Aleksandra A. Panyutina
Leonid P. Korzun
Alexander N. Kuznetsov

Flight of Mammals: From Terrestrial Limbs to Wings

Springer

Flight of Mammals: From Terrestrial Limbs to Wings

Aleksandra A. Panyutina • Leonid P. Korzun
Alexander N. Kuznetsov

Flight of Mammals: From Terrestrial Limbs to Wings

Springer

Aleksandra A. Panyutina
Department of Morphological
Adaptations of Vertebrates
Severtsov Institute of Ecology and Evolution
Russian Academy of Sciences
Moscow
Russia

Department of Vertebrate Zoology
Biological Faculty
Moscow State University
Moscow
Russia

Leonid P. Korzun
Department of Vertebrate Zoology
Biological Faculty
Moscow State University
Moscow
Russia

Alexander N. Kuznetsov
Department of Vertebrate Zoology
Biological Faculty
Moscow State University
Moscow
Russia

ISBN 978-3-319-08755-9 ISBN 978-3-319-08756-6 (eBook)
DOI 10.1007/978-3-319-08756-6
Springer Cham Heidelberg New York Dordrecht London

Library of Congress Control Number: 2014945367

© Springer International Publishing Switzerland 2015
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Foreword

This monograph is devoted to a particularly interesting scientific problem of the origin of flight in mammals. The first gliding mammal, known as *Volaticotherium*, appeared as early as the Jurassic, approximately 150 Ma. Subsequently, gliding flight emerged independently several times among marsupials, rodents, and colugos. On the contrary, flapping flight in mammals was only developed in chiropterans and became as perfect as in birds and extinct pterosaurs. The acquisition of this ability was a key adaptation, allowing a wide adaptive radiation of chiropterans; in the modern mammalian fauna, they display the second greatest species diversity just after rodents.

Bats appeared in the fossil record in the Eocene on all continents except for Antarctica and South America. North America has yielded complete skeletons of Early Eocene bats. These first reliable representatives of the order Chiroptera already had completely formed adaptations for flapping flight. Therefore, they provide very little information for understanding the initial causes of the appearance of this key adaptation. It is only possible to reconstruct them based on indirect characters provided by analysis of flying adaptations of living forms. This monograph is just devoted to this question.

Flapping flight in the atmosphere of the Earth imposes heavy demands on the flight apparatus of vertebrates. Great mechanical forces, work, and power produced in the shoulder girdle combined with fine adjustment of the angle of attack of the flapping wing pose stringent requirements upon the flight apparatus. The convergence of bats and birds in this respect is evident. It is not a gross exaggeration to assume that Chiroptera approach Aves in diversity. Against a background of general convergence of the two groups, it is particularly interesting how the same external requirements resulted in the appearance of peculiar general design of the flight apparatus in chiropterans. This is undoubtedly associated with ancestral morphological features; it is evident that ancestors of chiropterans already had parasagittal limbs and a perfect terrestrial locomotion, which was thoroughly investigated experimentally in many marsupials and placentals.

The study of the locomotor apparatus is of interest, since its adaptations form the general appearance of animals and directly reflect requirements of environments. At the same time, while running, digging, swimming, and climbing of mammals are

considered in many studies, flight of chiropterans has undeservedly received little attention. As compared with other locomotion patterns, flapping flight is more difficult to study experimentally and analyze, since it does not produce visible tracks, rapid wing movements escape video recording at a standard frame rate, and the distribution of external forces over the wing surface at natural interaction with air is difficult to model. As for morphological studies of bats, they have usually been restricted to this order itself without consideration of the most interesting points concerning evolutionary transition from non-flying to flying forms. As a result, the origin of flapping flight in mammals is discussed in much fewer publications than that of birds. A more or less detailed hypothesis for the origin of flight in mammals has not yet been proposed.

The present book prepared by employees of the Vertebrate Zoology Department of the Biological Faculty of Moscow State University, which is well-known for the old traditions of studies in the field of comparative anatomy and functional morphology, bridges this gap and opens a new page in the analysis of flight in mammals. The approach implemented by the authors combines the complex morphobiological method of K. A. Yudin and the method of the force–balance analysis of the musculoskeletal mechanisms developed by F. Ya. Dzerzhinsky, a teacher of all authors of this book. The purpose and problems posed in this work expand far beyond the framework of the study of chiropteran flight, which was developed by predecessors. Even the primary description of the morphological material discloses purposeful interest of the authors in the evolutionary development of flapping flight in mammals.

A particularly inspiring point is the fact that the topic chosen is rather new for the authors, so that they are not constrained by routine technique for studying the flight and bravely introduce approaches that were developed in neighboring fields of functional morphology. The flight apparatus seems as beneficial as the jaw apparatus of birds or limbs of cursorial mammals for the revelation of remarkable adaptations by the methods familiar to the authors. For example, the authors successfully apply graphic analysis of the static equilibrium, which was of great importance in the treatment of adaptive sense of a number of other musculoskeletal mechanisms, and corroborate that, in this case, it is also heuristic and fruitful. They show that the shoulder girdle of bats is enormously loaded, with forces being of an order of magnitude greater than the animal's weight; among mammals such heavy loading probably occurs in specialized diggers only. This results in prominent adaptations of chiropteran shoulder girdle, which the authors successfully treat by the analysis of general distribution of forces. There is no doubt that, in the future, detailed analysis of forces will provide a precise treatment of adaptive sense of particular differences between various bats in the elements of the shoulder girdle.

The ideas of the authors about the formation of flight in mammals are presented as an evolutionary scenario. In their opinion, the basic structural changes in the course of transition from terrestrial quadrupedal locomotion to flapping flight were associated with the change of the limb action plane from parasagittal to frontal. The authors have shown convincingly that this change was only possible through an intermediate stage of running along the vertical tree trunks; to grasp it animals had to sprawl forelimbs laterally as far as possible. The next step involved the development

of a wing membrane between the fore and hindlimbs on each body side for gliding from tree to tree. Subsequently, the formation of a membrane between fingers allowed movements of the manus to be used for more efficient manoeuvring during gliding. Apparently, the membranous manus has become extremely prospective, so further development resulted in the acquisition of flapping flight and, hence, appearance of a new mammalian order, Chiroptera. This elegant evolutionary scenario is attractive due to its simplicity and is supported by extensive factual evidence and observations provided in the monograph. This completely novel hypothesis can be tested by future paleontological findings, although they are extremely rare for tropical arboreal animals.

Thus, it is possible to state with confidence that the authors are highly qualified specialists and their hypothesis is a great scientific achievement – a real boon for future researchers in the field of mammal and vertebrate evolutionary morphology. Such hypotheses are necessary for a better understanding of the mechanisms of the evolutionary process and the development of key morphobiological adaptations. Therefore, this monograph is a great event not only for zoology, but also for general biology and evolutionary theory.

Laboratory of Theriology, Zoological Institute of the Russian Academy of Sciences
Professor, Doctor of Science
Peter P. Gambaryan

Laboratory of Theriology, Zoological Institute of the Russian Academy of Sciences
Professor, Head of Laboratory, Doctor of Science
Alexander O. Averianov

Acknowledgements

An important role in the creation of the present book was played by the Russian–Vietnamese Tropical Center, which provided almost all specimens examined by us.

The Zoological Museum of Moscow State University and Raffles Museum of Biodiversity Research (Department of Biological Sciences, Faculty of Science, National University of Singapore) allowed us to study their collection material.

A great help and support at all stages of investigation, during comprehension of results and preparation of the manuscript was rendered by F. Ya. Dzerzhinsky and E. L. Yakhontov.

Reasoning and remarks of our colleagues in the course of many discussions were particularly useful. We are sincerely grateful primarily to E. G. Potapova, I. A. Kolmanovsky, P. P. Gambaryan, E. N. Kurochkin, and S. V. Kruskop.

We are deeply thankful to N. Lim from the Raffles Museum of Biodiversity Research for help during field observations of colugos, discussion of various aspects of their biology, and granting photo and video materials.

N. M. Mylov, S. M. Forsunov, O. G. Ilchenko and M. A. Bragin contributed much to the technical maintenance of experiments.

T. Strickler, A. V. Borisenko, and S. V. Kovalsky helped us much with necessary literature.

We are grateful to B. A. Shulyak, A. K. Panyutin and D. E. Yakhontov for valuable discussions and methodical advice.

D. Youlatos supported us with his original quantitative data on muscles of *Tadarida teniotis*.

Photographs of animals for publication were kindly provided by Norman Lim, Peter Loh Tuck Kheong, Nick Garbutt, Julian W, Paul Chan, Tim Laman, Dietmar Nill, Daniel Riskin, E. L. Yakhontov, E. D. Popova-Bondarenko, E. P. Kuzmicheva, and E. A. Kovalev.

The study was supported by the Russian Foundation for Basic Research (projects no. 14-04-01132A and 15-04-05049A).

Methodical adviser B. A. Shulyak (30.01.2011) and A. K. Panyutin (19.10.2014) – deceased

Introduction

Locomotion supported by air is widespread among vertebrates. In the modern fauna, birds are absolute leaders in this respect. Not surprisingly, avian flight always remains in the center of attention of zoologists. The origin of flight, a question inseparably linked with evolutionary history of this group, remains urgent; this problem is still hotly debated and new hypotheses appear again and again (Peters 2002; Dial 2003; Dial et al. 2008; Kurochkin and Bogdanovich 2008).

In the shadow of birds, the origin of mammalian flapping flight attracts less attention, although more than 1200 bat species use this kind of locomotion. The hypotheses here, being rather numerous, are not so developed. In particular, a plausible comprehensive evolutionary scenario describing the key stages of the development of flapping flight in mammals has not been proposed.

The fossil record does not provide direct evidence of the origin of chiropterans. Transitional forms that could have shown successive stages of the appearance and improvement of the flight apparatus have not yet been recorded.

The earliest reliably identified chiropterans are known from the Lower Eocene; due to their good preservation, there is no doubt that these animals are very similar to extant bats of microchiropteran type. The most primitive presently known chiropteran is *Onychonycteris finneyi* (Simmons et al. 2008) from the Lower Eocene of Wyoming (dated 52.5 Ma). Its skeletal features allowed the authors of description to propose with confidence that the wing of *Onychonycteris* was approximately the same as in recent bats and it could use flapping flight. At the same time, *Onychonycteris* had claws in all five fingers of the forelimb (particularly strong in fingers I and II). Also, the hindlimbs were closer in length to the forelimbs than in extant bats (in which both limbs are longer relative to the body, but the hindlimbs not so much as the forelimbs). Based on these features, the authors of the description assumed that this animal could both fly and climb branches in tree crowns.

Interestingly, the same beds where *Onychonycteris* was recorded earlier yielded *Icaronycteris index* (Jepsen 1966) represented by several skeletons displaying a much more complete set of advanced characters. In the basic morphological features and proportions of the flight apparatus, it approaches recent microchiropterans. Primitive features include the absence of a spur on the hindlimb and the pres-

ence of rudimentary ungual phalanges of fingers III–V and a claw in finger II of the forelimb (Simmons and Geisler 1998).

Several Eocene bat genera are known from the Messel of Germany (dated 47 Ma). Perfectly preserved skeletons and, sometimes, imprints of soft tissues of *Palaeochiropteryx, Archaeonycteris, Hassianycteris,* and *Tachypteron* illustrate the beginning of adaptive radiation of the group like diverse feeding specializations and flight patterns (Simmons and Geisler 1998). The ear region of Eocene bats gives evidence of a rather advanced echolocation system (Novacek 1985, 1991; Habersetzer and Storch 1989, 1992). It is possible to assign with confidence the majority of fossil bats from the Middle–terminal Eocene of Europe, North America, Asia, Africa, and Australia to extant bat families. Undoubted records of fruit bats appear as late as the Miocene (Gunnell and Simmons 2005).

The age and morphological similarity of the most ancient chiropterans to extant members of the order suggest that mammals acquired flapping flight not later than the Palaeocene or, possibly, even earlier, at the end of the Mesozoic. It is evident that, although *Onychonycteris* is rather primitive, it should not be regarded as a "missing link" or model of the transitional form from quadrupedal to flying mammals.

Two basic scenarios for the appearance of flight in mammals are traditionally considered. The first hypothesis implies that the initial ancestral form was arboreal and combined climbing with gliding leaps (Smith 1977; Hill and Smith 1984; etc.). This hypothesis was developed for the first time by Darwin (1872, p. 140): "In certain bats in which the wing-membrane extends from the top of the shoulder to the tail and includes the hind-legs, we perhaps see traces of an apparatus originally fitted for gliding through the air rather than for flight". In its turn, the appearance of gliding ability is imagined as follows: an animal moving in tree crowns could use skin folds on body sides and between digits as a parachute surface, which increased the range of leaps and, thus, provided transition from ballistic leaping to gliding from tree to tree. Further, the increasing of manoeuvrability and of duration of air-borne time was achieved through the appearance of flapping flight. To date, the hypothesis of gliding ancestor has got many supporters and become generally accepted (Smith 1977; Hill and Smith 1984; Norberg 1985; Scholey 1986; Rayner 1988; Altringham 1998; Bishop 2008; Giannini 2012; etc.). Formerly, Padian also adhered to this hypothesis (Padian 1985). Although the main argument for him was the close filiation of bats to colugos (the point of view widely accepted at that time but abandoned today), Padian also noted that the presence in bats of membrane between the forelimbs and the hindlimbs can be hardly treated in the other way than as the trace of the gliding ancestral stage. Another argument in favor of the hypothesis of gliding ancestor is the fact that gliding mammals repeatedly appeared in the evolution of a number of different groups. Among living animals, examples are provided by marsupials, rodents, and colugos also called flying lemurs. A recent find of the specialized glider *Volaticotherium* in the Late Jurassic–Early Cretaceous deposits of China is evidence that mammals invaded the air at least 150–120 Ma (Meng et al. 2006). Recent estimates show that members of the class Mammalia adapted for gliding for at least nine times (Jackson and Thorington 2012).

Despite its obvious advantages, the hypothesis of gliding ancestor was consistently attacked throughout its 140-year history. In our opinion, the main reason for these attacks is the fact that all the time the advocates of this hypothesis only considered the general possibility of the gliding-to-flapping transition rather than reconstructed a convincing morphofunctional scenario supplied with the analysis of adaptive sense of presumed transitional stages. For opponents, this was the good subject for criticism (Jepsen 1970; Pirlot 1977; etc.); Padian (2011) has also abandoned this idea together with filiation of bats and colugos.

A positive idea was suggested by Bishop (2008) on the necessity to explore the continuity in improvement of aerial performance in the course of transition from short, rectangular, fur-covered wings of gliding mammals to long, tapered, smooth, flapping wings of bats. However, Bishop almost ignores the changes of the wing musculoskeletal machinery in the course of this transition.

The second widespread type of hypotheses on the origin of bat flight implies the total absence of gliding preliminary stage. (Jepsen 1970; Panyutin 1980; Caple et al. 1983; Kovtun 1984, 1988, 1990a; Padian 2011). Mostly they say that the bat ancestors were sitting on or hanging upside-down below the branches (Panyutin 1980; Kovtun 1984, 1988; Kovaleva 2013) and caught the by-passing insects by their hands supplied with membranes between the elongated fingers. Further, these imaginary animals began to leap into the air in chase of prey (in contrast to Smith's creatures they could not glide) and used hand flapping for soft landing. Still further, they began to use hand flapping to increase the chase distance of the prey in the air. Jepsen (1970) supposed that pre-bats could jump in chase of insects not only from tree branches down, but from the ground up. This leads to the idea of the non-arboreal but cave-living ancestor, which mode of life seems to better explain the dorsoventrally flattened body (allowing to hide in crevices) and reduced vision substituted by echolocation (Jepsen 1970). Recently, Padian (2011) has also adhered to the cave-origin hypothesis; he presumes that the bat ancestors flapped their rudimentary wings while parachuting from the cave ceiling to its floor where their prey was concentrated. In the absence of the gliding ancestor, the membrane between the fingers must have arisen initially for some non-flight performance such as insect catching (Jepsen 1970), crawling over swamps (Panyutin 1980), thermoregulation (Kovtun 1990a, b) and foetal skin breathing (Kovaleva 2013).

A mixed hypothesis was suggested by Pirlot (1977) and Caple et al. (1983) who regarded the bat ancestor as a hovering but not necessarily non-gliding animal. According to Pirlot, it hovered, that is flapped the wings, to slow down the fall while jumping from plant branches in chase of insects in the air (similar to Jepsen 1970; Smith 1977 and Caple 1983). Pirlot was immediately criticised by Clark (1977) in respect of hovering abilities of the hypothetical bat ancestor as well as the use of membranous wings as flycatchers.

Against "flycatching wing" hypotheses is the evidence that feeding on insects from the fixed perch is not repaid energetically (Speakman et al. 1989; Speakman 1993, 1999, 2001). Even more important discrepancy with reality is the assumption of the flycatcher advocates (Jepsen 1970; Panyutin 1980; Kovtun 1984, 1988,

1990a; etc.), that the first part of the future wing membrane to appear was its interdigital part (chiropatagium). The presumed initial absence of the membrane connected to the body side (plagiopatagium) implied inability to glide. Contrary to this assumption, the plagiopatagium develops in the bat ontogeny ahead of the chiropatagium (Elangovan et al. 2007).

Even easier target for criticism is the idea of an ancestor which started to leap from branches, tree trunks or cave walls into the air in chase of flying insects. Variations of this idea were repeatedly suggested by both the advocates of non-gliding (Jepsen 1970; Pirlot 1977 and Caple 1983) and gliding (Smith 1977) ancestor. This looks absolutely impossible because hunting flying insects is a difficult job even for such advanced professionals as modern bats and birds (e.g. flycatchers). Definitely, the primitive gliders or flap-aided leapers could not do it at all. The leaps from the ground could have been spectacular but not efficient, while those from high perch must have been crazy in fact. Indeed, an ancestral glider or flap-aided leaper should do its best simply to reach soft landing, and missing this chance in chase of prey would be suicidal.

We are forced to conclude that both main scenarios are by now speculative and lack a reliable factual support. In addition, these theoretical speculations imply that the major morphological change allowing mammals to acquire flapping flight was the elongation of the distal regions of the forelimbs and formation of interdigital membranes. For example, Kovtun (1990a) named this process "a key morphogenesis" in the evolution of chiropterans. At the same time, a complex set of morphofunctional changes required for transformation of the limb of terrestrial animal into the wing is disregarded. The elongation of metacarpals and phalanges appears to be not as big a problem as it is usually thought to be. The comparative embryological and genetic studies of bats and rodents (Sears et al. 2006; Cooper et al. 2012) show that the definitive length of metacarpals and phalanges is determined by the rate of proliferation and maturation of cartilaginous cells, which is controlled by bone morphogenetic proteins (BMP). It is probable that changes in these proteins or, more precisely, mutations in the genes encoding them, are the simple basis for changes in the length of limb elements. Having "mutation of elongation" been supported by the natural selection for any reason, the finger growth in the bat evolution can be regarded as the technically simplest neomorphic feature.

In general, the discussion of the origin of flight in mammals has usually been restricted to particulars and missed fundamental consideration of a complex set of ecological circumstances that caused transition from the limb of terrestrial animal to the bat wing as well as morphofunctional changes accompanying this process. In other words, the consistent evolutionary scenario of the origin of bats has not yet been reconstructed.

To date, a wealth of experience in elaboration of such retrospective scenarios for other objects has been accumulated. In particular, as the natural system of birds was developed, a complex morphoecological method, also called ecomorphological or morphobiological, was proposed (Yudin 1957, 1978; Dzerzhinsky 1972, 1977; Korzun 1986; etc.). The major idea behind Yudin's method is the study of the phylogeny

of birds as an adaptive process rather than formal changes in the so-called character matrix. As Dzerzhinsky (1972) noted, the basic theoretical prerequisite for this approach is the fact that the structures of biomechanical units of the musculoskeletal system of extant groups, which result from a long evolutionary pathway, still reflect the essence of successive steps of their history, each of which was marked by adaptation to particular environment.

Using this attitude, the chiropteran locomotor system in question should be considered as superposition of successive adaptations to different conditions, under which their ancestors dwelt. By decoding these "superimposed layers," we explore adaptive history of the groups under study; in so doing, the reliability of the proposed hypothesis (evolutionary scenario) is supported by abundant intrinsic functional links. The major criterion for verification of each reconstructed stage is its functionality and the presence of functional advantages allowing the natural selection to support the neomorphic features.

In the present study, we expand the field of investigation beyond the framework of the analysis of chiropterans, so that our comparative analysis involves animals which use a primitive terrestrial–arboreal locomotion supported by the firm substrate and gliding locomotion supported by air. In these animals, we expect to reveal morphofunctional prerequisites for the establishment of flapping flight.

In our study, terrestrial–arboreal and gliding animals are represented by members of the cohort Archonta; they are tree shrews and colugos, respectively. Although the recent molecular findings have finally disproved the assignment of Chiroptera to Archonta (O'Leary et al. 2013), our choice of tree shrews and colugos for comparison with bats is warranted morphofunctionally. Among extant mammals, the tree shrews look like the best model for generalized terrestrial–arboreal form, while colugos are the best gliders which are unique among other convergent mammals in possessing the interdigital membranes. To what extent are these animals appropriate for modelling the stages of the evolutionary history of bats, is the important task of our study.

So, in contrast to the current tendencies, our choice of study subjects is not rooted in phylogeny. This attitude is warranted by the fact that based on the morphological features only, the bats looked close enough to the tree shrews and colugos, so close indeed that they could not be subtracted from Archonta until phylogenetic application of molecular methods. Since morphology is not as good for phylogenetic reconstructions, hence, in its turn, phylogeny is not as good for morphologic ones. The chiropterans diverged from their insectivorous ancestor so long ago and have gone in their specialisation so far away that their closest true (molecular) relatives among modern mammals can hardly bear the structural prerequisites for flight which we are searching for. Contrary to this, the dermopterans, although far in molecular respect, bear pronounced structural adaptations for air-borne locomotion. The forelimb musculoskeletal features, which we can find in both bats and colugos but do not find in tree shrews, are definitely the bat–colugo convergences and are most probably associated with the flight adaptations. So, the full set of such features should help to restore the gliding ancestor of bats or prove that their ancestor was not a glider.

In this book, we decided to concentrate on the evolution of the forelimb, which always plays the major role in the flapping wings of tetrapods. However, we touch the hindlimb as far as it is necessary.

Anatomical Nomenclature and Terms

When describing the musculature, we followed the nomenclature proposed by Gourtovoy and Dzerzhinsky (1992) for rat (*Rattus norvegicus*) and mink (*Neovison vison*). Muscles that are absent in these animals are named using the terms from Norberg (1972) for the Egyptian fruit bat (*Rousettus aegyptiacus*). Tendons and skeletal structures are named according to the veterinary nomenclature (Nomina Anatomica Veterinaria 2005), supplemented with some terms from human anatomy (Voss and Herrlinger 1956). The combination of terms from these works has provided rather complete designations for all the structures described.

To identify short muscles of the manus of the colugo and tree shrew, we used the data of Aristov (1981), Voss and Herrlinger (1956) and Nozdrachev and Polyakov (2001). Carpal bones were homologized based on the data on the development of the manus in members of the cohort Archonta (Stafford and Thorington 1998).

In the present study, we use designations of anatomical planes and surfaces generally accepted in descriptions of tetrapods (Figs. 1 and 2). To avoid confusion, all of these designations are retained in descriptions of the colugo and bats.

The scapular borders are designated as dorsal (upper, or vertebral), cranial (anterior) and caudal (posterior); the surfaces are medial and lateral (Fig. 2). Although the scapular borders and surfaces in bats are traditionally designated using other terms which indicate the current orientation of elements in these animals (the vertebral border is termed medial, the caudal border is lateral, the lateral surface is

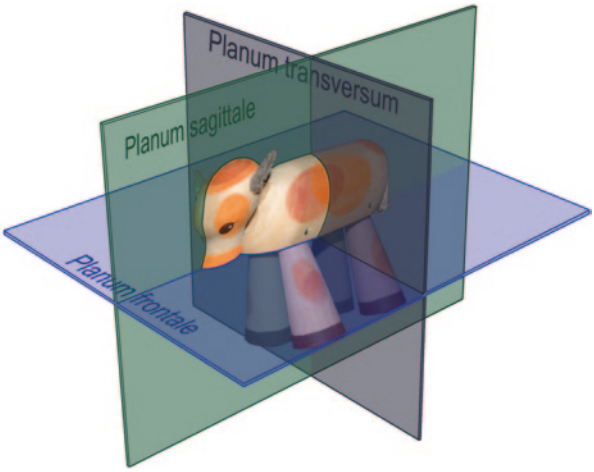


Fig. 1 Main planes used in anatomy. *Planum sagittale* – sagittal plane, *planum transversum* – transverse plane, *planum frontale* – frontal plane

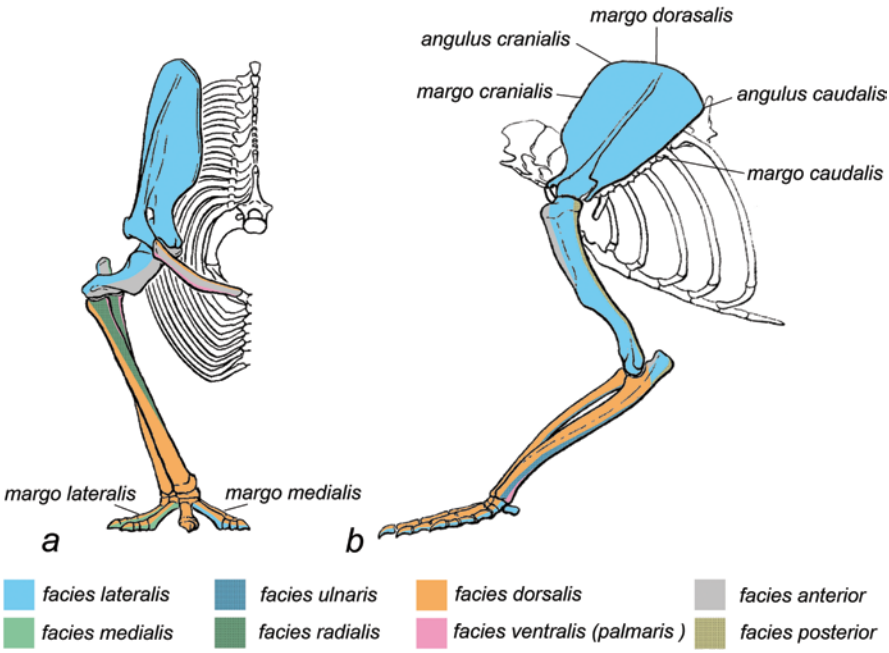


Fig. 2 The terms used in describing the surfaces, edges and faces of the skeletal elements. *a*. Anterior view, right forelimb. *b*. Lateral view, left forelimb

dorsal, and the medial surface is ventral), we refrained in this case from a special nomenclature to retain uniformity in descriptions.

In the humerus, the anterior (ventral), posterior (dorsal), medial and lateral surfaces are recognized. The description of the distal articular surface of the humerus requires some specification. In human anatomy, veterinary anatomy, and many other anatomical handbooks, the articular surface is divided into the *capitulum humeri* and *trochlea humeri* (Miller 1964; Voss and Herrlinger 1956; Nozdrachev and Polyakov 2001; Nomina Anatomica Veterinaria 2005). However, in many other morphological studies (e.g. Gambaryan and Aristov 1981; Gourtovoy and Dzerzhinsky 1992), the term trochlea is applied to the entire articular surface, which is divided into the lateral and medial condyles. We came to the conclusion that the second one better agrees with the joint structure of the animals under study. Therefore, hereinafter, the distal articular surface of the humerus is described as the trochlea consisting of *condylus lateralis* (the human *capitulum humeri*) and *condylus medialis* (the human *trochlea humeri*).

For the antebrachium (excluding olecranon, for which the terms of the humerus are kept), the sides are designated as dorsal, palmar, radial and ulnar (notice the typical torsion of the antebrachium on Fig. 2). In the manus, the surfaces are named dorsal and ventral (palmar) and borders are medial and lateral. The same terms are applied to each finger. The adduction and abduction of elements in the manus are described with reference to the longitudinal midline of the manus instead of the

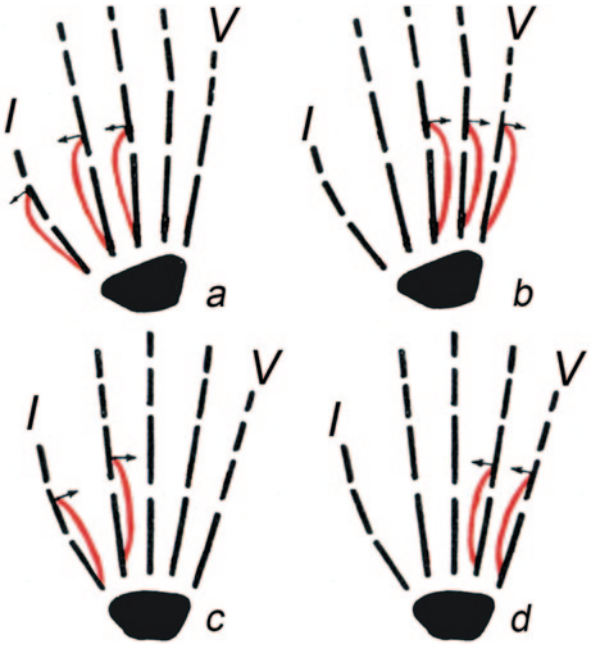


Fig. 3 The terms used in describing adduction and abduction of digits. *a*. Medial abduction. *b*. Lateral abduction. *c*. Lateral adduction. *d*. Medial adduction

body (Fig. 3). To treat these movements unequivocally, adduction of the first and second digits is named lateral and that of the fourth and fifth is medial adduction; abduction of these digits is designated as medial and lateral, respectively. Side deflexions of the third digit from the longitudinal axis of the manus are designated as medial and lateral abduction.

The abbreviations used in the present study are listed in the list of abbreviations.

References

Altringham JD (1998) Bats biology and behavior. Oxford University Press

Aristov AA (1981) Short muscles of the hand in the Murinae (Rodentia, Muridae). Zool Zh 60(11):1675–1682 (in Russian with English summary)

Bishop KL (2008) The evolution of flight in bats: narrowing the field of plausible hypotheses. Quart Rev Biol 83(2):153–169

Caple G, Balda RP, Willis WR (1983) The physics of leaping animals and the evolution of preflight. Am Nat 121(4):455–476

Clark BD (1977) Energetics of hovering flight and the origin of bats. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns in vertebrate evolution. Plenum Press, New York, p 423–425

Cooper NL, Cretekos CJ, Sears KE (2012) The evolution and development of mammalian flight. Wiley Interdisc Rev Dev Biol 1(5):773–779

Darwin CR (1872) Origin of species by means of natural selection: or, the preservation of favored races in the struggle for life. AMS Press, New York

Dial KP (2003) Wing-assisted incline running and the evolution of flight. Science 299(5605):402–404

Dial KP, Jackson BE, Segre P (2008) A fundamental avian wing-stroke provides a new perspective on the evolution of flight. Nature 451(7182):985–989
Dzerzhinsky FY (1972) Biomechanical analysis of the jaw apparatus of birds. MGU Publ, Moscow (in Russian)
Dzerzhinsky FY (1977) On the significance of biomechanical analysis in the reconstruction of the phylogeny of birds. In: Il'ichev VD (ed) Adaptive features of the evolution of birds. Nauka, Moscow, p 53–60 (in Russian)
Elangovan V, Yuvana Satya Priya E, Raghuram H, Marimuthu G (2007) Wing morphology and flight development in the short-nosed fruit bat *Cynopterus sphinx*. Zoology (Jena) 110(3):189–196
Gambaryan PP, Aristov AA (1981) Muscles and skeleton. In: Bashenina NV (ed) Bank vole. Nauka, Moscow, p 53–84 (in Russian)
Giannini NP (2012) Toward an integrative theory on the origin of bat flight. In: Gunnell GF, Simmons NB (eds) Evolutionary history of bats: fossils, molecules and morphology. Cambridge University Press, p 353–384
Gourtovoy NN, Dzerzhinsky FY (1992) Practical zootomy of vertebrates. Birds and mammals. Visshaya shkola, Moscow (in Russian)
Gunnell GF, Simmons NB (2005) Fossil evidence and the origin of bats. J Mammal Evol 12(1/2):209–246
Habersetzer J, Storch G (1989) Ecology and echolocation of the Eocene Messel bats. In: Hanak V (ed) European bat research 1987. Charles University Press, Prague, p 213–233
Habersetzer J, Storch G (1992) Cochlea size in extant Chiroptera and middle Eocene microchiropterans from Messel. Naturwissenschaften 79(10):462–466
Hill JE, Smith JD (1984) Bats, a natural history. University of Texas Press, Austin
Jackson SM, Thorington RW Jr (2012) Gliding mammals: taxonomy of living and extinct species. Smiths Contr Zool 638:1–117
Jepsen GL (1966) Early Eocene bat from Wyoming. Science 154(3754):1333–1339
Jepsen GL (1970) Bat origins and evolution. In: Wimsatt WA (ed) Biology of bats, vol 1. Academic Press, New York, London, p 1–64
Korzun LP (1986) The key trophic adaptation of forest birds revealed by means of functional morphology. In: Abstracts of the 1st congress of the all-union ornithological society and the 9th all-union ornithological conference, Zoological Institute, Leningrad, 16–20 December 1986 (in Russian)
Kovaleva I (2013) Integrative approach to Chiroptera origin problem. Nauchniy Dialog 3(15): 57–74 (in Russian with English summary)
Kovtun MF (1984) Structure and evolution of locomotion organs in bats. Naukova Dumka, Kiev (in Russian)
Kovtun MF (1988) On the origin of flight in bats. In: Topachevskiy VA, Kovtun MF (eds) Bats (morphology, ecology, echolocation, parasites, protection). Naukova Dumka, Kiev, p 5–12 (in Russian)
Kovtun MF (1990a) Problems of evolution of bats. Vestn Zool 3:3–12 (in Russian)
Kovtun MF (1990b) Problems of evolution of bats. Communication 2. Evolution of flight of bats. Vestn Zool 6:3–9 (in Russian)
Kurochkin EN, Bogdanovich IA (2008) On the origin of avian flight: compromise and system approaches. Biol Bull 35(1):1–11
Meng J, Hu Y, Wang Y, Wang X, Li C (2006) A Mesozoic gliding mammal from northeastern China. Nature 444(7172):889–893
Miller ME (1964) Anatomy of the dog. Saunders company, Philadelphia
Nomina anatomica veterinaria (2005), 5th edn. ICVGAN
Norberg UM (1972) Functional osteology and myology of the wing of the dog–faced bat *Rousettus aegyptiacus* (E. Geoffroy) (Mammalia, Chiroptera). Z Morph Tiere 73:1–44
Norberg UM (1985) Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. Am Nat 126(3):303–327

Novacek MJ (1985) Evidence for echolocation in the oldest known bats. Nature 315(6015):140–141
Novacek MJ (1991) Aspects of the morphology of the cochlea in microchiropteran bats: an investigation of character transformation. Bull Am Mus Nat Hist 206:84–100
Nozdrachev AD, Polyakov EL (2001) Anatomy of the rat (Laboratory animals). Lan, St. Petersburg (in Russian)
O'Leary MA, Bloch JI, Flynn JJ et al (2013) The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339(6120):662–667
Padian K (1985) The origins and aerodynamics of flight in extinct vertebrates. Palaeontology 28(3):413–433
Padian K (2011). Phylogenetic distribution of ecological traits in the origin and early evolution of bats. In: Program and Abstracts, 71st Annual Meeting Society of Vertebrate Paleontology, Paris Las Vegas, Las Vegas, Nevada USA, November 2–5, 2011
Panyutin KK (1980) Origin of flight of bats. In: Kuzyakin AP, Panyutin KK (eds) Chiroptera. Nauka, Moscow, p 276–286 (in Russian)
Peters DS (2002) Anagenesis of early birds reconsidered. Senck lethaea 82(1):347–354
Pirlot P (1977) Wing design and the origin of bats. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns in vertebrate evolution. Plenum Press, New York, p 375–410
Rayner JMV (1988) The evolution of vertebrate flight. Biol J Linn Soc 34(3):269–287
Scholey K (1986) The evolution of flight in bats. Biona Rep 5:1–12
Sears KE, Behringer RR, Rasweiler JJ, Niswander LA (2006) Development of bat flight: morphologic and molecular evolution of bat wing digits. Proc Nat Acad Sci 103(17):6581–6586
Simmons NB, Geisler JH (1998) Phylogenetic relationships of *Icaronycteris, Archaeonycteris, Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. Bull Am Mus Nat Hist 235:1–182
Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2008) Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451(7180):818–822
Smith JD (1977) Comments on flight and the evolution of bats. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns in vertebrate evolution. Plenum Press, New York, p 427–438
Speakman JR (1993) The evolution of echolocation for predation. Symp Zool Soc Lond 65:39–63
Speakman JR (1999) The evolution of flight and echolocation in pre–bats: an evaluation of the energetics of reach hunting. Acta Chiropterologica 1(1):3–15
Speakman JR (2001) The evolution of flight and echolocation in bats: another leap in the dark. Mammal Rev 31(2):111–130
Speakman JR, Anderson ME, Racey PA (1989) The energy cost of echolocation in pipistrelle bats (*Pipistrellus pipistrellus*). J Comp Physiol A 165(5):679–685
Stafford BJ, Thorington RW Jr (1998) Carpal development and morphology in archontan mammals. J Morphol 235(2):135–155
Voss H, Herrlinger R (1956) Taschenbuch der Anatomie. Band 1. Einführung in die Anatomie. Bewegungsapparat. VEB Gustav Fischer Verlag, Jena
Yudin KA (1957) On problems of morphological studies in ornithology. Zool Zh 36(1):113–121 (in Russian)
Yudin KA (1978) Classical morphological characters and the modern classification of animals. Trans ZIN 76:3–8 (in Russian)

List of Abbreviations

m.	*Musculus*
mm.	*Musculi*
p.	*Pars*
c.	*Caput*
lig.	*Ligamentum*
DI–DV	*Digits I–V*
McI–McV	*Ossa metacarpalia I–V*
$PhI_{1\text{-}2}$–$PhV_{1\text{-}3}$	*Phalanges digitorum*

Contents

1 Forelimb Morphology of Tree Shrews 1
Skeleton 1
Joints 9
Musculature 12
Muscles of Shoulder Girdle 12
Musculature of Shoulder Joint 19
Musculature Originating from Trunk 19
Intrinsic Musculature of Shoulder Joint 23
Musculature of Free Limb 29
Musculature of Humerus 29
Musculature of Antebrachium 32
Intrinsic Muscles of Manus 41
References 49

2 Forelimb Morphology of Colugos 51
Wing Membrane 52
Skeleton 53
Joints 59
Musculature 64
Musculature of Shoulder Girdle 65
Musculature of Shoulder Joint 68
Muscles Extending from Trunk 68
Intrinsic Musculature of Shoulder Joint 73
Musculature of Free Limb 85
Musculature of Humerus 85
Musculature of Antebrachium 87
Intrinsic Muscles of Manus 103
Musculature of Wing Membrane 112
References 113

3 Forelimb Morphology of Bats 115
Wing Membrane 116
Skeleton 117
Joints 129
Musculature 139
Musculature of Shoulder Girdle 139
Musculature of Shoulder Joint 158
Musculature Originating from Trunk 158
Intrinsic Musculature of Shoulder Joint 162
Musculature of Free Limb 174
Musculature of Humerus 174
Muscles of Antebrachium 177
Intrinsic Muscles of Manus 194
Musculature of Wing Membrane 201
References 202

4 Functional Analysis of Locomotor Apparatus of Colugos 205
Some Biological Aspects of Colugos 205
Locomotion of Colugos 208
Gliding 208
Climbing up Trunks 210
Climbing under Branches 211
Mobility of Shoulder Girdle 212
Static Analysis 215
Clinging Flat onto Trunk 216
Gliding 219
References 225

5 Functional Analysis of Locomotor Apparatus of Bats 227
Locomotor Features of Chiropterans 227
Kinematics of Chiropteran Wing 233
Interaction of Wing with Air 242
Internal Biomechanics of Wing 245
Static Analysis of Downstroke 247
References 255

6 Comparative Morphofunctional Analysis 259
Morphofunctional Features of Shoulder Girdle 259
Morphofunctional Features of Free Limb 269
Discussion on Comparative Morphology 274
Flight and Primitive Locomotion of Prototherians 274
Flight and Brachiation 275
Flight and Gliding 276
References 278

7 Evolutionary Scenario for Establishment of Flapping Flight 281
References 290

Citation Index 291

Anatomical Index 295

Chapter 1
Forelimb Morphology of Tree Shrews

Classical studies of Le Gros Clark (1924, 1926) and Davis (1938) were devoted to the anatomy of tree shrews. Osteology and some groups of locomotor muscles were described by Carlsson (1922), Miller (1935), Verma (1965), George (1977), and Sargis (2002d). Haines (1955) described the hand muscles in two species and supplied the set of histological cross-sections of the whole manus, which helps to trace in detail the arrangement of muscles which are most difficult for dissection. Subsequently, the morphology and functional analysis of limbs of tree shrews was investigated primarily in the context of mammalian adaptation for the arboreal mode of life and the origin of primates (Jenkins 1974; George 1977; Sargis 2001, 2002a, b, c, 2004).

For a detailed description of the musculature, we prepared one specimen of *Tupaia belangeri*[1] (Scandentia: Tupaiidae) provided by the Zoological Museum of Moscow State University (ZMMU). The structure of the skeleton and joints is described based on a syndesmological preparation[2] and a dry skeleton[3].

Skeleton

The shoulder girdle of tree shrew displays the structure generally typical for quadrupedal mammals with terrestrial locomotion (Fig. 1.1) (Gambaryan 1974; Kuznetsov 1999). *Tupaia belangeri*, which we studied, does not show considerable differences in the forelimb osteology as compared with the published data on the other tree shrews. So, we provide here the generalized description.

[1] Specimen ZMMU, no. s-173368.

[2] Syndesmological preparation of skeleton is wet preparation obtained completely removing the musculature and retaining all articular ligaments. It is used for the study of mobility in the joints.

[3] Specimen ZMMU, no. s-169721.

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_1

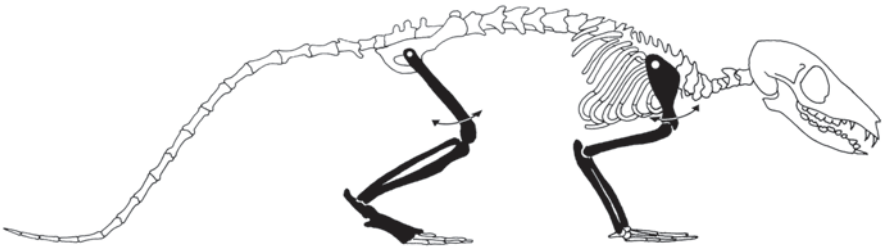


Fig. 1.1 Scheme of the tree shrew skeleton; lateral view. Arrows indicate the direction of swinging movements of the first elements of three-segment Z-like limbs.

Scapula (Fig. 1.2, Fig. 1.3) The scapula is positioned in the parasagittal plane. Its structural details are well described in *Anathana ellioti* by Verma (1965). Its dorsal border (*margo dorsalis*) gently passes into the cranial border (*margo cranialis*); therefore, the dorsocranial angle (*angulus cranialis*) is not pronounced.

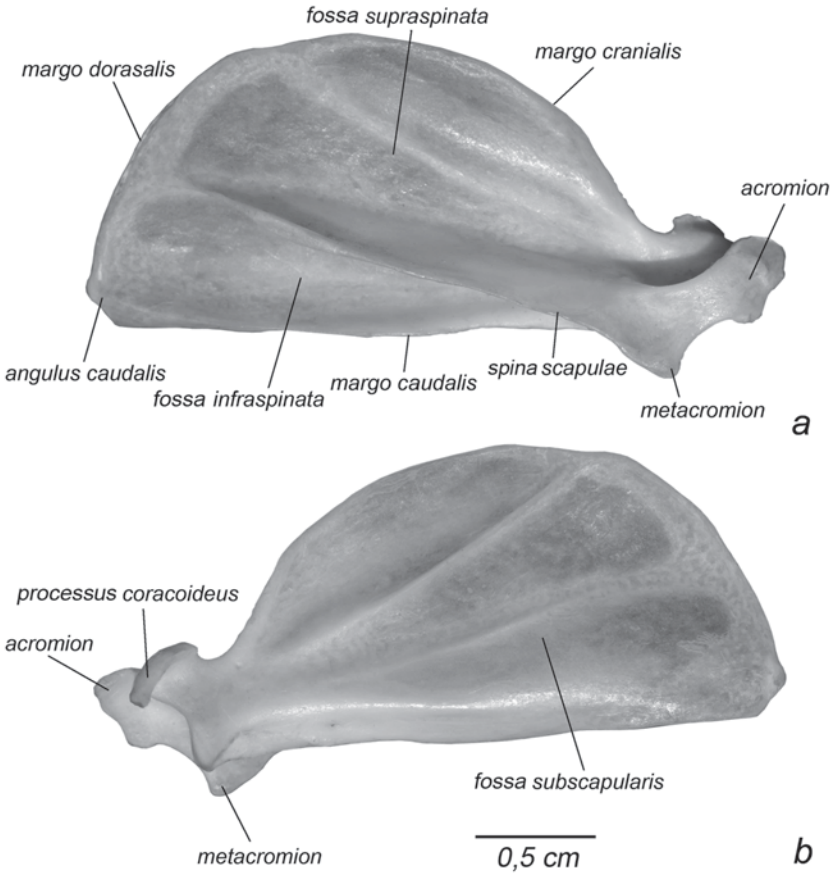


Fig. 1.2 The scapula of *Tupaia belangeri,* right forelimb. *a. Lateral view b. Medial view*

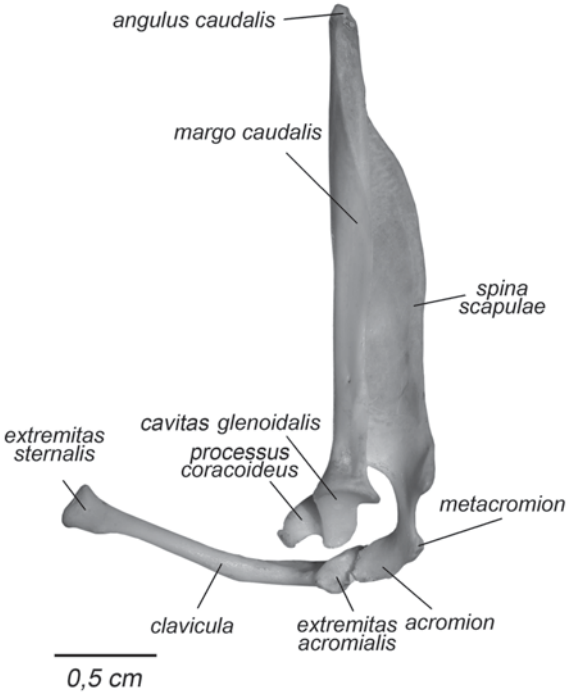


Fig. 1.3 The clavicle and scapula of *T. belangeri,* right forelimb, posterior view.

The dorsocaudal angle (*angulus caudalis*), on the contrary, is distinct. The straight caudal border (*margo caudalis*) is curved externally and forms a wide shelf which is mostly (including the flattened area at the dorsocaudal angle) occupied by the origin of the *m. teres major*; near glenoid the shelf is occupied by the origin of the *m. triceps brachii caput longum*. According to our data and to the description of Verma (1965), the supraspinous fossa (*fossa supraspinata*) is somewhat larger than the infraspinous fossa (*fossa infraspinata*). However, Le Gros Clark (1926) notes for the pen-tailed tree shrew (*Ptilocercus lowii*) the prevalence of the infraspinous fossa; this is confirmed by Sargis (2002b). The scapular spine (*spina scapulae*) is high, the acromion is very well developed. Its cranial part is articulated with the clavicle. The metacromion is poorly pronounced. On the contrary, the coracoid process (*processus coracoideus*) is very well developed. The medial surface of the scapula, subscapular fossa (*fossa subscapularis*), has two low crests (Verma 1965) mentions only one for *Anathana*). The glenoid (*cavitas glenoidalis*) is narrow, extended, and rather flat. The supraglenoid tubercle (*tuberculum supraglenoidale*) at its cranial border is developed rather well.

Clavicula (Fig. 1.4) The clavicle is dorsoventrally flattened. Its proximal two-thirds are slightly convex ventrad and the distal one-third is deflected caudad.

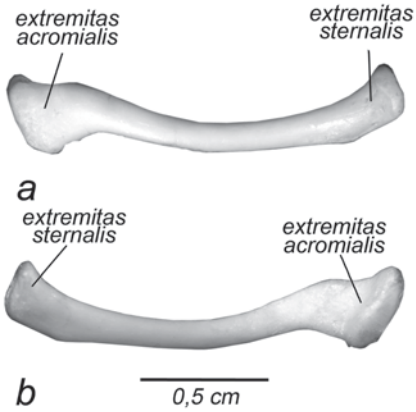


Fig. 1.4 The clavicle of *T. belangeri,* right forelimb. *a. Anterior view b. Posterior view*

The expanded oval ends (*extremitas sternalis* and *extremitas acromialis*) have flattened articular facets (*facies articularis sternalis* and *facies articularis acromialis*).

Humerus (Fig. 1.5, Fig. 1.6) The humerus is rather massive. The greater tubercle (*tuberculum majus*) on its proximal end is hardly visible and the lesser tubercle (*tuberculum minus*) is somewhat better developed; however, neither has a distinct neck. Crests on the tubercles are rather low. The pectoral crest (*crista pectoralis*) is present but extremely small. On the distal epiphysis, the lateral epicondyle (*epicondylus lateralis = ectepicondylus*) is poorly developed, but bears a long crest (*crista supracondylaris lateralis*). The medial epicondyle (*epicondylus medialis = entepicondylus*), on the contrary, is very wide, but its crest (*crista supracondylaris medialis*) is slightly shorter than the lateral crest. In tree shrews, the lateral and medial condyles equally participate in the trochlea. On the posterior humeral surface, proximal to the trochlea, there is a shallow fossa for the olecranon (*fossa olecrani*). In turn, on the anterior surface, proximal to the trochlea, there is a similar shallow fossa, which is not subdivided into typical radial and coronoid parts. We designate it as the radial fossa,[4] since the coronoid process of the ulna is undeveloped and, as the elbow is flexed, the ulna does not reach the bottom of the fossa; thus, this fossa only houses the radius. The *fossa radialis* and *fossa olecrani* are separated by a relatively thick bony wall.

[4] We use this term in descriptions of all animals.

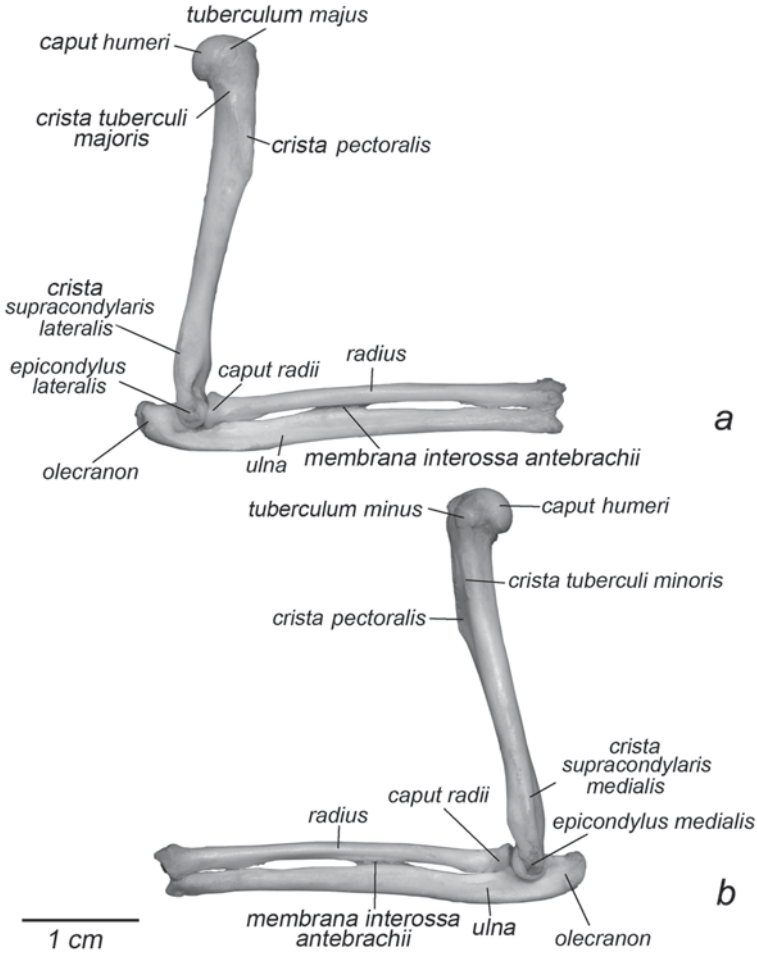


Fig. 1.5 The humerus and antebrachium of *T. belangeri,* right forelimb. *a. Lateral view b. Medial view*

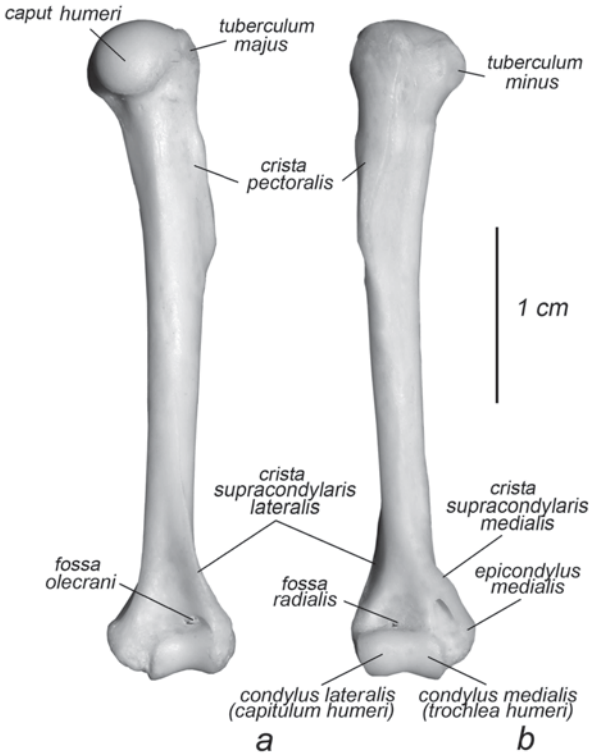


Fig. 1.6 The humerus of *T. belangeri,* right forelimb. *a. Posterior view b. Anterior view*

Antebrachium (Fig. 1.5) The **ulna** and **radius** are almost equally developed in the antebrachium. Close to the midlength, they are connected by a narrow collagenic *membrana interossa antebrachii*. The olecranon is well pronounced on the ulna, although it is not excessively developed. The distal end of the ulna is sharpened to form the styloid process which reaches the carpus. The distal end of the radius bears its own styloid process, which is however much wider and is not in fact styloid shaped.

Carpus (Fig. 1.7, Table 1.1) The carpus consists of eight bones: *scapholunatum* (produced by fusion of two proximal carpals, the *radiale* and *intermedium*), *cuneiforme*, *centrale*, *pisiforme*, *trapezium*, *trapezoideum*, *capitatum*, and *uncinatum* (produced by fusion of distal carpals IV and V). The most proximal position is occupied by the *pisiforme*, which lies at the level of the antebrachiocarpal joint slit. The *scapholunatum* and *cuneiforme* form the proximal row and the distal row consists of four bones: *trapezium*, *trapezoideum*, *capitatum*, and *uncinatum*. The *centrale* wedges in between the proximal and distal rows and, along with the *trapezoideum*, is not visible from the ventral side (Fig. 1.7b). Similar descriptions are given by Carlsson (1922) and Sargis (2002b). For *Anathana*, Verma (1965) notes the lack of *centrale*, the fusion of *trapezium* with *trapezoideum*, and the fusion of *capitatum* with *uncinatum*. In our opinion, *centrale* could be fused to *scapholunatum* indeed,

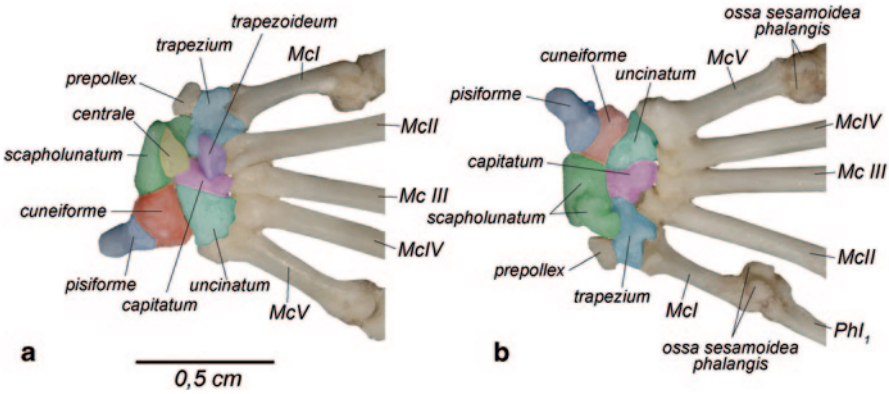


Fig. 1.7 The carpus of *T. belangeri,* right forelimb. *a. Dorsal view b. Ventral view*

but both mentioned fusions in the distal row are doubtful as they are extremely rare among mammals beyond ungulates. Probably, the boundaries between the distal bones were simply hidden by the connecting ligaments which were not thoroughly removed by Verma (1965). In *Ptilocercus*, nine separate bones are usually reported in the wrist, due to non-fused condition of *scaphoideum* and *lunatum* (Le Gros Clark 1926; Stafford and Thorington 1998; Sargis 2002d). The similar presence of separate *scaphoideum* and *lunatum* is noted for *Dendrogale* by Stafford and

Table 1.1 Carpal bones

Taxa	Proximal and central rows		Distal row	
Tree shrews	Terms used	Synonyms	Terms used	Synonyms
	Scapholunatum	*Radiale* (*scaphoideum*) + *intermedium* (*lunatum*)	***Trapezium***	*Carpale distale 1, multangulum majus, cubiforme*
	Centrale		***Trapezoideum***	*Carpale distale 2, multangulum minus*
	Cuneiforme	*Ulnare, triquetrum, pyramidale*	***Capitatum***	*Carpale distale 3, magnum*
	Pisiforme[a]		***Uncinatum***	*Carpale distale 4 + 5, unciforme, hamatum*
Colugos and bats[b]	***Scaphocentralolunatum***	*Radiale + intermedium* (*lunatum*) *+ centrale*	*The same as in tree shrews*	
	Cuneiforme	*Ulnare, triquetrum, pyramidale*		
	Pisiforme			

[a] The *pisiforme* is an ancient sesamoid bone ascribed to the proximal row arbitrarily. It is placed proximal to the rest of the carpus in tree shrews, ventral to the *cuneiforme* in colugos, and at the distal row of carpals in bats

[b] According to Stafford and Thorington (1998)

Thorington (1998) and Sargis (2002d). However in the other publication, Sargis (2002b) points out that in both of these genera of tree shrews *scaphoideum* and *lunatum* are not entirely separate.

Digits (Fig. 1.8, Table 1.2) The prepollex is well developed, positioned at the medial side of the carpus at the level of the *trapezium*. The phalangeal formula is typical of mammals: two phalanges (*phalanges digitorum*) in finger I and three in fingers II–V. Horny sheaths completely cover the bony ungual phalanges. Claws are equally well developed in all fingers and have sharp edges.

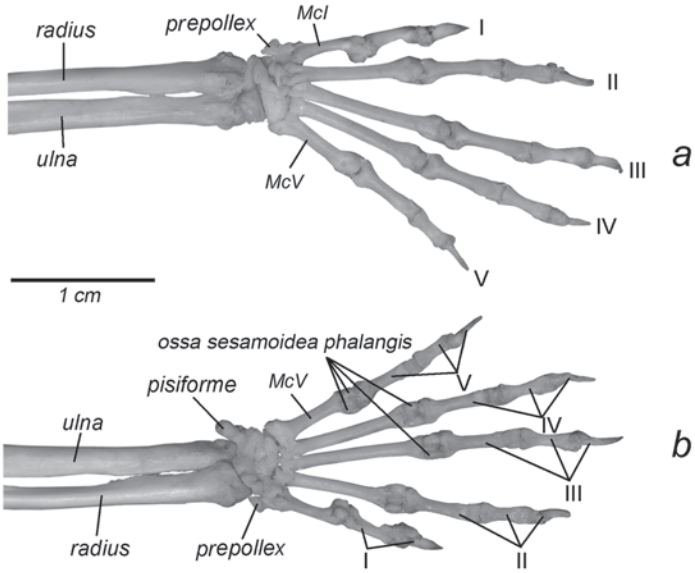


Fig. 1.8 The manus of *T. belangeri,* right forelimb. *a. Dorsal view b. Ventral view*

Table 1.2 Digits

Taxa	*Prepollex*	Number of phalanges				
		Digit I	Digit II	Digit III	Digit IV	Digit V
Tree shrews	+	2	3	3	3	3
Colugos	+	2	3	3	3	3
Fruit bats	+	2	3	2–3[a]	2	2
Microbats	+	2	0–1	2–3	2–3	2–3

[a] The third phalanges of digits III–V in Pteropodidae, Rhinopomatidae, Emballonuridae, Rhinolophidae, Hipposideridae, Nycteridae, Megadermatidae, Natalidae, Furipteridae, Noctilionidae is cartilaginous, often rudimentary, and can be completely absent. (Walton and Walton 1970)

Joints

We judged about the mobility of joints based on the structure of articular surfaces, using manipulations with the syndesmological preparations, and from the photographs and video records of live animals.

As in other animals investigated by us, the scapula of tree shrews is connected to the sternum by the clavicle.

The **sternoclavicular articulation** (*articulatio sternoclavicularis*) is provided with the *ligamentum sternoclaviculare*, connecting the proximal (sternal) end of the clavicle to the medial part of the cranial border of the *manubrium streni* (Fig. 1.9). This ligament restricts the distance between the sternal end of the clavicle and the sternum, but allows a wide range of other mobility.

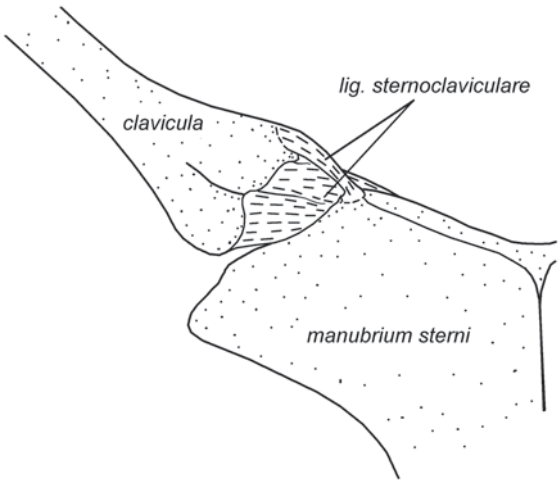


Fig. 1.9 The sternoclavicular articulation of *T. belangeri,* right forelimb, ventral view.

The **acromioclavicular articulation** (*articulatio acromioclavicularis*) is similarly provided with the *ligamentum acromioclaviculare*, connecting the end of the acromion process of the scapula with the distal (acromial) end of the clavicle (Fig. 1.10). The ligament allows mobility in all directions within its reach. In addition, the position of the clavicle relative to the scapula is controlled by the *ligamentum coracoclaviculare*. It connects the distal end of the clavicle with the base of the coracoid process of the scapula (Fig. 1.10).

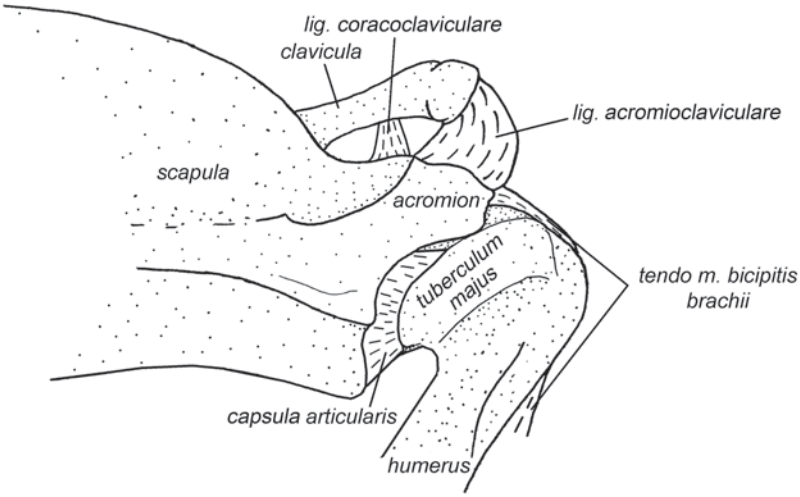


Fig. 1.10 The acromioclavicular articulation and shoulder joint of *T. belangeri,* right forelimb, lateral view.

The articular capsule of the **shoulder joint** (*articulatio humeri*) of tree shrews is formed by loose connective tissue. It includes two small firm ligaments. One connects the lateral border of the glenoid with the neck of the humeral head (*caput humeri*) (Fig. 1.10) and the second connects the medial border of the glenoid with a groove between the humeral head and the lesser tubercle. The articular capsule (*capsula articularis*) incorporates the distal tendons of the three muscles: *m. supraspinatus*, *m. infraspinatus*, and *m. subscapularis*. The spheric shape of the joint and its loose capsule provide a wide range of mobility (retraction/protraction, rotation, abduction/adduction).

The **elbow joint** (*articulatio cubiti*) is formed by three bones, humerus, ulna, and radius. The humeral trochlea consisting of the medial and lateral condyles fits into the respective articular concavity of the antebrachium (see Fig. 1.5). The entire posterior part of the trochlea contacts only with the ulna, the anterior part of the lateral condyle is only articulated with the radius, while the anterior part of the medial condyle, with both bones. In addition, at the point of contact of the proximal head of the radius (*caput radii*) with ulna, there is a sliding articulation.

When the elbow is maximally extended, the border of the articular surface of the olecranon comes into the *fossa olecrani* of the humerus and its cranial surface (proximal to the articular border) rests against the area between epicondylar crests. When maximally flexed, the border of the articular surface of the radius comes into the *fossa radialis*.

The elbow joint structure allows certain axial rotation of the antebrachium, as is confirmed by manipulations with the syndesmological preparations. Pronation and supination is mainly achieved by the movement of the two antebrachial bones as a single unit over the humeral trochlea. Mutual mobility between the ulna and radius

is very weak but exists too, as is shown by the presence of the *m. pronator quadratus*, which can do nothing else than shifting the two bones relative to each other. The total rotation range, combined from rotation of the ulna and radius together relative to the humerus and rotation of the radius relative to the ulna, can approach 80º. This allows tree shrews to move with pronated antebrachium (fingers point forwards) over a flat surface (ground or thick trunks) and with supinated antebrachium (fingers point laterally) along relatively thin branches, grasping them from the two sides by the left and right hands.

Both bones of the antebrachium participate in the formation of the **antebrachiocarpal joint** (*articulatio antebrachiocarpea*) (Fig. 1.8). Distally, the joint is formed by the *scapholunatum* and *cuneiforme*. In addition to flexion/extension, this joint allows certain adduction and abduction of the wrist and also slight rotation which is added to the just described rotation in the antebrachium.

Bones of the proximal and distal rows of the carpus are articulated by the **mediocarpal joint** (*articulatio mediocarpea*), which is stiff (*amphiarthrosis*) in tree shrews. The **intercarpal joints** (*articulationes intercarpeae*) between bones within the proximal and distal rows are also rigid. All joints between the carpals are strengthened by interosseous intercarpal ligaments, which connect bones of the distal and proximal rows. The ligaments are named according to the bones which they connect.

Of **carpometacarpal joints** (*articulationes carpometacarpeae*), the first one (between the *trapezium* and metacarpal I) shows the greatest range of mobility. Carpometacarpal joints II–V are almost immobile.

Mutual mobility of metacarpals II–V is additionally limited in the **intermetacarpal joints** (*articulationes intermetacarpeae*); the sides of the proximal heads of metacarpals tightly adjoin each other and are connected by ligaments.

The **metacarpophalangeal joints** (*articulationes metacarpophalangeae*) of neighboring fingers from second to fifth are connected to each other by transverse ligaments, called *ligamenta metacarpea transversa profunda*, which restrict divergence of metacarpals (Fig. 1.51). The distal ends of all metacarpals have a spheric condyle, which fits into a rounded concavity on the proximal end of respective basal phalanx (Fig. 1.11a). Therefore, the metacarpophalangeal joints allow a wide range

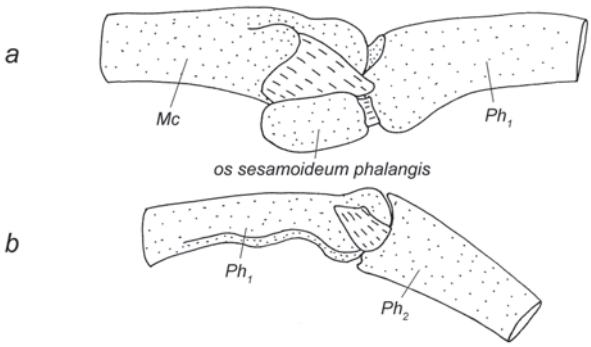


Fig. 1.11 The digital joints of *T. belangeri,* lateral view. *a. Metacarpophalangeal joint b. Interphalangeal joint*

of mobility, except for flexion, which is strongly restricted by paired sesamoid bones (*ossa sesamoidea phalangis proximalia*) incorporated in the ventral wall of the articular capsule. These triangular bones lie in paired incisures on the ventrolateral surfaces of the metacarpal condyle and, when the joint is flexed, their distal ends rest against outgrowths on the ventrolateral surfaces of the proximal end of the basal phalanx. As soon as the proximal shift of sesamoid bones along the metacarpal is prevented by ligaments of the articular capsule, flexion in the joint is stopped.

The **interphalangeal joints** (*articulationes interphalangeae manus*) lack sesamoid bones. The distal head of a more proximal phalanx has a tochlear articular surface, in a deep medial groove of which, a respective ridge of a concave proximal end of a more distal phalanx slides (Fig. 1.11b). Collateral ligaments of the articular capsule restrict mobility of this joint to flexion–extension. Since the articular surface of the trochlea extends more on the ventral side of the distal head of the phalanx, rather than on its dorsal side, hyperextension in the joint is small. The structure of distal interphalangeal joints differs somewhat. The articular trochlea has a shallower groove and, hence, the ridge of the ungual phalanx sliding along it is less developed.

Musculature

Muscles of Shoulder Girdle

Musculus sternocleidomastoideus (Figs. 1.12, 1.13, 1.15–1.16, 1.21) originates with the help of a small aponeurosis from the lateral part of the occipital crest of the skull and from the mastoid. At the end of the first one-third of its extent, the muscle is divided into two portions. *Pars sternomastoideus* inserts on the *manubrium sterni* from its midline (contralateral muscles are attached very closely) almost to the sternoclavicular articulation. *Pars cleidomastoideus* inserts on the proximal end of the clavicle on its cranial side.

The portions of this muscle provide depression and lateral movements of the head.

In all animals we have dissected the **trapezius muscle** (*m. trapezius*) portions are well differentiated; therefore, we treat them and name as separate muscles.

Musculus clavotrapezius is absent in tree shrews.

Musculus acromiotrapezius (Figs. 1.12, 1.13) is flat and very wide. It originates from the occipital crest and the midline of the dorsal surface of the neck (up to the third thoracic vertebra), line-on-line with the contralateral muscle. The cranioventral border of the muscle is thicker, and the caudal border is closely connected with the *m. spinotrapezius*. It inserts on the scapular spine somewhat apart from its dorsal end; near acromion the attachment occupies the whole anterior surface of the spine.

The muscle pulls the whole scapula craniomedially.

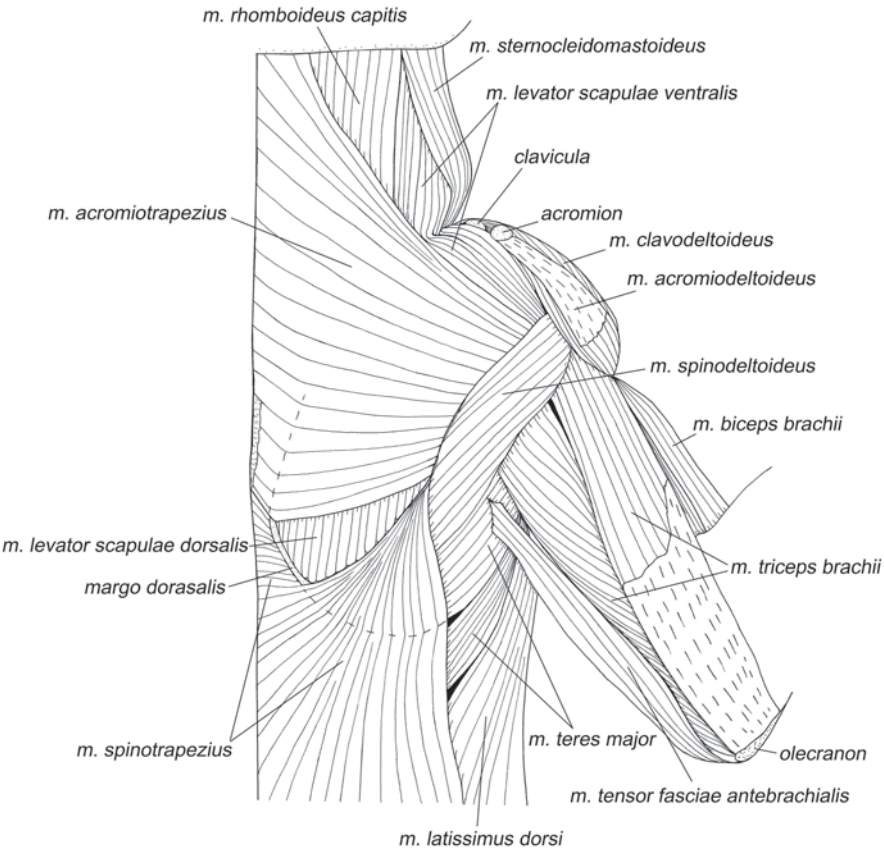


Fig. 1.12 Forelimb muscles of *T. belangeri,* dorsal view, layer I.

Musculus spinotrapezius (Figs. 1.12, 1.13) originates from apices of the neural spines and interspinous ligaments (*ligamenta interspinalia*)[5] from the third thoracic through the first lumbar vertebrae. It inserts on the scapular spine somewhat apart from its dorsal end; some fibers insert by an aponeurosis on the dorsal border of the scapula cranial to the spine. The most anterior fibers are inseparable from caudal fibers of the *m. acromiotrapezius*.

The muscle pulls the dorsal part of the scapula caudally and somewhat medially.

The **rhomboid muscles** (*mm. rhomboidei*) of tree shrews are represented by three well-differentiated muscles, as in many other quadrupedal terrestrial mammals.

Musculus rhomboideus capitis (Figs. 1.12–1.15, 1.19) originates as a wide band from the occipital crest and inserts on the dorsal border of the scapula cranial to the spine. Most of its distal part is covered by the *m. rhomboideus cervicis*.

The muscle pulls the dorsal border of the scapula cranially.

[5] The interspinous ligaments connect apices of neural spines of neighboring vertebrae.

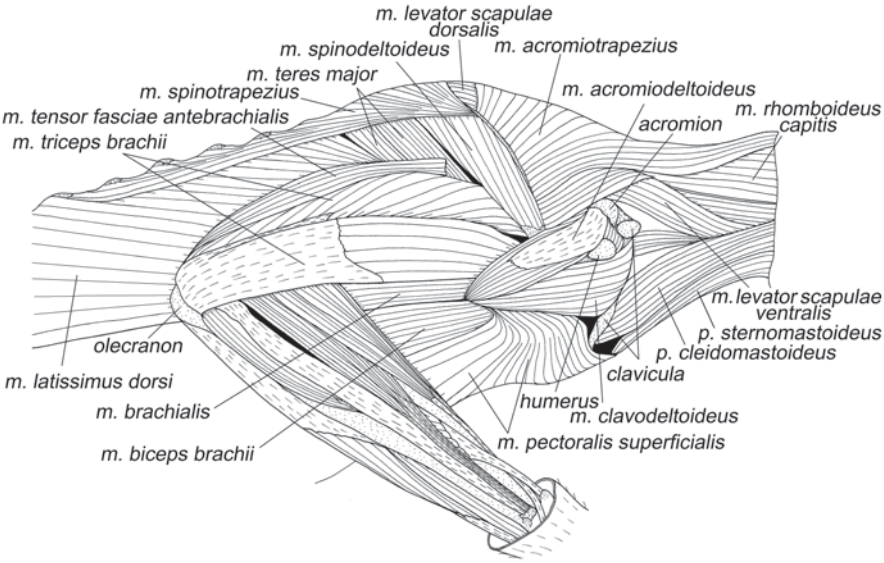


Fig. 1.13 Forelimb muscles of *T. belangeri,* lateral view, layer I.

Musculus rhomboideus cervicis (Figs. 1.14, 1.19) is very wide at the base, originates from the midline of the dorsal surface of the neck, line-on-line with the contralateral muscle, from the epistropheus through thoracic vertebra 5. It inserts on the dorsal border of the scapula adjacent to the spine, partially by an aponeurosis. The cranial part of the end covers the end of the *m. rhomboideus capitis* and the caudal part, in turn, is covered by the *m. rhomboideus dorsi*. The muscle tends to differentiate: there are two bands inserted on the scapula with a slight overlap.

The muscle pulls the dorsal border of the scapula craniomedially.

Musculus rhomboideus dorsi (Fig. 1.19) originates from apices of the neural spines and interspinous ligament of thoracic vertebrae 5 and 6. It inserts on the dorsal border of the scapula between the spine and dorsocaudal angle. It overlaps the end of the *m. rhomboideus cervicis*.

The muscle pulls the dorsal border of the scapula medially.

Tree shrews have two (dorsal and ventral) levators of the scapula.

Musculus levator scapulae dorsalis (= *m. atlantoscapularis*) (Figs. 1.12–1.15, 1.17) originates by a short, rounded in section aponeurosis from the ventral surface of the transverse process of the atlas. It inserts on the dorsal border of the scapula cranial to the spine and on the dorsal part of the spine.

The muscle pulls the dorsal part of the scapula towards the head.

Musculus levator scapulae ventralis (= *m. atlantoacromialis*) (Figs. 1.12–1.15, 1.17) originates from the ventral surface of the atlas as a wide band and inserts on the metacromial process of the spine.

The muscle pulls the ventral part of the scapula cranially.

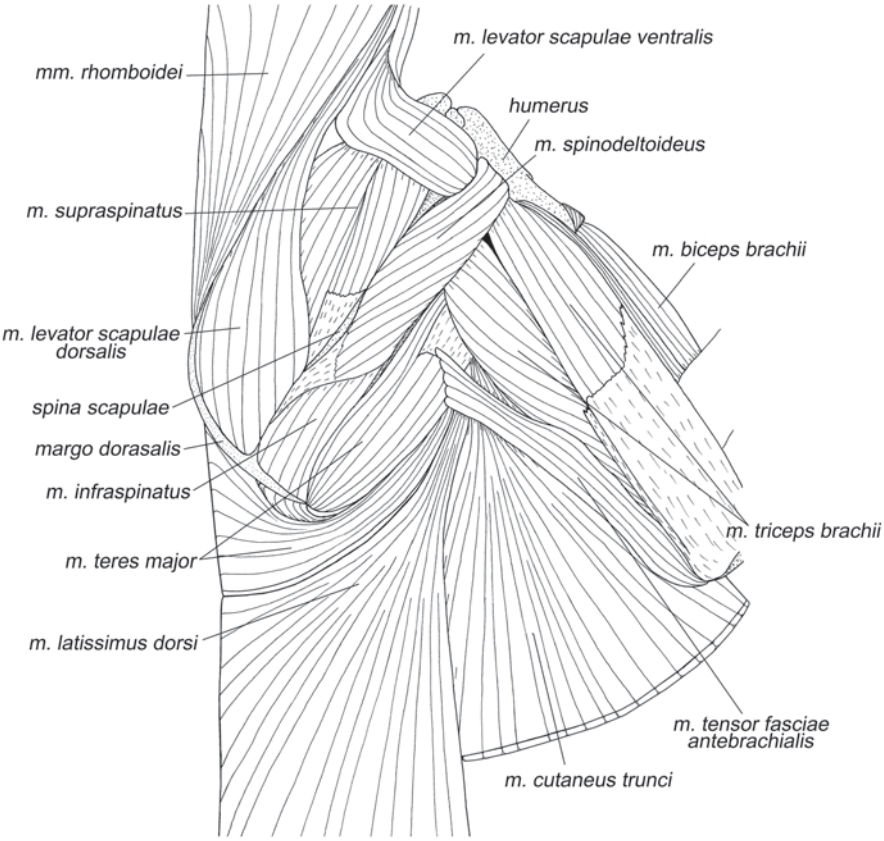


Fig. 1.14 Forelimb muscles of *T. belangeri,* dorsal view, layer II.

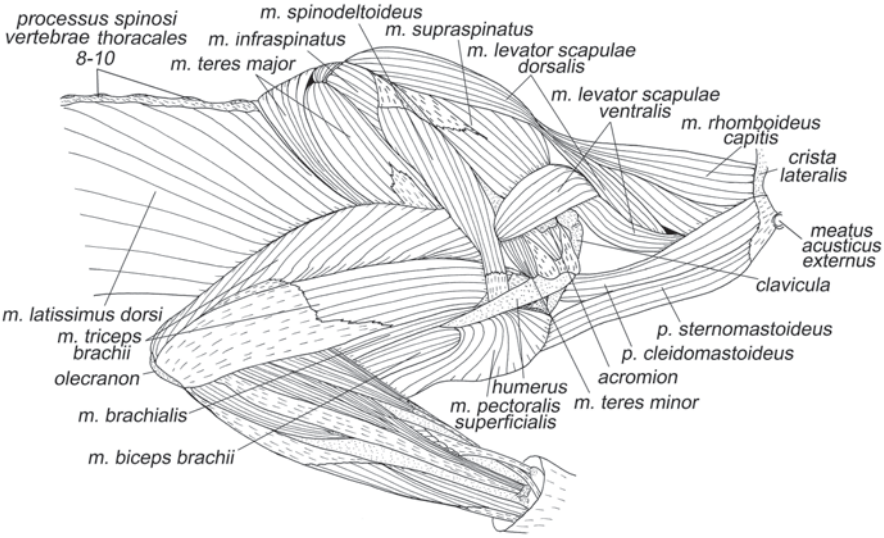


Fig. 1.15 Forelimb muscles of *T. belangeri,* lateral view, layer II.

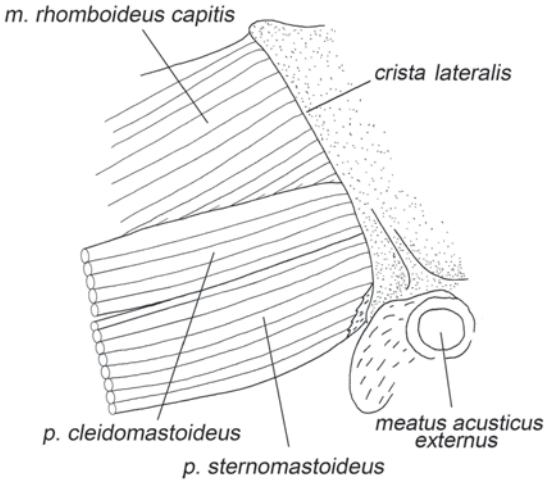


Fig. 1.16 Origin of the *m. sternomasoideus* and *m. cleidomastoideus* of *T. belangeri,* lateral view.

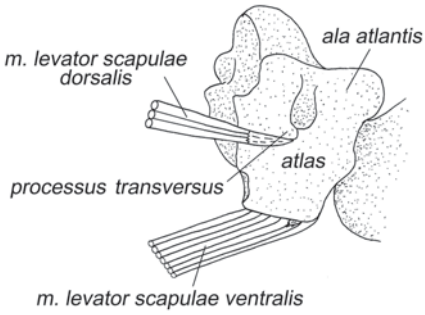


Fig. 1.17 Origin of the *mm. levatores scapulae* of *T. belangeri,* lateral view.

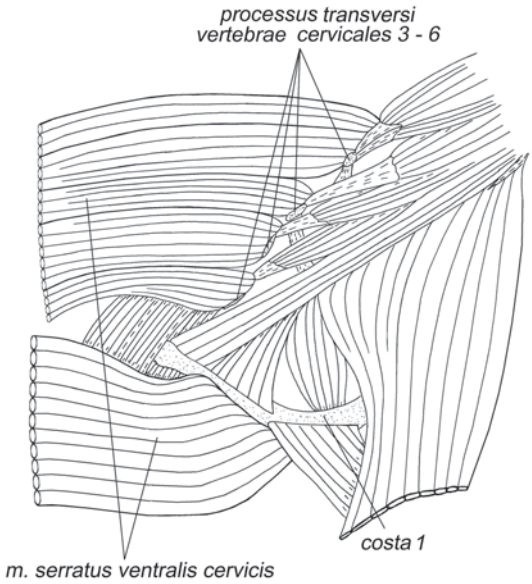


Fig. 1.18 Origin of the *m. serratus ventralis cervicis* of *T. belangeri,* ventral view.

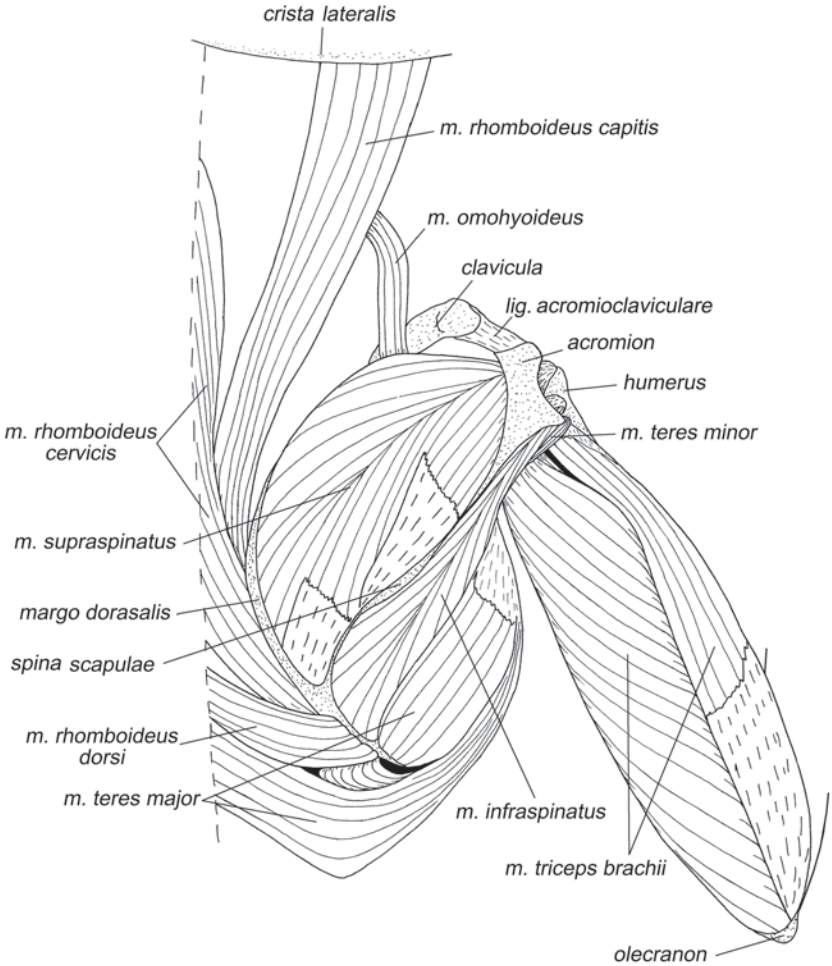


Fig. 1.19 Forelimb muscles of *T. belangeri,* dorsal view, layer III.

Musculus serratus ventralis is typically subdivided into the cervical and thoracal parts.

Musculus serratus ventralis cervicis (Figs. 1.18, 1.24, 1.25) is represented by the two wide bands. The cervical band originates by four slips from the transverse (costal) processes of cervical vertebrae 3–6 and from the adjacent aponeuroses of axial muscles of the neck. The costal band originates along the lower part of the dorsal (bony) segment of the first rib. The two bands unite to insert on the medial side of anterior two-thirds of the dorsal border of the scapula.

The muscle suspends the neck and thorax to the scapula and can play a role of the shock-absorber for the head and neck when landing after jumps.

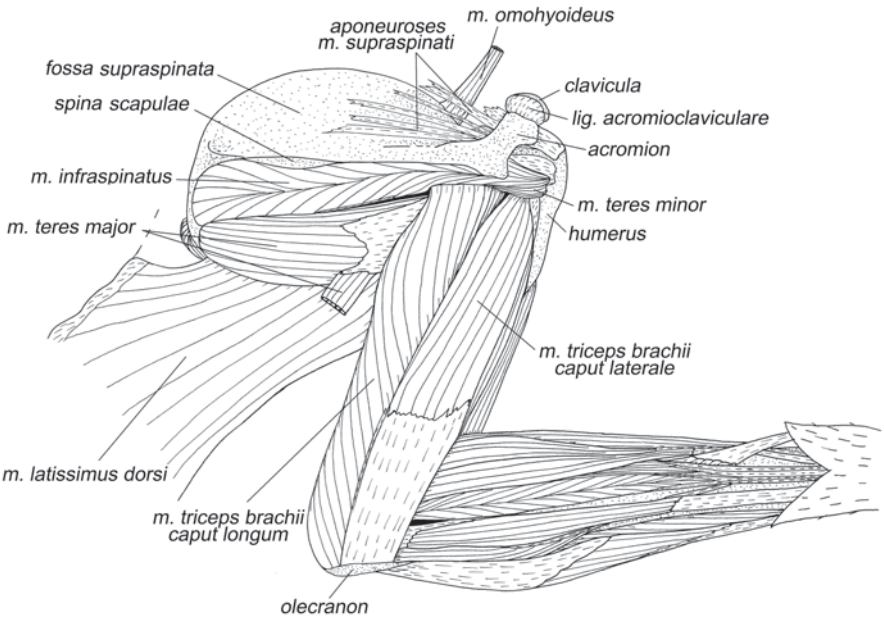


Fig. 1.20 Forelimb muscles of *T. belangeri,* lateral view, layer III.

Musculus serratus ventralis thoracis (Figs. 1.21, 1.24, 1.25) originates by five distinct slips from the external surface of the middle part of ribs 4–8 (and also rib 9 in some species, according to George 1977) and from aponeuroses of intercostal muscles. It inserts fleshy as well as by thin short aponeuroses on the medial surface of the scapula along the posterior one-third of the dorsal border.

The muscle suspends the thorax to the scapula.

Musculus omohyoideus (Figs. 1.19, 1.20) according to George (1977) originates from the posterior border of the hyoid bone lateral to the *m. sternohyoideus*, but we did not find this connection with the hypoglossal apparatus. The muscle arises in connective tissue ventral to the levators of the scapula as a very narrow band along the side of the neck and inserts on the cranial border of the scapula.

The muscle is rudimentary and probably plays a minor role, if at all.

Musculus subclavius (Figs. 1.22–1.24) originates from the middle part of the cranial border of the *manubrium sterni* and inserts on the dorsal surface of the distal part of the clavicle.

The muscle pulls the distal end of the clavicle caudally.

Musculature of Shoulder Joint

Musculature Originating from Trunk

Musculus latissimus dorsi (Figs. 1.12–1.15, 1.20–1.22, 1.24, 1.25, 1.27, 1.29, 1.30) originates from apices of the neural spines and interspinous ligaments from the seventh thoracic through second lumbar vertebrae by a very short and thin aponeurosis. Caudal to the second lumbar vertebra, fibers originate from the dorsal superficial fascia, with a gradually increasing indent from the vertebral column. A wide fan

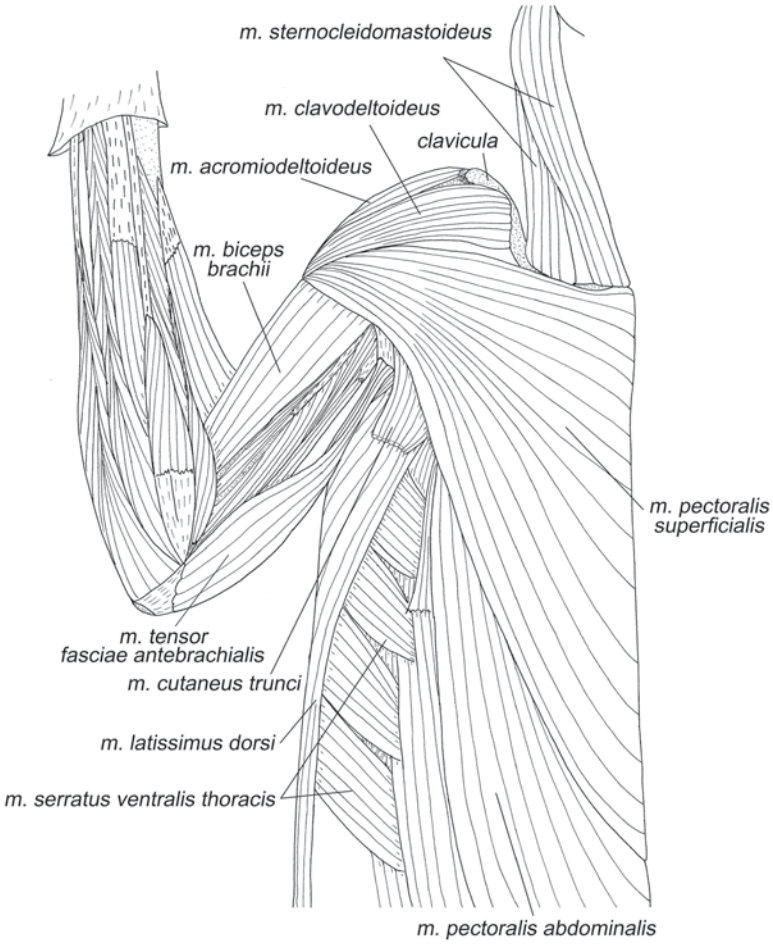


Fig. 1.21 Forelimb muscles of *T. belangeri,* ventral view, layer I.

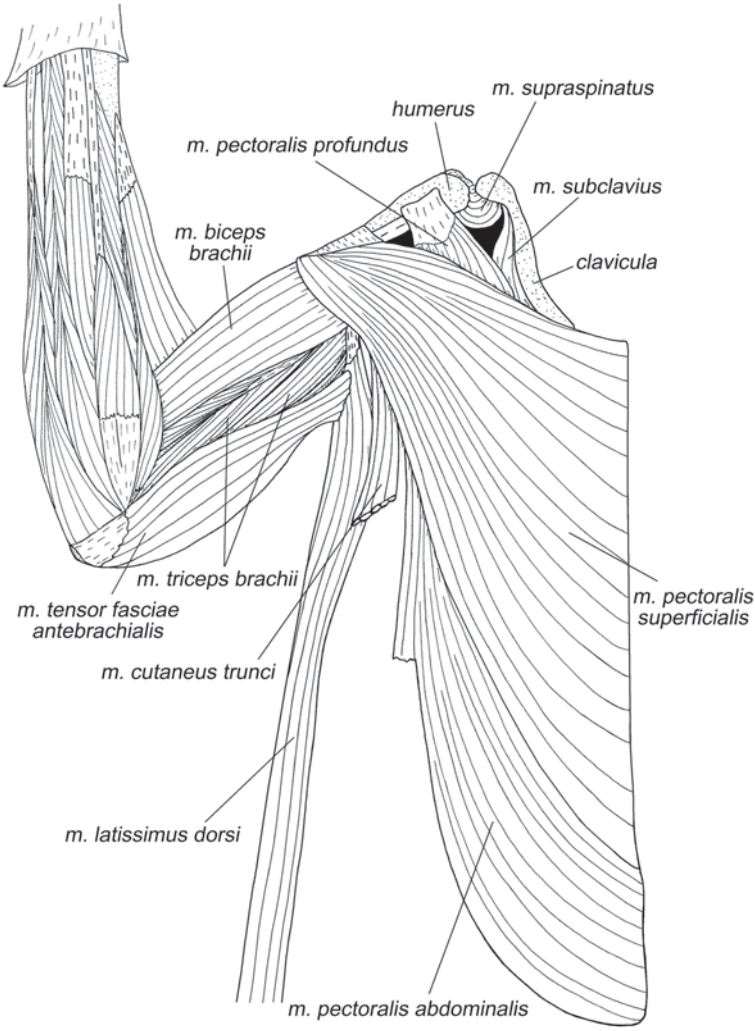


Fig. 1.22 Forelimb muscles of *T. belangeri,* ventral view, layer II.

of fibers converges onto a flat aponeurosis, which inserts on the neck of the lesser tubercle of the humerus near insertion of the terminal aponeurosis of the *m. teres major*.

This muscle pronates and retracts the humerus and, indirectly, via the shoulder joint, retracts the scapula.

Tree shrews, as the majority of other mammals, have two (superficial and deep) **pectoral muscles** (*mm. pectorales*).

Musculus pectoralis superficialis (Figs. 1.13, 1.15, 1.21, 1.22) originates along the entire sternum and, more caudally, along the *linea alba* on the abdomen. It inserts by a wide and short aponeurosis on the edge of the pectoral crest.

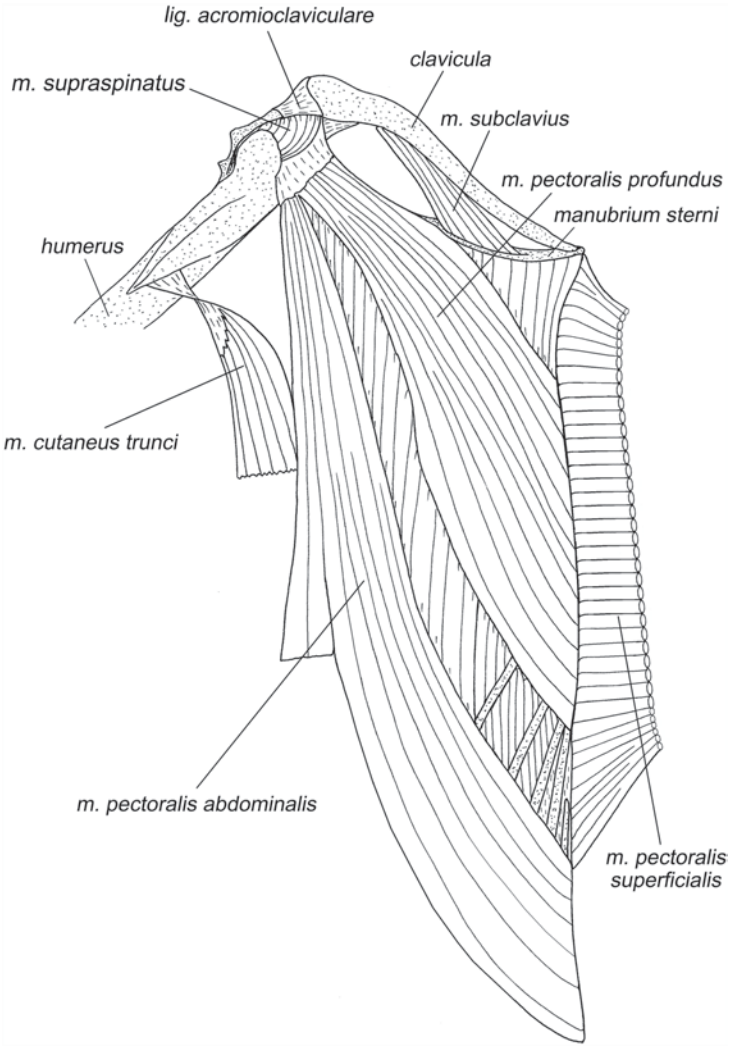


Fig. 1.23 Forelimb muscles of *T. belangeri,* ventral view, layer III.

Musculus pectoralis profundus (Fig. 1.23) is considerably weaker, originates from the sternum and sternal ends of ribs 3–8, extending not so far caudally as the *m. pectoralis superficialis* and, consequently, it is not visible from the outside. It inserts at the base of the humeral head by an aponeurosis shared with the *m. pectoralis abdominalis*. Notably, this humeral insertion is ancestral for the *m. pectoralis profundus* and occurs mostly in primitive mammals, for example, other Archonta (Dunlap et al. 1985) and marsupials (Jenkins and Weijs 1979). In the more advanced quadrupedal mammals, the insertion of the *m. pectoralis profundus* frequently shifts proximally onto the coracoid process of the scapula (Gambaryan 1960).

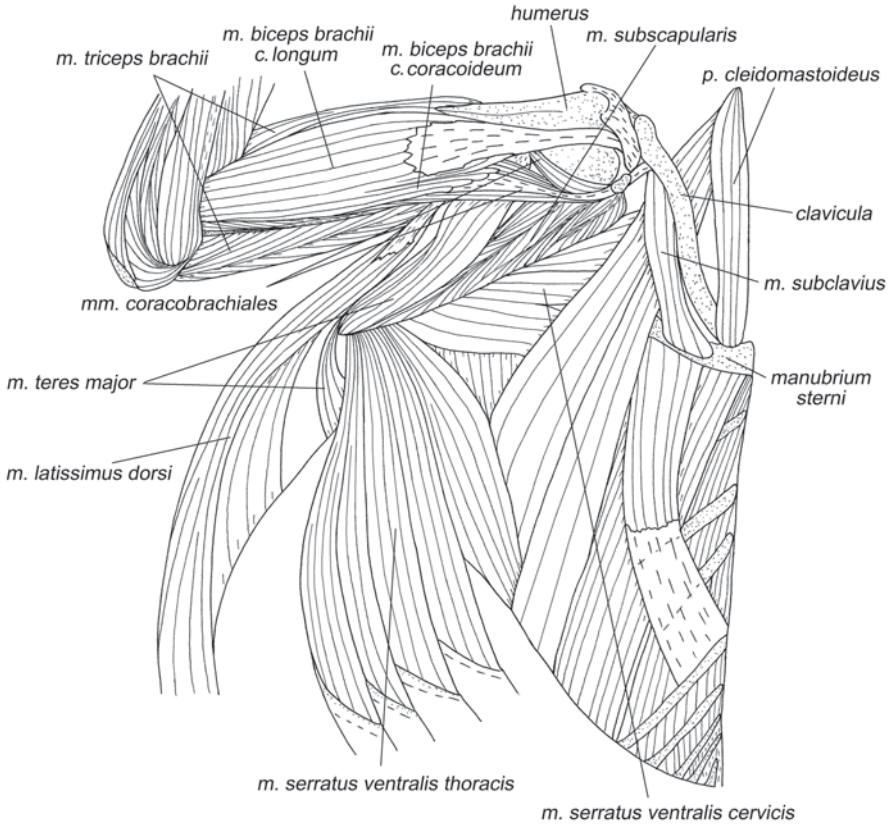


Fig. 1.24 Forelimb muscles of *T. belangeri,* ventral view, layer IV.

The two pectoral muscles are the main muscles adducting the limb. In addition, they retract the limb both along with the girdle and relative to it (*bending the shoulder joint*)*. The anterior part of the m. pectoralis superficialis is most effective in the humerus pronation.*

Musculus pectoralis abdominalis (Figs. 1.21–1.23) originates caudal to the *m. pectoralis superficialis* from a fascia of the *linea alba* of the abdomen. It inserts at the base of the humeral head by an aponeurosis shared with the *m. pectoralis profundus*.

This muscle participates in retraction and (*to a lesser extent*) *adduction of the limb by the humerus.*

Musculus cutaneus trunci (= *m. panniculus carnosus*) (Figs. 1.14, 1.21–1.23) forms a very wide and thin muscular sheet fused with the skin over the entire lateral side of the trunk posterior to the forelimb and up to the base of the tail. The muscular fibers pass in the longitudinal direction and, in the axillary region, converge onto an aponeurosis attached to the medial surface of the distal part of the pectoral crest.

This muscle controls the skin and retracts the limb by the humerus.

Intrinsic Musculature of Shoulder Joint

Musculus clavodeltoideus (Figs. 1.12, 1.13, 1.21) is relatively small, almost lacking aponeuroses. In tree shrews, it is typical of mammals, i.e., distinctly separate from the caudally adjacent *m. pectoralis superficialis*. The muscle originates from the ventral surface of the distal one third of the clavicle (except for its distal tip) and inserts along the edge of the pectoral crest of the humerus, overlapping the end of the *m. pectoralis superficialis*.

The muscle pronates the humerus and straightens the shoulder joint (*protracts the humerus*).

Musculus acromiodeltoideus (Figs. 1.12, 1.13, 1.21) originates from the upper part of the acromion of the scapula mostly by a wide superficial aponeurosis. It inserts along the entire lateral side of the pectoral crest of the humerus.

The muscle straightens the shoulder joint.

Musculus spinodeltoideus (Figs. 1.12–1.15) spreads along the scapular spine. It originates from the upper three fourths of the posterior surface of the spine, partially by the aponeurosis. It inserts by a flat aponeurosis on the lateral surface of the humerus along the base of the pectoral crest.

The muscle supinates the humerus and bends the shoulder joint.

Musculus teres minor (Figs. 1.15, 1.19, 1.20, 1.26, 1.28) is a diminutive muscle, which originates from the posterior border of the scapula caudal to the glenoid by a very small aponeurosis. It inserts on the base of the greater tubercle of the humerus. Le Gros Clark (1924), Davis (1938), and Verma (1965) regarded the *m. spinodeltoideus* as the *m. teres minor*. Carlsson (1922) and Miller (1935) noted the absence of this muscle in the genus *Tupaia*. Most probably, all these authors failed to dissect the *m. teres minor* from the *m. infraspinatus.* More thorough dissection allowed us to distinguish the *m. teres minor* in all the mammals we have studied.

This muscle contributes very little to the supination of the humerus. More probably, it is retained as a sensor of the angle in the shoulder joint.

Musculus teres major (Figs. 1.12–1.15, 1.19, 1.20, 1.24–1.27, 1.29–1.31) originates fleshy from the shelf of the caudal border of the scapula and from the lateral surface of its dorsocaudal angle. Also, the anterior fibers originate on an aponeurosis shared with the *m. infraspinatus*, and the posterior fibers originate on an aponeurosis shared with the *m. subscapularis*. In tree shrews (probably except for *Ptilocercus* (Le Gros Clark 1926)), immediately caudal to the major part of the *m. teres major* an accessory vertebral portion is present – *pars spinohumeralis*, which originates posterior to the dorsocaudal angle of the scapula from fascias of underlying axial muscles and interspinous ligaments at the level of thoracic vertebrae 4–6. Both scapular and vertebral portions insert by a common aponeurosis on the medial surface of the humerus distal to the insertion of the *m. coracobrachialis brevis* and close to the insertion of the *m. latissimus dorsi*. Sometimes the accessory portion is described as the separate muscle – *m. spinohumeralis* (Davis 1938; Le Gros Clark 1924). George (1977) regarded it as the part of the *m. latissimus dorsi*. In fact, this interpretation differs from ours not so much as it may seem,

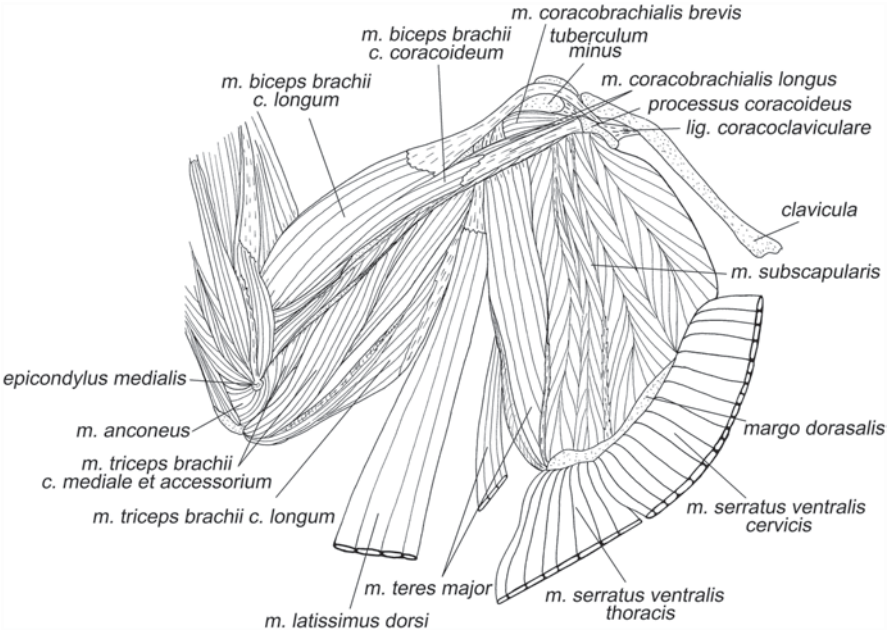


Fig. 1.25 Forelimb muscles of *T. belangeri,* medial view, layer I.

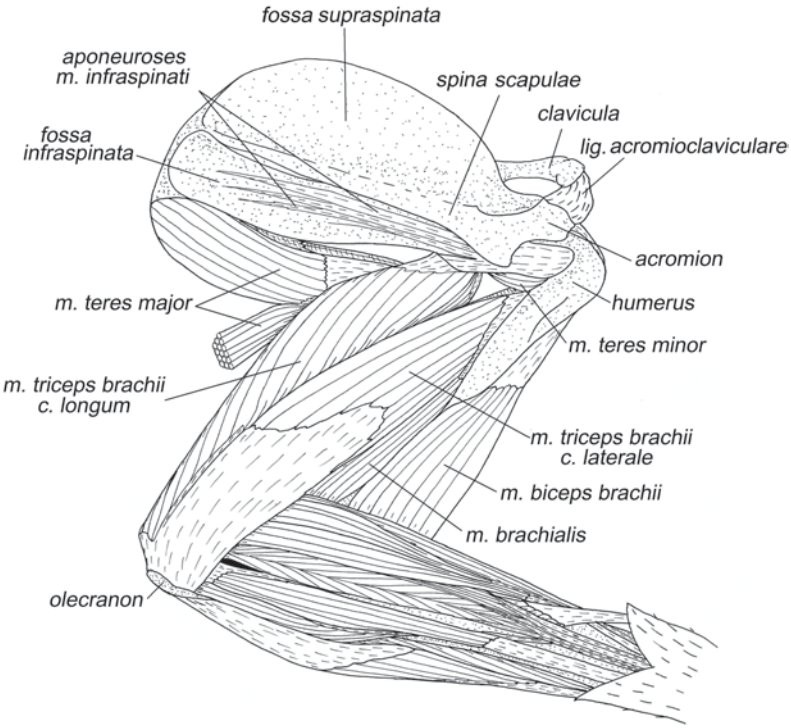


Fig. 1.26 Forelimb muscles of *T. belangeri,* lateral view, layer IV.

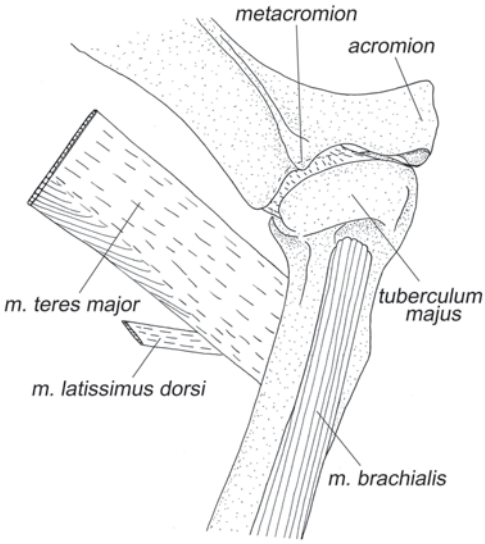


Fig. 1.27 Insertion of the *m. teres major* and *m. latissimus dorsi* of *T. belangeri,* lateral view.

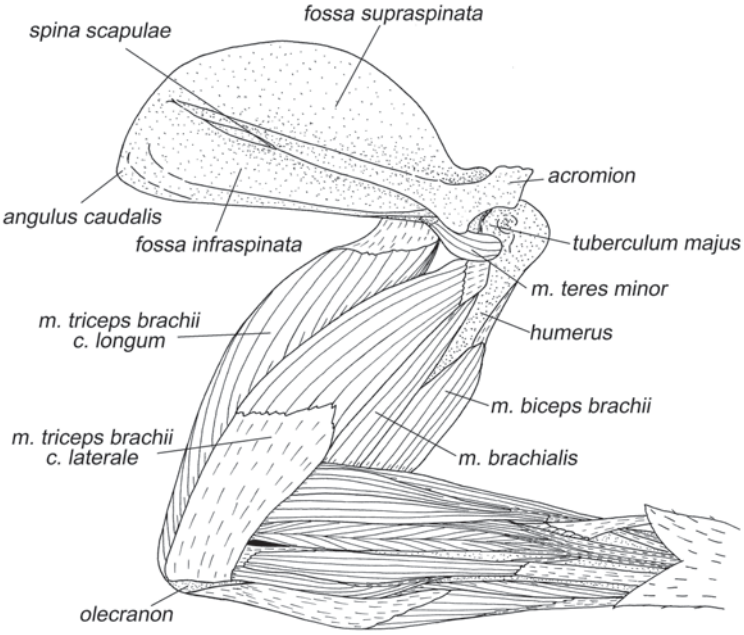


Fig. 1.28 Forelimb muscles of *T. belangeri,* lateral view, layer V.

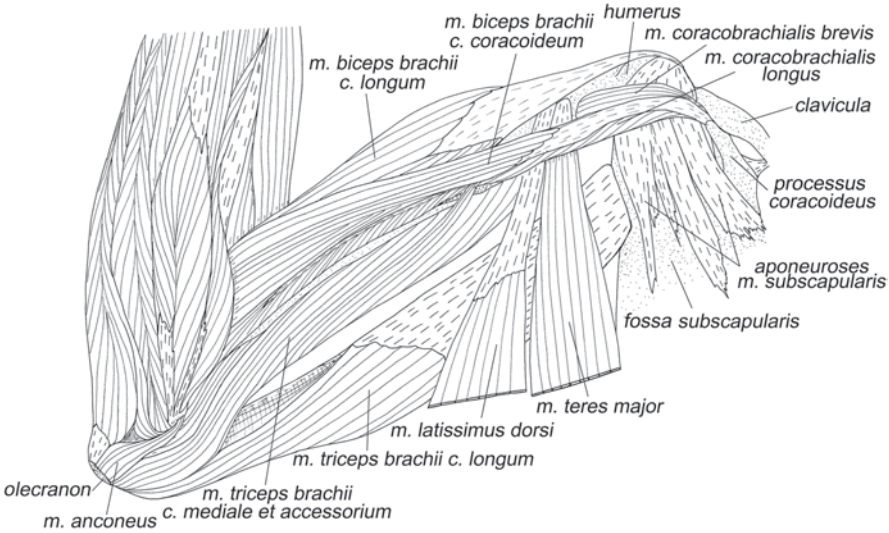


Fig. 1.29 Forelimb muscles of *T. belangeri,* medial view, layer II.

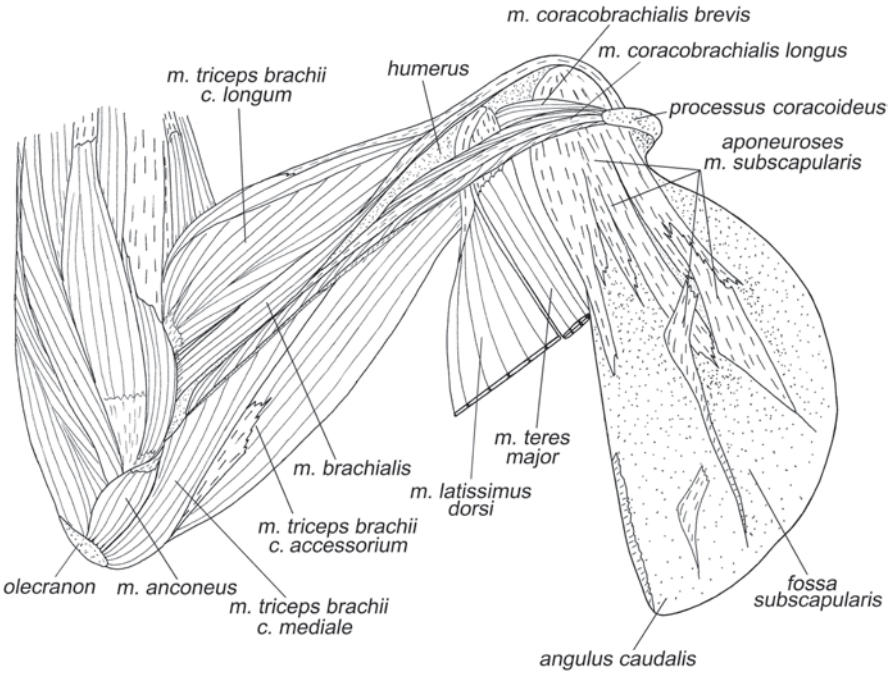


Fig. 1.30 Forelimb muscles of *T. belangeri,* medial view, layer III.

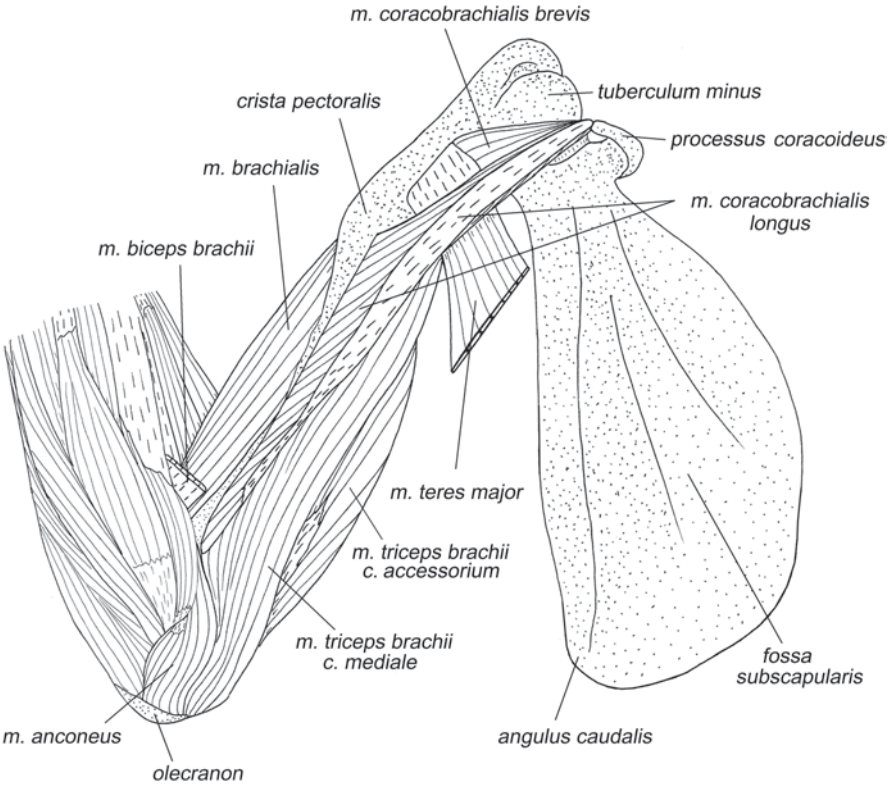


Fig. 1.31 Forelimb muscles of *T. belangeri,* medial view, layer IV.

because the *m. teres major* as a whole is the specific mammalian derivative of the *m. latissimus dorsi* (Howell 1937). Apparently, *pars spinohumeralis* is the trace of the early stage of separation of the *m. teres major* from the *m. latissimus dorsi*, while the major scapulohumeral portion of the *m. teres major* represents the final stage of invasion of this new muscle onto the scapula. In order to emphasize the consistency of this evolutionary trend, we decided to ascribe *pars spinohumeralis* to the *m. teres major* rather than to the *m. latissimus dorsi*.

This muscle bends the shoulder joint (*retracts the humerus*) *and pronates the humerus.*

Musculus subscapularis (Figs. 1.24, 1.25, 1.30) is a large muscle, which occupies the entire medial surface of the scapula. The aponeuroses of the origin and insertion are positioned perpendicular to the scapular plane (alike the spine, but at the medial side of the scapular blade), and the short muscular fibers which connect them form an octapennate structure. Among the aponeuroses of origin, which originate from the medial surface of the scapula, four large aponeuroses are most prominent. The posterior aponeurosis, shared with the *m. teres major*, originates along the caudal border of the scapula; three middle aponeuroses originate from the

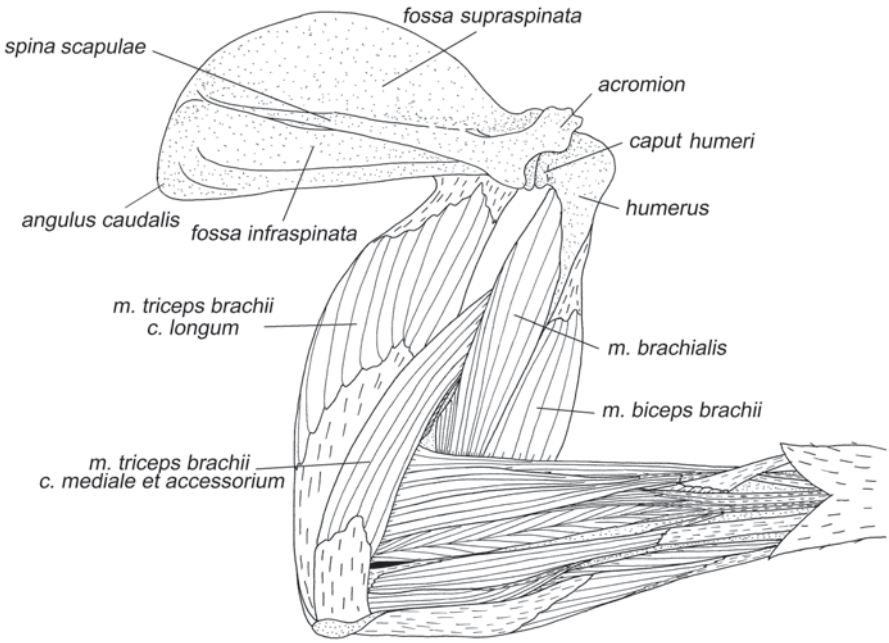


Fig. 1.32 Forelimb muscles of *T. belangeri,* lateral view, layer VI.

subscapular fossa, two of them from longitudinal crests; the anterior aponeurosis originating from the cranial border is weakest. Four aponeuroses of insertion (passing from between those of origin) converge on the lesser tubercle of the humerus. The terminal tendon is incorporated in the articular capsule of the shoulder joint.

The muscle is the main pronator of the humerus.

Musculus supraspinatus (Figs. 1.14, 1.15, 1.19, 1.20, 1.22, 1.23) occupies the supraspinous fossa. Its fibers originate from the entire surface of this fossa and from the dorsal part of the anterior surface of the scapular spine. The muscle inserts on the craniolateral surface of the greater tubercle of the humerus by a stout terminal tendon which is incorporated in the articular capsule of the shoulder joint.

The muscle straightens the shoulder joint, protracting the humerus.

Musculus infraspinatus (Figs. 1.14, 1.15, 1.19, 1.20, 1.26) occupies the infraspinous fossa. Its fibers do not originate from the surface of the fossa but only from its edges, that is from the spine, dorsal border, dorsocaudal angle, and caudal border of the scapula, as well as from an aponeurosis projecting from the caudal border which is shared by this muscle with the *m. teres major*. The muscular belly contains several long narrow internal aponeuroses, which are fused together to insert on the lateral surface of the humerus distal to the greater tubercle. The terminal tendon is incorporated in the articular capsule of the shoulder joint.

The muscle mostly supinates the humerus and probably participates in bending of the shoulder joint.

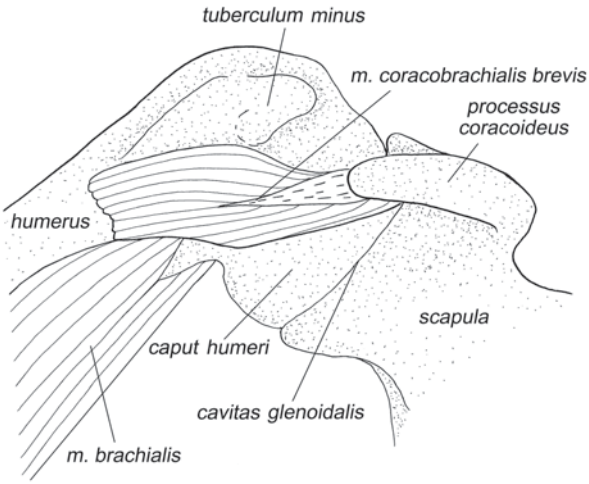


Fig. 1.33 The *m. coracobrachialis brevis* of *T. belangeri*, medial view.

Tree shrews have both **coracobrachial muscles** (*mm. coracobrachiales*) characteristic of mammals. Miller (1935) mentions the presence of the third coracobrachial muscle in *Tupaia picta* but does not describe it.

Musculus coracobrachialis brevis (Figs. 1.24, 1.25, 1.29–1.31, 1.33) originates by an aponeurosis from the coracoid process of the scapula lateral to the *m. coracobrachialis longus* and inserts on the medial surface of the humerus between the base of the lesser tubercle and terminal aponeurosis of the *m. teres major*.

Since this muscle is very small, it is probably only a sensor of the position in the shoulder joint.

Musculus coracobrachialis longus (Figs. 1.24, 1.25, 1.29–1.31) is ribbon-like, originates from the apex of the coracoid process by a superficial aponeurosis which extends along almost the entire muscle belly. Short muscle fibers insert on the medial surface of the humerus from the terminal aponeurosis of the *m. teres major* to the base of the medial epicondyle.

The muscle participates in adduction of the humerus.

Musculature of Free Limb

Musculature of Humerus

Posterior Group of Muscles

Musculus tensor fasciae antebrachialis (Figs. 1.12–1.14, 1.21, 1.22) originates as a wide band from the edge of the terminal aponeurosis of the *m. teres major* and as a narrower band from the terminal tendon of the *m. latissimus dorsi*. The two bands (heads) fuse together and insert by an aponeurosis on the medial and posterior sur-

faces of the olecranon. According to Miller (1935) this muscle has only one origin and it is associated with the *m. teres major*. George (1977) has found the second head originating from *pars spinohumeralis* (see above) but not from the *m. latissimus dorsi* in the narrow sense. However the descriptions given for various species of tree shrews by Carlsson (1922) and Le Gros Clark (1924, 1926) better agree with ours.

This muscle participates in extension of the elbow.

Musculus triceps brachii (Figs. 1.12–1.15, 1.19–1.22, 1.24–1.26, 1.28–1.32, 1.35, 1.36, 1.38, 1.39) is very well developed and has all the four heads recorded in mammals – *caput longum*, *c. laterale*, *c. mediale*, and *c. accessorium*, of which the latter two are poorly differentiated from each other. The *caput longum* is distinctly separated from others. It originates with the help of an aponeurosis from the caudal border of the scapula above the glenoid medial to the *m. teres minor* and lateral to the *m. teres major*. Its relatively short fibers insert by the distal aponeurosis on the apex of the olecranon. The *caput laterale* originates by an aponeurosis from the posterior (dorsal) surface of the proximal half of the humerus. This head inserts on the lateral surface of the olecranon by a wide aponeurosis shared with the next two heads. The *caput mediale* and *caput accessorium* originate together from the wide area covering the entire posterior and medial surfaces of the humerus. We regard the fibers which originate from the distal half of the humerus as the *caput mediale* in the narrow sense, and the more proximal part of this muscular mass as the *caput accessorium* (Figs. 1.30, 1.31). These two heads insert together on the anterior surface of the olecranon and on the aponeurosis shared with the *caput laterale*. George (1977) and many other researchers did not divide the *caput accessorium* from the *caput mediale* and regarded them together as the medial head. Le Gros Clark (1926) has ascribed the fibers of the *caput accessorium* to the *caput laterale*, while Davis (1938) has ascribed the fibers of the *caput mediale* to the *caput laterale* and regards the *caput accessorium* as the medial head.

All heads of the m. triceps brachii extend the elbow. The caput longum also bends the shoulder joint.

Musculus anconeus (= *m. epitrochleoanconeus*) (Figs. 1.25, 1.29–1.31, 1.38) is a small fascicle of fibers at the medial side of the elbow passing from the posterior surface of the medial epicondyle of the humerus and its crest to the medial side of the olecranon.

The muscle participates in supination of the antebrachium.

In a few mammals, lateral to the elbow the second *m. anconeus* is found (see Howell 1937) which passes from the lateral epicondyle of the humerus to the lateral side of the olecranon.

Anterior Group of Muscles

Musculus biceps brachii (Figs. 1.12–1.15, 1.21, 1.22, 1.24–1.26, 1.28–1.30, 1.32, 1.34) has two unequally developed heads – *caput longum* and *caput coracoideum*. The *caput longum* is developed very strongly. Its proximal tendon originates from the

lateral surface of the base of the coracoid process of the scapula, then it turns around the proximal end of the humerus onto its medial side, where it is divided into two aponeuroses, which embrace the proximal part of the belly. The muscle inserts on the antebrachium by long aponeuroses. One of them inserts on the palmar surface of the ulna, just proximal to the *m. brachialis*, and the second is attached somewhat more distally on the ulnar surface of the radius. The *caput coracoideum* is a thin fascicle of long fibers, which arises from the surface of the aponeurosis of origin of the *m. coracobrachialis longus* on the coracoid process of the scapula and blends distally into the long head. Davis (1938) has found only the *caput longum* in *Dendrogale*, as also did George on one side of *Urogale* and *Tupaia glis*; however both heads were present on the other side of the same specimens (George 1977).

The caput longum straightens the shoulder joint, flexes the elbow, and participates in supination of the antebrachium. The caput coracoideum participates in the elbow flexion and supination of the antebrachium; in addition, it can adduct the humerus.

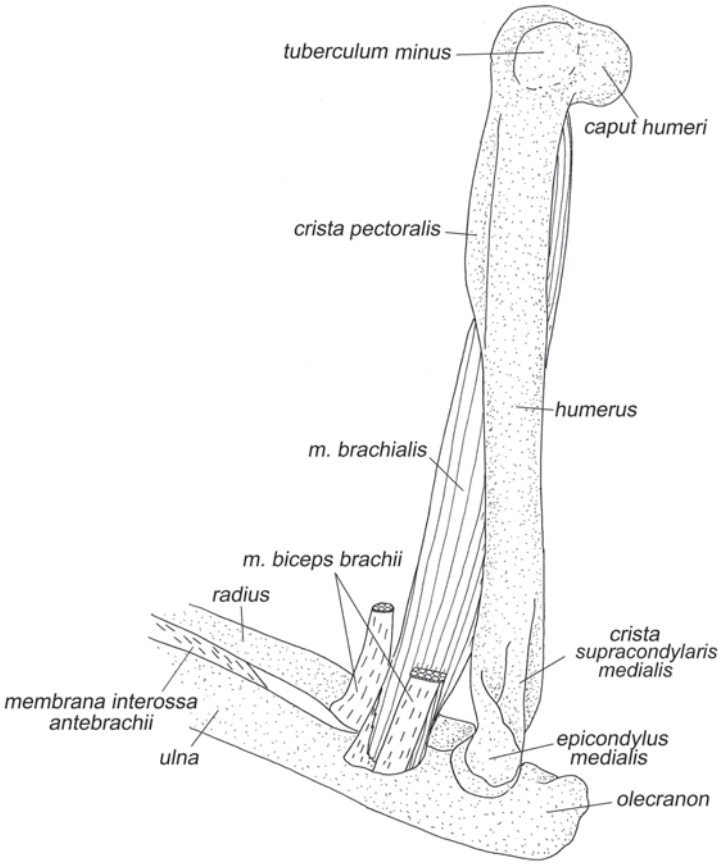


Fig. 1.34 Forelimb muscles of *T. belangeri*, medial view, layer V.

Musculus brachialis (Figs. 1.13, 1.15, 1.26–1.28, 1.30–1.32, 1.34–1.36, 1.38–1.41, 1.44) is very well developed, originates from the posterior and lateral surfaces of proximal two-thirds of the humerus distal to its articular head. It passes between the two distal tendons of the *m. biceps brachii* to inserts by a short aponeurosis on the palmar surface of the proximal part of the ulna just distal to one of these tendons.

This muscle flexes the elbow and supinates the antebrachium.

Musculature of Antebrachium

Muscles of Dorsal Surface

Musculus supinator (Figs. 1.36, 1.41, 1.43) originates from the anterior border of the lateral epicondyle of the humerus by a wide superficial aponeurosis covering almost completely the muscle. The aponeurosis contains a large sesamoid bone at the base – the lateral sesamoid. Very short muscular fibers insert on the radial surface of the proximal one-third of the radius.

Apparently, the muscle mostly prevents medial abduction of the antebrachium rather than supinates it.

Musculus brachioradialis (Figs. 1.35, 1.36, 1.38, 1.45) originates from the lateral surface of the humerus, wedging in between the *m. triceps brachii caput mediale*, *m. brachialis*, and *m. extensor carpi radialis longus*. Fibers converge on the tendon, which inserts on the radial side of the radius at the base of its distal head. According to Le Gros Clark (1926) this muscle is absent in *Ptilocercus*, in contrast

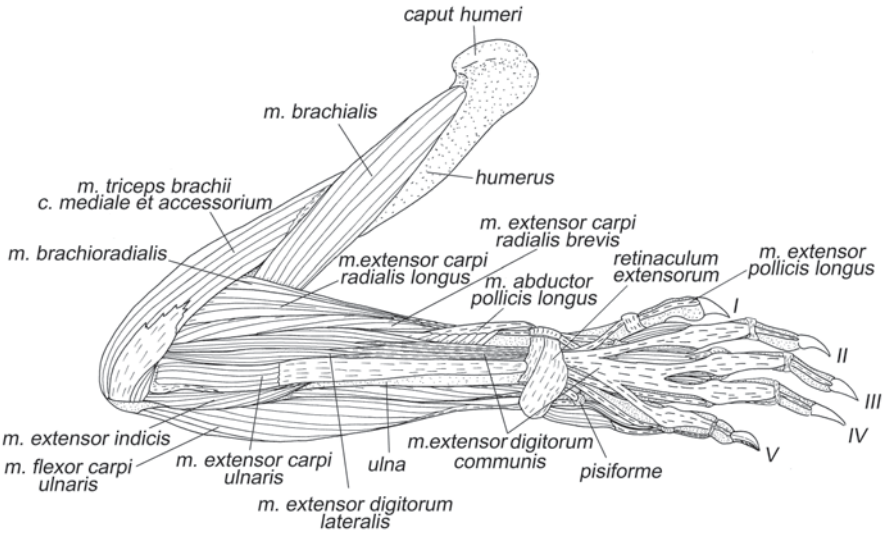


Fig. 1.35 Fore extremity muscles of *T. belangeri*, lateral view, layer I.

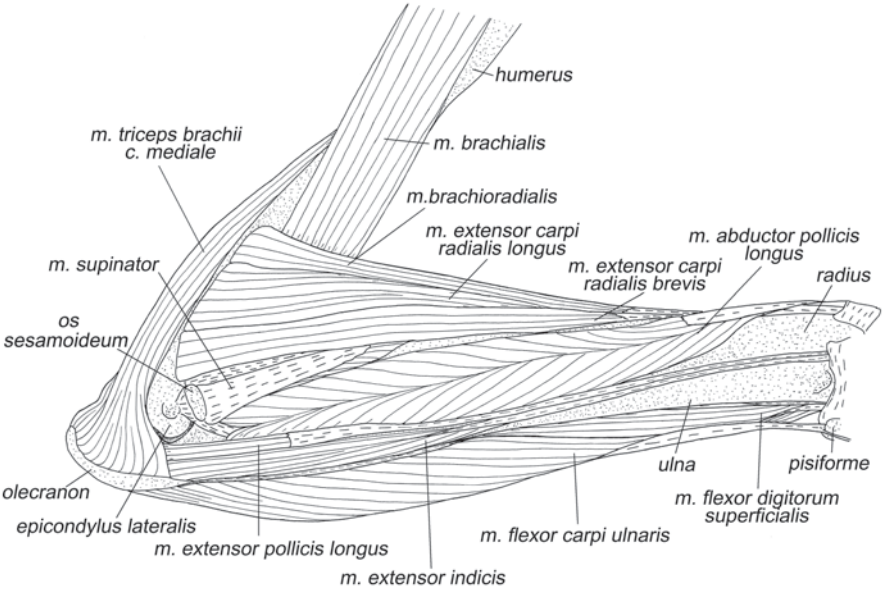


Fig. 1.36 Fore extremity muscles of *T. belangeri*, lateral view, layer II.

to various species of the genus *Tupaia*, but according to Carlsson (1922) it is also absent in *Tupaia javanica*.

The muscle bends the elbow and participates in supination of the antebrachium.

Musculus extensor carpi radialis longus (Figs. 1.35–1.38) originates along the crest of the lateral epicondyle of the humerus distal to the *m. brachioradialis*. Long muscular fibers run along the palmar side of the radial surface of the radius and at the middle of its length produce a long terminal tendon which passes under the medial ligament of the *retinaculum extensorum* (= *ligamentum carpi dorsale*)[6] to insert on the second metacarpal close to the middle of its dorsal surface.

The muscle extends the manus and abducts it medially as well as supinates the antebrachium. It can participate in the elbow flexion.

Musculus extensor carpi radialis brevis (Figs. 1.35–1.38) originates with the help of a small aponeurosis distal to the previous muscle from the crest of the lateral epicondyle of the humerus and from its proximal part. Long muscular fibers produce the terminal tendon at the level of the beginning of the distal one-third of the antebrachium. Along with the tendon of the previous muscle, it passes under

[6] In tupaias, the *retinaculum extensorum* (Fig. 1.37) is divided into two ligaments. A relatively small medial ligament forms a bridge on the medial side of the distal end of the radius and a wide lateral ligament passes across the dorsal side of the carpus from the medial side of the distal end of the radius to the lateral side of the distal end of the ulna and also to the *pisiforme*. The inner surface of the lateral ligament has fibrous septa which divide the space under it into several passages for the tendons of extensors of the manus and digits.

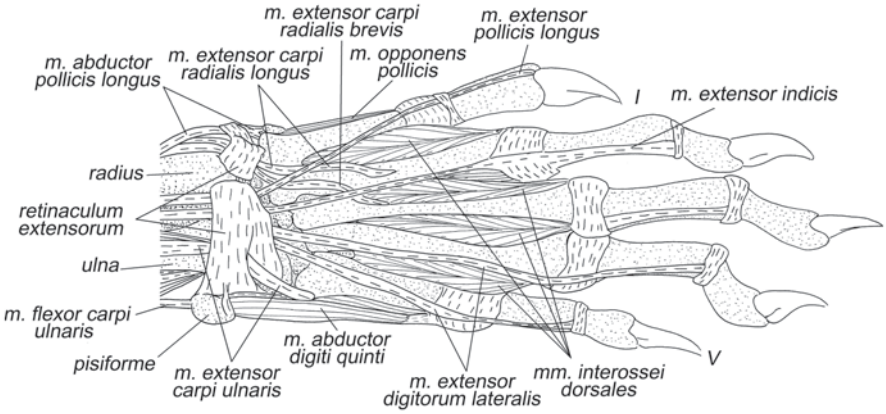


Fig. 1.37 Muscles of the manus of *T. belangeri*, dorsal view.

the medial ligament of the *retinaculum extensorum* onto the manus to insert on the medial side of the dorsal surface of the third metacarpal slightly distal to its proximal head.

Like the previous one, this muscle extends the manus, abducts it medially, supinates the antebrachium, and can participate in the elbow flexion.

Musculus extensor digitorum communis (Fig. 1.35) originates mostly from the proximal part of the lateral epicondyle of the humerus and, partially, from the crest of the epicondyle by an aponeurosis which underlies the muscular belly and is shared by this muscle with the *m. extensor digitorum lateralis*. The muscle produces four distal tendons, which along with tendons of the *m. extensor digitorum lateralis* pass under the lateral ligament of the *retinaculum extensorum* and, on the dorsal side of the carpus, unite into the *aponeurosis extensorum superficialis*. Approximately at the midlength of the metacarpals, the tendons separate again and pass along the dorsal sides of digits II–V up to the bases of ungual phalanges. At the metacarpophalangeal and proximal interphalangeal joints, they are fused with respective articular capsules.

The muscle extends the manus and digits II–V.

Musculus extensor digitorum lateralis (Figs. 1.35, 1.37) originates from the lateral side of the aponeurosis shared with the previous muscle. It produces two distal tendons, which along with terminal tendons of the previous muscle pass under the lateral ligament of the *retinaculum extensorum*. Further, the medial tendon runs along the fourth metacarpal and proximal phalanx of digit IV and inserts through the articular capsule of the proximal interphalangeal joint on the lateral side of phalanx 2. The lateral tendon has similar insertion on phalanx 2 of digit V.

The muscle extends and abducts laterally digits IV and V.

Musculus extensor pollicis longus (Fig. 1.35–1.37) originates from the dorsal surface of the ulna just distal to the elbow joint. A short belly occupies at most

one-fifth of the antebrachium length and produces a long terminal tendon, which along with the tendon of *m. extensor indicis*, passes under the lateral ligament of the *retinaculum extensorum* and inserts on the dorsal surface of the base of the ungual phalanx of digit I. Miller (1935), George (1977), and many other researchers do not distinguish this muscle from the *m. extensor indicis* and treat them together as a single unit.

The muscle extends the first digit.

Musculus abductor pollicis longus (Figs. 1.35–1.41, 1.45, 1.48) originates from proximal two-thirds of the dorsal surface of the radius and radial surface of the ulna. A long belly of the muscle is composed of rather short muscular fibers, which converge on the internal aponeurosis. This aponeurosis passes into a terminal tendon which runs along the radial side of the antebrachium and under the medial ligament of the *retinaculum extensorum*. Distal to the ligament, the tendon bifurcates and inserts on a rudimentary prepollex and on the medial side of the proximal end of the first metacarpal. According to George (1977) the second branch of the tendon inserts not only on the first metacarpal but on the *trapezium* as well, but Le Gros Clark (1924, 1926) reported that in *Ptilocercus* and *Tupaia minor* the insertion is restricted to the base of the first metacarpal.

The muscle supinates the antebrachium and abducts the manus medially.

Musculus extensor indicis (Fig. 1.35–1.37) originates from the ulna behind the *m. extensor pollicis longus* and has about twice longer a belly. Distal to the lateral ligament of the *retinaculum extensorum*, the terminal tendon of this muscle runs along the lateral side of the second metacarpal and proximal phalanx of digit II, having fusion with the articular capsule of the metacarpophalangeal joint, and, finally, inserts on the lateral side of the base of the second phalanx of digit II (like the *m. extensor digitorum lateralis* inserts on digits IV and V). According to Miller (1935) and George (1977) the muscle has the second tendon passing to digit III.

The muscle extends and adducts laterally digit II.

Musculus extensor carpi ulnaris (Figs. 1.35, 1.37) originates from the lateral epicondyle of the humerus by a wide aponeurosis, which underlies the muscular belly. It inserts by another wide aponeurosis covering the external surface of the belly and narrowing into a terminal tendon, which passes under the lateral ligament of the *retinaculum extensorum* and inserts on the lateral tubercle of the dorsal surface of the proximal head of the fifth metacarpal. The muscle was reported to originate not only from the lateral epicondyle of the humerus but also from the olecranon process of the ulna in *Tupaia minor* (Le Gros Clark 1924) and *Tupaia glis* (Straus 1941).

The muscle extends and abducts the manus laterally.

Musculus extensor pollicis brevis is absent in tree shrews. The claim of its presence in *Tupaia picta* (Miller 1935) is very doubtful especially in the absence of its description in the publication cited. This muscle is very rare in mammals, being definitely described only in humans (e.g. Voss and Herrlinger 1956) and some apes (Diogo and Wood 2012).

Muscles of Palmar Surface

Musculus pronator teres (Figs. 1.38–1.40) originates with the help of an aponeurosis from the medial epicondyle of the humerus. It inserts with the help of a wide aponeurosis on the radial surface of the middle one-third of the radius. According to Jones (1916), *Tupaia ferruginea* possesses the second head of this muscle which arises from the proximal extremity of the ulna. It is typical to man, but nobody else has found the ulnar head of the *m. pronator teres* in tree shrews.

The muscle pronates the antebrachium and participates in adduction of the antebrachium and flexion of the elbow.

Musculus flexor carpi radialis (Figs. 1.38, 1.39, 1.48, 1.50–1.52) originates from the medial epicondyle of the humerus by aponeuroses shared with the *m. flexor digitorum profundus* and *m. palmaris longus*. A long distal tendon passes under the *retinaculum flexorum superficiale*[7], then, at the level of the prepollex, under the *ligamentum palmaris profundum*[8], and inserts on the ventral surface of the proximal head of the third metacarpal, or, according to Le Gros Clark (1924, 1926), on the second metacarpal, or, according to George (1977), on both of them.

The muscle flexes the wrist.

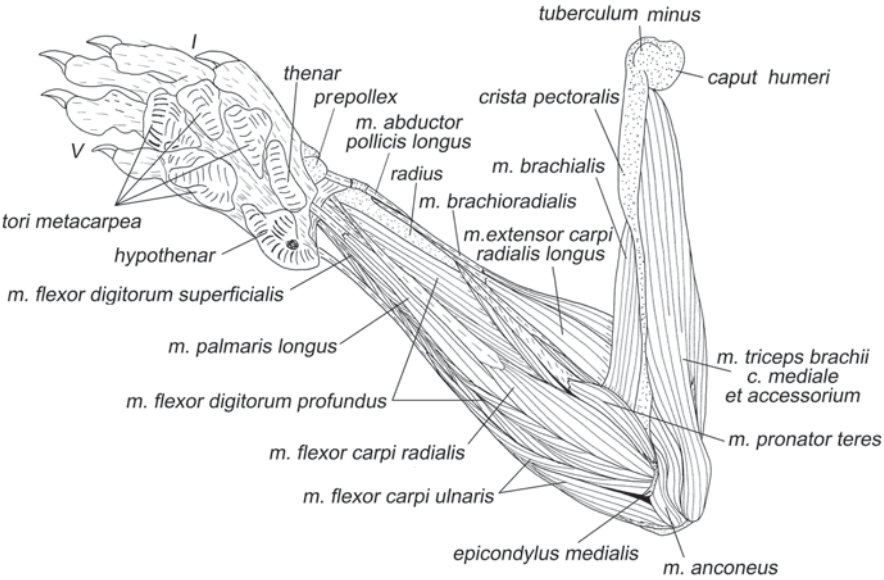


Fig. 1.38 Fore extremity muscles of *T. belangeri*, medial view, layer I.

[7] The *retinaculum flexorum superficiale* (Fig. 1.45) of tree shrews is a relatively thin transverse ligament, which connects the prepollex with the *pisiforme*.

[8] The *ligamentum palmaris profundum* (Fig. 1.50, 1.51) covers the ventral surface of the carpals. It connects the *pisiforme*, ventral surface of the distal ends of the ulna and radius, and the prepollex with the ventral surface of the bases of the metacarpals.

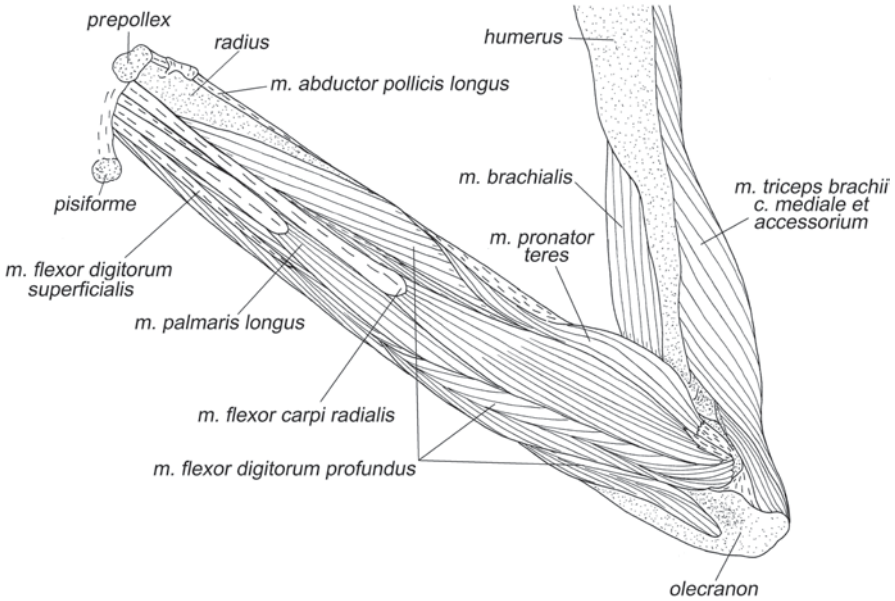


Fig. 1.39 Fore extremity muscles of *T. belangeri*, medial view, layer II.

Musculus palmaris longus (Figs. 1.38, 1.39, 1.45). Fibers of the muscle arise from the distal one-third of the length of the aponeurosis originating from the medial epicondyle of the humerus, which is shared with the humeral heads of the *m. flexor digitorum profundus*. The muscle produces a long, somewhat expanding, and flattened distal tendon, which is fuses with the *retinaculum flexorum superficiale* and inserts on the medial side of the proximal radial pad.[9]

The muscle prevents distal displacement of the proximal radial pad and indirectly, through the retinaculum flexorum superficiale, flexes the wrist joint.

Musculus flexor digitorum superficialis (Figs. 1.36, 1.38–1.42, 1.46–1.48). In opinion of other authors (e.g. Le Gros Clark 1924, 1926; George 1977), this muscle originates along with other flexors from the medial epicondyle of the humerus. However, according to our data, short fibers of this muscle originate in the distal part of the antebrachium from the terminal tendon of the *caput humerale superficiale* of the *m. flexor digitorum profundus*. This origin of this muscle should be regarded as a primitive condition, since the homologue of this muscle in reptiles and monotremes is the short rather than long flexor of the manus. Among therian mammals, such a distal origin is preserved not only in tree shrews, but also in some felids (Haines 1950). In the majority of other therian mammals, the origin of this muscle

[9] The palmar surface of the manus of tree shrews has six pads (Fig. 1.38). Only the radial proximal (thenar) pad is supplied with the musculature.

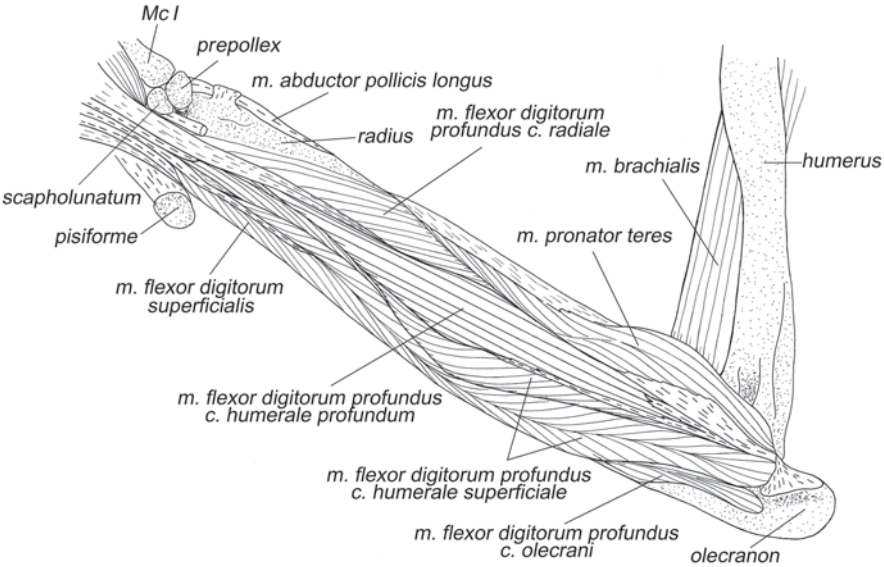


Fig. 1.40 Fore extremity muscles of *T. belangeri*, medial view, layer III.

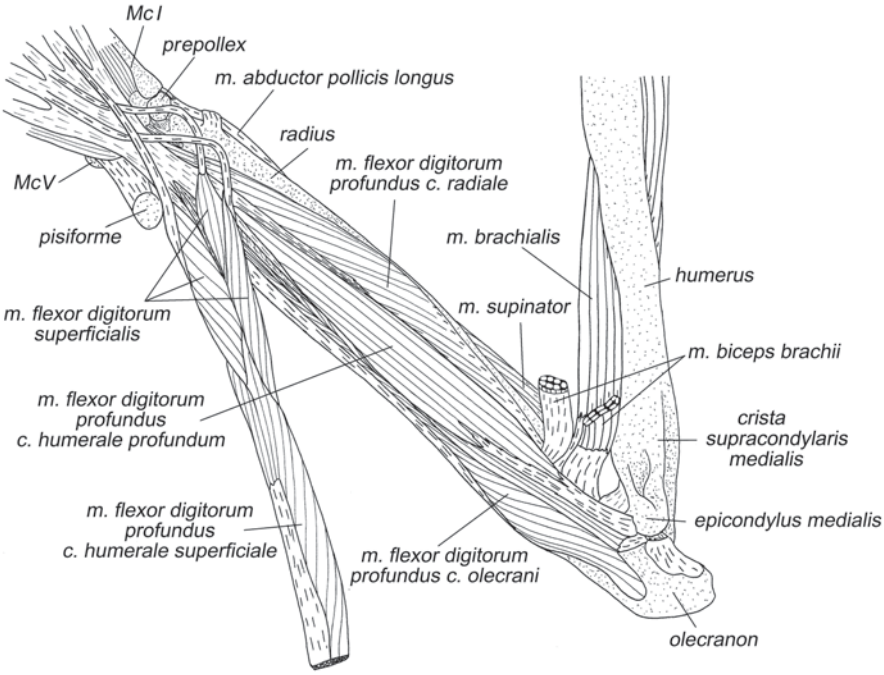


Fig. 1.41 Fore extremity muscles of *T. belangeri*, medial view, layer IV.

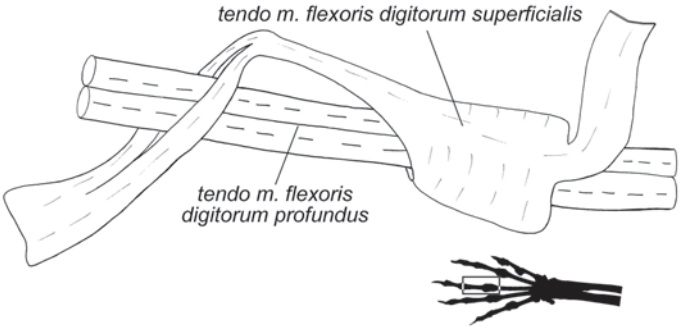


Fig. 1.42 The perforated tendon of *m. flexor digitorum superficialis* of *T. belangeri*, lateral view.

is displaced over the *caput humerale superficiale* of the *m. flexor digitorum profundus* onto the medial epicondyle of the humerus. The cited misunderstandings of the origin of the *m. flexor digitorum superficialis* in tree shrews appear to be due to difficulties in separation of its fibers from those of the *caput humerale superficiale* of the *m. flexor digitorum profundus*. Because of this problem, it seemed to Le Gros Clark (1924) and George (1977) that the *m. flexor digitorum superficialis* sends one of its terminal tendons into the common terminal aponeurosis of the *m. flexor digitorum superficialis*. According to our dissection, this tendon is just the continuation of the terminal tendon of the *caput humerale superficiale* of the *m. flexor digitorum profundus*, from which the fibers of the *m. flexor digitorum superficialis* arise.

The muscle consists of three well-differentiated heads corresponding to digits II–IV. The head to digit III originates from the superficial (palmar) side of the above-mentioned tendon of the *caput humerale superficiale* of the *m. flexor digitorum profundus*, and the heads to digits II and IV originate from its deep (dorsal) side. Each head produces an independent terminal tendon, which passes under the *retinaculum flexorum profundum*[10] and inserts on the ventral surface of the proximal head of the second phalanx of the respective digit. Before the metacarpophalangeal joint, the tendon forms a ring on its deep (dorsal) side, and before the insertion the tendon bifurcates; both the ring and the bifurcation, for which such tendon is called perforated, serve as a passage for the respective terminal tendon of the *flexor digitorum profundus* to the end of the finger (Fig. 1.42). In *Ptilocercus*, Le Gros Clark (1926) has found the fourth terminal tendon to digit V, which fuses at the level of the fifth metacarpal with the terminal tendon of the *m. flexor brevis manus* into a common perforated tendon of this finger.

The muscle bends digits II–IV, except for the ungual joints.

Musculus flexor digitorum profundus (Figs. 1.38–1.41, 1.43, 1.45–1.48) is the largest antebrachial flexor. It originates from the medial epicondyle of the hu-

[10] The *retinaculum flexorum profundum* (Fig. 1.47) connects the ligament between the *pisiforme* and the base of the metacarpal V with the medial side of the distal end of the radius, *scapholunatum*, and dorsal side of rudimentary prepollex. It forms a sheath, which encloses tendons of the long flexors of digits. Its surface is also origin of certain short muscles of the manus.

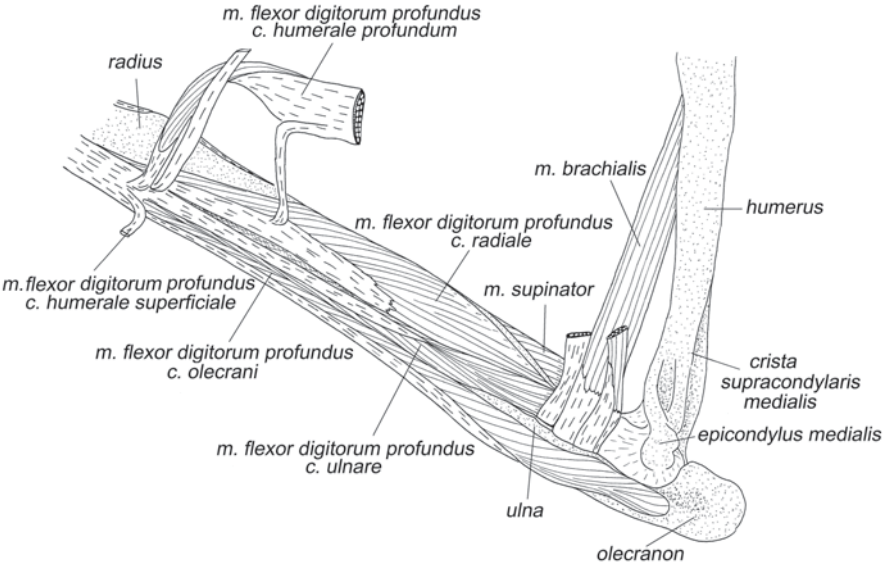


Fig. 1.43 Fore extremity muscles of *T. belangeri*, medial view, layer V.

merus and from the antebrachium by five separate heads – *caput humerale superficiale*, *c. humerale profundum*, *c. olecrani*, *c. ulnare*, and *c. radiale*. The terminal aponeuroses of all the five heads fuse together at the level of the distal one-third of the antebrachium into a thick common tendinous plate (*aponeurosis flexoria communis*[11]), which passes under the *retinaculum flexorum profundum* and, in the proximal part of the metacarpus, divides into five tendons running along fingers.

The *caput humerale superficiale* originates from the medial epicondyle of the humerus with the help of two aponeuroses, one of which is shared with the *caput humerale profundum*, and inserts on the *aponeurosis flexoria communis* by the terminal tendon, which also gives rise to the fibers of the *m. flexor digitorum superficialis* (see above). The *caput humerale profundum* originates from the medial epicondyle under the previous head, mostly via their shared aponeurosis, and inserts on the *aponeurosis flexoria communis* by several tendinous fascicles. The *caput olecrani* originates from the proximal two-thirds of the ulnar surface of the ulna and inserts by a single tendon on the *aponeurosis flexoria communis*, most laterally as compared with tendons of the other heads. The fibers of the *caput ulnare* originate from the palmar surface of the middle part of the ulna, of the proximal part of the radius, and of the aponeurosis shared with the radial head (over almost the entire distal half of the antebrachium); it inserts by a single tendon on the *aponeurosis flexoria communis*. The *caput radiale* occupies the most medial position, originates from the proximal two-thirds of the palmar surface of the radius, and inserts by a single tendon on the *aponeurosis flexoria communis*.

[11] The term *aponeurosis flexoria communis* designating a common tendinous plate of all the heads of the *m. flexor digitorum profundus* is introduced here for the first time for convenience.

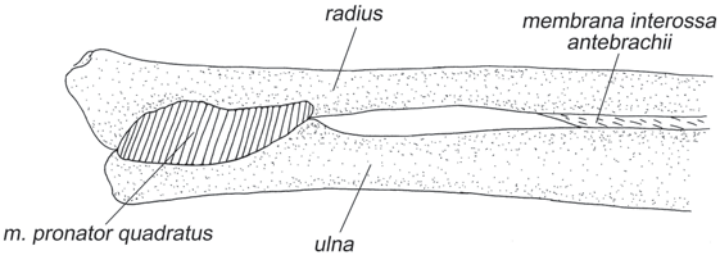


Fig. 1.44 The *m. pronator quadratus* of *T. belangeri*, medial view.

Le Gros Clark (1924) erroneously ascribed the *caput humerale superficiale* to the *m. flexor digitorum superficialis* (see above), and, consequently, regarded the *caput humerale profundum* of the *m. flexor digitorum profundus* as its superficial humeral head.

The *aponeurosis flexoria communis* blended from the terminal aponeuroses of all the five heads divides again into five so-called perforating tendons of the *m. flexor digitorum profundus* (the five terminal tendons do not correspond directly to the five muscular heads). Each tendon passes through the ring and bifurcation of the respective perforated tendon of the *m. flexor digitorum superficialis* or (in the fifth finger) *m. flexor brevis manus* (Fig. 1.42), then runs inside the *vagina fibrosa digiti*,[12] and finally inserts at the base of ungual phalanx. Over a significant extent, these tendons are split into two, but their halves do not diverge.

The muscle can flex all the joints of every finger.

Musculus flexor carpi ulnaris (Figs. 1.35–1.38, 1.45) originates from the palmar surface of the proximal part of the ulna (including the olecranon) and from the medial epicondyle of the humerus (most of fibers arise from the external surface of the aponeurosis shared with the *m. flexor digitorum profundus*). The terminal tendon inserts on the *pisiforme*. Some fascicles of the tendon continue distally to fuse into a thick *ligamentum pisometacarpeum*.

The muscle abducts the manus laterally.

Musculus pronator quadratus (Figs. 1.44, 1.50, 1.51) is present in tree shrews, but is absent in colugos and bats. It is located within the distal one-fourth of the antebrachium, where it connects adjacent surfaces of the ulna and radius by transverse fibers.

The muscle pronates the radius and, hence, the manus relative to the ulna.

Intrinsic Muscles of Manus

Musculus palmaris brevis (Fig. 1.45) is the muscle of the paw pads and is very difficult to dissect from surrounding connective tissue. In our specimen of tree shrew, we were able to locate only the fibers attachment on the deep (dorsal) side of a

[12] The *vaginae fibrosae digitorum* are fibrous tunnels or sheaths on the ventral surface of the distal ends of the first phalanges of digits, which enclose tendons of the flexors.

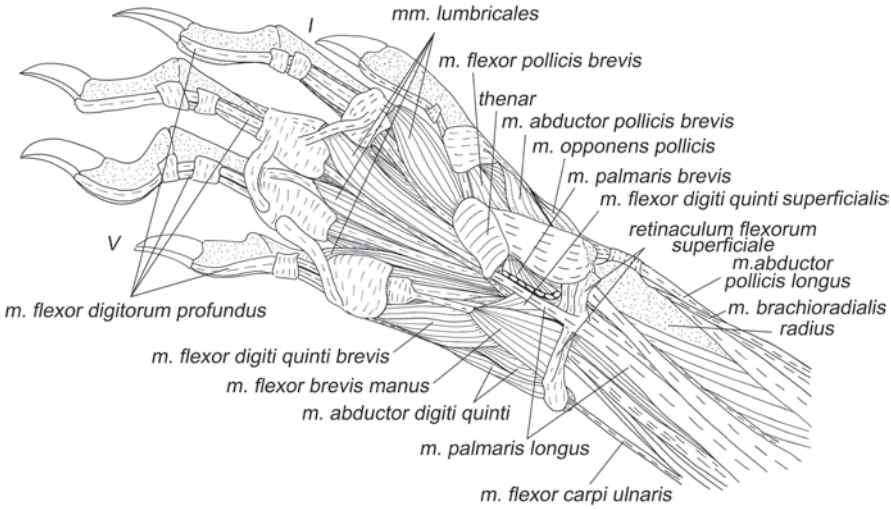


Fig. 1.45 Muscles of the manus of *T. belangeri*, ventral view, layer I.

very thick and wide ligament connecting the prepollex with the radial proximal pad (thenar). According to the previous review (George 1977), the opposite attachment of the muscle is in the ulnar proximal pad (hypothenar).

The muscle can participate in adjustment of the palmar surface to substrate relief.

Musculus opponens pollicis (Figs. 1.37, 1.45, 1.46) originates from the *retinaculum flexorum profundum* and from the ventral side of the *scapholunatum* and prepollex along their distal borders. It inserts on the medial surface of the distal head of metacarpal I. Frequently, this muscle is regarded as a part of *m. flexor pollicis brevis* (e.g. Haines 1955), or as a part of the *m. abductor pollicis brevis* (e.g. Le Gros Clark 1924). Nevertheless, we adhere to the separate nomination of all these muscles as is established in the human anatomy (among mammals, the human set of the short muscles of the manus is one of the most complete).

The muscle abducts medially metacarpal I and participates in its flexion (*lowering relative to the carpus*).

Musculus abductor pollicis brevis (Fig. 1.45) is most superficial among muscles forming the so-called "eminence" of digit I. It originates from the *retinaculum flexorum superficiale* and deep (dorsal) side of the ligament between the prepollex and thenar as well as the thenar base. It inserts with the help of a small tendon on the medial surface of the articular capsule of the first metacarpophalangeal joint and so, by means of it, on the medial side of the base of the first phalanx of digit I.

The muscle lowers (*flexes*) *metacarpal of digit I and abducts medially its proximal phalanx.*

Musculus flexor pollicis brevis (Figs. 1.45–1.47) originates from the *retinaculum flexorum profundum* at the level of the second metacarpal and inserts somewhat lateral to the *m. opponens pollicis* on the medial sesamoid bone of the articular capsule of the metacarpophalangeal I joint. In *Tupaia minor* it inserts on both sesamoid bones of this joint (Le Gros Clark 1924).

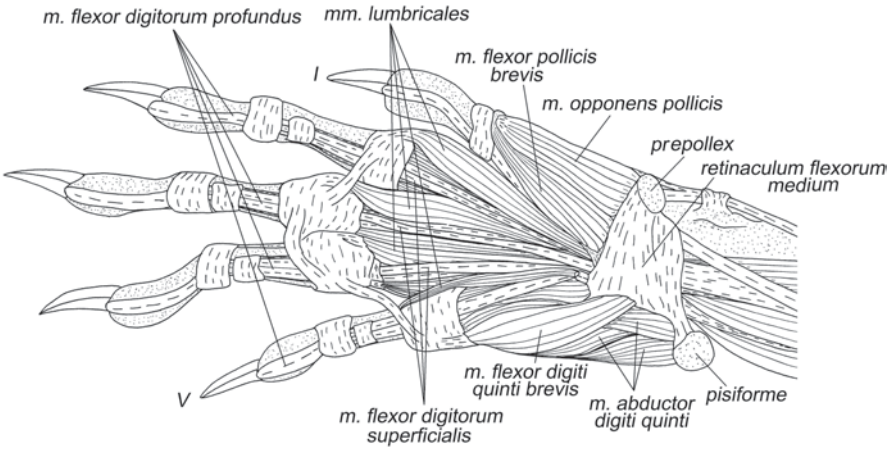


Fig. 1.46 Muscles of the manus of *T. belangeri*, ventral view, layer II.

The muscle participates in flexion and lateral adduction of the metacarpal and digit I.

Musculus flexor pollicis brevis profundus (Figs. 1.48, 1.50) originates from the *ligamentum palmaris profundum* at the level of metacarpal II, proximal to the origin of the *m. adductor pollicis*. It inserts under the *m. flexor pollicis brevis* on the medial sesamoid bone of the metacarpophalangeal I joint. Usually, this muscle is included in the *m. flexor pollicis brevis* (Le Gros Clark 1924, 1926; Haines 1955; George 1977). In the majority of mammals it is absent, but not in humans where it is known as the deep head of the *m. flexor pollicis brevis*. In tree shrews, this head is so definitely separate from the major (superficial) *m. flexor pollicis brevis*, that we decided to give it this new name – *m. flexor pollicis brevis profundus*.

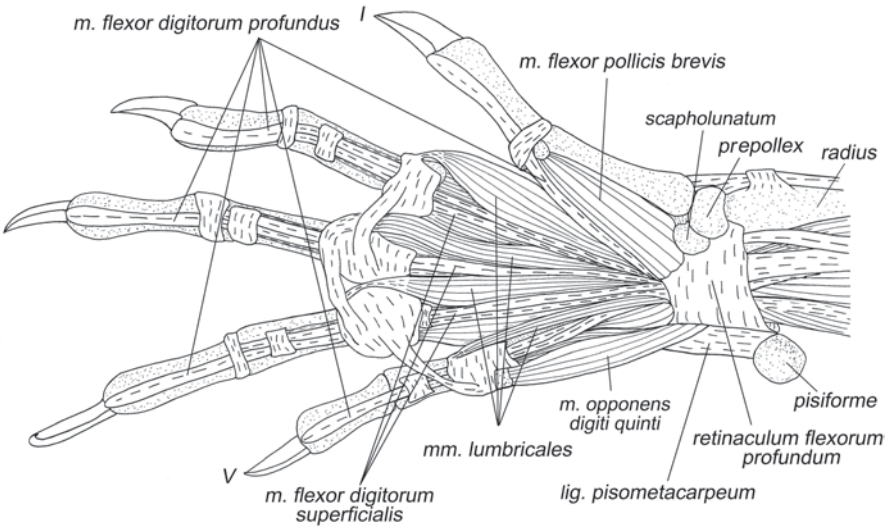


Fig. 1.47 Muscles of the manus of *T. belangeri*, ventral view, layer III.

The muscle flexes digit I and participates in its lateral adduction, including its metacarpal.

Musculus adductor pollicis (Figs. 1.48, 1.50) originates at the level of metacarpal II from the edge of the *ligamentum palmaris profundum* distal to the origin of the *m. flexor pollicis brevis profundus*. It inserts on the lateral surface of the articular capsule of the metacarpophalangeal joint of digit I.

The muscle adducts laterally digit I, including its metacarpal.

Musculi lumbricales (Figs. 1.45–1.47, 1.49) are four muscles located in the interspaces between the five terminal perforating tendons of the *m. flexor digitorum profundus*. The *m. lumbricalis digiti secundi* arises from the ventral surface of *aponeurosis flexoria communis* just proximal to the point of divergence of the perforating tendons to digits I and II and passes between these tendons to insert on the medial surface of the metacarpophalangeal articular capsule of digit II. Similar relations are found in the other three *mm. lumbricales*, which insert on the medial surface of the metacarpophalangeal articular capsules of digits III–V. The statement of Straus (1942) and George (1977), that the *m. lumbricalis digiti tertii* arises from the terminal tendon of the superficial digital flexor, instead of the deep one, is wrong and results from the erroneous ascription of the *caput humerale superficiale* of the *m. flexor digitorum profundus* to the *m. flexor digitorum superficialis* (see above).

Each muscular head flexes, pronates, and displaces medially respective digit.

Musculus abductor digiti secundi (Figs. 1.48, 1.50–1.52) originates from the distal edge of the *ligamentum palmaris profundum* medial to the *m. adductor digiti secundi* by a long tendon (Fig. 1.51). It inserts, along with the *m. interosseus dorsalis digiti secundi*, on the medial sesamoid bone of the metacarpophalangeal joint of digit II. This muscle seems to be never described in other mammals and is rarely

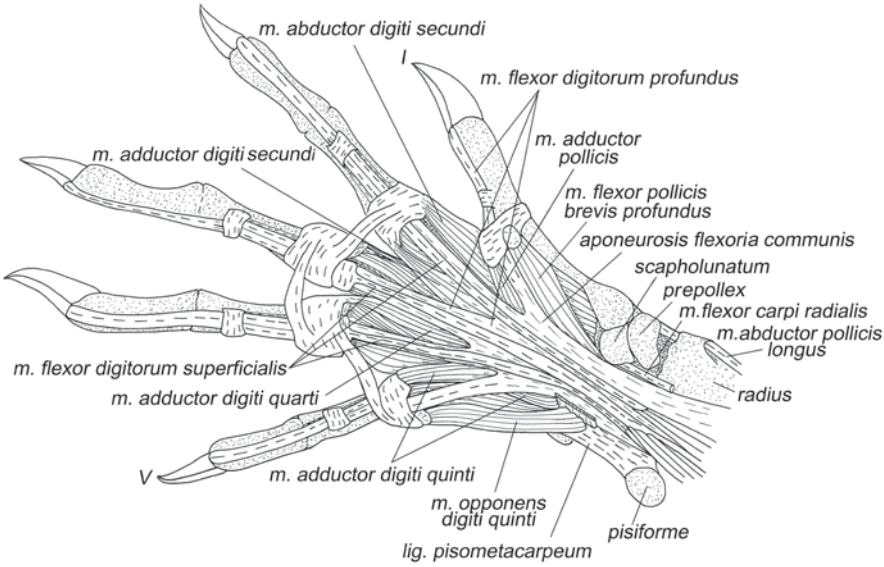


Fig. 1.48 Muscles of the manus of *T. belangeri*, ventral view, layer IV.

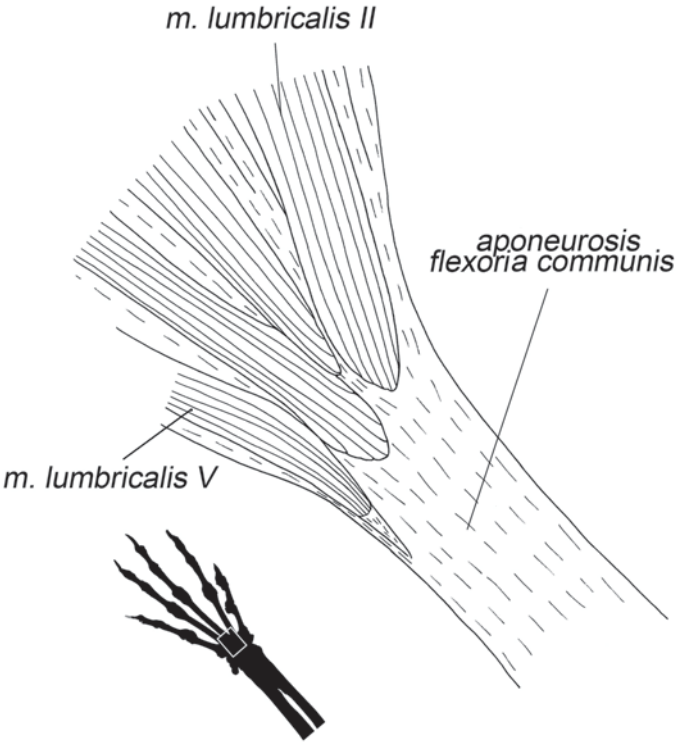


Fig. 1.49 Origin of the *mm. lumbricales* of *T. belangeri*, ventral view.

present in tree shrews. Our finding could be regarded as an artefact of dissection, but George (1977) has mentioned that a pair of superficial accessory interossei were present in the right manus of one *Urogale*, one of which additional muscles appears to be similar to our *m. abductor digiti secundi*. Another similar structure can be noticed on the cross-section of the manus of *Tupaia tana* published by Haines (1955, Fig. 11 therein); it looks like a subdivision of the interosseous muscular mass near the second finger. Apparently, the *m. abductor digiti secundi* develops by splitting off from the *mm. interossei palmares* and shifting the origin towards the palm center along the edge of the *ligamentum palmaris profundum*.

The muscle indirectly, via the metacarpal, abducts medially and flexes the second finger.

Musculus adductor digiti secundi (Figs. 1.48, 1.50, 1.51) originates by a very short aponeurosis from the distal edge of the *ligamentum palmaris profundum* at the level of metacarpal III and from the proximal aponeurosis of the *m. interosseus palmaris digiti secundi*. It inserts on the lateral surface of the articular capsule of the metacarpophalangeal joint of digit II. George (1977) describes the deeper part of this muscle in *Urogale* as the second of the two superficial accessory interossei mentioned above.

The muscle adducts laterally digit II.

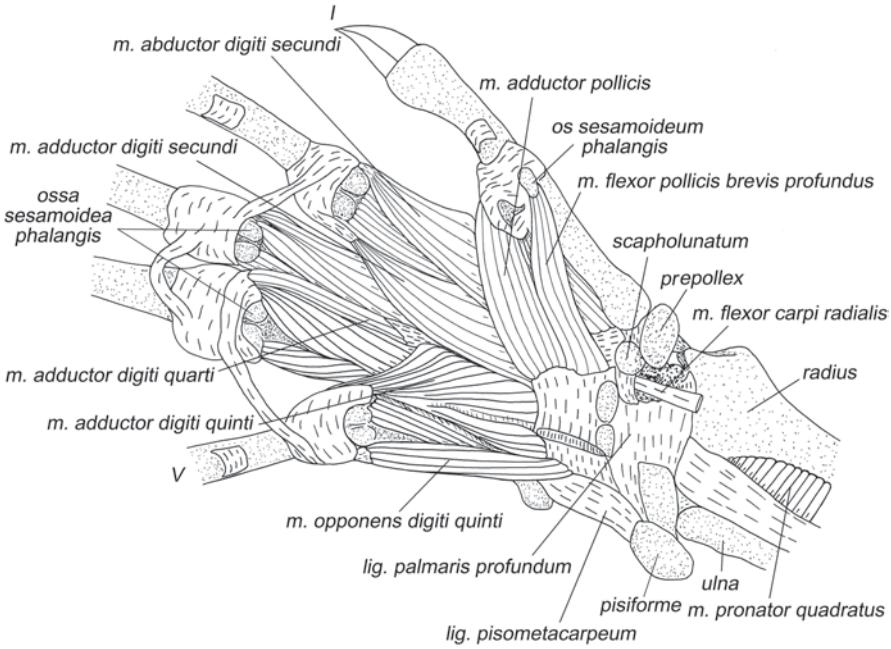


Fig. 1.50 Muscles of the manus of *T. belangeri*, ventral view, layer V.

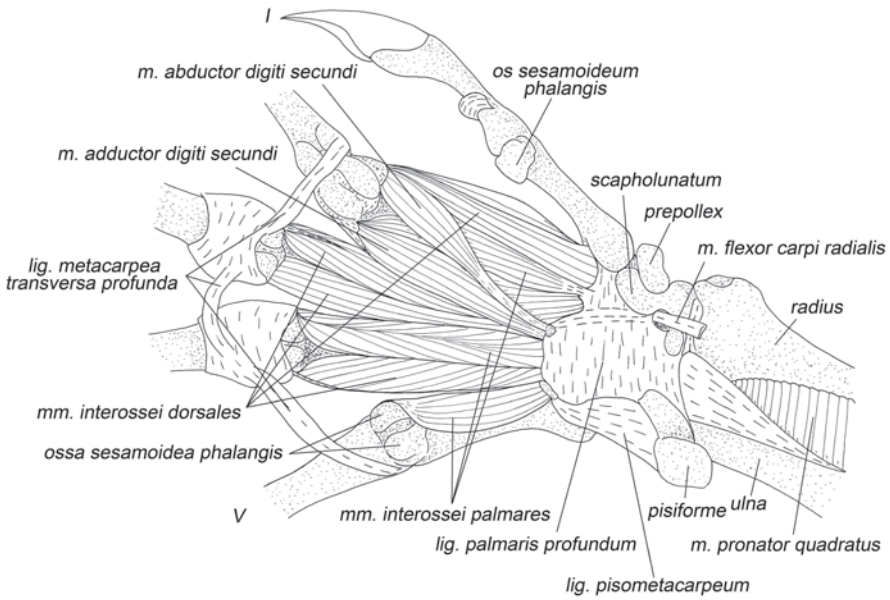


Fig. 1.51 Muscles of the manus of *T. belangeri*, ventral view, layer VI.

Musculus adductor digiti quarti (Figs. 1.48, 1.50) originates with the help of an aponeurosis from the distal edge of the *ligamentum palmaris profundum* between digits III and IV and from the ventral surface of the proximal aponeurosis of the *m. interosseus palmaris digiti quarti*. It inserts by a very short aponeurosis on the medial surface of the articular capsule of the metacarpophalangeal joint of digit IV.

The muscle adducts medially digit IV.

Musculus adductor digiti quinti (Figs. 1.48, 1.50) originates from the lateral edge of the *retinaculum flexorum profundum* at the point of its transition into the *ligamentum palmaris profundum*, from the distal edge of this ligament at the level of metacarpal IV, and from the proximal aponeurosis of the *m. interosseus palmaris digiti quarti*. It inserts on the medial surface of the articular capsule of the metacarpophalangeal joint of digit V.

The muscle adducts medially digit V.

Musculus flexor brevis manus (Fig. 1.45) is small, triangular in shape, and one of the most superficial muscles of the palmar surface of the manus. It originates from the ulnar part of the *retinaculum flexorum superficiale* and inserts on the ventral surface of the base of the second phalanx of digit V by a perforated tendon shared with the *m. flexor digiti quinti superficialis*. A typical perforated terminal tendon of this muscle shows that it belongs to the system of the *m. flexor digitorum superficialis* as a separate head, which retains the ancestral (characteristic of reptiles and a few other mammals) location in the manus rather than in antebrachium. The ancestral integrity of the two muscles is supported by the above-mentioned fact (Le Gros Clark 1926) that in *Ptilocercus* the perforated tendon of digit V is shared by the *m. flexor brevis manus* and *m. flexor digitorum superficialis*.

The muscle flexes digit V.

Musculus flexor digiti quinti superficialis (Fig. 1.45) originates widely from the middle one-third of the *retinaculum flexorum medium*[13] and also from the middle part of the *retinaculum flexorum superficiale*. It has the common insertion with the *m. flexor brevis manus* by the perforated tendon to the fifth finger. This muscle was never described before. Our predecessors have found in tree shrews some variation in the structure of the *m. flexor brevis manus*, but not this separate head, which we name the *m. flexor digiti quinti superficialis* for its obvious relation with the superficial system of digital flexors.

This muscle helps the m. flexor brevis manus to flex digit V.

Musculus flexor digiti quinti brevis (Figs. 1.45, 1.46) originates from the *retinaculum flexorum medium* at the level of the metacarpal of digit IV. It inserts by a short aponeurosis, shared with the *m. abductor digiti quinti*, on the lateral surface of the articular capsule of the metacarpophalangeal joint of digit V and, through it, on the lateral side of the base of its first phalanx.

This muscle participates in flexion and lateral abduction of digit V.

---

[13] The *retinaculum flexorum medium* (Fig. 1.46) is a wide palmar ligament connecting the lateral part of the *retinaculum flexorum profundum* with the lateral side of the lower surface of the prepollex.

Musculus abductor digiti quinti (Figs. 1.37, 1.45, 1.46) originates from the *pisiforme* and the *ligamentum pisometacarpeum*. It inserts, together with the *m. flexor digiti quinti brevis*, on the lateral surface of the articular capsule of the metacarpophalangeal joint of digit V and, through it, on the lateral side of the base of its first phalanx.

This muscle abducts laterally digit V.

Musculus opponens digiti quinti (Figs. 1.47, 1.48, 1.50) originates from the *ligamentum pisometacarpeum* and the *retinaculum flexorum profundum* at its lateral attachment and, thus, fills the groove formed at the point of fusion of these ligaments. It inserts on the lateral side of the distal head of the fifth metacarpal. Previously, this muscle was considered to be absent in tree shrews (Carlsson 1922; Le Gros Clark 1924), or was not mentioned at all (e.g. George 1977); in the second case it was probably regarded as an integral part of the *m. abductor digiti quinti*.

This muscle abducts laterally the fifth metacarpal.

Musculi interossei palmares (Figs. 1.51, 1.52). Tree shrews have three of them: one lateral of digit II and two medial of digits IV and V. The *m. interosseus palmaris digiti secundi* originates with the help of an aponeurosis from the distal edge of the *ligamentum palmaris profundum* at the level of the base of the second metacarpal, runs along the lateral side of the second metacarpal, and inserts on the lateral collateral ligament of the metacarpophalangeal joint of digit II. The *m. interosseus palmaris digiti quarti* originates fleshy from the distal edge of the *ligamentum palmaris profundum*, runs along the medial side of metacarpal IV, and inserts by an aponeurosis on the medial collateral ligament of the metacarpophalangeal joint of digit IV. *M. inter-*

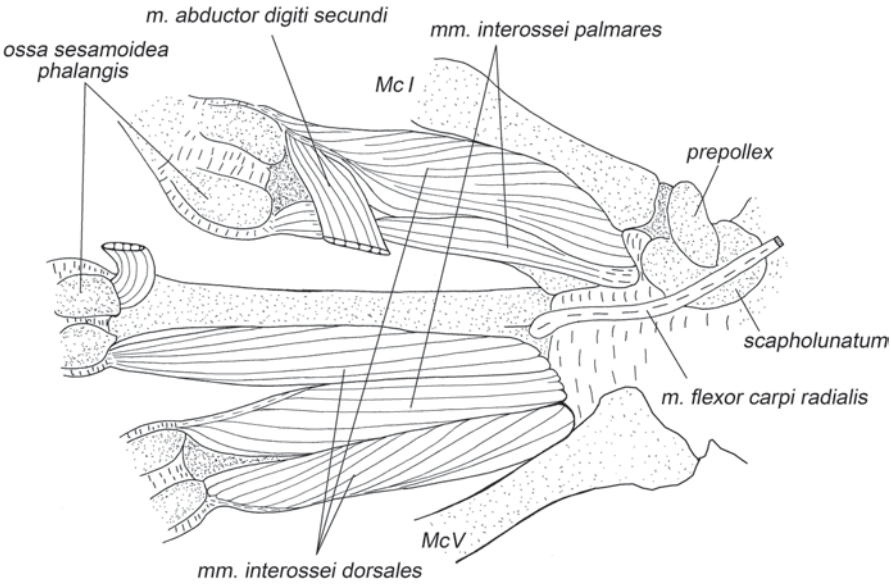


Fig. 1.52 Muscles of the manus of *T. belangeri*, ventral view, layer VII.

osseus palmaris digiti quinti originates from the lateral part of the distal edge of the *ligamentum palmaris profundum* and from a small sesamoid bone incorporated in it, runs along the medial side of metacarpal V, and inserts with the help of an aponeurosis on the medial collateral ligament of the metacarpophalangeal joint of digit V.

The muscles adduct digits II, IV, and V to the midline of the manus.

Musculi interossei dorsales (Figs. 1.51, 1.52) actually belong to the palmar (flexor) muscles, but squeeze in between metacarpals. Tree shrews possess the complete set of four muscles, characteristic of the majority of mammals: the medial muscle of digit II, lateral and medial muscles of digit III, and lateral muscle of digit IV. The *m. interosseus dorsalis digiti secundi* originates from the distal edge of the *ligamentum palmaris profundum* between digits I and II and from the facing each other surfaces of the first and second metacarpals, and inserts by an aponeurosis on the medial sesamoid bone and the medial collateral ligament of the second metacarpophalangeal joint along with the *m. abductor digiti secundi*. The *m. interosseus dorsalis digiti tertii medialis* originates from the distal edge of the *ligamentum palmaris profundum* between digits II and III, the lateral surface of the proximal part of the second metacarpal, and from the ventromedial surface of almost the entire third metacarpal; it inserts on the medial sesamoid bone and the medial collateral ligament of the third metacarpophalangeal joint. The *m. interosseus dorsalis digiti tertii lateralis* is opposed to the previous muscle symmetrically relative to digit III. The *m. interosseus dorsalis digiti quarti* originates from the distal edge of the *ligamentum palmaris profundum* between digits IV and V and from the facing each other surfaces of the fourth and fifth metacarpals, and inserts on the lateral sesamoid bone and the lateral collateral ligament of the metacarpophalangeal joint of digit IV.

The muscles abduct digits II–IV from the midline of the manus.

References

Carlsson A (1922) Über die Tupaiidae und ihre Beziehungen zu den Insectivora und den Prosimiae. Acta Zool 3(2–3):227–270

Davis DD (1938) Notes on the anatomy of the treeshrew *Dendrogale*. Field Mus Nat Hist Zool Ser 20(30):383–404

Diogo R, Wood BA (2012) Comparative anatomy and phylogeny of primate muscles and human evolution. Taylor & Francis, Oxford

Dunlap SS, Thorington RW Jr, Aziz MA (1985) Forelimb anatomy of New World monkeys: myology and the interpretation of primitive anthropoid models. Am J Phys Anthropol 68(4):499–517

Gambaryan PP (1960) Adaptive features of locomotion organs in burrowing mammals. Acad Sci Publ, Erevan (in Russian)

Gambaryan PP (1974) How mammals run: anatomical adaptations. Halsted Press/John Wiley and Sons, New York

George RM (1977) The limb musculature of the Tupaiidae. Primates 18(1):1–34

Haines RW (1950) The flexor muscles of the forearm and hand in lizards and mammals. J Anat 84(1):13–29

Haines RW (1955) The anatomy of the hand of certain insectivores. Proc Zool Soc Lond 125 (3–4):761–777

Howell AB (1937) Morphogenesis of the shoulder architecture. Part VI. Therian Mammalia. Quart Rev Biol 12(4):440–463

Jenkins FA Jr (1974) Tree shrew locomotion and the origins of primate arborealism. In: Jenkins FA Jr (ed) Primate locomotion. Academic Press, New York, p 85–116

Jenkins FA Jr, Weijs WA (1979) The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). J Zool Lond 188(3):379–410

Jones FW (1916) Arboreal man. Edward Arnold, London

Kuznetsov AN (1999) Structural types of limbs and evolution of running technique in tetrapods. Zool Issled 3:5–94 (in Russian with English summary)

Le Gros Clark WE (1924) The myology of the tree-shrew (*Tupaia minor*). Proc Zool Soc Lond 94(2):461–497

Le Gros Clark WE (1926) On the anatomy of the pen–tailed tree–shrew (*Ptilocercus lowii*). Proc Zool Soc Lond 96(4):1179–1309

Miller RA (1935) Functional adaptations in the forelimb of the sloths. J Mammal 16(1):38–51

Sargis EJ (2001) The grasping behavior, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). J Zool Lond 253(4):485–490

Sargis EJ (2002a) A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications. Mammalia 66(4):579–598

Sargis EJ (2002b) Functional morphology of the forelimbs of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. J Morphol 253(1):10–42

Sargis EJ (2002c) Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. J Morphol 254(2):149–185

Sargis EJ (2002d) The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae): an analysis of primatomorphan and volitantian characters. J Mammal Evol 9(1–2):137–160

Sargis EJ (2004) New view on tree shrews: the role of tupaiids in primate supraordinal relationships. Evol Anthrop 13(2):56–66

Stafford BJ, Thorington RW Jr (1998) Carpal development and morphology in archontan mammals. J Morphol 235(2):135–155

Straus WL Jr (1941) The phylogeny of the human forearm extensors. Hum Biol 13(1):23–50

Straus WL Jr (1942) The homologies of the forearm flexors: urodeles, lizards, mammals. Amer J Anat 70(2):281–316

Verma K (1965) Notes on the biology and anatomy of the Indian tree-shrew, *Anathana wroughtoni*. Mammalia 29(3):289–330

Voss H, Herrlinger R (1956) Taschenbuch der Anatomie. Band 1. Einführung in die Anatomie. Bewegungsapparat. VEB Gustav Fischer, Jena

Walton DW, Walton GM (1970) Post-cranial osteology of bats. In: Slaughter BH, Walton DW (eds) About bats: a chiropteran biology symposium. South Methodist University, Dallas (Fondren Sci Ser 11:93–126)

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.

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_2

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.

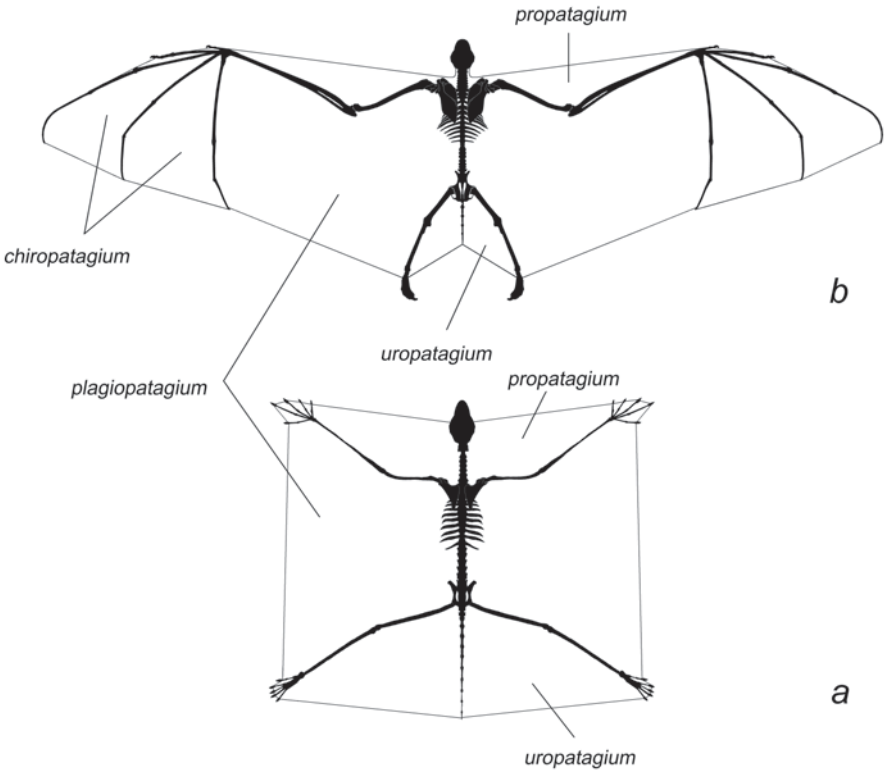


Fig. 2.1 Scheme of the main parts of patagium. *a. Colugos b. Bats*

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

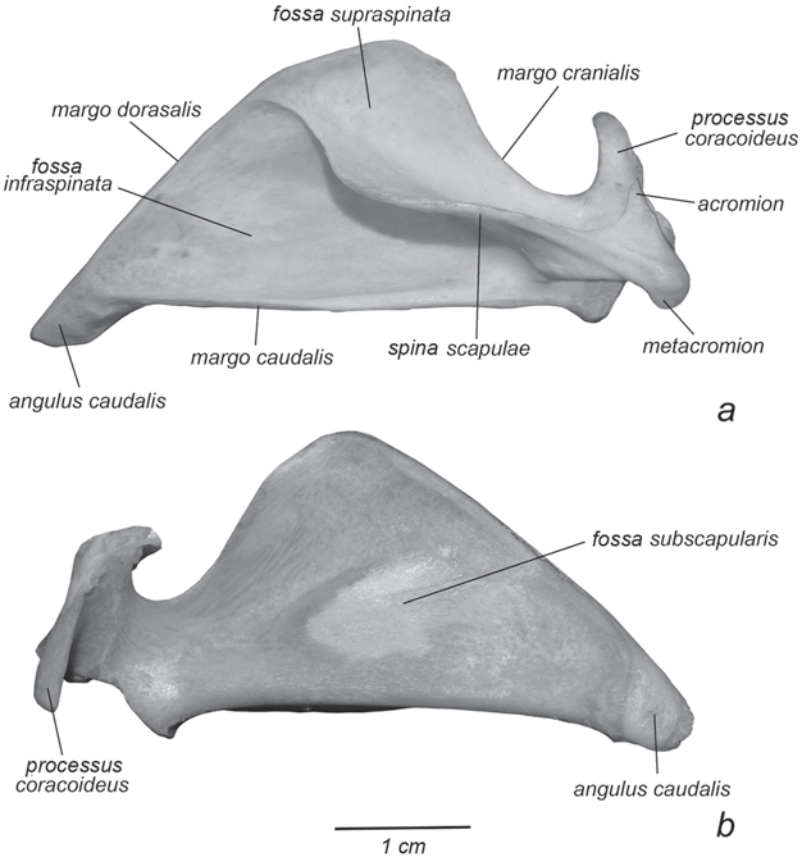


Fig. 2.2 The scapula of colugo, right forelimb. *a. Lateral view* (*Cynocephalus variegatus, adult*) *b. Medial view* (*Cynocephalus volans, subadult*)

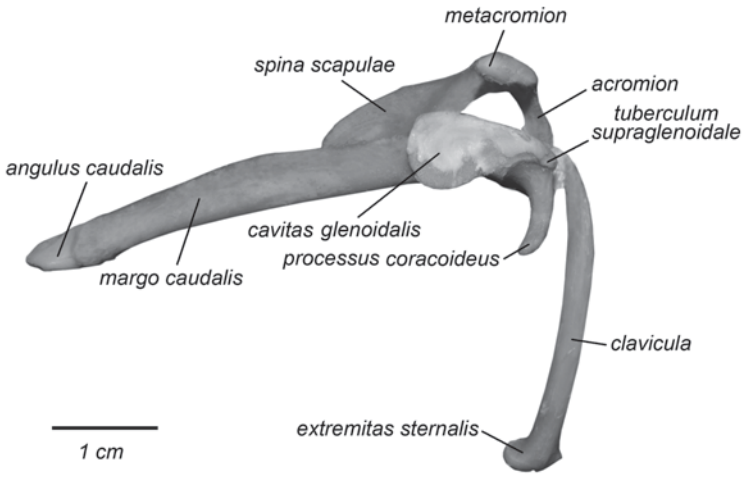


Fig. 2.3 The clavicle and scapula of *C. volans,* right forelimb, subadult, posterior view.

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.

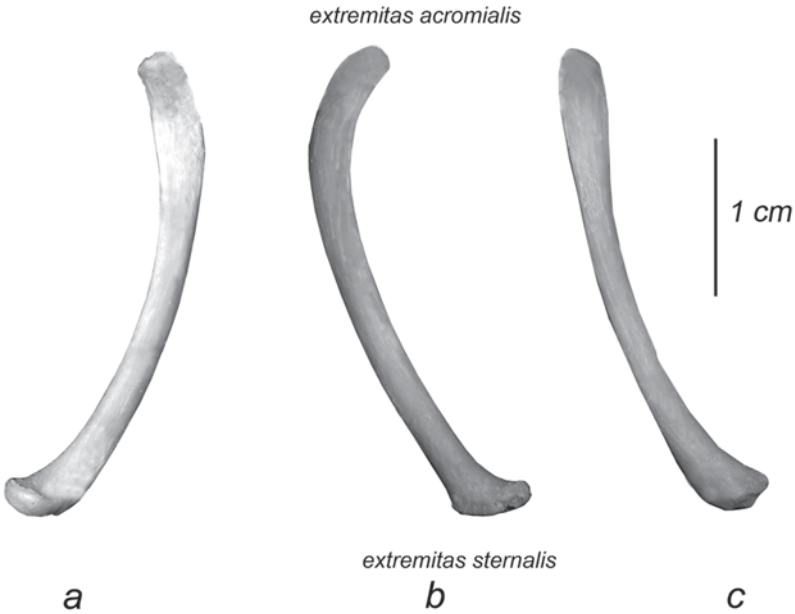


Fig. 2.4 The clavicle of *C. volans,* right forelimb. *a. Lateral view b. Medial view c. Anterior view*

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

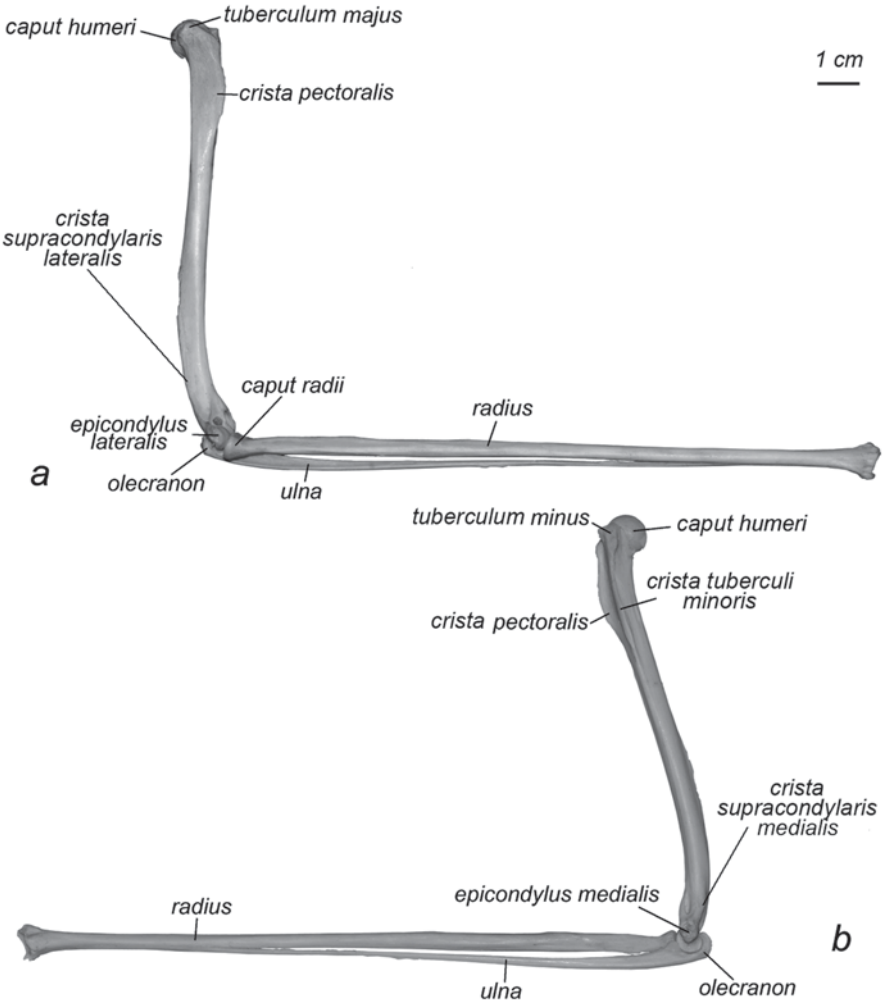


Fig. 2.5 The humerus and antebrachium of *C. volans,* right forelimb. *a. Lateral view b. Medial view*

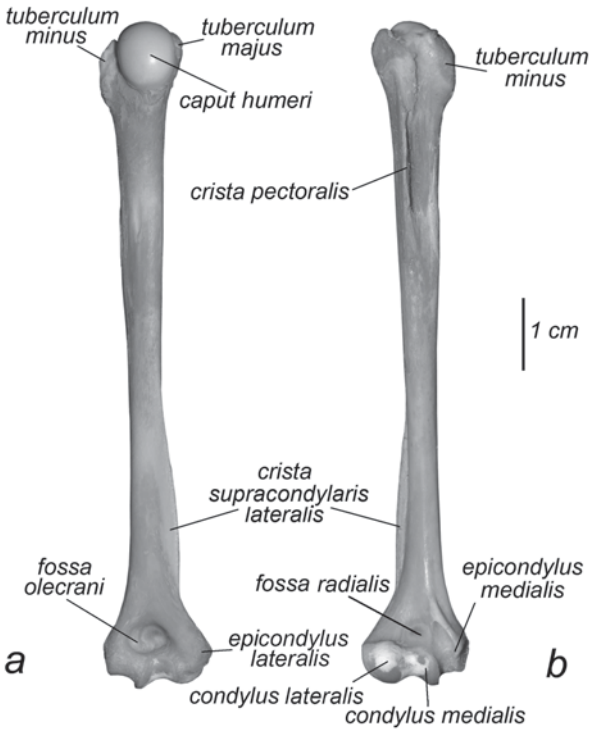


Fig. 2.6 The humerus of *C. volans,* right forelimb. *a. Anterior view* *b. Posterior view*

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*

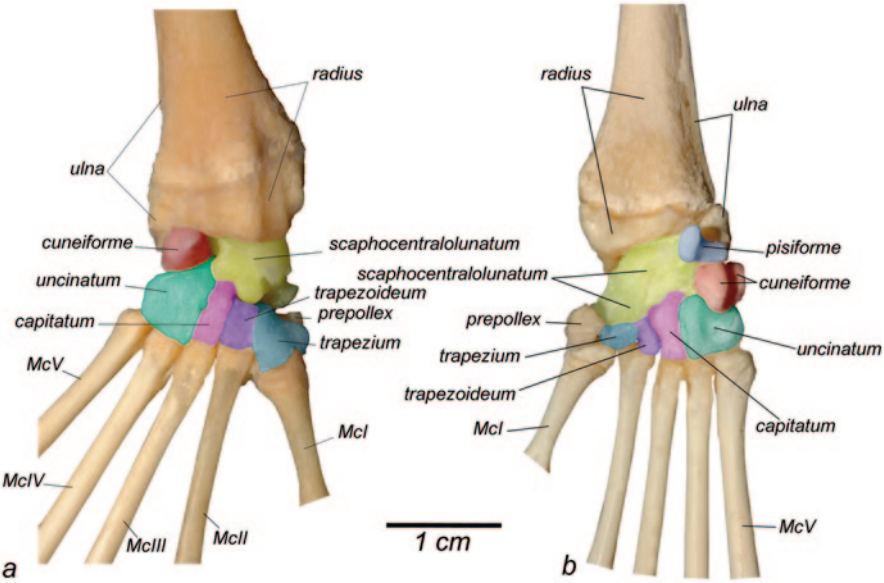


Fig. 2.7 The carpus of *C. volans,* right forelimb, subadult. *a. Dorsal view b. Ventral view*

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).

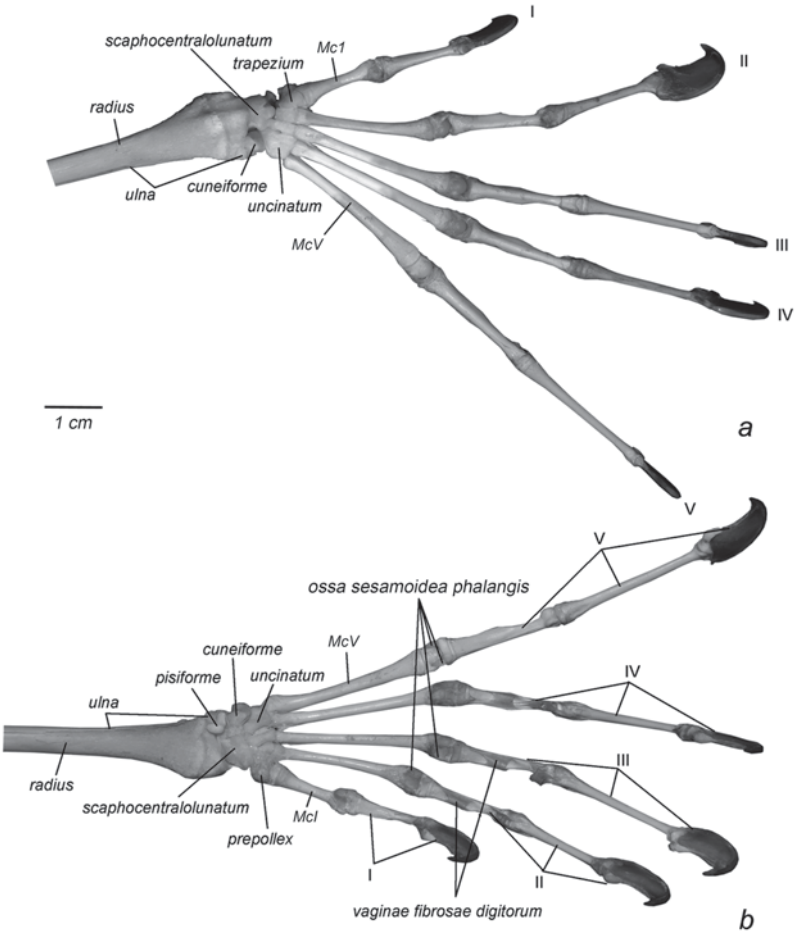


Fig. 2.8 The manus of *C. volans,* right forelimb. *a. Dorsal view b. Ventral view*

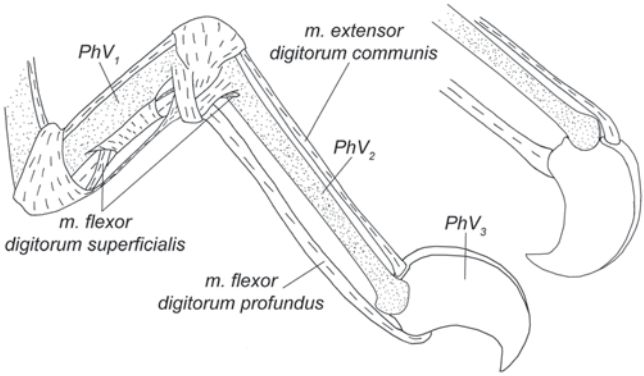


Fig. 2.9 The fifth finger of *C. volans*. Flexed and hyperextended ungual phalanx, lateral view.

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-*

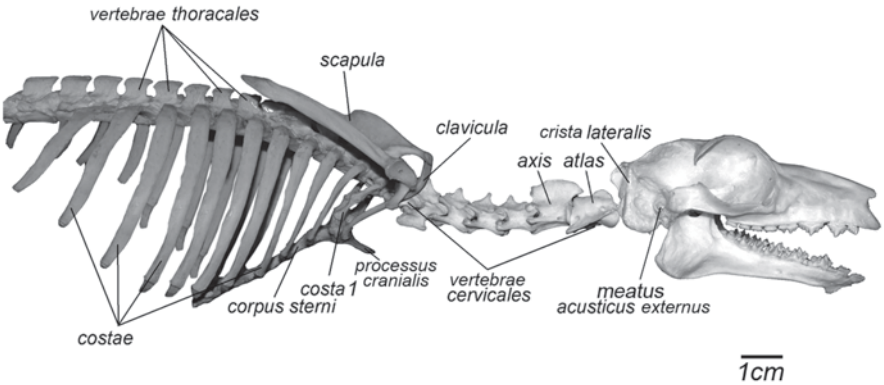


Fig. 2.10 The axial skeleton of *C. variegatus* with shoulder girdle, lateral view.

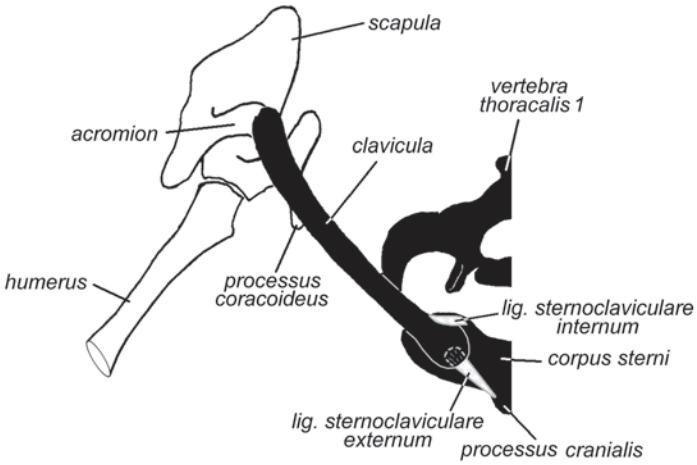


Fig. 2.11 Scheme of the sternoclavicular articulation of *C. volans,* right forelimb, anterior view.

[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).

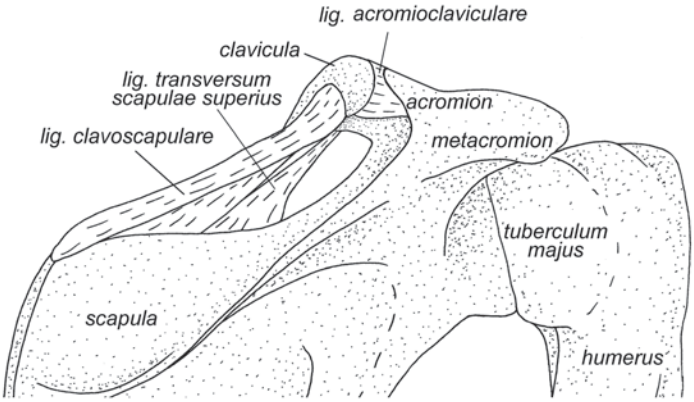


Fig. 2.12 The acromioclavicular articulation of *C. volans,* right forelimb, dorsal view.

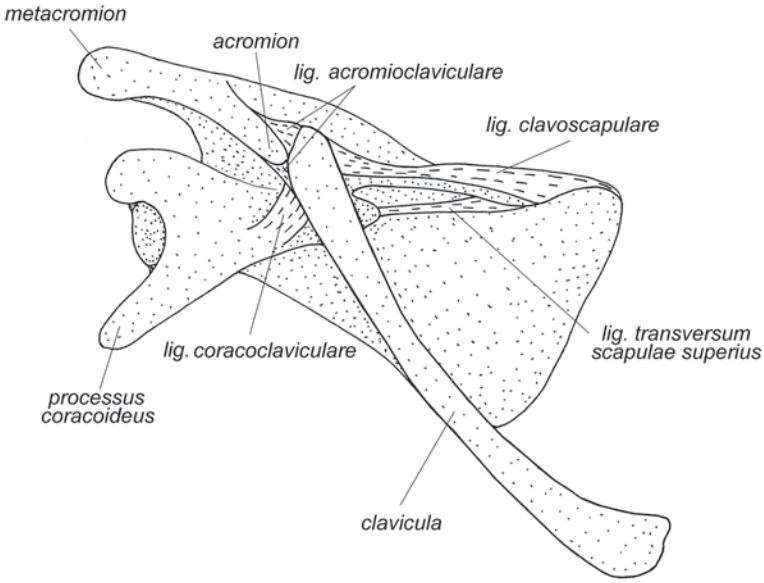


Fig. 2.13 The acromioclavicular articulation of *C. volans,* right forelimb, anterior view.

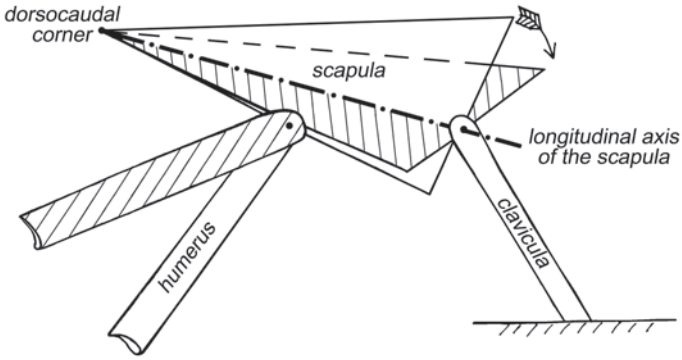


Fig. 2.14 Scheme of the scapula rotation relative to clavicle in colugo. Arrow indicates the direction of possible twist of the scapula; hatching indicates the final position of the scapula and humerus.

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*

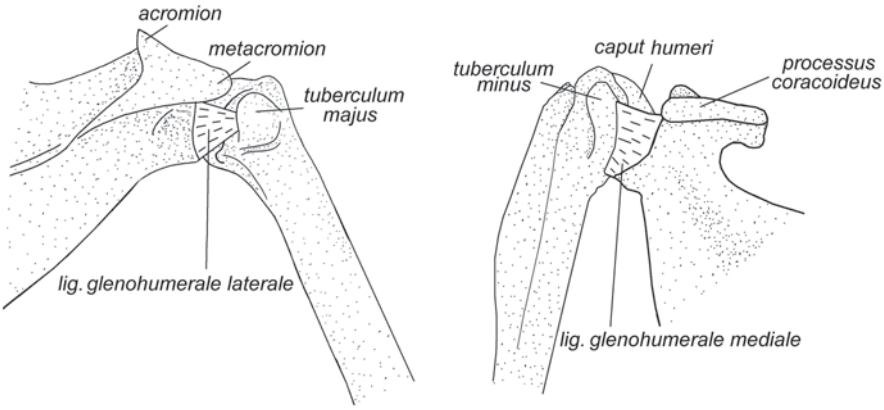


Fig. 2.15 The shoulder joint of *C. volans,* right forelimb. *a. Dorsal view b. Ventral view*

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.

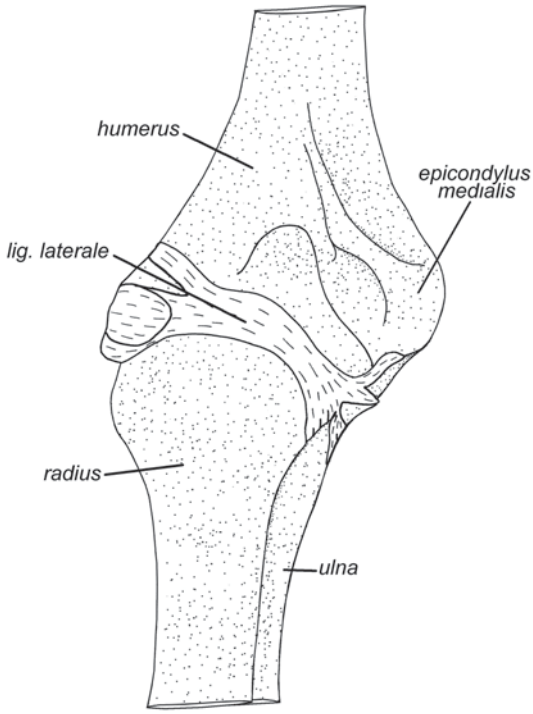


Fig. 2.16 The elbow joint of *C. volans,* right forelimb, anterior view.

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).

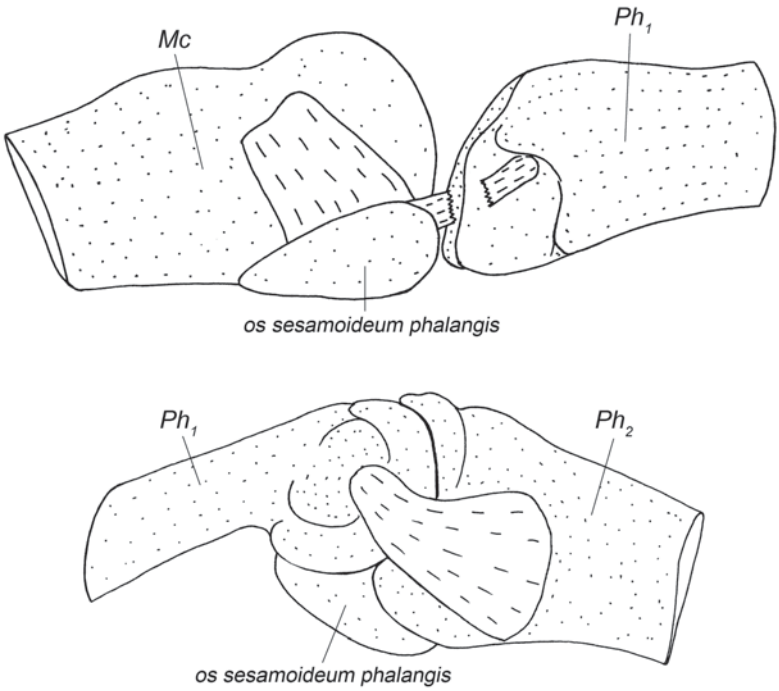


Fig. 2.17 The digital joints of *C. volans*. *a. Metacarpophalangeal joint (collateral ligament cut) b. Interphalangeal joint*

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*.

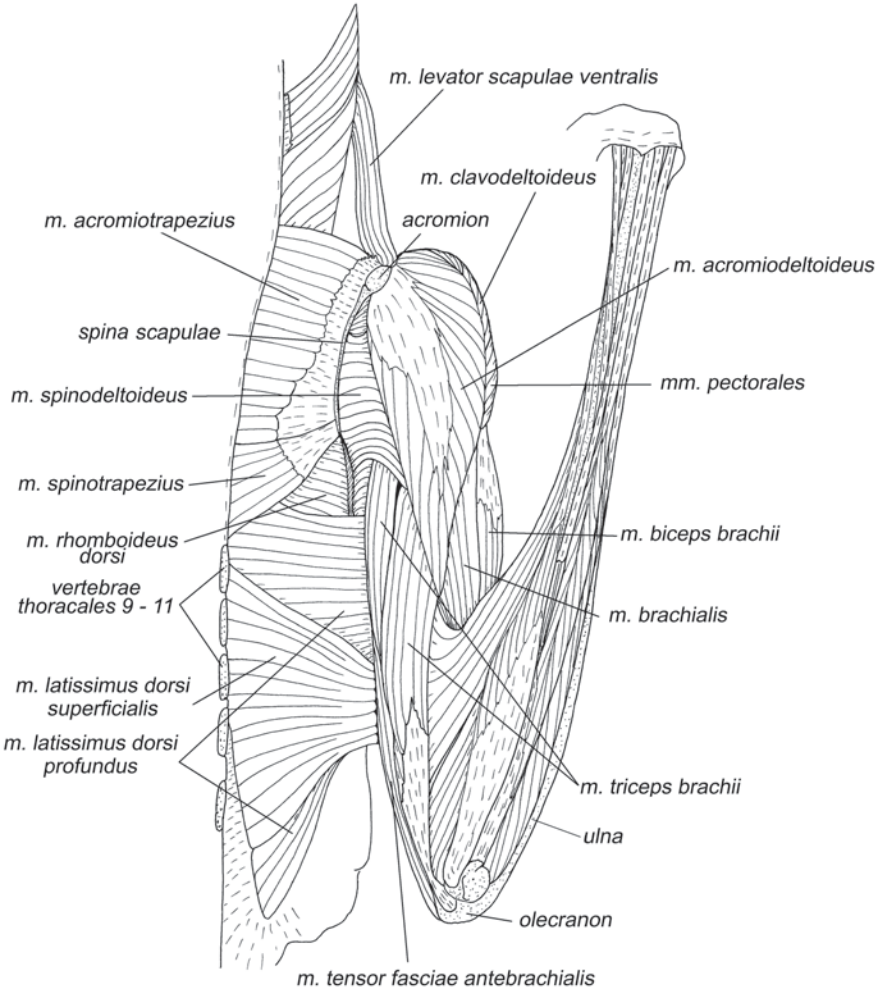


Fig. 2.18 Forelimb muscles of *C. volans,* dorsal view, layer I.

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.

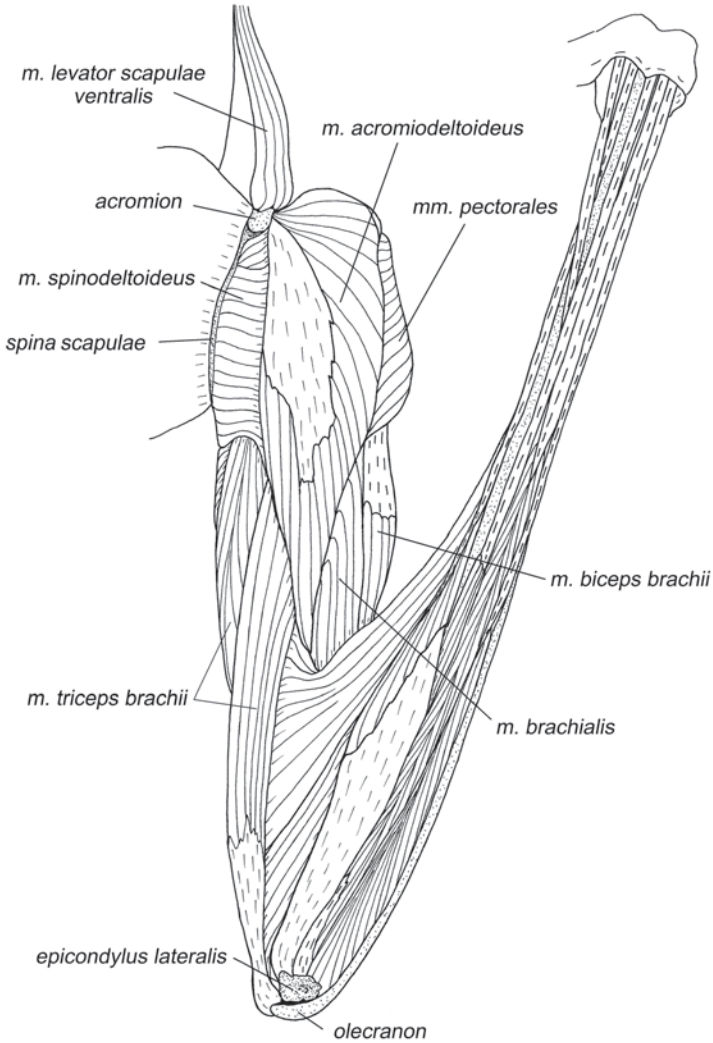


Fig. 2.19 Forelimb muscles of *C. volans,* dorsal view, layer II.

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.

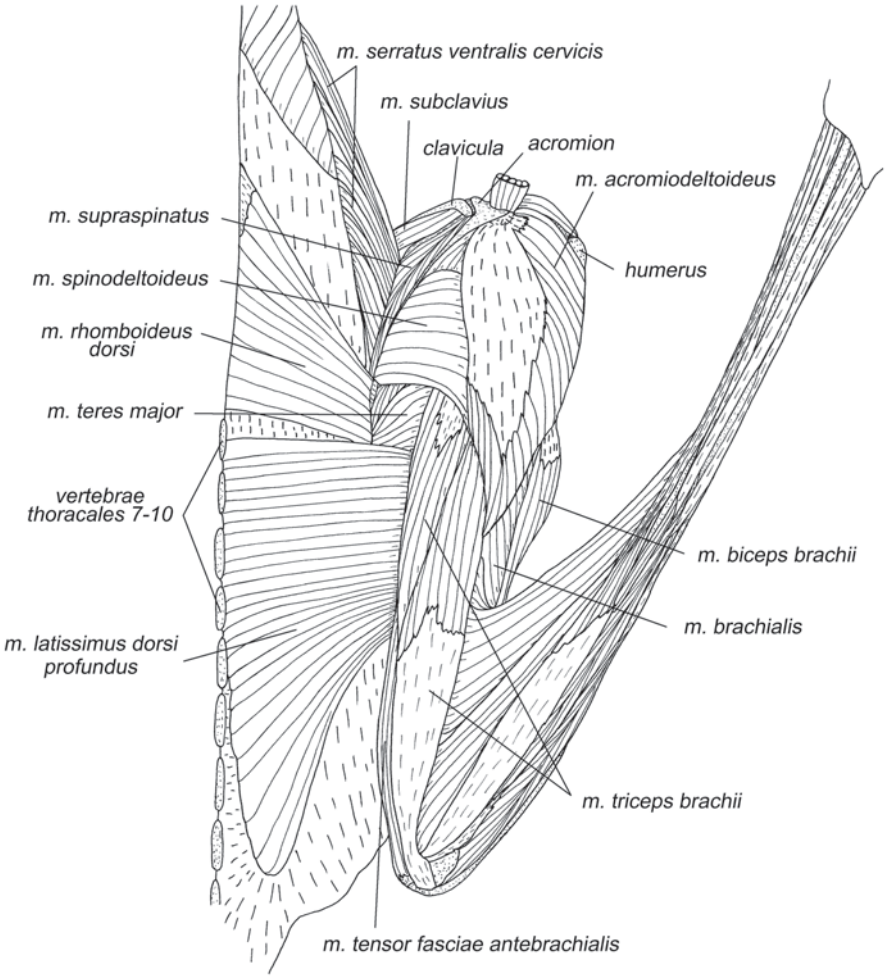


Fig. 2.20 Forelimb muscles of *C. volans,* dorsal view, layer III.

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,

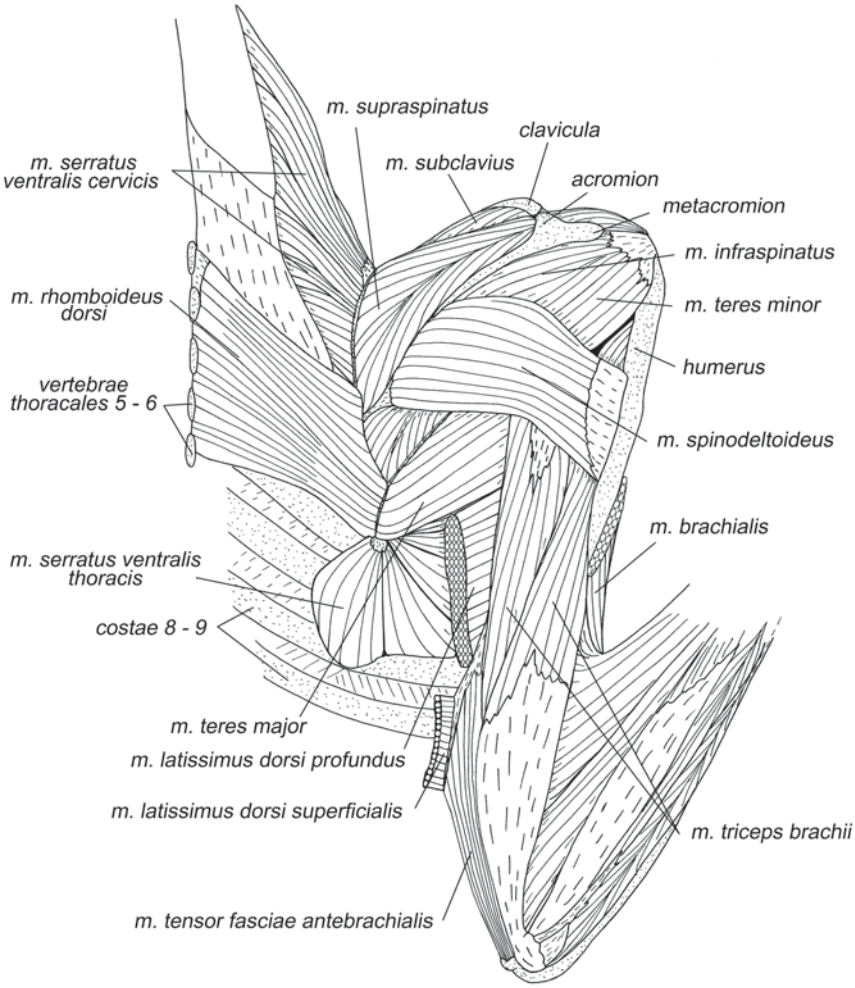


Fig. 2.21 Forelimb muscles of *C. volans,* dorsal view, layer IV.

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

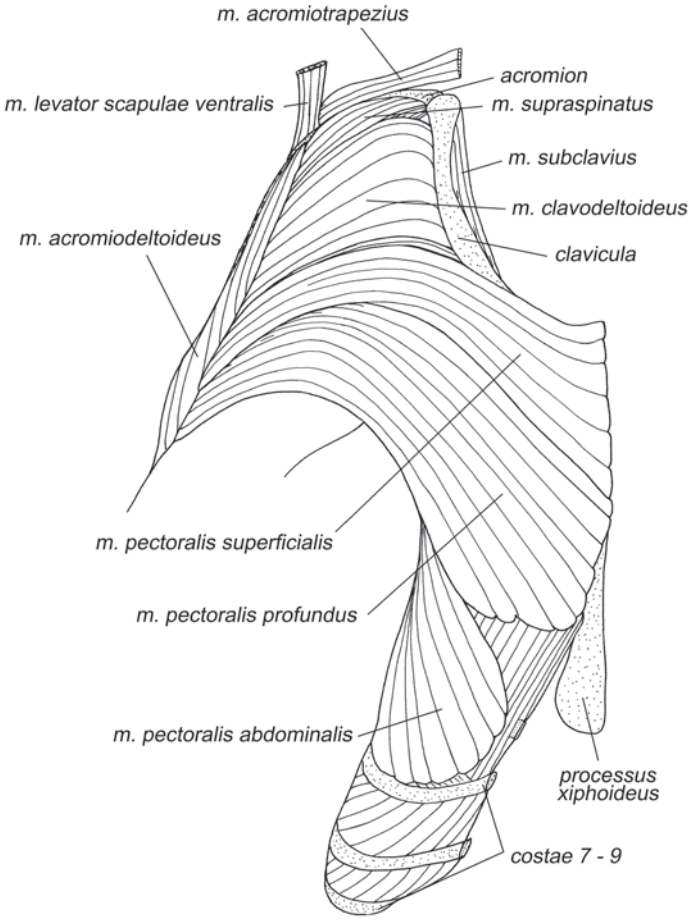


Fig. 2.22 Forelimb muscles of *C. variegatus,* ventral view, layer I.

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.

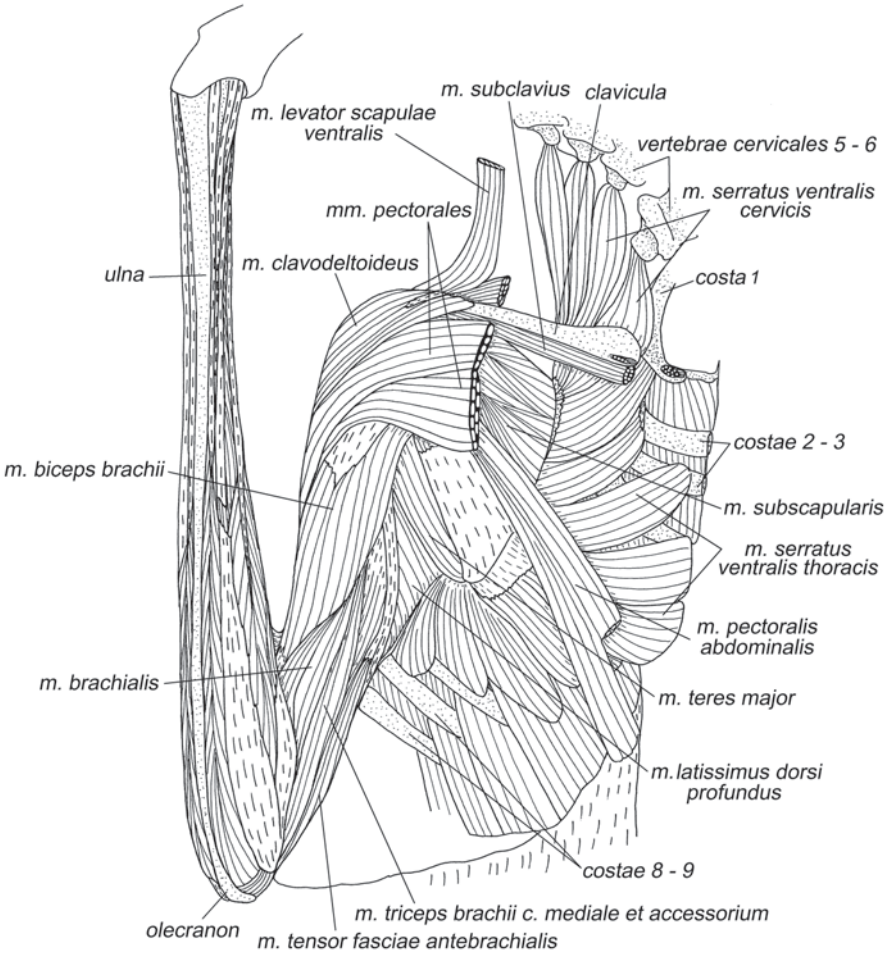


Fig. 2.23 Forelimb muscles of *C. volans,* ventral view, layer II.

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

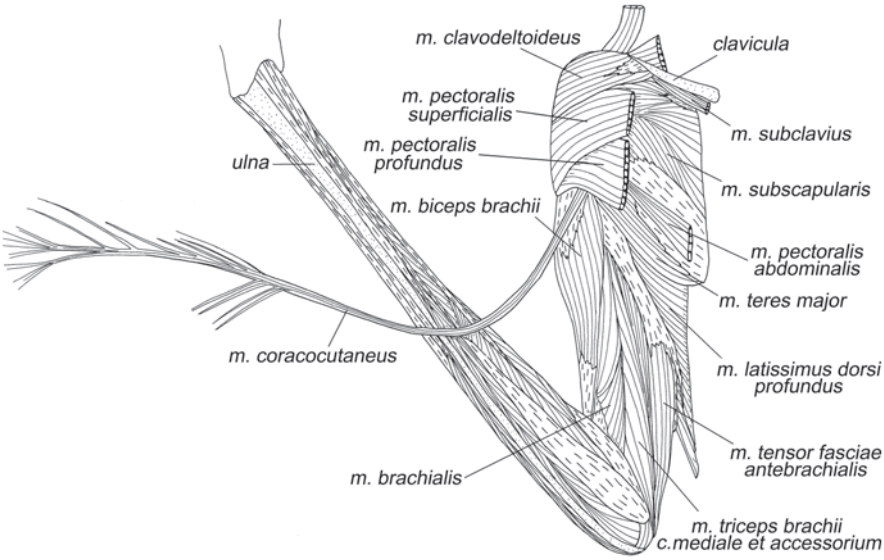


Fig. 2.24 Forelimb muscles of *C. volans,* ventral view, layer III.

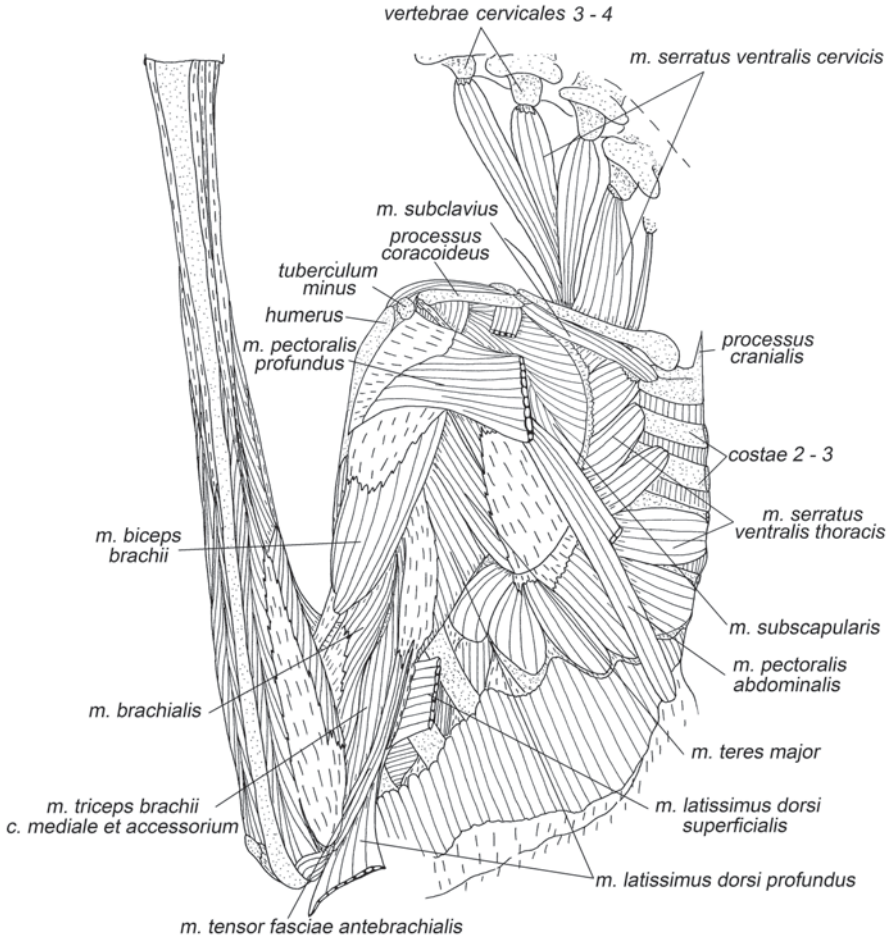


Fig. 2.25 Forelimb muscles of *C. volans,* ventral view, layer IV.

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.

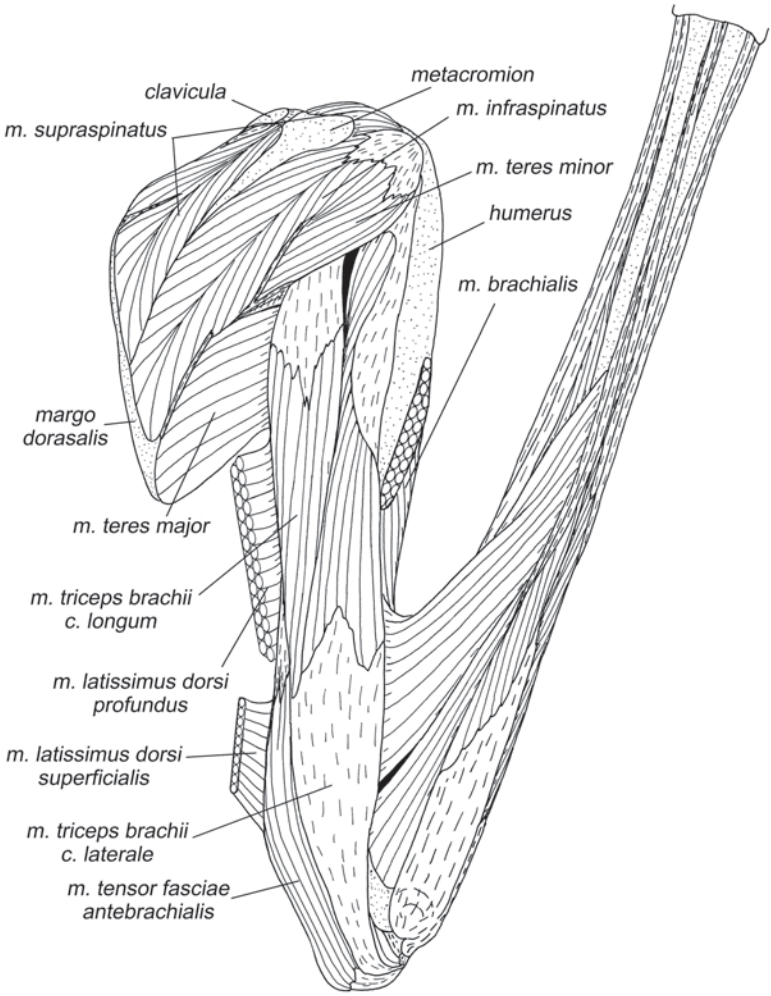


Fig. 2.26 Forelimb muscles of *C. volans,* dorsal view, layer V.

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.

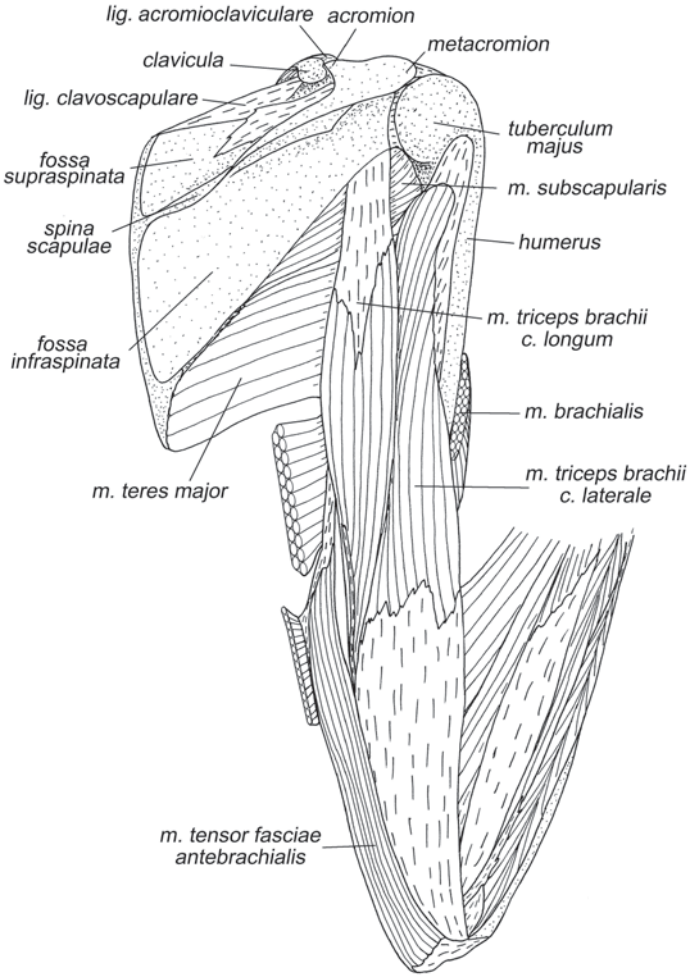


Fig. 2.27 Forelimb muscles of *C. volans,* dorsal view, layer VI.

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.

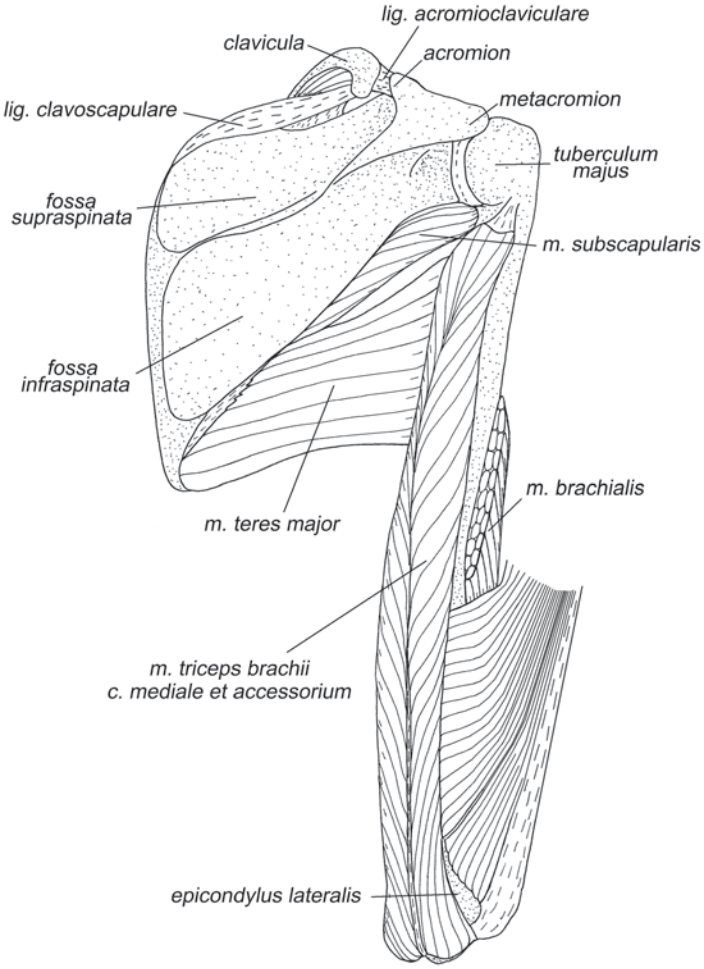


Fig. 2.28 Forelimb muscles of *C. volans,* dorsal view, layer VII.

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.

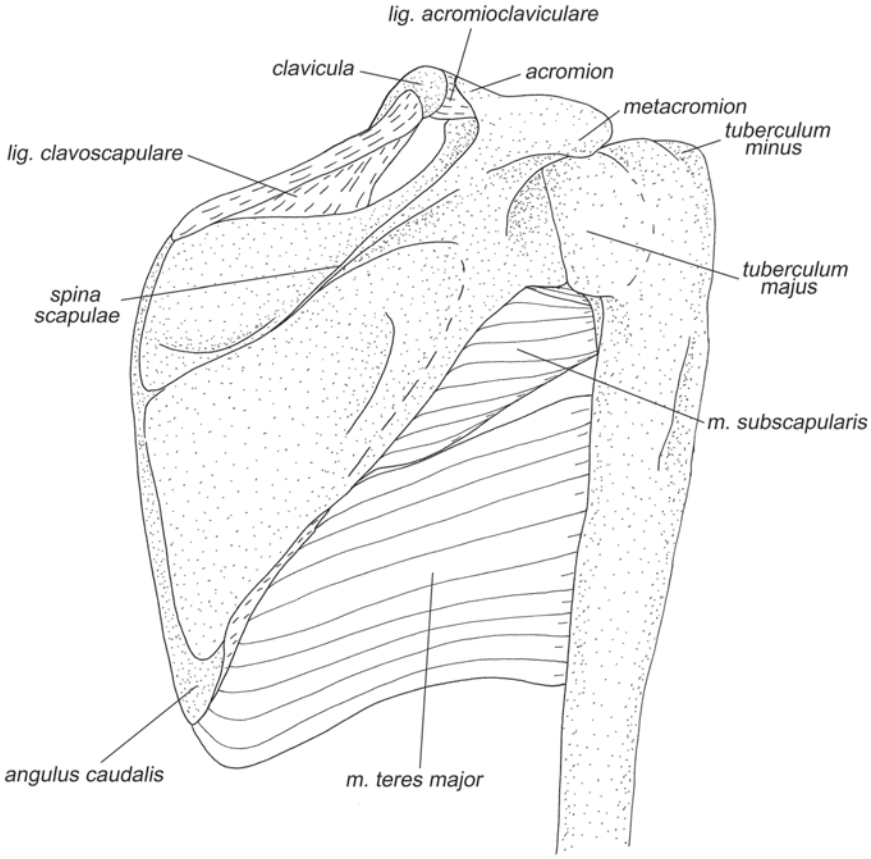


Fig. 2.29 Forelimb muscles of *C. volans,* dorsal view, layer VIII.

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

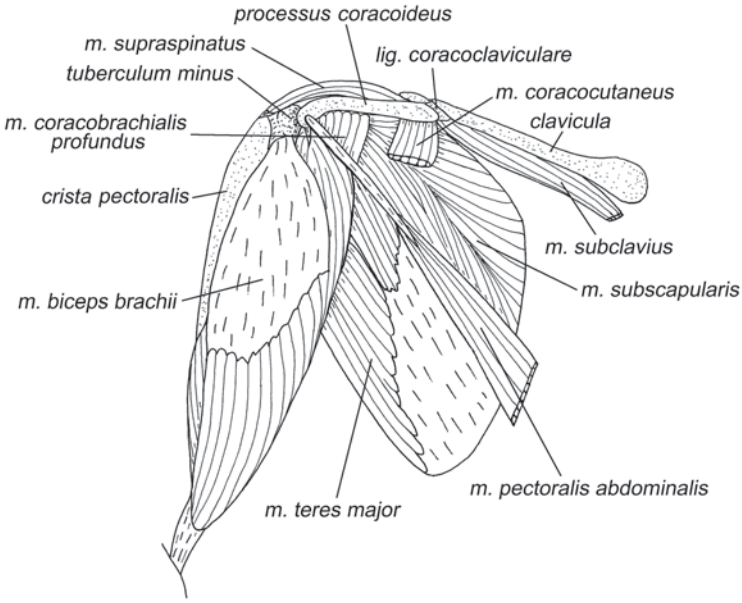


Fig. 2.30 Forelimb muscles of *C. volans,* ventral view, layer V.

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*.

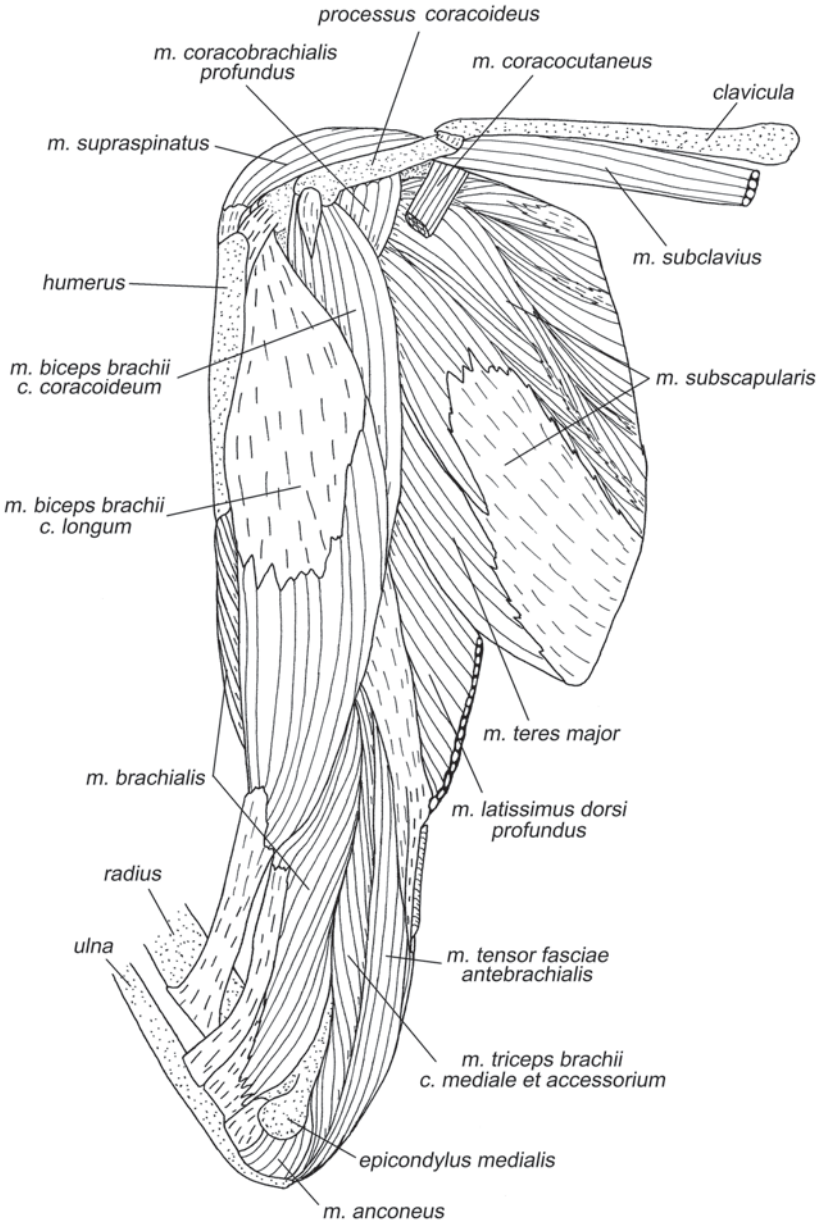


Fig. 2.31 Forelimb muscles of *C. volans,* ventral view, layer VI.

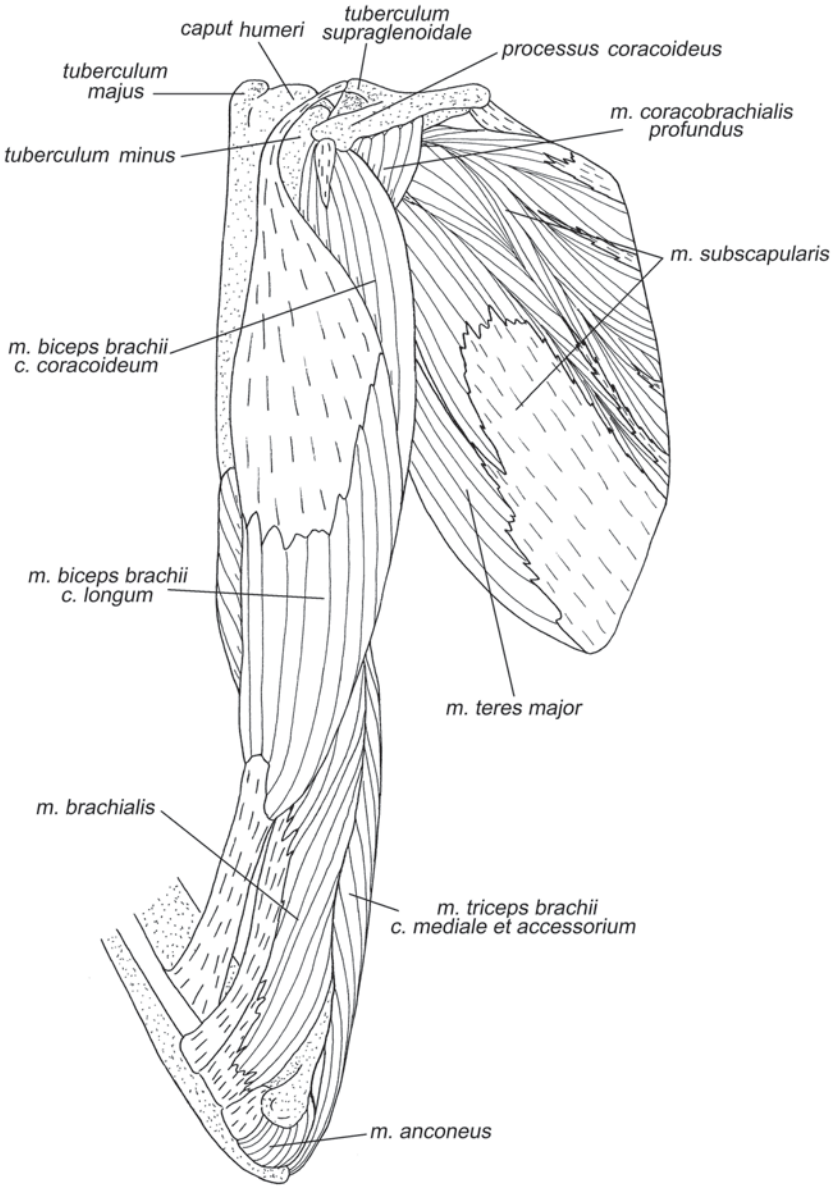


Fig. 2.32 Forelimb muscles of *C. volans,* ventral view, layer VII.

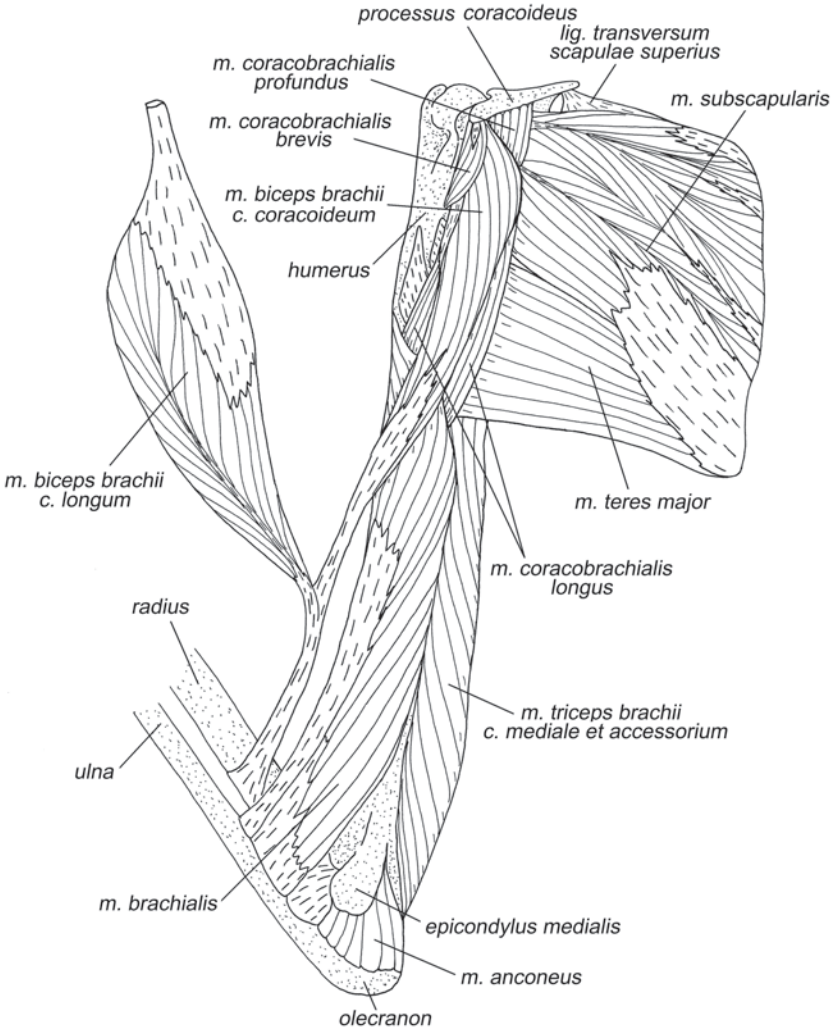


Fig. 2.33 Forelimb muscles of *C. volans,* ventral view, layer VIII.

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.

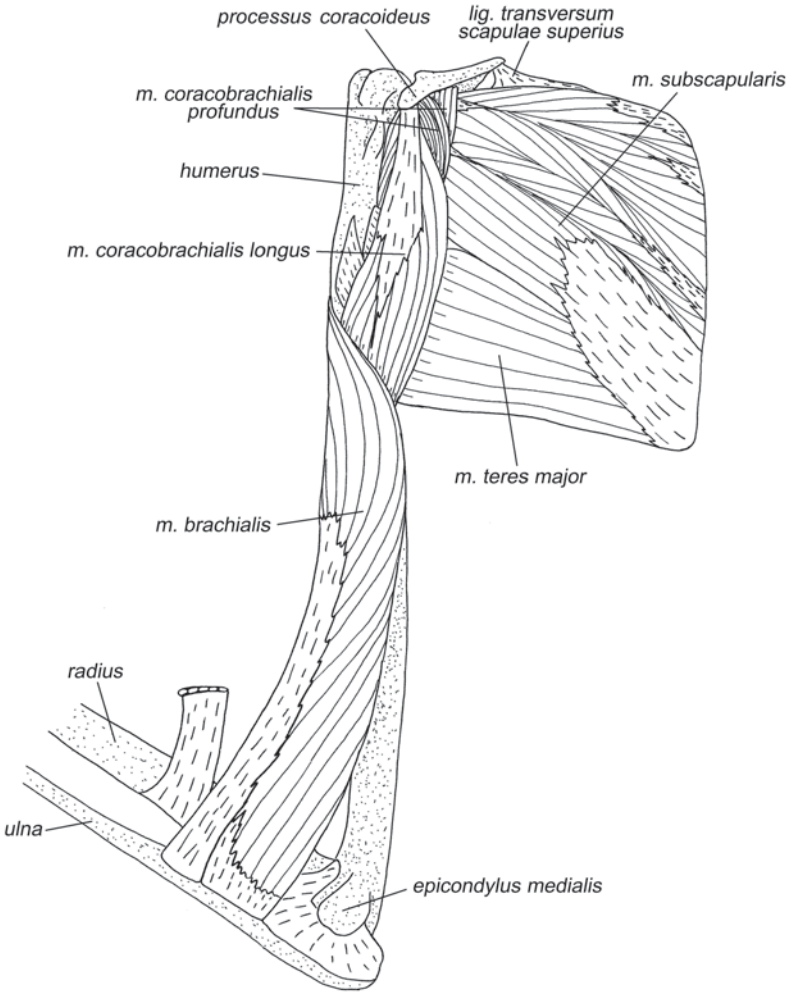


Fig. 2.34 Forelimb muscles of *C. volans,* ventral view, layer IX.

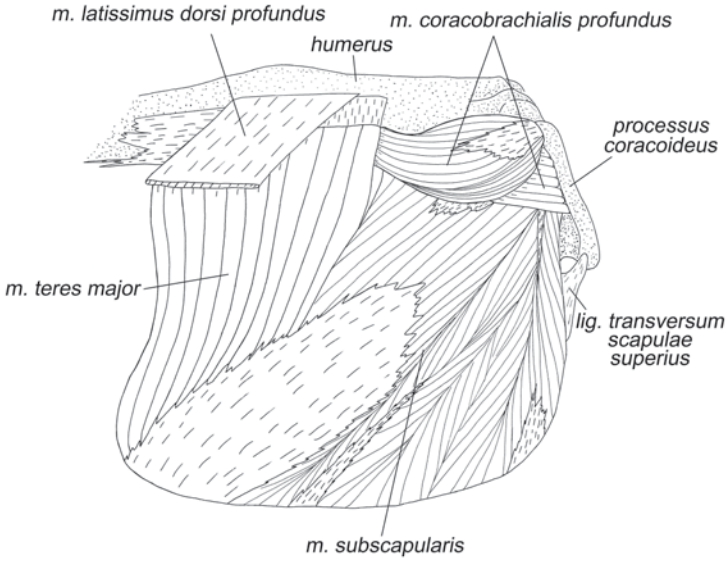


Fig. 2.35 Forelimb muscles of *C. volans,* ventral view, layer X.

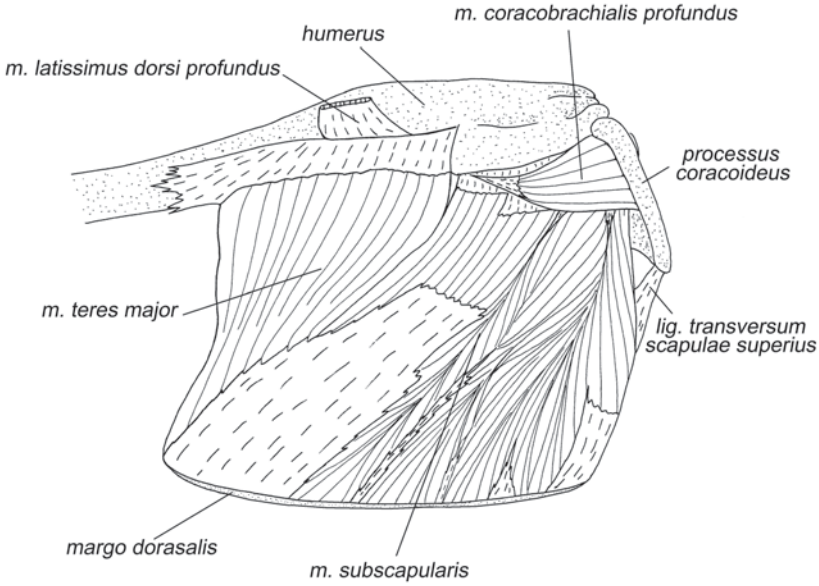


Fig. 2.36 Forelimb muscles of *C. volans,* ventral view, layer XI.

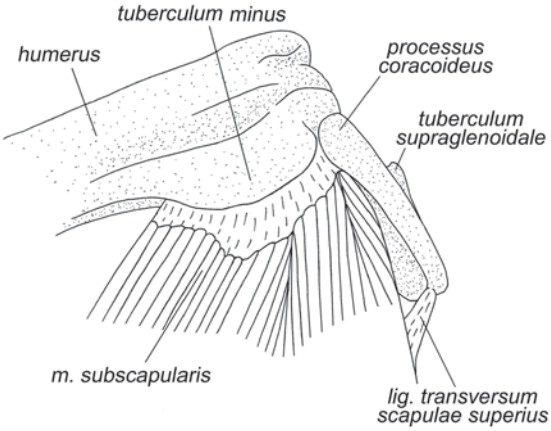


Fig. 2.37 Insertion of the *m. subscapularis* of *C. volans,* ventral view.

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.

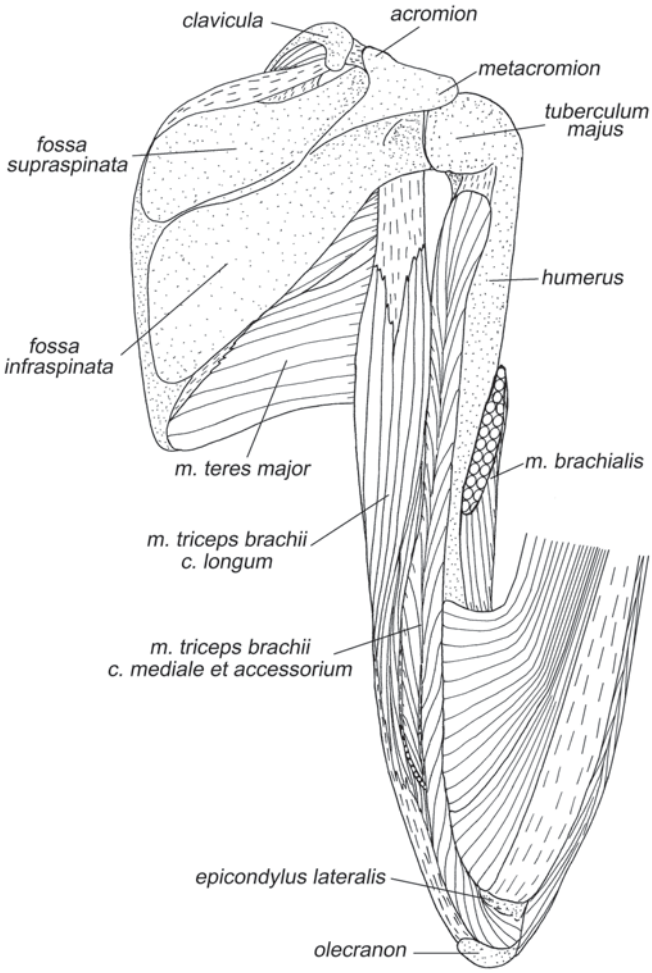


Fig. 2.38 Forelimb muscles of *C. volans,* dorsal view, layer IX.

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

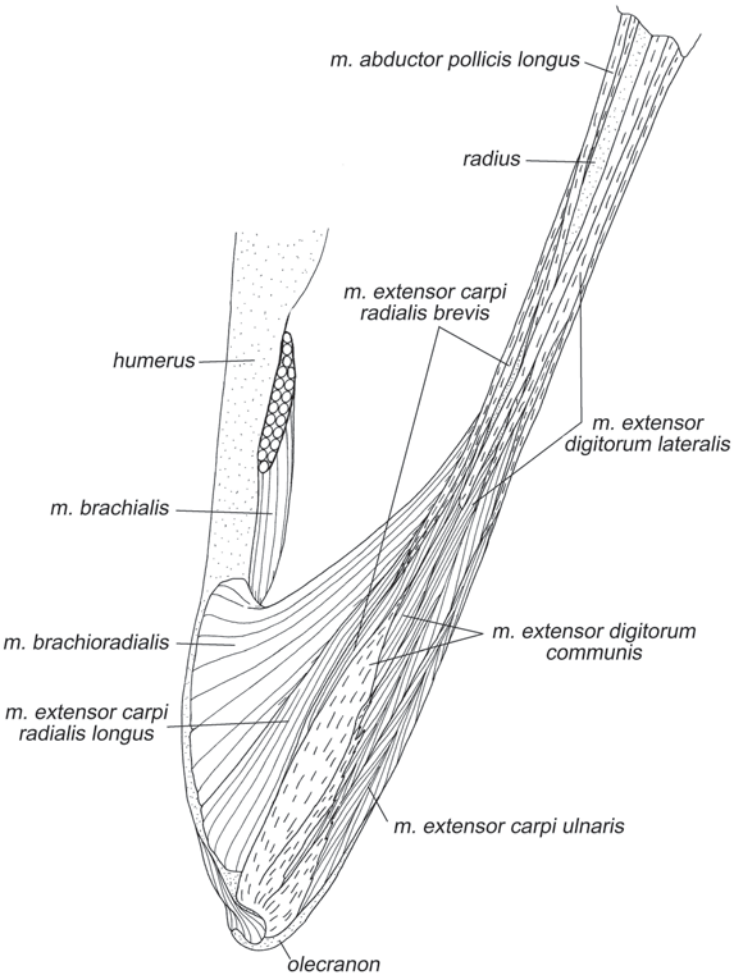


Fig. 2.39 Fore extremity muscles of *C. volans,* lateral view, layer I.

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.

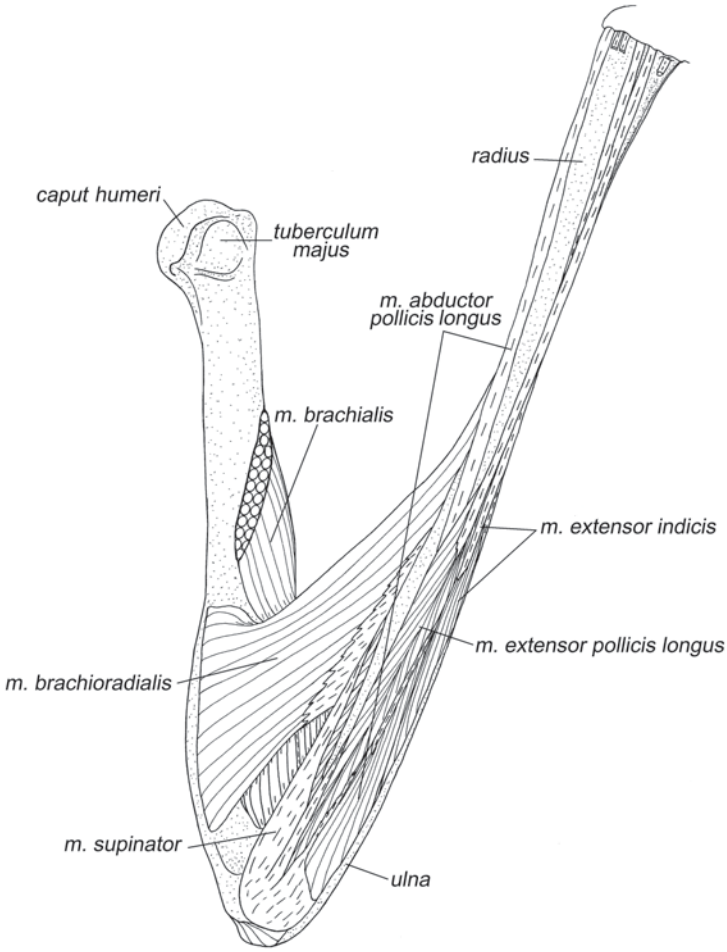


Fig. 2.40 Fore extremity muscles of *C. volans,* lateral view, layer II.

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-*

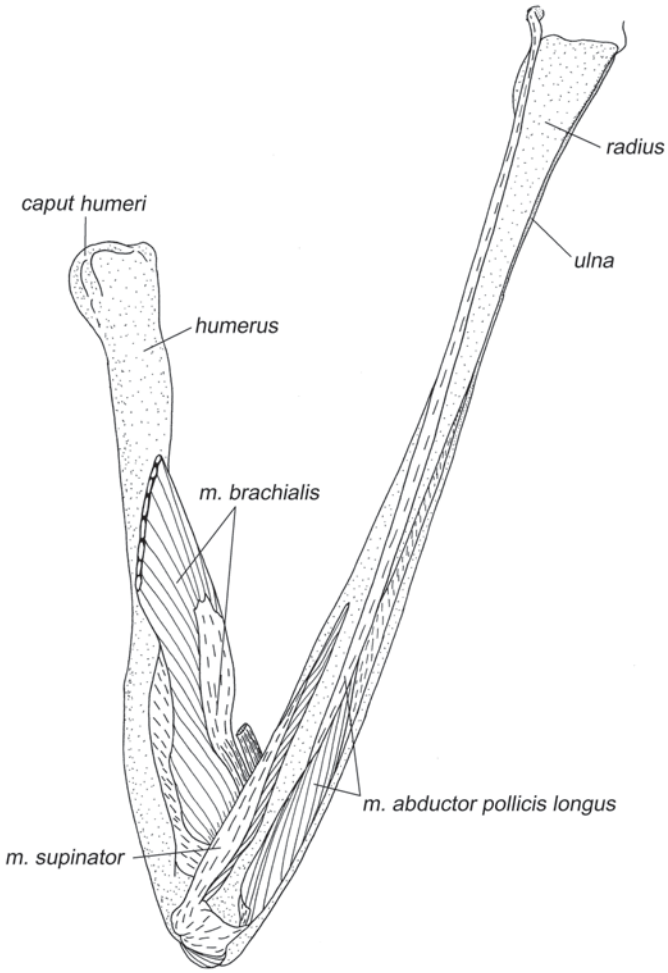


Fig. 2.41 Fore extremity muscles of *C. volans,* lateral view, layer III.

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.

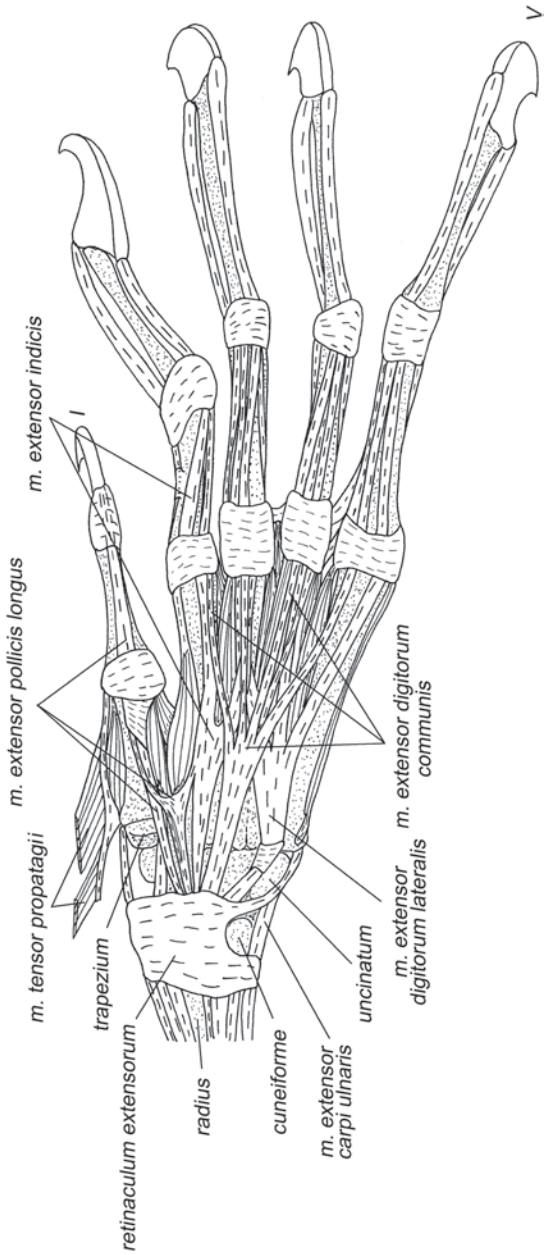


Fig. 2.42 Muscles of the manus of *C. volans*, dorsal view, layer I.

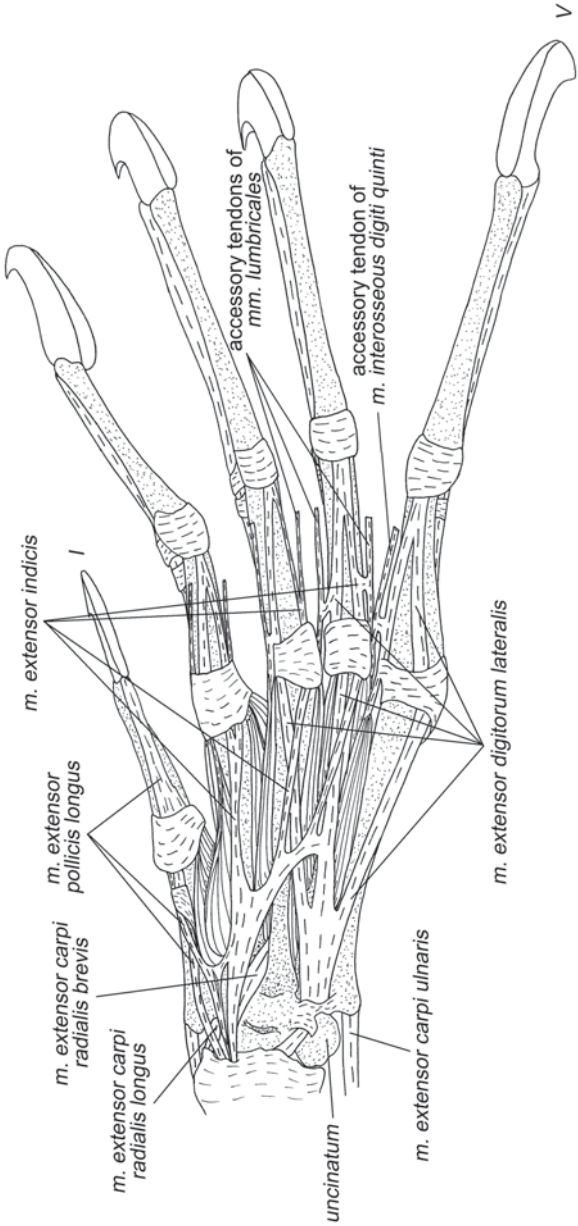


Fig. 2.43 Muscles of the manus of *C. volans,* dorsal view, layer II.

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.

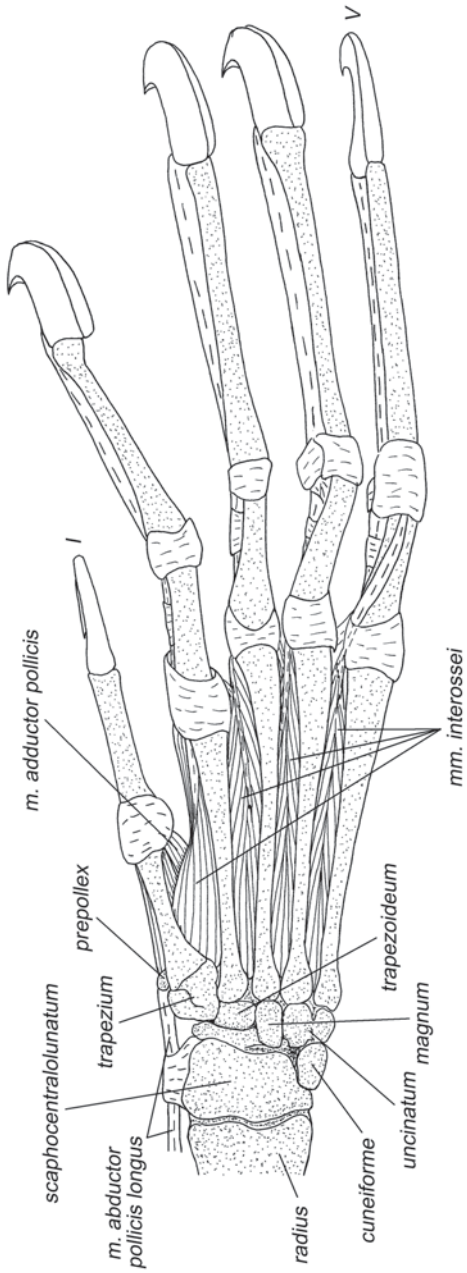


Fig. 2.44 Muscles of the manus of *C. volans*, dorsal view, layer III.

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-

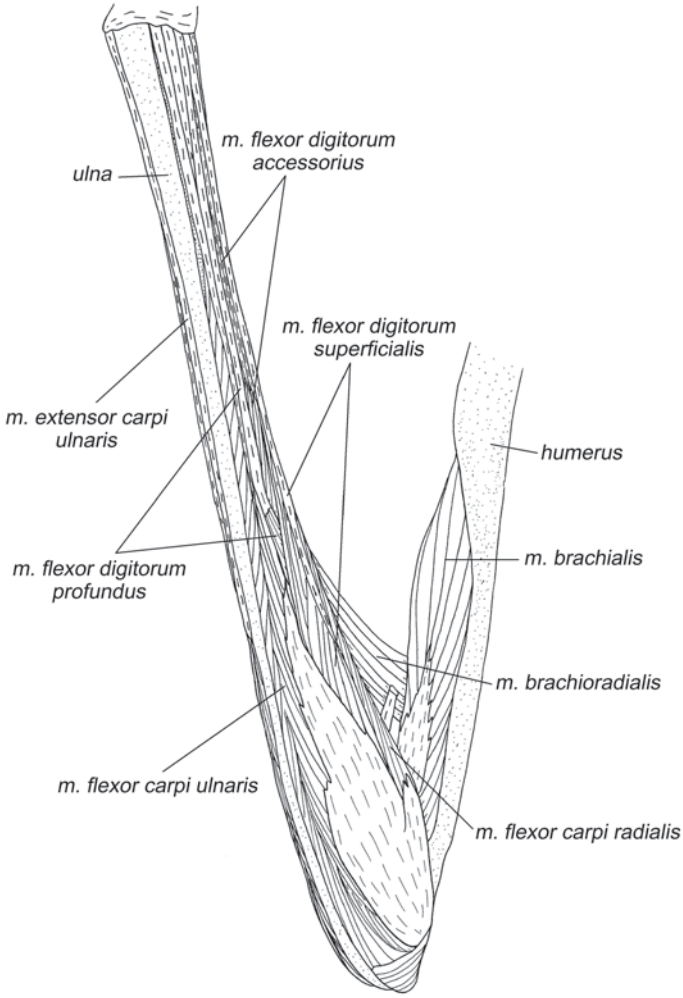


Fig. 2.45 Fore extremity muscles of *C. volans,* medial view, layer I.

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

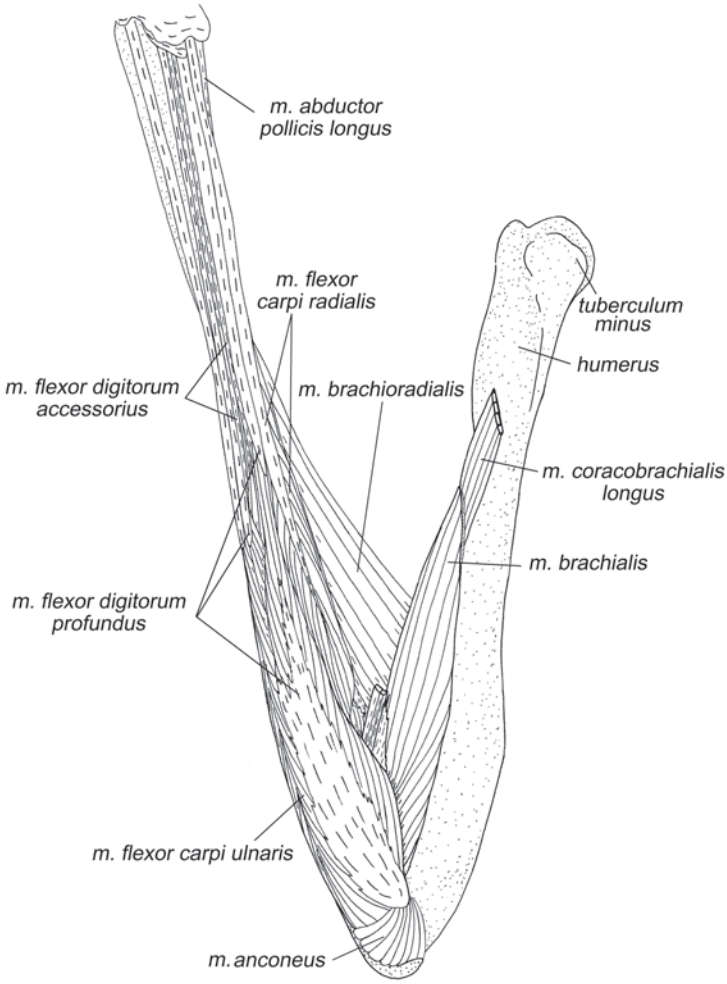


Fig. 2.46 Fore extremity muscles of *C. volans,* medial view, layer II.

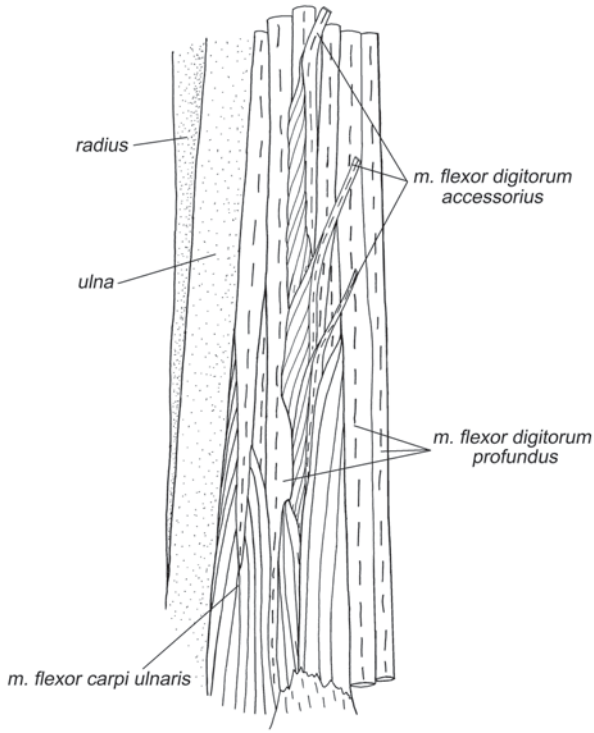


Fig. 2.47 Origin of the *m. flexor digitorum accessorius* on the fifth tendon of *m. flexor digitorum profundus* of *C. volans,* ventral view.

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.

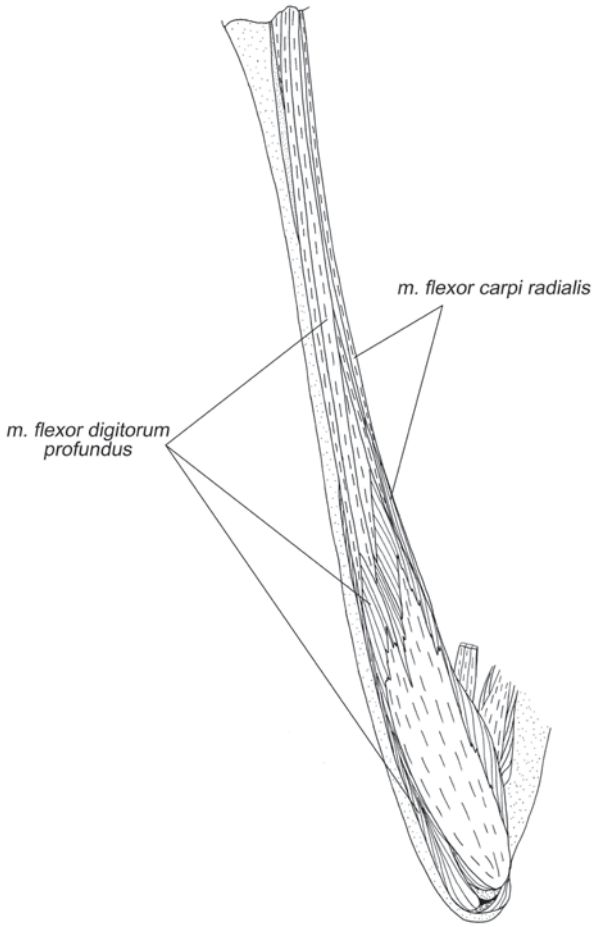


Fig. 2.48 Fore extremity muscles of *C. volans,* medial view, layer III.

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 mid-length 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*

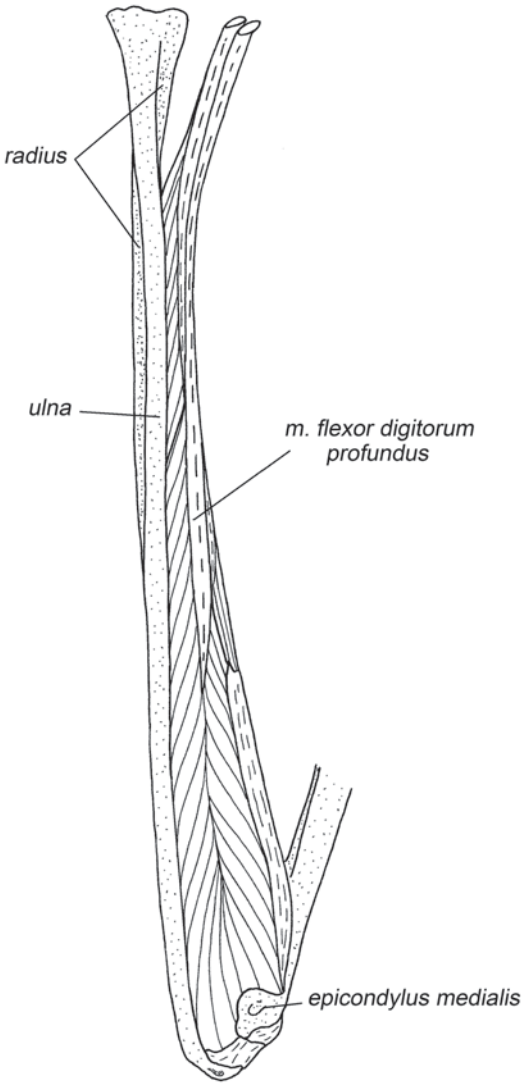


Fig. 2.49 Fore extremity muscles of *C. volans,* medial view, layer IV.

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

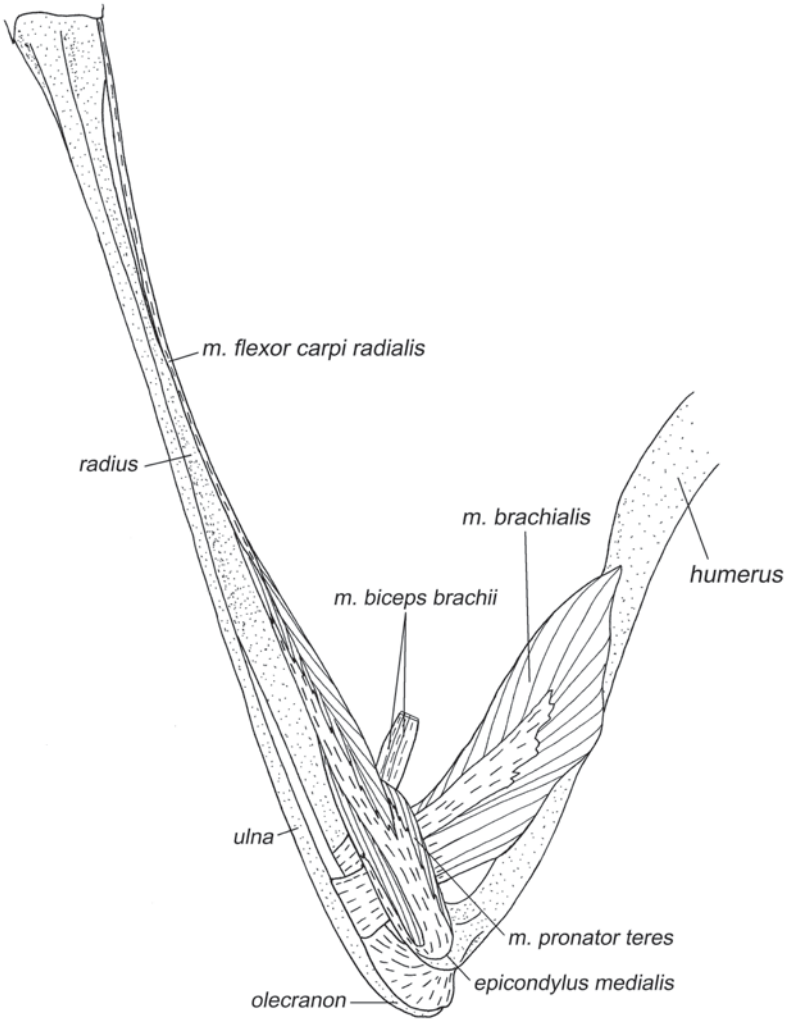


Fig. 2.50 Fore extremity muscles of *C. volans,* medial view, layer V.

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

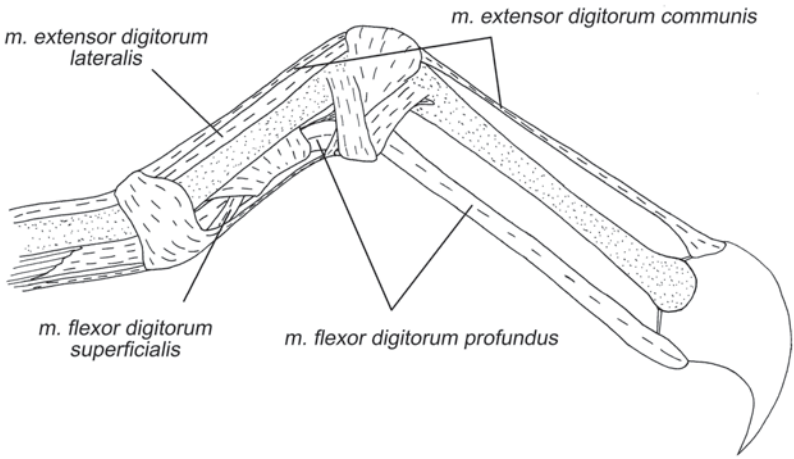


Fig. 2.51 The distal tendons of digital flexors and extensors of *C. volans,* lateral view, fifth finger.

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.

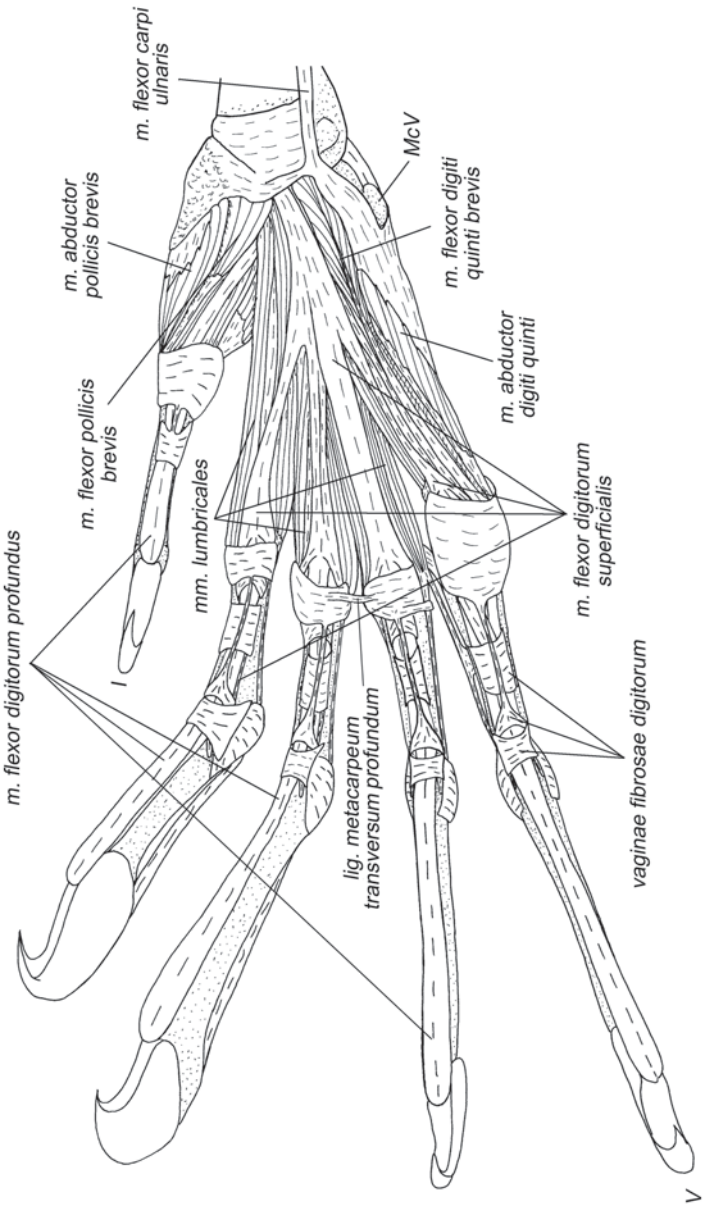


Fig. 2.52 Muscles of the manus of *C. volans*, ventral view, layer I.

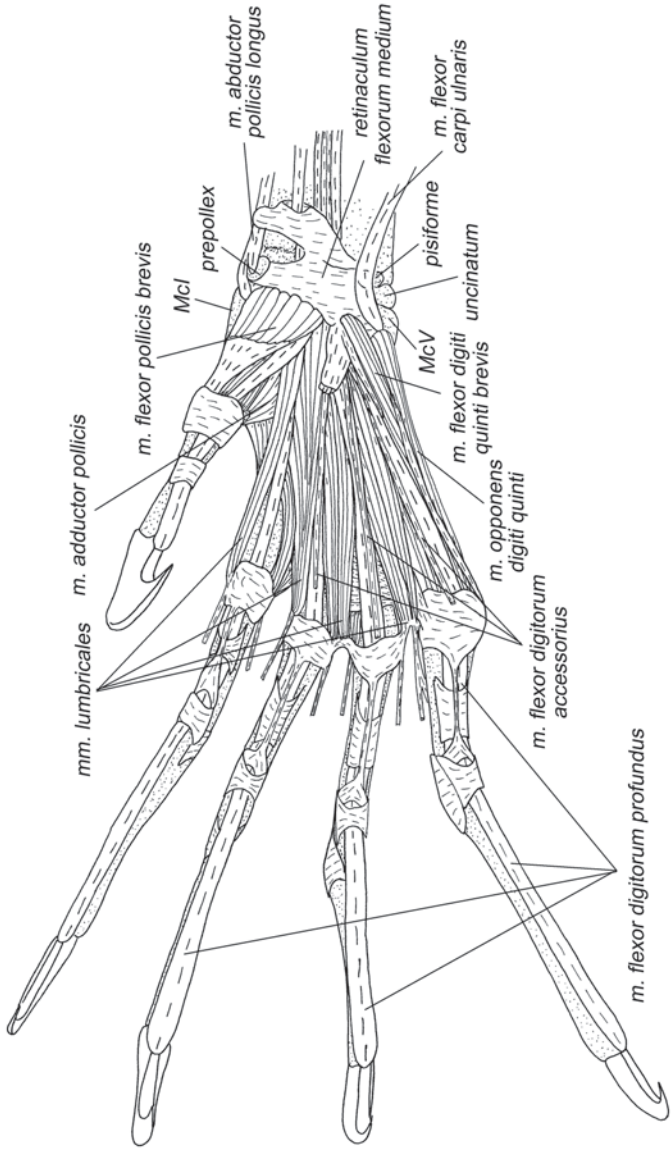


Fig. 2.53 Muscles of the manus of *C. volans*, ventral view, layer II.

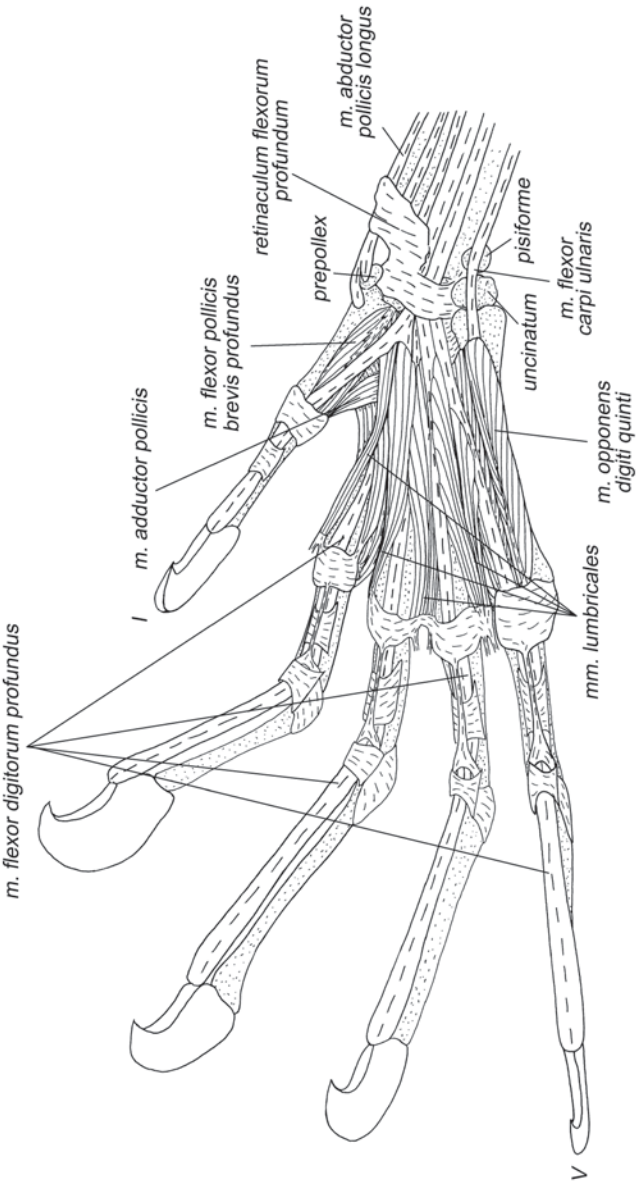


Fig. 2.54 Muscles of the manus of *C. volans*, ventral view, layer III.

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.

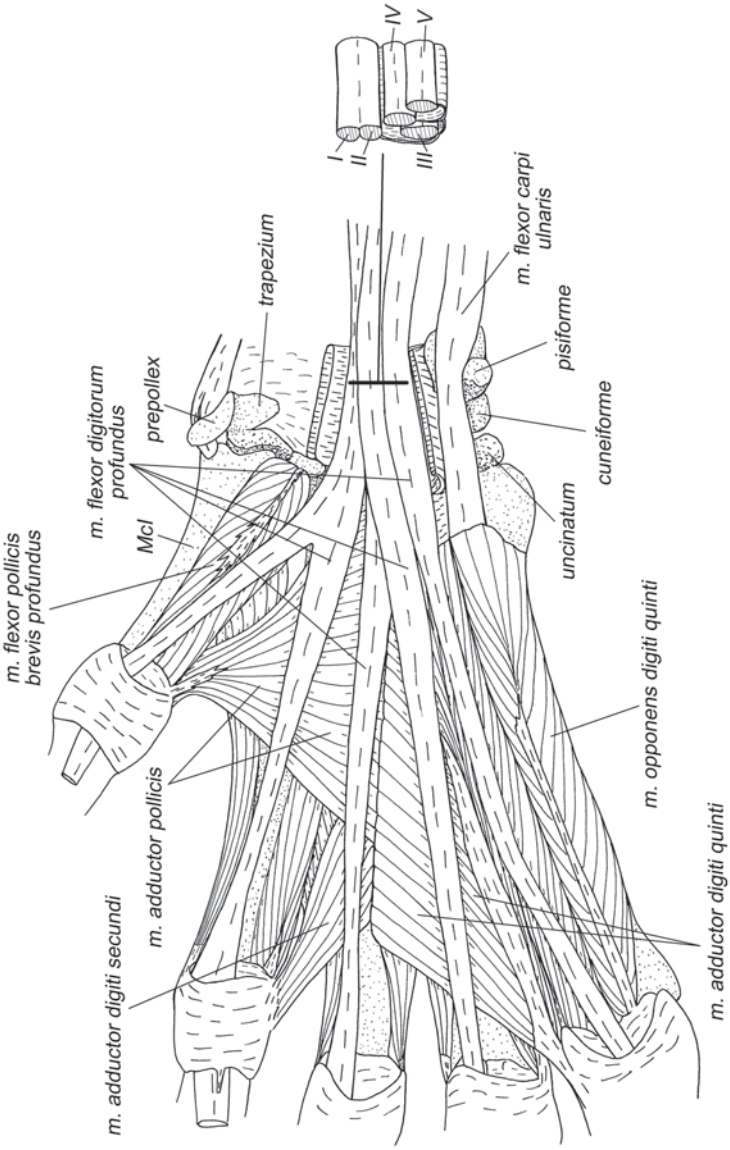


Fig. 2.55 Muscles of the manus of *C. volans*, ventral view, layer IV.

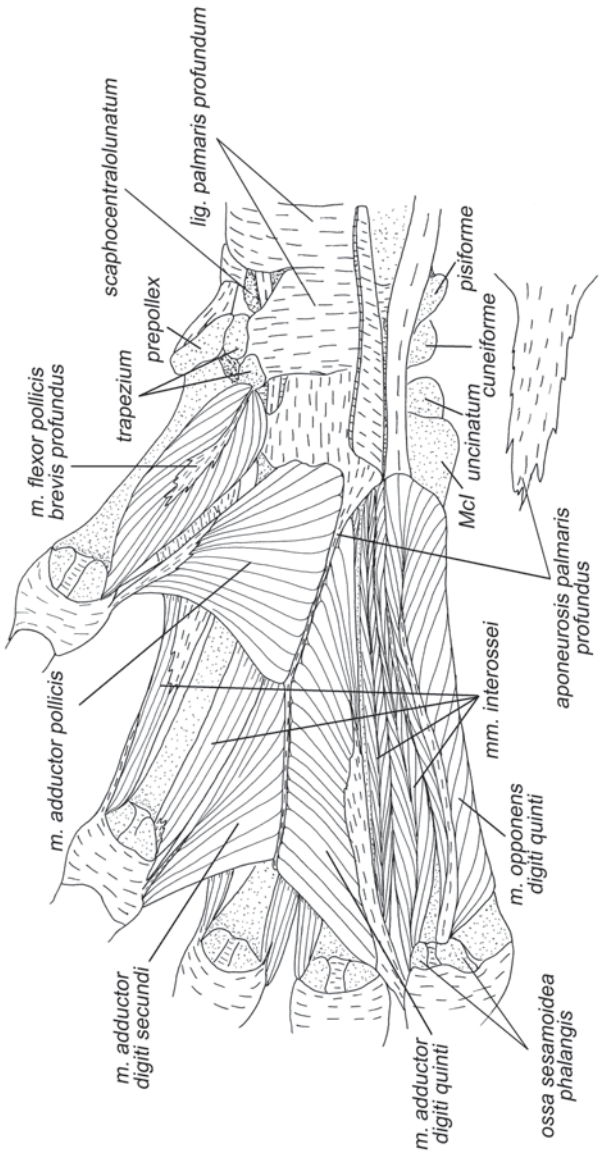


Fig. 2.56 Muscles of the manus of *C. volans,* ventral view, layer V.

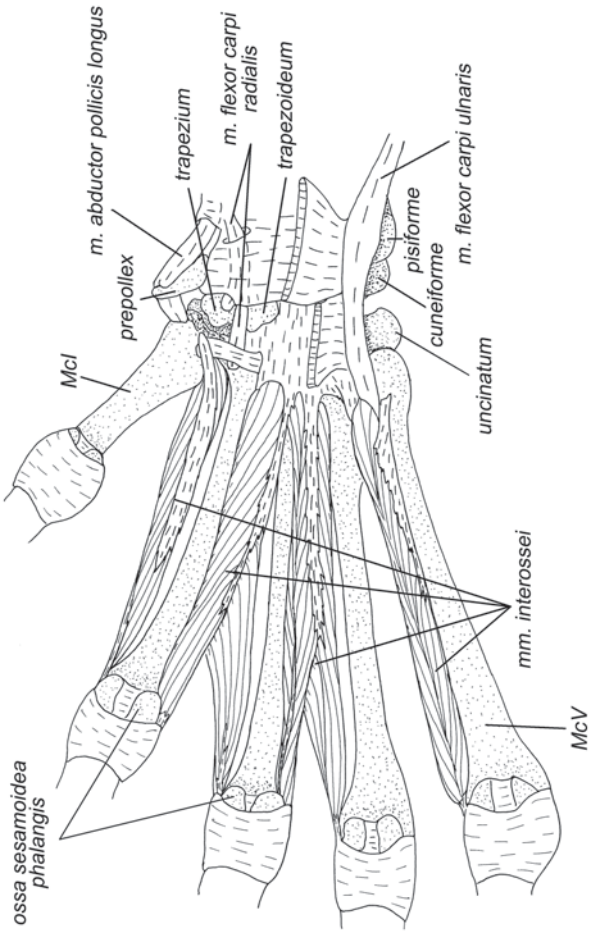


Fig. 2.57 Muscles of the manus of *C. volans*, ventral view, layer IV.

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.

References

Chapman HC (1902) Observations upon *Galeopithecus volans*. Proc Acad Nat Sci Phil 54(1):241–254

Diogo R (2009) The head and neck muscles of the Philippine colugo (Dermoptera: *Cynocephalus volans*), with a comparison to tree–shrews, primates, and other mammals. J Morphol 270(1):14–51

Grassé PP (1955) Ordre des Dermoptères. In: Grassé PP (ed) Traité de zoologie, anatomie, systématique, biologie. T XVII, fasc 2. Mammifères. Les ordres: anatomie, éthologie, systématique. Masson, Paris, p 1713–1728

Howell AB (1937) Morphogenesis of the shoulder architecture. Part V. Monotremata. Quart Rev Biol 12(2):191–205

Howell AB, Straus WL Jr (1931) The brachial flexor muscles in primates. Proc US Nat Mus 80(2913):1–31

Leche W (1886) Über die Säugetiergattung *Galeopithecus*. Eine morphologische Untersuchung. Kongl Sv Vet-Akad Handlingar 21(11):1–92

Macalister A (1872) The myology of the Chiroptera. Phil Trans Roy Soc Lond 162:125–172

Owen R (1868) On the anatomy of vertebrates. Vol III. Mammals. Longmans, Green, and Co, London

Shufeldt RW (1911) The skeleton in the flying lemurs, Galeopteridae. Phil J Sci 6(3):139–165 and 6(4):185–213

Stafford BJ, Thorington RW Jr (1998) Carpal development and morphology in archontan mammals. J Morphol 235(2):135–155

Szalay FS, Lucas SG (1993) Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In: MacPhee RDE (ed) Primates and their relatives in phylogenetic perspective. Plenum Press, New York, p 187–226

Chapter 3
Forelimb Morphology of Bats

Of the three mammalian orders, which we have investigated, morphological features of chiropterans are considered in the literature most completely. The structure of the musculoskeletal system of particular species and comparisons of different chiropteran groups are discussed in many studies. The earliest anatomical descriptions were already published in the second half of the nineteenth century (Humphry 1869; Macalister 1872), and the golden age of this field has fallen on the second half of the twentieth century (Vaughan 1959, 1966, 1970a, b; Jullien 1969; Kovtun 1970, 1976, 1977, 1978; Norberg 1970, 1972; Vaughan and Bateman 1970; Walton and Walton 1970a, b; Strickler 1978; Altenbach 1979; Hermanson and Altenbach 1983, 1985; Arganbright 1984; Foehring and Hermanson 1984; Glass and Gannon 1994; Schlosser-Sturm and Schliemann 1995; Schliemann and Schlosser-Sturm 1999; etc.). In the twenty-first century, anatomical studies of the bat locomotorium become scarce (Lopez-González and Polaco 2001; Maniakas and Youlatos 2012). The major efforts were invested in ecological interpretations of morphological features of particular members of the order or in comparison with birds, almost neglecting comparisons with other mammals.

Although in the literature dealing with the origin of chiropterans, both tree shrews and colugos are regarded as the nearest relatives and, sometimes, as hypothetical ancestors, studies devoted to the analysis of musculoskeletal system of chiropterans in comparison with members of these orders of Archonta are almost absent. Only a few solitary works are devoted to comparison of flying and gliding mammals and usually consider special cases, for example, the structure and innervation of muscles in the wing membrane of chiropterans and colugos (Thewissen and Babcock 1993) or innervation of the membrane in bats and other mammals (Kovtun 1984; Thewissen and Babcock 1991).

To describe the musculature, we dissected six specimens of four bat species (*Cynopterus sphinx*[1], *Rousettus aegyptiacus*[2], *Rhinolophus ferrumequinum* (three

[1] ZMMU, no. s-165073.

[2] ZMMU, no. s-177963.

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_3

specimens[3]), and *Hipposideros larvatus*[4]) of three families (Chiroptera: Pteropodidae, Rhinolophidae, and Hipposideridae). In addition, we studied selected muscles of *Lavia frons*[5] and *Chaerephon pumilus*[6] (Chiroptera: Megadermatidae, Molossidae). All specimens were provided by ZMMU.

Later in the text, we present generalized descriptions based on our own dissections as well as on published data (Macalister 1872; Vaughan 1959; Norberg 1970, 1972; Kovtun 1978; Strickler 1978; etc.) on different bat groups.

Osteological description is based on syndesmological preparations obtained at the final stage of myological dissections, when muscles were entirely removed; in addition, we examined dry skeletons of the following bat species: *Rousettus aegyptiacus*[7], *Pteropus lylei*[8], *Pteropus tonganus*[9], *Cynopterus sphinx*[10], *Rhinolophus ferrumequinum*[11], *R. borneensis*[12], *Hipposideros armiger*[13], *Myotis blythi*[14], and *Vespertilio superans*[15] from ZMMU and Department of Vertebrate Zoology of the Biological Faculty of Moscow State University.

The joint mobility is described based on the study of the aforementioned syndesmological preparations as well as fresh corpses of bats from the Moscow Region fauna (*Myotis daubentonii*, *Myotis dasycneme*, *Plecotus auritus*, and *Eptesicus nilssoni*) and two tropical species (*Rousettus aegyptiacus* and *Carollia perspicillata*). In addition, the movements of the shoulder girdle elements were studied using X-ray video filming of flight of the Egyptian fruit bat (*R. aegyptiacus*). To keep it within the video frame, experimenter held the bat flapping wings either by its hindlimbs or by a leash with collar put on its neck.

Wing Membrane

The wing membrane of bats is very thin and almost lacks a fur cover. As in colugos, fibers of several skeletal muscles pass into the membrane, which, also, has well-developed intrinsic muscles.

[3] ZMMU, no. s-169457, s-169458, and s-169577.
[4] ZMMU, no. s-172576.
[5] ZMMU, no. s-184319.
[6] ZMMU, without no.
[7] ZMMU, no. s-180590.
[8] ZMMU, no. s-167611.
[9] ZMMU, no. s-95402.
[10] ZMMU, no. s-165407.
[11] ZMMU, no. s-168245.
[12] ZMMU, no. s-167564.
[13] ZMMU, no. s-167563.
[14] ZMMU, no. s-175745.
[15] ZMMU, without no.

The terms designating parts of the membrane are almost the same as in colugos: the anterior part is propatagium, middle part is plagiopatagium, and posterior part is uropatagium (Fig. 2.1b). However, they significantly differ in shape. In addition to the plagiopatagium, the middle part of the bat includes a distal extension called chiropatagium, which is formed by the manus. In contrast to colugos, the first finger is not incorporated in the membrane. The propatagium is narrow in anteroposterior dimension and is not attached to the head. The uropatagium is well developed in many bats, sometimes even better than in colugos (for example, in the majority of Vespertilionidae). However, in a number of bats even having a long tail, the uropatagium is strongly or almost completely reduced (for example, in Emballonuridae, Molossidae, etc.); in many chiropterans, the tail itself is also reduced (for example, in Pteropodidae and some Phyllostomidae). It should be noted that the disappearance of the tail not always results in complete reduction of the posterior membrane. For example, in false vampire bats (Megadermatidae), the tail is completely absent, while the uropatagium is well developed and directly connects the left and right hindlimbs.

Skeleton

The position of elements of the shoulder girdle of bats differs considerably from that of terrestrial quadrupedal mammals. The major features of postcranial skeleton were summarized by Walton and Walton (1970a). The scapula in bats is displaced from the parasagittal position to the dorsal side of the body, where it lies in the frontal plane (Figs. 3.1, 3.2). Consequently, the clavicles changed their direction from lateromedial to dorsoventral (Figs. 3.1, 3.2). The distal end of the clavicle is, as usual, connected to the acromial process of the scapula and the proximal end enters the clavicular articular fossa (*incisura clavicularis*) (Fig. 3.2). This fossa is formed by the *manubrium sterni* and sternal segment (*costa sternalis*) of the first rib (Fig. 3.1b). The latter is usually called the "first costal cartilage" (Vaughan 1959; Norberg 1970; etc.), although it ossifies in all chiropterans. With reference to horseshoe bats, some authors (Kovtun 1978; Strickler 1978) believe that this element is a projection of the sternum rather than the rib. Indeed, in these bats, the first rib is fused with the sternum, and their boundary is additionally masked by a peculiar wing-like outgrowth above the *incisura clavicularis* (Fig. 3.3). However, young horseshoe bats retain the sternocostal articulation as a suture between the sternum and this wing-like process, which, thus, belongs to the first rib; we call it the *processus alaris costae sternalis 1*[16]. This process of horseshoe bats is the place of origin of the *m. subclavius*, which also originates in other chiropterans from the sternal segment of the first rib.

[16] This term is introduced here for the first time.

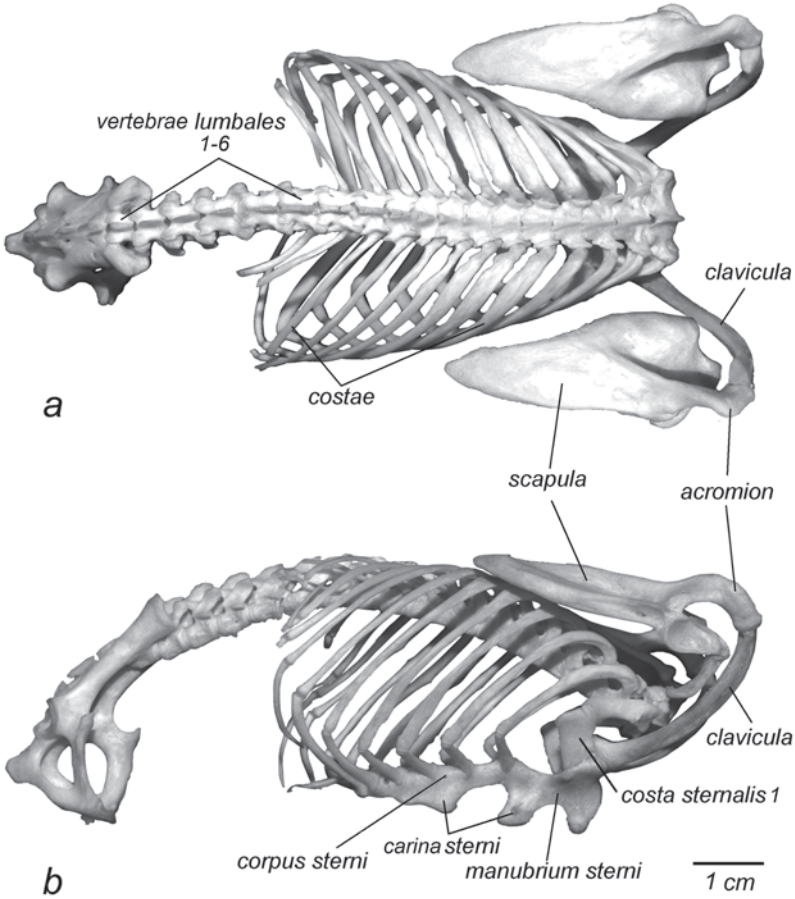


Fig. 3.1 The axial skeleton of *Pteropus lylei* with shoulder girdle. *a. Dorsal view b. Lateral view*

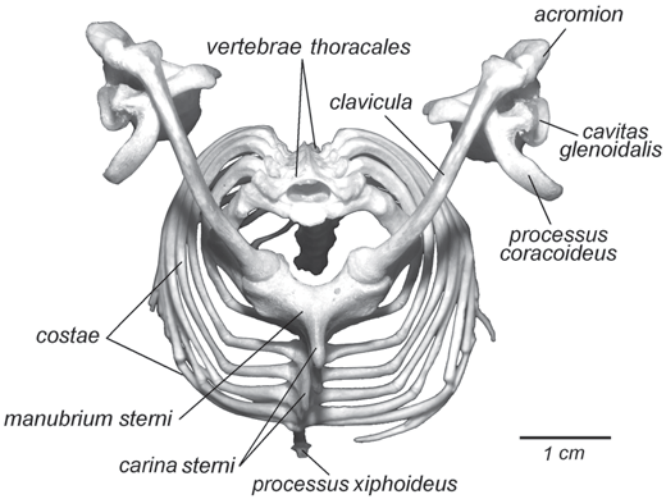


Fig. 3.2 The axial skeleton of *P. lylei* with shoulder girdle, anterior view.

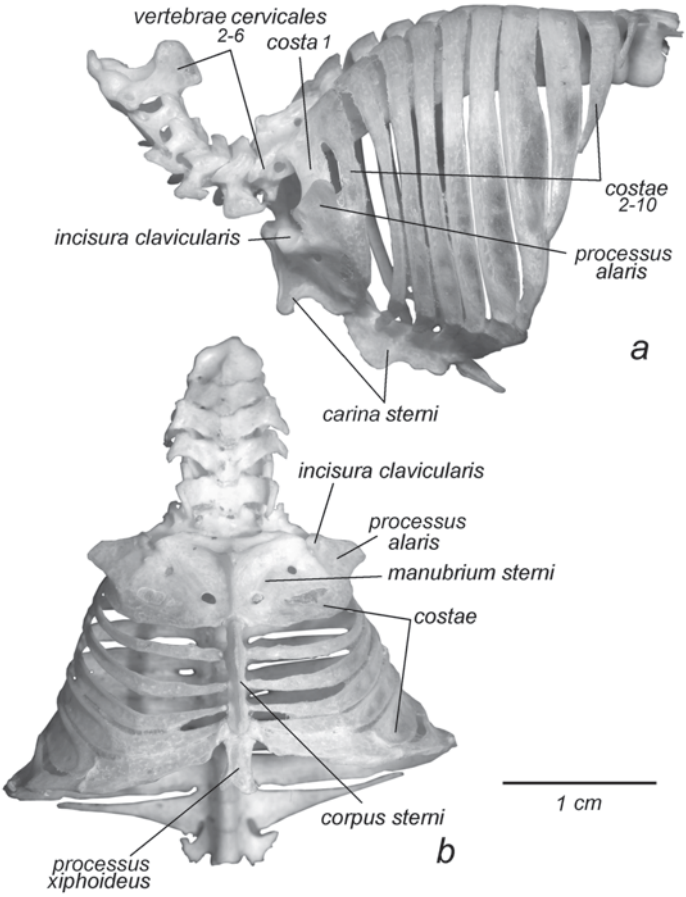


Fig. 3.3 The axial skeleton of *Hipposideros armiger*. *a. Lateral view b. Ventral view*

Since the scapula in bats lies in the frontal plane on the dorsal side of the body, in the literature devoted to the morphology of these animals, the borders and surfaces of the scapula are usually designated as in the anatomy of man rather than quadrupedal mammals (Vaughan 1959, 1966, 1970a, b; Kovtun 1970, 1976, 1977, 1978; Norberg 1970, 1972). The dorsal border of the scapula in bats is usually named vertebral (medial), and the caudal border is named lateral. In turn, the lateral surface of the scapula in bats is commonly named dorsal, and the medial surface is named ventral (costal). Although these terms indicate true orientation of the scapula, we follow the nomenclature accepted for quadrupedal mammals, which allows consistent comparative analysis with colugos and tree shrews based on homologies rather than derived positions of bones and muscles.

Scapula (Figs. 3.4a, b, 3.6a, b). The variety of the shape of the scapula in different chiropteran species was described in detail in a number of publications (e.g., Strickler 1978). In general, it is triangular, with a strongly posteriorly

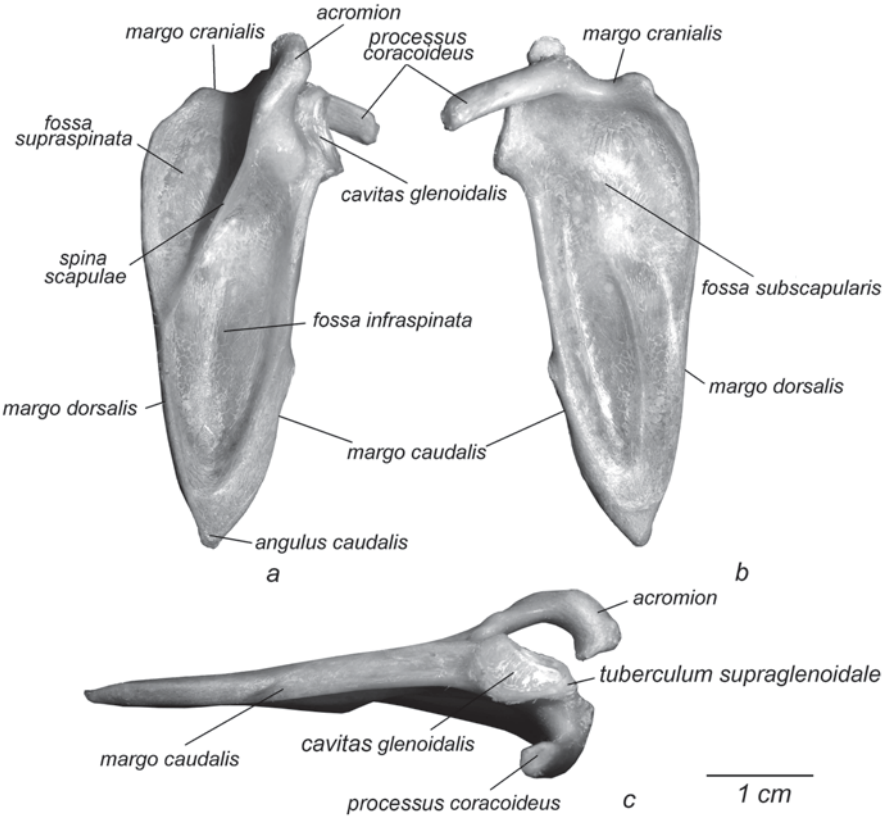


Fig. 3.4 The scapula of *Pteropus tonganus*, right forelimb. *a. External view b. Internal view c. Side view*

extending infraspinous part. In addition, the area of the dorsocaudal angle is supplemented with an accessory bone, which is apparently derived from a suprascapular cartilage. The suture between the accessory bone and the scapula itself is distinct in young fruit bats (Fig. 3.5). A peculiarity of the chiropteran scapula is the sharply pronounced rather than rounded dorsocranial angle, found in the majority of mammals. In contrast to fruit bats, the lateral surface of the scapula of microbats[17] has a more complex relief (Figs. 3.6a, b). In almost all microchiropterans, a wide additional area is formed caudal to the infraspinous fossa, being separated from it by a low additional crest. In the literature, it is usually named the posterolateral facet (e.g., Lopez-González and Polaco 2001). Its surface is occupied by the origin of the *m. teres major*, which in fruit bats

[17] The opposition of microbats as a whole to megabats (fruit bats) retains its morphological sense in spite of the recently proved paraphyly of the former respective to the latter.

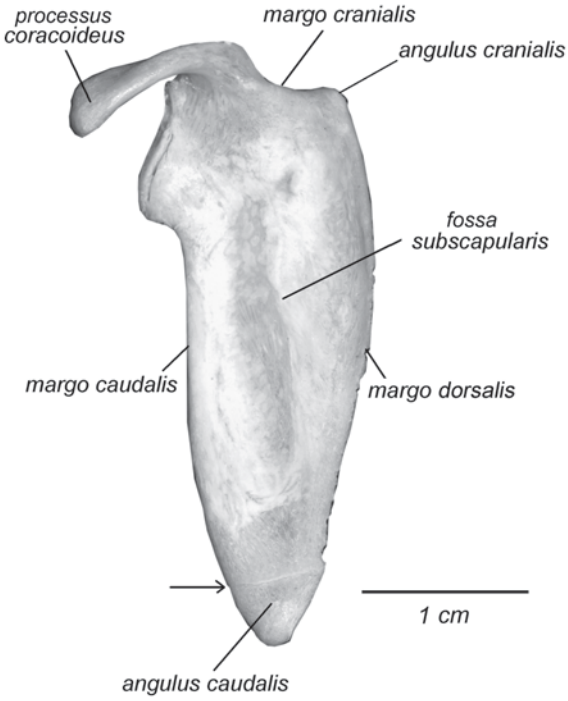


Fig. 3.5 The scapula of subadult *P. lylei*, right forelimb, medial view.

originates directly from the caudal border of the scapula. Thus, the posterolateral facet probably corresponds to a widened and externally turned caudal border. In addition, in some bat species, the infraspinous fossa itself is not flat but forms a deep trough parallel to the scapular spine; the slopes of this trough are frequently named anteromedial and intermediate facets (Kovtun 1978; Strickler 1978). According to the nomenclature accepted in the present study for borders and surfaces of the scapula (following that of quadrupedal mammals), they are termed the *facies anterior* and *facies intermedialis* of the *fossa infraspinata*. The aforementioned posterolateral facet, which does not belong to the infraspinous fossa, is named here the *facies posterior*. The supraspinous fossa of the scapula in all bats is considerably smaller than the infraspinous fossa. This is particularly distinct in comparison with terrestrial quadrupedal mammals, for example, tree shrews, which supraspinous fossa is considerably larger than the infraspinous fossa (Fig. 1.2a). The scapular spine is rather low, although the acromion is high (Figs. 3.4c, 3.6c). The coracoid process is excessively developed. The glenoid is subdivided into two parts. The posterior part forming the main articular surface is round or oval, and the anterior part is formed by the supraglenoid tubercle as narrow promontory. External to the glenoid, the lateral surface of the scapula of some bat groups has an additional articular area for contact with the greater tubercle of the humerus.

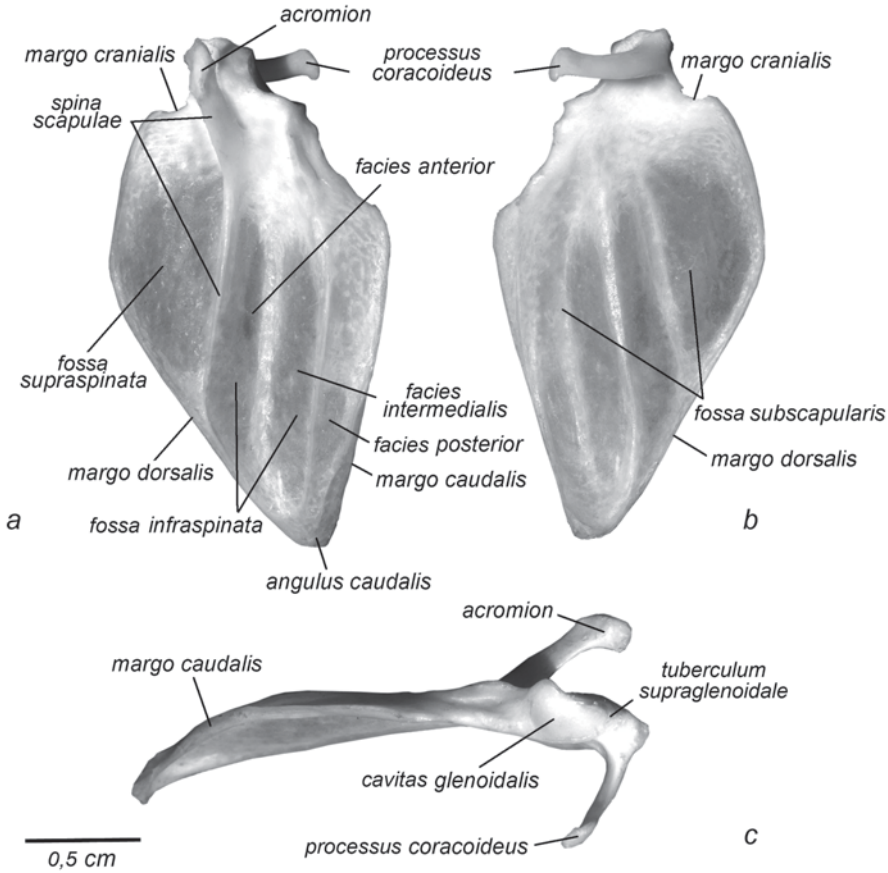


Fig. 3.6 The scapula of *H. armiger*, right forelimb. *a. External view b. Internal view c. Side view*

Clavicle. The clavicle of bats is saber shaped (Fig. 3.7) or, in some species, almost L shaped (Fig. 3.8); in the latter case, we name the straight sternal part of the bone the "stem." It is almost flat in bats that use flight as the only way of locomotion and rounded in section in less specialized species, primarily fruit bats. The sternal end of the clavicle is widened to form a head. Its flattened articular surface varies in outline from elongated to almost round. In some horseshoe bats, the posterolateral side of the sternal end of the clavicle bears a flat process (Fig. 3.8), which forms an additional prop against the *processus alaris costae sternalis 1*. The craniocaudally flattened distal part of the clavicle curves posterolaterally. In fruit bats, this end usually has an articular surface, which rests against respective articular surface on the acromial process of the scapula. In microbats, we have not found such articular surfaces.

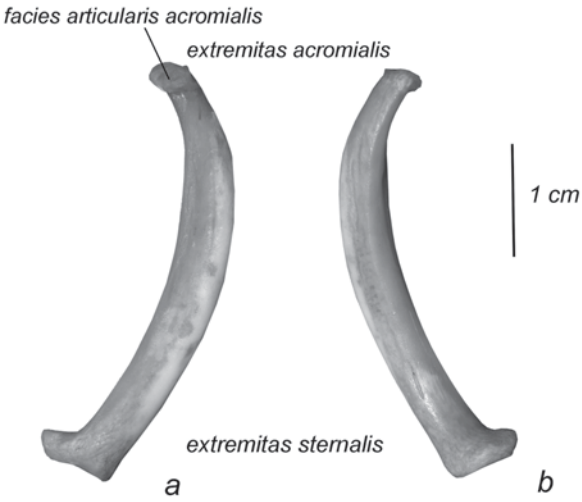


Fig. 3.7 The clavicle of *P. tonganus*, right forelimb. *a. Lateral view b. Medial view*

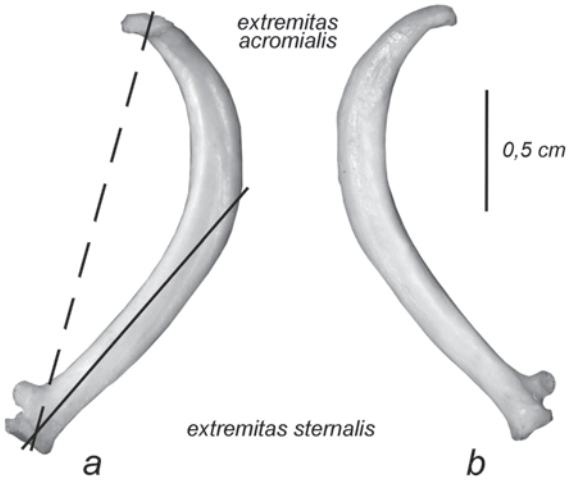


Fig. 3.8 The clavicle of *H. armiger*, right forelimb. — longitudinal axis of clavicle, – – – longitudinal axis of its proximal part (the stem). *a. Lateral view b. Medial view*

Humerus (Figs. 3.9, 3.10). The humerus is long and has well-developed greater and lesser tubercles with distinct necks. From each tubercle, a high crest extends distally. The crest of the lesser tubercle reaches the greatest height at the insertion of the *m. teres major*. This point Kovtun (1978) named "styloid protuberance," although its shape has nothing in common with a stylus (Figs. 3.10c, f); thus, in our opinion, this term is an unfortunate choice, but we do not introduce any other instead of it. This structure is only well pronounced in some taxa of chiropterans, for example, horseshoe bats (Rhinolophidae). The pectoral crest

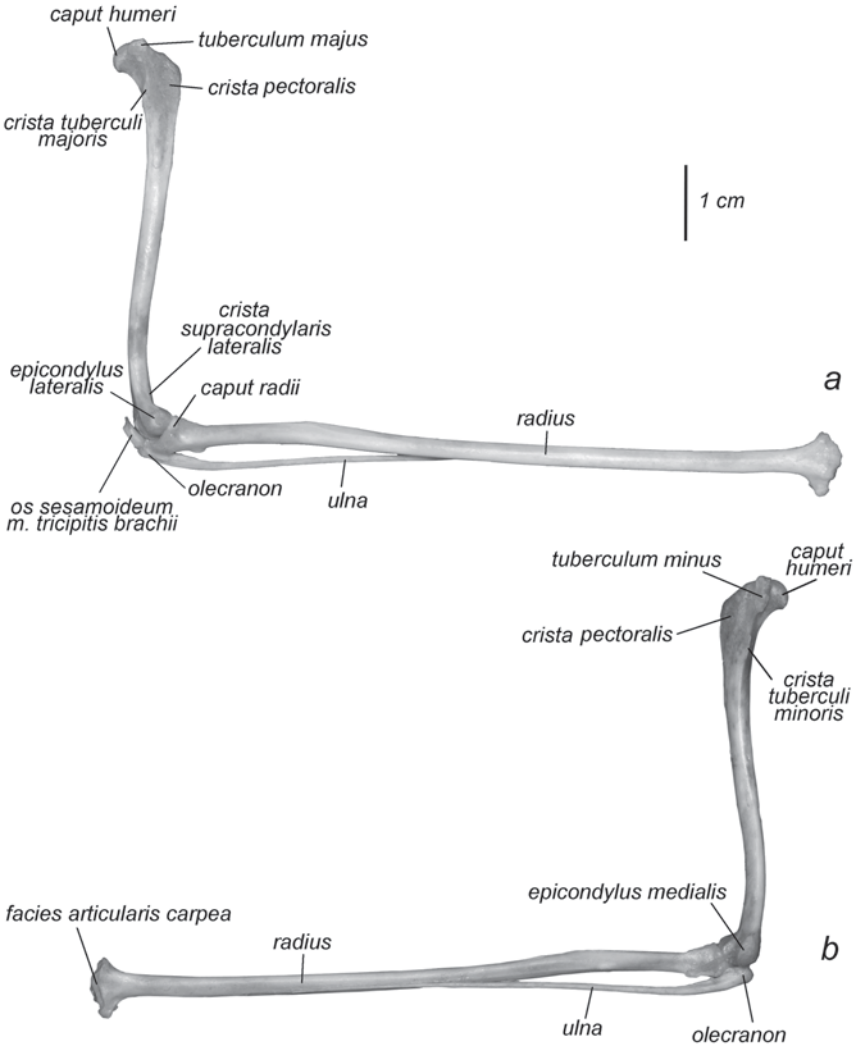


Fig. 3.9 The humerus and antebrachium of *Rousettus aegyptiacus*, right forelimb. *a. Lateral view b. Medial view*

in all chiropterans is very well developed. The large medial epicondyle of the humerus is considerably larger than the lateral epicondyle. The crests of epicondyles are almost indiscernible. In some bat families (for example, Mormoopidae, Molossidae, Rhinolophidae), the medial epicondyle has a specific distal outgrowth, the styloid process or spine (*spina entepicondyli*), which supplies an additional place of origin for flexor muscles of the antebrachium. Vaughan (1959, 1970a) supposed that when the elbow joint is being flexed by any exter-

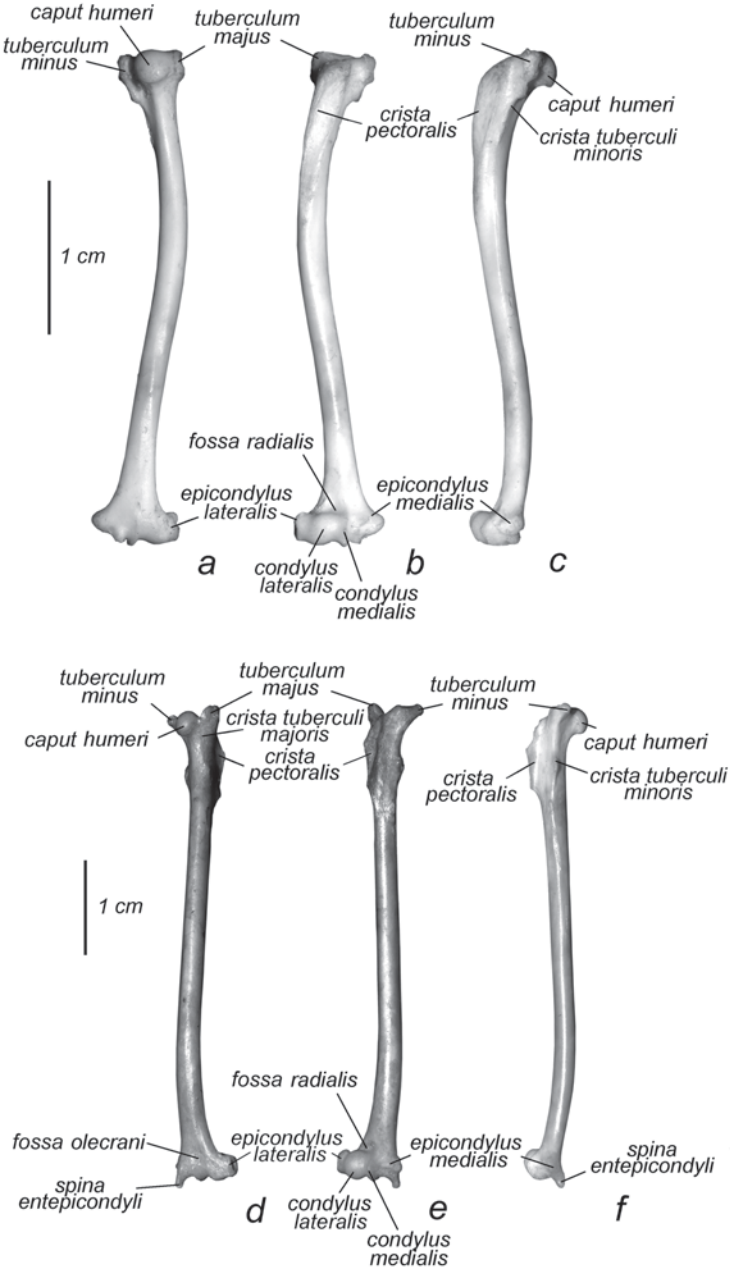


Fig. 3.10 The humerus of bats, right forelimb. *a. Cynopterus sphinx, posterior view b. C. sphinx, anterior view c. C. sphinx, medial view d. H. armiger, posterior view e. H. armiger, anterior view f. H. armiger, medial view*

nal force, the tip of the styloid process tends to move away from the *pisiforme*, and hence, the *m flexor carpi ulnaris*, which connects these two poins, undergoes tension and "automatically," without activation, transmits the elbow flexion into flexion of digit V via the *pisiforme* (for further detail, see the section devoted to muscles later in the text). Almost the entire anterior surface of the trochlea on the distal epiphysis is formed by the lateral condyle; the medial condyle is very poorly developed (Figs. 3.10b, e). The posterior surface of the trochlea has a groove, in which the olecranon slides; so, it is homologous to the medial (ulnar) condyle.

Antebrachium (Fig. 3.9). The **ulna** is much reduced. It is separate in the proximal half of the antebrachium and fuses into the radius in the distal half. At its proximal end, the ulna only slightly participates in the elbow joint, the olecranon being mostly preserved as the point of insertion of the distal tendon of the *m. triceps brachii*. Contrary to the ulna, the **radius** is well developed, being twice as long as the humerus. Its proximal end forms a wide *fovea articularis*, which houses the anterior part of the humeral trochlea (the lateral condyle). The proximal half of the radius is rounded in cross-section. Closer to the distal end, the radius is somewhat flattened dorsoventrally. Its distal epiphysis is widened. The articular surface for the carpus (*facies articularis carpea*) is a deep lateromedially extending trough (Fig. 3.9b), which houses the *scaphocentralolunatum*. The dorsal side of the distal epiphysis forms a shelf overhanging the radiocarpal joint and having a series of tubercles on the upper side (Fig. 3.9a). Extensor tendons pass to the manus between these tubercles. The ventral side of the epiphysis does not form a similar shelf and lacks tubercles.

Carpus (Fig. 3.11, Table 1.1). The carpus in bats is formed of the same set of bones as in colugos, although they differ somewhat in arrangement. The proximal row retains a very large *scaphocentralolunatum* and small *cuneiforme*. The distal row includes the *trapezium*, *trapezoideum*, *capitatum*, and *uncinatum*. The *pisiforme*, which usually lies at the side of the proximal row of carpal bones, is displaced in bats to the distal row and lies on the ventral surface of the *capitatum*. Macalister (1872) even regarded the *pisiforme* as a transverse process of the *capitatum*. Within the order Chiroptera, carpals vary in shape, as follows from both our studies and data of other authors (e.g., Vaughan 1959; Norberg 1970, 1972; etc.). Features of carpals that determine the specific mobility in the radiocarpal, mediocarpal, and carpometacarpal joints are described later in the section devoted to the joint structure in chiropterans.

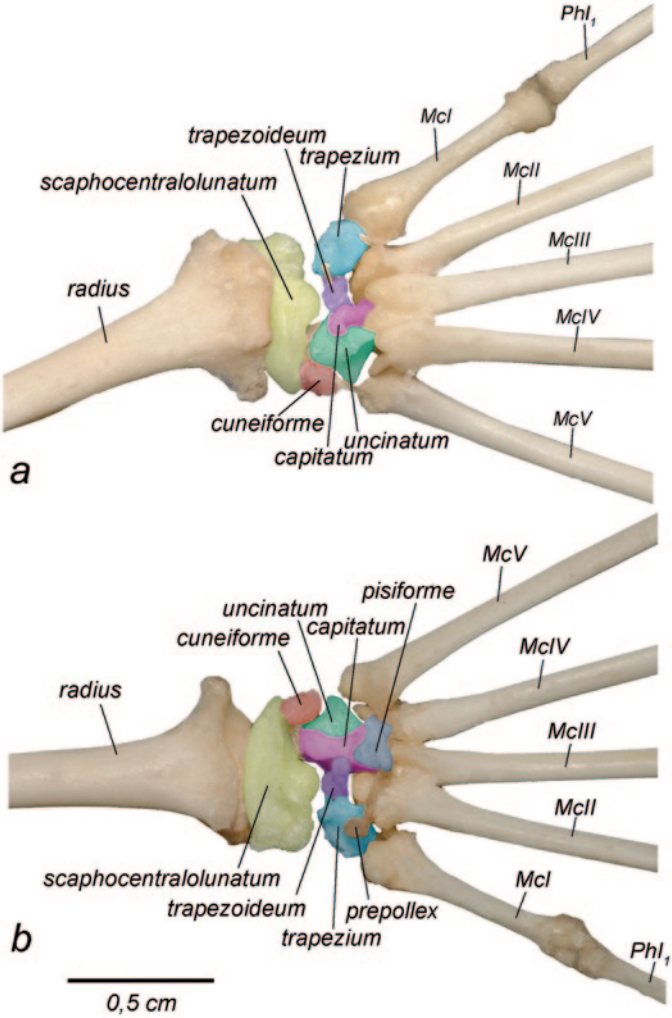


Fig. 3.11 The carpus of *C. sphinx*, right forelimb. *a. Dorsal view b. Ventral view*

Digits (Fig. 3.12, Table 1.2). The prepollex is rather small, but always present; sometimes it is misinterpreted as *scaphoideum* (Vaughan 1959, 1970a, b; Kovtun 1978). It is located on the ventral side of the medial border of the carpus. Since in spite of profound changes in the bat manus aimed at reduction of the wing inertia, this bone is retained, it probably plays an important role. Apparently, the prepollex

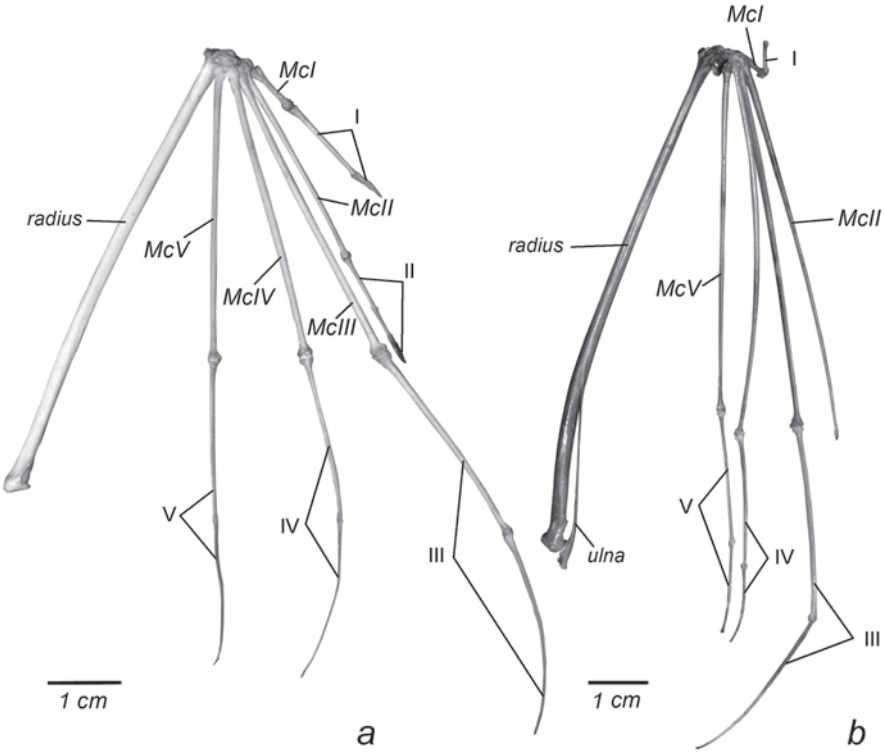


Fig. 3.12 The antebrachium and manus of bats, right forelimb, dorsal view. *a. C. sphinx (without ulna) b. H. armiger*

serves two important functions. First, due to the ventral position, it provides a lever for the muscle bending digit V (*m. abductor digiti quinti*). Second, it, along with the *pisiforme*, forms a canal that houses tendons of the long digital flexors. Metacarpals II–V contribute significantly to the elongation of the manus, so that each metacarpal is considerably longer than any phalanx. Their proximal heads are complex and asymmetrical in shape. The heads of metacarpals II–IV are provided with specific blade-like processes, which wedge in between carpals of the distal row. The metacarpal I is not elongated and lacks such a specific process. The phalangeal formula of bats is variable (Table 1.2). As is typical for mammals, the first digit in all chiropterans has two phalanges. In fruit bats, the second digit includes three phalanges, almost always with a minor claw on the distal one. Digit II of microbats has only one (proximal) phalanx or no phalanges at all (Fig. 3.12b). The phalangeal formula of three other digits is similar in megabats and microbats. Digit III has two or three phalanges, the third (ungual) one being usually cartilaginous and very short. Digits IV and V consist of two phalanges each. In extant species, digits III–V lack claws. The terminal phalanges are cartilaginous and flexible. Furthermore, the tips of digits IV and V are bifurcated in bats, which increases the areas of attachment for the membrane's trailing edge (Norberg 2002).

Joints

The **sternoclavicular articulation** is transformed into a true synovial joint, with a joint capsule and cartilaginous lining of articular surfaces, which are flattened and oval in outline. In addition to a thin joint capsule, there are two (medial and lateral) well-developed ligaments (Fig. 3.13). One of them, the obliquely oriented *ligamentum sternoclaviculare mediale*, connects the medial border of the proximal head of the clavicle with the anterior border of the *manubrium sterni*. The *ligamentum sternoclaviculare laterale* shortly connects the lateral borders of articular surfaces of the sternum and clavicle, which adjoin each other. This pair of ligaments restricts significantly the disarticulation of the joint, although allowing certain mobility of the clavicle. The main movement in the joint is rotation of the clavicle around the longitudinal axis of its proximal part (the stem). The range of rotation is limited by the length of the medial ligament, which is wound on the base of the clavicle, as it rotates. It should be noted that because the distal end is deflected, the axis of the straight proximal part does not coincide with the longitudinal axis of the clavicle as a whole, which passes through its sternal and acromial ends (Fig. 3.8). In addition to rotation, the design of the joint allows small deviations of the clavicle. The range of its deviations in flight is shown in X-ray video frames of a fruit bat (Fig. 3.14): (I) maximum lateral deviation, (II) minimum lateral deviation, (1) minimum protraction of the clavicle, the clavicle is raised, and (2) maximum protraction of the clavicle, the clavicle is lowered.

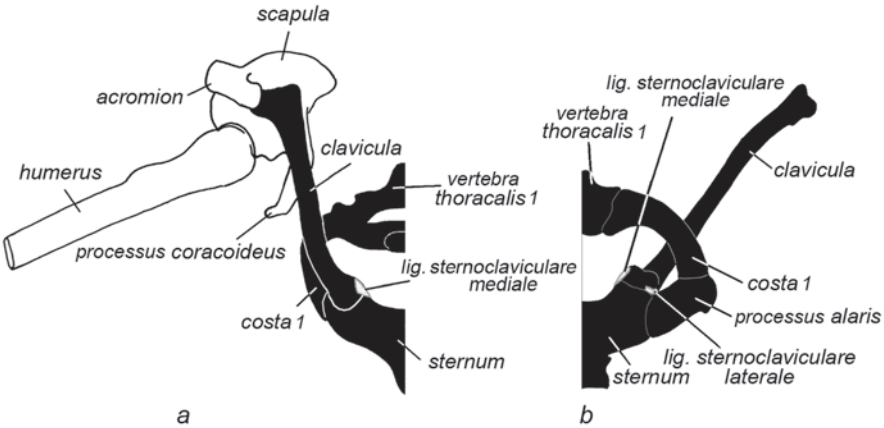


Fig. 3.13 Scheme of the sternoclavicular articulation of bats, right forelimb. *a. Anterior view b. Thorax from inside*

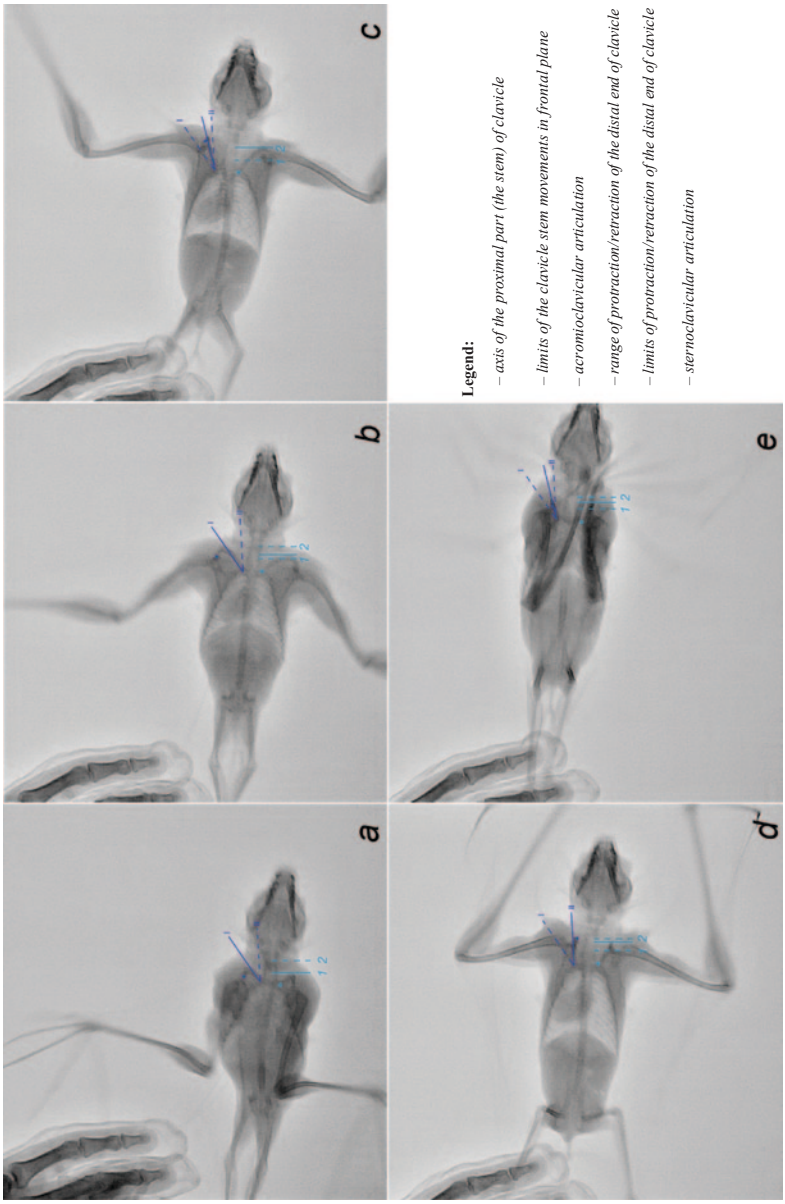


Fig. 3.14 X-ray images of wing beat cycle of *R. aegyptiacus*. *a. Early downstroke b. Late downstroke c. Early upstroke d. Middle upstroke e. Wings are at their upper position (point of transition from upstroke to downstroke)*

Acromioclavicular articulation (Fig. 3.15). In many species, the clavicle bears a smooth articular facet for acromion (*facies articularis acromialis*) (Fig. 3.7b). Manipulations with the syndesmological preparations show that the presence or absence of this facet has little effect on the mobility in the acromioclavicular articulation. More important are ligaments. There are always two of them: *ligamentum acromioclaviculare* and *ligamentum coracoclaviculare*. This pair of ligaments restricts mobility of the scapula relative to the clavicle, allowing some rotation of the scapula around its own longitudinal axis and around the longitudinal axis of the clavicle. The *ligamentum acromioclaviculare* often contains a sesamoid bone. Its length is variable among bat species. The *ligamentum coracoclaviculare* connects the cranial border of the base of the coracoid process of the scapula and the caudolateral side of the acromial end of the clavicle. As compared with other chiropterans, in horseshoe bats (Rhinolophidae and Hipposideridae), the *ligamentum coracoclaviculare* is significantly shorter than the *ligamentum acromioclaviculare*, and, hence, the acromial end of the clavicle is bound more tightly to the base of the coracoid process (Fig. 3.15b). However, mobility of the scapula relative to the clavicle is essentially the same as in other bats.

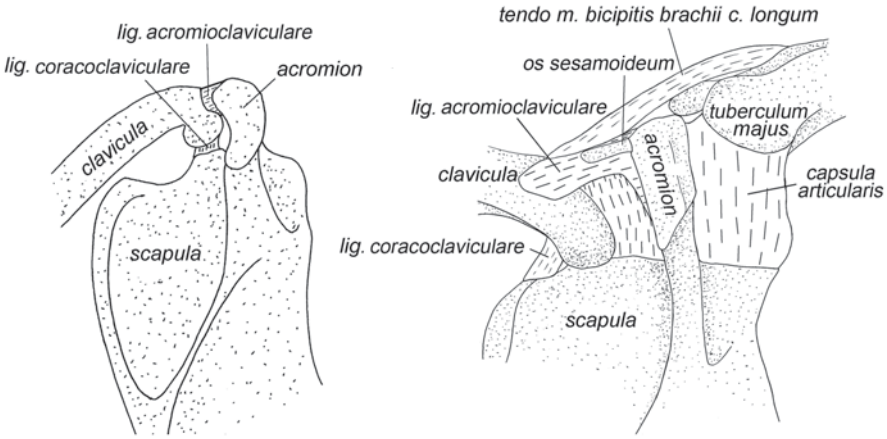


Fig. 3.15 The acromioclavicular articulation of bats, right forelimb, dorsal view. *a. C. sphinx b. Rhinolophus ferrumequinum*

The **shoulder joint** of bats is in general similar to that of other mammals. The articular capsule is thin and incorporates tendons of the *m. supraspinatus*, *m. infraspinatus*, and *m. subscapularis*. In this joint, the humerus displays a wide range of mobility, including abduction/adduction, retraction/protraction, and axial rotation (pronation/supination). Detailed studies of the shoulder joint in bats resulted in the recognition of three main structural types (Schlosser-Sturm and Schliemann 1995; Schliemann 1997; Schliemann and Schlosser-Sturm 1999): non-specialized (basic) joint, specialized joint with one articular surface, and specialized joint with two

articular surfaces. In the specialized joint of the first type, the glenoid and humeral head are significantly longitudinally extended, in contrast to that of the basic type, in which the humeral head is spheric and the glenoid is almost round. Specialized joint of the second type has an additional articulation between the humerus and scapula. It is formed due to excessive development of the greater tubercle of the humerus, which rests against respective articular facet on the scapula, located lateral to the glenoid. In addition, the supraglenoid tubercle of the scapula in some species is enlarged and, in the case of great protraction of the humerus, rests against the notch between its greater and lesser tubercles, thus, stopping this movement (Vaughan 1959). According to Schlosser-Sturm and Schliemann (op. cit.), the basic type of the shoulder joint is characteristic of Pteropodidae and Rhinopomatidae. The specialized joint of the first type occurs in Noctilionidae, Mormoopidae, Emballonuridae, Nycteridae, and Megadermatidae, and the specialized joint with two articular surfaces is found in Furipteridae, Natalidae, Thyropteridae, Myzopodidae, Mystacinidae, Vespertilionidae, Rhinolophidae, Craseonycteridae, and Phyllostomidae. According to Schliemann and Schlosser-Sturm (1999), both specialized types of the shoulder joint allow to restrict the rotational mobility of the humerus. In the first type of the shoulder joint, rotation is limited only in protracted, or also retracted, position of the humerus, depending on the degree of elongation of the humeral head; while in the second type of specialized joint, rotation is restricted only when the humerus is protracted.

The **elbow joint** (Fig. 3.16) is formed, as usual, by three bones: humerus, radius, and ulnar. The structure of the articular surfaces of the elbow joint in bats is considered in detail by Jullien (1969). High-quality images of these surfaces in *Pteropus* are supplied by Szalay and Lucas (1993). In general, the radius has almost completely crowded out the ulna from the elbow joint and, as a result, articulates not only with the lateral condyle of the humerus, but also with the medial condyle by a medial expansion of its articular fossa. The joint has well-developed collateral ligaments, which connect each epicondyle of the humerus with both bones of the antebrachium. Two ligaments arise from the medial epicondyle: the *ligamentum mediale radiale* runs to the radius and the *ligamentum mediale ulnare* to the ulna. The lateral epicondyle gives rise to a single wide ligament, which, then, bifurcates into two unequal parts, the short *ligamentum laterale radiale* running to the radius and the long *ligamentum laterale ulnare* to the ulna. There is a large sesamoid bone at the point of bifurcation, which is tightly fixed at the side of the elbow joint by the shorter ligament. This sesamoid provides an additional place of origin for the extensor musculature of the forearm. Since the *ligamentum laterale radiale* is attached to the radial side of the radius and the *ligamentum mediale radiale*, to the ulnar side, this pair of ligaments undergoes tension in the case of even slight pronation of the radius and, hence, prevents further rotation in this direction. At the same time, the placement of these ligaments allows certain supination. The *ligamentum laterale ulnare* and *ligamentum mediale ulnare*, in turn, strictly fix the position of the proximal end of the ulna in the elbow joint, excluding abduction or adduction disarticulations, which could otherwise occur when the powerful *m. triceps brachii* contracts.

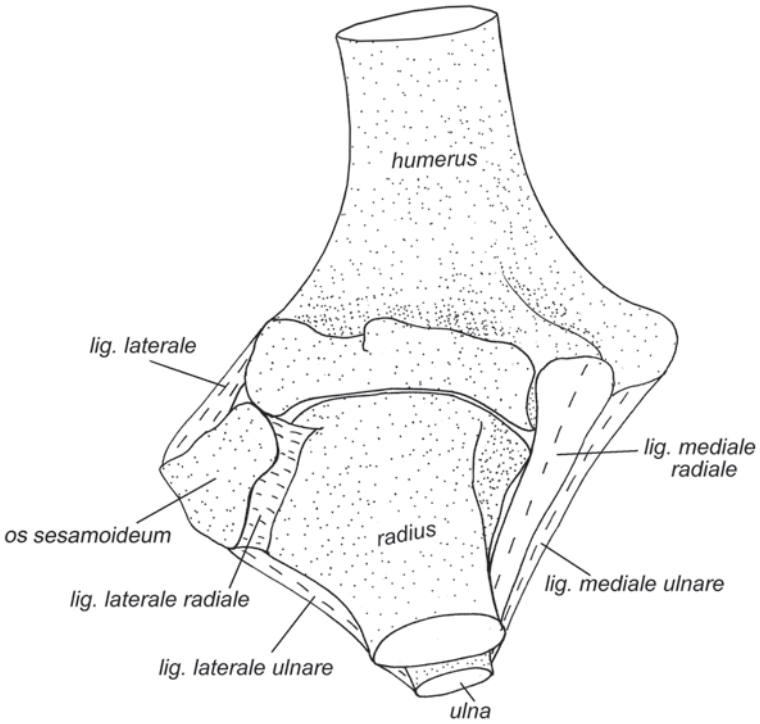
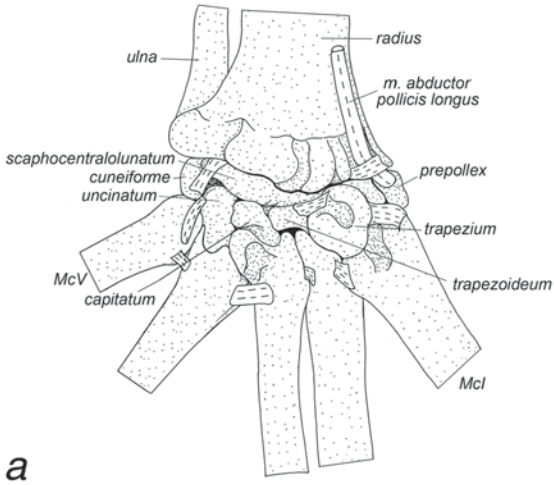
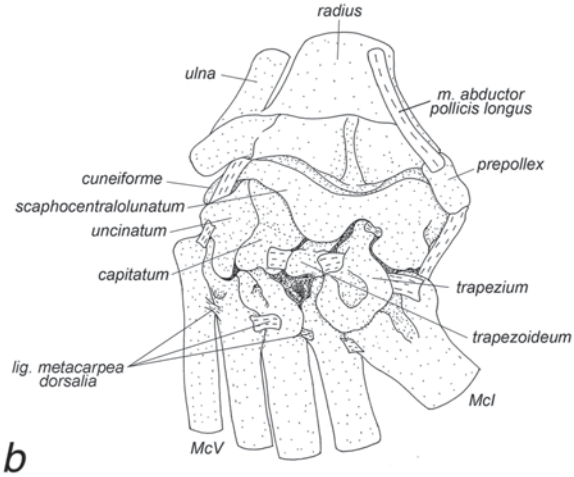


Fig. 3.16 The elbow joint of *C. sphinx*, right forelimb, anterior view.

The **radiocarpal joint** (*articulatio radiocarpea*) differs from the antebrachiocarpal joint of tree shrews and colugos by exclusion of the ulna, being reduced distally, from this joint. It is arranged like a simple door hinge: the lateromedially extended distal end of the radius bears a deep lateromedially directed articular trough, which houses respective torus of the *scaphocentralolunatum* (Fig. 3.11a). Due to this shape, the joint allows only flexion/extension (without hyperextension) and very weak lateral deflections, while axial rotation is almost completely prevented. The hyperextension is interfered by an opposition of the dorsal shelf-like border of the articular trough of the radius, with respective projection on the dorsal side of the *scaphocentralolunatum*.

The range of flexion in the radiocarpal joint does not provide complete folding of the wing; therefore, bats are distinguished by high mobility in the mediocarpal and carpometacarpal II–V joints, which are stiff in the majority of mammals.





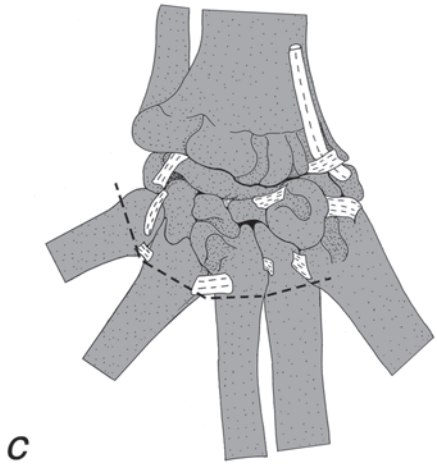


Fig. 3.17 The radiocarpal, mediocarpal and carpometacarpal joints of *R. aegyptiacus*, right forelimb, dorsal view.
a. Joints in extended position
b. Joints in flexed position
c. Scheme of the axes of rotation of the carpometacarpal joints (the axis of rotation shown by dashed line)

The **mediocarpal joint** is located between bones of the proximal (*scaphocentralolunatum* and *cuneiforme*, which, from the mechanical point of view, can be taken as a single whole) and distal (*trapezium*, *trapezoideum*, *capitatum*, and *uncinatum*) carpal rows. In the previous publications, we have not found discussions concerning mobility of this joint in chiropterans. In the plane of the manus, the joint space forms a zigzag cleft (Fig. 3.17). The *cuneiforme* forms a rounded condyle, which rests upon respective articular facet of the *uncinatum*. In turn, the *uncinatum* and *capitatum* form the second condyle, which fits into an extensive concavity in the lateral part of the articular surface of the *scaphocentralolunatum*. Medially, in the middle of the joint, the *scaphocentralolunatum* forms an opposite condyle, which is embraced by the *capitatum*, *trapezium,* and *trapezoideum*. Then, the *trapezium* has a peculiar knob, which lies in a deep, dorsally open notch in the *scaphocentralolunatum* (Fig. 3.17b). Finally, the medial border of the *scaphocentralolunatum* forms a support for the proximal head of metacarpal I (as a part of carpometacarpal joint I). The joint allows flexion, but abduction and adduction are impossible, as well as hyperextension. The extension is stopped, when the dorsal borders of bones of the proximal and distal carpal rows forming the joint set against each other, and the *ligamenta intercarpea interossea* on the ventral side of the joint, undergo tension.

Among **carpometacarpal joints**, the carpometacarpal I joint is relatively independent and allows a wide range of movements. It is formed by the *trapezium* and the proximal head of metacarpal I; the articular surfaces in different bat species vary from almost flat to saddle shaped. The carpometacarpal II–V joints of bats have acquired the ability of extensive flexion. Although they are rather diverse in bats (for detailed descriptions of particular species, see Vaughan 1959, 1970a; Kovtun 1978), these joints show a number of shared characters. Metacarpal II wedges between the *trapezium*, *trapezoideum*, and *capitatum*; metacarpal III wedges between the *capitatum* and *uncinatum*; metacarpal IV fits into respective notch in the *uncinatum*; and the proximal head of metacarpal V rests against the *uncinatum*.

Movements of the metacarpus II–V relative to the carpus are coupled with mutual mobility of the metacarpals in **intermetacarpal articulations**. They are formed by the blade-like proximal expansions of metacarpals II–IV, which overlap each other and the proximal end of metacarpal V (which virtually lacks such a blade). The tapering ends of the blades wedge in between bones of the distal row of the carpus (thus participating in the carpometacarpal joints). The blades are oriented obliquely to the plane of the manus (Fig. 3.18), and their inclination determines the plane of unfolding of the chiropatagium. Contrary to tree shrews, the distal ends of metacarpals II–V are not connected by *ligamenta metacarpea transversa profunda*, the absence of which allows wide divergence of metacarpals in the carpometacarpal joints. In a completely unfolded wing, metacarpals II and III are aligned with the antebrachium; metacarpal IV deviates caudally for at most 50°; and metacarpal V is positioned at almost a right angle. The divergence of metacarpals is achieved automatically, as the carpometacarpal joints are not coaxial, i.e., in digits II and III, their axes pass strictly lateromedially and, in digits IV and V, obliquely (Fig. 3.17c). The axis misalignment of carpometacarpal joints is determined by the metacarpal blades. The proximal ends of metacarpals II–V are connected by short dorsal ligaments (*ligamenta metacarpea dorsalia*) transferring the pull of extensors of the carpus from one bone to another.

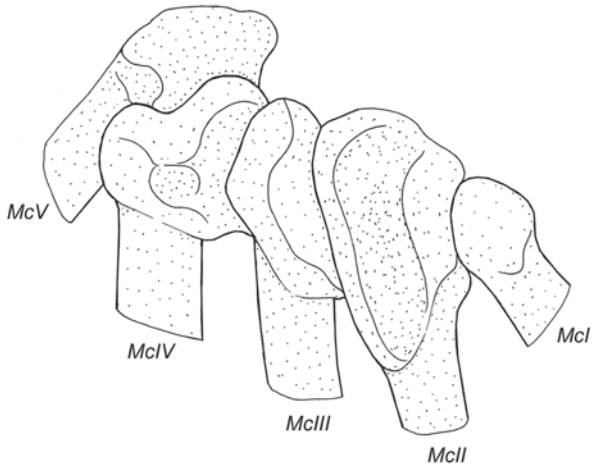


Fig. 3.18 The proximal metacarpal heads of *H. armiger*, right forelimb, distal view.

This mechanism provides coupled movements of metacarpals, as the wing is spread. Outwardly, this wing spreading looks like extension combined with lateral abduction (relative to the midline of the manus represented by the direction of metacarpal III) of digits IV and V. However, since the two movements are actually always coupled due to the inclination of the metacarpal blades and also by the wing membrane, this spreading movement may be named simply extension for brevity.

Among **metacarpophalangeal joints**, the metacarpophalangeal joint of digit I (Fig. 3.19a) allows hyperextension for an angle about 90° and flexion for a

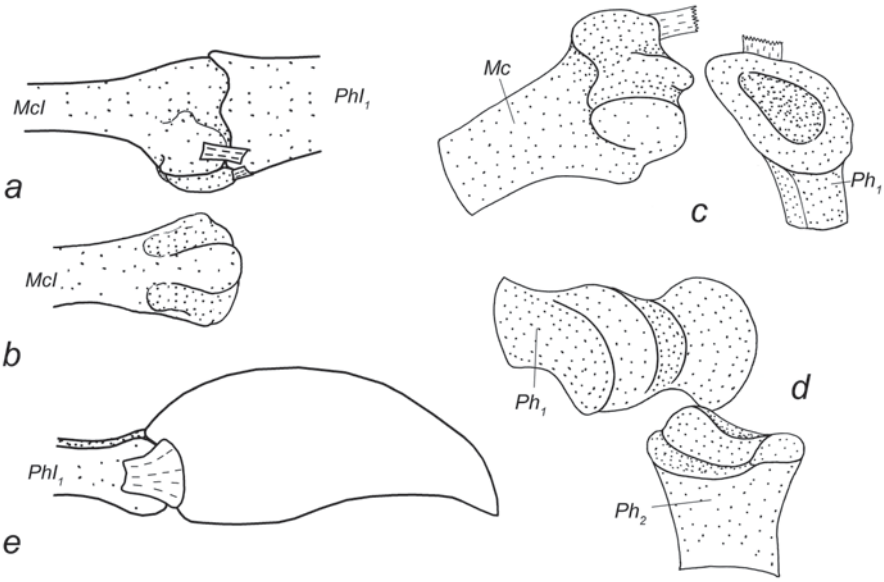


Fig. 3.19 The digital joints of bats. *a. Metacarpophalangeal joint I of R. aegyptiacus, lateral view b. Distal end of metacarpal I of R. aegyptiacus, ventral view c. Metacarpophalangeal joint V of H. armiger, ventral view d. Interphalangeal joint V of R. aegyptiacus, ventral view e. Preungual joint I of R. aegyptiacus, lateral view*

somewhat smaller angle. The joint also allows small adduction and abduction. A rounded condyle at the end of metacarpal I fits into a notch at the base of the proximal phalanx. Either side of the ventral surface of the distal head of the metacarpal I has a shallow notch (Fig. 3.19b), which houses a sesamoid bone formed inside the ventral ligaments of the joint. As the joint is flexed, the distal ends of these bones set against the ventral border of the proximal surface of the phalanx, limiting flexion. The metacarpophalangeal joints of digits II–V allow flexion for 90°–100° and very restricted adduction and abduction. The articular surface of the distal head of the metacarpal faces distally and ventrally and bears a longitudinal torus, which fits into a respective groove in the flattened proximal head of the first phalanx (Fig. 3.19c). As the joint is extended to a straight state, the dorsal borders of articular surfaces of the matacarpal and phalanx set against each other and the ligaments on the ventral side of the joint undergo tension, preventing hyperextension. Adduction and abduction in the joint are strongly restricted by collateral ligaments.

The **first interphalangeal joints of digits II–V** allow flexion for approximately 170°. The articular surface at the distal end of the proximal phalanx faces distally and ventrally and looks like a spool segment or saddle with a smoothly rounded outline. The proximal articular surface of the succeeding phalanx displays a complementary shape, so that its lateral and medial concavities (with a ridge between them) fit the respective tori of the spool of the preceding phalanx (Fig. 3.19d). The shape of the joint and its collateral ligaments exclude adduction and abduction, while hyperextension is prevented in the same way as in the metacarpophalangeal joints.

In microbats, the metacarpals are relatively longer than in fruit bats; therefore, when folding the wing, they tuck in all phalanges, beginning from the first. As a result, the metacarpal and phalanges become spirally arranged, with an angle about 20°–30° between segments. Thus, all digits are compactly curled under the antebrachium and do not clutch at substrate during crawling with a support on the radiocarpal joint and with a highly raised elbow (Fig. 3.20a).

Contrary to microbats, the metacarpophalangeal joints of fruit bats remain straightened, as the wing is folded (Fig. 3.20b), so that the first phalanges are aligned with metacarpals along with the antebrachium. In digits III and IV, because of torsion of the first phalanges toward pronation at approximately 90°, the axes of flexion in the first interphalangeal joints are turned at right angles to the membrane plane. In a folded wing, these joints are usually flexed at 90°–140°. Therefore, the second phalanges are positioned lateral to the elbow on the external wing side and, hence, do not interfere with climbing branches by embracing them from the sides by the fore- and hindlimbs (Fig. 3.20c). It is also possible that the pattern of digit folding in fruit bats is accounted for by the fact that many of them regularly fan themselves with wings to avoid overheating in daytime. Fruit bats regulate the efficiency of fanning by both the frequency of movements and changing the fan area of the semifolded wing by flexion or extension of distal phalanges.

A special arrangement giving a stiff leading edge of the chiropatagium is presented in bats. The distal end of the second digit (excluding the claw in fruit bats) and the base of the second phalanx of the third digit are connected by the ligament, forming a convex frame enclosing the so-called *dactylopatagium minus* (the mem-

Fig. 3.20 Quadrupedal locomotion of bats (photos by E. Yakhontov). *a. Locomotion of Pipistrellus pipistrellus on the horizontal substrate b. Locomotion under branches of Pteropus vampyrus c. Locomotion on the trunk of P. vampyrus, successive stages.*

brane between the second and third digits). This unit is stiff in the membrane plane (Norberg 1969).

The **preungual joints** are present in digits I–II in fruit bats and digit I in other bats. The structure of preungual joints (Fig. 3.19e) significantly differs from that of the first interphalangeal joints of digits II–V. Hyperextension almost equals flexion in range, as the articular surface almost equally spreads onto the dorsal and ventral sides of the distal head of the preungual phalanx. This articular surface is trochlear in shape, and in its median groove the ridge of the proximal head of the ungual phalanx slides in the course of flexion and hyperextension. Collateral ligaments of the articular capsule exclude adduction and abduction in the preungual joints.

Musculature

In the region of the shoulder girdle and humerus, bats have the same set of muscles as colugos: *m. rhomboideus capitis*, *m. rhomboideus cervicis*, and *m. levator scapulae dorsalis* characteristic to quadrupedal mammals are lost. However, they have the standard mammalian *m. clavotrapezius*, which is absent in tree shrews and colugos (this absence may be an apomorphy of Archonta). The musculature of distal regions is greatly reduced. Of the three mammalian orders investigated here, bats have the smallest set of muscles of the free limb: the humerus has 3 (in tree shrews and colugos, 5), the antebrachium has 15 (17 in tree shrews and 16 in colugos), and the manus has from 8 to 10 (26 in tree shrews and 23 in colugos). Bats lack not only the *m. palmaris longus*, *m. pronator quadratus*, *m. palmaris brevis*, *m. opponens pollicis*, *m. adductor digiti quarti*, *m. flexor brevis manus*, and *m. flexor digiti quinti superficialis*, which are already absent in colugos, but also the *m. tensor fasciae antebrachialis*, *m. anconeus*, *m. flexor pollicis brevis profundus*, and *m. adductor digiti quinti*. At the same time, as a result of development of the wing membrane, the *m. coracocutaneus* (analogous to that of colugos), *m. occipitopollicalis*, *m. dorsi patagialis*, *m. humeropatagialis*, and *mm. plagiopatagiales* are added.

Musculature of Shoulder Girdle

Musculus sternomastoideus (Figs. 3.21, 3.51, 3.53, 3.54). In the bats examined, the *m. sternocleidomastoideus* is only represented by this sternal portion, which is traditionally termed as a separate muscle. It originates from the lateral crest of the skull and behind it, within the area from the mastoid to jugular process. It inserts at the midline on the cranial surface of the *manubrium sterni*.

In bats, this muscle is not involved in locomotion. It participates in lowering and lateral movements of the head.

Musculus clavotrapezius (Figs. 3.22, 3.24, 3.27, 3.30–3.33, 3.37, 3.42, 3.52) is quadrangular in cross-section.

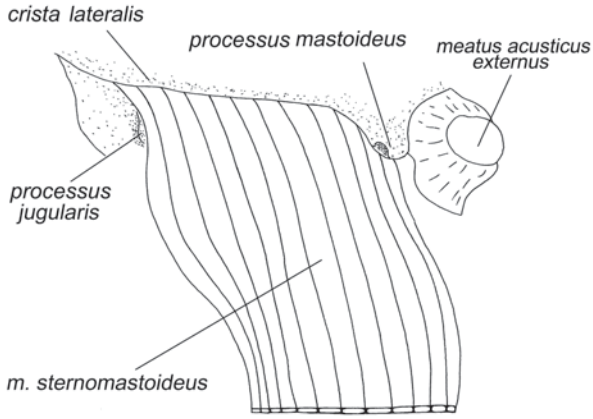


Fig. 3.21 Origin of the *m. sternomasoideus* of *R. ferrumequinum*, lateral view.

In **fruit bats**, it originates from the cervical fascia at the level of the cervical 5 through thoracic 1 vertebrae and inserts on the anterior surface of the distal part of the clavicle and onto the superficial aponeurosis of the *m. clavodeltoideus* and *ligamentum acromioclaviculare*. The posterior border of the muscle adjoins the *m. acromiotrapezius*; however, the boundary between them is usually distinct.

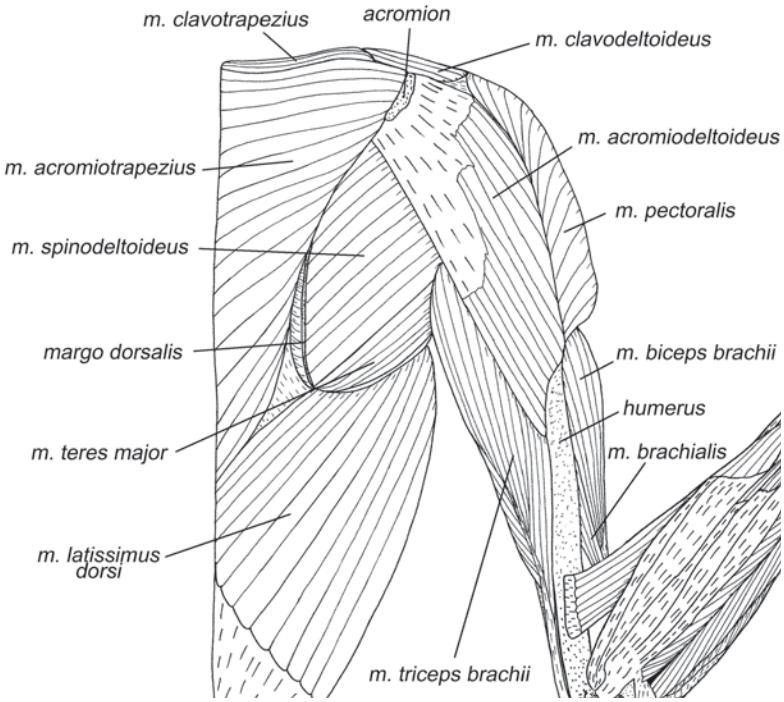


Fig. 3.22 Forelimb muscles of *C. sphinx*, dorsal view, layer I.

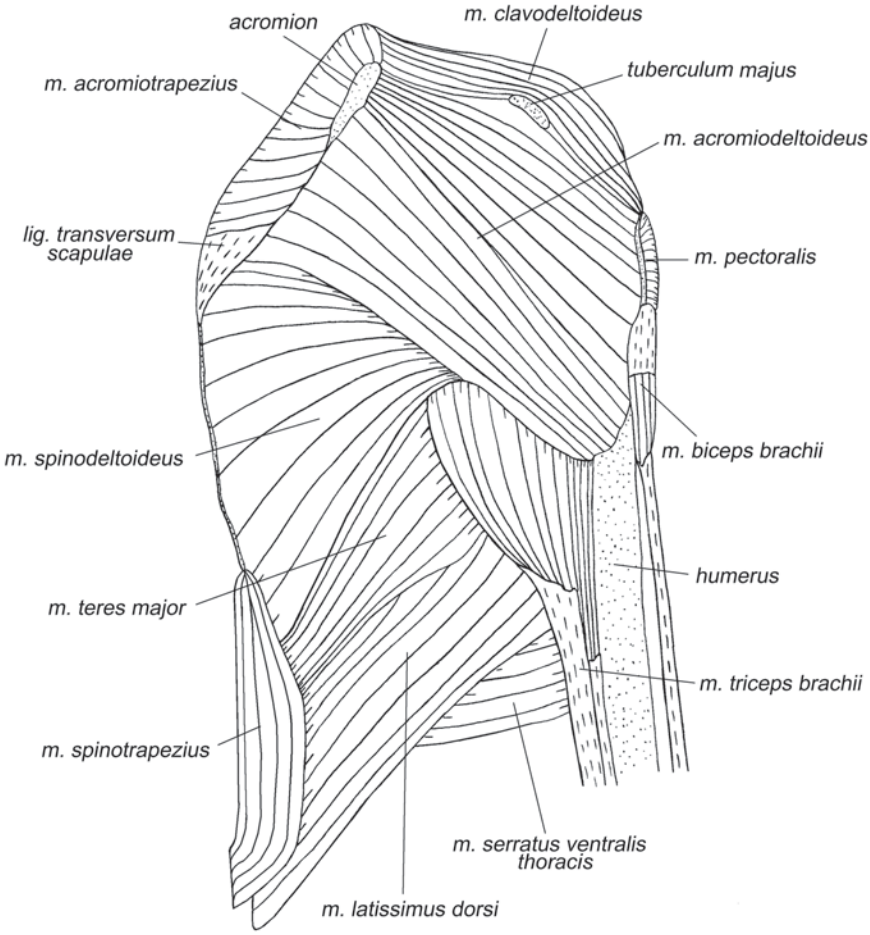


Fig. 3.23 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer I.

In **microbats**, this muscle originates from the apex of the neural spine of the first thoracic vertebra (according to Strickler (1978), in some species, also from cervical vertebra 7) and inserts on the internal surface of the distal one-third of the clavicle. Closer to the vertebral column, this muscle is inseparable from the *m. acromiotrapezius*, but becomes separate closer to the clavicle.

In fruit bats, this muscle pulls the distal end of the clavicle medially; in microbats, caudomedially. In addition, it prevents the lateral deviation of the clavicle.

Musculus acromiotrapezius (Figs. 3.22, 3.23, 3.25, 3.26, 3.28, 3.29, 3.34–3.37) is very wide and flat.

In **fruit bats**, it originates along the vertebral column from the fascias of axial muscles, at the level of the cervical 6 through thoracic 12 vertebrae.

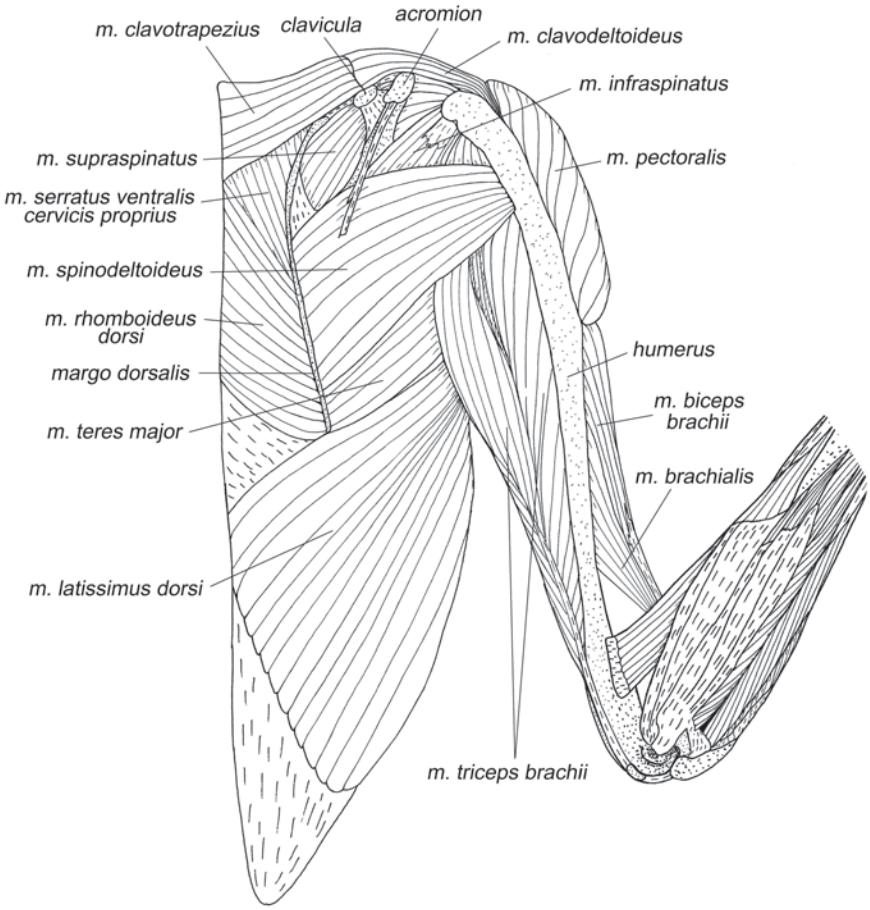


Fig. 3.24 Forelimb muscles of *C. sphinx*, dorsal view, layer II.

In **microbats**, it originates from the apices of the neural spines and interspinous ligaments of thoracic vertebrae 1–5 (or 6). Thus, the caudal part of the *m. acromiotrapezius* in fruit bats occupies the place where microbats have the *m. spinotrapezius*, which is absent in fruit bats. Muscular fibers insert mostly on the acromial process of the scapula and the *ligamentum transversum scapulae*[18].

This muscle pulls the scapula caudomedially. Due to the position of the muscle, the caudally directed component of its force is greater in fruit bats than in microbats, in which the caudally directed force is produced by the m. spinotrapezius.

[18] The *ligamentum transversum scapulae* extend over the supraspinous fossa parallel to the scapular spine from the acromial process to the dorsal border of the scapula (Fig. 3.39).

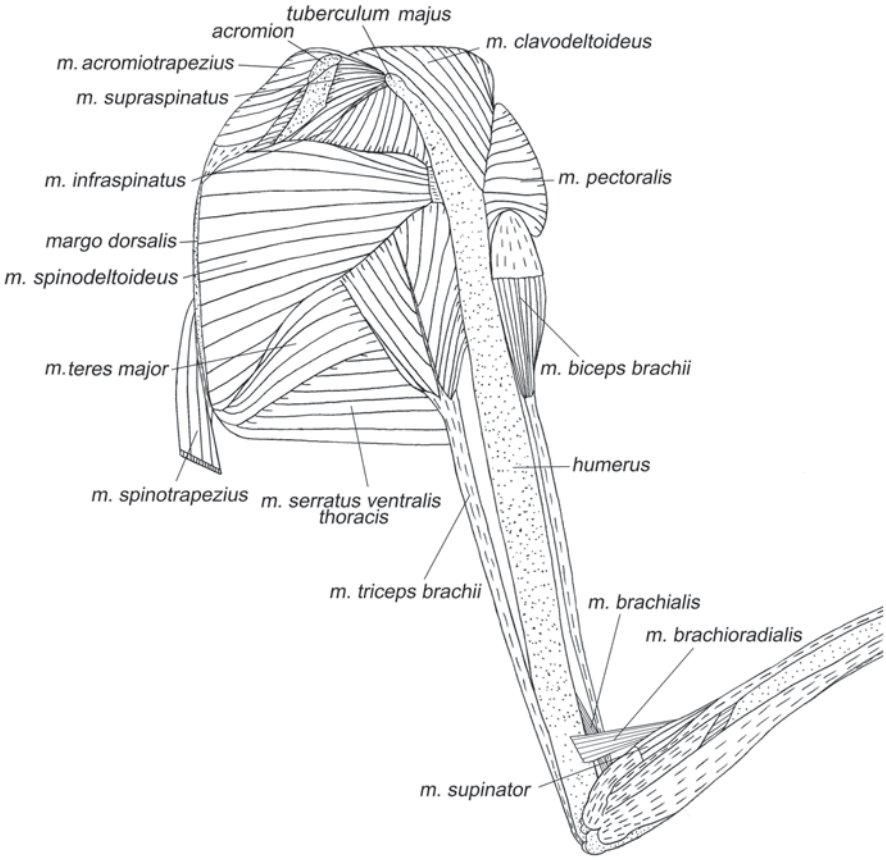


Fig. 3.25 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer II.

Musculus spinotrapezius (Figs. 3.23, 3.25) is absent in **fruit bats** as a separate muscle, its place being occupied by the caudal part of the significantly widened *m. acromiotrapezius*. Possibly, the latter is simply not divided in fruit bats into two, so it is more correct to name it the *m.acromiospinotrapezius*.

In **microbats**, this is a thin triangular muscle. Its fibers originate from the apices of the neural spines and interspinous ligaments from the eighth thoracic (in some species, tenth: Strickler 1978) through the first lumbar vertebra (second according to Strickler). The fibers converge onto a narrow and flat aponeurosis, which inserts on either the middle of the dorsal border of the scapula or caudal to the middle. In horseshoe bats (Rhinolophidae), this muscle inserts almost at the dorsocaudal angle.

The muscle pulls the scapula caudally. Strickler (1978) believed that the presence of a separate m. spinotrapezius in microbats is associated with adaptation to bound on horizontal substrates, since in Desmodus rotundus, this muscle is particularly

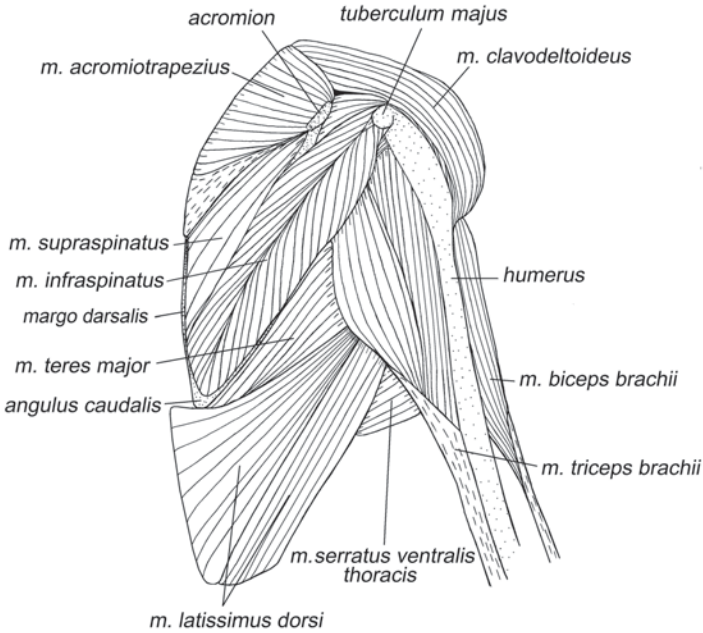


Fig. 3.26 Forelimb muscles of *Hipposideros larvatus*, dorsolateral view.

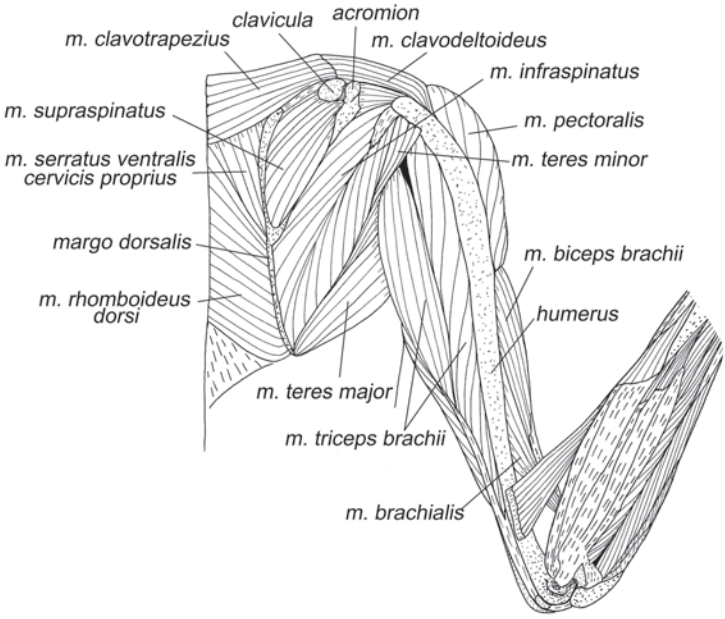


Fig. 3.27 Forelimb muscles of *C. sphinx*, dorsal view, layer III.

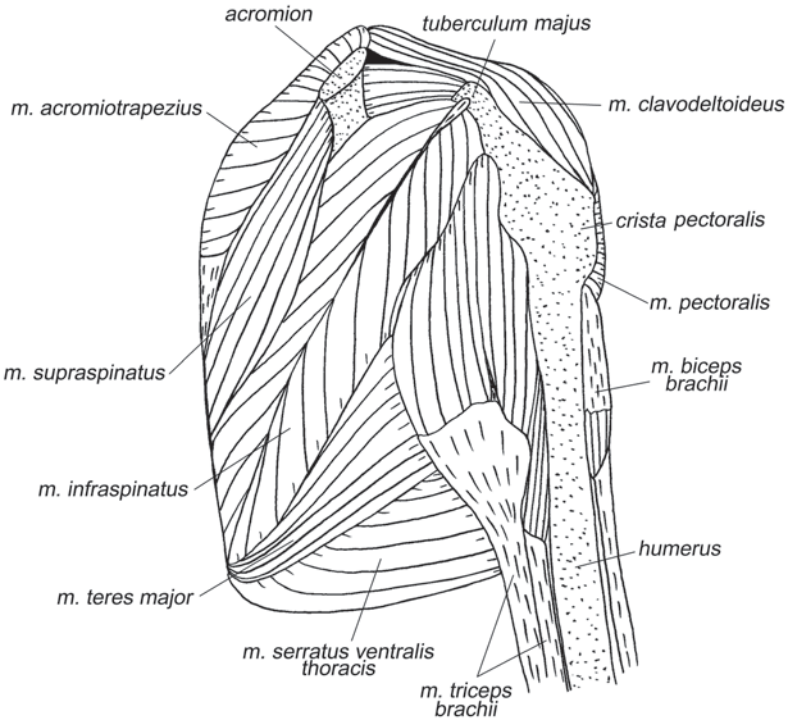


Fig. 3.28 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer III.

well developed. Electromyography (Altenbach 1979) has also shown that the m. spinotrapezius participates in bounding. This explanation is not comprehensive, since the overwhelming majority of bats do not use bound on solid surfaces and horseshoe bats never move on the ground.

Musculus rhomboideus dorsi (Figs. 3.24, 3.27, 3.30–3.31, 3.33, 3.37, 3.38, 3.42) of chiropterans is flat and relatively well developed. It lies under the *m. acromiotrapezius*.

In **fruit bats,** it originates from the cervical fascia and on apices of the neural spines and interspinous ligaments from first through fifth to seventh thoracic vertebra. It inserts on the dorsal border of the scapula, caudal to its spine and up to the dorsocaudal angle.

In **microbats,** it originates from the apices of the neural spines and interspinous ligaments of thoracic vertebrae 1–4 (or 5) (according to Strickler (1978), from cervical 7 through thoracic 9 vertebra). In many species, some fibers originate from the aponeuroses of origin of the *m. clavotrapezius* and *m. acromiotrapezius*. The muscle inserts on the dorsal border of the scapula caudal to the spine.

The muscle pulls the scapula craniomedially.

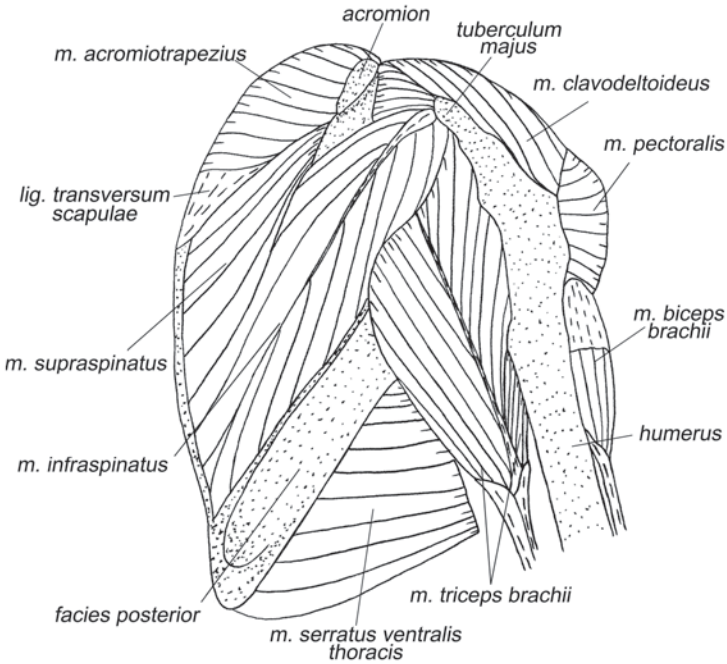


Fig. 3.29 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer IV.

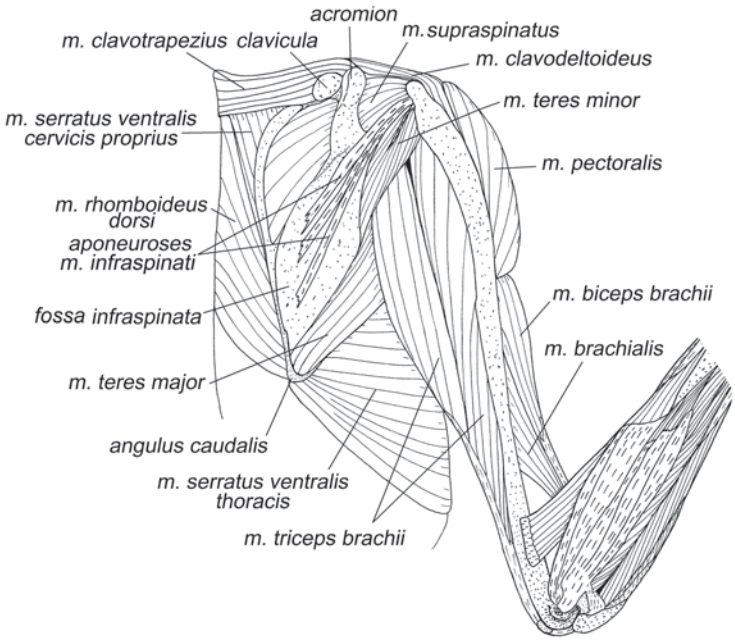


Fig. 3.30 Forelimb muscles of *C. sphinx*, dorsal view, layer IV.

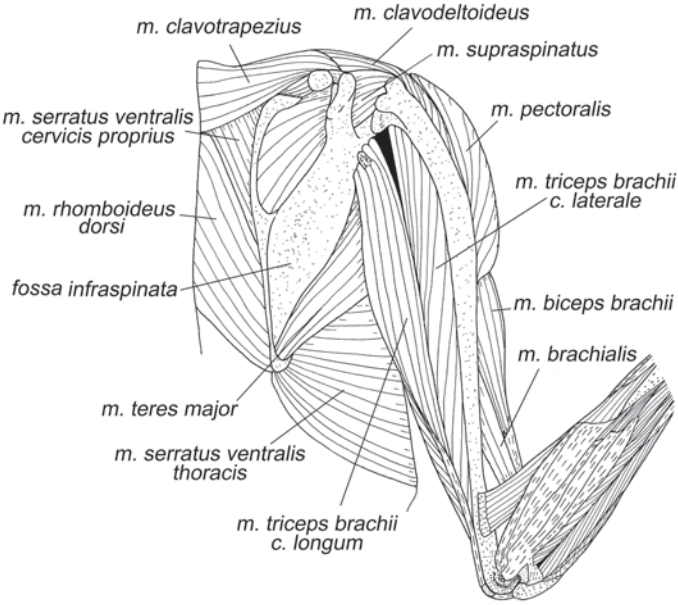


Fig. 3.31 Forelimb muscles of *C. sphinx*, dorsal view, layer V.

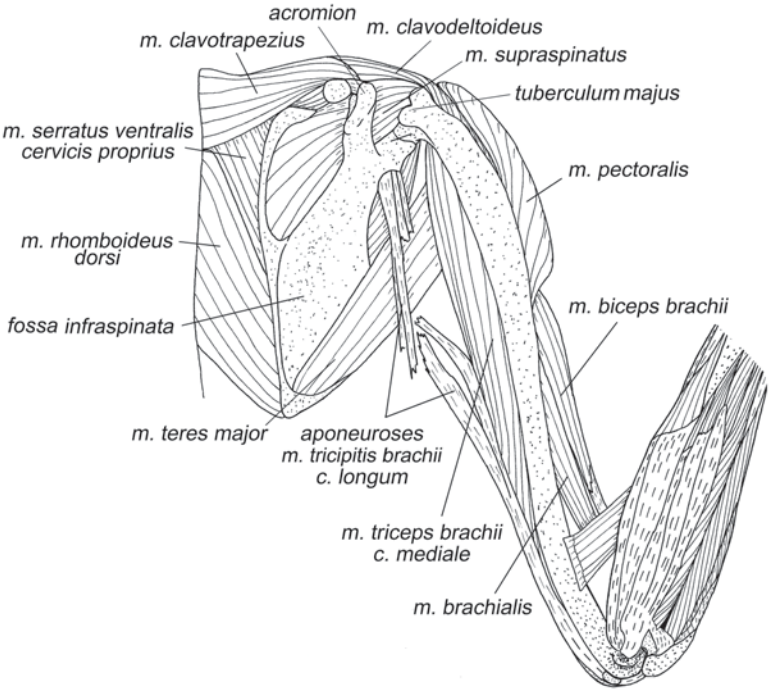


Fig. 3.32 Forelimb muscles of *C. sphinx*, dorsal view, layer VI.

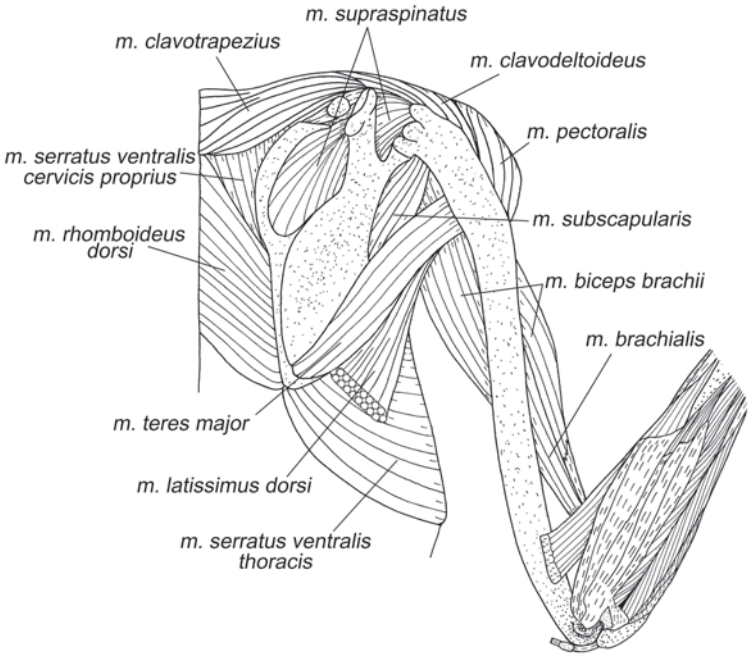


Fig. 3.33 Forelimb muscles of *C. sphinx*, dorsal view, layer VII.

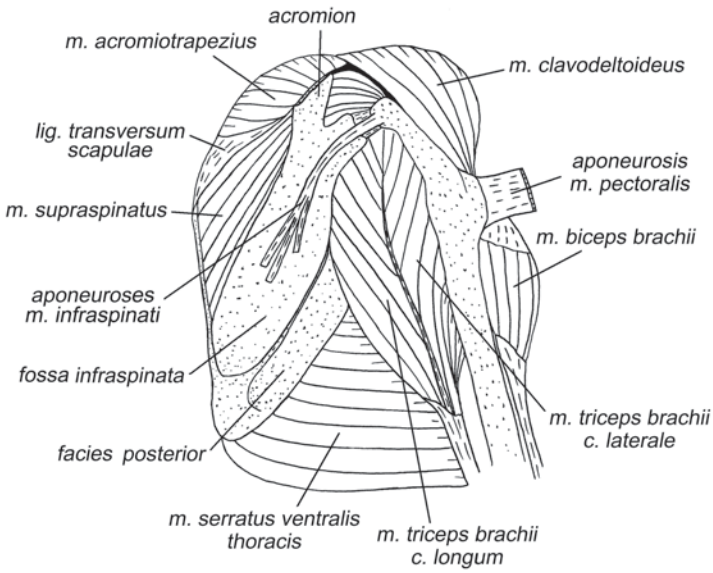


Fig. 3.34 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer V.

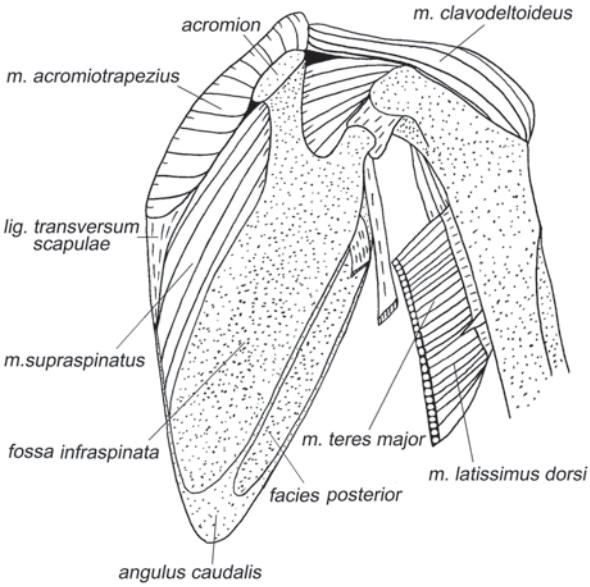


Fig. 3.35 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer VI.

Musculus levator scapulae ventralis (Figs. 3.38, 3.40, 3.41, 3.44, 3.51, 3.54, 3.60, 3.61) in **fruit bats** originates from transverse (costal) processes of cervical vertebrae 3–4 (4–5, according to Macalister (1872), and 2–3 in *Pteropus*, according to Humphry (1869)) and inserts on the dorsal surface of the distal part of the clavicle. This long ribbon-like muscle almost lacks aponeuroses. Other researchers (Vaughan 1959; Norberg 1972; Strickler 1978), without going into the problem of homology, introduce a special name for this muscle, the *m. omocervicalis*.

Among **microbats**, we have not found this muscle in horseshoe bats. This agrees with the data of Strickler, who wrote that this muscle (which he called the *m. omocervicalis*) is absent in the genera *Rhinolophus* and *Lasiurus*. According to Macalister (1872), it is also absent in *Plecotus*, but Norberg (1970) described it in this genus as a muscle connecting the atlas and acromion. Among microbats that retain this muscle, it usually arises from the atlas or from the third cervical vertebra (but Macalister (1872) reported its origin from the same cervical vertebrae 4–5 as in fruit bats). Strange enough, there are no data on the origin from the axis. The muscle inserts on either the acromial process of the scapula or the distal part of the clavicle. When the origin is on the atlas and insertion is on the acromial process (according to Vaughan 1959), as is observed in the genera *Eumops* and *Myotis* (according to Vaughan 1959) and also in *Pizonyx* and *Molossus* (according to Strickler 1978), the muscle represents the typical *m. levator scapulae ventralis*, which is frequently named the *m. atlantoacromialis*.

Depending on the type of insertion, the muscle pulls the scapula or clavicle craniomedially.

Musculus serratus ventralis in chiropterans displays an unusual topography.

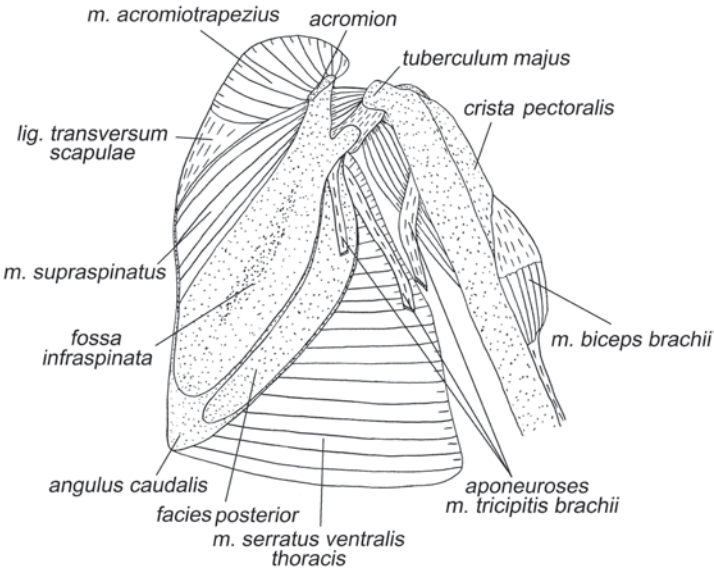


Fig. 3.36 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer VII.

The *m. serratus ventralis cervicis* is divided into two. The anterior portion has been properly ascribed to *m. serratus ventralis cervicis* by Hermanson and Altenbach (1985) but, more frequently, was taken for the *m. levator scapulae* (Humphry 1869; Macalister 1872; Vaughan 1959; Norberg 1972; Kovtun 1978; Strickler 1978; etc.), although it originates from more posterior vertebrae rather than the atlas, where the *m. levator scapulae dorsalis* should arise, together with the *m. levator scapulae ventralis*. The shift of the latter muscle in many bats onto the more posterior cervical vertebrae (see earlier in the text) may support the idea of Humphry and others that the muscular portion under consideration is indeed the *m. levator scapulae dorsalis*. However, its innervation by the *nervus dorsalis scapulae* (rami C4 or C4 + C5) (Vaughan 1959), but not by the C3 nerve, which typically supplies the *mm. levatores scapulae* (Le Gros Clark 1926), proves its homology with the *m. serratus ventralis cervicis*. That is why we conclude that chiropterans entirely lack the *m. levator scapulae dorsalis*, as also do most of the other mammals.

The posterior portion of the *m. serratus ventralis cervicis* originates from the first thoracal rib instead of the cervical vertebrae and, in the anatomy of chiropterans, is referred to as the *m. serratus anterior*. It was ascribed to the *m. serratus ventralis thoracis* by Hermanson and Altenbach (1985). However, its innervation by the *nervus dorsalis scapulae* (Vaughan 1959; Kovtun 1978) proves that it, indeed, belongs to the *m. serratus ventralis cervicis*, not to the *m. serratus ventralis thoracis* being normally supplied by the *nervus thoracicus longus*.

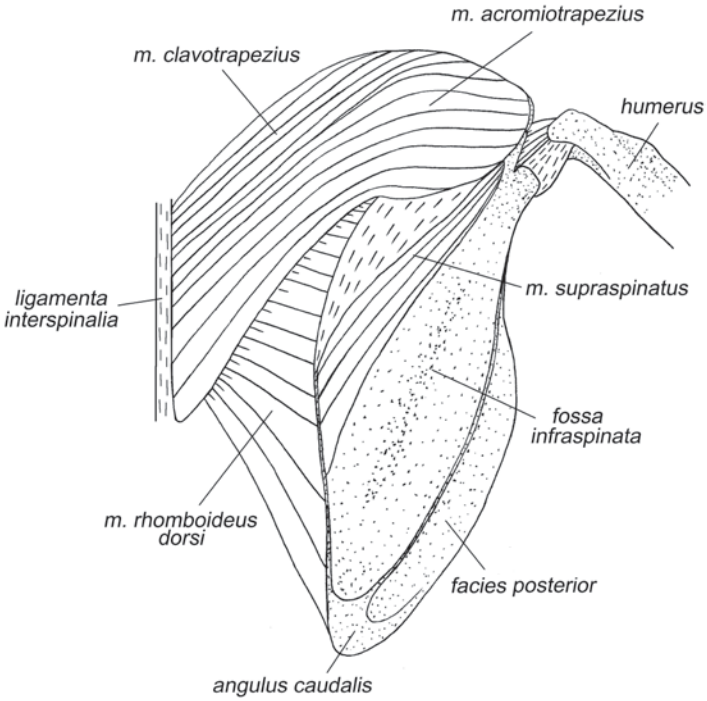


Fig. 3.37 Forelimb muscles of *R. ferrumequinum*, dorsal view, layer VIII.

The *m. serratus ventralis thoracis*, in contrast to the *m. serratus ventralis cervicis*, remains undivided, but is also greatly modified in chiropterans: it is much enlarged, and its insertion is displaced from the dorsocaudal angle of the scapula onto its caudal border. That is why, in the anatomy of chiropterans, it is referred to as the *m. serratus posterior*.

Thus, the designations proposed here based on homology correspond to the terms used in the preceding studies as follows: *m. serratus ventralis cervicis proprius = m. levator scapulae (dorsalis); m. serratus ventralis cervicis costalis = m. serratus anterior;* and *m. serratus ventralis thoracis = m. serratus posterior.*

Musculus serratus ventralis cervicis proprius (Figs. 3.24, 3.27, 3.30–3.33, 3.38, 3.40–3.44, 3.60, 3.61, 3.64) in **fruit bats** originates from the transverse (costal) processes of cervical vertebrae 4–6 (in *Rousettus aegyptiacus*, from vertebrae 3–7, according to Norberg 1972). It inserts on the cranial part of the dorsal border of the scapula, from its very dorsocranial angle and up to the spine.

In **microbats**, we found its origin on the transverse (costal) process of cervical vertebra 4. According to Macalister (1872), Altenbach (1979), and Strickler (1978), in different species, the origin ranges within cervical vertebrae 3–7. The muscle inserts on the cranial part of the dorsal border of the scapula, from its dorsocranial angle and up to the spine, sometimes extending more caudally.

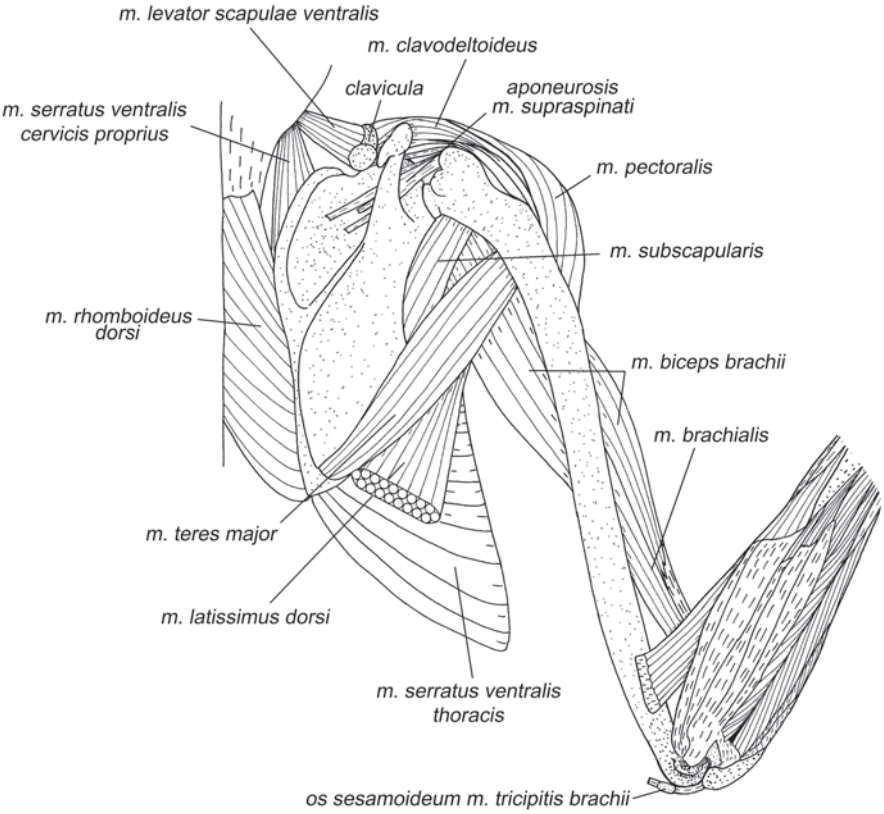


Fig. 3.38 Forelimb muscles of *C. sphinx*, dorsal view, layer VIII.

The muscle pulls the scapula craniomedially.

Musculus serratus ventralis cervicis costalis (Figs. 3.44–3.46, 3.53, 3.56, 3.59–3.65) in **fruit bats** originates mostly on the first rib, although some fibers arise from the second rib and fascias of intercostal muscles between the two. It inserts on the anterior one-third of the dorsal border of the scapula, wedging in between the *m. subscapularis* and *m. serratus ventralis cervicis proprius*.

In **microbats**, which we have studied, this short triangular in cross-section muscle originates by an aponeurosis from the external surface of the first rib under its *processus alaris* (in some other species, it originates from ribs 1–5: Macalister 1872; Vaughan 1959; Strickler 1978; etc.). It inserts by an aponeurosis on the anterior part of the dorsal border of the scapula, reaching in some species its dorsocranial angle.

The muscle pulls the dorsal border of the scapula ventrally.

Musculus serratus ventralis thoracis (Figs. 3.25, 3.26, 3.28–3.31, 3.33, 3.34, 3.36, 3.38–3.41, 3.48, 3.49, 3.52, 3.53, 3.56) in chiropterans shares the second place both in mass (Kovtun 1976; Strickler 1978; Foehring and Hermanson 1984;

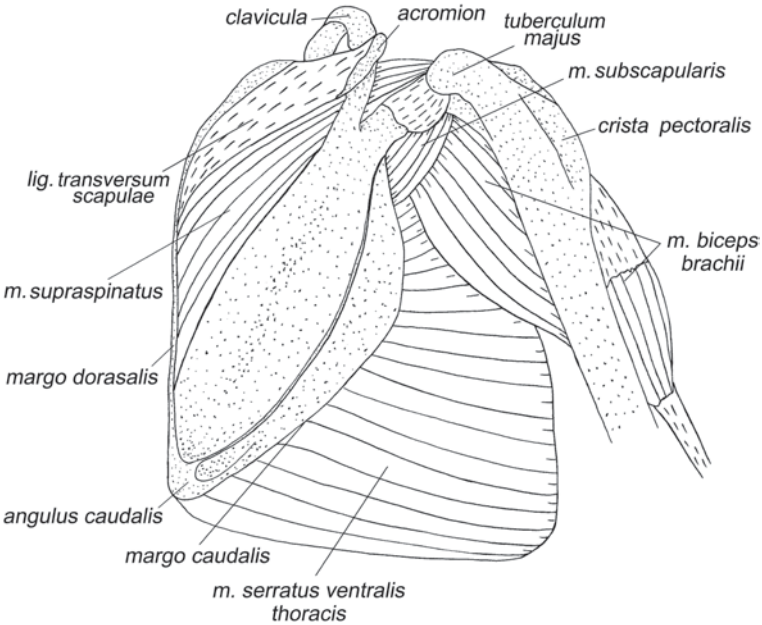
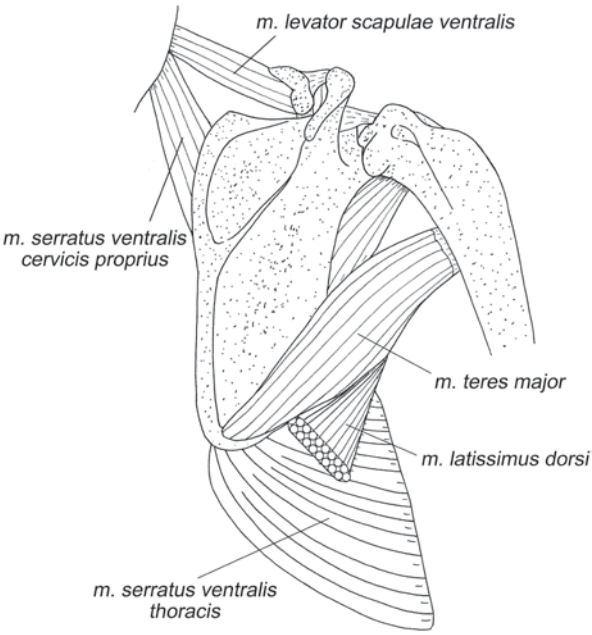


Fig. 3.39 Forelimb muscles of *R. ferrumequinum*, dorsolateral view, layer IX.

Fig. 3.40 Forelimb muscles of *C. sphinx*, dorsal view, layer IX.



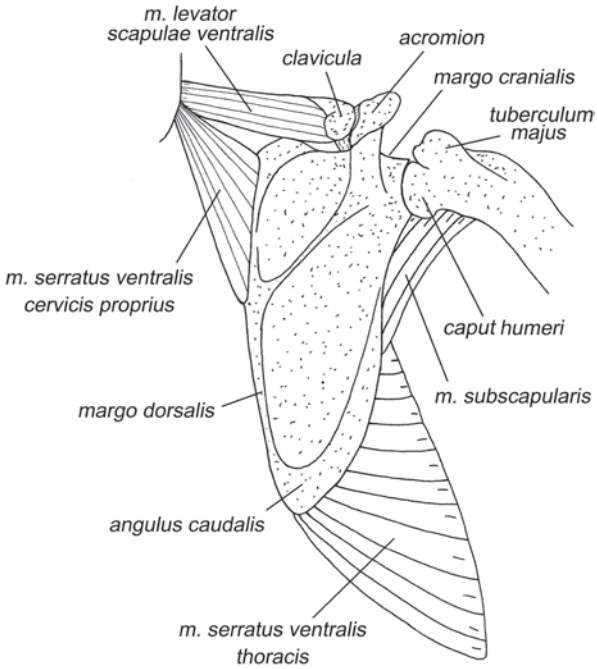


Fig. 3.41 Forelimb muscles of *C. sphinx*, dorsal view, layer X.

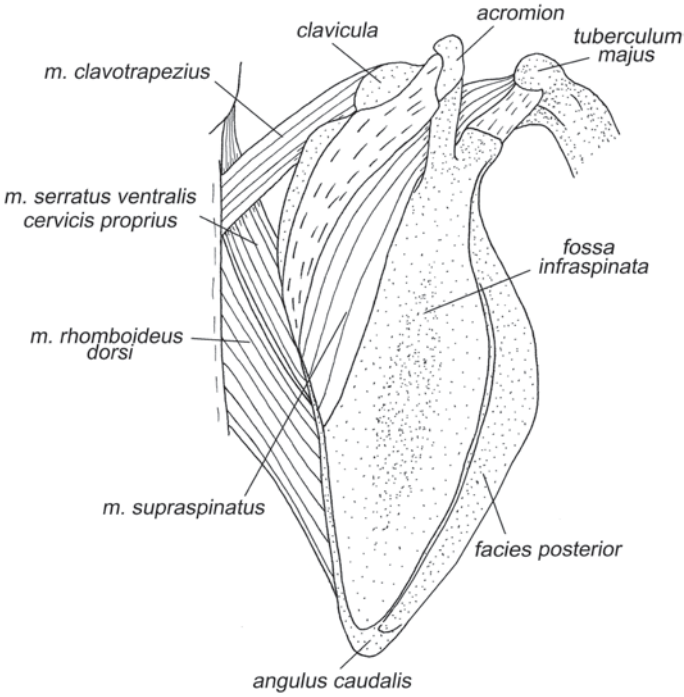


Fig. 3.42 Forelimb muscles of *R. ferrumequinum*, dorsal view, layer X.

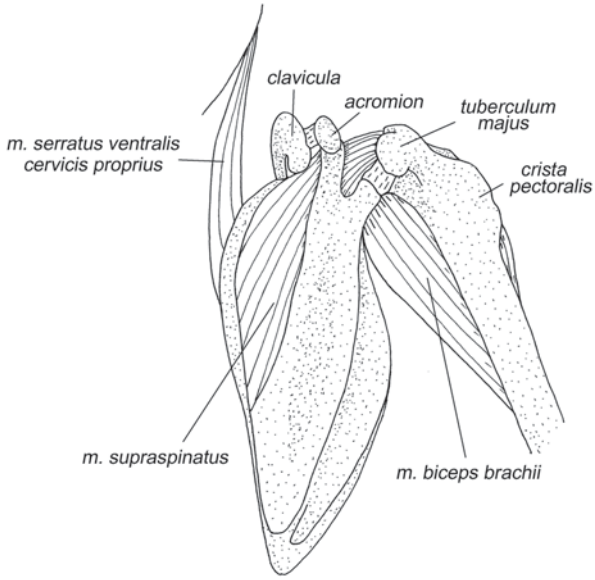


Fig. 3.43 Forelimb muscles of *R. ferrumequinum*, dorsal view, layer XI.

Maniakas and Youlatos 2012) and in physiological cross-sectional area (Maniakas and Youlatos 2012) with the *m. subscapularis*, being only inferior to the *m. pectoralis*.

In **fruit bats** (*Cynopterus*, original data), it forms wide slips originating from the external side of the distal part of the vertebral segments of ribs 2–8, near the articulations with the sternal segments. Sometimes, the origin expands from the first rib through ninth (*Rousettus*: data of Norberg 1972) and, in some species, up to the tenth (*Macroglossus*: data of Strickler 1978). The muscle inserts along the caudal border of the scapula, except for its one-third, nearest to the shoulder joint.

In **microbats**, this muscle is a wide thick belt embracing the entire thorax. It originates from ribs 1–13 and the lateral border of the *manubrium sterni* and inserts along the entire caudal border of the scapula, sometimes except for its one-fourth or, rarely, one-third (as in fruit bats), nearest to the glenoid.

The muscle pulls the caudal border of the scapula ventrally. The main role of this muscle is to suspend, together with the m. pectoralis, the body to the forelimbs in flight.

Musculus omohyoideus (Fig. 3.44) is only represented by a rudiment, which we have recorded as a very thin band only on one (right) body side of *Cynopterus*. It arose somewhere within the mass of connective tissue filling the spaces between the neck muscles and inserted on the cranial border of the scapula near the glenoid. According to published data (e.g., Strickler 1978), this muscle occurs in some fruit bats as well as some microbats, for example, members of the superfamilies Phyllostomoidea, Emballonuroidea, and Rhinolophoidae (except for *Rhinolophus* and *Hipposideros*).

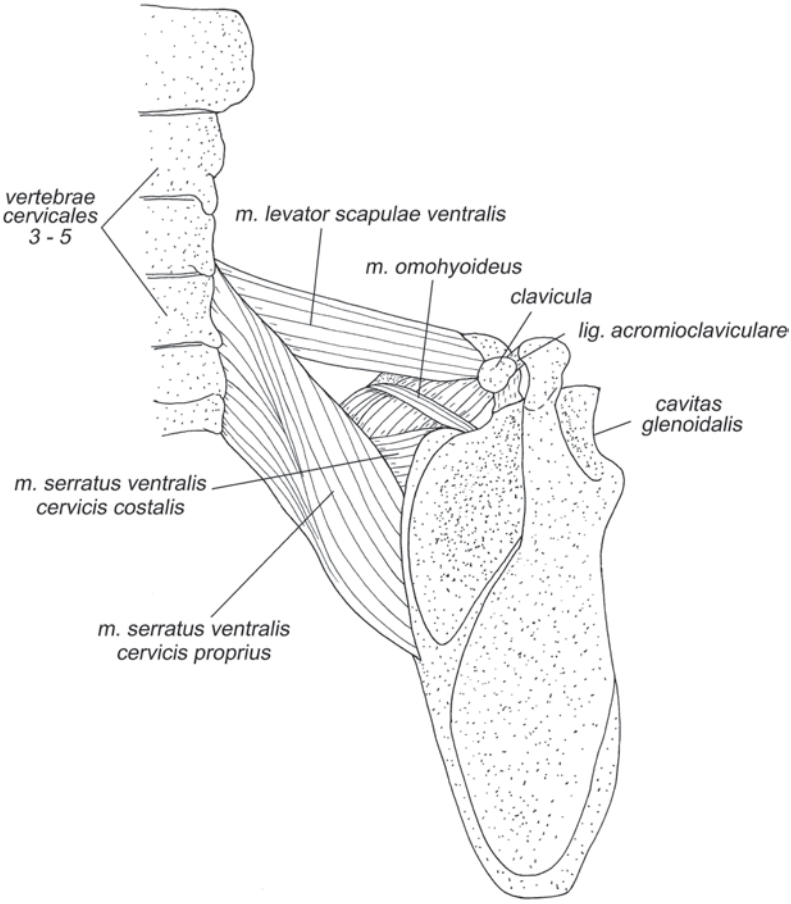


Fig. 3.44 Forelimb muscles of *C. sphinx*, dorsal view, layer XI.

If present in **fruit bats**, it originates from the area of the thyroid cartilage and inserts on the cranial border of the scapula (Strickler 1978).

If present in **microbats**, it originates from the hypoglossal skeleton and inserts on either the cranial border of the scapula (like in fruit bats) or, more often, the dorsal surface of the clavicle. In the latter case, it is probably the *m. sternohyoideus* rather than *m. omohyoideus*.

Even if present, this muscle hardly has any function in bats.

Musculus subclavius (Figs. 3.46, 3.47, 3.50, 3.51, 3.53–3.60, 3.62, 3.63, 3.65) originates from the entire external surface of the first rib (for example, in **fruit bats**), the anterior border of the sternal segment of this rib (for example, in some vespertilionids), or from the anterior border of the *processus alaris costae sternalis 1* (for example, in horseshoe and leaf-nosed bats of the Old World). It inserts on the

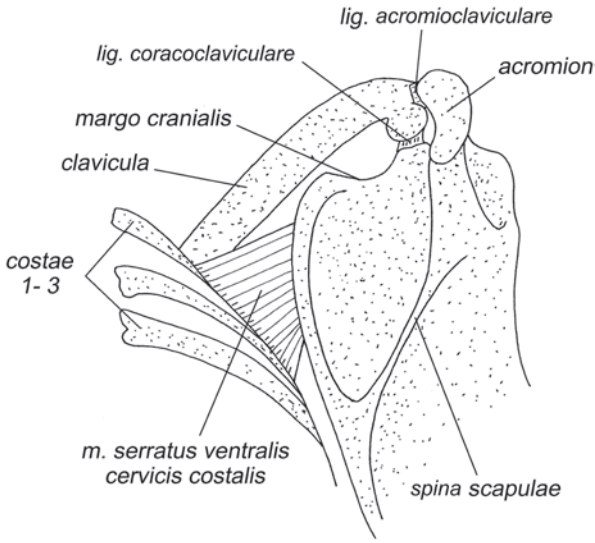


Fig. 3.45 The *m. serratus ventralis cervicis costalis* of *C. sphinx*, dorsal view.

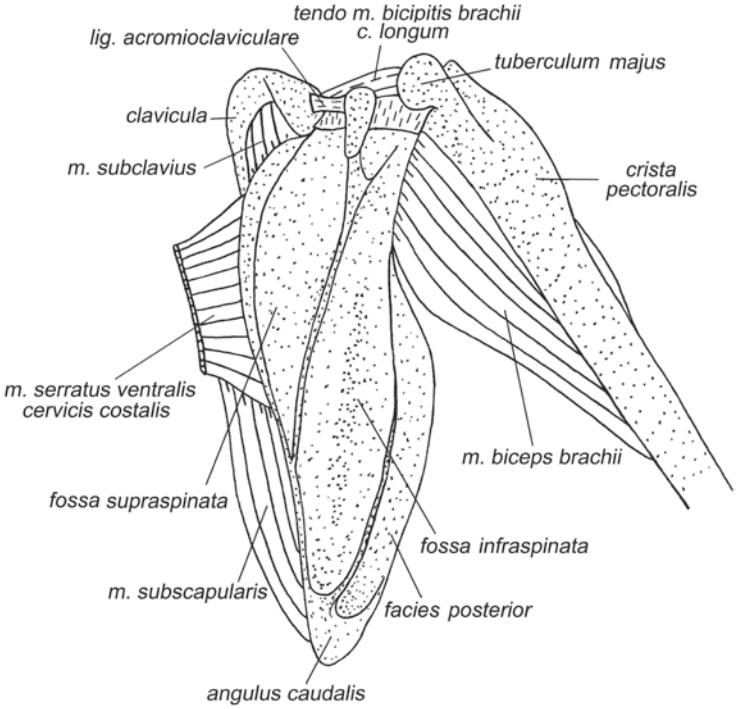


Fig. 3.46 Forelimb muscles of *R. ferrumequinum*, dorsal view, layer XII.

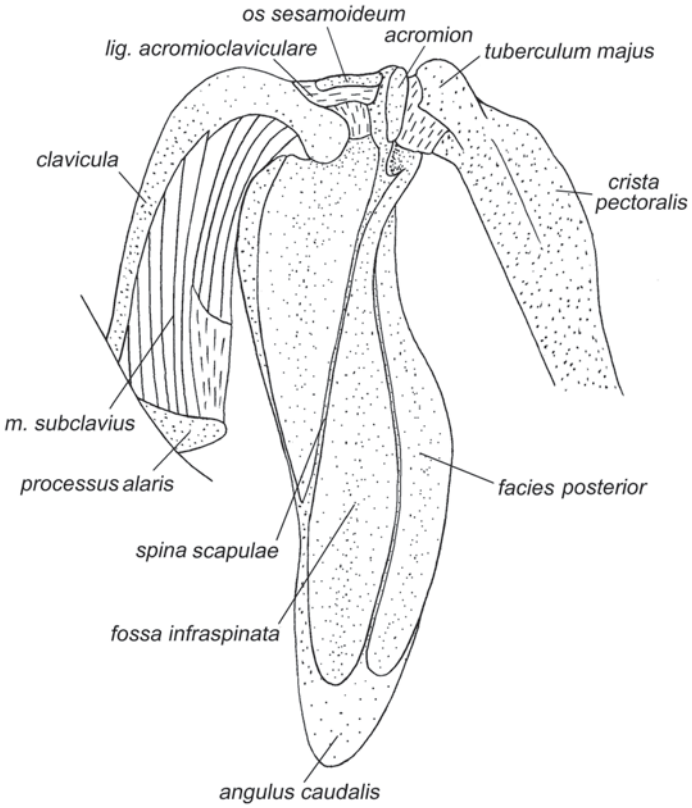


Fig. 3.47 The *m. subclavius* of *R. ferrumequinum*, dorsal view.

dorsal side of the distal part of the clavicle, occupying from one-third to two-thirds of its length.

The muscle pulls the clavicle caudally. In horseshoe bats, due to the wide processus alaris costae sternalis 1, the origin of the muscle is displaced laterally and, hence, it additionally pulls the clavicle laterally. Along with the m. clavotrapezius and m. levator scapulae ventralis, the muscle controls the sternoclavicular articulation.

Musculature of Shoulder Joint

Musculature Originating from Trunk

Musculus latissimus dorsi (Figs. 3.22–3.24, 3.26, 3.33, 3.35, 3.38, 3.40, 3.54–3.57) is flat, triangular, and very wide at its origin.

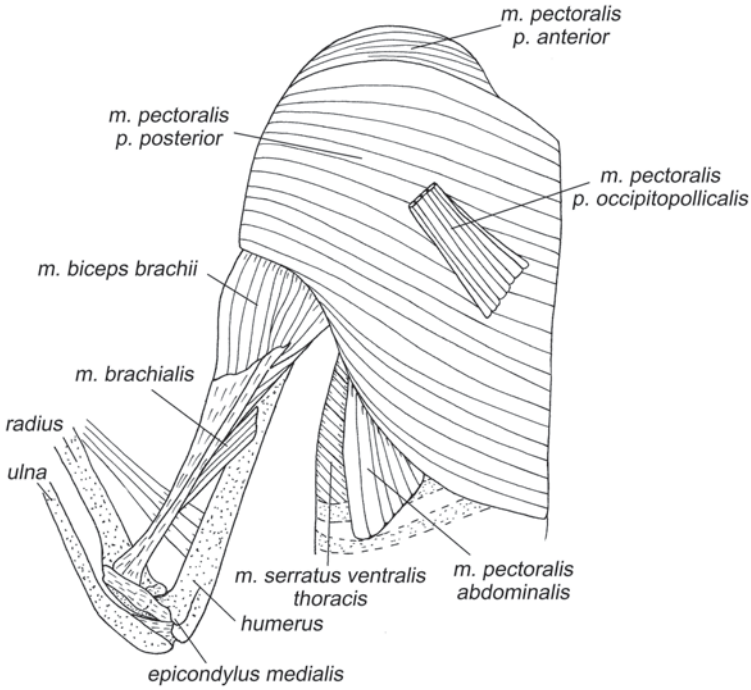
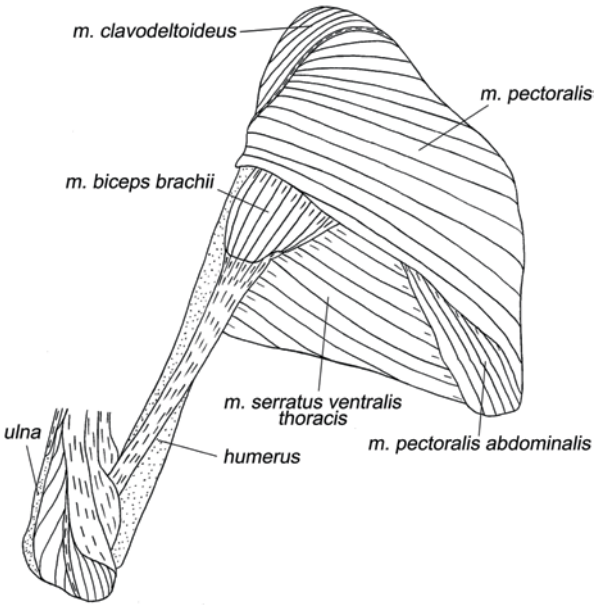


Fig. 3.48 Forelimb muscles of *C. sphinx*, ventral view, layer I.

Fig. 3.49 Forelimb muscles of *R. ferrumequinum*, ventrolateral view, layer I.



In **fruit bats**, it originates from the vertebral column and superficial fascia of the epaxial muscles from thoracic 10–11 to lumbar 3–4 vertebrae, passes under the belly of the *m. teres major*, and inserts by a tendon on the neck of the proximal head of the humerus. Macalister (1872) has found in *Pteropus* an additional superficial portion similar to the *m. latissimus dorsi superficialis* of colugos.

In **microbats**, the origin of this muscle considerably varies in extent. It originates from apices of the neural spines and interspinous ligaments between thoracic 9 and lumbar 5 vertebra; the number of vertebrae giving rise to this muscle varies from two to eight. It inserts by a flat tendon on the crest of the lesser tubercle of the humerus distal to the *m. teres major*. In horseshoe bats (Rhinolophoidea), it often has two well-pronounced portions and, according to Macalister (1872) and Strickler (1978), in Megadermatidae, Nycteridae, and some Phyllostomidae, these portions are divided not only at the origin, but also at the insertion. They insert by separate tendons at different sides of the *m. teres major* insertion (proximal and distal to it). In *Rhinolophus ferrumequinum,* Strickler has also recognized two portions, which, however, insert on the humerus together. Contrary to that, according to our data, the *m. latissimus dorsi* in this species is represented by only one portion (Fig. 3.23). We recognized two slightly split portions only in the leaf-nosed bat *Hipposideros larvatus* (Fig. 3.26). Apparently, the division into portion shows not only interspecific but also intraspecific variation.

The muscle pronates and retracts the humerus. Inmicrobats, a high crest of the lesser tubercle displaces the end of the muscle medially, away from the center of the shoulder joint, thus, increasing the lever for pronation. However, in fruit bats, the muscle inserts on the neck of the articular head and its pronation lever is relatively small.

Musculus pectoralis (Figs. 3.22–3.25, 3.27–3.33, 3.38, 3.48–3.52, 3.54) is the largest muscle of bats. It is divided into the *pars anterior* and *pars posterior*, the latter being much larger. Based on the fact that, at their insertion on the pectoral crest, the *pars anterior* overlaps *pars posterior*, they are apparently homologous to the *m. pectoralis superficialis* and *m. pectoralis profundus* of other mammals, respectively. Indeed, it is typical to mammals that the *m. pectoralis profundus* extends over the sternum more posteriorly than the *m. pectoralis superficialis*. Partial or full displacement of the origin of the latter muscle from the sternum forward onto the clavicle was enough to produce the chiropteran *m. pectoralis pars anterior*.

Musculus pectoralis pars anterior in **fruit bats** originates from the external side of the anterior surface of the proximal half of the clavicle. It inserts along the entire external border of the pectoral crest, covering the insertion of the *m. pectoralis pars posterior*.

In **microbats**, this muscle originates not only from the external side of the anterior surface of the proximal part of the clavicle, but also from the cranial border of the *manubrium sterni* and ventral surface of the *processus alaris costae sternalis 1*. It inserts on the external border of the pectoral crest (in many species, by an aponeurosis). Sometimes, the cranial border of this muscle is fused with the caudal border of the *m. clavotrapezius*.

Musculus pectoralis pars posterior in **fruit bats** originates from the *manubrium sterni* and *corpus sterni*, including the *carina sterni* and its connective-tissue extension (here the muscle closely adjoins the contralateral one), and from the external surface of sternal segments of all true ribs. It inserts along the entire pectoral crest, mostly by a wide flat aponeurosis. A small fascicle of fibers (*m. pectoralis pars occipitopollicalis*) usually runs into the skin to fuse into the *m. occipitopollicalis*.

In **microbats**, this muscle originates from the *manubrium sterni* and *corpus sterni*, from the connective-tissue surrogate of *carina sterni*, from the sternal segments of ribs 2–6, and upon the abdominal fascia along the caudal border of the thorax. It inserts on the medial surface of the pectoral crest with the help of a wide aponeurosis.

The m. pectoralis is the main depressor of the wing. Simultaneously, it pronates the humerus. The pars posterior, in addition, via humerus and scapula, pulls ventrolaterally the clavicle, while thedisplacement of the pars anterior onto the clavicle allowed it to depress and pronate the humerus, without influencing the sternoclavicular articulation (see Chap. 5).

Musculus pectoralis abdominalis (Figs. 3.48–3.50, 3.52) is, as usually, a thin band.

In **fruit bats**, it originates onto the abdominal fascia at the level of ribs 7–10. The origin of this muscle slightly varies among species but is always apart from the midline. It inserts by an aponeurosis on the proximal part of the pectoral crest of the humerus; the extent and exact point of insertion of the aponeurosis slightly vary in different species.

In **microbats**, this muscle originates from the abdominal fascia approximately at the level of the *processus xiphoideus* of the sternum or somewhat more cranially. The origin is either at the midline of the abdomen (according to Strickler (1978), such origin is characteristic of emballonurids and some American leaf-nosed bats) or much more laterally (in the majority of species). It inserts by a long flat aponeurosis on the proximal part of the base of the pectoral crest.

The muscle apparently contributes to pronation and retraction of the humerus.

Musculus cutaneus trunci was described by Norberg (1972) in the Egyptian fruit bat as the *m. bicipito-plagiopatagialis* and by Strickler (1978) in some horseshoe bats, emballonurids, and American leaf-nosed bats as the *m. dorsi patagialis*. In giving this name, Strickler followed Macalister (1872), who had properly defined its homology but described it untenably (in *Megaderma*, both Macalister and Strickler gave the same name to a slip of the *m. latissimus dorsi* in spite of its dorsal course relative to the brachial plexus). This muscle is also mentioned as the *m. cutaneus maximus* in the embryological research of *Carollia* (Tokita et al. 2012). We did not find it in the fruit bats or in horseshoe bats; probably we lost this extremely thin fascicle removing the skin. According to Norberg and Strickler, it originates from the tip of the coracoid process, sometimes by the tendon shared with the *m. coracocutaneus*, or from the surface of the *m. coracobrachialis longus*. According to Strickler, it inserts in the skin above the *m. latissimus dorsi*; according to Norberg, its fibers extend much more caudal and insert in the skin on the dorsal

side of the crus. Both insertions support its homology with the *m. cutaneus trunci* of typical mammals.

This rudimentary muscle may still control the skin of the body as in typical mammals.

The *m. coracocutaneus* and *m. humeropatagialis* of the membrane (see later in the text) may be also derivatives of the *m. cutaneus trunci*, like the *m. coracocutaneus* and *m. humerocutaneus* of colugos.

Intrinsic Musculature of Shoulder Joint

Musculus clavodeltoideus (Figs. 3.22–3.35, 3.38, 3.48–3.50, 3.52) in chiropterans is tightly connected with the *m. pectoralis pars anterior*. As a result, the boundary between them is sometimes determined incorrectly. In particular, Norberg (1972) included, in fruit bats, into the clavicular deltoid muscle not only the true *m. clavodeltoideus*, but also the clavicular part of the strongly enlarged *m. pectoralis pars anterior*. However, Vaughan (1959), examining not only topography but also innervation of these muscles, has distinguished them with certainty.

In **fruit bats**, fibers of this relatively small muscle originate from the anteroventral surface of the distal half of the clavicle and insert on the lateral side of the proximal part of the pectoral crest of the humerus. Externally, this muscle is almost

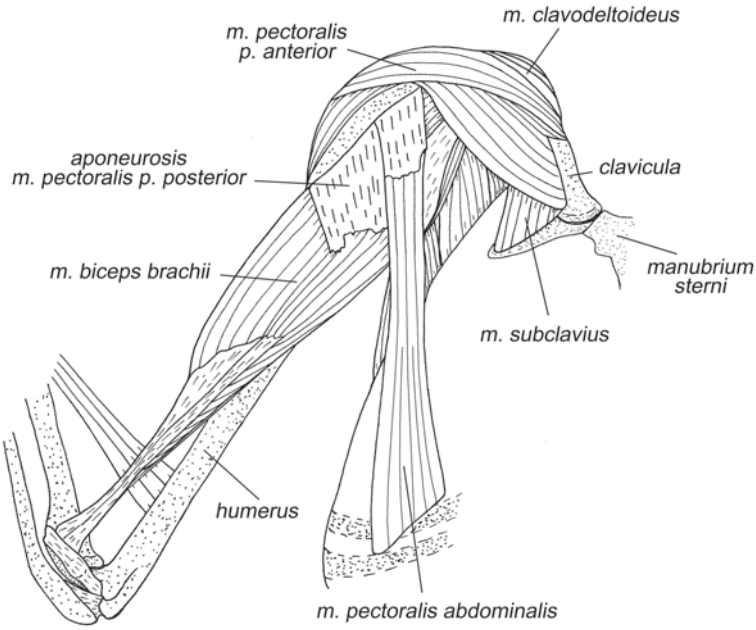


Fig. 3.50 Forelimb muscles of *C. sphinx*, ventral view, layer II.

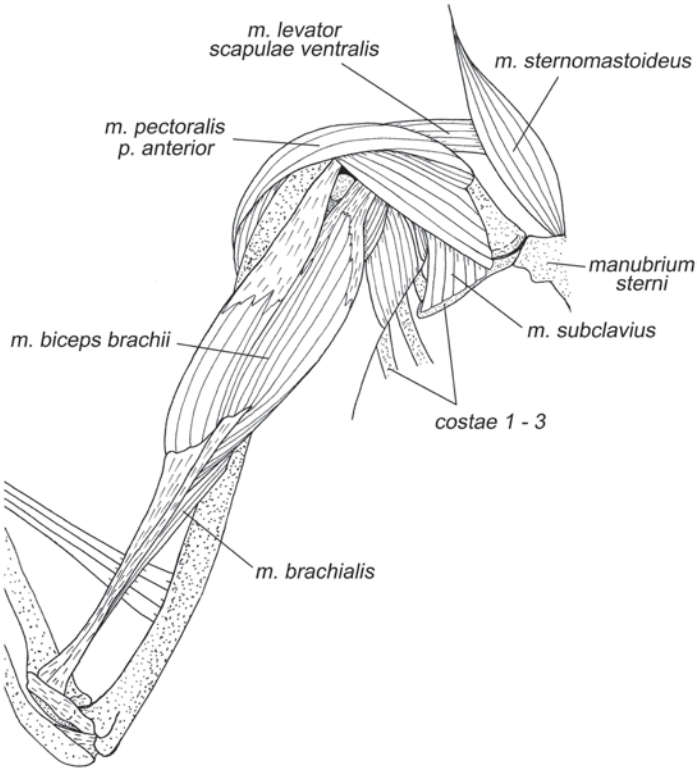


Fig. 3.51 Forelimb muscles of *C. sphinx*, ventral view, layer III.

completely overlapped by the *m. pectoralis pars anterior*. A distinct boundary between these muscles can be only found near their insertion on the humerus.

In **microbats**, this muscle is better developed than in fruit bats. It originates from the ventral surface of the distal part of the clavicle, occupying in different species from one-fourth to half of its length. The muscle inserts on the pectoral crest of the humerus proximal to the *m. pectoralis pars anterior*, with which its caudal border is usually fused.

The muscle protracts and pronates the humerus.

Musculus acromiodeltoideus (Figs. 3.22, 3.23) is a large muscle in all chiropterans. It originates from the acromial process and posterior edge of the *ligamentum transversum scapulae*. The extent of its origin on this ligament varies among species. For example, in **fruit bats**, it is almost completely confined to the acromial process, and, in horseshoe bats, it extends throughout the spinous ligament. The muscle inserts on the lateral side of the pectoral crest and a significant area of the anterolateral side of the humerus.

The muscle retracts, supinates, and raises (abducts) the humerus. Note that its lever arm for retraction increases with the extension of its origin along the

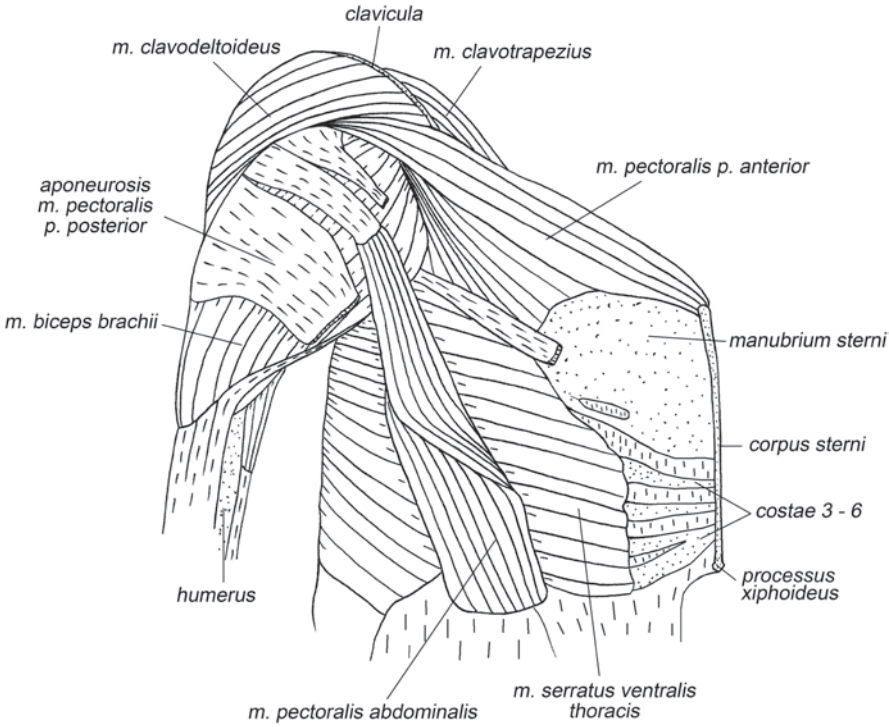


Fig. 3.52 Forelimb muscles of *R. ferrumequinum*, ventrolateral view, layer II.

ligamentum transversum scapulae toward the dorsal border of the scapula. In fruit bats, as the shoulder joint is completely straightened (the humerus being extremely protracted), the retractor effect almost disappears, and the muscle can only raise and supinate the humerus. In horseshoe bats, the topography of this muscle makes it an effective retractor of the humerus even in the extremely protracted position.

Musculus spinodeltoideus (Figs. 3.22–3.25) in all chiropterans is wide and flat, originating from the dorsal border of the scapula caudal to the spine and, sometimes, from the *ligamentum transversum scapulae*. It inserts on the distal part of the crest of the greater tubercle of the humerus, frequently by a short aponeurosis.

The muscle retracts and supinates the humerus and contributes to raising it from the lowered position and to lowering from a raised position.

Musculus teres minor (Figs. 3.27, 3.30) in chiropterans is very small, as in tree shrews, and contrary to that of colugos.

In **fruit bats**, it is better developed than in microbats and originates by an aponeurosis from the caudal border of the scapula, just at the glenoid, occupying from one-fourth to half length of this border. It inserts on the lateral surface of the base of the greater tubercle of the humerus distal to the *m. infraspinatus*.

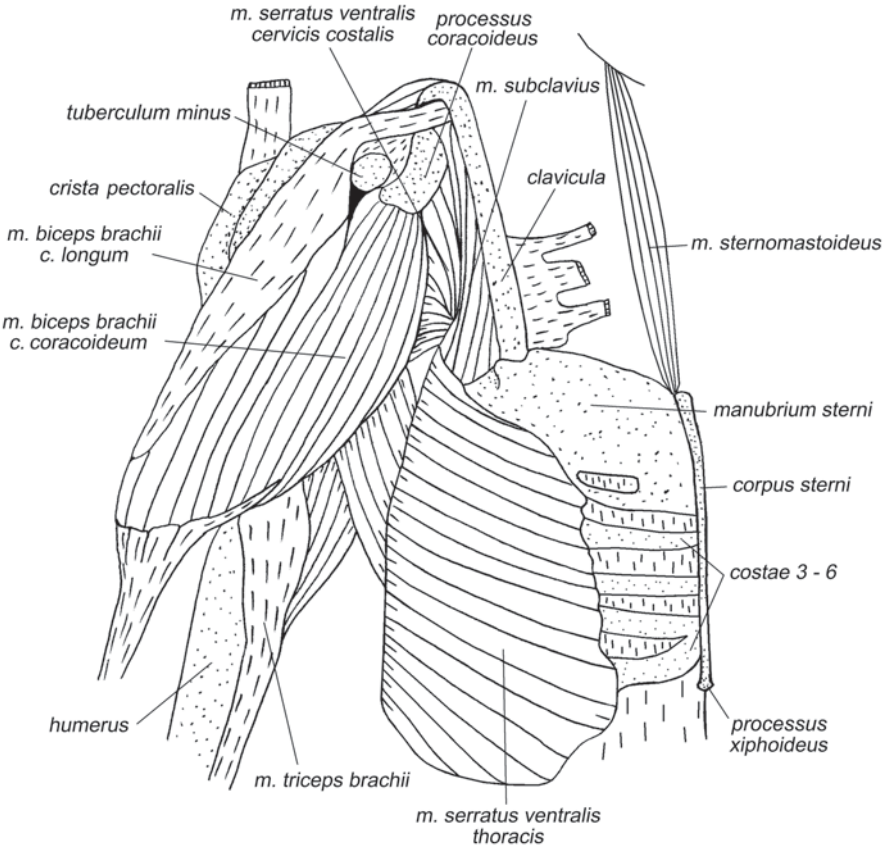


Fig. 3.53 Forelimb muscles of *R. ferrumequinum*, ventral view, layer III.

Among **microbats,** this muscle is best developed in Desmodontinae and weaker in horseshoe bats (Rhinolophoidea) (e.g., Vaughan 1959; Norberg 1970; Strickler 1978; our data). It originates along the caudal border of the scapula, occupying at most one-fourth of its length near the glenoid. It inserts on the lateral surface of the greater tubercle distal to the *m. infraspinatus*.

The muscle is a very weak retractor of the humerus and probablyserves as a sensor of the degree of retraction in the shoulder joint.

Musculus teres major (Figs. 3.22–3.28, 3.30–3.33, 3.35, 3.38, 3.40, 3.55, 3.57) in **fruit bats** originates from the external surface of the widened caudal border of the scapula. It inserts by a wide tendon along the crest of the lesser tubercle of the humerus dorsal and, usually, slightly distal to the *m. latissimus dorsi*.

In **microbats**, the muscle originates from the caudal border of the scapula and its *facies posterior*, if it is developed, and, frequently, from the aponeurosis of origin of the *m. infraspinatus*. It inserts on the crest of the lesser tubercle of the humerus dorsal to the *m. latissimus dorsi*.

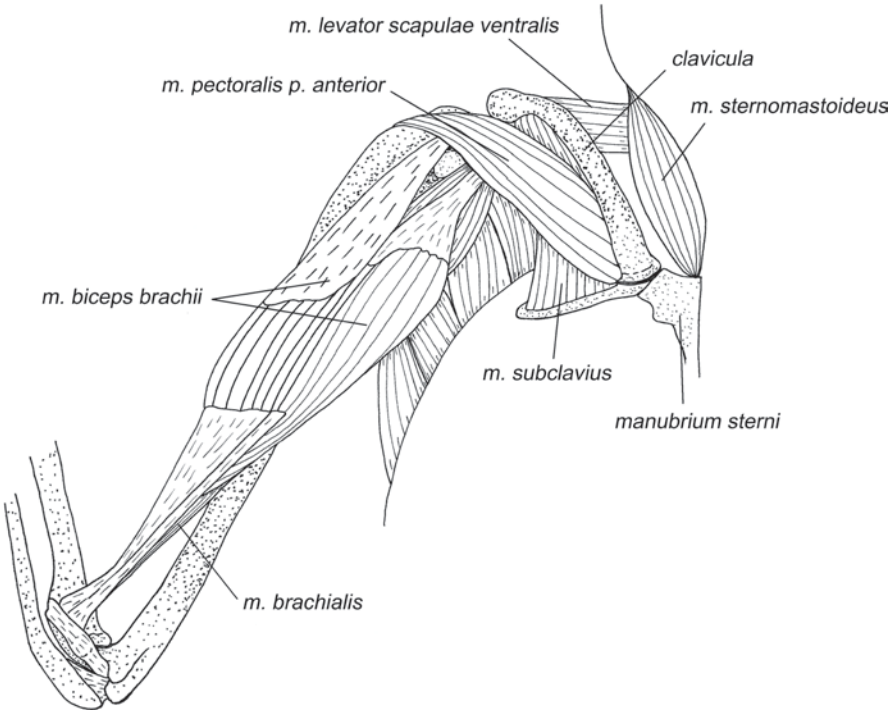


Fig. 3.54 Forelimb muscles of *C. sphinx*, ventral view, layer IV.

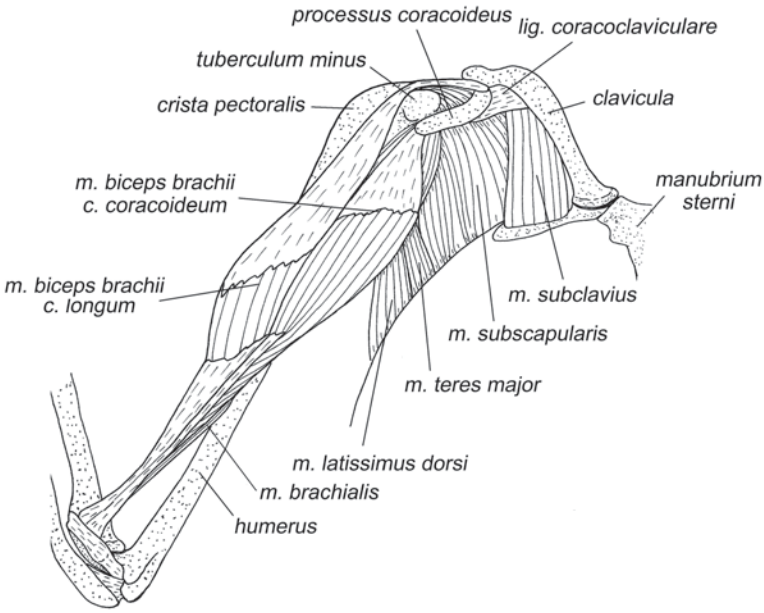


Fig. 3.55 Forelimb muscles of *C. sphinx*, ventral view, layer V.

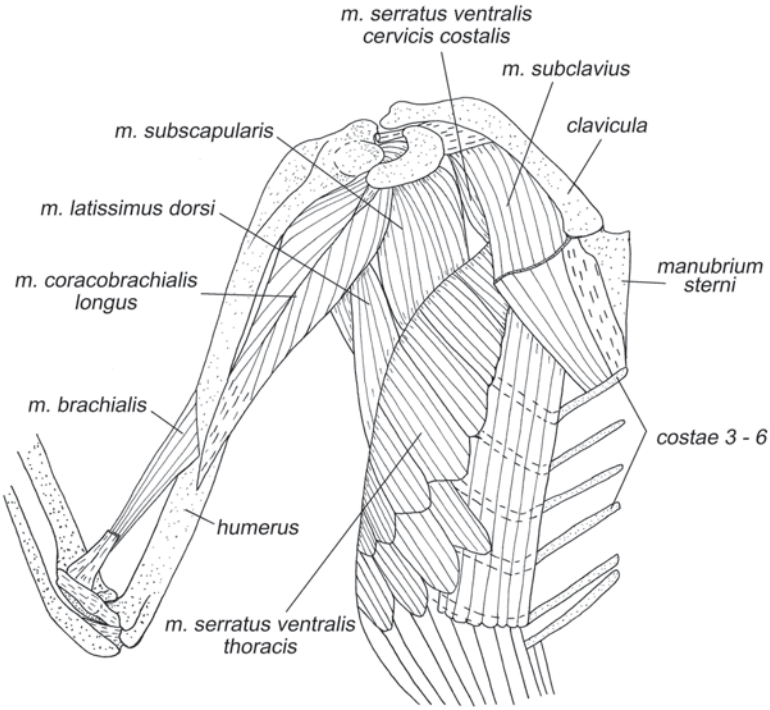


Fig. 3.56 Forelimb muscles of *C. sphinx*, ventral view, layer VI.

In chiropterans, this muscle mainly retracts the humerus. Its input in pronation is probably less pronounced than in tree shrews and colugos.

Musculus subscapularis (Figs. 3.46, 3.54–3.64) in chiropterans shares the second place both in mass (Kovtun 1976; Strickler 1978; Foehring and Hermanson 1984; Maniakas and Youlatos 2012) and in physiological cross-sectional area (Maniakas and Youlatos 2012) with the *m. serratus ventralis thoracis*, being only inferior to the *m. pectoralis*. The relative weight of this muscle in fruit bats is smaller

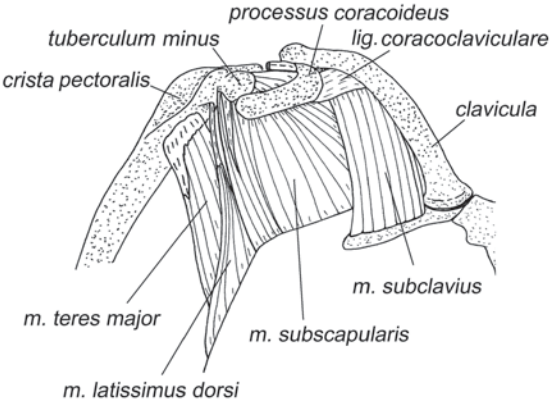


Fig. 3.57 Forelimb muscles of *C. sphinx*, ventral view, layer VII.

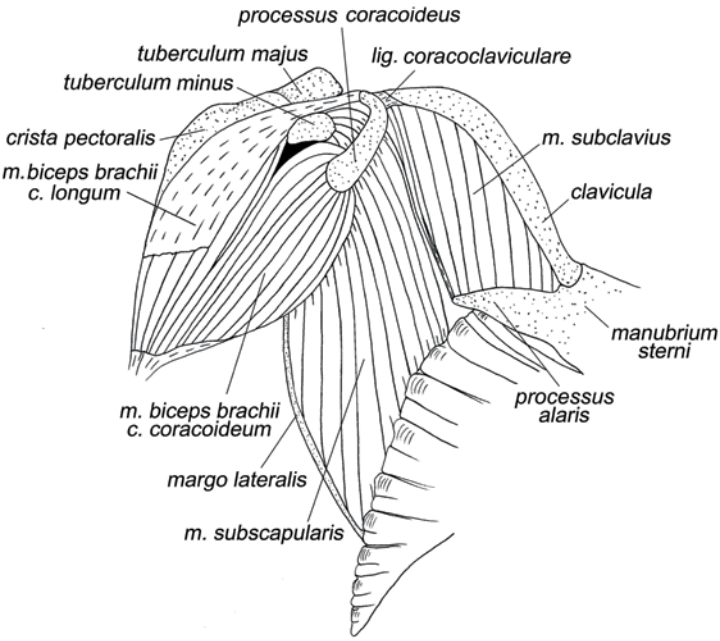


Fig. 3.58 Forelimb muscles of *R. ferrumequinum*, ventral view, layer IV.

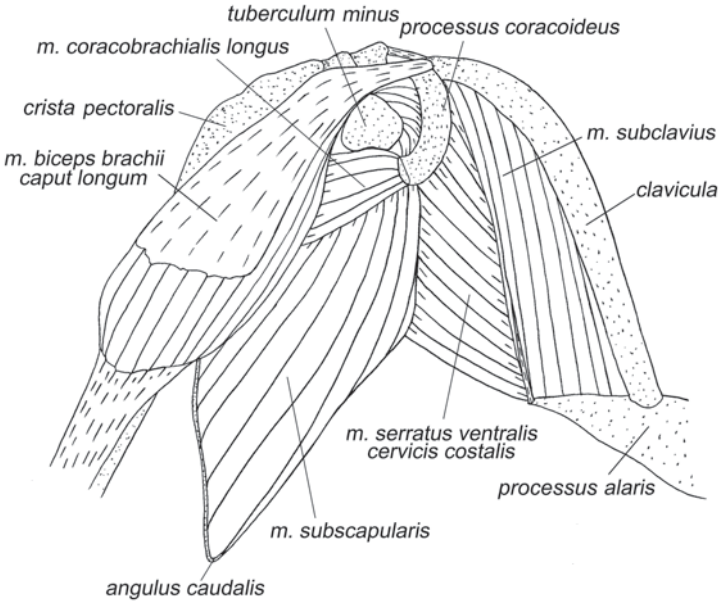


Fig. 3.59 Forelimb muscles of *R. ferrumequinum*, ventral view, layer V.

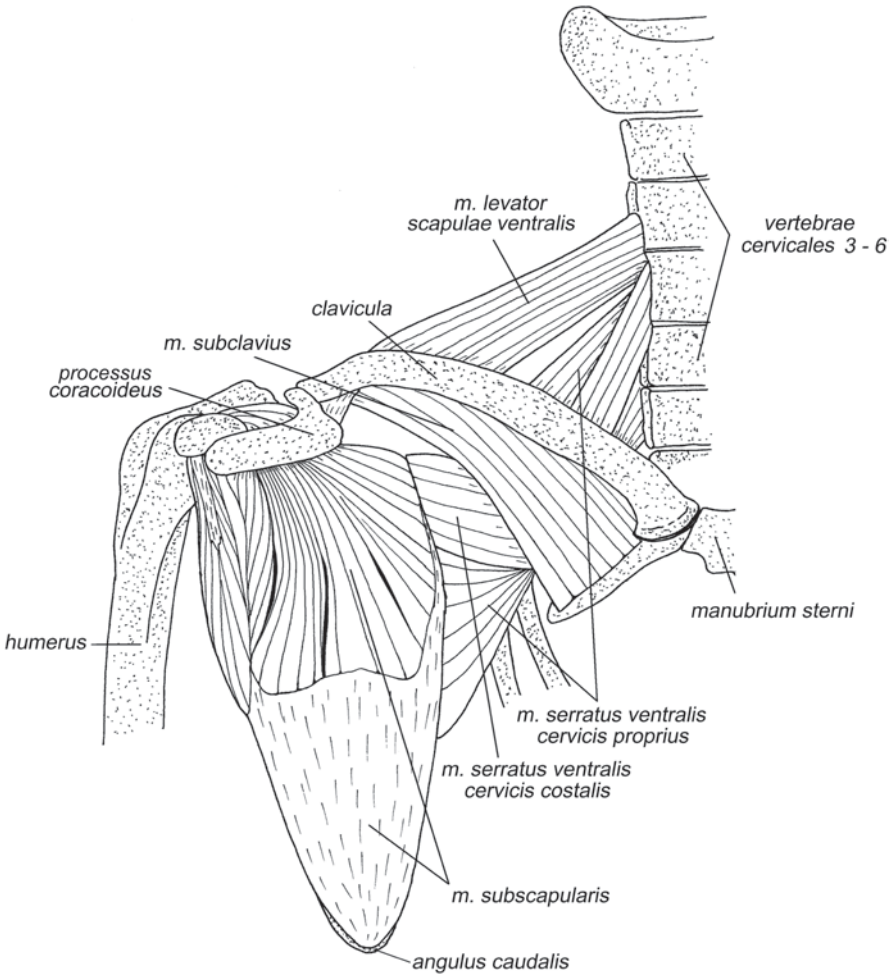


Fig. 3.60 Forelimb muscles of *C. sphinx*, ventral view, layer VIII.

than in microbats (Strickler 1978). As usual, it occupies the entire medial (internal) surface of the scapula and has a complex aponeurotic framework.

In **fruit bats**, its fibers originate from the surface of the subscapular fossa and, by means of aponeuroses, from its borders. It inserts on the lesser tubercle of the humerus by many converging aponeuroses. In *Cynopterus,* the small accessory lateral portion, which runs caudal to the scapula, is found. It originates from the caudal border of the scapula and inserts by a long separate tendon on the distal aspect of the lesser tubercle.

In **microbats**, this muscle is distinctly triangular in cross-section. It originates from the entire subscapular fossa, including its borders, fleshy and by means of aponeuroses. Its fibers converge onto long ribbon-like terminal aponeuroses, which, in

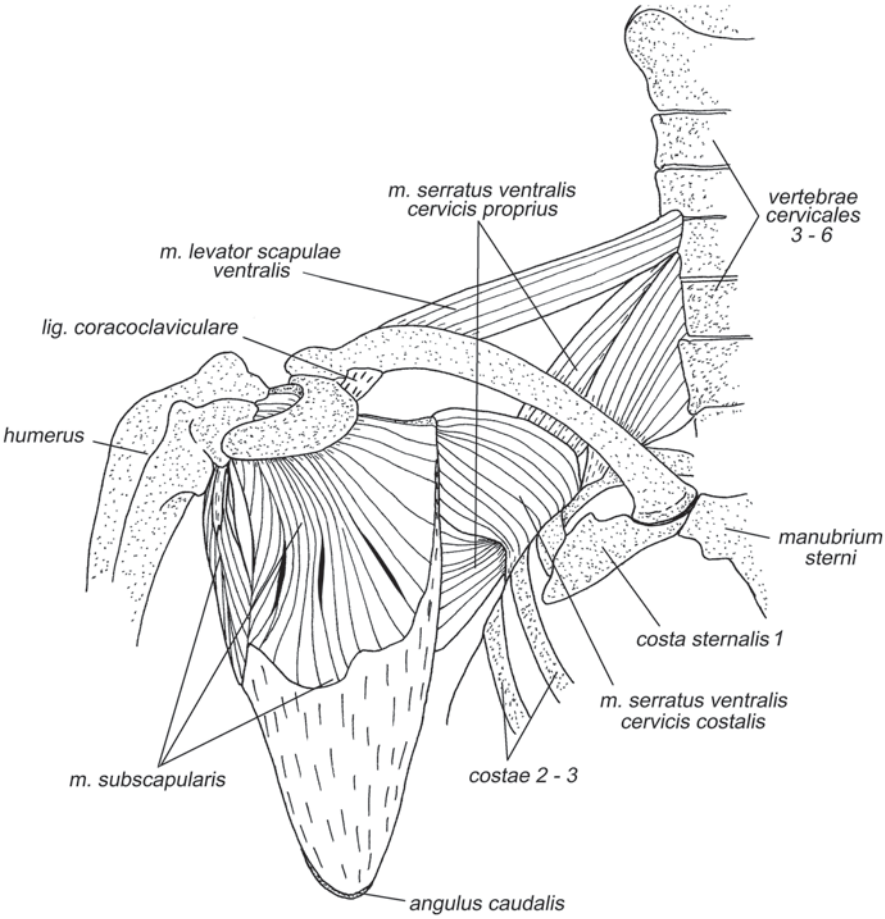


Fig. 3.61 Forelimb muscles of *C. sphinx*, ventral view, layer IX.

turn, converge to insert on the lesser tubercle of the humerus. Some muscular fibers directly, without the help of aponeuroses, insert on the distal and anterior aspects of the lesser tubercle of the humerus.

As usual, this muscle is the main pronator of the humerus, competing in this role with the m. pectoralis and m. latissimus dorsi. More unusual, as compared with quadrupedal mammals, is its function as the important one-joint depressor (adductor) of the humerus, when it becomes protracted in a spread wing.

Musculus supraspinatus (Figs. 3.24–3.39, 3.42, 3.43) in **fruit bats** originates from the entire surface of the supraspinous fossa and cranial side of the spine. It passes under the acromial process and inserts by a thick tendon on the anterolateral aspect of the greater tubercle.

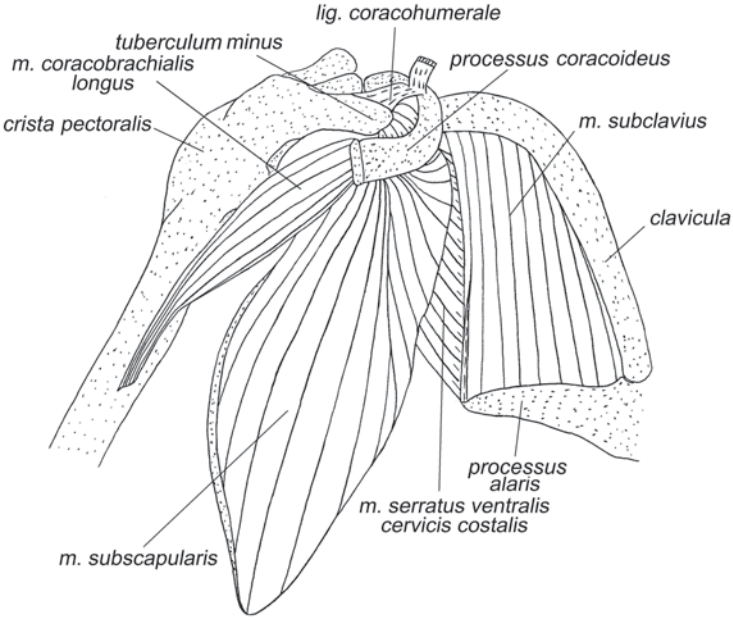
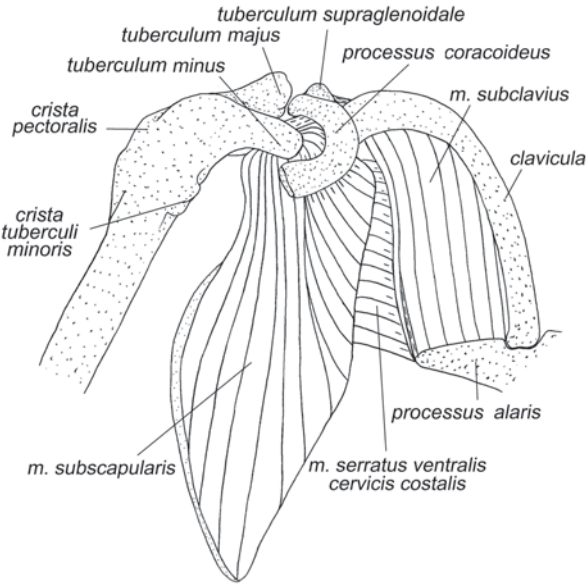


Fig. 3.62 Forelimb muscles of *R. ferrumequinum*, ventral view, layer VI.

Fig. 3.63 Forelimb muscles of *R. ferrumequinum*, ventral view, layer VII.



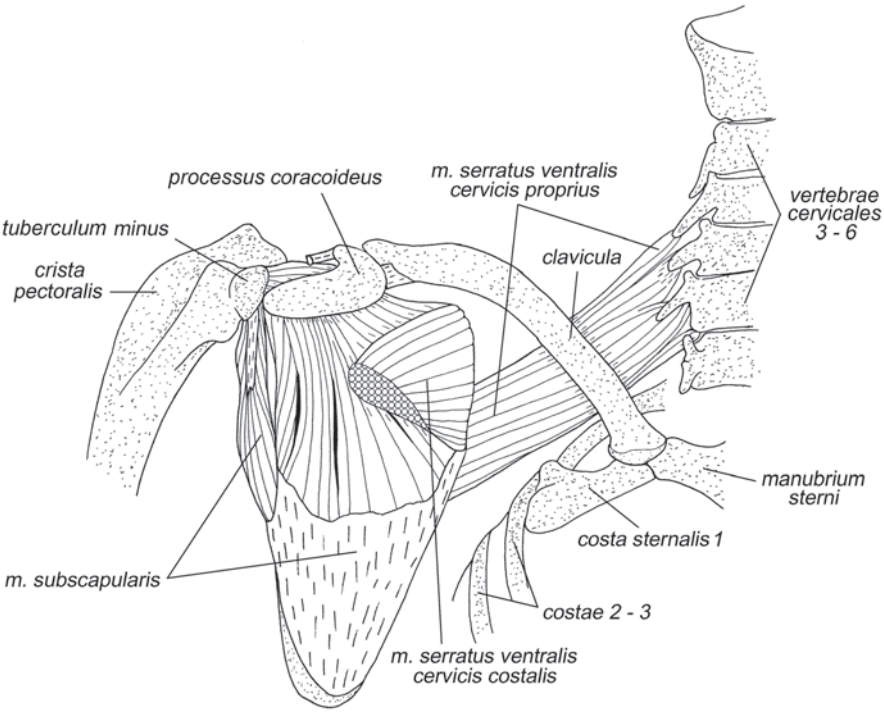


Fig. 3.64 Forelimb muscles of *C. sphinx*, ventral view, layer X.

In **microbats**, the origin of this muscle expands beyond the outline of the floor of the supraspinous fossa onto the dorsal border of the scapula and the *ligamentum transversum scapulae*, which covers a considerable area of this muscle. As in fruit bats, fibers insert by a thick tendon on the greater tubercle of the humerus proximal to the *m. infraspinatus*.

Strickler (1978) noted that the weakest *m. supraspinatus* is observed in fruit bats, while, in horseshoe bats, it is most strongly developed, in accordance with the relative size of the supraspinous fossa.

The muscle protracts the humerus.

Musculus infraspinatus (Figs. 3.24–3.30, 3.34) in bats is placed in the infraspinous fossa, as in other animals investigated. It has a well-pronounced pennate structure and triangular cross-section. The origin occupies the entire surface of the infraspinous fossa, including its dorsal border and caudal surface of the scapular spine, frequently spreading onto the acromion base. In some species possessing the *facies posterior*, the origin of this muscle expands onto it as well. Muscular fibers are short and converge onto numerous thick ribbon-like aponeuroses, which insert on the lateral aspect of the greater tubercle of the humerus.

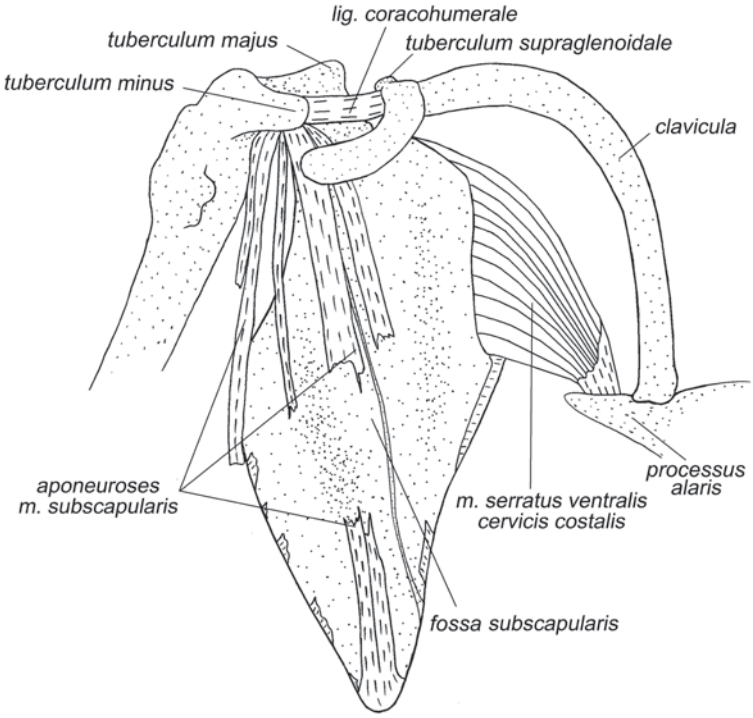


Fig. 3.65 Forelimb muscles of *R. ferrumequinum*, ventral view, layer VIII.

According to Strickler (1978), this muscle is less developed in frugivorous and slow-flying insectivorous forms (fruit bats and horseshoe bats), and it is much better developed in fast-flying insectivorous bats (emballonurids).

The muscle is the main supinator of the humerus. It also participates in its retraction (flexion of the shoulder joint).

Musculus coracobrachialis longus (Figs. 3.56, 3.59, 3.62, 3.66, 3.67) is the only coracobrachial muscle in all bats. It originates, sometimes by an aponeurosis, on the tip of the coracoid process of the scapula more lateral (closer to the humerus) than the *m. biceps brachii caput coracoideum*. It inserts by an aponeurosis on the medial surface of the middle part of the humerus. In some microbats (for example, members of the genus *Rhinolophus*), it is a very small ribbon-like muscle virtually lacking aponeuroses. According to Strickler (1978), it is completely absent in *Molossus*.

When the humerus is retracted (in a folded wing), this muscle prevents its protraction; when the humerus is protracted (in a spread wing), the muscle helps to depress it.

Musculature of Free Limb

Musculature of Humerus

Posterior Group of Muscles

Musculus triceps brachii (Figs. 3.22–3.32, 3.34, 3.36) in bats always includes *caput longum* and *caput laterale*, but the third head is absent in some species of *Mormoops* and *Balantiopteryx* (Strickler 1978). If present, it is called the *caput mediale*, and we shall follow this tradition avoiding the problem of its homology with either the *caput mediale* or *caput accessorium* of other mammals. Note that in human anatomy, the third head is also known as the *caput mediale*, although its position on the humerus rather implies its homology with the *caput accessorium* of the other mammals.

In **fruit bats**, the *caput longum* originates by an aponeurosis from the caudal border of the scapula near the glenoid. The *caput laterale* originates from the posterolateral surface of the proximal one-third of the humerus, distal to its greater tubercle. The *caput mediale* originates from the posteromedial surface of the proximal half of the humerus (by this proximal position, it rather corresponds to the *caput accessorium* of other mammals). The boundary between the two humeral heads is hardly discernible. Their terminal tendons fuse at first, and then, alongside the distal part of the humerus, they are also joined by the terminal tendon of the *caput longum*. The common terminal tendon inserts on the olecranon. Just before the insertion, a large sesamoid bone (the so-called *os sesamoideum m. tricipitis brachii*) is formed inside the tendon.

In **microbats**, the *caput longum* also originates by an aponeurosis from the caudal border of the scapula near the glenoid. It is separate throughout its length from other heads. Its terminal tendon passes to its separate insertion on the olecranon usually over a groove in the *os sesamoideum m. tricipitis brachii*; however, it is sometimes fused with the sesamoid bone. The *caput laterale* originates from the posterolateral surface of the proximal part of the humerus, occupying from one- to three-fourths of the humerus length. Its terminal tendon inserts on the olecranon either separately or after fusion with the terminal tendon of the *caput mediale*. The position and size of the *caput mediale* in various species differ considerably. In horseshoe bats, it originates most proximally, from the base of the lesser tubercle and medial surface of the proximal one-third of the humerus (by this proximal position, it rather corresponds to the *caput accessorium* of other mammals). In American leaf-nosed bats, the origin of the *caput mediale* is located most distally, on the posterior surface of the distal one-fourth of the humerus (by this distal position, it, indeed, corresponds to the true *caput mediale* of other mammals). The terminal tendon of this head inserts on the olecranon either (in the majority of microbats) along with that of the *caput laterale* or separately. In the first case (for example, according to Strickler (1978), in Vespertilionidae, Phyllostomidae, and Noctilionidae), the *os sesamoideum m. tricipitis brachii* is formed in the common distal-most segment of the tendons of the two humeral heads; in the second case, it is formed in the tendon of the *caput mediale*, while the tendon of the *caput laterale* can also form its separate sesamoid. It was found by Strickler (1978) in *Balantiopteryx* and *Saccopteryx* at the point of the tendon of the *caput laterale*, which passes over the *os sesamoideum m. tricipitis brachii* incorporated in the tendon of the *caput mediale*.

All heads extend the elbow; in addition, the caput longum retracts the humerus.

Anterior Group of Muscles

Musculus biceps brachii (Figs. 3.22–3.34, 3.36, 3.38, 3.39, 3.43, 3.46, 3.48–3.55, 3.58, 3.59, 3.66, 3.67) in bats has both typical heads, the *caput longum* and *caput coracoideum*, which are well differentiated, well developed, and approximately equal in size. Such great development of the *caput coracoideum* is unusual among mammals.

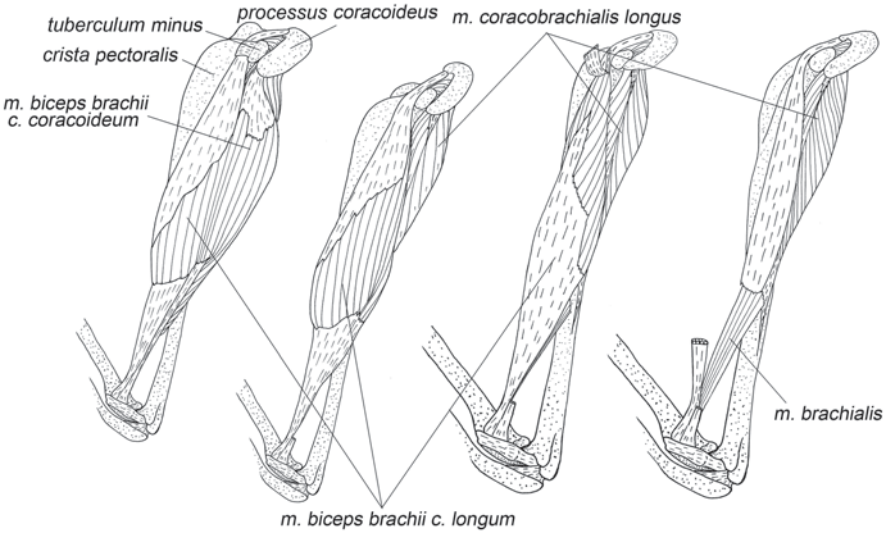


Fig. 3.66 The *m. biceps brachii* of *C. sphinx*, successive stages of dissection, ventral view.

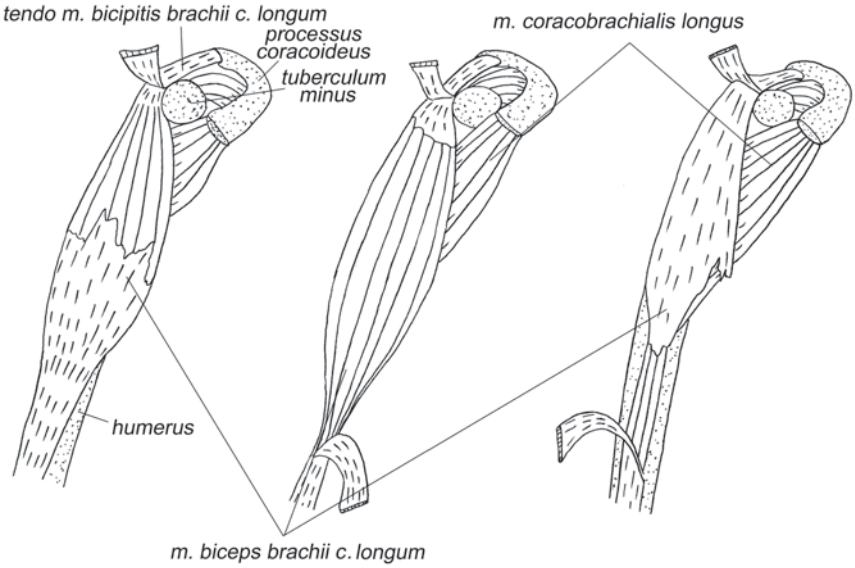


Fig. 3.67 The *m. biceps brachii caput longum* of *R. ferrumequinum*, successive stages of dissection, ventral view.

In **fruit bats**, a thick tendon of origin of the *caput longum* arises as usual from the supraglenoid tubercle of the scapula. At the level of the lesser tubercle of the humerus, the tendon divides into two wide superficial aponeuroses. From those, muscular fibers converge in a bipennate manner onto a terminal aponeurosis passing inside the belly, which inserts in a special groove on the palmar surface of the proximal end of the radius. The *caput coracoideum* originates from the tip of the greatly elongated coracoid process of the scapula by one (instead of two, as in the *caput longum*) short and wide aponeurosis. Its fibers insert on a long and thin terminal tendon, which either at once fuses with the tendon of the *caput longum* or remains separate and inserts near it in the groove on the radius.

In **microbats**, the *caput longum* is similar to that of fruit bats. It is also bipennate originating by a tendon, which bifurcates into a pair of superficial aponeuroses, wherefrom the fibers converge onto a thick terminal tendon. It inserts either separately or together with the *caput coracoideum* in a groove on the palmar side of the proximal end of the radius, leaving a small area in its proximal part for insertion of the *ligamentum mediale radiale* of the elbow joint. The *caput coracoideum* originates from the tip of the greatly elongated coracoid process of the scapula, sometimes spreading onto its medial and lateral borders, often fleshy. The terminal tendon of this head is usually fused with that of the *caput longum*, although sometimes they reach the radius separately.

The muscle is the main flexor of the elbow. In addition, the caput longum participates in protraction and the caput coracoideum in depression (adduction) of the humerus.

Musculus brachialis (Figs. 3.22, 3.24, 3.25, 3.27, 3.30–3.33, 3.38, 3.48, 3.51, 3.54–3.56, 3.66, 3.68, 3.76) in the majority of bats originates from the anterior surface of the middle part of the humerus. In some species, its origin is displaced much more proximally and reaches the pectoral crest. The muscle usually inserts in the aforementioned groove on the palmar surface of the proximal end of the radius. According to Strickler (1978), in some species (for example, *Macroglossus* and *Nycteris*), it inserts not on the radius but on the radial surface of the ulna. In a number of bats, for example, *Mormoops*, this muscle is absent (Strickler 1978).

The muscle could have participated in the elbow flexion but is so weak that probably only serves as a sensor of the degree of this flexion.

Muscles of Antebrachium

Muscles of Dorsal Surface

Musculus supinator (Figs. 3.25, 3.68–3.71, 3.75, 3.77) in all bats originates by a wide superficial aponeurosis from the lateral epicondyle of the humerus and lateral sesamoid bone of the elbow joint. The muscular fibers are short and insert on the radial surface of the proximal one-fourth of the radius.

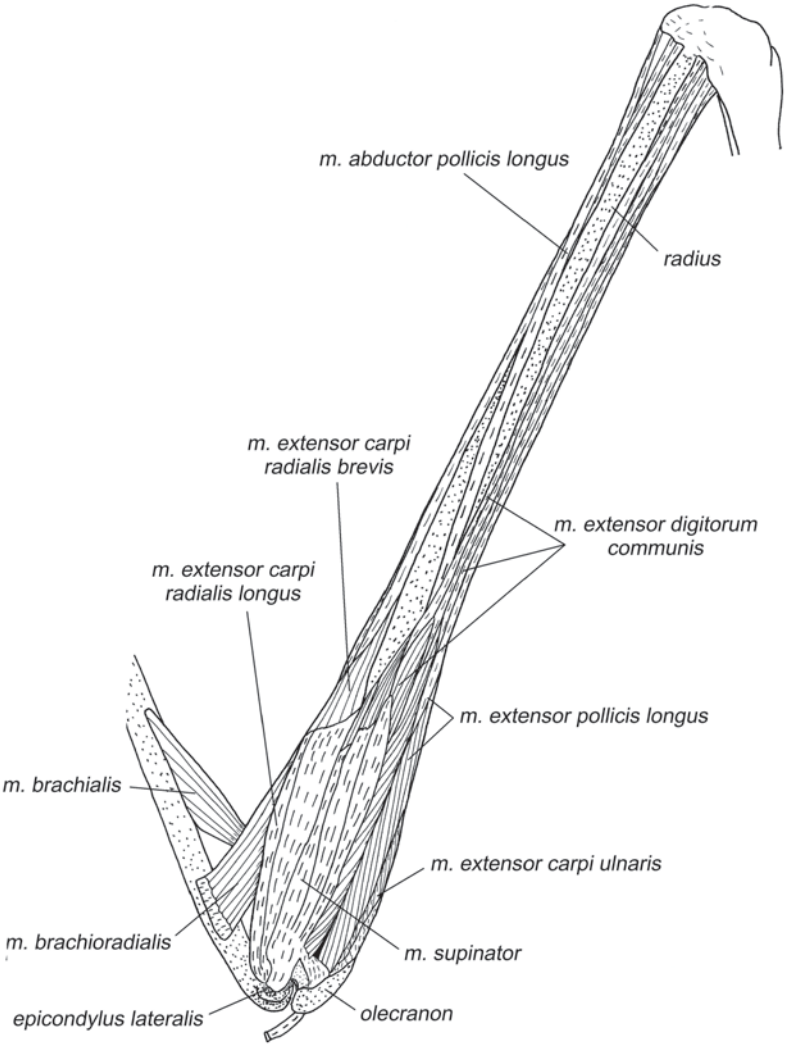


Fig. 3.68 Fore extremity muscles of *C. sphinx*, lateral view, layer I.

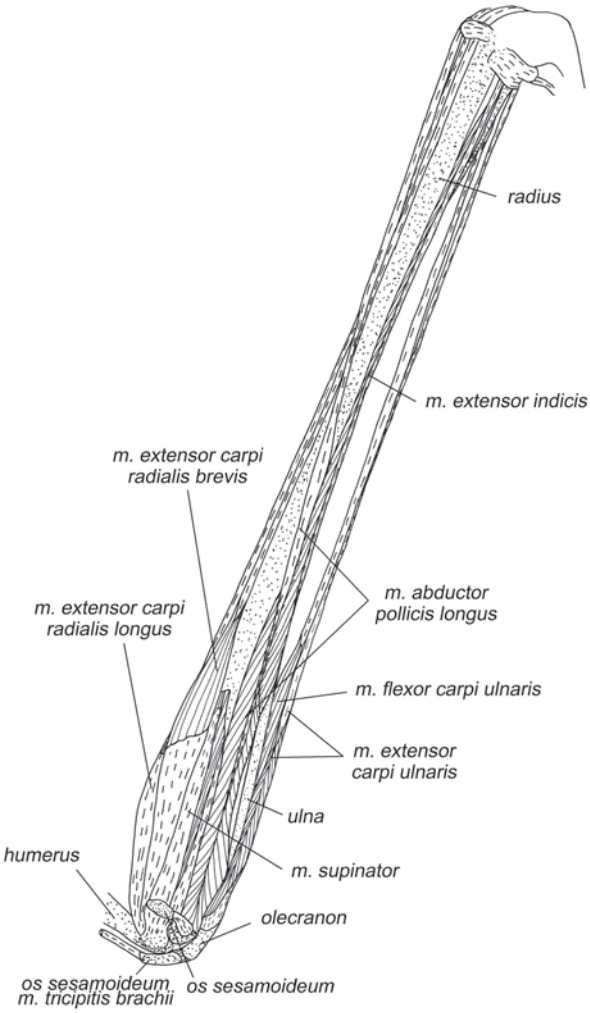


Fig. 3.69 Fore extremity muscles of *C. sphinx*, lateral view, layer II.

This muscle supinates the antebrachium for a small angle allowed by ligaments of the elbow joint, participates in elbow flexion, and prevents medial adduction of the antebrachium.

Musculus brachioradialis (Figs. 3.25, 3.68, 3.76) in **fruit bats** is a wide ribbon-like muscle originating by a short aponeurosis from the lateral surface of the humerus proximal to its lateral epicondyle. It inserts on the radial side of the radius at the end of its proximal one-third.

Among **microbats**, this muscle is absent in members of the families Vespertilionidae, Phyllostomidae, and Molossidae examined by Vaughan (1959) and Norberg (1970). We have found it in horseshoe bats as a very thin, hardly discernible, ribbon-like muscle. Vaughan (1970b) also recorded it in *Hipposideros armiger*, and

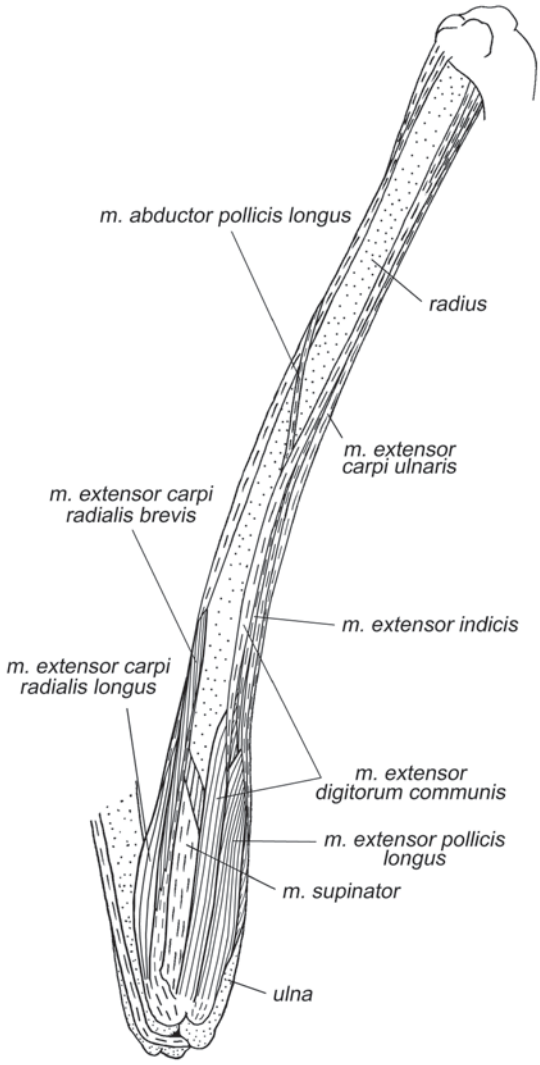


Fig. 3.70 Fore extremity muscles of *R. ferrumequinum*, lateral view, layer I.

Macalister (1872), in all the microbats he dissected, except for *Nyctalus* and *Pipistrellus*. If present, the muscle originates from the lateral surface of the humerus proximal to its lateral epicondyle and inserts on the radial side of the radius near its proximal end.

In fruit bats, this muscle probably still participates in elbow flexion, while in microbats, it is so weak that most likely only serves as a sensor of the degree of this flexion. Reduction of this muscle together with the m. brachialis in bats lies in the main stream of the mass reduction in the distal wing regions (e.g., Riskin et al. 2012). The function of elbow flexion is completely grabbed by the m. biceps brachii, the mass of which is confined to the proximal limb region.

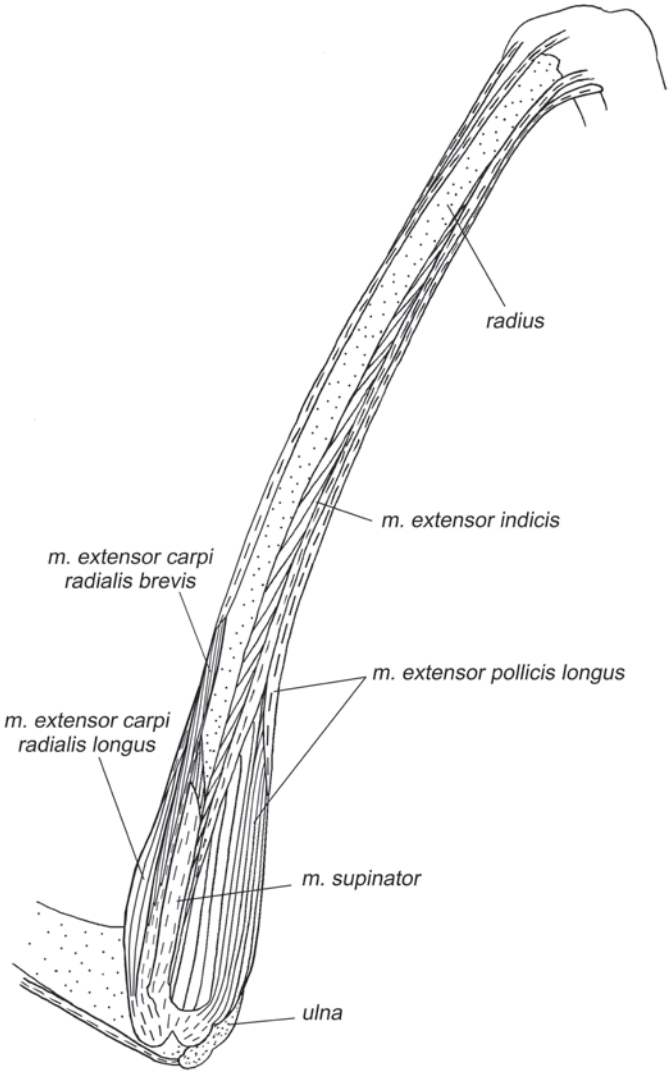


Fig. 3.71 Fore extremity muscles of *R. ferrumequinum*, lateral view, layer II.

Musculus extensor carpi radialis longus (Figs. 3.68–3.74, 3.76, 3.78, 3.80, 3.81) in all bats originates by a wide superficial aponeurosis from the crest of the lateral epicondyle of the humerus. The belly covers the proximal part of the radial side of the antebrachium. Fibers attach to a long distal tendon, which runs along the radial side of the antebrachium and, along with the tendon of the *m. extensor carpi radialis brevis*, passes onto the manus under the internal loop of the medial part of

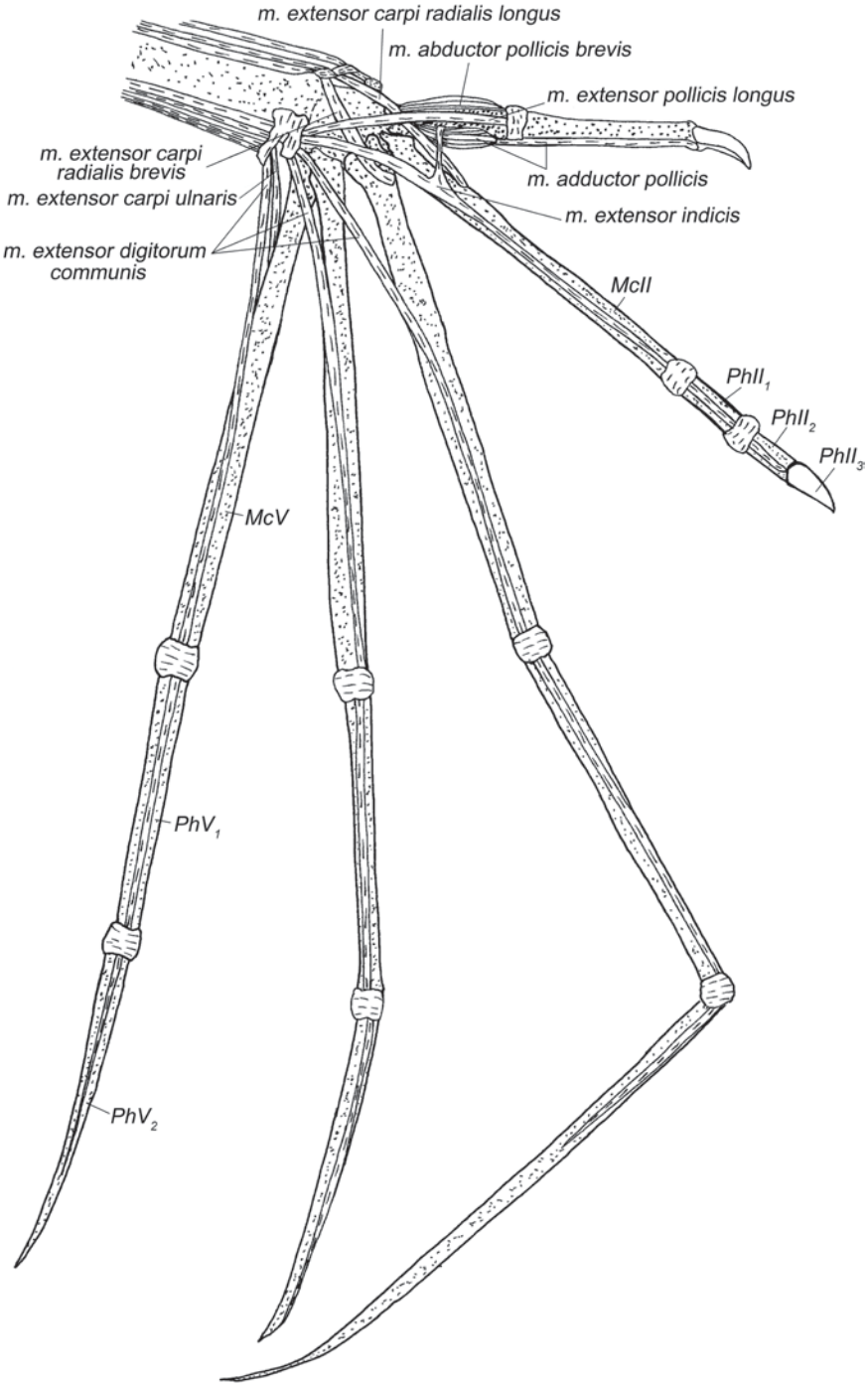


Fig. 3.72 Muscles of the manus of *C. sphinx*, dorsal view.

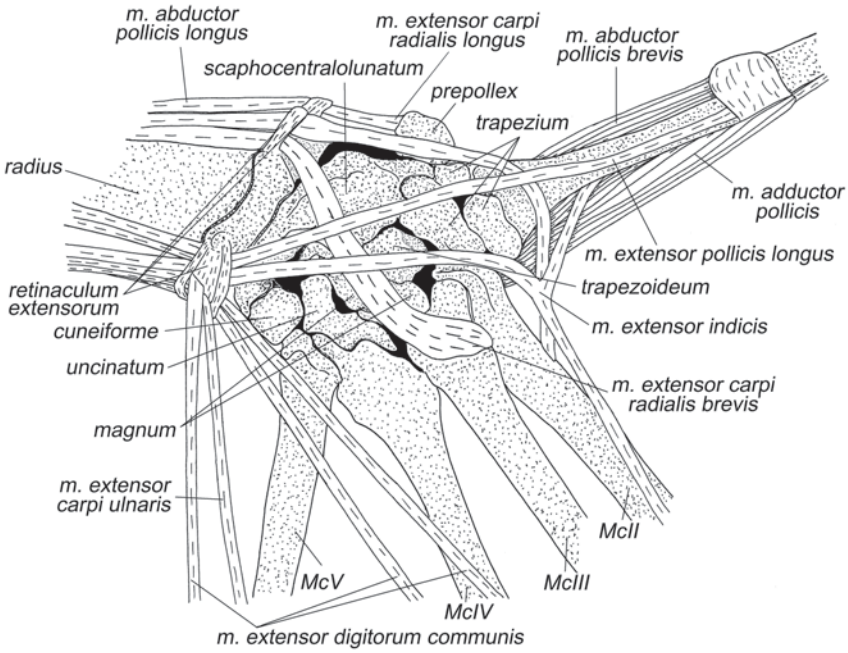


Fig. 3.73 Muscles of the carpal region of *C. sphinx*, dorsal view.

the *retinaculum extensorum*[19]. The tendon inserts on the medial surface of metacarpal II somewhat distal to its proximal head.

In **microbats**, the terminal tendon frequently gives an accessory branch to the lateral surface of the proximal head of metacarpal I. In some species, for example, *Nyctalus*, the terminal tendon bears a sesamoid bone at the level of the carpometacarpal joints (Ledenev 1988).

The muscle extends the radiocarpal joint and unfolds the chiropatagium by extension of the second carpometacarpal joint. In microbats, due to the accessory tendon, this muscle adducts the first digit to the second, when the wing is unfolded.

Musculus extensor carpi radialis brevis (Figs. 3.68–3.74, 3.80) in bats originates by a wide aponeurosis (which in many species has a small sesamoid bone at its base) either from the lateral epicondyle of the humerus or from its crest distal to the *m. extensor carpi radialis longus*. The belly covers from one-third to half of the length of the radial side of the radius. Muscular fibers attach to a long terminal tendon that runs parallel to that of the *m. extensor carpi radialis longus*. In the majority

[19] In bats, the *retinaculum extensorum* (Fig. 3.73) is divided into two parts, medial and lateral, which are placed at opposite sides of the distal end of the radius. The medial part forms two loops, one for tendons of the *mm. extensores carpi radiales* and the other (most medial) for tendon of the *m. abductor pollicis longus*. The lateral part consists of several parallel ligaments for tendons of the *m. extensor pollicis longus*, *m. extensor indicis*, *m. extensor digitorum communis*, and *m. extensor carpi ulnaris*.

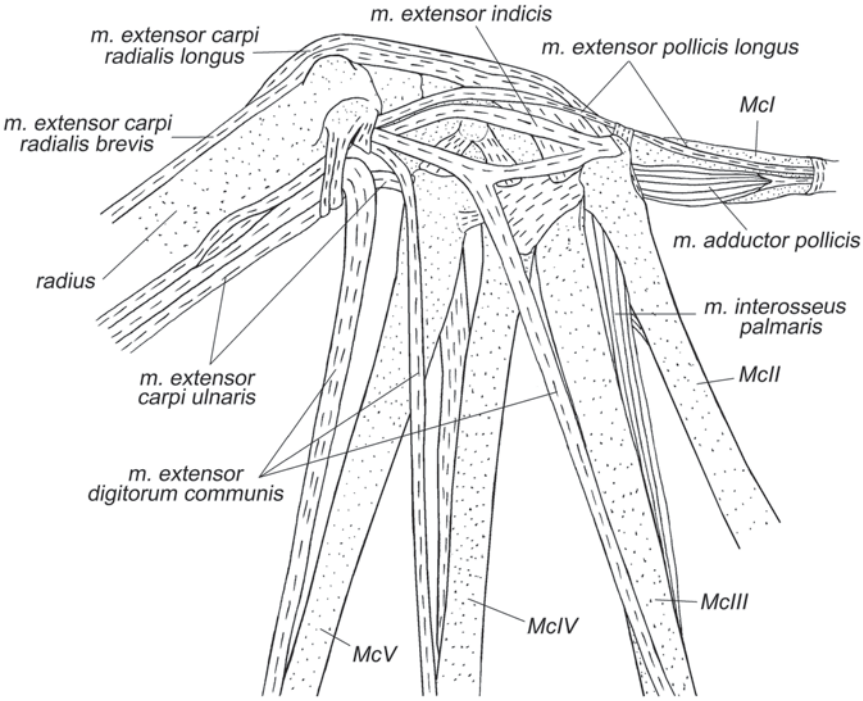


Fig. 3.74 Muscles of the carpal region of *R. ferrumequinum*, dorsal view.

of species, the widened end of the terminal tendon inserts on the lateral side of the proximal head of metacarpal III. However, in some species, it widens so much that its insertion covers the bases of two or even three metacarpals. For example, in the greater horseshoe bat, the insertion is on metacarpals II and III, and, in the Egyptian fruit bat, on metacarpals III–V. In this widened part of the tendon, a sesamoid bone is sometimes formed at the level of the carpometacarpal joints (Ledenev 1988).

This muscle extends the radiocarpal joint and unfolds the chiropatagium by the third metacarpal rather than the second, as the m. extensor carpi radialis longus does.

Many researchers believe in the so-called "automatic" spreading of the manus by the two mm. extensores carpi radiales. The idea (Vaughan 1959, 1970b) is that, since they pass in front of the axis of the elbow joint (as if they were its flexors), extension of this joint by any external force (for instance, produced by contraction of the m. triceps brachii) should cause tension in these muscles, and, hence, they will transmit the elbow extension into the extension of the radiocarpal joint "automatically," without activation. However, such mechanism appears to be impossible, as relaxed muscles are incapable of tramsmitting forces. We have confirmed the absence of such automatism by manipulations on living bats (Rousettus aegyptiacus and Carollia perspicillata): forced extension of the elbow joint virtually does

not result in extension of the radiocarpal joint from the flexed state (metacarpal II extends for at most 15°).

Musculus extensor digitorum communis (Figs. 3.68, 3.70, 3.72–3.74) in **fruit bats** originates by a wide aponeurosis from the lateral epicondyle of the humerus and lateral sesamoid bone of the elbow joint and also by a small accessory aponeurosis from the lateral surface of the olecranon. The belly is composed of very short muscular fibers and terminates by three separate tendons to digits III–V. They run along the ulnar side of the dorsal surface of the antebrachium and pass onto the manus under the lateral part of the *retinaculum extensorum*. Each tendon, having passed through articular capsules of the metacarpophalangeal and first interphalangeal joints of respective digit, becomes a very thin aponeurosis, which fuses with the dorsal surface of the second phalanx.

In **microbats**, the muscle originates by a thick aponeurosis from the lateral epicondyle of the humerus and lateral sesamoid bone of the elbow joint. Some fibers can also arise from the dorsal surface of the proximal ends of the ulna (except for the olecranon) and radius. The belly is large, multipennate, covers about proximal one-third of the radial side of the antebrachium, and terminates by one or two tendons. In the distal part of the antebrachium, this tendon (or two) splits into three terminal branches initially covered by the common connective-tissue sheath and, after passing under the lateral part of the *retinaculum extensorum*, diverging to digits III–V. The presence of the undivided proximal segment of the terminal tendon suggests that the independent extension of digits, characteristic to fruit bats, is not developed in microbats (like in tree shrews and colugos). The three terminal tendons pass through the capsules of metacarpophalangeal and first interphalangeal joints and insert on the dorsal surface of the second phalanx of respective digit, either on its proximal or distal end, or anywhere in-between depending on the particular species. The tendon to digit III frequently gives a branch to metacarpal II or the first phalanx of digit II.

The muscle extends the radiocarpal joint and all joints of digits III–V.

Musculus extensor digitorum lateralis. Vaughan (1959) and Altenbach (1979) revealed a muscle in the antebrachium of *Myotis*, *Macrotus*, and *Desmodus*, which they named the *m. extensor digiti quinti proprius*. Its fibers originate from the dorsal surface of the proximal part of the antebrachium along with the *m. extensor digitorum communis* and partially from the superficial aponeurosis of origin of the latter muscle in *Myotis* and *Macrotus*. In *Desmodus*, this muscle originates from distal edge of the lateral epicondyle. It inserts on the second phalanx of digit V. Apparently, this muscle is homologous to the *m. extensor digitorum lateralis* of other mammals, more precisely, to its part associated with digit V. In human anatomy, such muscle is termed the *m. extensor digiti minimi*.

The muscle extends digit V.

Musculus extensor pollicis longus (Figs. 3.68, 3.71–3.74) Many researchers (e.g., Vaughan 1959, 1970b; Norberg 1970, 1972) designate this muscle as the *m. extensor pollicis brevis* rather than *m. extensor pollicis longus*. Both extensors of digit I are simultaneously present in man. They are reliably distinguished by the fact that the terminal tendon of the *m. extensor pollicis brevis* passes under the *retinacu-*

lum extensorum adjacent to the *m. abductor pollicis longus*, whereas the *m. extensor pollicis longus* passes under the *retinaculum extensorum* adjacent to the *m.extensor indicis* (Voss and Herrlinger 1956). In the majority of mammals, including chiropterans, only one extensor of digit I is present. Based on the path of its distal tendon in chiropterans, it is possible to state with certainty that, in this case, we deal with the *m. extensor pollicis longus*.

In **fruit bats**, the muscle originates from the dorsal surface of the proximal one-fourth of the rudimentary ulna, partially spreading onto the *membrana interossa antebrachii*. A long terminal tendon passes onto the manus under the lateral part of the *retinaculum extensorum* and runs to digit I, where it inserts on the capsule of its metacarpophalangeal joint. In the Egyptian fruit bat, the tendon is attached to the capsule of the metacarpophalangeal joint, but does not terminate on it, extending further to the base of the ungual phalanx.

In **microbats**, the muscle originates from the dorsal surface of the proximal part of the rudimentary ulna, *membrana interossa antebrachii*, and, sometimes, from the ulnar side of the radius. Occasionally, some muscle fibers arise from the surface of aponeuroses of origin of the *m.extensor indicis* and *m. abductor pollicis longus*. The terminal tendon passes through the capsule of the first carpometacarpal joint, then, sometimes, gives branches to metacarpal I, and finally inserts on the dorsal surface of the base of either first or second (ungual) phalanx.

The muscle extends the radiocarpal joint and digit I.

Musculus abductor pollicis longus (Figs. 3.68–3.70, 3.73, 3.76–3.82) in **fruit bats** originates from the ulnar half of the dorsal surface of proximal one-third of the radius, the *membrana interossa antebrachii*, and partially from the dorsal surface of the ulna just distal to the elbow joint. The long terminal tendon of this muscle runs along the dorsal surface of the antebrachium, in distal one-third, passes onto its radial side, and, having passed under the most medial loop of the medial part of the *retinaculum extensorum*, inserts on the proximal aspect of the prepollex.

In **microbats**, this muscle originates from the ulnar surface of the proximal part of the radius. Very short muscular fibers (hardly discernible in many species) attach to the long terminal tendon, which curves radially around the radius, passes onto the manus under the medial loop of the medial part of the *retinaculum extensorum*, and inserts on the prepollex.

This muscle adducts the manus medially, but the extremely short fibers of the muscle are evidence of very small amplitude of contraction. So, more likely, it acts like a ligament preventing lateral abduction of the manus. Also, some researchers (Vaughan 1959; Norberg 1970, 1972) believe that, via the ligaments connecting the prepollex to pisiforme and base of metacarpal V, this muscle can prevent hyperextension of the fifth carpometacarpal joint during the wing downstroke.

Musculus extensor indicis (Figs. 3.69, 3.71–3.74) in **fruit bats** originates fleshy from the dorsal surface of the proximal part of the ulna, *membrana interossa antebrachii*, and from the ulnar surface of the distal half of the radius. Muscular fibers are short. The long terminal tendon passes onto the manus under the lateral part of the *retinaculum extensorum* and, at the level of the proximal head of metacarpal II, bifurcates into branches to digits II and I. The branch of digit II runs along its

dorsal surface and, after the first interphalangeal joint, becomes a thin aponeurosis fusing into the surface of the second phalanx. The branch of digit I does not reach phalanges but inserts on the lateral surface of proximal one-third of metacarpal I. In *Pteropus*, there is a single terminal tendon, which inserts on the last phalanx of digit II (Humphry 1869).

In **microbats**, the belly of this muscle also occupies the space between the radius and ulna. Its short fibers originate almost along the entire ulnar surface of the radius and from the radial surface of the ulna. The long terminal tendon passes under the lateral part of the *retinaculum extensorum* and inserts on the dorsal surface of the proximal head of metacarpal II.

In fruit bats, this muscle extends the first carpometacarpal joint and all joints of digit II, except for the preungual joint, and also pulls metacarpals I and II closer together. In microbats, in accordance with the reduction of phalanges of digit II (Table 1.2), the muscle only extends the second metacarpophalangeal joint.

Musculus extensor carpi ulnaris (Figs. 3.68–3.70, 3.72–3.74) in **fruit bats** has a small belly originating from the dorsal surface of proximal one-fourth of the ulna almost unaided by an aponeurosis. Its terminal tendon passes onto the manus under the lateral part of the *retinaculum extensorum* and inserts on the lateral surface of proximal one-fourth of metacarpal V.

In **microbats**, this muscle originates from the distal part of the ulnar side of the ulna. The terminal tendon passes under the lateral part of the *retinaculum extensorum*. Bat species display three variants of insertion. In horseshoe bats and American leaf-nosed bats, the tendon inserts on the dorsolateral surface of the proximal head of metacarpal V. In vespertilionids and free-tailed bats (Vaughan 1959, 1970b), it inserts on either the ligament connecting on the dorsal side metacarpals V and III or the dorsolateral surface of the proximal head of metacarpal III.

The bat groups differ in the function of this muscle. In fruit bats and microbats bearing insertion on metacarpal V, it abducts this metacarpal laterally, i.e., participates in unfolding the chiropatagium. In microbats bearing insertion on the ligament between metacarpals III and V, the muscle extends the third to fifth carpometacarpal joints and pulls digits III–V closer together (Vaughan 1959). According to Vaughan (1959, 1970b), in Eumops and Myotis bearing insertion on metacarpal III, this muscle is a flexor of the third carpometacarpal joint. However, we disagree with this idea, since the retinaculum extensorum prevents sliding of the terminal tendon of this muscle from the dorsal side of the carpus onto the medial side. Consequently, this muscle cannot act as a flexor, but acts, in the last case, as the extensor of the third carpometacarpal joint.

Muscles of Palmar Surface

Musculus pronator teres (Figs. 3.75–3.78) in **fruit bats** originates by a small aponeurosis from the proximal part of the medial epicondyle of the humerus and inserts by a very wide aponeurosis on the radial surface of the proximal part of the radius.

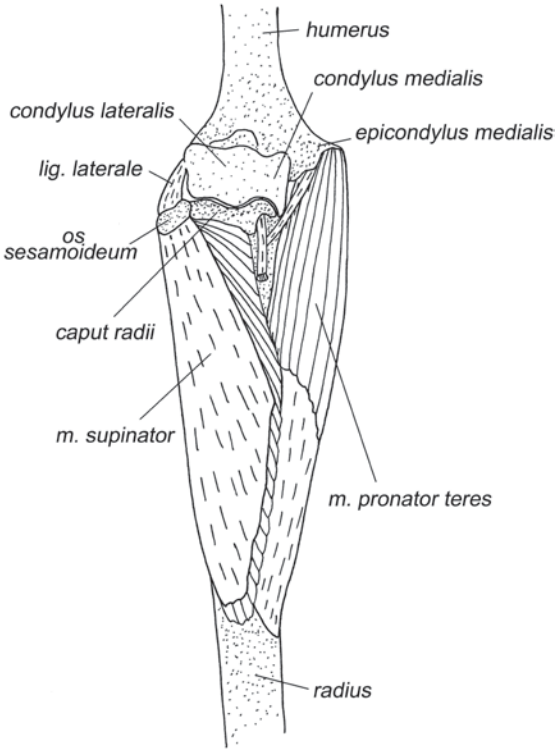


Fig. 3.75 The elbow joint of *C. sphinx*, anterior view.

In **microbats**, the muscle originates with the aid of an aponeurosis from the medial epicondyle of the humerus or the base of its styloid process, if present, and inserts by an aponeurosis on the radial surface of the proximal part of the radius, covering in different species from one-fifth to one-third of its length.

This muscle prevents supination of the antebrachium and returns it from a supinated to neutral position. In addition, it aids the ligamentum mediale radiale of the elbow joint to deter lateral abduction of the antebrachium relative to the humerus in a wing downstroke.

Musculus flexor carpi radialis (Figs. 3.76, 3.78, 3.80–3.83) of the majority of bats is very large. However, in some microbats, it is rudimentary (*Myotis, Eumops*, according to Vaughan 1970b) or absent (*Nyctalus*, according to Macalister 1872).

In **fruit bats,** it originates from the medial epicondyle of the humerus by a separate aponeurosis and the aponeurosis shared with the *m. pronator teres*. A long thick terminal tendon runs along the palmar surface of the antebrachium and inserts on the medial tubercle on the ventral surface of the proximal head of metacarpal II. According to Macalister (1872), in *Macroglossus,* the terminal tendon also gives branches to the *scaphocentralolunatum* and *trapezium*, although he could have taken for these branches the fibrous loop which binds the terminal tendon of the muscle to the palmar surface of the carpus.

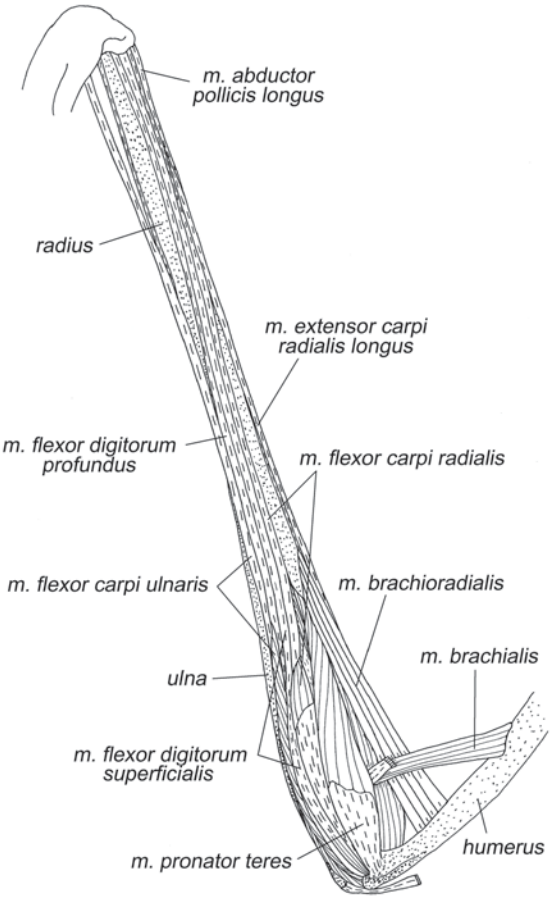


Fig. 3.76 Fore extremity muscles of *C. sphinx*, medial view, layer I.

In **microbats**, it originates from the base of the medial epicondyle of the humerus with the help of the aponeurosis shared with the *m. pronator teres*. The terminal tendon runs along the palmar surface of the antebrachium, passes under the *retinaculum flexorum* (Fig. 3.80), and, then, inserts on either the base of metacarpal I (for example, in free-tailed bats: Vaughan 1959), the base of metacarpal II (for example, in horseshoe bats (our data) and some vespertilionids: Vaughan 1959; Norberg 1970), or the base of metacarpal III (for example, in some American leaf-nosed bats: Vaughan 1959). Moreover, the tendon sometimes inserts on the ventral surface of the *trapezium* in *Platyrrhinus* (Macalister 1872). According to our dissection, in horseshoe bats (Fig. 3.78), the aponeurosis of origin of this muscle directly passes into its terminal tendon, as if they were a single ligament connecting the medial epicondyle of the humerus with the base of metacarpal II, the muscular fibers being embedded within the beginning of this ligament.

The muscle flexes the radiocarpal joint. Also, in the majority of bats, it bends the second carpometacarpal joint and, in some, the first or third carpometacarpal joint.

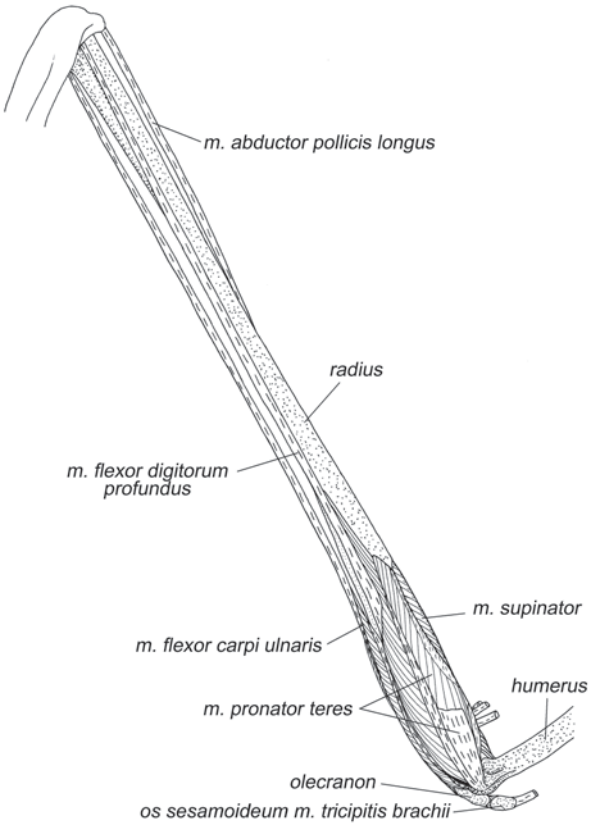


Fig. 3.77 Fore extremity muscles of *C. sphinx*, medial view, layer II.

Musculus flexor digitorum superficialis (Figs. 3.76, 3.78–3.81) of bats is used to be identified as the *m. palmaris longus* (e.g., Vaughan 1959, 1970b; Norberg 1970; Kovtun 1978; etc.). This tradition was started by Macalister (1872) in spite of the previous identification of this muscle as the *m. flexor digitorum superficialis* by Humphry (1869). Against Humphry is the non-perforated nature of its terminal tendons and their insertion on metacarpals (or, at maximum, on first phalanges) rather than on second phalanges, but this argument is easily repulsed by the fact of the general tendency in bats to reduce the extent of terminal flexor and extensor tendons of the antebrachial musculature. More profound is the argument against Macalister and the following tradition: the *m. palmaris longus* never inserts on bones among mammals, but blends into the skin. So, we regard the *m. palmaris longus* as lacking in bats (like in colugos), and follow the original homologization of Humphry.

In **fruit bats**, the *m. flexor digitorum superficialis* originates from the distal part of the medial epicondyle of the humerus between the *m. flexor digitorum profundus*, originating more proximally, and the *m. flexor carpi ulnaris*, originating even more distally. Its fibers attach to a superficial aponeurosis, which runs onto the manus under the *retinaculum flexorum*, passes through a fibrous loop on the medial side of

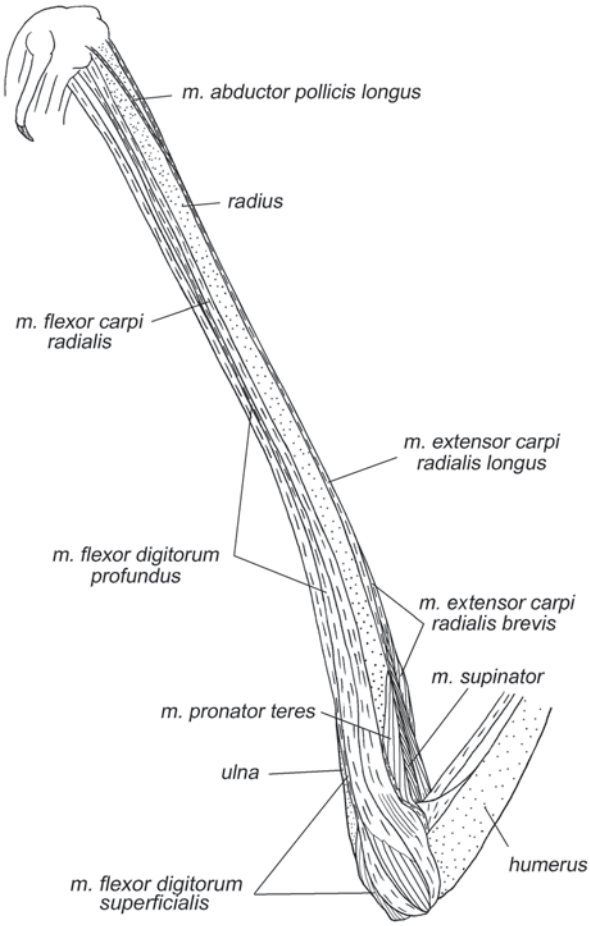


Fig. 3.78 Fore extremity muscles of *R. ferrumequinum*, medial view.

the prepollex, and, then, bifurcates into equal tendons of digits I and II. The tendon of digit I inserts on the ventral surface of either the distal head of the metacarpal I or sesamoid bone of the respective metacarpophalangeal joint; the tendon of digit II inserts on the ventral surface of either the distal head of the metacarpal II or articular capsule of the respective metacarpophalangeal joint. In *Pteropus*, the tendon of digit II reaches its second phalanx (Humphry 1869). The majority of fruit bats have a third tendon, which diverges at the point of bifurcation of the previous two and inserts on the ventral surface of metacarpal V not reaching the metacarpophalangeal joint.

In **microbats**, this muscle originates by an aponeurosis from the medial epicondyle of the humerus, or its styloid process, if present. The terminal tendon runs along the ulnar side of the antebrachium, along with tendons of other flexors. In the distal part of the antebrachium, it traverses onto its ventral surface and, then, passes onto the manus. Branching and insertion of this tendon widely vary; our own

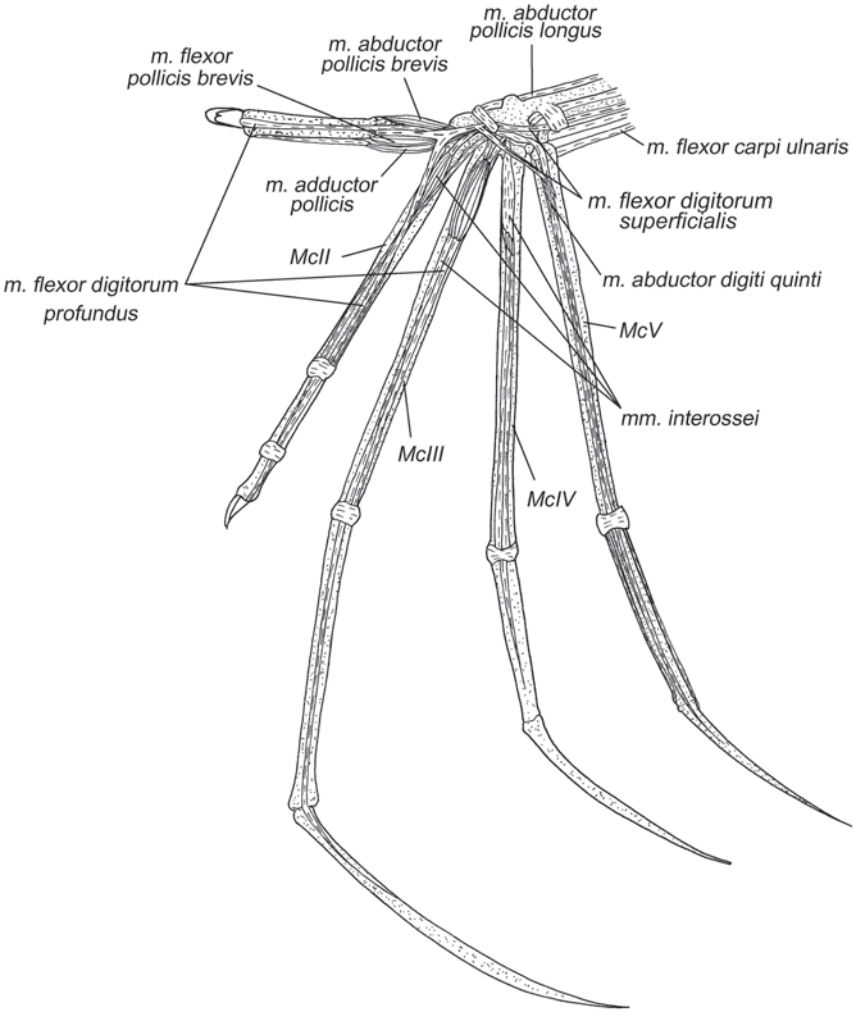


Fig. 3.79 Muscles of the manus of *C. sphinx*, ventral view.

findings combined with published data give the following picture. In horseshoe bats and, according to Macalister (1872), in false vampire bats, it inserts by two branches on metacarpals II and III; sometimes, a separate branch runs to the capsule of the first carpometacarpal joint. In free-tailed bats two branches run to digits I and V; in addition, the branch of digit I spreads into a wide aponeurosis, which splits into several thin bands fusing into the capsule of the first metacarpophalangeal joint (Vaughan 1970b). In vespertilionids, two branches supply either digits I and V (often with accessory branches from the point of the main bifurcation to the bases of matacarpals I and II: Norberg 1970), or digits I and II, or even digits III and

IV (Macalister 1872). In *Mormoops*, there is only one tendon to digit II (Vaughan and Bateman 1970). Most variable is the insertion in phyllostomatid bats (Macalister 1872; Vaughan 1959; Vaughan and Bateman 1970): one tendon to digit I; one tendon to digit II; two branches to digits I and II; two branches to digits I and III; three branches to digits I, II, III; three branches to digits I, III, V; and five branches to all digits. The point of insertion of the aforementioned branches varies among microbats from the base of respective matacarpal through the middle of proximal phalanx. This muscle is absent in *Myotis* (Vaughan 1970b), *Noctula* (Macalister 1872), and *Pteronotus* (Vaughan and Bateman 1970).

In all bats, the muscle flexes the radiocarpal joint and, depending on particular insertion, bends carpometacarpal and metacarpophalangeal joints of respective digits. In addition, it pulls closer together the digits involved.

Musculus flexor digitorum profundus (Figs. 3.76–3.82) in **fruit bats** originates under the *m. flexor carpi radialis* by the aponeurosis shared with the *m. pronator teres* from the medial epicondyle of the humerus, and fleshy from the palmar surface of the proximal one-third of the radius and, partially, from the palmar surface of the ulna. A thick terminal tendon passes through a special fibrous loop on the ventral surface of the carpus and, at the level of the prepollex, divides into three branches to three first digits. The branches of digits I and II insert on the ventral surface of the bases of respective ungual phalanges. At the level of proximal one-fourth of metacarpal III, the branch of digit III has a remarkable inset of muscular fibers in a manner of digastric muscles (Fig. 3.82). After this accessory belly, which we regard as the *m. lumbricalis digiti tertii* (see later in the text), there is a tendon again, which inserts on the proximal part of the second phalanx of digit III.

In **microbats**, the muscle has always a large belly but widely varies in origin and especially insertion. In the majority of species, it originates from the medial epicondyle of the humerus (from its styloid process, if present); frequently, fibers also arise from the palmar surface of the proximal part of the radius and ulna. In free-tailed bats, the muscle originates only from the radius (Vaughan 1959). The terminal tendon runs along the palmar surface of the antebrachium, passes under the *retinaculum flexorum*, and, then, divides into several branches. One of them always runs to digit I, while there is never a branch to digit II in accordance with reduction of this digit. Horseshoe bats have three branches passing to the base of the ungual phalanx of digit I, the second phalanx of digit III, and the first or second phalanx of digit IV; the branch of digit IV can be fused distally with the superficial terminal aponeurosis of the respective *m. interosseus*. Similarly, in vespertilionids, the three branches insert on the distal phalanges of digits I, III, and IV (Macalister 1872; Norberg 1970; Vaughan 1970b). American leaf-nosed bats either have the same three branches to digits I, III, and IV, or only two tendons to the ungual phalanx of digit I and distal phalanx of digit III (Vaughan 1970b; Vaughan and Bateman 1970). *Eumops* was claimed by Vaughan (1970b) to possess two branches terminating on the ungual phalanx of digit I and, unusually enough, at the fifth metacarpophalangeal joint. However, Vaughan's description and drawings allow us to state that he overlooked the third branch to digit III, which, having passed under the ligamentous loop at the *pisiforme*, bears the inset of muscular fibers directly corresponding to

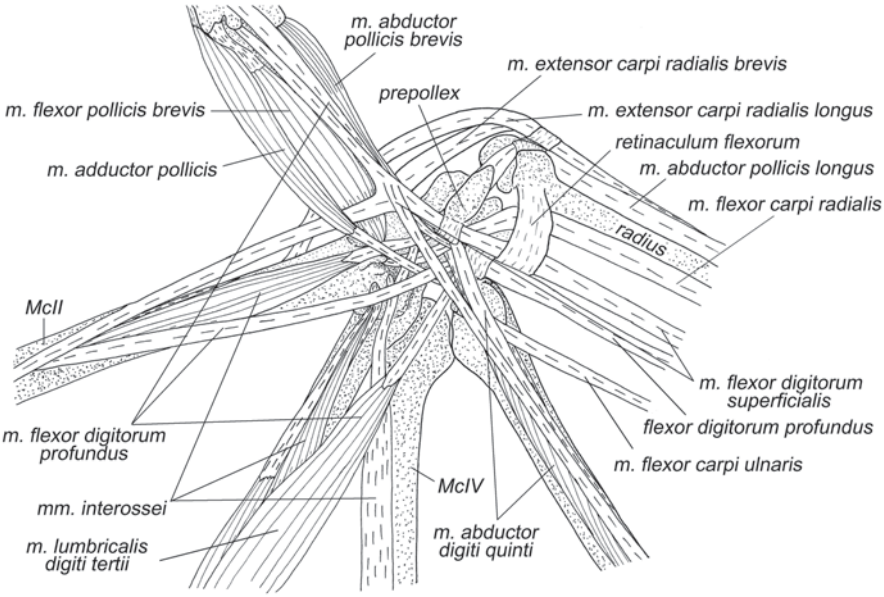


Fig. 3.80 Muscles of the carpal region of *C. sphinx*, ventral view, layer I.

the second muscular belly just described for fruit bats. We treat this belly as the *m. lumbricalis digiti tertii*, while Vaughan ascribed it to the *mm. interossei*; he decided that this muscle originates from the *pisiforme* (instead of passing over it), which is, in any case, a very strange point of origin for the *mm. interossei*. In some microbats, the terminal tendon of the *m. flexor digitorum profundus*, near its division into branches, gives rise to one or two *mm. lumbricales* more typical in appearance than those of fruit bats and *Eumops* (see later in the text).

In accordance with significant structural differences in this muscle, it widely varies in function among bats. In all cases, it flexes the radiocarpal joint and digit I up to its preungual joint. Depending on branching, it can also flex the second, third, or fourth digits and, in free-tailed bats, it folds the fifth carpometacarpal joint. This muscle also pulls digits together. Vaughan (1959) proposed that this muscle helps maintain the optimal camber of the plagiopatagium during the downstroke of the wing. However, this is only applicable to free-tailed bats, as other chiropterans have lost the tendon of digit V.

Musculus flexor carpi ulnaris (Figs. 3.69, 3.76, 3.77, 3.79, 3.80, 3.82, 3.83) in **fruit bats** originates from the distal part of the medial epicondyle of the humerus and the palmar surface of the rudimentary ulna in its proximal one-fourth by a small aponeurosis. A thick terminal tendon inserts on the crest on the ventral surface of the *pisiforme*.

In **microbats**, this muscle originates from either the medial epicondyle of the humerus (for instance, in *Myotis*: Vaughan 1970b) or the tip of its styloid process, if developed (for instance, in *Eumops*: Vaughan 1970b), or the palmar surface of

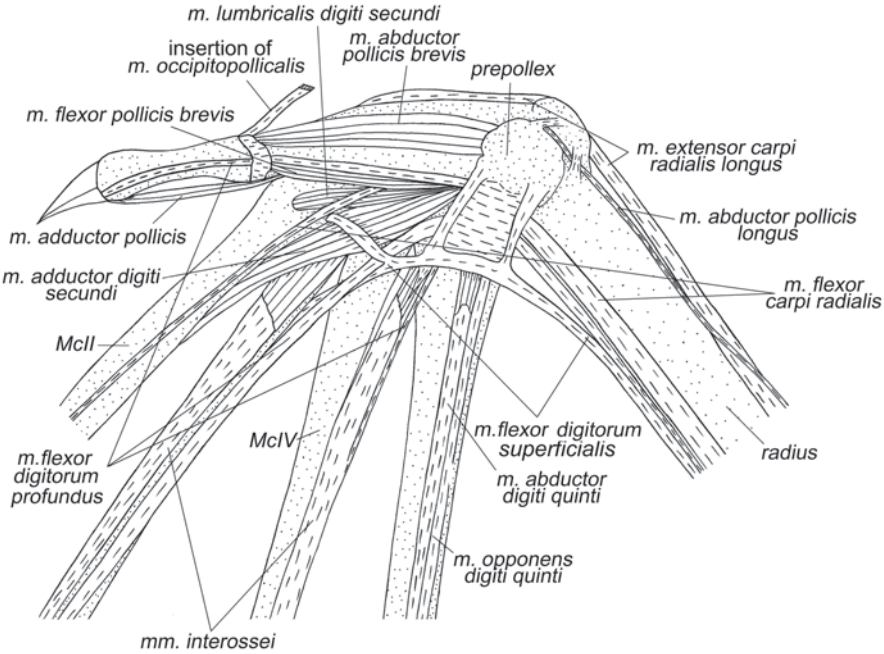


Fig. 3.81 Muscles of the carpal region of *R. ferrumequinum*, ventral view.

the ulna (for instance, in *Macrotus* (Vaughan 1970b) and *Hipposideros*). The belly of this muscle is relatively small and its fibers are short. The terminal tendon runs along the ulnar surface of the antebrachium and inserts on the *pisiforme*. In horseshoe bats, this muscle is almost completely reduced.

The muscle adducts the manus to the antebrachium. Vaughan (1959, 1970a) supposed that when the elbow joint is being flexed by any external force (for instance, produced by contraction of the m. biceps brachii), the tip of the styloid process tends to move away from the pisiforme, and, hence, the m flexor carpi ulnaris, which connects these two points, undergoes tension and "automatically," without activation, transmits the elbow flexion into flexion of digit V via the pisiforme. However, such mechanism appears to be impossible, as relaxed muscles are incapable of transmitting forces. Only a ligament could help in this case.

Intrinsic Muscles of Manus

As a result of morphofunctional changes accompanying the formation of the wing in chiropterans, short muscles of the manus have undergone essential transformations, primarily reduction. That is why the establishment of their exact homologies is usually extremely complicated. The synonymy of our terminology with that of other authors is represented in Table 3.1.

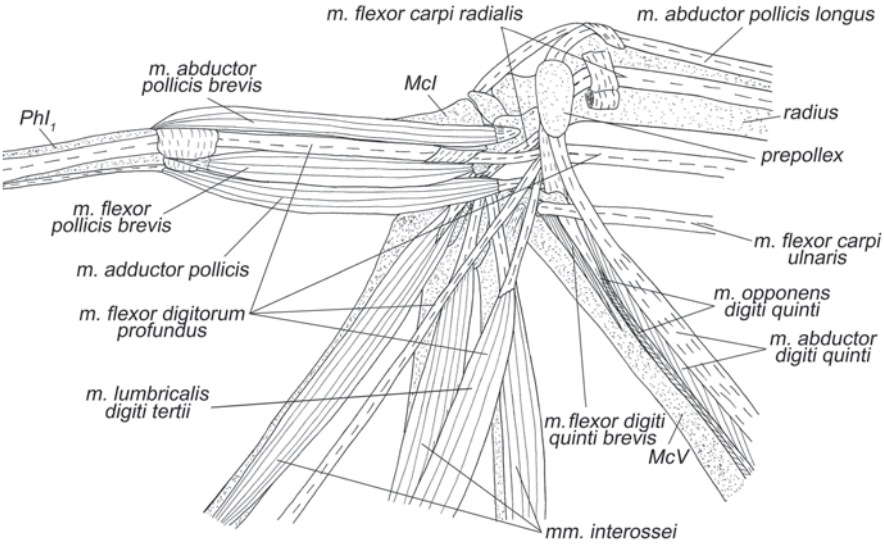


Fig. 3.82 Muscles of the carpal region of *C. sphinx*, ventral view, layer II.

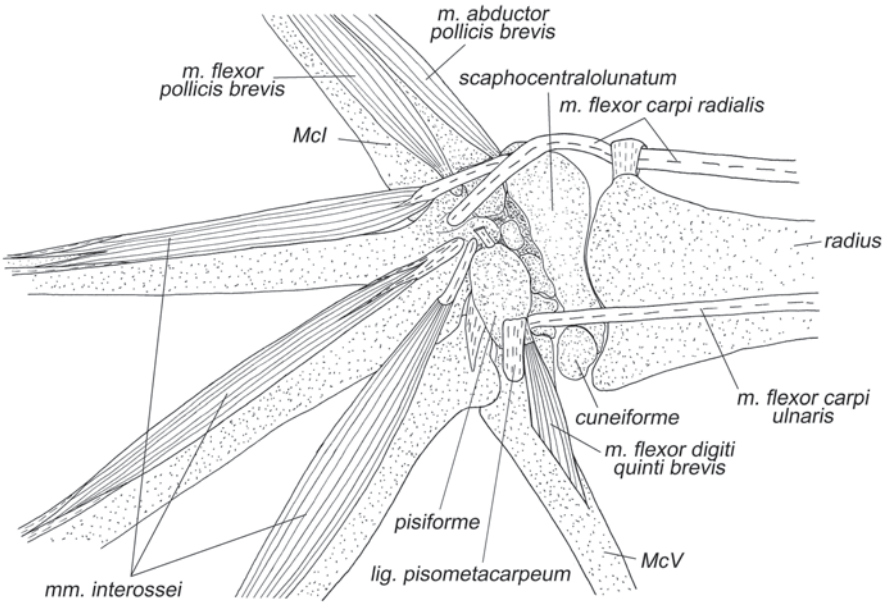


Fig. 3.83 Muscles of the carpal region of *C. sphinx,* ventral view, layer III.

Table 3.1 Intrinsic Muscles of the Manus of Bats (except for the *mm. lumbricales*)

Our data				Macalister (1872)	Vaughan (1959, 1970b)	Norberg (1970, 1972)	Kovtun (1978)
Muscle	Taxa	Origin	Insertion				
Muscles of digit I							
m. abductor pollicis brevis	Fruit bats	*Lig. scaphocentralolunatum-McI*	(*McI/PhI*$_1$)	+	x	+	x
	Microbats	*Prepollex* or *scaphocentralolunatum* or *trapezium*	(*McI/PhI*$_1$) or *PhI*$_1$		+	+	+
m. flexor pollicis brevis	Fruit bats	*McI* or *McII*	(*McI/PhI*$_1$)	*M. opponens pollicis, m. flexor pollicis brevis radialis, m. flexor pollicis brevis ulnaris*	x	+	x
	Microbats	*McI* or *McII*	(*McI/PhI*$_1$) or *PhI*$_1$		+	+ (Medial, innermost, outermost bellies)	+
m. adductor pollicis	Fruit bats	*Pisiforme*	*PhI*$_2$	+	x	+	x
	Microbats	*McI* or *McII*	*PhI*$_2$		+	+ (>(*McI/PhI*$_1$))	+
Muscles of digits II, III, and IV							
m. adductor digiti secundi	Fruit bats	—	—	?	x	—	x
	Microbats	*Capitatum* or *trapezoideum* or *trapezium*	*McII*	?	+	+	+
m. interosseus digiti secundi	Fruit bats	*Scaphocentralolunatum & trapezium*	(*McII/PhII*$_1$)	?	x	*Mm. interossei 1, 2* (>*D2*)	x
	Microbats	—	—	?	—	—	—
m. interosseus digiti tertii	Fruit bats	*McII*	(*McIII/PhIII*$_1$)	+ (*Capitatum & trapezoideum*>)	x	*Mm. interossei 3, 4* (>*D3*)	x
	Microbats	*McII*	*PhIII*$_1$	+	*M. interosseus 1 & m. interosseus dorsale*	*M. interosseus 1 & m. interosseus dorsale* (*McII & capitatum & trapezoideum* >(*McIII/PhIII*$_1$) & *PhIII*$_1$)	*M. interosseus palmare III & m. interosseus dorsale III*

Table 3.1 (continued)

Our data				Macalister (1872)	Vaughan (1959, 1970b)	Norberg (1970, 1972)	Kovtun (1978)
Muscle	Taxa	Origin	Insertion				
m. interosseus digiti quarti	Fruit bats	*McII*	(*McIV/PhIV*$_1$)	—	x	*Mm. interossei 5, 6* (>*D4*)	x
	Microbats	*Capitatum*	*PhIV*$_1$		*Mm. interossei 3, 4* (*McIII* & *McIV*>(*McIV/PhIV*$_1$))	*Mm. interossei 2, 3*	+
Muscles of digit V							
m. abductor digiti quinti	Fruit bats	*Prepollex*	*PhV*$_2$	*M. flexor digiti quinti brevis (radial interosseus D5)*	x	+	x
	Microbats	*Prepollex* or *pisiforme* or *lig. prepollex-pisiforme*	(*McV/PhV*$_1$) or *PhV*$_1$ or *PhV*$_2$		+	+	*M. flexor digiti minimi brevis*
m. opponens digiti quinti	Fruit bats	*Pisiforme*	*PhV*$_2$	*M. abductor digiti quinti*	x	+	x
	Microbats	*Pisiforme*	*PhV*$_1$, *PhV*$_2$		+	+	*M. abductor et opponens digiti minimi*
m. flexor digiti quinti brevis	Fruit bats	*Lig. pisometacarpeum*	*McV*	*M. opponens digiti quinti*	x	*M. interosseus 7* (>*D5*)	x
	Microbats	—	—	—	—	—	—

"x" – no data; "+" – the muscle is termed and described as in our study; "—" – the muscle is lacking; "?" – the description is not sufficient for homologization; *DI-DV* – digits I-V; *McI-McV* – metacarpals of digits I-V; *PhI-PhV* – phalanges of digits I-V; *Ph*$_1$-*Ph*$_2$ – proximal and distal phalanges; ">" – the sign linking origin and insertion in the data cited; "&" – the sign of combined attachment; "/" – the sign of a joint.
For instance, (*McIII* or *McIII* & *McIV*>(*McIV/PhIV*$_1$)) means that a muscle originates either from metacarpals III or from metacarpals III and IV and inserts on articular capsule of the metacarpophalangeal joint of digit IV.

Musculus abductor pollicis brevis (Figs. 3.72, 3.73, 3.79–3.83) in **fruit bats** originates by a very short aponeurosis from the ligament connecting the *scaphocentralolunatum* with the base of metacarpal I. The belly is composed of long fibers running along metacarpal I and inserting on the medial surface of the articular capsule and the medial sesamoid bone of the metacarpophalangeal joint of digit I.

In **microbats**, the muscle originates from the *scaphocentralolunatum* and ligament between it and metacarpal I (as in fruit bats), or from the prepollex and ligament between it and metacarpal I, or from the *trapezium*. The insertion is on the medial sesamoid bone of the metacarpophalangeal joint or the medial surface of the base of the first phalanx of digit I.

The muscle abducts medially digit I and participates in its flexion.

Musculus flexor pollicis brevis (Figs. 3.79–3.83) in **fruit bats** originates from the ventral surface of the proximal head of either first or second metacarpal. It inserts on the ventral surface of the articular capsule and on the lateral sesamoid bone of the first metacarpophalangeal joint.

In **microbats**, Macalister (1872) distinguished three separate muscles, which he termed *m. flexor pollicis brevis radialis*, *m. flexor pollicis brevis ulnaris*, and *m. opponens pollicis*. Norberg (1970) also recognized the three heads but, according to our data, this muscle is a single unit. It originates similarly to the respective muscle of fruit bats and inserts on the ventral surface of the articular capsule and the lateral sesamoid bone (for example, in horseshoe bats) or both sesamoid bones (for example, in vespertilionids: Vaughan 1959; Norberg 1970) of the first metacarpophalangeal joint, sometimes, also on the base of the first phalanx of digit I.

The muscle flexes the first metacarpophalangeal joint and, if it originates from metacarpal II, also participates in lateral adduction of metacarpal I.

Musculus adductor pollicis (Figs. 3.72–3.74, 3.79–3.82) in **fruit bats** originates from the ventral surface of the *pisiforme* by a tendon, which crosses the carpus almost transversely. From this tendon, the muscular fibers descend along the lateral side of metacarpal I and, at the level of the metacarpophalangeal joint, pass into a terminal tendon, which inserts on the lateral side of the base of the ungual phalanx of digit II. On the way, some muscular fibers may insert fleshy on the lateral side of the base of its first phalanx.

In **microbats**, it originates much more medially, from the base of metacarpal II or even the lateral side of the base of metacarpal I. Between the first and second digits, the muscle passes onto the dorsal side of digit I and inserts there on the base of the ungual phalanx.

In fruit bats, this muscle adducts laterally digit I, and, in microbats, it supinates digit I.

Musculi lumbricales (Fig. 3.80–3.82) are represented in **fruit bats** by *m. lumbricalis digiti tertii*, which forms an accessory belly interrupting the third terminal tendon of the *m. flexor digitorum profundus* at the level of metacarpal III. Macalister (1872) proposed that this accessory belly is the *m. interosseus digiti tertii* incorporated by the *m. flexor digitorum profundus*. However, beyond this, fruit bats already possess the fully developed *m. interosseus digiti tertii*; it has only one belly but two (lateral and medial) terminal tendons, which prove that the muscle is in fact

the fused *mm. interossei digiti tertii lateralis et medialis*. That is why, we adhere to the opinion of Humphry (1869), who has also found the accessory belly in the third tendon of the *m. flexor digitorum profundus* in the female *Pteropus* and noted its similarity with the *m. lumbricalis*. In other specimens of *Pteropus*, Humphry reports similar muscular fibers overlapping but not interrupting tendons II and III of the *m. flexor digitorum profundus*.

Some **microbats** have one or two lumbrical muscles represented by thin ribbon-like muscular fascicles, which originate at the branching point of the *aponeurosis flexoria communis* (looking in bats like a tendon) of the *m. flexor digitorum profundus*. Horseshoe bats have only the *m. lumbricalis digiti secundi*, which inserts on the lateral part of the ventral surface of the base of metacarpal II. In the brown long-eared bat, Norberg (1970) has found two heads, which insert on the lateral surface of proximal one-fourth of metacarpals II and III: *m. lumbricalis digiti secundi* and *m. lumbricalis digiti tertii*. In *Eumops*, as follows from Vaughan's (1970b) data, this muscle closely corresponds to that of fruit bats, looking like a second belly in the third tendon of the *m. flexor digitorum profundus*.

In microbats, the muscle participates in flexion and lateral displacement of digits II and III. In fruit bats and Eumops, its contraction switches on the transition of force of the m. flexor digitorum profundus onto digit III.

Musculus adductor digiti secundi (Fig. 3.81) is absent in **fruit bats**.

In the majority of **microbats,** this muscle is present and originates from the ventral surface of the *capitatum, trapezoideum*, or *trapezium*. Its fibers insert on the lateral surface of the proximal part of metacarpal II. According to Vaughan (1959), this muscle is particularly well developed in free-tailed bats and absent in American leaf-nosed bats.

The muscle adducts laterally digit II.

Musculus flexor digiti quinti brevis (Figs. 3.82, 3.83) is found only in **fruit bats** as a very weak rudiment. It originates by a very short aponeurosis from the *ligamentum pisometacarpeum* and inserts on the ventral surface of the proximal part of metacarpal V. Norberg (1972) regarded this muscle as the rudimentary *m. interosseus palmaris digiti quinti*, but this is obviously wrong, since the *mm. interossei* are used to originate rather than insert on metacarpals.

The small size of the muscle implies that it is rather a sensor than the effective flexor of the fifth carpometacarpal joint.

Musculus abductor digiti quinti (Figs. 3.79–3.82) was identified as such by Norberg (1970) and Vaughan (1959, 1970b). Kovtun (1978) believed that this muscle is homologous to the *m. flexor digiti quinti brevis* of other mammals, but there is a more probable candidate for this flexor in fruit bats (see the previous muscle).

In **fruit bats**, the *m. abductor digiti quinti* originates by a thick tendon from the lateral side of the prepollex. Therefrom, muscular fibers come onto the terminal aponeurosis (shared with the underlying *m. opponens digiti quinti*), which bifurcates into thin bands running along the sides of metacarpal V to the metacarpophalangeal joint. Having passed its articular capsule, these bands become thinner and thinner and, at the middle of the second (last) phalanx, blend into the periosteum of its ventral surface.

In **microbats**, this muscle originates by a thin tendon from the prepollex, *pisiforme*, or ligament between them. The belly is short and lies on the base of metacarpal V. A thin terminal tendon runs along the ventral side of digit V and inserts on the articular capsule of the metacarpophalangeal joint (in the majority of species), the first phalanx (in some vespertilionids), or the second phalanx (in horseshoe bats).

The muscle flexes digit V and, in the case of the origin on the prepollex, adducts it medially.

Musculus opponens digiti quinti (Figs. 3.81, 3.82) was named by Kovtun (1978) the *m. abductor et opponens digiti minimi*, apparently based on the fact that, as just mentioned, he took the true *m. abductor digiti quinti* for the *m. flexor digiti quinti brevis*.

In **fruit bats**, the *m.opponens digiti quinti* originates by a thick tendon from the ventral surface of the *pisiforme* and inserts by an aponeurosis shared with the *m. abductor digiti quinti* on the second (last) phalanx of digit V.

In **microbats**, this muscle originates by a tendon from the ventral surface of the *pisiforme*, has a thin belly lying along the proximal one-fourth of metacarpal V, and terminates by a tendon running along the ventral surface of digit V, parallel to the tendon of the *m. abductor digiti quinti*, to either proximal or distal phalanx.

The muscle flexes digit V.

Musculi interossei (Figs. 3.74, 3.79–3.83) are so reduced in bats that the traces of their division into the palmar and dorsal series are hardly visible. Based on the double terminal tendons, we agree with the point of view (Norberg 1972; Kovtun 1978) that the chiropteran *mm. interossei* were formed by a pairwise fusion of the ancestral muscles of the same digit.

Fruit bats have three such muscles. The *m. interosseus digiti secundi* originates either by a small double tendon from the *scaphocentralolunatum* and *trapezium* or only from the *scaphocentralolunatum*. It has two terminal tendons running along both sides of metacarpal II to the articular capsule of the metacarpophalangeal joint. The *m. interosseus digiti tertii* and *m. interosseus digiti quarti* originate close to each other from the ventral surface of the proximal head of metacarpal II; muscular fibers of both are long. Similarly to the previous head, each one terminates by a pair of tendons running along both sides of respective metacarpal to the articular capsule of the metacarpophalangeal joint of digits III and IV.

In **microbats**, we distinguish only two muscles of this series: the *m. interosseus digiti tertii* and *m. interosseus digiti quarti*.

The *m. interosseus digiti tertii*, in horseshoe bats, originates from the lateral surface of the proximal head of metacarpal II, and in long-eared bats (Norberg 1970), also from *trapezoideum* and *capitatum*. A short belly passes into two thin terminal tendons, which insert on the ventral surface of the first phalanx of digit III. In *Plecotus* (Norberg 1970) and *Eumops* (Vaughan 1959, 1970b), this muscle retains more pronounced traces of its paired origin, its medial part having been regarded as the remnant of the dorsal interosseous muscles (see Table 3.1).

The m. *interosseus digiti quarti* originates by a very short tendon from the palmar surface of the *capitatum*. Its thin belly lies along the proximal part of metacar-

pal IV and terminates by a pair of tendons running along both sides of the ventral surface of the metacarpal to the first phalanx of digit IV.

One of the short flexors of digit III of *Eumops,* which was also ascribed to the *mm. interossei* by Vaughan (1970b), is in fact the *m. lumbricalis digiti tertii* (see earlier in the text).

The muscles flex metacarpophalangeal joints of respective digits but can hardly pull them together or spread sidewise, since they pass closely parallel to the metacarpals.

Musculature of Wing Membrane

Musculus occipitopollicalis is specific to chiropterans being probably derived from the *m. platysma* as is shown by its innervation by the *nervus facialis* (Tokita et al. 2012); note that the same innervation is found in the propatagial muscle of colugos (Thewissen and Babcock 1993), which we call the *m. tensor propatagii*. The *m. occipitopollicalis* of chiropterans originates from the midline of the *supraoccipitale* or, in *Pteropus* (Humphry 1869), by four strands: from the occipital crest, lower jaw, throat, and the *m. pectoralis*. The muscle runs as a thin strap of long fibers along the entire anterior border of the propatagium. In the majority of species, its middle part receives one or two thin fascicles from the *m. pectoralis pars anterior* or *m. clavodeltoideus*. Some fibers insert on the base of the first phalanx of digit I, and other on the metacarpal of digit II.

This muscle tightens the anterior border of the propatagium and helps medial abduction of the first finger.

Musculus coracocutaneus shares innervation and embryonic muscular progenitor with the *m. cutaneus trunci* (Tokita et al. 2012). This muscle is found in all chiropterans as a long thin band, which originates from the coracoid process of the scapula and passes inside the plagiopatagium toward digit V, but does not reach it being vanished in the skin.

Electromyography shows, that this muscle contracts during the latter two-thirds of the upstroke (Arganbright 1984). Tension of the plagiopatagium by this muscle makes its camber shallower. In addition, the muscle participates in folding the wing membrane.

Musculus humeropatagialis shares innervation and embryonic muscular progenitor with the *m. cutaneus trunci* (Tokita et al. 2012). It was described in *Eumops* by Vaughan (1970b), as well as in *Noctilio*, Nycteridae, Megadermatidae, some species of Phyllostomidae, Mormoopidae, Molossidae, and Emballonuridae by Strickler (1978). Its fibers arise on the medial side of the elbow from the *fascia antebrachialis*, run parallel to the antebrachium, and vanish into the plagiopatagium.

Musculi plagiopatagiales are the intrinsic (non-skeletal) muscles of the wing membrane of chiropterans. They are thin fascicles of muscular fibers running inside the plagiopatagium perpendicular to the antebrachium.

These muscles play a very important role during the flight, tightening the plagiopatagium and, hence, shallowing its camber. In addition, they participate in folding the wing membrane.

We dismiss in the current research the fascicles sent into the plagiopatagium by the hindlimb muscles (Humphry 1869; Macalister 1872), as well as the *m. uropatagialis*, which passes along the border of the uropatagium in fruit bats and some microchiropterans (Norberg 1972; Glass and Gannon 1994).

References

Altenbach JS (1979) Locomotor morphology of the vampire bat, *Desmodus rotundus*, American Society of Mammalogists Special Publications, Pittsburgh 6:1–137

Arganbright K (1984) Electromyographic analysis of an intrinsic wing muscle in *Antrozous pallidus*. J Mammal 653(3):480–481

Foehring RC, Hermanson JW (1984) Morphology and histochemistry of flight in free-tailed bats, *Tadarida brasiliensis*. J Mammal 65(3):388–394

Glass PJ, Gannon WL (1994) Description of *M. uropataginalis* (a new muscle), with additional comments from a microscopy study of the uropatagium of the fringed myotis (*Myotis thysanodes*). Can J Zool 72(10):1752–1754

Hermanson JW, Altenbach JS (1983) The functional anatomy of the shoulder of the pallid bat, *Antrozous pallidus*. J Mammal 64(1):62–75

Hermanson JW, Altenbach JS (1985) Functional anatomy of the shoulder and arm of the fruit-eating bat *Artibeus jamaicensis*. J Zool Lond 205(2):157–177

Humphry GM (1869) The myology of the limbs of *Pteropus*. J Anat Physiol 3(2):294–319

Jullien R (1969) Interprétation des surfaces articulaires du coude des chiroptères. Mammalia 33(4):659–665

Kovtun MF (1970) Morpho-functional analysis of shoulder muscles of bats in connection with their flight. Vestn Zool 1:18–22 (in Russian with English summary)

Kovtun MF (1976) Comparative morphology of the shoulder girdle muscles in Horseshoe bat (Chiroptera, Rhinolophidae). Vestn Zool 5:19–24 (in Russian with English summary)

Kovtun MF (1977) Comparative morphology of the free thoracic limb muscles in Horseshoe bat (Chiroptera, Rhinolophidae). Vestn Zool 3:24–32 (in Russian with English summary)

Kovtun MF (1978) Locomotor apparatus of bats. Naukova Dumka, Kiev (in Russian)

Kovtun MF (1984) Structure and evolution of locomotion organs in bats. Naukova Dumka, Kiev (in Russian)

Le Gros Clark WE (1926) On the anatomy of the pen-tailed tree-shrew (*Ptilocercus lowii*). Proc Zool Soc Lond 96(4):1179–1309

Ledenev SYu (1988) Features of the wrists structure in bats of the genus *Nyctalus*. In: Topachevskiy VA, Kovtun MF (eds) Bats (morphology, ecology, echolocation, parasites, protection). Naukova Dumka, Kiev, p 26–29 (in Russian)

Lopez-González C, Polaco OJ (2001) Descripción y variación del esqueleto postcraneal de *Glossophaga morenoi* Martínez y Villa-R., 1938 (Chiroptera: Phyllostomidae). Acta Zool Mex 83:1–28

Macalister A (1872) The myology of the Chiroptera. Phil Trans R Soc Lond 162:125–172

Maniakas I, Youlatos D (2012) Myological adaptations to fast enduring flight in European free-tailed bats, *Tadarida teniotis* (Molossidae, Chiroptera). Ital J Zool 79(4):574–581

Norberg UM (1969) An arrangement giving a stiff leading edge to the hand wing in bats. J Mammal 50(4):766–770

Norberg UM (1970) Functional osteology and myology of the wing of *Plecotus auritus* Linnaeus (Chiroptera). Ark Zool 22(2):483–543

Norberg UM (1972) Functional osteology and myology of the wing of the dog-faced bat *Rousettus aegyptiacus* (E. Geoffroy) (Mammalia, Chiroptera). Z Morph Tiere 73:1–44

Norberg UM (2002) Structure, form, and function of flight in engineering and the living world. J Morphol 252(1):52–81

Riskin DK, Bergou A, Breuer KS, Swartz SM (2012) Upstroke wing flexion and the inertial cost of bat flight. Proc R Soc B 279(1740):2945–2950

Schliemann H (1997) Das sekundare Schultergelenk der Vespertilionoidea (Mammalia: Chiroptera). Z Saugetier 62:321–329

Schliemann H, Schlosser-Sturm E (1999) The shoulder joint of the Chiroptera—morphological features and functional significance. Zool Anz 238(1/2):75–86

Schlosser-Sturm E, Schliemann H (1995) Morphology and function of the shoulder joint of bats (Mammalia: Chiroptera). J Zool Syst Evol Res 33(2):88–98

Strickler TL (1978) Functional osteology and myology of the shoulder in the Chiroptera. Contrib Vertebr Evol 4:1–198

Szalay FS, Lucas SG (1993) Cranioskeletal morphology of archontans, and diagnoses of Chiroptera, Volitantia, and Archonta. In: MacPhee RDE (ed) Primates and their relatives in phylogenetic perspective. Plenum Press, New York, p 187–226

Thewissen JGM, Babcock SK (1991) Distinctive cranial and cervical innervation of wing muscles: new evidence for bat monophyly. Science 251(4996):934–936

Thewissen JGM, Babcock SK (1993) The implications of the propatagial muscles of flying and gliding mammals for archontan systematics. In: MacPhee RDE (ed) Primates and their relatives in phylogenetic perspective. Plenum Press, New York, p 91–107

Tokita M, Abe T, Suzuki K (2012) The developmental basis of bat wing muscle. Nature Communications 3, Article number: 1302. doi:0.1038/ncomms2298

Vaughan TA (1959) Functional morphology of three bats: *Eumops, Myotis, Macrotus*, University of Kansas Publications, Museum of Natural History, Lawrence 12(1):1–153

Vaughan TA (1966) Morphology and flight characteristics of molossid bats. J Mammal 47(2):249–260

Vaughan TA (1970a) The skeletal system. In: Wimsatt WA (ed) Biology of bats, vol 1. Academic Press, New York, p 97–138

Vaughan TA (1970b) The muscular system. In: Wimsatt WA (ed) Biology of bats, vol 1. Academic Press, New York, p 139–194

Vaughan TA, Bateman GC (1970) Functional morphology of the forelimb of mormoopid bats. J Mammal 51(2):217–235

Voss H, Herrlinger R (1956) Taschenbuch der Anatomie. Bd 1. Einführung in die Anatomie. Bewegungsapparat. VEB Gustav Fischer, Jena

Walton DW, Walton GM (1970a) Post-cranial osteology of bats. In: Slaughter BH, Walton DW (eds) About bats: a chiropteran biology symposium, Fondren Science Series 11. Southern Methodist University Press, Dallas, p 93–126

Walton GM, Walton DW (1970b) Post-cranial osteology of *Chilonycteris psilotis*. Rev Biol Trop 17(2):147–164

Chapter 4
Functional Analysis of Locomotor Apparatus of Colugos

Some Biological Aspects of Colugos

Typical habitats of colugos are primary high tropical forests of Southeastern Asia. At the same time, with the advent of secondary tropical forests, rubber plantations, and oil-palms, colugos adapted to the new conditions.

The entire life cycle of these animals is confined to trees. According to Lim (2007), about 80 % of their lifetime, colugos roost mostly clinging to the trunk surface or suspending from the branches. Active movements take about 10 % of their time, and approximately the same time is spent on feeding, during which colugos also move in the forest canopy. Terrestrial locomotion of colugos has not been described, but it is believed that they are virtually helpless on the ground (Vaughan et al. 2011); however, an animal released after capturing demonstrates ability for moving by leaps, as it tries to reach the nearest tree.

The most typical posture of resting colugos is clinging flat onto a vertical tree trunk; they do not use hollows and other similar shelters, though Dzulhelmi (2013) presents data indicating that sometimes colugos hide in wide vertical trunk cracks. It should be noted that they are always positioned head upward; no inverted position characteristic of chiropterans has been recorded. The forelimbs are sprawled laterally; the shoulder and elbow joints are slightly bent, with a varying angle (Fig. 4.1). The hindlimbs with bent joints remain in the parasagittal plane and are tucked under the body, so that feet rest on the trunk surface. The large claws of fore and hind limbs firmly attach animal to the bark, so that forelimbs pull the body to the support to prevent reclining.

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_4

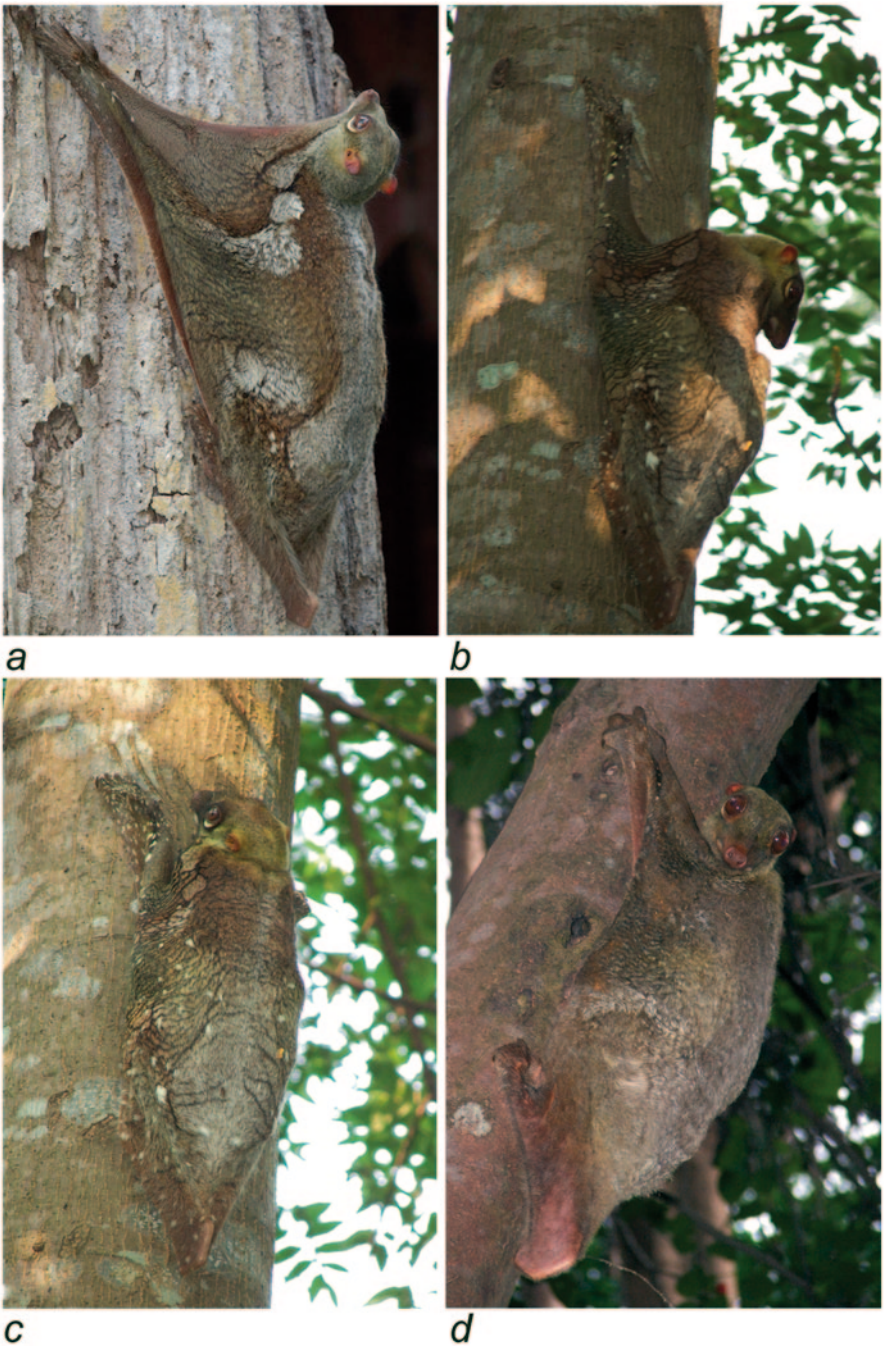


Fig. 4.1 Colugos clinging onto trunks (photo by: *a* – Paul Chan, *b, c, d* – Peter Loh Tuck Kheong).

Fig. 4.2 Colugo suspended below the horizontal support (photo by Nick Garbutt).

In addition to clinging in upright posture along a trunk, colugos use certain other way of roosting, i.e., suspending from relatively thin horizontal branches, although they spend considerably less time in this position (Fig. 4.2). In this case, forelimbs are completely straightened and palms are turned inside (to the extremely supinated state). The hindlimbs are positioned similarly, but the knee and talocrural joints are usually slightly bent.

Colugos can suspend using only fore or hind limbs, and even only one limb, but these postures never last for a long time.

Movement in a search for food is the major vital activity of colugos. The point is that these leaf-eating animals refrain from consuming leaves rich in tannin and are very selective with reference to feeding objects. In their habitats, forage trees (in Singapore, these are primarily plants of the family Myrtaceae) show mosaic distribution and only account for about 5% of the total forest stand (Agoramoorthy et al. 2006; Lim 2007). Moreover, they consume only young foliage. It is known that colugos cover even greater distances than leaf-eating primates. During one night, they can move over 1.5 km, while, for example, monkeys of the subfamily Colobinae usually migrate for at most 800 m per day (Wischusen and Richmond 1998). Lim (2007) believes that this difference is associated with the fact that, in colugos, digestion is not delayed for fermentation and food passes through the digestive tract approximately ten times more rapidly than in arboreal leaf-eaters which are characterized by long fermentation of cellulose. In this connection, efficiency of extraction of nutrients from food is significantly lower, and colugos have to cover large distances searching for juicy young leaves of suitable trees.

Colugos can travel horizontally passing from branch to branch, although they normally use gliding for this purpose. Gliding leaps enable rapid movements for great distances and, even taking into account the time spent for climbing up the tree trunk, this locomotor pattern is more rapid than running from one tree to another along branches (Byrnes et al. 2011). Moving by air between trees located at a considerable distance is not only faster, but also more economical and safer than running on the ground. Gliding may have emerged in primary high tropical forests, with free space under the forest canopy and scarcity of lianas. The indirect evidence

for this is the repeated appearance of gliding in different vertebrate groups inhabiting tropical forests of the Eastern Hemisphere. A link between the emergence of gliding and structure of forests is discussed in a number of studies (Emmons and Gentry 1983; Dudley and DeVries 1990). It should be noted that colugos are the indisputable champions in gliding among mammals; they can glide for more than 130 m at an angle 5° to the horizon (Jackson 2000). Later, the maximal gliding distance of about 150 m was registered (Byrnes et al. 2008). However, even twice as long distances or more are theoretically attainable for colugos given that their gliding angle is 5° and the medium tree height in primary forest, according to Dudley and DeVries (1990), exceeds 30–40 m.

Animals of the same size, the giant flying squirrels *Petaurista petaurista*, rank the second place in gliding performance among mammals; they cover almost the same distances as colugos (up to 120 m), although their gliding angle exceeds 10° (Scholey 1986), which implies an approximately twofold height loss per unit distance of horizontal progression.

Locomotion of Colugos

Gliding

Colugo begins a glide by a starting leap, pushing itself away from a support. The starting leap is performed from different postures, e.g., sitting on a trunk or thin vertical branch (Fig. 4.3a) or suspending from a branch. In the first two cases, like a lemur leaping from a trunk, colugo first turns the head in the direction of the forthcoming leap, and then, draws hindlimbs in the position optimum for a thrust (Figs. 4.3b, c), and, finally, takes away its forelimbs and pushes the body by the hindlimbs (Fig. 4.3d). During the thrust, colugo turns its body in the direction of forthcoming leap, its forelimbs being stretched posteriorly along the body (Figs. 4.3d, e). By the end of the thrust, hindlimbs are also stretched posteriorly (Figs. 4.3e, f). Having left the support, the colugo draws its forelimbs laterally and anteriorly, spreading the wing membrane (Figs. 4.3f–h). In so doing, the elbow joint remains slightly flexed so that olecranon points up above the back, and the manus moves anteriorly in the frontal plane. Simultaneously, the hindlimbs are sprawled laterally in the frontal plane too. Initially, the femur is perpendicular to the longitudinal body axis and the crus is parallel to it. Spreading of the membrane is completed with straightening all limbs: dorsal side of the elbows and knees faces upward, the manae are at the level of the head, the feet are at the level of the midlength of the tail, and all digits are widely spread (Fig. 4.4). In the manus, the first and fifth fingers are somewhat flexed (depressed), and the second through fourth ones, on the contrary, are extremely hyperextended, so that the manus as a whole is shaped similar to the terminal winglet of an aircraft. In general, the flight apparatus of colugo resembles a pentagonal kite, with an adjustable framework (composed of four limbs, head, and tail). Normally, the head is tilted muzzle down, so that the leading

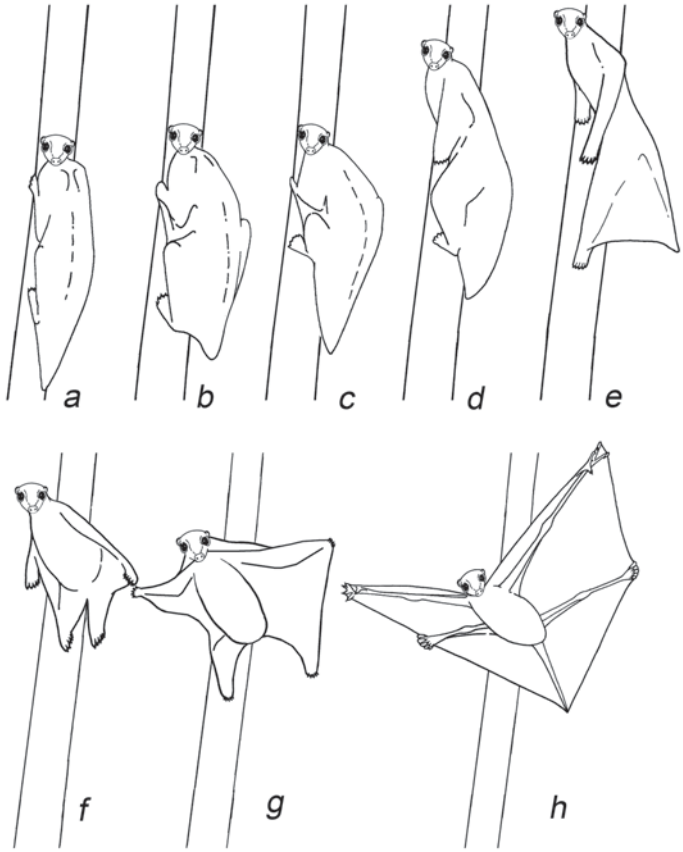


Fig. 4.3 Successive stages of colugo's take-off for a glide (traced from video).

edge of the membrane is V-shaped in anterior view, which apparently provides stability against side-slipping. In addition, the forelimbs are pronated (most probably, in the shoulder joint), and thus the palm faces somewhat posteriorly and the leading edge of propatagium forms a wing camber. To change the speed and direction of gliding, colugo changes the configuration of the wing membrane by repositioning the elements of its framework (limbs, head or tail).

The main difference of take-off from a horizontal branch is that the body initially falls downward rather than moves sideward, as in the take-off from a trunk. Only after spreading the membrane, colugo becomes enabled for horizontal motion. Meanwhile, the general algorithm of limb movements remains the same.

An important advantage of gliding as compared to simple leaping is that the distance covered does not considerably depend on the initial velocity, and hence, the mechanical work of limb muscles at take-off may be reduced.

In steady gliding, colugos lose about 1 m of height per 10 m of the horizontal progression (Jackson 2000), and the average horizontal speed is about 10 m/s

Fig. 4.4 Gliding colugo (photo by Norman Lim).

(Byrnes et al. 2008). According to Byrnes et al. (2008) colugos landed on near horizontal surfaces in only 4 of the 222 glides. On vertical surfaces, they always land strictly head up. Before landing, colugo moves its head and limbs so as to increase the angle of attack; therefore, the body turns almost upright, and kinetic energy of the body is converted back into potential energy so that the animal rises and, at the same time, slows down to about 4 m/s (Byrnes et al. 2008). The decrease of speed is necessary for soft landing, For the same purpose, the braking distance is increased by stretching the limbs forward as much as possible just before landing; all four limbs touch the tree trunk simultaneously in order to take part in braking the body. It was shown that colugos undergo the greatest braking forces after the shortest glides (Byrnes et al. 2008), and that most gliding mammals avoid short distance glides (Scholey 1986). Apparently, this is because at short distances the ballistic leap does not yet turn into the steady gliding, and, hence, the aerodynamic slowing down by conversion of kinetic energy of the body into potential energy is hardly possible.

Climbing up Trunks

Since gliding is accompanied by an inevitable height loss, climbing up a tree trunk is an immanent element of locomotion of colugos, which requires special adapta-

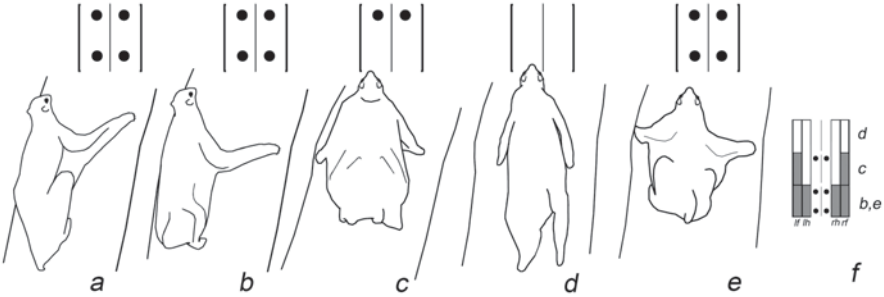


Fig. 4.5 Running of colugo up tree trunk – "pronk" with the forelimb prevalence (traced from video). *a. Typical posture on the trunk b–e. Successive stages of the gait f. Gait diagram. lf* – left forelimb, *lh* – left hindlimb, *rh* – right hindlimb, *rf* – right forelimb.

tions. To ascend as high as possible, the animal has to climb particularly tall trees, which are the thickest in the forest. Observations in Singapore showed that the diameter of trees used by colugos exceeded 45 cm (Byrnes et al. 2008). Speed of vertical progression of colugos on tree trunks is about 1 m/s (Byrnes et al. 2011).

The limb posture at the beginning of upward thrust is similar to that at rest, with the body clinging flat to the trunk surface: the hindlimbs are tucked under the body and forelimbs project anteriorly and laterally, the elbow joints being slightly flexed and fingers pointing anterolaterally (Fig. 4.5a). The thrust is initiated synchronously by four limbs (Fig. 4.5b), although forelimbs are longer and, hence, retain contact with the trunk even when hindlimbs are taken away (Fig. 4.5c). When forelimbs also lose contact with the trunk, they are stretched posteriorly along the body, as hindlimbs (Fig. 4.5d). In a vertical leap along the trunk (unsupported stage of the locomotor cycle) colugo covers a distance approximately equal to its body length. By the end of this stage, the forelimbs are drawn laterally and anteriorly in the frontal plane (Fig. 4.5e) and embrace the trunk, attaching to it by claws. Simultaneously, the hindlimbs are bent and tucked under the body in the parasagittal plane (Fig. 4.5e), taking the initial position for the next thrust. In general, the colugo's running up tree trunks belongs to asymmetrical gaits. Among these, by the sequence of limb movements, the gait most resembles the so-called pronk of some artiodactyls and rodents (Hildebrand 1977), but differs from it, in that, the colugo's forelimbs contact with the substrate for a longer time than the hindlimbs (Fig. 4.5f). Therefore, we classify this gait as the pronk with forelimb prevalence.

Climbing under Branches

Moving along relatively thin horizontal or slightly inclined branches, colugo suspends from below, like a sloth (Fig. 4.2). In this case, not only the hindlimbs move

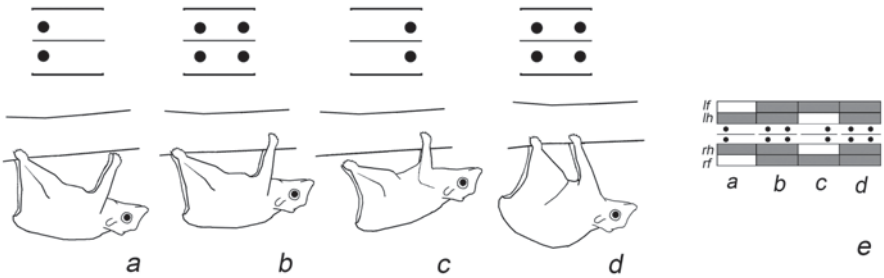


Fig. 4.6 Running of colugo under branch – "bound" (traced from video), *a–d. Successive stages of the gait, e. Gait diagram*. *lf* – left forelimb, *lh* – left hindlimb, *rh* – right hindlimb, *rf* – right forelimb.

in the parasagittal plane, but the forelimbs do so as well. As in the case of ascending trunks, the gait is asymmetrical and coupled, that is the left and right limbs of each pair move in strict synchrony with each other. However, to avoid falling down, the unsupported stages (leaps) when all four limbs are taken away from the substrate are excluded and grips by fore and hind limb pairs are alternating rather than synchronous (Fig. 4.6). The locomotor cycle begins by taking forelimbs away from the branch and straightening the hindlimbs, which thus push the body forward but also downward, away from the branch (Fig. 4.6a). Then, the forelimbs having stretched anteriorly grip the branch and pull the body forward and upward again, toward the branch (Fig. 4.6b). Subsequently, hindlimbs are taken away from the branch (Fig. 4.6c) and are protracted to grip it closer to the forelimbs (Fig. 4.6d). Thus, the gait is represented by the series of alternating four-limb and two-limb stages of support. So, this gait is a kind of bound (Hildebrand 1977), which we classify as the very slow bound, since it lacks unsupported stages. In the fast bound of terrestrial mammals, there are the stages of unsupported leaps instead of the four-limb stages. The four-limb stage of colugo (Fig. 4.6b) following the two-hindlimb stage corresponds to the stage of leap in extended position of the fast bound, while the four-limb stage (Fig. 4.6d) following the two-forelimb stage corresponds to the stage of leap in gathered position of the fast bound.

Mobility of Shoulder Girdle

The analysis of photo- and videomaterials has shown key morphofunctional features associated with the locomotion patterns of colugos described above.

As an animal clings flat onto a thick vertical trunk or glides (membrane being unfolded), the glenoids of the scapulae face laterally and, hence, the scapulae are positioned almost frontally (Fig. 4.4). This allows colugos to spread

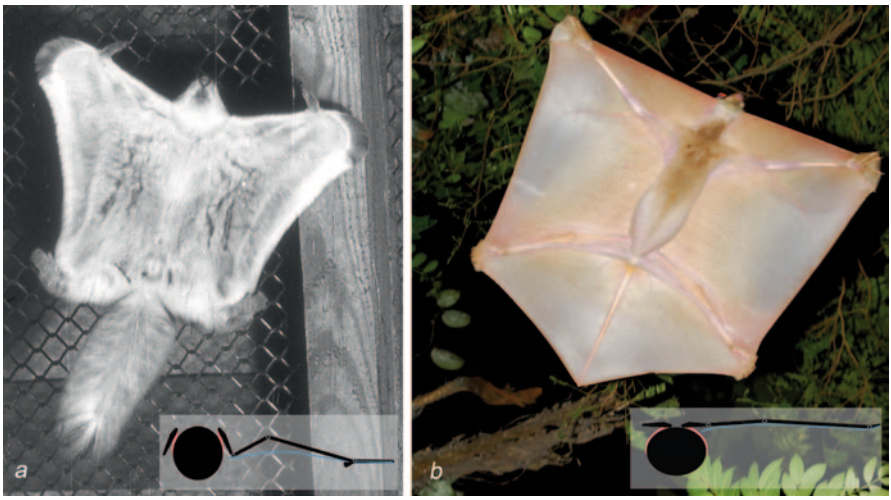


Fig. 4.7 Variants of the flight apparatus in gliding mammals with schemes of the membrane stretching mechanisms in cross section. *a. Pteromys volans* (photo by E.D. Popova-Bondarenko) *b. Cynocephalus variegatus* (photo by Norman Lim)

widely their limbs. In flying squirrels (Pteromyinae), which also can ascend thick trunks and glide, when they do so, the scapulae are inclined in such a manner that the glenoids face ventrolaterally (Fig. 4.7a). Thus, their scapulae occupy an intermediate position between parasagittal (typical to quadrupedal therians) and frontal (achieved by colugos). Consequently, they cannot sprawl the humeri laterally by the shoulder joint elevation, as colugos do (Fig. 4.7b). To stretch further the membrane in the frontal plane, flying squirrels partially compensate this imperfection by lengthening the distal part of the forelimb with cartilaginous spur attached to the lateral side of the manus (Fig. 4.7a). On the contrary, colugos have no need of an extra extension piece for the forelimb skeleton (Fig. 4.7b). Due to the different inclination of scapulae in colugos and flying squirrels, the shoulder joint of the first is elevated to the level of the vertebral column, while in the second, it remains close to the level of the sternum. Therefore, the trunk of colugo is suspended entirely under the membrane, while the trunk of flying squirrel projects both above it and below (Fig. 4.7).

However, the scapulae of colugos are not always positioned frontally. At the start of gliding, when the forelimbs are stretched posteriorly (Fig. 4.3, 4.8), or when the animal is suspended under relatively thin branches (Figs. 4.2, 4.6), the scapulae are positioned parasagittally, alike in the majority of quadrupedal therians. This is evident from the photographs showing the position of the shoulder joint (Fig. 4.8) and dorsal (vertebral) border of the scapula (Fig. 4.2).

Fig. 4.8 Colugo has pushed off and prepares to spread the membrane for a glide (photo by Julian W).

A wide range of locomotor patterns of colugos, including running up thick trunks succeeded by gliding over long distances and climbing under branches is based on their ability to reorient the scapulae from the parasagittal to frontal plane and vice versa, depending on functional requirements. The capability of colugos to change

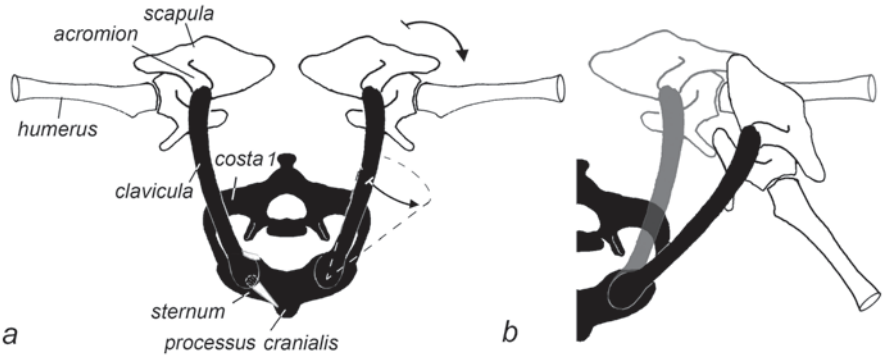


Fig. 4.9 Scheme of mobility in the shoulder girdle of colugo in the transverse plane, anterior view. *a. Spread position (clavicle is adducted medially, scapula is in the frontal plane);* arrows indicate the directions of limb adduction to the parasagittal plane, dotted lines indicate the limits of clavicle mobility. *b. Parasagittal position;* spread position is shown in grey.

the scapula orientation according to conditions is ensured by the increased mobility of the scapula in the transverse plane. In this ability colugos sharply differ from quadrupedal therians, which scapular mobility is more or less restricted to the parasagittal plane. Our manipulations with the syndesmological preparation of colugo have shown that transition of its scapula from the parasagittal to frontal position and back is accompanied by adduction and abduction of the clavicle in the sternoclavicular articulation and rotation of the scapula around its own longitudinal axis, which passes through the acromioclavicular articulation and its dorsocaudal angle (Fig. 4.9).

Apparently, during the starting leap which precedes gliding (Fig. 4.3), the reorientation of scapula is being initiated by the *m. acromiotrapezius* while the protraction of humerus is produced by the *m. acromiodeltoideus* and *m. supraspinatus*. The final frontal position of the limb and, hence, the scapula, results from the action of aerodynamic forces unfolding and tightening the membrane.

During gliding, the elbow joint is completely straightened, the manus is slightly adducted medially, and digits of both manus and foot are widely spread. Adduction of the manus is controlled by the *mm. extensores carpi radiales*, the fingers are dilated apart by tension of the propatagium and plagiopatagium, and the toes by tension of the plagiopatagium and uropatagium. Muscles of the manus and foot only adjust position of digits for fine manoeuvring.

For landing, the forelimbs are adducted back to the parasagittal plane by the *mm. pectorales*; in so doing, the membrane loses tension and does not counteract gathering of limbs together. We suppose that it is just at this instant of time that the scapula returns to the parasagittal position (Fig. 4.9b), since only this can allow the *m. serratus ventralis* to take part in achieving soft landing: the braking distance is increased by sagging of thorax between the two parasagittal scapulae (just the same mechanism is used by quadrupedal therians when they land after great leaps). Note that colugos have gained a muscle specialized for returning the scapula to the parasagittal plane. It is the *m. pectoralis abdominalis*, which is unique in the shift of its insertion from the humerus onto the tip of the specifically elongated coracoid process of the scapula (Fig. 2.3).

Static Analysis

For the analysis of distribution of forces in the locomotor apparatus we apply the method of graphic statics.

Clinging Flat onto Trunk

To estimate the role of particular muscles in fixing the colugo's body on the tree trunk, we introduce the following model (Fig. 4.10). The forelimbs attached to the trunk by claws prevent downward sliding along the trunk and simultaneously pull the body close to it. The hindlimbs tucked under the body, serve as a strut between the body and trunk and do not apply to it considerable forces in the frontal plane (that is tangential to the trunk). Judging from photographs of animals clinging flat onto the trunk, the antebrachium and manus are usually placed along the same line pointing anterolaterally (Figs. 4.1a, b, d); if the antebrachium is placed parallel to the vertebral column (Figs. 4.1c, 4.10c), the manus is significantly abducted from the longitudinal axis of the antebrachium to retain anterolateral direction necessary for sideways stability of the body. The constancy of the angle of declination of fingers from the body axis irrespective of the direction of the antebrachium suggests that it is this angle that determines proper interaction of the forelimbs with the trunk. Apparently, the force F of this interaction, that is the force of claws applied to the substrate, acts posteromedially along the line given by the arrangement of the tips of the major claws. Hence, the opposite force F_r of substrate reaction acts on the forelimb ($F_r = -F$).

Let us consider the transfer of the force F_r from claws onto the body in the case shown on Fig. 4.10b. Firstly, this force is directly transferred onto the antebrachium by the *m. flexor digitorum profundus*, holding the claws stuck into the bark. In the antebrachiocarpal joint, the force F_r provokes lateral abduction of the manus, which can be counterbalanced by the *m. flexor carpi radialis* and *mm. extensores carpi radiales*. In the elbow, the force F_r provokes extension, which can be counterbalanced by the well-developed *m. brachialis* and *m. brachioradialis*, aided also by the *m. extensor carpi radialis longus*. Then, the force F_r provokes protraction of the humerus, which can be counterbalanced by the *m. latissimus dorsi*. On Fig. 4.10b, the line of action of the force F_{lat} of the *m. latissimus dorsi* coincides with that of the external force F_r, and so this muscle is not only able to balance the humerus, but also to transfer the force F_r directly onto the body. Hence, other muscles are not required to balance the shoulder girdle, which stays unloaded by any forces. Finally, the force F_{lat} of the *m. latissimus dorsi* meets on the animal's midline with the symmetrical force F'_{lat} of the contralateral *m. latissimus dorsi* to balance gravity; as a result, a complete equilibrium of the animal's body on the tree is achieved. It should be noted that colugos have a very massive *m. latissimus dorsi* additionally strengthened by the accessory *m. latissimus dorsi superficialis*, which is absent in the majority of therians.

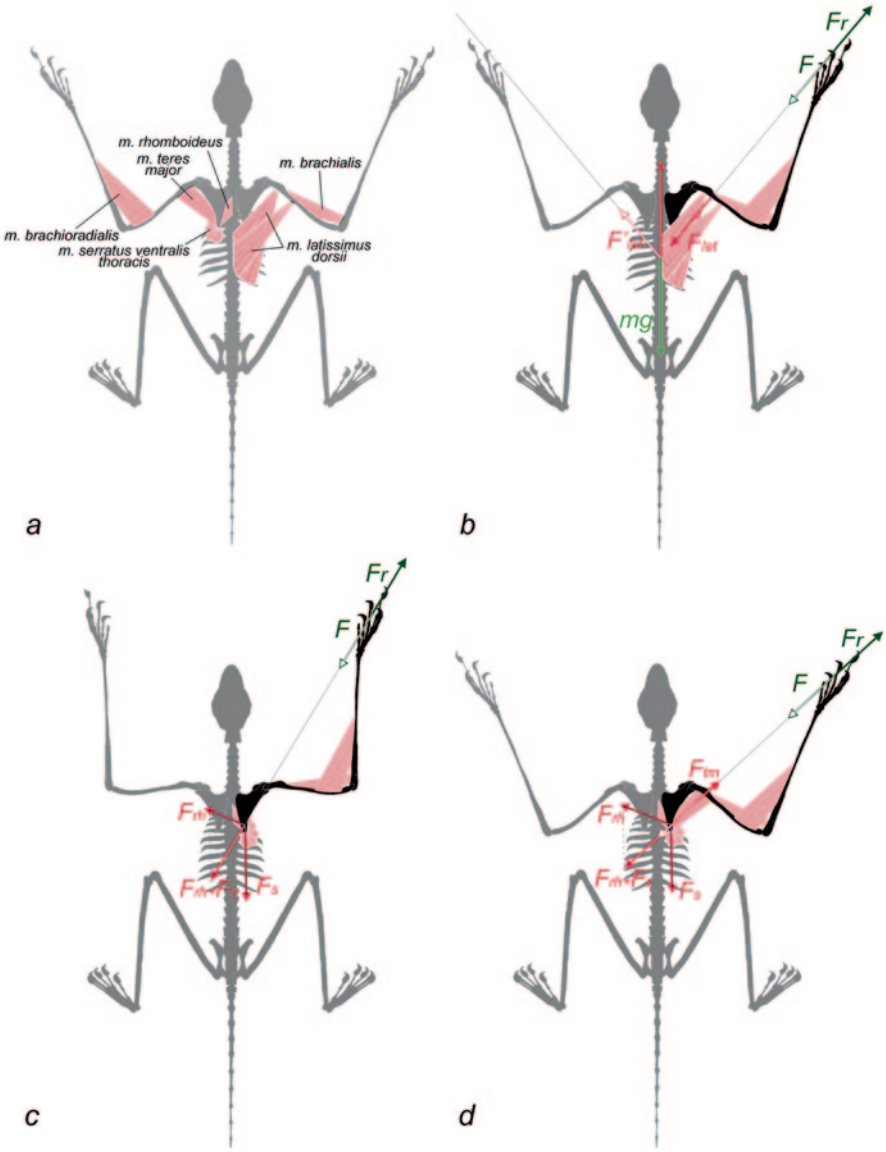


Fig. 4.10 Static equilibrium of the shoulder girdle and forelimb of colugo clinging onto tree trunk, frontal plane. F – force of the claws applied to the substrate, F_r – the substrate reaction force, F_{lat} – force of the *m. latissimus dorsi*, F_{rh} – force of the *m. rhomboideus*, F_s – force of posterior part of the *m. serratus ventralis thoracis*, F_{tm} – force of the *m. teres major*, mg – force of gravity of the body. *a. Main muscles of the shoulder girdle involved b–c. Variants of force distribution*

The ability of the colugo's *m. latissimus dorsi* to perform such suspension of the body may be checked by simple calculation based on general properties of striated muscles in mammals of similar size. For instance, in locomotor muscles of the kangaroo rat (Biewener et al. 1988), the stresses (forces divided by cross-sectional areas) reach 10 H/cm^2 when they actively shorten, 20 H/cm^2 when they keep constant length (isometric contraction), and 35 H/cm^2 when they are being forcibly stretched. In the colugo at rest, muscles act in the isometric mode; therefore, approximate estimate of the available force of the *m. latissimus dorsi* can be obtained by multiplication of its cross-sectional area by 20 H/cm^2. A single *m. latissimus dorsi profundus* of the specimen preserved in alcohol, which we dissected, weighed 3.2 g. Since the density of fresh muscles is known to be about 1.06 g/cm^3 and preservation in alcohol somewhat decreases it, the life-time volume of the *m. latissimus dorsi profundus* can be estimated with confidence as at least 3.2 cm^3. Its muscular fibers were 3.5 cm long. Dividing the volume by the fiber length, we obtain the cross-sectional area of 0.914 cm^2. Multiplying this value by the maximum isometric stress of the kangaroo rat muscles (20 H/cm^2) we, finally, get the approximate estimate of available isometric force of a single *m. latissimus dorsi profundus* of the colugo, which is F_{lat}=18.3 H. At the same time, for a colugo, weighing on average about 1.5 kg, F_{lat}=9.6 H would be quite sufficient, as follows from Fig. 4.10b. Thus, the isometric property of the *m. latissimus dorsi profundus* is almost twice greater than the required force, even if neither the accessory *m. latissimus dorsi superficialis* nor other muscles of the shoulder girdle or hindlimbs contribute to suspension (hindlimbs are apparently involved on the downside of inclined trunks, as in Fig. 4.1d).

As mentioned above, the position of forelimbs sometimes differs from that shown in Fig. 4.1b; therefore, we consider two more postures of suspension on the trunk (Figs. 4.10c, d), in which the line of action of the external force F_r applied to the claws does not coincide with the line of action of the *m. latissimus dorsi* passing more anteriorly, through the dorsocaudal angle of the scapula. Hence, other means are required to balance the humerus and scapula (equilibrium in the elbow joint is always achieved similarly).

Consider, at first, the posture with horizontal humerus and vertical antebrachium, the humerus being perpendicular to the vertebral column and the elbow being flexed at a right angle (Fig. 4.10c). Since the manus is abducted laterally, the line of action of the force F_r passes now through the shoulder joint axis rather than lateral (posterior) to it. Hence, the shoulder joint is in equilibrium without the need of muscular activity, and the scapula is loaded by the force F_r longitudinally, that is along the line connecting the glenoid and the dorsocaudal angle. In this situation, the scapula can be effectively balanced by the force F_{rh} of *m. rhomboideus dorsi* together with the force F_s of *m. serratus ventralis thoracis*, which produce the resultant force $F_{rh}+F_s$ aligned and opposite in direction to the external force F_r ($F_{rh}+F_s=-F_r$). The evidence for feasibility of this suspension mechanism are the particularly well-developed posterior slips of the *m. serratus ventralis thoracis* in colugos, which are able to exert a caudally directed force on the scapula indeed.

Consider now the posture, where the line of action of the force F_r passes again through the dorsocaudal angle of the scapula but lateral (posterior) to the shoulder

joint axis (Fig. 4.10d). Hence, in this joint, the force F_r provokes protraction of the humerus, which can be counterbalanced by the force F_{tm} of the well-developed *m. teres major*. Having balanced the humerus by the force F_{tm}, this muscle exerts on the dorsocaudal angle of the scapula the opposite force $-F_{tm}$, which, in the current example, coincides by the line of action with the external force F_r and, so, is equal to it ($-F_{tm}=F_r$). In this situation, the scapula can be balanced at its dorsocaudal angle in the same way as in the previous case, that is by the *m. rhomboideus dorsi* together with posterior slips of the *m. serratus ventralis thoracis*.

Note that the above variants of equilibrium are not rigidly coupled with postures. For instance, in the case of postures, shown in Figs. 4.10c, d, the force F_r may act on the claws more vertically, and then the equilibrium can be achieved with the help of the *m. latissimus dorsi*, as in Fig. 4.10b. And vice versa, in the case of the posture, shown in Fig. 4.10b, the force F_r may act on the claws more horizontally, and then the equilibrium can be achieved with the help of the *m. teres major*, *m. rhomboideus dorsi*, and posterior slips of the *m. serratus ventralis thoracis*, as in Fig. 4.10d.

When climbing up a trunk, during the stage when the animal clutches only by the forelimbs, the above variants of muscular recruitment succeed each other in one or another order, depending on the limb position and bark relief. During powered retraction of the humerus (Figs. 4.5b, c), simultaneous contraction of the *m. teres major* and *m. latissimus dorsi* may be required, because in active shortening the maximum muscular stress is about twice less than in the isometric mode (see above). At certain instances of time, the external force F_r may pass anterior rather than posterior to the shoulder joint provoking retraction rather than protraction of the humerus; in this situation the *m. supraspinatus* (humeral protractor) is necessary for balance, while the *m. teres major* and *m. latissimus dorsi* must be switched off.

As colugo suspends under a branch, it holds the angle in the elbow joint by the *m. brachialis* and *m. brachioradialis*, while the *m. latissimus dorsi* is generally enough to balance the humerus against the force of substrate reaction in the similar way to that on the tree trunk (Fig. 4.10b).

Gliding

When colugo is in the glide, the plagiopatagium connecting its fore and hind limbs undergoes tension by the aerodynamic force F acting on it from below according to the prevalence of air pressure at the lower side of the membrane (Fig. 4.11). The tension of the plagiopatagium results in the force F_{fl} applied to the forelimb and the force F_{hl} applied to the hindlimb[1]. These forces have no leverage to provoke

[1] In fact, there are two ways of transition of the aerodynamic force F onto the fore and hind limbs, direct and indirect. The direct way involves tension of longitudinal collagen fibers in the membrane, which anterior attachments are distributed throughout the length of the forelimb and posterior attachments throughout the hindlimb. The indirect way involves tension of transverse collagen fibers, which medial attachments are distributed throughout the side of the body and lateral attachments throughout the free edge of the membrane. Inevitably, this edge caves in dorsomedially under the tension of transverse collagen fibers and transmits this tension onto the fore

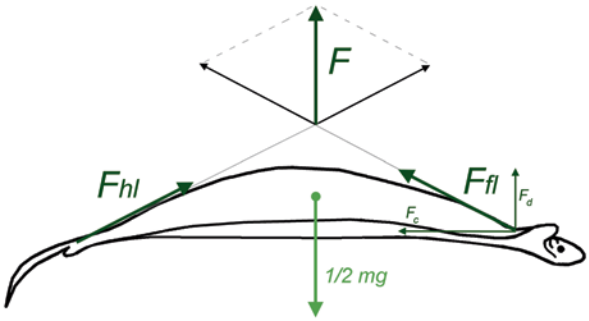


Fig. 4.11 Forces acting on the membrane and limbs of colugo in steady glide, sagittal plane. F – total aerodynamic force (support reaction force) acting on the plagiopatagium of the one side of the body, F_{fl} – membrane tension force applied to the forelimb, F_d – vertical component of the force F_{fl}, F_c – horizontal component of the force F_{fl}, F_{hl} – membrane tension force applied to the hindlimb, mg – force of gravity of the body.

either pronation or supination of the limbs but tend to pull them together and, due to membrane cambering, upward. We are going to consider only the action of the force F_{fl} on the forelimb. For convenience, we divide it into the horizontal component F_c acting in the caudal direction and the vertical component F_d acting in the dorsal direction (the transverse component of the propatagium tension is regarded as negligible). The magnitude of the vertical component F_d in steady gliding is about 1/4 mg, provided that the body weight is almost equally distributed between the four limbs.

Our analysis of static equilibrium of the forelimb and the shoulder girdle is based on the following assumptions.

1. The forces of gravity acting upon the membrane and the free limb are not taken into account, being, obviously, negligible as compared to membrane tension and other forces involved.
2. The resultant force of tension of the plagiopatagium and propatagium acts upon the antebrachium strictly longitudinally, like the rib of an umbrella, so that the required muscular control of the elbow is minimized.
3. The clavicle is regarded as a simple strut being loaded strictly longitudinally, along the line passing through the sternoclavicular and acromioclavicular articulations; no muscles attached to the clavicle are involved.
4. According to the so-called principle of solidification, widely used in statics, the free forelimb together with the scapula are regarded as a solid body; in this way

and hind limbs lengthwise again. Hence, irrespective of the involved fibers, the limbs are being subjected to longitudinal forces rather than transverse. More than that, the indirect way appears to be disadvantageous in respect of the required isometric forces in limb muscles, since the tension of transverse collagen fibers is applied via the membrane edge to the very distal end of the limbs, while the tension of longitudinal fibers is distributed up to axilla and inguen. Hence, we suppose that in plagiopatagium of colugos the longitudinal fibers prevail over transverse ones. The minor longitudinal folds near the free edge of the plagiopatagium on Fig. 4.4 are the evidence for reduced transverse tension in the membrane.

we put off calculation of forces of one-joint muscles of the shoulder joint (such as the *m. supraspinatus*) presuming that they can be supplied if necessary.

The result of our calculation of 3D equilibrium is shown in Figs. 4.12–4.14 representing three orthogonal planes, the frontal, the sagittal, and the transverse. The following forces are involved: the horizontal F_c and vertical F_d components of the plagiopatagium tension applied to the antebrachium, the force F_{prop} of propatagium tension applied to the antebrachium, the vector resultant F_1 of the plagiopatagium and propatagium tension acting along the antebrachium ($F_1 = F_c + F_d + F_{prop}$), the force F_p of the *m. pectoralis* (*superficialis* and *profundus*) applied to the pectoral crest of the humerus, the force F_s of the *m. serratus ventralis thoracis*[2] applied to the

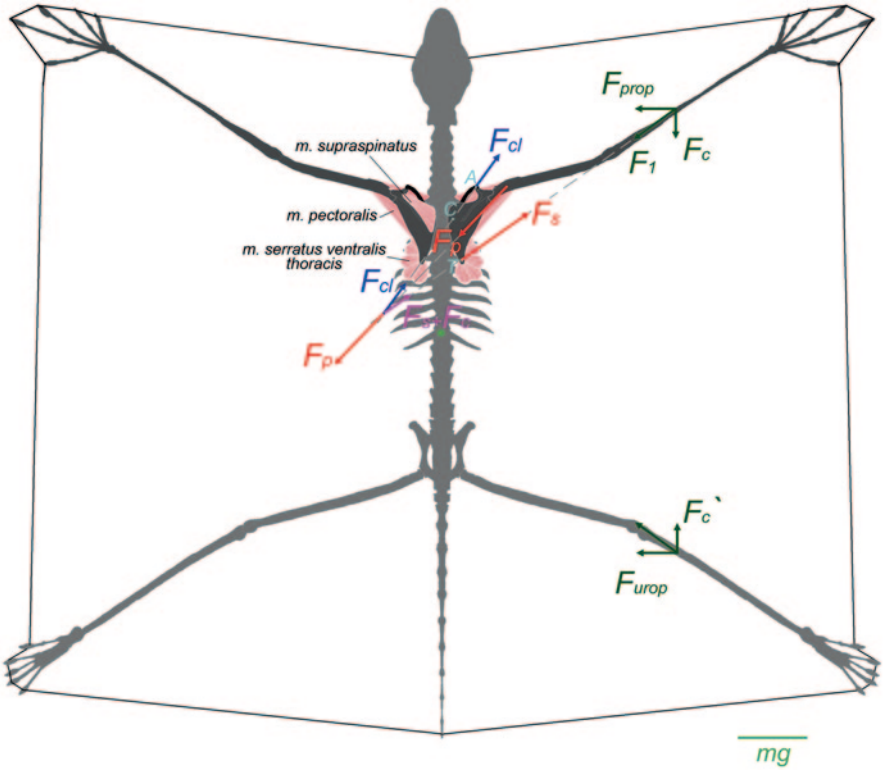


Fig. 4.12 Static equilibrium of the shoulder girdle and forelimb of colugo in gliding, frontal plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_c – horizontal component of the force F_{fl} (see Fig. 4.11), F_{prop} – force of the propatagium, F_1 – resultant of F_c and F_{prop}, F_p – force of the *m. pectoralis*, F_s – force of the *m. serratus ventralis thoracis*, F_{cl} – force of the clavicle reaction, F_c' – horizontal component of the force F_{hl}; for the scale of force vectors the value of gravity force is shown (*mg*).

[2] In contrast to the above analysis of clinging to tree trunk (Figs. 4.10 c, d), the whole *m. serratus ventralis thoracis* is involved in gliding, not only its posterior-most slips.

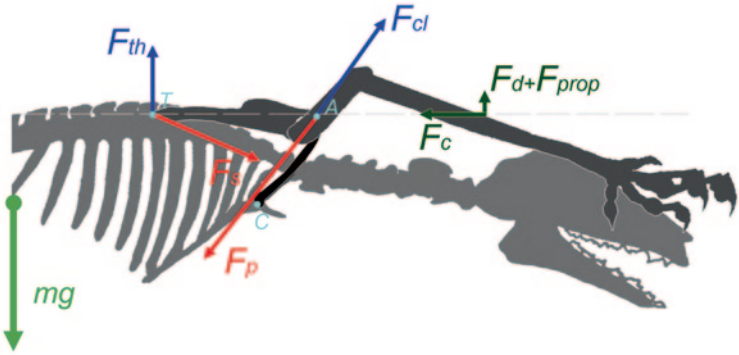


Fig. 4.13 Static equilibrium of the shoulder girdle and forelimb of colugo in gliding, sagittal plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_d – vertical component of the force F_{fl} (see Fig. 4.11), F_{prop} – force of the propatagium, F_p – force of the *m. pectoralis*, F_s – force of the *m. serratus ventralis thoracis*, F_{cl} – force of the clavicle reaction, F_{th} – force of the thorax reaction; *mg* – force of gravity of the body.

dorsocaudal angle of the scapula (point *T*), the force F_{cl} of reaction of the longitudinally compressed clavicle applied to the tip of acromion (point *A*), and the strictly vertical force F_{th} of reaction of the thorax applied to the dorsocaudal angle of the scapula (point *T*), which leans on it.

The equilibrium shows several important points in the frontal plane (Fig. 4.12). The total force F_1 of membrane tension is aligned in this plane with the dorsocaudal angle of the scapula (point *T*) and with the opposite and greater in magnitude force F_s of the *m. serratus ventralis thoracis*. Note, that this muscle is shaped as a wide fan covering the thorax and inserting, in colugos, along the entire dorsal border of the scapula. So, any reasonable force F_1, which line of action falls in the range of this extended insertion can be met by the force F_s through adjustment of contraction forces of different slips of this powerful muscle. Therefore, this scheme of balance works for a good range of forelimb positions. The resultant force F_1+F_s together with the force F_{cl} of the clavicle reaction is counterbalanced by the force F_p of the *m. pectoralis* at the point of their intersection in the frontal plane, which point is located posterior to the contralateral scapula.

Note also, that the total force F_1 of membrane tension passes posterior to the shoulder joint and, hence, provokes retraction of the humerus, which should be counterbalanced by the *m. supraspinatus*; however, based on the principle of solidification, calculation of the necessary magnitude of the force of this one-joint shoulder protractor is beyond our current analysis.

We shall not describe in detail the equilibria in the sagittal and the transverse planes, since they are well visible in Figs. 4.13 and 4.14, respectively. Instead, we suggest the following qualitative description of the involved forces and torques to represent the six underlying equations of statics.

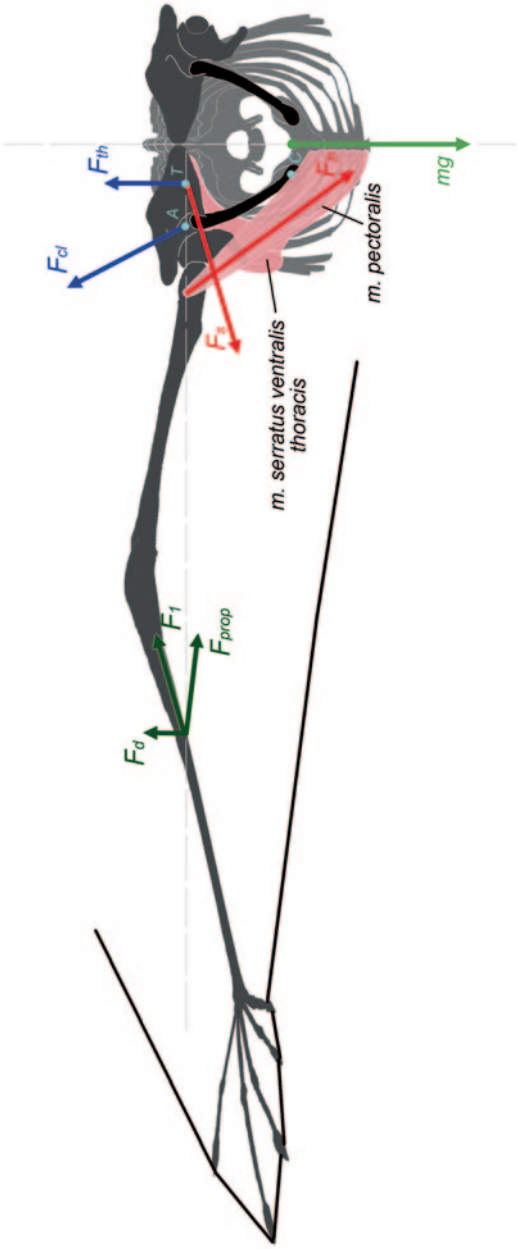


Fig. 4.14 Static equilibrium of the shoulder girdle and forelimb of colugo in gliding, transverse plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_d – vertical component of the force F_{fl} (see Fig. 4.11), F_{prop} – force of the propatagium, F_l – resultant of F_d and F_{prop}, F_p – force of the *m. pectoralis*, F_s – force of the *m. serratus ventralis thoracis*, F_{cl} – force of the clavicle reaction, F_{th} – force of the thorax reaction, *mg* – force of gravity of the body.

1. The forces F_d, F_{cl}, and F_{th} act upon the forelimb and the shoulder girdle in the upward direction; they are counterbalanced by the forces F_{prop} (very small downward component), F_p, and F_s acting in the downward direction. The forces applied to the body are $-F_{cl}$, $-F_{th}$, $-F_{prop}$, $-F_p$, and $-F_s$. Obviously, the sum of their vertical components is equal to $F_d = -1/4\ mg$ (Fig. 4.11); hence, the body gravity is balanced, provided that each of the three other limbs carries a quarter of the weight too.
2. The forces F_{prop} and F_p act upon the forelimb and the shoulder girdle in the medial direction; they are counterbalanced by the forces F_s and F_{cl} acting in the lateral direction.
3. The forces F_c and F_p act upon the forelimb and the shoulder girdle in the backward direction; they are counterbalanced by the forces F_s and F_{cl} acting in the forward direction.
4. Relative to the center of gravity of the body, the forces F_{prop} and F_p produce the yawing torque toward the opposite side; it is counterbalanced by the forces F_c, F_s, and F_{cl} producing the opposite torque (Fig. 4.12).
5. Relative to the center of gravity of the body, the forces F_d, F_{cl}, and F_{th} produce the pitching torque increasing the angle of attack; it is counterbalanced by the forces F_{prop} (very small downward component), F_p, and F_s producing the opposite torque (Fig. 4.13).
6. Relative to the center of gravity of the body, the forces F_d, F_{cl}, and F_{th} produce the wing-up rolling torque; it is counterbalanced by the forces F_{prop} (very small downward component), F_p, and F_s producing the opposite torque (Fig. 4.14).

An important feature of the described 3D equilibrium is that the forces of the *m. pectoralis* (F_p) and *m. serratus ventralis thoracis* (F_s) have opposite in sign and similar in magnitude transverse and lengthwise components. In fact, they are partial antagonists in the frontal plane (which is also the plane of the membrane and the scapula) (Fig. 4.12). Imagine, that the shown equilibrium of the shoulder girdle in this plane is disturbed, and the scapula begins to shift in the direction of pull of one of the two antagonistic muscles. This muscle begins to shorten, while the other undergoes forcible stretching. We have noted above, that the ratio of muscular stresses in the two modes of contraction is about 1/3.5. So, the muscle which pulls begins to lose force relative to the muscle which is pulled immediately after the disturbance. The negative feedback arises, which automatically restores the position of equilibrium without the need of nervous control.

Note, that the laterally directed transverse component of the force F_s of the *m. serratus ventralis thoracis* required for this balance in gliding, is gained in colugos exclusively due to the temporary transposition of the scapula into the frontal plane. Otherwise, if it stayed in the parasagittal plane, as in quadrupedal therians (or even in colugos at the initial stage of a starting leap), the force F_s of the *m. serratus ventralis thoracis* would be confined to the same plane and, hence, would lack any transverse component, which is absolutely necessary to prevent displacement of the scapulae toward the vertebral column (Fig. 4.15).

As to the hindlimb, it is loaded by the membrane tension similarly to the forelimb. In the sagittal plane, the plagiopatagium acts on it by the force F_{hl}, which is,

Fig. 4.15 Scheme of the *m. serratus ventralis thoracis* attachment in transverse cross section. *a. Tree shrew b. Colugo: at start of gliding leap (left), at gliding and clinging (right)*

relative to the transverse plane through the center of gravity of the body, approximately symmetrical to the force F_{fl} on the forelimb (Fig. 4.11). In the frontal plane, the cranially directed horizontal component F_c' of the force F_{hl} is summed up with the force F_{urop} of the uropatagium tension to produce longitudinal compression in the skeleton of the straightened hindimb (Fig. 4.12). So, the uropatagium serves here as a counter-string to the plagiopatagium, like the propatagium in case of the forelimb.

References

Agoramoorthy G, Sha CM, Hsu MJ (2006) Population, diet and conservation of Malayan flying lemurs in altered and fragmented habitats in Singapore. Biodivers Conserv 15(7):2177–2185

Biewener AA, Blickhan R, Perry AK et al (1988) Muscle forces during locomotion in kangaroo rats: force platform and tendon buckle measurements compared. J Exp Biol 137(1):191–205

Byrnes G, Libby T, Lim NTL, Spence AJ (2011) Gliding saves time but not energy in Malayan colugos. J Exp Biol 214(16):2690–2696

Byrnes G, Lim NTL, Spence AJ (2008) Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*). Proc Roy Soc B 275(1638):1007–1013

Dudley R, DeVries P (1990) Tropical rain forest structure and the geographical distribution of gliding vertebrates. Biotropica 22:432–434

Dzulhelmi N (2013) Natural history of the colugo. Penerbit Universiti Kebangsaan, Malaysia

Emmons LH, Gentry AH (1983) Tropical forest structure and the distribution of gliding and prehensile tailed vertebrates. Amer Nat 121(4):513–524

Hildebrand M (1977) Analysis of asymmetrical gaits. J Mammal 58(2):131–156

Jackson SM (2000) Glide angle in the genus *Petaurus* and a review of gliding in mammals. Mammal Rev 30(1):9–30

Lim NTL (2007) Colugo. The flying lemur of South–East Asia. Draco Publ, Singapore

Scholey K (1986) The climbing and gliding locomotion of the giant red flying squirrel *Petaurista petaurista*. Biona report 5:187–204

Vaughan TA, Ryan JM, Czaplewski NJ (2011) Mammalogy. 5th edn. Jones and Bartlett Publishers, Sudbury

Wischusen EW, Richmond ME (1998) Foraging ecology of the Philippine flying lemur (*Cynocephalus volans*). J Mammal 79(4):1288–1295

Chapter 5
Functional Analysis of Locomotor Apparatus of Bats

Locomotor Features of Chiropterans

Chiropterans have developed a travelling mode essentially unusual for mammals, that is, flapping flight. The forelimbs were charged with the major job of propelling the body into the air, and all their regions (except for the carpus) have become greatly elongated to form an airframe for the wing membrane. The formation of the wing involved hindlimbs as well, which are also rather elongated relative to the body. They help to tighten the trailing edge of the membrane and may participate in the flapping movements. In many species, the flight apparatus includes the uropatagium, a piece of the membrane stretched between the hindlimbs and tail.

Normally, the speeds of horizontal flapping flight vary from 2 to 8 m/s in majority of bats, but reach 15 m/s in some specialized species (Hayward and Davis 1964; Neuweiler 2000). The optimal flight speed is the speed of maximum lift to drag ratio. For instance, among the most studied species, it is ~3.5 m/s in *Glossophaga soricina* and ~5 m/s in *Leptonycteris yerbabuenae* (Muijres et al. 2011). At the lowest speeds, below 1 m/s, the flight performance is most complicated due to deficiency of the wing speed relative to the air (e.g., Muijres et al. 2008; Adams et al. 2012).

In general, in the horizontal flight of bats, the wings move obliquely relative to the body, from the raised and retracted position at the beginning of the downstroke to the lowered and protracted position at the downstroke-to-upstroke transition, and back again in the upstroke. This contrasts to birds, which move the wings in the horizontal flight almost vertically relative to the body (Hedenström et al. 2009). In the frame of reference of the external world (i.e., relative to still air), the wing moves in a wavy path (Fig. 5.1) whose shape depends on the speed of progression as this speed is summed up with the oblique movement of the wing relative to the body. As a result, the downstroke segments of this wavy path are always inclined downward and forward, while the upstroke segments are inclined upward and backward (the so-called 'tip-reversal' upstroke or backward 'flick') at slower speeds, but upward and forward at higher speeds. At medium speeds, the upstroke of the wing is almost vertical relative to the still air (the forward speed of the body is being cancelled here by wing retraction relative to the body). The hindlimbs and tail (if present) follow the movements of the forelimbs probably passively, driven by the plagiopatagium, or sometimes participate in the special strokes by the uropatagium (Adams et al. 2012).

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_5

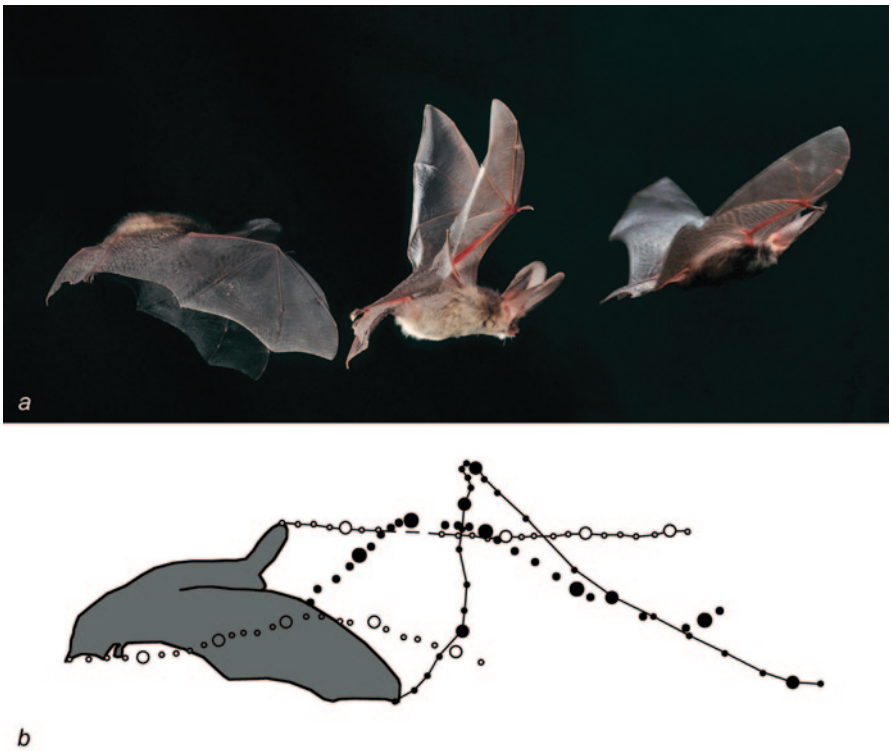


Fig. 5.1 Flight of bats. *a. End of downstroke, start of downstroke, middle of downstroke of Plecotus* (photo by Dietmar Nill) *b. Tracks of selected wing points in horizontal flight of Plecotus auritus. Forward speed 2.25 m/s, stroke duration 0.08 s. (data from 300 fps video record by Casio EX-F1).*

In the air, the upstroke is not as useful as the downstroke, and in the upstroke bats tend to reduce the aerodynamic wing loading by partially folding the shoulder and elbow joints, and the joints of the manus. This centripetal motion requires additional muscular work, but it is shown to be overridden by the savings associated with the reduction of the moment of inertia of the shortened wing which has to be elevated quickly (Riskin et al. 2012). As a result, the upstroke movement and action are more complicated. It not only folds but supinates as well. Depending on the degree of supination, the wing may retain positive or acquire negative angle of attack (in backward flick at low speeds), and, if the supination of the proximal part is greater than that of the distal part, the wing becomes twisted so that the proximal part retains positive angle of attack, while the distal part gains negative one (Hedenström et al. 2007). The backward flick of the chiropatagium has deserved special attention as a peculiar feature of upstroke at low flight speeds. Having estimated body accelerations in six bat species at various speeds, Aldridge (1987b) decided that the backward flick generates thrust at low

speeds, so that the body is accelerated forward during the upstroke. Recently, this conclusion has been supported for slow flight of *Glossophaga soricina* based on wing kinematics (Norberg and Winter 2006) as well as vortex wakes (Hedenström et al. 2007). However, consideration of inertia of the wing itself in *Cynopterus brachyotis* (Iriarte-Díaz et al. 2011) has shown that even at low speeds, the center of mass of the whole body does not accelerate forward during the upstroke; in fact, the positive impulse of force applied to the trunk is cancelled by the negative impulse of force applied to wings, which are always retracted relative to the trunk in the upstroke of bats.

In addition to the horizontal flight, some bats use upward flight, hovering (that is on-site flapping flight), gliding, and even soaring, as well as combined flap-gliding flight called 'undulating' due to the wavy trajectory of the body. In accordance with the general constraint of decrease of the available muscular power per unit body mass with the growth of animal size, hovering and upward flight are limited to smaller species (almost all microchiropterans), while gliding and soaring are preferred by larger ones (megachiropterans).

Hovering is the on-site flight allowing a bat, bird, or insect to hang over a food source or any other target point. It may be regarded as the slower-most flight, which requires no thrust. In its turn, the vertical flight may be regarded as a kind of overloaded hovering with the use of aerodynamic lift as a thrust against gravity and drag. In both cases, a bat places its body more upright than in forward flight and performs wing strokes more horizontally, almost in dorsoventral direction in respect of the body axis. For the first time, the kinematics was described and associated aerodynamic calculations were performed, for hovering, on *Plecotus auritus* by Norberg (1976c) and, for vertical flight, on *Rhinolophus ferrumequinum* by Aldridge (1991). In the first study it was already proved, that the steady-state aerodynamic model is inappropriate in the absence of forward speed. The most important role of the backward flick of the chiropatagium in hovering and upward flight was already noticed by Aldridge (1991) and further considered by Norberg and Winter (2006). The glossophagine flower bats, which weigh no more than 32 g, are the largest hovering animals (see the experimental data on hovering in hypodense air of ~25 g *Leptonycteris curasoae*: Dudley and Winter 2002). So, hovering flight is unattainable for heavyweight megabats, notwithstanding how advantageous it would be for these fruit-eaters and nectar-feeders.

Indeed, fruit bats avoid expensive wing flapping and, whenever possible, prefer static wing-wrestling to glide or even soar in thermals (Norberg et al. 2000; Thomson et al. 2002). As compared to flapping flight, gliding is simple in kinematics and better fits steady-state aerodynamics, that is why it became first to be studied. In the first research of gliding, performed by Pennycuick (1971) on a 120 g *Rousettus aegyptiacus* in the speed range from 5.5. to 11 m/s, it was shown that bats are inferior to birds in the ability to increase gliding speed by reducing the wing area. This is the structural constraint of a membranous wing, which loses stiffness when excessively folded.

Contrary to fruit bats, the microbats rarely use prolonged gliding but rather employ this mode of flight intermittently, mainly in the form of the so-called undulating flight. It is composed of brief flapping and gliding periods which regularly alternate. After several wing strokes, reaching a certain speed, the bat glides with motionless open wings. For the first time, the undulating flight was studied in *Pipistrellus pipistrellus* by Thomas et al. (1990). Bats use this travelling mode more rarely than birds. Apparently, the membranous wing is not as good as the feathered one in respect of the aerodynamic performance in gliding and, hence, the height loss in gliding phase of undulating flight would be too big in bats for efficient usage of this flight mode (see comparison with the swift by Muijres et al. 2012a).

Much more frequent than undulating flight in bats is the foraging flight over water, at a wing-touch distance from its surface. Aldridge (1988) has shown on *Myotis lucifugus*, that the so-called ground effect comes into action in this case, which reduces significantly the aerodynamic power cost of locomotion. So, this flight is twice advantageous, since it not only gives better chance to meet insect prey but also saves muscular expenditures of energy in the hunting voyage.

The special issue in the research of flight performance in bats is the influence of pregnancy. Significant growth of wing loading in pregnancy was shown on *Antrozous pallidus* (Davis 1969) and on *Pipistrellus pipistrellus* (Hughes and Rayner 1993), and growth of required flight power was shown on *Glossophaga soricina* (Voigt 2000). Surprisingly, the scope for selecting flight speed in pregnant *Pipistrellus pipistrellus* appeared very much wider than that of lactating and postlactating individuals, the average speeds remaining the same, as if in pregnancy an ability is enhanced to adjust the speed to its momentary optimum (Hughes and Rayner 1993). The influence of extra load was also studied on the fruit bat *Cynopterus brachyotis* by means of intra-peritoneal injections of saline solution, up to ~20 % of body weight. It appeared that, in forward flight, the extra load was compensated for by increasing either wingbeat frequency or wing area and camber (Iriarte-Diaz et al. 2012). In climbing flight (which is not truly vertical), the overloaded *Cynopterus brachyotis* did not increase the flight power and, so, tended to ascend slower, that is less steeply (MacAyeal et al. 2011).

In general, bats are significantly outperformed by birds in efficiency of forward flight (Muijres et al. 2012b) but are better in maneuvering, especially at slower speeds (Hartman 1963; Pennycuick 1971; Hedenström et al. 2009). However, Voigt and Holderied (2012), by measuring the flight CO_2 metabolism in molossid bats, have proved that maneuvering is rather expensive for long-winged species, because, when turning tightly, they have to fly slower than the optimal speed. Advanced maneuvering was described in *Otomops* и *Nyctalus* Norberg (1976a); maneuvers, which precede landing on a ceiling, were considered in *Cynopterus brachyotis*, *Carollia perspicillata*, and *Glossophaga soricina* (Riskin et al. 2009); lateral turning was studied in *Plecotus auritus* (Rayner and Aldridge 1985; Aldridge 1987a), *Rhinolophus ferrumequinum, R. hipposideros, Myotis mystacinus, M. daubentonii*,

and *Pipistrellus pipistrellus* (Aldridge 1987a). The different role of the upstroke and downstroke in turning was shown on *Cynopterus brachyotis* (Iriarte-Díaz and Swartz 2008).

In the vast variety of bats, maneuvering abilities differ across species very much. There are dozens of papers which consider relations of wing shapes and flying modes. They are generalized, for instance, by Findley et al. (1972), Norberg and Rayner (1987), and, more recently, by Bullen and McKenzie (2001). However, most of such studies confine the subject to superficial correlations of wing shapes and flying modes, not coming into in-depth analysis of their causal relations or morphofunctional basis.

The modern knowledge on bat flight is summed up in the recent review by Swartz et al. (2012). Beyond this, remember, that their body mass varies from ~1.5 g to ~1.6 kg, the upper limit being about 10 times lower than in flying birds. There are two reasons for such a big difference, external and internal. The external one is the fact, that the aerodynamic efficiency of bat flight apparatus is significantly lower than in birds (Muijres et al. 2012b). The internal shortcoming of bats is the lower mass proportion of flight muscles in the body and the lower limit of wingbeat frequency, which together cannot produce as much a muscular power as in birds (Norberg and Norberg 2012).

Beyond flying, many bats frequently climb vertical and inclined branches, tree trunks, and cave walls. Depending on the head-up or head-down direction of movement, the role of hooks to hang by is played by, respectively, the thumbs or the feet, which are reversed back to front, so that the toes point posteriorly and the claws are curved down (Fig. 5.2b).

Most bats are also capable of quadrupedal locomotion on horizontal ground. In this case, the forelimb contacts the substrate by the wrist bend and the thumb, while the hindlimb gains contact by the sole of the foot pointing anterolaterally (Lawrence 1969) (Fig. 5.2a). The most usual terrestrial gait of bats is the so-called lateral-sequence walk with slight forelimb prevalence, that is the prevalence of the forelimb over hindlimb contact duration (Riskin et al. 2006). In slower walking, the tail may also help to support the body touching the ground twice during the locomotor cycle, while in faster walking, the forelimbs tend to sprawl much more laterally than the hindlimbs are placed (Lawrence 1969). Normally, bats walk over relatively short distances, since the wings have become poorly adapted for locomotion beyond flight. However, some species have improved their walking ability considerably. In particular, the New Zealand *Mystacina tuberculata* hunts earth worms in leaf litter walking fast or almost running with the use of the quadrupedal gait just described (Riskin et al. 2006), but flies for the only purpose to reach the hunting area.

The more rare quadrupedal gait, which was once observed in *Nyctalus noctula* (Lawrence 1969) and has been better described in the true vampire bat *Desmodus rotundus* (Riskin and Hermanson 2005; Riskin et al. 2006), is bound with significant forelimb prevalence. They touch the ground a little later, but lose contact con-

Fig. 5.2 Locomotion of bats on solid substrates. *a. Common vampire bat (Desmodus rotundus) bounding on a horizontal surface* (photo by Daniel Riskin and John Hermanson) *b. Common noctule (Nyctalus noctula) descends the tree trunk head down clinging by hindlimbs* (photo by E. Yakhontov)

siderably later than the hindlimbs. Apparently, the forward thrust is supplied by the forelimbs, due to their prevailing length, while the hindlimbs serve as, more or less, passive struts for the body. In contrast to bounding mammals, e.g., rodents, the leap of bats follows the forelimb rather than the hindlimb thrust, and, hence, is more similar to the gathered rather than extended position *sensu* Hildebrand (1977). In fact, this gait is very similar to the above described pronk with forelimb prevalence, used by colugos to run up tree trunks. The major advantage of pronk is the coupled beginning of the contact phases of all the four limbs, which may help colugo to develop greater muscular power needed to propel the body upward.

Some bats are not capable of any locomotion on horizontal ground (Lawrence 1969). In Rhinolophidae and Hipposideridae, this may be associated somehow with the loss of spine flexibility due to development of a monolithic thorax, which, in its turn, gives firmer basis for flight muscles.

Kinematics of Chiropteran Wing

In the membranous wing, the skeleton is immediately visible, and its elements are rather easy to trace throughout the wingbeat cycle based on motion pictures. This allowed the study of wing kinematics from the elbow to the very tip in much detail (Norberg 1976b; Aldridge 1988; Tian et al. 2006; Norberg and Winter 2006; Swartz et al. 2006; Swartz et al. 2007; Riskin et al. 2008; etc.).

For the first time, the bat wing kinematics in horizontal flight was described in detail on *Plecotus auritus* at its typical slow speed by Norberg (1976b). Then, the wing kinematics at various flight speeds were studied in *Rhinolophus ferrumequinum* by Aldridge (1986) and in many other bats by many other authors. Finally, the general model for correlations between different kinematic variables in a certain speed range has been suggested, based on data on *Cynopterus brachiotis* (Riskin et al. 2008). Beginning with the first study by Norberg (1976b), the data on wing kinematics were used to calculate aerodynamic parameters, such as lift and drag forces, and respective mechanical power required from muscles, based on, in earlier studies, steady-state aerodynamic models or taking into account the recent findings on unsteady effects (especially pronounced at lower speeds). As exemplified by *Leptonycteris yerbabuenae* and *Glossophaga soricina* (Busse et al. 2012), the wing area, the angle of attack, and the camber, which are determinants of the aerodynamic lift production, tend to decrease with the speed increase, while the optimal flight speed, which is the speed of maximum lift to drag ratio, is best indicated in kinematics by the minimum angular velocity of the wing in the stroke plane relative to the shoulder joint. The angular amplitude also comes to minimum near the optimal flight speed in *Leptonycteris yerbabuenae* and *Glossophaga soricina*. On the contrary, in *Pipistrellus pipistrellus*, according to earlier findings of Hughes and Rayner (1993), it ranged from ~55° to ~85° irrespective of the speed, nor was it related to wingbeat frequency, wing span, wing area, wing loading, or body mass.

The independence of the wing angular amplitude (as well as the downstroke relative duration, stroke plane angle, and wing camber) from the body mass was confirmed on the interspecific scale by comparison of kinematics of six pteropodid species ranging in mass from ~28 g to ~1.15 kg (Riskin et al. 2010). However, this constancy is kept only among the bats of similar flight style. For instance, the rather slow *Cynopterus brachyotis* and the fastest *Tadarida brasiliensis* extremely contrast each other in the amplitude and kinematic pattern of wing strokes (Hubel et al. 2012). In the first one, the wings are raised very high at the beginning of the downstroke and fold by its end so much that their tips meet under the body, while in the second one, the wings are kept almost flat and show rather restricted up and down deviations from the frontal plane.

Contrary to the elbow and more distal points of the wing, the shoulder joint position was rarely traced on motion pictures (Aldridge 1988; Swartz et al. 2007), since it is technically difficult to locate even with the help of skin markers (Riskin et al. 2008). The motion of the shoulder girdle is even harder to analyze since the scapula and clavicle are incorporated in the thorax. Therefore, the previously developed views on the function of the shoulder girdle in bats were mainly hypothetical, except for a single article representing two frontal plane radiograms of *Antrozous pallidus* which was flapping its wings while the experimenter held it by the uropatagium (Hermanson 1981). Hermanson did not consider the movements of scapula, and for the clavicle he described only lateromedial deflections in the transverse plane. He concluded that the clavicle moves in phase with the wing: when the wing goes down, the clavicle deflects with it laterally, and during the upstroke medially.

A well-known graphic scheme of the stroke movement of the humerus and shoulder girdle of bats was proposed for the first time by Hill and Smith (1984). According to this scheme (Fig. 5.3b), the wing stroke is mainly produced by a coupled swing of the shoulder girdle and humerus relative to the rib cage. Hill and Smith presumed that the sternoclavicular articulation is very loose and allows the clavicle to turn relative to the sternum for more than 60° in the transverse plane, from almost vertical position at the beginning of the downstroke to almost horizontal by its end. Consequently, the scapula connected with the distal end of the clavicle was proposed to slide over the ribs along an arc-like trajectory, from the frontal position on the dorsal side of the thorax at the beginning of the downstroke to almost the parasagittal position on the lateral side by its end. This hypothesis is based on the idea of a scapulo-humeral lock (Fig. 5.3a) suggested earlier by Vaughan (1959, 1970). He believed that at the highest point of upstroke the greater tubercle of humerus locks against the additional articular facet of scapula found above the glenoid in specialized bats (shoulder joint of the second type according to Schlosser-Sturm and Schliemann 1995), which promotes the involvement of the strong *m. serratus ventralis thoracis*, connecting the ribs with the caudal border of scapula, into the braking of upstroke. Vaughan thought that in case of high wing beat frequency such a mechanism stopping upstroke would provide recover time for the *m. pectoralis*, since the downstroke could be initiated by the *m. serratus ventralis thoracis* if its force applied to scapula was transferred onto humerus via the proposed lock.

However, the available data on the shoulder joint displacements, though scarce, do not support the above cited idea (Hill and Smith 1984) of an extensive swing of

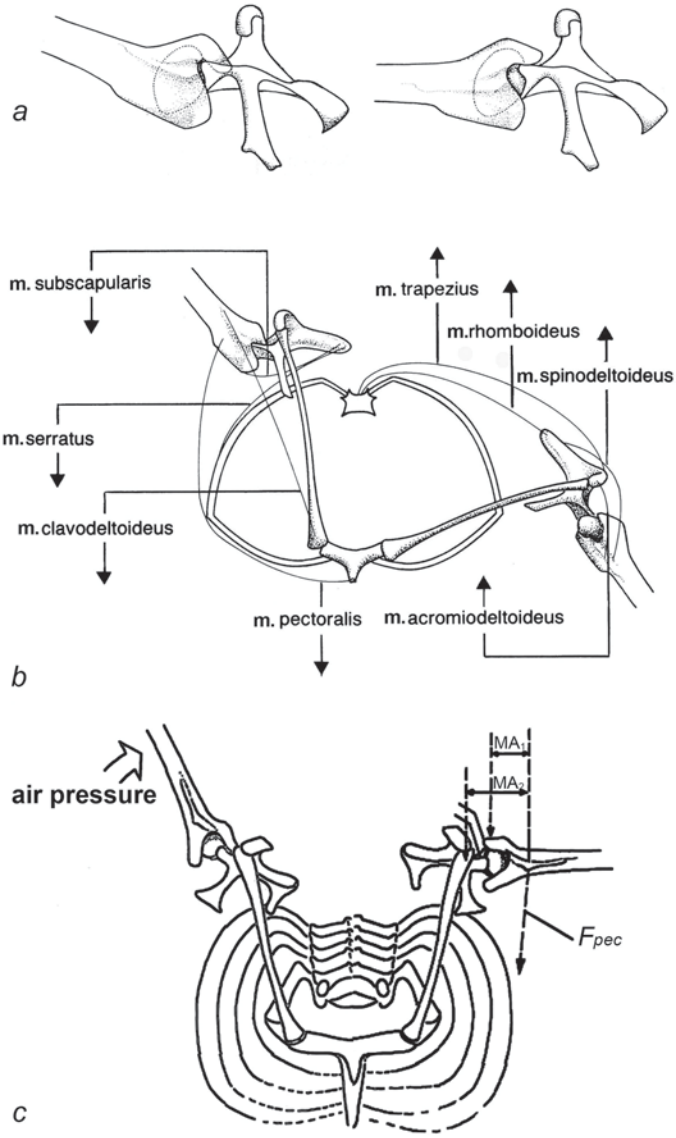


Fig. 5.3 Models of action of the upper scapulo-humeral locking mechanism, anterior view. Left – wing in the upper position, the lock is established; right – wing horizontal, the lock is disarticulated. *a. Close-up view of the mechanism, exemplified by Cheiromeles torquatus (Molossidae) according to Hill and Smith (1984). b. Model of stroke movements in the shoulder girdle of bats according to Hill and Smith (1984). Arrows pointing up mark upstroke muscles and pointing down – downstroke ones. c. Model of stroke movements modified after Altenbach and Hermanson (1987). Fpec – vector of force applied to the humerus by the m. pectoralis;* MA_1 *– horizontal moment arm of the m. pectoralis relative to the scapular fulcrum, the lock being disabled;* MA_2 *horizontal moment arm of the m. pectoralis relative to the clavicular fulcrum, the lock being enabled.*

the scapula in a wing stroke. Aldridge (1988) studied the flight of *Myotis lucifugus* close to water surface. In such a flight the wing depression below the body is inevitably restricted, while the elevation is significantly increased instead. Hence, all the kinematic reserves should be employed to keep the vertical wing amplitude, including, if possible indeed, the vertical displacement of the scapula. Contrary to this, *Myotis lucifugus* showed almost horizontal track of the shoulder joint above the water (in contrast to the wavy path of the wing tip), and thus, did not use the presumed scapular elevation even in such a *force majéur* flight mode.

Also, the order of activation of the flight muscles implied by Vaughan's lock-hypothesis, was disproved by further electromyographic research. Altenbach and Hermanson (1987) showed on *Artibeus*, *Antrozous*, and *Eptesicus* that the burst of electric activity in the *m. pectoralis* precedes rather than follows that in the *m. serratus ventralis thoracis*, both sustaining activity from the end of upstroke through the beginning of downstroke. In addition, the authors tested the movements of the scapula relative to the humerus in the same three species by implanting a pair of thin steel pins in the acromion and humeral shaft, which pins projected percutaneously and were visible on 200–250 fps cine photographs of operated bats flying on a tether. According to these experiments, the clavicle deflection in the transverse plane is restricted to no more than 15°, and, hence, the scapula does not slide down over the ribs but rather rotates in the acromioclavicular articulation about its own longitudinal axis (which passes through acromion and dorsocaudal angle). As a result, Altenbach and Hermanson introduced a new model of the shoulder girdle kinematics with the different, as compared with Vaughan's idea, usage of scapulo-humeral lock (Fig. 5.3c). When the humerus is being raised above the shoulder joint at the end of upstroke, the lock is established so that the fulcrum for the humerus is transferred from the axis of the shoulder joint onto the supraglenoid facet of the scapula. This new fulcrum is located more proximally and so makes the lever arm of the *m. pectoralis* ~1.5 times greater. The lock (fulcrum) is said to be subsequently maintained by contraction of the *m. pectoralis* which allows subsequent contraction of the *m. serratus ventralis thoracis* to provide additional downstroke effort. In any case, the scapular movement is still considered to be strictly coupled with the humeral downstroke.

Very small vertical displacements of the shoulder joint relative to the body were proved in the detailed kinematic analysis of *Cynopterus brachiotis* (Swartz et al. 2007). In this fruit bat the wingspan is 30–40 cm, while the vertical displacements of the shoulder joint in flight are less than 1 cm (median error 0.5 cm). More than that, these displacements are not in phase with the wing strokes. The phase-advanced elevation of the shoulder joint in respect of the wing tip at the upstroke to downstroke transition is shown, which obviously contradicts the idea of any scapulo-humeral lock since in both versions (Vaughan 1959, 1970; Altenbach and Hermanson 1987) it implies the leading role of humeral elevation.

Our morphofunctional analysis of the bat flight apparatus based on dissections, manipulations on syndesmological preparations, and fluoroscopic research of flight has shown that a number of statements of the lock hypotheses are wrong and allowed the introduction of an alternative kinematic model of the bat shoulder girdle (Panyutina et al. 2011, 2013). Below is its overview.

Manipulations on syndesmological preparations of bats have revealed that mobility of the clavicle in the sternoclavicular articulation consists of three components

(Fig. 5.4), whose limits are determined by ligaments and relief of articular facets (see description in Chap. 3). The first component is lateromedial and the second is craniocaudal deflections. In sum, they allow circumduction of the clavicle within the cone shown in Fig. 5.4a. The third is rotation of the clavicle about the longitudinal axis of its straight proximal part (the stem). As a result of this rotation, the posterolaterally curved distal (acromial) end of the clavicle turns by an arc in the plane which is perpendicular to the stem (Fig. 5.4b). Depending on the direction of rotation, we term it either pronation or supination, alike the respective movements of the humerus, etc. The range of axial rotation of the clavicle varies somewhat in different bat groups; in primitive taxa, mobility is greater than in specialized bats, such as *Hipposideros*. In any case, rotation of the clavicle, due to the pronounced deflection of its distal end, can make more important contribution in the displacements of the acromion and the shoulder joint than the lateromedial and craniocaudal deflections relative to the sternum.

Fluoroscopy was never applied to bat flight before. We used it to study kinematics of *Rousettus aegyptiacus* flying on a tether. It was rather free to move, and we obtained X-ray frame sequences (24 fps) representing cyclic motions of its shoulder girdle and wing in various aspects. The typical sequences in the frontal and sagittal planes are shown in Fig. 5.5. The data were not enough for quantitative analysis

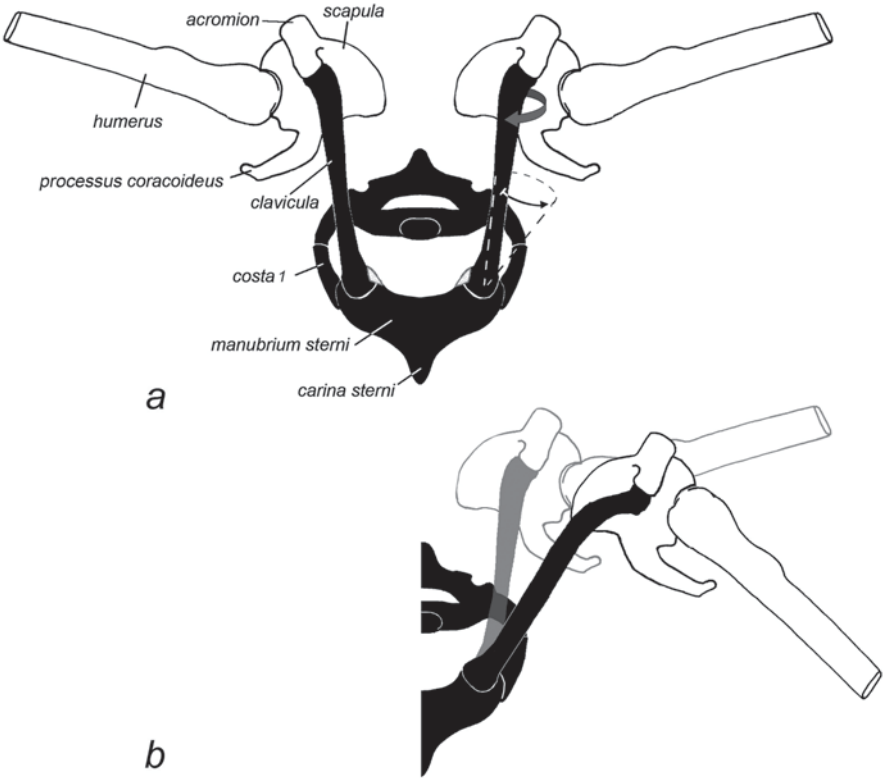


Fig. 5.4 Scheme of mobility in the shoulder girdle and humerus of bats in the transverse plane, anterior view. *a. Start of upstroke – clavicle is in the medial position, humerus is raised;* arrows indicate the directions of further movement, dotted lines indicate the limits of clavicle mobility. *b. End of downstroke;* preceding position is shown in grey.

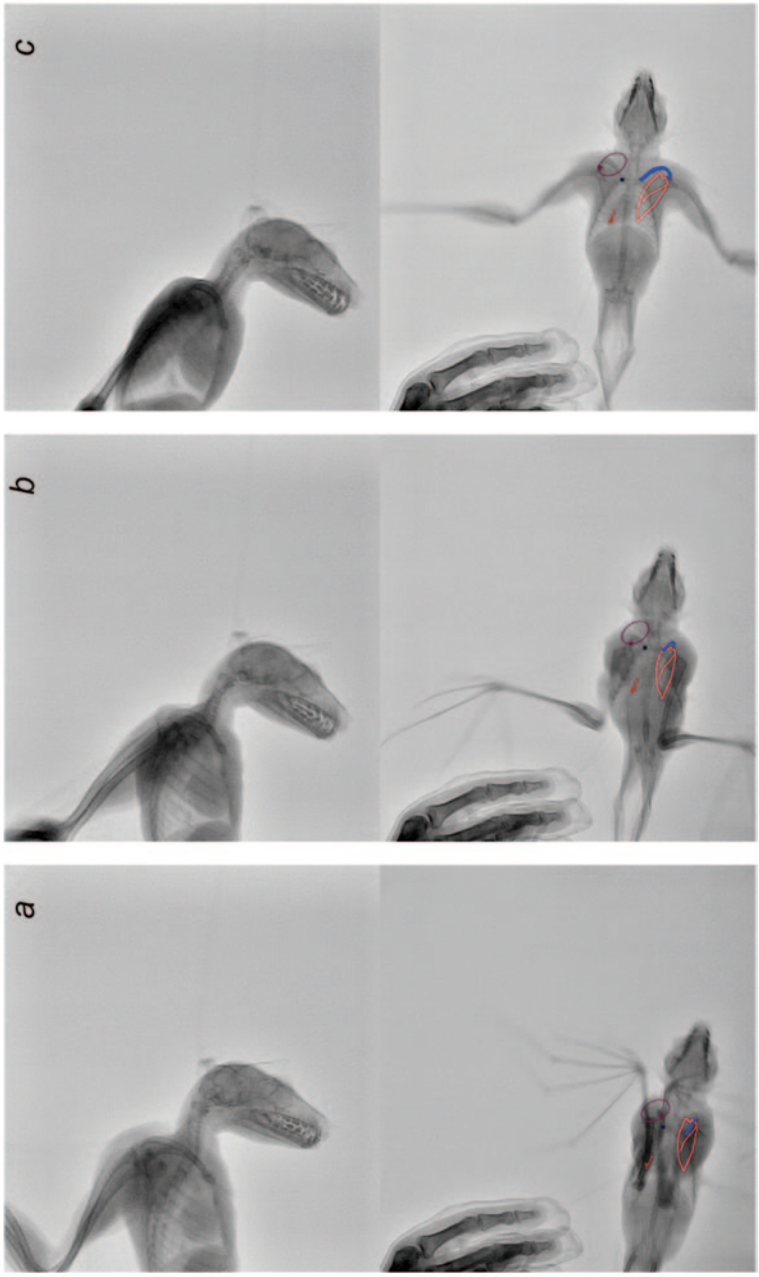


Fig. 5.5 X-ray images of successive wing beat phases of *Rousettus aegyptiacus* in sagittal and frontal planes. Wing beat cycle duration 1/5 s and 1/6 s for the sagittal and frontal views, respectively. To bring stages in both series into better accordance one frame between *c* and *d* in the sagittal view series was omitted. On one side of the body, the clavicle is filled with blue, and the scapula is outlined by red. *a, a' Wings in the uppermost position (point of upstroke to downstroke transition) b, c Downstroke d, e Upstroke*

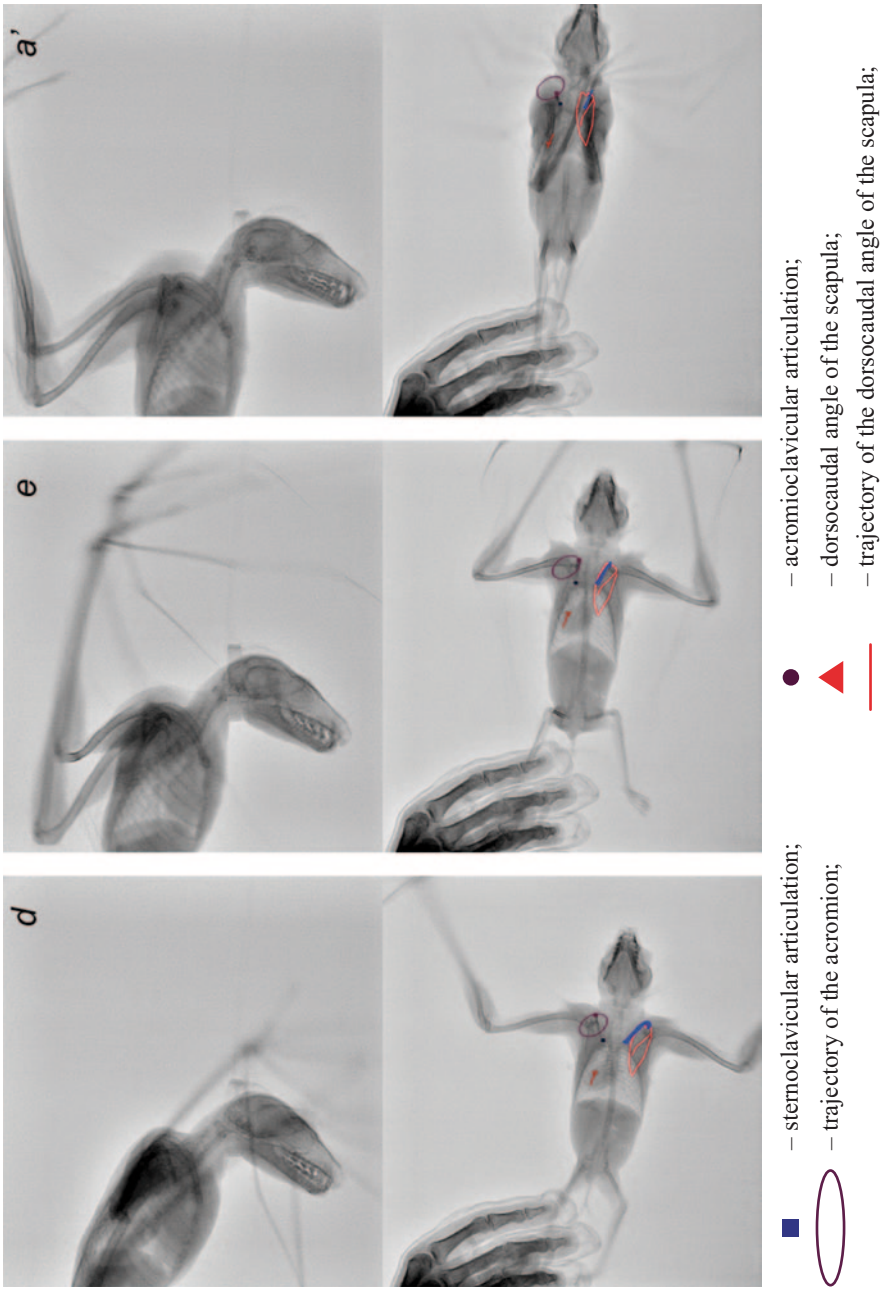


Fig. 5.5 (continued)

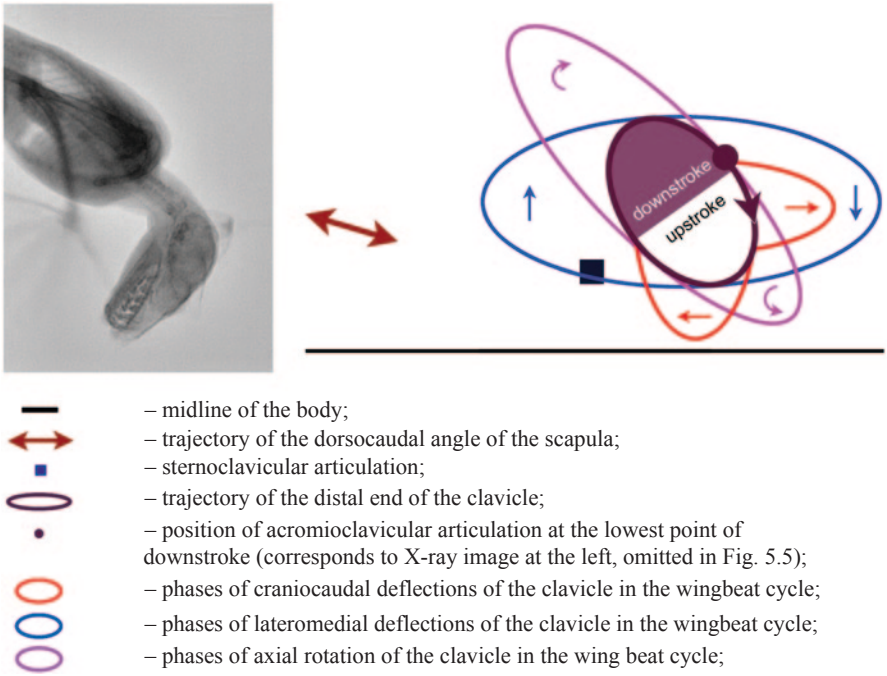


Fig. 5.6 Scheme of clavicle mobility in the wingbeat cycle of *Rousettus aegyptiacus* based on X-ray data. Left side, dorsal view. Arrows indicate direction of movements.

of the shoulder girdle motions, but allowed to make a rather reliable qualitative description thereof, as follows. The scapula rests horizontally on the dorsal side of the rib cage and does not go away from this frontal plane considerably. In this plane, the dorsocaudal angle of the scapula shifts back-and-forth almost parallel to the vertebral column, while the acromion, together with glenoid and the distal end of the clavicle, circulates by an elliptic trajectory (Fig. 5.6). Superficially, the whole movement is similar, in the frontal view, to that of a crank-and-rod mechanism, the clavicle acting as a crank and the scapula as a rod.

The greater diameter of the elliptic trajectory of the acromion somewhat declines from the perpendicular to the vertebral column, so that the lateral pole of the ellipse is found slightly caudal to its medial pole. The acromion passes the posterior part of the ellipse moving away from the vertebral column and the anterior part moving towards the vertebral column. The anteromedial and posterolateral parts of the ellipse are passed by the acromion during the upstroke and downstroke of the wing, respectively.

As the acromion moves along its elliptic trajectory, it leans on the clavicle, which circumscribes a cone with the apex in the sternoclavicular articulation. More precisely, the clavicle moves as follows (Fig. 5.6). Its supination and pronation are coupled with the downstroke and upstroke, respectively. The lateral and medial deflections are somewhat phase-advanced in respect of supination and pronation, respectively. The cranial deflection is restricted to the beginning of the upstroke, while the caudal deflection continues throughout the rest of this phase; no considerable craniocaudal deflections are found in the downstroke. So, at the beginning of the downstroke, the clavicle is being already deflected laterally (Fig. 5.5b) and, somewhat later, its supination also contributes to the lateral displacement of the acromion (Fig. 5.5c) due to the distinctive curvature of the clavicle. As the acromion passes the lateral pole of its orbit, the lateral deflection of the clavicle changes to the medial deflection, and the supination decays, so that, by the end of the downstroke, the acromion begins to go medially. The upstroke starts with the coupled pronation and cranial deflection of the clavicle, which also continues to deflect medially. In the first half of upstroke, the acromion reaches the most anterior point of its orbit, where the cranial deflection of the clavicle changes to the caudal deflection. Somewhat later, the medial deflection of the clavicle changes to the lateral deflection as well. Finally, at the upstroke to downstroke transition, pronation changes to supination (Figs. 5.5d, 5.5e). Then, the cycle repeats.

On the whole, the components of mobility in the sternoclavicular articulation employ the following ranges. The amplitude of rotation of the clavicle about its stem is at least 45°, the amplitude of lateromedial deflections is at most 30°, and the craniocaudal deflections are too small in range to be estimated accurately.

The trajectory of the shoulder joint relative to the body closely resembles the elliptic one of the acromioclavicular articulation, since the two points are adjacent on the scapula. The craniocaudal displacements of the shoulder joint are slightly less than 20 mm per cycle, while its lateromedial as well as dorsoventral displacements are slightly more than that. These values obtained by fluoroscopic research of *Rousettus aegyptiaeus* are roughly similar to respective displacements in *Cynopterus brachiotis*, which were measured in flight with the help of skin markers (Swartz et al. 2007). In this fruit bat, being about twice smaller in wingspan than ours (30–40 cm against 60 cm in *Rousettus aegyptiaeus*, according to Norberg 1972), the craniocaudal, lateromedial, and dorsoventral displacements of the shoulder joint are at most 6, 4, and 8 mm per cycle, respectively.

Note that all the above movements of the scapula and clavicle make a minor contribution to the wing strokes, since they are considerably less than the range of humeral movements relative to the scapula in the shoulder joint. The predominant role of the shoulder joint in the wing movements is evident from our fluoroscopic, video, and syndesmologic data, as well as from the literature. Thus, wing strokes during the bat flight are produced mostly by movements of the humerus relative to the weakly mobile shoulder girdle. Note however, that the movements of humerus relative to shoulder girdle in flight employ only the caudal-most sector of available shoulder joint mobility (Panyutina et al. 2013).

However, despite the above criticism against the scapulo-humeral lock idea it deserves further research. Indeed, there is a promising aspect of the hypothesis of Altenbach and Hermanson (1987) in the suggested shift of the wing fulcrum in the powered stroke from the shoulder joint axis more proximally (e.g., upon the articulation of the greater tubercle of humerus with the supraglenoid facet of scapula). It may be of advantage, if the *m. pectoralis* performs the power stroke about the proximal fulcrum, and all the rest, less strenuous, activities (e.g., wing folding) about the shoulder joint. Since the fiber length (as well as the cross-sectional area and the force) of the *m. pectoralis* is given in each particular bat, they shorten by the same linear magnitude irrespective of what fulcrum is employed. About the shoulder joint, the lever arm is smaller, and, hence, the muscle exerts a smaller moment over a larger angular amplitude; this is good for wing folding. About the more proximal articulation, the lever arm is greater, and, hence, the muscle exerts a greater moment over a smaller angular amplitude; this is good for wing stroke. Without such shift of fulcrum, the muscle should be necessarily more massive to combine the large amplitude for folding with the large moment of force for the stroke. In fact, the usage of the accessory proximal fulcrum does not need locking of the greater tubercle of humerus against the supraglenoid facet of scapula, but simply their contact and disarticulation of the humeral head and glenoid.

Interaction of Wing with Air

Having gained an idea of kinematics of bat wing skeleton and shoulder girdle in flight, let us turn to the action of the major muscles powering the flight. For this purpose the external forces exerted on the wing should be considered first.

Experimental research of bat aerodynamics has a rather long history. The only reliable basis to estimate the actual forces of the wing-air interaction is the vortex wake, which is produced in the air behind a flying animal by its wing strokes. So, the wake flow should be visualized. For the first time this was done for the horizontal flight of *Nyctalus noctula* by Rayner (1987), 8 years after the first visualization of a bird wake (Kokshaysky 1979). Rayner fitted his interpretation of the wake traces of *Nyctalus* in the general concept of flapping flight aerodynamics which became conventional at that time based on bird wakes. The concept states the existence of two discrete ‘gaits’ of forward flight, the slow ‘vortex ring gait’, and the fast ‘continuous vortex gait’. In the first one, the downstroke produces a single closed vortex ring being shed from wings when they exert lift and thrust, while the upstroke is passive, that is the wings do not considerably interact with air and, hence, do not produce a wake. In the second gait, the wings continue to interact with air throughout the wingbeat cycle, and so the wake is not interrupted, but is shed from wing tips as a pair of tube-shaped trailing vortices which repeat the wavy path of the wing tips. The upstroke is active in this case; it produces lift, but also a parasitic retard-

ing force canceling part of the downstroke thrust[1]. So, Rayner (1987) reported for *Nyctalus* the vortex ring gait at the flight speed of 3 m/s, and the continious vortex gait at the speed of 7.5 m/s.

The next experimental visualization of bat vortex wake was obtained almost 20 years later on *Cynopterus brachyotis* (Tian et al. 2006), but the data was not enough to build a three-dimensional picture of the wake. This was done exactly 20 years after Rayner on *Glossophaga soricina* by Hedenström et al. (2007).

Based on the modern experimental technique (particle image velocimetry), the new 3D wake reconstruction for *Glossophaga* (Hedenström et al. 2007) entirely contradicts the earlier results on *Nyctalus* (Rayner 1987). Neither the vortex ring gait at slow speeds nor the continuous vortex gait at high speeds is found in *Glossophaga*. In the speed range from 1.5 through 7 m/s, the vortex wake shows gradual transformation rather than any kind of discrete 'gaits'[2]. In addition, three important unexpected points have been found out. The first is that the body is not included in the lifting surface and, hence, the left and right wings produce separate vortex wakes. The second point is that the circulation on the wing changes continuously. The third point is in the nature of the wing-air interaction in the upstroke. At slow speeds, the upstroke is not passive (i.e., wake-less, as was regarded by Rayner); instead, the backward flick of the wing produces thrust, as well as lift, due to the negative angle of attack (as was envisaged by Aldridge 1987b, see above). At medium and higher speeds, the plagiopatagium and chiropatagium interact with air differently in the upstroke. The plagiopatagium 'inherits' the positive angle of attack from the downstroke and thus sustains lift but produces a parasitic retarding force (as in continuous vortex gait of Rayner). At the same time, the chiropatagium gains the negative angle of attack due to its pronation and produces thrust together with a minor parasitic downward force. As a result, separate vortex ring is shed from the chiropatagium at the end of the upstroke at medium and higher speeds, which rotates in the opposite direction as compared with the vortex shed from the plagiopatagium (and in the same direction as the vortex ring shed from the whole wing in its backward flick at slow speeds)[3]. On the whole, the thrust of the chiropatagium cancels the retarding force of the plagiopatagium, whose lift, in its turn, overbalances the downward force of the chiropatagium, and, hence, the resultant aerodynamic force produced by the wing as a whole in the upstroke at medium and higher speeds acts almost upwards providing only weight support (Wolf et al. 2010).

Comparison of vortex wakes produced by *Glossophaga soricina* and *Leptonycteris yerbabuenae*, which is twice heavier, has shown their general similarity (Muijres et al. 2011). The vortex wake 3D structure was also reconstructed for *Cynop-*

[1] In the upstroke of the continuous vortex gait, the downstroke muscles (e.g., the *m. pectoralis*) should be kept active to withstand the excess air pressure from below which results in aerodynamic lift. However, since the wings are being raised, these muscles are inevitably forcibly stretched. So, they produce negative work reducing the kinetic energy of the body.

[2] By that time, based on the same technique, the concept of discrete gaits has been already disproved for birds, and the upstroke wake was found at their slow speeds (Spedding et al. 2003).

[3] Such separate vortex rings with reversed rotation shed from the distal part of the wing in the upstroke were not reported in birds (Hedenström et al. 2009).

terus brachyotis (Hubel et al. 2009, 2010). Contrary to *Glossophaga soricina*, the body of *Cynopterus brachyotis* is better integrated into the lifting surface of the wings, and the reversed vortex rings shed from the chiropatagium by the end of the upstroke are not inclined to the horizon (Hubel et al. 2010), which implies that chiropatagium does not provide thrust at this time but only generates downward force, which seems bad for flight since it only cancels part of the lift generated by the plagiopatagium. Consideration of wing inertia suggests that *Cynopterus brachyotis* fails to produce thrust even by the backward flick at slow flight speeds, since the center of mass of the whole body does not show forward acceleration in the downstroke (Iriarte-Díaz et al. 2011).

Recently, the vortex wake 3D structure was reconstructed for *Tadarida brasiliensis* being one of the fastest bats (Hubel et al. 2012). The speed range from 2.8 through 8.3 m/s was studied. At lower speeds the wake pattern is similar to that of bats studied before: the body is not included in the lifting surface and reversed vortices are shed from chiropatagium at the end of the upstroke. However, at higher speeds the body becomes fully integrated into the lifting surface in the downstroke and, so, fully participates in lift generation throughout its duration, while the upstroke becomes aerodynamically passive and leaves no wake in the air. As a result, a rather typical vortex ring 'gait' arises in the fast flight of *Tadarida*. This is surprising, since, initially, such wake structure was presumed for slow flight of bats (Rayner 1987) as well as birds.

At slowest speeds, such as 1 m/s and below, the wing performance is complicated by insufficient velocity of wings relative to the still air. However, increased lift generation in the downstroke can be achieved by extraordinarily enlarged angle of attack and wing camber due to the appearance of unsteady leading-edge vortex on top of the anterior edge of the wing, which was discovered in *Glossophaga soricina* (Muijres et al. 2008). Also, the uropatagium, if present, shows active strokes in minimal-speed and take-off flight (Adams et al. 2012). These strokes are not always in phase with the wing strokes. They are powered by hind limbs and provide additional thrust and perhaps lift to accelerate and rise up.

On the whole, the picture of the wing-air interactions in the full speed range of horizontal flight in bats looks as follows. At the slowest speeds, there are leading-edge vortices in the wing downstroke for additional lift and uropatagium strokes for additional thrust; at medium-slow speeds, there is a backward flick in upstroke for lift and thrust generation associated with formation of reversed vortex rings, one per wing; at medium-high speeds, the plagiopatagium provides lift in upstroke, while the chiropatagium provides thrust shedding a separate and reversed vortex ring; at the highest speed, there is a vortex-ring 'gait', the body being integrated into the lifting surface in the downstroke, while the upstroke is passive.

The current state of bat flight biomechanics is reviewed by Swartz and co-authors (Swartz et al. 2006, 2012). The two reviews, when compared, show an important trend in bat aerodynamics, which is the increasing emphasis on unsteady effects in the wing-air interactions.

Internal Biomechanics of Wing

The aerodynamic forces are distributed over the wing membrane and are roughly perpendicular to its surface at every point. These forces are transformed into the forces of membrane tension which are tangential to its surface at every point. The shape of the wing camber represents an instantaneous balance of aerodynamic and tension forces (as well as inertial forces) on the membrane. The forces which are transferred onto the wing skeleton of bats are the tension forces, which, hence, may be regarded as external forces in the musculoskeletal biomechanics. So, the membrane structure is crucial for understanding of mechanics of the skeletal airframe of the wing.

The first attempt to analyze distribution of tension forces in the bat wing membrane and transformation thereof into longitudinal compression forces in the digits was undertaken by Pennycuick in 1971 in the course of wind tunnel experiments on *Rousettus aegyptiacus* gliding (Pennycuick 1971); the role of the hindlimbs together with the *m. extensor carpi radialis longus* and *m. occipitopollicalis* in membrane stretching was considered. More detailed analysis of membrane tension and digits compression was developed a year later by Norberg (1972), who paid special attention to the angled position of certain phalanges in the plain of the chiropatagium as a means to sustain its span without muscles.

In 1978, a detailed description was published of a network of combined elastin plus collagen fibers in the plagiopatagium, chiropatagium, and propatagium of *Tadarida brasiliensis* (Holbrook and Odland 1978). For our biomechanical analysis in the following section, the most important finding is that, in the plagiopatagium, these fibers are arranged as a roughly orthogonal mesh with chordwise fibers running from the humerus and radius to the trailing edge of the plagiopatagium, while the spanwise fibers run from the body side and the hindlimb to the fifth finger. Until now, there are no comparative studies of this network in various bat species.

The research of elastic properties of various regions of the membrane has shown its profound anisotropy (Swartz et al. 1996; Swartz et al. 2006; Swartz et al. 2012). Beyond the interspecific differences, the uropatagium is the strongest part of the membrane, while the plagiopatagium is the weakest and most extensible; the plagiopatagium and the chiropatagium are most stiff in the chordwise direction and most extensible spanwise (Swartz et al. 1996). The difference between the chordwise and spanwise stress to strain relations is smallest in the chiropatagium, and greatest in the propatagium and antebrachial portion of the plagiopatagium, its humeral portion being intermediate in this respect and most extensible in both directions (Swartz et al. 2006; Swartz et al. 2012).

Also unequal are the flexural properties of different segments of the wing skeleton. The proximodistal gradient of decreasing mineralization makes the digits more flexible than the proximal wing bones (Swartz and Middleton 2008).

Direct measurements of stresses in the humerus and radius in free flight were obtained on *Pteropus poliocephalus* (Swartz et al. 1992). These data were used to

verify the most complete, until now, biomechanical model of the bat wing Watts et al. (2001). All forces distributed over the membrane were taken into account, inertial, tensile, and aerodynamic, but the aerodynamic model was based on the constant-circulation hypothesis which, later, has been experimentally disproved (Hedenström et al. 2007). In fact, the model allowed the calculation of all muscular forces in the wing as well as loading of the shoulder girdle elements, but the authors restricted their deductions to estimation of stresses in the humerus and radius for verification purposes. That is why it could not help us, to our regret, to develop the biomechanical model of the bat shoulder girdle and its muscles described in the following section.

The order of activation of the major wing muscles in flight was studied by means of electromyography in *Artibeus jamaicensis*, *Antrozous pallidus*, *Eptisicus serotinus*, and *Eptesicus fuscus* (Kovtun and Moroz 1973, Hermanson and Altenbach 1981, 1983, 1985; Altenbach and Hermanson 1987). On the whole, 15 muscles were studied in this way; in some of them, different portions were treated separately. One of the major findings, already mentioned in the context of the scapulo-humeral lock idea, is the somewhat earlier activation of the *m. pectoralis*, as compared with the *m. serratus ventralis thoracis*. Even more surprising is the fact, that both of these powerful muscles did not show an electric activity in the last two thirds of the downstroke. Rather, their activity was associated with the upstroke to downstroke transition; switching on occurred in the last third of the former and switching off in the first third of the latter. Most of the other muscles studied were also active at the upstroke to downstroke transition, at the downstroke to upstroke transition, or both (e.g., *m. subscapularis*). Partially, this phase advance in the electric activity of the downstroke muscles relative to the actual beginning of the downstroke, as well as respective advance in the activity of the upstroke muscles, may be due to delay between the start of electric activity and force generation, which is typical to muscles. According to direct measurements on the *m. biceps brachii caput coracoideum* in *Tadarida brasiliensis* (Altenbach and Hermanson 1987), this delay is roughly about 20 % of the wingbeat cycle duration. The rest of this phase advance may be useful indeed, since the muscular forces are necessary not only to propel the wing through the air but also to accelerate it. The peak circumferential accelerations take place just at the transitional points where the direction of wing movement relative to the body reverses.

Power requirement for wing accelerations depends on the moment of inertia of the wing, whose values were estimated for bats by Thollesson and Norberg (1991) and Riskin et al. (2012). The aerodynamic and inertial power expenses were compared in *Glossophaga soricina* (Norberg et al. 1993). For a 10 g bat, hovering implies 0.15 W aerodynamic power and 0.19 W inertial power, while horizontal flight at 4.2 m/s (the optimal speed is ~3.5 m/s: Muijres et al. 2011) implies 0.10 W aerodynamic power and 0.4 W inertial power.

Obviously enough, the kinetic energy of the wing relative to the center of mass of the body (called for brevity the internal kinetic energy or inertial energy) has

maxima at mid-downstroke and mid-upstroke and drops at transitions from one to another. Its fluctuations in a wingbeat cycle were quantified by Riskin et al. (2012). The mid-downstroke and mid-upstroke energy maxima correspond to the maximal magnitudes of angular velocity and centripetal acceleration, while drops of energy at up-and-down transitions are associated with zero angular velocity and centripetal acceleration. Naturally, circumferential (angular) accelerations should have directly opposite position of the extreme and zero values in the wingbeat cycle.

As the wings are accelerated circumferentially, downward and forward or upward and backward relative to the center of mass of the whole body, the trunk is accelerated in the opposite direction. These accelerations were calculated by Iriarte-Díaz et al. (2011) as the difference between the accelerations of a skin marker on the sternum and the accelerations of the estimated center of mass of the whole body. Expectedly, the estimated accelerations (vertical and horizontal) showed sinusoid-like fluctuations in time, one period per wingbeat cycle, with maximal magnitudes near up-and-down transitions and zero values near the mid-downstroke and mid-upstroke.

Obviously, the inertial power expenses are mainly associated with circumferential accelerations of the wing. That is why the wing is partially folded in the upstroke. However, this folding also requires some power to overcome virtual centrifugal forces of inertia (Riskin et al. 2012). In the downstroke, the centrifugal forces may help spreading the wing, like they spread the propeller of a helicopter.

Static Analysis of Downstroke

In contrast to birds, the bat wing is composed of two biomechanically and evolutionary distinct regions (Fig. 5.7). It looks like a hybrid model, whose proximal region works similar to the membrane of gliding mammals while the distal one may be roughly compared to the avian wing. The first region is represented by the proximal part the plagiopatagium stretched between the forelimb and the hindlimb similarly to the whole plagiopatagium of colugos. The second is the rest of the wing which is relatively free from the hindlimbs. We suggest to term the proximal region of the bat wing the “archeopatagium” and the distal one the “neopatagium” to emphasize the similarity of the former with the gliding membrane of colugos and other gliding mammals and the novelty of the latter. Their partial functional independence can be seen on many photographs of flying bats as a fold crossing the membrane from the elbow to the foot, just along the presumed boundary of the archeopatagium and neopatagium. This fold shows that the spanwise tension in the plagiopatagium does not traverse the boundary, at least in certain phases of the wingbeat cycle.

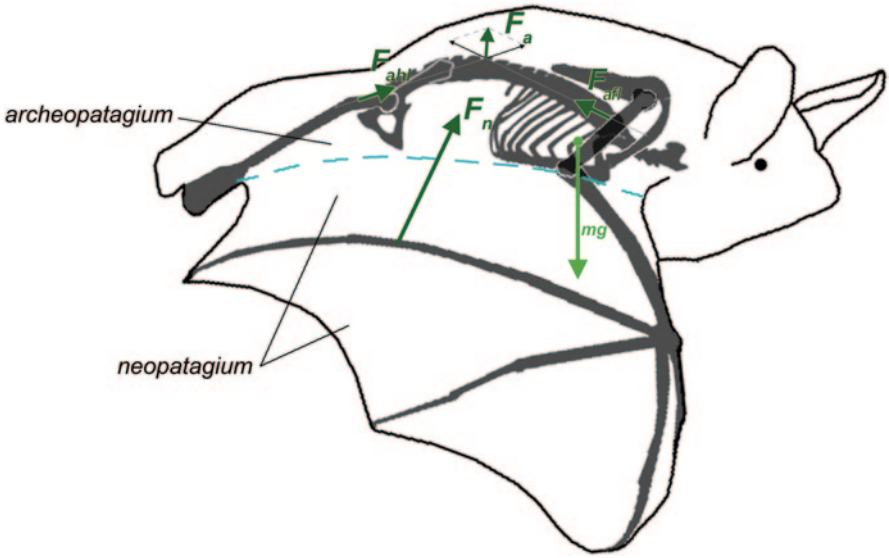


Fig. 5.7 Forces acting on the membrane and limbs of bats in the middle of downstroke, sagittal plane. F_a – aerodynamic force acting on the archeopatagium, F_{afl} – tension force of the archeopatagium applied to the forelimb, F_{ahl} – tension force of the archeopatagium applied to the hindlimb, F_n – aerodynamic force acting on the neopatagium, mg – force of gravity of the body.
boundary between archeo- and neopatagium

As was described in the previous sections, the bat wing performance is very variable and complicated; for instance, it sometimes involves the backward flick and negative angle of attack in the upstroke at low speeds. Below we shall confine our consideration to the downstroke at high flying speed, since our main purpose here is to analyze the extreme forces required from the major flight muscles.

The aerodynamic force F_a applied to the archeopatagium in the downstroke is transferred via the membrane onto the fore and hind limbs in the same manner as in colugos (cf. Figs. 4.11, 5.7) producing forces F_{afl} and F_{ahl} acting on the fore and hind limbs, respectively. These forces are approximately equal in magnitude and tend to pull the limbs together.

The effect of the aerodynamic force F_n acting upon the neopatagium, whose skeletal airframe is formed by the antebrachium and fingers, differs essentially. The trailing edge of this part of the membrane is not reinforced by the hindlimb. As a result, the aerodynamic force F_n is transferred to the trunk through the forelimb alone.

The neopatagium has a much greater surface area than the archeopatagium and its speed relative to the still air is greater too, due to the flapping motions of the wing. Hence, the force F_n of the neopatagium is much greater than the force F_a of the archeopatagium. Also, due to the wing twisting (pronation), which is well

known in birds too, the neopatagium usually develops greater thrust-to-lift ratio in the downstroke than the archeopatagium (see the forward inclination of the vector F_n relative to F_a in Fig. 5.7). As a result, the force F_{afl} exerted by the archaeopatagium on the humerus is approximately perpendicular to the force F_n applied to the manus.

Having outlined the forces exerted on the forelimb as a result of the wing-air interaction, let us consider the respective musculoskeletal mechanics in detail. We shall attempt to analyze the conditions of equilibrium at mid-downstroke of a fast flying bat exemplified by the *Tadarida*, one of the most comprehensively studied genera in respect of the wing structure and performance (Holbrook and Odland 1978; Altenbach and Hermanson 1987; Hubel et al. 2012; Maniakas and Youlatos 2012). Such an analysis has never been elaborated before for any bat.

Further analysis of equilibrium of the forelimb and the shoulder girdle of *Tadarida* at mid-downstroke requires more assumptions than for colugo gliding (Chap. 4); they are as follows.

1. The forces of gravity acting upon the wing are not taken into account being, obviously, negligible as compared with the membrane tension and other forces involved (the same as for colugo).
2. The centrifugal 'inertia forces'[4] virtually acting upon the wing, though maximal at mid-downstroke, are neglected, since they are, presumably, directly counterbalanced by tension in the spanwise elastin plus collagen fibers of the plagiopatagium (Holbrook and Odland 1978) and, via these fibers, transferred onto the body bypassing interference with muscular and skeletal forces which we analyze.
3. The circumferential 'inertia forces' virtually acting upon the wing are not taken into account being close to zero at mid-downstroke (Iriarte-Díaz et al. 2011).
4. The magnitude of the vertical component of the aerodynamic force acting upon the neopatagium is assumed to be equal to body weight *mg* and, as such, is taken as a scale for the other forces involved. This assumption seems reasonable enough for the fast flight of *Tadarida*, since the upstroke in this case is aerodynamically passive and the lift is exclusively provided in the downstroke (Hubel et al. 2012).
5. The total force of sub-chordwise tension of the archeopatagium is assumed to act, in the frontal plane, along the line connecting the mid-length of the humerus and the knee. In fact, the magnitude of this tension is found to be very small

[4] In the static equilibrium, all parts of a body are at rest or in uniform rectilinear motion. In the presence of accelerations of certain parts, D'Alembert's principle is applicable, which states that a body would be in equilibrium under the action of all the applied forces, together with introduced virtual inertia forces opposite in direction and corresponding in magnitude to these accelerations and inertial torques similarly opposing angular accelerations. Based on this, it is possible to analyze even complex movements, having divided them into successive stages.

(~0.13 *mg*); in some trials of equilibrium calculation, it was even reduced to zero, but we decided to show it here because it is interesting in the evolutionary perspective.

6. The clavicle is regarded as a simple strut being loaded strictly longitudinally, along the line passing through the sternoclavicular and acromioclavicular articulations; no muscles attached to the clavicle are involved (the same as for colugo).
7. According to the so-called principle of solidification, widely used in statics, the free forelimb together with the scapula are regarded as a solid body; in this way we put off calculation of forces of one-joint and two-joint muscles of the shoulder and elbow joints (such as the *m. subscapularis*, *m. teres major*, *m. infraspinatus*, *m. triceps brachii*, and *m. biceps brachii*) presuming that they can be supplied if necessary (the same as for colugo).
8. The ratio of force magnitudes of the *m. pectoralis* and the *m. serratus ventralis thoracis* is taken from the data on their physiological cross-sectional areas in *Tadarida teniotis* (Maniakas and Youlatos 2012).
9. The force of the *m. serratus ventralis thoracis* is vertical in the sagittal plane; this assumption is not necessary but rather realistic.

The result of our calculation of 3D equilibrium is shown in Figs. 5.8–5.10 representing three orthogonal planes, the frontal, the sagittal, and the transverse. The

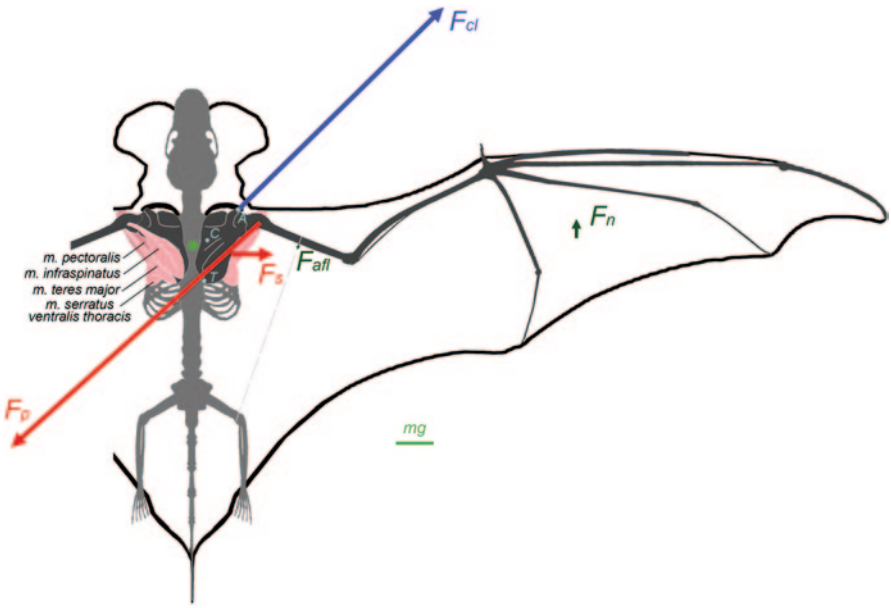


Fig. 5.8 Static equilibrium of the shoulder girdle and forelimb of bats in the middle of downstroke, frontal plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_{afl} – tension force of the archeopatagium, F_n – aerodynamic force of the neopatagium, F_p – force of the *m. pectoralis*, F_s – force of the *m. serratus ventralis thoracis,* F_{cl} – force of the clavicle reaction; for the scale of force vectors the value of gravity force is shown (*mg*)

following forces are involved: the total aerodynamic force F_n of the neopatagium applied to the wing between digits IV and V, the force F_{afl} of the archeopatagium tension applied to the humerus at its midlength, the force F_p of the *m. pectoralis* (*superficialis et profundus*) applied to the pectoral crest of the humerus, the force F_s of the *m. serratus ventralis thoracis* applied to the scapula at midlength of its caudal border, the force F_{cl} of reaction of the longitudinally compressed clavicle applied to the tip of acromion (point *A*), and the strictly vertical force F_{th} of reaction of the thorax applied to the dorsocaudal angle of the scapula (point *T*), which leans on it.

For better understanding of the equilibria in the frontal, sagittal, and transverse planes shown in Figs. 5.8–5.10, see the following qualitative description of the involved forces and torques, which represent the six underlying equations of statics.

1. The forces F_n, F_{afl} (very small), F_{cl}, and F_{th} act upon the forelimb and the shoulder girdle in the upward direction; they are counterbalanced by the forces F_p and F_s acting in the downward direction.
2. The forces F_{afl} (very small) and F_p act upon the forelimb and the shoulder girdle in the medial direction; they are counterbalanced by the forces F_s and F_{cl} acting in the lateral direction.

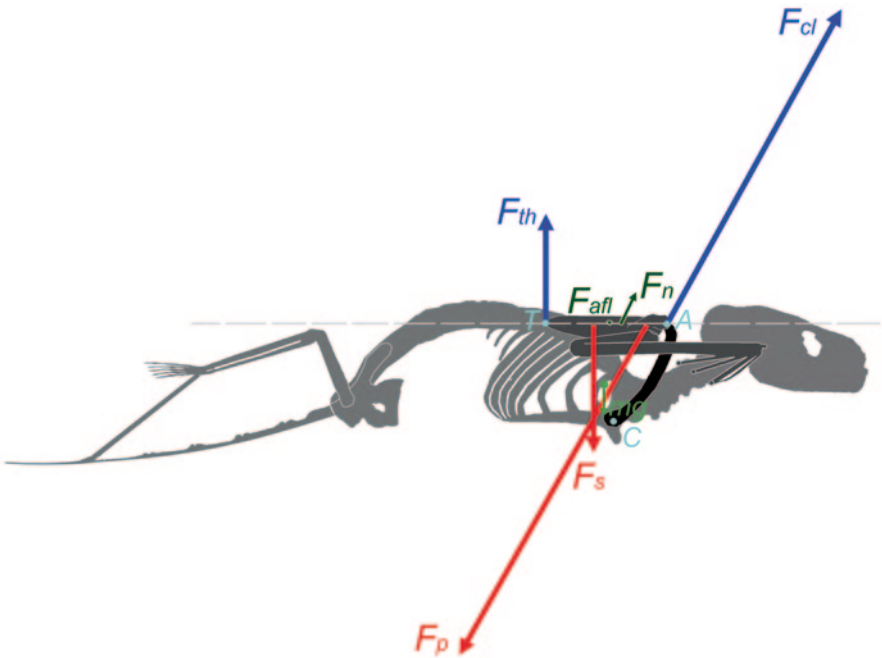


Fig. 5.9 Static equilibrium of the shoulder girdle and forelimb of bats in the middle of downstroke, sagittal plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_{afl} – aerodynamic force of the archeopatagium, F_n – aerodynamic force of the neopatagium, F_p – force of the *m. pectoralis,* F_s – force of the *m. serratus ventralis thoracis,* F_{cl} – force of the clavicle reaction, F_{th} – force of the thorax reaction; *mg* – force of gravity of the body.

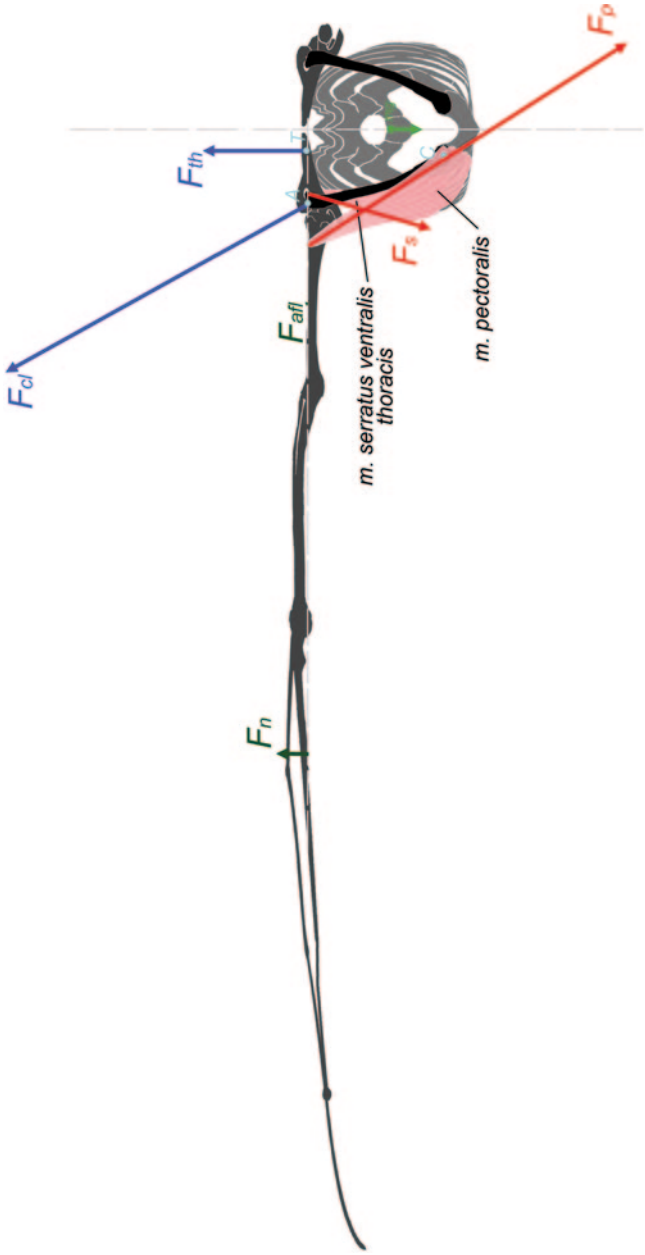


Fig. 5.10 Static equilibrium of the shoulder girdle and forelimb of bats in the middle of downstroke, transverse plane. *A* – acromioclavicular articulation; *C* – sternoclavicular articulation; *T* – dorsocaudal angle of the scapula, F_{afl} – aerodynamic force of the archeopatagium, F_n – aerodynamic force of the neopatagium, F_p – force of the *m. pectoralis*, F_s – force of the *m. serratus ventralis thoracis*, F_{cl} – force of the clavicle reaction, F_{th} – force of the thorax reaction; *mg* – force of gravity of the body.

3. The forces F_{afl} (very small) and F_p act upon the forelimb and the shoulder girdle in the backward direction; they are counterbalanced by the forces F_n and F_{cl} acting in the forward direction.
4. Relative to the center of gravity of the body, the forces F_n, F_s, and F_{cl} (negligible lever arm relative to the assumed position of the center of gravity) produce the yawing torque towards the opposite side; it is counterbalanced by the forces F_{afl} (very small) and F_p producing the opposite torque (Fig. 5.8).
5. Relative to the center of gravity of the body, the forces F_{afl} (very small), F_s, and F_{cl} produce the pitching torque increasing the angle of attack; it is counterbalanced by the forces F_n, F_p, and F_{th} producing the opposite torque (Fig. 5.9).
6. Relative to the center of gravity of the body, the forces F_n, F_{afl} (very small), F_{cl}, and F_{th} produce the wing-up rolling torque; it is counterbalanced by the forces F_p and F_s producing the opposite torque (Fig. 5.10).

The most important points in this 3D equilibrium are best represented in the sagittal plane (Fig. 5.9). In fact, the forces which hold the body aloft are the force $-F_p$ of the *m. pectoralis* applied to the sternum and the force $-F_s$ of the *m. serratus ventralis thoracis* applied to the ribs. It can be readily shown, that their upward components overbalance the downward components of the force $-F_{cl}$ of the pressure of the clavicle on the sternum and the force $-F_s$ of the pressure of the scapula on the thorax by the value, which is equal to the upward components of the wing forces F_{afl} and $F_n = -mg$. Note also, that the forces of the two muscles pass in the sagittal plane at the opposite sides of the center of gravity; this helps to achieve pitching balance of the body. Thus, the peculiar features of the *m. serratus ventralis thoracis* of bats gain the biomechanical explanation. It would not have a large enough vertical component if its insertion did not shift from the dorsal onto the caudal border of the scapula (Fig. 5.11), and it would be unable to pitch the body head-down if the scapula did not elongate posterior to the center of gravity (Fig. 5.12). Relaxing anterior or posterior slips, the *m. serratus ventralis thoracis* is capable to shift its resultant force backward or forward through almost the entire length of the scapula and thus, increase or decrease the pitching effect.

Now, let us put off the principle of solidification to specify the intrinsic limb muscles which are necessary to balance the joints of the free forelimb against the force F_n (see again Figs. 5.8–5.10). It is convenient to start from the distal joints where only the latter force should be counterbalanced.

In the interphalangeal and metacarpophalangeal joints, the force F_n (or, more precisely, its part distributed over the membrane portion which is distal to each particular joint) provokes hyperextension. It is resisted passively due to the special design of articular surfaces and the joint ligaments.

Fig. 5.11 Scheme of the *m. serratus ventralis thoracis* attachment in transverse cross section. *a. Colugo (at gliding and clinging) b. Bat*

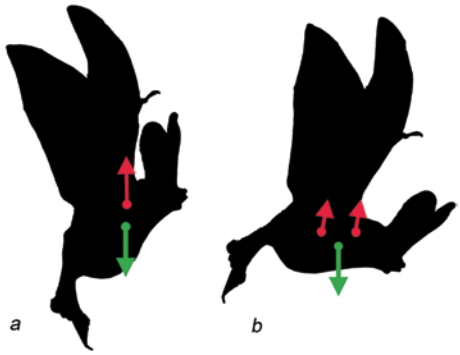


Fig. 5.12 Mechanism of maintaining of proper body position in flight. *a. Incorrect position, m. serratus ventralis thoracis does not work b. Proper position, m. serratus ventralis thoracis works*

In the carpometacarpal, mediocarpal, and radiocarpal joints, the force F_n provokes hyperextension too. For counteraction, the passive articular mechanisms are aided here by muscles, such as the *m. flexor carpi radialis*, *m. flexor carpi ulnaris*, *m. flexor digitorum profundus*, and *m. flexor digitorum superficialis*.

In the elbow joint, the force F_n provokes upward abduction, pronation, and flexion. The abduction and pronation are completely excluded by the special design of articular surfaces and ligaments of the elbow joint, while flexion is prevented by contraction of the *m. triceps brachii* and spanwise tension of the plagiopatagium which is directly transferred onto the body side.

In the shoulder joint, not only the force F_n but also the force F_{afl} of the archeopatagium tension and the force F_p of the *m. pectoralis* should be taken into account, since they were already involved in the 3D equilibration of the acromioclavicular and the sternoclavicular articulations. For complete balance in the shoulder joint, the *m. subscapularis* is required as a humeral depressor, the *m. infraspinatus* as a supinator, and the *m. teres major* as a retractor (the *m. triceps brachii caput longum* can also help).

The involvement of the shoulder girdle and forelimb muscles in the mid-downstroke, which follows from our analysis, generally agrees with the electromyographic data on *Artibeus jamaicensis*, *Antrozous pallidus*, and *Eptesicus fuscus* (Hermanson and Altenbach 1981, 1983, 1985; Altenbach and Hermanson 1987).

The above analysis of the equilibrium of the shoulder girdle and the forelimb in the downstroke of bats shows three important differences from colugos in a glide (cf. Figs. 4.12–4.14 and 5.8–5.10), which are definitely associated with the appearance of the neopatagium.

1. In bats, the force F_p of the *m. pectoralis* is greater than the body gravity by an order of magnitude, while in colugos it is the same order as the gravity. It is this excess force in bats that allows for wing flapping. Remember that the lift and thrust generation in the upstroke is problematic (it may be aerodynamically passive or produce either negative thrust or lift) and, so, the downstroke is obliged to provide excess positive force.

2. In bats, the vertical component of the force F_s of the *m. serratus ventralis thoracis* surpasses its transverse component, while the longitudinal component is zero; on the contrary, in colugos, the transverse and longitudinal components of its force almost equally surpass the vertical one. Thus, in bats this muscle mainly suspends the body aloft, while in colugos it draws the scapula anterolaterally to stretch the membrane by the straightened forelimb.
3. The most general difference of chiropterans from colugos is the unequal distribution of the membrane loading between the fore and hind limbs. In colugos (Fig. 4.11), the aerodynamic force F is equally divided via the plagiopatagium between the fore and hind limbs, so that the anterior half of the body is suspended by the *m. pectoralis* and the posterior half by femoral adductors. In bats (Fig. 5.7), only the aerodynamic force F_a acting on the archaeopatagium is distributed between the fore and hind limbs, like in colugos. On the contrary, the aerodynamic force F_n, which is an order of magnitude greater, acting on the neopatagium is only transferred to the body through the forelimb. In this situation, if the body was suspended to the forelimb by the *m. pectoralis* alone, the body would pitch head-up until the center of gravity of the body reached the vertical line of action of the *m. pectoralis*; otherwise, the equilibrium in flight would be impossible (Fig. 5.12a, Panyutina et al. 2010). Therefore, to keep the horizontal position of the body in horizontal flight using neopatagium, bats need the second suspension of the body to the forelimb, which should be placed posterior to the center of gravity (Fig. 5.12b). This function is performed by the *m. serratus ventralis thoracis*, which is displaced posteriorly by means of peculiar elongation of the scapula. As a result, anterior to the center of gravity, the body is held aloft by the *m. pectoralis* and, posterior to it, by the the *m. serratus ventralis thoracis* together with femoral adductors.

References

Adams RA, Snode ER, Shaw JB (2012) Flapping tail membrane in bats produces potentially important thrust during horizontal takeoffs and very slow flight. PLoS ONE 7(2):e32074 doi:10.1371/journal.pone.0032074

Aldridge HDJN (1986) Kinematics and aerodynamics of the greater horseshoe bat, *Rhinolophus ferrumequinum*, in horizontal flight at various flight speeds. J Exp Biol 126(1):479–497

Aldridge HDJN (1987a) Turning flight of bats. J Exp Biol 128(1):419–425

Aldridge HDJN (1987b) Body accelerations during the wingbeat in six bat species: the function of the upstroke in thrust generation. J Exp Biol 130(1):275–293

Aldridge HDJN (1988) Flight kinematics and energetics in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae), with reference to the influence of ground effect. J Zool Lond 216(3):507–517

Aldridge HDJN (1991) Vertical flight in the Greater horseshoe bat *Rhinolophus ferrumequinum*. J Exp Biol 157(1):183–204

Altenbach JS, Hermanson JW (1987) Bat flight muscle function and the scapulohumeral lock. In: Fenton MB, Racey P, Rayner RMV (eds) Recent advances in the study of bats. Cambridge University Press, p 100–118

Bullen R, McKenzie NL (2001) Bat airframe design: flight performance, stability and control in relation to foraging ecology. Austral J Zool 49(3):235–261
Busse R von, Hedenström A, Winter Y, Johansson LC (2012) Kinematics and wing shape across flight speed in the bat, *Leptonycteris yerbabuenae*. Biol Open 1(12):1226–1238
Davis R (1969) Wing loading in Pallid bats. J Mammal 50(1):140–144
Dudley R, Winter Y (2002) Hovering flight mechanics of neotropical flower bats (Phyllostomidae: Glossophaginae) in normodense and hypodense gas mixtures. J Exp Biol 205(23):3669–3677
Findley JS, Studier EH, Wilson DE (1972) Morphologic properties of bat wings. J Mammal 53(3):429–444
Hartman FA (1963) Some flight mechanisms of bats. Ohio J Sci 63(2):59–65
Hayward B, Davis R (1964) Flight speeds in western bats. J Mammal 45(2):236–242
Hedenström A, Johansson LC, Spedding GR (2009) Bird or bat: comparing airframe design and flight performance. Bioinsp Biomim 4(1):015001. doi:10.1088/1748-3182/4/1/015001
Hedenström A, Johansson LC, Wolf M et al (2007) Bat flight generates complex aerodynamic tracks. Science 316(5826):894–897
Hermanson JW (1981) Functional morphology of the clavicle in the Pallid bat, *Antrozous pallidus*. J Mammal 62(4):801–805
Hermanson JW, Altenbach JS (1981) Functional anatomy of the primary downstroke muscles in the Pallid bat, *Antrozous pallidus*. J Mammal 62(4):795–800
Hermanson JW, Altenbach JS (1983) The functional anatomy of the shoulder of the pallid bat, *Antrozous pallidus*. J Mammal 64(1):62–75
Hermanson JW, Altenbach JS (1985) Functional anatomy of the shoulder and arm of the fruit–eating bat *Artibeus jamaicensis*. J Zool Lond 205(2):157–177
Hildebrand M (1977) Analysis of asymmetrical gaits. J Mammal 58(2):131–156
Hill JE, Smith JD (1984) Bats, a natural history. Univ of Texas Press, Austin
Holbrook KA, Odland GF (1978) A collagen and elastic network in the wing of the bat. J Anat 126(1):21–36
Hubel TY, Hristov NI, Swartz SM, Breuer KS (2009) Time-resolved wake structure and kinematics of bat flight. Exp Fluids 46(5):933–943
Hubel TY, Hristov NI, Swartz SM, Breuer KS (2012) Changes in kinematics and aerodynamics over a range of speeds in *Tadarida brasiliensis*, the Brazilian free-tailed bat. J Roy Soc Interface 9(71):1120–1130
Hubel TY, Riskin DK, Swartz SM, Breuer KS (2010) Wake structure and wing kinematics: the flight of the lesser dog-faced fruit bat, *Cynopterus brachyotis*. J Exp Biol 213(20):3427–3440
Hughes P, Rayner JMV (1993) The flight of pipistrelle bats *Pipistrellus pipistrellus* during pregnancy and lactation. J Zool Lond 230(4):541–555
Iriarte-Díaz J, Riskin DK, Breuer KS, Swartz SM (2012) Kinematic plasticity during flight in fruit bats: individual variability in response to loading. PLoS ONE 7(5):e36665. doi:10.1371/journal.pone.0036665
Iriarte-Díaz J, Riskin DK, Willis DJ et al (2011) Whole-body kinematics of a fruit bat reveal the influence of wing inertia on body accelerations. J Exp Biol 214(9):1546–1553
Iriarte-Díaz J, Swartz SM (2008) Kinematics of slow turn maneuvering in the fruit bat *Cynopterus brachyotis*. J Exp Biol 211(21):3478–3489
Kokshaysky NV (1979) Tracing the wake of a flying bird. Nature 279(5709):146–148
Kovtun MF, Moroz VF (1973) Study of the bioelectric activity of the shoulder girdle muscles in *Eptisicus serotinus* Schreb. (Chiroptera). Dokl AN SSSR 210:1481–1484 (in Russian)
Lawrence MJ (1969) Some observations on non-volant locomotion in vespertilionid bats. J Zool Lond 157(3):309–317
MacAyeal LC, Riskin DK, Swartz SM, Breuer KS (2011) Climbing flight performance and load carrying in lesser dog-faced fruit bats (*Cynopterus brachyotis*). J Exp Biol 214(5):786–793
Maniakas I, Youlatos D (2012) Myological adaptations to fast enduring flight in European free-tailed bats, *Tadarida teniotis* (Molossidae, Chiroptera). Ital J Zool 79(4):574–581
Muijres FT, Henningsson P, Stuiver M, Hedenström A (2012a) Aerodynamic flight performance in flap-gliding birds and bats. J Theor Biol 306:120–128

Muijres FT, Johansson LC, Barfield R et al (2008) Leading-edge vortex improves lift in slow-flying bats. Science 319(5867):1250–1253

Muijres FT, Johansson LC, Bowlin MS et al (2012b) Comparing aerodynamic efficiency in birds and bats suggests better flight performance in birds. PLoS ONE 7(5):e37335. doi:10.1371/journal.pone.0037335

Muijres FT, Johansson LC, Winter Y, Hedenström A (2011) Comparative aerodynamic performance of flapping flight in two bat species using time-resolved wake visualization. J R Soc Interface 8(63):1418–1428

Neuweiler G (2000) The biology of bats. Oxford University Press

Norberg UM (1972) Functional osteology and myology of the wing of the dog–faced bat *Rousettus aegyptiacus* (E. Geoffroy) (Mammalia, Chiroptera). Z Morph Tiere 73(1):1–44

Norberg UM (1976a) Some advanced flight manoeuvres of bats. J Exp Biol 64(2):489–495

Norberg UM (1976b) Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. J Exp Biol 65(1):179–212

Norberg UM (1976c) Aerodynamics of hovering flight in the long-eared bat *Plecotus auritus*. J Exp Biol 65(2):459–470

Norberg UM, Brooke AP, Trewhella WJ (2000) Soaring and non-soaring bats of the family Pteropodidae (flying foxes, *Pteropus spp*.): wing morphology and flight performance. J Exp Biol 203(3):651–664

Norberg UM, Kunz TH, Steffensen JF et al (1993) The cost of hovering and forward flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory. J Exp Biol 182(1):207–227

Norberg UM, Norberg RA (2012) Scaling of wingbeat frequency with body mass in bats and limits to maximum bat size. J Exp Biol 215(5):711–722

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Phil Trans R Soc Lond B 316(1179):335–427

Norberg UM, Winter Y (2006) Wing beat kinematics of a nectar-feeding bat, *Glossophaga soricina*, flying at different flight speeds and Strouhal numbers. J Exp Biol 209(19):3887–3897

Panyutina AA, Korzun LP, Kuznetsov AN (2010) Unique role of serratus muscle in locomotion of bats. Plecotus et al 13:5–11 (in Russian with English summary)

Panyutina AA, Korzun LP, Kuznetsov AN (2011) Kinematics of the shoulder girdle in bats. Doklady Biol Sci 439:240–243

Panyutina AA, Kuznetsov AN, Korzun LP (2013) Kinematics of chiropteran shoulder girdle in flight. Anat Rec 296(3):382–394

Pennycuick CJ (1971) Gliding flight of the dog-faced bat *Rousettus aegyptiacus* observed in a wind tunnel. J Exp Biol 55(3):833–845

Rayner JMV (1987) The mechanics of flapping flight in bats. In: Fenton MB, Racey P, Rayner JMV (eds) Recent advances in the study of bats. Cambridge University Press, p 23–42

Rayner JMV, Aldridge HDJN (1985) Three-dimensional reconstruction of animal flight paths and the turning flight of microchiropteran bats. J Exp Biol 118(1):247–265

Riskin DK, Bahlman JW, Hubel TY et al (2009) Bats go head-under-heels: the biomechanics of landing on a ceiling. J Exp Biol 212(7):945–953

Riskin DK, Bergou A, Breuer KS, Swartz SM (2012) Upstroke wing flexion and the inertial cost of bat flight. Proc Roy Soc B 279(1740):2945–2950

Riskin DK, Hermanson JW (2005) Independent evolution of running in vampire bats. Nature 434(7031):292

Riskin DK, Iriarte-Díaz J, Middleton KM et al (2010) The effect of body size on the wing movements of pteropodid bats, with insights into thrust and lift production. J Exp Biol 213(23):4110–4122

Riskin DK, Parsons S, Schutt WA Jr et al (2006) Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*. J Exp Biol 209(9):1725–1736

Riskin DK, Willis DJ, Iriarte-Díaz J et al (2008) Quantifying the complexity of bat wing kinematics. J Theor Biol 254(3):604–615

Schlosser-Sturm E, Schliemann H (1995). Morphology and function of the shoulder joint of bats (Mammalia: Chiroptera). J Zool Syst Evol Res 33(2):88–98

Spedding GR, Rosén M, Hedenström A (2003) A family of vortex wakes generated by a thrush nightingale in free flight in a wind tunnel over its entire natural range of flight speeds. J Exp Biol 206(14):2313–2344

Swartz SM, Bennett MB, Carrier DR (1992) Wing bone stresses in free flying bats and the evolution of skeletal design for flight. Nature 359(6397):726–729

Swartz SM, Bishop K, Aguirre M-FI (2006) Dynamic complexity of wing form in bats: implications for flight performance. In: Zubaid A, McCracken GF, Kunz TH (eds) Functional and evolutionary ecology of bats. Oxford University Press, p 110–130

Swartz SM, Groves MS, Kim HD, Walsh WR (1996) Mechanical properties of bat wing membrane skin. J Zool Lond 239(2):357–378

Swartz SM, Iriarte-Díaz J, Riskin DK et al (2007) Wing structure and the aerodynamic basis of flight in bats. 45th AIAA Aerospace Sciences Meeting and Exhibit, Reno, Nevada, 8–11 January 2007

Swartz SM, Iriarte-Díaz J, Riskin DK, Breuer KS (2012) A bird? A plane? No, it's a bat: An introduction to the biomechanics of bat flight. In: Gunnell GF, Simmons NB (eds) Evolutionary history of bats: fossils, molecules and morphology. Cambridge University Press, p 317–352

Swartz SM, Middleton KM (2008) Biomechanics of the bat limb skeleton: scaling, material properties and mechanics. Cells Tissues Organs 187(1):59–84

Thollesson M, Norberg UM (1991) Moments of inertia of bat wings and body. J Exp Biol 158(1):19–35

Thomas ALR, Jones G, Rayner JMV, Hughes PM (1990) Intermittent gliding flight in the pipistrelle bat (*Pipistrellus pipistrellus*) (Chiroptera: Vespertilionidae). J Exp Biol 149(1):407–416

Thomson SC, Brooke AP, Speakman JR (2002) Soaring behavior in the Samoan flying fox (*Pteropus samoensis*). J Zool Lond 256(1):55–62

Tian X, Iriarte- Díaz J, Middleton K et al (2006) Direct measurements of the kinematics and dynamics of bat flight. Bioinsp Biomim 1(4):10–18

Vaughan TA (1959) Functional morphology of three bats: *Eumops, Myotis, Macrotus*. Univ Kansas Publ Mus Nat Hist 12(1):1–153

Vaughan TA (1970) The skeletal system. In: Wimsatt WA (ed) Biology of bats, vol 1. Academic Press, New York, London, p 97–138

Voigt CC (2000) Intraspecific scaling of flight power in the bat *Glossophaga soricina* (Phyllostomidae). J Comp Physiol B 170(5-6):403–410

Voigt CC, Holderied MW (2012) High manoeuvring costs force narrow-winged molossid bats to forage in open space. J Comp Physiol B 182(3):415–424

Watts P, Mitchell EJ, Swartz SM (2001) A computational model for estimating the mechanics of horizontal flapping flight in bats: model description and validation. J Exp Biol 204(16):2873–2898

Wolf M, Johansson LC, von Busse R et al (2010) Kinematics of flight and the relationship to the vortex wake of a Pallas' long tongued bat (*Glossophaga soricina*). J Exp Biol 213(12):2142–2153

Chapter 6
Comparative Morphofunctional Analysis

In our work, as a model of initial mammalian parasagittal three-segment Z-shaped limb (Kuznetsov 1999), we used the locomotor apparatus of tree shrews. In these animals, the forelimb design and the principles of functioning are essentially the same as in non-specialized insectivores (Neveu and Gasc 2002) and also primitive marsupials (Jenkins and Weijs 1979; Stein 1981). Morphofunctional analysis of musculature and skeleton of the shoulder girdle and forelimbs of colugos and bats has shown that these animals underwent a number of essential changes compared with the shoulder girdle and forelimbs oftree shrews (Fig. 6.1a).

Morphofunctional Features of Shoulder Girdle

In therian mammals, the shoulder girdle is connected to the axial skeleton only through the sternoclavicular articulation, if the clavicle is present. The mobility within the shoulder girdle (i.e., between the clavicle and the scapula) is provided by the acromioclavicular articulation. Thus, the movements of the scapula relative to the thorax are determined by the range of mobility in the two articulations, the role of which differs depending on the locomotion type.

Mammals, with their parasagittal three-segment limb, show a wide range of mobility of the sternoclavicular and acromioclavicular articulations due to their loose articular ligaments. In general, the mobility of the clavicle relative to the sternum can be described as a wide cone with the apex in the sternoclavicular articulation. At the same time, the acromioclavicular articulation allows for various turns of the scapula relative to the clavicle. However, in spite of a wide freedom of mobility, the scapula in most mammals with parasagittal three-segment limbs moves only in the parasagittal plane. While running, the scapula swings in the parasagittal plane around its dorsocaudal angle, like the femur in the hip joint (Fig. 6.1a). While doing so, the acromion together with the shoulder joint, undergoes some transverse

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_6

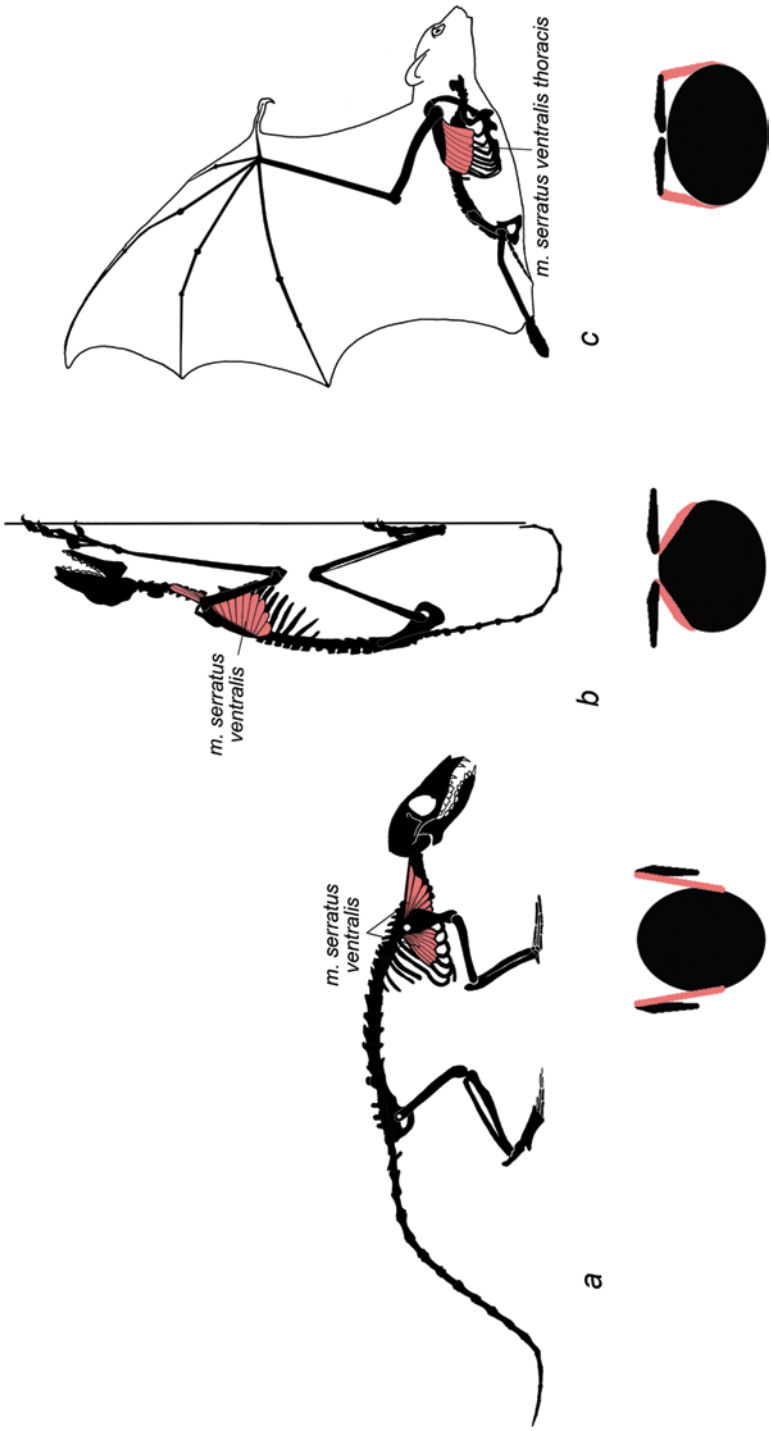


Fig. 6.1 Scheme of the *m. serratus ventralis thoracis* attachment, lateral view and anterior view in transverse cross section. *a. Tree shrew b. Colugo c. Fruit bat*

deviations given by the length of the clavicle, which, otherwise, follows scapular movements rather passively.

In colugos, the mobility of the clavicle relative to the sternum also falls within a certain cone, although the range of mobility is significantly narrower; ligaments of the sternoclavicular articulation are shortened and differentiated (Fig. 6.2a). The acromioclavicular articulation is also considerably less mobile than in tree shrews and, what is more important is that its mobility is limited in direction, i.e., the scapula rotates relative to the clavicle mostly around its own axis passing through the acromioclavicular articulation and dorsocaudal angle of the scapula; the range of this rotation is rather small (Fig. 6.2a).

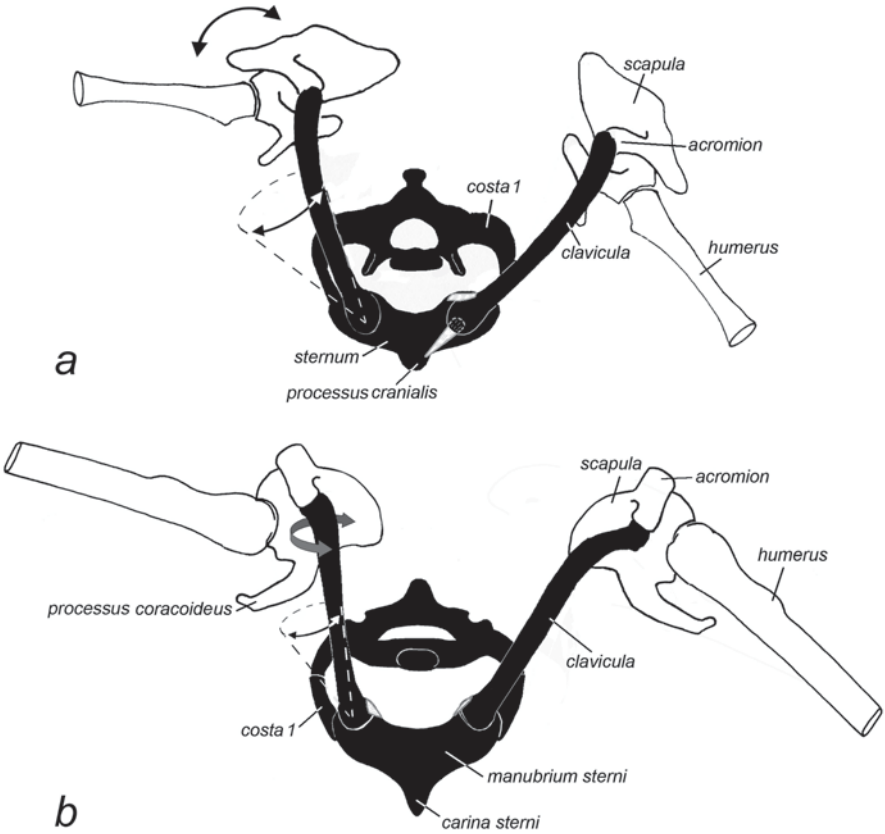


Fig. 6.2 Scheme of the mobility in the shoulder girdle and humerus in the transverse plane, anterior view. Arrows indicate the directions of movement of the clavicle and scapula, dotted lines indicate the limits of clavicle mobility. *a. Colugo: gliding on the left; take-off on the right (based on syndesmological preparation) b. Bat: end of upstroke on the left; end of downstroke on the right (based on syndesmological preparation and fluoroscopy)*

However, despite general similarity in the available movements, actual kinematics of the shoulder girdle of colugos essentially differs from that of tree shrews. Due to the combination of movements in the two articulations of the shoulder girdle, the scapula can change positions in the transverse plane. As the clavicle is abducted to the extreme lateral position and the scapula is rotated as much as possible around its longitudinal axis in the same direction (dorsal border away from the midline of the body), it is close to the parasagittal plane, as in quadrupedal mammals (Fig. 2.14). On the contrary, as the clavicle is adducted and the scapula is rotated by its dorsal border to the vertebral column, it lies almost horizontally on the dorsal surface of the thorax. The capability of reorientation of the scapula acquired by colugos has opened prospects for developing various locomotor patterns in the tropical forest environment (see Chap. 4).

In bats, the design of the sternoclavicular articulation strongly restricts lateral, and particularly, craniocaudal deflections of the clavicle, but allows axial rotation (Fig. 6.2b). Hence, the shoulder girdle as a whole is only slightly mobile relative to the thorax. In the acromioclavicular articulation, the scapula can rotate relative to the clavicle around its own longitudinal axis, as in colugos; however, this mobility is used for retention of the horizontal position of the scapula irrespective of the sideways movements of the clavicle rather than for reorientation of the scapula (Fig. 6.2b). The thick clavicle rigidly articulated with the sternum and acromion (see Fig. 3.1b) makes it an efficient strut in the wing downstroke (Figs. 5.8–5.10). On the contrary, in terrestrial therians such as tree shrews, the clavicle is loaded mostly by tension rather than compression.

Thus, in terrestrial therian mammals, the scapula moves mostly in the parasagittal plane, in colugos, it is transposed in the transverse plane, and in bats, it moves only slightly in the frontal plane.

The essential changes in the character of mobility of the scapula in colugos and bats correspond to certain features of the musculature of the shoulder girdle. In the majority of mammals, including tree shrews (Figs. 6.3a, 6.3d), a number of muscles of the shoulder girdle originate from the occipital region of skull and neck, which are the *m. sternocleidomastoideus*, *m. clavotrapezius*, *m. acromiotrapezius*, *m. rhomboideus capitis*, *m. rhomboideus cervicis*, *m. serratus ventralis cervicis*, and both *mm. levatores scapulae*. In colugos and bats, the *m. acromiotrapezius* has lost connection with the skull and at least five anterior cervical vertebrae (Figs. 6.3e, 6.3f), while the *m. rhomboideus capitis*, *m. rhomboideus cervicis*, and *m. levator scapulae dorsalis* have vanished (Figs. 6.3b, 6.3c). In addition,the origins of the *m. levator scapulae ventralis* and *m. serratus ventralis cervicis* tend to shift onto the last cervical vertebrae in bats (Figs. 3.42–3.44).

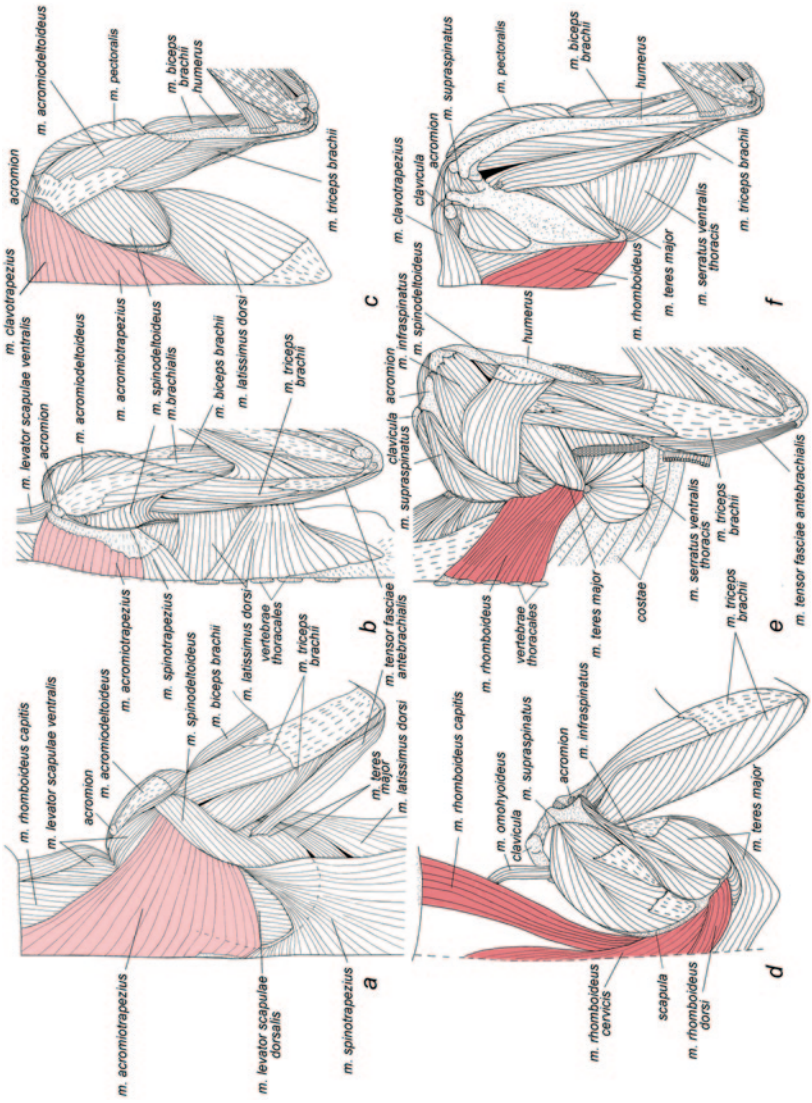


Fig. 6.3 The *m. acromiotrapezius* and *m. rhomboideus,* dorsal view. *a, d. Tupaia belangeri b, e. Cynocephalus volans c, f. Cynopterus sphinx*

Kovtun (1978) explains changes in the rhomboid and trapezius muscles of bats by the necessity for autonomisation of head and neck movements from movements of the scapula and wing. However, the author did not explain why the head of bats had to be more independent of the shoulder girdle than that of other mammals.

Having studied various aspects of locomotion of colugos and bats, we came to conclusion that the key role in the above changes was played not by the necessity to deliver the head from the influence of the locomotor musculature, but rather by the loss of necessity in the muscles protracting the scapula combined with the cruel necessity for a considerable increase in weight of the *m. pectoralis*. In the competition for mass under severe restrictions on body weight in flying animals, the advantage is given to those muscles whose mechanical performance is most crucial for locomotion, while others are reduced according to the principle of competitive exclusion.

The *m. acromiotrapezius* and *m. levator scapulae ventralis* of tree shrews control swings of the scapula around its dorsocaudal angle pulling the glenoid region towards the head. These muscles play a vital role as actuators of three-segment parasagittal forelimb.

In gliding colugos, the scapula is subject to the force pushing it caudomedially. This force is counterbalanced by the *m. serratus ventralis thoracis*, which drives it craniolaterally (Fig. 4.12) rather than craniomedially, as the *m. acromiotrapezius* and *m. levator scapulae ventralis* would do. In case of moving up tree trunk, the forelimb of colugos is subject to the force opposite to that during gliding. The forelimb is also loaded longitudinally, but by tension rather than compression. The force of substrate reaction as if pulls the limb along with the scapula craniolaterally (Fig. 4.10). The balance of the scapula requires muscles pulling it caudomedially towards the trunk. This action may be provided either by the *m. latissimus dorsi* (Fig. 4.10b) or by the posterior slips of the *m. serratus ventralis thoracis* aided by the *m. rhomboideus dorsi* (Figs. 4.10c, 4.10d). The more caudal is the origin of the latter muscle on the vertebral column, smaller is the force required from it. Muscles pulling the scapula craniomedially (to the head) are of no use in this case, as well as in gliding. Thus, both major locomotion patterns of colugos do not require muscular protraction of the scapula with a medial inclination; therefore, its protractors directed to the head and neck disappeared.

As is considered in the previous chapter, during the downstroke of bats, the aerodynamic force exerted on the forelimb has a propulsive (anteriorly directed) component, i.e., the thrust. Hence, the muscles of the shoulder girdle must pull the forelimb posteriorly and the body anteriorly; this is performed by the major flying muscle, i.e., the *m. pectoralis* (Figs. 5.8, 5.9). In this case, it is not required to pull the shoulder girdle anteriorly.

It is possible that the described disruption of muscular connection between the head and the shoulder girdle provided colugos and chiropterans with new opportunities of head mobility; however, it undoubtedly resulted from this disruption rather than caused it.

A number of key features of the shoulder girdle of colugos and chiropterans are associated with the pattern of suspension of the body to the shoulder girdle. In quadrupedal mammals, the body is suspended to the forelimb by the *m. serratus ven-*

tralis thoracis, which is shaped as a wide fan of slips originating from the ribs and converging onto the dorsocaudal angle of the parasagittal scapula (Fig. 6.1a). In colugos climbing vertical trunks, the main role in suspension of the body to forelimbs is performed by the *m. latissimus dorsi* (Fig. 4.10b), and only the posterior slips of the *m. serratus ventralis thoracis* can participate in this job (Figs. 4.10c, 4.10d). In gliding, the function of suspension of the body to the forelimbs is performed by the *m. pectoralis* rather than the *m. serratus ventralis thoracis*. The latter, due to the transposition of the scapula on the back, curves around the rib cage, and hence, gains a horizontal component of force, which it applies to the scapula, instead of the vertical component (Fig. 6.1b). As a result, the muscle acquires a new function in colugos, preventing caudomedial shift of the scapula provoked by the resultant force of tension of the plagiopatagium and propatagium (Fig. 4.12). The *m. serratus ventralis thoracis* is adapted to this new function by expansion of its insertion along the entire dorsal border of the scapula. It should be noted that, if the muscle were not curved around the rib cage due to the transposition of the scapula, it would have stayed in the parasagittal plane, which is almost perpendicular to the resultant force of the membrane tension applied to the forelimb in gliding, and so could not prevent displacement of the scapula towards the vertebral column.

In bats, muscular connection between the thorax and shoulder girdle looks even more unusual. In flight, their body is suspended under long, horizontally positioned scapulae (Fig. 6.1c). In contrast to colugos, the aerodynamic force is mostly applied to the neopatagium, i.e., the newly expanded distal region of the wing membrane, wherefrom it is entirely transferred onto the body via the forelimb, without participation of the hindlimb. Therefore, the *m. pectoralis*, which originates anterior to the center of gravity of the body is insufficient alone, and the more posteriorly located *m. serratus ventralis thoracis* is involved in suspension too. The insertion of this muscle has been displaced onto the caudal (lateral in bats) border of the scapula, so that its force has acquired (or rather, returned) a vertical (parasagittal) direction of force (Fig. 6.1). By this force, the body is suspended to the scapula posterior to the center of gravity. Since, the forces of the *m. pectoralis* and *m. serratus ventralis thoracis* pass anteriorly and posteriorly to the center of gravity, respectively, they together balance the body under the wings in respect of pitching (Fig. 5.9). A relatively small aerodynamic load is more or less equally distributed between the fore and hind limbs via tension of archeopatagium (i.e., the proximal part of the plagiopatagium). This minor load falls on the hindlimb adductors (depressors), while in colugos they are loaded by almost half of the full aerodynamic force, as the neopatagium is lacking in these gliders.

With the development of the neopatagium in ancestors of chiropterans, the vertical component of the aerodynamic force was more and more unequally distributed between the fore and hind limbs. The weaker load fell on hindlimbs, the greater load fell on the posterior slips of the *m. serratus ventralis thoracis*. To provide a required vertical force, these slips have to be positioned in the parasagittal plane. In the frontal position of the scapula, this is only possible if insertion of these slips on the scapula is displaced from the initial position on the dorsal border onto the caudal one; this is exactly what is observed in chiropterans.

This brings up the question, how could the *m. serratus ventralis thoracis* be translocated from the dorsal to caudal border of the scapula in gradual evolution, without saltations. The following ways are possible.

(1) The first way implies simple migration of the muscle from the typical to quadrupedal therians (e.g., tree shrews) point of insertion on the dorsocaudal angle along the caudal border of the scapula. In this process, the initially posteriormost slip was to move ahead of the others closer and closer to the glenoid, and finally, the more anterior is the rib of origin of a slip, the more posteriorly it was to insert on the caudal border of the scapula. Since, this cross of slips is not observed in bats, it is evident that this way is least plausible.
(2) The more probable starting point is that the *m. serratus ventralis thoracis* of bat ancestors already inserted as in colugos, i.e., not only on the dorsocaudal angle of the scapula, but also along the entire dorsal border. Possibly, the muscle did not follow the transposition of the scapula from the parasagittal to frontal plane, and thus retained the parasagittal position. If this was the case, the insertions of the slips of this muscle could have slid in parallel to each other from the dorsal border of the scapula over the superficial fascia of the *m. subscapularis,* and stopped at the caudal border between the *m. subscapularis* and *m. teres major*. However, the intermediate evolutionary stage with insertion of the powerful *m. serratus ventralis thoracis* on the *m. subscapularis* seems non-functional.
(3) The third variant also presumes that the *m. serrarus ventralis thoracis* inserted in bat ancestors along the entire dorsal border of the scapula. However, interference with the *m. subscapularis* could be avoided. It is well-known that this muscle, typically to the so-called secondary muscles of the shoulder girdle, grows in the embryo from the body to the girdle. The posterior border of the scapula is closer to the origin of this muscle on ribs than the dorsal border. Therefore, it is likely that the insertion of this muscle changed merely by stopping in the embryo of upward growth of the slip anlages before they reached the typical "destination point". We believe that, as the neopatagium developed, it was necessary to involve more and more slips in the new mechanism of suspension of the body by vertical muscular slings behind its center of gravity. Presumably, the slips were recruited in this mechanism one by one, beginning with the most posterior one, which is most crucial in counterbalancing the *m. pectoralis* with respect to body pitching. Translocation of the more anterior slips onto the caudal border of the scapula could be retarded for a good reason, since the horizontal, laterally directed force component is urgent as long as the neopatagium-based flapping flight is imperfect yet, and alternates with gliding for respite (Norberg 1985). As long as the propatagium retains its attachment to the head and neck, the distribution of membrane tension in gliding is such that the resultant force tends to push the forelimb and the scapula medially, as in the colugos. It is in order to efficiently counteract this effect that the anterior slips could keep the horizontal component of force longer than the posterior ones due to retention of insertion on the dorsal border of the scapula. So, the colugo-like mechanism of horizontal connection of the scapula and thorax by anterior

slips could coexist in evolution with the bat-like mechanism of vertical suspension by posterior ones and was "crowded out" gradually. The last residual dorsal-border slip in bats is the *m. serratus ventralis cervicis costalis*. It may be not involved in the translocation of insertion point for two reasons. First, it is rather vertical already due to the narrowness of the thorax at the anteriormost rib, wherefrom it originates. Second, it does not belong to the *m. serrarus ventralis thoracis* system, indeed, as is suggested by its innervation (see Chap. 3).

The body suspension to the shoulder girdle may be generalized as follows. In the running tree shrew, it is suspended by the *m. serrarus ventralis thoracis* in the gliding colugo by the *m. pectoralis*, and in the flying bat, by both muscles. However, this does not necessarily mean that the *m. serrarus ventralis thoracis* considerably shortens in the downstroke, as is implied by the scapulo-humeral lock advocates. In our opinion, more likely is its isometric, i.e., length-sustaining contraction.

The researchers of bats traditionally paid particular attention to the prevailing *m. pectoralis* being the main depressor of the wing. A distinctive feature of this muscle in bats is that the *m. pectoralis superficialis* and *m. pectoralis profundus* characteristic of other mammals cannot be recognized. Instead, the *pars anterior* and *pars posterior* are present. The *pars anterior* is probably formed from the *m. pectoralis superficialis* as a result of the anterior displacement of its origin, even onto the clavicle. Therefore, in contrast to the majority of mammals, this muscle ceased to retract the humerus in bats. This function, ensuring the wing thrust, is retained by the *pars posterior* only. The migration of some anterior fibers onto the clavicle may help to reduce a little, the compression in the sternoclavicular articulation which is extremely loaded by the rest of the *m. pectoralis* at least in the downstroke (Figs. 5.8–5.10).

Although, the *m. pectoralis* of colugos is similarly partitioned to that of tree shrews, it already shows considerable strengthening. It enables this gliding animal to hold its forelimbs in the horizontal plane, counteracting elevation provoked by the aerodynamic lift. Moreover, it has already increased the transverse force component in colugos at the expense of the longitudinal one. The caudal limit of the origin of the *m. pectoralis superficialis* on the sternum is at the third rib, while in tree shrews it extends along the whole sternum and even caudal to it onto the *linea alba*. The caudal extent of the *m. pectoralis profundus* origin in colugos has also been reduced, but not as much. So, the *m. pectoralis* of colugos exemplifies some morphofunctional preadaptation for flapping flight.

It is interesting to compare the sizes of the supraspinous fossa of the scapula in the animals under study. In tree shrews, this fossa is very large representing a good development of the *m. supraspinatus* which is placed there. In colugos, the scapula is more similar in shape to that of bats; however, their supraspinous fossa is still relatively larger. In bats, it is smaller (Fig. 3.4a) as well as the *m. supraspinatus*. Also, its pennation structure is simpler than in the *m. infraspinatus*. The different development of the *m. supraspinatus* is apparently accounted for by the type of locomotion. In tree shrew running, the muscle protracts the humerus in the swing

phase of the forelimb and, more importantly holds the shoulder joint against bending in its contact phase loaded by the body weight. In colugo running up the tree trunk, it protracts the humerus in the swing phase of the forelimb too, but is not required in its contact phase, and hence there is no need of strong development of this muscle in case of trunk climbing. However, in gliding, the *m. supraspinatus* helps the propatagium to prevent retraction of the humerus provoked by tension of the plagiopatagium together with the horizontal component of the *m. pectoralis* force (Fig. 4.12). In bats, the propatagium has lost the protracting effect on the shoulder joint. However, the aerodynamic thrust of the neopatagium alone overbalances the retracting component of the *m. pectoralis* force together with the backward pull of the reduced archeopatagium, and hence, the additional contraction of the *m. teres major* rather than the *m. supraspinatus* is needed for balance. At least, this is true for the mid-downstroke being the most loaded point in the whole wingbeat cycle (Fig. 5.8). It is plausible that reduction of the archeopatagium in favor of the neopatagium in the evolution of chiropterans entailed the reduction of both active and passive protracting structures of the shoulder such as the *m. supraspinatus* and the propatagium, respectively.

The *m. clavotrapezius*, which is present in all chiropterans, is of particular interest. The point is that, although this muscle is found in the majority of quadrupedal mammals, it is lacking in some members of the cohort Archonta. In particular, among platyrrhines the *m. clavotrapezius* is present (as in chiropterans) in *Saimiri, Ateles, Lagothrix,* and *Alouatta*, and is absent (as in colugos and tree shrews) in all Callitrichinae, *Callimico,* and *Callicebus*; capuchins (*Cebus*) usually lack it, but some individuals have a well pronounced clavicular portion of the *m. trapezius* (Dunlap et al. 1985). Thus, the presence or absence of this muscle is not a criterion for phylogenetic relationships of a group, but is rather associated with functional demands on the shoulder girdle design. In general, the preservation in bats of any muscle without a forcible functional need is highly improbable in conditions of cruel necessity to increase the weight of the main flight muscles. Consequently, the presence and perfect development of the *m. clavotrapezius* strongly suggests that it participates in flight. This muscle shows the high electric activity in the upstroke; however, lower activity is also observed during the downstroke (Hermanson and Altenbach 1985). Recollect also, the *m. subclavius* which is the only one-joint muscle of the sternoclavicular articulation and an almost direct antagonist of the *m. clavotrapezius*. They together hold the clavicle efficiently against hazardous distortions in the sternoclavicular articulation in bats, whose clavicle is subject to extreme compression in flight (Figs. 5.8–5.10). Apparently, the development in the most specialized bats (Fig. 3.58) of the expanded *processus alaris costae sternalis 1* which becomes the place of origin of the *m. subclavius*, is accounted for by the necessity to increase the lever arm of this muscle. Otherwise, it is too short as compared to that of the antagonistic *m. clavotrapezius*. Till date, the origin of the *processus alaris costae sternalis 1* has not got any other *raison d'être*.

Morphofunctional Features of Free Limb

The first thing that attracts attention in the forelimb of colugos and bats is its elongation. Not only the humerus and antebrachium are elongated in these mammals, but also the digits including metacarpals. Moreover, in case of bats, the degree of elongation of the digits substantially exceeds that of the humerus and antebrachium. Obviously, this elongation is required as the airframe for the wing membrane. However, many more features are also involved in ensuring its functionality.

In colugos and bats, directions of the typical locomotor movements of the humerus essentially differ from that in tree shrews. In the latter ones, the major movements of the humerus occur in the parasagittal plane. In colugos, while climbing up tree trunks, it performs a kind of circumduction being, on the whole, abducted much laterally. In gliding, the humeri are sprawled and even protracted in the frontal plane. As follows from photo and video materials, at the beginning of gliding, just after take-off from the trunk, the forelimbs are stretched posteriorly along the body. Then, the humerus is protracted, so that the elbow joint moves along an arch, in the upper point of which, it is raised to the level of the vertebral column or even higher. Finally, the humerus is drawn out anterolaterally in the frontal plane and keeps this position throughout the glide. In bats travelling over a solid substrate, the humerus is abducted laterally and performs circumduction, as in colugos. In flapping flight, the humerus performs circumduction as well. As exemplified by *Rousettus aegyptiacus* (Fig. 5.5; Panyutina et al. 2013), only the posterior most sector of available mobility in the shoulder joint is employed in flight, so that the elbow remains posterior to the dorsocaudal angle of the scapula throughout the wingbeat cycle. The elbow moves mainly dorsoventrally, but its way in the downstroke passes more anteriorly than in the upstroke; in the highest point it is raised well above the vertebral column, while the lowest point is at the level of the thorax mid-height. Besides circumduction, the humerus pronates or supinates to adjust the angle of attack of the wing.

Tree shrews actually use a minor part of available range of axial rotation of the humerus in the shoulder joint. The lever arms of the main pronators of the humerus (the *m. pectoralis* and *m. subscapularis*) are rather short, since the pectoral crest, and lesser tubercle where these muscles insert are very poorly developed (Fig. 1.5b). Also, tree shrews have a poorly developed greater tubercle, which is the place of insertion of the *m. infraspinatus*, the main supinator of the humerus (Figs. 1.5a, 6.4a). In colugos, the rotators of the humerus have more advantageous lever arms, because the processes for their insertion (pectoral crest, greater, and lesser tubercles) project from the humeral shaft more (Figs. 2.5, 6.4b). Apparently, the great rotational mobility in their shoulder joint compensates for significant limitation of rotation in the elbow. In bats, the processes for insertion of the main rotators of the humerus show the maximum relative size. The pectoral crest and the greater tubercle are enlarged rather proportionally to each other (Figs. 3.9, 6.4c); so, the greater tubercle gives the *m. infraspinatus* an appropriate lever arm for supination enabling it to counterbalance the pronating effect of the *m. pectoralis* and aerodynamic force. The lesser tubercle is also significantly enlarged, increasing the lever arm of the

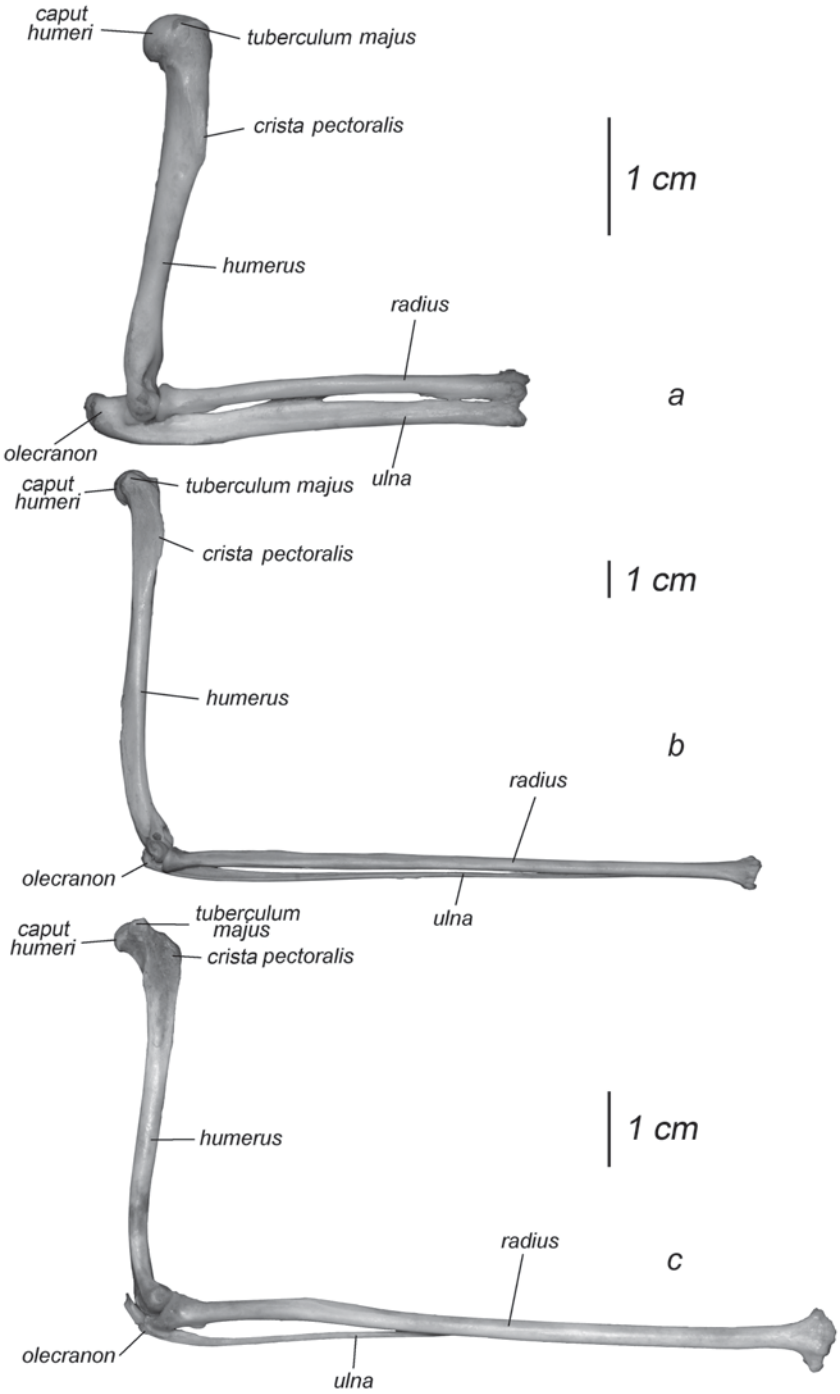


Fig. 6.4 The humerus and antebrachium, lateral view. *a. T. belangeri b. C. volans c. Rousettus aegyptiacus*

m. subscapularis. We believe that the major function of this muscle has changed in bats as compared to quadrupedal mammals. When the humerus comes to a well protracted position in a spread wing, the *m. subscapularis* becomes a depressor of the humerus rather than pronator. Note that there are no other one-joint humeral depressors. As such, the *m. subscapularis* can help the *m. pectoralis* to counterbalance the aerodynamic lift of the neopatagium relative to the shoulder joint. The *m. pectoralis* is probably strong enough to do it alone, but its main task (together with the *m. serratus ventralis thoracis*) is to ensure such a balance of the forelimb together with the scapula that the clavicle is loaded strictly longitudinally as a simple strut (Figs. 5.8–5.10). This implies equilibria in both the sternoclavicular and acromioclavicular articulations but not in the shoulder joint, relative to which the *m. pectoralis* should be aided in the downstroke by one-joint muscles, i.e., the *m. subscapularis* as depressor, the *m. teres major* as retractor, and the *m. infraspinatus* as supinator of the humerus.

In the structure of the antebrachium, the development of the ulna has engaged our primary attention. The olecranon of colugos is relatively shorter than that in tree shrews, and in bats, it is almost absent. The ulna of tree shrews is in general somewhat better developed than the radius; both bones equally participate in the formation of the antebrachiocarpal joint (Fig. 6.4a). In colugos, the ulna is considerably reduced relative to the radius; in the distal one-third, it is fused with the radius and is almost excluded from the antebrachiocarpal joint (Fig. 6.4b). In bats, the ulna is extremely narrow, fuses with the radius over distal two-thirds of the antebrachium, and does not articulate with the carpus; so the joint is radiocarpal rather than antebrachiocarpal (Fig. 6.4c).

Thus, in the series tupaia–colugo–bat, one of the two antebrachial bones is gradually excluded, as occurs in some other mammalian groups as well. In particular, in the series of perissodactyls from tapirs to horses, the ulna is being strongly reduced and elephants show reduction of the radius. It is generally accepted that reduction of one of these bones is an indicator of a decrease in rotational mobility in the antebrachium. This is corroborated by our data: tree shrews show significant degree of available supination and pronation relative to, say, neutral position. In colugos and bats, rotation of the antebrachium is sharply asymmetrical relative to the neutral position from which supination is only possible. In colugos, supination in the antebrachium is required to turn the palm inside for a sloth-like suspension whereas, the pronation from the neutral position is not vitally important; thus, it has been lost, since it is always unfavorable to retain a greater range of joint mobility than is necessary, because this requires extra fiber length of respective muscles and so, extra muscular weight. In bats, pronation of the antebrachium in a spread wing from the palm-down to the palm-back position is blocked for obvious reasons. In the downstroke, the aerodynamic force is applied to the neopatagium posterior to the longitudinal axis of the antebrachium, and hence, tends to pronate it. This force could have been counterbalanced by supinator muscles; however, to lighten the distal wing which is crucial for flapping flight, it is more favorable to block pronation of the antebrachium by ligaments and special design of the articular surfaces. The similar design restricting rotational mobility is observed in the radiocarpal joint

of bats (see Chap. 2, Sect. Joints). The restriction of rotational mobility of joints of the free limb is compensated by the great freedom of rotation in the shoulder joint. Although, the weight of muscles controlling it in bats is considerable, they cannot essentially increase the moment of inertia of the wing being placed at its base.

Thus, in our opinion, the primary reason for reduction of the ulna is a decrease in rotational mobility in the antebrachium. However, this also helps lightening the elongated forelimbs of colugos and bats.

A novelty acquired by bats is the ability to flex the mediocarpal and carpometacarpal joints, which are known as stiff articulations in other mammals and are virtually immobile indeed. This new mobility, combined with usual mobility in the antebrachiocarpal joint, allows bats to fold wings at rest bending the manus almost by 180° relative to the antebrachium from completely straightened to tightly pressed with respect to the antebrachium position. Colugos and tree shrews possess in this region the antebrachiocarpal mobility only allowing flexion in the range from the straightened state to about 90° between the antebrachium and manus.

A remarkable feature in the musculature of the free limb of colugos is strengthening and complication of the system of long muscles which control digits; this is accounted for by the combination of adaptations for clinging to tree trunks and gliding. Colugos cling to trunks by driving their large, flattened from the sides, and distally hooked claws into the bark. The distinctive high bases of these claws provide increased lever arms (Figs. 2.9, 2.51) for both the *m. flexor digitorum profundus* and its antagonists, i.e., the *m. extensor digitorum communis* and *m. extensor pollicis longus*. These large levers enable the *m. flexor digitorum profundus* to stick claws forcibly, and extensors to neatly release the "anchored" claws from the bark for running and leaping. However, other long flexors and extensors of digits of colugos also play an important role in the action of claws, although these muscles do not reach ungual phalanges. The precise control of a claw positioned at the end of a multijoint kinematic chain composed of metacarpal and phalanges is not a simple task, as might appear at first glance. When being stuck in the bark, a claw encounters resistance of the substrate and one of the more proximal joints can bend unpredictably; as a result, the claw would not obtain a required force. This unpredictable event is opposed by simultaneous action of not only the *m. flexor digitorum profundus* but also two shorter extensors, i.e., the *m. extensor digitorum lateralis* and *m. extensor indicis*. Not unexpectedly, both extensors have acquired in colugos accessory terminal tendons; with their help, the *m. extensor indicis* controls digits III and IV (in addition to II), and the *m. extensor digitorum lateralis* controls digit III (in addition to IV and V). All these tendons together form on the dorsal surface of the manus a network of fastened ties which prevent uncontrolled flexion of metacarpophalangeal and interphalangeal joints. Thus, the *m. flexor digitorum profundus* has acquired an exclusive ability to flex the preungual joint alone, applying to the claw a force required for sticking it in the substrate. Similarly, as the claw is pulled out, the *m. extensor digitorum communis* is aided by the *m. flexor digitorum superficialis* which prevents hyperextension of the metacarpophalangeal and interphalangeal joints of digits II–V.

In gliding, the *m. flexor digitorum profundus* also plays an important role; it counteracts the aerodynamic force, which tends to hyperextend the digits. In addition to the newly increased lever arms on the claws, the *m. flexor digitorum profundus* of colugos is distinguished by the unique structure. In all other tetrapods, the terminal tendons of this muscle are united at their beginning into a common plate which we named the *aponeurosis flexoria communis* (e.g., Figs. 1.48, 1.49), while in colugos, this junction is strongly reduced. As a result, the terminal tendons have acquired sufficient longitudinal mobility relative to each other allowing relatively free distribution of muscular forces between digits. Hence, the typical heads of this muscle have also undergone essential rearrangement for independent control of terminal tendons. As a result, colugos have acquired the ability to control the position of all digits independently of each other, and consequently, to voluntarily change the camber shape of the interdigital membrane during glide.

The *m. flexor digitorum accessorius*, a small unique muscle of colugos deserves special attention. It originates from the terminal tendon of the *m. flexor digitorum profundus* running to digit V and inserts on three terminal tendons of the *m. flexor digitorum superficialis* running to digits III–V. The *m. flexor digitorum accessories* is obviously too weak compared with the two muscles, whose terminal tendons it interconnects, to participate in their action mechanically, but it can perceive relative positions of these tendons, and thus, serve as a sensor of the camber shape of the membrane stretched between digits III–V during glide.

Both colugos and bats have lost the *m. palmaris longus* which drives paw pads in many arboreal mammals. These soft pads ensure adjustable friction surface being flattened in the tight grip of a branch. Colugos do not grip branches but rely on their claws in climbing tree trunks, so the soft paw pads and their muscular supply are of no use in these animals. It is even more true for bats.

The internal mobility of the manus in colugos is restricted by interdigital membranes due to which fact it is functionally less universal than in generalized quadrupedal mammals. Colugos no longer use it to manipulate food, but only pull sprigs to the mouth when feeding. The reduced mobility has affected the system of short muscles of the manus. As compared to tree shrews, colugos have lost the *m. palmaris brevis*, *m. opponens pollicis*, *m. adductor digiti quarti*, *m. flexor brevis manus*, and *m. flexor digiti quinti superficialis*. However, the leverage of all short adductors pulling metacarpals closer together has increased which is important for regulation of the camber shape of the interdigital membrane during glide.

The rearrangements in the bat manus are much more profound. All digits except for digit I have lost both manipulative ability and ability to support the body in terrestrial locomotion. The need for lightening the distal regions of a flapping wing resulted in significant reduction of all possible muscles including the long extensors and even flexors, despite large aerodynamic forces tending to hyperextend the digits. Thus, the antebrachium of tree shrews and colugos has 17 and 16 muscles, respectively, while bats have only 14. In the downstroke, counteraction to hyperextension in the joints of the manus, especially in mediocarpal and carpometacarpal joints, is provided by a complex arrangement of well-adjusted carpals and

metacarpals restricting mobility towards extension, rather than by the long flexors. Digits III–V including their metacarpals are actually transformed into flexible ribs reinforcing the membranous wing like an umbrella (Norberg 2002). When the wing camber is formed by a joint action of aerodynamic forces and membrane tension, the segments of the digits are loaded longitudinally (compressed), and so, do not need considerable muscular control neither in the plane of the wing membrane nor perpendicular to it (Pennycuick 1971; Norberg 1972). The shape of articular surfaces and the ligaments of metacarpophalangeal and interphalangeal joints ensure their integrity.

Therefore, the manus has almost completely lost short muscles; bats have from 8 to 10 muscles of initial 26 observed in tree shrews (colugos have 23). Even in the thumb, which plays an important role in locomotion on solid substrates and is frequently used for manipulations with food, only three short muscles out of five are retained.

Discussion on Comparative Morphology

The key changes in the shoulder girdle and forelimbs of colugos and bats suggest general, functional and evolutionary conclusions. The locomotion of these animals demands that their limbs should be sprawled sideways in the frontal plane. To ensure transposition of the limbs from the initial parasagittal plane to the new one, the glenoid was reoriented; in bats, it persistently faces laterally; while in colugos, such orientation is only employed in gliding and clinging flat on thick tree trunks; and in the majority of quadrupedal mammals exemplified by tree shrews, the glenoid persistently faces ventrally. To provide this reorientation of glenoid, the scapula of colugos and bats is transposed from the lateral to dorsal side of the thorax where it lies in the horizontal plane (Fig. 6.1, cross sections). At the same time, the mobility of the shoulder girdle is essentially changed.

The understanding of functional sense of the morphological changes described above allows creating justified hypotheses on the origin of flapping flight in mammals.

Flight and Primitive Locomotion of Prototherians

Let us begin from the question of the possible direct origin of colugos and bats from some very primitive ancestors with sprawling (not yet parasagittal) position of the limbs as in monotremes (as well as reptiles and amphibians). Since the limbs of colugos and bats are also sprawling laterally, it could be hypothesized that their ancestors never passed an evolutionary stage with the parasagittal limb position. Nevertheless, structural features of the musculature and skeleton of the shoulder girdle of both colugos and chiropterans unequivocally show that they did pass the stage of the parasagittal position. This is evident from the orientation of the humerus, and

hence, glenoid relative to the plane of the scapular blade. In ancestors of therian mammals, with their laterally sprawling limbs as in monotremes, the humerus is almost perpendicular to the scapular blade which is already positioned parasagittally. On the contrary, in bats and colugos the humerus and scapula are found in a single plane as is typical of quadrupedal therians. It is possible to draw the following general conclusion: in therian ancestors, the free limb alone was transposed from the monotreme-like initial sprawling posture in the transverse plane to the parasagittal plane of the scapula, and then in colugos and chiropterans, a coupled transposition of the free limb with the scapula from the parasagittal to frontal plane has occurred.

Flight and Brachiation

Extant mammals include one more group which demonstrates transposition of the scapula from the parasagittal to frontal plane. This is primates.

Several genera of apes and platyrrhines have adapted for brachiation, which is the way to travel under branches swinging by elongated forelimbs from one handhold to another. This implies the necessity to find and reach a new reliable handhold which can appear in the forest canopy on every side (even from behind), and often farther than at arm's length. Therefore, a wide range of forelimb movements in the transverse plane (which is horizontal in this case due to upright position of the body) is needed. This requirement is fulfilled in brachiators through the lateral orientation of the glenoid by means of transposition of the scapula onto the dorsal side of the thorax, as in colugos and bats. The gradual transposition of the scapula from the parasagittal to frontal plane is exemplified by a series of platyrrhines: the capuchin *Cebus*, howler *Alouatta*, and the spider monkey *Ateles*, the most specialized brachiator among platyrrhines (Youlatos 1994). The scapula of capuchin occupies a position typical for the majority of primates and other quadrupedal mammals, while that of the spider monkey lies frontally on the back, as in chiropterans. A similar arrangement of the shoulder girdle is observed in Hominoidea including brachiators such as gibbons (Hylobatidae) and orangutans (*Pongo*). This suggests that transposition of the scapula occurred independently in different primate lineages in the course of adaptation for brachiation. In addition, the forelimbs of all brachiating primates are considerably elongated, increasing the radius, and hence, the distance of swinging movements.

The similar position of the scapula together with the free forelimb elongation and wide range of shoulder mobility may suggest that gliding of colugos or flapping flight of chiropterans could be preceded by an evolutionary stage associated with locomotion in the forest canopy by means of brachiation. This stage could make the three mentioned morphofunctional features ready for aerial locomotion.

However, these features exhaust the morphological similarity of gliding and flying mammals to brachiators. As reaching a handhold requires as much free movements of the forelimb as possible, brachiators possess a wide range of pronation and supination not only in the shoulder joint, but also in the antebrachium. In all

brachiators, both antebrachial bones are very well developed and the palm can turn for a large angle both inside (pronation of the antebrachium) and outside (supination). On the contrary, colugos and bats are characterized by reduction of the ulna and a decrease in rotational mobility in the antebrachium.

The basic specialization of the manus of brachiators is the prehensile strength of the fingers which provides reliable swinging under branches. This specialization has an indelible effect: the thumb is either opposed (in apes) or reduced (in platyrrhines), fingers II–V are hooked and show a limited range of flexion and extension. On the contrary, all gliding mammals irrespective of taxonomic group, use clinging by claws rather than grasping by digits. Since gliding is inevitably accompanied by the height loss, this way of locomotion is inseparably linked with the necessity to return on the top of tall trees climbing up their thick trunks with the help of claws.

The main argument against the idea that, at early evolutionary stages, ancestors of colugos or bats could alternately glide and brachiate (even the slow brachiation, such as that observed in spider monkeys), is the controversy which arises when one attempts to analyze the possibility of development in brachiators of a gliding membrane connecting the limbs, i.e., the plagiopatagium. When brachiator swings, its forelimb holding a branch is stretched up and the ipsilateral hindlimb hangs down, both being aligned with the upright spine. In this posture, any kind of plagiopatagium would tie up movements if it was not extremely compliant, but on the other hand, such a compliant membrane would be absolutely unusable in gliding. The point is that, if the membrane connecting the limbs was able to stretch so much as to allow hand-up foot-down posture for swinging under branches, it would sag in the gliding position where the fore and hind limbs are much closer to each other. Hypothetically, tension of the membrane in such an extraordinary case could be generated by longitudinal (chordwise) muscular fibers of the *m. cutaneus trunci* if it filled the plagiopatagium throughout, between the two skin layers. The muscular layer should have been thick enough to provide required tension force in gliding, and its fibers should have been long enough to provide required compliance in brachiation; on the total, the muscle should have been heavy enough may be too heavy for flight. Remember that, both colugos and bats show reduction rather than progressive development of the *m. cutaneus trunci*.

It is possible to conclude that brachiation and flight are two different terminal stages of mammalian specialization in arboreal locomotion. The two trends require a considerable set of morphofunctional changes, many of which exclude each other. The similarities indicated above are an example of the so-called paraconvergence, first described by Gambaryan (1974), and termed so by Iordansky (1994).

Flight and Gliding

Although, locomotor specializations of chiropterans and colugos result from the evolution of essentially different phylogenetic lineages, many morphological characters of colugos fit well from the functional standpoint into the gap between terrestrial therians and chiropterans. This allows discarding again the attempts of some

researchers to completely exclude gliding ancestors from hypotheses on the origin of chiropterans (Norberg 1985). Ecological features of extant colugos help to restore conditions which could stimulate the formation of flapping flight in bats.

As is generally believed (e.g. Vaughan 1959; Kovtun 1990; etc.), the major difficulties encountered in explanation of the appearance of bat flight are associated with the origin of the distal wing part reinforced by the elongated digits (chiropatagium or neopatagium, in our terms[1]), because, at intermediate stages, natural selection would ostensibly act against elongation of digits, as this provides, they say, only minor advantage for flight and is inconvenient for locomotion on a solid substrate.

However, the morphofunctional model of a gliding bat ancestor, based on colugo, shows that such a gliding animal retains efficient locomotion on vertical surfaces, in spite of long limbs or, may be, even due to them. Indeed, it has already undergone the influence of natural selection in favor of improvement of aerodynamic performance through limb elongation. Their length helps now to embrace a support when climbing. If the support is rather wide and flat, claw clinging is used, and the long fore limbs are helpful again in sprawling on the vertical surface for stability. Moreover, adaptation for gliding combined with climbing vertical walls makes the key morphofunctional features of the locomotor apparatus ready for transition to flapping flight. One of the main features is the frontal position of the scapula with the laterally facing glenoid, because to perform powerful strokes for flight, the forelimbs (wings) should be able to move in the transverse plane through a wide angle, not only coming below the body but also raising above it. If the scapula remained close to parasagittal plane, the glenoid would face downwards, the wings would only flap below the body and the aerodynamic force would lack a considerable upward component.

It is also easy to imagine the appearance of the wing membrane. Various skin scallops or membranes on body sides or between digits are found in many tetrapods which use not only gliding over long distances, but also short gliding leaps. Among anurans, the species of the family Rhacophoridae and the genus *Boophis* (Mantellidae) have membranes between digits (a kind of chiropatagium). Among squamates, the agamid lizard *Draco* has a membrane between the ribs projecting to the sides of the body, the gecko *Uroplatus* has skin scallops on body sides, while the gecko *Ptychozoon* has scallops on both sides of the body and between digits. Among mammals, more or less developed plagiopatagium, propatagium, and sometimes, uropatagium is observed in several marsupial families (Acrobatidae, Petauridae, some Burramyidae, and Phalangeridae), scaly-tailed squirrels (Anomaluridae), and flying squirrels (Pteromyinae). In colugos, the chiropatagium is added. Probably, it should not be even regarded as a new formation but rather as a paedomorphosis, as the interdigital sheet of embryonic tissue is present in all tetrapods but is usually resorbed; not so in colugos and bats (Sears 2008).

[1] Neopatagium is not the same as chiropatagium. It also includes the distal part of the plagiopatagium, which has a free trailing edge, while the proximal part of the plagiopatagium (which we call the archeopatagium) is stretched between the fore and hind limbs, as the whole plagiopatagium in colugos.

As to the redistribution of muscular mass, a colugo-like gliding stage already makes the forelimb carrying capacity in the air half ready for flapping flight. Indeed, gliding of colugos almost equally loads the fore and hind limbs (Fig. 4.11), while in bats, almost the entire load falls on the forelimbs (Fig. 5.7). Roughly speaking, it is enough to translocate all the hindlimb muscles onto the forelimb, and the source of mechanical power for flapping flight will be supplied. In this respect, gliding is a much better transitional state to flapping flight than bipedal terrestrial locomotion, which in opinion of some researchers, released the forelimbs for getting a new flying function. Such a release from the locomotor function is the worst way, in fact, since it results in a decrease in size of the forelimbs including their muscles in favor of the muscular mass of the hindlimbs which are now forced to carry all the body weight. This can be illustrated by the disproportionately small forelimbs of kangaroos, springhare, jerboas, etc. As a result, the forelimbs of these forms become too weak to provide a support both on the ground and in the air. For the same reason, bipedal ancestors of birds are hardly possible too. The major morphofunctional preadaptation for flapping flight of any vertebrate is the increased muscular mass of the *m. pectoralis*.

References

Dunlap SS, Thorington RW Jr, Aziz MA (1985) Forelimb anatomy of New World monkeys: myology and the interpretation of primitive anthropoid models. Am J Phys Anthropol 68(4):499–517

Gambaryan PP (1974) How mammals run: anatomical adaptations. Wiley, New York

Hermanson JW, Altenbach JS (1985) Functional anatomy of the shoulder and arm of the fruit-eating bat *Artibeus jamaicensis*. J Zool Lond 205(2):157–177

Iordansky NN (1994) Macroevolution: systemic theory. Nauka, Moscow (in Russian)

Jenkins FA Jr, Weijs WA (1979) The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). J Zool Lond 188(3):379–410

Kovtun MF (1978) Locomotor apparatus of bats. Naukova Dumka, Kiev (in Russian)

Kovtun MF (1990) Problems of evolution of bats. Vestn Zool 3:3–12 (in Russian)

Kuznetsov AN (1999) Structural types of limbs and evolution of running technique in tetrapods. Zool Issled 3:5–94 (in Russian with English summary)

Neveu P, Gasc J-P (2002) Lipotyphla limb myology comparison. J Morphol 252(2):183–201

Norberg UM (1972) Bat wing structures important for aerodynamics and rigidity (Mammalia, Chiroptera). Z Morph Tiere 73(1):45–61

Norberg UM (1985) Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. Am Nat 126(3):303–327

Norberg UM (2002) Structure, form, and function of flight in engineering and the living world. J Morphol 252(1):52–81

Panyutina AA, Kuznetsov AN, Korzun LP (2013) Kinematics of chiropteran shoulder girdle in flight. Anat Rec 296(3):382–394

Pennycuick CJ (1971) Gliding flight of the dog-faced bat *Rousettus aegyptiacus* observed in a wind tunnel. J Exp Biol 55(3):833–845

Sears KE (2008) Molecular determinants of bat wing development. Cells Tissues Organs 187(1):6–12

Stein BR (1981) Comparative limb myology of two opossums, *Didelphis* and *Chironectes*. J Morphol 169(1):113–140

Vaughan TA (1959) Functional morphology of three bats: *Eumops, Myotis, Macrotus*. Univ Kansas Publ Mus Nat Hist 12(1):1–153

Youlatos D (1994) Maitrîse de l'espace et accès aux ressources chez le singe hurleur roux (*Alouatta seniculus*) de la Guyane Française. Etude morpho-fonctionnelle. PhD Dissertation, Museum National d'Histoire Naturelle, Paris, France

Chapter 7
Evolutionary Scenario for Establishment of Flapping Flight

The origin of flapping flight of chiropterans, like any other great morphofunctional changes of living organisms, as they are discussed from the standpoint of adaptive evolution, requires the use of the so-called principle of succession of functions (Dohrn 1875). Actually, excluding a miraculous acquisition of the flight apparatus through an accidental saltation, it should be proposed that gradual development of adaptations for flight started from the point when natural selection 'caught' at morphological characters involved in certain other functions. By virtue of a posteriori reasoning, we can regard these characters as preadaptations to the development of flight, whereas in real time, they were adaptations within the ecological niche occupied by their owners.

Our study of morphofunctional features and locomotion of mammals moving with a support on air allow reconstruction of a plausible evolutionary scenario for such succession of functions in the locomotor apparatus in the history of chiropterans. This scenario is based on locomotor specializations and its biological sense is derived from the reconstruction of ecological conditions which could result in the development of particular features treated a posteriori as preadaptations to flapping flight.

The main events in our evolutionary scenario are associated with changes in locomotor adaptations, accompanied by transition of limb action from the parasagittal to transverse plane. In our opinion, the locomotor patterns characteristic of colugos and respective structural features of their musculoskeletal apparatus display probable preadaptations for the establishment of flapping flight of chiropterans.

The complex arrangement of tree crowns and space under the canopy of the tropical forest are rather perspective for the formation and development of various locomotor patterns, in particular, overcoming long distances between trees by air. A need for this locomotor pattern in the tropical forest is corroborated by repeated emergence of gliding forms among arboreal mammals of the Eastern Hemisphere.

For many arboreal vertebrates leaping from one support to another in tree canopy is an essential element of their locomotion. Even those animals that lack flying membrane sometimes try to flatten body to get aerodynamic lift which helps them to increase the length of the leap (e.g., Demes et al. 1991). The formation of the lateral membrane considerably increasing the distance of leaps, could initially

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6_7

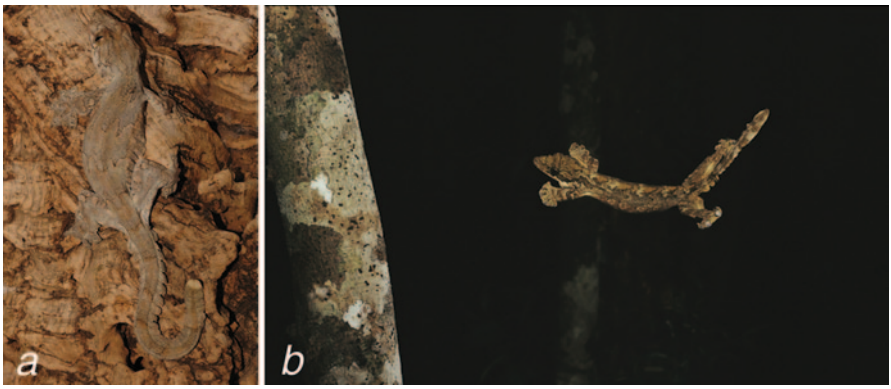


Fig. 7.1 Flying Gecko *Ptychozoon a. Cryptic on bark background* (photo by E. Yakhontov) *b. In glide* (photo by Tim Laman, www.timlaman.com)

play a different, masking, role. The skin folds on the body sides perfectly mask its contour on the background of a sculptured bark surface and remove shadows. It is generally believed that the skin scallops of *Ptychozoon* (Fig. 7.1) and *Uroplatus* primarily provide camouflage effect on the substratum and its flying function is secondary (Marcellini and Keefer 1976).

Emergence of gliding in such circumstances looks like a completely logical process. This mode of locomotion not only reduces the time spent on the move, but also is a huge advantage in rescuing from predators. Moreover, steady gliding with a large speed reserve (relative to the minimum required for stable interaction with the air) allows gain of altitude before landing, choosing the most convenient place, as well as significantly slowing down before landing, which is very important in preventing injuries at impact with hard surface.

However, gliding, contrary to a more or less horizontal movement along the branches, inevitably implies the height loss and successive return to tree crowns by climbing up thick trunks. For an animal with a masking membrane on body sides and a need for climbing up tree trunks, the ability to sprawl the forelimbs laterally was favorable in two aspects, for lateral extension of the membrane during gliding and for clinging the body close to a thick trunk at rest and upward running. On vertical surfaces such a posture prevents the undesirable lateral tilting of the body or tumbling on the back, because, as the body is as close to the trunk as possible, the torque produced by gravity is minimized. It is evident that the closer the body is placed to the trunk (i.e., the smaller distance is between the center of gravity and the surface of support), the more stable position is occupied and the smaller the clinging forces required to equilibrate the body (Fig. 7.2). Therefore, an animal running up a trunk tends to sprawl its limbs as widely as possible. For reptiles, the sprawling position of limbs is normal; therefore, transition to the arboreal mode of life does not require additional morphological changes in the shoulder girdle. On the contrary, in therian mammals, this requires considerable re-arrangement. Most of them, including many gliding forms, are unable to abduct the humerus laterally,

Fig. 7.2 External forces acting on the colugo clinging to a vertical trunk (photo by Norman Lim). F_{fl}, F_{hl} – substrate reaction forces transmitted to the body by front and hind limbs in the sagittal plane, *mg* – force of gravity of the body. *a. Actual forces acting upon the body held close to the trunk b. Presumed forces acting upon the body held apart from the trunk* (*forces* F_{fl}, F_{hl} *become greater*)

because their scapula is in the parasagittal plane with the glenoid facing ventrally. Protraction of the humerus (which is much better developed in therians than abduction in accordance with their technique of quadrupedal running) cannot be used for lateral displacement of the forelimb. As a result, they can move the forelimbs sideways almost exclusively by supination (rather than abduction) in the shoulder joint; in so doing, the elbow joint remains closely pressed to the thorax and only the antebrachium is being drawn aside (Fig. 7.3). The more strongly the scapula and, hence,

Fig. 7.3 Locomotion of squirrels (Sciuridae) on tree trunks. *a. Sciurus vulgaris* (photo by E.A. Kovalev, www.fotolenta.net) *b. Pteromys volans* (photo by E. Kuzmicheva) *c. Funambulus pennantii* (photo by Thomas Schoch, wikipedia.org)

the forelimb is turned from the parasagittal towards the frontal plane, the greater the contribution to sprawling made by protraction of the humerus. For example, in the Russian flying squirrel (*Pteromys volans*) the sprawling ability is more developed than in the red squirrel (*Sciurus vulgaris*). This is due to the fact that the scapula of flying squirrels is slightly declined from the parasagittal plane, so that the glenoid faces ventrolaterally. This shows that mammals combining the arboreal mode of life with gliding tend to increase the sprawling range of limbs by all available means. Marsupial sugar-gliders (*Petaurus*) are even more capable of declining the scapula towards the frontal plane. Nevertheless, none of these mammals have developed this ability as much as colugo.

So why do not all gliding mammals acquire the ability to transpose the scapula to the frontal plane in order to sprawl the forelimbs far apart? Apparently, the answer to this question is associated with the problems caused in terrestrial locomotion when the scapula is subhorizontal. The ability to sprawl limbs wider apart acquired by marsupial gliders and to some extent by flying squirrels affects their terrestrial locomotion. Our high-speed video recording of running of various gliders (*Pteromys volans*, *Acrobates pygmaeus*, *Petaurus breviceps*) shows that the sprawling forelimb posture developed for climbing trunks is also used in their running. Perhaps this partial refusal of parasagittal posture may account for increased running costs and lower speeds found in the flying squirrel *Glaucomys sabrinus* as compared with the squirrel *Sciurus niger* by Flaherty et al. (2010). According to our data, *Acrobates pygmaeus* and *Petaurus breviceps* do not use the true gallop at all lacking the so-called gathered unsupported stages which usually occur after the forelimb thrust; in our opinion, this is caused by the inability to draw the hindlimbs more laterally than the forelimbs since the latter are sprawling too much. This limits the speed of progression, and apparently leads to an increase in energy consumption during terrestrial locomotion. This tendency is much more pronounced in colugos. They spend most of their lives on tree trunks and are almost unable to move normally on the ground sprawling their forelimbs in a lizard manner. The entire muscular apparatus of the shoulder girdle in colugos is accommodated for loads mainly at horizontal position of the scapula. As a result, they are forced to produce thrust against the ground by humeral depression in the transverse plane instead of retraction in the parasagittal plane. Such movement is powered by transverse rather than longitudinal part of the *m. pectoralis*. This illustrates the idea that, to gain the ability of sprawling the forelimbs, mammals have to give up the efficiency of terrestrial locomotion.

On the other hand, acquisition of the great mobility of the shoulder girdle in the transverse plane allowed colugos to take priority among gliding mammals. In addition, the sprawling ability together with camouflaging pattern of the membrane help to mask the body contour on the trunk surface even in the daytime and, hence, obviate the necessity for searching for scarce refuges in hollows of trees. Due to this membrane, the colugo looks from afar like a natural outgrowth on the trunk (Fig. 7.4) and, if a predator approaches it along the trunk and exposes a fraud, the same protective cloak provides an escape of the colugo by gliding to a neighboring tree, immediately getting rid of the pursuer.

Fig. 7.4 Cryptic coloration and typical posture of colugo sitting on the bark background (photo by E. Yakhontov).

Arboreal ancestors of chiropterans probably passed similar evolutionary stages of morphofunctional changes. Presumably, these animals were smaller than colugos and, so, may have climbed and rested on not only vertical trunks, but also skeletal branches in tree crowns. This locomotion pattern is sometimes observed in fruit bats (Fig. 3.20c), corroborating the possibility of the presence of a stage in their history, at which this locomotion pattern was usual, as in colugos.

Such ancestors could also move among rather thin and dense branches grasping those by the fingers (as do colugos when feeding in canopies). Actually, as ancestors of chiropterans acquired the ability to sprawl widely the elongated forelimbs and even transpose them onto the back, they expanded the sector accessible for the forelimb to a spherical cone and hence, could freely reach a new support and readily move in tree crowns. Among extant chiropterans, about 150 species (all members of the family Pteropodidae) have a claw not only on the thumb, but also on digit II, which is incorporated in the wing membrane. They actively use these claws for climbing branches (Fig. 3.20b). Microbats also use the claw of the thumb for climbing. The highly autonomous thumb of bats shows that, apparently, in their ancestry, the membrane reached only its base (in contrast to colugos) (Fig. 7.5a).

The membranes stretched between the elongated digits of the forelimb (the chiropatagium) allowed ancestors of chiropterans (Fig. 7.5a) to use manus as a rudder controlling the body careen and, so, direction of glide. Such a steering technique is actively used today by colugos. The manus is the best possible rudder for rolling torque production, indeed, since it is placed farthermost laterally relative to the body's center of mass.

Either, the ancestral chiropatagium could be used as a winglet. This is a wingtip deflected upward (or downward) which slows down the airflow from beneath of the wing onto its top over the tip and, thus decreases the energy lost in rotation of the trailing vortex left behind the tip. This energy loss accounts for a significant part of the so-called induced drag of the wing, so the winglet finally increases the lift-to-drag ratio of the wing which is the main measure of its flight performance;

for instance, the greater the ratio, the less steep is the glide. The camber of the chiropatagium and its persistent deflection from the plane of plagiopatagium in gliding colugos indicates that they use it as a winglet indeed; this may be the main reason for the record low gliding angle among similar mammals. The idea of the winglet function of the manus in colugos and gliding petaurids, as well as of the flap of skin supported by a wing spur in flying squirrels and scaly-tailed flying squirrels, was considered by Jackson and Schouten (2012), being proposed for the first time for flying squirrels by Thorington et al. (1998).

Further elongation of the chiropatagium (Fig. 7.5b), which initiated the formation of the future neopatagium, could be promoted by the benefits of the high aspect ratio of the wing (span divided by chord) as the best way to reduce its induced drag. We noted above that winglets reduce the kinetic energy of tip vortices; similarly the increased wing span reduces the energy of the downwash, which is the downward airflow, as wide as the wing span, coupled with lift generation. The wider is the wing span for any given wing area, the wider is the downwash, the greater is its mass per unit time, the lower is its induced speed (since the mass per unit time, multiplied by speed, equals lift), the lower is its kinetic energy (since in its equation the speed is squared and the mass is not), the lower is the induced drag of the wing, and, finally, the higher is its lift-to-drag ratio. The energy lost in the downwash accounts for a much larger part of induced drag than the energy of trailing vortex and, hence, is a much more promising item for minimization. On the whole, the induced drag is inversely proportional to the wing span; hence an animal with elongated wings (Fig. 7.5b) has a better gliding performance than an animal with a square membrane (Fig. 7.5a).

It is rather difficult to judge how the chiropatagium was transformed from a deflected winglet into the elongated and integrated into the main lifting surface neopatagium, since the balance of energy losses in trailing vortices and downwash in these animals is difficult to estimate. However, only after the development of high enough aspect ratio of the wings considerably enhancing aerodynamic performance, the evolutionary development of flapping motions of the forelimbs could arise[1] The matter is that, for effective flapping flight, the aerodynamic passivity or harm (such as negative force or lift: see Chap. 5) of upstroke should be overbalanced by the aerodynamic benefits of the active downstroke.

An aerodynamic model of gradual transition from gliding to flapping flight was developed by Norberg (1985). This model proves that under certain conditions even the very slight flapping motions could be efficient enough in lift and thrust generation to ensure that intermittent flapping during gliding (say, in a manner of undulating flight), could help reduce the overall height loss inevitable in pure gliding. In terms of vortex wake (Chap. 5), Norberg regarded the so-called continuous-vortex gait as the initial flight style of bats, which, at that time, was considered to be typical of both birds and bats at high speeds. Today, the presence of such vortex wake in

[1] Colugos also have membranes between digits of the foot (Fig. 4.4); however, in ancestors of chiropterans, they were either initially absent or secondarily reduced with the appearance of the neopatagium and consequent decrease in the role of hind legs in the wing support.

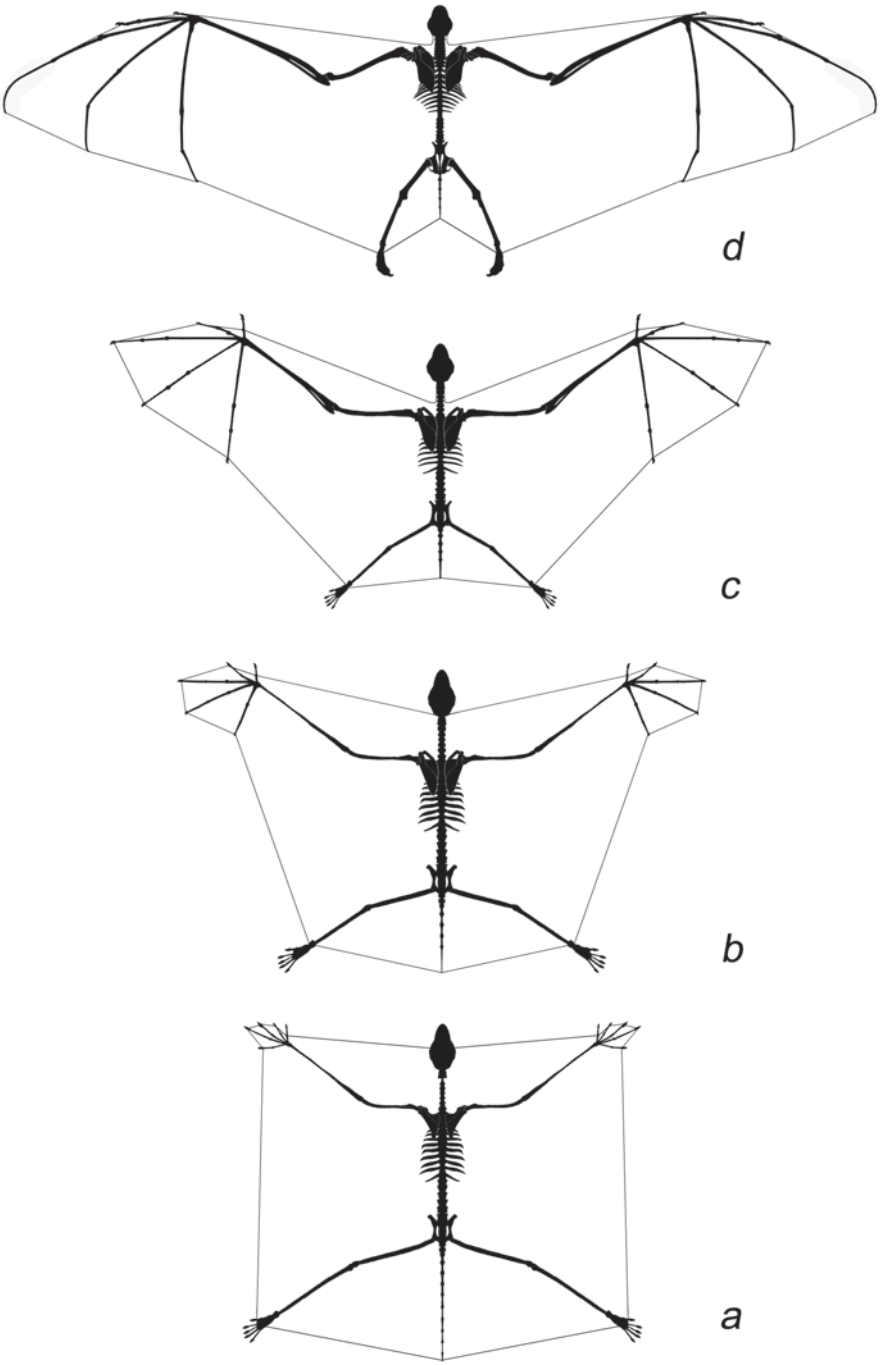


Fig. 7.5 Hypothetical transitional stages from gliding to flapping flight. *a. Gliding like colugos b. Gliding with enlarged distal parts of the wings c. Primitive flapping flight d. Perfect flapping flight*

any bat and at any speed is entirely disproved. However, we agree with the idea that the evolution of flapping flight in bats started from high speeds, while the ability to fly slowly was gained by the end of this process.

Probably in the early stages of development of flapping motions, the wing of bat ancestors produced more lift than thrust due to the predominance of archeopatagium. However, the presence of some neopatagium, small at least, was absolutely necessary for flapping flight origination. The reason is that the neopatagium, by our definition, is the part of membranous wing, which protrudes laterally beyond the reach of the hindlimb and so has a free trailing edge. This distinctive feature allows the neopatagium to twist (pronate or supinate) and, thus, differentially adjust the angle of attack along the wingspan, which is necessary for thrust generation. Even the yet underdeveloped neopatagium, due to its pronation in the downstroke, could have a good thrust-to-lift ratio. Taking into account that this distal part of the wing produces the maximum in magnitude aerodynamic force due to the greatest speed relative to the air, its thrust could be quite significant. Further, folding of the neopatagium in the upstroke could reduce its negative effect, and thereby achieve a positive balance of the lift and thrust in the whole wingbeat cycle. It is timely to recall that in steady gliding the gravity is balanced by the aerodynamic force, so even a small increase of the average lift in the wingbeat cycle is enough to prolong aerial travel (this is what was meant by Norberg 1985). Thus, in the presence of the laterally sprawling forelimbs highly mobile in the transverse plane and equipped with the skin membrane up to the tips of the elongated digits, the ancestors of chiropterans had to do only one step for transition from gliding to flapping flight (Fig. 7.5c). This step was of behavioral or neurophysiological rather than morphological and biomechanical nature, requiring but initiation of flapping movements. As was noted by Norberg (1985), even intermittent strokes can reduce or override the height loss in the gliding phase of such a mixed flight, because the flapping motion increases the wing speed relative to the air as compared with the static wing of the glider; as a result, additional lift appears. Further, since the circumferential speed of the flapping wing increases to its tip, the more distal wing regions produce greater lift and thrust forces than the more proximal ones, the subsequent progressive development of the neopatagium was predetermined. (Fig. 7.5d). The adaptation for gliding, which preceded this stage, as though prepared the musculature for flapping flight. Even at the stage modelled morphologically by colugo some redistribution of muscular mass has already occurred. The *m. pectoralis* is not only enlarged, but also shifted along the sternum anteriorly as compared with generalized therians (e.g., tree shrew). Subsequent growth of the neopatagium for powered flight required further enlargement of this muscle, so the muscular mass should have been reduced somewhere else. To the point, transition to flapping flight resulted in a decrease in the role of the archeopatagium and, hence, the hindlimb in holding the body aloft, and its muscular mass was reduced in favor of the forelimb. In the heavy job of transferring the aerodynamic forces from the neopatagium onto the body, the *m. pectoralis* was aided by the *m. serratus ventralis thoracis*, the insertion of which was gradually, slip by slip, translocated from the dorsal to caudal border of the scapula, which at the same time elongated in

the posterior direction (see Chap. 5). Throughout the transformation, the clavicle keeps the role of longitudinally compressed subvertical strut between the wing skeleton (namely, the scapula) and the sternum, which role was formerly acquired for gliding.

As flapping flight developed, the archeopatagium decreased in size relative to the neopatagium. In this process, the backward pull of the archeopatagium on the forelimb gradually decreased, while the forward thrust by the neopatagium increased. Consequently, it became possible to reduce the propatagium which initially counterbalanced the archeopatagium at the shoulder joint and in the new situation would only restrict the wing retraction in the upstroke. Therefore, in the evolution of chiropterans it gradually decreased in extent. In extant bats, its proximal attachment has 'slipped down' from the head and neck onto the shoulder (Fig. 7.5d).

Flapping motions of wings give them enough speed relative to the air for lift generation even at very low speeds of the body (hovering is the extreme example). This allows reduction of speed of the body at landing. Having gained in this way a time to get accustomed with the target point before landing, ancestors of bats received an opportunity to choose the most comfortable places on the substrate for clinging. However, head-down posture at landing in bats was probably developed later. The establishment of such an inverted posture most likely happened after the final refusal of running up tree trunks as powered flight became a more convenient way to rise than climbing. Body orientation of the modern bats in roosting is determined by the fact that the hindlimbs, being peculiarly reversed to 'flying position' and equipped with well developed claws, are more suitable for suspension than the forelimbs with only one finger, the thumb, fit for this purpose. Nevertheless, many modern bats can still climb head-up using claws of thumbs.

A late stage of the establishment of the extant appearance of chiropterans is well exemplified by *Onychonycteris* (Fig. 7.5c) recently described from the Lower Eocene (Simmons et al. 2008). Judging from the entire set of its morphological features, this primitive bat already used flapping flight, alternating it with gliding. It is remarkable that all five fingers of *Onychonycteris* are equipped with well-developed claws, which are particularly large on fingers I–III. *Onychonycteris* probably used these claws along with claws of the hindlimbs for clambering in tree crowns, as extant fruit bats. Apparently, *Onychonycteris* demonstrates the critical point in the evolution of flight. Before this point it was progressing slowly because the advantages of aerial locomotion but slightly overbalanced the losses in efficiency of quadrupedal locomotion associated with destruction of the Z-like parasagittal limbs. Having passed this point, prebats suddenly got access to the full scale and spectrum of flight advantages, abandoned quadrupedal locomotion, turned into bats, and flourished.

The evolutionary scenario proposed here is still very far from completeness; however, in our opinion, it is non-contradictory and naturally treats presently known morphofunctional features of the flight apparatus of chiropterans and illustrates the main stages of probable history of the establishment of their locomotion.

References

Demes B, Forchap E, Herwig H (1991) They seem to glide. Are there aerodynamic effects in leaping prosimian primates? Z Morphol Anthropol 78(3):373–385

Dohrn A (1875) Der Ursprung der Wirbeltiere und das Prinzip des Functionswechsel. Verlag von FCW Vogel, Leipzig

Flaherty EA, Ben-David M, Smith WP (2010) Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding. J Comp Physiol B 180(7):1067–1078

Jackson SM, Schouten P (2012) Gliding Mammals. CSIRO Publ, Melbourne

Marcellini DL, Keefer TE (1976) Analysis of the gliding behavior of *Ptychozoon lionotum* (Reptilia: Gekkonidae). Herpetologica 32(3):362–366

Norberg UM (1985) Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. Am Nat 126(3):303–327

Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2008) Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451(7180):818–822

Thorington RW Jr, Darrow K, Anderson CG (1998) Wing tip anatomy and aerodynamics in flying squirrels. J Mammal 79(1):245–250

Citation Index

Note: Figures, tables, and footnotes are indicated by *"f", "t",* and *"n"* respectively.

A
Adams, R.A., 227, 244
Agoramoorthy, G., 207
Aldridge, H.D.J.N., 228–231, 233, 234, 236, 243
Altenbach, J.S., 115, 145, 150, 151, 184, 235*f*, 236, 242, 246, 249, 254
Altringham, J.D., xiv
Arganbright, K., 115, 201
Aristov, A.A., xviii, xix

B
Biewener, A.A., 218
Bishop, K.L., xiv, xv
Bullen, R., 231
Busse, R.v., 233
Byrnes, G., 207, 208, 210, 211

C
Caple, G., xv, xvi
Carlsson, A., 1, 6, 23, 30, 33, 48
Chapman, H.C., 51, 52, 65
Clark, B.D., xv
Cooper N.L., xvi

D
Darwin, C.R., xiv
Davis, D.D., 1, 23, 30, 31
Davis, R., 230
Demes, B., 281
Dial, K.P., xiii
Diogo, R., 35, 51, 65
Dohrn, A., 281
Dudley, R., 208, 229
Dunlap, S.S, 21, 268
Dzerzhinsky, F.Y., xvi, xvii, xviii, xix
Dzulhelmi, N., 205

E
Elangovan, V., xvi
Emmons, L.H., 208

F
Findley, J.S., 231
Flaherty, E.A., 284
Foehring, R.C., 115, 152, 167

G
Gambaryan, P.P., xix, 1, 21, 276
George, R.M., 1, 18, 23, 30, 31, 35–37, 39, 42, 44, 45, 48
Giannini, N.P., xiv
Glass, P.J., 115, 202
Gourtovoy, N.N., xviii, xix
Grassé, P.P., 51, 52
Gunnell, G.F., xiv

H
Habersetzer, J., xiv
Haines, R.W., 1, 37, 42, 44, 45
Hartman, F.A., 230
Hayward, B., 227
Hedenström, A., 227–230, 243, 246
Hermanson, J.W., 115, 150, 234, 246, 254, 268

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6

Hildebrand, M., 211, 212, 233
Hill, J.E., xiv, 234, 235*f*
Holbrook, K.A., 245, 249
Howell, A.B., 27, 30, 78
Hubel, T.Y., 234, 244, 249
Hughes, P., 230, 233
Humphry, G.M., 115, 149, 150, 186, 189, 190, 199, 201, 202

I
Iordansky, N.N., 276
Iriarte-Díaz, J., 229–231, 244, 247, 249

J
Jackson, S.M., xiv, 208, 209, 286
Jenkins, F.A., Jr., 1, 21, 259
Jepsen, G.L., xiii, xv, xvi
Jones, F.W., 36
Jullien, R., 115, 132

K
Kokshaysky, N.V., 242
Korzun, L.P., xvi
Kovaleva, I., xv
Kovtun, M.F., xv, xvi, 115–117, 119, 121, 123, 127, 135, 150, 152, 167, 189, 196*t*, 197*t*, 199, 200, 246, 264, 277
Kurochkin, E.N., xiii
Kuznetsov, A.N., 1, 259

L
Lawrence, M.J., 231, 233
Le Gros Clark, W.E., 1, 3, 7, 23, 30, 32, 35–37, 39, 41–44, 47, 48, 150
Leche, W., 51, 65, 66, 68, 72, 78, 87, 91, 94, 97, 99, 100, 104, 108, 112, 113
Ledenev, S.Yu, 182, 183
Lim, N.T.L., 205, 207
Lopez-González, C., 115, 120

M
Macalister, A., 68, 115, 116, 126, 149–152, 160, 161, 179, 187–189, 191, 192, 196*t*, 197*t*, 198, 202
MacAyeal, L.C., 230
Maniakas, I., 115, 155, 167, 249, 250
Marcellini, D.L., 282
Meng, J., xiv
Miller, R.A., xix, 1, 23, 29, 30, 35
Muijres, F.T., 227, 230, 231, 243, 244, 246

N
Neuweiler, G., 227
Neveu, P., 259
Nomina Anatomica Veterinaria, xvi, xvii
Norberg, U.M., xiv, xvii, 115–117, 119, 126, 128, 139, 149–151, 155, 161, 162, 165, 178, 184, 185, 188, 189, 191, 192, 196*t*, 197*t*, 198–200, 202, 229–231, 233, 241, 245, 246, 266, 274, 277, 286, 288
Novacek, M.J., xiv
Nozdrachev, A.D., xviii, xix

O
O'Leary, M.A., xvii
Owen, R., 51, 57

P
Padian, K., xiv, xv
Panyutina, A.A., 236, 241, 255, 269
Pennycuick, C.J., 229, 230, 245, 274
Peters, D.S., xiii
Pirlot, P., xv, xvi

R
Rayner, J.M.V., xiv, 230, 242–244
Riskin, D.K., 170, 228, 230, 231, 233, 234, 246, 247

S
Sargis, E.J., 1, 3, 6–8
Schliemann, H., 115, 131, 132
Schlosser-Sturm, E., 115, 131, 132, 234
Scholey, K., xiv, 208, 210
Sears, K.E., xvi, 277
Shufeldt, R.W., 51, 53, 56
Simmons, N.B., xiii, xiv, 289
Smith, J.D., xiv–xvi
Speakman, J.R., xv
Spedding, G.R., 243*n*
Stafford, B.J., xviii, 7, 7*t*, 51, 56, 57
Stein, B.R., 259
Straus, W.L., Jr., 35, 44
Strickler, T.L., 115–117, 119, 121, 141, 143, 145, 149–152, 155, 156, 160, 161, 165, 167, 169, 172–174, 176, 201
Swartz, S.M., 231, 233, 234, 236, 241, 244, 245
Szalay, F.S., 51, 57, 62, 132

T
Thewissen, J.G.M., 115, 201
Thollesson, M., 246

Thomas, A.L.R., 230
Thomson, S.C., 229
Thorington, R.W., Jr., 286
Tian, X., 223, 243
Tokita, M., 161, 201

V
Vaughan, T.A., 115–117, 119, 124, 126, 127, 132, 135, 149, 150, 152, 162, 165, 178, 183–189, 191–194, 196*t*, 197*t*, 198–201, 205, 234, 236, 277
Verma, K., 1, 2, 3, 6, 7, 23
Voigt, C.C., 230
Voss, H., xviii, xix, 35, 185

W
Walton, D.W., 8*t*, 115, 117
Walton, G.M., 115
Watts, P., 246
Wischusen, E.W., 207
Wolf, M., 243

Y
Youlatos, D., 275
Yudin, K.A., xvi

Anatomical Index

Note: Figures, tables, and footnotes are indicated by *"f", "t",* and *"n"* respectively. The major descriptions of anatomical structures are in bold.

A

Acromion 2*f*, 3*f*, 53*f*, 54, 54*f*, 59*f*, 118*f*, 120*f*, 121, 122*f*, 222, 237*f*, 239*f*, 240, 241, 251

Angulus caudalis scapulae (dorsocaudal angle) xix*f*, 2*f*, 3, 3*f*, 53, 53*f*, 54*f*, 120, 120*f*–122*f*, 221*f*, 222, 222*f*, 223*f*, 239*f*, 240, 240*f*, 250*f*, 251, 251*f*, 252*f*, 253, 259, 261, 265, 266

Angulus cranialis scapulae (dorsocranial angle) xix*f*, 2, 121*f*

Antebrachium 5*f*, **6**, 55*f*, **56**, 124*f*, **126**, 128*f*, 269, 270*f*, 271, 272, 275, 276

Aponeurosis extensorum superficialis 34

Aponeurosis flexoria communis **40***n*, 44*f*, 45*f*, 103, 273

Aponeurosis palmaris profunda **104***n*, 110*f*

Archeopatagium **247**, 248, 248*f*, 249, 250*f*, 251, 251*f*, 252*f*, 254, 255, 265, 268, 277*n*, 288, 289

Articulatio acromioclavicularis (acromioclavicular articulation) **9**, 10*f*, **60**, 60*f*, 61, 130*f*, **131**, 131*f*, 221*f*, 222*f*, 223*f*, 236, 239*f*, 240*f*, 241, 250, 250*f*–252*f*, 259, 261, 262

Articulatio antebrachiocarpea (antebrachiocarpal joint) **11**, **63**, 271

Articulatio cubiti (elbow joint) **10**, **62**, 62*f*, **132**, 187*f*, 254

Articulatio humeri (shoulder joint) **10**, 10*f*, **61**, 61*f*, **131**, 133*f*, 236, 241, 242, 254, 268, 269, 271, 272, 275, 283

Articulatio mediocarpea (mediocarpal joint) **11**, 134*f*, **135**, 254, 272, 273

Articulatio radiocarpea (radiocarpal joint) **133**, 134*f*, 254, 271

Articulatio sternoclavicularis (sternoclavicular articulation) **9**, 9*f*, **59**, 59*f*, **129**, 129*f*, 130*f*, 221*f*–223*f*, 234, 236, 239*f*, 240*f*, 241, 250, 250*f*–252*f*, 259, 261, 262, 267, 268

Articulationes carpometacarpeae (carpometacarpal joints) **11**, **63**, 134*f*, **135**, 254, 272, 273

Articulationes intercarpeae (intercarpal joints) **11**

Articulationes intermetacarpeae (intermetacarpal joints) **11**, **135**

Articulationes interphalangeae manus (interphalangeal joint) 11*f*, **12**, **64**, 64*f*, 136*f*, **137**, 139, 253, 272, 274

Articulationes metacarpophalangeae (metacarpophalangeal joints) **11**, 11*f*, **63**, 64*f*, **136**, 136*f*, 253, 272, 274

Atlas 16*f*, 59*f*

Axis 59*f*

C

Capitatum 6, **7***f*,*t*, 56, 57*f*, 126, 127*f*, 134*f*, 135

Capitulum humeri, see *condylus lateralis humeri* xix

Capsula articularis (articular or joint capsule) 10, 10*f*, 59, 61, 64, 129, 131, 131*f*

Caput humeri (humeral head) 5*f*, 6*f*, 10, 55*f*, 56*f*, 124*f*, 125*f*, 270*f*

Caput radii (proximal head of radius) 5*f*, 10, 55*f*, 62, 187*f*

Carina sterni 118*f*, 119*f*

Carpale distale 1, see also *trapezium* 7*t*

Carpale distale 2, see also *trapezoideum* 7*t*

Carpale distale 3, see also *capitatum* 7*t*

Carpale distale 4 + 5, see also *uncinatum* 6, 7*t*

Carpus **6**, 7*f*, **56**, 57*f*, **126**, 127*f*

Cartilago suprascapularis (suprascapular cartilage) 120

Cavitas glenoidalis (glenoid) 3, 3*f*, 54, 54*f*, 61, 118*f*, 120*f*, 121, 122*f*, 132, 234, 242, 274, 275, 277, 283, 284

© Springer International Publishing Switzerland 2015

A. A. Panyutina et al., *Flight of Mammals: From Terrestrial Limbs to Wings,*
DOI 10.1007/978-3-319-08756-6

Centrale 6, **7***f*,*t*, 56, 57
Centralolunatum 57
Chiropatagium 52*f*, **117**, 228, 229, 243–245, 277, 277*n*, 285, 286
Clavicula (clavicle) **3**, 3*f*, 4*f*, 20*f*, **54**, 54*f*, 59*f*, 118*f*, **122**, 123*f*, 129*f*, 214*f*, 220, 221*f*–223*f*, 234, 236, 237, 237*f*, 238*f*, 240, 240*f*, 241, 250, 250*f*–252*f*, 253, 261, 261*f*, 262, 267, 289
Condylus lateralis humeri xix, 6*f*, 55, 56*f*, 62, 125*f*, 126, 132, 187*f*
Condylus medialis humeri xix, 6*f*, 55, 56*f*, 62, 125*f*, 126, 132, 187*f*
Corpus sterni 59*f*, 118*f*, 119*f*
Costae (ribs) 59, 59*f*, 118*f*, 119*f*, 277
Costae sternalis (sternal segment of rib) 118*f*
Crista lateralis occipitalis (occipital crest) 15*f*, 16*f*, 17*f*, 59*f*, 140*f*
Crista pectoralis (pectoral crest) 4, 5*f*, 6*f*, 55, 55*f*, 56*f*, 123, 124*f*, 125*f*, 269, 270*f*
Crista supracondylaris lateralis humeri (crest of lateral epicondyle) 5*f*, 6*f*, 55, 55*f*, 56*f*, 124*f*
Crista supracondylaris medialis humeri (crest of medial epicondyle) 4, 5*f*, 6*f*, 31*f*, 55*f*
Crista tuberculi majoris humeri (crest of greater tubercle) 5*f*, 124*f*, 125*f*
Crista tuberculi minoris humeri (crest of lesser tubercle) 5*f*, 55*f*, 123, 124*f*, 125*f*
Cubiforme, see also t*rapezium* 7*t*
Cuneiforme 6, **7***f*,*t*, 56, 57*f*, 58*f*, 63, 95*f*, 109*f*–111*f*, 126, 127*f*, 134*f*, 135, 182*f*, 195*f*

D
Dactylopatagium minus (membrane between digits I and II) 137

E
Ectepicondylus, see also *epicondylus lateralis humeri* 4
Entepicondylus, see also *epicondylus medialis humeri* 4
Epicondylus lateralis humeri (lateral epicondyle) 4, 5*f*, 55, 55*f*, 56*f*, 124, 124*f*, 125*f*
Epicondylus medialis humeri, (medial epicondyle) 5*f*, 6*f*, 55, 55*f*, 56*f*, 124, 124*f*, 125*f*
Extremitas acromialis claviculae (acromial end of the clavicle) 3*f*, 4, 4*f*, 54*f*, 55, 123*f*
Extremitas sternalis claviculae (sternal end of the clavicle) 3*f*, 4, 4*f*, 54, 54*f*, 122, 123*f*

F
Facies anterior scapulae (anteromedial facet) 121, 122*f*
Facies articularis acromialis claviculae (acromial articular facet of clavicle) 4, 123*f*, 131
Facies articularis carpea (articular surface for carpus) 124*f*, 126
Facies articularis sternalis claviculae (sternal articular facet of clavicle) 4
Facies intermedialis scapulae (intermediate facet) 121, 122*f*
Facies posterior scapulae (posterolateral facet) 120, 121, 122*f*
Fossa infraspinata scapulae (infraspinous fossa) 2*f*, 3, 53*f*, 54, 120*f*, 121, 122*f*
Fossa olecrani humeri (fossa for olecranon) 4, 6*f*, 10, 55, 56*f*, 63, 125*f*
Fossa radialis humeri (fossa for radius) 4, 6*f*, 10, 55, 56*f*, 63, 125*f*
Fossa subscapularis scapulae (subscapular fossa) 2*f*, 3, 53*f*, 120*f*–122*f*
Fossa supraspinata scapulae (supraspinous fossa) 2*f*, 3, 53*f*, 54, 120*f*, 121, 122*f*, 267
Fovea articularis radii (fossa on head of radius) 62, 126

H
Hamatum, see also *uncinatum* 7*t*
Humerus **4**, 5*f*, 6*f*, **55**, 55*f*, 56*f*, **123**, 124*f*, 125*f*, 237*f*, 245, 246, 261*f*, 269, 270*f*, 275, 284
Hypothenar (proximal ulnar pad) 36*f*, 42

I
Incisura clavicularis (clavicular articular fossa) 117, 119*f*
Intermedium, see also *lunatum* 6, 7*t*, 56

L
Ligamenta glenohumeralia (scapulohumeral ligaments) 61
Ligamenta intercarpea interossea 135
Ligamenta interspinalia (interspinous ligaments) 13, 13*n*, 151*f*
Ligamenta metacarpea dorsalia 134*f*, 135
Ligamenta metacarpea transversa profunda (transverse metacarpal ligaments) 11, 46*f*, 64, 104, 105*f*, 135
Ligamentum acromioclaviculare 9, 10*f*, 17*f*, 18*f*, 21*f*, 24*f*, 60, 60*f*, 76*f*–78*f*, 131, 131*f*, 156*f*–158*f*

Ligamentum carpi dorsale, see also *retinaculum extensorum* 33
Ligamentum clavoscapulare 60*f*, 61, 76*f*–78*f*, 131*f*
Ligamentum coracoclaviculare 9, 10*f*, 24*f*, 60, 79*f*, 131, 166*f*, 170*f*
Ligamentum coracohumerale 173*f*
Ligamentum glenohumerale laterale (lateral scapulohumeral ligament) 61, 61*f*
Ligamentum glenohumerale mediale (medial scapulohumeral ligament) 61, 61*f*
Ligamentum laterale (lateral ligament of elbow joint) 62*f*, 63, 133*f*, 187*f*
Ligamentum laterale radiale 132, 133*f*
Ligamentum laterale ulnare 132, 133*f*
Ligamentum mediale radiale 132, 133*f*
Ligamentum mediale ulnare 132, 133*f*
Ligamentum palmaris profundum 36, **36***n*, 46*f*, 110*f*
Ligamentum pisometacarpeum 43*f*, 44*f*, 46*f*, 195*f*
Ligamentum sternoclaviculare 9, 9*f*
Ligamentum sternoclaviculare externum 59, 59*f*
Ligamentum sternoclaviculare internum 59, 59*f*
Ligamentum sternoclaviculare laterale 129, 129*f*
Ligamentum sternoclaviculare mediale 129, 129*f*
Ligamentum transversum scapulae 141*f*, **142***n*, 146*f*, 148*f*–150*f*, 153*f*
Ligamentum transversum scapulae superius 53, 60*f*, 64*f*, 82*f*, 83*f*
Lunatum 7, 7*t*, 8, 57

M

Magnum, see also *capitatum* 7*t*, 95*f*, 182*f*
Manubrium sterni 9, 59, 117, 118*f*, 119*f*, 237*f*, 261*f*
Manus 8*f*, 58*f*, 128*f*
Margo caudalis scapulae (caudal border) xviii, xix*f*, 2*f*, 3, 3*f*, 53, 53*f*, 54*f*, 119, 120*f*, 121, 121*f*, 122*f*, 265, 266, 288
Margo cranialis scapulae (cranial border) xviii, xix*f*, 2, 2*f*, 53, 53*f*, 120*f*–122*f*
Margo dorsalis scapulae (dorsal border) xviii, xix*f*, 2, 2*f*, 53, 53*f*, 119, 120*f*–122*f*, 265, 266
Membrana interossa antebrachii 5*f*, 6, 31*f*, 41*f*
Metacarpus 8*f*, 128, 135
Metacromion 2*f*, 3*f*, 25*f*, 53*f*, 54, 54*f*
Multangulum majus, see also *trapezium* 7*t*
Multangulum minus, see also *trapezoideum* 7*t*
Musculi interossei 95*f*, 110*f*, 111*f*, **112**, 191*f*, 193*f*–195*f*, **200**
Musculi interossei dorsales 34*f*, 46*f*, 48*f*, **49**
Musculi interossei palmares 46*f*, **48,** 48*f*, 183*f*
Musculi lumbricales 42*f*, 43*f*, **44,** 45*f*, 93*f*, **104,** 105*f*, 106*f*, 107*f*, **198**
Musculi plagiopatagiales 139, **201**
Musculus abductor digiti quinti 34*f*, 42*f*, 43*f*, **48,** 105*f*, **108**, 191*f*, 193*f*, 194*f*, 195*f*, 197*t*, **199**
Musculus abductor digiti secundi 44*f*, **45,** 46*f*, 48*f*, **199**
Musculus abductor et opponens digiti minimi, see also *musculus opponens digiti quinti* 200
Musculus abductor pollicis brevis **42,** 42*f*, **103,** 105*f*, 181*f*, 182*f*, 191*f*, 193*f*–195*f*, 196*t*, **198**
Musculus abductor pollicis longus 32*f*–34*f*, **35,** 36*f*–38*f*, 42*f*, 44*f*, 88*f*, 89*f*, 90*f*, **91,** 95*f*, 97*f*, 106*f*, 107*f*, 111*f*, 177*f*–179*f*, 182*f*, **185,** 188*f*–191*f*, 193*f*–195*f*
Musculus acromiodeltoideus 13*f*, 14*f*, 19*f*, **23,** 66*f*, 67*f*, 69*f*, 71*f*, **73,** 140*f*, 141*f*, **163,** 215, 235*f*
Musculus acromiospinotrapezius 143
Musculus acromiotrapezius **12**, 13*f*, 14*f*, **65,** 66*f*, 71*f*, 140*f*, **141**, 141*f*, 143*f*–146*f*, 148*f*–151*f*, 215, 235*f*, 262, 263*f*, 264
Musculus adductor digiti quarti 44*f*, 46*f*, **47,** 64
Musculus adductor digiti quinti 44*f*, 46*f*, **47, 108**, 109*f*, 110*f*, 139, 273
Musculus adductor digiti secundi 44*f*, **45,** 46*f*, **108**, 109*f*, 110*f*, 139, 194*f*, 196*t*
Musculus adductor pollicis **44,** 44*f*, 46*f*, 95*f*, **104,** 106*f*, 107*f*, 109*f*, 110*f*, 181*f*–183*f*, 191*f*, 193*f*–195*f*, 196*t*, **198**
Musculus anconeus 24*f*, 26*f*, 27*f*, **30,** 36*f*, 80*f*–82*f*, **86,** 97*f*, 139
Musculus atlantoacromialis, see also *musculus levator scapulae ventralis* 14, 149
Musculus atlantoscapularis, see also *musculus levator scapulae dorsalis* 14
Musculus biceps brachii 13*f*–15*f*, 19*f*, 20*f*, 24*f*, 25*f*, 27*f*, 28*f*, **30,** 31*f*, 38*f*, 66*f*, 67*f*, 69*f*, 72*f*–74*f*, 79*f*, **86,** 101*f*, 140*f*–148*f*, 150*f*, 152*f*, 153*f*, 155*f*, 157*f*, 159*f*, 162*f*–164*f*, 166*f*, **175**, 175*f*
Musculus biceps brachii caput coracoideum 22*f*, 24*f*, 26*f*, **30,** 80*f*–82*f*, **86,** 165*f*, 166*f*, 168*f*, 175*f*, **176**, 246

Musculus biceps brachii caput longum 22*f*, 24*f*, **30,** 80*f*–82*f*, **87,** 157*f*, 165*f*, 166*f*, 168*f*, 175*f*, **176**
Musculus bicipito-plagiopatagialis 161
Musculus brachialis 14*f*, 15*f*, 24*f*–28*f*, 31*f*, **32,** 32*f*, 33*f*, 36*f*–38*f*, 66*f*, 67*f*, 69*f*, 70*f*, 72*f*–77*f*, 80*f*–83*f*, 86*f*, **87,** 88*f*–90*f*, 96*f*, 97*f*, 101*f*, 140*f*, 142*f*–144*f*, 146*f*–148*f*, 152*f*, 159*f*, 163*f*, 166*f*, 167*f*, **176**, 177*f*, 188*f*, 216, 217*f*, 219
Musculus brachioradialis **32,** 32*f*, 33*f*, 36*f*, 40*f*, 42*f*, **87,** 88*f*, 89*f*, 96*f*, 97*f*, 143*f*, 177*f*, **178**, 188*f*, 216, 217*f*, 219
Musculus clavodeltoideus 13*f*, 14*f*, 19*f*, **23,** 66*f*, 71*f*–73*f*, **73,** 140*f*–149*f*, 152*f*, 159*f*, **162,** 162*f*, 164*f*, 235*f*
Musculus clavotrapezius **12**, 65, **139**, 140*f*, 142*f*, 144*f*, 146*f*–148*f*, 151*f*, 154*f*, 164*f*, 268
Musculus cleidomastoideus 65
Musculus coracobrachialis brevis 22*f*, 24*f*, 26*f*, 27*f*, **29,** 29*f*, 78, **79**, 82*f*
Musculus coracobrachialis longus 22*f*, 24*f*, 26*f*, 27*f*, **29,** 78, **79**, 82*f*, 83*f*, 97*f*, 167*f*, 168*f*, 171*f*, **173**, 175*f*
Musculus coracobrachialis profundus **79**, 79*f*, 80*f*–84*f*
Musculus coracobrachialis superficialis, see also *musculus coracobrachialis longus* 78
Musculus coracocutaneus 65, 73*f*, 79*f*, **112**, 139, **201**
Musculus cutaneus trunci 15*f*, 19*f*–21*f*, **22, 72,** 112, **161,** 201, 276
Musculus dorsi patagialis 139, 161
Musculus dorso-brachialis, see also *musculus latissimus dorsi superficialis* 68
Musculus epitrochleoanconeus, see also *musculus anconeus* 30, 30
Musculus extensor carpi radialis brevis 32*f*, **33,** 33*f*, 34*f*, **87,** 88*f*, 93*f*, 177*f*–182*f*, **182**, 183*f*, 190*f*, 193*f*, 215
Musculus extensor carpi radialis longus 32*f*, **33,** 33*f*, 34*f*, 36*f*, **87,** 88*f*, 93*f*, 177*f*–180*f*, **180,** 181*f*–183*f*, 188*f*, 190*f*, 193*f*, 194*f*, 215, 216, 245
Musculus extensor carpi ulnaris 32*f*, 34*f*, **35,** 88*f*, 92*f*, 93*f*, **94,** 96*f*, 177*f*–179*f*, 181*f*–183*f*, **186**
Musculus extensor digiti minimi 184
Musculus extensor digiti quinti proprius 184
Musculus extensor digitorum communis 32*f*, **34, 88,** 88*f*, 92*f*, 102*f*, 177*f*, 179*f*, 181*f*, 183*f*, **184,** 272
Musculus extensor digitorum lateralis 32*f*, **34,** 34*f*, 88*f*, **89,** 92*f*, 93*f*, 102*f*, **184,** 272
Musculus extensor indicis 32*f*–34*f*, **35,** 89*f*, 92*f*, 93*f*, **94,** 178*f*–183*f*, **185,** 272
Musculus extensor pollicis brevis 35, 184
Musculus extensor pollicis longus 32*f*, 33*f*, **34,** 34*f*, 89*f*, **91,** 92*f*, 93*f*, 177*f*, 179*f*–183*f*, **184,** 272
Musculus flexor brevis manus 42*f*, **47,** 64, 139, 273
Musculus flexor carpi radialis **36,** 36*f*, 37*f*, 44*f*, 46*f*, 48*f*, **96,** 96*f*, 97*f*, 99*f*, 101*f*, 111*f*, **187,** 188*f*, 190*f*, 193*f*–195*f*, 216, 254
Musculus flexor carpi ulnaris 32*f*–34*f*, 36*f*, **41,** 42*f*, 96*f*, 97*f*, **103,** 105*f*, 106*f*, 107*f*, 109*f*, 111*f*, 178*f*, 188*f*, 189*f*, 191*f*, **193,** 193*f*, 195*f*, 254
Musculus flexor digiti quinti brevis 42*f*, 43*f*, **47,** 105*f*, 106*f*, **108,** 195*f*, 197*t*, **199**
Musculus flexor digiti quinti superficialis 36*f*, 37*f*, 42*f*, **47,** 65, 96*f*, 139, 273
Musculus flexor digitorum accessorius 65, 96*f*–98*f*, **99,** 106*f*, 273
Musculus flexor digitorum profundus 36*f*, 37*f*, **39**, 39*f*, 40*n*, 42*f*–44*f*, 96*f*–100*f*, **102**, 102*f*, 105*f*–107*f*, 109*f*, 188*f*–191*f*, **192,** 193*f*–195*f*, 216, 254, 272, 273
Musculus flexor digitorum profundus caput humerale profundum 38*f*, **40**, 40*f*, 102
Musculus flexor digitorum profundus caput humerale superficiale 38*f*, **40**, 40*f*, **102**
Musculus flexor digitorum profundus caput olecrani 38*f*, **40**, 40*f*, **102**
Musculus flexor digitorum profundus caput radiale 38*f*, **40**, 40*f*, **102**
Musculus flexor digitorum profundus caput ulnare **40**, 40*f*, **102**
Musculus flexor digitorum superficialis 33*f*, **37,** 38*f*, 39*f*, 43*f*, 44*f*, **97**, 102*f*, 105*f*, 188*f*, **189,** 190*f*, 191*f*, 193*f*, 194*f*, 196*t*, 254, 272
Musculus flexor pollicis brevis 42*f*, **43,** 43*f*, **104,** 105*f*, 106*f*, 191*f*, 193*f*–195*f*, **198**
Musculus flexor pollicis brevis profundus **44,** 44*f*, 46*f*, **104,** 107*f*, 109*f*, 110*f*, 139
Musculus humerocutaneus 65, **112**
Musculus humeropatagialis 139, **201**
Musculus infraspinatus 15*f*, 17*f*, 18*f*, **28,** 70*f*, 75*f*, **77,** 142*f*–146*f*, 148*f*, **172**, 250*f*, 254, 267, 269, 271
Musculus interosseus digiti quarti 197*t*, **200**
Musculus interosseus digiti quarti lateralis **112**

Musculus interosseus digiti quarti medialis **112**
Musculus interosseus digiti quinti medialis 93*f*, **112**
Musculus interosseus digiti secundi 196*t*, **200**
Musculus interosseus digiti secundi lateralis **112**
Musculus interosseus digiti secundi medialis **112**
Musculus interosseus digiti tertii 196*t*, 198, **200**
Musculus interosseus digiti tertii lateralis **112**
Musculus interosseus digiti tertii medialis **112**
Musculus interosseus dorsalis digiti quarti **49**
Musculus interosseus dorsalis digiti secundi **49**
Musculus interosseus dorsalis lateralis digiti tertii **49**
Musculus interosseus dorsalis medialis digiti tertii **49**
Musculus interosseus palmaris digiti quarti **48**
Musculus interosseus palmaris digiti quinti **49**, 199
Musculus interosseus palmaris digiti secundi **48**
Musculus jugalis propatagii 113
Musculus latissimus dorsi 13*f*–15*f*, 18*f*, **19,** 19*f*, 20*f*, 22*f*, 24*f*–26*f*, **68,** 140*f*–142*f*, 144*f*, 148*f*, 149*f*, 152*f*, 153*f*, **158,** 166*f*, 167*f*, 216, 217*f*, 218, 219, 264, 265
Musculus latissimus dorsi profundus 66*f*, **69,** 69*f*, 70*f*, 72*f*–75*f*, 80*f*, 84*f*, 218
Musculus latissimus dorsi superficialis 66*f*, **69,** 70*f*, 74*f*, 75*f*, 160, 216, 218
Musculus levator scapulae dorsalis 13*f*, **14,** 14*f*–16*f*, 64, 139, 150, 151, 262
Musculus levator scapulae ventralis 13*f*, **14,** 15*f*, 16*f*, 66*f*, **67,** 67*f*, 71*f*, 72*f*, **149,** 152*f*–154*f*, 156*f*, 163*f*, 166*f*, 169*f*, 170*f*, 262, 264
Musculus lumbricalis digiti quarti lateralis **104,** 108
Musculus lumbricalis digiti quarti medialis **104,** 108
Musculus lumbricalis digiti quinti medialis **104,** 108
Musculus lumbricalis digiti secundi **44,** 194*f*, **199**
Musculus lumbricalis digiti secundi lateralis **104,** 108
Musculus lumbricalis digiti secundi medialis **104,** 108
Musculus lumbricalis digiti tertii **44,** 192, 193, 193*f*, 195*f*, **198,** 199
Musculus lumbricalis digiti tertii lateralis **104,** 108
Musculus lumbricalis digiti tertii medialis **104,** 108
Musculus occipitopollicalis 139, 194*f*, **201**, 245
Musculus omocervicalis, see also *musculus levator scapulae ventralis* 149
Musculus omohyoideus 17*f*, **18,** 18*f*, 64, **155**, 156*f*
Musculus opponens digiti quinti 43*f*, 44*f*, 46*f*, **48,** 106*f*, 107*f*, **108**, 109*f*, 110*f*, 194*f*, 195*f*, 197*t*, **200**
Musculus opponens pollicis 34*f*, **42,** 42*f*, 43*f*, 64, 139, 198, 273
Musculus palmaris brevis **42,** 42*f*, 64, 139
Musculus palmaris longus 36*f*, **37,** 37*f*, 42*f*, 64, 99, 101, 139, 189, 273
Musculus panniculus carnosus, see also *musculus cutaneus trunci* 22
Musculus pectoralis **20,** 66*f*, 67*f*, **70,** 72*f*, 140*f*–148*f*, 152*f*, 159*f*, **160,** 215, 221, 221*f*, 222, 222*f*, 223*f*, 224, 234, 235*f*, 236, 242, 243*n*, 246, 250, 250*f*, 251, 251*f*, 252*f*, 253, 255, 264, 265, 267–269, 271, 278, 284, 288
Musculus pectoralis abdominalis 19*f*–21*f*, **22,** 71*f*, **72**, 72*f*–74*f*, 79*f*, 159*f*, **161,** 162*f*, 164*f*, 215
Musculus pectoralis pars anterior 159*f*, **160,** 162*f*–164*f*, 166*f*, 267
Musculus pectoralis pars occipitopollicalis 159*f*, 161
Musculus pectoralis pars posterior 159*f*, **161,** 162*f*, 164*f*, 267
Musculus pectoralis profundus 20*f*, **21**, 21*f*, **71,** 71*f*, 73*f*, 74*f*, 160, 267
Musculus pectoralis superficialis 14*f*, 15*f*, 19*f*, **20,** 20*f*, 21*f*, **70,** 71*f*, 73*f*, 160, 267
Musculus platysma 113, 201
Musculus pronator quadratus **41,** 41*f*, 46*f*, 64, 65, 139
Musculus pronator teres **36,** 36*f*–38*f*, **96,** 101*f*, **186,** 187*f*–190*f*
Musculus rhomboideus 13, 15*f*, 217*f*, 235*f*, 263*f*
Musculus rhomboideus capitis **13**, 13*f*, 14*f*–17*f*, 64, 139, 262, 263*f*
Musculus rhomboideus cervicis **14,** 17*f*, 64, 139, 262, 263*f*

Musculus rhomboideus dorsi **14,** 17*f*, **66,** 66*f*, 69*f*, 70*f*, 142*f*, 144*f*, **145,** 146*f*–148*f*, 151*f*, 152*f*, 154*f*, 218, 219, 263*f*, 264
Musculus serratus anterior 150
Musculus serratus posterior 151
Musculus serratus ventralis **17, 67, 149,** 215, 235*f*, 260*f*
Musculus serratus ventralis cervicis 16*f*, **17,** 22*f*, 24*f*, **68,** 69*f*, 70*f*, 72*f*, 74*f*, **150,** 262
Musculus serratus ventralis cervicis costalis 151, **152,** 156*f*, 157*f*, 165*f*, 167*f*—173*f*, 267
Musculus serratus ventralis cervicis proprius 142*f*, 144*f*, 146*f*–148*f*, **151,** 152*f*–156*f*, 169*f*, 170*f*, 172*f*
Musculus serratus ventralis thoracis **18,** 19*f*, 22*f*, 24*f*, **68,** 70*f*, 72*f*, 74*f*, 141*f*, 143*f*–148*f*, 150*f*, 151, **152**, 152*f*–154*f*, 159*f*, 164*f*, 165*f*, 167*f*, 172*f*, 217*f*, 218, 219, 221, 221*n*,*f*, 222, 222*f*, 223*f*, 224, 225*f*, 234, 236, 246, 250, 250*f*, 251, 251*f*–253*f*, 253, 254*f*, 255, 260*f*, 264–266, 267, 288
Musculus spinodeltoideus 13*f*–15*f*, **23,** 66*f*, 67*f*, 69*f*, 70*f*, **73,** 140*f*–143*f*, **164,** 235*f*
Musculus spinotrapezius **13**, 13*f*, 14*f*, **65**, 66*f*, 141*f*, **143**, 143*f*
Musculus sternocleidomastoideus **12**, 13*f*, 19*f*, **65**
Musculus sternocleidomastoideus pars cleidomastoideus **12**, 14*f*–16*f*, 22*f*
Musculus sternocleidomastoideus pars sternomastoideus **12**, 14*f*–16*f*
Musculus sternohyoideus 156
Musculus sternomastoideus 65, **139**, 140*f*, 163*f*, 165*f*, 166*f*
Musculus subclavius **18,** 20*f*, 21*f*, 22*f*, **68,** 69*f*–74*f*, 79*f*, 80*f*, **156,** 157*f*, 158*f*, 162*f*, 165*f*–169*f*, 171*f*, 268
Musculus subcoracoideus, see also *musculus coracobrachialis profundus* 79
Musculus subscapularis 22*f*, 24*f*, **27,** 72*f*–74*f*, **75**, 76*f*–85*f*, 148*f*, 152*f*–154*f*, 157*f*, 166*f*, **167**, 167*f*, 168*f*, 170*f*–172*f*, 235*f*, 246, 254, 266, 269, 271
Musculus supinator **32,** 33*f*, 38*f*, 40*f*, **87,** 89*f*, 90*f*, 143*f*, **177**, 177*f*–180*f*, 187*f*, 189*f*, 190*f*
Musculus supraspinatus 15*f*, 17*f*, 18*f*, 20*f*, 21*f*, **28,** 69*f*, 70*f*, 71*f*, 75*f*, **76,** 79*f*, 80*f*, 142*f*–151*f*, 153*f*–155*f*, **170**, 215, 219, 221, 221*f*, 222, 267, 268
Musculus tensor fasciae antebrachialis 13*f*–15*f*, 19*f*, 20*f*, **29,** 66*f*, 69*f*, 70*f*, 72*f*–76*f*, 80*f*, **85**, 139
Musculus tensor propatagii 92*f*, **113**, 201
Musculus teres major 13*f*–15*f*, 17*f*, 18*f*, 22*f*, **23,** 24*f*–27*f*, 69*f*, 70*f*, 72*f*–74*f*, **74,** 75*f*–84*f*, 86*f*, 140*f*–147*f*, 149*f*, 152*f*, 153*f*, **165**, 166*f*, 167*f*, 217*f*, 219, 250*f*, 254, 268, 271
Musculus teres minor 15*f*, 17*f*, 18*f*, **23,** 24*f*, 70*f*, **73,** 75*f*, 144*f*, 146*f*, **164**
Musculus triceps brachii 13*f*–15*f*, 17*f*, 20*f*, 22*f*, **30,** 66*f*, 67*f*, 69*f*, 70*f*, **85,** 140*f*–146*f*, 150*f*, 165*f*, **174**, 254
Musculus triceps brachii caput accessorium 24*f*, 26*f*–28*f*, **30,** 32*f*, 36*f*, 37*f*, 72*f*–74*f*, 77*f*, 80*f*–82*f*, **85,** 86*f*, **174**
Musculus triceps brachii caput laterale 18*f*, 24*f*, 25*f*, **30,** 75*f*, 76*f*, **85,** 147*f*, 148*f*, **174**
Musculus triceps brachii caput longum 18*f*, 24*f*–26*f*, 28*f*, **30,** 75*f*, 76*f*, **85,** 86*f*, 147*f*, 148*f*, **174**, 254
Musculus triceps brachii caput mediale 24*f*–28*f*, **30,** 32*f*, 33*f*, 36*f*, 37*f*, 72*f*–74*f*, 77*f*, 80*f*–82*f*, **85,** 86*f*, 147*f*, **174**
Musculus uropatagialis **202**

N

Neopatagium **247**, 248, 248*f*, 249, 250*f*, 251, 251*f*, 252*f*, 254, 255, 265, 266, 268, 271, 277, 277*n*, 286, 286*n*, 288, 289

O

Olecranon 5*f*, 55*f*, 56, 124*f*, 126, 270*f*, 271
Os sesamoideum musculi tricipitis brachii (sesamoid bone of *M. triceps brachii*) 11*f*, 124*f*, 152*f*, 174, 178*f*, 189*f*
Ossa metacarpalia (metacarpals) 8*f*, 57, 58*f*, 128*f*, 135, 136*f*, 269
Ossa sesamoidea phalangis (sesamoid bones of digits) 7*f*, 8*f*, 12, 46*f*, 48*f*, 58*f*, 63, 64, 110*f*, 111*f*

P

Palatopatagium, see also *plagiopatagium* 52
Phalanges digitorum (phalanges) 8, 8*f*,*t*, 57, 58*f*, 128, 128*f*, 137
Pisiforme 6, **7***f*,*t*, 8*f*, 43*f*, 44*f*, 46*f*, 56, 57*f*, 58*f*, 109*f*, 110*f*, 111*f*, 126, 127*f*, 195*f*
Plagiopatagium **52,** 52*f*, 113, **117**, 201, 215, 219, 220, 220*n*,*f*, 221, 225, 243–245, 247, 249, 254, 255, 265, 268, 276, 277, 277*n*, 286
Prepollex 7*f*, 8*f*,*t*, 43*f*, 44*f*, 46*f*, 48*f*, 56, 57, 57*f*, 58*f*, 95*f*, 109*f*–111*f*, 127, 127*f*, 134*f*, 182*f*, 193*f*–195*f*
Processus alaris costae sternalis 1 **117**, 119*f*, 158*f*, 268

Processus coracoideus (coracoid process) 2*f*, 3, 3*f*, 29*f*, 53, 53*f*, 54*f*, 59*f*, 118*f*, 120*f*, 121, 121*f*, 122*f*
Processus cranialis sterni (cranial process of sternum) 59, 59*n*,*f*
Processus jugularis (jugular process) 140*f*
Processus mastoideus (mastoid process) 140*f*
Processus xiphoideus (xiphoid process) 118*f*, 119*f*
Propatagium **52,** 52*f*, 113, **117**, 201, 209, 220, 221, 221*f*–223*f*, 225, 245, 265, 266, 268, 277, 289
Pyramidale, see also *cuneiforme* 7*t*

R
Radiale + *intermedium* + *centrale*, see also *scaphocentralolunatum* 7*t*
Radiale + *intermedium*, see also *scapholunatum* 7*t*
Radiale, see also *scaphoideum* 6, 7*t*, 56
Radius 5*f*, **6**, 8*f*, 55*f*, **56**, 57*f*, 58*f*, 124*f*, **126**, 134*f*, 193*f*, 245, 246, 270*f*, 271
Retinaculum extensorum 32*f*, 33, **33***n*, 34*f*, 92*f*, **182***n*,*f*
Retinaculum flexorum 193*f*
Retinaculum flexorum medium 43*f*, **47***n*, **98***n*, 106*f*
Retinaculum flexorum profundum **39***n*, 43*f*, **98***n*, 107*f*
Retinaculum flexorum superficiale **36***n*, 42*f*, **104***n*

S
Scaphocentralolunatum **7***t*, 56, 57*f*, 58*f*, 63, 95*f*, 110*f*, 126, 127*f*, 133, 134*f*, 135, 182*f*, 195*f*
Scaphoideum 7, 7*t*, 8, 56, 127
Scapholunatum 6, **7***f*,*t*, 43*f*, 44*f*, 46*f*, 48*f*
Scapula **2**, 2*f*, 3*f*, **53**, 53*f*, 54*f*, 59*f*, 118*f*, **119**, 120*f*–122*f*, 214*f*, 224, 234, 236, 237*f*–239*f*, 240, 241, 253, 255, 259, 261, 261*f*, 262, 265, 274, 275, 277, 284
Semilunare, see also *centralolunatum* 57
Spina entepicondyli humeri (styloid process of medial epicondyle) 124, 125*f*
Spina scapulae (scapular spine) 2*f*, 3, 3*f*, 53, 53*f*, 54*f*, 120*f*, 121, 122*f*
Sternum 129*f*, 214*f*, 261*f*

T
Thenar (proximal radial callosity or pad) 36*f*, 37*n*, 42*f*, 91, 91*n*
Tori metacarpea 36*f*
Trapezium 6, **7***f*,*t*, 8, 28*f*, 56, 57*f*, 63, 95*f*, 109*f*–111*f*, 126, 127*f*, 134*f*, 135, 182*f*
Trapezoideum 6, **7***f*,*t*, 56, 57*f*, 95*f*, 126, 127*f*, 134*f*, 135, 182*f*
Triquetrum, see also *cuneiforme* 7*t*
Trochlea humeri, see also *condylus medialis humeri* xix, 55, 62, 126
Tuberculum majus humeri (greater tubercle) 4, 5*f*, 6*f*, 55, 55*f*, 56*f*, 76*f*, 123, 124*f*, 125*f*, 132, 234, 242, 269, 270*f*
Tuberculum minus humeri (lesser tubercle) 4, 5*f*, 6*f*, 55, 55*f*, 56*f*, 123, 124*f*, 125*f*, 132, 269
Tuberculum supraglenoidale scapulae 3, 54, 54*f*, 120*f*, 121, 122*f*

U
Ulna 5*f*, **6**, 8*f*, 55*f*, **56**, 57*f*, 58*f*, 124*f*, **126**, 270*f*, 271, 272
Ulnare, see also cuneiforme 7*t*
Unciforme, see also *uncinatum* 7*t*
Uncinatum 6, **7***f*,*t*, 56, 57*f*, 58*f*, 95*f*, 109*f*–111*f*, 126, 127*f*, 134*f*, 135, 182*f*
Uropatagium **52,** 52*f*, 113, **117**, 202, 215, 225, 227, 244, 245, 277

V
Vaginae fibrosae digitorum 41*n*, 58*f*, 103*n*, 105*f*
Vertebrae cervicales (cervical vertebrae) 59*f*, 119*f*
Vertebrae lumbales (lumbar vertebrae) 118*f*
Vertebrae thoracales (thoracic vertebrae) 59*f*, 118*f*