COMPARATIVE MYOLOGY OF JAW, HYOID, AND PECTORAL APPENDICULAR REGIONS OF NEW AND OLD WORLD HYSTRICOMORPH RODENTS

CHARLES ARTHUR WOODS

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 147: ARTICLE 3 NEW YORK: 1972
COMPARATIVE MYOLOGY OF JAW, HYOID, AND PECTORAL APPENDICULAR REGIONS OF NEW AND OLD WORLD HYSTRICOMORPH RODENTS

CHARLES ARTHUR WOODS
Assistant Professor of Zoology
The University of Vermont

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF MASSACHUSETTS

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 147: ARTICLE 3 NEW YORK: 1972
BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 147, article 3, pages 115–198, figures 1–17

Issued February 21, 1972

Price: $2.85 a copy

Printed in Great Britain by Lund Humphries
ABSTRACT

The musculature of 13 genera of New World and Old World hystricomorphous rodents was studied by dissection. The genera investigated were Proechimys, Echimys, Isothrix, Mesomys, Myocastor, Oedonot, Ctenomys, Erethizon, Cavia, Chinchilla, and Dasyprocta of the New World, and Thryonomys and Petromus of the Old World. The objective of the investigation was to explore the myological characteristics of these rodents as an aid in better understanding their evolutionary history.

The hystricognathous mandible that is found in most hystricomorphous rodents is associated with pars reflexa of the superficial masseter muscle. The elongated angular process is associated with the internal pterygoid muscle and with the superficial masseter. The posterior deep part of the lateral masseter muscle lies horizontally, and is associated with the post-condyloid process of these rodents. The temporal muscle is composed mainly of the posterior division. All of these specializations are probably related to the anterior-posterior movement of the jaw.

The stylohyoid muscle is missing in all genera investigated (and in bathyergids). The scalenius anterior is present in all genera except Erethizon. The scapuloclavicularis muscle is found in all genera, and is similar in Thryonomys and Dasyprocta. The cutaneous maximus is similar in all genera and unlike the muscle in any other group of rodents.

The evidence indicates that New World and Old World hystricomorphs probably represent a common group. This group might have evolved from a hystricognathous paramyid subgroup in the mid-Eocene. Another view is that the group might be a consequence of an invasion of South America by African forms via rafting across the then narrower Atlantic Ocean.

INTRODUCTION

Because of their great similarity, hystricomorph rodents have puzzled investigators for many years. There are found primarily in areas of South America and Africa. The fossil record from North America, Europe, and Asia does not include any intermediate forms. Therefore, the evolutionary relationship of hystricomorph rodents of the New and Old world is not easily understood, in spite of the apparent morphological similarities of these animals.

In the present investigation I have studied the jaw, hyoid, and pectoral appendicular musculature of thirteen genera of rodents. These rodents have often been classified together in the suborder Hystromorpha. The New World genera that I dissected are Proechimys, Echimys, Isothrix, Mesomys, Myocastor, Oedonot, Ctenomys, Erethizon, Cavia, Chinchilla, and Dasyprocta. In most recent classifications these rodents are considered to be in the suborder Caviomorpha (Wood, 1965; Romer, 1966; Patterson and Pascual, 1968; Herschkowitz, 1969). The Old World genera dissected are Thryonomys and Petromus. Recently these two genera have been treated as members of separate monotypic families of unknown subordinate relationships (Wood, 1965, 1968; Cooke, 1968; Bigalke, 1968). For purposes of simplicity, the group of thirteen New World and Old World genera are referred to as hystricomorphs. This descriptive word does not necessarily imply one phylogenetic unit. The New World genera plus the Old World thryonomyids, petromurids, and hystricids will be referred to as the Hystromorpha (sensu stricto). I will refer to the group including the New World genera and the Old World thryonomyids, petromurids, hystricids, anomalurids, bathyergids, ctenodactylyids, and pedetids as the Hystromorpha (sensu lato).

The hystricomorphous rodents have many unusual characteristics in common. Most similarities are among members of the Hystromorpha (sensu stricto), but the bathyergids also share many of them. The characteristics that these rodents of the New and Old world have in common are listed in Waterhouse (1839, 1848), Parsons (1894a, 1896, 1898, 1899), Tullberg (1899, pp. 69-71, 82-83), Korvenkontio (1934), Winge (1941), Meinertz (1941b), Wood (1950, 1955, 1965, 1968), Schaub (1953), Landry (1957a), and Wood and Patterson (1959). Some of the characteristic morphological features are also found in the anomalurids, ctenodactylyids and pedetids, but in none of these other groups are all the similarities found.
These inconsistencies are noted for Pedetes by Wood and Patterson (1959, p. 293), and for ctenodactylids by Landry (1957a, pp. 76–77). The same type of inconsistencies is found in the anomalurids.

The presence in these three groups of only some of the unusual features shared by hysticomorphs in general is frequently used as evidence that these similar features arose via parallelism. The argument is also applied to genera of the New and Old world of the more consistently similar Hystricomorpha (sensu stricto) (Wood, 1950 and later). Because there is no fossil evidence indicating intermediate conditions between New World and Old World forms, in many current works (Romer, 1966; Patterson and Pascual, 1968) the hysticomorphs of the New and Old world are considered to be un-related at the subordinal level. Most common morphological features are explained as being the result of extreme parallelism (Wood and Patterson, 1959).

There are current indications, however, that the similar features of hysticomorphs may not be due to parallelism (Landry, 1957a; Lavocat, 1969; Hoffstetter and Lavocat, 1970). The recent information in the literature supporting the concept that the continents moved in their relative positions to each other also is an important reason to reexamine the relationships of hysticomorph rodents. It is my hope that the morphological investigation of the myology of hysticomorph rodents presented here will make it more possible to understand the evolutionary history of these unusual rodents.

**MUSCLES AS INDICATORS OF MAMMALIAN RELATIONSHIPS**

Muscles have been used as indicators of mammalian relationships (Parsons, 1894a, 1896; Tullberg, 1899; Hill, 1937; Meinertz, 1941b; Bryant, 1945; Wood and White, 1950; Reed, 1951; Rinker, 1954, 1963; Davis, 1964; Klingener, 1964; and others). The justification for using muscles was summarized by Hill (1937, p. 159) when he stated that, “although great modifications of attachment occur in the muscular system of mammals, ‘heritage’ exerts a great influence on the muscular system.” Both Hill (1937) and Rinker (1954, 1963) used muscles as indicators of relationships below the family level. Hill stated (1937, p. 159) that, “the evidences of relationship drawn from the muscular system, while important within families, are too complex to be of much importance in more comprehensive groups.” Most of the other workers mentioned above use muscles as indicators of relationships above the family level. Parsons (1894a, 1896) carried out his analysis at the subordinal level.

The main problem in using muscles as indicators of relationships at higher levels is that information on the anatomy of enough genera is not available to understand properly the amount of variation to be expected in large assemblages of mammals, such as suborders. Investigators, therefore, either do not have information on other genera with which to compare their findings, or they must rely on the older literature. This literature is often based on misinterpretations and rarely contains complete myological descriptions. If it is accepted uncritically, there is a definite possibility of erroneous findings being carried along from one investigation to another, resulting in false generalizations. The lack of consistency in the older literature causes some current investigators to refrain from placing much confidence in the usefulness of muscles as taxonomic characteristics. Wood and Patterson (1959, p. 290), for example, stated that, “of all the characteristics that have been used to classify rodents, there are none so subjective as variations in muscles, no two authors ever seeming to give the same description for a given group of muscles. There are also few systems in the order where individual variation is less well understood.”

Muscles have been modified from the primitive rodent condition in many ways via natural selection. These modifications may conceal true phylogenetic relationships because they have occurred by parallelism or convergence. I believe, however, that a careful examination of the muscles of a number of different species, genera, and families can: (1) point out the amount of variation within members of the same
genus and within and between families; (2) check the observations in the older literature and reinterpret them using the much more complete understanding of mammalian myology currently in the literature; (3) establish which myological characteristics are primitive, and therefore of little taxonomic value, and which are functional specializations and therefore subject to parallelism; (4) establish which myological similarities are derived from the primitive rodent configuration and therefore indicate possible phylogenetic relationships. The presence of complex, derived myological characteristics in different rodents indicates a probable common ancestor also having such myological characteristics. This premise was supported by Klingener (1964) and more generally by Brundin (1966).

There is a rich literature on rodent myology. The major papers that I consulted on the musculature of hysticomorph rodents are: Owen (1830, 1832), Martin (1835, 1836), Mivart and Murie (1866), Wood (1870), Mivart (1882), Dobson (1894), Windle (1888, 1897), Beddard (1891, 1892), Parsons (1894a, 1894b, 1896, 1898, 1899), Tullberg (1899), Alezais (1900), Lesbre (1907), Langworthy (1923), Meinertz (1932, 1941b, 1944, 1951), Muller (1933), Enders (1934), Wood and White (1950), and Olborth (1964). Dr. Albert E. Wood of Amherst College has made available to me unpublished honors theses done by the following students under his direction: Berkowitz, Brown, Elton, Guthrie, Hodge, Hoyer, Lane (see Bibliography). These theses are on the myology of a number of New World and Old World genera of hysticomorph rodents. All the theses are useful, but have been consulted with caution.

MATERIALS AND METHODS

Fluid preserved specimens of the following species were dissected:
Proechimys gypaenensis (in alcohol)
Six specimens, Dept. de Santa Cruz, Bolivia
Proechimys centralis (in alcohol)
One specimen, banana boat, New Orleans, Louisiana
Proechimys semispinosus (in 10 per cent formalin)
Two specimens, Canal Zone, Panama
Echimys armatus (in alcohol)
Four specimens, Tobago, Trinidad, West Indies
Isotrichis sp. (in alcohol)
Two specimens, origin unknown, the American Museum of Natural History
Mesomys sp. (in alcohol)
One specimen, origin unknown, U. S. National Museum, Smithsonian Institution
Myocastor coyopus (in 1:18 formalin + NaCl)
Four specimens, L. S. U. Forestry Station, Louisiana
Octodon degus (in 1:18 formalin + NaCl)
Five specimens, laboratory stock, M.I.T.
Ctenomys talarum (in alcohol)
Three specimens, Prov. de Buenos Aires, Argentina
Ctenomys nauilinus (in alcohol)
One specimen, Prov. de Malleco, Chile
Erethizon dorsatum (1:18 formalin + NaCl)
Three specimens, Hampshire Co., Massachusetts
Cavia porcellus (1:18 formalin + NaCl)
Six specimens, laboratory stock, Univ. of Massachusetts

Chinchilla laniger (two in alcohol, one in 1:18 + NaCl)
Three specimens, laboratory stock, Univ. of Massachusetts
Dasypus punctata (in alcohol)
One specimen, Puntarenas, Costa Rica
Thryonomus suwenderianus (in 1:18 formalin + NaCl)
Two specimens, Ngoma, Zambia
One specimen, Pietermaritzburg, South Africa
Petromus typicus (in alcohol)
Two specimens, South Africa
One specimen, South West Africa
Aplodontia rafa (in 10 per cent formalin)
Two specimens, Thurston Co., Washington
Tamias striatus (in 1:18 formalin + NaCl)
Two specimens, Hampshire Co., Massachusetts
Eutamias quadriovittatus (in 1:18 formalin + NaCl)
One specimen, Clear Creek Co., Colorado
Sciurus carolinensis (in embalming fluid)
One specimen, Hampshire Co., Massachusetts
Marmota monax (in embalming fluid)
One specimen, Hampshire Co., Massachusetts

The specimens preserved in one part commercial formalin to 18 parts water saturated with NaCl were the most suitable for dissection (Schultz, 1924; Rinker, 1954; Klingener, 1964). These animals were pliable enough to allow for movement of the muscle parts without damage to the musculature. This method works well on small rodents. The general weakness of the solu-
tion makes it difficult to preserve larger rodents, however. The rodents preserved in alcohol were adequate for dissection, but not nearly so desirable. The muscles were easily torn or damaged, and dissections had to be carried out with extreme care. The musculature of the alcohol-preserved animals also tended to dry out rapidly. The animals were easier to work with when they were partially dry. For this reason I stored the specimens in plastic bags or large containers between dissection periods. A cloth saturated with the fluid was placed inside the container to keep the atmosphere moist. This prevented the specimens from completely drying out and obviated the need for storing them under fluid.

A complete set of drawings was made for every genus dissected. For purposes of the present report, however, Proechimys is considered to be the standard genus. Therefore, the drawings are almost exclusively of Proechimys, and the descriptions of the other 12 genera are mainly in terms of how they compare with Proechimys. Illustrations of other genera are presented when the configurations of their musculature are unusual and important enough to warrant separate treatment.

The work by Parsons (1894a) on hystricomorph rodents is used as the standard on which this investigation is based. Synonyms for the nomenclature of Parsons are presented with each muscle description. I have chosen to follow Parsons because his work is the last in which the myology of a large series of hystricomorph rodents was investigated. The other works that I found very useful as guides in my dissection work were Hill (1937), Bryant (1945), Rinker (1954), and Klingener (1964). The unpublished senior honors theses by Amherst College students under the direction of Albert Wood were also useful.

ACKNOWLEDGMENTS

I am indebted to the members of my doctoral committee, Drs. David J. Klingener, Lawrence M. Bartlett, Theodore D. Sargent, and Albert E. Wood, for their thoughtful guidance during the course of the study and for their careful reading of the manuscript. I am also indebted to my fellow graduate student Miss Carolyn Creswell for her valuable criticism and friendship. To my wife, Missy, I am especially grateful for her patience and help during the study, and for typing the manuscript. To her and to our two children, Stott and Julie, this study is affectionately dedicated.

The collections and facilities of the University of Massachusetts and of Amherst College were freely opened to me by Drs. Klingener and Wood. For additional specimens of critical genera I am indebted to: Mr. W. F. H. Ansell, Kalomo, Zambia; Dr. Rollin Baker, The Museum, Michigan State University; Dr. R. C. Bigalke, Pietermaritzburg, South Africa; Dr. Joel E. Brown, Department of Biology, Massachusetts Institute of Technology; Dr. Theodore Fleming, Department of Biology, University of Missouri (St. Louis); Dr. Charles O. Handley, Jr., United States National Museum of the Smithsonian Institution; Dr. Emmet T. Hooper, Museum of Zoology, University of Michigan; Dr. George Lowery, Museum of Natural Science, Louisiana State University; Mr. Elio Massoia, Castelar, Argentina; Dr. Guy G. Musser, Department of Mammalogy, American Museum of Natural History.

I am grateful to Drs. Guy G. Musser and Richard Van Gelder for their help and encouragement in seeing this study through to publication.
DESCRIPTION OF THE MUSCLES
BRANCHIOMERIC MUSCULATURE

Masticatory Group
The masseter muscle complex is generally considered to be divided into three layers. A review of the literature indicates what appears to be a large amount of variability in this muscle, but it is difficult to relate the findings of one worker to those of another. What is often described as variability in this muscle group seems to be variability in interpretation by different authors. My dissections indicate an important and consistent pattern in the masseter muscle group. I have found this general pattern in squirrels and Aplodontia. Both Rinker (1954) and Klingener (1964) reported finding the same divisions of the masseter in muroids and dipodoids. Hill (1937) presented a list of synonyms for the masseter muscle that is helpful when consulting the older literature.

I am following the nomenclature of Hill, Rinker, and Klingener. This nomenclature is not consistent with that used by Schumacher and Rehmer (1962), and Yoshikawa and Suzuki (1969). These authors divided M. masseter medialis into a M. maxillo-mandibularis and a M. zygomatico-mandibularis. These two parts are not synonymous with the pars anterior and posterior of the medial masseter. Yoshikawa and Suzuki considered the maxillo-mandibularis and zygomatico-mandibularis to be completely independent of the more lateral parts of the masseter muscle complex. Becht (1953, p. 510) also believed that “M. zygomatico-mandibularis represents an independent member of the group with a history of its own.” Becht grouped the maxillo-mandibularis and zygomatico-mandibularis under the common name M. zygomatico-mandibularis. This muscle is synonymous with M. masseter medialis. The nomenclature used by these authors does not correspond in any way to that used by most other workers in rodent myology. The homologies of the masticatory muscles in other mammals, and vertebrates in general, were discussed in Edgeworth (1916, 1935) and Adams (1919).

The masseter muscle group in hystricomorph rodents is similar to the general pattern of other rodents, but in hystricomorphs this pattern is modified in several unusual and highly characteristic ways. (See below).

The muscles of this group are innervated by the masticatory nerve.

**M. masseter superficialis**
Figures 2, 3B
masseter—anterior part (Parsons, 1894a)

**Origin:** By a round strong tendon from the posteroverentral surface of the inferior zygomatic root of the maxilla. The tendon is continuous with a very thin aponeurosis which originates along the lateral edge of the flat ventral surface of the zygomatic arch as far posterior as the middle of the eye. The separate anterior part takes origin from the anterior surface of the tendon, and the anterior fascial covering of the muscle.

**Insertion:** On the mandible via three separate insertions. The primary insertion is on the ventral and ventromedial aspects of the inflected angle. The second (pars reflexa) is a continuation of the tendon, and is reflected medially, passing around the lateral aspect of the mandible in a groove and inserting along the whole

**Standard Rodent**
M. masseter superficialis

M. masseter lateralis profundus, pars posterior
superficial division
deep division

M. masseter medialis anterior
M. masseter medialis posterior

**Hystricomorph Rodent**
M. masseter superficialis but also having:
1. large pars reflexa
2. separate part from anterior margin of
tendon (called anterior part)

same
undergoes important reorganization
to become a separate part
same
same

123
posterior half of the medial surface of the mandible. Its posterior end is in contact with the insertion of M. pterygoideus externus on the posteromedial side of the condylar process below and posterior to the condyle. Pars anterior, the third, also passes medially and inserts on the ventral and medial aspects of the alveolar sheath.

Other Genera: The configuration of the main part of the muscle in *Echimys*, *Isothrix*, *Ctenomys*, and *Octodon* is the same as in *Proechimys*. In *Erithizon*, *Cavia*, *Myocastor*, *Thryonomys*, and *Petromus* the flat aponeurotic origin posterior to the round tendon is also present, but its extent may vary intraspecifically. This same variation was found between sides of the single specimen of *Dasyprocta* dissected. It may be insignificant or it may extend as far back as the posterior margin of the eye. In *Thryonomys* the fibers from the zygomatic arch are very heavy; in the other genera they are thin and fascial. In *Chinchilla* the origin is via a single tendon, but because of the narrow inferior zygomatic root, the tendon is flattened.

Pars anterior is present in *Echimys*, *Isothrix*, *Myocastor*, *Ctenomys*, *Octodon*, *Chinchilla*, and *Petromus*. In *Echimys* the insertion is partially continuous with the medial part. In *Thryonomys* the muscle was a vestige on one side of one specimen and missing in the others. Pars anterior is missing in *Erithizon*, *Cavia*, and *Dasyprocta*.

Remarks: In most rodents the superficial masseter inserts on the angle of the mandible. In some rodents there is a small reflected part that passes a short distance onto the medial side (Rink, 1934). In *Dipodomys* (Howell, 1932), dipodoids (Klingener, 1964), and squirrels and *Aplodontia* (Hill, 1937) a more significant part of the masseter superficialis passes onto the medial side of the mandible. In these animals, the reflected part inserts in the area behind and below the sheath of the incisor. Tullberg (1899) reported the same situation for *Ctenodactylus*, *Anomalurus*, and *Pedetes*. In hystricomorphs of the New and Old worlds, however, the muscle and tendon pass onto the medial side of the mandible in a groove and continue almost to the condyle. Tullberg (1899) referred to this part as pars reflexa. The passage of pars reflexa onto the medial side of the mandible might cause the formation of the groove that is associated with the hystricognath jaw. The deep medial fossa and the insertion of pars reflexa of the superficial masseter high up, near and posterior to the condyle, are characteristics consistently shared by hystricomorphs of the New and Old worlds. Tullberg (1899, p. 70) considered this one of the characteristics of his "Tribus Hystricognathi."

This situation, in my opinion, is associated with another important characteristic, the hystricognath jaw. Miller and Gidley (1918) presented a similar conclusion. Forster (1928–1929a) noted the presence of a "faisceau reflechi du masseter externe" (= pars reflexa) in *Cavia*, and (1928–1929b, 1930) he described the configuration of the lower jaw of various hystricomorph rodents in association with this part of the muscle. Ellerman (1940) incorrectly reported that the hystricognath jaw is correlated with the insertion of the lateral masseter muscle.

The origin of masseter superficialis in rodents is usually from the inferior zygomatic root, by a round or flattened tendon. In all genera dissected except *Chinchilla*, however, elements of the muscle also originate from the lateral margin of the zygomatic arch. In most such cases the superficial head of masseter lateralis profundus, pars posterior, has become partially associated with masseter superficialis. Therefore, the fascial origin on the zygomatic arch is made up of elements of both muscles.

The anterior part is distinct, and is found in forms of the New and Old world. It is totally missing only in *Erithizon*, *Cavia*, and *Dasyprocta*. Lane (ms.) reported finding this part in *Echimys armatus*. He considered the muscle to be unique in rodents, and called it M. masseter superficialis minor. Tullberg (1899) illustrated the part in his drawings of *Myocastor*, *Ctenomys*, and *Castor*, but did not describe the condition well in the text. In his illustration of *Echimys cavanennsis* (= *Proechimys guayanensis*) he did not show this part, but I have found it in my specimens of *Proechimys guayanensis*, *Proechimys centralis*, and *Proechimys semispinosus*. This part of the muscle certainly represents a specialized and relatively unusual condition. It is found in many, but not all, rodents with a hystricognath jaw. *Castor* is the only non-hystricognathous rodent in which the anterior part is reported.

M. masseter lateralis profundus, pars anterior

Figure 2B

masseter—posterior superficial part, part (Parsons, 1894a)

Origin: From the ventral surface of the maxillary part of the zygomatic arch, and from the
ventral surface of the anterior half of the jugal. The part of this muscle on the flattened undersurface of the inferior zygomatic root is heavy. Posteriorly the part becomes thinner as the maxilla tapers down, and is thinnest along the bladelike ventral surface of the jugal.

**Insertion:** On the edge and flattened dorsal surface of the masseteric crest. The insertion is also partially on the lateral surface of the mandible where the muscle grades into the fibers of pars posterior, deep division. It is closely associated with pars posterior, superficial division, and in some specimens the two muscles appear to be continuous with each other.

**Other Genera:** In *Echimys, Isothrix, Ctenomys,* and *Octodon,* the same origin on the maxillary and narrow jugal is evident. In *Echimys* and *Isothrix* the insertion is the same as in *Proechimys,* but in *Ctenomys* and *Octodon* the insertion is on the anterior half of the dorsal surface of the masseteric crest only. In *Petromus* the muscle originates on the ventral surface of the maxilla and the anterior half of the jugal, and in the jugal fossa. The insertion is dorsal to the masseteric crest to the tip of the angle. In *Cavia, Erethizon,* and *Chinchilla* the origin is along the relatively narrow ventral surface of the posterior half of the maxilla and the anterior half of the jugal. The insertion is on the dorsal surface of the anterior half to two-thirds of the masseteric crest, and in *Erethizon* the fibers are continuous with those of pars posterior, deep division. In *Dasyprocta, Myocastor,* and *Thryonomys* the origin is from the ventral surface of the fairly flattened and heavy maxilla and from the ventrolateral margin of the anterior half of the jugal in the position of the missing jugal fossa. The insertion in *Dasyprocta* is along the anterior half of the
dorsal surface of the masseteric crest. The insertion in *Myocastor* and *Thryonomys* is on the lateral side of the mandible dorsal to the masseteric crest. It passes to the tip of the angular process as in *Petromus*.

**Remarks:** There is some variation in this muscle related to the size of the flattened ventral surface of the zygomatic arch. Two characteristic patterns are present. In *Proechimys, Echimys, Isothrix, Clenomys, Octodon,* and *Petromus* a deep jugal fossa (fig. 1A) is present above the line of origin of this muscle. The deep fossa constricts the jugal into a narrow, bladelike ridge. In *Myocastor, Erethizon, Cavia, Chinchilla, Dasyprocta,* and *Thryonomys* there is no jugal fossa above the origin of this muscle. In these genera the posterior half of the jugal is flattened and bends upward. The origin of the masseter lateralis profundus, pars posterior, deep division, is from the margin of the jugal fossa in all genera having such a fossa except *Petromus*. In *Petromus* the pars anterior originates in the jugal fossa. Therefore, even though there is a jugal fossa in *Petromus*, the configuration of the masseter lateralis profundus in this genus is more similar to that in *Myocastor, Erethizon, Cavia, Chinchilla, Dasyprocta,* and *Thryonomys*.

The insertion of pars anterior appears to pass to the tip of the angle in *Myocastor, Thryonomys, Petromus, Proechimys, Echimys,* and *Isothrix*. In all these cases it may be pars anterior grading into pars posterior, superficial head, which makes the insertion look broader than it is.

![Diagram of masseter muscles](image_url)
M. masseter lateralis profundus, pars posterior

Figure 2

masseter—posterior superficial part, part, and questionably, posterior deep part (Parsons, 1894a)

This portion is composed of two divisions. Superficial division:

Origin: By a thin fascial sheet from the lateral edge of the flattened ventral surface of the maxilla, and from the ventrolateral edge of the bladelike anterior half of the jugal, below the anterior part of the jugal fossa.

Insertion: It passes posterodorsally to insert on the lateral edge of the massteric crest, from mid-eye level posteriorly to the tip of the angle. Part of these fibers are continuous with masseter superficialis.

Other Genera: The situation in Echimys and Isothrix is the same. In Ctenomys and Octodon the origin is the same as above, but the insertion is along the entire masseteric crest, covering most of pars anterior. Petromus, which has a zygomatic arch resembling the above genera, is very different. The origin is along the lateral edge of the maxillary and the lateral edge of the anterior half of the jugal above the fossa. The insertion is as usual. Cavia, Erethizon, Chinchilla, and Dasyprocta have the usual origin, but as the jugal fossa is not present, the origin is broadly from the jugal. The insertion is as usual. In Myocastor and Thryonomys this division does not seem to be present. However, in both of these genera the origin of masseter superficialis is broader than usual, and it is my belief that the superficial division has become incorporated into masseter superficialis.

Remarks: Lane (ms.) and Elton (ms.) interpreted this muscle division to be part of pars anterior. I believe, however, that it is homologous to the superficial part of pars posterior found in squirrels (personal observ. and Bryant, 1945), Reithrodontomys (Rinker and Hooper, 1950), and Sigmodon, Oryzomys, and Peromyscus (Rinker, 1954).

In all the genera studied, this division is closely associated with masseter superficialis. In Myocastor and Thryonomys it is part of the masseter superficialis, originating in common with it and inserting on its surface. In Chinchilla and Dasyprocta it stands out clearly as a separate, superficial portion on top of pars anterior. In some specimens of Erethizon and Cavia the division becomes associated with pars anterior, and is difficult to separate.

Deep division:

Origin: In the jugal fossa and on the ventromedial margin of the posterior half of the jugal.

Insertion: The fibers pass caudally. Those from the fossa insert on the expanded posterior margin of the condyloid process (= postcondyloid process). Those from the ventral margin insert underneath the others on the lateral side of the ascending ramus and anteriorly toward the line of insertion of masseter lateralis profundus, pars anterior.

Other Genera: The situation is the same in Echimys, Isothrix, Ctenomys, and Octodon. In Petromus there is a jugal fossa, but the fibers of this division originate instead from the ventral margin of the posterior half of the jugal. In Dasyprocta, Myocastor, Erethizon, and Thryonomys there is no jugal fossa. The origin is from the ventromedial edge and the flattened ventral surface of the posterior half to two-thirds of the jugal. The insertion is the same as in Proechimys. In these genera the muscle is not as pronounced as it is in the first four genera. In Cavia the muscle originates on the ventral and ventromedial area of the posterior quarter of the jugal, and is very small. In Chinchilla the origin is from the ventral and ventromedial edge of the posterior half of the jugal. The insertion is, as above, on the lateral and expanded posterior surface of the condyloid process.

Remarks: This muscle division is consistent in form within all genera investigated. The insertion below the condyle on the expanded posterior margin of the condyloid process is a unique situation, seemingly not characteristic of any other group of rodents. This division is related to the deep layer of fibers reported by Bryant (1945), Rinker and Hooper (1950) and Rinker (1954). Proechimys, Echimys, Isothrix, Ctenomys, and Octodon show the greatest degree of development of the division; Cavia shows the least.

This important and characteristic muscle division has not been described before. Lane (ms.) and the later workers under Albert Wood of Amherst College mentioned that the insertion of the posterior part of the lateral masseter is on the condyloid process, but they did not comment on its significance. Parsons (1894a) mentioned a posterior deep division which Hill (1937) concluded is synonymous with masseter medialis, pars posterior. Brown (ms.) concluded that Parsons was referring to masseter lateralis profundus, pars posterior. Because of the pro-
ounced nature of this muscle in the hystricomorphs studied, I agree with Brown.

The deeper fibers of this division are often continuous on the side of the mandible with fibers of pars anterior. Generally the two muscles can be separated from each other by the masseteric nerve, which passes between them. The M. masseter medialis posterior, which also lies behind the masseter nerve can be separated from the present muscle by the direction of the fibers. The fibers of masseter medialis posterior course caudoventrally.

The origin of the muscle is in a deep fossa on the lateral surface of the jugal bone. I have called this fossa the jugal fossa. Landry (1957a) called it the zygomatic fossa, and erroneously associated it with the origin of the superficial masseter. He correctly noted that it is especially well developed in echimyids and octodontids, but stated that its presence in other hystricomorphs is due to parallelism.

**M. masseter medialis, pars anterior**

**Figures 2B, 3A**

**Origin:** From the fossa on the lateral side of the rostrum, the superior zygomatic root, and the medial surface of the maxillary and jugal parts of the zygomatic arch.

**Insertion:** The fibers from the fossa and superior zygomatic root coalesce into a strong tendon, which passes vertically to insert at the anterior end of the masseteric crest below the level of the first molar. The fibers from the medial side of the zygomatic arch insert on the above tendon, the lateral crest below the last two molars, and in the masseteric fossa on the lateral surface of the mandible posteriorly to the level of the coronoid process.

**Other Genera:** In all genera the insertion is via a tendon and sheet of fibers. In *Echimys, Isothrix, Myocastor,* and *Thryonomys* the origin and insertion are the same as in *Proechimys.* In *Ctenomys* and *Octodon* the insertion of the fibrous sheet is along the dorsal aspect of the masseteric fossa. The origin is as above. In *Erethizon, Chinchilla, Dasyprocta,* and *Petromus* the insertion of the fibers is along the line of the lateral crest. The crest, however, is not enlarged. The origin is normal. In *Cavia* the fibers insert in a deep fossa on the dorsomedial side of the extremely enlarged lateral crest. The origin of this muscle in *Cavia* is more restricted, and the infraorbital foramen is flattened.

**Remarks:** The origin of the muscle on the rostral fossa and its passage through the enlarged infraorbital foramen are characteristic of the hystricomorphous condition. The condition is consistent in all genera studied. Some variation exists in the insertion of the muscle. *Cavia* and *Hydrochoerus* represent an extreme in which the insertion is very high on the side of the mandible and medial to the enlarged lateral crest. The other extreme is found in *Myocastor,* in which the side of the mandible above the masseteric crest is flat and the insertion of the fibrous portion of the muscle is along the ventral margin of the masseteric fossa. In other genera, intermediate stages between these two extremes can be found.

How this muscle corresponds to what Parsons reported is questionable. Parsons's (1894a, p. 253) description of the “anterior deep part” is certainly the same as the rostral and superior zygomatic arch elements of this muscle. However, Parsons did not mention any parts from the medial side of the zygomatic arch. Part of his “posterior deep part,” therefore, must also belong to the present muscle.

**M. masseter medialis, pars posterior**

**Figure 2A**

Not reported by Parsons (1894a)

**Origin:** From the ventral and medial aspect of the zygomatic process of the squamosal.

**Insertion:** The muscle fibers pass anteroven-trally to insert on the lateral surface of the coronoid process and in a depression between the root of the incisor and the posterior margin of the mandibular notch. The muscle is large and partially covered by fibers of masseter medialis pars anterior. The masseteric nerve splits the muscle into two unequal parts with most of the muscle lying posterior to the nerve.

**Other Genera:** The muscle is clearly present in *Isothrix, Myocastor, Octodon, Chrynomys, Erethizon, Chinchilla,* and *Dasyprocta.* It is posterior to the masseteric nerve in all of these genera. In *Echimys and Petromus* the muscle is actually present but is small and anterior to the masseteric nerve. In *Thryonomys* it is small and split by the nerve in one specimen and seemingly missing in the others. In *Cavia* the muscle is present, but the insertion is in the posterior region of the deep fossa above the expanded lateral crest.
REMARKS: As Hill (1937) pointed out, this small muscle was missed by several earlier investigators. I disagree with Hill's interpretation that it is the "posterior deep part" of Parsons (1894a, p. 253). I believe instead that Parsons must be describing at least part of masseter lateralis profundus, pars posterior, deep division. That muscle can be separated from the present one by the direction of the fibers. The fibers of masseter lateralis profundus, pars posterior, deep division, pass posterodorsally whereas those of masseter medialis, pars posterior, course anterodorsally. Lane (Ms.) and others missed this point and mistook the deeper fibers of masseter lateralis profundus, pars posterior, deep division, for the present muscle. The possibility of confusion is compounded because both muscles usually lie posterior to the masseteric nerve.

M. TEMPORALIS
Figures 2, 3
temporal (Parsons, 1894a)

ORIGIN: A small muscle composed of three closely associated parts. The main part (le faisceau moyen du temporal, Kunstler, 1887; medial part, Bryant, 1945; deep section, Rinker, 1954) originates from the surface of a long and narrow fossa in the temporal region, and from the superior temporal ridge, inferior
temporal ridge, and lambdoidal crest. The orbital part (le faisceau superieur du temporal, Kunstler, 1887; anterior part, Bryant, 1945; superficial part, Rinker, 1954) takes origin from the surface of the frontal and squamosal bones within the orbit and from the most proximal part of the temporal ridge. Much of the orbital part is covered by the main part. The posterior part (le faisceau inferieur du temporal, Kunstler, 1887; posterior part, I think, Bryant, 1945; not mentioned by Rinker, 1954) takes origin from the anterior and ventral surface of the zygomatic root of the squamosal.

**INSERTION:** The main part is a large bipinnate muscle. It narrows to a tendon to insert on the tip and anterior surface of the coronoid process. The orbital part inserts mostly on the medial part of the coronoid process. Some fibers insert near the tip and others pass to the base of the coronoid process where there is a pit just behind the third molar. The posterior part is small and inserts on the lateral surface of the coronoid process.

**OTHER GENERA:** The muscle is composed of these three parts in all genera studied. The posterior part is well developed in Cavia, Erethizon, Proechimys, Isothrix, Myocastor, and Thryonomys. In Myocastor and Thryonomys the insertion is on the tendon of the main part. In Echimys, Ctenomys, Octodon, Dasypodidae, Chinchilla, and Petromus the muscle is reduced and continuous with masseter medialis, pars anterior. The insertion is as usual on the lateral side of the coronoid process, however.

The main muscle mass in Erethizon is heavy. It is not in contact with its partner on the other side, however. In Myocastor the origins are the same, but because the coronoid process is reduced or missing, the insertions of the main and orbital parts are directly onto the flattened dorsal surface of the mandible. In Chinchilla the muscle is very reduced, especially the orbital part. The reduction may be associated with the enlargement of the bullae.

**REMARKS:** The parts of this muscle are difficult to homologize in various groups of rodents. The relationship is closest to that of squirrels (see Kunstler, 1887; Bryant, 1945). The important difference is the loss in all hystricomorphs dissected of the superficial fibers that cover the main muscle mass. These fibers are a continuation of the orbital part out of the orbit and onto the surface of the main part. The superficial nature of this part can be seen in Marmota (Kunstler, 1887), Neotoma (Howell, 1926), Thomomys (Hill, 1937), Reithrodontomys (Rinker and Hooper, 1950), and muroids (Rinker, 1954). In their excellent paper on Reithrodontomys, Rinker and Hooper (1950) discussed the nature of the temporal muscle parts. They concluded that the temporal muscle is important in grinding the molar teeth back and forth. Klingener (1964) describing an idea of Rinker’s suggested that the posterior fibers (=the main part) are more important in grinding food, whereas the anterior fibers (=the orbital or superficial part) are more important in crushing food. Klingener went on to state (p. 12): “the progressive disappearance of the anterior fibers of the temporals seen in jerboas could be associated with the transformation of the molars from tuberculate to flat, high crowned teeth, and with the probable shift from crushing to grinding movements of the mandible during mastication.” The genera studied, with the exception of Petromus, all have high-crowned teeth with flattened surfaces. The molars of Petromus are high crowned but less flattened.

**M. PTERYSTEGOIDUS EXTERNUS**

Figure 3B

pterygoid, external (Parsons, 1894a)

**ORIGIN:** From the edge of the lateral pterygoid plate, the surface of the alisphenoid bone, and the adjacent edge of the maxillary bone.

**INSERTION:** The muscle passes posterodorsally to insert below and posterior to the condyle on the medial surface of the condyloid process.

**OTHER GENERA:** The situation is basically the same in all genera. In Erethizon the alisphenoid bridge is missing, but the origin is still from the reduced lateral pterygoid plate, the edge of the maxillary bone, and the alisphenoid bone. The origin in Chinchilla is expanded, especially on the maxillary bone. The point of origin in this animal is from as far forward as the second molar, quite high up into the region of the orbit. In all genera the muscle is large and the insertion usually pushes outward onto the postcondyloid process.

**REMARKS:** Wood and White (1950) observed the posterior expansion of the mandible in their paper on Chinchilla, and they related this phenomenon with M. pterygoideus externus. Wood (1949) said that this expansion is apparent in both Santa-crucian erethizontids and
recent South American hysticomorphs, but not in *Petromus* or *Thryonomys*. However, *Ctenomys* is just as lacking in a post-condyloid expansion as is *Petromus*, and *Thryonomys* does have a moderate expansion. Pterygoideus externus does insert on the expanded area of the mandible, especially in *Erethizon* and *Dasyprocta*. A secondary and related reason for the expanded area, however, is the unusual insertion of M. masseter lateralis profundus, pars posterior, deep division, on the posterior margin of the condyloid process. In animals which have an enlarged post-condyloid expansion, such as *Erethizon* and *Dasyprocta*, the insertions of both muscles are on this expansion. In *Ctenomys*, in which the pterygoideus externus is somewhat small, the expansion has moved laterally and exists as a tubercle on the posterior-dorsal aspect of the condyloid process. Therefore, the expansion is related to both muscles. The expansion is slightly developed in *Petromus* and *Thryonomys*, and is moderately developed in *Hystrix javanica* and *Thecaxerus* sp. This character, therefore, is not useful in separating New World and Old World forms.

Merriam (1895) noted that the external pterygoid is more important than the internal pterygoid in moving the mandible forward. The posterior extension of the condyloid process would accentuate this action. It is possible, therefore, that the development of this muscle and of the expanded condyloid area is related with the flat-crowned teeth of hysticomorphs and with propalinal jaw movement.

**INTERNAL PTERYGOID GROUP**

The muscles of this group are innervated by the medial branch of the mandibular nerve.

**M. pterygoideus internus**

*Figure 3*

pterygoid, internal (Parsons, 1894a)

**Origin:** From the entire margin of the pterygoid fossa, and from deep inside the fossa itself. The muscle splits into two incompletely separated parts. The smaller part is from the edge of the lateral pterygoid plate, the larger from the pterygoid process and deep inside the pterygoid fossa.

**Insertion:** The medial side of the mandible on the dorsal surface of the flattened angular process. The two parts are almost continuous. The smaller inserts anterior and deep to the larger, and the larger is visible from the lateral side of the mandible as a sheet of muscle passing posterovertrally to the medial tip of the angle.

**Other Genera:** The muscle is basically the same in all genera. It originates from deep within the pterygoid fossa in all the specimens studied. In *Echimys, Isothrix, Cavia*, and *Petromus* the two parts are flattened and somewhat separate. In *Ctenomys, Octodon, Dasyprocta, Chinchilla*, and *Thryonomys* the two parts of the muscle are not separate, but the muscle is flattened. In *Myocastor* and *Erethizon* the two parts are not separate, and the muscle is large and round.

**Remarks:** Parsons (1894a) noted that the internal pterygoid is two-parted in *Sphingurus* (= *Coendou*), but he did not report it for any other genera. My observations indicate that the two-parted condition is fairly widespread. Becht (1953) and Schumacher and Rehmer (1962) also reported two parts to this muscle in hysticomorphous rodents.

The main trends within the hysticomorphs studied are toward elongation of the internal pterygoid and horizontal positioning of the muscle. These trends come about in two ways: the movement of the origin of the muscle deep into the pterygoid fossa, and the movement of the insertion to the tip of the extended and laterally displaced angle. The extension of the muscle into a more horizontal position would result in more anteroposterior (propalinal) movement to the jaw. These conditions are found in all hysticomorphs dissected and must be somehow associated with propalinal chewing.

The other muscles of this group were not dissected.

**MYLOHYOID GROUP**

The muscles of this group are innervated by the mylohyoid branch of the mandibular nerve.

**M. mylohyoideus**

*Figures 4A, 5A*

mylo-hyoid (Parsons, 1894a)

**Origin:** From the medial side of the mandible in the area below the molar teeth. The origin is broad and weak.

**Insertion:** On the median raphe from the symphysis of the mandible posteriorly to the basihyal, and along the lateral surface of the ventral wings of the basihyal. The broad insertion is barely covered near the mandibular symphysis by the small M. transversus mandibu-
laris. The muscle is not covered by the widely separated parts of M. digastrocnemius anterior.

Other Genera: The origin of M. mylohyoideus is similar in all genera. Echimys, Isothrix, Cavita, and Chinchilla have the same insertion as Proechimys. In all of these genera the insertion on the median raphe is almost in contact with the mandibular symphysis. In Chinchilla there is a separate tendinous arcade part of the posterior digastic, but no fibers of the mylohyoid insert on it. In Myocastor the insertion is on the posterior quarter of the median raphe between the mandibular symphysis and the basihyal, and onto the basihyal. In this animal the sternohyoid muscle also inserts onto the median raphe, and some fibers of the mylohyoid insert onto it. In Thryonomys the insertion is totally onto the body and ventral wings of the basihyal. There is a separate tendinous arcade to the posterior digastic, but as in Chinchilla, the mylohyoid does not insert onto the tendinous arcade. In Erethizon the insertion is onto the posterior half of the median raphe, the tendon of the posterior digastic, and the basihyal. The tendon of the posterior digastic is not a separate tendinous arcade, but rather a tendinous separation between the anterior and posterior digastic. This tendon attaches to the basihyal, and some fibers of the mylohyoid insert on it. In one specimen of Erethizon some fibers of M. mylohyoideus lift off the main muscle mass and stand out as a separate transverse part. In Dasyprocta the insertion is on the posterior quarter of the median raphe, the separate tendinous arcade of the posterior digastic, and the basihyal. In Octodon the insertion is as in Dasyprocta, and also along the proximal half of the thyrohyal. The tendinous arcade is small, but the fibers of the mylohyoid do insert on it. In Clemomys the insertion is only on the basihyal and the proximal half of the thyrohyal. In Petromus the insertion is along the median raphe from almost the level of the mandibular symphysis, the basihyal, and the entire length of the thyrohyal.

Remarks: The variation in the insertion of the mylohyoid seems to be partially related to the proportions of the neck, and the presence or absence of the tendinous arcade of the posterior digastic. Parsons (1894a, 1896) stated that the mylohyoid inserts on the tendinous arch in sciuromorphs and myomorphs, but not in hystricomorphs. However, Howell (1926, 1932), Hill (1937), Bryant (1945), Rinker (1954), and Klingener (1964) did not report an insertion of the mylohyoid on the tendinous arch in the non-hystricomorphs they studied. I observe an insertion on the tendinous arcade in Octodon and Dasyprocta. In Erethizon there is an insertion on the tendon of the posterior digastic which is probably homologous with the tendinous arcade. In Chinchilla and Thryonomys there is an arcade, but no insertion on it. There is a poorly developed arcade in Petromus.

Windle (1897) noted the arcade and insertion on it in Dasyprocta, as did Brown (ms.). It is interesting to note that while the mylohyoid does not insert onto the tendinous arcade in Chinchilla, the hyoglossus does. (For an interpretation of the homologies of the tendinous arcade see the explanation under the posterior digastic muscle.)

M. transversus mandibulæ

Figures 4A, 5A

Transverse mandibular (Parsons, 1894a)

Origin: From the ventral margin of the mandible, slightly covered by the insertion of M. digastrocnemius (anterior belly), and lying ventral to the most anterior fibers of M. mylohyoideus. It is a small muscle, confined to the area near the mandibular symphysis.

Insertion: Into the fibers of its mate.

Other Genera: The muscle is present and confined to the area near the mandibular symphysis in all genera. It is slightly better developed in Myocastor and Dasyprocta than in the other genera.

Remarks: Parsons (1894a) considered the absence of this muscle to be one of the main differences between the Hystricomorpha and the Sciuromorpha. Tullberg (1899), however, reported that the muscle is found within the hystricomorphs (= hystricognaths). Tullberg believed that the muscle is usually reduced, but that it is well developed in Echinomys cayennensis (= Proechimys), Dasyprocta, and several other genera. I find that the muscle is reduced in Proechimys but that it is fairly well developed in Dasyprocta. The usual explanation (Wood and White, 1950; Landry, 1957a) for the reduction of M. transversus mandibulæ is that as the two halves of the mandible become more closely fused, the muscle becomes less important and less well developed. It is significant that the two halves of the mandible are less closely associated in Dasyprocta than in any of the other genera. The
Fig. 4. Hyoid musculature of Proechimys guyannensis. A. Superficial muscles. B. Deep muscles.

Muscle appears to have been incorrectly identified in *Myopotamus* (= *Myocastor*) by Cords (1918).

The muscle, therefore, is present but reduced in all genera. The two halves of the lower jaw are closely associated and the whole lower jaw probably moves as a unit.

**M. digastricus, anterior belly**

Figures 4A, 5A

digastric, part (Parsons, 1894a)

**Origin:** The muscle is continuous with the fibers of the posterior belly. There is a slight constriction between the anterior and posterior bellies, but the muscle fibers are not separated by a tendon.

**Insertion:** The anterior bellies of the two sides are not in contact with each other. The insertion is on the ventral surface of the mandible posterior to the symphysis. There is no solid attachment to the hyoid.

**Other genera:** The conditions in all genera except *Dasyprocta* and *Erethizon* are the same as in *Proechimys*. In *Dasyprocta* the pattern is the same, but there is a greater constriction between the anterior and posterior bellies. In *Erethizon*, however, the situation is different. The origin is from the strong tendon of the posterior belly.
No fibers of the anterior and posterior bellies are continuous with each other.

Remarks: The "hystricomorphine" type of digastric as described by Parsons (1894a, p. 254) is characterized in part by the separation of the two anterior bellies from each other "by a distinct interval in which the mylohyoid is exposed." This condition is shared by all hystricomorph genera. Hill (1937), however, reported that the anterior bellies of this muscle are separated in Thomomys, as did Howell (1932) for Dipodomys, and Parsons (1896) for Heteromys. Therefore, although the separation of the anterior bellies seems to be a consistent character within the hystricomorphs, it is not confined to them.

The usual condition in hystricomorphs of a direct continuation between the anterior and posterior bellies of M. digastricus also forms part of Parsons (1894a) "hystricomorphine" type of digastric. Erethizon does not follow this pattern, however, nor does Coendou (Parsons, 1894a). Aside from the hystricomorphs Parsons (1896) reported that Cricetus, Microtus, Myodes (= Lemmus), Hydromys, Bathyergus, and Georychus all have almost continuous anterior and posterior bellies.

**Hyoid Constrictor Group**

The muscles of this group, which were dissected, are innervated by the digastric branch of the facial nerve. M. stapedius, which was not dissected, is innervated by the stapedial branch of the facial nerve.

**M. digastricus, posterior belly**

Figures 4A, 5A, 8 digastric, part (Parsons, 1894a)

Origin: From the paroccipital process.

Insertion: The insertion is continuous with fibers of the anterior belly. There is only a slight constriction between the two bellies, and no pronounced attachment to the hyoid bone. A thin tendon lying along the surface of the thyrohyal and basihyal probably represents the vestigial remains of the old tendinous arcade.

Other Genera: The origin is from the paroccipital process in all genera. In Ctenomys and Octodon the paroccipital process has become flattened onto the surface of the bulla. In Cavia and Dasyprocta the process is fused with the lambdoidal ridge and in the same vertical line with it. In Myocastor, the process is extremely enlarged and in nearly the same vertical line as the lambdoidal crest but not fused with it.

The insertion is continuous with the fibers of the anterior belly in all genera except Erethizon. In Erethizon the muscle inserts via a tendon which is firmly attached to the surface of the basihyal. The anterior belly originates from the entire surface of this tendon, but no fibers of the two bellies are continuous with each other. In Chinchilla, Thryonomys, and less completely in Petromus there is a separate slip of the digastric which splits off from the dorsomedial surface of the main muscle mass and inserts onto the basihyal. In Chinchilla part of M. hyoglossus originates from the surface of the separate slip. In Dasyprocta and Octodon the same separate dorsomedial part is present, but it forms a loop over the surface of the mylohyoid. The part is small in Octodon. In Dasyprocta and Thryonomys the part is separable for the entire length of the posterior digastricus.

Remarks: In hystricomorphs other than Erethizon and Coendou the anterior and posterior bellies of this muscle are continuous with each other. The two parts pass in an almost straight line from the origin of the posterior belly on the paroccipital process to the insertion of the anterior belly on the mandible. As I reported in the discussion of the anterior belly, there are non-hystricomorph rodents that also have an uninterrupted transition between the anterior and posterior bellies. However, in most other genera of rodents there is a tendinous separation between the two bellies. The tendon meets its mate from the other side to form, in effect, a tendinous arch (Hill, 1937; Bryant, 1945; Rinker, 1954; Klingener, 1964). This type of situation was considered by Parsons (1894a) to be the sciuromorphine type of digastric. Hill (1937, p. 105) believed that, "the 'sciuromorphine' type of digastric is probably the more primitive being more like that in other orders of mammals."

The myological situation found in most hystricomorphs represents a condition derived from the primitive sciuromorphine type. The derived condition would occur when the parts of the anterior belly originating on the lateral margin of the tendon bypassed the tendon and became continuous with the fibers of the posterior belly. A subsequent step in the development of the hystricomorphine digastric would be the movement of the entire digastric (anterior and
posterior bellies) into a straight line from the paroccipital process to the symphysis. This could possibly result in the degeneration of the connection between the anterior bellies, which would no longer be necessary (Landry, 1957a). *Chinchilla*, *Dasyprocta*, and *Thryonomys* could be interpreted as being in this stage. Further reduction of the old tendinous arcade would result in a situation such as in *Octodon*, where it is small, in *Petromus*, where it has been lost in some specimens, and in *Proechimys*, where the tendon is isolated on the surface of the basihyal. When the old arch has been completely lost the situation would be as it is in most hystricomorphs.

The intermediate stages of the theoretical change from a sciromorphine digastric type to a hystricomorphine can be found throughout the hystricomorphs. In some other genera of rodents the above changes might also be at work. *Neotoma* (Howell, 1926), *Dipodomys*, *Allactaga* (Howell, 1932), *Thomomys* (Hill, 1937), as well as the four genera reported by Parsons (1896) are all exceptions to the sciromorphine digastric type. All of these genera illustrate conditions that resemble the hystricomorphine digastric
type. Many of them share other characters with hystricomorphs such as an enlarged infraorbital foramen (Alitagata), or somewhat flat crowned teeth [Neoehina, Dipodomys, Thomomys, Myodes (=Lemmus), and Microtus].

M. stylohyoideus

I did not find the stylohyoideus muscle in any of the hysticromorph genera dissected. There is clearly no separate muscle ventral to the hypoglossal nerve which can be considered to be this muscle. The stylohyoideus is embryonically very closely associated with the posterior belly of M. digastricus, however, and it is possible that the stylohyoideus is fused with the posterior belly. As both muscles have the same innervation, it would be impossible to separate them. It would be possible to consider the separate tendinous slip of the posterior digastricus in hystricomorphs as homologous with the stylohyoideus. The situation would then resemble that in Sus, Felis, and Tarsius as described and illustrated in Edgeworth (1935). However, squirrels have a typical sciuromorph gastrica digastric with a primitive tendinous arcade and a distinct and very separate stylohyoideus. It seems more probable, therefore, that M. stylohyoideus is missing in hystricomorphs. It is interesting that Edgeworth (1935, p. 116) concluded that the muscle “is absent in Bathergus among the Rodentia; in Meles, Hyaena striata, Proteles and Mustelidae among the carnivora.”

M. jugulohyoideus

Figures 4, 5

Not reported by Parsons (1894a)

ORIGIN: From the anterior surface of the paroccipital process deep to the origin of M. digastricus (posterior belly).

INSERTION: On the ventromedial surface of the stylohyal cartilage.

OTHER GENERA: The origin and insertion are the same in all genera. The muscle is larger in M.ycastor and Chinchilla than in the others. Because of the close association of the paroccipital process with the tympanic bulla in Ctenomys and Octodon, the muscle in these two genera appears to come from the surface of the bulla itself.

REMARKS: The muscle is present in this form in rodents that have a well-developed stylohyal cartilage, including squirrels and Aplodontia (Hill, 1937), Peromyscus (Rinker, 1954), and most dipodoids (Klingener, 1964). In the genera I investigated the stylohyal cartilage was thin and tendinous from the area of the stylomastoid foramen to the point of insertion of M. jugulohyoideus. From this level to the body of the hyoid the stylohyal is either of heavy cartilage or bone and quite substantial. There is a well-developed ceratohyal in Dasyprocta, Chinchilla, Thyronomys, and Petromus. In the other genera the ceratohyal is either reduced or lost.

It is quite possible that Parsons (1894a) and others who reported a M. stylohyoideus for hystricomorphs were really describing M. jugulohyoideus. In cases where earlier authors described a stylohyal they usually failed to note the presence of the usually well-developed jugulohyoideus.

GLOSSOPHARYNGEAL GROUP

The muscles of this group are innervated by branches of the glossohyal nerve.

M. stylpharyngeus

Figures 4B, 5B

Not reported by Parsons (1894a)

ORIGIN: From the dorsal surface of the stylohyal.

INSERTION: The muscle passes anterodorsally into the musculature of the pharynx.

OTHER GENERA: The muscle is present in the same basic form in all genera of hystricomorphs investigated. In Cavia and Erethizon the muscle is large and a few fibers may also insert onto the tip of the thyrohyal. In Ctenomys and Octodon the muscle originates from the surface of the tympanic bulla.

REMARKS: The muscle in hystricomorphs conforms to the general condition for rodents in which there is a well-developed stylohyal cartilage. An excellent discussion of the situation in other rodents is presented by Klingener (1964, p. 22).

M. glossopharyngeus

Figures 4, 5B

Not reported by Parsons (1894a)

ORIGIN: From the lateral surface of the stylohyal cartilage anterior to the insertion of M. jugulohyoideus.

INSERTION: On the lateral surface of M.
hyoglossus and the lateral surface of M. geniollogus near the base of the tongue. Some fibers are continuous with those of the constrictor muscles of the pharynx.

Other Genera: In Echimys, Isothrix, Octodon, Otomys, and Chinchilla the arrangement of the muscle is as in Proechimys. In all of these genera the origin of the muscle is not closely associated with M. styloglossus. In Myocastor, Cavia, Erethizon, Thryonomys, and Petromus the origin is closely associated with M. styloglossus. In Dasyprocta the origin is separate from M. styloglossus, but lies alongside of it. The above variations are a result of changes in the origin of M. styloglossus.

Remarks: This muscle was present in all hysticomorphs that I examined, as well as in my specimens of Oryctolagus, Aptodontia, Tamias, Eutamias, Sciurus, and Marmota. It forms a prominent part of the muscles associated with the stylohyal cartilage.

In his description of the hyoid musculature of Oryctolagus, Meinertz (1956) described the muscle under the name M. stylohyoides minor. He stated, however, that both this muscle and M. stylopharyngeus are innervated by N. hypoglossus. My dissections indicate that both muscles are innervated by N. glossopharyngeus. Reighard and Jennings (1935) described this muscle in the cat. The insertion of the muscle in the cat differs from the usual condition in rodents, but the basic pattern and innervation are the same. Schön (1968) mentioned a similar muscle in the Red Howling Monkey (Alouatta) under the name M. constrictor pharyngis superior, pars glossopharyngea.

The close association of the muscle with M. styloglossus makes M. glossopharyngeus seem to be merely a part of M. styloglossus. Indeed, in humans (Gray and Lewis, 1943), Oryctolagus (Meinertz, 1956), and the dog (Miller, Christiansen, and Evans, 1964) there are two or more parts reported for M. styloglossus. In all rodents that I dissected, however, I could only demonstrate an innervation via N. glossopharyngeus. It is therefore not possible to consider the muscle as a second part of M. styloglossus.

I believe that M. glossopharyngeus in rodents is usually modified from its original pharyngeal constrictor condition by the loss of its insertion on the pharynx. The remaining muscle would have attachments on both the stylohyal and the hyoglossus/genioglossus muscles. The attachment to the stylohyal cartilage has become the origin. The muscle is probably involved in the movement of the tongue. In some genera, such as Proechimys, there are still some elements of the muscle inserting on the pharynx.

Trapezius Group

The muscles of this group are innervated by the inferior branch of the spinal accessory nerve and branches of the second and third cervical nerves.

M. sternomastoideus

Figures 8–11

sterno-mastoid (Parsons, 1894a)

Origin: From the anterior edge of the manubrium of the sternum.

Insertion: On the tip of the mastoid process. The muscle passes anterodorsally parallel with M. cleidomastoideus, with which it is closely associated. The two muscles are easily separated, however.

Other Genera: In all genera except Myocastor, the basic configuration of the muscle is the same as in Proechimys. In Cavia the origins of M. sternomastoideus and M. cleidomastoideus are more separated than in the other genera [Parsons (1894a) also comments on this separation]. In Myocastor the origin of this muscle is normal, but the insertion is on the tip of the enlarged paroccipital process.

Remarks: In the older literature (Mivart and Murie, 1866; Parsons, 1894a) the insertion of this muscle was occasionally stated to be on the paroccipital process. Among the animals dissected, only Myocastor had such an insertion. The probable reason for the confusion is the movement of the paroccipital process into the same line as the lambdoidal crest in some genera. In Cavia and Dasyprocta, for example, the paroccipital process and lambdoidal crest are so closely associated that the muscle appears to be inserting on the paroccipital process. Landry (1957a) commented on this situation, as did Winge (1941). Landry (1957a, p. 41, fig. 12) demonstrated some transitional forms of this condition.

M. cleidomastoideus

Figures 8, 10, 11

cleido-mastoid (Parsons, 1894a)

Origin: From the sternal end of the clavicle.
**Insertion:** On the mastoid process with M. sternomastoideus.

**Other Genera:** The conditions in all genera except Cavia and Myocaster follow the pattern described above. In Cavia the origin is on the clavicle underneath and in common with the large M. cleido-occipitalis. The clavicle of Cavia is reduced, and the origin of the muscle is along the entire length of the bone. In Myocaster the origin is normal, but as with M. sternomastoideus, the insertion is on the paroccipital process.

**Remarks:** There is little variation in the configuration of the cleidomastoid. Among most genera, the main variation is only in the exact point of origin on the clavicle. In Cavia the unusual condition is a result of the enlargement of M. cleido-occipitalis and the reduction in size of the clavicle.

**M. cleido-occipitalis**

Figure 9

Not reported by Parsons (1894a) but probably part of his M. cleidomastoideus.

**Origin:** From the sternal end of the clavicle in common with M. cleidomastoideus.

**Insertion:** On the most distal margin of the lambdoidal crest. The muscle is not separable from M. cleidomastoideus except at the point of insertion.

**Other Genera:** In all genera except Cavia, the muscle is poorly developed and closely associated with the cleidomastoid. In Myocaster, Octodon, and Ctenomys it is so poorly developed that in some specimens it may be missing. In Cavia the muscle is well developed and inserts broadly on the lambdoidal crest. It is in contact with M. acromiotrapezius at its insertion. The muscle in Cavia lies on top of and is closely associated with M. cleidomastoideus at the origin and for most of its length.

**Remarks:** This muscle has been described by some workers as M. clavotrapezius (Ballard, ms.) or included as part of M. cleidomastoideus (Parsons, 1894a; Lane, ms.; Olborth, 1964). The muscle was first described by John Wood in 1867, and he further elaborated on it in 1870. It is primitively very closely associated with the cleidomastoid (Hill, 1937; Rinker, 1954; Klingener, 1964), and lies ventral to the emerging N. auricularis magnus. This nerve is a useful feature in separating the muscle from M. clavotrapezius.

**M. acromiotrapezius**

Figures 8, 9

Trapezius, anterior portion (Parsons, 1894a)

**Origin:** From the area of the dorsal midline from the level of the rear of the skull to the second thoracic vertebra.

**Insertion:** On the anterior surface of M. spinotrapezius, the anterior surface of the distal (= clavicular) two-thirds of the scapular spine, the surface of the acromion and metacromion processes, and the scapular three-fourths of the clavicle. The insertion on the anterior surface of the spinotrapezius is lacking in some specimens.

**Other Genera:** The origin of the muscle in Erethizon, Dasyprocta, Thryonomys, and Petromus is partially from the lambdoidal crest. Posterior to the crest the origin is, as in all other genera, along the dorsal midline. In Myocaster, Octodon, Ctenomys, and Cavia the origin does not extend as far posterior as the second thoracic vertebra. The insertion of the muscle in Echimys, Isothrix, Mesomys, Myocaster, and Thryonomys is the same as in Proechimys. In Erethizon the insertion is confined to the tip of the clavicle, the acromion process, the spine of the scapula, and the anterior surface of M. spinotrapezius. In Octodon and Ctenomys the insertion is on the spinotrapezius, the spine of the scapula, and the acromion and metacromion processes, but not on the clavicle. In Cavia, Chinchilla, and Petromus the insertion is only on the spinotrapezius, the spine of the scapula and the metacromion process. In Dasyprocta the insertion is onto the surface of M. spinotrapezius, the spine of the scapula, and the metacromion process. The insertion on the spinotrapezius and spine of the scapula is via a thin fascial sheet, much as in Thryonomys.

**Remarks:** The configuration of this muscle varies greatly. In some specimens of Proechimys, Echimys, and Isothrix the insertion on the anterior surface of the spinotrapezius is missing. In Proechimys and Echimys some specimens had a good clavicular insertion, whereas others did not. In Cavia, a few specimens had a broad insertion on the spine of the scapula, whereas others had an insertion only on the metacromion process. Such variation must account for Parsons's (1894a) observations of a clavicular insertion in Octodon, a cranial origin in Chinchilla, and an insertion on the forearm in Dasyprocta. In addition, in some specimens of Proechimys and Echimys the origin was not as far posterior as the second thoracic vertebra.
The insertion on the clavicle can be explained by Hill's (1937, p. 109) assertion that this muscle in rodents "probably corresponds to clavicular and acromial parts of the trapezius of other mammals."

**M. spinotrapezius**
Figures 6, 8, 9

**Origin**: From the dorsal midline from the level of the third thoracic vertebra posteriorly into the lumbodorsal fascia.

**Insertion**: The muscle is divided into three parts. The posterior part inserts at a point on the spine of the scapula one-fourth of the way distally from the vertebral border. The anterior part inserts on the dorsal fascial extension of the first. The third part, called the auricular slip, lies on the posterior part and inserts on the facial muscles of the lateral side of the head.

**Other Genera**: The origin of the muscle is almost the same in all genera. In *Echimys*, *Isothrix*, *Mesomys*, *Erethizon*, *Chinchilla*, *Dasyprocta*, *Thryonomys*, and *Petromus* the origin is from as far forward as the third thoracic vertebra. In *Myocastor*, *Octodon*, *Ctenomys*, and *Cavia* the origin is from as far forward as the fourth thoracic vertebra. The auricular slip is present in *Echimys*, *Isothrix*, *Mesomys*, *Myocastor*, *Octodon*, *Erethizon*, and *Thryonomys*. In *Ctenomys* it is present and extremely enlarged. The auricular slip is not present in *Cavia*, *Chinchilla*, *Dasyprocta*, or *Petromus*.

**Remarks**: Parsons (1894a) stated that in many genera of hysticomorphs the trapezius is divided into an anterior and posterior part. He never observed an auricular slip. I found this separation into anterior and posterior parts in some specimens of *Proechimys*, *Echimys*, and *Isothrix*, but in most specimens of these three genera the muscles are continuous with each other. In *Mesomys*, *Erethizon*, *Chinchilla*, *Dasyprocta*, *Thryonomys*, and *Petromus* the acromiotrapezius and spinotrapezius muscles are always continuous with each other at their origins. In *Myocastor*, *Octodon*, *Ctenomys*, and *Cavia* the muscles are not continuous. In addition, in *Cavia*, *Dasyprocta*, and *Thryonomys* there is an open window of fascia between the two muscles in the area of the vertebral border of the scapula. This gives the appearance that the muscles are separate, but only *Cavia* has a separated origin. I conclude that the condition is too variable to be of any taxonomic significance. Hill (1937) stated that squirrels and *Aplodontia* have an undivided trapezius, and concluded that this is the primitive condition.
The presence of an auricular slip is fairly widespread in rodents (Klingener, 1964, 1970). The large superficial slip in Aplodontia (Klingener, 1970) is similar to the conditions in Ctenomys. Klingener believed that the superficial slip in Aplodontia represents a primitive superficial trapezial slip. This slip reflects the primitive rodent condition which has been modified in many rodents in one of three ways: the loss of the slip; the incorporation of the slip into the cheek pouch retractor muscles; and the vestigial presence of the slip as a thin auricular slip. The large superficial slip in Ctenomys can be viewed as representing a more primitive condition than exists in other hystricomorphs. The slip in Ctenomys is closely associated with the facial muscles, and is probably in the process of becoming a cheek pouch retractor of the kind seen in Thomomys (Hill, 1937; Klingener, 1970).

**MYOTOMIC MUSCULATURE**

**LINGUAL GROUP**

The muscles of this group are innervated by branches of the hypoglossal nerve.

**M. GENIOGLOSSUS**

*Figures 4B, 5B*

genio-hyo-glossus, part (Parsons, 1894a)

**Origin:** From the medial side of the mandible above the middle of the mandibular symphysis.

The origin is dorsomedial to the origin of M. geniohyoideus, and closely associated with it.

**Insertion:** Via two parts, one on the anterior margin of the basihyal, the other on the tongue. The muscle is not split by a branch of the hypoglossal nerve.

**Other Genera:** The muscle is variable. In Echimys and Ctenomys the insertion is mainly into the tongue. In Erethizon the entire insertion is
into the tongue. In Dasyprocta, one side had both insertions, the other only the insertion on the tongue. All other genera had both insertions of nearly equal size. There is also considerable variation as to whether the more lateral head is split by a branch of the hypoglossal nerve. In Thryonomys and Petromus (one specimen) the more lateral head has a branch of the nerve passing into it, but not splitting it. In Echimys, Myocastor, Octodon, Chinchilla, Dasyprocta, and Petromus (one specimen) the nerve passes between the two main parts of the muscle. In the other genera the nerve could not be followed in the region of the muscle.

Remarks: This muscle is too variable to be of any taxonomic value. In addition, the primitive condition of this muscle is not clearly understood.

M. hyoglossus
Figures 4, 5B
genio-hypoglossus, part (Parsons, 1894a)

Origin: From the anterolateral aspect of the basihyal and thyrohyal.

Insertion: The muscle passes anterolaterally to insert into the lateral part of the tongue.

Other Genera: The situation is the same in all genera except Chinchilla. In Chinchilla the muscle also takes origin from the tendinous arch of the posterior digastric.

Remarks: The muscle lies dorsal to M. mylohyoideus and lateral to M. geniohyoideus. The hypoglossal nerve passes over its surface before passing deep between this muscle and the geniohyoid.

There are fibers of a muscle originating from the stylohyal cartilage and passing into and below the lateral surface of this muscle. This extra muscle part appears to be part of the hyoglossus muscle which has extended its origin outward onto the stylohyal cartilage. The more lateral muscle is innervated by fibers of the glossopharyngeal nerve, however, and cannot be considered as part of M. hyoglossus.

M. styloglossus
Figures 4, 5B

Origin: From the tip of the bony pterygoid process.

Insertion: The muscle passes as a straplike band over the surface of M. hyoglossus to insert into the tongue.

Other Genera: The origin is also from the pterygoid process in Echimys, Isothrix, and Chinchilla. In some specimens of Octodon the origin is from the pterygoid process, while in others it is from the stylohyal cartilage close to the pterygoid process. In Thryonomys the origin is from the stylohyal cartilage close to the pterygoid process. In Myocastor, Erethizon, Cavia, and Thryonomys the origin is from the stylohyal cartilage anterior to the insertion of M. jugulo-hyoides. In Petromus and Dasyprocta the origin is along the stylohyal cartilage lateral and posterior to the insertion of M. jugulo-hyoides.

Remarks: As remarked for M. glossopharyngeus and M. hyoglossus, there are muscle fibers originating on the stylohyal cartilage in many genera that seem to be continuous with M. styloglossus. The innervation of these fibers indicates that they are not part of M. styloglossus, however.

The functional explanation for the shift of the styloglossus is not clear. Possibly the enlarging pterygoid process is associated with the change in the origin of the internal pterygoid and the styloglossus has secondarily become associated with this process. However, in Dasyprocta and Erethizon the pterygoid processes are enlarged (relative to the ventral dimensions of the skull), but the styloglossus is not associated with the pterygoid process in these animals. A more likely explanation is that a constriction of the inter-bulla distance (by the medial movement of the bulla for unknown reasons), plus an elongation of the head may have combined to create a situation in which the origin of the muscle has shifted in order to maintain a suitable mechanical advantage. The shift of the origin of the styloglossus in echimyids, Chinchilla, and to a lesser extent in octodontids seems to be a unique condition among rodents.

Medial Ventral Cervical Group

The innervation of M. geniohyoideus is via a small branch of the hypoglossal nerve. The remaining muscles, called the infrahyoid muscles, are innervated by a branch from the loop passing between the first and second cervical nerves. Edgeworth (1916) reported that muscles of this group have the same embryonic origin.

M. geniohyoideus
Figures 4, 5B
genio-hyoid (Parsons, 1894a)

Origin: From the medial side of the mandible
above the middle of the mandibular symphysis. The origin is ventral to that of M. genioglossus and closely associated with but separable from it.

**Insertion:** On the anterior surface and ventral tip of the basihyal. The muscle is closely associated with its antimeres to form what appears to be a single muscle.

**Other Genera:** The conditions of this muscle in the other genera are usually as they are in *Proechimys*. In *Dasyprocta* a few fibers insert onto the tendinous arcade of the posterior digastric along with some fibers of M. mylohyoideus. In *Erethizon* and *Thryonomys* the two antimeres are separable from each other, whereas in all other genera they are not.

**Remarks:** Parsons (1894a) used the separation of the antimeres of this muscle as a hysticomorph characteristic. In most of the hysticomorphs that I dissected the muscle was so closely associated with its antimeres that the parts were inseparable. This condition is similar to that of sciuromorphs (Parsons, 1894a), myomorphs (Parsons, 1896), pocket gophers (Hill, 1937), and squirrels (Bryant, 1945). It therefore seems safe to say that this condition is widespread in rodents and of little taxonomic significance. There is a significant amount of individual variation associated with this muscle.

**M. sternohyoideus**

*Figures 4A, 8, 11*

**Origin:** From the dorsal surface of the first sternebra and the anterior surface of the sternal end of the second rib. The origin is in common with M. sternothyroideus.

**Insertion:** On the posterior surface and tip of the basihyal.

**Other Genera:** The basic conditions are the same for all genera. In *Myocastor* the insertion is also on the surface of M. mylohyoideus and the median raphe, as reported by Parsons (1894a). The muscle in *Echimys, Octodon, and Chironomys* is fused with M. omohyoideus for a distance posterior to the insertion.

**Remarks:** The condition of this muscle is similar to the general rodent condition (Hill, 1937; Rinker, 1954; Klingener, 1964). The reported observation of the origin of this muscle from the anterior or dorsal surface of the manubrium (Ballard, ms.; Lane, ms.; Wood and White, 1950; Olborth, 1964) is not consistent with my observations. The observation by Bryant (1945) that this muscle originates on the dorsal surface of the manubrium in squirrels might reflect the more primitive rodent condition. Howell (1932) also implied that the manubrial origin is the more primitive.

**M. sternothyroideus**

*Figures 4A, 8*

**Origin:** In common with M. sternohyoideus, with which it is very closely associated.

**Insertion:** On the surface of the thyroid cartilage of the larynx. The muscle is considerably thinner than the sternohyoid from which it splits off beyond the level of the manubrium.

**Other Genera:** The muscle is similar in all the genera dissected. In *Cavia* it is extremely small, as Parsons (1894a) also noted. In *Dasyprocta* the muscle is large. It dominates M. sternothyroideus, and the origin is from the sternal end of the first rib, as well as the first costal cartilage and the sternal end of the second rib.

**Remarks:** The topographical relationships of this muscle are consistent in all genera. There is some variation in its size relative to the size of M. sternothyroideus.

**M. thyrohyoideus**

*Figure 4A*

Not reported by Parsons (1894a)

**Origin:** From the surface of the thyroid cartilage of the larynx.

**Insertion:** On the posterior surface of the thyrohyoid for almost the entire length.

**Other Genera:** In *Myocastor* and *Dasyprocta* the muscle is broad, and inserts on the posterior margin of the basihyal as well as the thyrohyal. This is true in *Erethizon* also, but the insertion on the basihyal is via a narrow slip that is separate from the main insertion on the thyrohyal. In *Cavia* and *Petromus* the muscle is restricted to the basihyal and the anterior half of the thyrohyal. In all other genera the muscle has the same configuration as it does in *Proechimys*.

**Remarks:** The unusual expansion of the insertion of M. mylohyoideus onto the entire length of the thyrohyal in *Petromus* might be responsible for restricting the area of insertion of M. thyrohyoideus.

Elton (ms.) mentioned the presence in *Dasyprocta* of an extra medial slip inserting onto the
medial portion of the hyoid and thought it to be separate from M. thyrohyoideus. The condition is similar to the extra medial slip I observed in Erethizon; however, I believe that the fibers are associated with M. thyrohyoideus. Bryant (1945, p. 320) reported that in squirrels M. thyrohyoideus inserts on the "posteromedial surface of the posterior process of the hyoid." I believe, therefore, that the primitive insertion is broadly onto the thyrohyal bone (= Bryant's "posterior process of the hyoid"). The more medial slip may possibly represent the part of the muscle that forms the insertion in muroids (Rinker, 1954) and dipoidoids (Klingener, 1964).

M. omohyoideus

Figure 5A

omo-hyoid (Parsons, 1894a)

The muscle is not present in any of my specimens of Proechimys.

Other Genera: The muscle is lacking also in Isothrix, Mesomys, Myocastor, Cavia, Chinchilla, and Dasyprocta. The muscle is present in Echimys, Octodon, Ctenomys, Erethizon, Thryonomys, and Petromus.

In Echimys, Octodon, and Ctenomys the insertion is onto the fibers of M. sternohyoideus, and therefore the muscle has a common insertion with M. sternohyoideus on the basihyal bone. In Erethizon the insertion is onto the tendon of M. digastricus (posterior belly), and the common insertion is on the basihyal bone. In Petromus and Thryonomys the insertion is onto the basihyal, close to, but not fused with the sternohyoideus.

The origin of the muscle in Echimys, Octodon, Ctenomys, and Erethizon is the cranial border of the scapula near, but not on, the coracoid process. In Petromus the origin is on the coracoid process. In Thryonomys the origin is on the coracoid process and the surface of M. supraspinatus.

Remarks: Parsons (1894a) remarked that the muscle is often lacking in hystricomorphs, but is always present in sciuromorphs and (1896) myomorphs. Howell (1932) reported that the muscle is missing in Zapus, which would make it the one reported exception among non-hystricomorphs. Klingener (1964) reported an omohyoid in his specimens of Zapus, however, and we must therefore assume that Howell overlooked this muscle.

I confirm Parsons's (1894a) observations that the omohyoid is present in Octodon, Erethizon, and Thryonomys. In addition I found it in Echimys (as did Lane, ms.), Ctenomys (as did Hoyer, ms.) and Petromus (as did Berkowitz, ms.). Parsons (1894a) reported that it is also found in Capromys and Sphingurus (= Coendou). In Hystrix the muscle is poorly developed or missing (Parsons, 1894a; Lesbre, 1907).

I confirm Parsons's (1894a) observations that the muscle is missing in Myopotamus (= Myocastor), Chinchilla, Dasyprocta, and Cavia. In addition I found it missing in Proechimys, Isothrix, and Mesomys. Parsons (1894a, 1898) reported that it is also missing in Lagostomus, Coelogenys (= Cuniculus), Ceredon (= Kerodon), and Dolichotis and Pedetes. The muscle is therefore reported as missing in twelve genera of hystricomorphs and in Pedetes.

The muscle is present in squirrels (Bryant, 1945), and is large in Aplodontia (Hill, 1937). These observations indicate that the presence of a M. omohyoideus is probably the primitive condition, and that the loss of the muscle is a derived situation. The consistency of my observations with the observations of the other workers indicates that the muscle exhibits little individual variation.

APPENDICULAR MUSCULATURE

MUSCLES OF THE PECTORAL GIRDLE AND LIMB

Extensor System
costi-spino-scapular group

All muscles of this group except M. serratus anterior are innervated by the dorsal scapular nerves. M. serratus anterior is innervated by the long thoracic nerve.

M. levator scapulae and M. serratus anterior

Figure 10

levator anguli scapulae and serratus magnus (Parsons, 1894a)

Origin: From the transverse processes of the last five cervical vertebrae, and from the lateral surface of ribs one through seven. In some
specimens the part from the surface of the second rib is missing, causing some separation into anterior and posterior parts.  

Insertion: As a single sheet on the medial side of the vertebral border of the scapula. The insertion is very broad and covered by the inserting fibers of M. rhomboideus. 

Other Genera: The insertion of the muscle is the same in all genera. In Echimys, Isothrix, and Mesomys the origin is the same as in Proechimys. In Myocastor, Octodon, Ctenomys, and Dasyprocta the origin is also from the eighth rib. In Cavia the origin is from the second cervical vertebra to the ninth rib. In Thryonomys and Petromus the origin is from the atlas to the eighth rib, and in Erethizon the origin is from the atlas to the ninth rib. 

Remarks: These two muscles are sometimes separate in mammals, but they are continuous in most rodents, and therefore treated as one muscle group. Howell (1926) separated the two parts of the muscle in his description of the wood rat, but Parsons (1894a), Howell (1932), Hill (1937), Bryant (1945), Rinker (1954), and Klingener (1964) all considered the muscles to be one group. 

The origin of this muscle is characterized by a large amount of individual variation. My specimens of Thryonomys, Octodon, Dasyprocta, and Cavia all differed in some points from the origins described by Parsons (1894a). Rinker (1954) also pointed out some variation of this muscle in muroids. 

A critical point concerning this muscle is the presence or absence of an origin from the atlas. Such an origin exists in Erethizon, Thryonomys, and Petromus. In Erethizon and Thryonomys a M. atlantoscapularis posterior is also present. Howell (1932) considered M. atlantoscapularis superior (= M. atlantoscapularis posterior) to be the part of M. serratus magnus (anterior part of which = M. levator scapulae) that arises from the atlas. Because of the presence of both an atlantal slip of M. levator scapulae and M. atlantoscapularis in Erethizon and Thryonomys, as well as in squirrels (Bryant, 1945 and personal observ.), I believe that Howell (1932) was incorrect in his interpretation. 

M. rhomboideus anterior 

Figure 10 
rhomboideus minor (Parsons, 1894a) 

From the sequence of his presentation, it appears that Parsons is confusing pars major with pars minor. Parsons’s descriptions are not complete enough, however, to know with certainty. The pars minor of human terminology is a synonym for pars anterior. 

Origin: From the dorsal midline along the ligamentum nuchae. The muscle is not continuous with M. occipitoscapularis, but is with M. rhomboideus posterior. 

Insertion: On the medial side of the vertebral border of the scapula posterior to the spine. Some fibers of the insertion are covered by the more superficial fibers of rhomboideus posterior. 

Other Genera: The insertion is the same in all genera. The origin is from the proximal half of the lambdoidal crest in Echimys, Mesomys, and Cavia. The origin is continuous with that of M. occipitoscapularis in these genera, as it is in all other genera except Octodon. In all genera the muscle is more or less continuous with M. rhomboideus posterior, but the muscles are separable from each other. 

Remarks: Whether this muscle forms a single sheet with M. occipitoscapularis, or is separable, does not seem to have any taxonomic value. It forms a single sheet in all but four genera of squirrels investigated by Bryant (1945), in Xerus and Spermophilus (Parsons, 1894a), Aplodontia (Lewis, 1949), geomyids (Hill, 1937), Scirtopoda (= Jaculus) (Howell, 1932), and Jaculus (Klingener, 1964). Most hystricomorphs have the continuous situation described above. However, Proechimys and Octodon have a separation between the muscles as do Dolichotis (Windle, 1897), Dipodomys, Allactaga, and Lepus (Howell, 1932), Neotoma (Howell, 1926), and Rattus (Greene, 1935). The variation in the condition of this muscle does not seem to follow any taxonomic pattern. The single continuous sheet is surely the more primitive condition. 

M. rhomboideus posterior 

Figure 10 
rhomboideus major (Parsons, 1894a) 

Origin: From the ligamentum nuchae posterior to the origin of M. rhomboideus anterior and from the neural spine of the second thoracic vertebra. 

Insertion: On the medial side of the border of the scapula, posterior to the spine. The muscle is superficial to parts of M. rhomboideus anterior.
**WOODS: HYSRICHOMORPH RODENTS**

**Fig. 8.** Lateral view of neck and thorax of *Proechimys guyannensis*.

**Other Genera:** The insertion is the same in all genera. The origin is the same as in *Proechimys, Echimys, Isothrix, Mesomys, Myocastor, Octodon, Ctenomys,* and *Petromus*. In *Cavia* and *Chinchilla* the origin is to as far posterior as the spine of the fourth thoracic vertebra. In *Dasyprocta* the origin extends back to the third thoracic vertebra, and is continuous with *M. latissimus dorsi*. In *Erethizon* and *Thryonomys* the origin extends as far back as the sixth thoracic vertebra. The origin in *Erethizon* is not continuous with that of *M. latissimus dorsi*, whereas it is continuous in *Thryonomys*.

**M. occipitoscapularis**

*Figures 8, 10, 12*

**rhomboideus capitis** *(Parsons, 1894a)*

**Origin:** From the lambdoidal crest. In some specimens the muscle is not continuous with *M. rhomboideus anterior*, while in others it is.

**Insertion:** On the proximal end of the scapular spine and the lateral edge of the vertebral border of the scapula.

**Other Genera:** In *Echimys, Isothrix, Mesomys, Erethizon, Cavia,* and *Petromus* the origin of the muscle on the lambdoidal crest is extensive, and the muscle is continuous with *M. rhomboideus anterior*. The insertion of the muscle in these genera is the same as it is in *Proechimys*. In *Myocastor* and *Ctenomys* the origin is on the whole lambdoidal crest, while in *Octodon* the origin is restricted to the central part of the crest. In *Myocastor* and *Ctenomys* the muscle is continuous with *M. rhomboideus anterior*. In these two genera and in *Octodon* the insertion is on the lateral edge of the vertebral border of the scapula. In *Chinchilla* and *Dasyprocta* the origin is on the whole lambdoidal crest, but in both of these animals the insertion tends to be on the medial side of the vertebral border, between the insertion of the rhomboideus and levator scapulae muscles. In *Chinchilla* the muscle also inserts on the lateral margin of the vertebral border. In *Thryonomys* the origin is from the whole lambdoidal crest and the transverse process of the atlas. The part from the atlas I interpret as being the *M. atlantoscapularis posterior*. The insertion is on the lateral margin of the vertebral border and the tip of the spine of the scapula.

**Remarks:** The situation in *Proechimys* and *Octodon* in which the muscle is not continuous with the rhomboideus is subject to individual
variation. In some cases in each of these genera I found specimens in which the origin of the muscle was broad and continuous with M. rhomboideus anterior. In addition, I found the origin of the muscle to be broad in my specimens of Chinchilla, but Wood and White (1950) reported that it was narrow in their specimens. These observations indicate the possibility of individual variation in the other genera.

The muscle is closely associated with M. atlantoscapularis posterior at its insertion, and when the insertion of one muscle varies, the other varies accordingly. In addition, in Thryonomys the origins of M. occipitoscapularis and M. atlantoscapularis posterior are continuous. The atlantoscapularis posterior is probably derived from the occipitoscapularis, not from the levator scapulae.

M. ATLANTOSCAPULARIS POSTERIOR

Figures 8, 10, 12

Not reported by Parsons (1894a)

ORIGIN: From the transverse process of the atlas.

INSERTION: On the proximal one-fifth of the spine of the scapula. The muscle is partially covered by M. occipitoscapularis and closely associated with it.

OTHER GENERA: The muscle is present in all genera except Ctenomys, Cavia, Dasyprocta, and Petrodus. The origin is the same in all genera in which the muscle is present. In Echimys, Isothrix, Mesomys, and Erethizon the insertion is on the spine of the scapula, just as it is in Proechimys. In Myocastor the insertion is similar, but because of the reduction of the proximal end of the scapular spine, the insertion is also on the aponeurosis of M. spinodeltoideus near its insertion. In Octodon the scapular spine is also reduced and the insertion is totally restricted to the vertebral border of the scapula. In Chinchilla and Thryonomys the insertion is inseparable from M. occipitoscapularis on the spine of the scapula. The muscle is thin in Chinchilla, and in Thryonomys is totally fused with the occipitoscapularis for its entire length.

REMARKS: The conditions of this muscle in other mammals are difficult to relate with my findings. Howell (1932) assumed that it is merely the part of M. levator scapulae (his main cervical part of M. serratus magnus) which originates from the atlas. This interpretation is followed by Klingener (1964) for dipodoids. In his treatment of the Red Howling Monkey, Alouatta fusca, Schön (1968) followed the same interpretation and presented a good discussion of the historical treatment of this muscle in primates. I believe, however, that this muscle in primates is not separable from M. levator scapulae and is not homologous with the true M. atlantoscapularis posterior.

I have observed a M. atlantoscapularis in Erethizon and Thryonomys. In both of these animals M. levator scapulae also originates from the atlas, making it unlikely that M. atlantoscapularis is part of M. levator scapulae. In addition, the close association of the muscle with M. occipitoscapularis in Thryonomys, and the relatively close association in other hystricomorph genera indicate a more probable relationship with M. occipitoscapularis. Olbornth (1964) treated the fibers that I am calling this muscle as part of his M. rhomboideus capitis (= my M. occipitoscapularis) in the Chinchilla. Further evidence that M. atlantoscapularis posterior is not related to M. levator scapulae is found in squirrels (Bryant, 1945; personal observ.). M. levator scapulae originates from the scapula, and there is a M. atlantoscapularis posterior in Eutamias, Marmota, Ammospermophilus, Spermophilus, Cynomys, Sciurus, Tamiasciurus, and Glaucomys.

I conclude that the M. atlantoscapularis posterior of many hystricomorphs and sciurinomorphs is different from the M. atlantoscapularis posterior that Howell (1932) and Schön (1968) described in their animals. Howell and Schön were probably merely describing the most anterior fibers of M. levator scapulae, which often appear, as in Thryonomys, to be a separate muscle. The primitive condition I interpret to be reflected in those hystricomorphs and sciurinomorphs where there is both a M. atlantoscapularis posterior and an origin of M. levator scapulae from the atlas.

It therefore becomes impossible to tell exactly what muscle Parsons (1894a, p. 277) was referring to when he described M. levator scapulae (his levator anguli scapulae) as having “a separate slip rising (sic) from the atlas” in some genera. It is also difficult to establish the homologies of this muscle with the M. atlantoscapularis posterior (= anterior) of the Rhesus Monkey (Howell and Straus, 1933) or the M. levator scapulae minor of the rabbit (Bensley, 1931).
The innervation of this muscle is via the same dorsal scapular complex that innervates M. levator scapulae and M. occipitocapularis.

**M. omocervicalis**

*Figures 6, 8-11*

*levator claviculae (Parsons, 1894a)*

**Origin:** From the ventral arch of the atlas.

**Insertion:** On the metacromion process, the surface of M. acromiodeltoideus, and onto the tip of the deltoïd crest of the humerus with M. cutaneus maximus.

**Other Genera:** The origin of this muscle is from the ventral arch of the atlas in *Echimys*, *Isothrix*, *Myocastor*, *Octodon*, *Ctenomys*, *Erethizon*, *Chinchilla*, and *Petromus*. The origin is from the surface of the basioccipital in *Cavia*, *Dasyprocta*, and *Thryonomys*.

The insertion of the muscle is the same in *Erethizon* as it is in *Proechimys*. The insertion is restricted to the metacromion process in *Echimys*, *Isothrix*, *Mesomys*, *Myocastor*, *Cavia*, *Chinchilla*, and *Petromus*. In *Octodon* it inserts on the metacromion and acromion processes. In *Ctenomys*, it inserts on the acromion process and the scapular three-fourths of the clavicle. In *Dasyprocta* the muscle inserts on the tip of the metacromion process, the surface of M. acromiodeltoideus, and the forearm. There is a distinct extra insertion on the scapular end of the clavicle. In *Thryonomys* the insertion is on the metacromion process and, as in *Dasyprocta*, via a small extra part on the scapular end of the clavicle.

**Remarks:** This muscle is extremely variable in rodents and probably of little taxonomic significance. Hill (1937) presented an excellent discussion of the variation of this muscle in different groups of rodents. He concluded (p. 114) that "the primitive origin seems to be the transverse process of the atlas; the primitive insertion is the acromion." However, Hill also stated that in squirrels and *Aplodontia* the insertion is on the acromion process, whereas I find the insertion to be on the metacromion process. My observations are substantiated by Bryant.
(1945) for squirrels and Lewis (1949) for *Aplodontia*. In addition, squirrels and *Aplodontia* have an origin from the ventral arch of the atlas, as do the more primitive hysticomorphs. For primitive hysticomorphs I am using the interpretations of Landry (1957a, p. 64) on *Petromys (= Petromus)* and echimyids, of Moody and Doniger (1956) on *Erethizon*, and Wood and Patterson (1959) on *Octodon*. I therefore do not agree with Hill's (1937) interpretation of the primitive rodent condition. I believe that the primitive origin probably is the ventral arch of the atlas, and the primitive insertion is the metacromion process.

Parsons (1894a) reported that in *Myopotamus* (= *Myocaster*) the origin is from the basioccipital, but in my specimens the origin is always from the ventral arch of the atlas.

**LATISSIMUS-SUBSCAPULAR GROUP**

The innervation of the muscles of this group is via the subscapular nerves. (The most posterior of the subscapular nerves is called N. thoracodorsalis.)

**M. LATISSIMUS DORSI**

*Figures 8, 12, 14, 16*

**Origin:** From the last five thoracic vertebrae and the lumbodorsal fascia.

**Insertion:** On the medial side of the humerus below the lesser tuberosity. The muscle joins with M. teres major to insert via a common tendon. There is a separate part lifting off the posterior margin of the main muscle and inserting on the surface of the pectoralis minor near its insertion on the deltoid ridge. This separate part, called a latissimus Achselbogen, passes over the surface of the nerves of the arm and over the biceps muscle.

**Other Genera:** The conditions in *Echimys*, *Isthrix*, *Mesomys*, and *Ctenomys* are the same as they are in *Proechimys*. In *Myocaster*, *Octodon*, and *Cavia* a latissimus Achselbogen is also present. In *Myocaster* and *Cavia* the latissimus dorsi originates from the posterior seven thoracic vertebrae and from the lumbodorsal fascia, while in *Octodon* the origin is from the last three thoracic vertebrae and the lumbodorsal fascia. In *Erethizon*, *Chinchilla*, *Dasyprocta*, *Thryonomys*, and
Petromus the latissimus Achselbogen is missing. In all of these genera, however, there are slight indications of a vestigial Achselbogen and of fibers of M. cutaneus maximus becoming associated with the main part of M. latissimus dorsi. In Chinchilla the origin is from the last thoracic vertebra and the lumbodorsal fascia. In Petromus the origin is from the last six thoracic vertebrae and the lumbodorsal fascia. In Erethizon the origin is from the last five thoracic vertebrae, the lumbodorsal fascia and the surface of the more caudal ribs. The insertion of the muscle in Erethizon is on the medial side of the humerus, separately from the insertion of M. teres major. In all other genera of hystricomorph rodents investigated the muscle inserts in common with the teres major. In Dasyprocta and Thryonomys the origin is from farther anterior than in the other genera, and is absolutely continuous with M. rhomboideus posterior. In Thryonomys the origin extends forward to the sixth thoracic vertebra; in Dasyprocta to the third.

Remarks: This muscle has not been completely described in the older literature. Parsons (1894a, p. 276), in passing, noted what must be the latissimus Achselbogen when he stated, "very often some of the fibers of the muscle are continued across the axilla to blend with the pectoralis major." In addition, Alezais (1900) presented a description of this part for Cavia and several other rodents. Alezais called this part of the muscle "Arc axillaire." Böse (1904) described and illustrated the Achselbogen in Cavia. The muscle is more completely treated in Langworthy (1925) which includes good discussions of the situation in Cavia and Erethizon. A latissimus Achselbogen is also frequently reported in humans, and in dogs and cats (Langworthy, 1924, 1925). Langworthy in both papers stated that the muscle in dogs and cats is not homologous with the muscle in humans. He believed that the muscle in humans develops from the pectoralis major (= cutaneus maximus), while in dogs and cats it develops from the latissimus dorsi.

I do not agree completely with Langworthy's ideas. The Achselbogen that is present in the hystricomorphs dissected was innervated by both the thoracodorsal and the anterior thoracic nerves. The dual innervation indicates that the muscle is probably formed by elements of both the latissimus dorsi and the cutaneus maximus. This would be consistent with the conditions in those hystricomorphs which lack an Achselbogen, but which have indications of a slip splitting off from the main latissimus muscle mass. In Erethizon, Chinchilla, and Thryonomys there are indications of this small slip of M. latissimus dorsi. In all these genera the cutaneus maximus also lies in close contact with the latissimus dorsi. In Erethizon the cutaneus maximus has even split into a separate part, and is closely associated with the latissimus dorsi. This extra part was noted in Erethizon by Langworthy (1925). I therefore believe that the latissimus Achselbogen is formed by elements of both the latissimus dorsi and the cutaneus maximus. The condition in humans, which Langworthy (1925) speaks of as being different from that of animals such as Cavia and the dog and the cat, probably represents only the cutaneus maximus contribution, and is therefore similar to the situation in Erethizon (as Langworthy also noted). Langworthy (1924, 1925) presented an excellent historical discussion of the latissimus Achselbogen problem.

The primitive origin of the cutaneus maximus is probably from the spines of the posterior thoracic vertebrae, the lumbodorsal fascia, and the more caudal ribs; the primitive insertion includes the presence of a latissimus Achselbogen.

M. teres major
Figures 13, 14, 16

Origin: From the most posterior margin of the vertebral border and the dorsal third of the axillary border of the scapula. Some fibers also originate from the fascial surface of M. infraspinatus and M. subscapularis.

Insertion: The muscle passes into the axillary region where it joins the tendon of M. latissimus dorsi. The combined muscle inserts as a common tendon on the medial side of the humerus distal to the lesser tuberosity.

Other Genera: The muscle is the same in all other genera except Erethizon. In Erethizon the muscle does not join the tendon of the latissimus, but instead inserts separately. This insertion is deep to the insertion of the narrow tendon of the latissimus dorsi.

Remarks: The insertion of this muscle is more distal on the shaft of the humerus in Erethizon and Ctenomys than in the other genera. The mechanical advantage of the muscle in these two genera, therefore, indicates habits requiring
strength rather than speed (Maynard Smith and Savage, 1956).

Parsons (1894a), Windle (1897), and Brown (ms.) noted that the muscle in their specimens of Dasyprocta does not have a common insertion with the latissimus dorsi. This differs from my observation, and those of Mivart and Murie (1866), and Elton (ms.) in which the muscle does insert via a common tendon with the latissimus dorsi. This individual variation is not found in the other genera investigated. Parsons (1894a) reported a common insertion in many genera of hystricognathi. Wood and White (1950) noted a common insertion in Chinchilla, but they implied that in most rodents the insertions are separate. A review of the works of Hill (1937) on geomyids, Bryant (1945) on squirrels, Lewis (1949) on Aplodontia, Rinker (1954) on muroids and Klingener (1964) on dipodoids indicates that a common insertion is widespread in rodents.

M. subscapularis

Figure 14

subscapularis (Parsons, 1894a)

ORIGIN: From the entire subscapular fossa of the scapula.

INSERTION: On the lesser tuberosity of the humerus.

OTHER GENERA: The muscle is basically the same in all genera.

REMARKS: The muscle is subdivided into a number of parts. The composition of these parts shows little variation among the genera studied. The surface of the muscle in Cavia is covered by a heavy fascial sheet that lifts off with the connective tissue surrounding the brachial plexus. This shiny fascial sheet was less well developed in other genera.

DELTOID GROUP

The muscles of this group are innervated by the axillary nerve.

M. clavodeltoideus

Figures 9, 11, 12
deltoid, clavicular portion (Parsons, 1894a)

ORIGIN: From the scapular three-fourths of the clavicle.

INSERTION: On the anterior margin and tip of the deltoiod crest of the humerus. The muscle is closely associated with M. acromiodeltoideus and M. pectoralis major.

OTHER GENERA: The conditions are basically the same in all genera except Cavia and Dasyprocta. The only variation in most genera is the extent of the origin on the clavicle. In some genera, such as Myocastor,Octodon, and Ctenomys the clavicle is hooked, and the origin of the muscle is from the middle three-fourths of the bone.

In Cavia (see fig. 9) the muscle originates on the posterior surface of the entire clavicle. The clavicle is reduced to a small rod. The insertion is at the distal end of the humerus on the inside surface of the medial epicondylar ridge. In Dasyprocta the origin is on the scapular half of the clavicle; the insertion is on the anterolateral surface of the distal one-half of the humerus. In both Cavia and Dasyprocta the muscle is still closely associated with the pectoralis major complex.

REMARKS: The muscle is closely associated with M. acromiodeltoideus, and in most genera the muscle probably could best be treated as M. clavo-acromiodeltoideus. The separation of the muscles in Cavia and Dasyprocta, however, would make such a grouping of these muscles less precise.

The extension of the insertion of this muscle to the distal end of the humerus in Cavia and Dasyprocta creates a muscle that looks like the clavobrachialis of the cat and other carnivores. The clavodeltoid and the clavobrachialis must certainly be the same muscle, but the description of the clavodeltoideus in squirrels (Parsons, 1894a; Bryant, 1945) implies that they may be separate parts of the same muscle. The movement of the insertion of M. clavodeltoideus to the distal end of the humerus (or the hypertrophy of the more superficial fibers of the muscle if the implications of Bryant's description are followed) might be associated with the tendency of Cavia and Dasyprocta to be stronger runners. In addition, the near fusion of the clavodeltoideus with the cleidoccipitalis in Cavia represents one of the primary modifications for speed in running (Howell, 1944).

M. acromiodeltoideus

Figure 12
deltoid, acromial slip (Parsons, 1894a)

ORIGIN: From the ventral edge of the acromial process of the scapula.

INSERTION: On the posterior edge and tip of the deltoid ridge of the humerus. The muscle
also inserts onto the fibers of M. clavodeltoideus and the tendinous surface of M. spinodeltoideus near their respective insertions.

**Other Genera:** The configuration of this muscle is the same in all genera. The relative size of the muscle varies somewhat. It is the least well developed in *Clenomys*; the best developed in *Thryonomys*. In *Myocastor*, *Octodon*, *Clenomys*, *Erithizon*, *Cavia*, and *Thryonomys* the fibers of this muscle also originate from at least part of the ventral surface of the metacromion process. As noted earlier, the muscle is not associated with M. clavodeltoideus in *Cavia* or *Dasyprocta*.

**Remarks:** This muscle shows almost no variation in most rodents, and is therefore of little taxonomic significance. The presence in *Thryonomys* of a joint in the scapular spine proximal to the acromion and metacromion processes has been noted by Tullberg (1899). The reason for this joint is not clear, but I suggest that it is caused by the great enlargement of the acromion and metacromion processes. These two processes are more enlarged in *Thryonomys* than in any other rodent dissected in this study. The muscles originating and inserting on these processes do so over a much greater horizontal angle than is usual, and therefore place an increased strain on the thin scapular spine.

**M. Spinodeltoideus**

**Figure 12**

deltoid, part from spine (Parsons, 1894a)

**Origin:** From the posterior edge of the deltoid four-fifths of the spine of the scapula.

**Insertion:** On the posterior edge of the deltoid ridge of the humerus, deep to the insertion of M. acromiodeltoides.
Other Genera: The insertion of the muscle is the same in all genera. The muscle has the same origin in *Echimys*, *Isothrix*, and *Mesomys* as it does in *Proechimys*. In *Octodon* and *Ctenomys* the origin is from a tubercle on the spine one-fourth the distance from the vertebral border, and along the distal three-fourths of the spine. In *Myocastor* the origin is the same as in *Octodon* and *Ctenomys*, but there is an additional origin via an aponeurosis on the surface of *M. infraspinatus* near the vertebral border of the scapula. In *Cavia* the muscle is relatively small, and the origin is from the distal half of the scapular spine. In *Dasyprocta* the origin is also from the distal half of the spine, but it is additionally from the surface of *M. infraspinatus* via an aponeurosis and from the medial surface of the metacromion process. In *Erethizon*, *Thryonomys*, and *Petromus* the muscle is well developed and originates from the distal three-fourths of the spine, and via an aponeurosis over the infraspinatus. In *Thryonomys* there is a part of the muscle originating on the medial surface of the metacromion, just as in *Dasyprocta*. In *Chinchilla* the origin is from the distal three-fourths of the scapular spine.

Remarks: The extent to which the muscle originates via the aponeurosis on the surface of *M. infraspinatus* is variable. I did not observe any aponeurotic origin in my specimens of *Chinchilla*, but Wood and White (1950) did report an origin from the fascia over the infraspinatus.

Parsons (1896) stated that the spinal part of his *M. deltoidei* is the smallest of the three parts in the Hystricomorpha. I do not agree with this observation. The description of this muscle in Mivart and Murie (1866) is inadequate.

The muscle does narrow down to a thin tendon in all genera, and fibers of *M. acromiodeltoideus* insert onto the surface of the tendon. In *Dasyprocta* and *Thryonomys* there are fibers of the muscle originating on the medial surface of the metacromion process and passing directly onto the tendon of the remaining part of the muscle. It is not known if this condition partially accounts for the presence of an extra joint in the spine of the scapula of *Thryonomys* proximal to the acromion and metacromion processes. *Dasyprocta* does not have such a joint.
Tullberg (1899, pl. 30) illustrated the scapulae of *Dasyprocta* and *Thryonomys*.

**M. teres minor**

*Figure 13*

**Origin:** From the distal two-fifths of the axillary border of the scapula, and from the anterior surface of the well-developed aponeurotic envelope. The muscle is small, and largely covered by *M*. infraspinatus.

**Insertion:** On the distal edge of the greater tuberosity. The insertion is via a tendon and is distal to and separate from the insertion of *M*. infraspinatus.

**Other Genera:** The muscle is small in *Octodon* and *Cavia*, but well developed in all other genera. In *Cavia* the separate insertion is covered by the inserting tendon of *M*. infraspinatus; in all other genera the insertion is distal to that of *M*. infraspinatus. In all genera there is a well-developed aponeurotic envelope.

**Remarks:** The aponeurotic envelope was described by Rinker (1954), and also seems to have been observed by Parsons (1894a) for *Lagostomus* and (1896) for *Rhizomys*. Howell (1932) for *Dipodomys*, and Klingener (1964) for *Sicista*, *Zapus*, and *Jaculus*. This aponeurotic envelope originates from the axillary border of the scapula between the origins of *M*. teres minor and teres major and then loops up and over the surface of the teres minor and infraspinatus muscles. The insertion is on the posterior margin of the base of the spine, and the posterodorsal tip of the metacromion process. The condition is present in all hysticomorphs that I examined, and in the murid rodents examined by Rinker (1954). It is possible that the condition is widespread in rodents, and has been overlooked.

**Suprascapular Group**

The muscles of this group are innervated by the suprascapular nerve.

**M. supraspinatus**

*Figure 13*

**Origin:** In two closely associated parts. One part is from the anterior surface of the proximal half of the scapular spine, the ventral surface of the spine in the region of the great scapular notch, and the surface of the septum separating
this muscle from M. infraspinatus. The remaining larger part is from the supraspinous fossa, the superior border of the scapula, and the anteromedial surface of M. subscapularis.

Insertion: The part from the scapular spine is more superficial than the second part, and inserts onto its surface. The combined parts narrow to a thin tendon which inserts on the dorsocranial surface of the greater tuberosity.

Other Genera: The conditions are basically the same in all genera. In Cavia and Erethizon the larger part of the muscle seems to be divided into two portions. In Erethizon there is also a small extra group of fibers along the anterior margin of the muscle near its insertion. The muscle parts are moderately fused in Myocastor, Octodon, Ctenomys, and Chinchilla. The parts are fused in Dasyprocta.

Remarks: The separation of this muscle into two parts is widespread in rodents, and of little taxonomic significance.

M. INFRASPINATUS

Figure 13

Origin: From the surface of the infraspinous fossa, the dorsal margin of the axillary border under M. teres major, the vertebral border, and the spine of the scapula. The part of the muscle from the spine originates on the posterior margin of the spine proximal to the great scapular notch and on the ventral surface of the spine in the region of the notch.

Insertion: The muscle narrows to a tendon and inserts on the greater tuberosity of the humerus. The muscle passes anteroventrally beneath the spine of the scapula (great scapular notch). The notch extends along the distal two-thirds of the length of the scapular spine.

Other Genera: The conditions of this muscle are the same in Echimys, Isithrix, Mesomys, Myocastor, Ctenomys, and Petromus. In all of these genera the great scapular notch extends along the distal two-thirds of the scapular spine. In Erethizon, Cavia, Chinchilla, Dasyprocta, and Thryonomys the notch extends for only the distal one-fourth of its length. In the last five genera the origin is from the fossa, the proximal axillary border, the vertebral border, the spine of the scapula, and the ventral surface of the metacromion process and aponeurotic envelope.

Remarks: The reason for the shift of M. infraspinatus under the open area of the scapular

spine is difficult to explain functionally. This muscle appears to be constant in most mammals. Howell (1944) stated that the infraspinatus does not undergo any modifications in animals that are becoming specialized for speed.

The muscle is multipennate in hystricomorphs, as it is in many other rodents (Hill, 1937; Rinker, 1954; Klingener, 1964). In those genera in which there is a large great scapular notch, the muscle is closely associated with M. supraspinatus. Indeed, in Proechimys there is a part originating from the ventral margin of the open spine which is impossible to assign clearly to either group. The muscles are closely associated with each other embryonically. This close embryonic association was pointed out by both Howell (1936, 1937) and Cheng (1955), who also believed that the M. infraspinatus and M. supraspinatus probably should be grouped with the ventral muscles on the basis of phylogenetic and embryonic origins.

TRICEPS GROUP

The muscles of this group are innervated by the radial nerve.

M. DORSOEPITROCHLEARIS

Figures 14, 15

Lateralis dorsi, part, dorso-epitrochlearis (Parsons, 1894a)

Origin: From the dorsolateral border of the latissimus dorsi. The muscle is thin, and the origin is often fascial. A small aponeurosis may pass onto the surface of the teres major.

Insertion: On the posteroventral aspect of the olecranon process of the ulna.

Other Genera: The configuration of the muscle is the same in all genera investigated. In all genera except Erethizon and Thryonomys the muscle is relatively thin. In these two genera the muscle is well developed and the origin is solidly from the central area of the latissimus dorsi. The insertion in Thryonomys is additionally onto the posteroventral surface of the enlarged M. flexor carpi ulnaris.

Remarks: The question of whether this muscle is related to the latissimus dorsi or the long head of the triceps has received some attention in the literature. Parsons (1894a) and other early workers considered the muscle to be part of the latissimus dorsi, as did Howell (1937) and Cheng (1955). Howell (1937, p. 455)
acknowledged the common innervation shared by the dorsoepitrochlearis and the triceps, but explained it by saying the “innervation shifted to allocation with N. radialis in response to the law of fasciculation.” Hill (1937) thought that the muscle is derived from the long head of the triceps, a premise which Howell (1937, p. 455) was “loath to accept.” The exact pre-mammalian homolog remains a mystery.

Howell (1937) remarked that this muscle is absent in Chiroptera, Cetacea, Sirenia, ante-lopes and many primates, and that the normal origin is the tendon of the latissimus dorsi. Such an origin on the latissimus dorsi is also found in all hystricomorphs dissected by me, and in several other rodents (Howell, 1926; Rinker, 1954) and insectivores (Reed, 1951). However, an origin on the scapula and/or on the teres major appears to be more widespread in rodents (Howell, 1932; Hill, 1937; Bryant, 1945; Klingener, 1964). The exact primitive configuration of this muscle is unknown but it seems reasonable that the muscle has enlarged and shifted posteriorly in these forms. The functional implications of the enlargement and posterior shift in the origin of this muscle in Erethizon and Thryonomys are unknown. Ziegler (1964) observed a similar enlargement of the muscle in the chimpanzee, and believed that it is associated with climbing and brachiating. The selective pressures in Erethizon may be similar.

M. triceps brachii, caput lateralis
Figures 12, 15
triceps, external head (Parsons, 1894a)

Origin: From the ventrolateral surface of the greater tuberosity via fibers of a strong tendon, and from the proximal three-fourths of the posterior edge of the deltoid ridge via a thin aponeurosis.

Insertion: On the ventralateral surface of the olecranon and onto the surface of M. triceps brachii, caput longus.

Other Genera: The muscle is the same in all genera except Ctenomys, Erethizon, and Cavia. In these genera the origin is restricted to the ventrolateral surface of the greater tuberosity. In

![Fig. 14. Medial view of front limb of Proechimys guyannensis.](image-url)
Thryonomys the origin passes only partially onto the deltoid ridge.

Remarks: In all genera in which the origin is partially via the deltoid ridge, the aponeurosis lies on the surface of M. brachialis. In some specimens of Echimys, Myocaster, and Octodon the aponeurosis appears to come from the surface of the brachialis.

M. triceps brachii, caput medialis

Figures 13–16

triceps, inner head (Parsons, 1894a)

Origin: From the posteromedial surface of the distal two-thirds of the humerus. The muscle is incompletely divided into a superficial and a deep layer, with the superficial layer originating from the middle area of the shaft.

Insertion: On the posterodorsal surface of the olecranon. The deep fibers are continuous with M. anconeus and insert on the lateral aspect of the olecranon.

Other Genera: The origin of this muscle is the same in Echimys and Isothrix as it is in Proechimys. In Mesomys, Chinchilla, Thryonomys, and Petromus the origin is from the distal three-fourths of the humerus; in Erethizon and Cavia the origin is from the entire posteromedial side of the humerus. In all the above genera the muscle is divided into superficial and deep parts. In Octodon, Ctenomys, and Dasyprocta the origin is from the distal four-fifths of the shaft of the humerus, but the muscle is not clearly separated into superficial and deep parts. There is an extra flap of the muscle present in Dasyprocta which lies on top of M. anconeus on the lateral side of the arm. In Myocaster the origin is from the distal four-fifths of the humerus, and from the surface of the coracobrachialis near the insertion of that muscle. There is a lateral flap of the muscle covering the anconeus, as in Dasyprocta.

Remarks: The deeper fibers of this muscle are continuous with the fibers of M. anconeus in all genera examined.

Parsons’s (1894a) notations concerning this muscle are accurate. In the description of this muscle by Wood and White (1950) the enlarged superficial part of the triceps medialis is erroneously described as M. epitrochleoanconeus. Olborth (1964) correctly noted that this group of fibers is part of the triceps group, and called it M. triceps brachii, caput accessorium. It is best considered merely as part of the medial triceps. The partial origin of this muscle from the coracobrachialis in Myocaster is unusual, and

Fig. 15. Deep medial view of front limb of Proechimys guyannensis.
has not been previously reported. Olborth (1964) seemed to have confused this part with the long head of the coracobrachialis. The fibers, however, are clearly innervated by the radial nerve, and are therefore part of the triceps.

M. triceps brachii, caput longus
Figures 12, 13, 15
triceps, middle or long head (Parsons, 1894a)

Origin: From the distal fifth of the scapula along the axillary border, and more laterally from the surface of the well-developed aponeurotic envelope.

Insertion: On the posterior surface of the olecranon process of the humerus.

Other Genera: The conditions are the same in all genera except Erethizon. In Erethizon the muscle is closely associated with, but not always firmly attached to, the aponeurotic envelope.

Remarks: The aponeurotic envelope mentioned in the description of M. teres minor is an important point of origin for the long head of the triceps. The origin from this aponeurosis is easily missed in small mammals, and therefore may have been overlooked by some earlier workers. Olborth (1964) did not comment on the aponeurotic envelope.

M. anconeus
Figure 13

Origin: From the distal third of the postero-lateral margin of the humerus, and from the lateral epicondyle. The muscle is separable from the medial triceps near the origin but is completely fused with it near the insertion of the two muscles.

Insertion: On the posterior surface of the olecranon. The muscle is partially covered by the lateral triceps.

Other Genera: In Octodon, Ctenomys, Cavia, and Dasyprocta the muscle tends to be covered by the lateral triceps. In all other genera the muscle is only partially covered.

Remarks: As mentioned by Rinker (1954) this muscle has been frequently missed or incorrectly identified (Howell, 1926; Greene, 1935, fig. 83, although her description in the text is correct; Ballard, ms.; Wood and White, 1950; Berkowitz, ms.). The important criterion is that the muscle lies on the lateral side of the arm, and is innervated by the radial nerve. The muscle often confused with it lies on the medial side of the arm and is innervated by the ulnar nerve (Hill, 1937; Rinker, 1954).

Extensor Group of the Forearm
The muscles of this group are innervated by the radial nerve.

M. brachioradialis
supinator longus (Parsons, 1894a)

This muscle is missing in all hystricomorphs dissected except Erethizon. In Erethizon the muscle is well developed. The origin is on the intermuscular septum between the brachialis and the lateral triceps muscles, and on the proximal end of the lateral epicondylar ridge. The insertion is on the outer edge of the styloid process of the radius.

The muscle was reported for Erethizon by Mivart (1882), Windle (1888) and Parsons (1894a). It has not been reported for any other hystricomorph. Parsons (1894a, 1896) reported that it is missing in all hystricomorphs except Erethizon and in all myomorphs, but present in all sciuromorphs except Caster and in the Dipodidae. Howell (1932) and Klingener (1964) confirmed its presence in the dipodoids they dissected, and Bryant (1945) reported it present in Nearctic Sciuricace. Hill (1937) stated that it is absent in geomyids and in Aplodontia, and Rinker (1954) wrote that it is missing in his muroids. The muscle is present, but very thin, in two specimens of Aplodontia I dissected.

M. extensor carpi radialis longus
Figures 12, 14
extensor carpi radialis longior (Parsons, 1894a)

Origin: From the proximal end of the lateral epicondylar ridge. The origin is proximal to and partially covers the origin of M. extensor carpi radialis brevis.

Insertion: On the dorsomedial side of the proximal third of the second metacarpal.

Other Genera: In all genera other than Myocastor and Thryonomys the configuration of the muscle is the same as it is in Proechimys. In Myocastor and Thryonomys, however, M. extensor carpi radialis brevis is much larger than the extensor carpi radialis longus, and largely covers it. Parsons (1894a) also noted this size difference in Myocastor. In Chinchilla the muscle is covered near its origin by the enlarged M. extensor digitorum. In all genera there is some variation...
as to the exact point of insertion on the second metacarpal. The insertion is on the proximal third of the metacarpal in *Isothrix*, *Mesomys*, *Cavia*, and *Petromus*; the middle third in *Octodon*, *Chinchilla*, *Dasyprocta*, and *Thryonomys*; the distal third in *Echimys*, *Myocastor*, *Clenomys*, and *Erethizon*.

**M. extensor carpi radialis brevis**

Figure 12

Extensor carpi radialis brevis (Parsons, 1894a)

**Origin:** From the lateral epicondylar ridge distal to the origin of *M. extensor carpi radialis longus*.

**Insertion:** On the dorsomedial side of the proximal third of the third metacarpal.

**Other Genera:** The configuration of this muscle is the same in all genera except *Myocastor* and *Thryonomys*. The muscle is extremely enlarged in these two genera, completely dominating the extensor carpi radialis longus. In *Chinchilla* this muscle is covered by the enlarged extensor digitorum. The exact points of insertion vary. The muscle inserts on the proximal third of the metacarpal in *Isothrix*, *Mesomys*, *Octodon*, *Cavia*, *Chinchilla*, *Dasyprocta*, and *Petromus*; the middle in *Echimys*, *Ctenomys*, and *Thryonomys*; the distal third in *Myocastor* and *Erethizon*.

**Remarks:** The exact point of insertion in all genera is probably subject to some individual variation. This is also true of *M. extensor carpi radialis brevis*.

**M. supinator**

Figures 12, 13

Supinator brevis (Parsons, 1894a)

**Origin:** From the surface of the radial collateral ligament and from the deep surface of the distal end of the lateral epicondyle. The origin is somewhat variable and in some specimens can be only from the lateral epicondyle, deep to the radial collateral ligament.

**Insertion:** On the proximal half of the lateral surface of the radius.

**Other Genera:** The origin of the muscle is the same in all genera except *Cavia*. In *Cavia* the ligament is missing and the origin is primarily from the capitulum of the humerus.

The insertion on the radius varies. In *Echimys*, *Isothrix*, and *Mesomys* it is on the proximal half, just as in *Proechimys*. In *Myocastor* the origin is on the proximal three-fifths; in *Ctenomys*, *Erethizon*, *Thryonomys*, and *Petromus* it is on the proximal two-thirds. In *Cavia*, *Chinchilla*, and *Dasyprocta* the muscle is reduced. Its insertion is the proximal third of the humerus in *Cavia*, the proximal quarter in *Chinchilla*, and the proximal fifth in *Dasyprocta*.

**Remarks:** Parsons (1896) observed the presence of a sesamoid bone in the tendon of this muscle in myomorphs. He did not observe it in hystricomorphs, nor do I. Rinker (1954) noted the presence of a radial collateral ligament in *Oryzomys* and *Sigmodon*, and stated that the origin of the supinator is deep to the radial collateral ligament. In some specimens of *Proechimys* and *Echimys* I found the muscle to be deep to the radial collateral ligament, but in most specimens the origin of the muscle has become fused with the ligament. In all other genera except *Cavia* the origin is fused with the ligament. The ligament was especially well developed in *Erethizon*. In the genera other than *Cavia* it is moderately developed. Ballard (Ms.) reported that the supinator was missing in his specimens of *Cavia*, but the muscle is reduced in *Cavia* and I believe that Ballard probably overlooked it.

**M. extensor pollicis brevis**

Rinker (1954) listed the muscle for muroids, as did Klingener (1964) for dipodoids. In both of these groups the insertion is given as the base of the falciform bone. The tendon of the muscle crosses over the tendon of M. abductor pollicis longus as it passes to its insertion.

Neither Rinker (1954) nor Klingener (1964) gave their reasons for stating why this muscle is identified as such. Most workers prior to Rinker did not recognize the muscle as distinct from M. abductor pollicis longus. In fact, Hill (1937, p. 117) stated that “in rodents, as in most mammals, there is no extensor pollicis brevis.” Howell and Straus (1933) stated that the extensor pollicis brevis is absent in the Rhesus monkey, as did Schönh (1968) for the Red Howling monkey. Both Howell and Straus, and Schönh described situations in which M. abductor pollicis longus is divided into two parts, inserting partly on the base of the first metacarpal and partly on the radial sesamoid (falciform). Bryant (1945) made the same observation about the condition of the abductor pollicis longus muscle in squirrels. In soricoid insectivores the muscle also splits into two parts.
(Reed, 1951). The same doubling of M. abductor pollicis longus occurs in humans even when there is a good M. extensor pollicis brevis. Therefore, there is substantial evidence in mammals for the loss of extensor pollicis brevis and the existence of a two-part abductor pollicis longus.

**M. abductor pollicis longus**

Figures 12-14, 17

Extensor ossis metacarpi pollicis (Parsons, 1894a)

**Origin:** From the proximal half of the radius, the interosseous membrane, and the proximal two-thirds of the ulna beyond the semilunar notch.

**Insertion:** The main tendon passes onto the base of the first metacarpal. A small accessory tendon forms from the more distal fibers and crosses over the main tendon to insert on the radial side of the large palmar ossicle (= falciform bone).

**Other Genera:** The origin of the muscle in *Cavia* and *Chinchilla* is the proximal half of the radius, the interosseous membrane, and the ulna; in *Thryonomys* and *Petromus* it is on the proximal third of the radius and ulna. In all other genera the origin is the same as in Proechimys. The extra tendinous slip is present in *Echimys, Isothrix, Mesomys, Myocastor, Octodon, Erethizon,* and *Dasyprocta.* In all these genera it is thin (extremely thin in some specimens), and in all specimens the insertion is onto the palmar ossicle (= falciform bone). The extra slip to the palmar ossicle is not present in *Ctenomys, Cavia, Chinchilla, Thryonomys,* and *Petromus.* In *Ctenomys,* however, there is a slight insertion of the main tendon onto the palmar ossicle; in the remaining four genera there is no such insertion.

The insertion of the main tendon in all genera except *Cavia* is on the base of the first metacarpal. In *Cavia* the thumb is completely missing, and the insertion is onto the small trapeziun bone (also called carpal 1 or greater multangular bone).

**Remarks:** The tendon (tendons) of this muscle crosses over the tendons of extensor carpi radialis longus and brevis and are therefore easily located. The separate tendons represent different parts of M. abductor pollicis longus.

I consider the large palmar ossicle that characteristically lies across the volar surface of the hand of so many hystricomorphs to be the radial sesamoid bone (= falciform bone). The bone is elongated and in many genera it appears to be an extra digit folded over the volar surface of the hand.

**M. extensor digitorum**

Figure 12

Extensor communis digitorum (Parsons, 1894a)

**Origin:** From the lateral epicondyle of the humerus between extensor carpi radialis brevis and the extensor digiti minimi.

**Insertion:** On the dorsal surface of the terminal phalanges of the second through fifth digits. The insertions are via thin tendons.

**Other Genera:** The basic configuration is the same in all genera except *Chinchilla.* In *Chinchilla* the muscle is unusually large. The origin is along the lateral surface of the proximal half of the lateral epicondyle, covering the origins of the extensor carpi radialis longus and brevis muscles.

The pattern of the inserting tendons varies, but in all genera the tendons insert onto the dorsal surface of the second through fifth digits.

**Remarks:** The pattern of the tendons of this muscle is extremely variable. Rinker (1954) and Klingener (1964) noted that there are usually four discrete tendinous slips present in the animals they dissected. Howell (1926) reported that there are only three main parts present, but that there are four separate tendinous slips. There are four tendinous slips in the hysticomorphs dissected. The radial slip (most medial) passes onto the second digit. The radial-central slip passes onto the third digit. These two tendons are often fused for much of their length.

The ulnar-central slip passes onto the fourth digit, and the ulnar slip (most lateral) passes onto the fifth digit. The ulnar-central and ulnar slips are rarely fused. The ulnar tendon often has a small accessory slip passing under the others to the third digit. On the dorsal surface of the hand the tendons are often bound together by fascial bands which make identifying the thin tendinous slips difficult.

Neither Rinker (1954) nor Klingener (1964) reported much individual variation in the configuration of the tendinous slips. I have noted, however, such variation as: fusion of all tendons; fusion of the three most radial tendons; fusion of the three most ulnar tendons; fusion of the radial with the radial-central and the ulnar with the ulnar-central tendons. There often appear to be additional small accessory slips present on
the dorsal surface of the hand. This variation follows no consistent taxonomic pattern, and often occurs on opposite sides of the same specimen. The other extensor muscles of the arm do not show much individual variation.

The muscle passes through the third wrist compartment. In Proechimys, Echimys, Isothrix, Mesomys, Erethizon, Cavia, and Thryonomys the third compartment is closely associated with the fourth compartment, as it is in dipodoids (Klingener, 1964). In Myocastor, Octodon, and Ctenomys the compartments are close to each other, and in Chinchilla, Dasyprocta, and Petromus they are separate. The compartments are completely fused in squirrels (Bryant, 1945) and Aplodontia.

M. extensor indicis

Figures 12, 13

ORIGIN: From the middle third of the ulna.

INSERTION: On the dorsal surface of the second digit. In most specimens the actual point of insertion is difficult to establish, but it is probably the middle phalanx. The tendon also inserts via a very thin side tendon on the terminal phalanx of the pollex.

OTHER GENERA: The origin is the middle third of the ulna in Echimys, Isothrix, Mesomys, Myocastor, Octodon, Ctenomys, and Chinchilla. The origin is the distal third in Erethizon, Dasyprocta, Thryonomys, and Petromus; in Cavia it is the proximal third. In some specimens of Myocastor and Octodon there is a thin tendinous connection to the capsule of the elbow.

The insertion of the muscle on the dorsal surface of the second digit is the same in all genera. In Thryonomys there is a thin separate tendon inserting on the third digit. The solid insertion onto the pollex is present in Echimys, Isothrix, Mesomys, Octodon, Ctenomys, Erethizon, Dasyprocta, and Petromus. In Myocastor and Chinchilla it is present in a vestigial condition. It is not present in Cavia or Thryonomys. The insertion on the pollex in Mesomys is via a completely extra tendon. In the other genera the insertion is via a side branch of the main tendon.

REMARKS: The tendinous branch of the pollex is curious, and has not been widely noted. Windle (1897) reported its presence in Dasyprocta, but Parsons (1894a) and most other early workers missed it. It inserts onto the terminal phalanx of the pollex, and has an ossicle associated with it near the point of insertion. Hill (1937) and Reighard and Jennings (1935) believed that M. extensor pollicis brevis is fused with this muscle. If that is so, then the slip to the pollex could represent the remains of the extensor pollicis brevis. This idea is substantiated by the condition in Mesomys, in which the tendon to the metacarpal of the pollex is separate for its entire length.

Hill (1937) stated that in Aplodontia, Citellus (= Spermophilus), and Sciurus the slip to the pollex is missing, and Bryant (1945) did not mention a slip to the pollex in squirrels. In my specimens of Aplodontia there was no slip to the pollex, but it was present in my specimens of Sciurus carolinensis.

The separate thin tendon in Thryonomys that inserts on the third digit is probably M. extensor digiti tertii proprius.

M. extensor digiti tertii proprius

Probably part of extensor minimi digiti (Parsons, 1894a)

This muscle is not mentioned by Parsons (1894a) or by other early workers. Parsons (1894a) did note an insertion of "extensor minimi digiti" in Sphingurus (= Coendou) and Sciurus onto the third digit. Bryant (1945) mentioned part of extensor digit quinti proprius (= extensor digiti minimi) which passes through the medial compartment of the wrist with the extensor digitorum communis (= extensor digitorum) and inserts on the third digit. Parsons and Bryant were probably describing M. extensor digiti tertii proprius. Klingener (1964) expressed the same belief about Bryant’s description.

This muscle is not present in any genera except Thryonomys. It is present in all three specimens of Thryonomys that I dissected. If my interpretation of Parsons’s (1894a) description is correct, then the muscle is also present in Coendou.

M. extensor digiti minimi

Figure 12

extensor minimi digiti (Parsons, 1894a)

ORIGIN: From the lateral epicondyle of the humerus. The origin is between M. extensor digitorum and M. extensor carpi ulnaris, and is closely associated with M. extensor digitorum at the point of origin.

INSERTION: On the dorsal surface of the middle phalanx of the fourth and fifth digits.
Other Genera: The origin of the muscle is the same in all genera except Dasyprocta. In Dasyprocta the origin is also from the proximal half of the lateral aspect of the ulna. In Thryonomys this muscle is completely fused with the extensor digitorum near the point of origin, but the muscles are separated distally.

The insertion is the same in all genera. In Echimys, Myocastor, and Ctenomys the tendinous insertion on the fourth digit is poorly developed. In all genera, the insertion can sometimes be on the proximal end of the terminal phalanx, but it is usually on the middle phalanx.

Remarks: This muscle is probably subject to individual variation. Mivart and Murie (1866) reported that in Dasyprocta the muscle originates from both the lateral epicondyle and the ulna, but Parsons (1894a) did not mention this. However, Parsons (1894a) reported that the extensor communis digitorum ( = extensor digitorum) is closely associated with this muscle, and that it originates along the ulna. Parsons (1894a) might have mistaken the parts of the two closely associated muscles, or the origin of the muscle may vary. Parsons (1894a) reported that the muscle was completely fused with the extensor communis digitorum ( = extensor digitorum) in Aulacodus ( = Thryonomys). I did not find the muscles completely fused in my specimens.

The insertion of the muscle also varies. In one specimen of Ctenomys the slip onto the fourth digit is very thin. Parsons (1894a) and Wood and White (1950) reported that it is missing in their specimens of Chinchilla, and Elton (Ms.) reported that it is missing in his specimen of Dasyprocta. The slip onto the fourth digit is present in squirrels and Aplodontia and in most other rodents (Bryant, 1945; Hill, 1937). The presence of an insertion on the fourth digit was considered by Hill (1937) to represent the primitive condition. In all hysticomorphs the muscle passes through the fourth compartment of the wrist. This compartment is closely associated with the third compartment, but is separate. Klingener (1964) presented a good discussion of the primitive deep extensor muscles of the forearm, of which this muscle is a part.

M. extensor carpi ulnaris

Origin: From the distal part of the lateral epicondyle and from the lateral edge of the proximal half of the ulna distal to the middle of the semilunar notch.

Insertion: On the lateral side of the base of the fifth metacarpal.

Other Genera: The origin of the muscle is the same in all genera except Chinchilla and Dasyprocta. In these two genera the origin is from the lateral epicondyle only. The insertion of the muscle is the same in all genera except Chinchilla and Dasyprocta. In these two genera the insertion is on the dorsolateral aspect of the base of the fifth metacarpal, whereas in all other genera it is on the lateral or ventrolateral aspect.

Remarks: The presence of the part of this muscle originating from the ulna is the usual condition in rodents. Chinchilla and Dasyprocta are exceptions, as Wood and White (1950) and Elton (Ms.) confirmed. Mivart and Murie (1866), however, reported an origin from the ulna in Dasyprocta.

The tendon of this muscle passes through a groove in the styloid region of the ulna, and through the fifth compartment of the wrist. The tendon then passes ventrally to insert on the base of the fifth metacarpal. In all genera except Chinchilla and Dasyprocta the insertion is ventrolateral, resembling Parsons’s (1894a) description of the condition in Sphingurus ( = Coendou).

Flexor System

Pectoral Group

The muscles of this group are innervated by the subclavius, the lateral anterior thoracic, and the medial anterior thoracic nerves.

M. subclavius

Figures 9–11, 14

Sterno-scapularis, part subclavius (Parsons, 1894a)

Origin: From the anterior border of the base of the first rib.

Insertion: On the posterior edge of the scapular half of the clavicle. A few fibers may be continuous with M. scapuloavicularis.

Other Genera: The configuration of this muscle is the same in Echimys, Isothrix, Mesomys, Myocastor, and Petromus, as it is in Proechimys. It is almost the same in Octodon and Ctenomys, except that in some specimens of these two genera there is also a tendinous insertion onto the tip of the coracoid process. In Chinchilla the origin is as usual on the first rib, but the insertion is on the scapular end of the clavicle and the
base of the scapula. In *Cavia* the origin is on the first rib; the insertion is on the scapular half of the clavicle, the scapuloclavicularis, and the acromion process of the scapula. In *Erethizon* the origin is broad. In some specimens it originates from the manubrium of the sternum, as well as the first rib. The insertion of the muscle in *Erethizon* is on the central area of the clavicle. In the above genera the configuration of the muscle is basically the same, but it is very different in *Dasyprocta* and *Thryonomys*. In *Dasyprocta* the origin is broadly from the first rib and manubrium of the sternum, as in some specimens of *Erethizon*. The muscle passes over the medial side of the clavicle, however, to insert by a few fibers on the most scapular end of the clavicle. The remaining and largest part of the muscle grades into the fibers of M. scapuloclavicularis. Some of the fibers grading into scapuloclavicularis can still be separated all the way to the spine of the scapula. Some parts of this muscle may be fused with the pectoralis minor. In *Thryonomys* the origin is variable. In one specimen the origin was via two heads; one from the base of the first rib, the second from the manubrium of the sternum. The insertion of the first part is on the scapular tip of the clavicle and the coracoid and acromion processes. The second part inserts on the sternal half of the clavicle, and is continuous with the scapuloclavicularis. In the other two specimens only the first part is present. The second part has probably become fused with the clavicular head of the pectoralis minor.

**Remarks:** The configuration of this muscle in most hystricomorphs is similar to the general rodent condition. In *Dasyprocta* and *Thryonomys*, however, the configuration of the muscle differs from the general rodent plan. Two parts of the muscle are present in one specimen of *Thryonomys* I dissected, and in the specimen dissected by Beddard (1892). In two of my specimens of *Thryonomys*, and in the specimen dissected by Parsons (1894a), only one part of the muscle is present. Mivart and Murie (1866) mentioned the presence of a separate origin for this muscle in their specimens of *Dasyprocta*. Windle (1897), however, and Elton (ms.) did not mention a separate origin in their specimens of *Dasyprocta*. Windle did, however, mention the presence of a separate part in one side of his specimen of *Dolichotis patagonica*. I believe that the manubrial head of the subclavius in both *Dasyprocta* and *Thryonomys* has become associated with the pectoralis minor. This results in a compound muscle looking much like a normal clavicular part of the pectoralis minor, but which is continuous with the scapuloclavicularis.

Wood (1870) gave an excellent early historical account of the interpretation of this muscle in the literature. He presented evidence that the extra part of the subclavius, which he calls the sterno-clavicular muscle, may actually be a separate muscle in many mammals. He believed that the sterno-clavicular is a division of the over-all sternoscapular muscle. Another division of this muscle passes from the clavicle to the scapular blade and is called the scapuloclavicularis. Wood cited various mammals in which differing patterns of this muscle are found. The same variation can be found in humans (Gray and Lewis, 1942), but the usual interpretation in humans is that these are abnormal conditions of the subclavius muscle. Some insectivores (Wood, 1870; Reed, 1951) also have a second part of the subclavius muscle. This part is usually treated as a separate muscle, the costoscapularis. In Howell (1937) there is a brief discussion of the subclavius and sternoscapularis muscles. Howell considered them to be divisions of the same muscle mass.

The subclavius has fibers that are continuous with those of M. scapuloclavicularis in some specimens of *Proechimys*, *Echimys*, *Ctenomys*, and *Erethizon*, and in all specimens of Myocastor, *Cavia*, *Chinchilla*, *Dasyprocta*, *Thryonomys*, and *Petromus*. This continuous nature plus the common innervation indicate that the muscle is closely related to M. scapuloclavicularis. Parsons (1894a) considered them to be parts of the same muscle. In *Cavia* (see fig. 9) a significant part of the insertion (labelled "subclavius, part") is onto the anterior border of the acromion process. This condition is similar to that reported by Parsons (1894a) for *Cerodon* (= *Kerodon*). Parsons illustrated this condition (1894a, p. 261, fig. 2).

**M. scapuloclavicularis**

*Figures* 9, 12, 14

**Origin:** From the anterior surface of the clavicle for its entire length.

**Insertion:** On the vertebral border of the
scapula in front of the spine, and on the anterior surface of the scapular spine for its entire length.

**Other Genera:** The origin is the entire clavicle in *Octodon, Cavia,* and *Chinchilla;* the scapular three-fourths of the clavicle in *Echimys, Isothrix, Mesomys, Myocastor, Ctenomys,* and *Petromys.* In *Erethizon* it is from the scapular third of the clavicle. In *Dasyprocta* and *Thryonomys* the origin is variable, but it is usually from the scapular half of the clavicle and also is continuous with the subclavius. In some specimens of *Dasyprocta* and *Thryonomys* the muscle is continuous with the clavicular part of the pectoralis minor.

The insertion of the muscle is along the entire length of the scapular spine in *Echimys, Isothrix, Mesomys, Octodon,* and *Petromys.* The insertion is also along the entire length of the spine in *Erethizon, Dasyprocta,* and *Thryonomys,* but the area of the muscle lying over the M. supraspinatus is thin and fascial. The insertion of the muscle is along the distal two-thirds of the scapular spine in *Myocastor, Ctenomys,* and *Chinchilla.*

**Remarks:** The presence of a M. scapuloclavicularis is an unusual feature of hystricomorphs. Wood and White (1950, p. 569) reported that the muscle is "characteristic of the South American 'hystricomorphs,' apparently being found as a distinct muscle only in that group." I have found it in both New World and Old World hystricomorphs, however. It is also found in hystricids (Parsons, 1894a), bathyergids (Parsons, 1896), *Dasyprocta* (Wood, 1870), lagomorphs (Mivart and Murie, 1866; Bensley, 1931), horses (Sisson and Grossman, 1953), tapirs (Sjörrman, 1932), and some marsupials (Howell, 1937).

The origin of the muscle is consistent in all genera except *Dasyprocta* and *Thryonomys.* In these two genera the origin is variable and can be: (1) mostly on the clavicle (Elton, ms. for *Dasyprocta;* one of my specimens for *Thryonomys*); (2) partially from the clavicle and partially from the subclavius (my specimen of *Dasyprocta* and one of my specimens of *Thryonomys*); (3) almost totally from the subclavius (Mivart and Murie, 1866, for *Dasyprocta,* and one side of one of my specimens of *Thryonomys*). In addition, in some specimens of both genera a part of the pectoralis minor passes toward the sternal end of the clavicle and is continuous with the scapuloclavicularis. This part of the pectoralis minor, as previously discussed, is probably a compound muscle in *Dasyprocta* and *Thryonomys* composed of elements of both the subclavius and the pectoralis minor. The muscle, therefore, is present in some form in all genera. In *Dasyprocta* and *Thryonomys,* where it is variable, it is often partially associated with M. pectoralis minor.

**M. pectoralis major**

Figures 9–12, 15

pectoral muscles, part alpha and beta (Parsons, 1894a)

**Origin:** From the manubrium of the sternum, and from the sternebrae as far posteriorly as the fourth rib. The muscle is not clearly divisible into two parts.

**Insertion:** On the deltoid crest of the humerus.

**Other Genera:** The muscle is not clearly separable into two parts in *Echimys, Isothrix, Mesomys, Myocastor, Octodon, Ctenomys, Thryonomys,* and *Petromys.* It is barely separable in *Erethizon* and *Chinchilla* and clearly separable in *Cavia* and *Dasyprocta.* The origin of the muscle is usually from as far back as the fourth rib, but in *Erethizon, Cavia,* and *Thryonomys* it is only from as far back as the second rib. In *Myocastor, Chinchilla,* and some specimens of *Petromys* the origin includes all the sternebrae.

The insertion of the muscle is the same in all genera except *Cavia* and *Dasyprocta.* In these two genera a separate superficial part of the muscle also inserts onto the distal end of the humerus.

**Remarks:** The muscle is always closely associated with the clavodeltoid. When the insertion of the clavodeltoid is on the distal end of the humerus, as in *Cavia* and *Dasyprocta,* the anterior part of the pectoralis major (called the pectoralis superficialis, fig. 9) crosses over the main part to insert on the humerus with the clavodeltoid. The pectoralis superficialis in these two genera stands out as a separate superficial part, but in all other genera dissected it is inseparably fused with the pectoralis major.

Parsons (1894a) reported that a separate part of this muscle also exists in *Hystrix* and *Sphingurus* (= *Coendou*). He also stated that the muscle is separable into two parts in *Erethizon* and *Octodon,* and that it is fused in *Chinchilla.* Wood and White (1950) reported that the two parts are fused in *Chinchilla.* I report that the muscle is fused in *Octodon,* and is barely separable in *Erethizon* and *Chinchilla.* The cause of these noted
differences is surely a result of interpreting the relative separation involved in most "hystricomorph" genera. Squirrels and Aplodontia also demonstrate this relatively fused condition (Hill, 1937; Bryant, 1945; personal observ.). I believe that it is best to say, therefore, that only Cavia and Dasyprocta have the muscle clearly separated into superficial and deep parts.

The muscle occasionally originates from the sternal end of the clavicle in all the genera dissected.

**M. pectoralis minor**

Figures 10, 11, 14

*Origin:* From the sternum. The muscle originates as a heavy sheet from the level of the second costal cartilage posteriorly onto the xiphisternum.

*Insertion:* The muscle separates into two parts. One part inserts on the central area of the clavicle. The second part inserts on the greater tuberosity of the humerus, the coracoid process of the scapula, and as a broad thin aponeurosis along the deltoid ridge of the humerus.

*Other Genera:* The origin of the muscle is the same in all genera. The insertion is the same in Echimys, Isotrichs, Mesomys, and Petromus as in Proechimys. In Petromus the muscle is closely associated near its insertion with the pectoralis abdominalis. In Octodon the same pattern is present, but there is no part looping over the bicipital groove to insert on the coracoid process. In Cavia the muscle seems to be divided into three parts; one inserts on the clavicle; the second on the greater tuberosity; the third on the deltoid crest. In Cavia there is no part to the coracoid process. In Ctenomys the part to the coracoid process is also missing, and the part to the deltoid crest appears to be missing. The latter, however, is fused with the pectoralis abdominalis and is present in Ctenomys. In Chinchilla the part to the deltoid crest is missing, as is the part to the coracoid process. In Erethizon the part to the clavicle is missing, but all other insertions are as in Proechimys. In Dasyprocta and Hystrix the muscle is very large, the part to the coracoid process being especially well developed. The parts to the greater tuberosity and the deltoid ridge are normal, but the part to the clavicle is variable. The clavicular part can be missing, normal, or continuous with the scapuloclavicularis.

**Remarks:** As stated in the discussion of the subclavius and scapuloclavicularis muscles, the configuration of the pectoralis minor in Dasyprocta and Thryonomys is complex and variable. In these two genera part of the subclavius is often fused with the clavicular part of the pectoralis minor. The muscle is invariably present, however. The absence of an insertion on the clavicle in Erethizon, Hystrix, and Sphingurus (= Coendou) was noted by Parsons (1894a). The differing descriptions of the insertion of the muscle on the shoulder capsule by Mivart (1882), Windle (1888) and Parsons (1894a) indicate that this part of the insertion in Erethizon may be subject to some individual variation.

The secondary slip of M. latissimus dorsi, called the latissimus Achselbogen, passes onto the tendon of M. pectoralis minor and inserts with it on the base of the deltoid crest. The M. pectoralis abdominalis is also often closely associated with M. pectoralis minor near the insertion of the two muscles. In Petromus and Ctenomys the muscles are inseparable.

**M. pectoralis abdominalis**

Figures 10, 11, 14

*Origin:* From the surface of the xiphisternum and from the muscles of the midventral line posterior to the sternum.

*Insertion:* On the lesser tuberosity of the humerus.

*Other Genera:* The origin is the same in all genera. The insertion is also on the lesser tuberosity in Echimys, Isotrichs, Mesomys, Myocastor, and Octodon. It is on the lesser tuberosity and coracoid process in Cavia, Dasyprocta, Thryonomys, and Petromus. The insertion is on the base of the deltoid crest in Chinchilla and Erethizon. In Ctenomys the insertion is inseparable from that of the pectoralis minor and is on the central area of the deltoid ridge.

*Remarks:* My observations are consistent with others in the literature. The insertion in squirrels (Bryant, 1945) is restricted to the shoulder capsule and the lesser tuberosity. This is basically similar to the insertion in most hystricomorphs, and probably represents the primitive rodent condition. In Ctenomys the insertion is in on the deltoid ridge, as it is in pocket gophers and Aplodontia (Hill, 1937). It is possible that the movement of the insertion onto
the deltoid ridge is associated with modifications of the front limb for digging. The pattern is most similar between *Ctenomys* and pocket gophers, and *Erethizon* and *Aplodontia*. The point of insertion of this muscle can vary from the greater tuberosity to the central area of the deltoid ridge in *Chinchilla*.

**M. cutaneus maximus**

Figures 6–9, 11

panniculus carnosus (Parsons, 1894a)

In establishing the origins and insertions of this complex muscle I am following Langworthy (1925).

**Origin:** The muscle is composed of four separate parts. Pars dorsalis originates on the fibers of its mate along the dorsal midline from the level of the scapula, posteriorly to the base of the tail. The fibers from the base of the tail take origin from the spines of the first few caudal vertebrae. Pars thoracoabdominalis originates along the ventral midline from beneath the pectoralis abdominals, where it is a thin aponeurosis, posteriorly to the level of the hind legs. Pars pudenda originates from the surface of pars thoracoabdominalis on the ventrolateral surface of the abdomen. Pars femoralis originates from the surface of pars thoracoabdominalis on the lateral surface of the thigh. The fibers of pars femoralis pass at a right angle to the fibers of pars thoracoabdominalis.

**Insertion:** Pars dorsalis passes anteroventrally to insert on the distal end of the scapular spine, the tip of the metacromion process, a fascial sheet in common with *M. omocervicaleus*, and the tip of the deltoid crest. Pars thoracoabdominalis sweeps posterodorsally and passes under the fibers of pars dorsalis, merging with them. It also inserts on the musculature of the thigh and rump. Pars pudenda passes into the inguinal region where it inserts onto and around the genitalia. Pars femoralis passes down the lateral side of the thigh to insert onto the tibia, and, via an aponeurosis, onto the medial side of the leg.

**Other Genera:** The configuration of this muscle is the same in *Echimys*, *Isothrix*, *Mesomys*, *Octodon*, and *Chinchilla* as it is in *Proechimys*. In *Myocastor*, *Ctenomys*, and *Petromus* pars pudenda is continuous with pars dorsalis, which has a ventral division sweeping over the side anteroventrally toward the inguinal region. In all of these genera pars dorsalis also inserts on the lateral surface of the front leg beyond the elbow. Pars femoralis in *Myocastor* loops anteroventrally from the rear of the leg, instead of ventrally from the lateral surface of the thigh. The configuration of pars femoralis in *Petromus* is normal. In *Erethizon* there is a separate part lying between pars thoracoabdominalis and pars dorsalis and in close contact with the latissimus dorsi. This part represents the part of pars thoracoabdominalis that has split off to become part of the latissimus Achselbogen. All other parts of the cutaneus maximus in *Erethizon* are as in *Proechimys*. In *Cavia* there is a group of fibers passing from the ventral midline anterodorsally to join the pars dorsalis on the lateral side of the arm. These fibers lie on the surface of the pectoral muscles and pars thoracoabdominalis, and are referred to by Langworthy (1925) as the anterior division. In *Cavia* there is a poorly developed pars femoralis which loops over the thigh as a continuation of pars thoracoabdominalis. The pars pudenda was missing in my specimens of *Cavia*. In *Dasyprocta* pars dorsalis inserts on the spine of the scapula at a point one-fourth of the distance from the distal end, and then sweeps over the surface of the shoulder to a major insertion via an aponeurosis in common with *M. omocervicaleus*. Also in *Dasyprocta*, the ventral part (= anterior division of Langworthy, 1925) of pars dorsalis is missing, pars thoracoabdominalis and pars pudenda are normal, and pars femoralis is present as a looped continuation of pars thoracoabdominalis. In *Thryonomys* there is a ventral part (= anterior division of Langworthy, 1925) of pars dorsalis, and pars femoralis is a looped continuation of pars thoracoabdominalis. Pars thoracoabdominalis and pars pudenda are normal in *Thryonomys*, but the origin of pars dorsalis is covered by the large platysma myoides (see fig. 7) which lies on its surface.

**Remarks:** The insertion of pars dorsalis of this muscle on the lateral side of the arm and shoulder is an unusual condition in rodents. The only non-hysticomorph rodent in which I can find an indication of a lateral insertion is the Greenland Lemming, *Dicrostonyx* (Meinertz, 1941a). Only a few fibers, however, insert on the lateral side of the arm in *Dicrostonyx*.

A useful description of this muscle for hysticomorphs has been made by Langworthy (1925), Meinertz (1932), and Enders (1934). Parsons (1894a) mentioned an insertion on the outer side
of the arm, and also what must be a pars pudenda and a pars femoralis.

Both Langworthy (1925) and Enders (1934) believed that pars femoralis is related to pars thoracoabdominalis, and probably represents a modified part of it. I agree with this interpretation. The situation in Cavia, Dasyprocta, and Thryonomys, in which the pars femoralis is a continuation of pars thoracoabdominalis, is a further indication of this relationship. The condition of this muscle in Myocastor is difficult to explain. The pars femoralis is often thin and easy to miss, which may account for its not being reported by Ballard (Ms.) for Cavia, and Wood and White (1950) for Chinchilla.

Langworthy (1925) believed that the ventral part in the inguinal region (= pars pudenda of Enders, 1934) is related to pars thoracoabdominalis because the ventral part in Erethizon is innervated by a ventral branch of the anterior thoracic nerve. Because of the continuation of pars pudenda with a ventral group of fibres from pars dorsalis in Myocastor, Ctenomys, and Petromus, it is probable that pars pudenda is related to pars dorsalis. Ballard (Ms.) also described a condition in his specimens of Cavia that supported this idea. The innervation of the muscle is difficult to work out with accuracy.

The part of pars thoracoabdominalis in Erethizon which has split off from the rest of the muscle was referred to by Langworthy (1925) as the fifth portion of the panniculus carnosus (= cutaneus maximus). He referred to it as being similar to the human Achselbogen. It is more probable, however, that this is the contribution of the cutaneous maximus to the true latissimus Achselbogen which in most other hystricomorphs has become part of M. latissimus dorsi. There is no latissimus Achselbogen in Erethizon.

The latissimus Achselbogen is also missing in Chinchilla, Dasyprocta, Thryonomys, and Petromus; and in all of these genera there is an anterior part of pars thoracoabdominalis lying in close contact with the latissimus dorsi and strongly resembling it.

The part of pars dorsalis which passes over the surface of the pectoral muscles is found in both Cavia and Thryonomys. Both Meinertz (1932) and Langworthy (1925) illustrated it, with Meinertz calling it the pectoral division. It is certainly part of pars dorsalis, and in both Cavia and Thryonomys the fibers from this part pass onto the inserting fibres of pars dorsalis and insert onto the forearm. The muscle is subject to some individual variation; it was present in all specimens of Thryonomys, but missing in two specimens of Cavia.

FLEXOR GROUP OF THE ARM

The innervation of the biceps brachii and the coracobrachialis is via the musculocutaneous nerve. The brachialis is innervated primarily by the musculocutaneous nerve, and secondarily by a small branch of the radial nerve.

M. CORACOBRACHIALIS

Figures 14-16

coracobrachialis (Parsons, 1894a)

ORIGIN: From the tip of the coracoid process in common with the biceps brachii.

INSERTION: On the medial side of the central area of the humerus. The insertion lies distal to the common tendon of the latissimus dorsi–teres major, and proximal to the medial epicondylar ridge.

OTHER GENERA: The origin is in common with the short head of the biceps brachii in Echimys, Isothrix, Mesomys, and Erethizon. It is separate from the origin of the short head of the biceps in Myocastor, Octodon, Ctenomys, Chinchilla, Thryonomys, and Petromus. The short head of the biceps is missing in Cavia and Dasyprocta. The configuration of this muscle is the same in Isothrix, Octodon, Ctenomys, Cavia, Chinchilla, and Petromus as it is in Proechimys. The insertion of the muscle is broader in Echimys and Mesomys and a few fibers may barely pass onto the proximal edge of the medial epicondylar ridge. In Myocastor the configuration is the same as in Proechimys except that part of the medial triceps originates from the surface of this muscle near its point of origin.

In Erethizon the insertion in some specimens is onto the middle of the humerus, whereas in other specimens it is onto the central area of the humerus via one part, and onto the medial epicondylar ridge via another. In specimens in which both parts are present, they are separated by the median nerve. In all the above genera the muscle lies distal to the musculocutaneous nerve, and inserts distal to the common tendon of the latissimus dorsi–teres major. In Dasyprocta and Thryonomys there is a second part inserting on the humerus proximal to the common tendon of the latissimus dorsi–teres major, and of the musculocutaneous nerve.
Remarks: According to Wood (1867), there are three possible parts of this muscle. The main or middle part is the one most commonly present. It inserts on the middle of the inner surface of the humerus. Wood (1867, p. 48) called the median part the “coraco-brachialis proprius vel medius.” A second, less common, part can be present inserting on the upper part of the internal epicondylar ridge. Wood (1867) noted that it is superficial to the middle part, and that the median nerve and brachial vessels often pass between the middle and long parts. Wood (1867, p. 49) called the long part the “coraco-brachialis longus.” A third and quite rare part can be present inserting on the anatomical neck of the humerus, and lying proximal to both the common tendon of the latissimus dorsi—teres major, and the musculocutaneous nerve. Wood (1867, p. 49) called this short part the “rotator humeri or coraco-brachialis superior vel brevis.” For simplicity it is better to refer to these portions as the short, middle, and long parts.

The middle part only is present in Proechimys, Isothrix, Myocastor, Octodon, Ctenomys, Cavia, Chinchilla, and Petromus. In spite of a few fibers passing onto the most proximal edge of the medial epicondylar ridge in some specimens of Echimys and Mesomys, this does not indicate that fibers other than the middle part are present in these genera. The middle and long parts are present in some specimens of Erethizon, and only the middle in others. The short and middle parts are present in both Dasyprocta and Thryonomys.

Parsons (1894a) agreed with most of these observations. He did not report a short head for Aulacodus (= Thryonomys), however, nor did Beddard (1892). The short head was present in all three of my specimens of Thryonomys. The presence of a short head is also indicated for Coelogenys (= Cuniculus) by Parsons (1894a) and Windle (1897), but Beddard (1891) only reported the middle head in his specimen of Dolichotis. The presence of both the middle and long heads in Erethizon was reported by Mivart (1882), Windle (1888), and Parsons (1894a). None of these workers noted any specimens in which only the middle head is present. It is not clear from the descriptions by Mivart (1882) or Windle (1888) if the median nerve passes between the middle and long heads of this muscle in their animals. Parsons (1894a) did not appear to have actually dissected any specimens of Erethizon, but used the information reported by Mivart (1882) and Windle (1888). I believe that when the long head is present, it lies beyond the median nerve (see fig. 16). Parsons (1894a) dissected a specimen of Sphingurus (= Coendou), and noted that the median nerve separated the long head from the middle head.

The short part is present in sciurids (Bryant, 1945), Aplodontia (Hill, 1937; but not Lewis, 1949), geomyids (Hill, 1937), heteromyids (Howell, 1932), dipoidoids (Klingener, 1964), and Cricetus, Cricetomys (Parsons, 1896), Neotoma, and Peromyscus (Rinker, 1954) among the murids.

The middle and long parts are considered fused into “one continuous insertion from the middle of the humerus to the internal condyle” by Parsons (1896, p. 169) for most myomorphs. This is the condition in sciurids (Bryant, 1945), Aplodontia (Lewis, 1949), and possibly in other rodents. The exact homology of the “fused” middle and long parts in these animals with the originally described parts by Wood (1867) is difficult to establish with certainty. It is not known, therefore, what the primitive rodent condition of this muscle is, or how the configuration in the various hystricomorphs relates with the form of the muscle in other groups of rodents.

M. biceps brachii
Figures 13–16
biceps cubiti (Parsons, 1894a)

Origin: Short head: From the tip of the coracoid process in common with the coracobrachialis. Long head: From the base of the coracoid process and lip of the glenoid fossa. The long head passes along the margin of the humeroscapular joint, and through the bicipital groove of the humerus before it passes distally down the anterior margin of the arm.

Insertion: The two heads merge into one muscle which inserts primarily on the brachial ridge of the ulna. There is a secondary insertion on the radius distal to the primary insertion. The insertion on the radius is almost in the interosseus area.

Other Genera: The short head arises in common with the coracobrachialis in Echimys, Isothrix, Mesomys, and Erethizon. The origin of the short head is covered by the origin of the coracobrachialis in Myocastor, Chinchilla, and in
most specimens of Octodon. The origin covers the origin of the coracobrachialis in one specimen of Octodon, and in Ctenomys, Thryonomys, and Petrobus. The short head of the biceps is missing in Cavia. On one side of my specimen of Dasyprocta the short head is missing, but on the other side a vestige is present. The insertion of the muscle is the same in all genera except Erethizon, in which the radial insertion is dominant.

Remarks: In all genera the muscle splits just before it inserts. The main part passes to the ulna, and the secondary part to the radius. The insertion of M. brachialis is deep to the ulnar part, and between the ulnar and radial parts. This condition is similar to the insertion of the muscle in Sigmodon and Oryzomys (Rinker, 1954).

The muscle inserts on both the radius and ulna even in Cavia and Dasyprocta in which only the long head is present. In these two genera the radial insertion is poorly developed, however, and easily missed. Parsons (1894a) reports that the muscle inserts only on the ulna in Dasyprocta Coelogenys (= Cuniculus), Cavia, Ceredon (= Kero- don), and Dolichotis. Parsons (1894a) probably missed the radial insertion. Windle (1897) found a radial insertion in his specimen of Dolichotis.

The short head is present in most sciurids (Bryant, 1945), and in geomyids (Hill, 1937), and Aplodontia (Hill, 1937; Lewis, 1949). This indicates that the presence of a short head is probably primitive. Hill (1937), following the idea of Leche (1900), stated that the two heads
of the biceps probably are relatable to two distinct premammalian muscles.

**M. brachialis**

Figures 13, 15, 16

_brachialis anticus_ (Parsons, 1894a)

**ORIGIN:** Via two heads: (1) from the neck of the humerus on the medial, posterior, and lateral sides; (2) from the anteromedial surface of the humerus on the tip of the deltoid ridge and beyond.

**INSERTION:** On the brachial ridge of the ulna. The fibers from the shaft of the humerus insert proximal to the ulnar insertion of the biceps; those from the neck of the humerus insert on the ulna between the two insertions of the biceps.

**OTHER GENERA:** The two heads of this muscle are present in all genera. The medial head is not well developed in any of the genera, however, and in some it is easily overlooked. The origin of the long head is additionally from below the lesser tuberosity on the medial side of the humerus in all genera except _Erethizon_ and _Cavia_. In these two genera it is restricted to the posterior and lateral aspects of the neck of the humerus. In _Erethizon_ and _Myocastor_ part of the muscle originates from the surface of, or is closely associated with, the lateral triceps.

**REMARKS:** The inconspicuous nature of the medial head has probably led to some inconsistent observations in the literature. It is present in Chinchilla, but Parsons (1894a) and Wood and White (1950) reported that it is absent. Beddard (1891) reported the presence of a medial head in _Dolichotis_, but Windle (1897) did not report one. I can find two heads of this muscle in _Cavia_, as did Ballard (ms.), but both Mivart and Murie (1866) and Parsons (1894a) reported only one head. The medial head is especially poorly developed in _Cavia_, however, and could easily be overlooked. There is a medial head in sciurids and _Aplodontia_ (Hill, 1937; Bryant, 1945; Lewis, 1949) but it is not well developed.

The origin of the long head in most rodents is from the lateral and posterior aspect of the neck of the humerus (Howell, 1932; Hill, 1937; Bryant, 1945; Lewis, 1949; Rinker, 1954; Klingener, 1964). In most hysticomorphs, however, the origin is also from the medial side of the neck of the humerus below the lesser tuberosity. In _Cavia_ and _Erethizon_ the origin from the medial side of the humerus seems to be restricted by the elongated origin of the medial triceps. Parsons (1894a) indirectly noted the extension of the origin onto the posteromedial side of the humerus.

**FLEXOR GROUP OF THE FOREARM**

The muscles of this group are innervated by both the median and ulnar nerves. In most mammals the ulnar nerve supplies the flexor carpi ulnaris, the epitrochleoanconeus, and the ulnar head of the flexor digitorum profundus. The median nerve supplies the remaining muscles of the forearm (Howell, 1932; Howell and Straus, 1933; Hill, 1937; Schön, 1968). Both Rinker (1954) and Klingener (1964), however, reported that in their specimens the ulnar head of the flexor digitorum profundus is innervated by the median nerve, not the ulnar nerve.

The ulnar nerve in hysticomorphs innervates _M. epitrochleaoanconeus_, _M. flexor carpi ulnaris_, and the ulnar head of _M. flexor digitorum profundus_, thus following the configuration reported by Howell (1932) and Hill (1937). In addition I find that the nerve usually innervates _M. flexor digitorum superficialis_ and _M. palmaris longus_. I can find no other reference in the literature indicating an ulnar innervation of these muscles in rodents (or in any mammal). This condition at first appears to be unique to hysticomorphs, but dissections also indicate the same muscles are innervated by the ulnar nerve in _Sciurus_, _Eutamias_, and _Aplodontia_. In _Thryonomyx_ the palmaris longus is not innervated by the ulnar nerve, but the epitrochleoanconeus, the flexor digitorum superficialis, the flexor carpi ulnaris, and the ulnar head of the flexor digitorum profundus all are. The flexor muscles of the forearm are all probably closely interrelated and illustrate no consistent pattern of innervation. Hysticomorphs, squirrels, and _Aplodontia_, however, do have an unusual arrangement of these muscles. The relationships of the forearm flexors are problems that need further study. The homologies of the forearm flexor muscles in amphibians, reptiles, and other mammals are discussed by McMurrich (1902, 1903) and Dastugue (1963).

**M. epitrochleaoanconeus**

Figures 14, 16

_epitrochleaoanconeus_ (Parsons, 1894a)

**ORIGIN:** From the medial epicondyle of the humerus.

1972

WOODS: HYSTRICOMORPH RODENTS

169
INSERTION: On the medial aspect of the olecranon process of the ulna.

OTHER GENERA: The muscle is very thin in four specimens of Cavia, and completely missing in two. It is well developed in all other genera, and especially so in Petromus.

REMARKS: The muscle forms a bridge between the medial epicondyle and the olecranon. The ulnar nerve passes deep to it, and a small branch of this nerve innervates the muscle. Howell (1926) and Wood and White (1950) incorrectly referred to this muscle as M. anconeus. Greene (1935) in her text confused this muscle with M. dorsoepitrochlearis. The muscle is present in sciurids (Bryant, 1945), Aplodontia (Lewis, 1949, under the name anconeus medialis), soricoid insectivores (Reed, 1951, also under the name anconeus medialis) and indeed in most mammals except humans (Hill, 1937).

M. flexor carpi ulnaris
Figures 12, 14–17

ORIGIN: From the medial and ventral surfaces of the olecranon and proximal eighth of the ulna beyond the olecranon.

INSERTION: On the surface of the pisiform bone.

OTHER GENERA: The origin of the muscle is restricted to the ventral surface of the olecranon and proximal end of the ulna in Echimys, Isothrix, Mesomys, Myocastor, Octodon, and Ctenomys. This is a result of the enlarged olecranon slip of palmaris longus, which has forced the origin of

Fig. 17. Palmar view of left manus of Proechimys guyannensis.
the flexor carpi ulnaris ventrally. In *Cavia, Chinchilla, Dasyprocta*, and *Thryonomys* the configuration of the muscle is similar to the muscle in *Proechimys*. In *Petromus* the origin is additionally from the surface of the palmaris longus. In *Erethizon* the origin is from the medial epicondyle as well as from the medial surface of the olecranon and the ventral surface of the proximal half of the ulna itself via an aponeurosis. In *Thryonomys* the muscle is large and the origin of *M. dorsoepitrochlearis* is partially from its surface.

**Remarks:** The origin of this muscle was partially from the medial epicondyle only in *Erethizoz*. Mivart (1882) also reported the muscle originating from the internal condyle (= medial epicondyle) in *Erethizon*. The description of this muscle by Parsons (1894a) is incomplete, but he does report that the condylar (= medial epicondylar) origin is lacking in Octodontidae and Dasyproctidae.

Both Wood and White (1950) and Olborth (1964) reported a two-parted muscle in *Chinchilla* that originates from both the medial epicondyle and the olecranon. This is not consistent with my observations. Neither Wood and White (1950) nor Olborth (1964), however, reported the presence of a palmaris longus. There is a palmaris longus present in my specimens with a feeble tendinous insertion. I believe, therefore, that Wood and White (1950) and Olborth (1964) confused the palmaris longus with what they call the medial epicondylar part of the flexor carpi ulnaris. Parsons (1894a) implied the presence of two parts to this muscle, and listed the palmaris longus as missing in *Chinchilla*, so he probably was making the same error.

The lack of the part from the epicondyle is not unusual in rodents. The part is missing in *Castor, Spermophilus (= Citellus), Rhizomys, Bathyergus* (Parsons, 1894a, 1896), *Dipodomys* (Howell, 1932), geomyids (Hill, 1937), and dipodoids (Klingener, 1964). In sciurids (Bryant, 1945), *Aplodontia* (Lewis, 1949), and in most other rodents (Parsons, 1894a, 1896) the origin is from both the medial epicondyle and the olecranon. Hill (1937) believed that the presence of a medial epicondylar head is the primitive condition.

**M. palmaris longus**

**Figures 14-16**

**Origin:** From both the distal tip of the medial epicondyle and the medial surface of the olecranon. The relative size of the head from the olecranon is variable from small to large.

**Insertion:** On the fascia of the palm, and the ulnar side of the large palmar ossicle (= falciform bone). The two heads unite into a single muscle which passes down the ventromedial side of the arm as a shiny tendon.

**Other Genera:** The head from the olecranon is large in *Echimys, Isothrix, Mesomys, Octodon*, and *Ctenomys*. In some specimens of *Ctenomys* the head from the medial epicondyle is thin. In *Myocastor* the head from the medial epicondyle is missing. In *Cavia* the head from the medial epicondyle is large, and in most specimens the head from the olecranon is missing. In *Erethizon, Chinchilla, Dasyprocta, Thryonomys*, and *Petromus* the origin is restricted to the medial epicondyle. In all five of these genera, and in *Cavia* the muscle is closely associated with the flexor digitorum profundus and the flexor digitorum sublimus.

**Remarks:** The muscle is present in all genera, although in *Dasyprocta* it is relatively thin, and in *Chinchilla* the insertion is often thin. The muscle was incorrectly reported as missing in *Chinchilla* by Parsons (1894a), Wood and White (1950) and Olborth (1964). It is probable that all of these workers included it in their descriptions of flexor carpi ulnaris. In echimyids and octodontids the origin from the olecranon is the larger. Mivart and Murie (1866) described the muscle in *Dasyprocta* as a small slip from the internal condyle (= medial epicondyle) and closely associated with the flexor sublimis (= flexor digitorum superficialis). Parsons (1894a) and Elton (Ms.) reported that the muscle is missing in their specimens of *Dasyprocta*.

The muscle, as Parsons (1894a) noted, is subject to a large amount of individual variation. I found two heads clearly present in *Octodon*, but Parsons (1894a) only reported one. In my specimens of *Proechimys, Echimys, Mesomys, Ctenomys, Cavia*, and *Dasyprocta* there was individual variation in the muscle. The muscle certainly is of little over-all taxonomic value, but there is a major difference between the echimyid-octodontid group, in which the origin is primarily from the olecranon, and the remaining genera. There is no difference between New World and Old World forms.

In all genera in which the origin of the muscle is mainly from the medial epicondyle,
the palmaris longus is closely associated, or partially fused, with the flexor digitorum superficiales and the flexor digitorum profundus. The muscle is innervated by the ulnar nerve in all genera except *Dasyprocta* and *Thryonomys*. In *Dasyprocta* the muscle is vestigial and in *Thryonomys* the innervation is via the median nerve.

**M. flexor carpi radialis**

*Figures 14–16*

**Origin:** From the medial epicondyle between the origins of the pronator teres and the flexor digitorum profundus.

**Insertion:** On the base of the second and third metacarpals.

**Other Genera:** The muscle is the same in all genera except *Myocastor*. In *Myocastor* the muscle additionally originates from the surface of the pronator teres in one specimen, and the surface of the medial head of the flexor digitorum profundus in two other specimens.

**Remarks:** The insertion is usually on the second and third metacarpals. There is some individual variation, however; some specimens have an insertion on the second and third metacarpals, and some have an insertion on the first through third metacarpals. The origin is variable in *Myocastor*. I do not find that the origin of the muscle is fused with the pronator teres in my specimens of *Chinchilla*, but Wood and White (1950) and Olborn (1964) do find such a common origin. The muscle is, therefore, subject to a certain amount of individual variation.

**M. pronator teres**

*Figures 14, 16*

**Origin:** From the most proximal end of the medial epicondyle.

**Insertion:** On the proximal half of the craniomedial surface of the radius.

**Other Genera:** The origin of the muscle is the same in all genera. In *Echimys* and *Isthrix* the insertion is the same as it is in *Proechimys*. In *Metamys* the insertion is on the proximal two-thirds of the radius. In *Myocastor* and most specimens of *Octodon* the insertion is on the middle third of the radius. In one specimen of *Octodon* the insertion was on the proximal third of the radius. In *Ctenomys* the muscle is large and the insertion is on the middle two-thirds of the radius. In *Erethizon* the muscle is huge, and the insertion is the distal half of the radius. In *Chinchilla* the insertion is the proximal quarter of the radius; in *Dasyprocta*, *Thryonomys*, and *Petro-mus* it is the middle quarter.

**Remarks:** The size and distal movement of the insertion of the muscle in *Ctenomys* and *Erethizon* could be associated with a more powerful front limb in these two genera. However, the muscle is also large in geomyids, and in squirrels and *Aplodontia* (Hill, 1937; Bryant, 1945; Lewis, 1949), and this may reflect the primitive condition of the muscle.

The muscle is very small in *Cavia*, and was missing in one specimen. Ballard (ms.) reported the muscle absent in his specimens of *Cavia*, but Mivart and Murie (1866) found it in theirs.

**M. flexor digitorum superficialis**

*Figures 14–17*

**flexor sublimus digitorum** (Parsons, 1894a)

**Origin:** From the medial epicondyle. The muscle is covered at its origin and for most of its length by the medial head of the flexor digitorum profundus, and by the palmaris longus. In the distal region of the arm the muscle passes from under the ulnar side of the flexor digitorum profundus, and comes to lie on the surface of the latter.

**Insertion:** The muscle splits into three tendons which pass out onto the base of the second, third, and fourth digits. Beyond the metacarpophalangeal junction each tendon splits into two small branches which pass out on either side of the large tendon of the flexor digitorum profundus and insert on the base of the second phalanx.

**Other Genera:** The muscle is the same in all genera except *Myocastor*, *Erethizon*, and *Cavia*. In one specimen of *Myocastor* the muscle is composed of two heads, one from the median epicondyle and the other from the olecranon. In the other specimens of *Myocastor* this extra head was not found. In *Erethizon* the muscle divides into tendons which pass onto the second through fifth digits. This was true of all specimens of *Erethizon* dissected. In *Cavia* the slip onto the fifth digit is present in one specimen, but missing in all others.

**Remarks:** A loop forms on each tendon of this muscle at the point where the tendon splits to pass on either side of the flexor digitorum profundus. These loops pass around the larger
tendon of the flexor digitorum profundus. Either on top of this loop, or slightly distal to it, another loop passes over both the dividing flexor digitorum superficialis and the penetrating flexor digitorum profundus. This second loop is inserted on the two sesamoid bones that lie at the metacarpophalangeal joint. It is important to stress that the loop formed by each tendon of the flexor digitorum superficialis at the point where the tendon divides does not insert upon the sesamoid bones, but rather continues as a loop under the tendon of the flexor digitorum profundus. This loop from the flexor digitorum superficialis was described by Rinker (1954) for Sigmodon, but according to Rinker the loop passes directly to the sesamoid bones. It is possible that Rinker was not able to separate the inner and outer loops in his much smaller specimens, or the conditions in Sigmodon may differ from those in hystricomorphs. Parsons (1894a) was the first worker to note these tendinous loops.

The slip passing to the fifth digit in Erethizon and in one specimen of Cavia probably represents the primitive condition of the muscle. Mivart and Murie (1866) reported finding a slip to the fifth digit on one side of their specimen of Dasyprocta. Such an extra slip is the usual condition in squirrels and Aplodontia (Hill, 1937; Bryant, 1945; Lewis, 1949).

In those genera in which there is no tendon to the fifth digit, there is a loop and set of paired tendons passing out on either side of the flexor digitorum profundus onto the fifth digit. Parsons (1894a) interpreted this as representing the part of the flexor digitorum superficialis remaining behind after the tendinous connection with the main part of the muscle has been lost. His explanation is probably correct. It is interesting to note that Castor also has an extra origin from the olecranon, as did one specimen of Myocastor.

This muscle is innervated by the ulnar nerve in all genera.

M. flexor digitorum profundus

**Figures 12, 14–17**

flexor profundus digitorum (Parsons, 1894a)

**Origin:** Via four heads. The first, or medial, is from the medial epicondyle by the origins of the flexor carpi radialis and the palmaris longus, and it is large. The second, or deep medial, is from the medial epicondyle deep to the first part, and is thin. The third, or radial, is from the proximal two-thirds of the radius, and is well developed. The fourth, or ulnar part, is from the proximal two-thirds of the ulna, and is also well developed. The radial and ulnar parts are deep to the others.

**Insertion:** The four parts of this muscle unite in the region of the wrist. The tendons of the three deeper parts join the tendon of the medial. The muscle passes through the wrist as a large tendon and then divides into four tendons. The tendons pass out onto the ventral surface of the second through fifth digits to insert on the terminal phalanx. From the tendon to the second digit a side tendon develops that passes out onto the first digit.

**Other Genera:** The muscle is the same in Echimys, Isothrix, Mesomys, Octodon, and Cleomys. In Thryonomys the muscle is basically the same but the medial part is extremely large and the tendon of the deep medial part joins the tendon of the radial part. In Chinchilla the muscle is also basically the same, but the radial and ulnar parts are inseparable for most of their length and originate on the proximal third of the radius and ulna. In Myocastor the insertion pattern of the muscle is the same, but the origin of the medial part is via two heads; one from the medial epicondyle, and the other from the olecranon. In Erethizon, Cavia, Dasyprocta, and Petromus the side tendon that inserts onto the pollex is not present. In Cavia there are small tendons that lift off of the surface of the tendons to the second through the fifth digits, and pass to the surface of the palm.

**Remarks:** As pointed out earlier, this muscle is closely associated with the flexor digitorum superficialis and the palmaris longus in Erethizon, Cavia, Chinchilla, Dasyprocta, Thryonomys, and Petromus. The insertion of this muscle may be subject to some individual variation. Mivart (1882) reported a side tendon to the pollex in Erethizon, but I did not find such a tendon in my specimens. I did find the side tendon to the pollex in my specimens of Chinchilla, but Wood and White (1950) and Olborth (1964) did not report such an insertion. Also, the insertion on the pollex was variable in my specimens of Echimys and Octodon. Lane (ms.) did not report the side tendon to the pollex in his specimen of Echimys. Bryant (1945) reported some variation in the insertion of this muscle onto the pollex in sciurids.

The radial and ulnar parts are large in all
genera except *Cavia*. The ulnar head can in many cases be seen bulging outward on the distal end of the posteroverentral surface of the forearm between the extensor carpi ulnaris and the flexor carpi ulnaris. This is especially true in *Thryonomys* in which all the forearm muscles are large. In *Chinchilla* the radial and ulnar heads are united for most of their length, and appear to be one muscle. This condition is found in many rodents (Windle, 1890; Hill, 1937; Rinker, 1954).

The ulnar head of this muscle is definitely innervated by the ulnar nerve; the remaining three heads are innervated by the median nerve. This observation is consistent with that of Howell (1932) and Hill (1937) for their rodents, and for most mammals. Rinker (1954) and Klingener (1964), however, reported only median innervations for the ulnar head in the rodents they dissected. I also found an ulnar innervation for the flexor digitorum superficialis and the palmaris longus in all the animals dissected except *Thryonomys* and *Dasyprocta*.

The lumbrical muscles originate from the tendinous surface of this muscle. In all genera except *Cavia* there are four lumbricales present. In *Cavia* there are only three. *Cavia*, however, does have a set of three extra tendinous slips present from the surface of the flexor digitorum profundus. The extra slips are not present in any of the other genera.

Windle (1882) reported four lumbricales in *Erethizon*, but Mivart (1882) described only three. Mivart and Murie (1866) and Parsons (1894a) mentioned three lumbricales for *Dasyprocta*, but I can locate four. Both Mivart and Murie (1866) and Parsons (1894a) reported only three lumbricales in *Cavia*.

**M. pronator quadratus**

*Figure 15*

**Origin:** From the distal third of the ulna. The muscle originates along the radial side of the ulna, and fills the interosseus area.

**Insertion:** On the opposite surface of the radius.

**Other Genera:** The muscle is the same in *Echimys*, *Isothrix*, *Mesomys*, and *Erethizon*. In *Myocastor* and *Octodon* the muscle varies in extent from the distal third of the forearm to the distal half. In *Petromus* it varies between the distal third of the forearm and the entire length. In *Chinchilla* it is along the distal three-fourths of the forelimb. In *Dasyprocta* and *Thryonomys* it is along the entire length of the forelimb. In *Ctenomys* and *Cavia* I could not see the muscle. Dastugue (1963), however, showed it as being well developed in *Cavia*.

**Remarks:** The muscle is more extensive in many hystricomorphs than it is in most other rodents (Parsons, 1894a). Hill (1937) stated that the primitive condition was as an extensive interosseus muscle. The reduction in size of the muscle is probably a result of several factors. In *Cavia* and *Ctenomys*, where the muscle is reduced, the radius and ulna are close together. The extent of the muscle also seems to be inversely associated with the size and point of origin of the radial head of the flexor digitorum profundus. The range of variation of this muscle within hystricomorphs, and the amount of individual variation exhibited limit the use of this muscle as a taxonomic characteristic. Parsons (1894a) considered the great extent of this muscle to be an important hystricomorph feature.
The structure of rodent jaw muscles is associated with the manner of movement of the mandible in feeding and chewing. The enlargement of the incisors and the presence of a pronounced diastema have resulted in the separation of the gnawing (or digestive) and the chewing (or masticatory) acts. Maynard Smith and Savage (1959) and Hiemae and Ardren (1968) have pointed out that the two acts are carried out with the jaw in two different positions. The great anteroposterior shift necessary to bring the incisors or the molar series into contact is allowed by the elongation of the glenoid fossa in an anteroposterior direction.

Because of the structure of the glenoid fossa, many early workers assumed that rodents chew in a propalinal manner. The movement of the rodent mandible in an anteroposterior manner in the transition from gnawing to chewing is obviously propalinal. Hiemae and Ardren (1968) did not believe, however, that rodents chew in a predominantly propalinal manner, and their experimental animal, the laboratory rat, probably does not. Becht (1953) and Krapp (1965) also did not believe that rodents chew in a propalinal manner. Landry (1957a), however, believed that Becht was not interpreting his data correctly. Tullberg (1899), Landry (1957a), and Maynard Smith and Savage (1959) all believed that the Hystricomorpha (sensu stricto) chew propalinally.

The hystricomorphous condition of the medial masseter muscle, and the hystricognathous condition of the angle of the mandible are merely two component parts of the modified masticatory apparatus of these rodents. Moss (1968) in his functional analysis of the mammalian mandible, observed that in Cavia, Hydrochoerus, and Myocastor the angular processes are large, and the coronoid processes are small. In relation to these conditions he believed that there is “massive evidence” that skeletal structure is not directly controlled by genetics. “Rather, it appears that it is the functional matrices which are the target of such activity” (p. 443). One such functional matrix is the masseter muscle complex, plus the internal pterygoid muscle (Moss, 1968, p. 439). Moss believed that the muscular and skeletal anatomy of the mammalian mandible evolves in units (= functional matrices) in response to functional demands. One of the most important functional demands acting on the masticatory apparatus of the hystricomorpha (sensu stricto) is associated with propalinal chewing.

The main conditions of the masticatory apparatus that might be associated with the manner in which these animals chew are: (1) chewing with both left and right molar tooth rows in contact simultaneously; (2) flat-crowned teeth; (3) reduction of the superficial or anterior part of the temporal muscle; (4) horizontal position of the superficial masseter; (5) development of the reflected part (= pars reflexa) of the superficial masseter; (6) horizontal position of the posterior deep part of the lateral masseter; (7) increased relative size and length of the internal pterygoid; (8) straight and uninterrupted configuration of the anterior and posterior digastrics; (9) reduction in the size of the transverse mandibular muscle.

In most rodents and lagomorphs chewing occurs on only one side of the jaw at a time (Ardren, Kemp, and Ride 1958; Hiemae and Ardren, 1968). Maynard Smith and Savage (1959) reported that in Hystrix, Erethizon, Coendou, Hydrochoerus, Cavia, Dasyprocta, Lagostomus, Chiinchilla, and Myocastor the molar tooth rows on both sides of the jaw are in occlusion simultaneously. Chewing is therefore propalinal, with the movement of the jaw guided by the angle of the teeth against each other. Landry (1957a) stated that chewing is propalinal in the Hystricomorpha (sensu stricto) and in Pedetes, anomalurids, bathyergids, and ctenodactylids. The angle of chewing is at about 50 degrees to the line of the tooth rows, however, in Landry’s definition of propalinal chewing. I have examined Coendou, Dasyprocta, Ctenomys, and Erethizon, and find that the two tooth rows are almost in contact, but that chewing must be mostly on one side or the other, as Landry reported. In Myocastor, Capromys, Cavia, Hydrochoerus, Octodon, Proechimys, Echimys, Chiinchilla, Thecurus, and Hystrix the two rows are solidly in contact and chewing probably includes both sides simultaneously. The
Hysticomorpha (*sensu stricto*), therefore, do show a strong tendency to chew with both of their tooth rows together, or closely together, and in a propalinal manner. However, the problem of how specific rodents chew is in need of further studies such as those by Ardran, Kemp, and Ride (1958), Hiiemae (1967), and Hiiemae and Ardran (1968). For example, Crompton and Hiiemae (1969) believed that the only way precisely to determine the manner in which mammals chew is to study living forms. They believed that in *Didelphis* the information from the occlusion patterns and tooth wear is not consistent with their findings from cinefluorographic studies.

Many hysticomorphs (*sensu stricto*) have flat-crowned teeth. Other groups of rodents also have flat-crowned teeth, for example, geomyoids, glirids, otomyines, microtines, *Neotoma*, and others (Merriam, 1895; Landry, 1957a). In geomyoids, microtines, and *Neotoma* there are conditions of the internal pterygoid muscle and the pterygoid fossa that resemble the condition in hysticomorphs (*sensu stricto*), indicating the possibility of similar selective pressures acting on the jaw musculature. Anomalurids, bathyergids, ctenodactylids, and pedetids also have flat-crowned teeth (Bohlin, 1946; Stehlin and Schaub, 1951; Landry, 1957a). In many of the above-mentioned rodents the teeth are not nearly as flat-crowned in juveniles as they are in adults (Wood, 1965). The increase in flatness of the tooth surfaces during the life of the rodent is a further indication that the animal chews propalinally.

The temporal muscle is closely associated with the maseter muscle complex, and with chewing. Indeed, Allen (1880) and Tullberg (1899) considered the two muscles to be indistinct from each other; and Krapp (1965) pointed out how easily they can be confused. Hiiemae and Jenkins (1969) investigated the masticatory muscles of *Didelphis*, and were unable to separate effectively these two muscles in that mammal. Most workers describe the temporal muscle in rodents as being composed of either two or three parts. The main divisions are the superficial (or anterior) and the deep (or posterior). It has been known for a long time that the temporal muscle operates both to shut the mouth and to slide the mandible posteriorly (Merriam, 1895; Rinker and Hooper, 1950; Vendeloo, 1953). Hiiemae (1967) stated that the two parts of the temporal muscle function independently of each other. The anterior part stabilizes and elevates the mandible. Klingener (1964), following an idea of Rinker's, has suggested that in animals in which mastication is primarily grinding rather than crushing there is a progressive reduction in the size of the anterior fibers of the temporal. In the hysticomorphs dissected the anterior part of the temporal is very reduced, and I believe that this reduction is correlated with propalinal chewing. In most squirrels, in which propalinal chewing is not important, the anterior temporal is well developed.

In hysticomorphs the superficial maseter muscle lies almost horizontally and is therefore able to force the mandible anteriorly in propalinal chewing (see fig. 2 and also Maynard Smith and Savage, 1959). The position of the superficial maseter is also horizontal in other groups of rodents, but the area of insertion is broadly over the rounded angular process (see plates in Tullberg, 1899; Vendeloo, 1953; Wood, 1965). In hysticomorphs the superficial maseter is inserted along the ventral surface of the posteriorly elongated angle of the mandible all the way to the horizontally elongated tip (see figs. 1 and 2 and Wood, 1965, fig. 3). The direction of force is, therefore, almost anteroposterior. The large reflected part (= pars reflexa) of the superficial maseter which is so characteristic of hysticomorphs also seems to function in the anteroposterior movement of the jaw. In most rodents this part of the muscle inserts on the ventral margin of the angle, but in all hysticomorphs it has migrated around to the postero-medial side of the mandible. This extends the muscle and causes its over-all force to pass more anteroposteriorly. The extension of the reflected part of the muscle onto the medial side of the mandible is associated with the groove lying anterior to the angle, and with the hystricognathous jaw. This condition of the superficial maseter is found in both New World and Old World hysticomorphs and in bathyergids. It is not found in ctenodactylids, anomalurids, *Pedetes* or any other group of rodents.

The deep division of maseter lateralis profundus, pars posterior lies horizontally in hysticomorphs (see fig. 2). This part is homologous to the vertically lying part of the lateral maseter in squirrels which lies posterior to the maseteric nerve. The muscle is often associated with a posterior expansion of the mandible (= post-
condyloid process). This expansion is also present in Reithroparameters (a paramyid) and Platypittamys (a New World hysticomorph). Tullberg (1899) illustrated this muscle as a part of his "portio superficialis masseteris lateralis," but did not describe it extensively. He showed that it is present in most hysticomorphs and possibly in Pedetes, but not in any other group of rodents. Muller (1933) described this part as M. masseter pars profunda, pars posterior in Hydrochoerus. This horizontally lying muscle is an important component of the propalinal masticatory apparatus of these rodents, and functions in forcing the jaw anteriorly in propalinal chewing.

In my interpretation of the masseter muscle complex, I am following the nomenclature of Hill (1937). Other investigators have also described the anatomy and function of the masseter muscle complex (Forster, 1928–1929a; Muller, 1933; Becht, 1953; Schumacher, 1961; Schumacher and Rehmer, 1962; Heinze, 1964, 1969; Krapp, 1965, 1969; Yoshikawa and Suzuki, 1969). Most of this work is on large domestic animals, but the masseters of Oryctolagus, Cavia, Myocastor, Hydrochoerus, and Spalax are also described. The nomenclature used by these workers is different from that used by Hill and other American investigators. Unquestionably the work by Yoshikawa and Suzuki is carefully done, but they interpret the various layers of the masseter group erroneously. Their interpretation and that of Muller (1933) seem overly split to me (Hiemae and Jenkins, 1969). The work by Heinze (1964, 1969) employs muscular diagrams to analyze the various parts of the masseter as a single unit. This method is too general to correctly interpret the various parts of the masseter, or their functions. There is also a good but not comprehensive study of the jaw muscles of Ondatra by Vendeloo (1953).

The pterygoid muscles are important components of the rodent jaw musculature. Both the internal and external pterygoids have come to lie in a more horizontal plane. This has occurred in the case of the internal pterygoid by the movement of the insertion distally onto the posteriorily extended angle of the mandible, and by the movement of the origin of the muscle deep into the pterygoid fossa. The pterygoid fossa in all hysticomorphs except Hydrochoerus is modified inside and opens into the orbit or braincase (Tullberg, 1899; Landry, 1957a). The open nature of the fossa allows for an increase in the length of the muscle. As a result the muscle lies more horizontally. The shift of the angle of action of the internal pterygoid enables the muscle to function in the anteroposterior movement of the jaw. The fossa is not open in Hydrochoerus because of the increased length of the third upper molar (Landry, 1957a). The fossa is open in bathyergids and geomyoids, but it is not in Pedetes. The condition in geomyoids is possibly a result of parallelism and is associated with the flat-crowned teeth, simultaneously opposing molar tooth rows, and similar action of the lower jaw in these animals.

The external pterygoid also lies in a more horizontal plane in most hysticomorph genera. This change is associated with the posterior expansion of the mandible in the area behind the mandibular condyle. The condition of the external pterygoid differs markedly in animals such as the giant panda, which chews somewhat laterally. In the giant panda the external pterygoid has an almost frontal course (Sicher, 1944).

The digastric muscle is modified in hysticomorphs in such a way that it lies in a straight line. The muscle, therefore, passes uninterrupted from the paroccipital process to the ventral surface of the mandible. The bellies of the anterior digastric are not in contact with each other in most hysticomorphs. Parsons (1894a, 1896) referred to this configuration of the digastric as the "hysticomorphine type." Dobson (1882) correlated the presence or absence of the tendinous intersection with the position in which the head is held while feeding. He reported that the reason there is no tendinous intersection in Bathyergus (=Bathyergus) is that these rodents hold their heads in line with their bodies while feeding. According to Dobson (1882, p. 262), animals that sit erect while feeding have united anterior bellies of the digastric with "intermediate tendons well developed and connected by fascial bands with the hyoid bone." There is no over-all correlation within the hysticomorphs I have examined, however, that would substantiate Dobson's ideas.

The observed lack of contact between the two anterior bellies and the continuity of the anterior and posterior digastrics are secondary conditions resulting from the shift of the digastrics into straight lines. Merriam (1895) suggested that the function of the digastric in those geomyid genera in which the teeth are flat
crowned and the tooth rows meet simultaneously is to draw the jaw posteriorly. Hill (1937) pointed out that the structure of the digastrics in geomyids is similar to that in hystricomorphs. Landry (1957a) made the same observation for heteromyids. In Neotoma, Microtus, Lemmus, and bathyergids that also have flat-crowned teeth the digastrics tend to resemble the hystricomorphine condition (Parsons, 1896; Howell, 1926; Landry, 1957a). The condition of the digastric in geomyoids and microtines is probably another example of parallelism in response to the functional demands of the propalinal masticatory apparatus. The condition in bathyergids may indicate a relationship with hystricomorphs. The condition of the digastric muscle in all of these genera strongly supports my contention that the hystricomorphine digastric is a functional component of propalinal chewing.

The transverse mandibular muscle probably functions to separate the tips of the lower incisors during gnawing and to permit scissor-like motion of the two lower incisors against each other (Kunstler, 1887; Landry, 1957a). The muscle may also regulate the position of the molar tooth rows during chewing (Merriam, 1895). The muscle in hystricomorphs is poorly developed, a condition that is undoubtedly associated with the near fusion of the mandibles (Landry, 1957a). There is a functional advantage in having the lower part of the masticatory apparatus fused into one solid shelf in animals that chew on both sides of the jaw at the same time and in a predominantly propalinal manner. Conversely, in animals that mainly crush their food and need to regulate the position of the two separately functioning halves of the mandible, the transverse mandibular muscle is important. The muscle is well developed in squirrels (Kunstler, 1887; Tullberg, 1899), Haplodon (=Aploodontia) (Tullberg, 1899), and Rattus (Tullberg, 1899; Greene, 1933); all are non-propalinal chewers. However, the muscle is also well developed in Neotoma (Tullberg, 1899; Howell, 1926) and geomyids (Hill, 1937), animals that probably chew in a manner somewhat similar to hystricomorphs. It is well developed in bathyergids, which certainly chew in a manner similar to most hystricomorphs (Landry, 1957a). The muscle is reduced in hystricomorphs, and in Castor (Tullberg, 1899) and Dipodomys (Howell, 1932). All of these rodents have flat-crowned teeth and probably chew propalinally. Therefore, there is a possible functional correlation between propalinal chewing and the transverse mandibular muscle, but it is not absolute.

The passage of the medial masseter muscle through the enlarged infraorbital foramen and onto the snout is the characteristic feature of the classical suborder Hystricomorpha (Brandt, 1855). This feature is certainly not restricted to hystricomorphs, however. According to Wood (1965), the result of this condition is an almost horizontal line of action of the medial masseter, augmenting the horizontal action of the superficial masseter. In contrast to Wood's view, Maynard Smith and Savage (1959) and Krapp (1965) concluded that the main axis of action of the medial masseter is vertical, and that the muscle cannot be associated with antero-posterior movement of the jaw. Hiðemæ (1967) presented basially the same conclusion. Maynard Smith and Savage, Hiðemæ, and Krapp all believed that the main function of the medial masseter is to stabilize the mandible during chewing. My observations support the findings of these workers. Therefore, the similarity of the medial masseter probably is not associated simply with functional modifications of the jaw for propalinal chewing.

Muller (1933), Becht (1953), and Yoshikawa and Suzuki (1969) believed that the inner parts of the masseter muscle complex have evolved independently of the remaining parts. The part that passes through the infraorbital foramen is called M. maxillo-mandibularis. If this muscle has evolved independently of the remaining parts of the masseter muscle complex, then it is possible that the hystricomorphous condition of the medial masseter of so many different rodents could be a result of parallelism. The medial masseter could be a part of a different "functional matrix" (Moss, 1968). Therefore, dipodoids, anomalurids, ctenodactylids, and pedetids could have evolved a hystricomorphous condition of the medial masseter independently. The other parts of the masseter muscle complex, which are similar in rodents of the Hystricomorpha (sensu stricto) and possibly the bathyergids, could be part of a separate functional unit. The many similarities of both of these possible functional units in the hystricomorphs that I dissected indicates either extreme parallelism, or a common relationship of some sort.
I have described what I believe to have been the main selective forces and primary functional modifications of the masticatory apparatus in these rodents. I believe that most of the modifications of the jaw are associated with propalinal chewing. These modifications have often been quite complex, and they are all derived from the primitive rodent condition. For some of these individual modifications, similar conditions in response to similar selective pressures can be demonstrated in other rodents. The preceding examples further substantiate my ideas. The presence of these complex, derived characteristics in all hystricomorphs, whereas other rodent groups have only a few of these modifications, is a strong argument for placing the New World and Old World genera of these rodents together in the same taxonomic unit.

The hyoid muscles of hystricomorphs are unusual in several ways. The muscles of this region are often small and complex. It is not surprising, therefore, that their treatment in the older literature has been inconsistent. The primitive condition of the hyoid apparatus includes a well-developed stylohyal cartilage passing into the stylomastoid foramen and a full set of hyoid muscles originating on both the stylohyal and the paroccipital process (Klingener, 1964). The primitive conditions of the hyoid apparatus are found in sciurids, Aplodontia, Peromyssus, Sicista, and Zapus (Hill, 1937; Bryant, 1945; Rinker, 1954; Klingener, 1964). The primitive condition also includes the presence of a well-developed ceratohyal, as in Sciurus (Romankowowa, 1962). Various rodents have modified the basic hyoid apparatus in several ways (Hill, 1937; Sprague, 1942; Rinker, 1954; Sharma and Sivaram, 1959; Klingener, 1964).

In hystricomorphs the stylohyoid muscle has been lost. Such a loss is unusual when the basic primitive skeletal configuration of the hyoid apparatus is retained. Many early workers, such as Parsons (1894a), reported the presence of a stylohyoid muscle in hystricomorphs, but I believe that they are confusing the jugulohyoid muscle with this muscle. It is interesting that the stylohyal muscle is also missing in Bathyergus.

In some hystricomorphs, the origin of the styloglossus muscle has shifted from the stylohyal to the pterygoid process. Such an origin is extremely unusual in rodents. Many hystricomorphs have lost the omohyoid muscle. The loss of this muscle, however, does not follow any systematic pattern within the over-all hystricomorph group. The omohyoid muscle fuses with the sternohyoid muscle in Echimys, Octodon, and Ctenomys. The condition in Bathyergus is the same (Parsons, 1896). Parsons (1894a) used the tendency toward the loss of the omohyoid as one of his hystricomorph characters. He also noted that the opposite sides of the geniohyoid muscle tend to be distinctly separated in hystricomorphs, but certainly this situation is not consistently true. A glossopharyngeus muscle is found in all hystricomorphs that I dissected. Although this muscle has not been widely reported in rodents, I suspect that it is probably present in most primitive rodent groups and is part of the primitive rodent configuration.

Therefore, it can be seen that hystricomorphs have a primitive type of hyoid apparatus. The musculature of the apparatus is generally of the normal primitive configuration, but in the case of the stylohyoid muscle in all hystricomorphs, the musculature has been modified. These modifications are unusual and represent a departure from the conditions reported in other rodents.

The cleido-occipitalis is present in all genera dissected, but it is usually closely fused with the more dominant cleidomastoid. In Cavia the cleido-occipitalis is the dominant muscle, and is easily confused with the clavotrrapezius (see fig. 9). Using the emergence of the great auricular nerve, however, as the point of separation between the cleido-occipitalis and the trapezius muscles (Hill, 1937; Rinker, 1954; Klingener, 1964), the clavotrapezius must be interpreted as being incorporated into the acromiotaepiuus. This is the condition in most rodents.

The acromiotaepiuus is a variable both within and between genera. This variation is probably a result of the fusion with the clavotrapezius. The origins of the acromiotaepiuus and spino-trapezius are continuous in primates (Howell, 1932; Hill, 1937), squirrels (Hill, 1937), and in Aplodontia (Hill, 1937; Lewis, 1949). I have confirmed this observation in squirrels and Aplodontia. Hill (1937) considered this to be the primitive mammalian condition. I find the origins of the trapezius muscles to be separable in four genera. In two additional genera the origins appear to be separable only because of the presence of an enlarged fascial window on the lateral surface of the proximal half of the scapula. Wood and Patterson (1959) reported
that the muscles are separate in *Petromus*, but this is not consistent with my observations. Therefore, in some hystricomorphs there is a modification of the basic primitive condition. The condition in *Dasyprocta* and *Thryonomys* represents one kind of modification, whereas that in *Myocastor*, *Octodon*, and *Ctenomys* represents the other. These modifications may indicate relationships within hystricomorphs, but I do not believe that they represent an over-all subordinal distinction of the kind Parsons (1894a) or Wood and Patterson (1959) believed.

The auricular slip is present in all but four genera I dissected. The presence of an auricular slip probably represents a vestige of the primitive superficial trapezial sheet (Klingener, 1970). This vestige is found in some sciurids, murines, microtines, cricetines, and bathyergids. The large primitive superficial trapezial sheet is found in *Ctenomys*, and in *Aplodontia* (Klingener, 1970). In hystricomorphs, therefore, the trapezius group illustrates a considerable amount of variation. This variation spans the range from conditions that are primitive to those that are modified. Some intraspecific variation is found in all parts of this muscle group.

The presence of a scalenus anterior muscle ventral to the brachial plexus was considered by Parsons (1894a) to be characteristic of his Hystricomorpha. Parsons reported that it is present in all hystricomorphs except his hystricids (= New World and Old World porcupines). In most rodents the scalenus anterior is not present (Howell, 1932; Hill, 1937). I can find a scalenus anterior present and ventral to the brachial plexus in all the genera dissected except *Dasyprocta* and *Erethizon*. The condition in *Dasyprocta* is unusual since Mivart and Murie (1866), Parsons (1894a), Windle (1897), Elton (ms.), and Brown (ms.) all reported that the scalenus anterior is present in *Dasyprocta*. However, Mivart and Murie stated that Meckel (1829) did not find the muscle in *Dasyprocta*. The muscle is probably missing in *Coendou* (Parsons, 1894a) and is missing in *Hystrix* (Parsons, 1894a; Lesbre, 1907) and *Atherura* (Parsons, 1894b). The muscle is supposedly present in bathyergids and *Gerbillus* (Parsons, 1896). The presence of a scalenus anterior may, therefore, be an indication of a relationship between New World and Old World hystricomorphs and also bathyergids. The lack of a scalenus anterior in erethizontids is difficult to explain and is in need of further study.

The levator scapulae and the serratus anterior are continuous in all genera. The origin of the levator scapulae is variable. There is a slip of the levator scapulae from the atlas in *Erethizon* and *Thryonomys*, and there is a well-developed atlantoscapularis posterior. This indicates that the atlantoscapularis posterior is probably not homologous with the atlantal slip of the levator scapulae. The atlantoscapularis posterior is found in sciurids (Alzeais, 1900; Bryant, 1945), *Blarina* (Reed, 1951; Gaughran, 1954), primates (Howell and Straus, 1933) and the mink (Klingener, personal commun.). The presence of the muscle probably is a primitive mammalian condition.

Both the origin and insertion of the omo-cervicalis are variable among the hystricomorphs dissected. I do not agree with Hill's (1937) interpretation of the primitive rodent origin or insertion of this muscle. I believe that the primitive origin is on the ventral arch of the atlas, and the insertion is on the metacromion process. Within the hystricomorphs several functional groups can be distinguished: (1) *Proechimys* and *Erethizon* in which the insertion of the muscle is broad and includes the deltidial crest; (2) *Dasyprocta* and *Thryonomys* in which the origin is the basioccipital and the insertion includes a small slip onto the clavicle (the condition of the muscle in *Cavia* is similar to the conditions in *Dasyprocta* and *Thryonomys*, but the small clavicular slip is missing); (3) the insertion of the muscle in *Ctenomys* is mainly onto the clavicle and the acromion process, much as it is in geomyoids (Howell, 1932; Hill, 1937); (4) in the remaining genera the primitive origin and insertion exist. Therefore, the muscle is variable and complex. The groups probably reflect functional grades differing in response to unknown selective pressures rather than cladistic units.

The primitive origin of the latissimus dorsi is partially on the more posterior ribs. This condition is found in squirrels, *Aplodontia* (Hill, 1937), and *Erethizon*. There is a latissimus Achselbogen associated with the latissimus dorsi in all hystricomorph genera dissected except *Erethizon*, *Chinchilla*, *Dasyprocta*, *Thryonomys*, and *Petromus*. In some of these genera, however, there are indications of a vestigial Achselbogen. My dissections indicate that a good Achselbogen is also
found in squirrels and Aplodontia. I conclude, therefore, that the presence of an Achselbogen is a primitive rodent characteristic, and that it is formed of elements from both the latissimus dorsi and the cutaneus maximus.

The deltoids of hystricomorphs are separable into clavicular, acromial, and spinal parts (see fig. 12). In geomyoids, Aplodontia, primates, and muroids (Howell, 1932; Hill, 1937; Rinker, 1954) the three parts are fused into one continuous sheet. In squirrels and dipodoids the muscle group is divided into an acromioclavicular and a spinal part (Hill, 1937; Bryant, 1945; Klingeneder, 1964). The separation of the clavicular and acromial parts is most pronounced in Cavia and Dasyprocta. In these two genera the insertion of the clavodeltoid muscle extends onto the distal end of the humerus (see fig. 9). The resulting configuration resembles the carnivore situation in which the muscle is called the clavobrachialis. This modification may be associated with speed in running (Howell, 1944). It is a moot question whether the primitive condition of this muscle group is reflected in the continuous muscles of Aplodontia or the somewhat separable ones of squirrels. Howell (1937) stated that the muscle primitively originated from the clavicle only, but that it is found in three separate parts in Chiroptera, Dermoptera, Perissodactyla and in most Insectivora, Carnivora, and Rodentia. Reed (1951) found three separate parts in most of his soricoid insectivores.

It appears, therefore, that the primitive rodent condition was a separation of the three deltoid parts. The fusion of the cleidomastoid and cleido-occipitalis with the clavodeltoid, which Howell (1944) spoke of as a modification for speed in running, was referred to by Howell (1937) as the cephalohumeral muscle. He reported this fused muscle in some marsupials, edentates, carnivores, pinnipeds, proboscidians, hyracoids, sirenians, perissodactyls, and artiodactyls. The condition of the muscle in Cavia and Dasyprocta cannot be viewed, therefore, as an indicator of relationships among particular hystricomorphs.

The interpretation of the triceps complex has led to some confusion. Problems are especially common in the literature concerning the triceps medialis and the anconeus. These two muscles are fused with each other, and both are innervated by the radial nerve. The medial aspect of the triceps medialis in nine genera of hystricomorphs has a superficial layer which has been confused by some workers with the epitrochleoanconeus. The epitrochleoanconeus, however, is innervated by the ulnar nerve. The insertion of the triceps medialis is partially onto the coracobrachialis in Myocastor. This extra point of insertion results in a condition resembling the long head of the coracobrachialis, which Myocastor does not have. The long head of the triceps inserts in part on the aponeurotic envelope in all genera except Erethizon. The origin of the muscle in porcupines is more solidly from the scapula, as in the chimpanzee. This condition may be associated with climbing (Ziegler, 1964). The aponeurosis also serves as a point of origin for the teres minor. The aponeurotic envelope has not been widely reported in mammals, and should be looked for in other groups. The triceps muscles, therefore, do not indicate any possible relationships within the hystricomorphs.

Parsons (1894a) used the absence of a brachioradialis in his Hystricomorpha as a point of separation between them and his Sciuromorpha. All squirrels have a brachioradialis (Hill, 1937; Bryant, 1945). Contrary to Hill (1937), I have seen a reduced brachioradialis in two specimens of Aplodontia. The muscle is reduced to the point of being vestigial, however, and was missing on one side of one animal. The presence of a brachioradialis, therefore, is probably the primitive rodent condition, and all hystricomorphs except Erethizon have departed from this condition. In some specimens of Erethizon the muscle is vestigial (Parsons, 1894a; personal observ.). The brachioradialis is missing in hystricids (Parsons, 1894a; Lesbre, 1907), bathyergids (Parsons, 1896), and pedetids (Parsons, 1898). Other groups have also lost the brachioradialis, such as all myomorphs, Castor, geomyids, and muroids (Parsons, 1896; Hill, 1937; Rinker, 1954).

The extensor pollicis brevis is missing in hystricomorphs, and the abductor pollicis longus is divided into two parts. This pattern is found in most rodents (Howell and Straus, 1933; Hill, 1937). One part of the abductor pollicis longus inserts on the base of the enlarged falciform bone. This enlarged bone is the large palmar ossicle that is characteristic of so many hystricomorphs. The extensor indicis is well developed and in some genera of both the New and Old worlds there is a solid side branch inserting on
the pollex. The side branch may represent the M. extensor pollicis brevis, which is probably fused with this muscle (Hill, 1937). The condition is unusual and not found in squirrels or Aplodontia (Hill, 1937). The presence of this side branch in Petromus, as well as in most New World hystricomorphs, is an indication of a probable relationship.

The tendons of the extensor muscles of the forearm pass through tendinous compartments in the wrist. In squirrels and Aplodontia the third compartment (for extensor digitorum and extensor indicis) and the fourth compartment (for extensor digitii minimi) are fused (Bryant, 1943; personal observ.). In Proechimys, Echimys, Isothrix, Mesomys, Erethizon, Cavia, and Thryonomys the third compartment is closely associated with the fourth compartment, but not fused with it. This condition resembles the pattern in dipodoids (Klingener, 1964). The third and fourth compartments lie close to each other in Myocastor, Octodon, and Ctenomys; whereas in Chinchilla, Dasyprocta, and Petromus they are separate. The configurations of the wrist compartments, therefore, are not consistent within the group. They do indicate, however, that the conditions in both Thryonomys and Petromus are more similar to other New World and Old World hystricomorphs than either is to the other. The configuration in Thryonomys probably resembles the primitive rodent pattern.

The subclavius muscle is similar to the general rodent condition in all genera except Dasyprocta and Thryonomys. The fibers of the subclavius are continuous with the fibers of the scapulocavicularis in some specimens of Proechimys, Echimys, and Ctenomys, and in all specimens of Myocastor, Cavia, Chinchilla, Dasyprocta, Thryonomys, and Petromus.

In Dasyprocta and Thryonomys the subclavius is composed of two heads, one head originating from the first rib and the other from the manubrium. The manubrial head becomes associated with part of the pectoralis minor in some specimens of both Dasyprocta and Thryonomys. The manubrial head probably represents the sternoclavicular division of the sternoscapular muscle. The presence of a subclavius muscle with two heads has not been widely reported in the literature on rodent myology. The immediate interpretation, therefore, is that the condition is derived from a primitive rodent configuration of one head, such as in squirrels (Bryant, 1945) and Aplodontia (Lewis, 1949). Another possibility is that the configuration of the subclavius in Dasyprocta and Thryonomys could reflect the primitive condition of this muscle in their nearest common ancestor, because there is also a moderately developed two-headed subclavius in Erethizon and hystricids (Parsons, 1894a, 1894b). The latter explanation is more probable. An indication of the possible primitiveness of this condition is reflected in the costoscapularis muscle of some insectivores (Reed, 1951), and part of the anterior deep pectoral muscle of the horse (Sisson and Grossman, 1953), the tapir (Stjernman, 1932), and some marsupials (Howell, 1937).

The scapulocavicularis muscle is also part of the sternoscapularis muscle (Parsons, 1894a; Howell, 1937). It is found in all hystricomorphs, hystricids, and bathyergids, but not in any other group of rodents. The presence of this muscle in the Hystricomorpha is noted by Parsons (1894a), who considered it to be an indication that these rodents form a common systematic unit. The muscle certainly represents a unique condition that differs from even the most primitive of living non-hystricomorph rodents. I do not agree with Wood and Patterson (1959) that the conditions of this muscle indicate a separation of these rodents into New World and Old World groups.

The configuration of the cutaneus maximus muscle is another characteristic that strongly indicates a common grouping of hystricomorphs. Parsons (1894a, p. 275) noted that the panniculus carnosus (= cutaneus maximus) inserts on the “outer side of the arm and the pectoral ridge of the humerus.” He also noted the presence of fibers on the ventral surface of the body along the margin of the leg and in the inguinal region. The illustration of Hystrix by Parsons is apparently incorrectly drawn, but there is an excellent figure in Lesbre (1907) illustrating the correct configuration of the cutaneus maximus for Hystrix. Parsons made the above observations, but he does not in any way note their importance.

The unusual pattern of the cutaneus maximus is described by Langworthy (1925) for Cavia and Erethizon, Meinhertz (1932) for Cavia, and Enders (1934) for Proechimys. All of these workers elaborated on the basic description by Parsons (1894a) and noted the presence of four basic parts to the cutaneus maximus. Landry (1957a) did not refer to any of the important earlier
observations on this muscle, but correctly noted for the first time that the insertion of the dorsal part of the panniculus (= cutaneus maximus) on the lateral side of the arm is probably a hysticomorph character. The observed pattern of the cutaneus maximus in these rodents is probably characteristic of the group. This characteristic pattern would include: (1) the insertion of the pars dorsalis on the lateral side of the arm; (2) the presence of a pars femoralis; (3) the presence of a pars pudenda. Meinertz showed that a few fibers of the pars dorsalis insert on the lateral side of the arm in Dicrostonyx (1941a) and Arvicola (1941b). These fibers, however, are only a minute part of the muscle, and none of the other characteristics mentioned above is found in microtines. The cutaneus maximus in geomyids, Aplodontia, sciurids, dipodoids, and muroids (Hill, 1937; Bryant, 1945; Lewis, 1949; Rinker, 1954; Klingener, 1964) is not divided into the parts mentioned above. Parsons (1898, fig. 3) illustrated this muscle in Pedetes, and showed it having a pars femoralis. The description in the text is poor, however, and the figure is not complete enough to tell if there is a pars pudenda or if pars dorsalis inserts on the lateral side of the shoulder. The pars dorsalis inserts on the lateral side of the shoulder in bathyergids (Meinertz, 1951). Therefore, the cutaneus maximus does have an unusual configuration in hysticomorphs and hystricids and bathyergids. A knowledge of the conditions of the muscle in pedetids, anomalurids, and ctenodactyldids is necessary before the phylogenetic significance of the different parts of the cutaneus maximus can be known with certainty.

The coracobrachialis muscle varies little in most genera dissected. The position of the musculocutaneous and median nerves in relation to the muscle indicates that only the middle head of the muscle is present in most genera (Wood, 1867; Parsons, 1894a). In some specimens of Erethizon there is a part of the muscle lying on top of the median nerve. If Wood's (1867) criteria is used, this part is the long head of the muscle. The same two parts of this muscle, separated by the median nerve, are reported in Sphingurus (= Coendou) (Parsons, 1894a). I therefore believe that in erethizontids the muscle is usually composed of both the middle and long heads. In Dasyprocta and Thryonomys the musculocutaneous nerve lies distal to fibers of this muscle that insert on the neck of the humerus. This insertion is proximal to the tendon of the fused latissimus dorsi—teres major. Wood (1867) indicated that muscle fibers in this position represent the short head of the coracobrachialis. In the configuration of this muscle Dasyprocta and Thryonomys are more similar to each other than to other New World or Old World hystricomorphs. The short head is present in sciurids, Aplodontia, geomyids, heteromyids, and a few muroids (Parsons, 1896; Howell, 1932; Hill, 1937; Bryant, 1945; Rinker, 1954). The presence of the short head in Dasyprocta, Cuniculus, and Thryonomys is probably the retention of a primitive condition.

The long and medial heads of the brachialis are present in all genera dissected. I do not agree with Wood and Patterson (1959) that there is a tendency for New World hystricomorphs to lose the medial head. The medial part is poorly developed in Cavia, however, and easily missed. Both parts of the brachialis are also present in sciurids and Aplodontia (Hill, 1937; Bryant, 1945; Lewis, 1949). In all hysticomorphs except Cavia and Erethizon the long head of the brachialis originates from the medial side of the neck of the humerus below the lesser tuberosity, as well as from the usual origin on the posterior and lateral aspects of the humerus. The long head of the brachialis, therefore, wraps almost completely around the humerus. The origin on the medial aspect of the humerus is not present in any squirrel or Aplodontia dissected, nor is it in any other rodent of which I am aware. The medial insertion is certainly a derived condition in these rodents, and may indicate a common phylogenetic relationship. It is important to know what the condition of the brachialis is in hystricids, bathyergids, anomalurids, pedetids, and ctenodactyldids, but this information is not currently available.

The condition of the palmaris longus is variable in most mammals; even in those in which it seems to be functionally important (Parsons, 1894a; Zeigler, 1964). Wood and Patterson (1959) believed that in New World hystricomorphs the origin of the muscle is from the olecranon, or else the muscle is entirely missing. In Old World hystricomorphs, erethizontids, and caviids they believed the origin to be on the medial epicondyle. Wood and Patterson, therefore, are using the origin of the muscle as an indication that New World and Old World hystricomorphs are unrelated. I confirm that
the origin of the muscle is from the medial epicondyle in *Erethizon*, *Thryonomys*, and *Petromus*. I have also found the origin from the medial epicondyle in *Chinchilla* and *Dasyprocta*. In *Petromus*, *Echimys*, *Lothrix*, *Masomys*, *Octodon*, *Ctenomys*, and *Cavia* the muscle originates from both the olecranon and the medial epicondyle. The condition of the muscle, therefore, does not indicate the separation of these rodents into New World and Old World groups. If anything, the muscle indicates a relationship of the Old World forms with *Erethizon*, *Chinchilla*, and *Dasyprocta*. In most myological characteristics the last three genera are quite primitive.

Wood and Patterson (1959) believed that the insertion of the pronator teres has shifted from the distal to the proximal area of the radius in Caviomorphs. In *Aplodontia* and squirrels the insertion is on the distal part of the radius, and this is probably the primitive insertion. The insertion of the muscle has shifted proximally in all the genera dissected except *Erethizon* and *Ctenomys*. There may be a functional reason for the distal insertion of the muscle in these two genera. Both *Erethizon* and *Ctenomys* have modified other limb muscles for increased power. I conclude, therefore, that the insertion of the pronator teres does not indicate a separation of these rodents into groups of the New and Old worlds.

Parsons (1894a) concluded that the pronator quadratus always attaches to the radius and ulna for more than the distal one-third of their length. I find that the muscle is almost missing in *Cavia* and *Ctenomys*. In all other genera the muscle does insert on the radius and ulna for more than one-third of their length. The extent of the muscle, however, is extremely variable in *Petromus*. In *Dasyprocta* and *Thryonomys* the muscle is associated with the radius and ulna for the entire length of the radius. The muscle, therefore, is variable and not consistently associated with more than one-third of the length of the limb bones. The condition of the muscle in *Dasyprocta* and *Thryonomys* sets these two genera apart from the other New World and Old World forms.

The ulnar nerve in all hystricomorphs except *Thryonomys* innervates *M. epitrochleoanconeus*, *M. flexor carpi ulnaris*, ulnar head of *M. flexor digitorum profundus*, *M. flexor digitorum superficialis*, and *M. palmaris longus*. In *Thryonomys* the palmaris longus is innervated by a branch of the median nerve. The innervation of the last two muscles by the ulnar nerve is unusual, if the information in the literature is accepted. Such an innervation has never been reported in a rodent before. I have examined the muscles in *Sciurus*, *Eutamias*, and *Aplodontia*, however, and the ulnar nerve innervates all five of the above muscles in all of these genera. Which muscles the ulnar nerve innervates in different groups of rodents should be investigated further. The conditions and relationships of the forearm flexor muscles are much more complex than most investigators realize.

HISTORICAL SURVEY OF HYSTRICOMORPH CLASSIFICATION

A review of the ways in which hystricomorph rodents have been classified follows. It is presented to summarize past classifications, to point out the extent of the morphological similarities shared by hystricomorphs, and to demonstrate the long-standing tradition of grouping them together. The complexity of the hystricomorph rodent problem is reflected in the different ways in which these rodents have been classified.

The validity and history of the generic names of these rodents are treated in Tate (1935), Allen (1939), Ellerman (1940), Roberts (1951), Ellerman, Morrison-Scott, and Hayman (1953), Cabrera (1961), and Ellerman and Morrison-Scott (1966). The important nomenclatorial problem of the generic name of the African rock rat is considered by Wood (1955, p. 184). I have chosen to follow Ellerman and Morrison-Scott (1966) and Wood (1955) in considering the most valid name for this rodent to be *Petromus*.

Both Simpson (1945) and Wood (1955) credited de Blainville with the first division of the Rodentia into groups resembling the classical suborders. Waterhouse (1839) divided the order into two main sections (excluding the lagomorphs, which he considered to be the third section of the Rodentia). One of these sections is the Hystricomorpha. In this group the angular
process "springs from the outer side of the alveolar portion" of the mandible (p. 92; the italics are his), and in most genera "the antorbital foramen is very large" (p. 91). Waterhouse, therefore, recognized two of the most important features of these rodents, and was the first investigator to propose classifying the Hystricomorpha (sensu stricto) with the bathyergids. His description of the laterally inflected angular process precedes Tullberg's (1899) work by 60 years. Waterhouse (1848) classified these rodents in the family Hystricidae. This family includes the Hystricomorpha (sensu stricto), but not the bathyergids.

The classification of rodents into the classical suborders Sciuromorpha, Myomorpha, and Hystricomorpha was first concretely proposed by Brandt (1855). His "Subordo Hystricomorphi" (p. 312) includes those rodents in which a part of the masseter medialis muscle passes through the infraorbital foramen from an origin on the rostrum. Brandt did not place Pedetes, Anomalurus, Bathyergus, or dipodids in this suborder. Many current workers no longer believe in the validity of suborders which are based mainly on the structure of the masseter muscle (Wood, 1955). It should be pointed out, however, that the classifications of both Waterhouse (1839, 1848) and Brandt (1855) are sophisticated enough so that the definitions of their respective hystricomorph groups exclude the pedetids, anomalurids, and dipodids (Landry, 1957a).

Alston (1876) presented the same basic classification of the hystricomorph genera as did Brandt. Thomas (1896) based a classification mainly on the degree of fusion of the tibia and fibula. He followed Brandt in leaving the anomalurids near the squirrels and in placing the bathyergids in the Myomorpha. He classified the pedetids, however, as a family within the Hystricomorpha. In the family Octodontidae Thomas placed Ctenodactylus and Petromys (= Petromus) as members of the subfamily Ctenodactylinae. He placed Thryonomys in the same family, but in a separate subfamily, as several New World genera. The hystricids and the erethizontids are treated by Thomas as members of different families within the Hystricomorpha.

Parsons (1894a, 1896) investigated the myology of 34 different rodents, and presented his ideas on their subordinal classification. Within the suborder Hystricomorpha he placed Aulacodus (= Thryonomys) in the family Octodontidae, and both the New World and Old World porcupines in the family Hystricidae. He did not mention anomalurids, ctenodactylids, or pedetids, but treated the bathyergids as members of the Myomorpha. In a later work on the anatomy of Pedetes, Parsons (1898, p. 890) concluded that, "a study of the muscles showed that Pedetes was allied to the Dipodidae, but had more hystricomorphine tendencies than those animals." A similar paper by Parsons (1899) on the myology of Anomalurus indicated that there are almost no hystricomorph tendencies in anomalurids.

Tullberg (1899) based his classification partially on the position of the angular process on the mandible. Both Waterhouse (1839, 1848) and Alston (1876) previously described this type of lower jaw within their hystricomorphs. In the hystricognath jaw the angular process originates on the lateral side of the incisor alveolar sheath (see fig. 1B). This type of jaw is not found in anomalurids, ctenodactylids, or pedetids. Tullberg, therefore, did not place any of these rodents in his tribe Hystricognathi. The bathyergids are hystricognathous (as Waterhouse noted 60 years earlier). They also share other characteristics with most of the Hystricomorpha (sensu stricto) such as: (1) fused incus and malleus; (2) a sacculus urethralis associated with the penis; (3) an open pterygoid fossa (Tullberg). The genera Aulacodus (= Thryonomys) and Petromys (= Petromus) are placed by Tullberg in different monotypic families within the Hystricognathi. He also separated the New World and Old World porcupines into different families. This classification is similar in form to that of Waterhouse (1839), and still retains the basic breakdown of the Rodentia into three divisions. The groupings within the Hystricognathi are much more reasonable, however, than earlier classifications. Ellerman (1940, p. 10) considered this "perhaps the best classification of the order that has been done."

Miller and Gidley (1918) departed radically from the three classical suborders by dividing the order into five superfamilies. The Hystricomorpha (sensu stricto) are classified in the superfamily Hystricoidae. Miller and Gidley classified the bathyergids in a separate superfamily that is apparently closely related to the superfamily Hystricoidae. These authors note that
the hystricognath angle in bathyergids is “distorted outward to allow passage of a specialized and enlarged distal anterior limb of the masseter lateralis superficialis” (pp. 443-444). They also noted that the zygomaseteric structure in the Hystricoidea is basically the same as in the Bathyergoidea.

Winge (1941) organized the order into nine families. This work (1941) is the English translation of Winge’s earlier publication (1924), and according to Simpson (1945), presented basically the same classification as Winge’s 1887 publication. The family Hystricidae of Winge is similar in composition to the Hystricomorpha of Thomas (1896). Winge classified the genera Aulacodus (=Thryonomys), Myopotamus (= Myocastor), Cynomys, and Plagiodon (= Plagiodontia) together in the same subfamily (= family of most other workers), and he placed Ctenodactylus and Petromys (= Petromus) in the same subfamily.

In his classification, Weber (1928) placed the bathyergids in the tribus Bathyergoidea. This tribe is separate from the tribus Hystricoidea but closely associated with it. Within his tribus Hystricoidea, Weber placed Thryonomys in a separate and monotypic family and Petromys (= Petromus) in the same family as Ctenodactylus. Porcupines of the New and Old worlds are classified in different families. The anomalurids and pedetids are treated separately from the Hystricoidea as members of the tribus Anomaluroidea.

The classification of these rodents by Ellerman (1940) is similar to the classification by Tullberg (1899). Ellerman placed the bathyergids near the Hystricomorpha (sensu stricto) in a group he called the Hystricognathi. The common characteristic of this group is the infected angle of the mandible. Within the Hystricomorpha series Thryonomys and Petromus are treated as members of monotypic subfamilies of the family Echimyidae. This family is equivalent to the superfamilys Octodontoidae of most later workers.

Ellerman also treated the New World and Old World porcupines as members of separate families. The anomalurids, ctenodactyliids, and pedetids were all treated as members of the Myomorph series.

Ellerman became doubtful of the value of suborders in his later works. He stated (1961, although the work was completed in 1946, p. 5) that “it seems to me that it is not possible to divide the order into natural suborders.” His work with Morrison-Scott (1966, p. 457) contains the statement that they were not using suborders because “they are held to be indefinable.” I am making these points to prove that even though Ellerman had become doubtful of the value of suborders, he still believed in uniting hystricomorph genera of the New and Old worlds into a single unit. Ellerman (1949) commented on Simpson’s (1945) classification, and made the point that he believed that the Hystricomorpha (sensu stricto) constitute a natural unit and have some affinity with the bathyergids. Ellerman (Ellerman, Morrison-Scott, and Hayman, 1953) classified both Thryonomys and Petromus in the family Octodontidae. He stated, however, (pp. 225–226) that “Thryonomys is a distinct genus and perhaps merits family rank, but the same cannot be said for Petromus, which is essentially morphologically an octodont.”

Simpson (1945) was critical of Ellerman’s (1940) classification, calling it more a key than a classification. He noted that there were increasing objections to the use of the classical suborders, but (p. 198) that “Brandt’s suborders have not yet outlived their usefulness.” Within the suborder Hystricomorpha, Simpson classified Thryonomys and Petromus as members of separate monotypic families within the Octodontidae. The porcupines of the New and Old worlds were placed in separate families. The bathyergids were classified in a separate group under the name “Hystricomorpha incertae sedis.” The discussion in Simpson is excellent, but the classification, as Simpson himself realized, represents a traditional approach.

Roberts (1951) presented a classification of mammals of the South Africa area. He treated the genera Hystrix, Thryonomys, Petromus, and Pedetes as members of the suborder Hystricomorpha. The bathyergids are treated as members of a separate suborder, the Bathyergomorpha. This work is more a key than a classification, however, and no mention is made of any hystricomorph character except the enlarged infraorbital foramen. It is not surprising, therefore, that Pedetes is included in the suborder Hystricomorpha, or that the bathyergids are not.

Schaub (1953), using information presented in Stehlin and Schaub (1951), presented an extensive classification of the Hystricomorpha. He considered the molar teeth of these rodents
to be derived from a theridomyid rodent prototype. Schaub (p. 391) believed that "the basic plan of *Theridomys* with its five anticlines, of which the third is the mesoloph, exists also in South America, as in Europe and Africa." Schaub named this suborder the Pentalophodonta, and separated the New World and Old World genera into separate infraorders. This separation indicated his belief that the New World and Old World genera developed independently and in complete isolation. Within this suborder the hystricids, thryonomyids, petromurids, and bathyergids are classified as probable members of the infraorder Pentalophomomorpha. All the New World genera are classified in the infraorder Notrotrogomorpha.

Grasse and Dekeyser (1955) expanded upon this classification. The genera within the suborder Pentalophodonta are classified exactly as they are by Schaub. The anomalurids and ctenodactylyids are classified in the suborder non-Pentalophodonta. The pedetids are classified as the non-Pentalophodonta *incertae sedis*. The suborder non-Pentalophodonta is basically the same as the suborder Sciuromorpha (without castorids, and with glirids, seleviniids, and ctenodactylyids). The suborder Myodonta corresponds to the suborder Myomorpha. The suborder Pentalophodonta represents the New World and Old World Hystricomorpha (*sensu stricto*), plus the bathyergids, thryonomyids, pseudosciurids, castorids, spalacids, and rhizomyids. Schaub (1958) followed this classification.

Wood (1955) presented a classification that separated the New World and Old World groups of hystricomorphs in different suborders. This classification is a logical development from his 1950 paper in which he stated (p. 97) that "the South American forms can be shown to have definite affinities with the North American Eocene Paramyidae, suggesting an orthodox geographical origin for these rodents. The Old World forms cannot have been derived from the same North American forms, but presumably are descended from Old World representatives of the basal rodent stock." He classified the New World genera in the suborder Caviomorpha. The hystricids and *Thryonomys* and *Petromus* are classified in the suborder Hystricomorpha; the bathyergids in the suborder Bathyergomorpha; the anomalurids in the newly created suborder Theridomyomorpha; the pedetids in the suborder Sciuromorpha or Theridomyomorpha *incertae sedis*; and the ctenodactylyids in the suborder Sciuromorpha.

In 1959 and 1965 Wood further revised his classification. The revision is based partially on a review of the rodents of the Deseadan Oligocene of South America (Wood and Patterson, 1959). The New World genera are still classified in the suborder Caviomorpha, but the families are rearranged among the superfamilies. The Old World genera are no longer classified in any suborder. It is clear that Wood does not consider the New World and Old World genera to be related. Wood (1968) presented evidence to show that *Thryonomys* and *Petromus* have evolved from phiomyid rodents. He stated that pedetids, bathyergids, anomalurids, and ctenodactylyids invaded Africa in the Miocene, and therefore are not related to the Thryonomyoidea. The Hystricidae "probably developed in southern Asia independently of the African thryonomyoids" (Wood, 1968, p. 83).

Wood earlier believed (Wood and Patterson, 1959, p. 419) that "the Hystricomorpha and Caviomorpha have derived those characters, which they hold in common, independently and subsequent to their geographic separation. This is extreme parallelism." Wood now believes that the similarities of hystricids and the Thryonomyoidea are also due to extreme parallelism.

Landry (1957a) presented a recent evaluation and classification of hystricomorph rodents. He gave a list of morphological similarities between New World and Old World genera based on a review of the literature. Some of these similarities are: (1) a hystricognath mandible; (2) a pterygoid fossa that opens into the orbit or braincase; (3) a fused malleus and incus; (4) a sacculus urethralis in the penis; (5) a tibia and fibula that are fused at the proximal end; (6) a reduction in the size of the alisphenoid bone; (7) an unusual multiserial arrangement of the incisor enamel; (8) a scapuloclavicularis muscle. He concluded that on the basis of these similarities the New World and Old World hystricomorphs must be closely related. Landry believed that rodents originated in the Cretaceous, that the hystricomorphs split off early, and that the primary dispersal of the hystricomorphs occurred in the Paleocene, before the widespread dispersal of the sciurognaths. The known fossil record flatly contradicts Landry's hypothesis (Wood and Patterson, 1959).
In Landry's classification the suborder Hystricomorpha is divided into four New World and five Old World superfamilies. The classification of the families within the New World group represents a major departure from most other recent classifications. The Old World genera, *Thryonomys* and *Petromys* (= *Petromus*), plus the hystricids are all classified in the Hystricomorpha. Landry believed (1957a, p. 65) that "there seems to be no basis for uniting the Petromyidae, Thryonomyidae, and Hystricidae in any category below the subordinal level. They represent widely separate stocks, and should therefore be placed in three separate superfamilies." The bathyergids are also classified as a superfamily in the Hystricomorpha. Landry believed (p. 75) "that some primitive ratlike hystricomorph similar in general appearance to *Petromus* gave rise to the Bathyergidae." Landry classified the ctenodactyliids as another superfamily within the Hystricomorpha. He admitted that these animals lack several of the most important hystricomorph characters, such as the hystricognath jaw and the open pterygoid fossa. He believed, however, that on the balance the over-all similarities with the Hystricomorpha indicated a relationship.

Ansell (1960) followed Wood (1955) and elevated *Thryonomys* to familial rank. He listed the rodent families in the same sequence as they are listed in Ellerman, Morrison-Scott, and Hayman (1953). He chose to omit categories above the family level, however, "until more is known of the history of the order" (p. 76).

Romer (1966, 1968) followed the ideas of Wood concerning the separation of New World and Old World genera at the subordinal level. He stated (1968, p. 225) that it "seems plausible to believe that the two sets of 'hystricomorph' members have developed in parallel fashion and that the supposed suborder is not a natural group." Romer went on to note the remarkable similarity of these supposedly unrelated rodents. The Old World forms of the Hystricomorpha (sensu stricto) are much less similar to one another than *Thryonomys* and *Petromus* are to the New World forms. Even though Romer rejected the subordinal unity of *Thryonomys* and *Petromus* with the New World genera, he hoped that the Old World forms of the Hystricomorpha (sensu lato) "will be found to be related, with the eventual reestablishment of an Old World true hystricomorph group" (1968, p. 227).

The search for some valid way to classify the Rodentia has reached an extreme in Thaler (1966). He separated the Rodentia into 16 different suborders, five of which are new and have no name. He treated the New World hystricomorphs as the suborder Caviomorpha, the hystricids as the suborder Hystricomorpha, and the genera *Thryonomys* and *Petromus* apparently as phiomyids in a suborder with no name. Also treated separately in suborders without names are the anomalurids, pedetids, bathyergids, and ctenodactyliids.

Lavocat (1969) returned to the idea that the suborder Hystricomorpha (sensu stricto), in the sense of Brandt, is a valid natural unit and should be retained. He is currently preparing a classification of these rodents using new information that he has gathered from the Miocene of Africa. This classification is in press (Lavocat, In press).

It can be seen that the rodents within the Hystricomorpha (sensu stricto) have been classified in a number of different ways. The evidence that is usually used to unite these genera is morphological, and comes from a number of different sources. The male reproductive tract has been investigated by Cole (1897), Tullberg (1899), Pocock (1922), Dathe (1937), Angulo and Alvarez (1948), Mirand and Shadle (1953), Layne (1960), Hooper (1961), Dellmann (1962), and Dubost (1968). This information indicates that the sacculus urethralis that is found in most hystricomorphs is unique and characteristic of the group. Hooper (1961, p. 15) noted how the penes in all New World hystricomorphs "accord with a single fundamental design which in important respects is unlike the structural plans seen in other major groups of rodents, for example the Muroidea and Sciuroidea (Simpson, 1945)." The morphology of the glans penis in Old World groups (including *Pedetes* and ctenodactyliids) is in need of further study. Particular attention should be paid to the presence or absence of a retractile apparatus associated with the sacculus urethralis. This information must be known before the true extent of the similarities of the reproductive tract will be known.

The ear ossicles have been investigated and the incus and malleus found to be fused in all the Hystricomorpha (sensu lato) except *Pedetes*
and anomalurids (Landry, 1957a). The incus and malleus in Pedetes are so closely associated, however, that Doran (1878) believed them to be fused. Wood and Patterson (1959) found them to be separable but complexly interlocked. The ear ossicles of some New World genera are also separable (Cockerell, Miller, and Printz, 1914). The morphology of the incus and malleus in some hysticomorph rodents was also reported by Tullberg (1899) and Fields (1957).

The unusual and characteristic laminations in the enamel layers of the incisors of hysticomorph rodents was first reported by Tomes (1850). Korvenkontio (1934) also reported this unusual multilayered pattern of enamel in hysticomorphs, and called it “multiserial-lamellar.” He reported finding this enamel pattern in New World hysticomorphs [Clenomys, Myocastor, Erethizon, Coendou, Lagostomus, Dasyprocta, Coelogenys (= Conicus), Cavia, Kerodon, and Dolichotis], hystricids (Atherura), bathyergids (Georychus, Cryptomys), ctenodactylids (Ctenodactylus), and pedetids (Pedetes). The anomalurids (Anomalurus and Idiurus) are not multiserial, however, but are uniserial. Korvenkontio showed that sciuromorphs and myomorphs have a uniserial pattern of enamel. He also reported that primitive rodents have an intermediate type of enamel pattern, which he called “pauciserial-lamellae.” Wood and Patterson (1959, p. 292) believed that multiserial enamel “could have been evolved independently by the ancestors of both the Hystricomorpha (sensu stricto) and the Caviomorpha.” Wahlert (1968) concurred that the pauciserial enamel condition could give rise to both the uniserial and multiserial conditions.

RELATIONSHIPS OF THE HYSTRICOMORPHA

I have described the configurations of 80 different muscles. Some of these muscles are multipartite or complex, and as a result 105 different myological characters are reported in the present investigation. All but five of these characters provide enough information to be of some taxonomic value.

Erethizon stands clearly apart from the other New World genera, and from the Old World forms. There are 17 unusual myological conditions in Erethizon, 12 of which are not found in any other “hysticomorph” genus dissected. Of these 17 conditions, 10 are unmistakably primitive and are also found in Aplodontia and squirrels. The muscles of Erethizon are more similar to those in Thryonomys and Petromus than to those in either echimyids or octodontids. This information suggests that either Wood (1955) and Wood and Patterson (1959) were correct in considering the erethizontids to have separated early from the other New World forms, or that the erethizontids represent a separate invasion of South America. The findings of Vanzolini and Guimaraes (1955) using lice, and of Moody and Doniger (1956) using serology also indicate that the erethizontids are isolated. I feel that Landry (1957a) was not correct in classifying the echimyids with Erethizon in the superfamilie Erithizontoidea.

My findings do not clearly indicate whether Myocastor is more similar to the echimyids, as Wood and Patterson (1959) and Patterson and Pascual (1968) believed, or to the octodontids as Landry (1957a) believed. The myology of Myocastor is not notably similar to that of Dasyprocta, however, indicating that Landry’s classification of the latter genus in a family near his family Myocastoridae in the superfamily Octodontoidea is questionable. The muscles of Myocastor are much more similar to those of Petromus than to Thryonomys. Both Thomas (1896) and Winge (1941) classified Thryonomys and Myocastor in the same family. The musculature, however, does not support this classification. Myocastor is certainly in the superfamily Octodontoidea, but the musculature indicates that this animal might best be classified in a family separate from both the echimyids and octodontids. I question, therefore, the conclusion by Wood and Patterson (1959) and Patterson and Pascual (1968) that Myocastor is best classified as a subfamily in the family Echimyidae.

The family Echimyidae was divided into five subfamilies by Wood and Patterson (1959) and Patterson and Pascual (1968). Ellerman (1940) did not subdivide the group, but noted that Echimys, Diplomys, and Isothrix are more similar to one another than to Proechimys. Landry
Thryonomys (1957a) did not divide the group at all. My findings indicate that Proechimys and Echimys are myologically more different from each other than would be expected if these genera were in the same subfamily. Because the musculature of both Isthrix and Mesomys was not complete, it is impossible to relate these two genera with either Proechimys or Echimys. The reported myological information supports the classification by Wood and Patterson, and Patterson and Pasqual, of Proechimys and Echimys in different subfamilies.

The muscles in Chinchilla are more similar to those of echimyids, octodontids, Cavia, and the two Old World genera than they are to Dasyprocta. I question, therefore, the placement by Wood and Patterson (1959) of the dasyproctids in the superfamily Chinchilloidea. The classification of Chinchilla in its own separate superfamily by Landry is more in agreement with the myological distinctness of these rodents. Dasyprocta is best classified as a family within the superfAMILY Cavioida.

Octodon and Ctenomys are similar morphologically, and probably are closely related. Wood (1955, 1965) considered these genera to be members of separate families in his superfamily Octodontoidae. Landry (1957a, p. 50) could “see little reason for putting Ctenomys and its relatives in a separate family or even superfamily.” There is more similarity between the musculature of Octodon and Ctenomys than between Proechimys and Echimys. The latter two genera are best classified as subfamilies within the same family. On the basis of the musculature, Octodon and Ctenomys are best classified in separate subfamilies of the family Octodontidae.

The Old World genera Thryonomys and Petromus in the past have often been classified in the same family or superfamily as Myocastor and the octodontids. The myological evidence does not support classifying either Thryonomys with Myocastor, or Petromus with the octodontids. These observations support Landry’s (1957b) opinions based on skull morphology, and the work of Wood.

The musculature of Thryonomys is as similar to Dasyprocta as it is to Petromus. In addition, Petromus is myologically more similar to Chinchilla and the echimyids than it is to Thryonomys. Therefore, the musculature does not indicate any clear separation between Thryonomys and Petromus on the one hand, and the New World forms on the other. Thryonomys and Petromus are myologically distinct from each other. Based on their myology, Thryonomys and Petromus should be classified in separate superfamilies.

The anatomy of the bathyergids was not investigated in the present study. The information in the literature, however, does indicate a strong morphological similarity between bathyergids and hystricomorphs. These similarities are especially pronounced in the jaw, hyoid, and front limb muscles. In addition, Meinertz (1951) indicated the presence of a configuration of the cutaneous maximus muscle in Heterocephalus that is similar to that found in hystricomorphs. Parsons (1896) indicated the presence of a scalenus anticus (= scalenus anterior) muscle in Georychus and Bathyergus. Mossman and Luckett (1968) showed that the fetal membrane morphology is the same in Bathyergus as it is in Erethizon, Cavia, Dasyprocta, Chinchilla, and Myocastor, and not similar to any known sciuriform or myomorph. Guthrie (1963, 1969) showed that the carotid artery pattern in Cryptomys and Bathyergus is unusual, but in many ways similar to the condition in the Hystricomorpha (sensu stricta). There are strong indications that bathyergids should be included in the same group as the New World and Old World hystricomorph genera dissected.

The complex and unique configurations of the masticatory and hyoid muscles of hystricomorphs are not found in any other group of rodents, even those which chew in a similar manner. In some of these non-hystricomorphs which chew propalinally a few of the important myological conditions of the jaw and hyoid musculature may be found. This indicates that these conditions might have originally developed in response to the selective pressures associated with propalinal chewing. The elaborate series of specializations shared by all hystricomorphs, however, is unique to the group. The hystricomorphous jaw and post-condyloid process of Platypitamys brachydont (Wood, 1949, fig. 2) indicate that the specialized jaw musculature of the New World forms goes back at least to the lower Oligocene (Deseadan) of South America. The early phiomyd genera Phiomys, Mastophiomys, and Gaudemus of the lower Oligocene (Fayum) of Africa are also hystricomorphs (Wood, 1968). The configurations of the cutaneous maximus and the scapuloclavicularis muscles are also unique in hystricomorph rodents. The probability of the many myological, osteological,
dental, histological, circulatory, and reproductive similarities shared by these New World and Old World genera all being a result of parallelism is surely small. It is more reasonable to imagine that both New World and Old World genera evolved from a common ancestor. This common ancestor was a paramyid that probably was already in the process of developing the conditions of the jaw, hyoid, and front-limb musculature spoken of above. This paramyid group would not necessarily have a hystricomorphous medial masseter. The hystricomorphous condition probably developed independently several times and may be part of a separate functional matrix.

Of all the possible explanations for the common origin of the suborder Hystricomorpha (sensu stricto), the most acceptable to me are either: (1) that these rodents evolved from a group of paramyid rodents living in the tropical and semitropical regions of North America and Asia; or (2) that hystricomorph rodents had a common origin in Africa, and that the South American forms are derived from African predecessors that rafted across to a then much narrower Atlantic Ocean.

The first possibility is more probable. The environmental conditions in tropical and semitropical regions of North America and Asia are poor for fossilization. This fact is partially responsible for the poor fossil record in these areas of the world. The paramyid ancestors of the hystricomorphs that might have been found in North America and Asia probably already had, or were well along toward developing, a horizontal masseter superficialis, an elongated internal pterygoid muscle, and a temporal muscle that was reduced in both size and relative proportion of the superficial (= orbital) part. These pre-hystricomorph paramyids could have been present in the middle Eocene. They would have spread into South America and Africa in the later Eocene. They might have closely resembled Platypitamyx and Cephalomyx of the early Oligocene of South America, and the early phiomyids of Africa. Erethizon might have split off from the remaining genera in the mid- to late Eocene, and remained morphologically isolated ever since. The hystricomorphous medial masseter is not an early or primary characteristic of hystricomorphs.

The conclusion that South American hystricomorphs might have evolved from African forms that rafted across the Atlantic remains a distinct possibility. The current literature on continental drift indicates that the continents were much closer to each other during the early Tertiary than they are at the present time. It is possible that floating islands might successfully cross 500 to 800 miles of ocean. Powers (1911) described such floating islands. Matthew’s (1939, p. 64) stated that he had “been unable to frame any hypothesis which will fit all of the facts of distribution in this group (hystricomorphs), except by assuming that the South American Hystricomorpha, which as Scott has shown are all clearly derived from a single stock, reached South America from Africa in the Oligocene by over-sea raft transportation.”

Matthew (1939) was reluctant to accept this explanation because of the great distances involved. However, the concept of continental drift makes Matthew’s statement more reasonable. Also, both Darlington (1957) and Burt (1958) noted that climate is a barrier to the dispersal of many mammals. Climate might have restricted the dispersal of hystricomorphs across the land areas of the north. If the rafting hypothesis is accepted, then the possibility exists that the erethizontids represent the descendants of a separate invasion via a separate raft.

In conclusion, I believe that the New World genera (= the suborder Caviomorpha of Wood, 1955) and Thryonomys and Petromus are myologically similar enough to be members of the same suborder. The literature on the myology of the hystricids is not complete enough for me confidently to classify these rodents. The most primitive living genus of hystricognathous rodents myologically is Erethizon, which is just as myologically isolated from the other New World genera as it is from the Old World genera. Thryonomys shares many myological characteristics with several New World genera, especially Dasypodidae. Most of these similarities are reflections of the myological conditions of primitive hystricomorphs.

An outline of the classification that the muscles of these genera indicate is presented in Abbreviated Classification (below). This classification is based totally on the configurations of the musculature of these genera, and does not take into account some of the excellent recent work on fossils and the male reproductive tract. By necessity and definition, therefore, the classification is typological. However the condi-
tions of the muscles in these genera must raise some serious questions concerning the validity of certain aspects of earlier classifications. I have chosen to use the subordinal name Hystricognatha to reflect the most important myological feature shared by these rodents, the hystricognathous jaw.

AN ABBREVIATED CLASSIFICATION BASED ON MYOLOGICAL CHARACTERISTICS

Order Rodentia
Suborder Hystricognatha
Superfamily Cavioidae
Family Caviidae

Family Dasyproctidae
Superfamily Chinchilloidea
Superfamily Octodontoidae
Family Echimyidae
 Subfamily Echimyinae
 Subfamily Heteropsomyinae
Family Octodontidae
 Subfamily Octodontinae
 Subfamily Ctenomyinae
Family Myocastoridae
Superfamily Petromuroidea
Superfamily Thryonomyoidae
Superfamily Bathyergoidae
Superfamily Erethizontoidea
Incertae sedis
Family Hystrixidae

BIBLIOGRAPHY


1892. On the brain and muscular anatomy of Aulacodus. Ibid., pp. 520–527.


BRANDT, JOHANNES FREDERICK

BROWN, KENNETH

BRUNDIN, BRYANT, MONROE W. WILLIAM
CABRERA, CHENG, THEODORE COCKERELL, VON PRINTZ M.

DARLINGTON, PHILIP J., JR.

DASTUGUE, J.

DATHE, H.

DAVIS, D. DWIGHT

DELLMANN, H. D.

DOBSON, GEORGE EDWARD


DORAN, ALBAN H. G.

DUBOST, G.

EDGEOworth, FRANCIS H.


ELLERMAN, JOHN REEVES


ELLERMAN, JOHN R. E. REEVES, AND T. C. S. MORRISON-SCOTT

ELLERMAN, JOHN R. E. REEVES, T. C. S. MORRISON-SCOTT, AND R. W. HAYMAN

ELTON, RICHARD C.

ENDERS, ROBERT K.

FIELDS, RICHARD W.

FORSTER, ANDRÉ


GAUGHAN, GEORGE R. L.

GRASSÉ, PIERRE P., AND P. L. DEREYSSER

GRAY, HENRY, AND WARREN H. LEWIS

GREENE, EUNICE CHASE

GUTHRIE, DANIEL A.


HEINZE, W.


HERSHKOVITZ, PHILIP

HIEMAE, KAREN

HIEMAE, KAREN, AND G. M. ARDRAN

HIEMAE, KAREN, AND FARISH JENKINS, JR.

HILL, JOHN ERIC

HODGE, A. TALBOT

HOFFSTETTER, ROBERT, AND RENÉ LAVOCAT

HOOPER, EMMET T.
HOWELL, ALFRED BRAZIER

HOWELL, ALFRED BRAZIER, AND WILLIAM L. STRAUS, JR.


KLINGENER, DAVID JOHN


KORVENKONTIO, V. A.

KRAPP, F.

KUNSTLER, J.

LANDRY, STUART O., JR.
1957a. The interrelationships of the New and Old world hysticomorph rodents. Univ. Cali-


LANGWORTHY, ORTHHELLO R.

LAVOCAT, RENÉ

LAYNE, JAMES N.

LECHE, WILHELM

LESBRE, FRANCIS XAVIER

LEWIS, THOMAS HOWARD

McMURRICH, J. FAIRPLAY

MARTIN, W.

MATTHEW, WILLIAM DILLER


1832. On the anatomy of Capromys fournier. Ibid., pp. 68–76.


1894b. On the anatomy of Altenua africana compared with that of other porcupines. Ibid., pp. 675–692.

1996. Myology of rodents. II. An account of the myology of the Myomorpha, together with a comparison of the muscles of the various suborders of rodents. Ibid., pp. 159–192.


REICHE, JACOB, and H. S. JENNINGS  
1935. Anatomy of the cat. ed. 3. New York,  
Holt, xxii + 486 pp.  
RINKER, GEORGE C.  
1954. The comparative myology of the mammalian genera Sigmodon, Oryzomys, Neotoma, and  
Peromyscus (Gritcinidae), with remarks on their intergeneric relationships. Misc. Publ.  
1963. A comparative myological study of three  
subgenera of Peromyscus. Occas. Papers Mus.  
RINKER, GEORGE C., and EMMET T. HOOPER  
1950. Notes on the cranial musculature of two  
subgenera of Reithrodonotomys (harvest mice).  
Occas. Papers Mus. Zool. Univ. Michigan,  
n. 528, pp. 1-11, pl. 1.  
ROBERTS, AUSTIN  
1951. The mammals of South Africa. Johannesburg,  
ROMAKOWA, ANNA  
1962. Comparative investigation of the skeleton of  
the hyoid apparatus in Polish Insectivora and Rodentia. Acta Theriologica,  
vol. 6, pp. 11-31.  
RÖMER, ALFRED HERRWOOD  
1956. Vertebrate paleontology. ed. 3. Chicago,  
1968. Notes and comments on vertebrate paleon-  
tology. Chicago, University of Chicago  
Press, viii + 304 pp.  
SCHAUB, SAMUEL  
1953. Remarks on the distribution and classification  
Paris, Masson et Cie, vol. 6, no. 2, pp. 1-  
962.  
SCHÖN, MICHAEL A.  
1968. The muscular system of the red howling  
pp. 1-183.  
SCHULZ, A. H.  
1924. Preparation and preservation of anatomical  
and embryological material in the field.  
SCHUMACHER, G. H.  
1961. Funktionsbedingter Strukturwandel des M.  
masseter. Morph. Jahrb., vol. 102, pp. 150-  
169.  
SCHUMACHER, G. H., and H. REISER  
1962. Ueber einige Unterschiede am Kaualapparat  
bei Lagonomorph und Rodentia. Anat.  
SHARMA, D. R., and S. SIVARAM  
SICHER, HARRY  
1944. Masticatory apparatus in the giant panda  
ser., vol. 29, no. 4, pp. 61-73.  
SIMPSON, GEORGE GAYLORD  
1945. The principles of classification and a classi- 
SISSON, SEPTIMUS, and J. D. GROSSMAN  
1953. The anatomy of the domestic animals. ed.  
SPRUNGE, JAMES M.  
Mammal., 23, pp. 405-411.  
STEHLIN, HANS G., and SAMUEL SCHAUB  
1951. Die Trigonodontidie der simplicidentaten  
Nager. Schweizerischen Palaeont. Ab- 
STERNENMAN, ROBERT O. G.  
1932. Vergleichend-Anatomische Studien über die Extremitäten-Muskulatur (Vorder- und  
Hintergliedmassen) bei Tapirus indicus.  
2, vol. 28, no. 5, pp. 1-154, figs. 1-35.  
TAKE, GEORGE HENRY HAMILTON  
1935. The taxonomy of the genera of Neotropical  
THALER, LOUIS  
1966. Les rongeurs fossiles du Bas-Languedoc  
da leurs rapports avec l'histoire des  
aunes et les stratigraphie du Tertiaire  
THOMAS, OLDFIELD  
1896. On the genera of the rodents: an attempt to  
bring up to date the current arrangement  
1012-1028.  
TOMES, JOHN  
1850. On the structure of the dental tissues of the  
London, pp. 528-567.  
TULLBERG, TYCHO  
1899. Ueber das System der Nagethiere, eine  
Soc. Sci. Upsalia, ser. 3, v+514 pp., pls. 1- 
57.  
VANZOLINI, P. E., and L. R. GUIMARAES  
1955. South American land mammals and their  
VENDENLOO, N. H. VAN  
1953. On the correlation between the masticatory  
muscles and the skull structure in the musk- 
Wahlert, John H.

Waterhouse, George Robert

Weber, Max, Othenio Abel, and H. M. Burlet

Winge, Herluf

Wood, Albert Elmer
1954. Comments on the classification of rodents.


Wood, Albert Elmer, and Brian Patterson

Wood, Albert Elmer, and R. R. White, III

Wood, John

Yoshikawa, Tetsuo, and Takashi Suzuki

Ziegler, Alan C.