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Comparative cranial anatomy of rattus norvegicus and proechimys trinitatus

Richard Marcin
Baruch College

COMPARATIVE CRANIAL ANATOMY OF RATTUS NORVEGICUS AND PROECHIMYS TRINITATUS

by
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ABSTRACT

The head of the rat, *Rattus norvegicus*, and head of a South American rodent, *Proechimys trinitatus,* were dissected, and nerves and blood vessels leaving and entering the skull were traced. Cranial foramina in *Proechimys* were identified and named on the basis of comparison with the rat and anatomical literature on the rat and other mammals. The purpose of this paper was to provide information on cranial morphology (especially on cranial foramina) of *Proechimys trinitatus,* a New World caviomorph (Guinea pigs and

their relatives), to point out its differences from the *Rattus norvegicus,* a myomorph rodent (rats, mice, hamsters, etc.), and, if possible, to use this comparison to comment on the current theories about rodent phylogeny. *Proechimys* and *Rattus* show many differencies in cranial anatomy that reflect different arrangements of parts of the masseter muscle that characterize the suborder of Rodentia to which they belong. The absence of several cranial foramina in *Proechimys* are associated with the lack of an internal carotid artery; its branches are a part of the external carotid system. This paper should provide meaningful new data about *Proechimys* that can be used in the future to better understand relationships between rodents.

INTRODUCTION

Guinea pig - a rodent or not?

It is known that the current classification of rodents is inadequate and unclear. Many controversies in classification arise because of this inadequate knowledge that we have about rodents. The guinea pig *(Cavia porcellus),* Suborder Caviomorpha (Guinea pigs and their relatives), has been classified as a New World (the Americas) hystricomorph rodent for about two centuries. However, Graur et al. (1991) suggested that guinea pigs and probably all of the caviomorphs and Old World (Eurasia and Africa) hystricomorphs might not even be rodents and thus should be separated from the Order Rodentia as a distinct Order Hystricomorpha. They theorized that guinea pigs diverged from myomorph rodents (mice, rats and their relatives) "before the separation between myomorph rodents and a lineage leading to primates and artiodactyls" (Graur et al., 1991). D'Erchia et al. (1996) studied all of the 14 complete mammalian mitochondrial DNA sequences that were available and that represented eight different orders. Their phylogenetic tree, based on the mtDNAs, showed clearly that the guinea pig does not belong among myomorph rodents (rat, mice) and is not derived from them. This is not surprising, as they have long been considered part of a separate branch of the Rodentia. D'Erchia et al. (1996), on the basis of mitochondrial DNA analysis, identified the guinea pig as an outgroup to Lagomorpha/Primates/Carnivora/Perissodactyla/Artiodactyla (+Cetacea), as opposed to Graur et al (1991), according to whom the guinea pig is an outgroup of myomorph rodents, primates and artiodactyls. These studies are flawed with respect to rodents because other basic branches such as the squirrels and dormice were not included.

It is generally agreed upon that a classification of animals "should reflect the underlying relationships of the animals involved" (Wood, 1955). Scientists often disagree however, on criteria that should be used to determine these relationships. Many relationships within the Order Rodentia are unclear. The best that can be done is to use "that type of classification, which involves the use of key characters, and sets up a classification based on arbitrary criteria, into which all forms can fit" (Wood, 1955). The problem with this approach is that some groups may seem unnatural from the phylogenetic point of view. This is the case of rodents.

"*The defining characteristics of the members of the order Rodentia are a brain with few convolutions; a cerebellum that is not covered by the cerebral lobes; a single row of superior chisel-shaped incisors and inferior incisors that exhibit continuous growth; a wide diastema between the incisors and cheek teeth into which the cheeks can extend and meet in the midline, thus separating the rostral and caudal portions of the mouth; four cheek teeth per side in upper and lower jaws; well-developed masseters; the presence of clavicles; a large cecum; and the fact that they are generally pentadactylous and plantigrade.*" (Feldhamer et al., 1999)

According to this definition, guinea pigs certainly are rodents, but it does not say anything about the evolutionary position of the guinea pig. A better definition would include a phylogenetic description besides a morphological description.

Rodents

The Order Rodentia is the largest mammalian order with approximately 2016 species in 28 families. Given such diversity and adaptability, it is not surprising that classification of rodents is extremely difficult and often controversial.

Three suborders of the Rodentia are recognized, based on three different arrangements of the divisions of the masseter muscle (the main adductor of the mandible) and on the skull structures that accommodate the muscle divisions. The primitive condition, from which the three modern divisions of rodents evolved, is the one in which the masseter muscle originated entirely on the zygomatic arch and is termed the protrogomorphous condition (See Fig. 1). Rodents rapidly diversified in the late Eocene (over 40 million years ago) in ways that allowed more effective gnawing with the incisors and grinding with the cheek teeth. The changes involved mainly the masseter muscle, its areas of attachment, and the infraorbital foramen, which lets nerves and blood vessels pass anteriorly through the zygomatic arch (cheek bone) to the side of the rostrum. Brandt (1855) subdivided the Order Rodentia based on this morphology (Fig. 1):

· Suborder Myomorpha (e.g. mice, rats, hamsters and their relatives): Most rodents, have a pattern of zygomasseteric specialization named myomorphous. "In such rodents, the anterior part of the lateral masseter originates on the highly modified anterior extension of the zygomatic arch (forming the zygomatic plate [which compresses the ventral part of the infraorbital foramen]) and the anterior part of the medial masseter originates on the rostrum and passes through the somewhat enlarged dorsal part of the infraorbital foramen" (Vaughan et al. 2000). This is a combination of the hystricomorphous and sciuromorphous conditions (see below), both of which contribute to more effective gnawing. The coronoid process and temporalis muscle are reduced in many myomorphs.

· Suborder Hystricomorpha (e.g. New and Old World porcupines, guinea pig, Proechimys): In the hystricomorphous condition, the infraorbital foramen is greatly enlarged and the medial masseter's origin is shifted from the inside of the zygomatic arch

through the enlarged infraorbital foramen and onto the side of the rostrum (Vaughan et al. 2000). This increases anterior pull for more effective gnawing. The size of the coronoid process and the temporalis muscle are variable among families and genera.

· Suborder Sciuromorpha (e.g. squirrels and beavers): In the sciuromorphous condition, the origin of the anterior part of the lateral masseter is shifted to the anterior surface of the zygomatic arch and externally onto the side of rostrum; this compresses the infraorbital foramen. The new arrangement permits a stronger anterior force for gnawing. The coronoid process of the jaw is of moderate size, and the large temporalis muscle, which arises on the cranial roof, inserts here (Vaughan et al. 2000). Thus, the temporal muscle is also an important adductor of the jaw.

Every rodent also has one of the two types of the lower jaw, and an alternate division of Rodentia is recognized (Tullberg, 1899):

· Suborder Sciurognatha: In sciurognathous rodents the masseter inserts in part on the angle of the jaw, which arises ventral to the molariform dentition; this condition is deemed primitive in rodents.

· Suborder Hystricognatha: In hystricognathous rodents the masseter inserts in part on a deflected angular process that is mostly lateral to the body of the jaw; this is a derived condition.

The Myomorpha and Sciuromorpha have a sciurognathous mandible. Most, but not all hystricomorphs have a hystricognathous mandible.

Problem of New World Hystricognaths

Caviomorphs, which include porcupines, guinea pigs, chinchillas and capybaras, are rodents that are mostly endemic to South America. They have a large infraorbital foramen with medial masseter passing through it and originating anteriorly on the rostrum. The lower jaw is hystricognathous. Both of these characters are shared with Old World porcupines and other hystricomorphs, which have been grouped in the Suborder Phiomorpha. Both phylogenetic and paleogeographic data were taken into consideration when Caviomorpha were named a distinct clade or branch that is separated from the Old World hystricomorph clade. This is to say, that there are no known fossil Old World rodents with morphology suggesting ancestry of caviomorphs (Wood, 1950). Thus it is a strange fact that caviomorphs and Old World hystricomorphs share almost the same morphological features. According to Wood (1955), "the resemblances to the caviomorphs of the forms here included in the Hystricomorpha are surely parallelisms, rather than due to any kind of trans-Atlantic transportation." Even though this conclusion was based on a fixed continent model of the geologic history, the problem remains since South America and Africa were already some distance apart in the Eocene, before these rodents could have diverged. The traditional explanation for the problem of the New

World caviomorphs has been affirmed by Patterson and Wood (1982); they proposed that the two hystricomorphous suborders (caviomorphs and phiomorphs) probably evolved independently of each other. The debate continues on this issue.


Scope of this study

The purpose of this paper is to describe the cranial anatomy of *Proechimys* (Caviomorpha, Echimyidae), a relative of the Guinea pig. Since *Proechimys* is much more primitive than the Guinea pig, its cranial anatomy is easier to compare with that of sciuromorph and myomorph rodents to assess relationships. This paper is based on comparison of cranial foramina of a rat (myomorph rodent) and *Proechimys*.

Foramina allow nerves, blood vessels and occasionally muscles to pass through the bones of the skull. The presence or absence and position of foramina can be very useful in determining evolutionary relations among rodents (e.g. Wahlert, 1983; Wahlert et al., 1993), when usual methods of comparing masticatory muscle divisions, mandibular shape, and cheek tooth morphology do not provide conclusive evidence.

Although there is a published anatomy of a Guinea pig (Cooper and Schiller, 1975), it contains many errors and misleading information; some of these are noted below.

Proechimys

Proechimys belongs to the family Echimyidae of the caviomorph hystricognath rodents. They are small rat-like rodents with short limbs and generally large eyes and ears. Proechimys has a life expectancy of 10.3 months, feeds of cottonseeds and prefers damp localities near rivers. The distribution of living *Proechimys* in South America is indicated at figure (2). The Family Echimyidae contains 20 genera and is one of 13 families of caviomorph rodents (Woods, 1992).
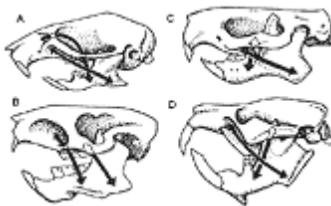
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Figure 1: Position of lateral and medial divisions of masseter muscle in rodents (superficial layer omitted). A, a myomorph, the lateral division is as in sciuromorphs, but the medial division has pushed up through the orbit and passes through the infraorbital foramen onto the rostrum. B, a hystricomorph, the lateral division of the masseter arises

on the zygomatic arch, but the medial division passes through the infraorbital foramen onto the rostrum. C, a protrogomorph, the entire masseter originates mainly from the lower edge of the zygomatic arch. D, an advanced sciuromorph, the lateral division of the masseter originates from the side of the rostrum, the medial division from the medial side of the zygomatic arch. (after Romer, 1966, fig. 437).

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Figure 2: Distribution of the Family Echimyidae. Reproduced from Anderson (1984).

MATERIALS AND METHODS

The head of a laboratory rat was dissected under a Nikon stereomicroscope using forceps and other fine tools. Observed structures were compared with the *Anatomy of the Rat* (Greene, 1935). The purpose of the dissection was to practice the method, to observe pathways of cranial nerves and blood vessels entering and leaving the skull, and to use this knowledge as a basis for comparison with *Proechimys*. *Proechimys* was also dissected under a Nikon stereomicroscope with fine tools. Several anatomical works served as guides to dissections and identifying structures: Greene, 1935; Miller, 1964; and Wahlert 1974. Skulls of *Rattus norvegicus* and *Proechimys trinitatus* were used to see the positions of foramina clearly during the dissection.

The skulls and alcoholic specimens used are as follows:

- *Proechimys trinitatis.* AMNH 209029 (alcoholic specimen dissected). Trinidad:
- *Cumaca.* Trinidad Regional Virus Lab.
- *Proechimys trinitatis*. AMNH (American Museum of Natural History) 7651/6037.
- AMNH 7651/6038 Trinidad and Tobago: Trinidad; Caura.
- *Rattus norvegicus.* AMNH 77723. Brooklyn Museum.
- *Rattus norvegicus.* AMNH 70184. New York.
- *Rattus norvegicus.* Preserved specimen dissected - purchased.

RESULTS

The focus of this section is on identification of skull structures (Figures 3-6), especially foramina, which are defined by the nerves and blood vessels that pass through them (Figures 7-19). The following description tells chiefly how nerves and blood vessels relate to the skull bones. Only one side of the head is described, since most nerves and blood vessels are bilaterally symmetrical. Pathways of the nerves and blood vessels and the corresponding cranial foramina are labeled in figures 3-19. The small size of vessels and poor preservation of *Proechimys* made it impossible to trace every connection of vessels; such vessels are thus described in isolation.

Cranial Nerves of the Rat and Proechimys

1. Olfactory - doesn't leave the skull.
2. Optic - emerges from the **Optic foramen** and extends into the retina of the eye. (Fig. 9)
3. Oculomotor - emerges from the **sphenoidal/orbital fissure** as the major nerve of the muscles of the eye.
4. Trochlear - also emerges from the **sphenoidal/orbital** fissure, supplies dorsal oblique muscle of the eye.
5. Trigeminal (Fig. 17)
    1. Opthalmic division - emerges from the **sphenoidal/orbital fissure**; all of its branches remain in the orbit, except one that goes to the **supraorbital foramen**. The opthalmic nerve is the major sensory nerve of the orbit.
    2. Maxillary division- the largest of the trigeminal branches, passes out of the skull with the opthalmic division through the **sphenoidal/orbital fissure**. It extends anteriorly over the floor of the orbit in the infraorbital fossa and is referred to as the infraorbital nerve. It is the major sensory nerve of the cheek, nose, soft and hard palates, nasopharynx and upper jaw.
    3. Mandibular division -emerges from the **foramen ovale** and divides into 2 major branches that are separated by a bony bridge:
        1. Anterior part: consists of the buccinator and masseteric nerves leaving through the **buccinator/masseteric foramen.**
        2. Posterior part: gives off lingual, auriculotemporal, mylohyoid and inferior alveolar nerves.
6. Abducens - emerges from the **sphenoidal/orbital fissure**, and goes to the lateral rectus muscle of the eye.
7. Facial -leaves the cranial cavity through the **stylo-mastoid foramen**, which is posterior to the auditory meatus. The nerve splits as it passes the meatus and the auriculopalpebral nerve extends to the auricle and exorbital lacrimal gland. (Fig. 13)
8. Acoustic - does not leave the skull (also called the Vestibulocochlear nerve).
9. Glossopharyngeal -leaves the skull through the **posterior lacerated foramen**, and its branches reach the parotid and salivary glands, the tongue and pharynx. (Fig. 7)

10. Vagus - the longest cranial nerve, it leaves the skull through the **posterior lacerated foramen**, and traverses the neck, thorax and abdomen. It emerges rostral to the hypoglossal and spinal accessory nerves and travels posteriorly to the neck. (Fig. 7)
11. Spinal Accessory - leaves through the **posterior lacerated foramen**. It emerges posterior to the vagus and lateral to the hypoglossal nerve. (Fig. 7)
12. Hypoglossal - leaves through the **hypoglossal foramen**. (Fig. 7)

Blood Vessels

Rat

The common carotid artery in the rat splits into the internal and external carotid arteries ventral to the auditory bulla. The internal carotid gives off the stapedial branch which enters the auditory bulla, while the main trunk continues anteriorly before it enters the carotid canal and supplies the brain. The external carotid continues anteriorly and supplies most of the structures of the head. (Fig. 10)

The stapedial artery emerges from the bulla and continues anteriorly as the pterygopalatine artery. One of its branches enters the orbit through the optic foramen and extends anteriorly in the infraorbital fossa as the infraorbital artery.

The infraorbital artery emerges in the orbit and supplies the eye muscles. Another branch of the artery continues anteriorly, passes through the orbit, and emerges from the infraorbital canal, onto the rostrum. It is accompanied by the infraorbital nerve and vein.

The external carotid artery gives off ascending pharyngeal and lingual arteries (Fig. 11) before it gives off the external maxillary, which continues anteriorly to the mandible and divides into smaller vessels. Branches of the anterior facial vein accompany most of the divisions of the external maxillary artery. Then the external carotid turns dorsally toward the ear and gives off the posterior auricular artery, which supplies the region posterior to the auditory bulla. The external carotid turns anteriorly and gives off the masseteric artery to the masseter muscle, and the anterior auricular artery, which supplies the region anterior to the auditory meatus and external ear; the latter is associated with the anterior auricular vein, which drains into the posterior facial vein.

The superficial temporal artery, with the superficial temporal vein, continues anteriorly along the surface of the masseter, giving off the middle temporal branch to the temporalis muscle. (Fig. 10)

Proechimys

Arteries

The Common Carotid Artery becomes the external carotid as it passes the ramus of the mandible even though it does not give off an internal carotid artery; it gives off these branches:

1. Superficial Temporal A. splits into
    1. Caudal Auricular - gives off 3 branches and continues to the posterior external ear
        1. Stylo-mastoid - enters the skull through the **stylo-mastoid foramen**.
        2. Unnamed branch #2 - supplies superficial tissues and muscles posterior to the ear
        3. Unnamed branch #3 - passes medial to the lateral supraoccipital process and splits into 2 branches: one enters **unnamed foramen** in the groove on the dorsolateral edge of the occipital bone; the other extends to the splenius muscle.
    2. Rostral Auricular - supplies anterior external ear, its infra-tympanic branch goes into the infra-tympanic canal.
2. Lingual - probably lost during the dissection
3. Facial - leaves the external carotid at the ramus of the mandible. It crosses the mandible and runs on the lateral surface toward the mouth. It supplies facial and cervical tissues.
4. Internal Maxillary - leaves the carotid at the temporomandibular joint and runs medially to the masseter.

Infraorbital artery - The origin of this artery was not discovered during the dissection. It gives off the following branches in the orbit before it leaves anteriorly via infraorbital canal and reappears on the rostrum. Branches:

Internal ethmoidal - enters ethmoidal foramen.
Maxillary alveolar - enters alveolar foramen.

Veins:

Since the walls of veins are composed mainly of thin connective tissue, it is extremely difficult to observe them in specimens such as this that were not fixed with formaldehyde. Only the largest veins are usually preserved. In the dissected *Proechimys*, only the vein coming from the transverse sinus (leaving the skull through the **post-glenoid foramen**) and joining the posterior facial branch of the external jugular was visible.

## Abbreviations for bones, their processes and cranial foramina:

ab, auditory bulla	mf, mastoid foramen

|	
ac, alisphenoid canal	ml, molar teeth
alf, anterior lacerated foramen	mlf, middle lacerated foramen
ap, alveolar process	n, nasal bone
apf, anterior palatine foramen	oc, occipital bone
as, alisphenoid bone	of, optic foramen
bmf, buccinator/masseteric foramen	p, parietal bone
bs, basisphenoid bone	pap, palatine process
cc, carotid canal	pc, occipital condyle
eam, external auditory meatus	pf, postglenoid foramen
epp, external pterygoid process	pl, palatine bone
f, frontal bone	plf, posterior lacerated foramen
fm, foramen magnum	pm, premaxillary bone
fn, anterior ethmoidal foramen	pmf, posterior maxillary foramen
fo, foramen ovale	pmn, posterior maxillary notch
ic, interpterygoid foramen	pop, paraoccipital process
if, infraorbital foramen	pp, paramastoid process
in, incisive foramen	ppf, posterior palatine foramen
int, interparietal bone	ps, presphenoid bone
ipp, internal pterygoid process	ptf, petrotympanic fissure
j, jugal bone	smf, stylomastoid foramen
lps, lateral process of the supraoccipital	sq, squamosal bone
m, maxillary bone	
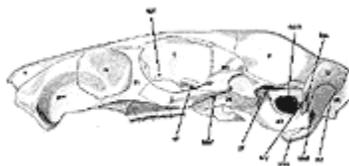
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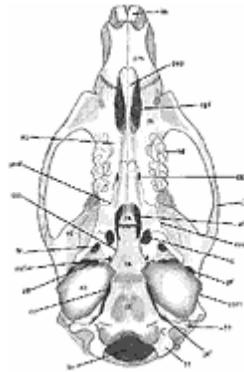Figure 3: Reproduced from laboratory drawing, R. Marcin: *Proechimys trinitatus*. (lateral view).
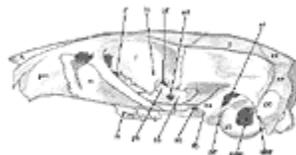
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Figure 4: Reproduced from laboratory drawing, R. Marcin: R*attus norvegicus*. (lateral view)
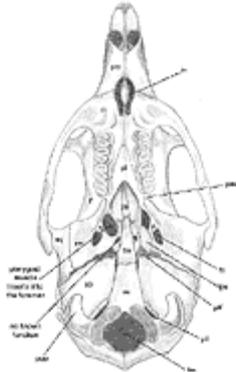
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Figure 5: Reproduced from laboratory drawing, R. Marcin: *Proechimys trinitatus*. (ventral view). Note: the lateral process of the supraoccipital (labeled lps) on the right side was removed to reveal the underlying structure.

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Figure 6: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*. (ventral view)

Cranial foramina and the blood vessels and/or nerves passing through them comparison of the rat and *Proechimys*. See Figures 3-6. Skull

- **Alisphenoid canal:** passes through the alisphenoid bone and contains the internal maxillary artery in the rat; the canal is missing in *Proechimys*.

- **Anterior Alveolar Foramen:** is situated on the floor of the infraorbital fossa and transmits the anterior alveolar nerve.

- **Buccinator/Masseteric foramen:** transmits the buccinator and the masseteric branches of the mandibular nerve.

- **Dorsal Palatine Foramen:** is found in the infraorbital fossa in the suture between the maxillary and palatine bones medial to the roots of the upper dentition. It is entirely missing in *Proechimys*. Its function is taken over by a notch and dorso-ventral channel behind the upper teeth.

- **Ethmoidal Foramen:** is a very small foramen in the frontal bone in the orbit; the internal ethmoidal artery, vein and nerve pass through it.

- **Eustachian Canal:** emerges on the dorsal side of the anteromedial portion of the auditory bulla. It carries the Eustachian tube from the middle ear to the throat.

- **Foramen Ovale:** is a large foramen that transmits the mandibular division of the trigeminal nerve. See Figures 5 and 6 for comparison between the rat and *Proechimys*.

- **Hypoglossal Canal:** is located between the condyle and the posterior lacerated foramen the hypoglossal nerve passes through it.

- **Incisive foramen:** has an oval shape and occupies about half of the diastemal length; the suture between the premaxillary and maxillary bones laterally intersects the pair of them. Palatine vein and artery enter the foramen but they are tiny and were lost in both dissections.

- **Infraorbital Foramen:** opens from the orbit to the rostrum; it is much larger in *Proechimys* (hystricomorphy) then in the rat (myomorphy). The maxillary bone encircles the foramen. Infraorbital artery, vein and nerve pass from the orbit to the rostrum, but only the nerve was actually observed during the dissection; the blood vessels were too small. There is a nonossified area, where lacrimal, maxillary and frontal bones meet in the rat. The nonossification is completely missing in the *Proechimys*; the region is completely ossified.

- **Infra-tympanic Canal:** transmits the infra-tympanic artery.

- **Internal Carotid Canal:** is present in the rat only; it is medial to the auditory bulla and transmits the internal carotid artery. This artery is obliterated in *Proechimys* as it is in most hystricognaths (the exception is *Erethizon*, the New World porcupine - also a caviomorph).

- **Lacrimal canal:** is situated in the lacrimal bone on the side of the rostrum in the rat, but in *Proechimys*, the canal is ventral to the lacrimal bone, within the maxillary bone, and in the primitive position near the anterodorsal edge of the orbit. Nasolacrimal duct (tear duct) passes through it.

- **Mastoid foramen:** situated in the suture between the occipital and mastoid bones in the rat. It is also present in **Proechimys**, but it is situated entirely within the dorsomedial end of the mastoid bone.

- **Middle Lacerated Fenestra:** is anterior and anteromedial to the bulla it is missing in *Proechimys* but transversed by the internal carotid artery in the rat.

- **Optic foramen:** is entirely within the presphenoid (orbitosphenoid) bone in both dissected rodents. The foramen is dorsal and slightly posterior to the third molar in the rat but is much farther posterior in *Proechimys*. Transmits the optic nerve.

- **Posterior Lacerated Foramen (Jugular Foramen):** transmits the glossopharyngeal, vagus, and spinal accessory nerves.

- **Posterior Maxillary Foramen:** is present only in the rat, just posterior to upper teeth and medial to posterior end of maxillary bone.

- **Posterior Maxillary notch:** is present in *Proechimys* only, it is homologous to the posterior maxillary foramen, and replaces the palatine foramina that are present in the rat (dorsal and posterior palatine foramina). It is posterior to a spur of the palatine bone behind the upper teeth.

- **Posterior Palatine Foramen:** is present in the rat, but not in the *Proechimys*. It lies in the palatine bone medial to upper teeth.

- **Postglenoid Foramen:** pierces the squamosal bone dorsal to the bulla in the rat and dorsoanteriorly to the bulla in the *Proechimys*. It transmits a vein from the transverse sinus.

- **Sphenoidal/Orbital Fissure:** has the alisphenoid bone as its outer wall. It transmits oculomotor nerve, trochlear nerve, maxillary and opthalmic div. of the trigeminal nerve, abducens nerve, and internal maxillary artery and vein.

- **Sphenopalatine foramen:** in the rat, is located in the junction of maxillary, frontal and palatine bones in the orbit, dorsomedial to the roots of the upper teeth. It transmits the sphenopalatine nerve, artery and vein. In *Proechimys* the foramen is divided into three parts that lie entirely within the maxilla. The palatine bone is restricted to the posterior orbital floor in *Proechimys*, whereas it extends as far as the foramen in the rat.

- **Stylo-mastoid Foramen:** is posterior to the auditory meatus. Facial nerve and stylomastoid artery pass through it.

- **Supra-orbital Foramen:** transmits a branch from opthalmic branch of the trigeminal nerve.

Mandible

- **Mandibular foramen:** is on the medial side of the jaw, dorsoposterior to the teeth. It's the site of entrance of the inferior alveolar nerve.

- **Mental foramen:** is situated anteroventral to the cheek teeth; it is the site of the exit of the inferior alveolar nerve, observable in the rat only. It is missing in the *Proechimys*.
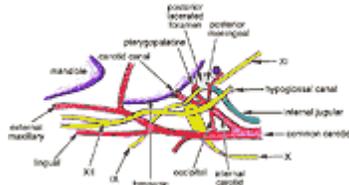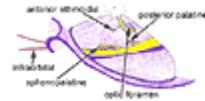

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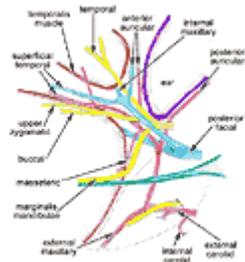Figure 7: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*. (ventral view)
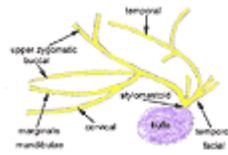
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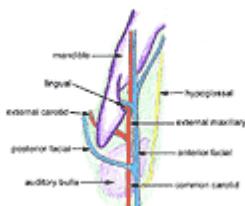Figure 8: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 9: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 10: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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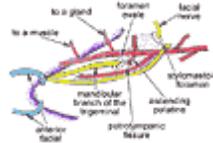Figure 11: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 12: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 13: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 14: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 15: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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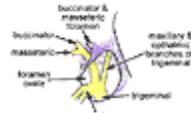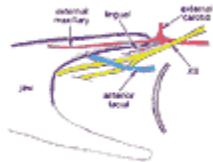Figure 16: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.
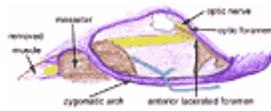

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Figure 17: Reproduced from laboratory drawing, R. Marcin: *Proechimys trinitatus*.

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Figure 18: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

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Figure 19: Reproduced from laboratory drawing, R. Marcin: *Rattus norvegicus*.

DISCUSSION

Both neontologists and paleontologists have been trying for the past two hundred years to understand the relationships among rodent groups. The major classification of Brandt (1855) divided rodents according to the origin and insertion of the masseter muscle and the morphology of the associated infraorbital foramen and zygomatic arch, into three suborders: Sciuromorpha, Myomorpha and Hystricomorpha. Tullberg (1899) based his classification on the angle of the jaw relative to its tooth bearing body and proposed two suborders: Hystricognatha and Sciurognatha. These two classifications are still in use and provide a good example of how difficult it is to classify rodents. Hystricognaths are only hystricomorphous, but sciurognaths can be protrogomorphous, sciuromorphous, hystricomorphous or myomorphous. The sciurognathous condition is presumably

primitive because it is found in the earliest rodents. Since the hystricomorphous condition is derived, then "several families (Anomaluridae, Ctenodactylidae, Dipoidae and Pedetidae) currently within Tullberg's (1899) Sciurognatha may actually represent a monophyletic group sister to the order Hystricognatha because they all share a hystricomorphous condition" (Nedbal et al. 1996), and they should be removed from the suborder Sciurognatha.

The New and Old World hystricomorphs share a series of morphological features including the ones in the masticatory apparatus. Therefore, one could claim, that they form a natural entity and share a common ancestor. As it was explained earlier, there are no fossils supporting this theory, because there are no known extinct Old World rodents that could be ancestors of the caviomorphs. Bugge (1971) studied cephalic arterial systems of the New and Old World hystricomorphs and concluded that they are nearly identical. The dissection has confirmed, too, that the caviomorphous cephalic arterial system does not have the internal carotid artery and that the vertebral artery supplies the brain. Cooper & Schiller's *Anatomy of the Guinea Pig* misses this very important point and claims that there is an internal carotid artery supplying the brain of the guinea pig.

Based on the dissections and comparison with the anatomical literature, cranial nerves appear to be quite constant not only in rodents but also in mammals. Miller's *Anatomy of the Dog* and Cooper's *Anatomy of the Guinea Pig* clearly confirm that there is little variation in pathways and target tissues of the cranial nerves. Arteries are variable (Bugge, 1971) and veins highly so. The positions of the cranial foramina reflect these differences as well as changes in the positions and functions of the bones that nerves, vessels and muscles penetrate. Since the foramina are defined by what passes through them, their presence or absence and their shifts in positions can reveal relationships between rodents that would otherwise not be so obvious. The following is a description of major differences in the positions and presence of the cranial foramina in the rat and *Proechimys*.

Rodents differ from other mammals in many aspects. The infraorbital canal is unique to rodents because the anterior part of zygoma has a box-like shape. In other mammals such as a cat or a dog, the anterior end of the zygomatic arch makes a smooth transition to the rostrum, while in rodents the arch turns sharply toward the rostrum. A feature typical of hystricomorph rodents is the medial division of the masseter muscle passing through the infraorbital canal with the vessels and nerves. This is a distinctive feature that is useful in classifying rodents. The guinea pig, for example, has the muscle passing through the foramen, and this poses a strong argument in favor of the guinea pig being a hystricomorph rodent. *Proechimys*, also a caviomorph hystricognath has the same large infraorbital foramen with a muscle passing through it. The rat, a myomorphous sciurognath has a considerably smaller infraorbital foramen with the muscle passing only through its dorsal part.

Palatine foramina are found in the rat only. The palatine nerve and artery enter the dorsal palatine foramen in the infraorbital fossa and exit through the posterior palatine foramen

to supply the hard palate. These foramina are completely missing in *Proechimys*, and the posterior maxillary notch posterior to upper dentition replaces them.

The lacrimal canal is within the lacrimal bone in the rat, but within the maxillary bone in Proechimys. Also, *Proechimys* has its lacrimal canal on the edge within the orbit while the rat has it shifted anteriorly onto the side of the rostrum.

Another feature found in *Proechimys* but not in the rat is presence of the lateral process of the supraoccipital. It is between the mastoid bone and the posterior end of the squamosal bone. According to Landry (1957), it is present in both hystricomorphs and nonhystricomorphs and, therefore, cannot be used as a feature to distinguish caviomorphs and Old World hystricognaths from the rest of rodents. The same applies to the paraoccipital process in *Proechimys*, which is deflected and follows the curvature of the tympanic bulla.

Blood vessels are more variable than nerves. In the rat, the common carotid artery extends anteriorly from the thorax and divides into the internal and the external carotid arteries. In *Proechimys*, the internal carotid is missing completely part of its function is replaced by the vertebral artery, which enters the skull through the foramen magnum.

The alisphenoid canal is also unique to rodents. In the rat, the internal carotid artery enters the canal through the posterior alar fissure and leaves the canal through the anterior alar fissure, which is lateral to the sphenoidal/orbital fissure in the braincase. This kind of long alisphenoid canal, covered laterally by the alisphenoid bone, is typical of rodents, but not all rodents have it. *Proechimys* has no alisphenoid canal since the internal carotid artery is missing completely. What looks like the alisphenoid canal on the skull is the pathway of the maxillary and opthalmic divisions of the trigeminal nerve. Other mammals, such as dogs, have a very short alisphenoid canal with the anterior opening being posterior to the sphenoidal/orbital fissure; many mammals lack the canal.

In the rat, the internal carotid gives off the stapedial artery upon reaching the tympanic bulla, and the main trunk continues forward for a short distance before it enters the carotid canal between the bulla and the occipital bone. The stapedial artery continues anteriorly out of the auditory chamber as the pterygopalatine artery. The vessel is named the infraorbital artery as it transverses the orbital fossa and gives off several branches to the orbit. In *Proechimys*, however, there is no internal carotid. The common carotid gives off branches that supply the neck and the face, but not the brain. In my dissection, I was unable to determine whether the infraorbital artery originates from the vertebral artery or from the external carotid, but I saw that it takes the same course as the corresponding artery in the rat. According to Bugge (1971), an anastomosis connects the facial arterial branch of the external carotid artery with the arterial system of the orbit in most caviomorphs. Since the internal carotid and the stapedial artery are missing, some outer vessel must deliver blood to the the orbit and brain in the case of the *Proechimys*; it is this new tube between the facial artery and infraorbital artery. Bugge's paper, however, does not describe the arterial pathways relative to the skull; from the absence of foramina, I presume blood supply to the orbit may come from outside of the cranium.

The venous system will not be discussed, as I was unable to trace the veins in *Proechimys*. The veins of the rat were injected with blue latex and were, therefore, visible. The venous system in the rat corresponds to the description given by Greene (1935) in the *Anatomy of the Rat.*

This work has pointed to several differences in anatomical features of the rat and Proechimys. It should serve as a basis for further study of caviomorphs and their relationships, especially to the Old World hystricomorphs. The data I have collected are not sufficient to confirm or repudiate any of the current controversies, but they do set stage for further research. As Wahlert (1974) showed, cranial foramina can be very useful in the further attempts to completely understand relationships among rodent groups.

The recent studies of Graur et al. and D'Erchia et al. use modern techniques of mtDNA sequencing for assessing relationships between rodents. However, it is still necessary to consider morphological data because fossils do not have DNA or have only small fragments that cannot be used comparatively, and cannot be, therefore, included in such studies.

This study reveals several anatomical differences in the rat and *Proechimys*. Since the genera belong to two different rodent suborders, based on either masseter or jaw morphology, differences are expected. Comparison of two genera cannot supply evidence to support or falsify the hypothesis that caviomorphs are not rodents. However, the many differences in foramina all relate to one character, the absence of the internal carotid in *Proechimys*. The different arterial connections of downstream vessels and different pathways and foramina are not each an independent character, and thus, caviomorphs are probably rodents.

To adequatly answer the question of relationship of caviomorphs to rodents as a whole and to the Old World hystricomorphs would require a broad study that compares samples of skulls of each genus of caviomorph rodent, of Old World hystricomorphs, and of the other rodent suborders - the Myomorpha and Sciuromorpha. Although fossil skulls are few, their inclusion would make an even more robust study.

The comparison of cranial anatomy of the rat and *Proechimys* that I have presented provides new data that can serve as a starting point for further research on the comparison of a much larger and wider sample of rodents.

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