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Cranial anatomy of *Jaculus orientalis* (Rodentia, Dipodea) : new evidence for a close relationship of dipodoid and muroid rodents

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CRANIAL ANATOMY OF *JACULUS orientalis* (RODENTIA, DIPOIDEA): NEW EVIDENCE FOR CLOSE RELATIONSHIP OF DIPODOID AND MUROID RODENTS

by
Brian S. Sheets ©

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ABSTRACT

The head of the Egyptian jerboa, *Jaculus orientalis*, was dissected and the pathways of vessels and nerves were traced and recorded in order to identify the cranial foramina. Comparison of this head with cleaned skulls indicated that the foramina through which vessels and nerves pass are relatively constant in dipodoids and are features that can be used to assess relationships with other rodents. Dipodoids share with muroids specialized features, such as an enlarged infraorbital canal, rostral entrance to the lacrimal canal, and branching outside the middle ear of the stapedia artery from the internal carotid. Dipodoids retain a more primitive origin of the lateral masseter than is seen in muroids, and they have a unique partitioning of the infraorbital canal. This study owed that jerboas are close relatives of muroids but have not evolved from any member of that group.

INTRODUCTION

Scope of this study

Jerboas, family Dipodidae, are a group of Palearctic and North African rodents that contains 10 living genera and approximately 26 species (Corbet, 1978). These rodents have been considered close relatives of the muroids, mice, rats, and their kin (Simpson, 1945), although the origins of the layers of the masseter muscle, a prominent muscle used in chewing and gnawing, differ (Klingener, 1964). This study uses new evidence derived

from dissection of the head of *Jaculus orientalis* and from examination of skulls to reexamine the hypothesis that these rodents are close relatives.

Traditionally, jaw musculature or the modifications of the skull and jaw resulting from changes in the musculature have been the main features used to determine the relationships of the subgroups of rodents. The pathways of blood vessels and nerves and the foramina that mark their passage through bone have not been examined in jerboas. In our study the soft tissues, mainly the nerves, arteries, and veins, were followed to the foramina where they penetrate bone, because the foramina are named according to the nerves and vessels that pass through them. In order to identify the nerves and vessels, they had to be traced to the tissues they innervate or to which they circulate blood. The information presented by this dissection of the soft tissues of *Jaculus orientalis* is now available for comparison to known cranial features in other living or extinct rodents.

Understanding the relationships of soft tissues to bone is the basis for interpreting the fossilized skulls of extinct animals. This study is significant in that it adds new anatomical data about the head of a dipodoid rodent to the basic information on rodent cranial anatomy. Similar studies of other groups have provided useful data for evaluating theories of relationship among rodents (Wahlert, 1974, 1985a).

The following general description of rodents is taken from Wood (1974) and Vaughan (1978). Sources for specific information about jerboas are Klingener (1984); Nowak and Paradiso (1983).

The Order Rodentia

Jerboas are a very small division of the Rodentia, the most abundant order of mammals. Fifty percent of the species of living mammals are rodents. Most rodents are small. Some mice and dormice measure 75 millimeters long, including the tail, and weigh as little as 20 grams. The largest living rodent, the capybara (*Hydrochoerus hydrochoeris*) of South America measures 1.3 meters in length and can weigh 50 kilograms. Rodents are generally herbivorous; seeds are the preferred food item, and acorns, fruits, berries, young leaves, buds, shoots, tubers and bulbs make up the list of other foods eaten by a wide variety of rodents. Others eat bird eggs, insects, fish and available carrion.

The most typical members of the order Rodentia are the small, ground living, scampering animals, that are commonly called rats and mice. Although most of these types spend a great deal of time on the ground, some climb plants and trees to gather food. Rodents of this scampering design, with limited burrowing or arboreal adaptations, include members of all major rodent groups: the myomorphs, mice and their relatives, the sciuriforms, squirrels and chipmunks, and the hystricomorphs, including spiny rats, chinchillas and South African rock rats. Certain rodents have become specialized in the ability to glide or jump. Some small squirrels have evolved a skin fold (patagium), that forms a flat surface

between the limbs and tail. This increase in surface area allows these rodents to leap in an outstretched posture from one tree to another and glide to a safe landing.

Other rodents have become bipedal jumpers, and they escape their enemies by long leaps. Notable examples of these saltators include the jerboas, the subject of this study, jumping mice, the New World relatives of jerboas, and the North American kangaroo rats of the family Heteromyidae. The bony covering of the middle ear, the tympanic bulla, is greatly enlarged in the saltatorial rodents that live in arid environments. It is believed that this is an adaptation to life in the desert. An enlarged tympanic bulla causes increased amplification of sound that allows the rodent to detect an approaching predator early. It is also suggested that an increase in the size of the bulla is equaled by the balancing and stabilizing activities of the ears.

The design for gnawing

All rodents gnaw, and they have one pair of upper and one pair of lower incisors. These incisors grow with age and must be worn off by gnawing at a rate equal to the growth rate. Studies have measured the growth of incisors in some species at around two millimeters per week. Gnawing involves the fore-and-aft movement of the lower jaw, with the upper incisors holding a hard object and the lower incisors cutting against it. Since enamel is restricted to the labial side of each incisor, the wear resulting from gnawing proceeds on an angle. The softer dentine in the rear of each incisor wears at a faster rate than the enamel on the front. This process maintains a sharp cutting edge at the front of each incisor while balancing the rate of extrusion of the tooth. Jaw articulation is such that when the incisors are in use, the molar teeth are not touching, and during chewing, the molars are in contact and the incisors are not.

Anteroposterior movement of the jaw is possible in rodents because the glenoid fossa in which the jaw articulates is elongated and has no limiting bony processes. Most other mammals have processes that limit movement. Chewing and gnawing involves all three of the main jaw muscles, the masseter, temporal, and pterygoid. Wood (1965) presented a synopsis of the evolutionary changes in the masseter. In the earliest and most primitive rodents, the protrogomorphs, the origin of the masseter was limited to the ventral part of the zygomatic arch and the muscle inserted on the mandible at the masseteric fossa. This arrangement, for the most part, pulled the jaw nearly straight up. In the course of evolution different portions of the masseter shifted their origins forward onto the rostrum (Figure 1). This change nearly doubled the length of the muscle and greatly augmented the anterior direction of its pull. Differences in origin of various layers of the masseter has served to distinguish major subgroups of rodents from one another.

In the sciuriforms the lateral layer of the masseter extends rostrally alongside the zygoma and compresses the infraorbital canal. In hystricomorphs the lateral masseter remains restricted to its primitive position, but the anterior part of the deeper medial layer passes anteriorly through the infraorbital canal onto the rostrum. Enlargement of the

infraorbital canal in some species is so great that it is bigger than the orbit. In muroids a combination of changes occurred. Here, both the lateral and medial layers of the masseter extend rostrally (the myomorphous condition); the medial masseter passes through the infraorbital canal, and the lateral masseter extends alongside it. The fact that both layers of the muscle are modified in muroids may make them most efficient gnawers among rodents and account for their enormous success in terms of numbers of species and of individuals.

Jerboas, although they are considered to be related to the muroids, have the hystricomorphous condition of the masseter muscle. They share many other specializations with muroids. Klingener (1964) proposed that enlargement of the infraorbital canal and rostral extension of the anterior part of the medial masseter, as seen in jerboas, was the first step in the evolution of true myomorphy.

Figure 1.



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Figure 1. Reproduced from Romer, 1966, Fig. 437. Modifications of jaw musculature.

A = protrogomorphous

B = sciurormorphous

C = myomorphous

D = hystricomorphous

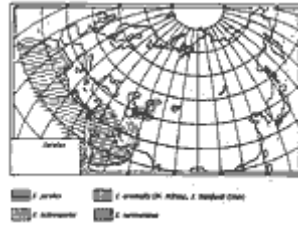
Jerboas

The jerboa family, the Dipodidae, is made up of 10 living genera and 26 species. They are generally steppe or desert dwellers that occur throughout the arid part of the southern Palearctic region, from the Sahara across southwestern and Central Asia to the Gobi Desert. Sizes of genera range from that of a small mouse to a large rat (i.e. the average weight of *Jaculus orientalis* is 134 grams according to Nowak and Paradiso). The distribution of *Jaculus*, the genus dissected, is illustrated in Figure 2.

Several physical features have enabled the jerboas to become excellent jumpers. Their hind legs are often over four times the length of their fore limbs. In all subfamilies other than Cardiocraniinae, the three central foot bones are fused into a single cannon bone. This feature gives added strength and support. The jerboas that live in loose, sandy soil have tufts of hair under the digits and soles of their hind feet. This feature aids in creating increased friction and helps to support the animal. The opening of the external ear is

protected from wind blown sand by bristly hairs located in the pinna region. The auditory bulla is greatly inflated.

Figure 2.



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Figure 2. Distribution of *Jaculus*. Reproduced from Corbet, 1978, Map 74.

Coloration of the pelage is somewhat variable. In *Jaculus orientalis* the upper portions are pale to dark sandy or buffy, the under parts, whitish with a whitish stripe on the hip; the eyes and ears are fairly large; the upper incisors are grooved, and there are no premolars.

Burrows are often in hard ground and at depths of 1-2 meters. Shredded vegetation or camel's hair usually line the sleeping chamber. *Jaculus orientalis* also excavates a food storage chamber. The diet of *Jaculus* includes roots, sprouts, seeds, grains and cultivated vegetables. Such food caching is important in distributing the seeds of desert plants, since those that are not eaten may grow.

ACKNOWLEDGEMENTS

I would like to thank Dr. John Wahlert for his remarkable patience, generous sharing of knowledge and insight and for the use of two unpublished drawings of skulls (*Jaculus orientalis*). I am grateful also, to the instructors of the Natural Sciences Department for preparing me to undertake such a project, to Dr. Ronald Schwizer for impressing upon me the importance of precision and accuracy when producing and labeling scientific illustrations, to Dr. Emil Gernert for aiding in my recognition of anatomical and physiological systems, to Dr. Guy Musser and the Department of Mammalogy at the American Museum of Natural History for their generous donation of specimens and office space, to Mr. Chester Tarka and Ms. Loraine Meeker for their help in preparation of visual aids required for my greater understanding of the anatomical structure of my specimen. And finally to my wife, Belinda, for her patience and support throughout the many months of research and also for her time spent typing the final paper.

MATERIALS AND METHODS

A head of *Jaculus orientalis*, the Egyptian jerboa, was dissected with fine forceps and a Nikon SMZ 10 stereomicroscope. A record of anatomical detail was kept in the form of labeled drawings. Specialized anatomical works served as guides to identify structures in the head: Greene, 1935; Howell, 1926; Klingener, 1964; Miller, 1964; Wahlert, 1974. Skulls of *Jaculus orientalis*, *Jaculus jaculus*, and *Allactaga bullata* were examined in order to verify the consistency of position of the foramina, the pathways of nerves and vessels through bone. Published data on the cranial characteristics of other kinds of rodents provided a basis for broader comparisons: Bugge, 1971; Musser and Newcomb, 1983; Wahlert, 1972, 1974, 1985b. No thorough study of foramina in hystricomorphs has been done, and detailed comparison with them was not possible. The alcoholic specimen and skulls examined are as follows:

Jaculus orientalis. AMNH (American Museum of Natural History) 201942 (alcoholic specimen dissected), AMNH 2363, AMNH 4329, AMNH 70003, AMNH 80007. New York Zoological Society.

Jaculus jaculus. AMNH 8005, AMNH 8006. New York Zoological Society.

Allactaga bullata. AMNH 58691. Mongolia.

Unidentified arvicolid (muroid rodent). No locality data.

RESULTS - CRANIAL ANATOMY OF JACULUS ORIENTALIS

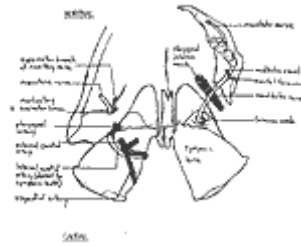
Vessels

Cranial foramina, the pathways of nerves and vessels through bone, are labeled in figures 3 - 17. The common carotid artery was found to split into the internal and external branches ventral to the auditory bulla. The internal carotid continues rostrally and travels along the medial surface of the bulla to enter the carotid canal between the bulla and the basal plate of the occipital bone. The vessel is then able to reach the interior of the skull and give off branches to the brain. The stapedia artery branches from the cervical portion of the internal carotid artery outside of the middle ear. It pierces the tympanic bulla in an area lateral to the jugular foramen, entering the stapedia foramen. The artery then traverses the middle ear by way of the stapedia artery canal and crosses the periotic (Wahlert, 1974). Another branch of the internal carotid is the pharyngeal artery; it descends just rostral to the tympanic bulla and supplies blood to the soft palate.

The external carotid artery continues anteriorly and gives rise to a major branch, the external maxillary artery. This branch extends rostrally in close association with the anterior facial vein and its divisions. Both the external maxillary artery and anterior facial vein pass between the superficial masseter muscle group and the digastric anterior

muscle. After both of the aforementioned arteries and vein give tiny branches to the cutaneous regions, the vessels continue rostrally and divide further. Many of the divisions of the external maxillary artery coincide with a matching division of the anterior facial vein. The submental artery arises from the external maxillary artery at the anterior belly of the digastric muscle. It travels between the digastric and the mylohyoid and supplies both muscles. The artery continues rostrally to the transversus mandibularis muscle, the platysma and the integument of the submental region.

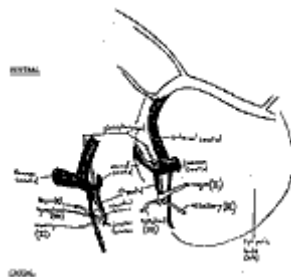
Figure 3.



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Figure 3. Reproduced from laboratory drawing, B. Sheets: *Jaculus orientalis*. [ventro-caudal view]

Figure 4.



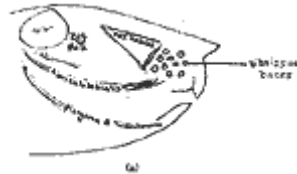
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Figure 4. Reproduced from laboratory drawing, B. Sheets: *Jaculus orientalis*. ventro-caudal view

Figure 5.

Figures 7 & 8. Reproduced from laboratory drawings, B. Sheets: *Jaculus orientalis*.
[Fig. 7: ventro-caudal view. Fig. 8: ventral view]

Figure 9a.



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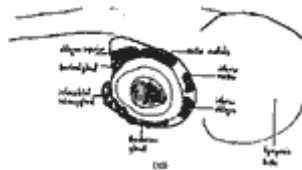
Figure 9b.



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Figures 9a & 9b. Reproduced from laboratory drawing, J. Wahlert: *Jaculus orientalis*.
[lateral view: right side]

Figure 10.



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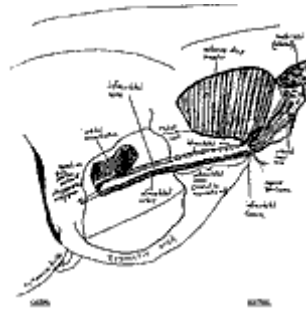
Figure 11.



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Figures 10 & 11. Reproduced from laboratory drawings, B. Sheets: *Jaculus orientalis*.
[left orbit]

Figure 12.



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Figure 12. Reproduced from laboratory drawing, B. Sheets: *Jaculus orientalis*. [lateral view: right side]

The external carotid continues laterally to a fork. The posterior auricular artery runs posteriorly in the space between the tympanic bulla and the ramus of the mandible. Partially covered by the parotid gland, it continues ventral and slightly caudal to the ear. This artery and a similar venous system supply and drain respectively, the levator auris longus muscle, the auricle and of the occipital region surrounding the ear. The external carotid turns anteriorly and immediately gives off the masseteric artery to the muscle and the anterior auricular artery. The artery divides into two branches after passing medial to the parotid gland. One branch supplies the exorbital lacrimal gland, the other continues dorsally to the anterior portion of the auricle. The associated anterior auricular vein, which drains these structures into the jugular vein is located ventro-caudal to the anterior auricular artery.

The superficial temporal travels rostrally along the lateral surface of the masseter, a branch of which enters and supplies the muscle. Another division, the middle temporal branch, supplies the temporalis muscle. The transverse facial artery is a branch of the internal maxillary. It follows the zygomatic arch rostrally and supplies the masseter muscle and the integument of the region.

The infraorbital artery emerges into the orbit from the cranium and sends small branches to the inferior rectus and inferior oblique muscles of the eye. Another branch crosses the orbit anteriorly, passes through the infraorbital canal, and emerges via the infraorbital foramen onto the side of the rostrum. It is accompanied by the infraorbital nerve and vein. The artery and vein supply and drain the levator labii muscle of the vibrissae. The nerve sends several branches ventrally to labial tissues along with divisions to each mystacial vibrissae and surrounding tissue. The infraorbital vein appears dorsal most. The nerve is ventral to the vein and dorsal to the infraorbital artery. The vessels and nerve are

separated in a bony passage from the anterior part of the medial masseter muscle that also passes through the canal.

Small portions of bag-like transverse sinuses can be seen within the postglenoid foramen. It is there that they unite with the internal maxillary vein before possibly joining with the superficial temporal vein. This was not clear in the dissection.

Nerves

The orbital fissure is a large unossified area, opening between the orbitosphenoid bone medially and alisphenoid laterally. The orbital fissure transmits the lacrimal, oculomotor (III,) trochlear (IV,) abducens (VI) nerves and several divisions of the trigeminal (V) nerve (Figures 11,13). The lateral wall of this region formed by the rostral edge of the alisphenoid bone is called the sphenoidal fissure. The large optic foramen which is entirely within the orbitosphenoid bone, transmits the optic nerve (II).

The trigeminal nerve branches into the maxillary and mandibular divisions. These buccinator and masseteric branches of the maxillary nerve travel anteriorly through the alisphenoid bone and emerge separately from the masticatory and buccinator foramina (Figure 3). After leaving the orbital fissure, the main trunk of the maxillary nerve in contact with the maxillary bone, travels rostrally into the infraorbital canal where it is named the infraorbital nerve (Figure 12). Rostral to the infraorbital foramen, various branches of the infraorbital nerve fan out as the external nasal and superior nasal nerves. The external nasal branches terminate at the nose and muzzle. Superior labial branches supply the skin of the upper lip and mucous membrane of the mouth.

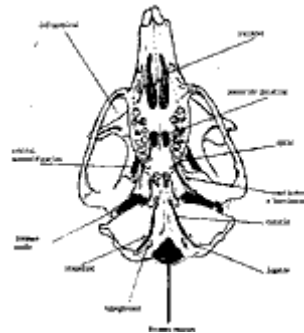
The mandibular division of the trigeminal nerve passes through the foramen ovale; rostrally it branches into several smaller lingual nerves that penetrate the tip of the tongue. Another division of the mandibular nerve continues around the pterygoideus internus muscle to the opening of the mandibular canal, the mandibular foramen, in the caudomedial surface of the mandible (Figure 3). The canal extends rostrally until it opens as the mental foramen on the lateral surface of the mandible. Within the mandible, small inferior dental branches of the mandibular nerve supply the molar teeth, and branches enter the incisor alveolus.

The contents of two foramina in the orbit could not be determined due to poor preservation of deep tissue. The artery, vein, and nerve that pass through the sphenopalatine foramen were not seen. The contents of the ethmoid and interorbital foramina, likewise, could not be found.

The facial nerve (VII) emerges from the stylomastoid foramen; it runs rostrally and ventral to the external auditory meatus (Figure 5). Ventral to the meatus the nerve splits and a dorsal branch diverges. A tiny ramus of this division extends caudally into the auricle. The greatest portion of this division, the auriculopalpebral nerve, runs dorso-

rostrally lateral to all carotid artery branches and terminates within the exorbital lacrimal gland. The second main division of the facial nerve, travels rostrally after passing ventral to the external auditory meatus. This branch, the buccolabial nerve, while remaining lateral to all carotid artery, branches, passes medial to the posterior and anterior auricular veins. It continues rostrally, lateral to the masseter muscle, until it reaches the superficial muscles of the face, nose and upper lip (Figure 9).

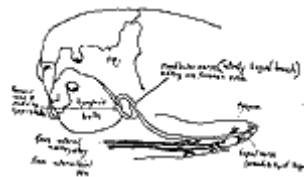
Figure 13.



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Figure 13. Cranial foramina of *Allactaga bullata* (AMNH 58691), ventral view. [Reproduced from laboratory drawing: B. Sheets]

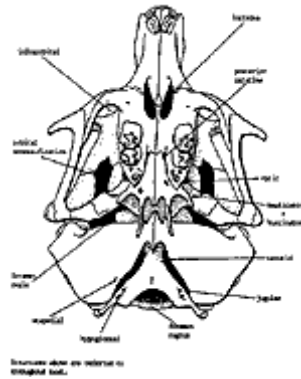
Figure 14.



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Figure 14. Reproduced from laboratory drawing, B. Sheets: *Jaculus orientalis*. [mandibular nerve & lingual dissection]

Figure 15.



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Figure 15. Cranial foramina of *Jaculus orientalis* (AMNH 8007), ventral view. [Reproduced from unpublished monograph: J. Wahlert]

In this dissection, the only clear divisions of the hypoglossal nerve (XII) were those which penetrated the infrahyoid muscles, the posterior belly of the digastric and sternohyoid muscles (Figure 8). This nerve group expands from the ansa hypoglossi of the upper neck region. The hypoglossal nerve (XII) emerges from the hypoglossal foramen.

Three major cranial nerves emerge together from the jugular foramen (Figure 4). The glossopharyngeal nerve (IX) passes medial to the external carotid artery as it travels rostrally. The main division continues anteriorly and passes medial to the anterior belly of the digastric immediately ventral to the lingual artery. The nerve continues rostrally to terminate in the stylopharyngeus muscle and mucous membrane of the tongue. As the vagus nerve (X) emerges from the jugular foramen a bulbous ganglion appears ventro-caudal to the opening. The vagus emerges rostral to the hypoglossal (XII) and spinal accessory (XI) nerves. After leaving the jugular foramen it travels caudally into the neck to the sympathetic plexus, which was not studied here. The spinal accessory nerve (XI) emerges from the jugular foramen caudal to the vagus nerve and lateral to the hypoglossal nerve. A small bulb of cervical ganglion exists (TX) antero-medial to the junction of the common carotid, external carotid and internal carotid arteries.

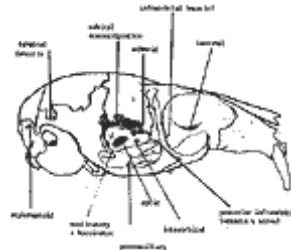
Other Cranial Structures

The lacrimal foramen pierces the maxillary bone anterior to the orbit and leads into the lacrimal canal or tear duct. The lacrimal gland and nerve were clearly visible in the specimen dissected, but the lacrimal duct was obscured by connective tissue.

Jerboas do not have temporal foramina. The temporal fenestra, a large window through the bone in the posterior part of the skull roof, does not transmit any vessels or nerves. It

is not the same as the foramen that has been described in other rodents. The angle of the mandible, the posteroventral flange, contains a large fenestra. It is covered with connective tissue and does not transmit anything.

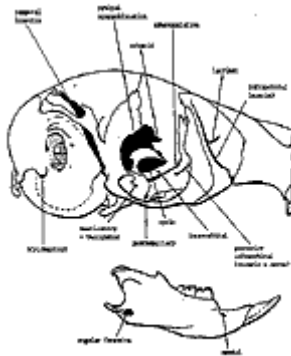
Figure 16.



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Figure 16. Cranial foramina of *Allactaga bullata* (AMNH 58691), lateral view. [Reproduced from laboratory drawing: B. Sheets]

Figure 17.



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Figure 17. Cranial foramina of *Jaculus orientalis* (AMNH 8007), lateral view. [Reproduced from unpublished monograph: J. Wahlert]

DISCUSSION AND CONCLUSIONS

A survey of other skulls of *Jaculus orientalis*, *Jaculus jaculus* and *Allactaga bullata* and comparison with descriptions in Corbet (1978) and Ellerman (1940) showed that the observed patterns of cranial foramina are relatively constant in jerboas. This study's determination of what passes through the foramina in *Jaculus orientalis* is a means by

which to link mammalogy with paleontology. Identification of the contents of cranial foramina by dissection of the specimen AMNH 201942 yielded information that can be compared with fossil skulls. Cranial foramina can be used for the classification of fossil skulls since no soft tissue remains. Since there are no thorough studies of muroid or sciurid cranial foramina that have been published, comparison of jerboas to them is limited to a few well known features summarized by Wahlert (1985b).

Several specialized features of dipodoids are shared with muroids and indicate common origin or close relationship. In jerboas and muroids the anterior part of the medial masseter passes through an enlarged infraorbital canal and arises from the rostrum. This feature does not occur in sciurids in which the medial masseter is restricted to the orbital side of the zygoma, the primitive condition. The sciurids have a small infraorbital canal that transmits only a nerve and several blood vessels. Another specialized feature common to both is the situation of the entrance to the lacrimal canal on the side of the rostrum anterior to the zygoma. In sciurids the entrance is in its primitive position in the anterodorsal part of the orbit. It is interesting to note that the hystricomorphs, which have a similarly extended medial masseter and enlarged infraorbital canal, retain the entrance to the lacrimal canal in its primitive orbital position (Wahlert, 1985b).

The stapedia artery branches from the internal carotid outside the middle ear in jerboas and muroids. The primitive branching point, seen in a few fossil protrogomorphous rodents (Wahlert, 1974) was within the middle ear. Wible (1985) demonstrated from embryos that the squirrels retain this primitive condition, but as development progresses the anterior continuation of the internal carotid artery disappears.

Temporal foramina are lacking in both jerboas and muroids. They are commonly present in sciurids and primitive rodents.

Although dipodoids and muroids share many specialized features that indicate their close relationship, there are also some differences. In dipodoids the lateral masseter remains restricted to the ventral part of the zygomatic arch as in protrogomorphs; it does not extend anteriorly as in muroids. The jugal bone retains its primitive anterior extent and reaches the lacrimal bone; in muroids the jugal is greatly reduced in length. Dipodoids have one peculiar characteristic that is not known in other groups of rodents. Within the ventral part of the infraorbital canal a small lamina of bone separates the vessels and nerve from the portion of the medial masseter that is also passing through to reach the rostrum. The combination of characters more primitive than those in muroids and the presence of the unique, specialized condition of the infraorbital canal show that although dipodoids may be closely related to muroids, they cannot have evolved from any known member of that group.

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