

MORPHOLOGY OF THE MUSCULATURE OF THE ARM AND SHOULDER GIRDLE IN MORMOOPIDAE, PHYLLOSTOMIDAE AND NOCTILIONIDAE (MAMMALIA, CHIROPTERA)

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RESUMO

Morfologia da musculatura do braço e cintura escapular em Mormoopidae Phyllostomidae e Noctilionidae (Mammalia, Chiroptera). A musculatura do braço e cintura peitoral dos morcegos *Phyllostomus hastatus* (omnívoro/carnívoro), *Glossophaga soricina* (nectarívoro), *Artibeus planirostris* (frugívoro), *Desmodus rotundus* (hematófago), *Noctilio leporinus* (piscívoro) e *Pteronotus gymnotus* (insectívoro) foi dissecada e descrita. Encontrou-se alguma variação interespecífica na origem e inserção dos músculos bem como na sua robustez. Nos seguintes músculos não se observou variação: *supraspinatus*, *triceps brachii – caput longum* e *caput laterale*, *biceps brachii – caput breve* e *caput longum*, *pectoralis major – pars clavicularis*, *pars sternocostalis* e *pars abdominalis*. Eles são os principais músculos na batida da asa e provavelmente estão sob forte pressão de seleção.

Palavras-chave: Musculatura, Braço e cintura peitoral, Mormoopidae, Phyllostomidae, Noctilionidae, Chiroptera.

ABSTRACT

Morphology of the musculature of the arm and shoulder girdle in Mormoopidae, Phyllostomidae and Noctilionidae (Mammalia, Chiroptera). The musculature of the arm and pectoral girdle of the bats *Phyllostomus hastatus* (omnivorous/carnivorous), *Glossophaga soricina* (nectarivorous), *Artibeus planirostris* (frugivorous), *Desmodus rotundus* (hematophagous), *Noctilio leporinus* (piscivorous) and *Pteronotus gymnotus* (insectivorous) was dissected and described. We found some inter-specific variation in origin and insertion of muscles as well as in their robustness. No variation was found in the muscles *supraspinatus*, *triceps brachii – pectoralis major – pars clavicularis*, *pars sternocostalis* and *pars abdominalis*, they are the principal muscles in the beating movement of the wing and probably are under stronger selection pressure.

Keywords: Musculature, Arm and shoulder girdle, Mormoopidae, Phyllostomidae, Noctilionidae, Chiroptera.

INTRODUCTION

Chiroptera are the only mammals capable to accomplish true flight. The wing of bats grew starting from the expansion of the dorsal and ventral epidermis along the lateral margin and caudal region of the body. It is formed by macroscopic fibers of collagen and elastine, being vascularized and innervated (SWARTZ, 1998).

The membranous wing is controlled by the pelvic and thoracic members and it is possible to notice some skeletal adaptations, as the reduction in the supraespinous fossa and enlargement of the infraespinous fossa of the scapula, the strongly arched acromion and the length and accentuated curvature of the clavicle (VAUGHAN, 1970a). Those adaptations provide surfaces for appropriate attachment of the musculature, which also suffers great modifications to make possible the aerial locomotion. In Microchiroptera, for instance, the pectoral crest (*Crista tuberculi majoris*) of the humerus is quite developed and acts as a place of insertion of the deltoid and pectoral, muscles both involved in flight (VAUGHAN, 1970a; BAKER et al. 1991). Besides the modifications in the pectoral girdle, the digits 2 to 5 of the hand are strongly prolonged and, with the membrane of the wing, they form a structure similar to an umbrella. The thumb can be moved freely, being used as a tool to hold, and it is the only digit with functional claw (NEUWEILER, 2000).

The musculature of the wing acquired a differentiated arrangement and following the aerodynamic principles, she concentrated its mass on the gravity center of the body, close to the medial line, the musculature of the member being reduced distally. This outstanding adaptation in Chiropterans facilitates the fast flight and maneuverability (VAUGHAN, 1970c; VAUGHAN and BATEMAN, 1970). The robust muscles, especially those that are in relationship with the pectoral girdle, provide mechanical force and energy support for the accomplishment of the flying activity, which demands great amount of energy. Many of the specializations in the histology and in the biochemistry, observed in the musculature involved in flight of bats are exclusive of this group (FENTON et al. 1987). LAWLOR (1973) affirms that structural characteristics of the wings as length, width, weight and position of the muscular insertions, influence the flight style and reflect the type of foraging behaviour (SWARTZ & NORBERG, 1998).

VAUGHAN (1970b) attributes the interspecific variations observed in the anatomy of the pectoral girdle and in the pectoral, serratus and subscapularis muscles, to the style of flight of the species. This author affirms also that the development of a great variety of flight styles has influenced the adaptative radiation to different ecological niches. VAUGHAN and BATEMAN (1970) verified that there are differences in the attachments as well as reduction and loss, in the muscles of the thoracic members between bats of the families Mormoopidae and Phyllostomidae, and they considered that these modifications are related to different functions, concluding that the morphology determines the style of flight and the type of foraging of the alimentary resources.

The aim of this study was to describe and to compare the wing

musculature in some representative species of the families Phyllostomidae, Noctilionidae and Mormoopidae giving emphasis to the patterns of origins and insertion of the muscles of the shoulder girdle and of the arm. We wish to give support to the line of works that relate the anatomy of the wing with the different flight types and these with the alimentary habits.

MATERIALS AND METHODS

The studied specimens are deposited in the Collection of Mammals of the Department of Systematics and Ecology of the Federal University of Paraíba (UFPB), conserved in ethanol 70°. The species were selected according to the alimentary guilds described by MACNAB (1971). In the following list the species name, alimentary guilds and the collection numbers of specimens dissected is given: *Phyllostomus hastatus* (omnivorous / carnivorous) UFPB 5132, 5130, 5133, 5131; *Glossophaga soricina* (nectarivorous) UFPB 5198, 5215, 5575, 5200; *Artibeus planirostris* (frugivorous) UFPB 5536, 5571, 5132, 5538; *Desmodus rotundus* (hematophagous) UFPB 5134, 5692, 5691, 5693; *Noctilio leporinus* (piscivorous) UFPB 4890, 4882, 4876, 4887; *Pteronotus gymnotus* (insectivorous) UFPB FO 232, FO 228, FO 233, FO 231. All the animals were adults.

For dissection the animals were fastened on a rubber platform with the aid of pins, the thoracic members being extended in *decubitus dorsalis* and later in *decubitus ventralis*. Specimens were dissected with micro dissection instruments under a stereomicroscope. After their description, the superficial muscles were cut transversally with the purpose of accessing the deeper muscles. The drawings were made with the aid of a camera lucida. We supplied a detailed description of the musculature of *A. planirostris*. For the remaining of the species we make only reference to those characteristics that differ from *A. planirostris*.

The International Anatomical Terminology and the nomenclature adopted by VAUGHAN (1970b) were used as a base for our descriptions. The comments about the function of the muscles are based on the origin, insertion and direction of the fiber bundles. We also considered the action of the muscle in other mammals and the conclusions of VAUGHAN (1970b) on this subject. The muscular groups were organized following the classification of VAUGHAN (1970b). In the descriptions we used the letters C, T and L together with a number to refer to the respective cervical thoracic and lumbar vertebrae.

RESULTS

Twenty-seven muscles were dissected and described as follows:

The *trapezius* group.

M. acromiotrapezius - It is a large flat muscle of triangular form. It covers the cranial third of the back of the thorax and the caudal portion of the posterior face of the neck (Fig. 2:1).

Origin: From the spinous processes of the vertebrae T1 to T5. It arises also from the costotransverse ligament, which is going from the transverse process of the first thoracic vertebra to the cervical face of the first rib.)

Insertion: To the distal 1/3 of the lateral surface of the clavicle, the acromion and the distal 1/3 of the spine of the scapula.

Action: It draws the clavicle and the scapula medially.

Comments: In *P. hastatus* the insertion extends to the middle or distal 2/3 of the spine of the scapula. In *P. gymnonotus* this muscle is reduced and its origin goes just to the spinous process of T4.

M. spinotrapezius - A long and thin muscle that runs obliquely from caudo-ventral to cranio-lateral (Fig. 2:2).

Origin: From the spinous processes of the vertebrae T9 to L2 and the thoracolumbar aponeurose.

Insertion: To the medial border of the scapula, some 2 mm above and 2 mm below the spine.

Action: It rotates the scapula raising the glenoid cavity and draws the scapula caudally and medially.

Comments: In *N. leporinus*, *P. hastatus* and *D. rotundus* the *M. spinotrapezius* inserts on the whole medial border of the scapula above the spine. In *N. leporinus* the origin is a little narrower, from the vertebrae T10 to L1 and the thoracolumbar aponeurose, while in *D. rotundus* the origin is more caudal, from T11 to L3 and the thoracolumbar aponeurose. A more cranial insertion provides a larger lever effect and an increase in the rotation angle of the scapula. In *D. rotundus* this effect is still more accentuated due to its more caudal origin. In *P. gymnonotus*, the muscle arises more cranially, from T8 to T12 and the thoracolumbar aponeurose. The insertion also includes the proximal extremity of the spine of the scapula.

The *costo-spino-scapular* group.

M. levator scapulae - A robust muscle, cylindrical and slightly twisted in its medial portion. It is situated deeper than the *M. acromiotrapezius* and immediately under the *M. rhomboideus minor* (Fig. 4:1).

Origin: From the transverse process of C7 to the cranial surface of the first rib.

Insertion: To the cranial angle of the scapula and along the next 2 mm of the

medial border.

Action: It draws the cranial angle of the scapula medially and slight cranially. It probably acts with the *Mm trapezius* and *rhomboideus* to fix the scapula during the abduction of the wing.

Comments: In *P. hastatus* and *G. soricina* the origin is only from the first rib. In *D. rotundus* the origin has larger surface going from the transverse process of the vertebra C6 to the first rib. In *G. soricina* and *P.gymnonotus* the insertion is restricted to the cranial angle of the scapula. Such small differences probably don't determine changes in the action of the muscle.

M. serratus anterior - A flat and wide Muscle that covers all the lateral portion of the thorax (Fig. 3:1).

Origin: From the external face of the ventral 1/3 of the 1st to 9th ribs.

Insertion: In the whole extension of the lateral border of the scapula and half of its caudal angle.

Action: It draws ventrally the lateral border of the scapula producing its rotation.

Comments: In *N. leporinus*, the origin goes from the 1st to the 7th rib and the insertion occupies only the proximal 3/4 of the lateral border of the scapula. In *P.gymnonotus* the origin extends from the 1st to the 8th rib.

M. rhomboideus major - A very wide muscle in relation to the smaller *M. rhomboideus minor*, flat and of rhombic outline. It lays deeper to the *M. trapezius* and covers a good part of the ribs (Fig. 4:2).

Origin: From the costotransverse ligament of T1 and the spinous processes of the vertebrae T1 to T6.

Insertion: To the medial border of the scapula, from the spine to the caudal angle.

Action: It draws the scapula medially and rotates it driving the glenoid cavity caudally. Acting together with the *M. trapezius* and the anteroposterior division of the *M. serratus anterior* this muscle helps in the control of the abduction of the wing.

Comments: In *P. hastatus*, *N. leporinus* and *G. soricina* this muscle originates from the vertebrae T1 to T7. *D. rotundus* has a reduction in the origin, only going from T1 to T4. In *P.gymnonotus* and *G. soricina* the origin is from T1 to T5. The reduction of the origin and the consequent increase of the inclination of the muscle, probably increase the rotation angle of the scapula.

M. rhomboideus minor - Some fiber bundles that run parallel to the *M. rhomboideus major* being usually twice narrower than this muscle.

Origin: From spinous processes of C3 to C6 (Fig. 4:3).

Insertion: To proximal half of the cranial angle of the scapula and in the cranial fourth of the medial border of this bone.

Action: Similar to that of *M. rhomboideus major*.

Comments: The insertion of this muscle in *P.gymnonotus* is restricted to the medial border 3 mm below and 2mm above the spine of the scapula. In *N.*

leporinus the origin goes from C2 to C6. In *D. rotundus* the origin is from C2 to C6, or to C7 in one specimen. The insertion in this species doesn't include the cranial angle of the scapula, being only in the next 2 mm of the medial border. In *G. soricina* the origin is from C4 to C7 and the insertion also excludes the cranial angle of the scapula.

The more cranial the origin and the more caudal the insertion larger will be the angle of rotation of the scapula. This is determined by the muscle length and the related increase in the contraction of the muscle. The muscles formed by parallel fiber bundles reduce considerably its length during contraction, being, therefore, the shortening degree directly proportional to its length.

The *latissimus-subscapular* group.

M. latissimus dorsi - A flat fan shaped and very wide muscle located caudal to the scapula. It covers dorsally, half of the latero-caudal surface of the trunk (Fig. 3:2).

Origin: From the spinous processes of the vertebrae T10 or T11 to T12, the lumbar vertebrae and the thoracolumbar aponeurose, that extends over de iliac and sacral regions.

Insertion: To the proximal part of the medial face of the humerus.

Action: It is a flexor of the escapulo-humeral articulation and rotates the humerus medially. During the abduction, the stability of the wing can be maintained partly by the *M. latissimus dorsi* and by the *M. teres major*, opposing the rotator *Mm. deltoideus* and *infraspinatus*.

Comments: In *P. hastatus*, *D. rotundus* and *N. leporinus* the muscle inserts in the crest of the lesser tubercle of the humerus. The origin in *P. hastatus* is wider, including T9 to T13, and in *N. leporinus* the origin starts from T8 or T9. In *D. rotundus* and *G. soricina* it originates from T10. In *P.gymnonotus* the origin is from T8. In all species the muscle arises from the caudal region of the thoracolumbar aponeurose. Due to the muscles length the different origins, possibly don't determine differences in action.

M. teres major - A fusiform muscle, robust and slightly convex in its dorsal surface. It covers the lateral border of the scapula (Fig. 4:4).

Origin: From the caudal angle of the scapula to the middle or proximal third of the lateral border of the bone.

Insertion: To the proximal part of the medial surface of the humerus, just medial to the insertion of the *M. latissimus dorsi*.

Action: It flexes the articulation of the shoulder, adduces and rotates the humerus medially.

Comments: *D. rotundus*, *P. hastatus* and *N. leporinus* insert to the cranial surface of the crest of the lesser tubercle of the humerus. In *D. rotundus* the origin is in the medial three fourths of the lateral border of the scapula but in *G. soricina* and *P. gymnonotus* it is reduced to the proximal third of that border, inserting respectively in the caudal face of the proximal third of the humerus and in the proximal part

of the medial face of that bone. In the animals that have the medial insertion, as *P. gymnonotus* and *D. rotundus*, the humerus has a larger rotation angle.

M. subscapularis - A triangular and less robust muscle that covers the ventral surface of the scapula (Fig. 3:3).

Origin: From the subscapular fossa.

Insertion: To the lesser tubercle of the humerus.

Action: It adduces and extends the humerus, the two most important movements of the wing during the flight. In the terrestrial locomotion of bats it aids in supporting the anterior portion of the body adducing the humerus.

Comments: In *P. hastatus* it also has origin in the lateral border of the scapula.

The *deltoides* group.

M. claviodeltoideus - A robust muscle that covers the clavicle dorsally. It has fiber bundles oriented almost parallel to those of the *M. pectoralis major pars clavicularis* up to a point where they meet to the same insertion. Usually it is difficult to distinguish both muscles (not figured).

Origin: From the distal half or third of the dorsal face of the clavicle.

Insertion: To the proximal half of the pectoral crest of the humerus.

Action: It extends and adduces the humerus, causing the wing beat. It probably controls the extension of the humerus at the beginning of the displacement of the upper member during the terrestrial locomotion.

Comments: In *P. hastatus* the insertion is also in the proximal extremity of the crest. There is no difference in action since the fiber bundles have the same direction.

M. acromiodeltoideus - A thick muscle with the shape of an inverted triangle. It covers the articulation of the shoulder and extends to the middle of the humerus (Fig. 2:3).

Origin: From the acromion, the distal third of the spine of the scapula and the distal extremity of the clavicle.

Insertion: To the distal portion of the pectoral crest (*crista tuberculi majoris*) and the deltoid tuberosity of the humerus.

Action: Abduction, lateral rotation, and flexion of the humerus.

Comments: In *D. rotundus* the origin doesn't include the extremity of the clavicle. In *P. gymnonotus* there is not an origin in the spine of the scapula and also the insertion is in the middle portion of the pectoral crista. In the last species, the muscle is more involved with the abduction, because of its lesser size and more proximal insertion, what should optimize the traction force of the muscle. In *D. rotundus* abduction, rotation and flexion are more accentuated, because the area of origin doesn't include the clavicle.

M. spinodeltoideus - A flat muscle of triangular shape shorter and wider than the

M. acromiodeltoideus. He lies over the *M. infraspinatus* covering all that portion of the scapula, caudal to the spine (Fig. 2:4).

Origin: From all the spine of the scapula and the medial border of this bone to its caudal angle.

Insertion: To the lateral face of the humerus, caudally to the pectoral crest.

Action: Elevation, flexion and lateral rotation of the humerus.

Comments: In *N. leporinus* the spinal origin occupies just the proximal half of the spine of the scapula. In *G. soricina* and *P. gymnonotus* this muscle originates from the proximal two-thirds of the spine of the scapula. The insertion in the last species is in the distal portion of the pectoral crest of the humerus. When the origin is limited to the proximal portion of the spine of the scapula the muscle acts mainly flexioning the articulation of the shoulder, and providing less lateral elevation and larger rotation of the humerus. This should be increased in *P. gymnonotus* where the insertion is more distal.

M. teres minor - A very thin and short muscle, the smallest of the muscles involved in flight. It lies just below the insertion of the *M. infraspinatus* and passes superficially to the lateral head of the triceps. In some cases, it is difficult to identify and seem to be part of the *M. infraspinatus* (Fig. 4:5).

Origin: From the distal end of the lateral border of the scapula.

Insertion: To the greater tubercle of the humerus, immediately distal to the insertion of the *M. infraspinatus*.

Action: It contributes to the flexion and lateral rotation of the humerus.

Comments: In *P. hastatus* and *G. soricina* the insertion is in the crest of the greater tubercle. In the last species the *M. teres minor* originates in the neck of the scapula. In *P. gymnonotus* the muscle originates from the infraglenoidal tubercle. The muscle has a similar size in all studied species and probably the same function.

The *suprascapular* group.

M. suprascapularis - A muscle with conical shape, covered by the *M. acromiotrapezius* and partially by the *M. spinodeltoideus*. It is lodged in the suprascapular fossa of the scapula and passes below the acromion (Fig. 4:6).

Origin: From the suprascapular fossa.

Insertion: To the greater tubercle of the humerus, proximal to the insertion of the *M. infraspinatus*.

Action: It abducts, extends and rotates laterally the humerus. At the end of the wing beat it helps to maintain the head of the humerus in the glenoid cavity of the scapula.

Comments: The origin and insertion were the same for all species.

M. infraspinatus - A triangular muscle covered by the *M. spinodeltoideus* and lodged in the infrascapular fossa (Fig. 4:7).

Origin: From the infraspinous fossa.

Insertion: To the greater tubercle of the humerus, immediately distal to the insertion of the *M. supraspinatus*

Action: It abducts, flexes and rotates laterally the humerus.. This muscle together with the *Mm. supraspinatus, teres minor* and *subscapularis* form a sort of sleeve which rotates the humerus and aids to maintain a good escapulo-humeral fitting.

Comments: In *P.hastatus* it also inserts in the crest of the greater tubercle, while in *N. leporinus* the insertion is lateral to the greater tubercle.

The *triceps* group.

The *M. triceps brachii* is a long and fusiform muscle. It divides in three heads in its more proximal portion that are named *caput longum, caput laterale* and *caput mediale*.

All the three divisions converge to a single tendon that inserts in the olecranon of the ulna.

M. triceps brachii - caput longum - It is located dorso-medially to the other heads.

Origin: From the infraglenoid tubercle of the scapula (Fig. 4:8).

Action: It produces the extension of the elbow articulation and adduction of the articulation of the shoulder.

Comments: the origin and insertion are similar in all species.

M. triceps brachii - caput laterale - It is located laterally to the former (Fig. 4:9).

Origin: From the neck and proximal third of the shaft of the humerus.

Action: extension of the elbow articulation.

Comments: The origin and insertion are similar in all species.

M. triceps brachii - caput mediale - It is thinner and more elongated than the two other heads. The fibers become scattered in the more distal portion (Fig. 3:4).

Origin: From the medial surface of the humerus shaft.

Action: Extension of the elbow articulation. In the species where the muscle is reduced like *P. gymnonotus* and *G. soricina* its contribution to the action of the *M. triceps brachii* is minimal in relation to the two other heads.

Comments: In *P. hastatus* the origin extends only over the medium third of the humerus shaft. In *D. rotundus*, however, the origin extends also over the distal part of the proximal third of the humerus. In *P. gymnonotus* it originates only from the distal portion of the proximal third of the shaft.

The *flexor of the arm* group.

M. coracobrachialis - It is a fusiform and elongated muscle (Fig. 3:5).

Origin: From the apex of the coracoid process of the scapula.

Insertion: To the medium third of the medial surface of the humerus shaft.

Action: Adduction, flexion and medial rotation of the humerus.

Comments: In *P. hastatus* and *G. soricina* the insertion is in the proximal third of the humerus. In this case there is a decrease of the adduction due to the shortening of the muscle. In *D. rotundus* the insertion occurs in the antero-medial surface of the humerus, what should result in a greater medial rotation of the bone.

The *M. biceps brachii* arises from two heads, a long and a short one. It is fusiform and elongated and is attached by a single tendon to the radial tuberosity. The radial tuberosity, in all the observed animals, is placed caudo-medially allowing the tendon of the *M. biceps brachii* to pass between the radius and the ulna. This location, more caudal than in primates, allows a larger supination angle, necessary to maintain the wing horizontal during flight.

M. biceps brachii - caput breve - (Fig. 3:6).

Origin: From extremity of the coracoid process.

Action: Flexion and mainly supination of the fore arm and extension of the shoulder articulation.

Comments: The origin and insertion are similar in all species.

M. biceps brachii - caput longum - (Fig. 3:7).

Origin: From the base of the coracoid process.

Action: Flexion and mainly supination of the fore arm and adduction of the shoulder articulation.

Comments: The origin and insertion are similar in all species. However, a clear difference was observed in length and robustness of the muscle between different species. In the larger species such as *A. planirostris*, *D. rotundus*, *N. leporinus* and *P. hastatus*, the belly of the biceps appears longer and proportionally more robust when compared to that of *P. gymnonotus*.

M. brachialis - A long muscle, flattened medio-laterally. It is located under the distal half of the biceps (Fig. 3:8).

Origin: From the distal third of the cranio-lateral surface of the humerus.

Insertion: To the tuberosity of the radius, ventral and proximal to the tendon of the *biceps brachii*.

Action: Flexion and supination of the fore arm.

Comments: In *D. rotundus* and *N. leporinus* it arises from the distal part of the medium third and the proximal part of the distal third of the cranial surface of the shaft of the humerus. We didn't find this muscle in *P. gymnonotus*. Due to the small size of this muscle, the differences observed among species in the origin of the *M. brachialis* should not determine important functional variations.

The *pectoralis* group.

The *M. pectoralis major* is the largest and more robust muscle of bats. It is divided in a clavicular portion an abdominal portion and a sternocostal portion. It is the most important muscle in the adduction of the wing.

M. pectoralis major - pars clavicularis - (Fig. 1:1).

Origin: From the proximal two thirds of the ventral surface of the clavicle.

Insertion: To the proximal portion of the pectoral crest of the humerus.

Action: Adduction of the arm, pulling cranial wards; medial rotation of the humerus.

Comments: Origin and insertion are the same in all species.

M. pectoralis major - pars sternocostalis - (Fig. 1:1).

Origin: From the body, manubrium and xiphoid process of the sternum as well as from de second to seventh costal cartilages.

Insertion: in the pectoral crest of the humerus distal to the insertion of the *pars clavicularis*.

Action: Adduction of the arm, pulling it medially and caudally; medial ward rotation of the humerus.

Comments: The origin and insertion are similar in all species. The separation from the *pars clavicularis* is not very well defined, being identified mainly by recognition of the origin and insertion.

M. pectoralis major - pars abdominalis - A long and thin muscle of parallel fiber bundles, covered partially by the *pars sternocostalis* and superficial to the intercostal muscles and *M. serratus anterior* (Fig. 3:9).

Origin: From the abdominal aponeurose and the sheath of the *M. rectus abdominis*.

Insertion: To the pectoral crest, medial and proximal to the insertion of the *pars sternocostalis*.

Action: Adduction of the arm, pulling it caudal ward and rotating the humerus medial ward.

Comments: The origin and insertion are similar in all species.

M. subclavius - A flat and triangular muscle (Fig. 3:3).

Origin: From the four distal fifth of the dorsal surface of the clavicle.

Insertion: To the cranial margin of the first costal cartilage.

Action: It moves the clavicle caudal and ventral ward and probably acts also in the fixation of the clavicle against the antagonistic dorsal musculature.

Comments: In *P. hastatus* and *G. soricina* the muscle also inserts in the lateral extension of the manubrium, what doesn't necessarily changes its action.

M. pectoralis minor - It is a thin and triangular muscle that lies superficial to the

intercostal muscles (Fig. 3:11).

Origin: From the second to the fourth costal cartilages.

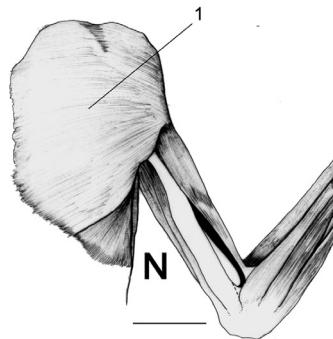
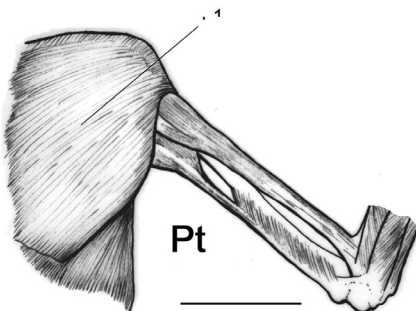
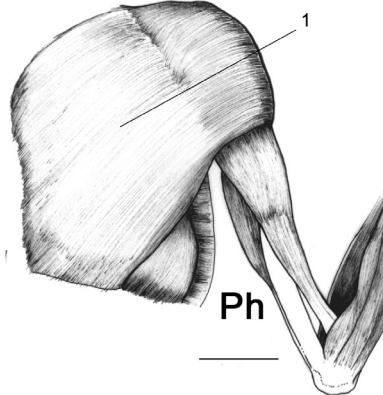
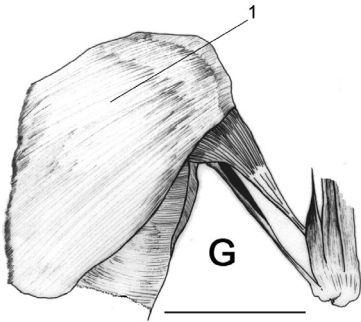
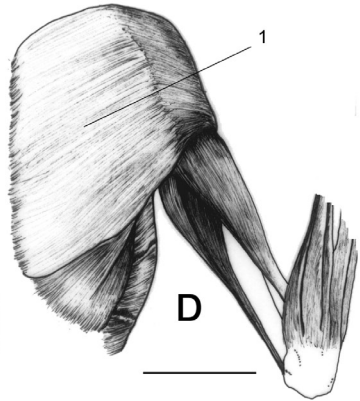
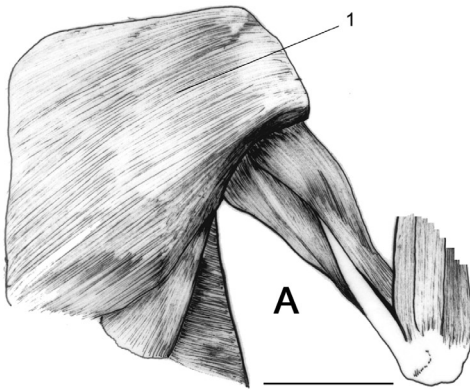
Insertion: To the caudal margin of the first costal cartilage.

Action: It elevates the second to fourth ribs. Probably it fixes the first rib and, consequently, the clavicle together with the *M. subclavius*.

Comments: In *P. hastatus*, *P. gymnonotus* and *G. soricina* it arises from the third to fifth costal cartilages. In *N. leporinus* it arises from the third to sixth costal cartilages, as well as from the body of the sternum. In *D. rotundus* this muscle arises from the body of the sternum, in level to the third to fifth sternal synchondroses. The different insertions probably don't determine functional differences.

Figure 1 - Ventral view of the superficial musculature of arm and shoulder girdle. The letters refer to the species described, **A** = *Artibeus planirostris*, **D** = *Desmodus rotundus*, **Ph** = *Phyllostomus hastatus*, **G** = *Glossophaga soricina*, **Pt** = *Pteronotus gymnonotus*, and **N** = *Noctilio leporinus*. **1** = *M. pectoralis major*- *pars clavicularis* and *pars sternocostalis*. The bar is 1cm.

For a better visualization of the *M. biceps brachii - caput longum*, (Figure 3) the distal part of the *M. biceps brachii - caput breve* were removed in *G. soricina* and *P.gymnonotus*. The *M. brachialis* could be shown only in *Artibeus planirostris* (**A**) and *Noctilio leporinus* (**N**) because of the difficult posture in which the specimens of the other species were fixed.



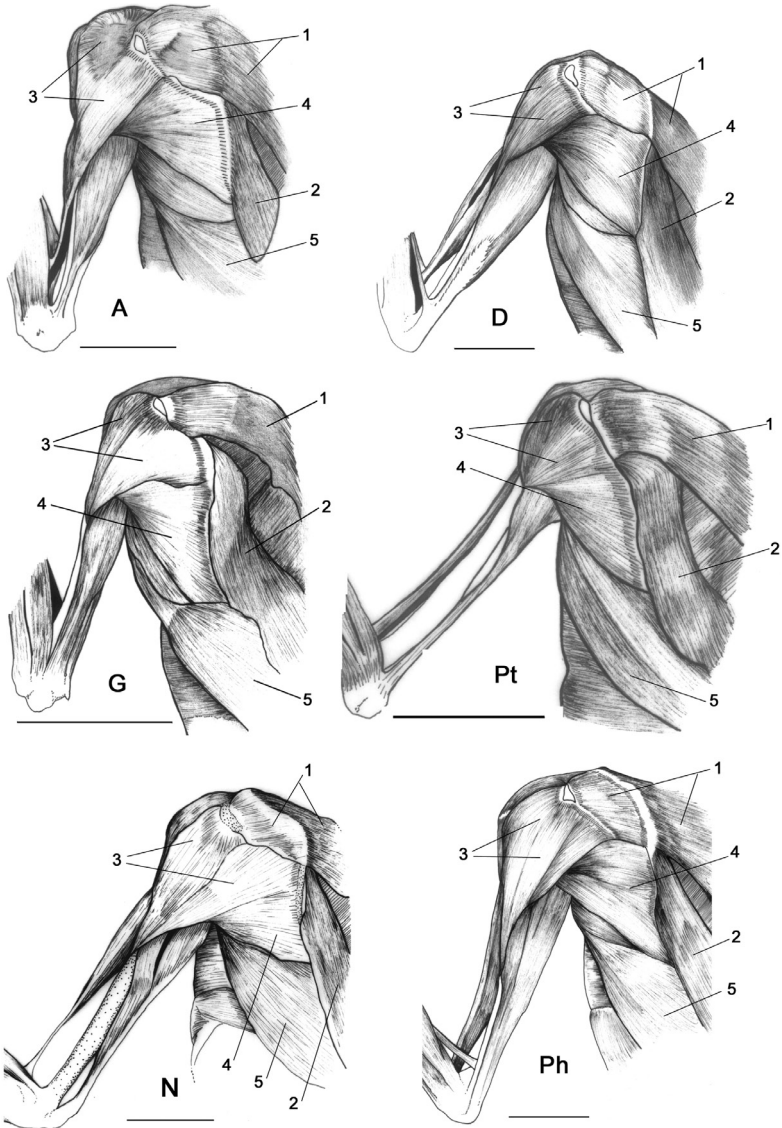


Figure 2. Dorsal view of the superficial musculature of arm and shoulder girdle. The letters refer to the species described, see Figure 1 for explanations. **1** = *M. acromiotrapezius*, **2** = *M. spinotrapezius*, **3** = *M. acromiodeltoideus*, **4** = *M. spinodeltoideus*, **5** *M. latissimus dorsi*.

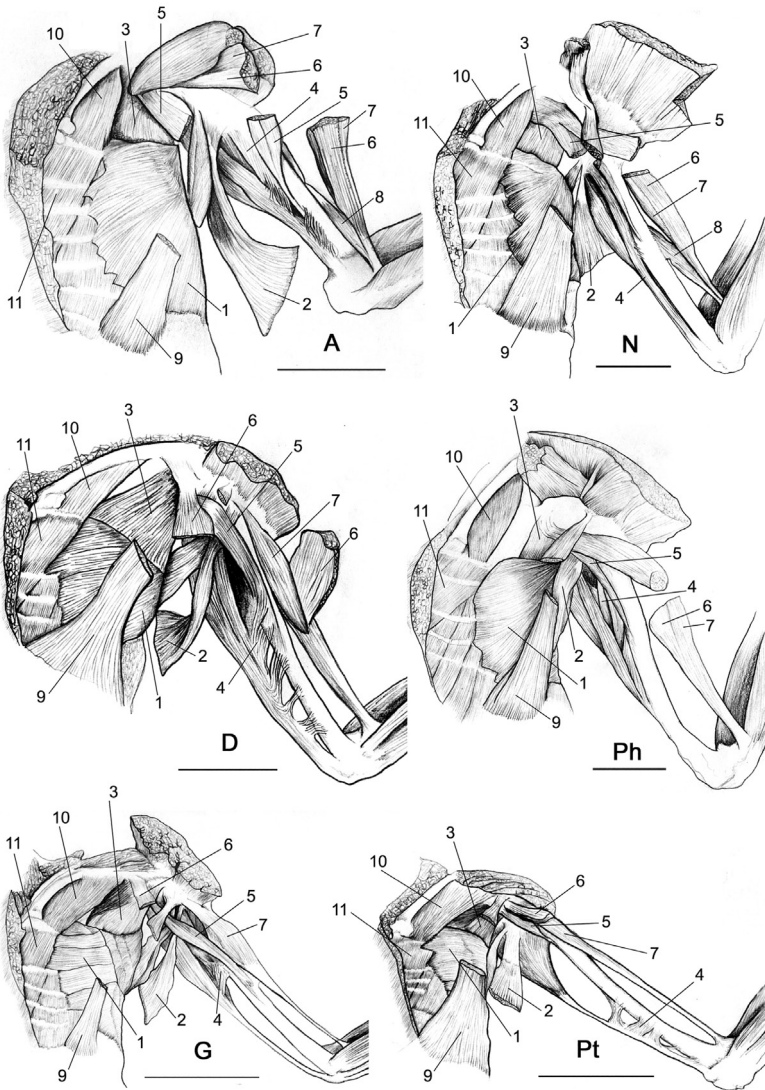


Figure 3. Ventral view of the deep musculature of arm and shoulder girdle. The letters refer to the species described, see Figure 1 for explanations. **1** = *M. Serratus anterior*, **2** = *M. latissimus dorsi*, **3** = *M. subscapularis*, **4** = *M. triceps brachii - caput mediale*, **5** = *M. Coracobrachialis*, **6** = *M. biceps brachii - caput breve*, **7** = *M. biceps brachii - caput longum*, **8** = *M. brachialis*, **9** = *M. Pectoralis major - pars abdominalis*, **10** = *M. subclavius*, **11** = *M. pectoralis minor*.

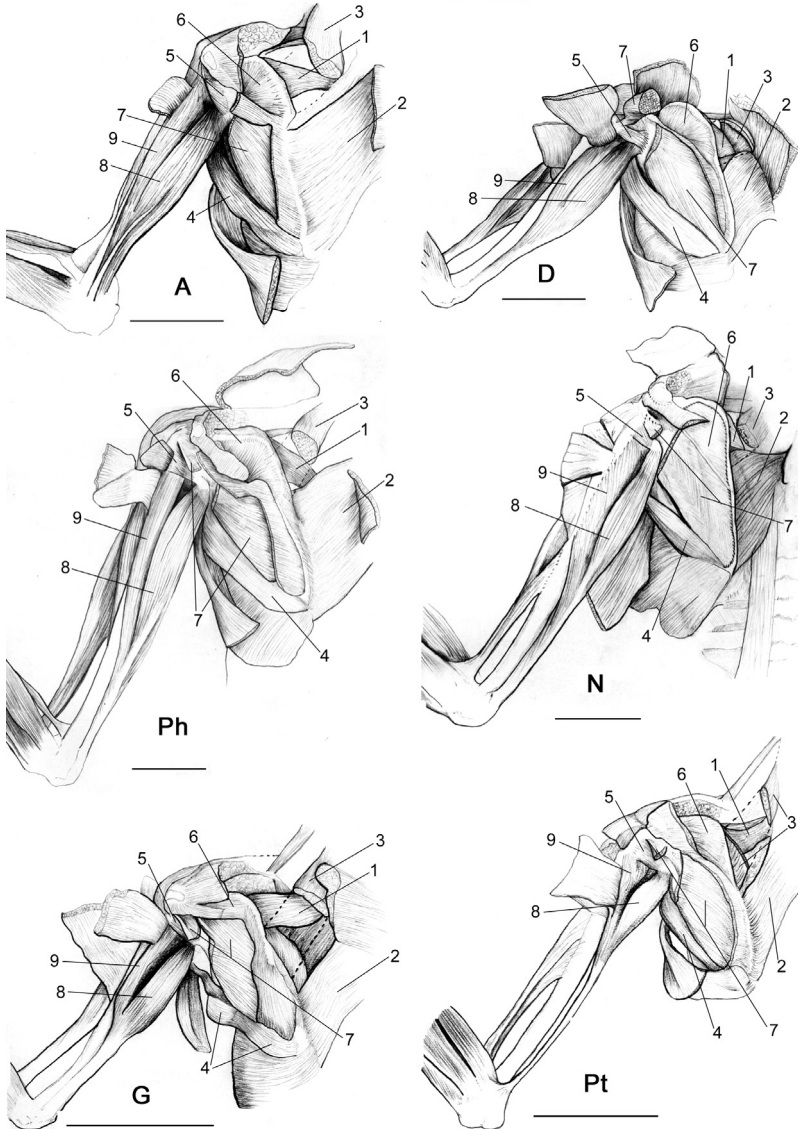


Figure 4. Dorsal view of the deep musculature of arm and shoulder girdle. The letters refer to the species described, see Figure 1 for explanations. 1 = *M. levator scapulae*, 2 = *M. rhomboideus major*, 3 = *M. rhomboideus minor*, 4 = *M. teres major*, 5 = *M. teres minor*, 6 = *M. supraspinatus*, 7 = *M. infraspinatus*, 8 = *M. triceps brachii - caput longum*, 9 = *M. triceps brachii - caput laterale*.

DISCUSSION

We observed a variation in robustness of some muscles. The muscles of the **triceps** group for instance show muscle fibers running down to the insertion in some species (*A. planirostris*, *P. hastatus* and *N. leporinus* *D. rotundus*) in others (*Pteronotus gymnonotus*) they occupy just the proximal third of the muscle the other 2/3 are formed mainly by tendons (Fig. 3).

Robustness may be related to foraging strategies. All the mentioned robust species carry some weight during flight. *A. planirostris* use to get fruits in one tree and to carry them to another “feeding” tree; *P. hastatus* do the same with small vertebrates; *N. leporinus* fish on the water surface, and transport its prey in flight to a dry feeding place (FINDLEY et al., 1972). The hematophagous *Desmodus* also show a robust musculature that may be related to the particular activities of climbing and quadruped displacement of the vampire bat, an unusual behavior in other species of Chiropterans (SWARTZ et al., 2003).

This species also make long lasting flights because of the wide distribution of its feeding resources (BOCCHIGLEIRI, 2000). The smaller *G. soricina* showed a widespread reduction in musculature. This characteristic is not only related to size but is observed in nectarivorous species, and according to BOCCHIGLEIRI (2000), members of the Glossophaginae show morphologic adaptations to hover-flight with reduction of the muscular load.

According to VAUGHAN and BATEMAN (1970) the family Mormoopidae has a reduction of the forearm musculature. This is what we observed in *P. gymnonotus*, our specimen showed the greatest degree of reduction of the wing musculature when compared to specimens of other families we studied. As an insectivorous bat that captures its prey during flight, he needs high maneuverability and speed. A small musculature is one of the main specializations for that type of flight; allowing greater lightness and a better performance of the chiroptagium as a functional unit (VAUGHAN and BATEMAN, 1970).

We agree with KALKO (1997) that defines diet and flight type as parameters for the characterization of the guilds of bats, and observes that those that fly in a similar way prefer the same feeding resources and are more frequent in certain habitat and microhabitat.

The variation in origins and insertion of muscles we observed in different species, do not have an apparent correlation with alimentary guild or flight type they may have a phylogenetic explanation. However, these conclusions should be supported by a larger number of species and of specimens. To better explain the relationship of morphology to flight function (or flight type) the origin and insertion of muscles should be associated to other parameters like muscle volume, weight and type of muscular fiber as well as to the morphology of the membranous wing.

It is interesting to note that variation occurred in a large number of muscles except in the following: *Mm. supraspinatus*, *triceps brachii* – *caput*

longum and *caput laterale*, *biceps brachii* – *caput breve* and *caput longum*, *pectoralis major* – *pars clavicularis*, *pars sternocostalis* and *pars abdominalis*. These are the principal muscles in the beating movement of the wing and probably are under stronger selection pressure to avoid variations. Among the other muscles here studied some variations may be irrelevant functionally or are important in controlling the different types of flight.

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