Chapter 2
Forelimb Morphology of Colugos

Colugos were examined morphologically much rarer than tree shrews. The first notes on the skull and the forelimb skeleton of colugo were done by Owen (1868). The most detailed classic description of its anatomy, including osteology and myology, was performed by Leche (1886), and Chapman (1902) published a summary of the most interesting features of its skeleton, musculature, etc. The hindlimb muscles were briefly described in a general textbook of zoology (Grassé 1955), and Diogo (2009) analyzed the jaw apparatus and also mentioned several muscles of the shoulder girdle originating from the head. The whole skeleton was described by Shufeldt (1911), and some bones were also studied by Szalay and Lucas (1993). The analysis of carpal bones has shown that colugos and chiropterans have a number of similar features (Stafford and Thorington 1998).

To describe the musculature, we dissected one specimen of either colugo species (Dermoptera: Cynocephalidae: *Cynocephalus volans*[1], *C. variegatus*[2]) from ZMMU; partial dissection of muscles and determination of the natural position of the clavicle were performed using three wet specimens of the Philippine colugo (*C. variegatus*[3]) in the Raffles Museum of Biodiversity Research (Department of Biological Sciences, Faculty of Science, National University of Singapore). The analysis of joints mobility was performed using syndesmological preparations obtained after dissection and a fresh corpse from Raffles Museum of Biodiversity Research. The skeleton was described based on the same syndesmological preparations and one more dry skeleton of the Philippine colugo[4] from the exposition of the ZMMU.

[1] ZMMU, no. s-113598.

[2] ZMMU, no. s-146228.

[3] without no.

[4] ZMMU, without no.

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Wing Membrane

Colugos have a relatively thick gliding membrane covered with rich fur. In the spread state, it is pentagonal, with the apices represented by the ends of tail and four limbs. The membrane is stretched between the head and forelimbs, between fore- and hindlimbs, and between hindlimbs and tail. At the head, the anterior edge of the membrane closely approaches the mouth angles; at limbs, it spreads up to the claw bases, so that the digits are incorporated in the membrane (Fig. 2.1a). The tail is completely included in the membrane.

The membrane contains some striated muscles. The largest is the coracocutaneus muscle. In addition, many separate muscular fascicles are enclosed between the dorsal and ventral skin layers of the membrane.

The lateral part of the membrane stretched between the fore- and hindlimbs is named the plagiopatagium or palatopatagium (Chapman 1902; Grassé 1955). The most anterior part of the membrane stretched between the forelimbs and head is named propatagium, and the caudal part stretched between the hindlimbs and tail is the uropatagium. The interdigital membranes of colugos are also present, but have not got special names.

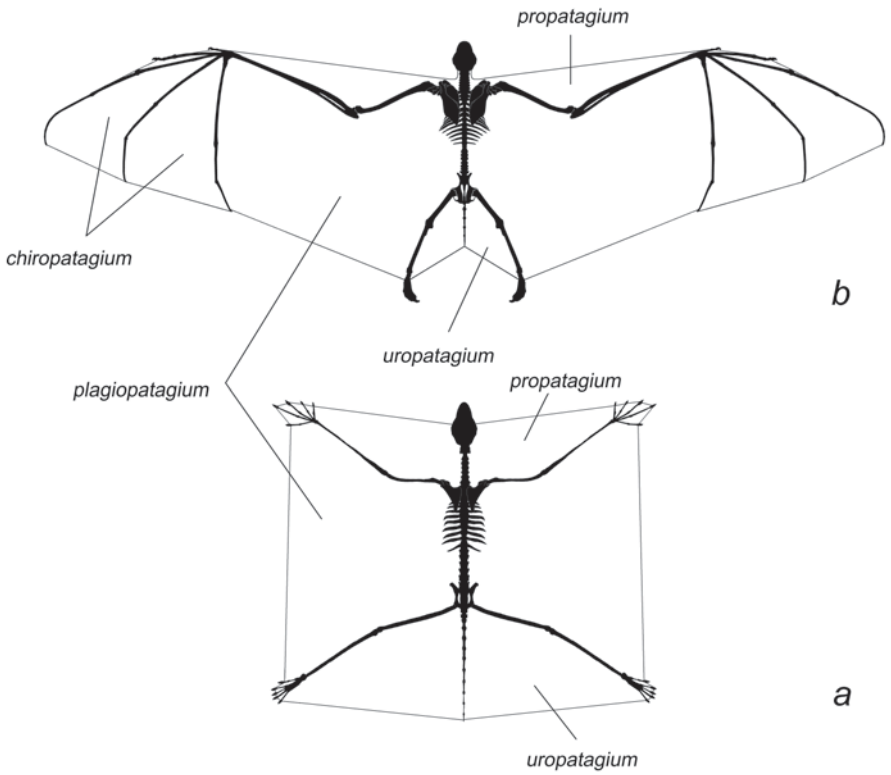


Fig. 2.1 Scheme of the main parts of patagium. *a. Colugos b. Bats*

Skeleton

The forelimb skeleton was described in detail by Shufeldt (1911).

Scapula (Fig. 2.2, Fig. 2.3). The scapula of colugos is distinctly triangular. In tree shrews, its dorsal border is less than half as long as the caudal border, whereas in colugos, they are approximately equal in length. The spine divides the dorsal border into two unequal parts; the posterior (infraspinous) part is almost straight, composes approximately two-thirds and the anterior (supraspinous) part is slightly rounded, one-third of the total length. The transition between the dorsal and cranial borders of the scapula is gradual. The cranial border gently passes into a long hooked coracoid process. Its base is connected with the cranial border of the scapula by the *ligamentum transversum scapulae superius* (Figs. 2.12, 2.13, 2.32–2.37). The caudal border of the scapula is the longest, perfectly straight. It deflects externally, forming a shelf parallel to the spine, similar to that of tree shrews. The dorsocaudal angle is supplemented with an extra ossification; the suture separating it from the

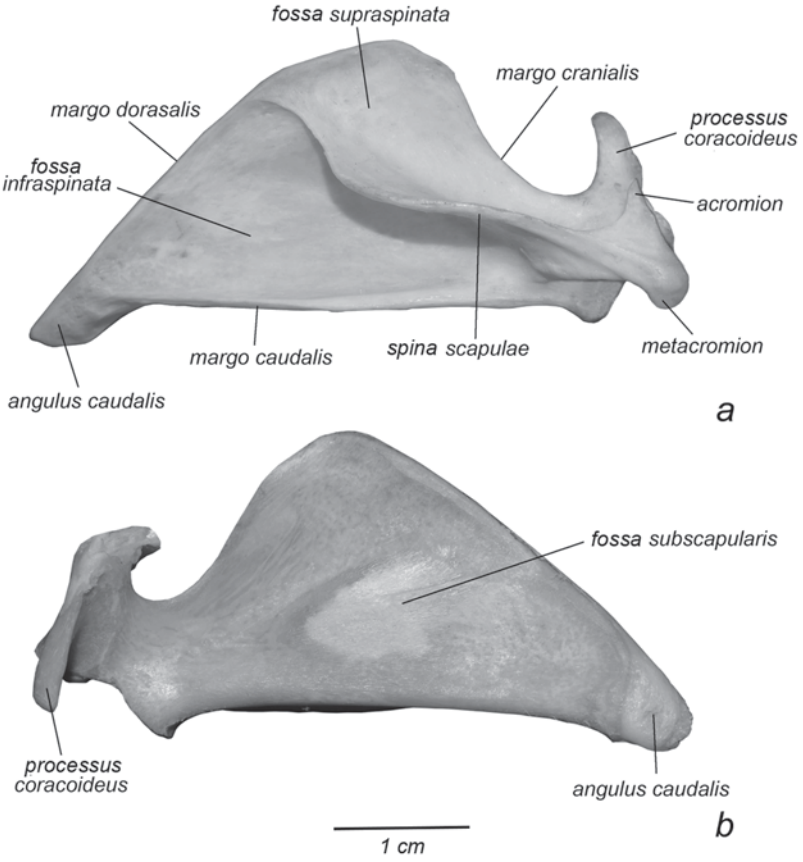


Fig. 2.2 The scapula of colugo, right forelimb. *a. Lateral view* (*Cynocephalus variegatus, adult*) *b. Medial view* (*Cynocephalus volans, subadult*)

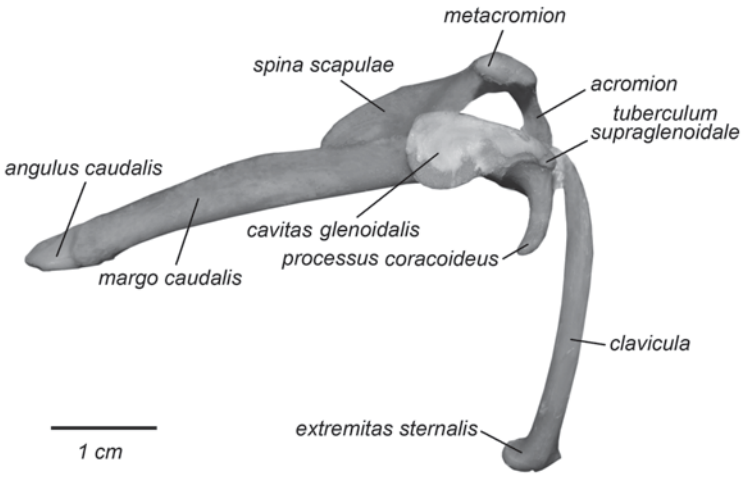


Fig. 2.3 The clavicle and scapula of *C. volans,* right forelimb, subadult, posterior view.

remaining scapula, is distinct in young animals (Fig. 2.2b). The supraspinous fossa is significantly smaller than the infraspinous fossa. The spine is very high. A long, tapering acromion curves anteriorly and internally. The metacromion is well pronounced and is thicker than the anterior part, that is the acromion itself. The glenoid is wide, piriform in outline; the supraglenoid tubercle is well developed.

Clavicula (Fig. 2.4). The clavicle is S-shaped and flattened slightly dorsoventrally. At the sternal end, the clavicle expands to form a rounded articular surface.

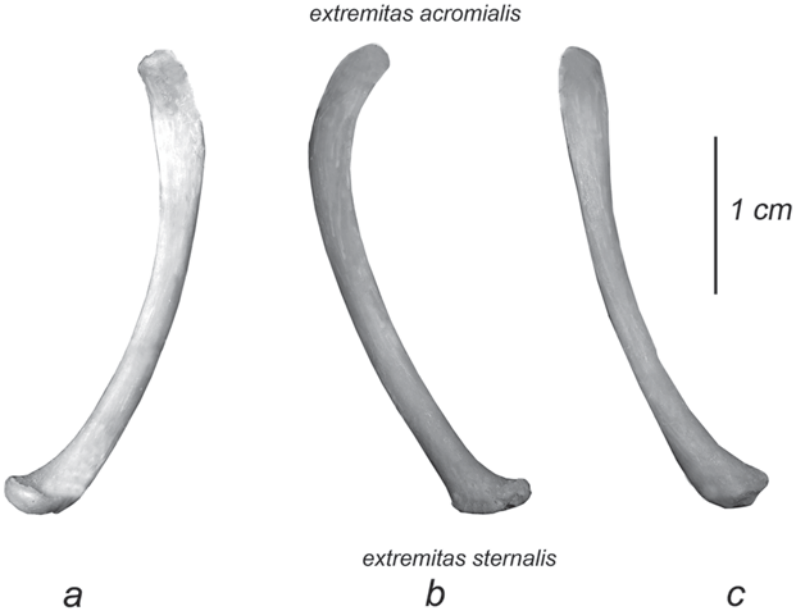


Fig. 2.4 The clavicle of *C. volans,* right forelimb. *a. Lateral view b. Medial view c. Anterior view*

Its acromial end curves posteriorly and does not have an articular facet for the acromion of the scapula, as acromion does not have for the clavicle.

Humerus (Figs. 2.5, 2.6). The humerus is longer relative to the body than in tree shrews. Its proximal end has well-developed greater and lesser tubercles, the latter being larger. The pectoral crest is high and approximately one-third as long as the humerus. The distal end of the humerus bears well-developed epicondyles; the lateral epicondyle is significantly smaller than the medial epicondyle. The crest of the lateral epicondyle is high and occupies almost half of the humerus length. The medial epicondyle is wide, but its crest is relatively short. The trochlea of the distal epiphysis extends well lateromedially. The large lateral condyle is spherical and faces only anteriorly. The smaller medial condyle is pulley-shaped and its articular surface

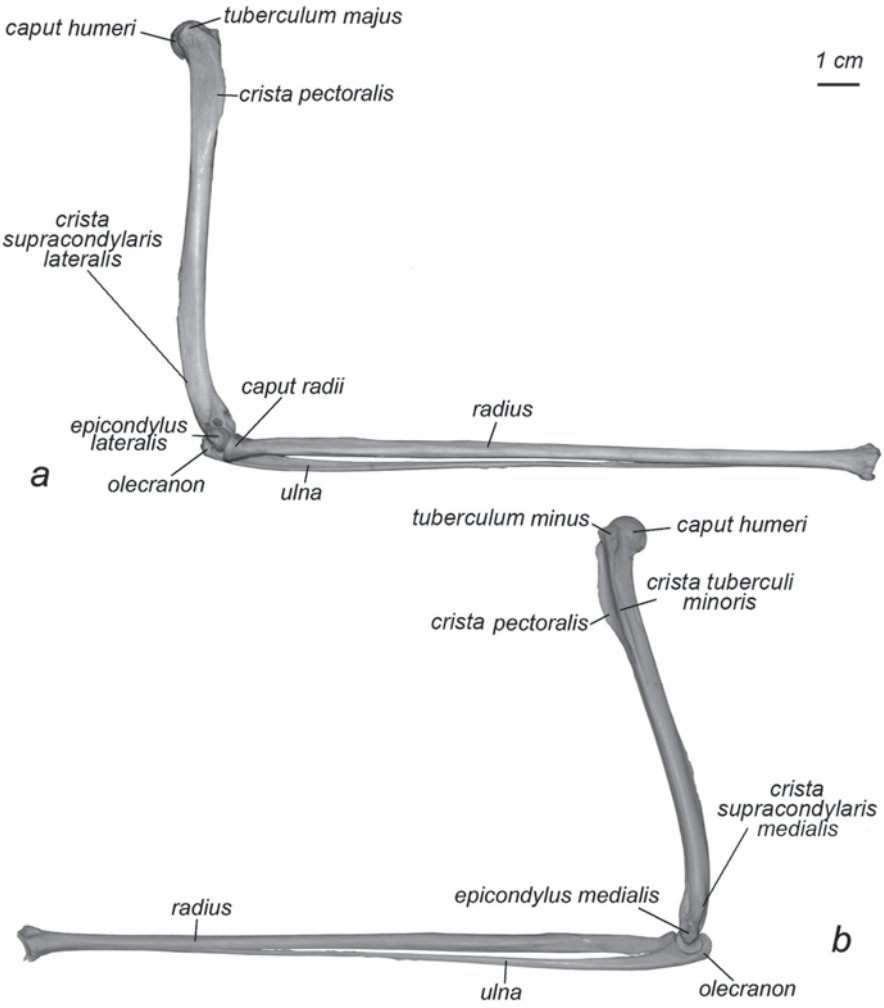


Fig. 2.5 The humerus and antebrachium of *C. volans,* right forelimb. *a. Lateral view b. Medial view*

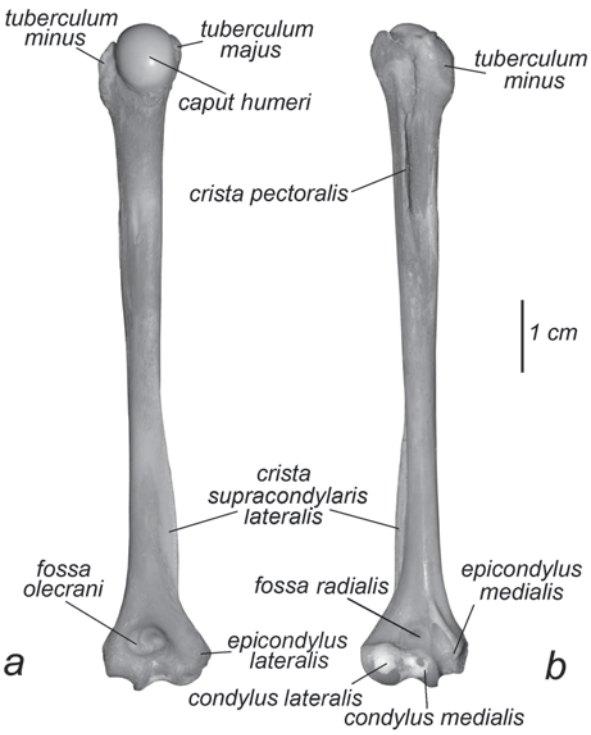


Fig. 2.6 The humerus of *C. volans,* right forelimb. *a. Anterior view* *b. Posterior view*

spreads over the anterior, distal, and posterior sides of the epiphysis reaching the *fossa olecrani*. The *fossa radialis* is almost indiscernible, and the *fossa olecrani* is, on the contrary, so deep that it is only separated from the *fossa radialis* by a thin bony wall.

Antebrachium (Fig. 2.5). The antebrachium in colugos is almost twice as long as the humerus, while in tree shrews, the humerus and antebrachium are approximately equal in length. The **radius** is developed much better than the **ulna**. The uncinate olecranon is very short. The distal one-third of the ulna tapers and fuses to the radius. Shufeldt (1911) reports, that, in some specimens, he could separate the ulna from the radius almost throughout its length, but probably this was due to condition of his material; indeed, after long fixation. The tapering distal end of the ulna frequently splits off from the radius. The process of narrowing of the ulna relative to the radius is well visible in a series of successive ontogenetic stages (Stafford and Thorington 1998). Comparing these stages with the relatively young (judging from the state of bones) specimen, which we have examined, it is possible to conclude that the ulna participates in the antebrachiocarpal joint by a small rounded fragment of its distal end, which is completely fused to the radius in older animals (Fig. 2.7a).

Carpus (Fig. 2.7, Table 1.1). In adults, the carpus is formed of seven separate bones. The bones are arranged in two rows: *scaphocentralolunatum* (produced by fusion of *radiale*, *intermedium*, and *centrale*), *cuneiforme*, and *pisiforme* form the proximal row; *trapezium, trapezoideum, capitatum,* and *uncinatum* form the distal row. Shufeldt (1911) reports four bones in the proximal row, but most probably his separate scaphoid is in fact the prepollex. Indeed, in ontogeny, the true *scaphoideum*

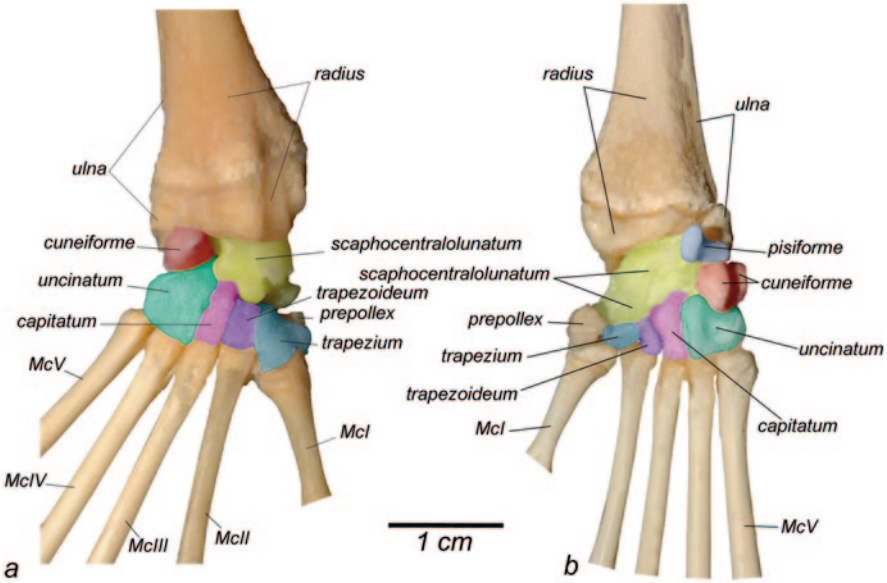


Fig. 2.7 The carpus of *C. volans,* right forelimb, subadult. *a. Dorsal view b. Ventral view*

fuses to *lunatum* even earlier than the *centrale* does (Stafford and Thorington 1998) and so the condition with the separate *scaphoideum* and fused *centralolunatum* (*semilunare* of Shufeldt) seems impossible.

Digits (Fig. 2.8, Table 1.2). The prepollex of colugos is smaller relative to the carpus than in tree shrews. It is located at the medial side of the distal row of carpals. The metacarpals (*ossa metacarpalia*) and distal phalanges make the main contribution to the length of the manus, which is in colugos considerably longer relative to the forelimb than in tree shrews. Digits III–V are the longest. Digit II is slightly shorter and digit I is almost half as long as the others. The phalangeal formula is ordinary, the same as in tree shrews. The palmar surface of proximal phalanx in each finger bears high crests forming a groove, which houses tendons of digital flexor muscles. Long, laterally compressed claws, with sharp and curved tips are equally well developed in all digits. They have an extraordinarily high bases, which give good leverage to the digital flexors and extensors (Fig. 2.9). The huge claws of colugos were already noticed by Owen in 1868. Similar size and shape of claws is found in some fossil Plesiadapidae (Szalay and Lucas 1993).

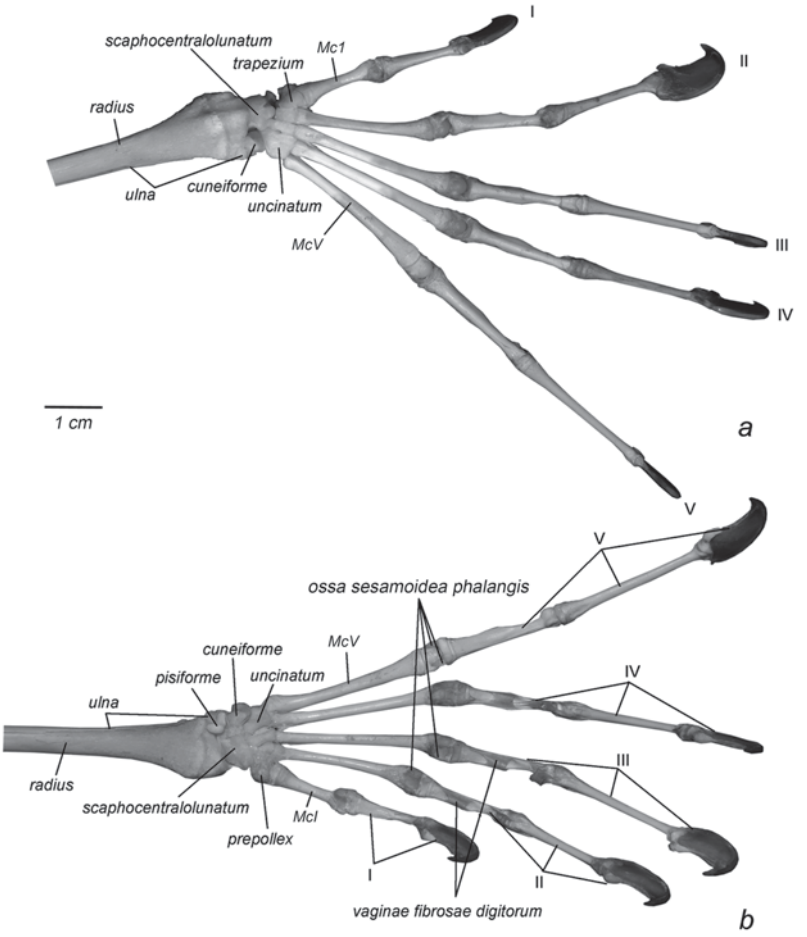


Fig. 2.8 The manus of *C. volans,* right forelimb. *a. Dorsal view b. Ventral view*

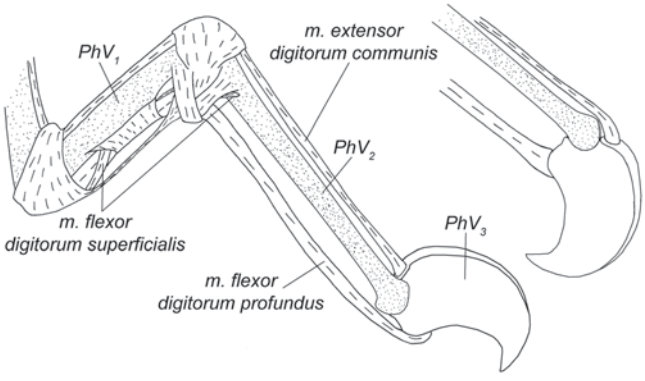


Fig. 2.9 The fifth finger of *C. volans*. Flexed and hyperextended ungual phalanx, lateral view.

Joints

In the **sternoclavicular articulation**, the sternal end of the clavicle fits into a shallow, smooth, anteriorly facing concavity formed by the *manubrium sterni* and the sternal end of the first rib (Fig. 2.10). Mobility of the sternoclavicular articulation is restricted by two wide ligaments (Fig. 2.11). The *ligamentum sternoclaviculare externum* originates from the dorsolateral surface of the base of the cranial process (*processus cranialis*[5]) of the *manubrium sterni*, which is specific to colugos, enters the articular capsule from anterior, and inserts on the articular surface of the sternal end of the clavicle. The *ligamentum sternocla-*

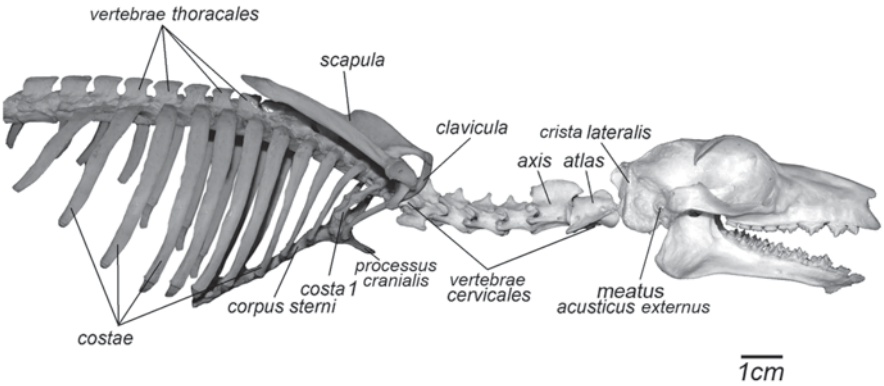


Fig. 2.10 The axial skeleton of *C. variegatus* with shoulder girdle, lateral view.

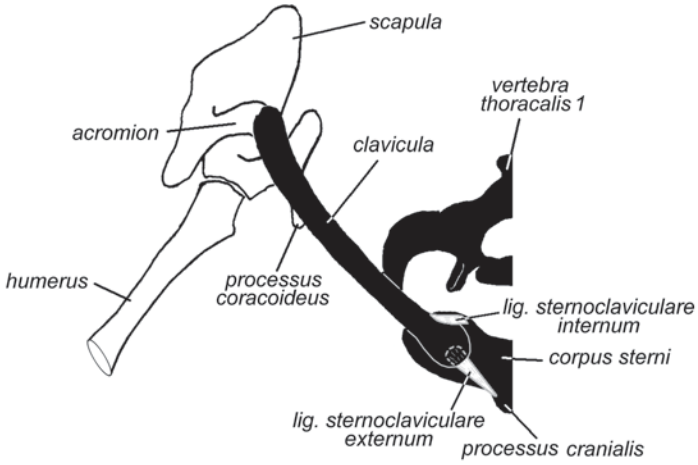


Fig. 2.11 Scheme of the sternoclavicular articulation of *C. volans,* right forelimb, anterior view.

[5] The term *processus cranialis* was never suggested before for this structure specific to colugos.

viculare internum connects the internal (dorsal) border of the anterior end of the *manubrium sterni* with the internal side of the sternal end of the clavicle. These ligaments together prevent displacement of the proximal end of the clavicle away from the sternum, but allow mobility of the clavicle within the cone with the apex at the sternoclavicular articulation.

The **acromioclavicular articulation**, like in tree shrews, lacks true cartilaginous sliding surfaces between the pointed apex of the acromion and the acromial end of the clavicle adjoining each other (Fig. 2.12). Mobility of this articulation in colugos is restricted not only by the *ligamentum acromioclaviculare*, which is very short, but also by the equally short *ligamentum coracoclaviculare*, which connects the acromial end of the clavicle with the base of the coracoid process, and by the third ligament specific to colugos (Fig. 2.13).

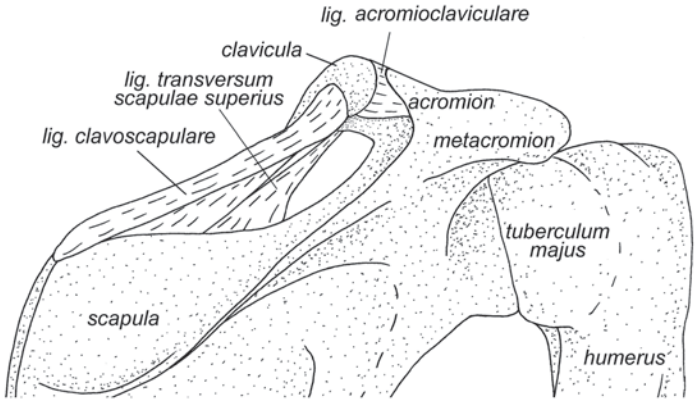


Fig. 2.12 The acromioclavicular articulation of *C. volans,* right forelimb, dorsal view.

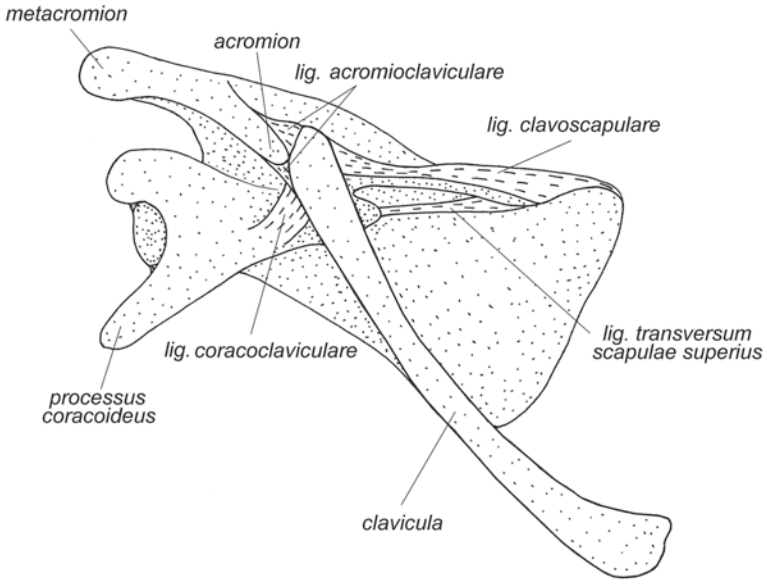


Fig. 2.13 The acromioclavicular articulation of *C. volans,* right forelimb, anterior view.

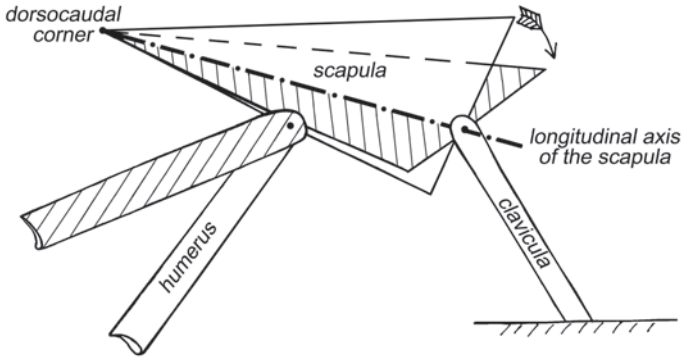


Fig. 2.14 Scheme of the scapula rotation relative to clavicle in colugo. Arrow indicates the direction of possible twist of the scapula; hatching indicates the final position of the scapula and humerus.

It is the *ligamentum clavoscapulare*, which connects the cranial border of the scapula with the dorsal surface of the acromial end of the clavicle to form an anterior extension of the supraspinous fossa supplying an additional area for the origin of the *m. supraspinatus*. The three ligaments together allow only rotation of the scapula relative to the clavicle around the axis passing through the acromioclavicular articulation and the dorsocaudal angle of the scapula (Fig. 2.14).

The articular capsule of the **shoulder joint** incorporates the distal tendons of the *m. supraspinatus*, *m. infraspinatus*, and *m. subscapularis*, as in tree shrews. The scapulohumeral ligaments are somewhat better developed than in tree shrews. The lateral ligament (*ligamentum glenohumerale laterale*) originates from the lateral border of the glenoid and inserts on the groove between the humeral head and greater tubercle (Fig. 2.15a). The medial ligament (*ligamentum glenohumerale*

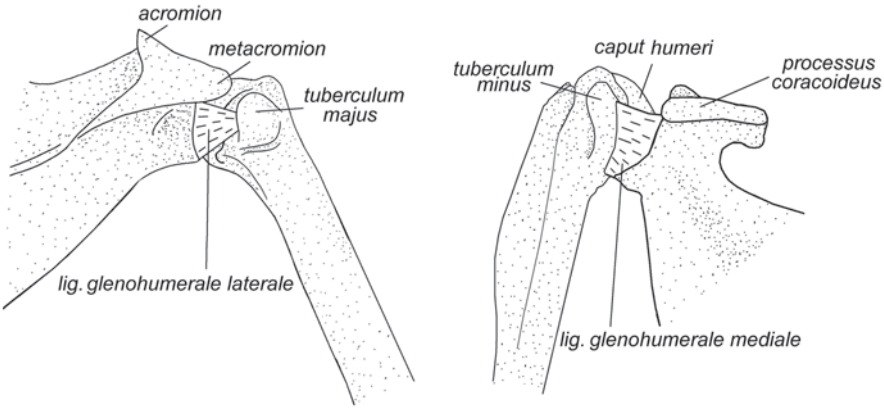


Fig. 2.15 The shoulder joint of *C. volans,* right forelimb. *a. Dorsal view b. Ventral view*

mediale) is wider and thicker and connects the medial border of the glenoid with the base of the lesser tubercle (Fig. 2.15b). The shoulder joint is highly mobile, as in tree shrews.

As usual, the **elbow joint** is formed by three bones: humerus, ulna, and radius. The detailed drawings of their articular surfaces were made by Szalay and Lucas (1993). A distinctly outlined *fovea articularis* on the head of the radius corresponds to a spherical lateral condyle of the humerus. The anterior side of the trochlear medial condyle contacts with the proximal head of the radius and other sides are embraced by a deep articular notch of the ulna. Thus, the radius "crowds out" the ulna from the anterior part of the humeral trochlea.

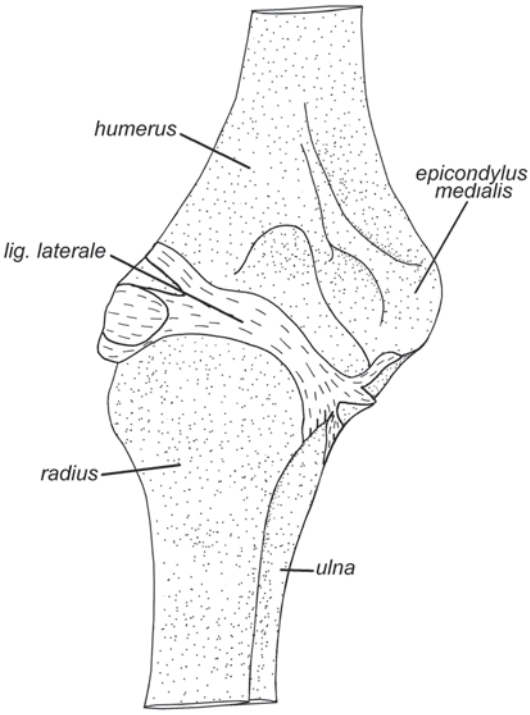


Fig. 2.16 The elbow joint of *C. volans,* right forelimb, anterior view.

A wide lateral ligament (*ligamentum laterale*) extends almost at right angles to the proximodistal axis of the limb from the lateral epicondyle of the humerus to the medial side of the proximal head of the radius (Fig. 2.16). This ligament restricts pronation in the elbow joint, but allows supination. Supination in the antebrachium is only achieved through rotation of the radius. Turning around its own longitudinal axis, it winds up the tapering distal part of the ulna on itself until it begins to prevent elastically further supination.

As mentioned above, in tree shrews, when the elbow joint is completely extended, the olecranon rests against the posterior surface of the distal end of the humerus. In colugos, the entire hook-shaped olecranon freely enters a particularly deep *fossa olecrani* on the posterior aspect of the humerus; thus, the limit of extension is reached with a more straightened elbow. In the case of the maximum flexion, the anterior border of the proximal head of the radius enters the shallow *fossa radialis* on the anterior aspect of the humerus.

The **antebrachiocarpal joint** is formed by the distal head of the radius fused laterally with a rudimentary distal end of the ulna and, on the carpal side, by the *scaphocentralolunatum* and *cuneiforme* (Fig. 2.7). The articular surface of the *scaphocentralolunatum* is rounded and freely turns in the socket formed by the distal epiphysis of the radius. Therefore, flexion and extension of the manus as well as adduction and abduction are performed mostly in this joint.

The **carpometacarpal I joint** is formed by the *trapezium* and the proximal head of metacarpal I (Fig. 2.7a). As the articular surfaces of these bones have some spherical curvature, the joint allows a greater range of flexion–extension and adduction–abduction than other carpometacarpal joints.

Mobility of the **carpometacarpal II–V joints** (Fig. 2.7) is strongly limited by ligaments and relief of articular surfaces. The articular surfaces of distal carpals and proximal heads of metacarpals are flat and rectangular in outline. Therefore, ligaments on the dorsal and palmar sides prevent flexion and extension, respectively. Adduction and abduction of these metacarpals are only possible in a range of backlash.

The **metacarpophalangeal joints** of colugos are formed by an ovate condyle at the distal end of the metacarpal, which fits into a fossa at the proximal end of the first phalanx (Fig. 2.17a). At both sides of the distal condyle of the metacarpal there are notches, which house triangular sesamoid bones. Respective projections on the palmar side of the proximal end of the phalanx rest against the distal surface of these sesamoids, restricting flexion of the joint, as in tree shrews. The articular surface of the distal condyle of the metacarpal is shaped on the palmar side as two rounded parallel crests and the groove between them, which passes into a longitudinal groove on the palmar surface of the proximal phalanx (characteristic of colugos).

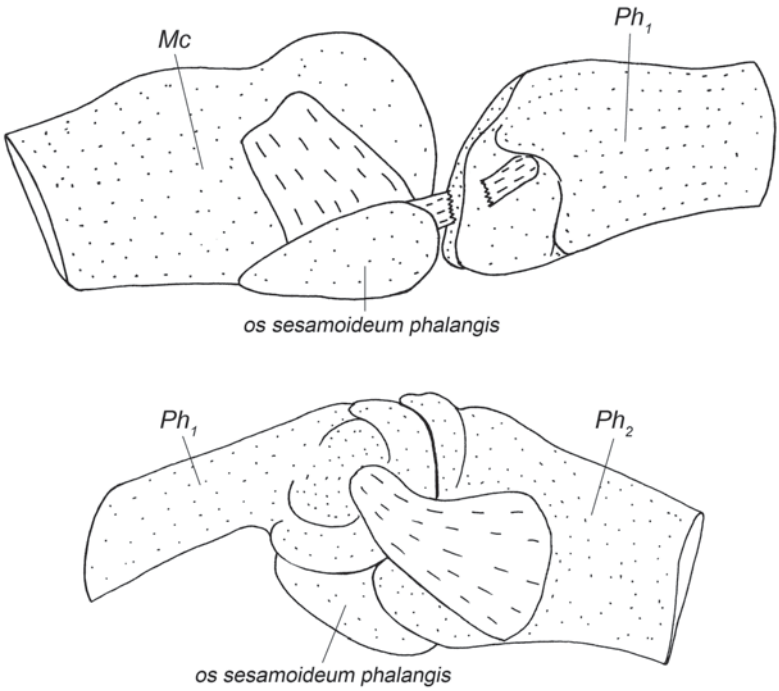


Fig. 2.17 The digital joints of *C. volans*. *a. Metacarpophalangeal joint (collateral ligament cut) b. Interphalangeal joint*

In contrast to tree shrews, the colugo has only one *ligamentum metacarpeum transversum profundum*, the one connecting the metacarpophalangeal III and IV joints (Fig. 2.52).

The **interphalangeal joints** are trochlear, as in tree shrews, (Fig. 2.17b); mobility is strictly limited to flexion–extension. In the palmar wall of the articular capsule, the proximal joints of digits II-V have one underdeveloped sesamoid bone. In the proximal interphalangeal joints, the articular surface of the distal head of the first phalanx faces distally and ventrally, but not dorsally, and hence, hyperextension is impossible. Contrary to this, in the preunguarl joints, the articular surface of the distal head of the second phalanx spreads equally onto the ventral and the dorsal sides, and so the claw is capable of flexion and hyperextension to approximately the same extent.

Musculature

The set of forelimb muscles of colugos differs considerably from that of tree shrews. They have lost *m. rhomboideus capitis, m. rhomboideus cervicis, m. levator scapulae dorsalis, m. omohyoideus, m. palmaris longus, m. pronator quadratus, m. palmaris brevis, m. opponens pollicis, m. adductor digiti quarti, m. flexor bre-*

vis manus, and *m. flexor digiti quinti superficialis*. Leche (1886) has found a few muscular fibers in the distal part of the antebrachium, which can be a rudiment of the *m. pronator quadratus*, but the claim of the presence of the *m. palmaris longus* (Leche 1886; Chapman 1902) is the result of wrong interpretation as such of the *m. flexor digitorum superficialis* which is present indeed. However, colugos possess several additional muscles as compared with tree shrews. In the limb it is the *m. flexor digitorum accessorius* (part of the *m. flexor digitorum superficialis*), and in the gliding membrane the new muscles are the *m. coracocutaneus* and *m. humerocutaneus* (probably derived from the *m. cutaneus trunci*), and some protrusions of skin musculature.

Musculature of Shoulder Girdle

Musculus sternocleidomastoideus. We could not see this muscle in colugos because this region in the available specimens was damaged. However, the cranial end of the *manubrium sterni* and the base of the clavicle preserved remains of fibers, which are probably fragments of the distal end of the *m. sternocleidomastoideus*.

In a paper devoted to the muscles of the head and neck of the Philippine colugo (*C. volans*), Diogo (2009) mentions *m. sternomastoideus* and *m. cleidomastoideus* as separate muscles. According to his study, both originate from the lateral crest of the skull and mastoid process and insert on the sternum: the *m. sternomastoideus* inserts medially, adjacent to the contralateral muscle, and the *m. cleidomastoideus* inserts more lateraly but not on the clavicle. Contrary to that, Leche (1886) describes the insertion of the *m. cleidomastoideus* on the clavicle and also notes that it is much thinner and weaker than the *m. sternomastoideus*.

Both parts of the muscle apparently contribute to lateral movements of the neck and head, as in tree shrews.

The **trapezius muscle** consists of only two parts, *m. acromiotrapezius* and *m. spinotrapezius*, while the typical third part (*m. clavotrapezius*) is absent, as in tree shrews.

Musculus acromiotrapezius (Fig. 2.18) is flat and very well developed. It originates from cervical fascia, apices of the neural spines, and interspinous ligaments from the sixth cervical through the fifth thoracic vertebrae and inserts on the acromion and adjacent two-thirds of the scapular spine by an aponeurosis shared with the *m. spinotrapezius*. The anterior border of the distal end of the muscle is almost fused with the *m. levator scapulae ventralis*.

The muscle pulls the scapula medially and, effectively using a high spine as a lever, produces a force couple with the m. serratus ventralis to pronate the scapula, that is to turn its dorsocranial part downward around the longitudinal axis passing through the acromioclavicular joint and the dorsocaudal angle (Fig. 2.14).

Musculus spinotrapezius (Fig. 2.18) originates posterior to the *m. acromiotrapezius* from apices of the neural spines and interspinous ligaments of thoracic vertebrae 6–7. It inserts on the scapular spine by an aponeurosis shared with the *m. acromiotrapezius*.

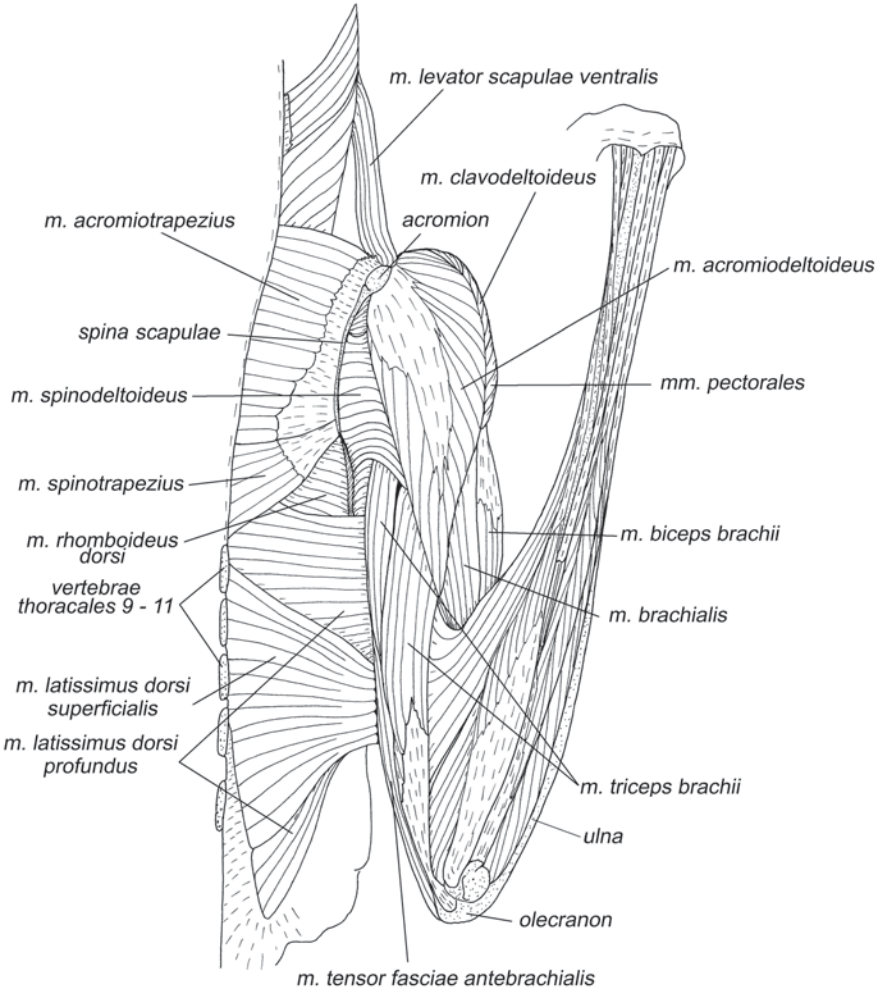


Fig. 2.18 Forelimb muscles of *C. volans,* dorsal view, layer I.

The muscle pulls the scapula caudomedially by the spine middle. As the previous muscle, it participates in pronation of the scapula and its displacement toward the midline.

Musculus rhomboideus dorsi (Figs. 2.18, 2.20, 2.21). Of three rhomboid muscles occurring in mammals, colugos have only this one, which is most posterior in the group. It originates from apices of the neural spines and interspinous ligaments of thoracic vertebrae II–VI (I–VI according to Leche) and inserts along the dorsal border of the scapula from its spine to the dorsocaudal angle. Anterior fibers insert on the superficial aponeurosis of the *m. infraspinatus*.

The muscle pulls the scapula medially and somewhat cranially.

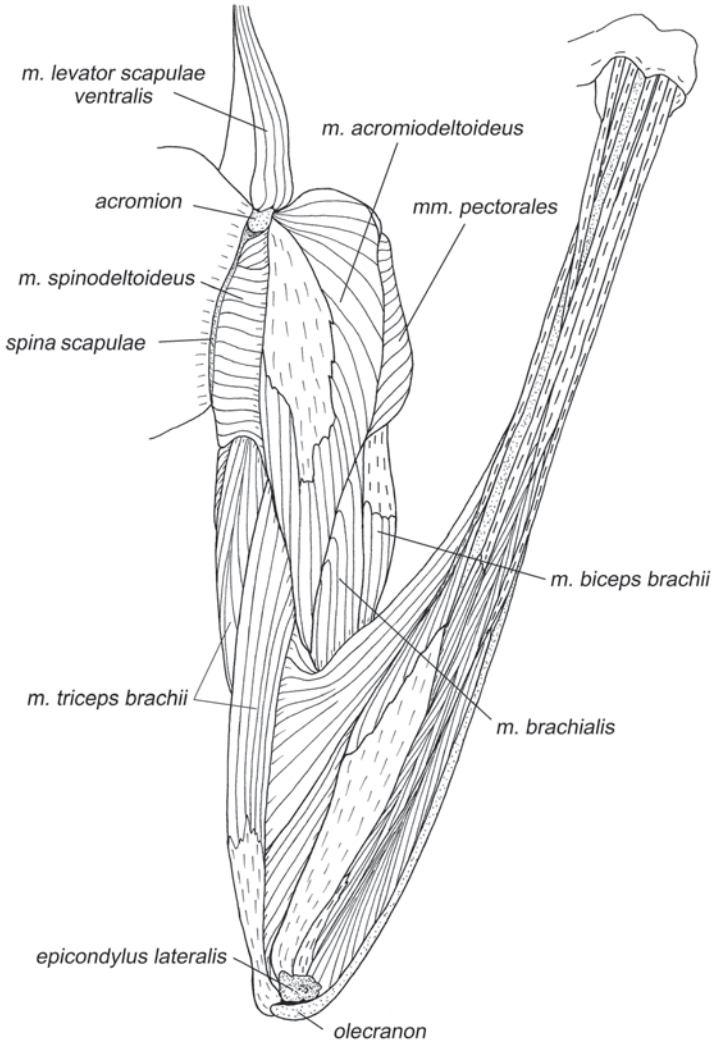


Fig. 2.19 Forelimb muscles of *C. volans,* dorsal view, layer II.

Musculus levator scapulae ventralis (Figs. 2.18, 2.19, 2.23). The colugo has only this one, ventral, levator of the scapula. This ribbon-like muscle originates from the posterior angle of the wing of the atlas and inserts on the metacromial process of the scapula.

The muscle pulls the acromial region of the scapula craniomedially. When other muscles of the shoulder girdle hold the scapula in its place, this muscle performs lateral abduction of the neck.

Musculus serratus ventralis (Figs. 2.20, 2.21, 2.23, 2.25) originates by 13 slips from cervical vertebrae and ribs.

Musculus serratus ventralis cervicis forms four slips, which originate from transverse (costal) processes of cervical vertebrae 3–6. A thin fascicle of fibers extends from the transverse process of vertebra 7 to the fourth slip; this is probably a rudimentary fifth cervical slip.

Musculus serratus ventralis thoracis includes nine slips. Narrow slips 1–3 originate from bony ribs 1–3, fleshy or by short aponeuroses. Wide slips 4–9 originate from ribs 4–8 and intercostal muscles: the fourth and fifth of them originate just from the sternal end of ribs, the sixth and seventh originate somewhat above the end, and the eighth and ninth originate from the middle part of rib 8 (at the articulation of the two rib segments).

All cervical and thoracic 1–6 slips insert mostly by aponeuroses on the medial side of the dorsal border of the scapula, the seventh inserts on the dorsocaudal angle, and eighth and ninth insert on the lateral side of the caudal border of the scapula at the dorsocaudal angle. Interestingly, the insertion of the *m. serratus ventralis thoracis* of the colugo expands from its typical position at the dorsocaudal angle both onto the caudal border (slips 8, 9) and onto the dorsal border (slips 1–6), crowding out the insertion of the *m. serratus ventralis cervicis*.

Forming a wide fan, the muscle controls position of the scapula in several directions. When all the slips contract simultaneously, they pull the scapula ventrolaterally; when only the most caudal slips contract, they pull the scapula posteriorly; contraction of the cranial slips pulls the scapula anteriorly, toward the neck (or the neck posteriorly, to the scapula); the middle slips participate in pronation of the scapula around its longitudinal axis, if they contract together with the trapezius muscle, as described above.

Musculus subclavius (Figs. 2.20–2.25, 2.30, 2.31) originates from the anterior surface of the sternal end of the first rib and inserts on the posterior surface of distal two-thirds of the clavicle. A small fascicle of fibers inserts on the medial side of the base of the coracoid process.

The muscle pulls the clavicle to the first rib.

Musculature of Shoulder Joint

Muscles Extending from Trunk

Musculus latissimus dorsi consists of two parts, the main, corresponding to the whole muscle of the majority of mammals, is the *m. latissimus dorsi profundus*, and an accessory muscle, the *m. latissimus dorsi superficialis*. Leche (1886) noticed their common innervation, but named the latter one *m. dorso-brachialis*, ascribed it to the musculature of the plagiopatagium and regarded (following Macalister 1872) as homologous to chiropteran *m. dorsi-patagialis*. However, Macalister's *m. dorsi-patagialis*, according to his description, is not the *m. dorsi-patagialis* in the modern sense, but just the *m. latissimus dorsi superficialis* which is characteristic of some bats as well as colugos.

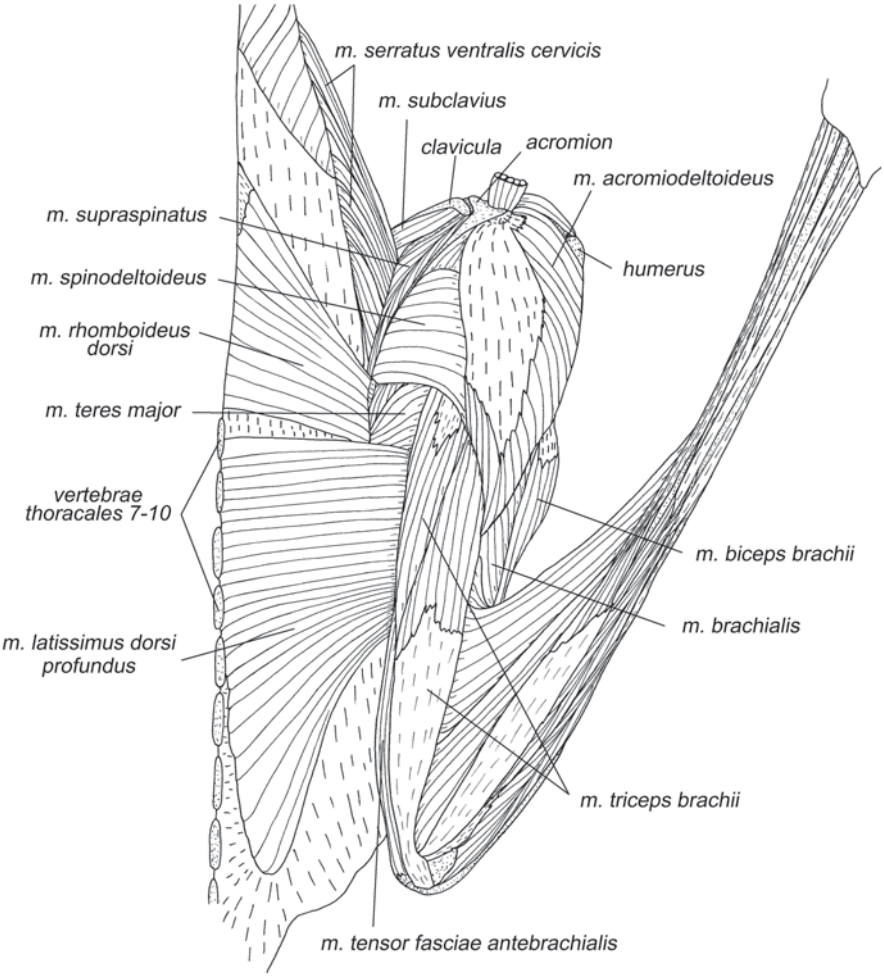


Fig. 2.20 Forelimb muscles of *C. volans,* dorsal view, layer III.

Musculus latissimus dorsi profundus (or *proprius*) (Figs. 2.18, 2.20, 2.21, 2.23–2.27, 2.31, 2.35) is rather thick and wide, similar to the single *m. latissimus dorsi* of the majority of mammals. It originates from apices of the neural spines and interspinous ligaments of thoracic vertebrae 7–11 and, more posteriorly up to the level of lumbar vertebra 2, via a dorsal fascia. Muscular fibers attach almost at right angles to a terminal aponeurosis, which inserts compactly on the medial surface of the humerus along the base of the pectoral crest.

Musculus latissimus dorsi superficialis (Figs. 2.18, 2.21, 2.25–2.27) appears to be an apomorphic feature of colugos (as well as of some bats). It originates from apices of the neural spines and interspinous ligaments of thoracic vertebrae 9–12,

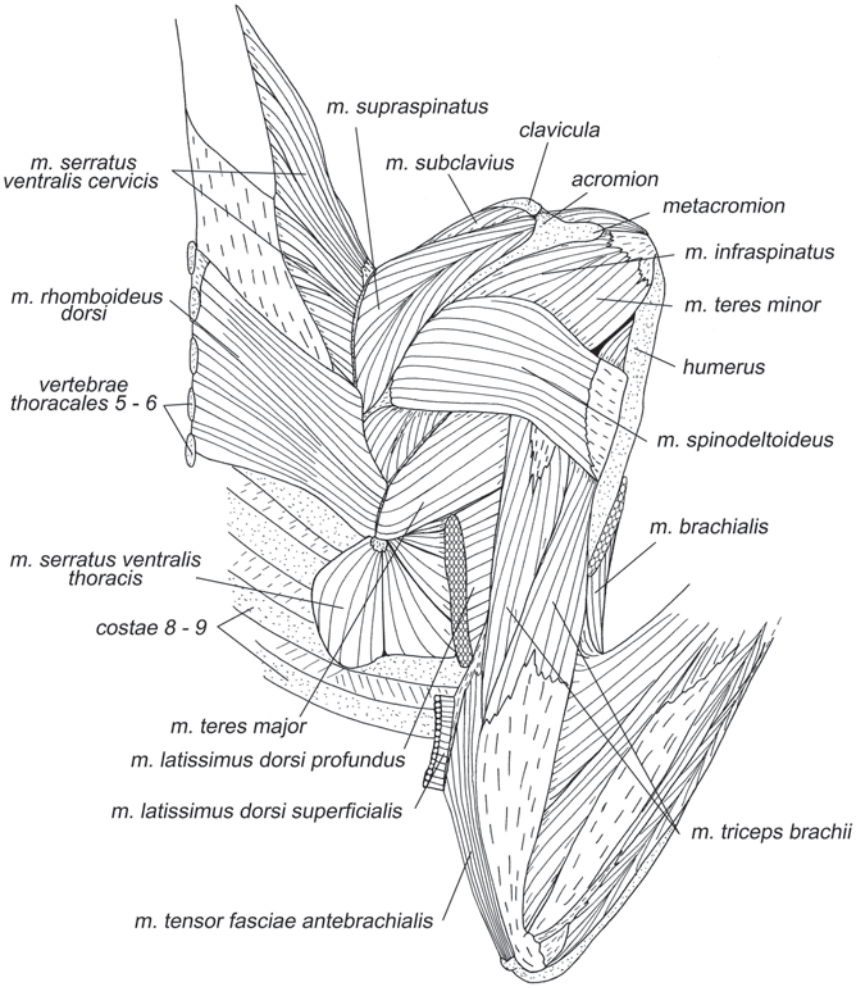


Fig. 2.21 Forelimb muscles of *C. volans,* dorsal view, layer IV.

and, via a dorsal fascia, from lumbar vertebra 1. Its fibers insert on the caudal part of the same terminal aponeurosis as the fibers of the *m. latissimus dorsi profundus*.

Both parts of the m. latissimus dorsi retract the humerus and scapula in the plane of the limb and participate in pronation of the humerus.

The **pectoral muscle** of colugos consists of three typical parts: *m. pectoralis superficialis*, *m. pectoralis profundus*, and *m. pectoralis abdominalis*.

Musculus pectoralis superficialis (Figs. 2.18, 2.19, 2.22–2.24) originates from the manubrium, cranial part of the sternal corpus, and the sternal ends of ribs 2–3; a thin fascicle of fibers originates from the ventral (external) surface of the sternal

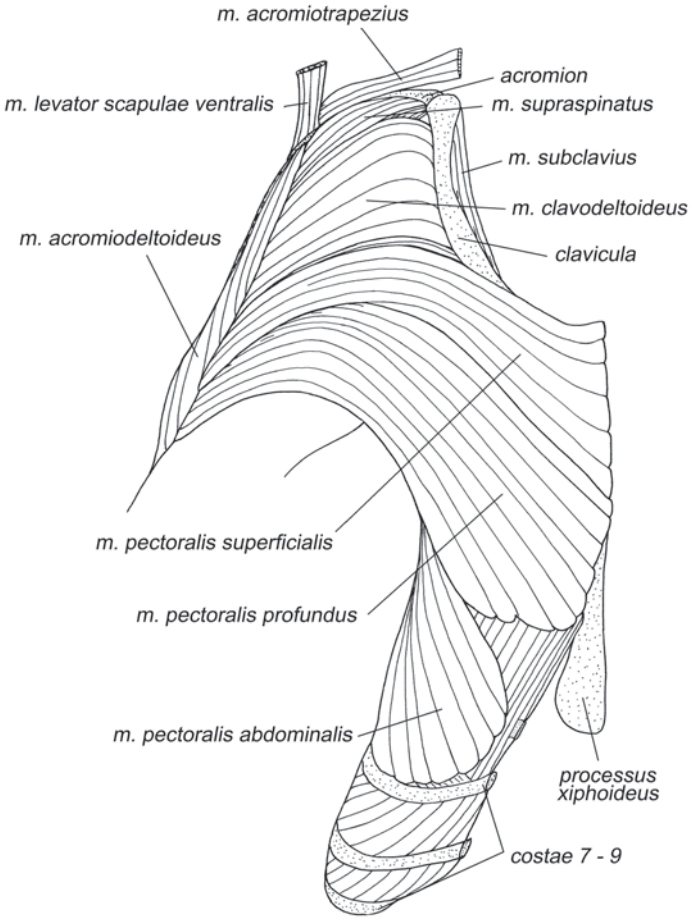


Fig. 2.22 Forelimb muscles of *C. variegatus,* ventral view, layer I.

end of the clavicle. The muscle inserts by an aponeurosis on the pectoral crest of the humerus.

The muscle pronates the humerus and adducts it, together with the scapula, from the frontal to parasagittal plane.

Musculus pectoralis profundus (Figs. 2.18, 2.19, 2.22–2.25) originates from sternal segments of ribs 2–7 and, partially, from the *corpus sterni* caudal and deep to the *m. pectoralis superficialis*. It inserts by a wide aponeurosis on the medial surface of the humerus along the base of the pectoral crest beneath the *m. pectoralis superficialis*.

The muscle more retracts and less adducts and pronates the humerus and scapula than the m. pectoralis superficialis.

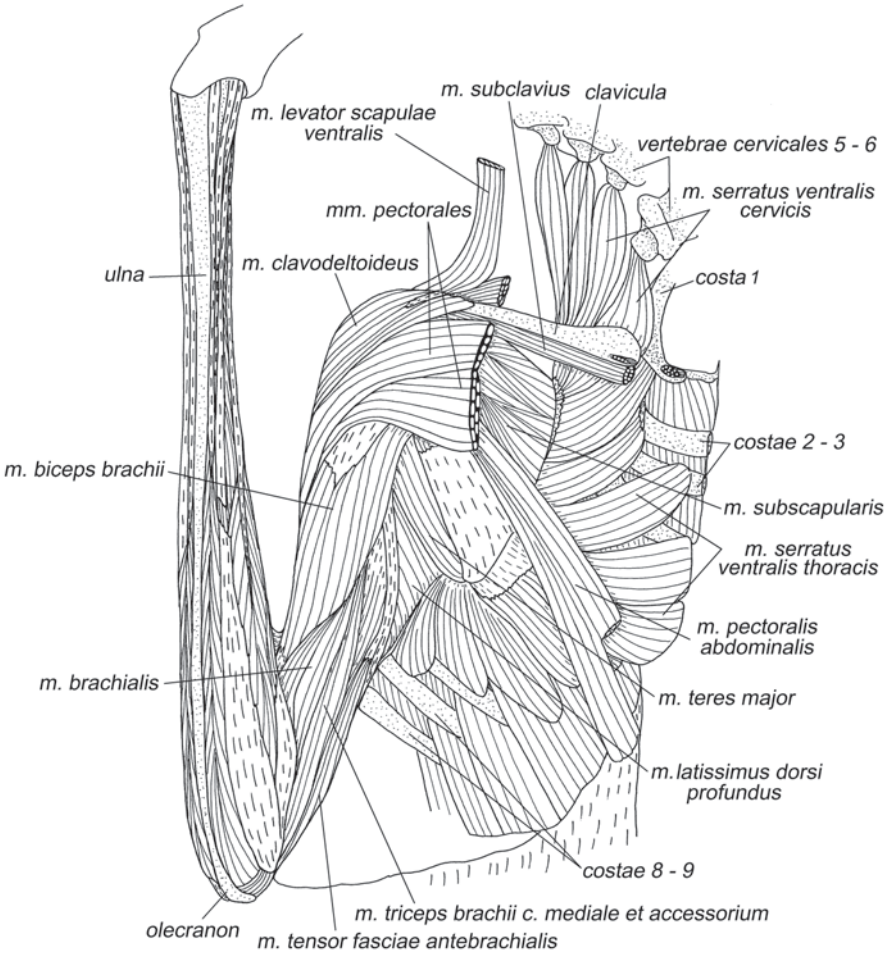


Fig. 2.23 Forelimb muscles of *C. volans,* ventral view, layer II.

Musculus pectoralis abdominalis (Figs. 2.22–2.25, 2.30) originates from sternal segments of ribs 6–7 (6–9 according to Leche) and adjacent surface of the external intercostal muscles. It inserts by a long, thin, rounded in section tendon on the tip of the coracoid process of the scapula, not on the humerus, as is usual.

This muscle acts similar to the m. pectoralis profundus, but its pull is applied to the scapula instead of the humerus.

Musculus cutaneus trunci is absent in its typical form, but the *m. coracocutaneus* and *m. humerocutaneus* in the plagiopatagium may represent its derivatives (see below).

Intrinsic Musculature of Shoulder Joint

The **deltoid muscle** consists of three typical parts: *m. clavodeltoideus*, *m. acromiodeltoideus*, and *m. spinodeltoideus*.

Musculus clavodeltoideus (Figs. 2.18, 2.22–2.24) originates from the anterior side of the distal one-third of the clavicle up to the acromioclavicular articulation. It inserts on the proximal part of the pectoral crest.

The muscle pronates and protracts the humerus and indirectly, via the shoulder joint, controls the position of the scapula relative to clavicle.

Musculus acromiodeltoideus (Figs. 2.18–2.20) is triangular, originates by a very wide superficial aponeurosis from the metacromial process of the scapula. Its fibers insert on the lateral surface of the proximal part of the humerus, including the entire pectoral crest (its lateral surface). Some fibers insert on the terminal aponeurosis of the *m. spinodeltoideus*.

The muscle supinates the humerus and abducts it from the plane of the scapula.

Musculus spinodeltoideus (Figs. 2.18–2.21) originates from the entire length of the scapular spine, except for its acromial region. It inserts by a wide aponeurosis on the lateral surface of the proximal part of the humerus.

The muscle retracts and supinates the humerus.

Musculus teres minor (Figs. 2.21, 2.26) of colugos is relatively well developed compared with tree shrews and bats; however, its cranial border is almost inseparable from the *m. infraspinatus*. It arises along the caudal border of the scapula from its middle to the origin of the *m. triceps brachii caput longum* and inserts

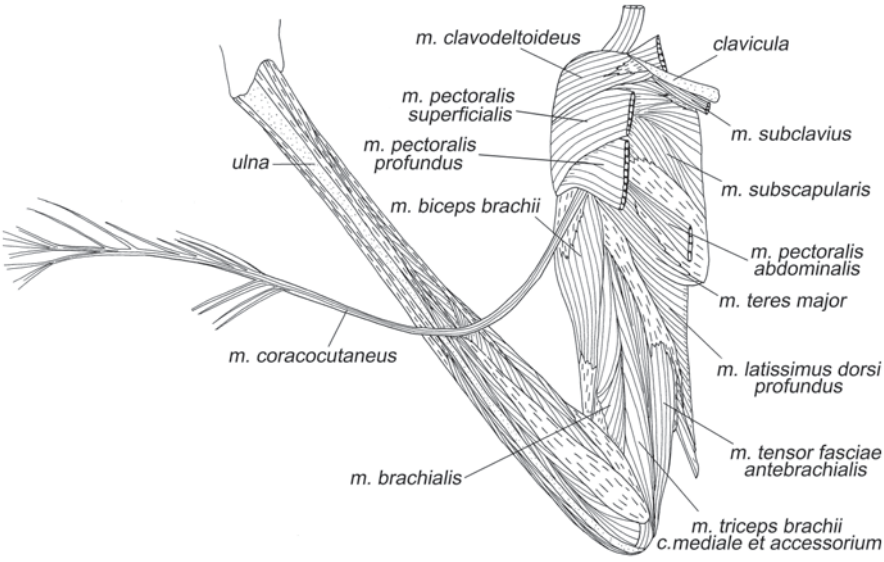


Fig. 2.24 Forelimb muscles of *C. volans,* ventral view, layer III.

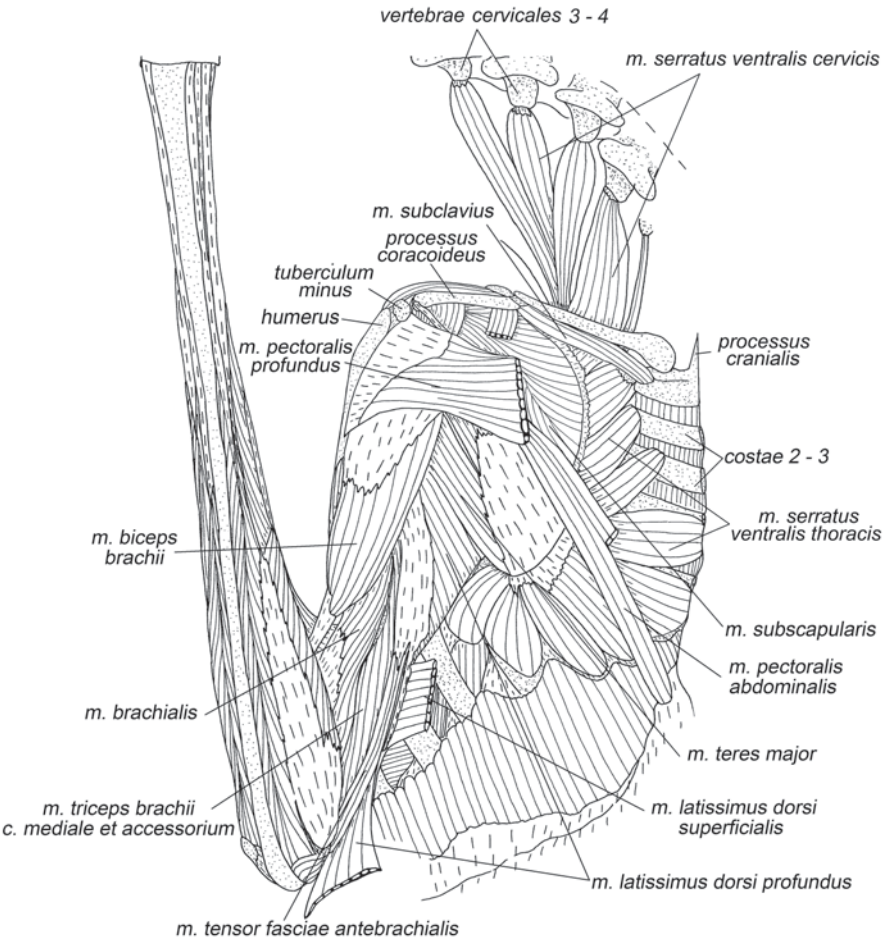


Fig. 2.25 Forelimb muscles of *C. volans,* ventral view, layer IV.

by an aponeurosis shared with the *m. infraspinatus* on the greater tubercle of the humerus.

This muscle participates in retraction and supination of the humerus. It is better developed than is usual due to an increased demand for the humeral retraction when running up tree trunks.

Musculus teres major (Figs. 2.20, 2.21, 2.23–2.36) originates from the caudal border of the scapula and lateral surface of its dorsocaudal angle, both fleshy and by aponeuroses shared with the *m. infraspinatus* and *m. subscapularis*. It inserts by a very wide aponeurosis on the medial surface of the humerus distal to the insertion of the *m. coracobrachialis profundus* and proximal to the origin of the *m. brachialis*.

The muscle retracts and pronates the humerus.

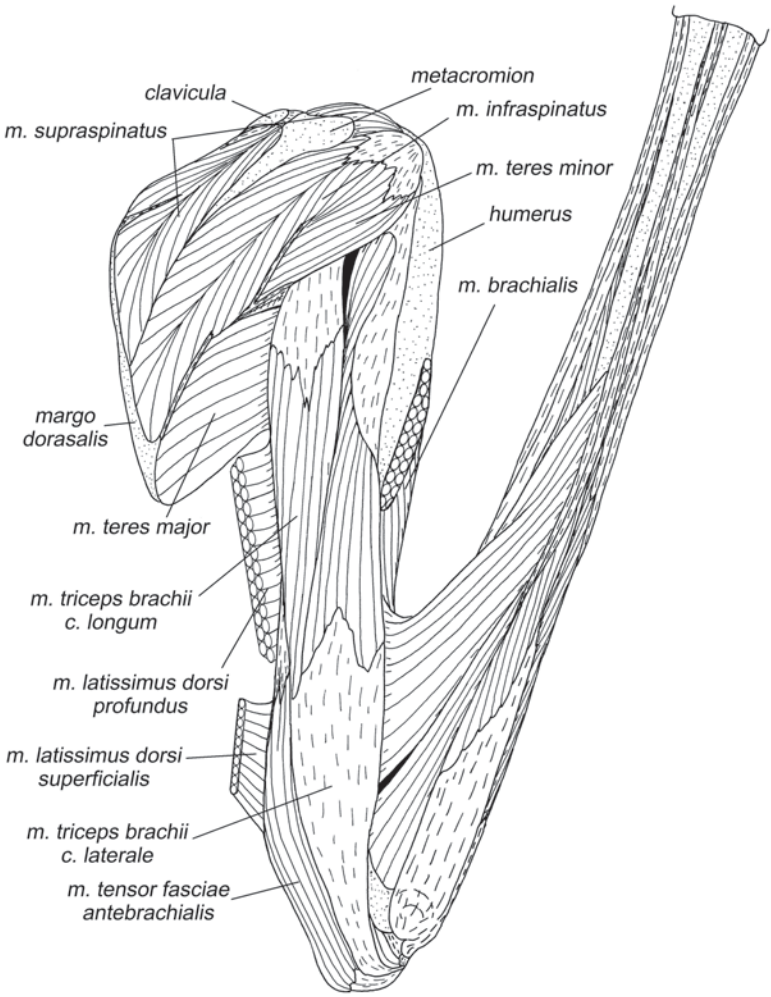


Fig. 2.26 Forelimb muscles of *C. volans,* dorsal view, layer V.

Musculus subscapularis (Figs. 2.23–2.25, 2.30–2.37) is a large muscle, which originates from the entire surface of the subscapular fossa both fleshy and by several aponeuroses. The original aponeuroses interdigitate with terminal ones to form a multipennate structure, which is immediately visible in the anterior part of the belly because the aponeuroses are perpendicular here to the surface of the scapula. In the posterior part of the belly, the aponeuroses are subparallel to the surface of the scapula and; therefore, the pennate structure can be only seen in cross-sections of the muscle. All the terminal aponeuroses converge and unite to insert on the humerus along the lesser tubercle and its crest.

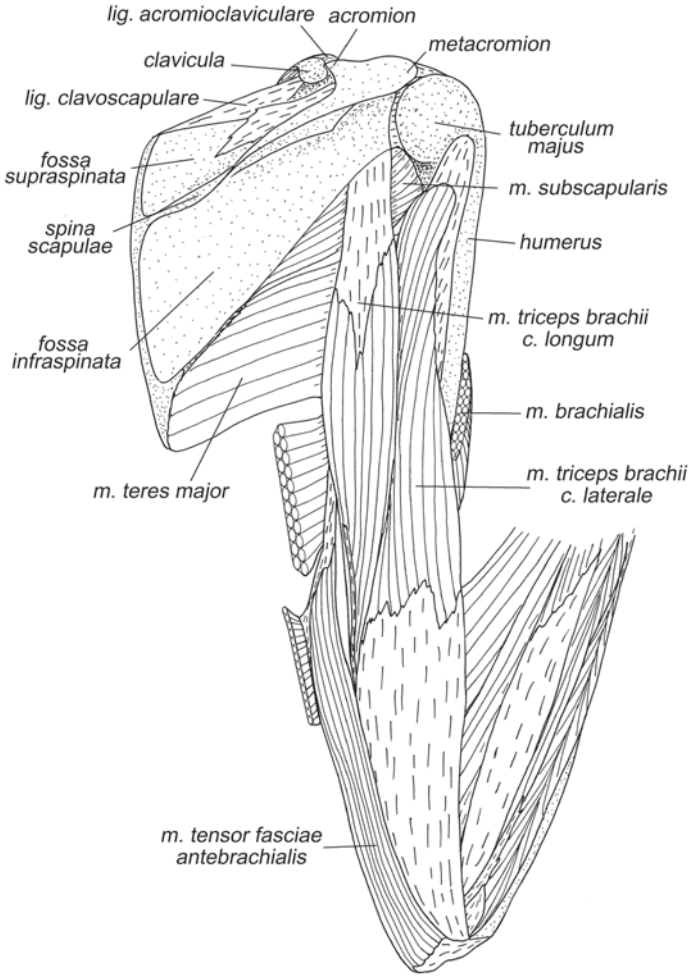


Fig. 2.27 Forelimb muscles of *C. volans,* dorsal view, layer VI.

The muscle is the main pronator of the humerus.

Musculus supraspinatus (Figs. 2.20, 2.21, 2.26, 2.31) is very well developed. It fills the entire supraspinous fossa of the scapula, as is characteristic of therian mammals. Muscular fibers originate from the entire surface of the fossa, anterior surface of the spine, internal surface of the wide *ligamentum clavoscapulare* specific of colugos, and even from the internal side of the acromion. It inserts by a well-developed system of aponeuroses on a groove between the head and greater tubercle of the humerus.

This muscle protracts the humerus, as in all other animals investigated in this study.

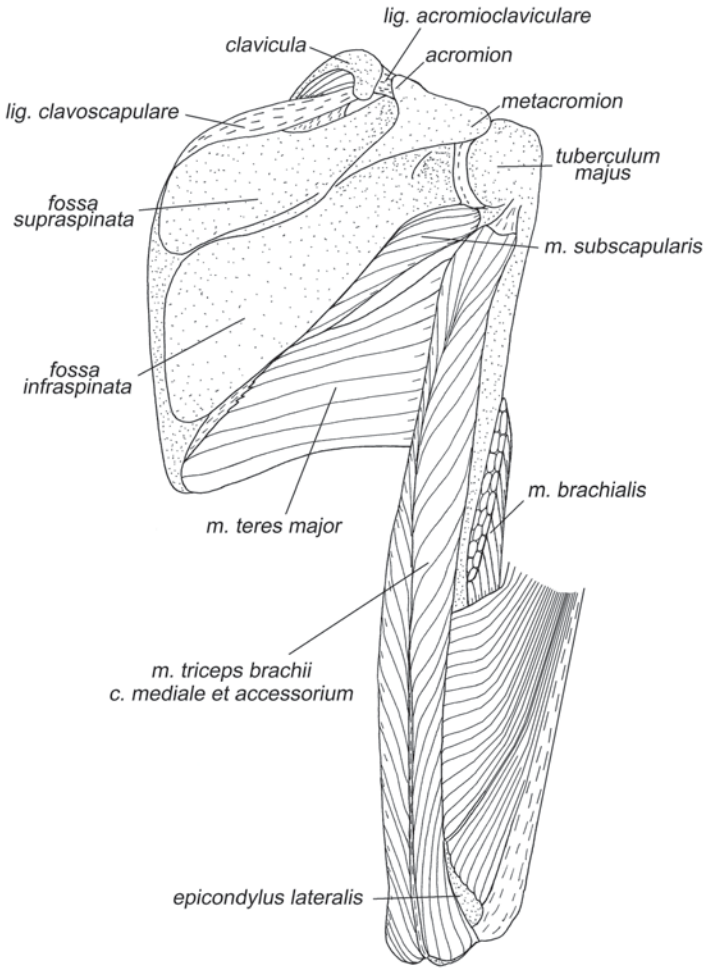


Fig. 2.28 Forelimb muscles of *C. volans,* dorsal view, layer VII.

Musculus infraspinatus (Figs. 2.21, 2.26) lies in the infraspinous fossa of the scapula, as in other mammals. However, it originates from borders rather than floor of the fossa: on the posterior surface of the spine and dorsal and caudal borders of the scapula. From the caudal border, muscular fibers arise by means of several relatively small aponeuroses, one of which is shared with the *m. teres major*. The muscle inserts on the greater tubercle of the humerus by a very strongly developed terminal aponeurosis.

This muscle supinates the humerus.

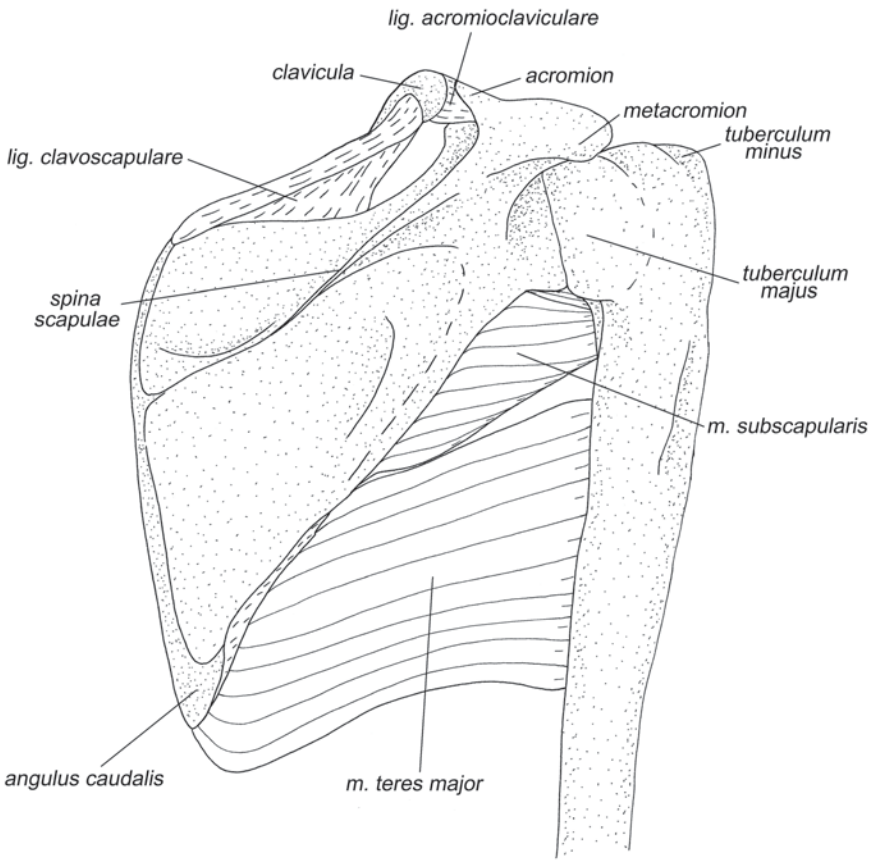


Fig. 2.29 Forelimb muscles of *C. volans,* dorsal view, layer VIII.

In addition to two **coracobrachial muscles** typical of mammals (*m. coracobrachialis brevis* and *m. coracobrachialis longus*), colugos have one more deep muscle (*m. coracobrachialis profundus*). Leche (1886) described in colugo only the two typical coracobrachial muscles, and the quality of his drawing does not allow to decide, whether the *m. coracobrachialis profundus* was absent indeed, or it was not separated from the *m. coracobrachialis brevis*, or even lost in the course of dissection. Although Howell and Straus (1931) noted the possibility of occurrence of three coracobrachial muscles in therian mammals, they apparently meant the *m. coracobrachialis brevis* and the two portions *m. coracobrachialis longus* but did not describe anything similar to *m. coracobrachialis profundus*. In *Ornithorhynchus*, Howell (1937) describes the two muscles – *m. coracobrachialis superficialis* (= *longus*) and *m. coracobrachialis profundus*, and, indeed, the description of the latter sounds similar

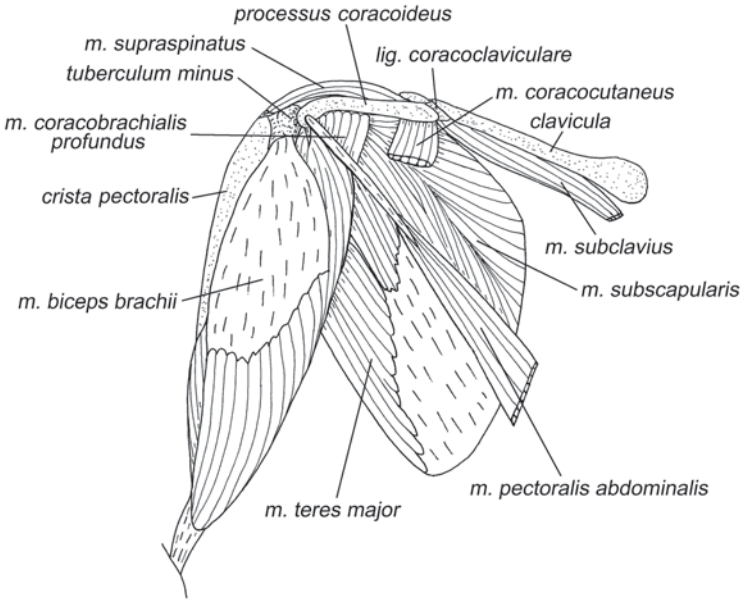


Fig. 2.30 Forelimb muscles of *C. volans,* ventral view, layer V.

to what we call so in colugos; Howell insists, by the way, that this muscle must not be regarded as homologous with the reptilian *m. subcoracoideus*.

Musculus coracobrachialis brevis (Figs. 2.33, 2.34) originates by an aponeurosis from the tip of the coracoid process of the scapula. Its fibers are very short and insert on the medial surface of the humerus along the crest of the lesser tubercle.

Musculus coracobrachialis longus (Figs. 2.33, 2.34) originates by a rather wide aponeurosis from the tip of the coracoid process of the scapula under the *m. coracobrachialis brevis* and inserts fleshy on the medial surface of the middle part of the humerus.

Musculus coracobrachialis profundus (Figs. 2.30–2.36) is apparently a relic structure in colugos. It is called so because it appears deeper than the previous two muscles when dissecting this region from the medial side; in fact, it is the lateral-most coracobrachial muscle. It originates by an aponeurosis from the tip of the coracoid process of the scapula and fleshy from its caudoventral border. The belly consists of three layers differing somewhat in the direction of fibers; the fibers of the lateral-most layer arise from the coracoid process farther away from the shoulder joint than the other two layers of this muscle and than the two previous *mm. coracobrachiales* as well. The muscle inserts fleshy on the medial surface of the humerus dorsal (posterior) to the insertion of the *m. teres major* and by a tendon on the medial surface of the terminal aponeurosis of the *m. subscapularis*.

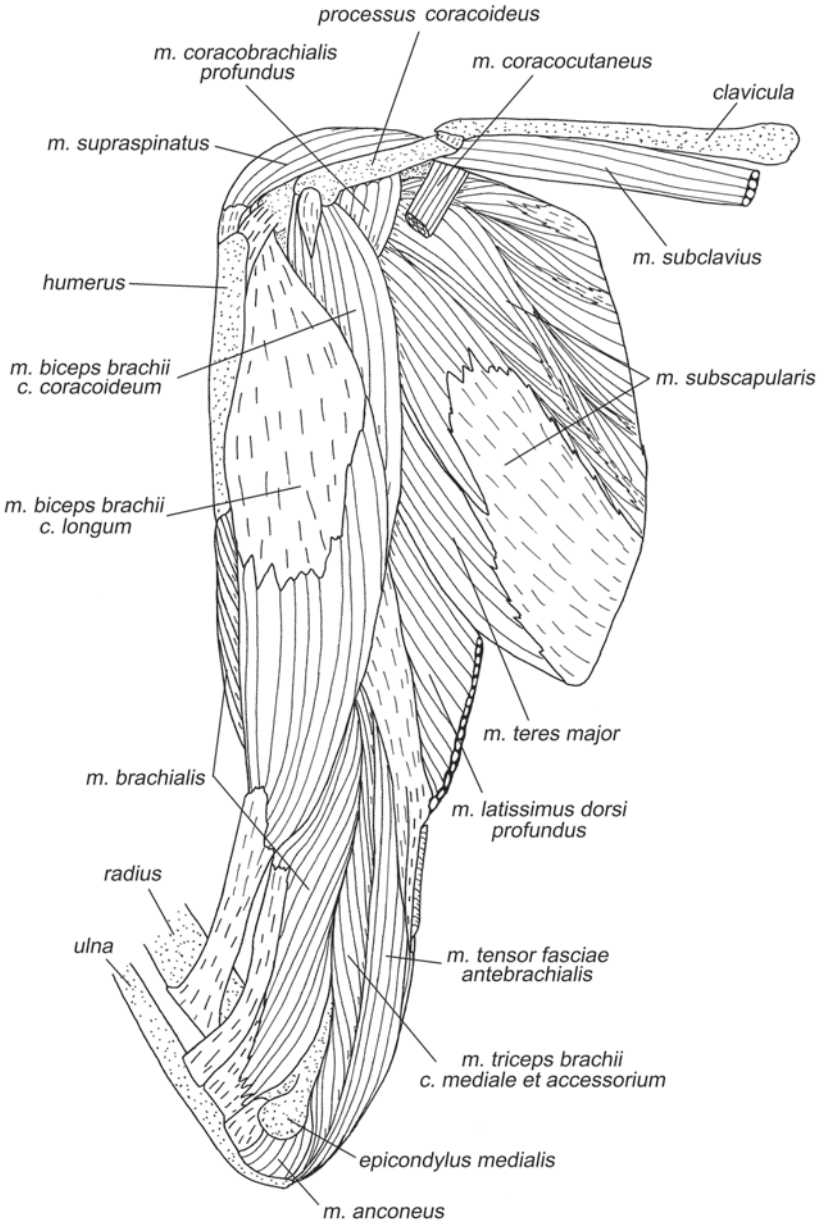


Fig. 2.31 Forelimb muscles of *C. volans,* ventral view, layer VI.

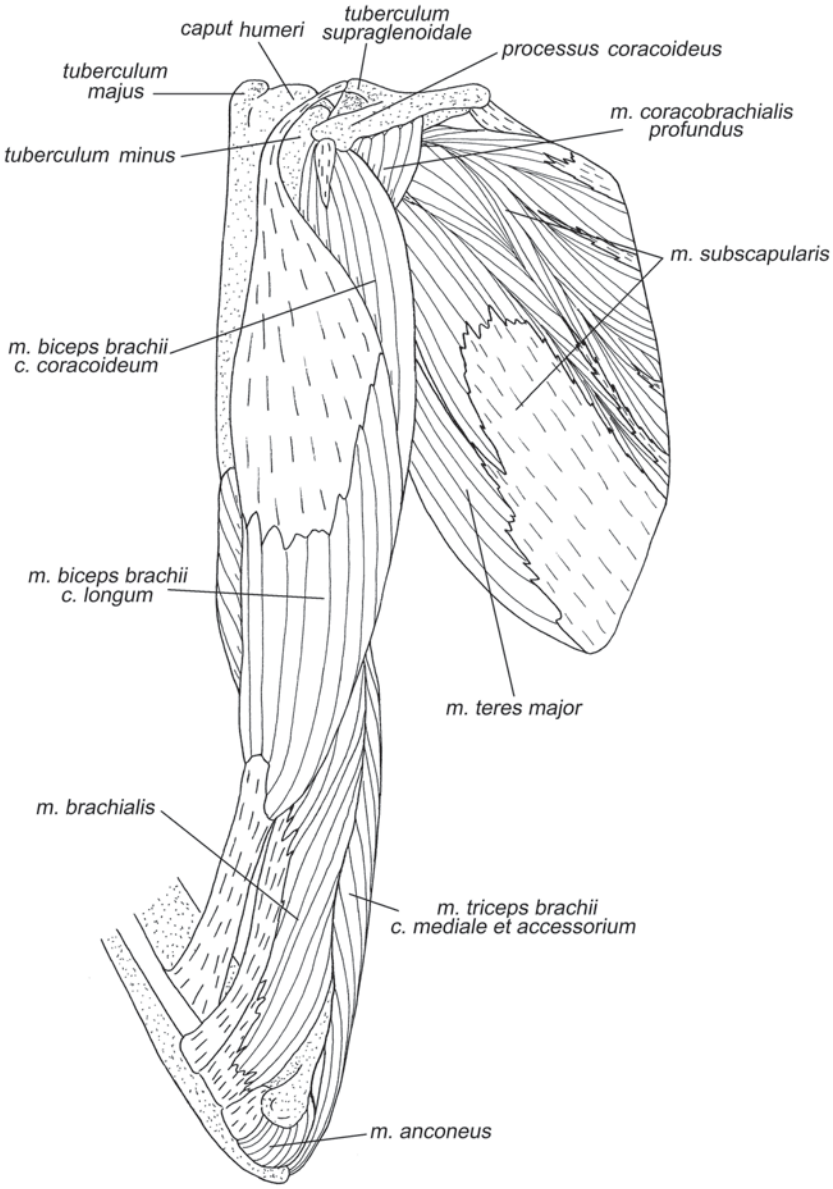


Fig. 2.32 Forelimb muscles of *C. volans,* ventral view, layer VII.

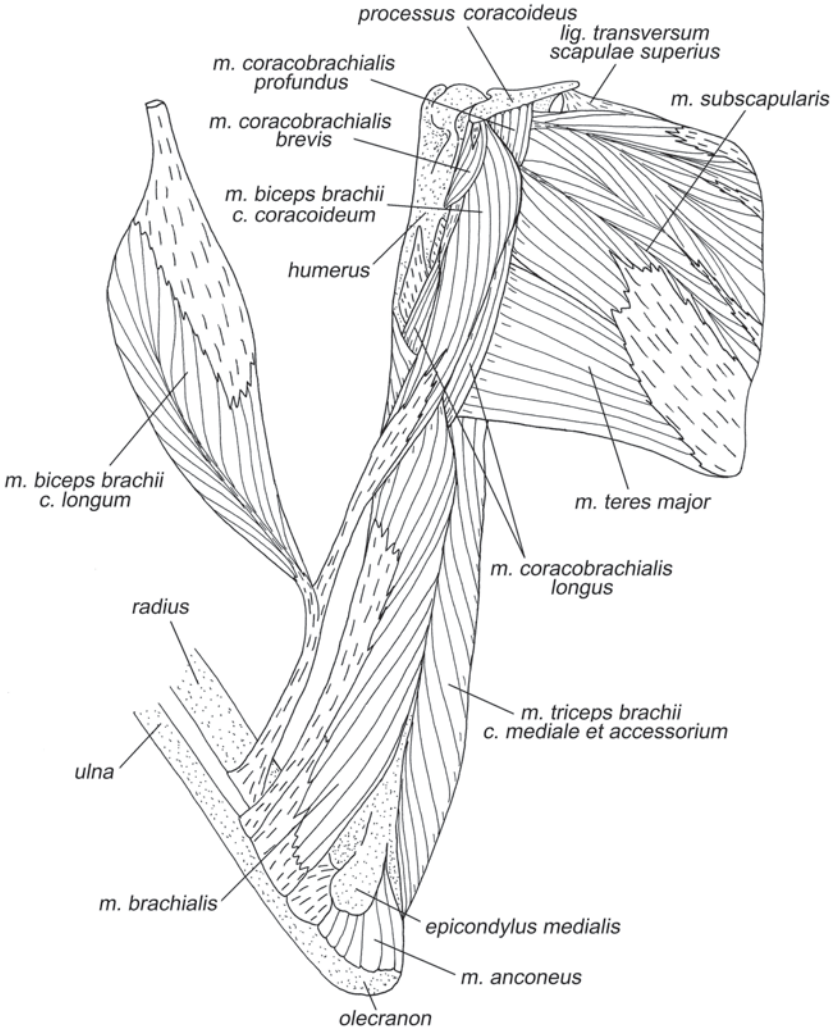


Fig. 2.33 Forelimb muscles of *C. volans,* ventral view, layer VIII.

The three mm. coracobrachiales adduct the humerus medially (ventrally, when the membrane is spread), retract and pronate it but unequally: the m coracobrachialis longus acts more as the adductor, and the m. coracobrachialis profundus acts more as the retractor.

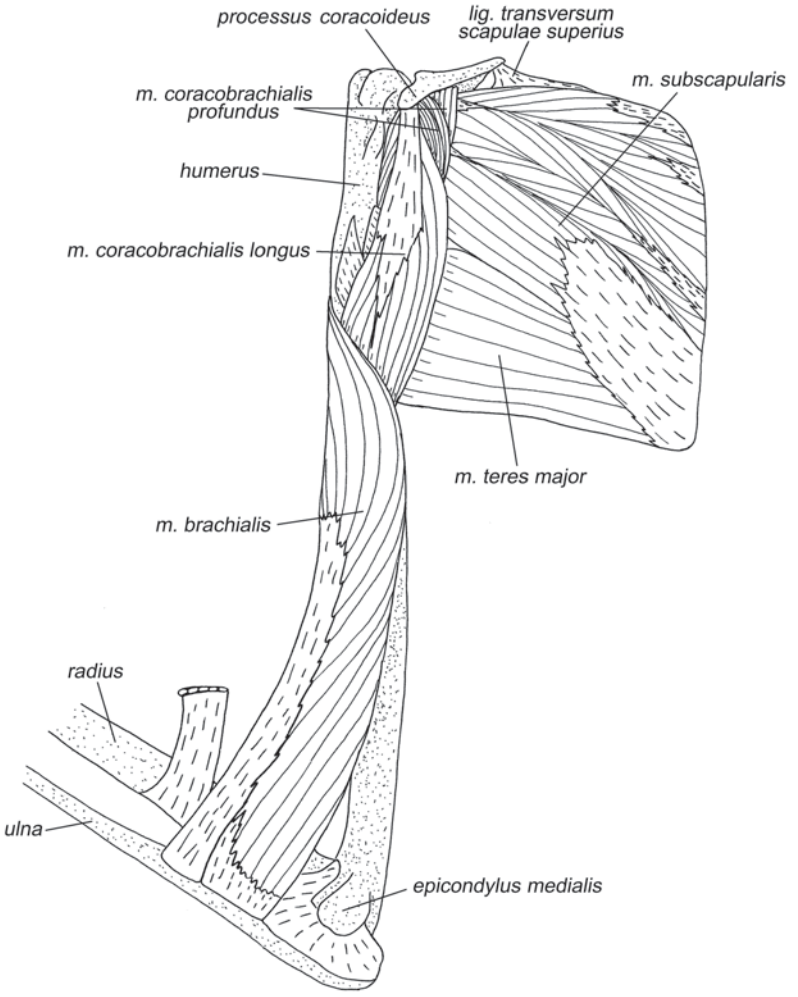


Fig. 2.34 Forelimb muscles of *C. volans,* ventral view, layer IX.

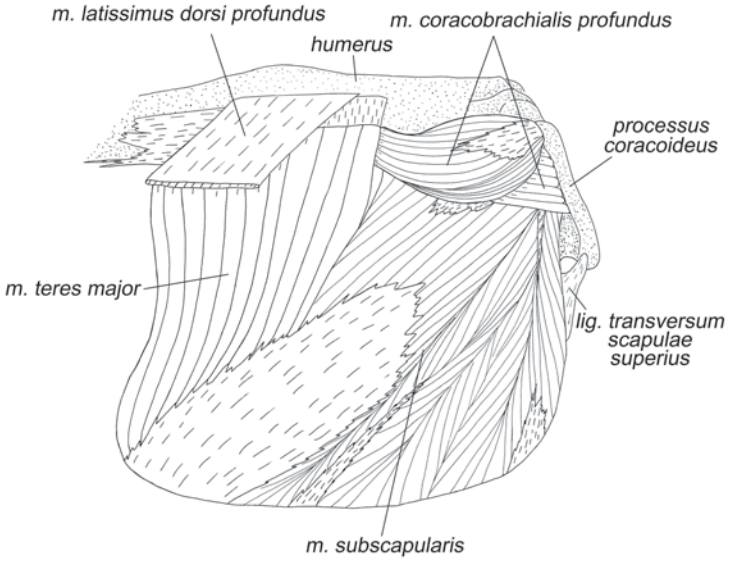


Fig. 2.35 Forelimb muscles of *C. volans,* ventral view, layer X.

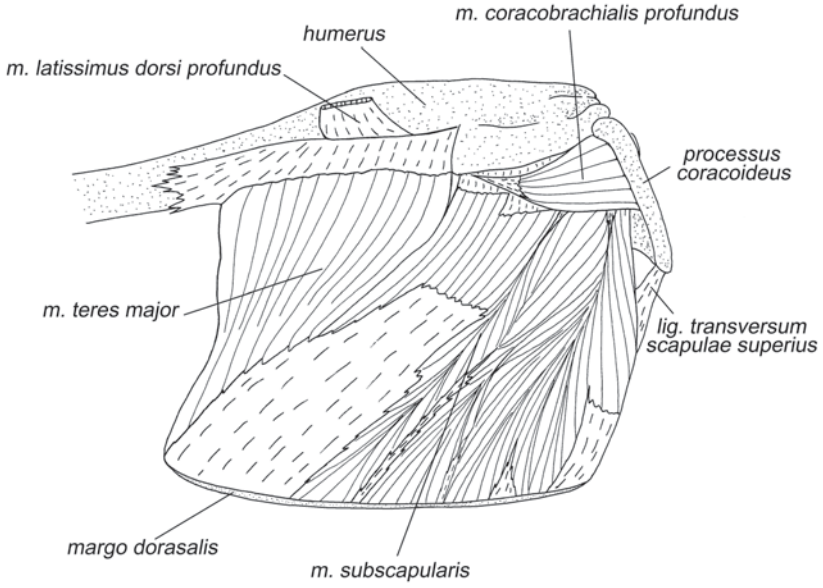


Fig. 2.36 Forelimb muscles of *C. volans,* ventral view, layer XI.

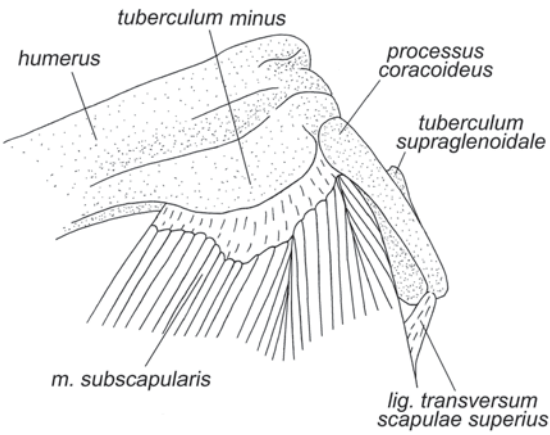


Fig. 2.37 Insertion of the *m. subscapularis* of *C. volans,* ventral view.

Musculature of Free Limb

Musculature of Humerus

Posterior Group of Muscles

Musculus tensor fasciae antebrachialis (Figs. 2.18, 2.20, 2.21, 2.23–2.27, 2.31) originates from the caudal part of the terminal aponeurosis of the *m. latissimus dorsi*, adjacent and at right angle to the ends of the fibers of the *m. latissimus dorsi superficialis* and of the posteriormost fibers of the *m. latissimus dorsi profundus*. The muscle passes over the posterior surface of the arm as a wide band and inserts on the tip of the olecranon above the triceps.

This muscle participates in extension of the elbow.

Musculus triceps brachii (Figs. 2.18–2.21, 2.24–2.28, 2.31–2.33, 2.38) of colugos includes the following heads: *caput longum*, *c. laterale*, and the union of the *c. mediale* and the *c. accessorium*. The *caput longum* originates by a wide tendon from the posterior border of the scapula close to the glenoid. Its belly is approximately half as long as the humerus. The terminal aponeurosis fuses with that of the *caput laterale* into a common tendon, which inserts on the olecranon. The *caput laterale* originates from the lateral surface of the proximal one-third of the humerus and inserts along with the previous head. The combined *caput mediale et caput accessorium* occupies the entire posterior surface and a significant part of the medial surface of the humerus. The short fibers converge on a long terminal tendon, which passes inside the belly of the muscle and inserts on the olecranon, fusing into the above-mentioned distal aponeurosis of the two other heads.

The muscle extends the elbow and its caput longum also participates in retraction of the humerus.

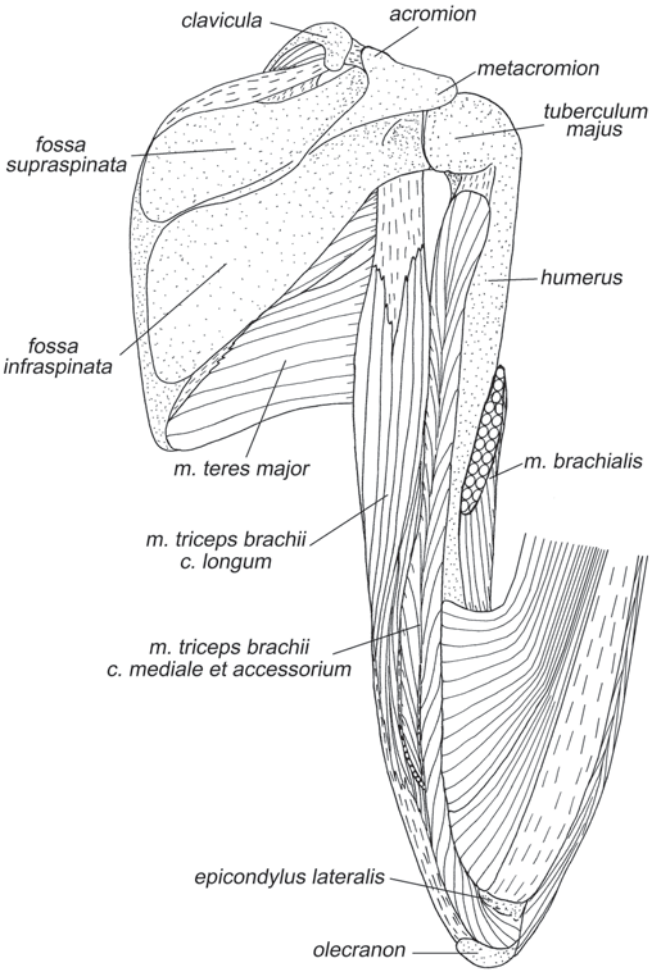


Fig. 2.38 Forelimb muscles of *C. volans,* dorsal view, layer IX.

Musculus anconeus (Figs. 2.31–2.33). The short fibers of this muscle originate from the posterior side of the crest of the medial epicondyle of the humerus and insert on the posterior and medial surfaces of the olecranon.

This muscle prevents medial adduction of the antebrachium.

Anterior Group of Muscles

Musculus biceps brachii (Figs. 2.18–2.20, 2.23–2.25, 2.30–2.33) includes two unequal heads: *caput coracoideum* and *caput longum*. The first one is considerably smaller. Its fibers arise from a significant piece of the aponeurosis of origin of the

m. coracobrachialis longus; in other words, this aponeurosis is shared by the two muscles. The terminal aponeurosis of the *caput coracoideum* fuses into that of the *caput longum* at the midlength of the humerus to insert on the ulnar side of the radius somewhat distal to the elbow joint. The *caput longum* originates from the supraglenoid tubercle of the scapula by a long thick tendon, which passes within the intertubercular groove (between the lesser tubercle and humeral head) and, then, divides into two wide aponeurotic sheets, from which the muscular fibers of this head arise in a bipennate manner. The fibers converge from two sides onto the terminal tendon which passes inside the middle of the belly and, finally, fuses with that of the *caput coracoideum* to insert as described above.

The muscle flexes the elbow and supinates the radius. The long head also participates in protraction of the humerus.

Musculus brachialis (Figs. 2.18–2.21, 2.23–2.28, 2.31–2.34, 2.39–2.41, 2.45, 2.46, 2.50) is very well developed. Its origin occupies the entire anterior surfaces of the distal part of the humerus. The muscle inserts by a wide aponeurosis on the radial side of the palmar surface of the ulna just near the elbow joint.

The muscle flexes the elbow.

Musculature of Antebrachium

Muscles of Dorsal Surface

Musculus supinator (Figs. 2.40, 2.41) is relatively small and is covered by the *m. extensor carpi radialis brevis*. It originates by a wide aponeurosis from the anterior part of the lateral epicondyle of the humerus and inserts fleshy on the radial surface of the proximal part of the radius. Its fibers are short and, hence, have a rather restricted shortening range.

The muscle apparently stabilises the elbow joint.

Musculus brachioradialis (Figs. 2.39, 2.40) is wide, ribbon-like, and very well developed. It originates by an aponeurosis from proximal two-thirds of the lateral epicondyle of the humerus above the *m. extensor carpi radialis longus* and inserts on the radial surface of the proximal part of the radius somewhat apart from the elbow joint.

The muscle flexes the elbow.

Musculus extensor carpi radialis longus (Figs. 2.39, 2.43) originates from the distal one-third of the crest of the lateral epicondyle of the humerus distal to the *m. brachioradialis*. It inserts by a long tendon, which runs along the radial side of the antebrachium, passes under the *retinaculum extensorum*, and inserts on the lateral tubercle of the dorsal surface of the proximal head of the first metacarpal (or on *trapezium*, according to Leche).

When the antebrachiocarpal joint is flexed, the muscle acts as its extensor; also, it prevents lateral abduction of the manus.

Musculus extensor carpi radialis brevis (Figs. 2.39, 2.43) has a relatively small belly. The muscle originates from the anterior side of the lateral epicondyle of the

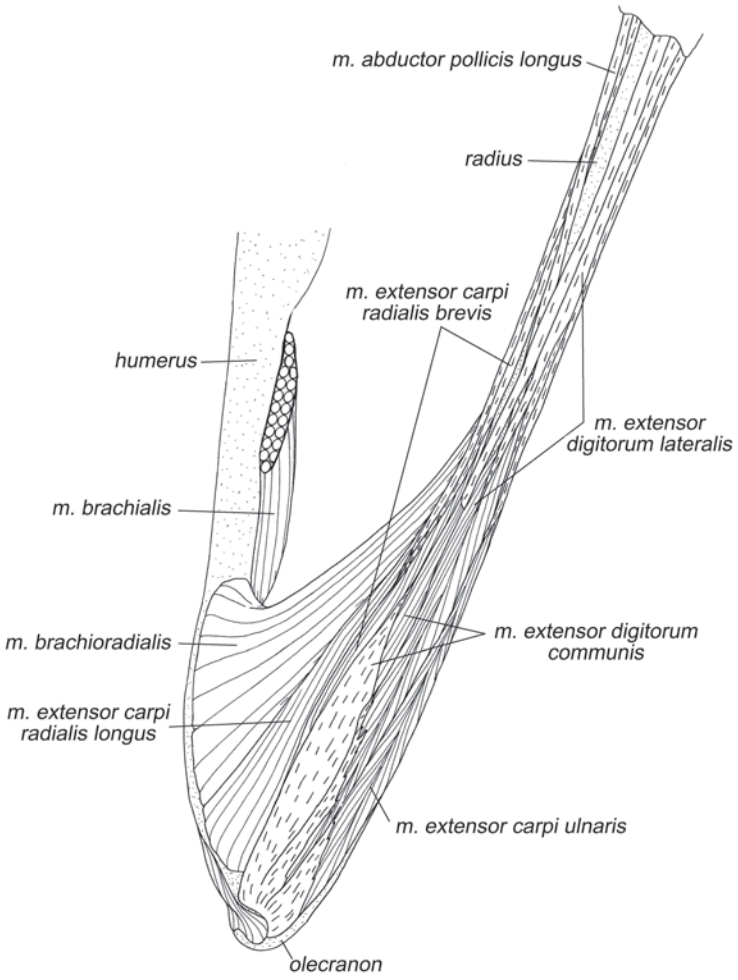


Fig. 2.39 Fore extremity muscles of *C. volans,* lateral view, layer I.

humerus by an aponeurosis shared with the *m. extensor digitorum communis*. Its fibers arise from the inner surface of this aponeurosis along its edge. A long terminal tendon runs to the manus together with that of the previous muscle, but inserts on the medial surface of metacarpal III slightly distal to its proximal head.

The muscle acts as the m. extensor carpi radialis longus, even more effectively preventing lateral abduction of the manus.

Musculus extensor digitorum communis (Figs. 2.39, 2.42, 2.51) originates from the lateral epicondyle of the humerus by a wide superficial aponeurosis supplied with additional aponeurotic sheets wedging into the belly. A long terminal tendon passes under the *retinaculum extensorum* onto the manus, expands there, and, at the level of the middle of the metacarpus, divides into four separate tendons.

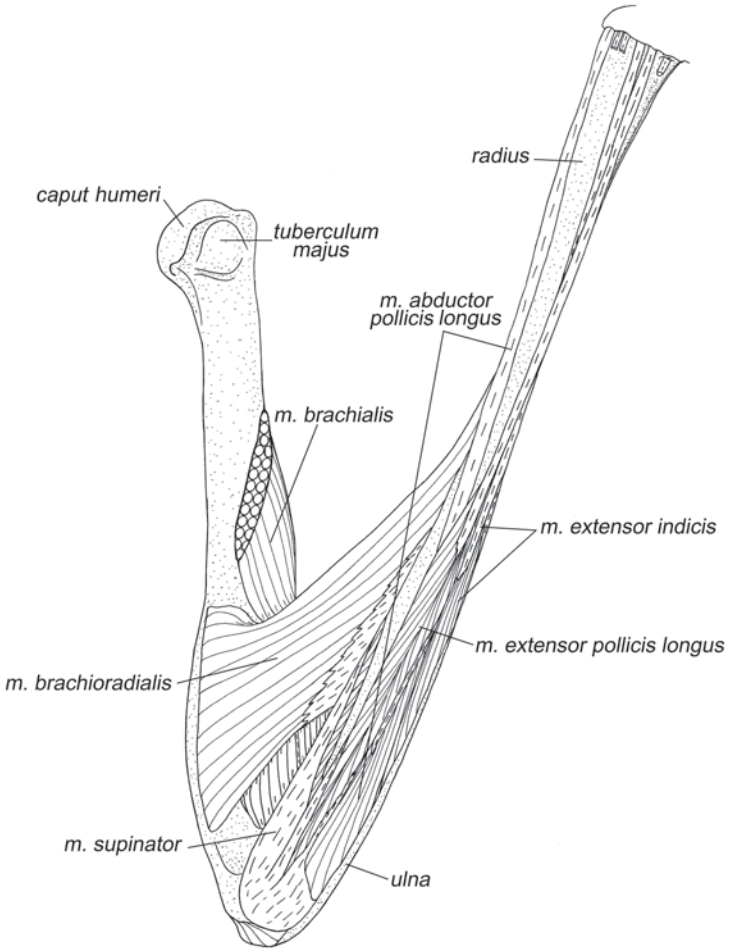


Fig. 2.40 Fore extremity muscles of *C. volans,* lateral view, layer II.

These tendons run along the dorsal surface of digits II–V, passing through articular capsules, and insert at the base of respective claws. At the proximal interphalangeal joints, thin terminal tendons of the *mm. lumbricales* squeeze from the palmar side between the digits and insert on the tendons of the *m. extensor digitorum communis*, laterally and medially in digits II–IV and only medially in digit V.

The muscle extends all joints of digits II–V and participates in extension of the antebrachiocarpal joint.

Musculus extensor digitorum lateralis (Figs. 2.39, 2.42, 2.43) originates by aponeuroses one of which is shared with the *m. extensor digitorum communis* from the lateral epicondyle of the humerus and fleshy from the dorsal surface of the proximal part of the radius. A long terminal aponeurosis passes under the *retinaculum exten-*

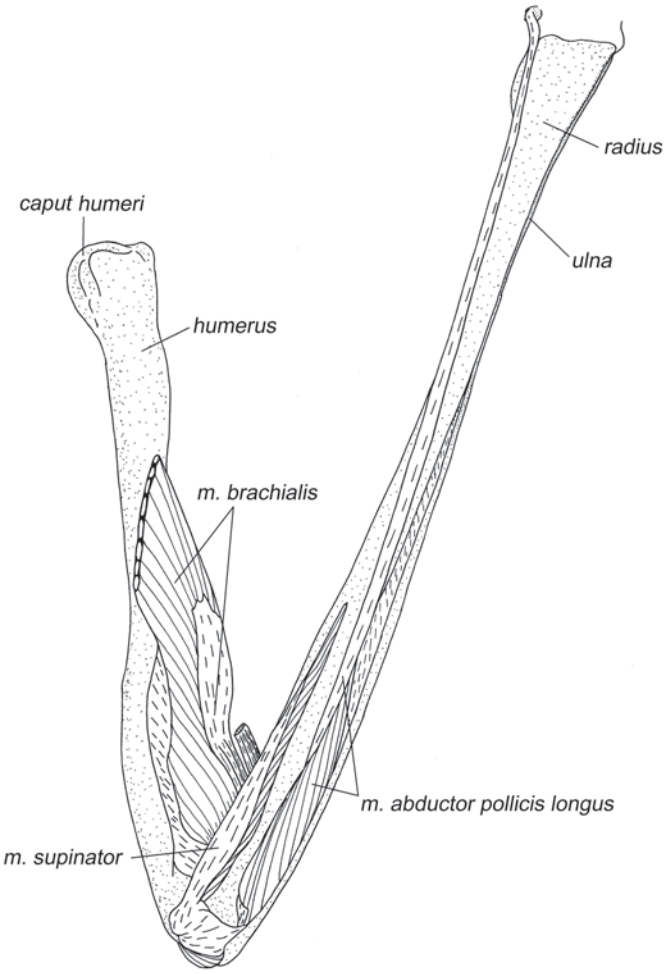


Fig. 2.41 Fore extremity muscles of *C. volans,* lateral view, layer III.

sorum, expands on the dorsal surface of the carpus, and divides into three tendons to digits III–V at the base of the metacarpus. Approximately at midlength of the metacarpus, there is a tendinous vinculum connecting the tendons of digit IV, which belong to this muscle and the *m. extensor indicis*. Then, the three terminal tendons (like those of *m. extensor indicis*) blend inseparably into the articular capsules of respective metacarpophalangeal joints but do not terminate there. Slightly distal to the metacarpophalangeal joints, the tendons of digits III and IV receive, from the medial side, tiny vinculi from the tendons of respective *mm. lumbricales*. More distally, the tendons run under those of the *m. extensor digitorum communis* along the medial side of the dorsal surface of digits III and IV and along the lateral side of the dorsal surface of digit V. At the proximal interphalangeal joints, the tendon of digit V fuses

with the terminal tendon of the *m. interosseus digiti quinti*, which runs along its opposite (medial) side of this digit. Similarly, the tendons of digits III and IV fuse with the terminal tendons of the *m. extensor indicis*, which run along the opposite (lateral) side of these digits. The insertions are on the articular capsules of the proximal interphalangeal joints. According to Leche (1886), in the fourth finger, the lateral tendon belongs to the *m. extensor digitorum lateralis* itself, not to the *m. extensor indicis*.

Because the terminal tendons are blended into the metacarpophalangeal articular capsules, which cannot be much shifted proximally, the muscle is incapable to hyperextend the metacarpophalangeal and interphalangeal joints, but it is able to extend (straighten) them from the previously flexed state. In addition, since the tendons pass medial (in digits III and IV) and lateral (in digit V) to the longitudinal axes of digits, this muscle abducts laterally digit V and displaces medially digits III and IV. The muscle also participates in extension of the antebrachiocarpal joint. The role of the muscle in the control of a multuijointed system of the manus will be considered in Chapter 6.

Musculus extensor pollicis longus (Figs. 2.40, 2.42, 2.43) originates from the proximal part of the antebrachium. Its fibers are short, arise along with the *m. extensor indicis* from the dorsal surface of the ulna and ulnar surface of the radius. The terminal tendon runs along the dorsal surface of the antebrachium and, approximately at its midlength, divides into two unequal branches, which pass under the *retinaculum extensorum* onto the manus. The thicker medial tendon runs to the ungual phalanx of digit I and inserts at its claw base. The thinner lateral tendon, at the level of the carpus, forms a vinculum with the not yet divided tendinous plate of the *m. extensor indicis* and, then, inserts on the medial side of the articular capsule of the metacarpophalangeal I joint. Both tendons are held at the dorsal side of metacarpal I by a ligamentous loop, which is placed somewhat proximal to the metacarpophalangeal joint. Leche (1886) found exactly the same pattern of the terminal tendons, but regarded the more proximal branch of the two as the *m. extensor pollicis brevis*. We cannot agree with such definition because the true *m. extensor pollicis brevis* (which is very rare in mammals as was mentioned in our description of the tree shrews) is associated with the *m. abductor pollicis longus* rather than with the *m. extensor indicis*, to which *m. extensor pollicis longus* adheres.

The thicker medial tendon is used to extend all joints of digit I and manus. The lateral tendon is used to abduct medially digit I.

Musculus abductor pollicis longus (Fig. 2.40, 2.41, 2.44, 2.53–2.57) originates from the dorsal surface of the proximal one-third of the ulna and from the adjacent interosseous membrane of the antebrachium. A relatively small fascicle of fibers originates by an aponeurosis from the ulnar side of the proximal head of the radius. At the end of the proximal one-third of the antebrachium, the belly of the muscle gives the terminal tendon, which, in the middle of the antebrachium, passes from the dorsal onto radial side. In the carpal area, the tendon bifurcates; the first branch inserts on the prepollex and cartilaginous plate of proximal radial callosity[6] and the second inserts on the medial surface of the proximal head of the first metacarpal.

The muscle abducts medially metacarpal I and manus as a whole.

[6] The palmar surface of the carpus and metacarpus of colugos bears a dense tough hairless pad. It includes several callosities, which are not supplied with muscles. Under the proximal radial callosity, there is a cartilaginous plate connected with the prepollex.

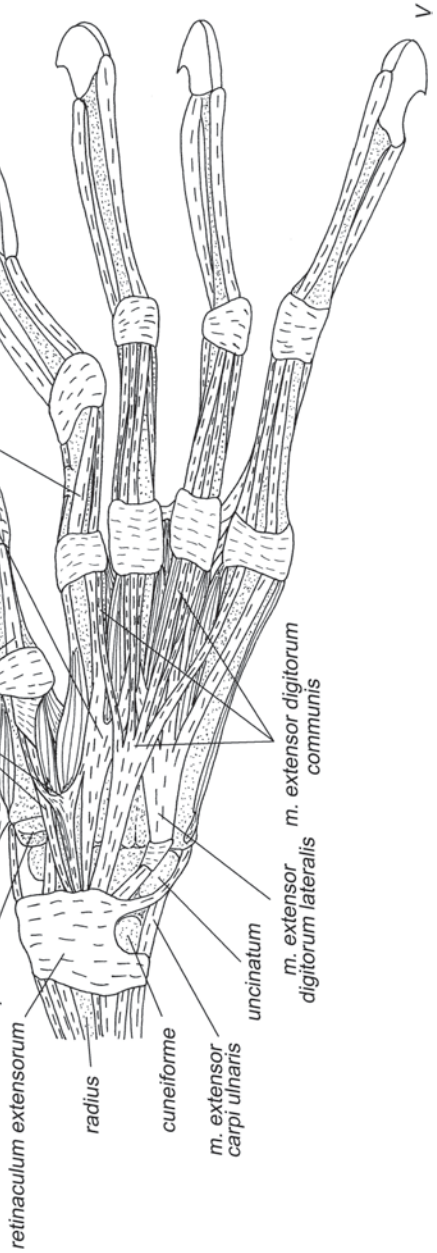


Fig. 2.42 Muscles of the manus of *C. volans*, dorsal view, layer I.

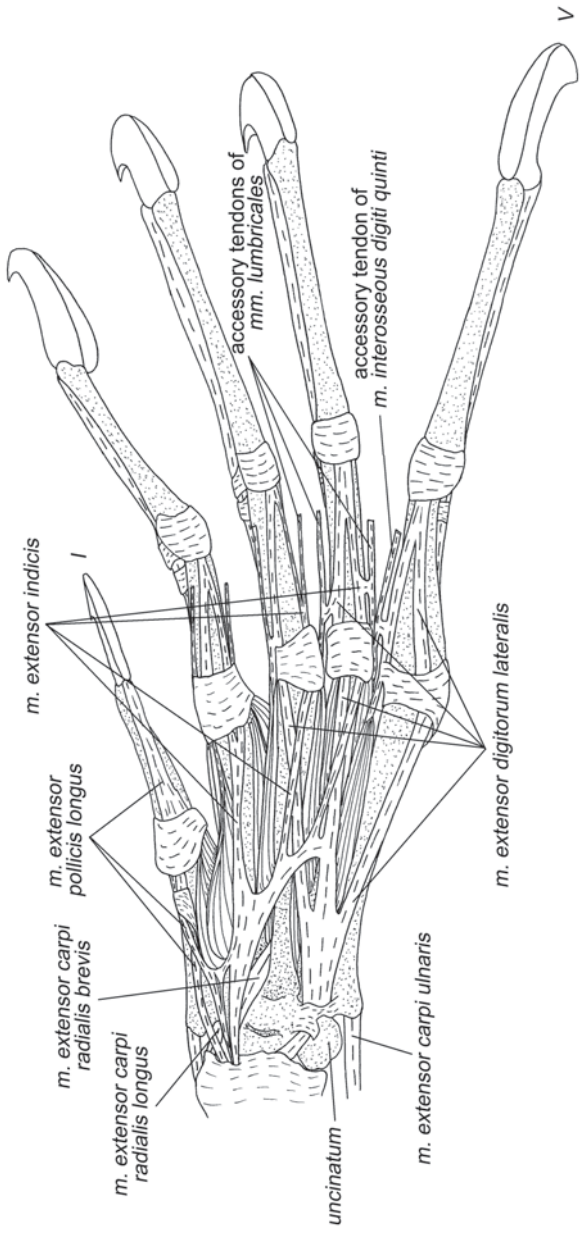


Fig. 2.43 Muscles of the manus of *C. volans,* dorsal view, layer II.

Musculus extensor indicis (Fig. 2.40, 2.42, 2.43) originates from the dorsal side of the ulna together with the *m. extensor pollicis longus*. The terminal tendon also parallels those of the *m. extensor pollicis longus*, passing onto the manus under the *retinaculum extensorum*. At the level of the proximal part of the metacarpus, the tendon expands into a plate, which gives terminal branch to digit II, then, to digit III and IV, the latter being connected by vinculum with respective tendon of the *m. extensor digitorum lateralis*. Before the metacarpophalangeal joints, the tendon of digit II additionally bifurcates into the medial and lateral bands, while two other tendons traverse onto the lateral side of digits III and IV over respective tendons of the *m. extensor digitorum lateralis* (which, on the contrary, pass onto the medial side of the same digits). All the terminal tendons are tightly fused with the articular capsules of respective metacarpophalangeal joints. Slightly distal to these joints, the tendons of the *m. extensor indicis* receive, from the lateral side, tiny vinculi from the tendons of respective *mm. lumbricales*, and the medial band of the tendon of digit II receives similar vinculum from the medial side. Over the proximal phalanx, just before insertion on the articular capsule of the proximal interphalangeal joint, the lateral and medial tendinous bands of digit II fuse together, and the tendons of digits III and IV similarly fuse with respective tendons of the *m. extensor digitorum lateralis*. According to Leche (1886), the muscle has only two terminal tendons, those of digits II and III, while the digit IV is exclusively supplied by the *m. extensor digitorum lateralis*.

Like the m. extensor digitorum lateralis, this muscle straightens metacarpophalangeal and proximal interphalangeal joints from the previously flexed state, but cannot hyperextend them. Since the tendons of digits III and IV are attached to the lateral side of respective articular capsules, they act asymmetrically; as a result, a slight lateral abduction of digits III and IV is produced. Also, the muscle participates in extension of the antebrachiocarpal joint and the manus as a whole.

Musculus extensor carpi ulnaris (Fig. 2.39) originates fleshy from the dorsal surface of the proximal part of the ulna, by an aponeurosis from the dorsal surface head of the radius, and from the lateral epicondyle of the humerus by an aponeurosis shared with the *m. extensor digitorum lateralis*. A long and thin terminal tendon passes onto the manus under the lateral part of the *retinaculum extensorum* and inserts on the lateral side of the proximal head of metacarpal V.

The muscle abducts laterally the manus.

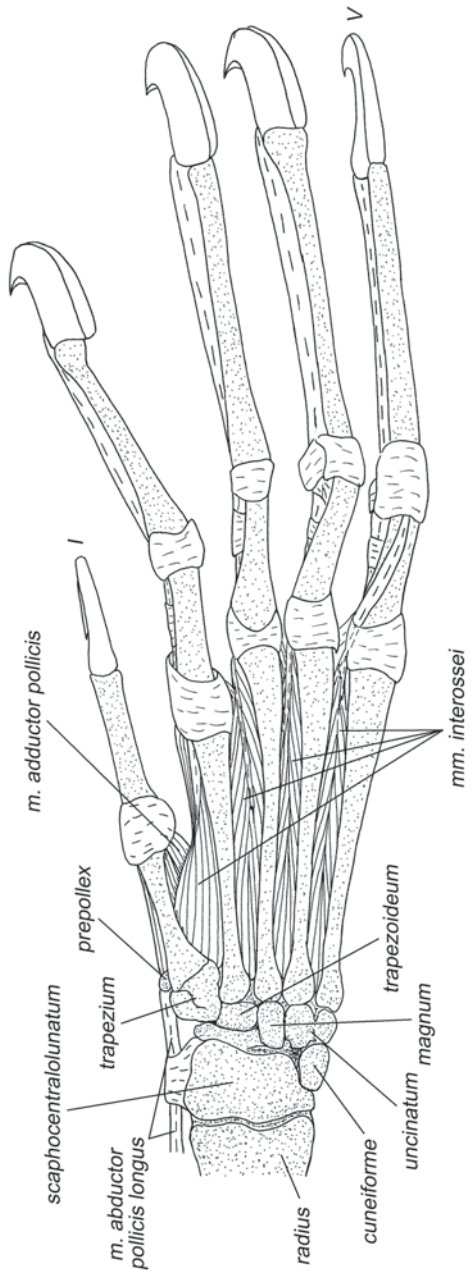


Fig. 2.44 Muscles of the manus of *C. volans,* dorsal view, layer III.

Muscles of Palmar Surface

Musculus pronator teres (Fig. 2.50) is better developed than the supinator. It originates by a wide aponeurosis from the medial epicondyle of the humerus. The muscle has short fibers, which insert on the radial surface of the proximal one-fourth of the radius distal to the insertion of the *m. biceps brachii*.

The muscle participates in flexion of the elbow and pronates the antebrachium from a supinated state.

Musculus flexor carpi radialis (Figs. 2.45, 2.46, 2.48, 2.50, 2.57) is the most radially placed muscle of the palmar side of the antebrachium. Its short fibers origi-

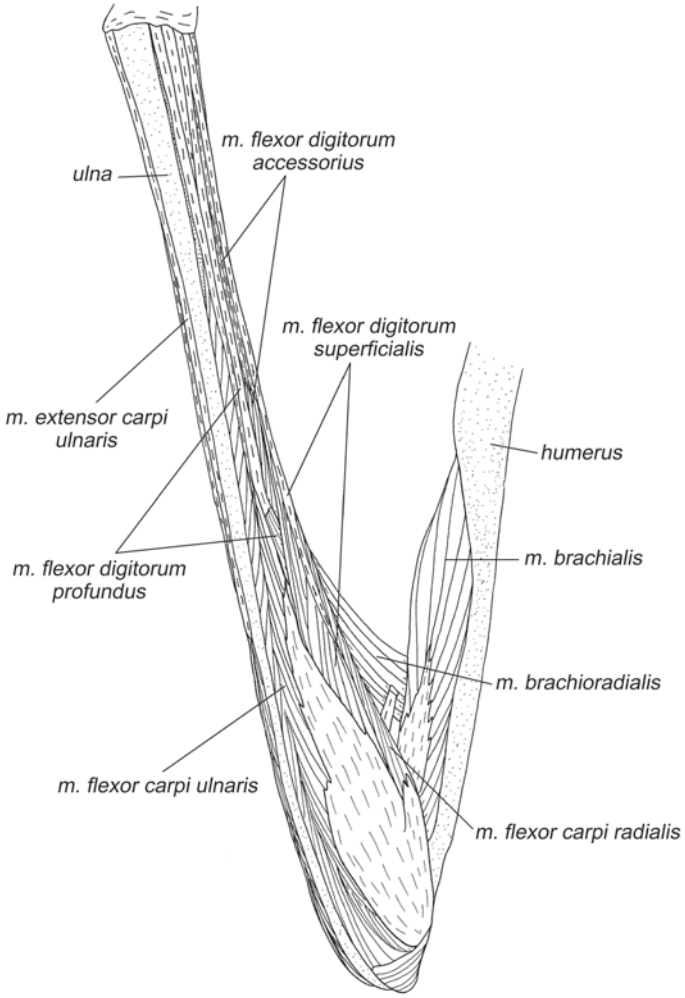


Fig. 2.45 Fore extremity muscles of *C. volans,* medial view, layer I.

nate from the superficial aponeurosis of origin of the *m. pronator teres*. The terminal tendon passes onto the manus under the *retinaculum flexorum profundum* in a separate tunnel and inserts on the medial part of the palmar surface of the base of the second metacarpal, and by a minor branch on the ventral surface of the *trapezium*. Leche (1886) noticed the second insertion only.

The muscle flexes the antebrachiocarpal joint.

Musculus flexor digitorum superficialis (Fig. 2.45, 2.51, 2.52) occupies the palmar side of the proximal part of the antebrachium. Its fibers originate from superficial aponeuroses of origin of underlying muscles, mostly the *m. flexor digitorum profundus*. The terminal tendon runs along the radial side of the antebrachium and

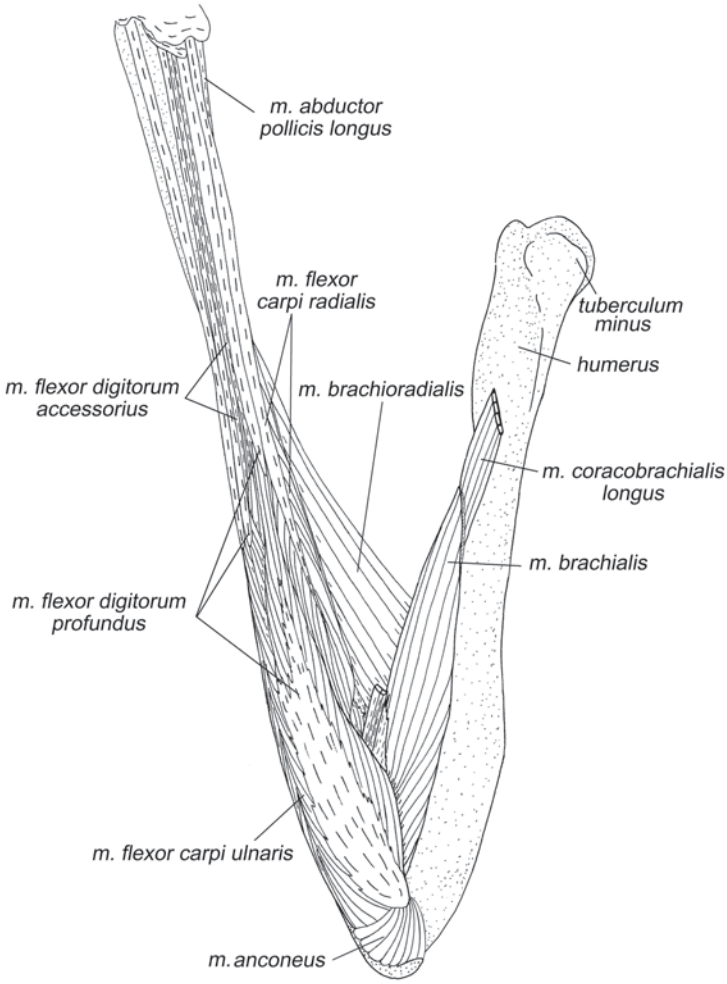


Fig. 2.46 Fore extremity muscles of *C. volans,* medial view, layer II.

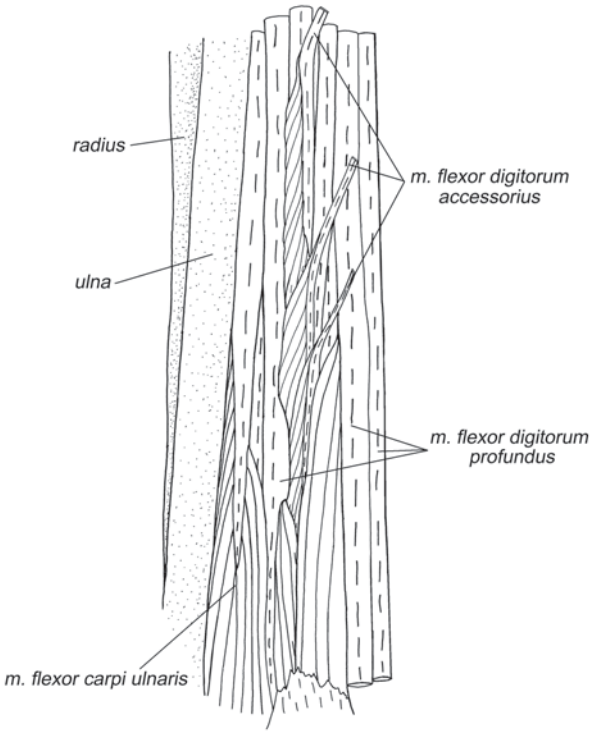


Fig. 2.47 Origin of the *m. flexor digitorum accessorius* on the fifth tendon of *m. flexor digitorum profundus* of *C. volans,* ventral view.

passes onto the manus under the *retinaculum flexorum medium*[7]. On the palmar surface of the manus, the tendon expands into a wide aponeurotic plate, which has a ligamentous connection with the *retinaculum flexorum profundum*[8]. In the middle of the metacarpus, the tendinous plate divides into terminal tendons, which run to digits II–V. Before the metacarpophalangeal joints, they give rise to short accessory side branches, which attach to the palmar surface of the distal heads of respective metacarpals. Further, at the level of the metacarpophalangeal joints, the tendons form rings on their dorsal surface for the passage of terminal tendons of the *m. flexor digitorum profundus*. Just distal to the metacarpophalangeal joints, the tendons of the *m. flexor digitorum superficialis* bifurcate, outflank (are perforated by) the respective tendons of the *m. flexor digitorum profundus*, and pass further under them. Somewhat distal to the metacarpophalangeal joints, the perforated tendons of digits III–V are joined by tendons of the *m. flexor digitorum accessorius* (see below). The insertions of the terminal tendons are on on the proximal heads of the

[7] The *retinaculum flexorum medium* (Fig. 2.53) is a wide ligament, which connects the ulnar side of the distal end of the radius and *uncinatum* with the radial side of the distal end of the radius and the cartilaginous plate of the proximal radial callosity.

[8] The *retinaculum flexorum profundum* of colugos (Fig. 2.54) passes from the ulnar side of the distal end of the radius, *scaphocentralolunatum*, and the base of metacarpal V to the radial side of the distal end of the radius and prepollex.

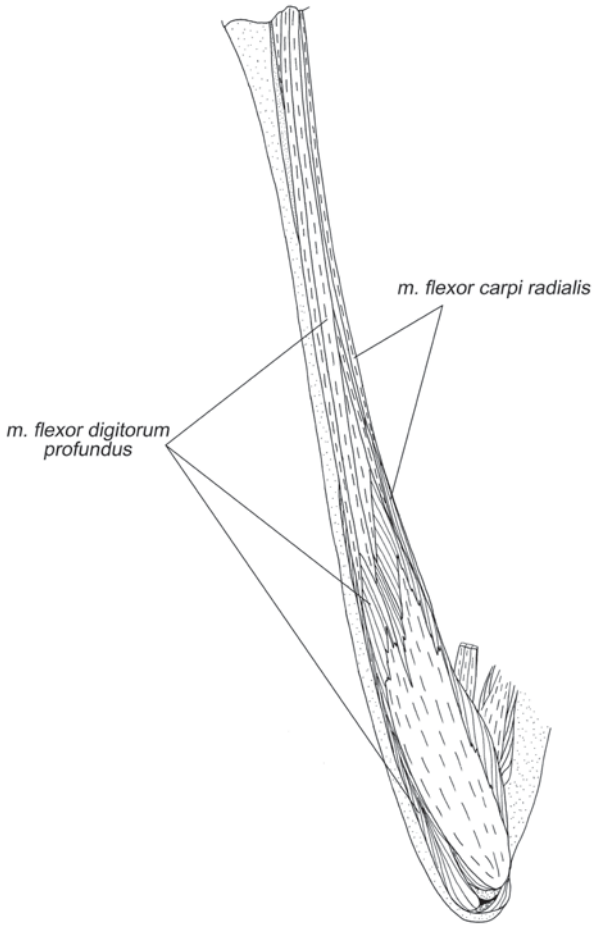


Fig. 2.48 Fore extremity muscles of *C. volans,* medial view, layer III.

second phalanges of digits II–V. In spite of the typical perforated tendons, Leche (1886) did not recognize the *m. flexor digitorum superficialis* and called it *m. palmaris longus*. Probably, this mistake was due to the above mentioned ligamentous connection of its terminal aponeurotic plate with the *retinaculum flexorum profundum*. In fact, the true *m. palmaris longus* with its typical insertion in the skin of the palm is absent in colugos.

The muscle flexes the antebrachiocarpal joint, the carpometacarpal, metacarpophalangeal and proximal interphalangeal joints of digits II–V; they do not operate only the claws. A specific functional role of this muscle will be discussed in Chapter 6.

Musculus flexor digitorum accessorius (Fig. 2.45–2.47, 2.53) originates at midlength of the antebrachium from the external (palmar) surface of the terminal tendon to digit V of the *m. flexor digitorum profundus*. The fibers are short and form three heads with separate thin terminal tendons, which pass under the *retinaculum*

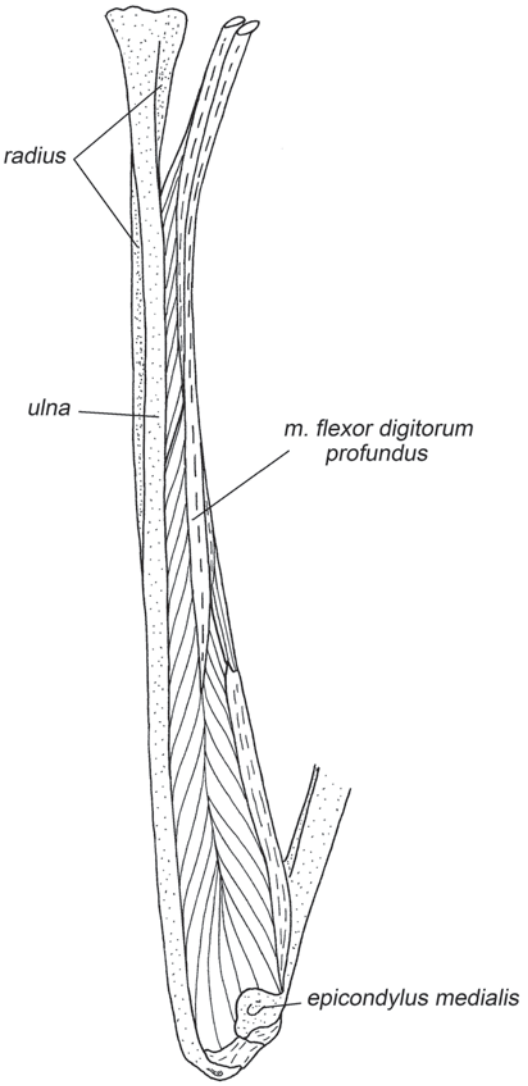


Fig. 2.49 Fore extremity muscles of *C. volans,* medial view, layer IV.

flexorum profundum to digits III–V (II–IV according to Leche 1886). Somewhat distal to the metacarpophalangeal joints, these tendons fuse into the palmar side of terminal tendons of the *m. flexor digitorum superficialis*. Leche (1886) regarded this tiny muscle as the superficial digital flexor itself. On the one hand, it is really similar to the *m. flexor digitorum superficialis* of the tree shrews in its origin on the terminal aponeurosis of the *m. flexor digitorum profundus*. On the other hand, colugos already possess the more typical mammalian *m. flexor digitorum superficialis* described above, which fibers arise not from the distal, but from the aponeurosis of

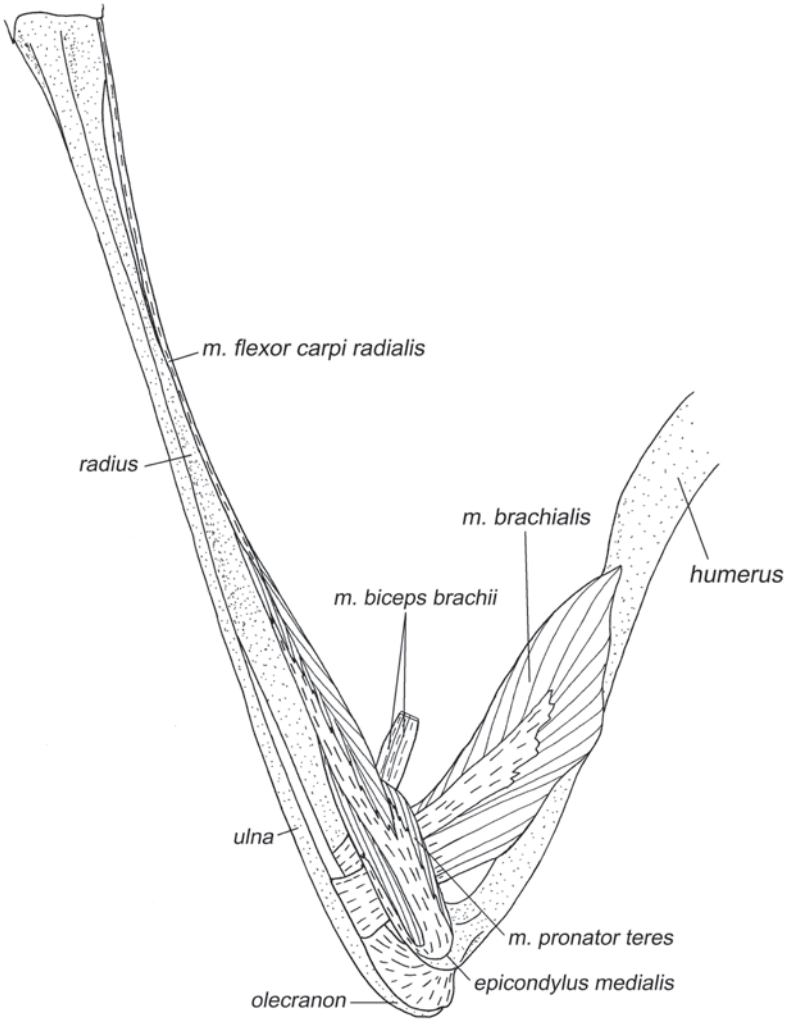


Fig. 2.50 Fore extremity muscles of *C. volans,* medial view, layer V.

origin of the same *m. flexor digitorum profundus*. This typical *m. flexor digitorum superficialis* is much more developed and makes the major input in the terminal perforated tendons, due to which, and contrary to Leche's claim (see above), it cannot be regarded as *m. palmaris longus*. We have introduced the term *m.flexor digitorum accessorius*, to distinguish the three tiny heads arising on the terminal aponeurosis of the *m. flexor digitorum profundus* from the rest of the *m. flexor digitorum superficialis*. Most probably, the latter migrated in the course of mammalian evolution from the manus onto the medial epicondyle of the humerus via the surface of the *m.*

flexor digitorum profundus, and the tiny *m.flexor digitorum accessorius* in colugos is the last trace of the ancestral stage.

As compared with other long digital flexors, this muscle is very weak. Possibly, it serves as a sensor. Its length directly depends on the longitudinal shift of terminal tendon V of the m. flexor digitorum profundus relative to terminal tendons III, IV, and V of the m. flexor digitorum superficialis. Thus, the head of digit V is able to signal about the position of its claw relative to the previous phalanx; no other muscle is capable to sense the degree of flexion in preungual joint. The heads of digits III and IV can signal about the degree of flexion of these digits relative to digit V.

Musculus flexor digitorum profundus (Figs. 2.45–2.49, 2.51–2.55) of colugos is unique in structure not only among mammals, but also all tetrapods. It originates from the entire palmar surface of the antebrachium (from the ulna, radius, and interosseous membrane) and, by a wide aponeurosis, from the medial epicondyle of the humerus. It is possible to recognize two unequal bipennate heads, which lie along the antebrachium one over the other. The superficial one is bigger, occupies most of the surface of the antebrachium and the medial epicondyle of the humerus, and is probably mixed from the *caput humerale superficiale* and *caput radiale* of the typical mammals (the *caput humerale profundum* is apparently completely lost). This head produces three tendons, which are separate from their very beginning: one tendon runs to digits I and II, the other to digit III, and the third one to digit IV. The first tendon, singular at its beginning, bifurcates into branches to digits I and II at the transverse vinculum (see below). The second (deeper) head is considerably smaller, originates fleshy from all the available surface of the ulna and, by an aponeurosis, from the distal part of the medial epicondyle of the humerus. It is probably mixed from the *caput olecrani*, *caput ulnare*, and part of the *caput humerale superficiale* of the typical mammals. The single distal tendon of this head runs to digit V. At

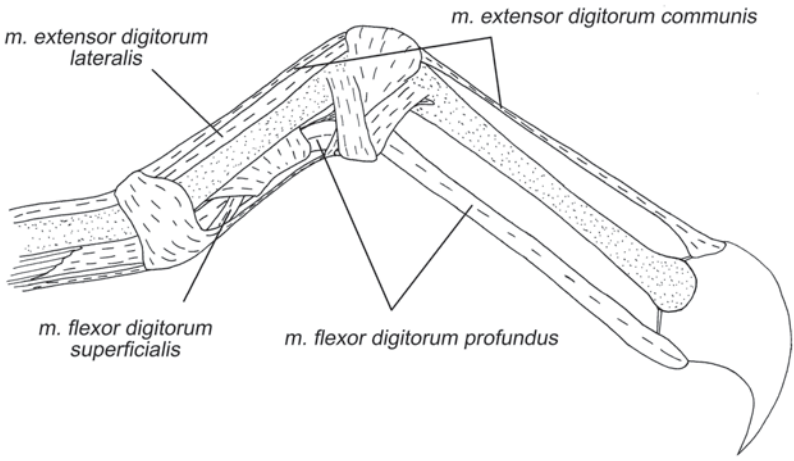


Fig. 2.51 The distal tendons of digital flexors and extensors of *C. volans,* lateral view, fifth finger.

the antebrachiocarpal joint, the four tendons (tendons to digits I and II are not yet divided here) get connection with each other by a transverse vinculum (Fig. 2.55), which is apparently a rudiment of the *aponeurosis flexoria communis*. The vinculum loosely envelopes the tendons from the dorsal side only, and does not hold them tightly together, allowing mutual longitudinal sliding. Distal to the vinculum the tendons are separate again, and there are already five of them. Each tendon passes through the ring on the underside of the respective perforated tendon of the *m. flexor digitorum superficialis* and, then, through *vaginae fibrosae digitorum*[9] to insert on the palmar side of the base of the ungual phalanx.

The muscle flexes all digits, including ungual joints. A unique feature among tetrapods is the completely separate beginning of tendons controlling different digits (except for the pair I and II), which enables colugos to distribute rather freely the muscular forces between claws, in particular, to apply the greatest force not only to the most extended digit, as inevitably occurs in the presence of the common stem at the beginning of the terminal tendons. In colugos, especially important is probably the fine control of digit V. Indeed, its tendon has a separate belly, and also the m. flexor digitorum accessorius arises only from the fifth tendon of the m. flexor digitorum profundus (see above). Apparently, such control is particularly important for gliding, as the position of digit V determines the outline of the anterolateral angle of the spread membrane.

Musculus flexor carpi ulnaris (Figs. 2.45, 2.46, 2.52–2.57) originates fleshy from the palmar and ulnar surfaces of the proximal part of the ulna and, by an aponeurosis shared with the *m. flexor digitorum profundus*, from the medial epicondyle of the humerus. A long and thin terminal tendon inserts on the base of metacarpal V and, before this, on the *pisiforme*.

The muscle flexes the antebrachiocarpal joint, participates in supination of the manus and also prevents the manus from medial adduction.

Intrinsic Muscles of Manus

Musculus abductor pollicis brevis (Fig. 2.52) originates from the prepollex and cartilaginous plate of the proximal radial callosity. It inserts by an aponeurosis on the medial surface of the articular capsule of the metacarpophalangeal I joint and on the terminal aponeurosis of the *m. flexor pollicis brevis*.

The muscle abducts medially the first digit together with its metacarpal.

[9] Digit I of colugos has only one *vagina fibrosa* in the middle of the proximal phalanx; digits II–V have three *vaginae fibrosae* each, and all the three are also on the proximal phalanx. The first one is placed just distal to the metacarpophalangeal joint, the second and third are closer to the proximal interphalangeal joint. The second *vagina fibrosa* is connected by a thin ligament with the capsule of the metacarpophalangeal joint (Fig. 2.52).

Musculus flexor pollicis brevis (Figs. 2.52, 2.53) originates from the base of metacarpals II and III, from the *retinaculum flexorum medium* and *retinaculum flexorum superficiale*[10], and from the prepollex. It inserts by an aponeurosis on the ventromedial surface of the articular capsule of the metacarpophalangeal I joint.

The muscle flexes the first carpometacarpal and metacarpophalangeal joints.

Musculus flexor pollicis brevis profundus (Figs. 2.54–2.56) originates by an aponeurosis from the *trapezium* and, partially, from the proximal aponeurosis of the *m. interosseus digiti secundi medialis*. It inserts on the lateral sesamoid bone of the metacarpophalangeal I joint. Leche (1886) ascribed this muscle to the previous one as its part.

The muscle participates in lateral adduction of digit I and flexion of this finger relative to its metacarpal.

Musculus adductor pollicis (Figs. 2.52–2.56) originates as a wide fan from the *aponeurosis palmaris profunda*[11] in the proximal part of the metacarpus. It inserts by an aponeurosis on the lateral side of the articular capsule of the metacarpophalangeal I joint.

The muscle adducts laterally the first digit.

Musculi lumbricales (Figs. 2.52–2.54) are located, as usual, in the inerspaces between the five terminal perforating tendons of the *m. flexor digitorum profundus*. Normally in mammals (see the description of tree shrews above), there is only one such muscle in each intarspace, which passes to the medial side of the digit, next to the respective interspace. In colugos, it is only true for the interspace between digits I and II. In the interspaces II–III, III–IV, and IV–V colugos have got a pair of *mm. lumbricales*, which are obviously the result of bifurcation accompanied with the shift of insertion of one of the twins from the medial side of the post-interspace digit onto the lateral side of the pre-interspace one. This shift of insertion could be achieved via *ligamenta metacarpea transversa profunda*, of which only the ligament of the III–IV interspace is currently retained in colugos; instead of such a ligament in the IV–V interspace, there remains a junction of the ends of the bellies of the respective pair of muscles. So, on the total, there are seven *mm. lumbricales* in colugos (only six, according to Leche). The *m. lumbricalis digiti secundi medialis*, which have not got a twin, originates from the point of divergence of tendons I and II of the *m. flexor digitorum profundus*. The pair of *m. lumbricalis digiti secundi lateralis* and *m. l. d. tertii medialis* originates from tendon II of the *m. flexor digitorum profundus* in the middle of the metacarpus. The pair of *m. lumbricalis digiti tertii lateralis* and *m. l. d. quarti medialis* originates from tendons III and IV of the *m. flexor digitorum profundus*. The pair of *m. lumbricalis digiti quarti lateralis* and *m. l. d. quinti medialis* originates from tendons IV and V of the *m. flexor digitorum*

[10] The *retinaculum flexorum superficiale* is a thin ligament connecting the *pisiforme* and prepollex, as in tree shrews.

[11] The term *aponeurosis palmaris profunda* is introduced here for the first time. This aponeurosis originates from the distal edge of the *ligamentum palmaris profundum*, so that its collagen fibers are perpendicular to this ligament and parallel to the metacarpals (Fig. 2.56). It serves as the place of origin for short adductors of the digits.

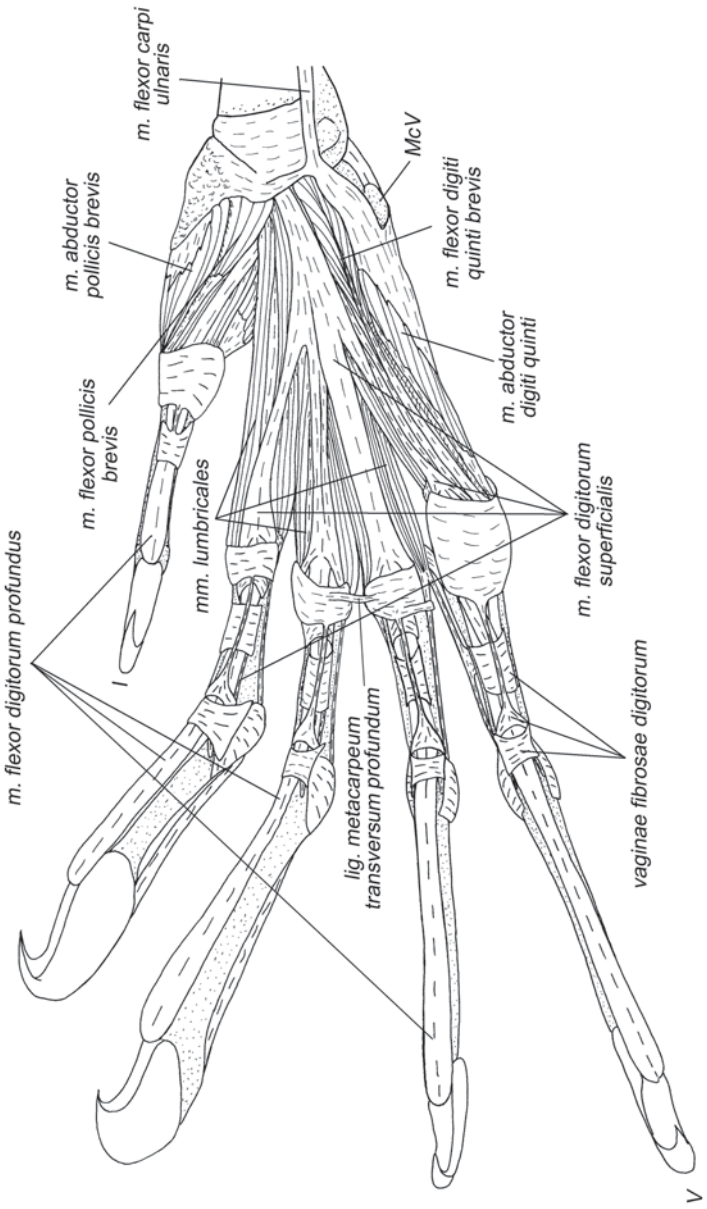


Fig. 2.52 Muscles of the manus of *C. volans,* ventral view, layer I.

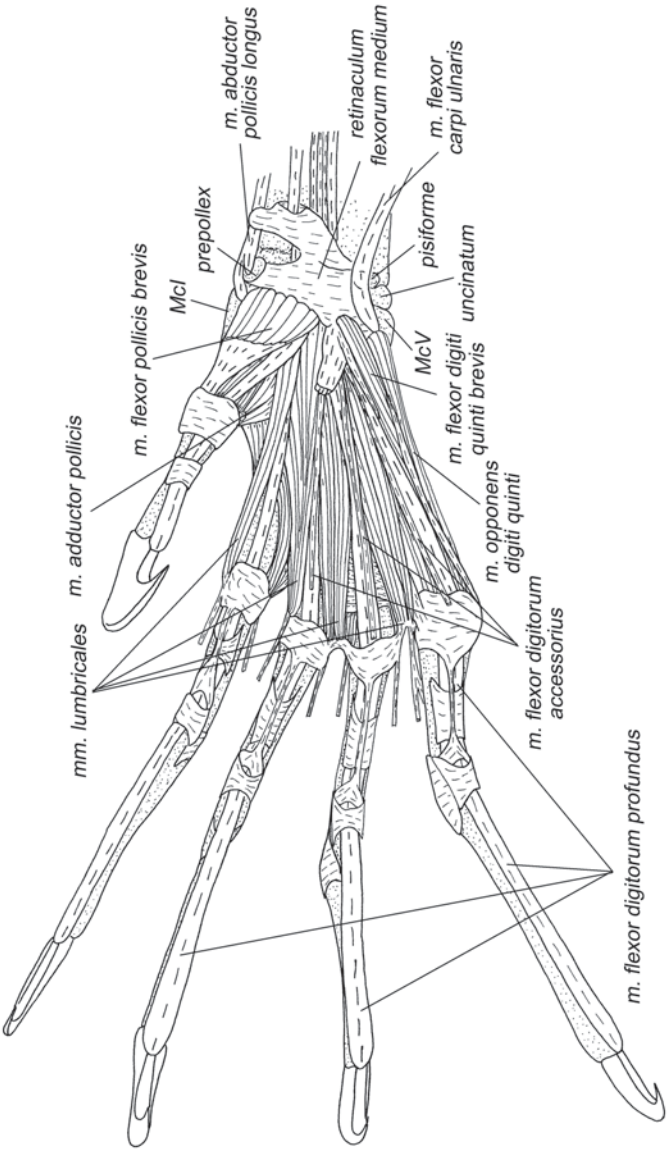


Fig. 2.53 Muscles of the manus of *C. volans*, ventral view, layer II.

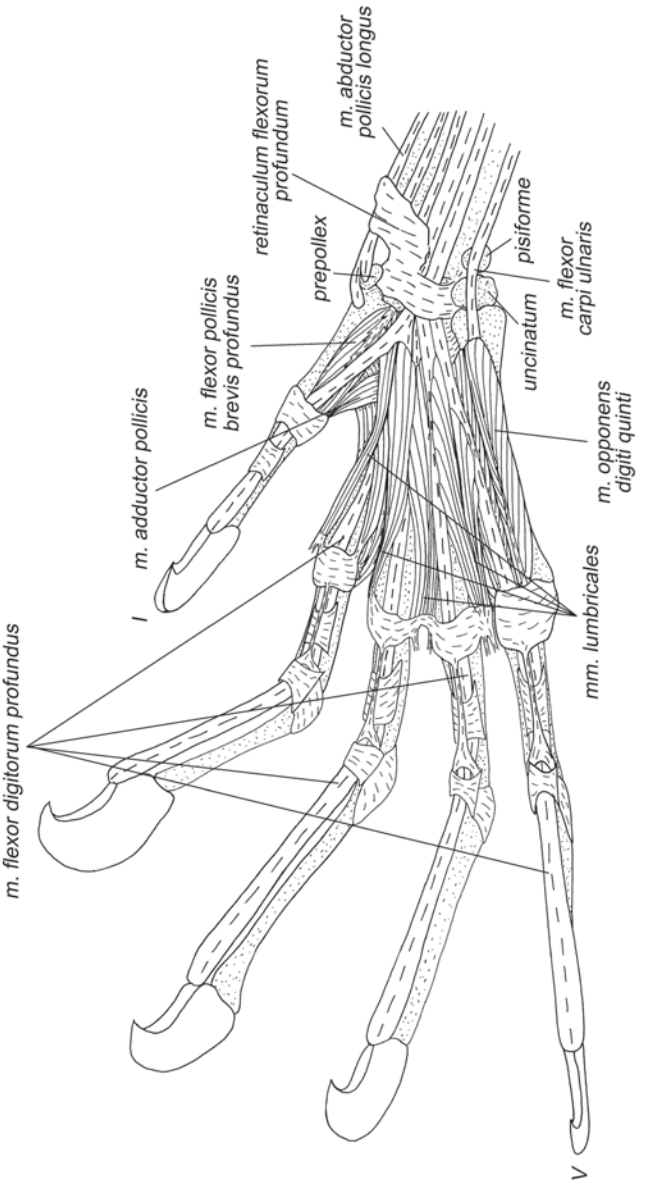


Fig. 2.54 Muscles of the manus of *C. volans,* ventral view, layer III.

profundus. Each *m. lumbricalis* inserts on the respective side of articular capsule of the respective metacarpophalangeal joint, and sends therefrom a tiny accessory tendon, which squeezes between the digits dorsally to join the respective side of the respective tendon of the *m. extensor digitorum communis* at the proximal interphalangeal joint. Just distal to the metacarpophalangeal joint, each tiny tendon is connected by a vinculum to the respective side of a deeper extensor tendon, as follows: *m. lumbricalis digiti secundi medialis*, *m. l. d. secundi lateralis*, *m. l. d. tertii lateralis*, and *m. l. d. quarti lateralis* – to the *m. extensor indicis; m. l. d. tertii medialis* and *m. l. d. quarti medialis* – to the *m. extensor digitorum lateralis*; *m. l. d. quinti medialis* – to the *m. interosseus digiti quinti*.

The muscles pull closer together all metacarpals, except for the first.

Musculus adductor digiti secundi (Fig. 2.55, 2.56) originates as a wide fan from the *aponeurosis palmaris profunda* in the distal part of the metacarpus, the proximal border coming under the *m. adductor pollicis*. It inserts by an aponeurosis on the lateral side of the articular capsule of the metacarpophalangeal II joint.

The muscle adducts laterally the second digit.

Musculus adductor digiti quinti (Fig. 2.55, 2.56) originates along the entire *aponeurosis palmaris profunda* and inserts by an aponeurosis on the medial side of the articular capsule of the metacarpophalangeal V joint.

The muscle adducts medially digit V.

In contrast to tree shrews, the m. adductor pollicis, m. adductor digiti secundi and m. adductor digiti quinti of colugos cover almost the entire palmar surface of the metacarpus and approach the metacarpals at a considerably greater angle, while in tree shrews, they actually run along the metacarpals Therefore, in colugos, they have much more advantageous leverage for adduction of respective digits to the midline of the manus. This implies that pulling the digits together in colugos sometimes requires significant muscular efforts. An opposite force that is to be overcome by the three adductor muscles is probably the tension of the pro- and plagiopatagium, which tend to pull apart the digits during gliding.

Musculus flexor digiti quinti brevis (Fig. 2.52, 2.53) originates under the fifth metacarpal mostly from the distal edge of the *retinaculum flexorum medium* and a part of the *retinaculum flexorum superficiale*. It inserts by an aponeurosis on the ventrolateral surface of the articular capsule of the metacarpophalangeal I joint.

The muscle flexes the fifth carpometacarpal and metacarpophalangeal joints.

Musculus abductor digiti quinti (Fig. 2.52) originates by a wide aponeurosis from the *retinaculum flexorum superficiale* at the base of digit V and from the proximal head of metacarpal V. The terminal aponeurosis inserts on the lateral side of the articular capsule of the metacarpophalangeal V joint.

The muscle abducts laterally digit V and participates in flexion of this finger relative to the metacarpus.

Musculus opponens digiti quinti (Fig. 2.53–2.56) originates from the ventrolateral surface of metacarpal V (from *uncinatum* according to Leche 1886). It inserts by an aponeurosis on the lateral sesamoid bone of the metacarpophalangeal V joint.

The muscle participates in flexion of the metacarpophalangeal V joint and lateral abduction of the fifth finger.

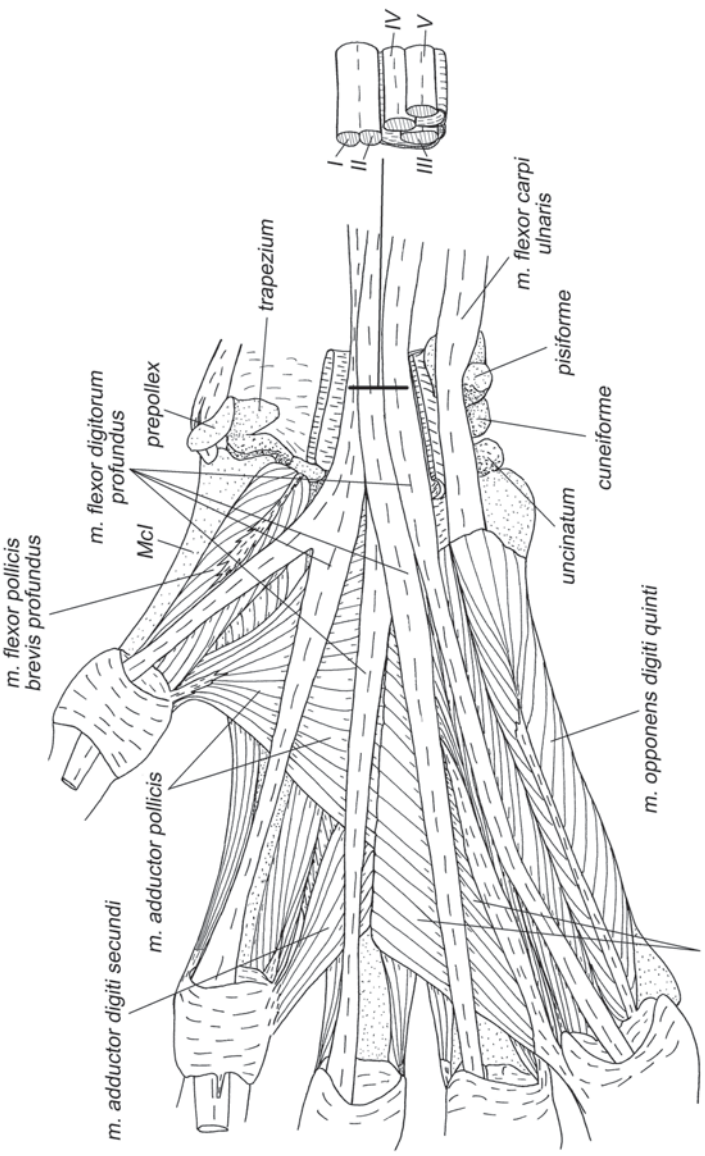


Fig. 2.55 Muscles of the manus of *C. volans,* ventral view, layer IV.

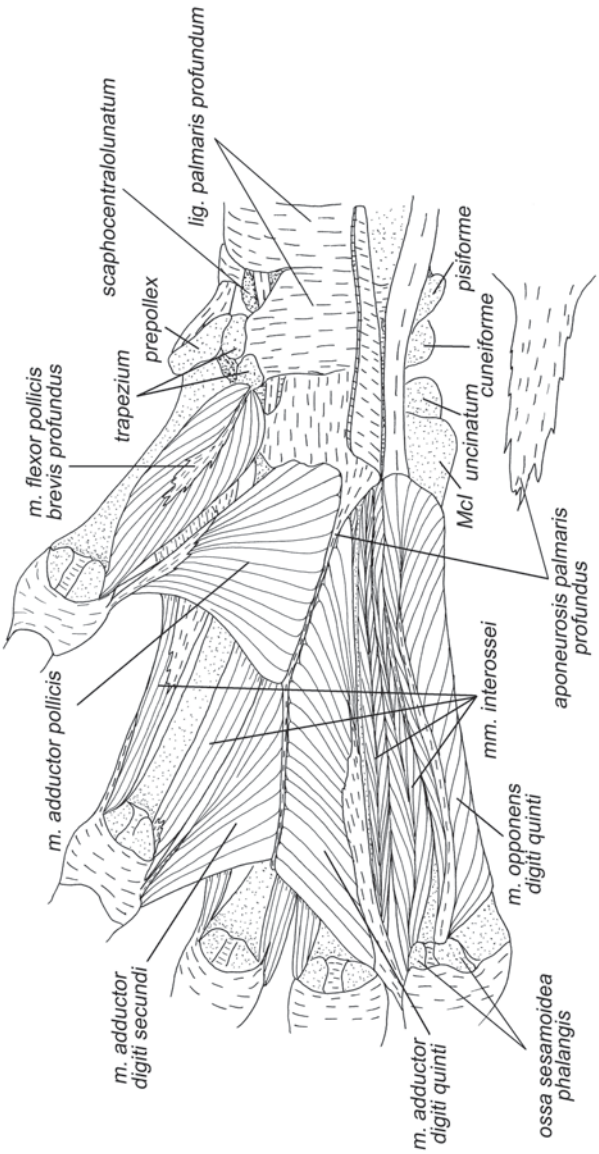


Fig. 2.56 Muscles of the manus of *C. volans,* ventral view, layer V.

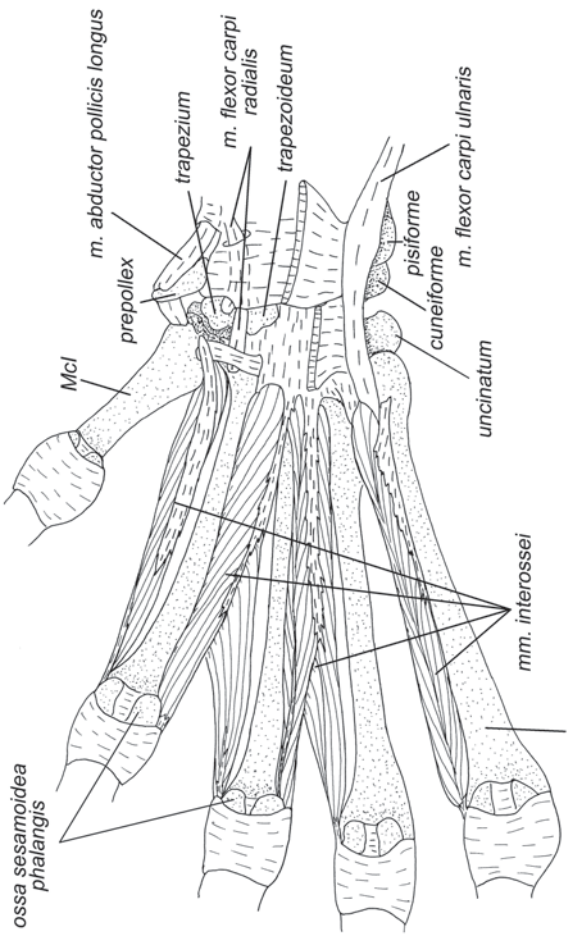


Fig. 2.57 Muscles of the manus of *C. volans,* ventral view, layer IV.

Musculi interossei (Figs. 2.44, 2.56, 2.57). Colugos have seven muscles in this series, as tree shrews. However, in contrast to tree shrews, they are not subdivided into *mm. interossei palmares* and *mm. interossei dorsales*. The *m. interosseus digiti secundi medialis* originates by a thick tendon from the ventrolateral surface of the proximal head of metacarpal I and, partially, from the *trapezium*; it inserts on the ventromedial side of the articular capsule of the metacarpophalangeal II joint. The *m. interosseus digiti secundi lateralis* and *m. i. d. tertii medialis* originate mostly by a common tendon from the *aponeurosis palmaris profunda* between the bases of digits II and III and, fleshy, from the lateral surface of metacarpal II; these two muscles insert on respective sides of the metacarpophalangeal joints of respective digits. The *m. interosseus digiti tertii lateralis* and *m. i. d. quarti medialis* have the same relations with digits III and IV as the previous pair of muscles has with digits II and III. Similarly, the *m. interosseus digiti quarti lateralis* originates by an aponeurosis from the base of metacarpal V and inserts on the lateral side of the metacarpophalangeal IV joint. The *m. interosseus digiti quinti medialis* originates by an aponeurosis shared with the previous muscle and from the *aponeurosis palmaris profunda*; it inserts on the medial side of the metacarpophalangeal V joint and, by a peculiar accessory tendon, which traverses over the medial side of digit V onto its dorsal side and fuses with the respective tendon of the *m. extensor digitorum lateralis* before their insertion on the articular capsule of the proximal interphalangeal joint.

Like mm. lumbricales, these muscles pull closer together all metacarpals, except for the first.

Musculature of Wing Membrane

Musculus coracocutaneus (probable derivative of the *m. cutaneus trunci*) (Fig. 2.24, 2.25, 2.30, 2.31) is formed by a thin fascicle of very long fibers. They originate from the caudal side of the base of the coracoid process of the scapula, come out from under the *mm. pectorales* and, behind the forelimb, pass inside the wing membrane to its lateral border. The distal half of the main fascicle gives rise to many fibers, which spread in various directions and insert in the skin.

Certainly, this muscle participates in the control of tension of the membrane during gliding. However, what is more important, it is probably the only skeletal muscle that reefs the membrane, pulling it closer to the body, during running.

Musculus humerocutaneus (probable derivative of the *m. cutaneus trunci*) was damaged in our specimens of colugos. However, at least on one side of every specimen, the fiber fragments were found arising from the distal half of the medial surface of the humerus. According to Leche (1886), this muscle originates from the humerus between the *m. brachialis* and *m. triceps brachii caput mediale*, wherefrom it passes inside the wing membrane along with the *m.coracocutaneus*.

In addition to the forelimb muscles described above, several intrinsic muscles of the membrane should be taken into account.

In the propatagium, Leche (1886) has distinguished two muscular layers, the ventral and the dorsal, which fibers pass more or less perpendicular to each other. The ventral layer is composed of isolated fascicles, which traverse the propatagium from the neck and shoulder toward its free anterior edge but do not reach it. The dorsal layer, which we name the *m. tensor propatagii* (Fig. 2.42), is formed by fibers of the *m. platysma myoides* and *m. jugalis propatagii*, which arise from the sides of the head (from the cheek in the case of the *m. platysma myoides* and from the cheek and jugal arch up to the acoustic meatus in the case of the *m. jugalis propatagii*), and run parallel to the free anterior edge of the membrane toward the first finger. According to our dissections, the *m. tensor propatagii* terminates in a tendon with double insertion, one on the proximal head of the first metacarpal and the other on the medial surface of the articular capsule of the first metacarpophalangeal joint.

In the plagiopatagium, Leche (ibid.) has also distinguished two muscular layers. One is composed by the *m. coracocutaneus* и *m. humerocutaneus* considered above. The other is represented by fibers, which run from the forelimb to the hindlimb and concentrate into a tiny band at the very edge of the membrane. According to our dissections, this band is only present in the posterior half of the edge of the plagiopatagium, while in its anterior half the band disappears being substituted by fibers of the *m. coracocutaneus*.

In the uropatagium, Leche (ibid.) describes only one muscular layer, which fibers pas from the hindlimb to the tail. As in the other regions of the membrane, these fibers concentrate into a pronounced, though thin, band at the edge of the membrane. In addition, a few fascicles are pronounced, which connect the shank with the dorsal side of the tail base.

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