (B), GSP specimen 8358, in left lateral view. *Brachyrhizomys choristos*, GSP specimen 4053, snout in two views, D1 (right lateral) and D2 (anterior). In *Kanisamys* (GSP 8358) most of the ascending plate of the zygoma is broken, but the base of the ventral slit is preserved. The area of origin of the deep masseter muscle extends far anteriorly on the snout. In *Brachyrhizomys*, GSP 4810 especially, this origin extends only a little beyond the lachrymal bone; however, the ascending plate of the zygoma is partly fused to the snout, permitting the lateral masseter muscle to extend onto the premaxilla. Bar scale equals 10 mm.

La morphologie zygomassétérienne et palatale des rhizomyidés du Miocène supérieur. *Brachyrhizomys tetracharax*, GSP 4810; A, palais en vue occlusale; C, rostre en vue latérale droite (C1) et vue antérieure (C2). *Kanisamys sivalensis* (B), GSP 8358, en vue latérale gauche. *Brachyrhizomys choristos*, GSP 4053, rostre en vue latérale droite (D1) et antérieure (D2). Le « plateau » antérieur du *Kanisamys* est cassé, mais la base de la fente ventrale est conservée. L'origine du muscle massétérien (médial) est bien antérieure sur le museau. La surface d'origine de cette partie du muscle massétérien l'est moins dans GSP 4810, mais la partie latérale s'étend sur le prémaxillaire. L'échelle représente 10 mm. F, frontal; Ic, canal infraorbitaire; L, lachrymal; M, maxillaire; N, nasal; P, palatin; Pm, prémaxillaire; V, fissure ventrale du foramen infraorbitaire.



1 cm



1 cm



nonburrowing rhizomyid, retained a keyhole shaped foramen with the ventral slit descending nearly to the base of the snout (fig. 3B). The reduced ventral slit of the burrowers *B. tetracharax* (fig. 3C1 and 3C2) and *B. choristos* (fig. 3D1 and 3D2) descended only to the midline of the snout. This is also the case in the burrower *B. nagrii* (Flynn, 1982). Cf. *B. pilgrimi* was modified further with a foramen restricted to well above the midline of the snout (fig. 1). Although none of these species may be directly ancestral to early *Rhizomys*, they show the pathway of transformation of its derived infraorbital foramen.

The foregoing arguments demonstrate that the rhizomyine snout is a derived form of the myomorphous zygoma. Primitive (mainly Oligocene) muroids are hystricomorphous, but by the early Miocene most members of the group exhibit myomorphy (see review in Flynn, Jacobs, and Lindsay, 1985). This is consistent with the estimated early Miocene origin for Rhizomyidae. Fossil rhizomyids suggest that the modern rhizomyid zygoma developed by upward migration of the infraorbital foramen in several stages, rather than in a single macroevolutionary event.

The evolution of the infraorbital foramen is important as an additional feature in diagnosing rhizomyid subfamilies. This foramen became reduced in both subfamilies, but was modified earlier and ultimately more extremely in Rhizomyinae than in Tachyoryctinae. While *Kanisamys sivalensis* remained conservative, its contemporary *Brachyrhizomys nagrii* had a shortened ventral slit (Flynn, 1982). Furthermore, the foramen of the rhizomyine *B. nagrii* resembles that of *Tachyoryctes splendens*, although the latter is 8 million years younger and is a tachyoryctine. Complete closure of the ventral slit appeared late in rhizomyine evolution and is a generic character for *Rhizomys*. Transformation of the zygoma is yet another element in the mosaic of traits that characterize living Rhizomyidae (see Flynn, 1984). The shape of the foramen can be useful in diagnosis of subfamilies as suggested by M. Sabatier (1982), but only when applied in combination with other characters.

The upward shift of the infraorbital foramen in rhizomyines coincided with their adoption of not only a burrowing lifestyle, but presumably also of a new source of food; that is, the roots and stalks eaten by living species. Apparently a strong lateral masseter muscle became more useful than was the deep masseter muscle. Hence lateral masseter expanded anterodorsally, while the deep masseter (and the infraorbital foramen) shrank in relative size and area of origin. The origin of the lateral masseter muscle was confined to the anterior plate of the zygoma in *Kanisamys*, while the deep masseter extended through the infraorbital foramen of that genus and anchored anteriorly on the nasal and premaxilla (fig. 3B). With loss of the ventral slit in *Brachyrhizomys*, the plate became continuous with the snout and the origin of the lateral masseter muscle expanded anteriorly onto the premaxilla (heavy lines in figs. 3C and 3D). The concomitant retreat of the deep masseter muscle was indicated by a smaller excavation for its origin, which was confined mainly to the lachrymal bone in *Brachyrhizomys* (figs. 3C and 3D).

COMPARISONS WITH BATHYERGOIDEA

The zygomatic condition seen among Rhizomyidae invites comparison with that of another fossorial group, the Bathyergidae. These distantly related hystricognaths are more modified for burrowing than are Rhizomyidae; however, they evidently underwent some of the same changes in zygomatic musculature as did the latter. In his monograph on Miocene fossil rodents from East Africa, R. Lavocat (1973) showed that at least some bathyergoids transmitted deep masseter muscle through the infraorbital foramen. Lavocat proposed that this was the primitive condition for the family. This is also suggested by some living *Cryptomys* (e.g., *C. bocagei*), which retain relatively large foramina. Perhaps the general phylogenetic retraction of the deep masseter and the diminution of the infraorbital foramen, which are characteristic for living bathyergids, are related to the fossorial lifestyle of the group.

Like rhizomyids, bathyergids are predominantly tooth diggers (Nevo, 1979). However, unlike rhizomyids, bathyergids have all of the lateral masseter muscle confined to the ventral border of the zygoma. It is unknown if this difference results from a lack of need (in either feeding or digging) of an anterior anchor on the snout for the lateral masseter. Alternatively, it should be recalled that rhizomyids are myomorphs and as a preadaptation had the lateral masseter in an anterior position where it would have been more easily expanded. Anterior expansion of the lateral masseter muscle in Bathyergidae would have required greater modification of the snout in that group.

SUMMARY

Well preserved cranial material of a large late Miocene rhizomyine is described. The specimen is important for future systematic work because it includes the upper dentition, a part of the anatomy poorly represented among large *Brachyrhizomys*. Based on size alone, this partial skull is compared to a species designated *Brachyrhizomys* cf. *B. pilgrimi* (see Flynn, 1982) from approximately 8 million year old deposits in Pakistan. This and other rhizomyid cranial material demonstrate how the myomorphous infraorbital foramen of early Miocene muroids was transformed into the high round foramen of extant *Rhizomys*. This derived condition is part of a complex mosaic of features that is applicable to higher level systematics when used in combination with other traits.

As the ventral slit retracted upward, the lateral portion of the masseter muscle expanded anteriorly onto the snout. Coupled with this was shrinkage of the infraorbital foramen and reduction in the area of origin of the deep masseter muscle. Evolution of the distantly related fossorial Bathyergoidea probably included convergent reduction of the deep masseter, but this group never showed expansion of the lateral portion of that muscle.

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