

COMPARATIVE MYOLOGY OF THE  
PECTORAL AND PELVIC APPENDAGES  
OF THE NORTH AMERICAN  
PORCUPINE (*ERETHIZON DORSATUM*)  
AND THE PREHENSILE-TAILED  
PORCUPINE (*COENDOU PREHENSILIS*)

JAMES STEPHEN McEVOY

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# CONTENTS

Abstract .....	339
Introduction .....	339
Acknowledgments .....	342
Materials and Methods .....	343
List of Abbreviations .....	343
Description of the Muscles .....	345
Branchiomic Musculature .....	345
Trapezius Group .....	345
Appendicular Musculature .....	347
Muscles of the Pectoral Girdle and Limb .....	347
Extensor System .....	347
Costo-Spino-Scapular Group .....	347
Latissimus-Subscapular Group .....	349
Deltoid Group .....	350
Suprascapular Group .....	352
Triceps Group .....	352
Extensor Group of the Forearm .....	354
Flexor System .....	357
Pectoral Group .....	357
Flexor Group of the Arm .....	359
Flexor Group of the Forearm .....	361
Muscles of the Pelvic Girdle and Limb .....	363
Extensor System .....	364
Iliacus Group .....	364
Gluteal Group .....	366
Quadriceps Femoris Group .....	371
Tibial Extensor Group .....	373
Peroneal Group .....	376
Flexor System .....	377
Adductor Group .....	377
Ischiotrochanteric Group .....	382
Hamstring Group .....	383
Flexor Group of the Leg .....	384
Flexor Group of the Pes .....	389
Discussion .....	397
Myological Conditions of the Appendages of the Erethizontidae .....	397
Forelimb .....	397
Hindlimb .....	405
Conclusion .....	409
Summary of the Myological Conditions of <i>Erethizon</i> and <i>Coendou</i> .....	409
The Evolutionary Relationship of <i>Erethizon</i> and <i>Coendou</i> .....	417
Literature Cited .....	419



## ABSTRACT

The myology of the pectoral and pelvic appendages of *Erethizon dorsatum*, the North American porcupine, and *Coendou prehensilis*, the prehensile-tailed porcupine, were compared by dissection. The data were used to hypothesize on the evolutionary relationship of these two species, and the arboreal adaptations within their musculature were identified.

Arboreal adaptations were observed most frequently in the forelimb. Several muscles may be important in caudal rotation of the scapula, a movement that is probably used as an aid to limb protraction during reaching movements. The cranial fibers of M. acromiotrapezius and the caudal fibers of the M. levator scapulae and M. serratus anterior complex probably function in caudal scapular rotation, but it is possible that the latter would be important in suspension of the thorax by the pectoral girdle during climbing. The cranial fibers of the M. levator scapulae and M. serratus anterior complex along with M. occipitoscapularis, M. rhomboideus anterior, and M. atlanto-scapularis posterior would be used in cranial scapular rotation (the glenoid moves caudoventrally). This motion is probably used as an aid to limb retraction during climbing. M. latissimus dorsi and M. teres major have configurations which also reflect the need for powerful limb retraction in erethizontids. Several muscles, particularly M. pectoralis major and M. clavodeltoideus, are responsible for limb adduction in order to maximize the frictional forces generated between the

manus and the arboreal substrate. The configuration of M. biceps brachii indicates that it is a powerful elbow flexor and an important supinator of the antebrachium. M. supinator is probably most important in maintaining the integrity of the humeroradial joint.

Arboreal adaptations in the pelvic appendage were primarily concerned with positioning the pes or improving its grasping capabilities. M. tibialis anterior and M. tibialis posterior are important for inversion of the pes toward the medially lying arboreal substrate. M. plantaris brevis and M. adductor ossis sesamoideus medialis would probably depress the preaxial pad, allowing the pes to "grasp" branches or conform to the curved substrate.

The musculature of the pectoral appendages of *Erethizon* and *Coendou* was found to be similar, although some minor interspecific differences were observed. However, major interspecific differences were observed in the pelvic appendages of these animals. M. caudofemoralis and M. adductor digiti secundi are present in *Erethizon* but absent in *Coendou*. The configurations of M. flexor digitorum tibialis and M. abductor hallucis brevis in *Coendou* are clearly derived from the more primitive conditions as represented by *Erethizon*. The myological data obtained in this study, along with other morphological and paleontological data from Frazer (1978), suggest that *Erethizon* and *Coendou* were derived from a common ancestor.

## INTRODUCTION

The purpose of the present study is to compare myological differences in the pectoral and pelvic appendages between *Erethizon dorsatum*, the North American porcupine, and *Coendou prehensilis*, the prehensile-tailed porcupine. Both animals are in the Erethizontidae, the New World porcupines. This descriptive material will be used to hypothesize on the evolutionary relationship between these two species and will help to contribute further information toward the understanding of arboreal adaptations in mammals.

*Erethizon dorsatum* is a widespread hystriognathous rodent found in timbered areas from Alaska to northern Mexico in the West

and as far south as the Appalachian Mountains in the East (Hall and Kelson, 1959; Woods, 1973; Walker, 1975). It is large, stoutly built, and has well-developed legs and tail. The normal range in weight is 3.5 to 7 kg., but large males have been recorded at 18 kg. (Woods, 1973; Walker, 1975). The feet are modified for semi-arboreal life with tiny epidermal tubercles for traction (Vaughan, 1972; Walker, 1975). There are four functional digits on the manus and five on the pes, all with long, curved claws used for climbing and manipulating food (Seton, 1953; Costello, 1966; Woods, 1973; Walker, 1975). The foot posture is plantigrade. The porcu-

pine is slow and deliberate both on the ground and in the trees. Although its terrestrial locomotion has been described as a "shuffle" or "waddle," the porcupine is, nevertheless, a skilled climber that spends considerable time in the trees feeding on bark, buds, and leaves (Seton, 1953; Hall and Kelson, 1959; Costello, 1966; Woods, 1973; Banfield, 1974; Walker, 1975).

Porcupines climb trees deliberately but skillfully and have an excellent sense of balance (Walker, 1975). The claws are applied to any available irregularities and are also used for grasping smaller branches when convenient (Costello, 1966). On trunks a few inches in diameter, the palmar and plantar aspects of the feet are turned medially and forced against the sides of the tree, thus taking advantage of the frictional forces generated between the epidermal tubercles and the substrate (personal observ.). The ventral surface of the tail is covered with short, stiff hairs and is also forced against the substrate during climbing and descent (Costello, 1966). The ankle can be rotated in order to turn the plantar aspect of the pes medially during climbing. The frictional forces generated by the feet and tail are powerful enough to allow the animal to maintain its position on a suitable vertical substrate without the use of its forelimbs. When climbing, porcupines usually advance one forefoot at a time and follow with either one or both hindfeet. They descend by backing down the trunk, using the tail as a sensory organ (personal observ.). When feeding in trees, they often use the forelimbs to bring the food toward the mouth (Seton, 1953; Costello, 1966; Banfield, 1974).

*Erethizon* is usually restricted to forested habitats throughout much of its range. However, it is found in marginal habitats such as the chaparral type and wanders far from the trees into open tundra, prairies, and higher elevations if suitable plant material is available (Hall and Kelson, 1959; Costello, 1966; Woods, 1973; Walker, 1975). Daily and seasonal ranges are usually restricted. During the winter, the animals will use suitable cover for den sites and make short trips to nearby feeding trees. They typically rely on the bark and twigs of the dominant tree species of the region (Costello, 1966; Woods, 1973). In the sum-

mer, the animals do not make use of dens and take longer forays to nearby fields, where they feed on herbaceous plant material (Seton, 1953; Costello, 1966; Woods, 1973). Porcupines are known to make longer seasonal migrations into different habitats in order to obtain other food sources, especially in the West (Costello, 1966; Woods, 1973; Walker, 1975). Normally, porcupines rely on their arboreal locomotor capabilities and their quills for protection. Their typical defensive tactic is to face away from an attacker with quills erect while protecting the head against a tree or rock (Seton, 1953; Banfield, 1974; Walker, 1975). However, they have been known to move rapidly away in a lumbering fashion when alarmed (Banfield, 1974). Thus, *Erethizon* is both a terrestrial and arboreal animal.

The biology of the prehensile-tailed porcupine is poorly known. The genus *Coendou* has a range which extends from the southern portion of Mexico, including the Yucatan Peninsula, to Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia (Hall and Kelson, 1959; Walker, 1975). Two species, *C. mexicanus* and *C. rothschildi*, are found in Central America (including Mexico). *Coendou prehensilis* is restricted to South America (Hall and Kelson, 1959). These animals are found exclusively in forested areas and are nocturnal and arboreal. Although they will take shelter in dens or shallow burrows, they spend most of their lives in trees (Leopold, 1972; Vaughan, 1972; Walker, 1975). They are smaller than *Erethizon*, and the average adult weights vary from 0.9 to 4.3 kg. The tail is longer than in *Erethizon* and is prehensile with a naked distal portion that curls dorsally. As in their North American counterparts, prehensile-tailed porcupines have feet that are modified for arboreal life, although each foot has four external digits (Walker, 1975). They possess a movable pad on the pes in place of the hallux (Jones, 1953; Vaughan, 1972).

*Coendou* feeds on leaves, roots, and tender stems to a greater extent than does *Erethizon* (Hall and Kelson, 1959; Leopold, 1972; Walker, 1975). Epiphytic plants, bark, and cambium are also eaten (Leopold, 1972). The differences in feeding habits between *Erethi-*



zon and *Coendou* are reflected in the skeletal morphology of the masticatory apparatus. Frazer (1978) reported that *Erethizon* was generally larger than *Coendou* in most cranial measurements, particularly in the width of upper P<sup>4</sup> and upper M<sup>1</sup>, the width of the skull at the zygomatics and the auditory meatus, and the alveolar length of the upper and lower tooth rows. The divergence and dorsoventral thickness of the zygomatics were also greater in *Erethizon*. The squamosal zygomatic processes extended laterally in contrast to those of *Coendou* which extended ventrolaterally. Finally, both Frazer (1978) and White (1970) concurred that the orthodont incisors of *Coendou* were not as efficient for scraping bark as the proodont incisors of *Erethizon*.

Few anatomical studies have been done on the musculoskeletal system of *Erethizon* or *Coendou*. Ballard (1937) did a comparative study of the entire anatomy of *E. dorsatum* and *Cavia cobaya*, using the latter as the reference species for comparison. He recorded numerous differences in the osseous and muscular systems between the two species and noted that the bones of *Erethizon* were heavily built and had well-developed tubercles and ridges for the attachment of powerful muscles. The scope of this study was so extensive that the specific details of the myology were often vague and sometimes erroneous. He did not record the specific innervation of each muscle. Although he mentioned the specific muscle actions for the guinea pig, he failed to consider the functional implications of the variations in musculoskeletal morphology between *Cavia* and *Erethizon* as they relate to semi-arboreal locomotion. This study was never published.

Several studies have considered various aspects of the osteology of *Erethizon*. Swena and Ashley (1956) described the entire skeleton and identified the major features of each bone. Although they included several good illustrations with their work, they did not discuss the significance of the skeletal characteristics in the light of arboreal adaptations. Ray (1958) examined the fusion of cervical vertebrae of *Erethizon* and *Dinomys* in detail and discussed the significance of this morphological character to the taxonomy of caviomorphs. Gupta (1966) briefly described

the differences between the skeletons of *Erethizon* and *Coendou*. Sutton (1972) discussed the intraspecific variation in the skeleton of *Erethizon* and also provided information on tooth eruption and replacement and on the sequence of cranial suture closure. He disagreed with Swena and Ashley (1956) on certain features of the cranial osteology and on the nomenclature of the sesamoid bones of the pes. Frazer (1978) did an extensive descriptive and morphometrical analysis of the known North American fossil erethizontids. The crania of *Erethizon* and *Coendou* were found to have substantial differences between them, some of which have been discussed previously. In the postcranial skeleton, the hindlimb and pes were found to differ significantly between the two genera. It was noted that differences in the tibia, fibula, astragalus, and calcaneus reflected differences in locomotor capabilities. *Erethizon*, the more terrestrial of the two forms, was found to have greater rotational ability of the pes to provide a wider ranging locomotor accommodation.

Mivart (1882) considered some aspects of the anatomy of *Erethizon*, including parts of the digestive and nervous systems. Although he also examined the musculature of the limbs, he did not include several muscles such as the trapezius and rhomboideus, and his descriptions were usually vague.

Windle (1888) described variation in the myology between "*E. dorsatus*" and *E. epixanthus*, which were then considered separate species. The latter is now considered as a subspecies of *E. dorsatum* (Hall and Kelson, 1959). Since this study only considered the differences between the two forms, it was understandably incomplete. The differences in myology that were described were generally not significant and fell within the normal range of variation for the species.

Parsons (1894) did an extensive study of the myology of some sciuriform and hystricomorph rodents including *Sphingurus* (= *Coendou*) but not *Erethizon*. However, he made use of Mivart's (1882) and Windle's (1888) studies for comparative purposes. He examined all muscle groups and summarized some of the major myological differences between the two suborders. He also briefly discussed some of the myological character-

istics of the hystricomorph families that were investigated. Eleven distinct differences were noted between the "Ground Porcupines" of the genus *Hystrix* and the "Tree Porcupines" of the genus *Sphingurus* (= *Coendou*) which, at the time, were placed in the same family (Hystricidae). Parsons granted that he lacked sufficient information with his study to determine if these differences were the result of different locomotor habits or different evolutionary histories. The scope of the study was reasonably complete, but the descriptions were quite generalized and illustrative material for the pelvic appendage was lacking. Also, there was no consideration of the functional aspects of the myology within the two groups of rodents.

Jones (1953) described some of the osteological and myological adaptations of the pedes of *Coendou prehensilis* and *Cyclopes didactyla* (Edentata) that allowed grasping of the substrate during arboreal locomotion. In *Coendou*, he observed a subcutaneous, sheet-like muscle which attached to the cartilaginous margin of the preaxial pad and was responsible for opposing that pad to the rest of the plantar aspect of the pes. He noted that this muscle, which he termed the *plantaris brevis*, was also present with modifications in *Erethizon* and *Cyclopes*. The relations of the extensors and flexors of the ankle and digits were also briefly discussed.

Woods (1972) studied the jaw, hyoid, and pectoral appendage of 13 genera of hystricomorph rodents, including *Erethizon* but not *Coendou*. Parsons (1894) was used as the standard reference for hystricomorph rodent anatomy because it compared a large number of animals from that group. Of all the rodents examined, *Erethizon* was found to be myologically the most primitive. It possessed 17 distinctive myological characters of which 12 were unique to that genus and 10 of which were definitely primitive. *Erethizon* was shown to be isolated morphologically from both New and Old World hystricomorphs. He therefore disagreed with Landry (1957) and placed the Erethizontidae in their own superfamily of the suborder Hystricognatha. Landry (1957) had grouped the Erethizontidae with the Echimyidae. Woods did not include the pelvic appendage with his study,

and he was primarily concerned with the systematics rather than the locomotor adaptations of hystricomorphs. However, his study is by far the most precise of its kind to date.

Recently, Hildebrand (1978) analyzed the insertions, relations, and important functions of three medial flexors of the hindlimb of representatives of 26 rodent families. In all, 56 genera were examined, including *Erethizon* and *Coendou*. A consistent relationship was demonstrated between *M. tibialis posterior* and the medial tarsal, one of two additional bones on the medial aspect of the pes. This relationship was indicative of the unique occurrence of this bone in rodents. The size, occurrence, anchorage, and functions of the other additional tarsal bone, called the medial sesamoid, were also described. In *Erethizon* and *Coendou*, this bone was shown to be functionally important in allowing the plantar aspect of the pes to grip the substrate, obviously advantageous for arboreal locomotion. This study clearly demonstrated the range of morphological and functional variation in an important biomechanical system in rodents.

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## MATERIALS AND METHODS

Four specimens of *Erethizon dorsatum* and three specimens of *Coendou prehensilis* were dissected. All were preserved by immersion in 10 percent formalin and maintained between dissecting periods by the method described in Woods (1972). In addition, postcranial skeletons of other specimens of the two genera were studied. Most of this material was borrowed from the American Museum of Natural History; some was from the University of Vermont.

For all muscle descriptions, *E. dorsatum* was used as the standard species to which *C. prehensilis* was compared. For a given muscle, the origin, insertion, important topographical relations, significant intraspecific variations, and significant interspecific differences were described for three specimens of each species. The innervation was usually not determined because this information has been thoroughly described for rodents by Rinker (1954), Klingener (1964), and Woods (1972). Measurements were usually made unilaterally wherever possible to make the descriptions more accurate and were taken using a drawing divider and a 30 cm. ruler. The data were recorded to the nearest 0.1 mm. and were usually used to calculate the relative length or position of a muscle attachment to a given bone to the nearest whole percent. For a given parameter (e.g., relative length of insertion), the average of all three specimens of each species was recorded and the range placed in parentheses. Statistical analysis of the numerical data was not performed due to the small number of specimens. Factors such as the position of the specimen, the nature of preservation, the precision of dissection, and the placement of the drawing dividers onto the specimen and the ruler would also have an effect on the recorded measurements and the subsequent calculations. Therefore, unless otherwise stated for a given parameter, specimens were said to vary intraspecifically or differ interspecifically

if the range or the numerical difference between the averages, respectively, were greater than or equal to 10 percent. Exceptions were made if a difference could be detected visually. A complete set of drawings for *Erethizon* was made. The forelimb of *Coendou* was not drawn because its variation with that of *Erethizon* was not substantial.

The reference used as the standard for nomenclature was Klingener (1964). Woods (1972) was used as a guide to the dissection of the forelimb since it precisely described the myology of a large number of hystricomorph rodents including *Erethizon*. Both Klingener (1964) and Rinker (1954) were used for the dissection of the hindlimb. Hollinshead (1974) was also frequently consulted during this study.

## LIST OF ABBREVIATIONS

A. fem., femoral artery  
 A. poplit., popliteal artery  
 annular lig., annular ligament  
 aponeur. env., aponeurotic envelope  
 astragalocal. lig., astragalocalcaneal ligament  
*C.*, *Coendou*  
 caud. pubic ram., caudal pubic ramus  
 com. flex. tend., common (subsidiary) flexor tendon  
 com. sub. tend., common subsidiary (flexor) tendon  
 com. tendons, common tendons  
 cran. pubic ram., cranial pubic ramus  
 deep palm. aponeur., deep palmar aponeurosis  
 dor. ischial ram., dorsal ischial ramus  
 dor. ridge, dorsal ridge  
*E.*, *Erethizon*  
 fib. col. lig., fibular collateral ligament  
 first caud. verte., first caudal vertebra  
 iliopect. eminence, iliopectineal eminence  
 inf. ischial ram., inferior ischial ramus  
 ischiotroch. group, ischiotrochanteric group  
 lat. head, lateral head  
 lig. troch., ligamentous trochlea  
 long plant. lig., long plantar ligament  
 M. abd. dig. min., M. abductor digiti minimi  
 M. abd. hal. brev., M. abductor hallucis brevis  
 M. abd. oss. met. quint., M. abductor ossis metatarsi quinti  
 M. abd. pol. lg., M. abductor pollicis longus  
 M. acromiodelt., M. acromiodeltoideus  
 M. acromiotrap., M. acromiotrapezius  
 M. add. brev., M. adductor brevis  
 M. add. dig. quint., M. adductor digiti quinti  
 M. add. dig. sec., M. adductor digiti secundi

- M. add. hal., M. adductor hallucis  
 M. add. lg., M. adductor longus  
 M. add. mag., M. adductor magnus  
 M. add. min., M. adductor minimus  
 M. add. oss. ses. med., M. adductor ossis sesamoides medialis  
 M. ancon., M. anconeus  
 M. atlantosc. post., M. atlantosc. posterior  
 M. biceps br., M. biceps brachii  
 M. biceps fem., M. biceps femoris  
 M. brachiorad., M. brachioradialis  
 M. caudofem., M. caudofemoralis  
 M. clavodelt., M. clavodeltoideus  
 M. coracobrach., M. coracobrachialis  
 M. cut. max., p. dor., M. cutaneous maximus, pars dorsalis  
 M. cut. max., p. fem., M. cutaneous maximus, pars femoralis  
 M. dorsoepitroch., M. dorsoepitrochlearis  
 M. epitroch., M. epitrochleoanconeus  
 Mm. ext. breves, Mm. extensores breves  
 M. ext. carpi rad. brev., M. extensor carpi radialis brevis  
 M. ext. carpi rad. lg., M. extensor carpi radialis longus  
 M. ext. carpi ul., M. extensor carpi ulnaris  
 M. ext. dig., M. extensor digitorum  
 M. ext. dig. lg., M. extensor digitorum longus  
 M. ext. dig. min., M. extensor digiti minimi  
 M. ext. dig. ter. prop., M. extensor digiti tertii proprius  
 M. ext. hal. brev., M. extensor hallucis brevis  
 M. ext. hal. lg., M. extensor hallucis longus  
 M. ext. ind., M. extensor indicis  
 M. ext. obl., M. external oblique  
 M. femorococcyg., M. femorococcygeus  
 Mm. flex. brev. acc., Mm. flexores breves accessorii  
 M. flex. carpi rad., M. flexor carpi radialis  
 M. flex. carpi ul., M. flexor carpi ulnaris  
 M. flex. dig. brev., M. flexor digitorum brevis  
 M. flex. dig. fib., M. flexor digitorum fibularis  
 M. flex. dig. min. brev., M. flexor digiti minimi brevis  
 M. flex. dig. prof., M. flexor digitorum profundus  
 M. flex. dig. sup., M. flexor digitorum superficialis  
 M. flex. dig. tib., M. flexor digitorum tibialis  
 M. gastroc., M. gastrocnemius  
 M. gem. inf., M. gemellus inferior  
 M. gem. sup., M. gemellus superior  
 M. glut. max., M. gluteus maximus  
 M. glut. med., M. gluteus medius  
 M. glut. min., M. gluteus minimus  
 M. grac., M. gracilis  
 M. infraspin., M. infraspinatus  
 Mm. inteross., Mm. interossei  
 M. lat. dorsi, M. latissimus dorsi  
 M. lev. scap. and M. ser. ant., M. levator scapulae and M. serratus anterior  
 M. obt. ext., M. obturator externus  
 M. obt. int., M. obturator internus  
 M. occipitosc., M. occipitosc. posterior  
 M. omocerv., M. omocervicalis  
 M. omohyoid., M. omohyoideus  
 M. palm. lg., M. palmaris longus  
 M. pect., M. pectineus  
 M. pect. abd., M. pectoralis abdominalis  
 M. pect. maj., M. pectoralis major  
 M. pect. min., M. pectoralis minor  
 M. per. brev., M. peroneus brevis  
 M. per. dig. min., M. peroneus digiti minimi  
 M. per. lg., M. peroneus longus  
 M. plant., M. plantaris  
 M. poplit., M. popliteus  
 M. pron. quad., M. pronator quadratus  
 M. pron. teres, M. pronator teres  
 M. psoas maj., M. psoas major  
 M. pubococcyg., M. pubococcygeus  
 M. pyriform., M. pyriformis  
 M. quad. fem., M. quadratus femoris  
 M. rect. fem., M. rectus femoris  
 M. rhomb. ant., M. rhomboideus anterior  
 M. rhomb. post., M. rhomboideus posterior  
 M. scapuloclav., M. scapuloclavicularis  
 M. semimemb., M. semimembranosus  
 M. semitend., M. semitendinosus  
 M. spinodelt., M. spinodeltoideus  
 M. spinotrap., M. spinotrapezius  
 M. sternomast., M. sternomastoideus  
 M. subclav., M. subclavius  
 M. subscap., M. subscapularis  
 M. supin., M. supinator  
 M. supraspin., M. supraspinatus  
 M. ten. fas. lat., M. tensor fascia lata  
 M. tenuis., M. tenuissimus  
 M. teres maj., M. teres major  
 M. teres min., M. teres minor  
 M. tib. ant., M. tibialis anterior  
 M. tib. post., M. tibialis posterior  
 M. tri. br., cap. lat., M. triceps brachii, caput lateralis  
 M. tri. br., cap. lg., M. triceps brachii, caput longus  
 M. tri. br., cap. med., M. triceps brachii, caput medialis  
 M. vast. intermed., M. vastus intermedius  
 M. vast. lat., M. vastus lateralis  
 M. vast. med., M. vastus medialis  
 med. head, medial head  
 med. sesamoid, medial sesamoid  
 med. tarsal, medial tarsal  
 N. obtur., obturator nerve  
 N. perin., perineal nerve  
 N. post. fem. cut., posterior femoral cutaneous nerve  
 N. sup. glut., superior gluteal nerve



N. to hamstrings, nerve to the hamstrings  
 peron. pr., peroneal process  
 plant. apon., plantar aponeurosis  
 pos. of inf. tub., position of inferior tuberosity

rad. col. lig., radial collateral ligament  
 sup. ischial tub., superior ischial tuberosity  
 tib. col. lig., tibial collateral ligament  
 trans. crur. lig., transverse crural ligament

## DESCRIPTION OF THE MUSCLES

### BRANCHIOMERIC MUSCULATURE

#### TRAPEZIUS GROUP

##### M. ACROMIOTRAPEZIUS

Figures 1, 2

**ORIGIN:** By fibers from the nuchal crest extending 83 percent (82–86%) of the distance from the midpoint of the skull to the level of the base of the mastoid process and mostly by aponeurosis from the dorsal midline to the level of the second thoracic vertebra.

**INSERTION:** By fascia proximally and by fibers distally onto the cranial surface of the distal 73 percent (71–74%) of the spine of the scapula, by fibers onto the cranial edge and somewhat onto the dorsal surface of the acromion, and by fibers onto the acromial 22 percent (11–28%) of the clavicle.

**REMARKS:** The segment of origin from the dorsal midline between the first and second thoracic vertebrae is by fibers in two specimens. In one specimen, the entire origin from the dorsal midline is fleshy.

The muscle is entirely continuous with M. spinotrapezius. Woods (1972) reported that the insertion included the cranial surface of that muscle, but I was not able to confirm this. The fascia of insertion is particularly prominent dorsally. The acromiotrapezius and spinotrapezius muscles were distinguished by tracing from the most dorsal extension of this fascia through the muscle fibers to the dorsal midline. This procedure consistently placed the boundary between the muscles at the second thoracic vertebra. The distal boundary between the fascia and the fibers of insertion onto the scapular spine is approximately at the level of the great scapular notch. In some specimens, it is situated a few millimeters proximal or distal to that level.

In *Coendou*, the origin from the nuchal crest is not as broad as in *Erethizon*, extending 72 percent (66–78%) of the distance to the level of the mastoid process. The muscle inserts onto the distal 80 percent (79–81%) of the spine of the scapula. The insertion includes the acromial 16 percent (13–21%) of the clavicle.

##### M. SPINOTRAPEZIUS

Figures 1, 2

**ORIGIN:** By fibers along the dorsal midline from the second to the seventh thoracic vertebra and from the lateral border of the cranial extension of the lumbodorsal fascia from the seventh to the level of the eighth thoracic vertebra a short distance from the dorsal midline.

**INSERTION:** There are three parts of this muscle. The cranial part inserts into the dorsal extension of the fascia of insertion of M. acromiotrapezius. The caudal part inserts by fascia onto 26 percent (25–26%) of the caudal surface of the spine of the scapula beginning at a point 28 percent (26–29%) of the length of the spine from the vertebral border. The third part is represented by a thin auricular slip which inserts onto the superficial surfaces of the parotid gland and the facial muscles in the region of the ear.

**REMARKS:** The muscle is entirely continuous with M. acromiotrapezius. The lumbodorsal fascia is visible superficially to the level of the seventh thoracic vertebra. Tracing the lateral border of the muscle through the fascia (which is actually an aponeurosis) places the most caudal point of origin at the level of the ninth thoracic vertebra. In one specimen, a short cranial segment of origin

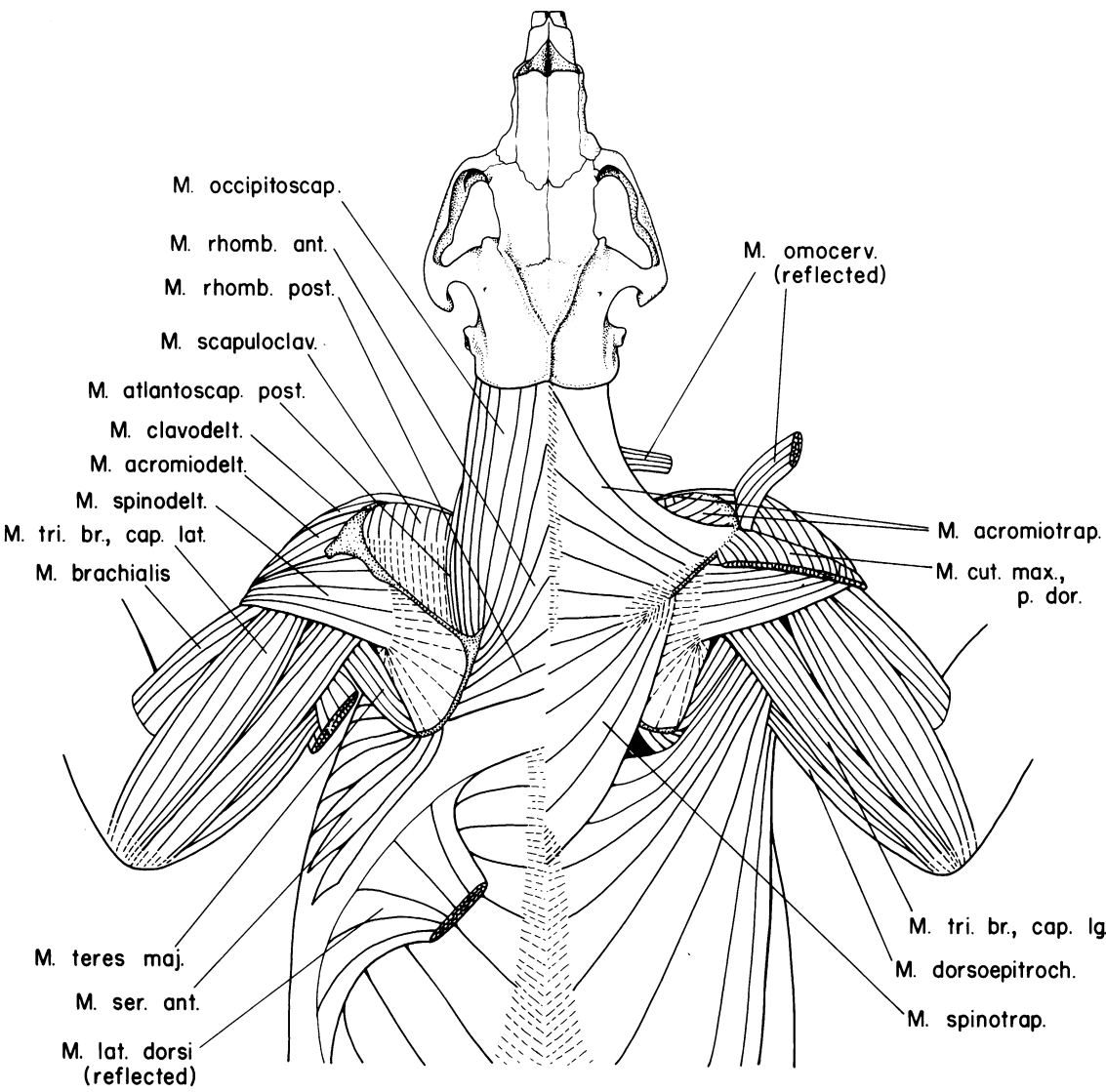


FIG. 1. Dorsal view of the muscles of the pectoral girdle and brachium of *Erethizon*. Superficial muscles are on the right. Deeper muscles are on the left.

from the second to the third thoracic vertebra is aponeurotic.

The auricular slip arises near the lateral border of the muscle. It courses craniad over the main portion of the muscle and over *M. acromiotrapezius* before fanning out to reach its insertion. In one specimen, the auricular slip is present but is not well developed. Woods (1972) noted the presence of this slip

in several genera of hystricomorphs. It has also been found in many other rodents as well (Rinker, 1954; Klingener, 1964). Woods (1972) concluded that the slip represented a primitive rodent feature that either remained unchanged, became incorporated into the retractor musculature of the cheek pouch, or was lost altogether.

In *Coendou*, the origin extends along the



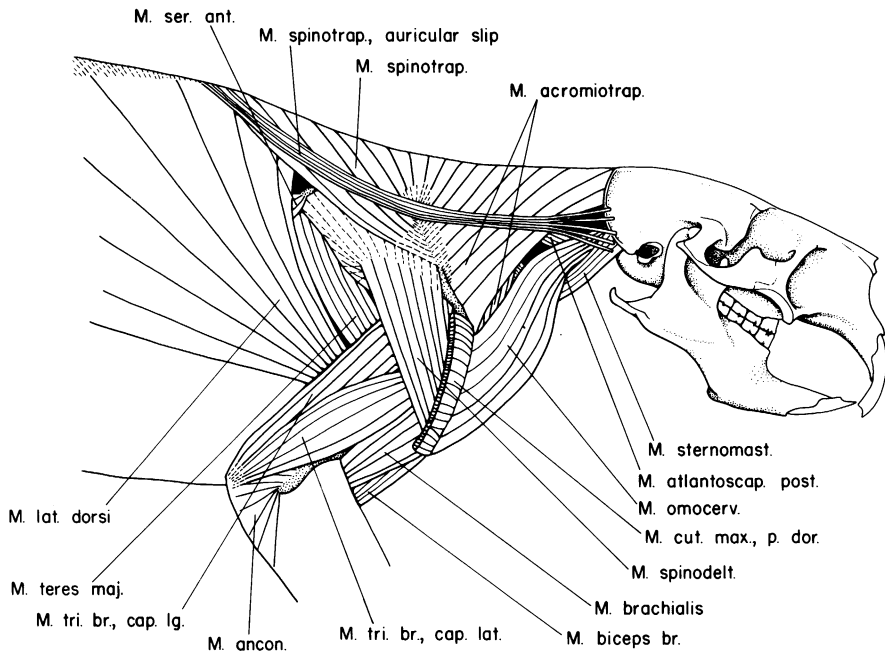


FIG. 2. Lateral view of the superficial muscles of the pectoral girdle and brachium of *Erethizon*.

dorsal midline from the second to the ninth thoracic vertebra. No part of the muscle arises from the lumbodorsal fascia, which extends cranially only as far as the eleventh thoracic vertebra. A short caudal segment of origin from the eighth to the ninth thoracic vertebra is aponeurotic. The insertion of the caudal

part of the muscle is not as broad nor does it begin or extend as far distally as in *Erethizon*. It inserts onto 16 percent (14–19%) of the caudal surface of the scapular spine beginning at a point 20 percent (17–21%) from the vertebral border.

## APPENDICULAR MUSCULATURE

### MUSCLES OF THE PECTORAL GIRDLE AND LIMB

#### EXTENSOR SYSTEM

##### COSTO-SPINO-SCAPULAR GROUP

#### M. LEVATOR SCAPULAE AND M. SERRATUS ANTERIOR

Figures 1, 2, 5

**ORIGIN:** From the lateral edge of the transverse process of the atlas, the transverse processes of the remaining six cervical vertebrae, and by muscular slips from the lateral surfaces of the ribs 1 through 8 or 9.

**INSERTION:** On a narrow portion of the costal surface of the scapula adjacent to the vertebral border and on the medial edge of the vertebral border.

**REMARKS:** These two muscles are separable only on the basis of innervation. Since they are entirely continuous with each other, they are described here as a single functional unit.

The extent of the origin from the ribs is variable. In two specimens, the origin extends as far caudally as the eighth rib while on one side of one specimen, a small muscular slip arises from the ninth rib as well. Woods (1972)

reported that the origin included the ninth rib in all of his *Erethizon* specimens.

Cranially, the muscle is relatively thin near its insertion. Caudally, it is thicker and fills the gap on the vertebral border between the insertion of *M. rhomboideus posterior* and the origin of *M. teres major*. The medial surface of the insertion is covered with the insertion fibers of *Mm. rhomboideus anterior* and *rhomboideus posterior*.

In *Coendou*, the origin extends caudally to the eighth rib in one specimen, to the ninth rib in one specimen (although the slip to rib 9 is poorly developed on one side), and by a small slip to the ninth rib on one side of the remaining specimen.

**M. OCCIPITOSCAPULARIS, M. RHOMBOIDEUS ANTERIOR, AND M. RHOMBOIDEUS POSTERIOR**  
Figures 1, 5

These muscles form a continuous sheet that is innervated by the dorsal scapular nerves. The muscles were distinguished on the basis of fiber direction and position of insertion. Although some slight separation of fibers occurred when the muscles were manipulated in some specimens, they were not consistent and could not be used as a basis for describing the boundaries of the muscles precisely. Therefore, since these muscles form one morphological and functional unit, they will be discussed jointly.

**ORIGIN:** *M. occipitoscapularis* arises broadly from the nuchal crest, extending to the level of the base of the mastoid process, and from a short cranial segment of the nuchal ligament. *M. rhomboideus anterior* arises from the nuchal ligament caudal to the origin of *M. occipitoscapularis*. *M. rhomboideus posterior* arises from the nuchal ligament caudal to the origin of *M. rhomboideus anterior* and extends to the level of the fourth thoracic vertebra.

**INSERTION:** *M. occipitoscapularis* inserts by aponeurosis onto the proximal 10 percent (8–12%) of the cranial surface of the spine of the scapula and by fibers onto a small segment of the vertebral border cranial to the plane of the scapular spine. *Mm. rhomboideus anterior* and *posterior* insert onto an extensive portion of the vertebral border from the level of the scapular spine to the caudal

attachment of *M. serratus anterior*. They also insert by a tough connective tissue onto the proximal portion of the medial surface of *M. levator scapulae* and *M. serratus anterior*.

**REMARKS:** These muscles lie deep to the trapezius muscles. The fibers of *M. occipitoscapularis* course caudad and then slightly dorsad to reach their insertion. Those of *M. rhomboideus anterior* course caudolaterad and slightly dorsad to the insertion. Those of *M. rhomboideus posterior* course almost directly laterad and slightly dorsad, although the cranial fibers follow a slight caudal line as well. The reason for the slight dorsal course of these muscles is that the vertebral border is slightly above the level of origin when the scapula is in a normal position. Woods (1972) reported that the origin of *M. rhomboideus posterior* extended caudally to the sixth thoracic vertebra. The origin did not extend that far caudally in any of my specimens.

In *Coendou*, the origin of *M. rhomboideus posterior* extends to the level of the third thoracic vertebra. There is no other variation from *Erethizon*. *M. occipitoscapularis* inserts onto the proximal 12 percent (9–15%) of the spine of the scapula.

**M. ATLANTOSCAPULARIS POSTERIOR**  
Figures 1–3, 5

**ORIGIN:** From the caudal portion of the ventral surface of the transverse process of the atlas.

**INSERTION:** By aponeurosis onto the proximal 13 percent (11–16%) of the cranial surface of the spine of the scapula and by fibers onto a short segment of the vertebral border cranial to the insertion of *M. occipitoscapularis*.

**REMARKS:** The insertion of this straplike muscle lies deep to that of *M. occipitoscapularis* and has a very similar arrangement. On one side of two specimens, the insertion does not reach the scapular spine due to poor development of the aponeurosis but instead, blends slightly with the aponeurosis covering *M. supraspinatus*.

In *Coendou*, the insertion is fleshy and more extensive than in *Erethizon*, attaching to the proximal 29 percent (28–32%) of the spine of the scapula. Hence, a distal portion does not lie deep to *M. occipitoscapularis*.

**M. OMOCERVICALIS**

Figures 1, 2

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

**INSERTION:** Onto the metacromion process of the scapula with *M. cutaneus maximus*, pars dorsalis, into the cranial border of the pars dorsalis, and with the pars dorsalis onto the lateral surface of the tip of the deltoid crest of the humerus in some specimens. A few fibers reach the surface of *M. acromiodeltoideus* immediately adjacent to its origin from the metacromion process.

**REMARKS:** The muscle is thick and relatively narrow near its origin, but as it courses laterad, it becomes thinner and broader. The insertion onto the deltoid crest is absent in two specimens. In one of these individuals, the most distal point of union between *M. omocervicalis* and *M. cutaneus maximus*, pars dorsalis is anchored by strong connective tissue to the lateral surface of *M. brachialis* just after it emerges from under cover of the *spinodeltoideus* muscle. In all specimens, the fibers of *M. omocervicalis* and *M. cutaneus maximus*, pars dorsalis do not interdigitate but are joined strongly by fascia. Woods (1972) did not include the attachment of these two muscles in his description of *M. omocervicalis* but included it in that of *M. cutaneus maximus*.

In two specimens of *Coendou*, the muscle is basically as described for *Erethizon* except that the insertion onto the deltoid crest is by aponeurosis. In one specimen, the insertion also includes much of the dorsal surface of the acromion. The muscle inserts onto the cranial border of *M. cutaneus maximus*, pars dorsalis, and both of these muscles insert quite strongly onto a tiny proximal portion of the surface of *M. acromiodeltoideus*. The insertion of *M. omocervicalis* does not extend distally beyond this point. Thus, there is a great deal of intra- and inter-specific variation associated with this muscle.

**LATISSIMUS-SUBSCAPULAR GROUP****M. LATISSIMUS DORSI**

Figures 1-6

**ORIGIN:** The origin of the muscle is extensive. The ventrolateral fibers arise by muscular slips from the last five ribs, although

the slip arising from the last rib does so by a lateral portion of the lumbodorsal fascia. The dorsomedial fibers arise from the lumbodorsal fascia and extend cranially to the sixth thoracic vertebra. The segment of origin from the eighth to the sixth thoracic vertebra is by a layer of the lumbodorsal fascia that lies deep to *M. spinotrapezius*.

**INSERTION:** By a tendon onto 16 percent (14-20%) of the medial surface of the humerus beginning at a point 28 percent (26-29%) from the proximal end.

**REMARKS:** There are 15 thoracic vertebrae and ribs in all specimens. On one side of two specimens, a few fibers arise from the tenth rib.

The muscle fibers converge acutely to reach the narrow tendon of insertion in the axillary region. The proximal portion of the tendon which receives the muscle fibers also gives rise on its ventral (distal) surface to *M. dorsoepitrochlearis*. The tendon then passes deep (lateral) to the brachial nerves and vessels, fans out somewhat, and reaches its insertion separate and just superficial (medial) to that of *M. teres major*.

Woods (1972) reported that remnant fibers of a latissimus Achselbogen were present in *Erethizon*, an observation which I confirm. These fibers are not well developed and are embedded in the heavy fascia of the axillary region. They are closely associated with a separate slip of *M. cutaneus maximus*, pars dorsalis which enters this region as well. The reader is referred to Woods (1972) for a more detailed description of this feature.

In *Coendou*, the origin of the ventrolateral fibers is not as extensive as in *Erethizon*, but there is considerable variability. In one specimen, the origin is from ribs 12 through 14. In another specimen, the muscular slips arise from ribs 13 and 14, and from rib 15 by a lateral portion of the lumbodorsal fascia, as in *Erethizon*. The slip to rib 14 is represented only by a few fibers. In the third specimen, the origin is from ribs 11 through 13 with the slip from rib 11 being small and lying deep to the main part of the muscle. A slip also arises from a lateral portion of the lumbosacral fascia and from the surface of the intercostal muscle between ribs 14 and 15.

The dorsomedial fibers are more extensive

in *Coendou*. They arise from the lumbodorsal fascia, which extends cranially to the eleventh thoracic vertebra, and by fibers from the dorsal midline and neural spines of the thoracic vertebrae from that point to the fifth thoracic vertebrae in two specimens and the fourth thoracic vertebra in one specimen. The portion cranial to the ninth thoracic vertebra lies deep to *M. spinotrapezius*. There are 16 thoracic vertebrae and ribs in all specimens.

There is no significant variation in insertion from *Erethizon*. The tendon inserts onto 11 percent (10–13%) of the medial surface of the humerus beginning at a point 31 percent (29–33%) from the proximal end.

#### M. TERES MAJOR

Figures 1–6

ORIGIN: From the proximal 40 percent (34–43%) of the axillary border of the scapula, from the adjacent surfaces of *M. subscapularis* and *M. infraspinatus*, and slightly from the aponeurotic envelope covering *M. infraspinatus*.

INSERTION: Onto 23 percent (23–24%) of the medial border of the humerus beginning at a point 25 percent (24–26%) from the proximal end.

REMARKS: The insertion is distal to that of *M. subscapularis* on the crest of the lesser tuberosity and is deep (lateral) to the tendon of *M. latissimus dorsi*.

In *Coendou*, there is no significant variation in origin and insertion from *Erethizon*. The origin includes the proximal 38 percent (33–44%) of the axillary border. The insertion is on 23 percent (21–25%) of the medial border of the humerus beginning at a point 21 percent (18–23%) from the proximal end.

The boundaries of the axillary border of the scapula were considered to be from the most proximal point of origin of *M. teres major* to the lip of the glenoid fossa. The glenovertebral (caudal) angle is rounded and tends to be variable in shape depending upon the degree of ossification. It is difficult to pinpoint precisely the division between the vertebral and axillary borders. Hence, the most proximal point of origin of *M. teres major* was used for the purpose of identifying the proximal end of the axillary border.

#### M. SUBSCAPULARIS

Figures 5, 6

ORIGIN: From the entire subscapular fossa of the scapula except for a narrow portion adjacent to the vertebral border where *M. levator scapulae* and *M. serratus anterior* insert, from the cranial border with *M. supraspinatus*, and from the axillary (caudal) border with *M. infraspinatus*.

INSERTION: By a tendon onto the caudal surface of the lesser tuberosity of the humerus and by fibers onto its associated crest.

REMARKS: The insertion is proximal to that of *M. teres major*. The muscle is multipinnate. I did not observe any significant variation in *Coendou*.

#### DELTOID GROUP

##### M. CLAVODELTOIDEUS

Figures 1, 3, 5

ORIGIN: From 48 percent (44–55%) of the ventral surface of the clavicle beginning at a point 12 percent (9–17%) from the acromial end.

INSERTION: Onto the anterior edge of the deltoid crest and the surface of the medial border of *M. acromiodeltoideus*.

REMARKS: The most distal point of insertion is proximal to the tip (the most prominent point) of the deltoid crest. Woods (1972) reported that the origin was from the scapular (=acromial) three-fourths of the clavicle in his specimens. In my specimens, the most distal portion of the clavicle is bound by connective tissue, but the fibers of *M. clavodeltoideus* do not arise from this segment.

There is no significant variation in *Coendou*. The origin is from 41 percent (35–46%) of the clavicle beginning at a point 16 percent (13–18%) from the acromial end.

##### M. ACROMIODELTOIDEUS

Figures 1, 3

ORIGIN: From the ventral edge of the acromion and metacromion processes.

INSERTION: Onto the anterior edge of the deltoid crest, onto the surface of the lateral border of *M. clavodeltoideus*, and strongly onto the aponeurosis of insertion of *M. spi-*



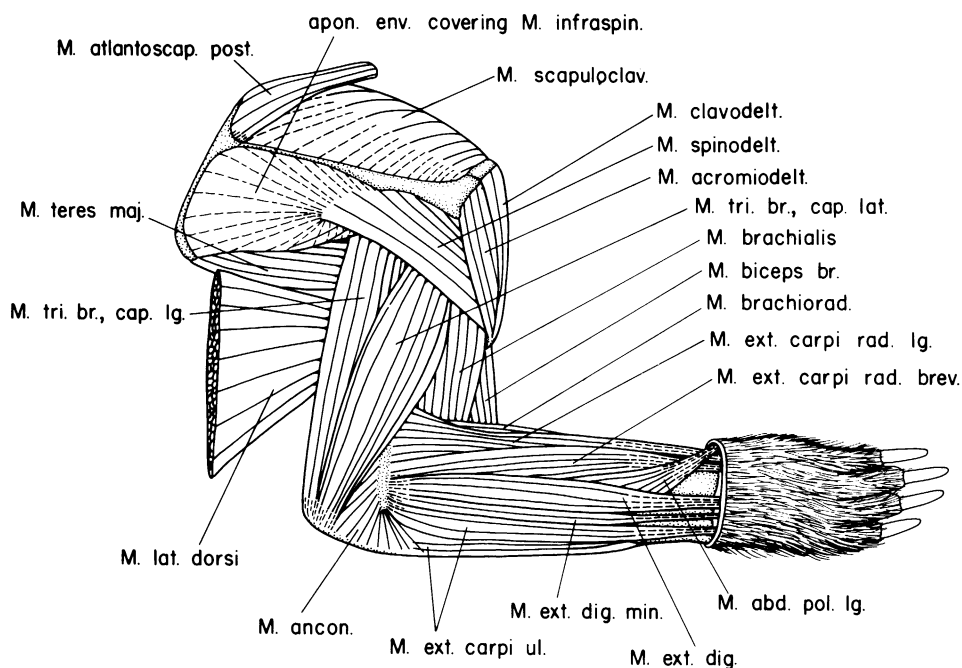


FIG. 3. Lateral view of the superficial muscles of the pectoral appendage of *Erethizon*.

nodelloideus. In two specimens, a few fibers insert onto the deep surface of *M. omocervicalis* near the attachment on the tip of the deltoid crest.

REMARKS: In *Coendou*, there is no insertion onto the deep surface of *M. omocervicalis*.

#### *M. SPINODELTOIDEUS*

Figures 1-3

ORIGIN: The origin of this muscle is complex. It arises by fibers from the distal 20 percent of the caudal edge of the spine of the scapula and the surface of the aponeurotic envelope covering *M. infraspinatus*. The muscle also arises by way of that aponeurosis from the proximal 80 percent of the caudal edge of the scapular spine and the narrow portion of the dorsal surface adjacent to the vertebral border just beyond the origin of *M. infraspinatus*.

INSERTION: By a tough aponeurosis onto the lateral surface of the deltoid crest deep to *M. acromiodeltoideus*.

REMARKS: This description differs somewhat from that of Woods (1972), who reported that in his specimens the origin was from the distal three-fourths of the scapular spine and from the aponeurotic envelope covering *M. infraspinatus*. In some of my specimens, tracing the caudal edge of the muscle through the aponeurosis places the origin at approximately this position. However, this does not work for all specimens. Furthermore, the aponeurotic envelope is extensive, and the portion attached to the dorsal surface of the scapula adjacent to the vertebral border also anchors the muscle. Hence, I believe that it is more precise to include this portion in the description of the origin. Most of the muscle blends inseparably with the aponeurosis. The aponeurotic envelope also attaches to the entire axillary border, although it tends to be weakly developed distally. It is attached to the proximal portion of the long head of the triceps muscle and serves as part of its origin. There is no significant variation in *Coendou*.

**M. TERES MINOR**

Figure 4

**ORIGIN:** Mostly by fibers from the dorsal edge of the distal 38 percent (34–42%) of the axillary border of the scapula and from the deep surface of the portion of the aponeurotic envelope between the muscle and the long head of the triceps.

**INSERTION:** By a short tendon onto the crest of the greater tuberosity just distal to the insertion of *M. infraspinatus*. The most proximal point of insertion is at the level of the epiphyseal line.

**REMARKS:** The muscle lies deep to the aponeurotic envelope described in the remarks for *M. spinodeltoideus*. The origin is covered by *M. infraspinatus*.

There is no significant variation in *Coendou*. The origin is from the distal 34 percent (30–40%) of the axillary border.

**SUPRASCAPULAR GROUP****M. SUPRASPINATUS**

Figures 4, 6

**ORIGIN:** Two closely associated parts of this muscle can be identified. The smaller part arises by fibers from the cranial surface of the spine of the scapula, the deep surface of the spine in the region of the great scapular notch, the intermuscular septum between the muscle and *M. infraspinatus*, and the aponeurosis of *M. scapuloclavicularis* superficial to the muscle. The larger part arises from the entire supraspinous fossa except for a narrow portion adjacent to the vertebral border and from the entire cranial border of the scapula and the adjacent surface of *M. subscapularis*. A few fibers arise from the insertion of *M. omohyoideus*. There is also a small group of accessory fibers on the cranial margin of the muscle near its insertion.

**INSERTION:** The first part blends into the second. The combined parts insert by a tendon onto the dorsocranial surface of the greater tuberosity of the humerus. The accessory fibers blend with the cranial portion of the tendon.

**REMARKS:** The smaller part lies superficial to the larger one. The latter is itself divided proximally into cranial and caudal parts. In two specimens of *Coendou*, the fibers arising

from *M. omohyoideus* were absent. There is no other variation from *Erethizon*.

**M. INFRASPINATUS**

Figure 4

**ORIGIN:** By fibers from the entire infraspinous fossa except for a narrow portion adjacent to the vertebral border, as well as from the caudal surface of the scapular spine proximal to the great scapular notch, the deep surfaces of the metacromion process and the spine in the region of the notch, the intermuscular septum between the muscle and *M. supraspinatus*, the axillary border of the scapula proximal to the origin of *M. teres minor*, and from the aponeurotic envelope covering the muscle.

**INSERTION:** By a tendon onto the caudo-dorsal surface of the greater tuberosity of the humerus.

**REMARKS:** The muscle is multipinnate. Woods (1972) reported that the origin included the vertebral border of the scapula, but I did not observe this in my specimens. I suspect that this discrepancy is due simply to minor differences in the interpretation of the vertebral border, the caudal portion of which is sometimes cartilaginous, depending upon the age of the specimen when preserved. The most proximal edge of origin lies on the boundary between the cartilaginous portion adjacent to the vertebral border and the main portion of the scapula. Since the former would not be preserved in a skeletal preparation, Woods may have labelled the edge of the main portion the "vertebral border" and correctly identified the muscle as arising from it. Woods did not mention the origin from the intermuscular septum between the muscle and *M. supraspinatus*, although he included the septum in his description of the latter. I did not observe any variation in the configuration of this muscle in *Coendou*.

**TRICEPS GROUP****M. DORSOEPITROCHLEARIS**

Figures 1, 5

**ORIGIN:** By fibers from the ventral border of the portion of the tendon of insertion of *M. latissimus dorsi* embedded in muscle

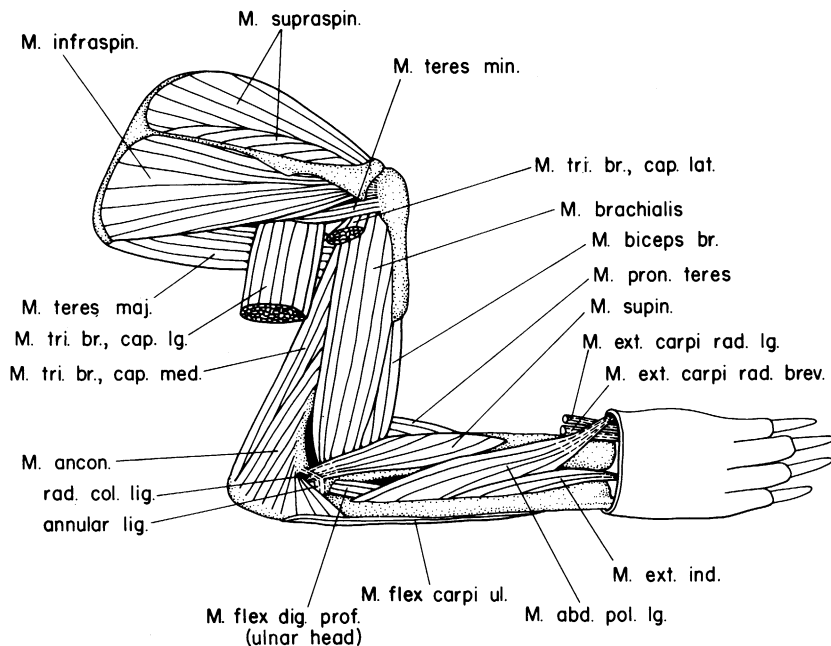


FIG. 4. Lateral view of the deep muscles of the pectoral appendage of *Erethizon*.

fibers. A short caudal segment of the muscle interdigitates with the adjacent fibers.

**INSERTION:** By fibers onto the ventral portion of the proximomedial aspect of the olecranon and into the fascia covering the medial aspect of the forearm.

**REMARKS:** Woods (1972) did not mention the insertion into the fascia of the forearm. There is no significant variation in *Coendou*.

#### M. TRICEPS BRACHII, CAPUT LATERALIS Figures 1-4

**ORIGIN:** By tendon and fibers from the caudolateral surface of the greater tuberosity.

**INSERTION:** Mostly by fibers onto the lateral aspect of the olecranon and into a distal portion of the adjacent surface of the long head of the triceps.

**REMARKS:** The tendinous portion of the origin is flat and lies superficial to the fleshy portion. A few fibers of *M. brachialis* arise from its cranial border. In one specimen of *Coendou*, it continues as an aponeurosis to anchor the proximal portion of the muscle to the surface of *M. brachialis*. There is no other

variation in the configuration of this muscle from *Erethizon*.

#### M. TRICEPS BRACHII, CAPUT MEDIALIS Figures 4-6

**ORIGIN:** The muscle is completely divided into superficial and deep parts, which proximally are difficult to separate. The superficial part arises from the distal 80 percent of the posteromedial surface of the shaft of the humerus between the deep part and the insertion of *M. teres major*. The deep part arises proximally from the posterior and posterolateral surfaces and distally from the posterior surface of the entire length of the shaft of the humerus.

**INSERTION:** The deep part inserts onto the dorsal surface of the olecranon. It also fuses with *M. anconeus* and continues with that muscle to its insertion on the lateral aspect of the olecranon. The superficial part fuses with the deep part and inserts into the medial aspect of the olecranon.

**REMARKS:** The deep part fuses strongly with the deep fibers of *M. anconeus*. The super-

ficial fibers of the latter muscle insert onto the surface of the deep part of the medial head of the triceps but are not as difficult to separate. In *Coendou*, the two parts of the muscle are inseparable and the deep part is completely fused with *M. anconeus*.

**M. TRICEPS BRACHII, CAPUT LONGUS**  
Figures 1-4

**ORIGIN:** By fibers from the distal 27 percent (23-34%) of the axillary border of the scapula and slightly from the aponeurotic envelope between the muscle and *M. teres minor*.

**INSERTION:** Mostly by fibers onto the proximal end of the olecranon.

**REMARKS:** In some specimens, it is difficult to determine if the muscle arises from the aponeurotic envelope or is simply closely associated with it. The envelope is described with *M. spinodeltoideus*. There is a tough, tendinous sheet on the lateral surface in contact with the lateral head, which inserts into the distal portion of this muscle.

There is no significant variation in *Coendou*. The muscle arises from the distal 35 percent (30-43%) from the axillary border.

**M. ANCONEUS**  
Figures 2-4

**ORIGIN:** By fibers from the distal 53 percent (50-55%) of the posterolateral surface of the shaft of the humerus, including the posterior surface of the lateral epicondyle and its crest, and from the distal surface of the lateral epicondyle mediolateral to the origin of *M. extensor carpi ulnaris*.

**INSERTION:** By fibers onto the proximal 31 percent (29-35%) of the lateral aspect of the ulna. The distal portion of insertion fuses slightly with the ulnar origin of *M. extensor carpi ulnaris*.

**REMARKS:** The deep fibers of the muscle are fused with those of the deep part of *M. triceps brachii, caput medialis*. The superficial fibers are closely associated with the surface of that muscle but are not difficult to separate.

In *Coendou*, the muscle is inseparable from the deep part of the medial head of the triceps. The origin is from the distal 36 percent (30-43%) of the shaft of the humerus, less extensive than in *Erethizon*. The muscle

inserts onto the proximal 26 percent (25-26%) of the ulna.

EXTENSOR GROUP OF THE FOREARM

**M. BRACHIORADIALIS**  
Figures 3, 5

**ORIGIN:** By an aponeurosis from the lateral epicondylar ridge of the humerus medial to the proximal portion of the origin of *M. extensor carpi radialis longus* and weakly from the surface of *M. brachialis*.

**INSERTION:** By a short, flat tendon onto the medial surface of the distal end of the shaft of the radius proximal to the styloid process.

**REMARKS:** The muscle is parallel-fibered and straplike distally. Woods (1972) reported that the muscle arose in part from the intermuscular septum between the lateral head of the triceps and the brachialis muscle, but I did not observe a distinct septum in my specimens. He also noted that the insertion was on the styloid process of the radius. The muscle was present in one specimen of *Coendou* with no significant variation in configuration from *Erethizon*.

**M. EXTENSOR CARPI RADIALIS LONGUS**  
Figure 3

**ORIGIN:** By fibers from the lateral epicondylar ridge of the humerus proximal to *M. extensor carpi radialis brevis* and lateral to *M. brachioradialis*. A few fibers arise from the aponeurosis of the latter.

**INSERTION:** By a tendon onto the middle of the dorsomedial surface of the second metacarpal.

**REMARKS:** This muscle is parallel-fibered. The fibers attach superficially to the tendon of insertion, which is visible on the deep surface of the muscle against *M. extensor carpi radialis brevis*. The tendon passes deep to *M. abductor pollicis longus* and the extensor retinaculum medial to that of *M. extensor carpi radialis brevis*. There is no significant variation in *Coendou*.

**M. EXTENSOR CARPI RADIALIS BREVIS**  
Figure 3

**ORIGIN:** By fibers and tendon from the lateral epicondylar ridge distal to *M. extensor*



carpi radialis longus. There is some fusion with *M. extensor digitorum* near the origin.

**INSERTION:** By a tendon onto the middle of the dorsomedial surface of the third metacarpal.

**REMARKS:** This muscle is bipinnate. The tendon of insertion is visible on the medial surface, which lies against *M. extensor carpi radialis longus*. It passes deep to *M. abductor pollicis longus* and the extensor retinaculum lateral to that of *M. extensor carpi radialis longus*. There is no significant variation in *Coendou*.

#### M. EXTENSOR DIGITORUM

Figure 3

**ORIGIN:** Mostly by tendon from the lateral epicondyle of the humerus distal to the origin of *M. extensor carpi radialis brevis* and proximal to that of *M. extensor digiti minimi*, with which it is partially fused.

**INSERTION:** The muscle splits into four tendinous slips which insert onto the dorsal surfaces of the bases of the terminal phalanges of digits 2 through 5.

**REMARKS:** The muscle is difficult to separate from *M. extensor digiti minimi* near the origin. The thin tendons of insertion are bound tightly together on the dorsal surface of the manus by tough fascia, making them difficult to separate. Woods (1972) observed this feature and also noted that there was considerable individual variation in the branching pattern of the tendons in all forms which he dissected. I did not observe such variation in my specimens. The configuration of this muscle in *Coendou* does not vary from that in *Erethizon*.

#### M. EXTENSOR DIGITI MINIMI

Figure 3

**ORIGIN:** By a tendon from the lateral epicondyle distal to the origin of *M. extensor digitorum* and by fibers from the lateral surface of the capitulum.

**INSERTION:** The tendon of insertion bifurcates into two branches which insert into the dorsal surfaces of the bases of the middle phalanges of digits 4 and 5. The tendons then continue distad to fuse with the lateral borders of the tendons of *M. extensor digitorum* to those digits.

**REMARKS:** The muscle is partially fused with *M. extensor digitorum* near the origin. The two branches of the tendon of insertion can be traced from the muscle belly but remain closely associated until they pass onto the dorsum of the manus. They then course distad along the dorsolateral surfaces of the proximal phalanges of digits 4 and 5 before reaching the insertion. The branch to digit 4 passes deep to the tendon of *M. extensor digitorum* to digit 5. Tracing the tendons through the region of the proximal interphalangeal joint is difficult because both they and the tendons of *M. extensor digitorum* are bound by the joint capsule. The portion of the tendon distal to the insertion on the base of the middle phalanx is also difficult to trace through the connective tissue in this region and may be missed in some specimens, especially if the digits are in a somewhat desiccated condition. Woods (1972) traced the insertion to the middle phalanges of the fourth and fifth digits, as well, and noted that in all of the genera which he dissected, the insertion was sometimes on the terminal phalanx of the digit. There is no significant variation in *Coendou*.

#### M. EXTENSOR DIGITI TERTII PROPRIUS

This muscle is absent in all specimens of *Erethizon* that I dissected, but I found it in one specimen of *Coendou*. It arises by a long, narrow tendon from the lateral epicondyle between the origins of *M. extensor digitorum* and *M. extensor digiti minimi*. I could not trace the tendon of insertion past the styloid region of the ulna. Woods (1972) did not observe this muscle in *Erethizon* but noted that Parsons (1894) had described a slip of *M. extensor digiti minimi* inserting on the third digit in *Sphingurus* (= *Coendou*). Woods concluded that Parsons was describing *M. extensor digiti tertii proprius*. Thus, it appears that this muscle is absent in *Erethizon* and occurs sporadically in *Coendou*.

#### M. EXTENSOR CARPI ULNARIS

Figure 3

**ORIGIN:** There are two heads of origin: (1) By a short tendon from the distal surface of the lateral epicondyle between the origins of *M. extensor digiti minimi* and *M. anconeus*;

and (2) By fibers from the ventral portion of 19 percent (16–23%) of the lateral surface of the ulna beginning at a point 29 percent (27–33%) from the proximal end. The proximal point of origin interdigitates slightly with *M. anconeus*.

**INSERTION:** By a tendon onto the ventrolateral surface of the base of the fifth metacarpal.

**REMARKS:** The ulnar origin is not well developed, and in one specimen, it is represented by an aponeurosis with a few embedded muscle fibers. The muscle is parallel-fibered, with most of the fibers attaching to the superficial surface of the tendon of insertion. The tendon passes over a groove on the lateral surface of the styloid process of the ulna in the fifth compartment of the wrist. It then courses distoventrad to reach the insertion. In two specimens of *Coendou*, the ulnar origin is represented by weak fascia and a few fibers. There is no other variation from the conditions in *Erethizon*.

#### M. SUPINATOR

Figure 4

**ORIGIN:** By a strong tendon from the distal portion of the lateral epicondyle deep to the origin of *M. extensor carpi ulnaris* and *M. extensor digiti minimi* and from the annular ligament of the humeroradial joint. The tendon is deep to and closely associated with the radial collateral ligament.

**INSERTION:** By fibers onto 60 percent (51–70%) of the lateral surface of the radius beginning at a point 11 percent (8–15%) from the proximal end. There is some slight fusion with *M. pronator teres*.

**REMARKS:** The tendon of origin is closely associated with but separable from the radial collateral ligament. The muscle is very large. The fibers insert broadly on the radius but form a small angle (approximately 10 degrees or less) to its longitudinal axis.

There is no significant variation in *Coendou*. The muscle inserts on 58 percent (56–62%) of the radius beginning at a point 11 percent (8–14%) from the proximal end.

#### M. EXTENSOR POLLICIS BREVIS

This muscle is absent in both *Erethizon* and *Coendou*.

#### M. ABDUCTOR POLLICIS LONGUS

Figure 4

**ORIGIN:** By fibers from 57 percent (50–64%) of the ulna beginning at a point 25 percent (18–34%) from the proximal end. In two specimens, the muscle arises proximally from the lateral surface at the level of the semilunar notch and distally from the dorsal (interosseous) surface. The muscle also arises from the proximal portion of the surface of the interosseous membrane, including the distinct interosseous ligament, and by fascia and scattered fibers from the interosseous surface of the radius proximal to the attachment of that ligament. In one specimen, the muscle arises from the dorsal surface of the ulna and from the interosseous membrane and adjacent surface of the radius distal to the attachment of the interosseous ligament. The origin does not extend proximally onto the lateral surface of the ulna or the proximal portion of the radius.

**INSERTION:** There are two closely associated tendons of insertion. The main tendon inserts on the ventrolateral surface of the base of the first metacarpal. The accessory tendon inserts on the radial side of the falciform bone on the volar surface of the manus.

**REMARKS:** The interosseous ligament is very distinct in all of my specimens and represents the proximal portion of the interosseous membrane. It passes from the interosseous surface of the ulna in a distomedial direction to attach to 12 percent (11–15%) of the interosseous surface of the radius beginning at a point 36 percent (32–39%) from the proximal end. In two specimens, much of the origin from the interosseous membrane is from this ligament. Woods (1972) reported that the origin was from the ulna, the proximal end of the radius, and the interosseous membrane. In my specimens, the origin from the proximal portion of the radius is poorly developed when present. However, in one specimen, the origin from the distal portion of the radius is well developed. Woods (1972) did not distinguish the interosseous ligament from the rest of the interosseous membrane.

The muscle fibers converge to reach the tendons of insertion superficially. Both tendons course distomedially through the first compartment of the wrist over a groove on the styloid process of the radius. The acces-

sory tendon is the more superficial of the two and crosses the path of the main tendon to insert on the falciform bone.

In *Coendou*, the muscle arises from a portion of the interosseous membrane distal to the interosseous ligament and from 61 percent (59–64%) of the ulna beginning at a point 19 percent (17–22%) from the proximal end. The origin extends proximally on the lateral surface of the ulna to the level of the semilunar notch. The muscle does not arise from the proximal portion of the radius. In two specimens, a few fibers arise from the interosseous surface of the radius distal to the interosseous ligament, which attaches to 10 percent (6–16%) of the radius beginning at a point 31 percent (30–32%) from the proximal end.

#### M. EXTENSOR INDICIS

##### Figure 4

**ORIGIN:** By fibers from the lateral and dorsolateral surfaces of 27 percent (22–30%) of the ulna beginning at a point 54 percent (48–63%) from the proximal end and weakly from the surface of *M. abductor pollicis longus* proximally in two specimens.

**INSERTION:** The tendon of insertion bifurcates on the dorsum of the manus. The main branch inserts onto the dorsal surface of the base of the middle phalanx of the second digit and then continues distad to fuse with the tendon of *M. extensor digitorum*. The medial branch inserts on the medial surface of the pollex.

**REMARKS:** There is some variation in the configuration of the origin. In one specimen, the muscle arises from the dorsolateral surface of the ulna and the surface of *M. abductor pollicis longus*. In another, the origin from *M. abductor pollicis longus* is absent. The muscle is slightly convergent and lies deep to *M. extensor digiti minimi* and *M. extensor digitorum*. Its tendon of insertion courses through the same compartment of the wrist as those two muscles. The main branch passes deep to the tendon of *M. extensor digitorum* to the second digit and then courses along the dorsolateral surface of the proximal phalanx. As with *M. extensor digiti minimi*, the portion of the tendon distal to the insertion on the base of the middle phalanx is difficult to trace and may be missed in some specimens.

Woods (1972) noted that the precise location of the insertion was difficult to determine but suggested that it was on the middle phalanx. The medial branch, somewhat wider and thinner than the main one, courses mediad to insert on the pollex.

In *Coendou*, the muscle arises from the dorsolateral surface of 26 percent (25–28%) of the ulna beginning at a point 57 percent (52–63%) from the proximal end. The muscle arises slightly from the surface of *M. abductor pollicis longus* in two specimens. In one specimen, the insertion to the pollex is represented by a wide band of fascia, whereas in another, the medial branch of the tendon is embedded in the proximal portion of this fascial band.

#### FLEXOR SYSTEM

##### PECTORAL GROUP

#### M. SUBCLAVIUS

##### Figure 5

**ORIGIN:** By fibers from the sternal end of the first costal cartilage and the adjacent surface of the manubrium.

**INSERTION:** In two specimens, the muscle inserts by fibers onto 45 percent (44 and 47%) of the caudoventral surface of the clavicle beginning at a point 29 percent (33 and 24%) from the sternal end. A group of caudal fibers fuses with the deep surface of *M. scapuloclavicularis*. In one specimen, the insertion is onto the acromial 67 percent of the clavicle. In this case, the caudal fibers insert onto the most distal portion of the clavicle and are closely associated but do not fuse with *M. scapuloclavicularis*.

**REMARKS:** In *Coendou*, the insertion is onto the acromial 55 percent (46–60%) of the clavicle beginning at a point 45 percent (40–54%) from the sternal end. Hence, the insertion begins farther distally than in *Erethizon*. Some of the caudal fibers fuse with *M. scapuloclavicularis*.

#### M. SCAPULOCLAVICULARIS

##### Figures 1, 3

**ORIGIN:** By fibers from the acromial 61 percent (54–69%) of the dorsocaudal edge of the clavicle.

**INSERTION:** By a broad aponeurosis onto

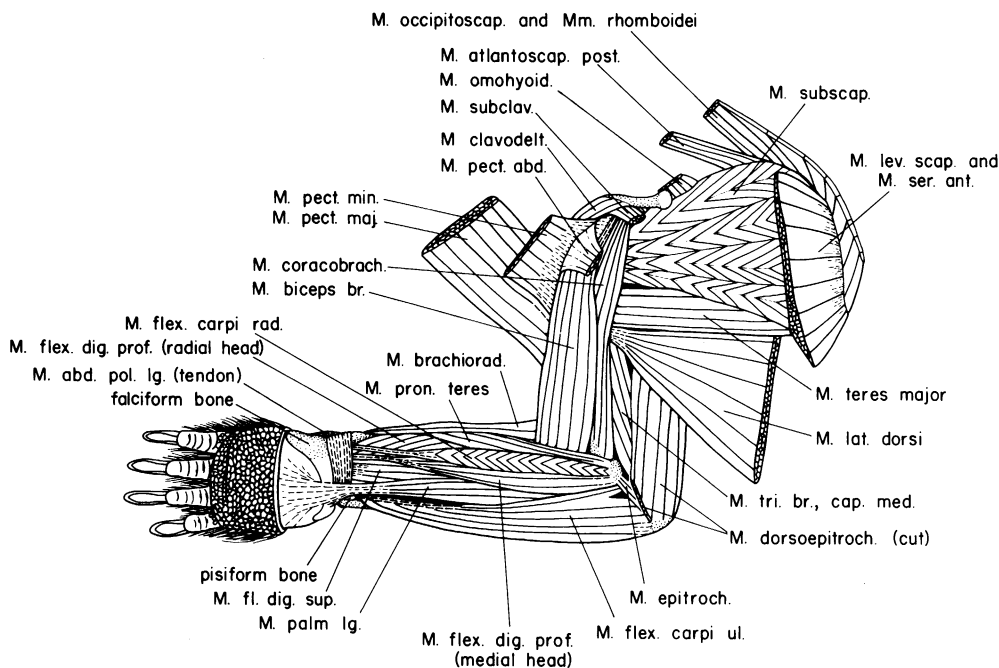


FIG. 5. Medial view of the superficial muscles of the pectoral appendage of *Erethizon*.

the vertebral border of the scapula cranial to the spine, onto the cranial surface of the spine, and slightly onto the surface of *M. supraspinatus*.

**REMARKS:** There is no significant variation in *Coendou*. The muscle arises from the acromial 61 percent (57–65%) of the clavicle.

#### M. PECTORALIS MAJOR

Figure 5

**ORIGIN:** By fibers from the ventral midline of the manubrium sterni and from the first three sternabrae in two specimens and first two sternabrae in one specimen.

**INSERTION:** Proximally by aponeurosis and distally by fibers onto the medial surface of the deltoid crest of the humerus beginning at a point 21 percent (19–23%) from the proximal end and extending to a point 3 to 5 mm. distal to the tip (the most prominent point) of the crest. A small group of fibers distal to this point fuses with *M. cutaneus maximus, pars dorsalis* and is anchored by connective tissue to the edge of the deltoid crest and surface of *M. brachialis*.

**REMARKS:** In all specimens, the superficial part of this muscle is only slightly separable from the major portion. This observation was also made by Woods (1972). The muscle is closely associated with but separable from *M. clavodeltoideus*.

In *Coendou*, the origin is from the manubrium and the first three sternabrae. The insertion is mostly by fibers beginning at a point 22 percent (20–23%) from the proximal end of the humerus and extending to a point as much as 4 mm. distal to the tip of the deltoid crest. As in *Erethizon*, there is some fusion with *M. cutaneus maximus, pars dorsalis*.

#### M. PECTORALIS MINOR

Figure 5

**ORIGIN:** By fibers from the second sternabra to the cranial end of the xiphisternum. A few fibers arise from the ventral surfaces of the sternal ends of the third or fourth through seventh costal cartilages.

**INSERTION:** By aponeurosis onto the tip of the coracoid process, the medial edge of the



tendon of *M. supraspinatus*, and the medial surfaces of the greater tuberosity and deltoid crest deep to *M. pectoralis major*. The insertion is onto the proximal 36 percent (35–37%) of the humerus.

REMARKS: Woods (1972) did not observe the insertion onto the tendon of *M. supraspinatus* in his specimens. In *Coendou*, the origin includes the ventral surfaces of the sternal ends of costal cartilages 3 through 7. The insertion is not as extensive as in *Erethizon* and is onto the proximal 24 percent (23–26%) of the humerus.

#### M. PECTORALIS ABDOMINALIS

Figure 5

ORIGIN: By fibers from the ventral surface of the xiphisternum and from the cranial portion of the linea alba.

INSERTION: In two specimens, the muscle inserts by aponeurosis onto the proximal portion of the medial surface of the deltoid crest deep to the insertion of *M. pectoralis minor*. In one specimen, the insertion is onto the coracoid process, the medial surface of the tendon of *M. supraspinatus*, and the greater tuberosity of the humerus.

REMARKS: A few fibers at the origin lie deep to *M. pectoralis minor*. On one side of one specimen, an extra slip is present cranial to the main part of the muscle and entirely deep to *M. pectoralis minor*. It arises by aponeurosis from the third sternabra to the cranial end of the xiphisternum and fuses with the main part near the insertion.

In *Coendou*, the origin of the muscle is confined to the xiphisternum, with a few fibers extending superficial to the caudal portion of *M. pectoralis minor*. The muscle inserts onto the proximal portion of the deltoid crest by a weak aponeurosis that blends proximally with that of *M. pectoralis minor*.

#### FLEXOR GROUP OF THE ARM

##### M. CORACOBRACHIALIS

Figures 5, 6

ORIGIN: By a tendon from the coracoid process of the scapula in common with the short head of *M. biceps brachii*.

INSERTION: By fibers onto the medial border of 26 percent (19–36%) of the humerus beginning at a point 56 percent (54–60%) from

the proximal end. In two specimens, the insertion includes the medial epicondylar ridge as far distally as the origin of *M. pronator teres*. In one specimen, the insertion is confined to the shaft of the humerus.

REMARKS: The insertion lies 5 to 11 mm. distal to that of *M. teres major*. Woods (1972) noted that there were three possible parts of insertion of this muscle in hystricomorphs: a short part lying proximal to the musculocutaneous nerve and the common insertion of *M. teres major* and *M. latissimus dorsi*; a middle part inserting on the middle of the humerus distal to the musculocutaneous nerve and the common insertion of *M. teres major* and *M. latissimus dorsi*; and a long part inserting onto the medial epicondylar ridge. In *Erethizon*, the middle and, in some specimens, both the middle and long parts are present. Woods (1972) noted that the median nerve passed between both parts, but I did not observe this condition in my specimens.

Both parts are present in all of my specimens of *Coendou*. The muscle inserts onto 31 percent (22–36%) of the humerus beginning at a point 55 percent (52–60%) from the proximal end. As in *Erethizon*, the median nerve did not pass between the two parts. However, Parsons (1894) reported that the alternative condition existed in *Sphingurus* (= *Coendou*). Therefore, this condition seems to be variable in both *Erethizon* and *Coendou*.

##### M. BICEPS BRACHII

Figures 2–6

ORIGIN: The short head arises by a tendon from the tip of the coracoid process in common with *M. coracobrachialis*. The long head arises by a tendon from the lip of the glenoid fossa and the base of the coracoid process.

INSERTION: The muscle belly divides into two heads of insertion. The more proximal ulnar head inserts by a small tendon onto the proximal portion of the brachial ridge of the ulna proximal to the insertion of *M. brachialis*. The distal radial head inserts by a strong, flattened tendon onto the radial tuberosity.

REMARKS: The tendon of the long head passes through the bicipital groove and emerges from under the shoulder joint cap-

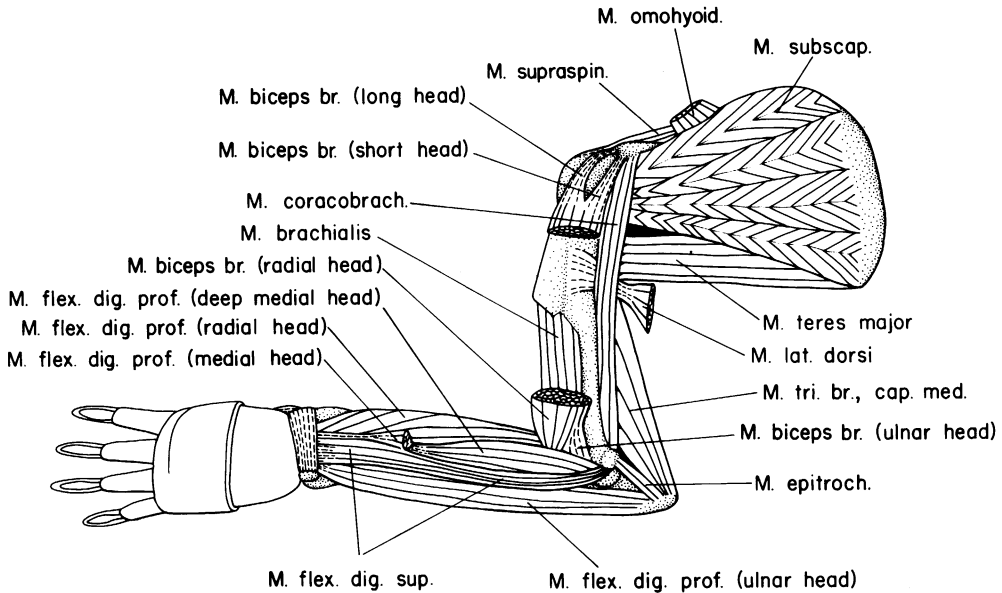


FIG. 6. Medial view of the deep muscles of the pectoral appendage of *Erethizon*.

sule before giving rise to the muscle fibers. The long and short heads fuse to form an extremely large muscle belly which becomes compressed near the insertion when it passes between *M. pronator teres* and *M. brachialis*. The insertion is dominated by the radial head with a relatively small proximal component forming the ulnar portion. *M. brachialis* passes between the two heads as it reaches its insertion. In one specimen, the ulnar head is represented by a thin fascia with a few embedded muscle fibers attached to the surface of *M. brachialis*. In *Coendou*, the configuration of this muscle does not vary from that in *Erethizon*.

#### M. BRACHIALIS

Figures 1-4, 6

**ORIGIN:** The muscle arises by two heads. (1) The long head arises by fibers from the posterolateral and posterior surfaces of the neck of the humerus deep to the lateral head of the triceps, from the lateral surface of the deltoid crest deep to the insertion of *M. spinodeltoideus*, and from the adjacent anterolateral surface of the shaft of the humerus. A few fibers arise from the proximal portion of

the lateral head of the triceps. (2) The medial head arises by fibers from the anterior edge of the deltoid crest distal to its tip (the most prominent point), with a few fibers arising from its medial surface, and from the anterolateral, anterior, and anteromedial surfaces of the shaft distal to this level. The entire origin is from the proximal 84 percent (83-85%) of the shaft of the humerus.

**INSERTION:** By fibers and tendon onto the brachial ridge of the ulna distal to the insertion of the ulnar head of *M. biceps brachii*.

**REMARKS:** The two heads of origin are partially separable laterally. The long head is larger than the medial. Woods (1972) noted that the origin of the long head was restricted to the neck of the humerus and did not arise from the deltoid crest or humeral shaft. The medial head was found to arise only from the tip of the deltoid crest and the anteromedial surface of the shaft. However, in my specimens, the origin includes the distal portion of the anterior and anterolateral surfaces as well. The muscle passes between the ulnar and radial heads of *M. biceps brachii* before reaching the insertion. Woods (1972) reported that part of the insertion lay proximal to the

ulnar head, but this is not the case in my specimens.

On one side of one specimen, the major portion of the long head does not fuse strongly to the medial portion of the muscle. It instead courses distad into the antebrachium medial to *M. brachioradialis* and inserts by a tendon onto the distal end of the shaft of the radius ventral to the insertion of the latter. Although this portion of the muscle has a similar insertion to *M. brachioradialis* and may be confused with that muscle, it is innervated by both the musculocutaneous and radial nerves. The configuration of the deeper fibers of the long head that arise from the deltoid crest and shaft of the humerus is as previously described.

There is no significant variation in *Coendou*. The muscle arises from the proximal 87 percent (86–87%) of the shaft of the humerus.

#### FLEXOR GROUP OF THE FOREARM

##### *M. EPITROCHLEOANCONEUR*

Figures 5, 6

**ORIGIN:** By fibers from the caudomedial surface of the distal portion of the medial epicondyle of the humerus and from the adjacent surface of the epicondylar origin of *M. flexor carpi ulnaris*.

**INSERTION:** The fibers pass distocaudad to insert on a well-developed ridge on the medial aspect of the olecranon distal to the insertion of the medial head of the triceps and partly deep to the ulnar origin of *M. flexor carpi ulnaris*.

**REMARKS:** The muscle is closely associated with but separable from the medial head of the triceps. The ulnar nerve passes deep to the muscle. In one specimen of *Coendou*, the muscle is thinner and the origin is aponeurotic. There is no other significant variation.

##### *M. FLEXOR CARPI ULNARIS*

Figures 4, 5

**ORIGIN:** There are two heads of origin. (1) The epicondylar head arises by tendon and fibers from the lateral surface of the distal portion of the medial epicondyle caudodistal to the origin of the medial head of *M. flexor digitorum profundus* and caudal to that of *M. palmaris longus* and from the adjacent

surface of *M. epitrochleoanconeus*. (2) The ulnar head arises by fibers from the edge of a prominent ridge on the medial aspect of the olecranon distal to the insertion of *M. dorsoepitrochlearis* and by aponeurosis from the medioventral surface of the olecranon and the proximal half of the ventral surface of the ulna adjacent to the ulnar head of *M. flexor digitorum profundus*. This aponeurosis continues distad to anchor the rest of the lateral border of the muscle to the lateral edge of the ventral ulnar surface between the ulnar head of *M. flexor digitorum profundus* and *M. extensor carpi ulnaris*.

**INSERTION:** By a strong tendon onto the ventral portion of the proximal surface of the pisiform bone.

**REMARKS:** The epicondylar head is small. The aponeurosis that attaches the muscle to the ventral surface of the ulna passes over the surface of the ulnar head of *M. flexor digitorum profundus*. The muscle is bipinnate, with the ulnar fibers reaching the lateral surface and the epicondylar fibers reaching the medial surface. The ulnar fibers extend farther distally, giving the distal portion of the muscle a unipinnate appearance. The muscle is closely associated with but separable with some difficulty from *M. palmaris longus*. There is no significant variation in *Coendou*.

##### *M. PALMARIS LONGUS*

Figure 5

**ORIGIN:** By a long, narrow tendon from the distal surface of the medial epicondyle distal to the origin of the medial head of *M. flexor digitorum profundus*, cranial to that of the epicondylar head of *M. flexor carpi ulnaris*, and proximomedial to that of *M. flexor digitorum superficialis*.

**INSERTION:** By a thin tendon onto the ulnar portion of the large falciform bone and into the fascia of the palm.

**REMARKS:** The muscle is closely associated but separable with some difficulty from *M. flexor carpi ulnaris* and the medial head of *M. flexor digitorum profundus* proximally. There is also a close association but no fusion with *M. flexor digitorum superficialis*. The falciform bone has its main center of ossification on the radial side of the palm but has an extensive cartilaginous portion which

reaches the ulnar side. The tendon of insertion passes over the ventral surface of the pisiform bone and fans out to insert onto the ulnar portion of this cartilaginous extension and the fascia of the palm. In one specimen of *Coendou*, the tendon of origin is thin and poorly developed. There is no other significant variation from *Erethizon*.

#### M. FLEXOR CARPI RADIALIS

Figure 5

**ORIGIN:** By fibers and tendon from the medial epicondyle of the humerus distal to the origin of *M. pronator teres* and proximal to that of the medial head of *M. flexor digitorum profundus*. The muscle is fused with *M. pronator teres* near the origin.

**INSERTION:** By a tendon onto the bases of the second and third metacarpals.

**REMARKS:** The muscle is bipinnate. The well-developed tendon of insertion passes through its own compartment of the wrist medial to the large tendon of *M. flexor digitorum profundus* and against the scapholunar bone. It then passes deep to an intrinsic adductor muscle of the manus and becomes wider without bifurcating to insert on the bases of the second and third metacarpals. In one specimen, a small accessory tendon separates from the dorsal surface of the main tendon and inserts on the scapholunar bone. There is no significant variation in *Coendou*. No accessory tendon was observed.

#### M. PRONATOR TERES

Figures 4, 5

**ORIGIN:** Mostly by fibers from the cranial surface of the proximal portion of the medial epicondyle proximal to the origin of *M. flexor carpi radialis*. The muscle is fused with *M. flexor carpi radialis* near the origin.

**INSERTION:** Broadly by fibers on the cranial (dorsal) edge of the medial surface of 43 percent (39–46%) of the radius beginning at a point 30 percent (20–38%) from the proximal end.

**REMARKS:** The muscle is massive proximally and diverges considerably to reach the broad insertion. Woods (1972) reported that the insertion was on the distal half of the

craniomedial surface of the radius, but in my specimens, the insertion did not extend all the way to the distal end. Further, the cranial (dorsal) surface is crestlike for much of its length, a feature which is accentuated by the concavity of the medial surface of the radius. Therefore, there is no true craniomedial surface of the radius in the region of the insertion. In *Coendou*, the insertion is on 34 percent (33–35%) of the radius beginning at a point 33 percent (32–38%) from the proximal end.

#### M. FLEXOR DIGITORUM SUPERFICIALIS

Figures 5, 6

**ORIGIN:** Mostly by fibers from the distal surface of the medial epicondyle distolateral to the origin of *M. palmaris longus*.

**INSERTION:** The muscle gives rise to four tendons which insert deep to the subsidiary tendons of *M. flexor digitorum profundus* on the bases of the middle phalanges of the lateral four digits (see remarks).

**REMARKS:** The proximal portion of the muscle lies deep to *M. palmaris longus*, the epicondylar origin of *M. flexor carpi ulnaris*, and partially deep to the medial head of *M. flexor digitorum profundus*. The distal portion becomes superficial and, as it nears the wrist, lies lateral to the medial head of *M. flexor digitorum profundus* and medial to *M. palmaris longus*. The muscle divides into four tendinous slips which pass through the carpal tunnel superficial (ventral) to the tendon of *M. flexor digitorum profundus*. Each tendon passes deep to a fibrous connective tissue loop attached to the medial and lateral sesamoids at the metacarpophalangeal joint. Just before doing so, each gives rise to a tendinous loop which passes around the subsidiary tendon of *M. flexor digitorum profundus*. It then bifurcates, sending medial and lateral branches distad around the tendon of *M. flexor digitorum profundus*. These branches fuse just before reaching their insertion on the base of the middle phalanx. The tendon to the fifth digit is smaller in diameter than those to the other three digits. There is no significant variation of the configuration of this muscle in *Coendou*.

**M. FLEXOR DIGITORUM PROFUNDUS**

Figures 5, 6

**ORIGIN:** The muscle arises by four heads.

(1) The medial head arises mostly by fibers from the tip and distal portion of the cranial surface of the medial epicondyle distal to the origin of *M. flexor carpi radialis*, proximal to that of *M. palmaris longus*, and superficial to the deep medial head. (2) The deep medial head arises by tendon and fibers from the cranial surface of the medial epicondyle deep to the medial head and distal to the deep portion of origin of *M. flexor carpi radialis*. (3) The radial head arises from the medial surface of 52 percent (50–56%) of the radius beginning at a point 21 percent (20–22%) from the proximal end at the level of the radial tuberosity. (4) The ulnar head arises from the ventral, medial, and dorsomedial surfaces of 68 percent (67–69%) of the ulna beginning at a point 9 percent (9–11%) from the proximal end. The origin includes the medial surface of the olecranon deep to *M. epitrochleoanconeus* and distal to the insertion of the medial head of the triceps. In one specimen, the origin includes the adjacent portion of the interosseous membrane.

**INSERTION:** The four heads unite in the region of the wrist to form a large common tendon which then divides into four subsidiary tendons that insert on the well-developed tubercles on the bases of the terminal phalanges of digits 2 through 5.

**REMARKS:** The medial head is fused slightly with *M. palmaris longus* and partially covers the proximal portion of *M. flexor digitorum superficialis*. The deep medial head is flattened and lies between the other heads of origin. The radial and ulnar heads are large and closely associated throughout their lengths but are separable with varying degrees of difficulty. The ulnar head lies deep to *M. flexor carpi ulnaris* and the aponeurosis that anchors that muscle to the ulna. Each of the subsidiary tendons of insertion passes through the tendinous loop formed by the tendon of *M. flexor digitorum superficialis* to reach the insertion on the distal phalanx. There is no tendon of insertion to the pollex.

The configuration of this muscle is not significantly different in *Coendou*. The radial

head arises from 50 percent (46–54%) of the radius beginning at a point 21 percent (20–22%) from the proximal end. The ulnar head arises from 68 percent (67–68%) of the ulna beginning at a point 5 percent (4–6%) from the proximal end. In all specimens, this head arises from the adjacent portion of the interosseous membrane. It is separable from the radial head with difficulty.

**MM. LUMBRICALES**

**ORIGIN:** There are four of these muscles present. The lateral three arise by fibers from the angles formed by the subsidiary tendons of *M. flexor digitorum profundus* and slightly from the ventral surface of the common tendon of that muscle. The medial lumbrical arises from the medial surface of the subsidiary tendon of *M. flexor digitorum profundus* to the second digit.

**INSERTION:** By small tendons onto the middle of the ventral edges of the medial surfaces of the proximal phalanges of digits 2 through 5.

**REMARKS:** There is no significant variation of these muscles in *Coendou*.

**M. PRONATOR QUADRATUS**

**ORIGIN:** By fibers from the dorsal surface of the distal 25 percent (24–25%) of the ulna.

**INSERTION:** By fibers onto the interosseous border and medial surface of the distal 28 percent (28–29%) of the radius.

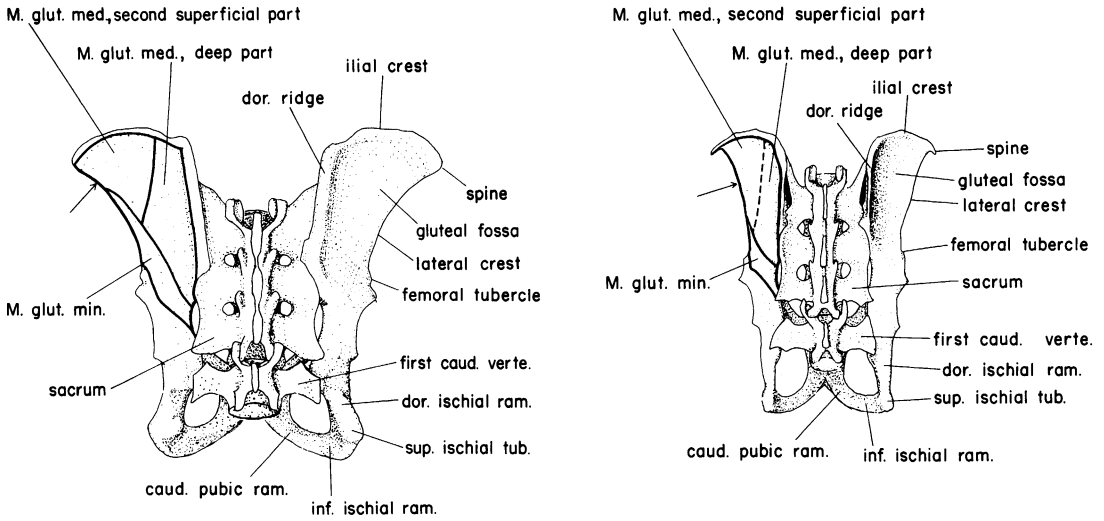
**REMARKS:** The border between the dorsal and medial surfaces of the ulna is marked by a crest in the region of the origin. The muscle does not extend onto the styloid processes of the radius or ulna.

There is no significant variation in *Coendou*. The muscle arises from the distal 29 percent (27–32%) of the ulna and inserts onto the distal 29 percent (28–31%) of the radius.

**MUSCLES OF THE PELVIC GIRDLE AND LIMB**

Some of the terminology used by Rinker (1954) and Klingener (1964) to identify parts of the os coxa is not appropriate for erethizontids. Both studies follow the terminology of Hill (1937) with some modifications. Hill





FIGS. 7, 8. (7) left. Dorsal view of the pelvis of *Erethizon* and (8) right, *Coendou*. The origins of *M. gluteus medius* and *M. gluteus minimus* are shown on the left of each figure. The arrow indicates the most proximal extent of the origin of *M. gluteus minimus* from the lateral crest.

(1937) described the cranial end of the ilium of *Thomomys* (Geomyidae) as consisting of a tubercle and a crest. The latter, not given a specific name, forms a spine laterally. I have chosen to follow Howell (1926) and designate the crest at the cranial end of the ilium the "ilial crest" (figs. 7 and 8).

Hill (1937) identified dorsal and ventral tuberosities of the ischium (the superior and inferior ischial tuberosities of Howell, 1926; Rinker, 1954; and Klingener, 1964) and placed the symphysis between the ischium and pubis distal to the ventral tuberosity. He admitted that his young specimens of *Thomomys* did not clearly show the symphysis between the ischium and pubis, but he inferred its position from the shape of the os coxa. Howell (1926) showed the symphysis in a similar position for *Neotoma*. In *Erethizon* and *Coendou*, the superior ischial tuberosity is present, and there is an inconspicuous tuberosity in the same position as the inferior one described above. However, in one young specimen of *Erethizon* (my collection) and one of *Coendou* (AMNH 210337), the symphysis between the ischium and pubis lies dorsal to the latter tuberosity, as shown in figure 9. That tuberosity is actually located on the pubis, not the ischium. However, I

have retained the term "superior ischial tuberosity" in my descriptions.

Hill (1937) described the pubis in geomyids as a straight bar forming the ventral border of the os coxa. It consisted of the body and ventral ramus, with the dorsal ramus being absent. This terminology was followed by Rinker (1954) and Klingener (1964). The pubis in erethizontids consists of a cranial ramus, body, and caudal ramus. This terminology is based on that of Cooper and Schiller (1975).

## EXTENSOR SYSTEM

### ILIACUS GROUP

#### *M. ILIACUS*

Figures 11–13, 16–18

**ORIGIN:** By fibers from the iliac fossa and the lateral portion of the ventral surface of the transverse process of the first sacral vertebra.

**INSERTION:** By a common tendon with *M. psoas major* onto the craniomedial surface of the lesser trochanter of the femur.

**REMARKS:** In all specimens, the muscle does not arise from a narrow cranial portion of the iliac fossa and the transverse process of the first sacral vertebra, but the width and extent

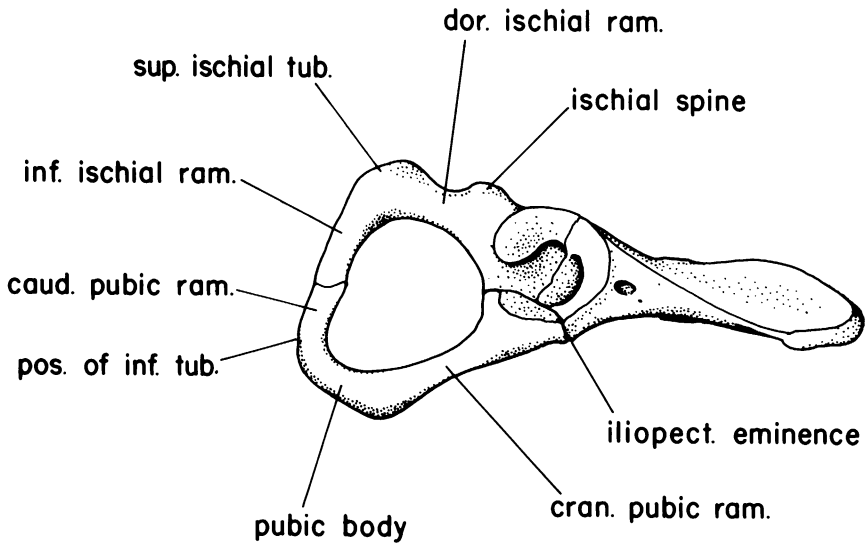


FIG. 9. Lateral view of the pelvis of a juvenile specimen of *Erethizon*.

of this portion are individually variable. The muscle is difficult to separate from *M. psoas major*. Both are inseparable at the insertion. The contribution of *M. iliacus* to the common insertion is much larger and lies deep and distal to that of *M. psoas major*.

In *Coendou*, the muscle arises from nearly all of the iliac fossa, except for a very small cranial portion in some specimens. The origin from the transverse process of the first sacral vertebra is as in *Erethizon* in one specimen, from the full length of the lateral portion of the transverse process in another, and from the craniolateral edge in a third. This variation does not have any apparent functional significance.

#### *M. PSOAS MAJOR*

Figures 16, 17

**ORIGIN:** By fibers from the surfaces of the vertebral bodies, transverse processes, and intervertebral discs of the last four lumbar vertebrae and from the cranial and medial portions of the ventral surface of the transverse process of the first sacral vertebra medial to the origin of *M. iliacus*. The origin is from the lateral surface of the body of the fourth to last and that of the cranial portion of the

third to last lumbar vertebrae deep (dorsal) to that of *M. psoas minor*. It also includes the ventrolateral surface of the body of the caudal portion of the third to last and the body of the second to last lumbar vertebra. In two specimens, the origin from the body of the last lumbar vertebra is from the lateral surface dorsal to the origin of *M. flexor caudae lateralis*. In one specimen, it also includes the ventrolateral surface and does not lie dorsal to that muscle.

**INSERTION:** By a flat tendon onto the craniomedial surface of the lesser trochanter in common with *M. iliacus*.

**REMARKS:** Distally, the muscle is difficult to separate from *M. iliacus*. The origin extends to the caudal edge of the ventral surface of the transverse process of the first sacral vertebra in two specimens but does not extend that far caudally in one. The tendon is inseparable from and lies proximosuperficial to that of *M. iliacus* near the insertion.

In two specimens of *Coendou*, the origin is from the bodies and transverse processes of the last four lumbar vertebrae and the medial portion of the transverse process of the first sacral vertebra. In one of these specimens, the muscle also arises from a short cranial portion of the body of the first sacral

vertebra dorsal to the origin of *M. flexor caudae lateralis*. In one specimen, the muscle arises from the last five lumbar vertebrae and the medial portion of the transverse process of the first sacral vertebra. The origin from the last lumbar vertebra lies dorsal to that of *M. flexor caudae lateralis*. Thus, there is a great deal of variation in the configuration of the origin of this muscle. This variation is not functionally significant.

#### *M. PECTINEUS*

Figures 16, 17

**ORIGIN:** Mostly by fibers from the surface of the small tubercle on the cranial pubic ramus dorsal (cranial) to the origin of *M. adductor longus* and from the lateral surface of the pubis ventral to the acetabulum.

**INSERTION:** Onto the caudomedial and caudal surfaces of 24 percent (22–25%) of the femur beginning at a point 33 percent (29–35%) from the proximal end. The proximal portion of the insertion is mostly by fibers onto the caudomedial and medial portion of the caudal surfaces of the femur beginning at the point where the lesser trochanter fuses with the shaft. The distal portion inserts by fibers and aponeurosis onto the caudomedial surface of the femoral shaft medial to the insertion of *M. adductor longus*.

**REMARKS:** The muscle consists of two closely associated but completely separable parts. The ventral (caudal) part arises from the small tubercle on the cranial ramus and forms the proximal portion of the insertion. The dorsal (cranial) part arises from that portion of the cranial pubic ramus ventral to the acetabulum and forms the distal portion of the insertion. In one specimen, the caudal portion of the dorsal part lies ventral to a cranial portion of the ventral part.

In *Coendou*, there is no significant variation in the origin of the muscle, but the two parts are difficult to separate. The caudal portion of the dorsal part lies deep to a cranial portion of the ventral part. The insertion extends farther distally onto 32 percent (30–34%) of the femur beginning at a point 25 percent (23–26%) from the proximal end. In all specimens, most of the insertion lies medial to that of *M. adductor longus* because of the more extensive development of the

latter. However, in one specimen, the muscle is divided into medial and lateral parts at the insertion. The ventral portion arising from the small tubercle on the cranial ramus becomes the lateral part, which inserts broadly by fibers and aponeurosis onto the caudal surface of the femoral shaft between the insertions of the medial part and *M. adductor longus* proximally and on the caudomedial surface of the shaft distally. The dorsal portion becomes the medial part, which inserts by fibers onto the caudomedial and caudal femoral surfaces proximally and caudomedial surface distally. This part is thicker and does not extend as far distally as the former.

#### GLUTEAL GROUP

##### *M. TENSOR FASCIA LATA*

Figures 10–13, 16–18

**ORIGIN:** By fibers from the iliac spine and via the gluteal portion of the lumbodorsal fascia from the ilial crest. Some specimens have a slightly fleshy origin from the extreme cranial portion of the lateral crest of the ilium.

**INSERTION:** The cranial fibers arising from the spine of the ilium insert onto the medial portion of the proximal surface of the patella. Those arising by the lumbodorsal fascia from the ilial crest insert by fascia onto the proximal and lateral surfaces of the patella superficial to and closely associated with the fascia of insertion of *M. femorococcygeus* and into a small distal portion of the lateral surface of the femur continuous with the insertion of *M. gluteus maximus*.

**REMARKS:** This muscle is completely continuous with *M. gluteus maximus* and is inseparable from it except on the basis of innervation. It is difficult to define precisely the boundary between the insertions of these two muscles because both insert by a continuous fascial sheet.

In *Coendou*, the muscle is visually distinguishable from *M. gluteus maximus*, but the two are connected by a sheet of fascia that contains the caudal fibers of *M. tensor fascia lata*. The cranial portion is well developed and inserts by fibers onto the proximal surface of the patella. The fascial sheet is difficult to trace to the patella and femur. It blends with the aponeurosis of *M. femorococcygeus* and into the distal portion of the surface of

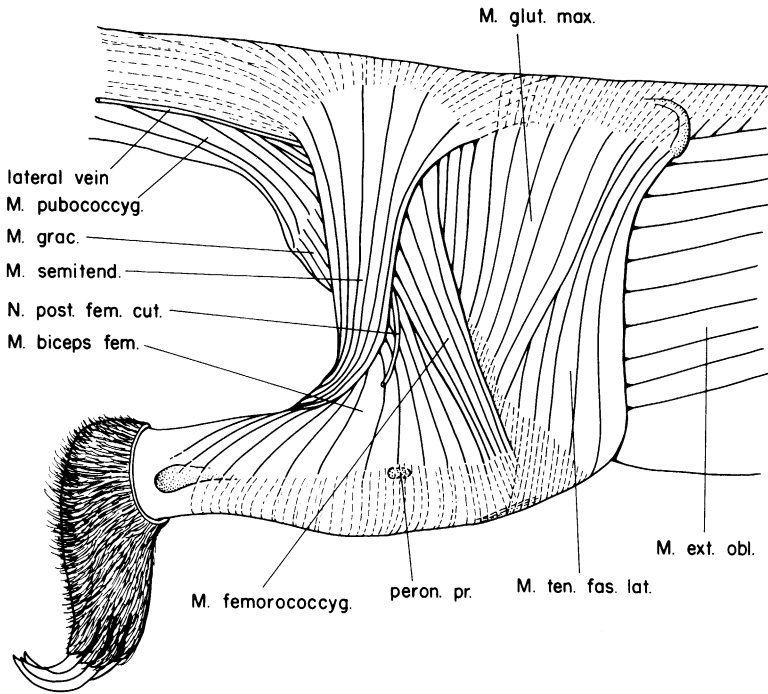


FIG. 10. Lateral view of the pelvic appendage of *Erethizon*. I. Superficial muscles.

*M. vastus lateralis*. In one specimen and on one side of another, the caudal fibers are weakly developed. On the opposite side of the latter and in a third specimen, they are well developed, and the configuration of the muscle approaches that in *Erethizon*.

#### M. GLUTEUS MAXIMUS

Figures 10, 11

**ORIGIN:** From the gluteal portion of the lumbodorsal fascia from the level of the first sacral to the first caudal vertebra.

**INSERTION:** By aponeurosis onto the distal portion of the lateral crest of the femur, including the third trochanter, beginning at a point 43 percent (40–45%) from the proximal end, and by fascia onto the lateral surface of the shaft of the femur continuous with the insertion of *M. tensor fascia lata*.

**REMARKS:** The muscle is continuous with *M. tensor fascia lata*. The origin is continuous with that of *M. femorococcygeus*, with the most caudal fibers passing slightly deep to that muscle near the origin. In two speci-

mens, the insertion extends slightly proximal to the third trochanter while, in one specimen, it does not. The most proximal portion of insertion is fleshy in one specimen.

There is only minor variation of this muscle in *Coendou*. In two specimens, the origin extends to the level of the second caudal vertebra. The most proximal point of insertion is on the third trochanter beginning at a point 45 percent (43–47%) from the proximal end. It is at least partially fleshy in two specimens. The distal portion of the insertion is traceable over the surface of *M. vastus lateralis* to the lateral surface of the femur, even in specimens where the fascia lata is not. The relations with *M. tensor fascia lata* have been discussed previously.

#### M. FEMOROCOCCYGEUS

Figures 10–13, 18

**ORIGIN:** From the deep layer of the caudal portion of the lumbodorsal fascia deep to *M. semitendinosus* extending from the level of the first to the third caudal vertebra. A well-

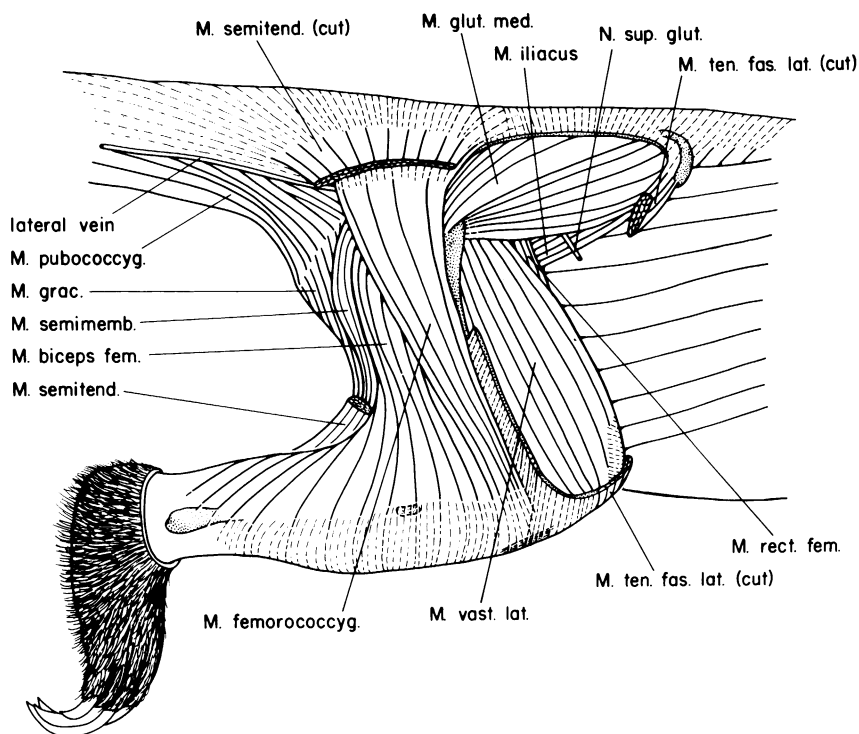


FIG. 11. Lateral view of the pelvic appendage of *Erethizon*. II. Deeper muscles.

developed slip deep to the caudal portion of the muscle arises by a short, flat tendon from the transverse process of the third caudal vertebra. A large blood vessel on the lateral aspect of the tail passes between this slip and the caudal portion of origin from the lumbodorsal fascia.

INSERTION: By fascia onto the lateral surface of the patella and patellar ligament.

REMARKS: The origin is continuous cranially with that of *M. gluteus maximus*. Proximally, the muscle is deep to *M. semitendinosus* between *M. gluteus maximus* and *M. biceps femoris* and is superficial to *M. caudofemoralis* and *M. tenuissimus*. The fascia of insertion lies partly deep to the fascia lata and is continuous with that of *M. biceps femoris*. The deep layer of the lumbodorsal fascia from which the muscle arises envelops the erector spinae (sacrospinalis) group. It is anchored to the spines and interspinous ligaments of the caudal vertebrae dorsally and the transverse processes of these vertebrae ventrally.

In two specimens of *Coendou*, the origin from the lumbodorsal fascia extends from the first to the third caudal vertebra, as in *Erethizon*. The deep caudal slip arises from the transverse processes of the second and third caudal vertebrae. In one specimen, the origin extends to the fourth caudal vertebra, with the deep caudal slip arising from the second through fourth caudal vertebrae, although primarily from the third and fourth.

#### *M. TENUISSIMUS*

Figures 12, 13, 16–18

ORIGIN: From the deep layer of the lumbodorsal fascia deep to the origin of *M. femorococcygeus* and cranial to that of *M. caudofemoralis*. The origin extends from the level of the first caudal vertebra to the interspinous region between the first and second caudal vertebrae.

INSERTION: Via the fascia on the medial side of the leg onto the calcaneus, the medial surface of the distal end of the tibia, and into the medial border of the plantar aponeurosis.



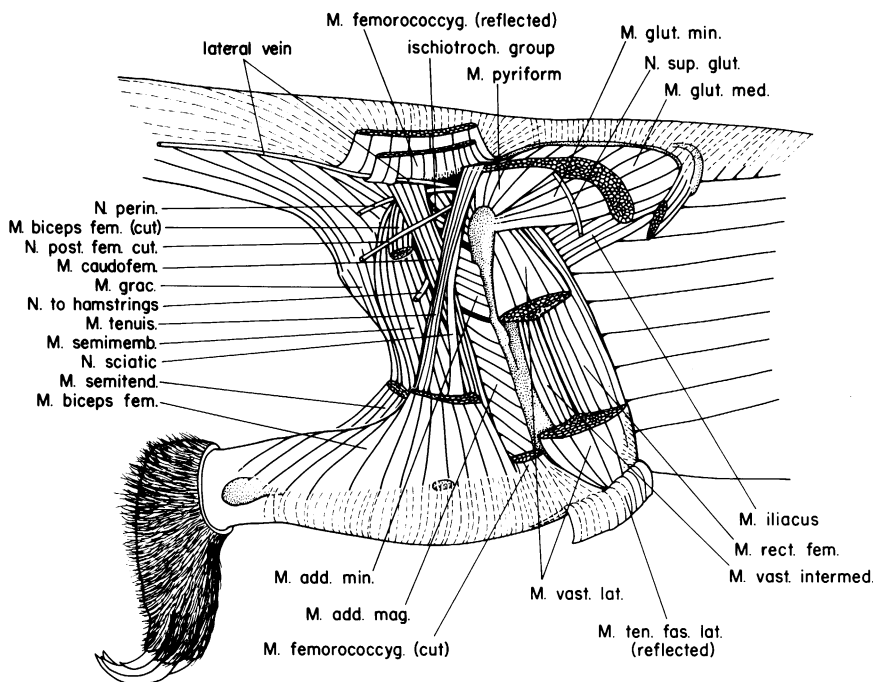


FIG. 12. Lateral view of the pelvic appendage of *Erethizon*. III. Deeper muscles.

**REMARKS:** The muscle is thin and straplike throughout its entire length. The origin lies caudal to the level of *M. gluteus maximus* and cranial to *M. caudofemoralis*. The muscle courses distad superficial to *M. caudofemoralis* and the posterior femoral cutaneous nerve and deep to *M. biceps femoris*.

In *Coendou*, the origin lies deep to the caudal portion of *M. gluteus maximus*. In two specimens, it extends from the level of the interspinous region between the third sacral and first caudal vertebrae to the first caudal vertebra. In one specimen, its boundaries are as in *Erethizon*. The insertion is by fibers onto the medial surface of the calcaneus, but the fascia on the medial side of the leg is attached to the cranial border of the muscle.

#### *M. GLUTEUS MEDIUS*

Figures 7, 8, 11–13, 18

**ORIGIN:** From the deep surface of the gluteal portion of the lumbodorsal fascia from the level of the last lumbar vertebra in two specimens and the second to last lumbar vertebra in one specimen to the level of the third

sacral vertebra, weakly from the lateral portion of the deep layer of the lumbodorsal fascia which envelopes the erector spinae (sacrospinalis) musculature in the region, from the dorsal ridge (gluteal crest), gluteal fossa, and cranial 29 percent (25–32%) of the lateral crest of the ilium, including the spine, and from the cranial surface of *M. pyriformis* and the lateral edges of the transverse processes of the second and third sacral vertebrae.

**INSERTION:** By fibers and tendon onto the greater trochanter and onto the caudal surface of the shaft of the femur lateral to the intertrochanteric crest and 3 to 5 mm. proximal to the insertion of *M. adductor minimus*.

**REMARKS:** Three closely associated parts of this muscle can be distinguished that correspond to similar parts observed by Rinker (1954). The first superficial element, corresponding to the "dorsolateral part" of Rinker (1954), arises from the deep surface of the gluteal portion of the lumbodorsal fascia and very weakly from the deep fascial layer covering the erector spinae musculature. These fibers converge caudolaterad and pass over

the proximal end of the greater trochanter to insert on its caudolateral and caudal surfaces and on a small proximal portion of the caudal surface of the femoral shaft lateral to the intertrochanteric crest. The most distal point of insertion lies 3 to 5 mm. proximal to the insertion of *M. adductor minimus*. The second superficial element is thick and arises from the cranial and lateral portions of the gluteal fossa and the cranial portion of the lateral crest of the ilium and the spine. It inserts by a flat tendon onto the lateral surface of the greater trochanter in common with that of *M. gluteus minimus* in two specimens and separate in one. In *Erethizon*, the "spine" is not prominent and represents the junction of the ilial and lateral crests. The deep part is massive and arises from the dorsal ridge, the caudal and medial portions of the gluteal fossa, the lateral edges of the transverse processes of the second and third sacral vertebrae, and the cranial surface of *M. pyriformis*. It inserts by tendon onto the proximal end and extreme proximal portions of the cranial and craniomedial surfaces of the greater trochanter continuous with the insertion of *M. pyriformis*.

In two specimens of *Coendou*, the first superficial element arises from the lumbodorsal fascia from the level of the interspinous region between the last lumbar and first sacral vertebrae to the second sacral vertebra. In an equal number of specimens, this part does not pass over the proximal end of the femur, and its insertion is restricted to the caudal surface of the greater trochanter and a short proximal portion of the femoral shaft lateral to the intertrochanteric crest. It is similar to that in *Erethizon* in one specimen. The origin of the second superficial element from the lateral crest of the ilium is more extensive from the cranial 63 percent (59–69%), including the prominent iliac spine. A small caudal part of the origin from the lateral crest lies dorsal to that of *M. gluteus minimus*. In one specimen, the origin also includes a narrow craniolateral portion of the iliac fossa lateral to the origin of *M. iliacus*. In one specimen, the insertion includes the extreme proximal portion of the medial surface of the greater trochanter in addition to the proximal, cranial, and craniomedial surfaces. In all spec-

imens, the three parts were more difficult to distinguish than in *Erethizon*, especially the second superficial and deep elements.

#### M. GLUTEUS MINIMUS

Figures 7, 8, 12, 13, 18

**ORIGIN:** From the caudal 74 percent (69–80%) of the lateral crest of the ilium, the caudolateral and caudal portions of the gluteal fossa, and posteriorly from the medial portions of the dorsal surfaces of the ilium and ischium extending to the level of the transverse process of the third sacral vertebra. A few fibers arise from the joint capsule of the hip.

**INSERTION:** The fibers which arise from the lateral crest of the ilium insert in two specimens via a common tendon with the second superficial element of *M. gluteus medius* onto the lateral surface of the greater trochanter. In one specimen, the insertion is by a separate tendon onto the lateral and craniolateral surfaces deep to that of *M. gluteus medius*. The medial and caudal fibers insert by tendon onto the cranial, craniomedial, and slightly onto the medial surfaces of the greater trochanter.

**REMARKS:** The muscle lies deep to *M. gluteus medius* and is separable only by tracing the superior gluteal nerve, which passes laterad between the two muscles to innervate them and *M. tensor fascia lata*. It is partially deep to but is separable from *M. pyriformis*. A small cranial portion of the origin from the lateral crest of the ilium lies ventral to that of *M. gluteus medius*.

In *Coendou*, the muscle arises from the caudal 63 percent (60–67%) of the lateral crest of the ilium. The origin from the gluteal fossa does not extend as far cranially due to the more extensive origin of *M. gluteus medius*. Consequently, a larger cranial portion of the origin from the lateral crest lies ventral to that of the latter muscle. In one specimen, the origin also includes a very narrow lateral portion of the iliac fossa. In all specimens, the caudal portion of origin is closely associated with the joint capsule of the hip and, in one specimen, is confined to the lateral portion of the dorsal surfaces of the ilium and ischium extending to the level of the transverse process of the third sacral vertebra.

There is no significant variation of the insertion of this muscle from *Erethizon*. The cranial fibers insert in common with *M. gluteus medius* onto the lateral surface of the greater trochanter.

#### M. PYRIFORMIS

Figures 12, 13, 18

**ORIGIN:** By fibers from the ventral surfaces of the transverse processes of the second and third sacral vertebrae.

**INSERTION:** By fibers onto the tendon of the deep part of *M. gluteus medius* and onto the medial surface of the greater trochanter.

**REMARKS:** This muscle lies deep to *M. gluteus medius*. A small cranial portion lies superficial to *M. gluteus minimus*. The muscle is closely associated with but reliably separable from *M. gluteus medius* based on the position of origin. Rinker (1954) observed a branch of the superior gluteal nerve passing between the two muscles, but I was not able to confirm this. There is no variation of this muscle in *Coendou*.

### QUADRICEPS FEMORIS GROUP

#### M. RECTUS FEMORIS

Figures 11–13, 16–18

**ORIGIN:** By a stout tendon from the femoral tubercle of the ilium.

**INSERTION:** Mostly by fibers onto the proximal surface of the patella.

**REMARKS:** Both Rinker (1954) and Klingener (1964) identified two heads of origin. The straight head arose from the femoral tubercle and the reflected head arose from the margin of the acetabulum. I did not observe a reflected head in any of my specimens. Distally, the lateral and deep surfaces of the muscle are tendinous. *M. vastus lateralis* inserts into the distal portion of the lateral surface. The muscle is closely associated with but separable from *M. vastus medialis*. There is no significant variation of this muscle in *Coendou*.

#### M. VASTUS LATERALIS

Figures 11–13, 18

**ORIGIN:** Mostly by fibers from the cranial and craniolateral surfaces of a small distal

portion of the greater trochanter and the shaft of 52 percent (50–54%) of the femur beginning at a point 7 percent (6–8%) from the proximal end. On the cranial surface, the origin extends to the most proximal point of origin of *M. vastus intermedius*. On the craniolateral surface, it extends slightly farther distally to the level of the distal end of the third trochanter at a point 59 percent (58–60%) from the proximal end of the femur.

**INSERTION:** Mostly by fibers into the distal portion of the lateral surface of *M. rectus femoris*, the fascia covering the distal portion of the cranial surface of that muscle, and onto the proximolateral aspect of the patella.

**REMARKS:** The origin from the greater trochanter lies deep to *M. gluteus minimus*. Proximally, the deepest fibers of the muscle are fused with *M. vastus medialis*. The muscle is difficult to separate from *M. vastus intermedius*. The surface in contact with *M. rectus femoris* is tendinous distally. The fascia covering the distal portion of the cranial surface of that muscle attaches to the proximal end of the patella. On one side of one specimen, a few fibers arise from the lateral surface of the lateral crest of the femur at a point 20 percent from the proximal end.

In *Coendou*, the origin from the craniolateral surface extends farther distally than in *Erethizon* to a point 73 percent (69–77%) from the proximal end of the femur. Hence, the origin is broader from 65 percent (62–70%) of the femur beginning at a point 8 percent (5–10%) from the proximal end. The deep fibers are fused slightly with *M. vastus medialis* in one specimen. The muscle is closely associated with *M. vastus intermedius* to varying degrees in two specimens.

#### M. VASTUS MEDIALIS

Figures 16, 17

**ORIGIN:** By fibers from the craniomedial and medial surfaces of the shaft of 35 percent (31–40%) of the femur beginning at a point 15 percent (13–17%) from the proximal end. The most proximal portion of origin is distal to the neck and cranial to the lesser trochanter.

**INSERTION:** By fibers onto the proximomedial surface of the patella.

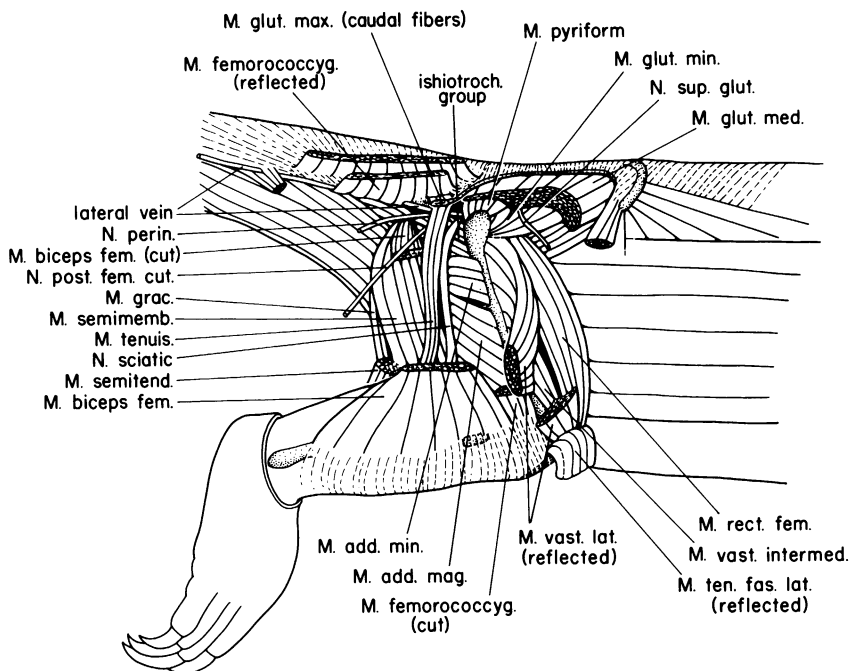


FIG. 13. Lateral view of the deeper muscles of the pelvic appendage of *Coendou*.

REMARKS: Proximally, the deepest fibers of the muscle are fused with those of *M. vastus lateralis*. In one specimen, there is some difficulty in separating the muscle from *M. vastus intermedius*.

In *Coendou*, there is no significant variation in the configuration of this muscle from *Erethizon*. The origin is from 40 percent (37–44%) of the femur beginning at a point 18 percent (16–19%) from the proximal end. On one side of one specimen, a small group of fibers arises from the tendon of the medial head of *M. gastrocnemius*, becomes closely associated with but separable with difficulty from the main part of the muscle, and inserts onto the proximal portion of the medial surface of the patella.

#### *M. VASTUS INTERMEDIUS*

Figures 12, 13, 18

ORIGIN: By fibers from the distal portion of the cranial surface of the shaft of the femur beginning at a point 51 percent (44–56%) from the proximal end and extending to the most proximal edge of the intercondylar fossa.

INSERTION: Broadly by a short aponeurosis onto the proximal aspect of the patella deep to the other quadriceps muscles. In two specimens, a few fibers insert into the synovial membrane of the knee.

REMARKS: The muscle is difficult to separate from *M. vastus lateralis* and is closely associated with the synovial membrane of the knee. In one specimen, it is somewhat difficult to separate from *M. vastus medialis*. *M. articularis genu* is absent in all specimens, although a few fibers on the medial side of the muscle in one specimen and on the lateral side in another insert into the synovial membrane of the knee. According to Hollinshead (1974), the *articularis genu* lies between the *vastus intermedius* muscle and the femur and inserts into a layer of the synovial membrane reflected downward onto the femur. The fibers described above do not have these relations. Therefore, I do not believe that they represent a true *M. articularis genu*.

In *Coendou*, the origin of *M. vastus intermedius* extends farther proximally on the average beginning at a point 41 percent

(32–58%) from the proximal end of the femur. However, in one specimen, the percentage distance from the most proximal point of origin to the proximal end of the femur is not significantly different from that in *Erethizon*. It was difficult to determine if any fibers were inserting directly into the synovial membrane of the knee.

#### TIBIAL EXTENSOR GROUP

##### M. EXTENSOR DIGITORUM LONGUS

Figures 14, 15, 19

**ORIGIN:** By a flat tendon from the most distal portion of the lateral epicondyle of the femur distocranial to the attachment of the fibular collateral ligament.

**INSERTION:** By four tendons onto the dorsal surfaces of the bases of the distal phalanges of digits 2 through 5.

**REMARKS:** The muscle is parallel-fibered and lies lateral to the tibial part and superficial to the fibular part of *M. tibialis anterior* and medial to the peroneal group. Distally, the muscle lies superficial to *M. extensor hallucis longus*. It divides into three tendinous slips deep to the transverse crural ligament. These pass onto the dorsum of the foot in a tendon sheath lateral to that of *M. extensor hallucis longus*. Part of the sheath is thickened into a ligamentous trochlea anchored to the cuboid. The lateral tendon courses distolaterad across the fourth metatarsal and distad along the dorsomedial surface of the proximal phalanx of the fifth digit toward its insertion. The middle tendon courses distad between the third and fourth metatarsals and along the dorsomedial surface of the proximal phalanx of the fourth digit toward its insertion. The medial tendon splits into two subsidiary tendons. The lateral one passes distad along the dorsal surface of the third metatarsal and digit. The medial branch courses mediodistad between the second and third metatarsals to the head of the former and then distad along the dorsal surface of the second digit. All tendons lie superficial to the short extensor muscles and are bound together by fascia.

In *Coendou*, the tendon of origin from the lateral epicondyle is narrower than in *Erethizon*. In two specimens, the muscle also arises by fibers from the medial surface of the peroneal

process of the fibula and the distal surface of the lateral tibial condyle superficial to the origin of *M. peroneus longus* and lateral to that of *M. tibialis anterior*, from a proximal portion of the adjacent surface of the latter muscle, and from the proximal one-fourth of the intermuscular septum between the tibial extensor and peroneal groups. In one specimen, the distal end of the tendon of origin attaches mostly to the medial portion of the superficial surface of the peroneal process. Only a few fibers arise from the process itself. The fibular collateral ligament is narrower than in the other specimens and attaches to the lateral portion of the superficial surface of the peroneal process. A small aponeurosis of insertion of *M. biceps femoris* attaches to that process between the ligament and the tendon of origin. The rest of the origin is similar to that in the other two specimens except that it includes the proximal one-half of the intermuscular septum between the tibial extensor and peroneal groups.

##### M. EXTENSOR HALLUCIS LONGUS

Figures 14, 15, 19

**ORIGIN:** By fibers from a narrow portion of the cranial surface of 37 percent (31–43%) of the fibular shaft beginning at a point 43 percent (41–47%) from the proximal end and from the adjacent surface of the septum between the muscle and the peroneal group.

**INSERTION:** By a tendon onto the dorsal surface of the base of the distal phalanx of the hallux and by an aponeurosis into the medial border of the tendon of *M. extensor digitorum longus* to the second digit at the level of the metatarsophalangeal joint.

**REMARKS:** This parallel-fibered muscle lies lateral to *M. tibialis anterior* and deep to *M. extensor digitorum longus*. The muscle fibers attach to the lateral side of the tendon of insertion, although in one specimen, a few fibers reach its medial surface. The tendon passes deep to the transverse crural ligament lateral to and in a common sheath with that of *M. tibialis anterior*. It then courses mediodistad over the dorsum of the foot, passes through a ligamentous trochlea attached to the distal portion of the dorsal surface of the medial sesamoid, and courses distad toward the hallux. A short distance

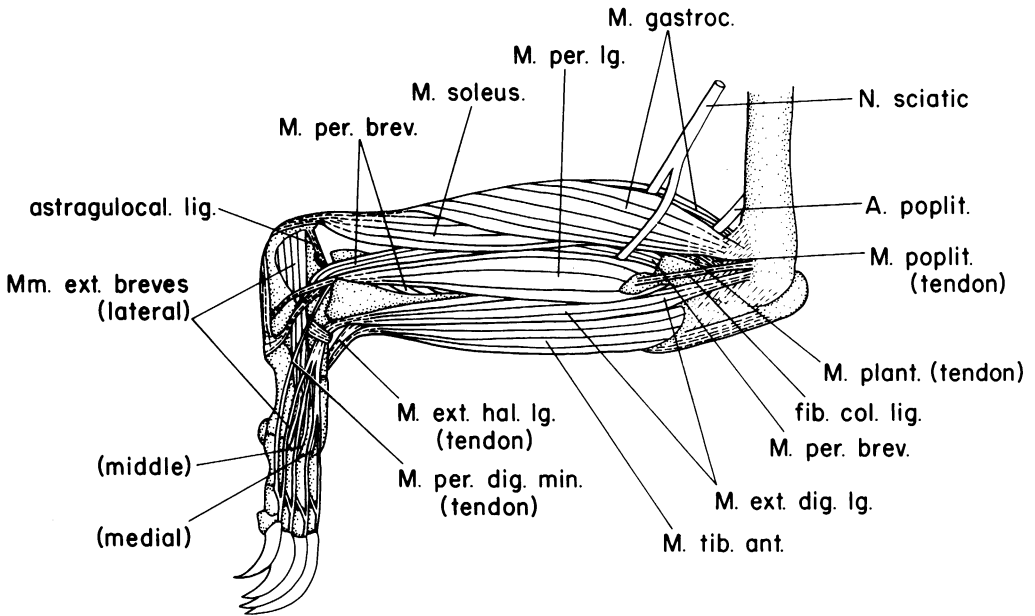


FIG. 14. Lateral view of the superficial muscles of the leg of *Erethizon*.

proximal to the metatarsophalangeal joint, the tendon bifurcates. The medial branch, forming the main insertion, courses distad along the dorsal surface of the hallux to the base of the distal phalanx. The lateral branch widens immediately into an aponeurosis which courses distolaterad to reach the tendon of *M. extensor digitorum longus* to the second digit at the level of the metatarsophalangeal joint. The aponeurosis is embedded in fascia.

In *Coendou*, the muscle arises from 28 percent (17–43%) of the craniomedial surface of the fibular shaft beginning at a point 38 percent (20–53%) from the proximal end. In two specimens, the origin is less extensive than in *Erethizon* (17 and 25%, respectively). In one specimen, the length of origin is similar to that in *Erethizon*, but it begins proximally at a point 20 percent from the proximal end of the shaft. In one specimen, the muscle is difficult to separate from *M. tibialis anterior*. The configuration of the insertion varies from that in *Erethizon*. Most of the fibers attach to the lateral surface of the tendon, but in two specimens, a few fibers reach the medial surface. The tendon courses mediolaterad across

the dorsum of the foot along the dorsomedial surface of the first metatarsal. Unlike *Erethizon*, the longitudinal axis of the first metatarsal is directed sharply mediolaterad. The trochlea through which the tendon passes is broad, flat, and convergent toward its distal end. The tendon then courses distad across the first metatarsal and along the dorsolateral surface of the hallux to insert on its distal end. At the level of the metatarsophalangeal joint, it gives rise to two aponeuroses. The medial one blends into the subcutaneous connective tissue on the medial side of the hallux. The lateral one inserts into the medial borders of the medial short extensor and the tendon of *M. extensor digitorum longus* to the second digit proximal to the metatarsophalangeal joint.

#### M. TIBIALIS ANTERIOR

Figures 14, 15, 19

**ORIGIN:** The muscle consists of tibial and fibular parts which are separate as distinct heads proximally for a short distance. The tibial part arises by fibers from the lateral fossa of the proximal 57 percent (50–65%) of

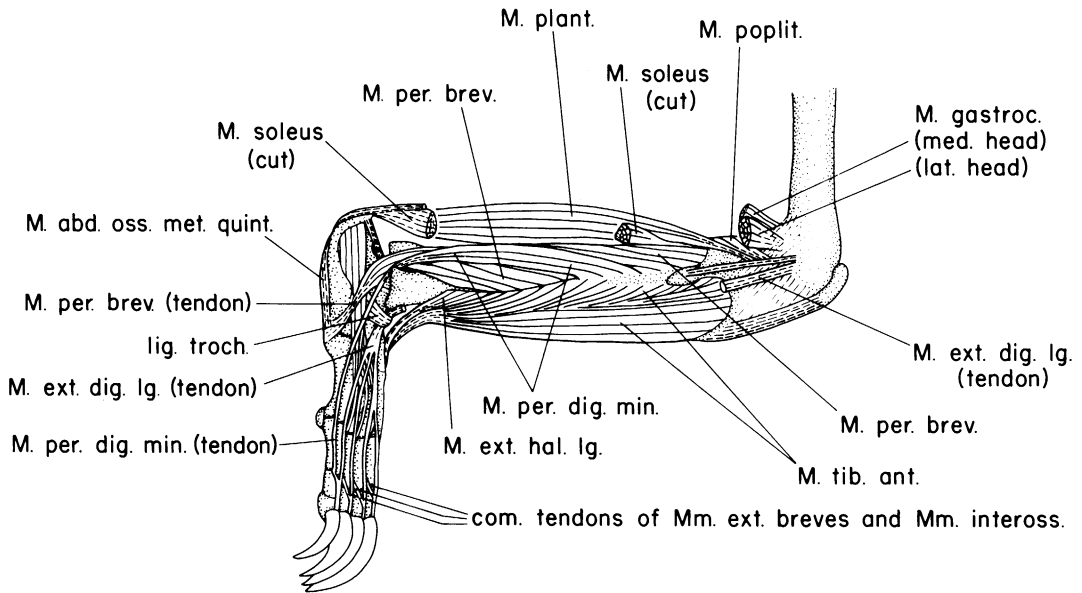


FIG. 15. Lateral view of the deep muscles of the leg of *Erethizon*.

the shaft of the tibia, from the surface of the tibial crest lateral to the insertion of *M. gracilis*, and from the distal surface of the lateral condyle. A proximal portion arises from the deep surface of the crural fascia on the cranio-lateral aspect of the leg. The fibular part arises by fibers from the medial surface of the head of the fibula and the proximal 55 percent (43–64%) of the craniomedial surface of the fibular shaft. A few fibers arise from the intermuscular septum between the tibial extensor and peroneal groups. Both parts arise from a proximal portion of the interosseous membrane. Distally, the fibular part arises from a narrow portion of that membrane adjacent to the origin from the shaft of the fibula.

**INSERTION:** Via two stout tendons onto the ventrolateral surface of the medial cuneiform and slightly onto the medial surface of the base of the first metatarsal.

**REMARKS:** The muscle is parallel-fibered. Most of the fibers attach to the lateral and deep surfaces of the tendon of insertion. The tibial and fibular parts lie medial and deep, respectively, to *M. extensor digitorum longus*. Distally, the origin from the fibular shaft lies medial to that of *M. extensor hallucis*

*longus*. The tendons of insertion pass deep to the transverse crural ligament medial to and in a common sheath with the tendon of *M. extensor hallucis longus*. They then course mediolateral across the dorsum of the foot and pass deep to the ligamentous trochlea guiding the tendon of *M. extensor hallucis longus* and deep to the muscle attached to the medial sesamoid and the first metatarsal. The medial tendon inserts proximally and the lateral tendon distally on the medial cuneiform. The lateral tendon also inserts slightly on the first metatarsal. The distal portion of the transverse crural ligament loops around the tendons of insertion and attaches to the dorsum of the foot in the region of the cuboid and the medial portion of the navicular. In one specimen, the medial tendon is partially separable with difficulty into two branches near the insertion.

There is only minor variation of this muscle in *Coendou*. The origin of the tibial part includes the proximal 62 percent (53–67%) of the shaft of the tibia. Its proximal portion arises from the deep surface of the crural fascia, with some fibers lying partially superficial to *M. extensor digitorum longus*. That muscle arises proximally from the adjacent sur-



face of *M. tibialis anterior*. The fibular portion arises in part from the proximal 59 percent (54–65%) of the shaft of the fibula. The medial tendon of insertion is separable with difficulty into two branches near its attachment to the medial cuneiform. Jones (1953) also observed this but noted that its insertion was on “the plantar surface of the proximal extremity of the first metatarsal.” He described the insertion of the lateral (his anterior) tendon as simply the dorsum of the foot.

#### MM. EXTENSORES BREVES

Figures 14, 15

**ORIGIN:** There are three of these muscles present. The lateral one arises by fibers from the lateral and dorsal surfaces of the calcaneus, including the dorsal surface of the trochlear process, beginning at a point at the level of attachment of the astragalocalcaneal ligament at the proximal epiphyseal line. A few fibers arise from the ligamentous trochlea for the tendons of *M. extensor digitorum longus* near its attachment to the calcaneus. The middle and medial short extensors arise from the distal end of the dorsal surface of the calcaneus and from the ligamentous trochlea of *M. extensor digitorum longus*. The medial short extensor is difficult to separate from the attachment of the transverse crural ligament to the dorsum of the foot.

**INSERTION:** By small tendons that fuse with those of the lateral interossei of digits 2 through 4, forming common tendons which insert onto the dorsal surfaces of the bases of the middle phalanges. The tendons continue distad to fuse with the lateral borders of the long extensor tendons to these digits.

**REMARKS:** The muscles are difficult to separate proximally. The fibers attach to the tendons of insertion in a bipinnate manner. The origin includes all of the lateral surface of the calcaneus except for the region of the proximal epiphysis.

In *Coendou*, a few medial fibers of the medial short extensor insert into the lateral aponeurosis of *M. extensor hallucis longus*.

#### M. EXTENSOR HALLUCIS BREVIS

This muscle is present on only one side of one specimen of *Erethizon* and has a very

small diameter. It arises by a narrow aponeurosis from the distal portion of the dorsal surface of the calcaneus medial to the attachment of the ligamentous trochlea of *M. extensor digitorum longus* and the origins of the short extensors. Its small tendon crosses the dorsal surface and fuses on the medial side of the tendon of *M. extensor hallucis longus*. The aponeurosis of origin is closely associated with but separable from the ankle joint capsule.

#### PERONEAL GROUP

##### M. PERONEUS LONGUS

Figures 14, 20–22

**ORIGIN:** Mostly by fibers from the medial, lateral, and adjacent edges of the superficial surfaces and distal edge of the peroneal process of the fibula and from the proximal half of the intermuscular septum between the peroneal and tibial extensor groups.

**INSERTION:** By a tendon onto the lateral portion of the plantar surface of the base of the first metatarsal in one specimen, onto a similar portion of the medial cuneiform in another, and onto the base of the first metatarsal and part of the medial cuneiform in a third.

**REMARKS:** There are some tendinous filaments visible superficially which arise from the edge of the superficial surface of the peroneal process. The muscle is parallel-fibered, with most of the fibers attaching to the superficial surface of the tendon. It lies superficial to the common peroneal nerve and the other peroneal muscles. The tendon courses around the lateral malleolus in a sheath lateral (superficial) to the other peroneal tendons. It then courses distocranially to the edge of the trochlear process of the calcaneus. There it passes in a groove on the plantar surface of the calcaneus deep to *M. abductor ossis metatarsi quinti* and continues mediodistad along a groove in the cuboid and across the plantar aspect of the pes deep to the deep palmar aponeurosis to reach the insertion.

In *Coendou*, the muscle also arises by fibers from the distal surface of the lateral tibial condyle deep to the origin of *M. extensor digitorum longus*. It does not arise from the medial edge of the superficial surface of the peroneal process. The origin includes the

proximal one-third of the intermuscular septum between the peroneal and tibial extensor groups. The insertion is on both the base of the first metatarsal and the medial cuneiform in two specimens and only the base of the first metatarsal in one.

#### M. PERONEUS BREVIS

Figures 14, 15, 20–22

**ORIGIN:** By fibers from the proximal 73 percent (63–81%) of the shaft of the fibula, the intermuscular septum between the tibial extensor and peroneal groups, and the distal half of the intermuscular septum between the peroneal group and the flexor group of the leg. Proximally, the origin is from the cranial and craniolateral surfaces of the fibular shaft anterior to the origin of *M. peroneus digiti minimi*. Distally, the origin is from the lateral and caudolateral surfaces of the shaft. In one specimen, the origin includes the distal 5 mm. of the medial surface of the fibular head.

**INSERTION:** By a stout tendon onto the proximolateral surface of the tuberosity on the ventrolateral aspect of the base of the fifth metatarsal and into the distal portion of *M. abductor ossis metatarsi quinti*.

**REMARKS:** This muscle is the largest of the peroneals and lies deep to *M. peroneus longus* and the common peroneal nerve. *M. peroneus digiti minimi* arises in part from its surface. Its fibers attach to the tendon in a bipinnate manner with the caudal fibers extending farther distally. The tendon courses distad along the caudal surface of the lateral malleolus medial (deep) to and in a common sheath with that of *M. peroneus digiti minimi*. It passes under the lateral malleolus and over the edge of the trochlear process cranial (distal) to that of *M. peroneus longus*.

In *Coendou*, there is only minor variation in the configuration of this muscle from *Erethizon*. The origin includes the proximal 69 percent (67–74%) of the fibular shaft. The fusion between the tendon of insertion and *M. abductor ossis metatarsi quinti* is slight.

#### M. PERONEUS DIGITI QUARTI

This muscle is absent in both *Erethizon* and *Coendou*.

#### M. PERONEUS DIGITI MINIMI

Figures 14, 15

**ORIGIN:** By fibers from the proximal 45 percent (40–49%) of the lateral surface of the shaft of the fibula posterior to the origin of *M. peroneus brevis*, the distal 4 to 7 mm. of the lateral surface of the fibular head, the adjacent surface of *M. peroneus brevis* proximally, and the intermuscular septum between the peroneal and flexor groups.

**INSERTION:** By a tendon of small diameter onto the dorsal surface of the base of the middle phalanx of the fifth digit. It continues distad to fuse with the lateral border of the long extensor tendon to that digit.

**REMARKS:** The muscle is parallel-fibered. The tendon passes under the lateral malleolus medial (deep) to that of *M. peroneus longus* and lateral (superficial) to and in a common sheath with that of *M. peroneus brevis*. It then courses distad along the dorsolateral surfaces of the fifth metatarsal and digit to the level of the proximal interphalangeal joint, where it becomes difficult to trace beyond this point. However, I have consistently observed a fusion with the long extensor tendon just before the insertion of that tendon on the distal phalanx.

There is no significant variation of this muscle in *Coendou*. The origin is from the proximal 36 percent (32–41%) of the shaft of the fibula and from the distal 5 to 9 mm. of the lateral surface of the fibular head. The configuration of the insertion as described for *Erethizon* was positively confirmed.

#### FLEXOR SYSTEM

##### ADDUCTOR GROUP

#### M. GRACILIS

Figures 10–13, 16–18

**ORIGIN:** By fibers from the lateral edge of the caudal surface of the caudal pubic ramus and the ventral surfaces of the pubic body and the ventral 38 percent (33–47%) of the cranial pubic ramus extending to the level of attachment of the inguinal ligament. The muscle also arises by aponeurosis from a caudal portion of the inguinal ligament even with the attachment of the lacunar ligament.

**INSERTION:** By a short, tough aponeurosis onto the craniomedial surface of the anterior

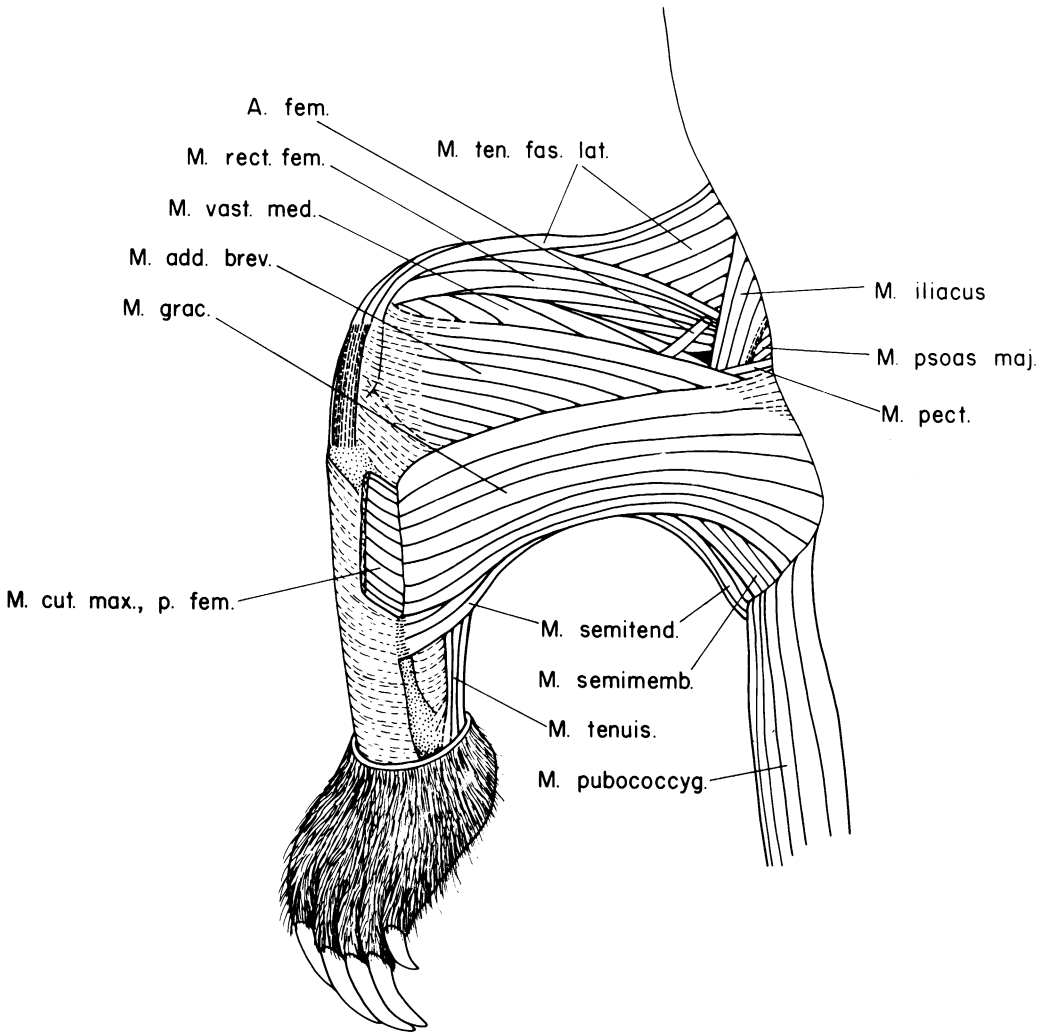


FIG. 16. Medial view of the superficial muscles of the pelvic appendage of *Erethizon*.

tibial crest on 33 percent (31–34%) of the tibia beginning at a point 22 percent (22–23%) from the proximal end. The cranial border of the muscle is anchored by tough fascia inserting onto the medial surfaces of the proximal portion of the tibia, the patellar ligament, and the distal portion of the patella.

REMARKS: The origin is superficial to that of *M. adductor brevis* and ventral to that of *M. semimembranosus*. The insertion lies superficial to a distal portion of that of *M. semimembranosus* and a small cranial portion of that of *M. semitendinosus*. The fascia

anchoring the cranial border of the muscle lies superficial to the rest of the insertion of *M. semimembranosus*. *M. cutaneus maximus*, pars femoralis fuses with the muscle at the insertion. The lacunar ligament attaches to the cranial pubic ramus, extending a short distance dorsal to the small tubercle for the origin of *M. pectineus* to a point 71 percent (61–81%) from the ventral end.

In *Coendou*, the basic configuration of the muscle is similar to that in *Erethizon*, but there are minor differences. The origin includes the ventral 54 percent (46–60%) of

the cranial pubic ramus. This is more extensive on the average than in *Erethizon*, but a small amount of overlap in the ranges is apparent. The muscle also arises cranially from the inguinal ligament by an aponeurosis that blends with the lacunar ligament to attach to the cranial pubic ramus. It extends dorsally to a point 81 percent (70–91%) from the ventral end. The aponeurosis of origin and the inguinal and lacunar ligaments are less distinct than in *Erethizon*. There are no important differences in the insertion of the muscle from the conditions in *Erethizon*. The insertion is by aponeurosis onto 37 percent (35–40%) of the tibia beginning at a point 19 percent (17–23%) from the proximal end. The cranial fascia blends with the aponeurosis of M. adductor brevis and cannot be traced to the patella.

#### M. ADDUCTOR LONGUS

Figure 17

**ORIGIN:** By fibers from the lateral surfaces of a tiny cranial portion of the body and the cranial ramus of the pubis deep to the origin of M. adductor brevis, ventral (caudal) to that of M. pectineus, and cranial to that of M. adductor magnus.

**INSERTION:** By a very short aponeurosis onto 22 percent (17–30%) of the caudal surface of the femur beginning at a point 46 percent (44–49%) from the proximal end. The insertion lies between those of M. pectineus medially and M. adductor magnus laterally. Proximally, the insertion is positioned toward the middle of the caudal surface of the femoral shaft while distally, it lies adjacent to the medial surface.

**REMARKS:** The muscle is thin throughout its length and lies between M. pectineus and M. adductor magnus deep to M. adductor brevis. In two specimens, the most distal point of insertion lies a short distance distal to that of M. pectineus (5 to 9% of the total length of the femur). In one specimen, the insertion is substantially broader and its most distal point lies a distance of 24 percent of the total length of the femur beyond M. pectineus. The obturator nerve passes between the muscle and M. adductor magnus to pierce M. adductor brevis.

In *Coendou*, the insertion is broader and

begins farther proximally than in *Erethizon*. The muscle inserts by fibers onto 39 percent (38–40%) of the caudal surface of the femur beginning at a point 30 percent (29–30%) from the proximal end. The most distal point of insertion lies 11 percent (6–15%) of the total femoral length distal to that of M. pectineus. In one specimen, the obturator nerve passes through the muscle near its origin.

#### M. ADDUCTOR BREVIS

Figures 16–18

**ORIGIN:** By fibers from the lateral surfaces of the caudal pubic ramus, body, and ventral portion of the cranial pubic ramus deep to M. gracilis and extending to the level of the small tubercle for the origin of M. pectineus. The origin from the caudal pubic ramus lies 3 to 9 mm. ventral to the most dorsal point of origin of M. gracilis.

**INSERTION:** By a weak aponeurosis onto the medial surfaces of the patella and patellar ligament and into the medial border of a short distal segment of M. tensor fascia lata. The aponeurosis blends with and appears to pass deep to the cranial fascia of M. gracilis. In two specimens, a small slip deep to the distal portion of the muscle inserts by aponeurosis into the capsule of the knee proximal to M. semimembranosus.

**REMARKS:** This muscle is thin. It lies deep to M. gracilis and superficial to M. adductor longus and M. adductor magnus. A small cranial portion of the origin lies superficial to part of M. pectineus. The popliteal artery lies deep to the muscle, and the obturator nerve pierces it before innervating M. gracilis. The aponeurotic insertion into the distal portion of M. tensor fascia lata is continuous with a weak fascial sheet that passes between that muscle and M. adductor brevis. Klingener (1964) identified two parts of this muscle in dipodoids. The genicular part inserted on the medial surface of the knee and the femoral part inserted on the shaft of the femur. Rinker (1954) also observed similar parts in cricetids. The muscle in *Erethizon* consists solely of the genicular part.

In *Coendou*, the origin is from a tiny cranial portion of the body of the pubis and the cranial pubic ramus to the level of the tubercle for the origin of M. pectineus. It is less

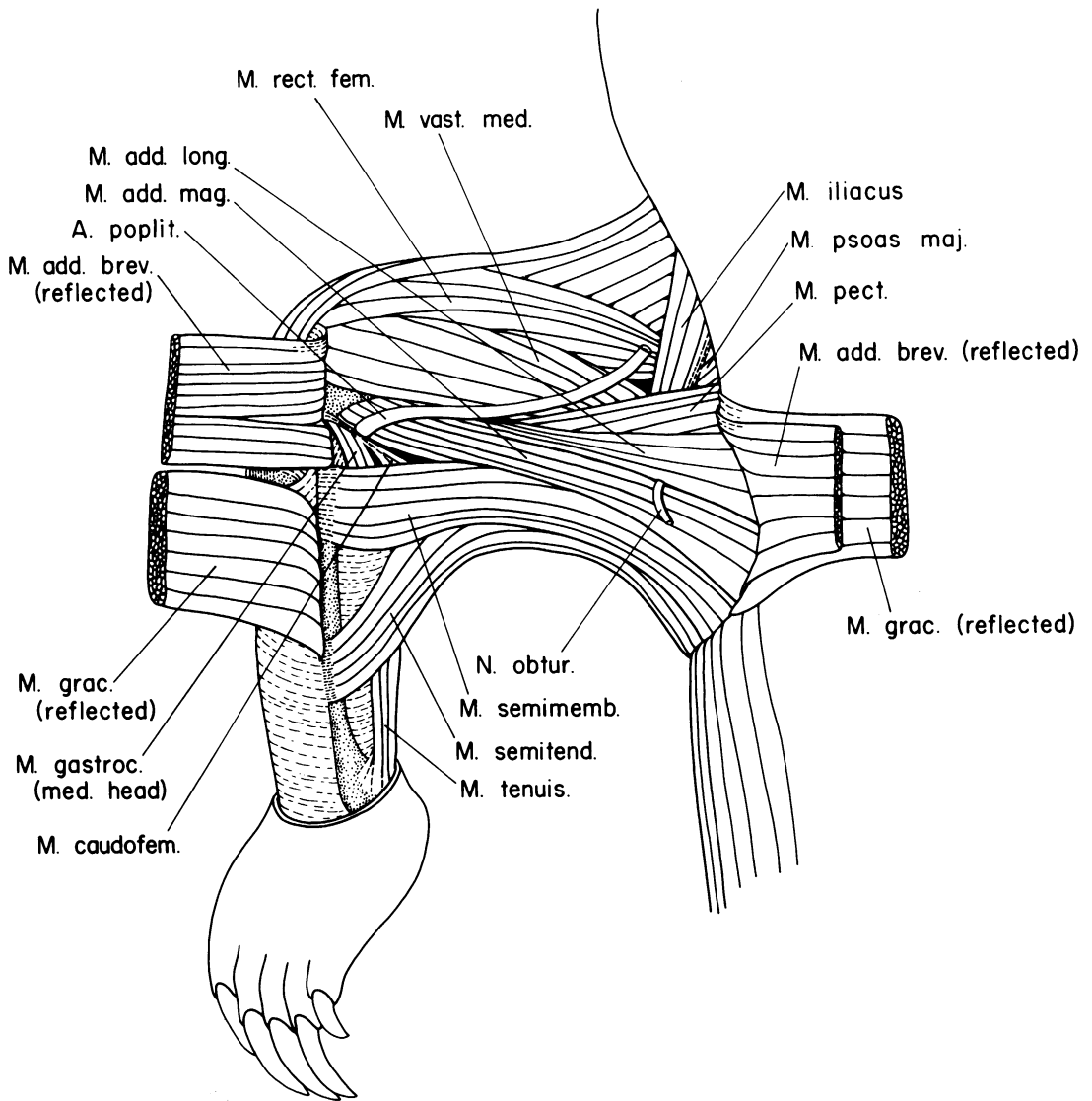


FIG. 17. Medial view of the deep muscles of the pelvic appendage of *Erethizon*.

extensive than in *Erethizon* and does not lie superficial to *M. adductor magnus*. The obturator nerve does not penetrate the muscle but passes caudal to it. There are no deep fibers inserting into the capsule of the knee.

#### *M. ADDUCTOR MAGNUS*

Figures 12, 13, 17, 18

**ORIGIN:** By fibers from the lateral surfaces of the caudal ramus and body of the pubis caudal to the origin of *M. adductor longus*

and deep to *M. adductor brevis*. The most dorsal point of origin from the caudal pubic ramus lies 4 to 5 mm. ventral to that of *M. gracilis*.

**INSERTION:** By fibers onto 50 percent (45–56%) of the caudal surface of the femur beginning at a point 33 percent (27–36%) from the proximal end and extending to the distal end of the femoral shaft.

**REMARKS:** Proximally, the insertion is thin and is situated on the lateral portion of the caudal femoral surface. Distally, the muscle

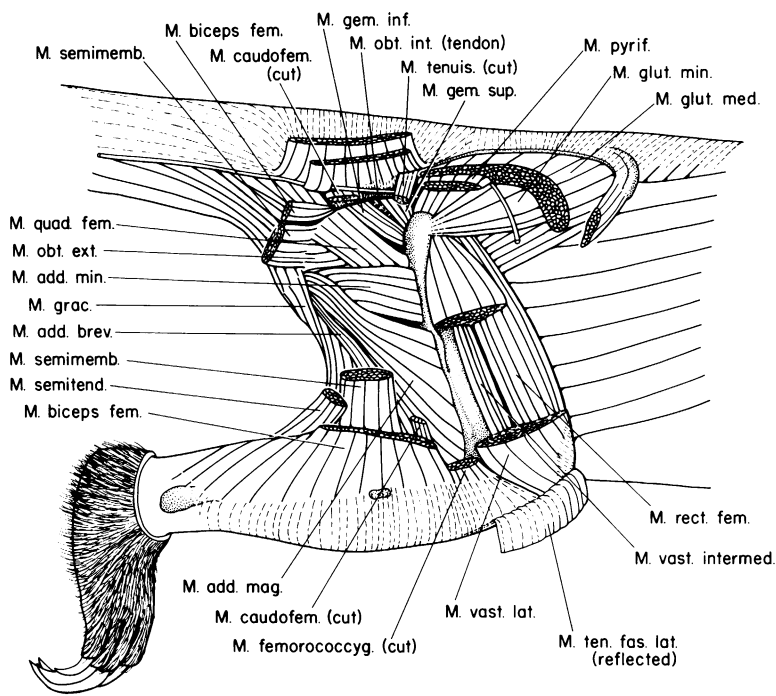


FIG. 18. Lateral view of the pelvic appendage of *Erethizon*. IV. Deeper muscles.

becomes much thicker and is positioned on the central and medial portions of the caudal surface proximal to the dorsal surface of the medial condyle.

In *Coendou*, the origin does not lie deep to *M. adductor brevis* because of the less extensive origin of that muscle. However, the position of the origin is identical with that in *Erethizon*. The insertion is not as broad and does not extend as far proximally. The muscle inserts onto 40 percent (37–43%) of the caudal surface of the femur beginning at a point 42 percent (40–44%) from the proximal end and extending to a point 3 to 5 mm. proximal to the dorsal surface of the lateral condyle. The insertion is positioned on the lateral and central regions of the caudal surface of the femoral shaft and does not reach the medial portion distally.

M. ADDUCTOR MINIMUS  
Figures 12, 13, 18

ORIGIN: Mostly by fibers from the lateral surfaces of the pubic body deep to *M. adductor magnus*, the ventral 18 percent (12–22%)

of the cranial pubic ramus deep to *M. adductor longus* and, in two specimens, from a ventral portion of the caudal pubic ramus. The most dorsal point of origin from the caudal ramus lies 8 to 16 mm. ventral to that of *M. gracilis*.

INSERTION: By aponeurosis and fibers onto the lateral portion of 12 percent (12–13%) of the caudal surface of the femur at the level of the lesser trochanter beginning at a point 19 percent (18–19%) from the proximal end.

REMARKS: The aponeurosis of insertion is situated on the deep (medial) surface of the muscle. Most of the fibers attach to its lateral surface, with some continuing directly onto the femur.

In *Coendou*, the muscle arises from the ventral 22 percent (11–38%) of the cranial pubic ramus and from the lateral surface of the pubic body. In one specimen, the caudal portion of origin is via a fascia from the ventral end of the caudal pubic ramus. The insertion is onto 24 percent (15–28%) of the caudal surface of the femur beginning at a point 17 percent (14–19%) from the proximal end. In

two specimens, the insertion is broader than in *Erethizon*.

#### M. OBTURATOR EXTERNUS

Figure 18

ORIGIN: By fibers from the lateral surfaces of the ischium and pubis at the rim of the obturator foramen and from the external surface of the obturator membrane.

INSERTION: By a stout tendon into the trochanteric fossa of the femur deep (medial) to the insertion of M. obturator internus and Mm. gemelli.

REMARKS: There is no significant variation of the configuration of this muscle in *Coendou*.

#### ISCHIOTROCHANTERIC GROUP

##### M. QUADRATUS FEMORIS

Figure 18

ORIGIN: By fibers from the lateral surfaces of the dorsal ischial ramus deep to M. gemellus inferior, the superior ischial tuberosity deep to M. biceps femoris, and the inferior ischial ramus deep to M. semimembranosus. The most ventral point of origin from the inferior ischial ramus lies 0 to 10 mm. dorsal to that of M. semimembranosus.

INSERTION: Mostly by fibers onto the tip and caudolateral surface of the lesser trochanter and, in two specimens, onto the adjacent portion of the caudal surface of the femoral shaft.

REMARKS: The muscle is closely associated with M. gemellus inferior. There is no variation of the origin in *Coendou*. The most ventral point of origin from the inferior ischial ramus lies 6 to 7 mm. dorsal to that of M. semimembranosus. In two specimens, the muscle inserts by fibers onto the tip and caudolateral surface of the lesser trochanter and onto a distal portion of the intertrochanteric crest extending to a level of 1 to 2 mm. distal to the insertion of M. gluteus medius. The insertion of the muscle reaches the caudal surface of the femoral shaft in one of these specimens. In a third specimen, it is as in *Erethizon*.

#### M. GEMELLUS SUPERIOR

Figure 18

ORIGIN: By fibers from the dorsolateral surface of the ischium at the base of the ischial spine extending from the level of the caudal border of the acetabulum to the point where the tendon of M. obturator internus crosses the dorsal surface of the ischium.

INSERTION: By fibers onto the cranial surface of the tendon of M. obturator internus and via a tendon into the trochanteric fossa.

REMARKS: There is some fusion of the Mm. gemelli beneath the tendon of M. obturator internus. The tendon of insertion of the muscle is also fused with that tendon. No significant variation in *Coendou* was observed.

#### M. GEMELLUS INFERIOR

Figure 18

ORIGIN: By fibers from the dorsolateral surface of the dorsal ischial ramus cranial to the superior ischial tuberosity and caudal to the point where the tendon of M. obturator internus crosses the dorsal surface of the ischium.

INSERTION: By fibers onto the caudal surface of the tendon of M. obturator internus and via a tendon into the trochanteric fossa.

REMARKS: The origin lies superficial to that of M. quadratus femoris. The tendon of insertion is fused with that of M. obturator internus. There is no significant variation in *Coendou*.

#### M. OBTURATOR INTERNUS

Figure 18

ORIGIN: By fibers from the medial surfaces of the dorsal ischial ramus, the pubic body, cranial ramus and, in some specimens, a small ventral portion of the caudal ramus adjacent to the obturator foramen, the cranial two-thirds of the internal surface of the obturator membrane, and the medial surface of the os coxa in the region of the acetabulum.

INSERTION: By a stout tendon into the trochanteric fossa of femur with Mm. gemelli. The insertion is superficial (lateral) to that of M. obturator externus.

REMARKS: The muscle is multipinnate and highly convergent. The tendon passes dorsocaudad and then laterad over a smooth sur-



face on the dorsal aspect of the dorsal ischial ramus caudal to the spine. The tendon receives the fibers of *Mm. gemelli* before reaching the insertion.

The origin is more extensive in *Coendou*. The muscle arises from the medial surfaces of the pubis and ischium adjacent to the obturator foramen, from all the internal surface of the obturator membrane, and from the medial surface of the pubis in the region of the acetabulum.

#### HAMSTRING GROUP

##### *M. CAUDOFEMORALIS*

Figures 12, 17, 18

**ORIGIN:** From the deep layer of the lumbodorsal fascia in the region of the second caudal vertebra deep to *M. femorococcygeus* and by way of this fascia from the transverse process of the second caudal vertebra. The origin is slightly broader than the transverse process and, in one specimen, reaches the caudal edge of the transverse process of the first caudal vertebra.

**INSERTION:** By a tendon into a notch formed by the caudal surface of the medial epicondylar ridge of the femur and the medial edge of the proximal surface of the medial condyle. The insertion is just medial to the origin of the medial head of *M. gastrocnemius*.

**REMARKS:** The muscle arises from the same layer of the lumbodorsal fascia that gives rise to *M. femorococcygeus* and lies deep to that muscle, *M. tenuissimus*, the blood vessel passing to the lateral aspect of the tail, and the posterior femoral cutaneous nerve. It lies superficial to the perineal nerve and the nerve to the hamstrings. The sciatic nerve lies along its lateral border. This muscle is absent in all my specimens of *Coendou*.

##### *M. SEMITENDINOSUS*

Figures 10–13, 16–18

**ORIGIN:** Extensively from the lumbodorsal fascia of the gluteal and sacral regions. The origin extends from the level of the third sacral to the third caudal vertebrae.

**INSERTION:** By a short, flat tendon onto the lateral surface of the tibial tuberosity beginning at a point 53 percent (50–54%) from the

proximal end of the tibia and into the crural fascia covering the distal portion of the medial aspect of the leg. This fascia attaches to the distal portion of the medial surface of the tibia and blends with the insertion of *M. tenuissimus*.

**REMARKS:** The origin cannot be traced through the lumbodorsal fascia to the axial skeleton. Rinker (1954) identified two heads of origin of this muscle in cricetids, one from the sacral and caudal portions of the axial skeleton and one from the superior ischial tuberosity. Both heads fused below the origin of the ischial head at a point marked by a tendinous inscription that has been observed in many mammals (Rinker, 1954; Klingener, 1964). The ischial head and tendinous inscription are not present in any of my specimens. On one side of one specimen, a small group of fibers is present deep to *M. semitendinosus* that arises from the superior ischial tuberosity and inserts into the region of the deep layer of the lumbodorsal fascia that gives rise to *M. femorococcygeus*. These fibers course craniodorsad and do not insert into *M. semitendinosus* in any way. Hence, it is unlikely that they represent the ischial head of the muscle. The tendon of insertion passes laterad over the tibial tuberosity to reach the insertion. A small proximal portion of the tendon lies deep to *M. gracilis*.

In two specimens of *Coendou*, the origin extends from the level of the first to the fourth caudal vertebrae. In one specimen, the main part of the muscle arises as described, but a well-developed caudal slip of fibers arises separately from the caudal portion of the lumbodorsal fascia at the level of the fifth caudal vertebra via a few fibers and by fascia from the transverse processes of the fourth through sixth caudal vertebrae. This slip is closely associated with but separable from *M. pubococcygeus*. The insertion begins at a point 45 percent (44–48%) from the proximal end of the tibia. The portion that lies deep to *M. gracilis* is slightly larger than in *Erethizon*.

##### *M. SEMIMEMBRANOSUS*

Figures 11–13, 16–18

**ORIGIN:** By fibers from the caudal surface of the superior ischial tuberosity ventral to

the origin of *M. biceps femoris* and from the caudal edge of the lateral surface of all of the inferior ischial ramus caudal to the origin of *M. quadratus femoris* and proximal to that of *M. gracilis*. The origin is from the dorsal 35 percent (29–39%) of the distance from the superior ischial tuberosity to the caudal border of the pubic symphysis.

**INSERTION:** The insertion is divided into two parts by the tibial collateral ligament. The superficial part inserts by a thin aponeurosis onto the medial surface of the proximal 27 percent (24–30%) of the tibia cranial to the tibial collateral ligament. A deep slip inserts by aponeurosis onto the proximal 15 percent (13–18%) of the medial aspect of the shaft of the tibia on the caudal surface of a crest deep to the tibial collateral ligament.

**REMARKS:** The superficial aponeurosis is extensive and passes over the tibial collateral ligament to reach the insertion. It blends with the fascia of the knee. The deep slip is thick and well developed.

The configuration of the insertion is somewhat different in *Coendou*. The muscle inserts by aponeurosis onto the proximal 20 percent (18–21%) of the medial aspect of the shaft of the tibia on the crest located deep to the tibial collateral ligament. The superficial aponeurosis is represented only by a small distal slip which inserts cranial to the tibial collateral ligament. The most distal point of insertion is at a point 25 percent (22–26%) from the proximal end of the tibia. Thus, in *Coendou*, the equivalent of the deep fibers forms most of the insertion.

#### *M. BICEPS FEMORIS*

Figures 10–13, 18

**ORIGIN:** By a stout tendon from the dorsocaudal surface of the superior ischial tuberosity.

**INSERTION:** Broadly into the crural fascia on the lateral aspect of the leg. This fascia is continuous with the aponeurosis of insertion of *M. femorococcygeus* and similarly inserts onto the lateral surfaces of the patella and patellar ligament. It attaches to the peroneal process and the distal portion of the lateral surface of the shaft of the fibula, the antero-lateral surface of the lateral tibial condyle, the surface of the tibial crest just beyond the

origin of *M. tibialis anterior*, the lateral surface of the tibial tuberosity with *M. semiten-dinosus*, and the anterior surface of the tibia distal to the tibial tuberosity. It thickens distally to form the transverse crural ligament.

**REMARKS:** On one side of one specimen, a caudal slip of fibers separates from the main part and passes superficial to *M. tenuissimus* to insert into the crural fascia on the medial aspect of the leg. *M. tenuissimus* passes between the caudal slip and the main portion of the muscle. On one side of another specimen, a small slip of fibers arises by aponeurosis from the transverse process of the second caudal vertebra posterior to *M. caudofemoralis*. It fuses with the cranial portion of the main part and forms part of the proximal portion of insertion onto the patella and patellar ligament. In all specimens, the cranial portion of the muscle forming the more proximal portion of the insertion is thicker than the caudal portion. The configuration of the muscle in *Coendou* resembles *Erethizon*.

#### FLEXOR GROUP OF THE LEG

##### *M. GASTROCNEMIUS*

Figures 14, 15, 19

**ORIGIN:** Lateral head: By a stout tendon from the caudal surface of the lateral epicondyle of the femur proximal to the attachment of the fibular collateral ligament. A few fibers on the medial side arise directly from the fibrous capsule of the knee. In two specimens, some fibers arise from the tendon of *M. plantaris*, which lies deep to the lateral head. Medial head: By a stout tendon from the caudal surface of the crest of the medial epicondyle and slightly from a small lateral portion of the dorsal surface of the medial condyle deep to the tendon of insertion of *M. caudofemoralis*.

**INSERTION:** By a flat tendon onto the caudal (proximal) end of the calcaneus with the tendon of *M. soleus*.

**REMARKS:** The tendons of both heads of origin are bound by the capsule of the knee. In two specimens, the lateral tendon is closely associated with but separable with varying degrees of difficulty from the tendon of *M. plantaris*. In one specimen, the tendon of *M.*

plantaris does not lie deep to the lateral head. The medial tendon is closely associated with but separable from the tendon of *M. caudofemoralis*. The medial head is somewhat thicker but slightly narrower than the lateral one. The tendon of insertion becomes fused with that of *M. soleus* before reaching the common insertion on the calcaneus.

There are only minor variations of this muscle in *Coendou*. The lateral head does not arise from the capsule of the knee or the tendon of *M. plantaris*, although its tendon is closely associated with the latter. Since *M. caudofemoralis* is absent in *Coendou*, the medial tendon of *M. gastrocnemius* is not closely associated with its tendon of insertion. On one side of one specimen, a small distal group of fibers of *M. vastus medialis* arises from the superficial surface of the medial tendon. On one side of another specimen, a few distal fibers on the medial side of *M. gastrocnemius* attach to the tendon of *M. soleus*. The tendon of *M. plantaris* passes between these fibers and the main portion of the muscle.

#### M. PLANTARIS

Figures 14, 15, 20

**ORIGIN:** In two specimens, the muscle arises by a stout tendon from the caudal surface of the lateral epicondyle deep to the tendon of origin of the lateral head of *M. gastrocnemius*. In one specimen, the origin is from the lateral surface of the lateral condyle cranial to the origin of *M. popliteus*, distal to the level of the fibular collateral ligament, and 6 mm. caudal to the origin of *M. extensor digitorum longus* from the distal portion of the lateral epicondyle.

**INSERTION:** Via the plantar aponeurosis onto the bases of all five digits, the proximal end of the fifth metatarsal, and the deep surface of the medial sesamoid bone.

**REMARKS:** The muscle lies deep to *M. gastrocnemius* except for a small distomedial portion visible just medial to the tendon of insertion of that muscle. In two specimens, the tendon of origin is closely associated with that of the lateral head of *M. gastrocnemius*, a few fibers of which arise from its surface. It is bound by the capsule of the knee. Its own fibers arise farther distally from its

superficial surface. In one specimen, the tendon of origin lies deep to that of *M. extensor digitorum longus* and the capsule of the knee with that of *M. popliteus*. It courses 11 mm. distad from the origin on the lateral surface of the lateral condyle to fuse somewhat with the tendon of *M. popliteus*. It receives some fibers from that muscle and gives rise to its own fibers on its superficial surface. The tendon of insertion does not fuse with those of *M. gastrocnemius* and *M. soleus* but passes in a sheath on the medial portion of the caudal end of the calcaneus to reach the plantar aspect of the pes. There it fans out to become the plantar aponeurosis.

The plantar aponeurosis extends somewhat onto the medial and lateral sides of the calcaneus, where it is well anchored by adjacent connective tissue. It lies superficial to and is very closely associated with the thick, ligamentous remnant of *M. abductor ossis metatarsi quinti*. On the medial side, it blends with the fascia of insertion of *M. tenuissimus*. There are two layers of the plantar aponeurosis which are not easily separable. The superficial layer courses distad and fans out to attach to the proximal end of the fifth metatarsal, the deep surface of the medial sesamoid, and the bases of all five digits, where it is embedded in a large amount of adipose and fibrous connective tissue. The deep layer of the plantar aponeurosis is very thin and serves as the origin for *M. flexor digitorum brevis*. It is not readily separable from the superficial layer and is anchored to the medial, plantar, and lateral surfaces of the caudal (proximal) end of the calcaneus. In certain regions, there are large amounts of fibrous and adipose connective tissue superficial to the plantar aponeurosis. A thick pad of this tissue is found on the medial half of the pes and is attached to the ventral edge and deep surface of the medial sesamoid, the integument, and the plantar aponeurosis. It also contains muscle fibers, the amount of which is individually variable, that attach to the ventral cartilaginous portion of the medial sesamoid and the plantar aponeurosis. This connective tissue gradually thins out to nothing in the middle of the pes. There is also a substantial amount of connective tissue at the bases of the digits and some laterally.

In *Coendou*, there is only minor variation of the configuration of the insertion from *Erethizon*. The plantar aponeurosis attaches to the proximal end of the fifth metatarsal, a small proximal portion of the deep surface of the medial sesamoid, and the bases of digits 2 through 5. I was not able to trace most of the plantar aponeurosis to an attachment on the medial sesamoid, although the small portion on the medial side of the calcaneus was traced to the proximal portion of the deep surface. The muscle embedded within the connective tissue pad was described by Jones (1953). He reported that it spread across all the plantar surface of the pes and attached to the medial sesamoid and a curved tendon at the interspace between the fourth and fifth digits. I was not able to observe the tendon or the portion of the muscle on the lateral portion of the pes. Jones (1953) noted that the muscle was responsible for opposing the preaxial pad to the rest of the sole.

#### M. SOLEUS

Figures 14, 15

**ORIGIN:** By a strong, flat tendon from a small tubercle on the lateral portion of the caudal surface of the head of the fibula and by fibers from the middle third of the intermuscular septum between the flexor and peroneal groups.

**INSERTION:** By a stout tendon onto the caudal (proximal) end of the calcaneus in common with *M. gastrocnemius*.

**REMARKS:** The fibers arise from the superficial surface of the tendon of origin. The tendon of insertion is large and lies deep to that of *M. gastrocnemius*. These two tendons fuse inseparably as they near the insertion. There is no significant variation in *Coendou*.

#### M. POPLITEUS

Figures 14, 15, 19

**ORIGIN:** By a tendon from the lateral surface of the lateral condyle 6 to 7 mm. caudal to the attachment of the tendon of *M. extensor digitorum longus* on the distal portion of the lateral epicondyle.

**INSERTION:** By fibers onto the proximal 62 percent (59–66%) of the medial surface of the shaft of the tibia extending to the level of the

tibial tuberosity, onto the caudal surface of the small crest on the proximal portion of the medial tibial surface to which the tibial collateral ligament and part of the insertion of *M. semimembranosus* are attached, and strongly onto the surface of *M. flexor digitorum tibialis*. A few fibers insert onto the distal attachment of the tibial collateral ligament.

**REMARKS:** The origin is marked by a depression on the lateral surface of the lateral condyle. The tendon of origin lies deep to the capsule of the knee, which is bound to its superficial surface. In one specimen, the tendon lies deep to and fuses somewhat with that of *M. plantaris*. As soon as the tendon enters the popliteal space, it gives rise to the muscle fibers. The proximal fibers pass medially toward their insertion at the level of the tibial collateral ligament. The distal fibers pass distomedially toward their insertion onto *M. flexor digitorum tibialis* and the more distal portions of the tibial shaft. In one specimen, the insertion extends to a point just distal to the tibial tuberosity.

In *Coendou*, the only differences are related to body size. The origin lies 2 mm. caudal to the tendon of *M. extensor digitorum longus*. The insertion is onto 48 percent (46–50%) of the shaft of the tibia. Although this is not quite as broad as in *Erethizon*, it occupies exactly the same position, extending to the level of the tibial tuberosity.

#### M. FLEXOR DIGITORUM TIBIALIS

Figures 19, 21, 22

**ORIGIN:** By a small aponeurosis from the medial portion of the caudal surface of the head of the fibula, mostly by fibers from 60 percent (56–66%) of the medial surface of the shaft of the tibia, including the medial surface of the interosseous crest, beginning at a point 20 percent (14–26%) from the proximal end, and from a very narrow portion of the fascia on the surface of *M. tibialis posterior* adjacent to the origin from the tibia.

**INSERTION:** The muscle inserts primarily by a common tendon with *M. abductor hallucis brevis* onto the tubercle at the base of the distal phalanx of the hallux and via the common subsidiary flexor tendon with that muscle and *M. flexor digitorum fibularis* onto the

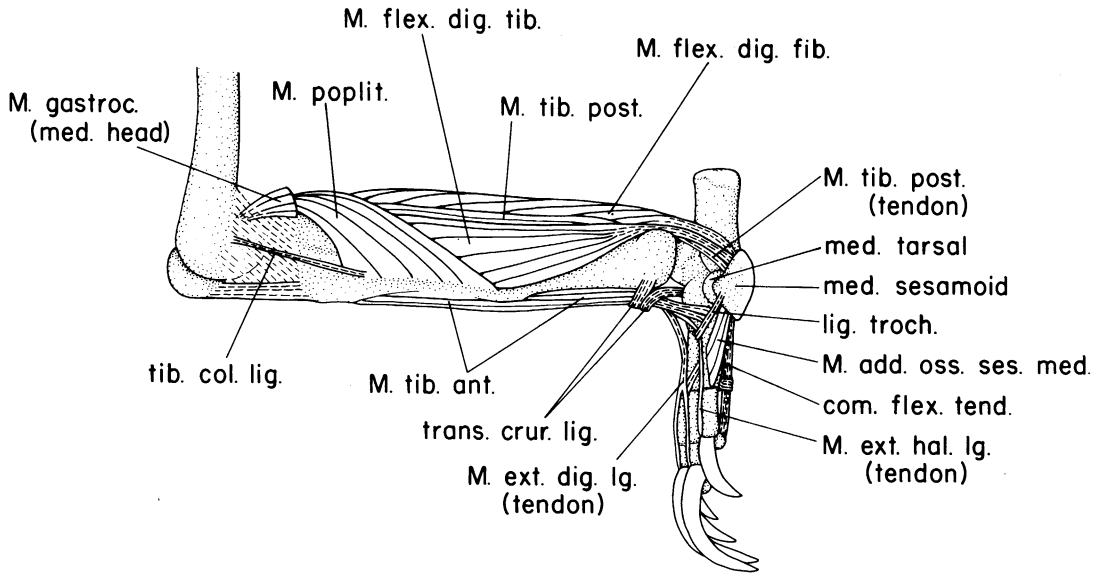


FIG. 19. Medial view of the deep muscles of the leg of *Erethizon*.

tubercle at the base of the distal phalanx of the second digit. It also has minor insertions with the subsidiary tendons of *M. flexor digitorum fibularis* onto the distal phalanges of digits 3 through 5.

**REMARKS:** The muscle is large and highly convergent. The aponeurosis of origin from the fibular head is closely associated with *M. tibialis posterior*. The proximal portion of origin from the tibia is aponeurotic. The aponeurosis from the head of the fibula also attaches in this region. The origin from the tibia lies caudal and distal to the insertion of *M. popliteus*, which inserts in part onto the proximal portion of the muscle. However, these two muscles can be separated in some specimens with difficulty. The most distal point of origin lies just distal to the tibial tuberosity. The degree of development of the origin from the fascia of *M. tibialis posterior* varies individually. The tendon of insertion passes through a deep groove on the medial side of the medial malleolus superficial to the tendon of *M. tibialis posterior*. It then passes deep to the flexor retinaculum and onto the plantar aspect of the foot. There it lies deep (dorsal) to *M. abductor hallucis brevis* and superficial (ventral) to the tendon of *M. flexor digitorum fibularis*. It divides into four sub-

sidary tendons which fuse with the tendons of *M. abductor hallucis brevis* and *M. flexor digitorum fibularis*. It inserts primarily by a common tendon with the former onto the hallux and via a common subsidiary tendon with both of those muscles onto the second digit. It also makes small contributions with *M. flexor digitorum fibularis* to the common subsidiary tendons to digits 3 through 5, although the contributions to digits 3 and 4 are represented by a few tendinous filaments, embedded in fascia, that are difficult to trace deep to the origin of the lumbricales of those digits.

There is only minor variation of the origin in *Coendou*. The muscle arises from 67 percent (65–68%) of the tibial shaft beginning at a point 10 percent (7–16%) of the total length of the tibia from the proximal end. The origin from the fascia of *M. tibialis posterior* is absent in one specimen. The aponeurosis from the head of the fibula tends to be weaker than in *Erethizon*. The muscle inserts by a common subsidiary tendon with *M. abductor hallucis brevis* and, in two specimens, with *M. flexor digitorum fibularis* onto the base of the distal phalanx of digit 2 and by common subsidiary tendons with the latter muscle onto

digits 3 through 5. The contribution to digits 3 and 4 is greater than in *Erethizon*.

In all specimens, I have observed a narrow tendinous filament that appears to attach proximally to the surface of *M. adductor hallucis*. It courses distad, passes deep to a fibrous loop between the sesamoids at the metatarsophalangeal joint of the hallux, and inserts on the distal end of the sole phalanx of that digit. It probably represents the vestigial common subsidiary tendon to the hallux.

#### *M. FLEXOR DIGITORUM FIBULARIS*

Figures 19, 21, 22

**ORIGIN:** By fibers from the medial and lateral surfaces of the head of the fibula, the proximal 77 percent (76–80%) of the shaft of the fibula, the intermuscular septum between the flexor and peroneal groups, the interosseous membrane, and the proximal 81 percent (75–85%) of the shaft of the tibia. The origin from the fibular shaft includes the caudal and mediocaudal surfaces proximally and the mediocaudal surface distally. The tibial origin includes the caudolateral surface proximally and a large portion of the caudal fossa distally.

**INSERTION:** By four common subsidiary tendons with *M. flexor digitorum tibialis* onto the tubercles at the bases of the distal phalanges of digits 2 through 5. The common subsidiary tendon to digit 2 contains elements from *M. abductor hallucis brevis* as well.

**REMARKS:** The origin from the head of the fibula and proximal portion of the shaft of the tibia is separated into two small heads with the anterior tibial artery passing between them. The fibers reach the tendon of insertion in a complex pattern. The large tendon then passes along a shallow groove on the caudal surface of the medial malleolus and under the sustentaculum tali onto the plantar aspect of the foot deep (dorsal) to that of *M. flexor digitorum tibialis*. It divides into four subsidiary tendons that fuse with those of *M. flexor digitorum tibialis* to form common subsidiary tendons which insert on the distal phalanges of the lateral four digits. Its contribution to the common tendon to digit 2 is much less than that of *M. flexor digitorum tibialis*. However, the reverse is true for digits

3 through 5, with the muscle forming nearly all of the common subsidiary tendons to digits 3 and 4. Elements of the tendon of *M. abductor hallucis brevis* are included in the common tendon to the second digit. The muscle is the equivalent of *M. flexor digitorum profundus* in the forelimb (Hollinshead, 1974). Similarly, the common subsidiary tendons pass through the tendinous loops formed by the slips of *M. flexor digitorum brevis*, then deep to the fibrous loops at the metatarsophalangeal joints, and finally between the branches of the short flexor tendons to reach the insertion.

In *Coendou*, the origin includes the proximal 74 percent (68–78%) of the shaft of the fibula and the proximal 76 percent (75–77%) of the tibial shaft. In two specimens there is no variation in insertion, whereas in one the insertion is confined to the lateral three digits.

#### *M. TIBIALIS POSTERIOR*

Figures 19, 21, 22

**ORIGIN:** By fibers from the medial and distal portions of the caudal surfaces of the head of the fibula, the aponeurosis of origin of *M. flexor digitorum tibialis* from the fibular head, the fascia on the proximal portion of the surface of that muscle, the adjacent surface of *M. flexor digitorum fibularis*, and the proximal 52 percent (40–62%) of the shaft of the tibia on the lateral surface of all of the interosseous crest.

**INSERTION:** By a stout tendon onto the ventral portion of the caudal surface of the medial tarsal bone.

**REMARKS:** The muscle is parallel-fibered. The origin from the tibia lies caudal to that of *M. flexor digitorum fibularis* and extends to the edge of the interosseous crest, although distally the crest is rounded. There is no origin from the caudal fossa of the tibia. The tendon passes in a deep groove on the medial side of the medial malleolus deep to the tendon of *M. flexor digitorum tibialis*. It passes distad under the medial malleolus deep (lateral) to the proximal portion of the medial sesamoid to reach the insertion.

In *Coendou*, the origin extends farther distally along the interosseous crest to include a short segment of the lateral border of the caudal fossa. The muscle arises from the prox-

imal 67 percent (63–69%) of the tibial shaft. There is no other significant variation.

#### FLEXOR GROUP OF THE PES

##### M. FLEXOR DIGITORUM BREVIS

Figure 20

**ORIGIN:** The muscle is divided into four slips which are closely associated proximally. It arises via the deep layer of the plantar aponeurosis from the lateral, plantar, and medial surfaces of the caudal (proximal) end of the calcaneus.

**INSERTION:** By small tendons onto the plantar aspects of the bases of the middle phalanges of digits 2 through 5. The tendons of the lateral three slips fuse with those of the accessory short flexors, forming common tendons of insertion.

**REMARKS:** The muscular slips appear to arise from the deep surface of the plantar aponeurosis. However, their origins were consistently traced to a deep aponeurotic layer that was very difficult to separate from the superficial one. Although the slips always arise near the proximal end of the pes, the pattern of origin is somewhat variable. In one specimen, the medial slip (to digit 2) arises from the portion of the deep layer of the plantar aponeurosis that is anchored to the medial and plantar surfaces of the calcaneus. In another specimen, it arises from a small portion of the deep layer of the plantar aponeurosis on the medial side of the pes and broadly by fibers from the distal portion of the flexor retinaculum deep to the fascia of insertion of *M. tenuissimus*. In a third specimen, the medial and lateral slips (to digits 2 and 5, respectively) are closely associated proximally and arise via the deep layer of the plantar aponeurosis from the medial surface of the calcaneus. In all specimens, the middle two slips (to digits 3 and 4) are closely associated through most of their lengths. The lateral slip is not as well developed as the other three. The tibial nerve passes deep (dorsal) to the muscles. These muscles are parallel-fibered but the fibers attach to the tendons of insertion in a variable manner. There is no accessory short flexor for the tendon to digit 2.

Each tendon of insertion courses distad and

passes deep to the fibrous loop between the sesamoids of the metatarsophalangeal joint of its respective digit. Just before it does so, it gives rise to a small tendinous loop that passes around the common subsidiary tendon of the long flexors. This loop is often difficult to observe. The tendon then bifurcates, sending medial and lateral branches distad and around the common subsidiary flexor tendon. These branches fuse just before reaching the insertion on the base of the middle phalanx.

The configuration of this muscle in *Coendou* is also quite variable. In one specimen, there are four slips which arise from the deep layer of the plantar aponeurosis as in *Erethizon*, with the medial slip arising from its medial portion. On one side of one specimen and on both sides of another, the slip to digit 4 is absent. In the latter specimen, that to digit 5 is also absent.

The tendons of *M. flexor digitorum brevis* contribute less to the common tendons of insertion than the accessory short flexors, the reverse of the conditions in *Erethizon*. However, the basic configuration of the insertions is similar between the two genera. In one specimen, the tendon to the fifth digit is weakly developed. On one side it bifurcates, sending a medial branch to blend with the fibrous loop at the metatarsophalangeal joint. The lateral branch becomes slightly fused with the tendon of the lateral accessory short flexor, then receives a few fibers from that muscle, and finally courses around the common long flexor subsidiary tendon to insert on the base of the middle phalanx. On the other side, the tendon fuses lightly with that of the accessory short flexor and blends with the fibrous loop. I could not observe a distinct tendinous loop for this slip.

##### MM. FLEXORES BREVES ACCESSORII

Figures 20, 21

**ORIGIN:** There are three of these muscles present. In two specimens, the middle and lateral accessory short flexors arise by fibers from the plantar surface of the tendon of *M. flexor digitorum tibialis* just proximal to the origin of the lumbricales to digits 4 and 5, respectively, and by fascia from the lateral border of the distal portion of *M. abductor*



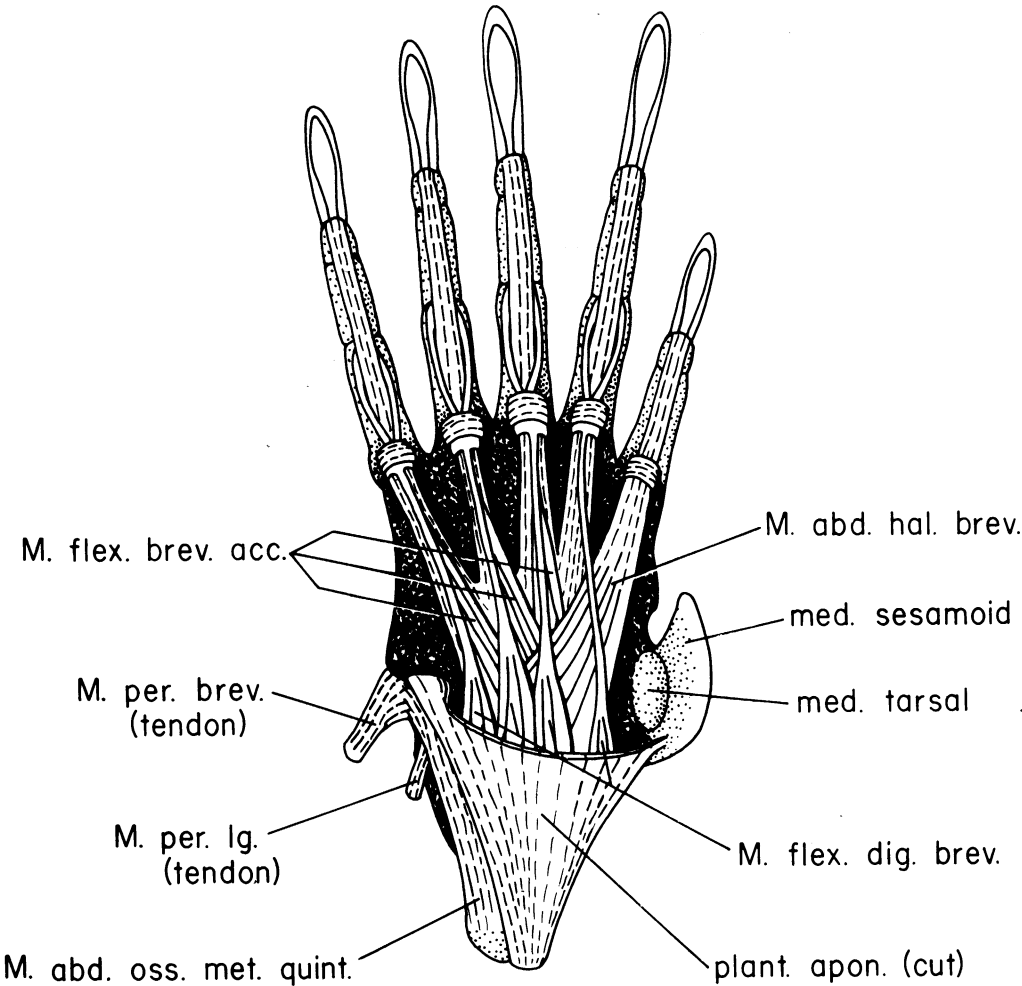


FIG. 20. Plantar view of the pes of *Erethizon*. I. Superficial muscles.

hallucis brevis. The medial accessory short flexor arises from the plantar surface of the tendon of *M. flexor digitorum tibialis* and the distal border of the tendon of *M. abductor hallucis brevis* just proximal to the origin of the lumbrical to digit 3. In one specimen, the lateral muscle arises by fibers from the plantar aspect of the common subsidiary flexor tendon to digit 5 and from a small portion of a group of lateral fibers of *M. abductor hallucis brevis* that inserts on the same subsidiary tendon. The middle accessory short flexor arises from the plantar surface and dis-

tal border of the fibers and tendon of *M. abductor hallucis brevis* and slightly from the plantar surface of *M. flexor digitorum tibialis*. The medial belly arises from the tendon of *M. abductor hallucis brevis* just proximal to the origin of the lumbrical to the third digit.

INSERTION: By small tendons that fuse with those of *M. flexor digitorum brevis*, forming common tendons which insert as described for that muscle onto the middle phalanges of digits 3 through 5. The tendons of the accessory short flexors are difficult to observe with-

out dissecting the muscles from the common tendons of insertion. As such, these muscles appear to insert by fibers onto the tendons of *M. flexor digitorum brevis*.

**REMARKS:** These muscles are parallel-fibered. There is no interdigitation of the fibers of origin with *M. abductor hallucis brevis*. The middle accessory short flexor is the largest of the three.

In two specimens of *Coendou*, the medial accessory short flexor arises from the tendons of *M. flexor digitorum tibialis* and *M. abductor hallucis brevis* as in two specimens of *Erethizon*. The origin also includes a tiny portion of the surface of the middle accessory short flexor in one of these specimens. In a third specimen, it arises in a similar manner but also strongly interdigitates with the medial fibers of *M. abductor hallucis brevis*, which appear to be continuous with this muscle. In all specimens, the middle accessory short flexor arises from the tendon of *M. flexor digitorum tibialis*. There is no origin from *M. abductor hallucis brevis*, although in two specimens, part of the origin lies deep to that muscle. The origin of the lateral accessory short flexor is also from the tendon of *M. flexor digitorum tibialis*. However, in one specimen, it includes a tiny portion of the middle accessory short flexor and the plantar surface and lateral border of *M. abductor hallucis brevis*. In another specimen, the muscle also arises slightly from the middle accessory short flexor but strongly interdigitates with both the medial and lateral fibers of *M. abductor hallucis brevis*. In a third specimen, the slight origin from the middle accessory short flexor is present, but there is no origin from *M. abductor hallucis brevis*.

In *Coendou*, these muscles are bipinnate and their tendons make larger contributions to the common tendons of insertion than do those of the short flexors. In specimens where some short flexor slips are absent, the configuration of the insertion is as described for *M. flexor digitorum brevis*. In one specimen, the lateral accessory short flexor fuses slightly with the tendon of the slip of *M. flexor digitorum brevis* to digit 5. Its tendon then passes to the lateral side of the proximal phalanx of the fifth digit. It appears to insert there, but I could not be certain of this because of the difficulty in tracing the tendon.

#### *M. ABDUCTOR HALLUCIS BREVIS*

Figures 20–22

**ORIGIN:** By fibers from a small portion of the medial surface of the calcaneus, including the surface of the tuber calcanei, from a small proximal portion of the long plantar ligament, and from the plantar surface of the calcaneus lateral to that ligament, medial to the plantar surface of the trochlear process, and proximal to the groove for the tendon of *M. peroneus longus*.

**INSERTION:** The tendon of the muscle fuses with part of the tendon of *M. flexor digitorum tibialis* to form a common tendon that inserts on the base of the distal phalanx of the hallux. Some tendinous elements course with *M. flexor digitorum tibialis* and *M. flexor digitorum fibularis* in the common subsidiary flexor tendon to the second digit. In one specimen, the muscle also inserts by fibers onto the distomedial portion of the tendon of *M. flexor digitorum tibialis* and laterally onto the common subsidiary flexor tendon to digit 5.

**REMARKS:** The muscle is closely associated with *M. abductor ossis metatarsi quinti*. In *Coendou*, the origin is not quite as extensive. Its most distal point lies 3 to 6 mm. proximal to the groove for the tendon of *M. peroneus longus*. In two specimens, the tendon of insertion fuses with that of *M. flexor digitorum tibialis* and courses with the common subsidiary flexor tendon to the base of the distal phalanx of the second digit. In one specimen, the muscle inserts by fibers onto the entire distal portion of the plantar surface of the tendon of *M. flexor digitorum tibialis* and slightly onto the surface of the middle accessory short flexor. Distally, it splits into two parts that strongly interdigitate with the medial and lateral accessory short flexors. The medial fibers also insert slightly onto the tendon of *M. flexor digitorum brevis* to digit 3. There is also a small tendon on the deep surface of the medial fibers that fuses with the subsidiary tendon of *M. flexor digitorum tibialis* to the second digit.

#### MM. LUMBRICALES

Figure 21

**ORIGIN:** There are four of these muscles present. They arise from the angles formed by the common subsidiary flexor tendons to

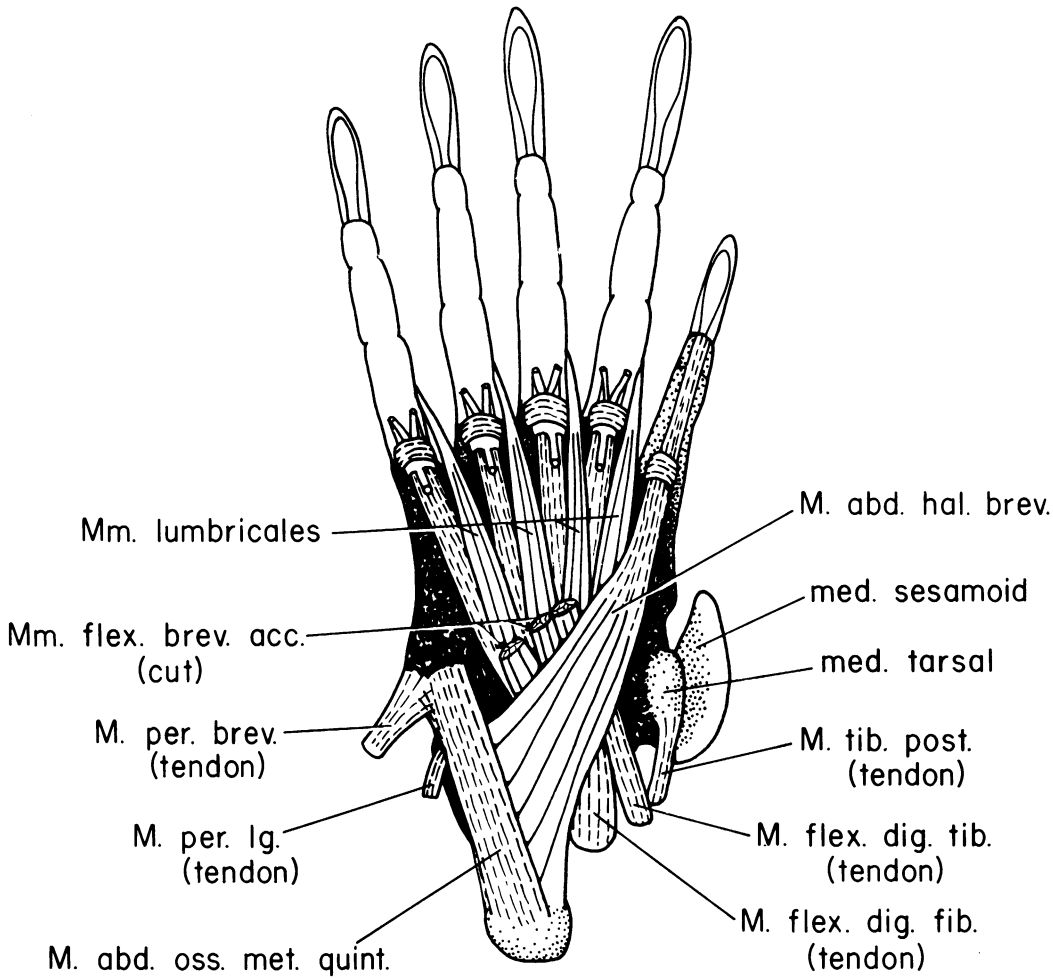


FIG. 21. Plantar view of the pes of *Erethizon*. II. Deeper muscles.

all five digits and slightly from the plantar surfaces of the tendons of *M. flexor digitorum tibialis*, *M. flexor digitorum fibularis*, and *M. abductor hallucis brevis* distal to the origin of the accessory short flexors. The lumbrical to digit 3 also arises from the distal border of the tendon of *M. abductor hallucis brevis*.

INSERTION: By small tendons onto the middle of the plantar edges of the medial surfaces of the proximal phalanges of digits 2 through 5.

REMARKS: In *Coendou*, there is no significant variation in the origins of the lateral three lumbricales. Since there is no common flexor tendon to the hallux, the medial lum-

brical arises from the medial border and slightly from the plantar surface of the tendon to the second digit. The tendons of insertion appear to be somewhat broader and flatter than in *Erethizon*. In one specimen, two small slips from the lumbricales to digits 4 and 5 insert by small, flat tendons onto the plantar edges of the lateral surfaces of the proximal phalanges of digits 3 and 4, respectively.

**M. ABDUCTOR OSSIS METATARSI QUINTI**  
Figures 14, 15, 20–22

This muscle is represented by a thick, flattened tendon that lies deep to and is closely

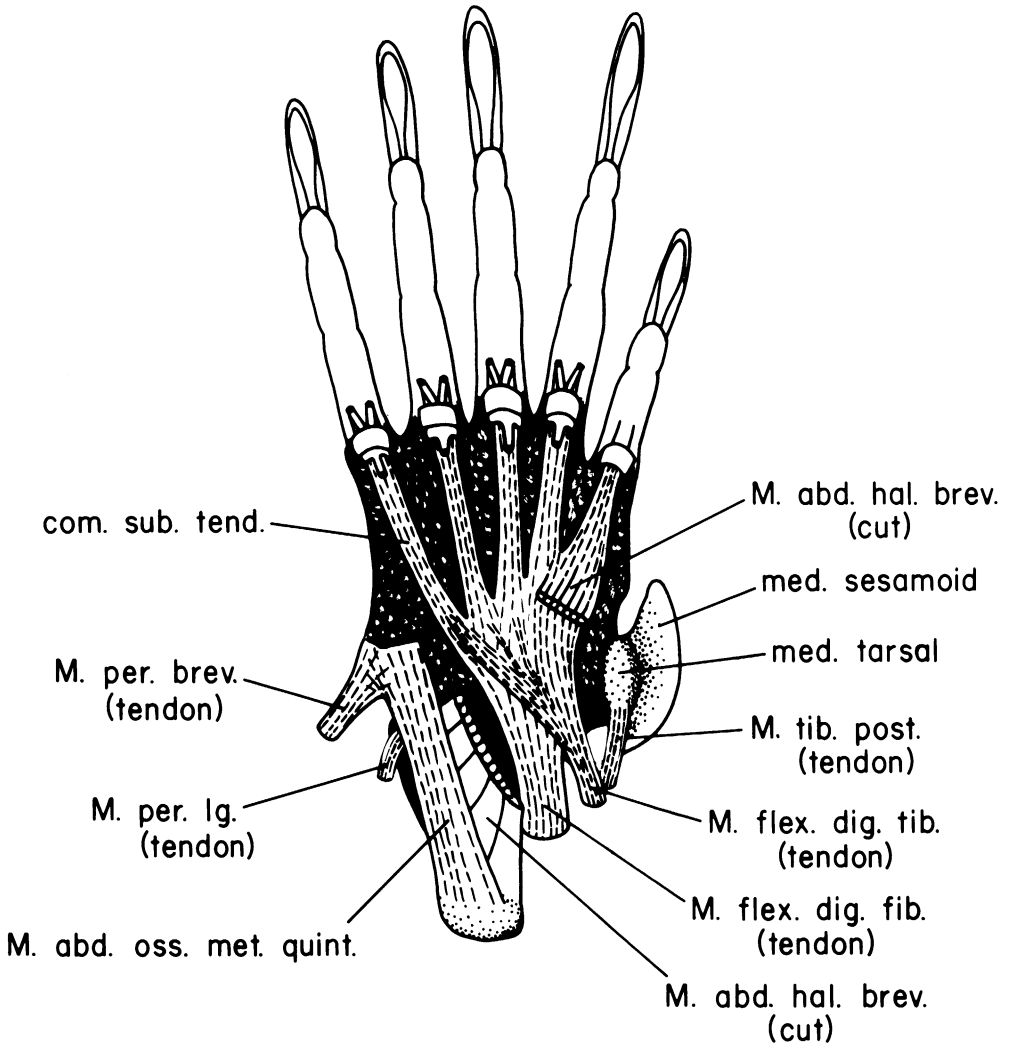


FIG. 22. Plantar view of the pes of *Erethizon*. III. Deeper muscles.

associated with the plantar aponeurosis. It arises from the plantar and a small portion of the lateral surfaces of the proximal end of the calcaneus and inserts onto the base of the fifth metatarsal and into the distal portion of the tendon of *M. peroneus brevis*. The origin of *M. abductor hallucis brevis* is closely associated with its deep surface. There appear to be faint indications of muscle fibers within the tendon, but I cannot be certain of their presence without histological studies. In *Coendou*, the tendon is not as thick as in

*Erethizon*, and it has only a small insertion into the tendon of *M. peroneus brevis*.

**M. ABDUCTOR DIGITI MINIMI**  
Figures 23, 24

**ORIGIN:** From the lateral portion of the deep palmar aponeurosis attached strongly to the base of the fifth metatarsal.

**INSERTION:** By a short aponeurosis onto the lateral surface of the lateral sesamoid bone at the metatarsophalangeal joint of the fifth

digit. A small tendon continues a short distance distodorsad to fuse with the tendon of *M. peroneus digiti minimi*.

REMARKS: The muscle is parallel-fibered and heavily invested with tough connective tissue. It appears to arise by fibers from the base of the fifth metatarsal, but it is actually attached via the deep palmar aponeurosis. The tendon of insertion is bound by the capsule of the metatarsophalangeal joint and is often difficult to distinguish. However, there is always a close association with the tendon of *M. peroneus digiti minimi*. There is no significant variation in *Coendou*.

#### M. FLEXOR HALLUCIS BREVIS

This muscle is absent in both *Erethizon* and *Coendou*.

#### M. FLEXOR DIGITI MINIMI BREVIS

Both Rinker (1954) and Klingener (1964) described this muscle as arising either from a sesamoid bone associated with the origin of *M. abductor digiti minimi* or directly from the calcaneus. A close association with *M. abductor digiti minimi* was always noted. The insertion was on the medial sesamoid bone at the metatarsophalangeal joint of the fifth digit. On one side of one specimen of *Erethizon*, a small slip of fibers probably representing this muscle was observed to arise from the deep palmar aponeurosis medial and closely associated with *M. abductor digiti minimi*. It inserts onto the caudomedial surface of the medial sesamoid at the metatarsophalangeal joint of the fifth digit. I observed similar fibers in two specimens of *Coendou*. The only variation from *Erethizon*, of little importance, is that the insertion is on the medial side of the fifth digit just dorsal to the medial sesamoid. Therefore this muscle is vestigial and its occurrence is sporadic in these two genera.

#### M. ADDUCTOR HALLUCIS

Figure 23

ORIGIN: The medial fibers form the main portion of the muscle and arise superficially from the medial portion of the deep palmar aponeurosis. The distolateral fibers arise from a narrow distal extension of the deep palmar

aponeurosis at the level of the middle metatarsal.

INSERTION: The two portions of the muscle converge to insert on the lateral surface of the lateral sesamoid bone at the metatarsophalangeal joint of the hallux.

REMARKS: In two specimens, the distolateral fibers are weakly developed and embedded in a fascial sheet continuous with the superficial origin from the deep palmar aponeurosis. In one specimen, they are somewhat better developed, and a distinct tendinous filament represents the distal extension of the deep palmar aponeurosis. On one side of one specimen, some deep fibers of the medial portion of the muscle insert via a small aponeurosis onto the base of the first metatarsal just medial to the origin of the medial interosseous muscle to the second digit. A small group of fibers arises from the lateral border of this aponeurosis and courses distolaterad to insert onto the deep transverse metatarsal ligament between the second and third digit and into the connective tissue on the lateral side of the second digit.

In two specimens of *Coendou*, the distolateral fibers are not present but are represented by a weak fascial sheet. In one specimen, the origin resembles *Erethizon*. The insertion is onto the lateral side of the hallux just dorsal to the lateral sesamoid at the metatarsophalangeal joint and, in two specimens, slightly onto that sesamoid. In all specimens, a narrow tendinous filament passing to the hallux attaches proximally to the surface of the muscle. Since it probably represents the vestigial tendon of *M. flexor digitorum tibialis*, it is described more completely with that muscle.

#### M. ADDUCTOR DIGITI QUINTI

Figure 23

ORIGIN: The lateral fibers arise superficially from the lateral portion of the deep palmar aponeurosis. The distomedial fibers arise from a narrow distal extension of the deep palmar aponeurosis at the level of the middle metatarsal.

INSERTION: The muscle converges to insert by fibers onto the medial surface of the medial sesamoid at the metatarsophalangeal joint of the fifth digit.

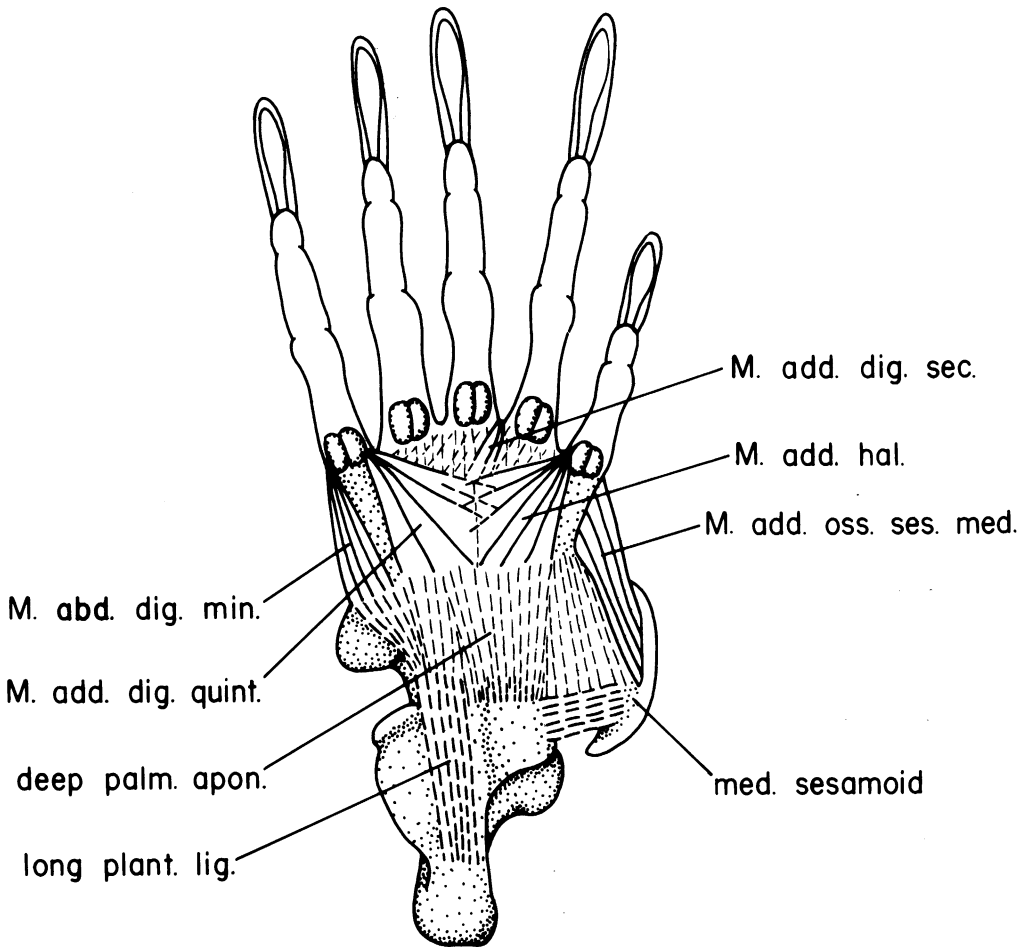


FIG. 23. Plantar view of the pes of *Erethizon*. IV. Deeper muscles.

REMARKS: The lateral fibers are the best developed. The distomedial fibers are weakly developed and embedded in a fascial layer continuous with the superficial origin from the deep palmar aponeurosis. As previously described for *M. adductor hallucis*, the narrow distal extension of the deep palmar aponeurosis is represented by a tendinous filament in one specimen.

In one specimen of *Coendou*, the origin is as described for *Erethizon*, although no tendinous filament between it and *M. adductor hallucis* was observed. In two specimens, the distolateral fibers and the fascial sheet are weaker than in *Erethizon*. The fascial sheet is anchored to the lateral border of *M. adduc-*

*tor hallucis*. In all specimens, the muscle inserts by fibers onto the medial surface of the fifth digit just dorsal to the medial sesamoid at the metatarsophalangeal joint.

**M. ADDUCTOR DIGITI SECUNDI**  
Figure 23

This muscle is vestigial and is present only in *Erethizon*. A few fibers arise in the region of the middle metatarsal from the distal portion of the distal extension of the deep palmar aponeurosis in which the fibers of *M. adductor hallucis* and *M. adductor digiti quinti* are embedded. They insert onto the deep transverse metatarsal ligament between digits 2 and 3.

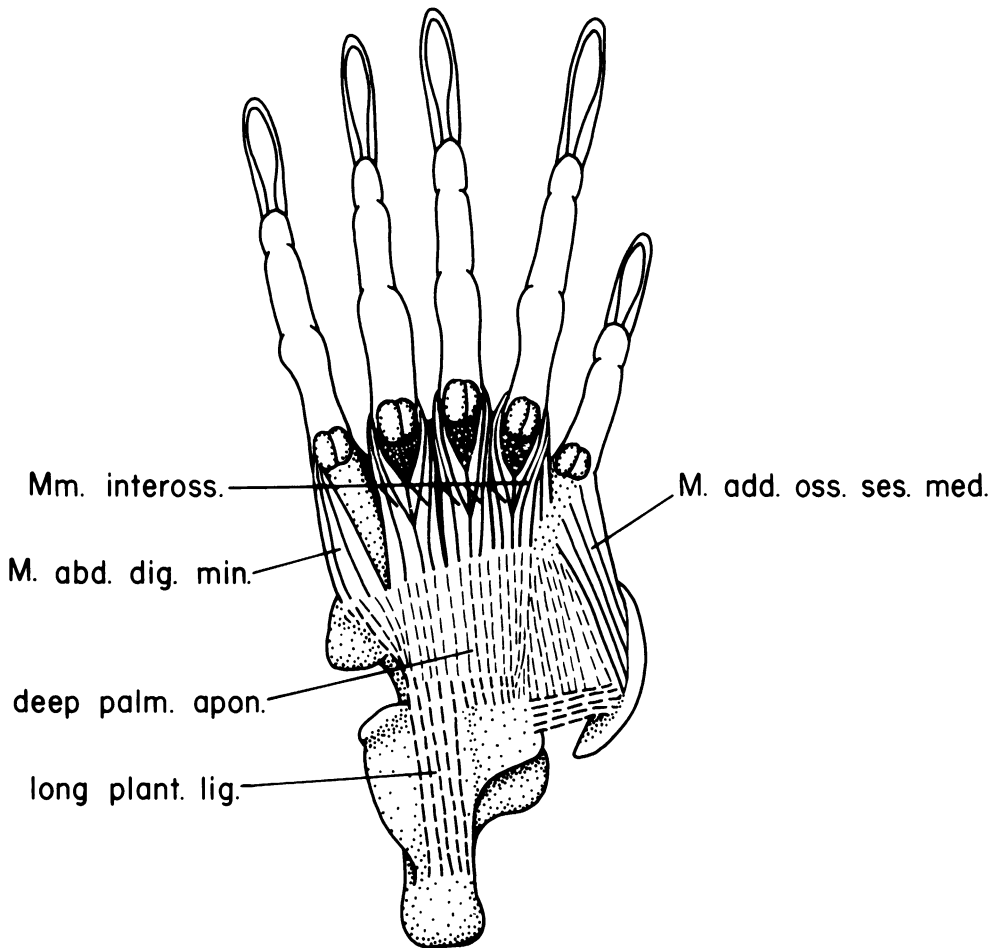


FIG. 24. Plantar view of the pes of *Erethizon*. V. Deeper muscles.

MM. INTEROSSEI  
Figure 24

There are three pairs of these muscles associated with the medial and lateral sides of the middle three digits. The medial portion of the medial interosseous muscle of digit 2 is separable from the lateral portion and arises broadly from the lateral portion of the plantar surface of the first metatarsal. The lateral portion of this muscle and all other interossei arise slightly by fibers from the bases of the lateral four metatarsals and from the distal end of the deep palmar aponeurosis. They give the appearance of arising totally by fibers from the bases of the metatarsals but are

actually attached via the deep palmar aponeurosis. The origin of the most lateral interosseus muscle lies medial to that of *M. abductor digiti minimi*. The medial and lateral interossei of each digit form a raphe between themselves proximally. The interossei of adjacent digits are also fused proximally, with a small tendinous filament sometimes visible between them.

The deep palmar aponeurosis (Rinker, 1954) gives rise superficially to *M. adductor hallucis* and *M. adductor digiti quinti*. Distally, it attaches to the plantar surfaces of the bases of the lateral four metatarsals. Medially it attaches to the medial cuneiform, the medial



tarsal bone, and by a thin layer to the deep surface of the medial sesamoid bone, blending with a ligament coursing between the medial sesamoid and the medial edge of the sustentaculum tali. Centrally, it attaches to the navicular, blending indistinguishably with a ligament from the navicular to the distal edge of the sustentaculum tali. Laterally, it attaches to the cuboid and blends indistinguishably with the long plantar ligament. In *Coendou*, the deep palmar aponeurosis does not appear to be attached to the medial sesamoid.

The lateral interosseous muscle of each digit gives rise to a tendon which courses a short distance distodorsad to fuse with that of the short digital extensor, forming a common tendon. This tendon and that of the medial interosseous muscle of each digit pass deep to the joint capsule of the proximal interphalangeal joint and insert on their respective sides of the dorsal surface of the base of the middle phalanx. The tendons then continue distad to fuse with the distal portion of the long digital extensor tendon. The portion of the tendon distal to the insertion on the base of the middle phalanx is difficult to trace and may be missed in some specimens. The interosseous muscles are also bound to the sides of their respective digits of insertion by the capsule of the metatarsophalangeal joint and adjacent connective tissue. In one specimen, a separate tendon for the medial portion of the medial interosseous muscle to digit 2 is

present and was traced to that of the lumbrical to the second digit. The configuration of these muscles does not vary significantly in *Coendou*.

A separate muscle located on the medial side of the pes was observed to arise by fibers from the medial surface of the first metatarsal, including the head, and to insert by fibers onto the deep surface of the medial sesamoid bone (figs. 19, 23, 24). This muscle appears to be slightly broader in *Coendou* and arises from the medial cuneiform as well as the first metatarsal. In two specimens, the origin includes the medial portion of the plantar surface of the first metatarsal in addition to the medial surface. This muscle was described in *Coendou* by Jones (1953) and more recently by Hildebrand (1978). Jones (1953) suggested that it represented an *M. abductor ossis metatarsi hallucis*, but Hildebrand (1978) left it unnamed. Jones (1953) noted that the preaxial margin of the pes could be depressed in a plantar direction because of the mobility of the medial tarsal (his *os naviculare tibiale*) and the "free articulation" of the medial sesamoid (his tibial ossicle). Hildebrand (1978) concluded that contraction of the muscle between the first metatarsal and the medial sesamoid would move the latter forward and inward rather than abduct the first metatarsal. Therefore, I have chosen to refer to this muscle in erethizontids as the *M. adductor ossis sesamoideus medialis*.

## DISCUSSION

### MYOLOGICAL CONDITIONS OF THE APPENDAGES OF THE ERETHIZONTIDAE

Some of the myological characters in *Erethizon* have been shown to be relatively primitive when compared with other hystricomorphs (Woods, 1972). The present study also supports this observation for both *Erethizon* and *Coendou*. The size and weight of these animals coupled with the presence of external adaptations for arboreal locomotion suggest that corresponding myological adaptations would also occur. One would expect the configurations of some muscles to be derived from the primitive condition or to

be convergent with those in other large arboreal mammals.

### FORELIMB

During climbing, the pectoral girdle would tend to be pulled cranially when the forelimb is used to bear the weight of the animal. The scapula would also rotate so that the glenoid would be forced craniodorsally and the vertebral border posteroventrally. This is defined as caudal rotation. Therefore, the scapula

must be well anchored by the attached musculature in order for the propulsive muscles of the forelimb to increase the altitude of the animal by advancing the thorax over the manus, which is stabilized against the substrate. Caudal scapular rotation would also be used advantageously by erethizontids to aid in limb protraction. Cranial scapular rotation (the opposite motion) may be important for limb retraction.

*M. acromiotrapezius* and *M. spinotrapezius* form a continuous sheet in erethizontids, a condition considered primitive for rodents (Hill, 1937; Woods, 1972). In erethizontids, these muscles may have several functions in arboreal locomotion. The insertion of *M. acromiotrapezius* is onto the scapular spine, the acromion, and the lateral portion of the clavicle. Hill (1937) and Woods (1972) concluded that the latter part of the insertion represented the clavicular portion of *M. trapezius* present in other mammals. *M. spinotrapezius* inserts primarily into a dorsal extension of the fascia of insertion of *M. acromiotrapezius* and onto the scapular spine. The cranial fibers of *M. acromiotrapezius* and perhaps the caudal portion of *M. spinotrapezius* may function in caudal rotation of the scapula (the glenoid would move craniodorsally). This would be important for reaching movements during climbing and feeding. However, the use of the caudal fibers of *M. spinotrapezius* in this motion would depend upon the position of the axis of rotation. Jenkins (1974) reported that significant scapular rotation (30 to 40 degrees) occurred in the rat during a normal propulsive movement on a horizontal substrate. The axis of rotation was located approximately at the intersection of the vertebral border and scapular spine. If the scapula has a similar axis of rotation in erethizontids, then *M. spinotrapezius* could not participate in caudal scapular rotation because it inserts distal to this axis. During propulsion in the rat, there was a net caudal displacement of the scapula from the level of the fourth or fifth cervical vertebra to that of the first or second thoracic vertebra. Similar movements were also observed in the opossum. Jenkins thus showed that the thorax moved farther forward during propulsion than the shoulder and suggested that the caudal

fibers of the trapezius would function with other muscles in drawing the thorax through the pectoral girdle during horizontal locomotion. Therefore, it seems likely that in erethizontids, *M. spinotrapezius* would be used in a similar fashion during climbing as well as terrestrial locomotion. The trapezius muscles would also retract the scapula dorsally from a protracted position and elevate the clavicle. They would probably also be used for stabilizing the scapulothoracic joint and for controlling the pectoral girdle during locomotion on a horizontal substrate.

*M. levator scapulae* and *M. serratus anterior* form a continuous muscle mass in erethizontids, as in most rodents (Hill, 1937; Bryant, 1945; Lewis, 1949; Rinker, 1954; Klingener, 1964; Woods, 1972). *M. serratus anterior* has been described as the most important muscle for supporting the weight of the thorax by the pectoral appendage (English, 1978; Taylor, 1978). Both muscles may act as a functional unit for body support in rodents. The cranial fibers arising from the cervical vertebrae may be used for cranial scapular rotation (the glenoid moves caudally) and would be important for stabilizing the pectoral girdle and perhaps for aiding in the retraction of the limb during climbing. The caudal fibers insert on the posterior portion of the vertebral border of the scapula. This part of the muscle is thick and fills the gap between the insertion of *M. rhomboideus posterior* and the origin of *M. teres major*. It is probably an important caudal rotator of the scapula and as such, may be used during reaching movements. Taylor (1978) stated that in *Didelphis*, the caudal fibers of *M. serratus anterior* functioned in posterior scapular rotation by pulling the caudal angle posteroventrally. The entire muscle functioned with *M. levator scapulae* in supporting the weight of the thorax on the forelimbs. Grand (1968a) and Schon (1968) stated that in *Alouatta*, a pronograde quadrupedal climber, the caudal portion of *M. serratus anterior* functioned with the superior (=cranial) fibers of *M. trapezius* in elevation of the shoulder during reaching. Both recognized that the muscle was also important for shoulder stability in these animals. Oxnard (1963) and Ashton and Oxnard (1964) stated that *M. trapezius* and

*M. serratus magnus* (=anterior) formed a muscular couple that rotated the scapula caudally for arm raising in various primates. They described several muscular and bony features that were most efficient for scapular rotation in brachiators and least efficient in quadrupeds. However, Stern et al. (1976) found that the caudal portion of *M. serratus magnus* (=anterior) showed more electromyographic activity during the support phase than during the swing phase of brachiation in *Ateles* and *Lagothrix* because it suspended the thorax from the pectoral girdle. The activity of the muscle during the swing phase was relatively low. However, it was relatively high during both the support and swing phases of vertical climbing. They therefore concluded that the muscle was more important for support of the body during brachiation than for arm raising and that it was also important for "other" antipronograde activities. It is possible that the caudal portion of *M. levator scapulae* and *M. serratus anterior* in erethizontids would also be used to suspend the thorax by the scapula during climbing, particularly when the weight of the animal is supported exclusively by the front limbs. This may explain why the caudal portion of the insertion is thick. Perhaps the caudal fibers of *M. spinotrapezius* would also have a similar function.

*M. occipitoscapularis*, *M. rhomboideus anterior*, and *M. rhomboideus posterior* are fused in erethizontids to form a continuous sheet that arises from the lambdoidal crest and nuchal ligament. Woods (1972) wrote that this represented the primitive configuration in hystricomorphs. In erethizontids, the cranial fibers corresponding to *M. occipitoscapularis* course almost directly caudad to insert onto the scapular spine and a small portion of the vertebral border cranial to the spine. They would therefore tend to rotate the scapula cranially, forcing the glenoid caudally and ventrally. The tendency of the shoulder to be forced cranially during climbing would thus be arrested by this muscle. It would probably also be used to aid in the retraction of the pectoral appendage, particularly while under heavy loading during climbing, and to reposition the scapula after caudal rotation. The fibers of *M. rhomboid*

*deus anterior* and *M. rhomboideus posterior* take a more lateral course from origin to insertion than do those of *M. occipitoscapularis*. When the scapula is in a normal position, the vertebral border lies slightly above the level of origin. Therefore, the fibers of these muscles course dorsad to reach their insertion and would function with the trapezius muscles and *M. levator scapulae* and *M. serratus anterior* in anchoring the scapula against the thorax. They would also retract the scapula from a protracted position. The cranial fibers of *M. rhomboideus anterior* may also assist *M. occipitoscapularis* in cranial scapular rotation.

As previously mentioned, the cranial fibers of the *M. levator scapulae* and *M. serratus anterior* complex in erethizontids would function in cranial scapular rotation and would thus be an important synergist of *M. occipitoscapularis* and the rhomboideus muscles. Taylor (1978) found this to be the case in *Tamandua*, where *M. levator scapulae* consisted of distinct anterior and posterior divisions. The fibers of the anterior division coursed caudodorsad and inserted onto the medial surface of the cranial angle of the scapula. Those of the posterior division coursed craniodorsad and inserted ventral to the anterior division. Both divisions tended to pull the cranial angle of the scapula ventrally, thus producing cranial scapular rotation. Taylor suspected that such a movement (in which the glenoid moved caudoventrally) was used during climbing, defensive, and feeding behaviors in these animals.

*M. atlantoscapularis posterior* is straplike and lies deep to *M. occipitoscapularis*. It inserts onto a small segment of the vertebral border of the scapula cranial to the insertion of that muscle and onto the proximal portion of the scapular spine. It would act synergistically with *M. levator scapulae*, *M. occipitoscapularis*, and the rhomboideus muscles in cranial rotation of the scapula. In *Erethizon*, the insertion is aponeurotic and in some specimens may blend with the aponeurosis covering *M. supraspinatus* instead of attaching to the spine. In *Coendou*, the insertion is fleshy and is broader than in *Erethizon*. It may be slightly more powerful in cranial scapular rotation. Woods (1972) discussed the

treatment of this muscle by various authors and concluded that it was related to *M. occipitoscapularis* and represented a primitive mammalian feature.

*M. omocervicalis* shows considerable intraspecific variation in erethizontids. It arises from the ventral arch of the atlas in both *Erethizon* and *Coendou*. Such an origin is primitive for hystricomorphs (Woods, 1972). The insertion is onto the metacromion process of the scapula, the cranial border of *M. cutaneus maximus*, pars dorsalis, and the surface of *M. acromiodeltoideus*. In some specimens of both *Erethizon* and *Coendou*, it included the tip of the deltoid crest. The muscle would tend to draw the shoulder dorsally and perhaps slightly cranially during reaching movements. It may function synergistically with the trapezius and rhomboideus muscles in preventing the pectoral girdle from being drawn ventrally during various arboreal maneuvers or in retracting it dorsally from a protracted position. Hence, it would probably be an important stabilizer of the scapulothoracic joint. It is doubtful that the intraspecific variation observed in erethizontids significantly alters its basic functions.

The configurations of *M. latissimus dorsi* and *M. teres major* in erethizontids reflect the need for powerful retraction of the humerus at the glenohumeral joint during climbing. The origin of the former is from the caudal ribs, the lumbodorsal fascia, and the posterior thoracic vertebrae either via the lumbodorsal fascia (as in *Erethizon*) or directly by fibers (as in *Coendou*). Woods (1972) considered this to be the primitive configuration of the origin of *M. latissimus dorsi* in hystricomorphs. In *Coendou*, the origin from the caudal ribs is less well developed than in *Erethizon* but shows considerable intraspecific variation. The insertion onto the medial surface of the humerus is separate from that of *M. teres major* in both genera. Woods (1972) found a common insertion in all of the hystricomorphs that he examined except *Erethizon*. A distinct *latissimus Achselbogen* is not present in erethizontids, but I observed a few remnant fibers of this structure in *Erethizon*. Woods (1972) considered it to be primitive for hystricomorphs.

There may be a functional explanation for the retention of the origin from the caudal ribs. Such an attachment would allow the ventrolateral fibers of the muscle to impart a more direct posterior force on the humerus for powerful retraction of the forelimb during climbing. The origin of *M. latissimus dorsi* from the more lateral aspects of the body wall may be functionally adaptive in other heavy arboreal mammals as well. The muscle arises from some ribs in *Alouatta* (Hill, 1962; Grand, 1968a; Schon, 1968), *Lagothrix*, *Brachyteles*, and *Ateles* (Hill, 1962; Rhoades, 1976). Ziegler (1964) found that the muscle arose extensively from the iliac crest in *Pan satyrus*. He noted that this portion of the origin was weakly developed in man but would help support the weight of the chimpanzee during suspension by the forelimb. The fibers arising from the caudal ribs in erethizontids would probably also support the weight of the thorax during climbing. Taylor (1978) noted that the origin of *M. latissimus dorsi* included the dorsolateral body wall in *Tamandua*. He suggested that the more direct posterior component of force generated by the muscle would allow these animals to powerfully retract the limb during climbing, feeding, and defensive behaviors.

*M. teres major* is also a powerful retractor of the forelimb in erethizontids. It arises from the proximal portion of the axillary border of the scapula and the surfaces of adjacent muscles. The morphology of the scapula in these animals also reflects the necessity for a large moment arm associated with this muscle. Smith and Savage (1956) found that the scapulae of aquatic and fossorial mammals, which require powerful limb retraction, were relatively wide. The axillary border tended to curve ventrally in order to increase the mechanical advantage of *M. teres major*. Secondary spines were often present, creating postscapular fossae for increasing the area of origin for that muscle. Taylor (1978) described similar adaptations in arboreal *Tamandua*. The scapulae of erethizontids do not possess secondary spines, but the infraspinous fossa is relatively wide and becomes progressively wider from the scapular neck to the vertebral border. This suggests that the moment arm of *M. teres major* is large.

The mechanical advantages of both *M. latissimus dorsi* and *M. teres major* appear to be large in erethizontids. Grand (1968a) computed the "insertion index" for each of these muscles in *Alouatta* by taking the ratio between the distance from the proximal end of the humerus to the most distal point of insertion and the total length of the humerus. The mean insertion indices for *M. latissimus dorsi* and *M. teres major* in *Alouatta* were 20.8 percent and 30.4 percent, respectively. Grand considered these to be "moderately good" lever arms for retraction of the limb during running and climbing. The "insertion index" can be computed for these muscles in my specimens of *Erethizon* and *Coendou* by simply adding the percentage distance from the proximal end of the humerus to the most proximal point of insertion with the percentage length of insertion. The mean insertion index of *M. latissimus dorsi* is 44 percent and 41 percent for *Erethizon* and *Coendou*, respectively. That of *M. teres major* is 48 percent and 44 percent, respectively. Thus, the leverage of these muscles in erethizontids appears to favor powerful retraction of the forelimb. Taylor (1978) observed that the insertion of *M. teres major* extended to the middle of the humerus in arboreal *Tamandua* and stated that it retracted the shoulder more powerfully than in the relatively unspecialized opossum.

Other muscles may also participate to a limited extent in the retraction of the humerus at the glenohumeral joint. *M. spinodeltoideus* inserts onto the lateral surface of the deltoid crest deep to the insertion of *M. acromiodeltoideus*. It would primarily function as an external rotator of the humerus along with *M. infraspinatus* and *M. teres minor*. However, the insertion is on the base of the deltoid crest rather than the tip and, as such, is relatively close to the longitudinal axis of rotation. It may therefore have a component of force in the caudal direction that would serve to retract the forelimb. *M. acromiodeltoideus*, on the other hand, would most likely be important in protraction and abduction of the limb during reaching movements. *M. triceps brachii, caput longus* arises from the distal portion of the axillary border and is the only member of the triceps group

that crosses the glenohumeral joint. It would assist in the retraction of the humerus during climbing because the elbow would either be fixed or undergoing flexion at that time. It may also help to stabilize the glenohumeral joint. Ziegler (1964) observed that the origin of the long head of the triceps was more extensive in *Pan satyrus* than in man and helped to suspend the weight of the animal during brachiation and to maintain the integrity of the shoulder joint. Both Grand (1968a) and Schon (1968) stated that it helped to retract the limb in *Alouatta*. However, it is unlikely that erethizontids utilize this muscle in true suspension because they do not ordinarily support themselves with their forelimbs extended to the degree observed in the chimpanzee or a true brachiator.

Erethizontids must rely on frictional and interlocking forces to maintain their position on a vertical substrate such as a tree trunk. The frictional forces can be maximized by increasing the coefficient of friction between the surfaces in contact by the selection of suitable substrates or by developing epidermal tubercles on the plantar surfaces of the feet. They can also be maximized by increasing the normal forces generated between the foot and the substrate with powerful adductor musculature (Hildebrand, 1974). Several muscles are responsible for adduction of the forelimbs in erethizontids. *M. pectoralis major* is large and is probably the most important of these. It inserts onto the medial surface of the prominent deltoid crest and would probably internally rotate the humerus as it adducted. The rotatory component would further serve to force the more distal parts of the pectoral appendage into the medially lying arboreal substrate when the elbow is in a flexed position. *M. clavodeltoideus* would act synergistically with the *pectoralis major* in both adduction and internal rotation.

*M. pectoralis minor* is also an important adductor and internal rotator in erethizontids. It is large and has an extensive insertion onto the coracoid process, the tendon of insertion of *M. supraspinatus*, and the greater tuberosity and deltoid crest of the humerus. Woods (1972) found that the insertion of the muscle consisted of two parts in *Proechimys*, *Echimyus*, *Isothrix*, *Mesomys*, and *Petromus*.

One part inserted onto the central portion of the clavicle. The other part inserted onto the coracoid process, the greater tuberosity, and the deltoid crest. The configurations of the insertions in other hystricomorphs were variations of this basic pattern. That in *Erethizon* and *Coendou* consists solely of the second part. Woods (1972) noted that Mivart (1882), Windle (1888), and Parsons (1894) differed in their descriptions of an insertion onto the shoulder joint capsule in *Erethizon* and conceded that this feature may vary intraspecifically.

*M. pectoralis abdominalis* has the most caudal origin of the pectoral muscles and shows some intraspecific variation in *Erethizon*. It inserts onto the deltoid crest in some specimens of that genus and all specimens of *Coendou*. In one specimen of *Erethizon*, the insertion resembles that of *M. pectoralis minor* except that there is no attachment to the deltoid crest. Woods (1972) found the deltoid crest insertion in all of his specimens of *Erethizon*, *Ctenomys*, and some specimens of *Chinchilla*. He suggested that such an attachment in *Ctenomys* may be an adaptation for fossorial locomotion. The muscle also inserts onto the deltoid crest in geomyids (Hill, 1937) and *Aplodontia* (Hill, 1937; Lewis, 1949). In erethizontids, the muscle would assist in the retraction and adduction of the humerus during climbing, except in those specimens of *Erethizon* that lack a deltoid crest insertion. Both the *pectoralis minor* and *pectoralis abdominalis* muscles would also resist the tendency of the pectoral girdle to be forced cranially and would help to suspend the weight of the thorax.

*M. subclavius* would also function in stabilizing the pectoral girdle. The muscle shows some intraspecific variability but is always closely associated with *M. scapuloclavicularis*. It inserts primarily onto the caudoventral surface of the clavicle and, in some specimens of both *Erethizon* and *Coendou*, into the deep surface of *M. scapuloclavicularis*. It would stabilize the pectoral girdle during climbing by resisting craniodorsal movement of the clavicle. Woods (1972) observed some intraspecific variation of this muscle in *Erethizon* and gave a good discussion of its configuration in hystricomorphs.

It is difficult to hypothesize on the function of *M. scapuloclavicularis* in erethizontids. Woods (1972) noted that it was present in all hystricomorphs, including hystricids (Parsons, 1894) and bathyergids (Parsons, 1896) but was not found in other rodents. He concluded that its presence provided evidence that hystricomorphs formed a cohesive group. He also noted that it was present in lagomorphs (Mivart and Murie, 1866; Bensley, 1931), horses (Sisson and Grossman, 1953), tapirs (Stjernman, 1932), and some marsupials (Howell, 1937). There does not seem to be any common locomotor pattern between these animals that can be used to elucidate the function of this muscle. It would probably be used to anchor the acromioclavicular joint, but further study is needed before any definite conclusions can be made regarding its function in locomotion.

During arboreal locomotion, the glenohumeral joint is subjected to stresses that would tend to dislocate it. Several intrinsic muscles of the shoulder, referred to by Grand (1968a) as "short stabilizers," help to maintain its integrity. The morphology of the scapulae of erethizontids reflects the need for stability at this joint. The cranial portion of the vertebral border and the coracoid border are rounded, and the cranial angle between them is indistinct. Smith and Savage (1956) observed similar adaptations in aquatic and fossorial mammals and suggested that they served to increase the surface area for the origin of the suprascapular muscles. The fiber architecture of the short stabilizer musculature in erethizontids favors powerful contraction with a short range of motion. *M. supraspinatus* consists of two major parts, as it does in many rodents (Woods, 1972). The larger part arising from most of the suprascapular fossa is further divided proximally into cranial and caudal parts. There is also a small group of accessory fibers on the cranial margin of the muscle near its insertion. Taylor (1978) observed that the muscle was pinnate in *Tamandua*, as in many mammals. He stated that it functioned primarily in stabilization of the glenohumeral joint but suggested that it also assisted the cephalohumeralis and acromiodeltoideus muscles in protraction of the humerus during climbing

and defensive posturing. In erethizontids, it would probably protract and abduct the humerus in reaching movements during climbing and feeding. *M. infraspinus* is bipinnate and *M. subscapularis* is multipinnate. Woods (1972) found that the configuration of the latter was relatively constant in the hystricomorphs that he examined. The muscle inserts onto the lesser tuberosity and its crest and would medially rotate the humerus as well as help maintain the integrity of the glenohumeral joint. Therefore, it may be used with the pectoral muscles and *M. clavodeltoideus* in forcing the distal portion of the forelimb into the medially lying arboreal substrate during climbing.

*M. coracobrachialis* may also function in maintaining the integrity of the glenohumeral joint in erethizontids. It consists of middle and long parts which insert onto the medial border of the humeral shaft distal to the insertions of *M. teres major* and *M. latissimus dorsi* and onto the medial epicondylar ridge, respectively. The long part is absent in one of my specimens of *Erethizon*. Woods (1972) observed similar intraspecific variation in his *Erethizon* specimens and noted that both parts, when present, were separated by the median nerve. *Erethizon* was the only hystricomorph examined that possessed both middle and long parts. Parsons (1894) observed the same configuration in *Sphingurus* (= *Coendou*). However, the median nerve did not pass between the middle and long parts in any of my specimens. Thus, there appears to be some variation in the configuration of this muscle in erethizontids. Woods (1972), following the original descriptions by Wood (1867) of the three possible parts of the coracobrachialis, contended that the long part was always separated from the middle one by the median nerve and that the presence of both parts represented the usual condition in porcupines. However, both parts are completely fused in my specimens of *Erethizon* and *Coendou*. The muscle has a similar configuration in geomyids (Hill, 1937), sciurids (Hill, 1937; Bryant, 1945), and *Aplodontia* (Hill, 1937; Lewis, 1949). I believe that the primitive configuration of the muscle in rodents includes the presence of the long part. This part may be separate or fused with

the middle part or lost altogether, as in some specimens of *Erethizon*.

*M. coracobrachialis* may have additional functions in erethizontids besides stabilizing the glenohumeral joint. Since its insertion onto the medial aspect of the humerus begins distal to those of *M. latissimus dorsi* and *M. teres major* and extends to the medial epicondyle, its mechanical advantage may allow moderately powerful adduction of the forelimb toward the medially lying arboreal substrate. It would also protract the humerus during reaching movements.

Porcupines must flex the elbow powerfully when climbing. Several muscles are responsible for this action. *M. biceps brachii* is extremely large in these animals and inserts via two heads onto the radial tuberosity and the brachial ridge of the ulna. The insertion, however, is dominated by the radial head. In one specimen of *Erethizon*, the ulnar head is represented by thin fascia with a few embedded muscle fibers. Woods (1972) reported that the ulnar head dominated the insertion of the biceps in all hystricomorphs that he examined except *Erethizon*. Thus, there may be a functional reason for the large size of the radial head in erethizontids. When porcupines climb a tree trunk a few inches in diameter, the antebrachium is supinated from the normal terrestrial position so that the palmar aspect of the manus faces medially toward the substrate. Contraction of the biceps would supinate the forearm because the muscle inserts onto the tuberosity of the radius. Once this has been accomplished, it would then act as a strong flexor of the elbow. The mechanical advantage of the radial head is larger than that of the ulnar one because its attachment to the radial tuberosity is located more distally than the attachment of the muscle to the brachial ridge of the ulna. The radial insertion is also dominant in cebids (Hill, 1960, 1962; Grand, 1968a; Schon, 1968; Rhoades, 1976) and lorids (Miller, 1943) among primates and sciurids (Hill, 1937; Bryant, 1945) and *Aplodontia* (Hill, 1937; Lewis, 1949) among rodents. *M. brachialis* would act synergistically with the biceps in elbow flexion but would have no supinating action on the forearm.

*M. brachioradialis* is present in all of my

specimens of *Erethizon* and one specimen of *Coendou*. Woods (1972) found it in *Erethizon* but not in any other hystricomorph that he examined. Parsons (1894) also did not find it in any hystricomorph including *Coendou*. The muscle is present in sciurids (Hill, 1937; Bryant, 1945) and is vestigial in *Aplodontia* (Woods, 1972). Hill (1937) and Lewis (1949) did not find it in their specimens of the latter. The muscle is a primitive rodent feature (Woods, 1972). There may be a functional reason why it has been retained in *Erethizon*. Upon contraction, the muscle would supinate the antebrachium so that the palmar aspect of the manus faces toward the medially lying arboreal substrate. It would then assist the biceps and brachialis muscles in flexion of the elbow during climbing. However, since its origin from the medial epicondylar ridge lies medial and not proximal to that of *M. extensor carpi radialis longus*, its moment arm at the elbow is quite short. It would therefore be a relatively weak flexor. Its loss in most specimens of *Coendou* may indicate that it is not crucial for powerful elbow flexion during climbing. Perhaps its retention in *Erethizon* is a reflection of the greater weight of these animals. *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis* may also assist in elbow flexion, but like *M. brachioradialis*, their mechanical advantages at this joint would be relatively small.

*M. supinator* is very large in erethizontids, and its insertion onto the radius extends distally to a point approximately 70 percent from the proximal end. The fibers of the muscle form an angle of  $10^\circ$  or less with the longitudinal axis of the radius. The fact that the brachium must be supinated from the normal terrestrial position when porcupines climb certain arboreal substrates does not explain why the muscle is so large or its angle of insertion so acute. Further, the biceps brachii is probably the most important supinator of the forearm because it would do so through a greater range of motion. Woods (1972) found that the extent of the insertion of *M. supinator* was quite variable among hystricomorphs. In generalized forms such as *Proechimys*, *Echimys*, *Isothrix*, and *Mesomys*, it inserted onto the proximal half of the radius. The insertion was on the proximal  $\frac{2}{3}$  in

*Erethizon*, *Ctenomys*, *Thryonomys*, and *Petromus* and on the proximal  $\frac{3}{5}$  in *Myocastor*. It was confined to the proximal  $\frac{1}{3}$ ,  $\frac{1}{4}$ , and  $\frac{1}{5}$  in *Cavia*, *Chinchilla*, and *Dasyprocta*, respectively. Thus, it appears that the insertion of *M. supinator* in hystricomorphs tends to be more extensive in forms such as *Erethizon* and *Ctenomys* which need powerful pectoral appendages for various activities. It is reduced in more cursorial forms such as *Cavia* and *Dasyprocta*. In erethizontids, the forces imposed upon the antebrachium during climbing would tend to dislocate the humeroradial joint. *M. supinator* would probably help to maintain the integrity of this joint and to support the weight of the animal. Taylor (1978) found the insertion of the muscle to be onto the proximal two-thirds of the radius in *Tamandua*. However, he believed that the supinator, along with *M. pronator teres*, was used to generate powerful tortional movements for tearing apart insect nests.

*M. abductor pollicis longus* is convergent and has an extensive origin primarily from the ulna and the distinct interosseous ligament. The main tendon inserts onto the first metacarpal and the accessory tendon onto the falciform bone. The muscle would function primarily as a supinator of the forearm rather than an abductor of the pollex because that structure is rudimentary and relatively immobile in erethizontids and is represented only by the first metacarpal. *M. extensor indicis* may also assist in supination of the forearm. Its origin from the ulna begins much farther distally than that of *M. abductor pollicis longus*, and its tendon of insertion has a medial branch that attaches to the pollex. The size and architecture of the abductor pollicis longus suggest that its action may be powerful. However, a functional explanation for such powerful supination in erethizontids is not apparent. The muscle may be an important supinator in chimpanzees and spider monkeys but for reasons relating directly to brachiation (Ziegler, 1964; Rhoades, 1976).

*M. pronator teres* is large in erethizontids, and its insertion extends distally to a point approximately 70 percent from the proximal end of the radius. Woods (1972) found that the extent and position of the insertion were variable among hystricomorphs. He reported



the muscle to be large in *Erethizon* and *Ctenomys*, a fossorial form, and to insert onto the distal half and middle two-thirds of the radius, respectively. He wrote that the size of the muscle and its distal insertion might reflect the need for powerful forelimbs in these animals. However, he acknowledged that this might represent the primitive condition because of a similar configuration in sciurids (Hill, 1937; Bryant, 1945) and *Aplodontia* (Hill, 1937; Lewis, 1949). In erethizontids, the muscle may function in stabilization of the humeroradial joint and in supporting the weight of the animal during climbing. Ziegler (1964) postulated that it was important for weight bearing during brachiation in *Pan satyrus*.

The flexors of the wrist and digits in erethizontids are important for ensuring that the palmar aspect of the manus and the claws are appressed against the arboreal substrate and for grasping branches and securing food. *M. flexor digitorum profundus* is large and consists of medial, deep medial, radial, and ulnar heads. The last two are particularly well developed, as noted by Woods (1972) for most hystricomorphs. A tendon to the pollex is not present in *Erethizon* and *Coendou*. Woods (1972) also did not find it in *Erethizon* or in *Cavia*, *Dasyprocta*, and *Petromus*.

### HINDLIMB

There are relatively few distinct myological adaptations for arboreal locomotion in the hindlimbs of erethizontids. The pelvic girdle is firmly attached to the axial skeleton at the sacroiliac articulation. The pectoral girdle, in contrast, is attached via the highly mobile sternoclavicular joint. Therefore, several muscles are needed to anchor and control it during locomotion. The acetabulum is relatively deep compared to the glenohumeral joint, and the hip does not have specific "rotator cuff" muscles. The hindlimb undergoes extension at the hip, knee, and ankle (=plantar flexion) during propulsion in both climbing and terrestrial locomotion. However, in the forelimb, the flexor system is needed to support the weight of the body or to advance it during climbing. Therefore, except for the muscles used in positioning the

pes or controlling its preaxial pad for "grasping," the myology of the hindlimb in erethizontids retains a fairly primitive configuration.

*M. caudofemoralis* is present in *Erethizon* and is absent in *Coendou*. It arises from the deep layer of the lumbodorsal fascia deep to *M. femorococcygeus* and via this fascia from the transverse process of the second caudal vertebra. It inserts by a tendon into a notch formed by the caudal surface of the medial epicondylar ridge and the proximal surface of the medial condyle of the femur. It is difficult to speculate on the possible reasons why the muscle is absent in *Coendou*. It would probably function as an extensor of the hip in *Erethizon*, but its absence in *Coendou* indicates that it is not crucial to arboreal locomotion.

As with the forelimb, adduction of the hindlimb would be important in arboreal locomotion. In order for this to be done forcefully when climbing a tree trunk a few inches in diameter, the femur would have to be somewhat abducted and perhaps externally rotated at the hip. With the limb in this position, the knee would then be flexed and the pes inverted and applied to the medially lying substrate by powerful adductors. Grand (1968a, 1968b) described the posture of the limbs of *Alouatta* during arboreal locomotion. The knees were flexed and bowed outward in an externally rotated position. The hip was flexed and adducted in order to stabilize the foot against the medially lying substrate. During propulsion, external rotation occurred at the hip and knee in addition to extension and adduction in order to pivot the body of the animal over the pes. These movements were correlated with well-developed muscles responsible for them (Grand, 1968b). Among carnivores, Jenkins and Camazine (1977) found that the ambulatory raccoon (*Procyon lotor*) positioned the femur at a 25- to 30-degree angle from the medial plane during quadrupedal standing. The femur was abducted at a 25-degree angle at the start of the propulsive phase and was then abducted 10 to 15 degrees more during propulsion. It was abducted to a lesser degree in the fox (*Vulpes fulva*) and not at all in the cat. These postural differences were then related to

structural differences in the morphology of the hip joint. Jenkins and Camazine concluded that the hip of the raccoon allowed rotation and abduction to occur beyond the normal range used in ambulation and that these movements were necessary for climbing and for negotiating uneven substrates. It is probable that a similar pattern of movement occurs at the hip of erethizontids. I am uncertain if external rotation at the hip would be an important propulsive movement in these animals during arboreal locomotion. However, of the muscles primarily responsible for this action, *M. obturator externus* and *M. obturator internus* are large, and the latter is multipinnate and hence, capable of powerful contraction.

*M. gracilis* is one of the most important adductors of the hip in erethizontids. The muscle has an extensive origin that includes the caudal pubic ramus, the pubic body, and the ventral portion of the cranial pubic ramus. It also arises by aponeurosis from the caudal portion of the inguinal ligament even or blending with the lacunar ligament. The latter itself attaches to the cranial pubic ramus and serves to anchor the origin of the muscle from the inguinal ligament. The *gracilis* would probably be a powerful flexor of the knee as well because the insertion extends distal to the midpoint of the tibia. The origin of the muscle from the inguinal ligament is an unusual feature that has not been reported in the literature on rodent myology. Grand (1968b) found such an attachment in *Alouatta caraya*, but Schon (1968) did not observe it in *A. seniculus*. Hill (1962) did not mention it in his description of the *gracilis* for this genus. The muscle was considered a powerful adductor of the hip and a flexor of the knee in these animals (Grand, 1968b; Schon, 1968). The extensive origin in erethizontids is probably related to the need for powerful adduction of the hindlimb during arboreal locomotion. The fibers arising from the inguinal ligament would have a larger moment arm for adduction at the hip than would be the case if they attached to the dorsal portion of the cranial pubic ramus. The muscles that function synergistically with *M. gracilis* in adduction of the hip include *M. pectineus*, *M. adductor longus*, *M. adductor brevis*, *M. adductor magnus*, and *M. adductor minimus*.

Porcupines must invert the pes in order to position its plantar aspect against the medially lying arboreal substrate. *M. tibialis anterior* is probably important in this action. The muscle is large and has an extensive origin consisting of well-developed tibial and fibular parts. The presence of a fibular origin is not unique to erethizontids and has been observed in sciurids by Bryant (1945) and in *Zapus*, *Napeozapus*, and *Jaculus* by Klingener (1964). However, in these forms it is usually poorly developed (except in *Jaculus*) and is always confined to the fibular head. Thus, the extensive origin in erethizontids may be an adaptation for powerful inversion of the pes. The muscle also has two tendons of insertion in these animals. This feature is not common among rodents, but it has been reported in cebid primates (Hill, 1960, 1962; Grand, 1968b; Schon, 1968). Its functional significance, if any, is not apparent. Grand (1968b) found that *M. tibialis anterior* contained 55 percent of the total muscle mass acting at the subtalar joint in howler monkeys (*Alouatta*) and was the only important inverter of the pes in these animals. He stated (Grand, 1968b, p. 171) that the muscle helped to determine "the major plane of muscular control" during arboreal locomotion when the foot was stabilized against the substrate.

*M. tibialis posterior* inserts onto the ventral portion of the caudal surface of the medial tarsal bone and is an extremely important inverter of the pes in erethizontids. Hildebrand (1978) noted that the muscle in rodents always inserted onto the medial tarsal bone, when present, usually attaching to the middle or ventral portions of its proximal (=caudal) surface. The medial tarsal was present in all rodents that he examined except *Pedetes* and appeared to be fused with the medial cuneiform in anomalurids. Its size varied considerably but was generally found to be medium to large in hystricomorphs. Hildebrand had difficulty correlating size with locomotor specialization but found it to be small in cursorial forms and sciuriforms and large in fossorial forms and hystricomorphs. However, among climbing rodents, it varied from small to large.

Hildebrand (1978) stated that the precise function of *M. tibialis posterior* in some rodents was dependent upon the position of

the pes at the talocrural joint. In *Cavia*, *Hydrochoerus*, and *Myocastor* it primarily inverted the pes at the astragalonavicular joint. However, the muscle also simultaneously plantar flexed the same joint if the talocrural joint was at an angle less than 120 degrees. If the angle approached 180 degrees (the talocrural joint was fully extended), then some slight dorsiflexion occurred at the astragalonavicular joint. Hildebrand stated that the angling of the tendon under the medial collateral ligament of the ankle might also affect the action of the muscle, but he did not speculate on the functional significance of this feature.

M. flexor digitorum tibialis and M. flexor digitorum fibularis are important plantar and digital flexors in erethizontids. Their tendons of insertion fuse with each other and with the tendon of M. abductor hallucis brevis and divide into common subsidiary tendons which insert on the distal phalanges of the digits. The fusion of the long flexors and M. abductor hallucis brevis does not allow independent digital flexion. This may be an adaptation to conserve energy or to increase power. If digital or plantar flexion must be maintained for long periods of time (e.g., while maintaining position on a vertical trunk), then M. flexor digitorum tibialis and M. flexor digitorum fibularis may be used alternately or at only a fraction of their full contractile capability. If extra power is required, then both may be used simultaneously. Grand (1967) found that in *Nycticebus*, the long flexor tendons were fused within the pes so that digital flexion occurred in one motion with no individual control. The pes in these animals was divided into proximal weight-bearing and distal prehensile portions. The latter was instrumental in maintaining the position of the animal on the arboreal substrate. Hill (1962), Grand (1968b), and Schon (1968) found the tendons of the flexor digitorum tibialis and flexor digitorum fibularis to be fused in *Alouatta*.

M. flexor digitorum tibialis forms the common subsidiary flexor tendon to the hallux with M. abductor hallucis brevis in *Erethizon*, but it contributes to the subsidiary tendons to the other digits as well. In *Coendou*, neither of these muscles inserts onto the hallux, but a narrow tendinous filament prob-

ably representing the common subsidiary tendon to that digit is present in all of my specimens. Therefore, the conditions observed in *Coendou* are surely derived from an arrangement similar to that in *Erethizon*.

Some of the intrinsic muscles of the foot show considerable intraspecific variation and some interspecific differences. M. flexor digitorum brevis usually divides into four slips which pass to the lateral four digits. Although their origin was consistently traced to a deep layer of the plantar aponeurosis that was difficult to separate from the superficial one, the position of origin of the individual slips varied intraspecifically. In some specimens of *Coendou*, the slips to digits 4 and 5 are absent unilaterally or bilaterally. There are three accessory short flexors in both *Erethizon* and *Coendou*. Their origins showed some intraspecific variation in both genera. The tendons of these muscles fuse with those of the lateral three slips of M. flexor digitorum brevis to form common tendons of insertion. The contributions of the accessory short flexors to these common tendons are greater in *Coendou* than in *Erethizon*. Both the short and accessory short flexors act at the proximal interphalangeal joint. As in the forelimb, digital flexion in the hindlimb would be used to force the claws into irregularities in the substrate during climbing and to "grasp" branches. However, the latter capability is probably better developed in the manus because it is used for manipulating food and for other delicate activities such as scratching.

Some of the muscles which abduct or adduct the pedal digits are poorly developed or show other modifications from the primitive conditions. M. abductor hallucis brevis is well developed, but its tendon is fused with the common subsidiary flexor tendons to the hallux and second digit in *Erethizon* and with that to the second digit in *Coendou*. The insertion of the muscle shows some intraspecific variation in both genera. The muscle arises primarily from the plantar surface of the calcaneus proximal to the groove for the tendon of M. peroneus longus. However, in other rodents, the origin is located farther distally. The muscle arises primarily from the navicular and inserts onto the medial sesamoid at the metatarsophalangeal joint of the

first digit in geomyids (Hill, 1937), cricetids (Rinker, 1954), and dipodoids (Klingener, 1964). Bryant (1945) stated that it arose from the navicular and the tip of the medial sesamoid and was closely associated with the continuation of the tendon of *M. flexor digitorum tibialis* distal to the latter in sciurids. Its insertion was similar to that in the other rodents mentioned above. Since the muscle in erethizontids has a more proximal origin and inserts into the long flexor tendons, its line of action would favor digital flexion rather than abduction of the hallux.

*M. adductor hallucis* and *M. adductor digiti quinti* are present in both *Erethizon* and *Coendou*, but only the medial and lateral fibers, respectively, are well developed. The medial fibers of the adductor hallucis correspond roughly to the "oblique head" of the muscle in man. However, neither of these muscles is divided into "heads." The distolateral and distomedial fibers of *M. adductor hallucis* and *M. adductor digiti quinti*, respectively, show some intraspecific variation but tend to be weakly developed. The former are absent in some specimens of *Coendou*. *M. adductor digiti secundi*, present only in *Erethizon*, is represented by a few fibers that insert onto the deep transverse metatarsal ligament between digits 2 and 3. Thus, the digital adductors tend to be reduced in erethizontids. It is difficult to speculate on their possible functions, but they are probably not crucial for arboreal locomotion.

Erethizontids possess myological and osteological adaptations related to the medial sesamoid bone that improve the ability of the pes to maintain the position of the animal on the arboreal substrate. Hildebrand (1978) found that the medial sesamoid showed considerable variation in size, shape, and occurrence in rodents. He stated that the bone represented a primitive rodent feature, but he could not correlate its size with locomotor adaptation. It served as a point of insertion for *M. flexor digitorum tibialis* in all sciuriforms, some myomorphs, and the bathyergids that he examined. In such cases, the function of that muscle was usually related to the first or second digit, but the precise nature of its action was dependent upon the morphological and functional characteristics

of the medial sesamoid. In the remaining myomorph families and all hystricomorphs examined except the bathyergids, *M. flexor digitorum tibialis* did not insert onto the medial sesamoid. Hildebrand noted that the bone was thus usually reduced or absent, but he found it to be large in erethizontids due to its importance for pedal grasping in these animals.

The pes contains a muscle embedded within its subcutaneous connective tissue that attaches to the ventral cartilaginous portion of the medial sesamoid and the plantar aponeurosis. Jones (1953) designated it the "plantaris brevis." In *Coendou*, the reduced hallux is incorporated into the well-developed preaxial pad along with the medial sesamoid. The plantaris brevis functions to depress the preaxial pad in a plantar direction in order to "oppose" it to the lateral portion of the sole (Jones, 1953). A crease in the plantar integument indicates the position where the folding occurs. Jones (1953) stated that this action allowed the pes to "grasp" branches despite the fact that the hallux was reduced and could not be used in opposition to the other digits as in the primates and other arboreal mammals. In *Erethizon*, the hallux is well developed, and a preaxial pad or plantar crease is not distinct. The plantaris brevis in these animals would function to depress the medial sesamoid and perhaps to adduct its ventral cartilaginous portion slightly. This action would "cup" the pes in order to make it conform to a curved substrate, particularly on smaller branches. True "grasping" of the substrate using this mechanism probably does not occur in *Erethizon*.

Both *Erethizon* and *Coendou* also possess a muscle that attaches primarily to the first metatarsal and the deep surface of the medial sesamoid. Jones (1953) observed this muscle in *Coendou* and designated it the abductor ossis metatarsi hallucis. Hildebrand (1978) also found it in erethizontids and other rodents but left it unnamed. Its functional significance is apparent only if the nature of the attachment of the medial sesamoid to the rest of the pedal skeleton is considered.

Hildebrand (1978) noted that the medial sesamoid was always anchored by the medial tarsal ligament, which usually attached proxi-

TABLE 1  
Synopsis of Interspecific Differences and Intraspecific Variations of the Musculature of the Pectoral Appendage

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
Trapezius Group			
M. acromiotrap.	Rel. len. attach.	Min. bilat. diff.	Min. bilat. diff.
M. spinotrap.	Arch., rel. size, deg. anat. dev. Rel. len. attach. Rel. pos. attach. <sup>a</sup>	Min. bilat. diff.	None
Costo-Spino-Scapular Group			
M. lev. scap. and M. ser. ant.	Not compared	Min. unilat. diff.	Min. bilat. diff. Min. unilat. diff.
M. occipitoscap.	None	None	None
M. rhomb. ant.	None	None	None
M. rhomb. post.	Rel. len. attach.	None	None
M. atlantoscap. post.	Arch., rel. size, deg. anat. dev. Rel. len. attach.	Min. unilat. diff.	None
M. omocerv.	Not compared	Maj. bilat. diff. Min. bilat. diff.	Maj. bilat. diff.

(Table continued on page 410.)

mally to the medial tarsal and distally to the base of the first metatarsal. In erethizontids, the bone was anchored at its proximal end close to the medial tarsal, thus allowing it to pivot in the sagittal plane. Hildebrand observed two synovial joints on the deep surface of the medial sesamoid in *Erethizon*: a circular one located proximally at the axis of rotation; and an elongated one positioned distally where the bone traveled in an arc when pivoting. Contraction of the associated muscle would tend to adduct the medial ses-

amoid because its ventral portion is cartilaginous, its mobility is restrained somewhat by its ligamentous attachments, and the first metatarsal is relatively immobile (Hildebrand, 1978). Therefore, I have chosen to designate this muscle in erethizontids the "M. adductor ossis sesamoideus medialis." It probably acts synergistically with the plantaris brevis in depression of the preaxial margin of the pes for "grasping" or for allowing the pes to conform to a curved arboreal substrate.

CONCLUSION

SUMMARY OF THE MYOLOGICAL CONDITIONS  
OF ERETHIZON AND COENDOU

Tables 1 and 4 catalogue the types of interspecific differences observed between *Erethizon dorsatum* and *Coendou prehensilis* and the intraspecific variations observed within each species. The term "interspecific difference" refers to a comparison of the average configuration of a given muscle within each

species. When numerical data were used in describing the relative length or position of attachment, a 10 percent or greater difference between the averages for each species was considered to indicate an "interspecific difference." A range of 10 percent or greater within a given species was considered to indi-

TABLE 1—(Continued)

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
Latissimus-Subscapular Group			
M. lat. dorsi	Rel. len. attach. Arch., rel. size, deg. anat. dev. Relat. muscles	Min. unilat. diff.	Min. bilat. diff.
M. subscap.	None	None	None
M. teres maj.	None	None	Min. bilat. diff.
Deltoid Group			
M. clavodelt.	None	Min. bilat. diff.	Min. bilat. diff.
M. acromiodelt.	None	Min. bilat. diff.	None
M. spinodelt.	None	None	None
M. teres min.	None	None	Min. bilat. diff.
Suprascapular Group			
M. supraspin.	None	None	Min. bilat. diff.
M. infraspin.	None	None	None
Triceps Group			
M. dorsoepitroch.	None	None	None
M. tri. br., cap. lat.	None	None	Min. bilat. diff.
M. tri. br., cap. med.	Arch., rel. size, deg. anat. dev. Relat. muscles	None	None
M. tri. br., cap. lg.	None	Min. bilat. diff.	Min. bilat. diff.
M. ancon.	Relat. muscles Rel. len. attach.	None	Min. bilat. diff.
Extensor Group of the Forearm			
M. brachiorad.	Not compared	None	Maj. bilat. diff.
M. ext. carpi rad. lg.	None	None	None
M. ext. carpi rad. brev.	None	None	None
M. ext. dig.	None	None	None
M. ext. dig. min.	None	None	None
M. ext. dig. ter. prop.	Not compared	None	Maj. bilat. diff.
M. ext. carpi ul.	None	Min. bilat. diff.	Min. bilat. diff.
M. supin.	None	Min. bilat. diff.	None
M. abd. pol. lg.	Not compared	Min. bilat. diff.	Min. bilat. diff.
M. ext. ind.	Not compared	Min. bilat. diff.	Min. bilat. diff.
Pectoral Group			
M. subclav.	Rel. pos. attach.	Min. bilat. diff.	Min. bilat. diff.
M. scapuloclav.	None	Min. bilat. diff.	None
M. pect. maj.	Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	None
M. pect. min.	Rel. len. attach.	Min. bilat. diff.	None
M. pect. abd.	Rel. len. attach. Relat. muscles	Maj. bilat. diff.	None

TABLE 1—(Continued)

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
Flexor Group of the Arm			
M. coracobrach.	None <sup>a</sup>	Maj. bilat. diff.	Min. bilat. diff.
M. biceps br.	None	Min. bilat. diff.	None
M. brachialis	None	Min. unilat. diff.	None
Flexor Group of the Forearm			
M. epitroch.	None	None	Min. bilat. diff.
M. flex. carpi ul.	None	None	None
M. palm. lg.	None	None	Min. bilat. diff.
M. flex. carpi rad.	None	Min. unilat. diff. <sup>b</sup>	None
M. pron. teres	None <sup>a</sup>	Min. bilat. diff.	None
M. flex. dig. sup.	None	None	None
M. flex. dig. prof.	None <sup>a</sup>	Min. bilat. diff.	None
Mm. lumbricales	None	None	None
M. pron. quad.	None	None	None

<sup>a</sup> See remarks in text.

<sup>b</sup> A small accessory tendon is present, but I am uncertain whether it is unilateral or bilateral due to the poor condition of one side of the specimen.

Key to Abbreviations

Minor Interspecific Differences	Abbreviations
Relative length of attachment	Rel. len. attach.
Relative position of attachment	Rel. pos. attach.
Portion of attachment	Por. attach.
Relations to other muscles	Relat. muscles
Relations to nerves and vessels	Relat. nerves, vessels
Architecture, relative size, or degree of anatomical development	Arch., rel. size, deg. anat. dev.
Major Interspecific Differences	
Muscle absent in one species	Muscle absent
Attachment of muscle to given structure absent in one species	Attach. absent
Intraspecific Variations	
One or more specimens have minor bilateral differences	Min. bilat. diff.
One or more specimens have minor unilateral differences	Min. unilat. diff.
One or more specimens have major bilateral differences	Maj. bilat. diff.
One or more specimens have major unilateral differences	Maj. unilat. diff.

cate “intraspecific variation.” Exceptions were made for *M. spinotrapezius* and *M. pectineus* because I could visually observe differences in the lengths of insertion even though the average percentage difference in length was slightly less than 10 percent. Numerical differences in relative length or position of attachment were considered

“minor” along with other features. A “major interspecific difference” refers to the presence or absence of a given muscle or muscular attachment. It is difficult to speculate if minor and major interspecific differences have functional significance. Intraspecific variations were categorized with regard to whether or not the differences between specimens were

TABLE 2  
Summary of Interspecific Differences in the Pectoral Appendage

Interspecific differences	Number of muscles	%
Rel. len. attach.	8	16
Rel. pos. attach.	2	4
Por. attach.	0	0
Relat. muscles	4	8
Relat. nerves, vessels	0	0
Arch., rel. size, deg. anat. dev.	5	10
Muscle absent	0	0
Attach. absent	0	0
Totals		
Muscles identical	32	65
Muscles with minor differences	11	23
Muscles with major differences	0	0
Muscles not compared	6	12
Total number of muscles	49	—

“minor” or “major” and unilateral or bilateral. For some muscles, intraspecific variation made the determination of an average configuration difficult. Therefore, these muscles were not compared interspecifically (tables 1 and 4).

Tables 2 and 3 show the number and percentage of muscles that differ interspecifically and vary intraspecifically within the forelimb. Of a total of 49 muscles described, 32 (65%) were identical between *Erethizon* and *Coendou* while 11 (23%) had minor interspecific differences (table 2). *M. coracobrachialis* was not considered to differ interspecifically even though the long part of the

muscle is absent in one specimen of *Erethizon* (table 1). *M. pronator teres* was considered identical, but the relative length of insertion was an average of 9 percent greater in *Erethizon* than *Coendou* and the ranges for the two genera did not overlap. However, I did not make an exception in this case because no obvious difference in length of insertion was apparent. *M. flexor digitorum profundus* is virtually identical, but the ulnar head does not arise from the adjacent portion of the interosseous membrane in *Erethizon*. No muscles had major interspecific differences, but six (12%) were not compared because they exhibited too much intraspecific variation. These include *M. levator scapulae* and *M. serratus anterior* (counted as one muscle), *M. omocervicalis*, *M. brachioradialis*, *M. extensor digiti tertii proprius*, *M. abductor pollicis longus*, and *M. extensor indicis*. Of these, *M. brachioradialis* is always present in *Erethizon* but occurs sporadically in *Coendou*. Conversely, *M. extensor digiti tertii proprius* is absent in *Erethizon*, but I found it in a vestigial condition in one specimen of *Coendou*. Parsons (1894) also apparently found the muscle in *Sphingurus* (= *Coendou*).

Muscles of the forelimb differed interspecifically most frequently in relative length of attachment (table 2). Relatively few muscles differed in position of attachment, relations to other muscles, or in architecture, relative size, or degree of anatomical development.

Table 3 shows that the intraspecific variation within the forelimb was fairly common but that most was of a minor nature. Only 16 muscles (33%) showed no intraspecific

TABLE 3  
Summary of Intraspecific Variations in the Pectoral Appendages

Intraspecific variations	Number of muscles			%		
	<i>E.</i>	<i>C.</i>	Total	<i>E.</i>	<i>C.</i>	Total
Min. bilat. diff.	17	17	27	35	35	55
Min. unilat. diff.	6	1	6	12	2	12
Maj. bilat. diff.	3	3	4	6	6	8
Maj. unilat. diff.	0	0	0	0	0	0
Totals						
Muscles varying intraspecifically	24	20	33	49	41	67
Muscles showing no intraspecific variation	25	29	16	51	59	33



TABLE 4  
Synopsis of Interspecific Differences and Intraspecific Variations of the Musculature of the Pelvic  
Appendage<sup>a</sup>

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
Iliacus Group			
M. iliacus	Not compared	Min. bilat. diff.	Min. bilat. diff.
M. posas maj.	Not compared	Min. bilat. diff.	Min. bilat. diff.
M. pect.	Rel. len. attach. <sup>b</sup>	Min. bilat. diff.	Min. bilat. diff.
Gluteal Group			
M. ten. fas. lat.	Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	Min. bilat. diff. Min. unilat. diff.
M. glut. max.	None	None	None
M. femorococcyg.	Por. attach.	None	Min. bilat. diff.
M. tenuis.	Relat. muscles Por. attach.	None	Min. bilat. diff.
M. glut. med.	Por. attach. Relat. muscles	Min. bilat. diff.	Min. bilat. diff.
M. glut. min.	Rel. len. attach. Relat. muscles	Min. bilat. diff.	Min. bilat. diff.
M. pyriform.	None	None	None
Quadriceps Femoris Group			
M. rect. fem.	None	None	None
M. vast. lat.	Rel. len. attach.	Min. unilat. diff.	Min. bilat. diff.
M. vast. med.	None	Min. bilat. diff.	Min. unilat. diff.
M. vast. intermed.	Rel. len. attach.	Min. bilat. diff.	Min. bilat. diff.
Tibial Extensor Group			
M. ext. dig. lg.	Arch., rel. size, deg. anat. dev. Por. attach.	None	Min. bilat. diff.
M. ext. hal. lg.	Por. attach.	Min. bilat. diff.	Min. bilat. diff.
M. tib. ant.	Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	Min. bilat. diff.
Mm. ext. breves	Por. attach.	None	None
M. ext. hal. brev.	Not compared	Maj. unilat. diff.	None
Peroneal Group			
M. per. lg.	Por. attach. Rel. len. attach.	Min. bilat. diff.	Min. bilat. diff.
M. per. brev.	Por. attach.	Min. bilat. diff.	None
M. per. dig. min.	None	None	None
Adductor Group			
M. grac.	Rel. len. attach. Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	Min. bilat. diff.
M. add. lg.	Rel. len. attach. Rel. pos. attach.	Min. bilat. diff.	Min. bilat. diff.

TABLE 4—(Continued)<sup>a</sup>

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
M. add. brev.	Rel. len. attach. Relat. muscles Relat. nerves, vessels Por. attach.	Min. bilat. diff.	None
M. add. mag.	Rel. len. attach. Rel. pos. attach.	Min. bilat. diff.	None
M. add. min.	Rel. len. attach.	Min. bilat. diff.	Min. bilat. diff.
M. obt. ext.	None	None	None
Ischiotrochanteric Group			
M. quad. fem.	Not compared	Min. bilat. diff.	Min. bilat. diff.
M. gem. sup.	None	None	None
M. gem. inf.	None	None	None
M. obt. int.	Por. attach.	Min. bilat. diff.	None
Hamstring Group			
M. caudofem.	Muscle absent	None	None
M. semitend.	Rel. pos. attach. Relat. muscles	Min. unilat. diff.	Min. bilat. diff.
M. semimemb.	Por. attach.	Min. bilat. diff.	None
M. biceps fem.	None	Min. unilat. diff.	None
Flexor Group of the Leg			
M. gastroc.	Relat. muscles Por. attach.	Min. bilat. diff.	Min. unilat. diff.
M. plant.	Por. attach.	Min. bilat. diff.	None
M. soleus	None	None	None
M. poplit.	Rel. len. attach. <sup>b</sup>	Min. bilat. diff.	None
M. flex. dig. tib.	Arch., rel. size, deg. anat. dev. Attach. absent	Min. bilat. diff.	Min. bilat. diff.
M. flex. dig. fib.	None	Min. bilat. diff.	Min. bilat. diff. Maj. bilat. diff.
M. tib. post.	Rel. len. attach.	Min. bilat. diff.	None
Flexor Group of the Pes			
M. flex. dig. brev.	Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	Maj. unilat. diff. Maj. bilat. diff. Min. bilat. diff. Min. unilat. diff.
Mm. flex. brev. acc.	Arch., rel. size, deg. anat. dev.	Min. bilat. diff.	Min. bilat. diff.
M. abd. hal. brev.	Rel. len. attach. Attach. absent	Min. bilat. diff.	Min. bilat. diff.
Mm. lumbricales	Por. attach. Arch., rel. size, deg. anat. dev.	None	Min. bilat. diff.

TABLE 4—(Continued)<sup>a</sup>

Muscle	Interspecific differences	Intraspecific variations	
		<i>Erethizon</i>	<i>Coendou</i>
M. abd. oss. met. quint.	Arch., rel. size, deg. anat. dev. Por. attach.	None	None
M. abd. dig. min.	None	None	None
M. flex. dig. min. brev.	Rel. pos. attach.	Maj. unilat. diff.	Maj. unilat. diff.
M. add. hal.	Por. attach.	Min. bilat. diff. Min. unilat. diff.	Min. bilat. diff.
M. add. dig. quint.	Rel. pos. attach.	None	Min. bilat. diff.
M. add. dig. sec.	Muscle absent	None	None
Mm. inteross.	None	Min. bilat. diff.	None
M. add. oss. ses. med.	Rel. len. attach.	None	Min. bilat. diff.

<sup>a</sup> Abbreviations are the same as for table 1.

<sup>b</sup> See remarks in text.

variation in either *Erethizon* or *Coendou*. Six muscles (12%) possessed minor unilateral differences or anomalies in *Erethizon*, but only one (2%) had this type of intraspecific variation in *Coendou*. There does not appear to be any correlation between the frequency of intraspecific variation within a given muscle group and the importance of that group to arboreal locomotion.

In conclusion, the musculature of the pectoral appendages of *Erethizon* and *Coendou* is similar and contains some adaptations for arboreal locomotion. Neither Gupta (1966) nor Frazer (1978) reported any important differences in their osteology. Therefore, they are probably used in a similar fashion.

The myology of the hindlimb exhibited many interspecific differences (tables 4 and 5). Of the 55 muscles described, only 13 (24%) were identical, and 34 muscles (62%) had minor interspecific differences. There was no apparent difference in the relative length of insertion of M. popliteus even though the percentage difference was greater than 10 percent (table 4). The insertion occupied the same position in both genera and extended to the level of the tibial tuberosity. M. iliacus, M. psoas major, M. extensor hallucis brevis, and M. quadratus femoris were not compared because they exhibited too much intraspecific variation.

Four muscles (7%) showed major interspecific differences (tables 4 and 5). M. caudo-femoralis is present in *Erethizon* but absent in *Coendou*. The configurations of M. flexor digitorum tibialis and M. abductor hallucis brevis in *Coendou* are derived from the more

TABLE 5  
Summary of Interspecific Differences in the Pelvic Appendages

Interspecific differences	Number of muscles	
		%
Rel. len. attach.	14	26
Rel. pos. attach.	5	9
Por. attach.	16	29
Relat. muscles	6	11
Relat. nerves, vessels	1	2
Arch., rel. size, deg. anat. dev.	9	16
Muscle absent	2	4
Attach. absent	2	4
Totals		
Muscles identical	13	24
Muscles with minor differences	34 <sup>a</sup>	62
Muscles with major differences	4	7
Muscles not compared	4	7
Total number of muscles	55	—

<sup>a</sup> Two muscles with both minor and major differences were not included in this tabulation.

TABLE 6  
Summary of Intraspecific Variations in the Pelvic Appendage

Intraspecific variations	Number of muscles			%		
	<i>E.</i>	<i>C.</i>	Total	<i>E.</i>	<i>C.</i>	Total
Min. bilat. diff.	31	28	39	56	51	71
Min. unilat. diff.	4	4	8	7	7	15
Maj. bilat. diff.	0	2	2	0	4	4
Maj. unilat. diff.	2	2	3	4	4	6
Totals						
Muscles varying intraspecifically	36	31	41	66	56	75
Muscles showing no intraspecific variation	19	24	14	35	44	26

primitive conditions as exhibited in *Erethizon*. An insertion onto the reduced hallux is absent, and a thin tendinous filament is all that remains of the common subsidiary flexor tendon to that digit. Finally, M. adductor digiti secundi, though vestigial, is present in *Erethizon* and absent in *Coendou*.

Muscles of the hindlimb differed interspecifically most often in portions of their attachments, but differences in relative length of attachment occurred frequently as well (table 5). Differences in architecture, relative size, or degree of anatomical development were also common, especially in the pes. Other types of interspecific differences were less frequent in occurrence.

As in the forelimb, intraspecific variation in the myology of the hindlimb was quite common and usually minor in nature (table 6). Only 14 muscles (26%) showed no intraspecific variation. Major differences between conspecific specimens occurred most often in the pes of *Coendou* (table 4).

The myology of the hindlimb retains a fairly generalized condition except for some adaptations for the positioning and grasping of the pes during arboreal locomotion. The frequency of interspecific differences may indicate that the hindlimbs of *Erethizon* and

*Coendou* are used in different ways. Gupta (1966) described several osteological differences in the pelvic girdles and limbs of these two animals. White (1968) stated that the "prehallux" (=medial sesamoid) was "highly specialized" in the more arboreal *Coendou* and "almost vestigial" in *Erethizon*. However, Hildebrand (1978) found the bone to be large in erethizontids. This discrepancy in the literature may be due to the fact that the ventral portion of the medial sesamoid is cartilaginous and was not preserved in the fossil material that White examined. Frazer (1978) stated that a greater posterior expansion of the medial malleolus of the tibia in *Coendou* reflected a difference in the articulation of the pes. He found several differences in the articular surfaces of the astragalus and calcaneus and suggested that they reflected "markedly different modes of locomotion." The "greater rotational ability" of the pes of *Erethizon* was consistent with the fact that these animals moved in both terrestrial and arboreal environments. *Coendou* would not need to rotate its pes to the extent necessary for terrestrial locomotion. Since these animals are almost totally arboreal, the pes would need to be inverted toward the medially lying arboreal substrate.

THE EVOLUTIONARY RELATIONSHIP OF *ERETHIZON* AND *COENDOU*

The myology of the appendages can be compared with other morphological data available in the literature to speculate upon the evolutionary relationship of *Erethizon* and *Coendou*. White (1968) observed that the cheek teeth of the mandible were convergent in *Erethizon* and subparallel in *Coendou*. He stated (White, 1968, p. 11) that "each of the masticatory strokes more closely parallels the longitudinal axis of the tooth row" in *Erethizon*, resulting in more efficient mastication. Since adult specimens of *Coendou* and juvenile specimens of *Erethizon* had subparallel cheek tooth rows and other similar features of the mandible, he suggested that a "paedomorphic relationship" existed between these two genera and concluded that either *Coendou* was ancestral to *Erethizon* or that both shared a common South American ancestor.

In a later paper, White (1970) described four fossil North American species of *Coendou*, with one (*C. cumberlandicus*) being morphologically intermediate between that genus and *Erethizon*. He stated that the morphology of *Coendou* reflected its arboreal habits because of the presence of a prehensile tail, a specialized pes, and a more laterally directed visual field as in tree squirrels, and orthodont incisors that were less efficient for eating bark than the proodont incisors of *Erethizon*. He concluded that *Coendou* was ancestral to *Erethizon* and that the evolutionary change occurred during the middle Pleistocene when the tail lost its prehensility. It was suggested that the shift in climate from warm to cold during that epoch might have favored the evolutionary loss of the distal portion of the longer prehensile tail in the ancestral form.

Frazer (1978) referred all known North American fossil erethizontids to the genus *Erethizon*, including all known species of *Coendou* recognized by White (1970). *Coendou cumberlandicus* was referred by Frazer (1978) to *Erethizon dorsatum*. A morphometrical analysis of the crania of recent specimens of *Erethizon* and *Coendou* showed the former to be larger in most dimensions. A cluster analysis divided these specimens into two groups: one containing all *Erethizon* and

some large *Coendou* specimens; and one containing only *Coendou*. Six measurements clearly separated the two genera with no overlap. Frazer suggested that these differences were related to differences in mastication. Other morphological features, including certain details of the auditory ossicles and the microscopic structure of the incisor enamel, also distinguished *Erethizon* and *Coendou*. The incisor enamel was found to be significantly thicker in *Erethizon*, as was expected in light of the dietary differences between these two genera. Frazer also observed differences in the postcranial osteology, as previously discussed.

Frazer (1978) thus recognized four species of erethizontids within the fossil material that he examined: *E. bathygnathum*, *E. cascoensis*, *E. kleini*, and *E. dorsatum*. All had similar morphological adaptations needed for feeding on bark and other coarse vegetation in a wide variety of habitats. He concluded that the genus immigrated to North America through Central America during the late Pliocene. He also suggested that the presence of temperate tree species in Central America as far back as the Miocene (Raven and Axelrod, 1975) may have favored the evolutionary development of the thicker incisor enamel and the other features of an efficient masticatory apparatus. Frazer (1978, p. 90) therefore concluded that "the probable place for *Erethizon* to begin differentiating from its immigrant ancestor was in subtropical Central America. It seems highly improbable that it came to North America from tropical South America as *Erethizon*, preadapted for eating conifer bark in temperate forests." He noted that White's (1970) hypothesis on the ancestral relationship of *Coendou* was not supported by the fossil record and suggested that it was more probable that *Erethizon* and *Coendou* evolved from a common ancestor.

The appendicular myology of *Erethizon* and *Coendou* lends support to Frazer's ideas. The absence of *M. caudofemoralis*, *M. adductor digiti secundi*, and (in some specimens) *M. brachioradialis* and the configurations of *M. flexor digitorum tibialis* and *M. abductor hallucis brevis* in *Coendou* are clearly derived from the more primitive con-

ditions as represented in *Erethizon*. The myological data therefore indicate that *Coendou* could not possibly have been ancestral to *Erethizon* as White (1970) contended. The reduction of the hallux and its incorporation into the preaxial pad of the pes provides corroborating evidence. However, this does not necessarily imply that *Erethizon* gave rise to *Coendou*. The presence of several morphological features for efficient mastication in *Erethizon* argues against such a hypothesis (Frazer, 1978). Furthermore, *M. extensor digiti tertii proprius* is present in some specimens of *Coendou* but not in *Erethizon*. Therefore, the hypothesis that *Erethizon* and *Coendou* are derived from a common ancestor is the one that best accounts for the available morphological evidence.

The appendicular myology of the ancestral form would most closely resemble that in *Erethizon*. The ancestor must have possessed a well-developed hallux, but the condition of its tail is open to speculation. It is probable that it was partially terrestrial rather than totally arboreal in locomotor habit. Frazer (1978) suggested that *Erethizon* and *Coendou* shared a common ancestor from the Miocene or early Pliocene of northern South America. He proposed that *Steiromys*, which has been found in several South American deposits (Landry, 1957), might be the ancestral form. He observed similarities in the microstructure of the incisor enamel between *Steiromys* and *Erethizon* and noted that Scott (1905), Friant (1936), and Fields (1957) found other similarities in their dentitions.

Two evolutionary pathways radiated from the common ancestor, probably in Central America as suggested by Frazer (1978). One favored the development of an efficient masticatory apparatus to cope with a diet of temperate vegetation and the retention of semiarboreal locomotion. This was the evolutionary course followed by *Erethizon*. *Coendou*, on the other hand, became specialized for arboreal locomotion with the development of a prehensile tail and "grasping" pes. Its hallux became reduced and incorporated into the preaxial pad at some point in its evolutionary history. Jones (1953,

p. 33) wrote that the reduction of the first digit in *Coendou* was the result of "a prolonged apprenticeship to pronograde terrestrial life." He stated that *Coendou* was obliged to develop the preaxial pad in order to obtain a "grasping pes" to be used in conjunction with the prehensile tail since it could not develop an opposable hallux as in other arboreal mammals with prehensile tails. However, the pes of *Erethizon* possesses myological and osteological adaptations for grasping similar to those in *Coendou* even though its hallux is well developed and its preaxial pad is not. The presence of these features in both genera may be an example of parallelism, but it may also indicate that they were already present in the ancestral form. While Jones's (1953) ideas on the development of the preaxial pad in *Coendou* may be true, it is equally possible that the enlargement of the medial sesamoid and the development of the plantaris brevis and adductor ossis sesamoides medialis muscles rather than the opposable hallux was more feasible evolutionarily. These adaptations would have been made more efficient in *Coendou* by the reduction of the hallux and its incorporation into the distinct preaxial pad. The locomotor habits of these animals may not require prehension of the pes to the degree seen in arboreal primates and marsupials with opposable halluces.

In conclusion, the evolutionary divergence of *Erethizon* and *Coendou* probably occurred in Central America in response to selective pressure for the development of an efficient masticatory apparatus to cope with coarse temperate vegetation (Frazer, 1978). If this is true, then the presence of *Coendou* in South America represents a secondary colonization. It is also possible that the common ancestor that immigrated to Central America from northern South America gave rise to *Erethizon* but became extinct. *Coendou* could have evolved in South America, become specialized for the arboreal environment, and immigrated to Central America in more recent times. A definitive conclusion can be made only when the fossil history of *Coendou* is known.

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## CONTENTS OF VOLUME 173

- Article 1. A Revision of the American Spiders of the Genus *Drassyllus* (Araneae, Gnaphosidae). By Norman I. Platnick and Mohammad U. Shadab. Pages 1–97, figures 1–281, maps 1–41. March 26, 1982. .... Price. \$7.60
- Article 2. Marine Bryozoans (Ectoprocta) of the Indian River Area (Florida). By Judith E. Winston. Pages 99–176, figures 1–94, tables 1–10. June 28, 1982. .. Price. \$5.30
- Article 3. A Revision of the Genus *Rattus* (Rodentia, Muridae) in the New Guinean Region. By J. Mary Taylor, John H. Calaby, and Hobart M. Van Deusen. Pages 177–336, figures 1–50, tables 1–34. July 30, 1982. .... Price. \$11.30
- Article 4. Comparative Myology of the Pectoral and Pelvic Appendages of the North American Procupine (*Erethizon dorsatum*) and the Prehensile-Tailed Porcupine (*Coendou prehensilis*). By James Stephen McEvoy. Pages 337–421, figures 1–24, tables 1–6. November 15, 1982. .... Price. \$6.40













