Proceedings of the Zoological Institute RAS Vol. 317, No. 3, 2013, pp. 226–245



УДК 599.324;591.473

# COMPARATIVE ANALYSIS OF FORELIMB MUSCULATURE IN LAONASTES AENIGMAMUS (RODENTIA: DIATOMYIDAE)

## P.P. Gambaryan, O.V. Zherebtsova and A.A. Perepelova

Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: hedgol@yandex.ru

## ABSTRACT

The forelimb musculature of the relict rodent *Laonastes aenigmamus* Jenkins et al., 2005 (Diatomyidae) was studied for the first time. *Ctenodactylus gundi* and *Chinchilla lanigera* were also first included in the morphological analysis for comparative purposes. These species belong to different infraorders, Ctenodactylomorphi and Hystricognathi, the members of which could be closely related to *Laonastes* according to available hypotheses. The peculiar features of the examined muscles, like the more primitive topography of the m. rhomboideus, the unusual insertion of the m. endopectoralis and absence of the m. flexor digitorum sublimis, were revealed in *Laonastes*. In addition, a number of common characters in the structure of the locomotor musculature were also observed in *Laonastes* and *Ctenodactylus*: a single undifferentiated condition of the m. trapezius; the muscular origin of the m. sternomastoideus; the unusual attachments of the m. latissimus dorsi and the unique origin of the m. dorsoepitrochlearis unnoted in other rodents. The majority of these features are probably indicative of more archaic organisation. The obtained results support the hypothesis of the close affinity between Diatomyidae and Ctenodactylidae proposed on the basis of the molecular-genetic and some morphological data.

Key words: Chinchilla lanigera, Ctenodactylus gundi, forelimb musculature, Laonastes aenigmamus, rodents

# СРАВНИТЕЛЬНЫЙ АНАЛИЗ МУСКУЛАТУРЫ ПЕРЕДНИХ КОНЕЧНОСТЕЙ LAONASTES AENIGMAMUS (RODENTIA: DIATOMYIDAE)

## П.П. Гамбарян, О.В. Жеребцова и А.А. Перепелова

Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия; e-mail: hedgol@yandex.ru

### РЕЗЮМЕ

Впервые проведено изучение мускулатуры передних конечностей реликтового грызуна *Laonastes aenigmamus* Jenkins et al., 2005 (Diatomyidae). В сравнительный морфологический анализ также впервые включены *Ctenodactylus gundi* и *Chinchilla lanigera*. Эти виды относятся к разным инфраотрядам, Ctenodactylomorphi and Hystricognathi, представители которых, согласно имеющимся гипотезам, могли состоять в близком родстве с *Laonastes*. Выявлены такие специфические особенности изучаемых мышц у *Laonastes* как более примитивная топография m. rhomboideus, необычное окончание m. endopectoralis и отсутствие m. flexor digitorum sublimis. Кроме того, обнаружен ряд общих черт в строении локомоторной мускулатуры у *Laonastes* и *Ctenodactylus*: единое, недифференцированное состояние m. trapezius, мышечное начало m. sternomastoideus, необычное окончание m. endopectoralis и отсутствие m. sternomastoideus, необычное осотояние m. trapezius, мышечное начало m. sternomastoideus, необычное особенностей являются, по-видимому, проявлением более архаичной организации. Полученные результаты поддерживают гипотезу о близком родстве между Diatomyidae and Ctenodactylidae, выдвинутую на основе молекулярно-генетических и некоторых морфологических данных.

Ключевые слова: Chinchilla lanigera, Ctenodactylus gundi, мускулатура передней конечности, Laonastes aenigmamus, грызуны

### **INTRODUCTION**

Laonastes aenigmamus Jenkins et al., 2005 (hereafter Laonastes) is a recently described relict form of rock rats from Laos. The skull of this species differs from that of all other recent rodents by an unusual combination of features which are characteristic both of sciurognathous and hystricognathous rodents (Jenkins et al. 2005). Currently, Laonastes is included in the family Diatomyidae, which together with its sister group, the family Ctenodactylidae, is placed outside infraorder Hystricognathi but within the common clade Ctenochystrica (Dawson et al. 2006; Huchon et al. 2007). The examination of the masticatory apparatus of *Laonastes* also revealed an unusual combination of characters inherent both in sciurognathous and hystricognathous rodents (Hautier and Saksiri 2009).

The forelimb musculature of the relict rodent Laonastes aenigmamus was studied for the first time to reveal its specific features, along with basic characters, that are typical of all Rodentia. *Ctenodactylus* gundi Rothmann, 1776 (hereafter Ctenodactylus) (Ctenodactylidae) and Chinchilla lanigera Bennett, 1829 (hereafter Chinchilla) (Chinchillidae) were also first included in the morphological analysis for comparative purposes. At present these species belong to different infraorders, Ctenodactylomorphi and Hystricognathi (Dieterlen 2005; Woods and Kilpatrick 2005), respectively. The members of the latter could be closely related to Laonastes according to one of the available hypotheses (Jenkins et al. 2005), however according to another hypothesis the origin of the relict rodent was connected with Ctenodactylomorphi (Dawson et al. 2006; Huchon et al. 2007). Besides, Ctenodactylus and Chinchilla, as well as Laonastes, are rock dwelling forms and probably similar to him on their locomotor adaptations. The preference for such habitats is determined by certain conditions: first, there are lots of plants among the rocks that would dry out in open landscapes; second, it is easier to find cover from predators under the rock debris.

For wider comparison, earlier obtained unpublished morphological data on other forms of rodents with different lifestyles and locomotion were also used in this research: more than 40 species of the majority of families of Sciuromorpha and Myomorpha; nearly 10 members of different phyletic lines of the hystricognathous rodents (Hystricognathi). Such a broad comparative analysis is of special interest because it allows us to reveal the general and specific features of *Laonastes* and to find additional criteria for determination of the taxonomic and phylogenetic relationships of the species.

The morphological data obtained will be discussed in relationship to the classification of rodents in the taxonomic review by Don E. Wilson and Dee A.M. Reeder, "Mammals species of the world" (see: Dieterlen 2005; Woods and Kilpatrick 2005).

### MATERIAL AND METHODS

Three species of rodents from the collections of the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint Petersburg) were investigated: the Laotian rock rat, *Laonastes aenigmamus* Jenkins et al., 2005 (n = 2;  $N_{\rm D}$  99491, 99496); the gundi, *Ctenodactylus gundi* Rothmann, 1776 (n = 1;  $N_{\rm D}$  6641); and the long-tailed chinchilla, *Chinchilla lanigera* Bennett, 1829 (n = 2;  $N_{\rm D}$  576 a, b). The adult specimens were preserved in 70° ethanol or 5% formalin. The forelimb musculature was examined using the total preparations with a binocular stereomicroscope *Leica* MZ6.

### RESULTS

The forelimb musculature

Visceral muscles: mm. clavotrapezius, acromiotrapezius, spinotrapezius, sternomastoideus and cleidomastoideus

**Mm. clavo-, acromio- and spinotrapezius** (Figs. 1–4). In *Laonastes* and *Ctenodactylus*, the m. trapezius is presented by a single undifferentiated muscle. Its cranial part as usual m. clavotrapezius originates muscularly in *Laonastes* at the skull on the vertical part of the lambdoid crest (its two vertical parts correspond to the temporal regions), barely extending onto its horizontal part (it corresponds to the occipital region of the skull). In *Ctenodactylus*, the cranial part of the muscle arises by aponeurosis from the middle third of the occipital part of the lambdoid crest. In *Laonastes* and *Ctenodactylus*, the cranial fibres of a single m. trapezius are inserted unusually: on the acromion and metacromion of the scapula.

*Chinchilla* has a typical individual m. clavotrapezius. It originates on the vertical part of the lambdoid crest and inserts onto the dorsal surface of the sternal part of the clavicle. However, the mm. acromiotrapezius and spinotrapezius, like those in *Laonastes* and *Ctenodactylus*, are presented by a single muscle. Its anterior edge arises from the middle of the occipital part of the lambdoid crest.

Further, in all three species investigated, the origin of the mm. acromio-spinotrapezius runs along the midline of the cervix to the spinal processes of the thoracic vertebrae and then, in the form of an aponeurosis, extends at least to the lumbar vertebrae. Here, the origin of the muscle fuses with the external fascia of the dorsal muscles by this means that its caudal border is hard to define.

In *Laonastes, Chinchilla*, and *Ctenodactylus*, the caudal fibres of the original region (from the level of middle of the scapula vertebral border until the caudal edge of the origin) converge and are inserted into the tuber of the scapulae spine. Apparently, this caudal part of a single muscle is homologous to the m. spinotrapezius. At the same time, in *Laonastes* and *Ctenodactylus*, the rest of a single mm. acromio-spinotrapezius inserts on the spine of the scapulae: from its tuber to the metacromion, where the m. atlanto-scapularis inferior also terminates. In *Laonastes*, the part of the most ventral fibres pass over the scapula processes and the external fascia of the m. atlanto-scapularis inferior to the caudal edge of the distal half of the m. spinodeltoideus (Fig. 4).

In *Chinchilla*, the acromial part of the mm. acromio-spinotrapezius inserts on the metacromion and then move to the acromion, whereas the insertion of the m. atlantoscapularis inferior envelops the muscle from the surface and from the dip.

**Mm. sterno- and cleidomastoideus** (Figs. 1–4). In *Laonastes*, the m. sternomastoideus originates muscularly on the skull at the base of the mastoid process over the m. cleidomastoideus which begins on the lambdoid crest by a strong tendon. The m. sternomastoideus is inserted on the front edge of the manubrium sterni; the m. cleidomastoideus terminates on the sternal extremity of the clavicle, covering the front half of its dorsal surface and meeting here the m. subclavius anterior.

In *Ctenodactylus*, a single mm. sternocleidomastoideus originates from the mastoid process muscularly, where the external part of the muscle origin is the m. sternomastoideus and the internal part is the m. cleidomastoideus. The muscle is inserted as in *Laonastes*.

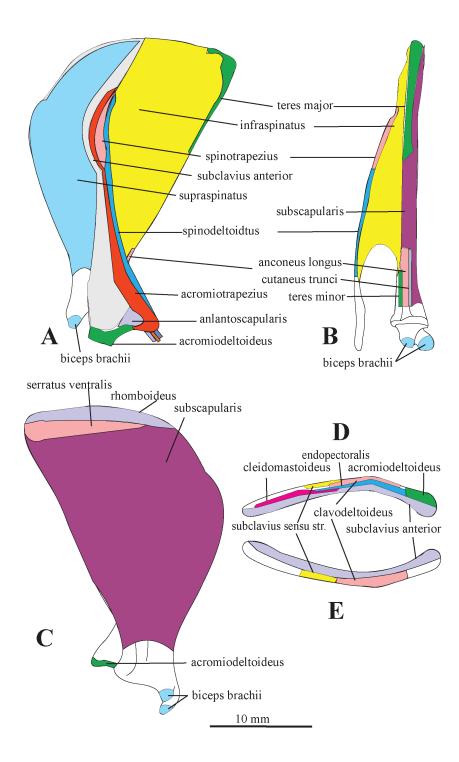
In contrast with the previous two forms, in *Chin-chilla*, the m. sternomastoideus originates on the mastoid process by a strong tendon and terminates on the forward extremity of the manubrium sterni, expanding under the insertion of the m. ectopectoralis. The m. cleidomastoideus originates tendinously on the same process as the m. sternomastoideus but is deeper and more caudal. The muscle belly is located in the enhanced channel formed by the m. sternomastoideus. The m. cleidomastoideus inserts on the craniodorsal surface of the sternal extremity of the clavicle.

**Mm. rhomboideus capitis and rhomboideus cer-vitis** (Figs. 1–4). In *Laonastes*, the m. rhomboideus capitis arises from the skull along the horizontal and slightly vertical parts of the lambdoid crest. Then the origin of the muscle discontinuously passes to the midline of the neck and the spinal processes of the first thoracic vertebrae, forming the m. rhomboideus cervitis. Both parts of the muscle terminate on the vertebral border of the scapula but only on its medial surface. That is why the cranial part can be named the m. rhomboideus capitis medialis (Gambaryan 1960).

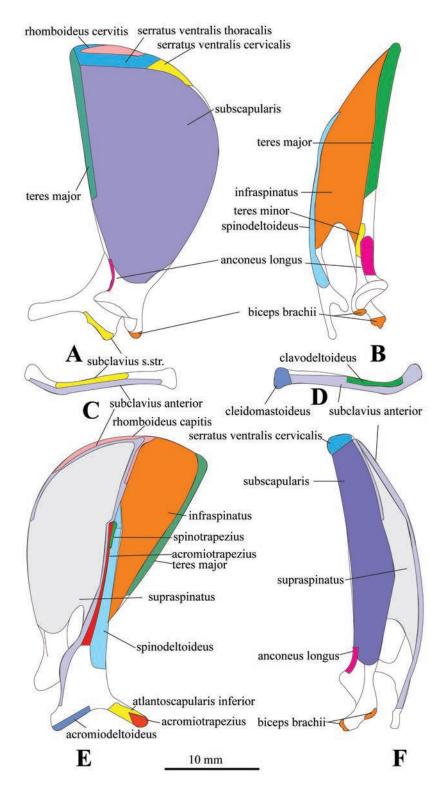
In *Ctenodactylus*, the m. rhomboideus capitis originates muscularly on the lambdoid crest, extending up to the mastoid process. This part of the m. rhomboideus inserts onto the spine of the scapula and on its vertebral border from the lateral side. Therefore, the cranial part of the muscle should be named m. rhomboideus capitis lateralis. The origin of the m. rhomboideus cervitis without interruption passes along the midline of neck up to the spinal processes of the first thoracic vertebrae. This part of the m. rhomboideus inserts on the medial side of the vertebral border of the scapula, extending to its caudal corner and along the caudal edge.

In Chinchilla, the m. rhomboideus capitis originates muscularly on the lambdoid crest near its middle part and passes slightly on its vertical part. The muscle terminates on the scapular spine and also on the vertebral border of the scapula from the lateral side, partly moving to the dorsal fascia of the m. infraspinatus. Moreover, the m. rhomboideus capitis covers the medial part of the vertebral border of the scapula, scarcely reaching the caudal insertion of the m. serratus ventralis. In this case the m. rhomboideus cervitis is not directly connected to the m. rhomboideus capitis, and it originates from the midline of the caudal part of the neck and the spinal processes of the first thoracic vertebrae. This muscle inserts on the whole vertebral border of the scapula from its medial side (Figs. 3, 4).

**M. latissimus dorsi** (Figs. 5–7). In *Laonastes,* the muscle originates muscularly from the spinal



**Fig. 1.** *Laonastes aenigmamus.* Muscles insertion on the scapula (left) (A–C) and clavicle (left) (D, E) in lateral (A), caudal (B, D), medial (C) and cranial (E) view.



**Fig. 2.** *Ctenodactylus gundi.* Muscles insertion on the scapula (left) (A, B, E, F) and clavicle (left) (C, D) in medial (A), caudal (B, D), cranial (C, F) and lateral (E) view.

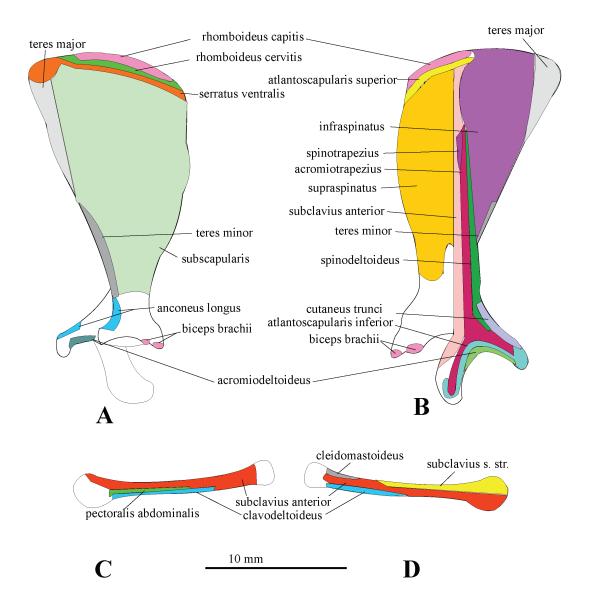


Fig. 3. Chinchilla lanigera. Muscles insertion on the scapula (left) (A, B) and clavicle (left) (C, D) in medial (A), lateral (B), cranial (C) and caudal (D) view.

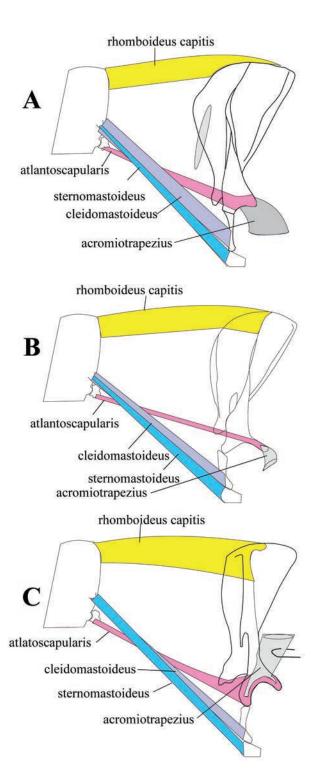


Fig. 4. Scheme of the muscles insertion on the skull, scapula, clavicle and sternum in: A – *Laonastes aenigmamus*; B – *Ctenodactylus* gundi; C – *Chinchilla lanigera*.

processes of thoracic vertebrae 5–9 and also traces as an aponeurosis until the spinal process of thoracic vertebra 13. Then, the origin of the muscle transfers to the lumbar fascia, where its caudal border is hard to define. Additionally, there are attachments on the two last ribs, by the muscular denses extending for more than dorsal half of the length of the ribs. The m. latissimus dorsi has different insertion. The main part of the muscle fibres locating lateral to the m. teres major fuses with its terminal tendon. Another part of the m. latissimus dorsi forms the own tendon which passes around the tendon of the m. teres major and lies deeper than the m. biceps brachii, inserting along the proximal half of the crista tuberculi majoris (Fig. 5).

In *Ctenodactylus*, the m. latissimus dorsi originates by an aponeurosis from the spinal processes of thoracic vertebrae 5-13 and then passes on the lumbar fascia. The muscle is inserted differently. The first end, as a thin aponeurosis goes under the m. biceps brachii and inserts onto the base of the crista tuberculi majoris, medially to the attachment of the m. pectoralis abdominalis. In this region, the termination of the m. cutaneus trunci is also located. The second ending of the m. latissimus dorsi connects to the terminal tendon of the m. teres major, spreading along its surface for two thirds of the width of the tendon. Here, the m. latissimus dorsi fuses with the second end of the m. cutaneus trunci, covering the whole lateral surface of the m. teres major (Fig. 6).

In *Chinchilla*, the m. latissimus dorsi originates by an aponeurosis from the spinal processes of thoracic vertebrae 10–13 and then begins inside the aponeurosis common with the m. spinotrapezius. Moreover, the muscle originates from the external fascia of the m. serratus dorsalis, extending for half the length of its muscular denses. There is no attachment on the ribs. The m. latissimus dorsi inserts by a single aponeurosis with the m. teres major on the crista tuberculi minoris of the humerus (Fig. 7).

**M.** dorsoepitrochlearis (Figs 8, 9). In *Laonastes* and *Ctenodactylus*, it originates on the external fascia of the cranial part of insertion of the m. cutaneus trunci. In one sample of *Laonastes*, the most ventral muscle fibres transverse the termination of the m. cutaneus trunci, inserting onto the tendon of the m. latissimus dorsi. The m. dorsoepitrochlearis inserts by an aponeurosis onto the surface of the m. anconeus longus and tendinously on the tip of the olecranon, extending on the proximal quarter of superficial fascia of the forearm.

In *Chinchilla*, the m. dorsoepitrochlearis originates from the external fascia of the m. latissimus dorsi and goes to the distal part of the olecranon and also to fascia of the forearm.

**M. ectopectoralis** (Figs. 5, 6). In *Laonastes*, it originates muscularly along the whole sternum until its last segment. From here, the muscle passes to the ventral midline of the neck, covering the insertion of the m. sternomastoideus and tensely fusing with its external fascia. The anterior part of the m. ectopectoralis inserts on the tip of the crista tuberculi major of the humerus whereas the insertion of its posterior part extends along the crest more proximally.

In *Ctenodactylus*, the muscle originates on the anterior edge of the manubrium sterni, extending caudally along the midline of the manubrium and sternum until the insertion of the m. cutaneus trunci. The latter is inserted on the sternum, beginning from the level of the first quarter of the processus xiphoideus, and then continues more caudally along the midline of the belly. The m. ectopectoralis inserts by an aponeurosis, passing into a muscular insertion on the distal part of the crista tuberculi majoris, some proximally from its tip and almost to the middle of the crest length (Fig. 6).

In *Chinchilla*, it originates on the small area before the front part of the manubrium sterni, extending up to the middle of the xiphoid cartilage. The anterior part of the muscle inserts on the distal region of the crista tuberculi major; the posterior part passes under the anterior one and inserts along the crest more proximally. Meanwhile, the whole insertion of the m. ectopectoralis is covered by the m. clavodeltoideus.

**M.** endopectoralis (Figs. 5, 6). In *Laonastes*, it originates on the sternum, from the level of the third costal cartilage and up to the whole xiphoid process and scapular widening of the sternum. The muscle inserts on the middle part of the crista tuberculi majoris, extending along it proximally until the ligamentum transversus. Along this tendon, the insertion of the m. endopectoralis continues to the tuberculum minus and its crista, passing also to the scapular extremity of the clavicula (Figs. 1, 5).

In *Ctenodactylus*, the muscle originates nearly from the first quarter of the processus xiphoideus and up to its end, not occupying the caudal edge of its widening. The muscle passes to the humerus, and inserts on it deeper than the m. ectopectoralis along the medial side of the crista tuberculi majoris. Extending proximally, the m. endopectoralis passes over the tendon of the m. biceps brachii and also inserts on the tuberculum minus of the humerus (Fig. 6).

In *Chinchilla*, it originates on the sternum from the level of the 4th sternebra and up to the base of the xiphoid cartilage. The caudal fibres of the muscle are covered by the m. pectoralis abdominalis. The m. endopectoralis inserts on the tuberculum minus of the humerus.

**M. pectoralis abdominalis** (Figs. 3, 5, 6). In *La*onastes, the muscle originates from the external fascia of the m. obliquus abdominis externus at the level of the scapular widening of xiphoid process, and then the muscle extends like a fan to costal cartilages 7–8. The m. pectoralis abdominalis inserts deeper than the m. endopectoralis on the crista tuberculi majoris, approximately in the middle of its broadening, and then the muscle passes to the crista tuberculi minoris, coming up to the distal half of the tuberculum minus.

In *Ctenodactylus*, there are two parts of the m. pectoralis abdominalis: the pars superficialis and the pars profundus. The first of them originates by a wide fan over the m. cutaneus trunci, reaching the level of the middle of false costal cartilages; this part inserts on the humerus, fusing with the deeper part. The latter originates from the level of the middle of the m. endopectoralis origin, covering it but not inserting on it. Then, the muscle extends on the anterior part of the belly white line under the m. cutaneus trunci. From this spacious original region, both parts of the muscle merge, and come to the humerus, inserting on the crista tuberculi majoris. Here, they pass proximally over the tendon of the m. biceps brachii, attaching on the tuberculum minus medially to the insertion of the m. endopectoralis. The area of their insertion overlaps distally with the aponeurosis of the second termination of the m. latissimus dorsi.

In *Chinchilla*, m. pectoralis abdominalis originates from the xiphoid cartilage of the sternum and from the white line of the belly. The muscle inserts by a narrow aponeurosis on the middle of the ventral surface of the clavicle, laterally meeting the insertion of the m. cutaneus trunci (Fig. 3).

**M.** subclavius s. str. In *Laonastes*, this muscle originates on the base of the first rib; it inserts under the m. endopectoralis on the middle part of the clavicle's dorsal surface, moving to its dorsal side (Fig. 1).

In *Ctenodactylus*, the m. subclavius s. str. originates on the lateral part of the front of the manubrium sterni; it inserts on the dorsal side of the clavicle's sternal extremity (Fig. 2).

In *Chinchilla*, the muscle originates on the anterior surface of the costal cartilage of the first rib and its base; it inserts onto the dorsal surface of the clavicle, departing from its sternal extremity for a third of its length (Fig. 3).

**M. subclavius anterior.** In *Laonastes*, the muscle originates muscularly from the whole external surface of the acromion and further along the spine of the scapula, transferring to its vertebral border and the proximal third of its anterior edge. The muscle inserts on the whole ventral surface of both (ventral and dorsal) surfaces of the clavicle (Fig. 1).

In *Ctenodactylus*, the m. subclavius anterior originates from the acromial process and from the anterior surface of the spine of the scapula, passing to its vertebral border deeper than the m. rhomboideus capitis. The muscle inserts on the ventral surface of the clavicle and also on its dorsal side, meeting there with m. subclavius s. str. (Fig. 2). The mm. subclavius s. str. and subclavius anterior have different innervations: the first is accompanied by the n. subscapularis and the second one – by the n. supraspinatus.

In *Chinchilla*, the muscle originates on the external fascia of the m. supraspinatus, departing from its proximal attachment, and also on the anterior edge of the scapular spine up to the acromial process. The muscle inserts on the ventral surface of the clavicle and passes on its dorsal side, meeting there with the m. subclavius s. str. The insertion of the m. subclavius anterior extends from the scapular extremity of the clavicle for more than half of its length.

**M.** serratus ventralis. In *Laonastes*, the origin of this muscle has five muscular denses on the 4–8th ribs (Fig. 1). There are no attachments on the second and third ribs. On the first rib, the muscular fibres originate from its tuberculum. Thus, this muscular dens can be related to cervical denses that originate medially to the m. scalenus from the transverse-costal processes of the last six cervical vertebrae. The muscle inserts on the medial surface of the scapula's vertebral border.

In *Ctenodactylus*, the m. serratus ventralis originates by two portions. The first presents as six muscular denses extending from the transversecostal processes of the last six cervical vertebrae. The denses from the first two ribs coincide in their fibre direction with the cervical ones. There are no attachments on the 3rd and 4th ribs. The second portion consists of six denses from the 5th to the 10th ribs. The muscle inserts on the medial side of the scapula's vertebral border, slightly beneath the attachment of the m. rhomboideus (Fig. 2). The cervical portion occupies nearly the whole length of the border, and the costal portion inserts near the caudal corner of the scapula.

In *Chinchilla*, the m. serratus ventralis originates as muscular denses on five ribs, from the 5th to the 9th (Fig. 3). The insertion of the muscle is the same as in the two previous forms.

**M.** atlantoscapularis (Figs. 1–4). In *Laonastes*, the muscle originates from the ventral tuberculum of the atlant and inserts on the metacromial process of the scapula under the attachment of the m. acromiotrapezius. There is one more muscular dens from the ventral edge of the muscle that passes under the m. acromiotrapezius to the distal half of the anterior border of the m. spinodeltoideus.

In *Ctenodactylus* and *Chinchilla*, the origin of the m. atlantoscapularis is the same as in *Laonastes*, but the insertion of the muscle is along the spine of the scapula from its tuber to the metacromial process.

**M. acromiodeltoideus.** In *Laonastes*, this muscle originates from the distal edge of the acromial process of the scapula, passing slightly to the dorsal surface of the clavicle, but there is no attachment on the metacromion (Fig. 1). The muscle inserts on the crista tuberculi majoris (Fig. 5).

In *Ctenodactylus*, the origin of this muscle is the same as in *Laonastes*. The m. acromiodeltoideus inserts together with the m. clavodeltoideus on the crista tuberculi majoris, slightly laterally and distally to the insertion of the m. ectopectoralis (Fig. 6).

In *Chinchilla*, the muscle originates from the caudodistal edge of the acromial process of the scapula and inserts on the crista tuberculi majoris (Fig. 3). The initial and final tendinous mirrors are on the external and internal surfaces of the muscle for a third of its belly length.

**M. clavodeltoideus.** In *Laonastes, Ctenodactylus* and *Chinchilla*, this muscle originates from the dorsal surface of the clavicle and inserts on the medial side of the crista tuberculi majoris (Figs. 1–3, 5–7).

**M.** spinodeltoideus. In three species studied, this muscle originates from the posterior edge of the scapular spine on the level of its tuber, extending up to the distal end of the metacromial process. The muscle passes under the m. acromiodeltoideus and m. clavodeltoideus, and it inserts by an aponeurosis on the proximal part of the crista tuberculi majoris (Figs. 1–3, 5–7).

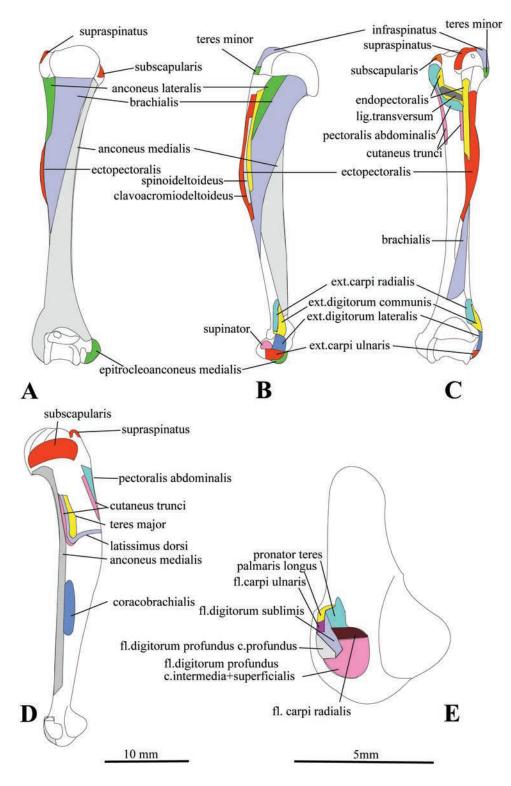
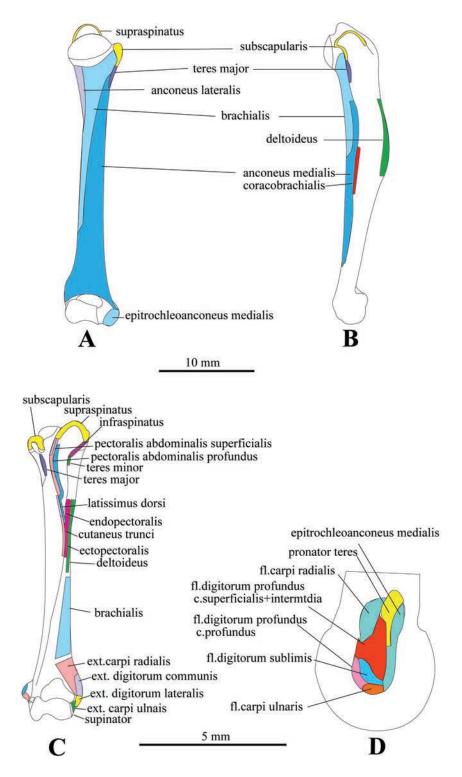


Fig. 5. Laonastes aenigmamus. Muscles insertion on the humerus (left) in volar (A), lateral (B), dorsal(C), medial (D) view and on its medial epicondile from the medial side (E). Abbreviations: c - caput; ext – extensor; fl – flexor; lig – ligamentum.



**Fig. 6.** *Ctenodactylus gundi*. Muscles insertion on the humerus (left) in volar (A), medial (B), dorsal (C) view and on its medial epicondile from the medial side (D). Abbreviations: c - caput; ext - extensor; fl - flexor.

236

**M.** supraspinatus (Figs. 1–3). In *Laonastes, Ctenodactylus* and *Chinchilla,* the muscle originates from nearly the whole surface of the fossa supraspinatus of the scapula and from the anterior surface of its spine. The anterior border of the muscle extends for the limits of the fossa supraspinatus, having here a common aponeurosis with the m. subscapularis. The m. supraspinatus inserts on the tip of the crista tuberculi majoris (Figs. 5–7).

**M. infraspinatus** (Figs. 1–3). In *Laonastes, Ctenodactylus* and *Chinchilla*, this muscle originates from the fossa infraspinatus and from the caudal surface of the scapular spine. The muscle inserts along the caudal edge of the tuberculum minus of the humerus, just distally to the insertion of the m. supraspinatus (Figs. 5–7).

**M.** subscapularis (Figs. 1–3). In *Laonastes, Ctenodactylus* and *Chinchilla*, this muscle originates from the medial surface of the scapula by a specific fascia, out of which the muscular fibres continue to three internal tendons, converging into a final aponeurosis. In the region of the scapular vertebral border, this muscle is slightly displaced by the insertion of the mm. rhomboideus and the m. serratus ventralis. The m. subscapularis inserts on the tuberculum minus of the humerus (Figs. 5–7).

**M. teres major**. In *Laonastes* and *Ctenodactylus*, the muscle originates from the lateral surface of the caudal corner of the scapula, from the caudal edge for a dorsal third of its length and also from the external fascias of the m. infraspinatus and m. subscapularis (Figs. 1, 2). The muscle inserts by the tendon on the crista tuberculi minoris (Figs. 5, 6). The final tendon transfers proximally into a tendinous mirror, extending for half of the muscle length. First the tendon of the m. latissimus dorsi reach the distal end of the tendon of the m. teres major.

In *Chinchilla*, the m. teres major originates from the lateral surface of the caudal corner of the scapula and from the caudal sides of the mm. infraspinatus and subscapularis (Fig. 3). The muscle inserts on the crista tuberculi minoris by a combined aponeurosis with the m. latissimus dorsi (Fig. 7). From the final aponeurosis, the tendinous mirror extends for a third of the muscle length.

**M. teres minor** (Figs. 1–3, 5–7). In *Laonastes, Ctenodactylus* and *Chinchilla,* the muscle originates tendinously and muscularly from the distal half of the caudal border of the scapula; it inserts on the

tuberculum major of the humerus, just distally to the insertion of the m. infraspinatus.

**M.** coracobrachialis. In *Laonastes, Ctenodac-tylus* and *Chinchilla*, the muscle originates from the internal surface of the coracoidal head of the m. biceps brachii. In *Laonastes* and *Ctenodactylus*, as the m. coracobrachialis intermedius the muscle inserts on the middle of the medial labium of the humerus, medially to the tendon of the m. teres major (Figs. 5, 6). However, *Chinchilla* has two heads of this muscle, mm. coracobrachialis brevis and longus (Fig. 7). First of them passes under the terminal tendon of the m. teres major and inserts on the humerus laterally to the latter. M. coracobrachialis longus terminates on the distal part of the medial labium of the humerus.

**M.** anconeus longus. In *Laonastes*, this muscle originates from the distal quarter of the scapular caudal border and inserts on the tip of the olecranon (Figs. 1, 8).

In *Ctenodactylus*, this muscle has dual origin. The first one is medial, as a strong aponeurosis, transforming in a tendinous mirror at the distal part of the caudal border of the scapula (Fig. 2). The second one is muscular, and it is situated laterally to the first. On the medial surface the muscular origin of the muscle transfers into the tendinous mirror, extending for half of the belly's length. A wide aponeurosis extends also proximally from the final tendon. There are muscle fibres among these two formations. The m. anconeus longus inserts by the same way as in *Laonastes* (Fig. 9).

In *Chinchilla*, the muscle originates from the whole caudal edge of the scapula below its corner (Fig. 3). Moreover, a strong tendon from the internal surface of the metacromial process fuses with the lateral surface of the muscle's head. On the medial surface of the muscle, the original tendon transfers into the mirror extending for a third of the belly's length. The second tendinous mirror passes from the terminal tendon along its ventral surface, penetrating into the muscle's belly for the 2/3 third of its length. The m. anconeus longus inserts to the tip of the olecranon and its medial labium.

**M. anconeus lateralis** (Figs. 5–9). In *Laonastes, Ctenodactylus* and *Chinchilla*, this muscle originates muscularly from the base of the tuberculum major of the humerus. Then, the muscle transforms into a thin aponeurosis. The latter can be observed up to the distal part of the crista tuberculi majoris, covering the original tendon of the m. brachialis. The muscle

inserts by aponeurosis from the tip to the base of the olecranon.

**M. anconeus medialis.** In *Laonastes*, the muscle originates laterally from the insertion of final tendon of the m. teres major, reaching the distal edge of the humerus caput. Further, the muscle origin passes on the volar surface of the humerus (Fig. 5).

In *Ctenodactylus* and *Chinchilla*, the m. anconeus medialis originates from the medial labium of the humerus slightly below its caput because the muscle is displaced by origin of the m. brachialis (Figs. 6, 7).

In *Laonastes, Ctenodactylus* and *Chinchilla,* m. anconeus medialis inserts on the cranial surface of the olecranon and also on its medial side, where on the tip the muscle attachment is displaced by the insertion of the m. epitrochleoanconeus medialis (Figs. 8, 9).

**M. epitrochleoanconeus medialis** (Figs. 5–9). In *Laonastes, Ctenodactylus* and *Chinchilla*, the muscle originates from the medial epicondyle of the humerus and inserts on the medial side of the olecranon tip.

**M. epitrochleoanconeus lateralis.** In *Ctenodactylus*, this muscle originates from the dorsal surface of the lateral epicondyle and inserts on the olecranon slightly distally of its tip along its lateral side, and also on the proximal third of the caudal border of the ulna (Fig. 9).

In *Laonastes* and *Chinchilla*, the m. epitrochleoanconeus lateralis is not determined.

**M. biceps brachii.** In *Laonastes, Ctenodactylus* and *Chinchilla,* the muscle originates by two tendons from the tuber of the scapula and its coracoidal process (Figs. 1–3). The first tendon lies inside the intertubercular fossa of the humerus, and the second one is situated over the tuberculum minus; from the latter the fibres of the m. coracobrachialis intermedius and of the m. coracobrachialis brevis (in *Chinchilla*) originates. Further, the muscle continues to the forearm, forming two tendons. One of them inserts distally to the terminal tendon of the m. brachialis inside the special groove of the ulna, whereas the other tendon inserts on the special tuberosity of the radius (Figs. 8, 9).

In *Laonastes, Ctenodactylus* and *Chinchilla*, there is a lacertus fibrosus on the dorsal surface of the distal third of the muscle belly passing to the external fascia of the m. pronator teres.

**M. brachialis.** In *Laonastes*, this muscle originates from the volar surface of the humerus and from the medial border of its caput (Fig. 5). In *Ctenodactylus* and *Chinchilla*, the proximal part of the muscle origin

slightly removes the attachment of the m. anconeus medialis (Figs. 6, 7). Then, the m. brachialis runs distally, passing from the volar surface of the humerus to the dorsal one, and further extends to the forearm.

In *Laonastes* and *Ctenodactylus*, the m. brachialis inserts by two endings: the first of them is on the radius, near and proximally to the tendon of the m. biceps brachii, and the second one together with the m. biceps brachii is near the elbow joint in the special fossa of the ulna (Figs. 8, 9).

In *Chinchilla*, the muscle inserts by the tendon near the elbow joint, and muscularly slightly higher than the first insertion. The tendon of the muscle fuses with the final tendon of the m. biceps brachii in the special fossa of the ulna, and there is an aponeurosis, going from this termination inside the muscle for a third of its length.

**M.** supinator. In *Laonastes, Ctenodactylus* and *Chinchilla,* this muscle originates from the base of the lateral epicondyle of the humerus deeper than the other muscles, and it inserts on the lateral and dorsal surfaces of the radius (Figs. 5–9).

**M. pronator teres.** In *Laonastes, Ctenodactylus* and *Chinchilla*, the muscle originates most proximally on the crest of the medial epicondyle of the humerus, and it inserts onto the medio-dorsal surface of the radius medially to the insertion of the m. supinator (Figs. 5–9). Additionally, the muscle has tendinous mirrors on its external and internal surfaces.

**M.** extensor capri radialis. In *Laonastes* and *Ctenodactylus*, the muscle originates from the crest of the lateral epicondyle of the humerus, proximally to the other extensors and deeper than the m. ext. digitorum communis onto the internal surface of the crest (Figs. 5, 6). At the beginning of the final tendon formation, the muscle divides into two branches that penetrate under the tendon of the m. abductor pollicis longus. The terminal tendons of the m. extensor capri radialis insert into special grooves on the medial sides of the proximal ends of the metacarpals II and III. In *Ctenodactylus*, there is an internal aponeurosis, extending from the terminal tendon inside the muscle for a third of its length.

In *Chinchilla* the m. extensor capri radialis also originates from the crest of the lateral epicondyle but deeper and distally to the m. extensor digitorum communis (Fig. 7). The insertion is the same as in *Laonastes* and *Ctenodactylus*.

**M.** extensor digitorum communis. In *Laon*astes, this muscle fuses at its origin with the m.

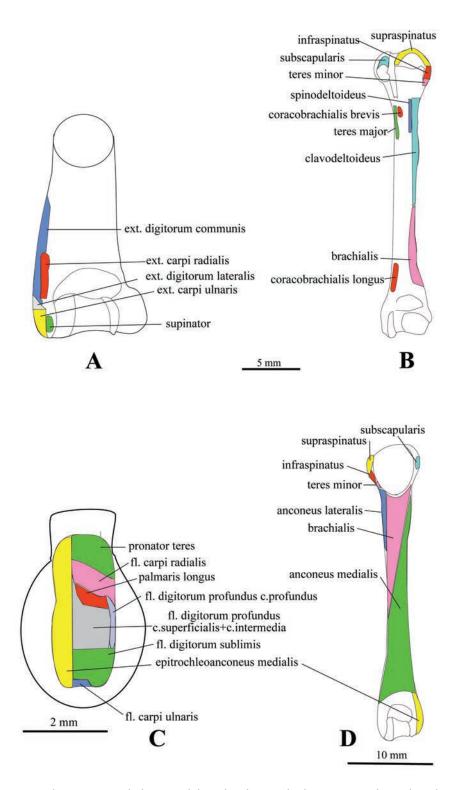
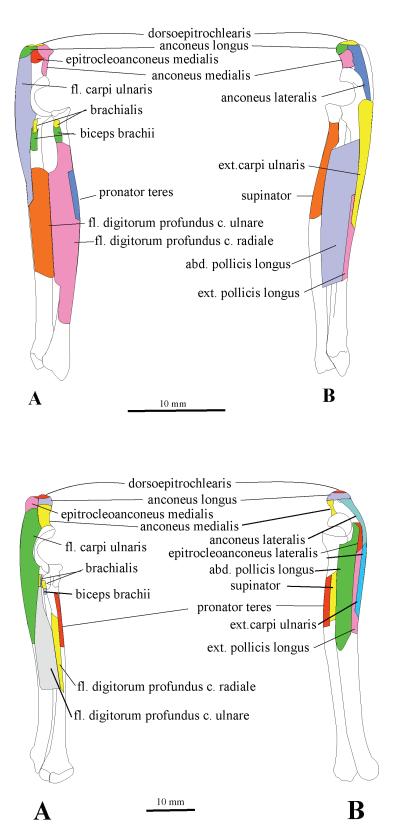
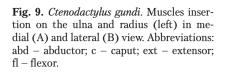


Fig. 7. *Chinchilla lanigera*. Muscles insertion on the humerus (left) in dorsal (B), and volar (D) view and on its lateral epicondile from the ventral side (A) and medial epicondile from the medial side (C). Abbreviations: c - caput; ext – extensor; fl – flexor.



**Fig. 8.** Laonastes aenigmamus. Muscles insertion on the ulna and radius (left) in medial (A) and lateral (B) view. Abbreviations: abd – abductor; c – caput; ext – extensor; fl – flexor.





ext. digitorum lateralis on the proximal part of the lateral epicondyle crest (Fig. 5). Near the middle of the forearm length, the muscles differentiate. At the level of the distal third of the anterbrachium, the m. extensor digitorum communis transforms into four independent tendons, passing between the bones to the manus. The tendons insert onto the proximal ends of the second phalanxes of four lateral digits. At the original region the muscle also takes the muscular fibres from the flat tendon, which goes from the lateral epicondyle to the middle of the ulna, and then from the external fascia of the m. ext. pollicis longus.

In Ctenodactylus, the m. extensor digitorum communis originates from the crest of the lateral epicondyle of the humerus, distally to the insertion of the m. extensor capri radialis (Fig. 6). At the middle of the forearm length, the muscle divides into four tendons, which pass under the transversal ligament connecting both bones of the forearm. Two medial tendons insert on the proximal ends of the second phalanxes of digits II and III. Two lateral tendons at the level of the distal terminations of the metacarpal bones bifurcate onto two branches to the lateral sides of digits IV and V. Before the insertion, all four tendons and their branches fuse strongly with the corresponding sesamoids, lying on the dorsal surfaces of the distal ends of the first phalanxes of digits II-V. From the surfaces of the sesamoids, pairs of ligamentums originate named the ligamentum dosales, which insert to both sides of the unguis phalanxes.

In *Chinchilla*, the m. extensor digitorum communis originates from the crest of the lateral epicondyle, proximally to the other extensors, and it covers the origin of the m. ext. capri radialis (Fig. 7). There is an initial aponeurosis from the dorsal surface of the muscle belly for a third of its length. The m. extensor digitorum communis divides into four tendons at the level of the proximal third of the forearm length. The final tendons of the muscle insert on the proximal ends of the second phalanxes of the four lateral digits.

**M.** extensor digitorum lateralis. In *Laonastes* and *Ctenodactylus*, this muscle originates on the crest of the lateral epicondyle of the humerus (Figs. 5, 6). At the middle of the forearm length it divides into two tendons that insert on the proximal ends of the second phalanxes of two lateral digits. The tendon to digit IV passes under the tendon of the m. extensor digitorum communis, going to digit V.

In *Chinchilla*, the origin of the m. extensor digitorum lateralis is the same as in *Laonastes* and *Cteno*- *dactylus* (Fig. 7). However, the muscle forms a single tendon at the level of the proximal third of the forearm. The latter bifurcates distally and comes to the manus as two tendons within special groove on the ulna. The tendon to digit V passes along its lateral side and fuses with tendon of the m. ext. digitorum communis at the end of the first phalanx. Together, these two tendons insert on the dorso-proximal part of the second phalanx. The tendon to digit IV passes under the tendon of the m. ext. digitorum communis and inserts similarly to the tendon to digit V.

**M. extensor pollicis longus.** In *Laonastes, Ctenodactylus* and *Chinchilla*, this muscle originates muscularly on the posterior edge of the lateral depression on the ulna, caudally to the m. abductor pollicis longus (Figs. 8, 9). The tendon of the muscle passes under the tendon of the m. ext. digitorum communis and divides onto two tendons which pass to digits I and II. Therein, the terminal tendons of the m. extensor pollicis longus insert on the proximal ends of the second phalanx of digit II and the first phalanx of digit I.

**M.** abductor pollicis longus. In *Laonastes*, the muscle originates along the lateral depression of the ulna and the interosseous space; it inserts onto the proximal end of the dorsal surface of the first meta-carpal bone and on the dorsal edge of the praepollex (Fig. 8).

In *Ctenodactylus*, the m. abductor pollicis longus originates from the lateral depression on the ulna, passing to the radius behind the attachment of the m. supinator (Fig. 9). From there, the muscle runs down deeper than the other two extensors of the digits. Further, the m. abd. pollicis longus forms a flat tendon, which covers the final tendons of the m. ext. capri radialis and inserts on the medial side of the proximal end of the metacarpale I.

In *Chinchilla*, this muscle originates very similarly to those of *Laonastes* and *Ctenodactylus*. At the level of the elbow joint, the muscle passes under the humeroulnar ligament. The terminal attachment is the same as in *Laonastes* and *Ctenodactylus*.

**M.** extensor capri ulnaris. In *Laonastes* and *Ctenodactylus*, this muscle has two heads. One of them, caput ulnaris originates from the proximal end of the lateral depression of the ulna near the base of the olecranon and extends along its caudal edge (Figs. 8, 9). The other, humeral caput originates from the latero-distal surface of the lateral epicondyle crest of the humerus (Figs. 5, 6). The final tendon penetrates inside the belly of the m. ext. capri ulnaris for nearly

whole length of the muscle. In both forms, the m. ext. capri ulnaris inserts by a tendon that arises at the level of the middle of the forearm length. The tendon passes through the special sulcus on the distal part of the ulna and inserts onto the carpalia I.

In *Chinchilla*, there is only one humeral head of the m. extensor capri ulnaris, which originates on the most distal end of the lateral epicondyle crest (Fig. 7). The insertion is the same as in *Laonastes* and *Ctenodactylus*.

**M. flexor capri ulnaris.** In *Laonastes* and *Cteno-dactylus*, the muscle also originates by two heads (Figs. 5, 6, 8, 9). The first of them originates from the caudal border of the proximal half of the ulna, meeting here with the attachment of the m. ext. capri ulnaris. The second head originates from the most distal part of the medial epicondyle of the humerus. Both heads fuse, and the muscle inserts by a single tendon on the os pisiforme.

In *Chinchilla*, in contrast with those in *Laonastes* and *Ctenodactylus*, the m. flex. capri ulnaris is very weak (Fig. 7).

**M. flexor capri radialis.** In *Laonastes* and *Ctenodactylus*, the muscle originates from the medial epicondyle of the humerus, distally to the attachment of the m. pronator teres and proximally to the origin of the three heads (profundus and joined intermedius and superficial) of the m. flex. digitorum profundus (Figs. 5, 6). At the middle of the forearm length, the muscle passes into the tendon, which inserts on the medial side of the proximal extremity of metacarpale III.

In *Chinchilla*, the m. flex. carpi radialis originates on the medial epicondyle of the humerus, directly distally to the attachment of the m. pronator teres (Fig. 7). In this region, the muscle is covered by the origin of the m. palmaris longus, which passes over the proximal head of the m. flex. digitorum sublimis. The latter meets up directly with the m. flex. capri radialis. There is an aponeurosis, extending from the initial tendon inside the muscle for two thirds of its belly length. The terminal attachment is the same as in *Laonastes* and *Ctenodactylus*.

**M. palmaris longus.** In *Laonastes*, this muscle originates from the medial epicondyle of the humerus, fusing there with the external fascia of the m. flex. capri radialis for a half of its belly length (Fig. 5). The muscle inserts on the transversal fascia, attaching on the bases of two pulvinus carpale.

In *Ctenodactylus*, the m. palmaris longus is not found.

In *Chinchilla*, the muscle originates from the medial epicondyle of the humerus, merging with the external fascias of the m. flex. digitorum profundus and m. flex. digitorum sublimis (Fig. 7). Further, the terminal tendon is enveloped by a common fascia with the final tendon of the m. extensor capri ulnaris. Before the manus, the tendon of the m. palmaris longus bifurcates and goes to the bases of two pulvinus carpale.

**M. flexor digitorum sublimis.** In *Laonastes*, this muscle is absent.

In *Ctenodactylus*, the m. flex. digitorum sublimis originates from the medial epicondyle of the humerus (Fig. 6). The muscle extends to the manus, where it bifurcates and attaches to the metacarpo-phalangeal sesamoids. The muscle inserts under the tendons of the m. flex. digitorum profundus on the first phalanxes of digits II-IV.

In *Chinchilla*, the m. flex. digitorum sublimis originates from the medial epicondyle of the humerus, embracing from inside and outside the intermedial head of the m. flex. digitorum profundus (Fig. 7). At the middle of the forearm, the muscle transforms into a triple tendon, inserting in the same way as in *Ctenodactylus*.

**M. flexor digitorum profundus.** This muscle has three humeral, one ulnar and one radial heads. In *Laonastes* and *Ctenodactylus*, two of these heads, the caput intermedia and the caput supeficialis fuse together, overlapping the insertion of the m. flex. capri radialis (Figs. 5, 6, 8, 9). The deep head, caput profundus originates by an independent tendon distally to the m. flex. carpi radialis. The caput radiale originates bellow the tuberculum for the final tendon of the m. biceps brachii, and it extends along the internal surface of the radius up to its distal extremity. The ulnar head, the caput ulnare originates from the whole medial surface of the ulna.

In *Chinchilla*, there are five autonomous original heads of the m. flex. digitorum profundus (Fig. 7). Caput superficialis originates on the medial epicondyle of the humerus most medially and directly distally to the origin of the m. palmaris longus. The caput intermedia is situated more laterally, enveloping by the m. palmaris longus from the lateral side. These two heads fuse together and can be distinguished only by the direction of their muscular fibres. Caput profundus is situated on the medial epicondyle deeper than the other heads. There is an aponeurosis, passing along the terminal tendon of the caput profundus inside the muscle belly for half of its length.

The caput ulnare inserts distally onto the olecranon along the anterior edge of the ulna, occupying also the whole medial surface of the ulna. The radial head covers the ulnar surface of the radius, and it soon fuses with the caput ulnare into a single tendon whose mirror continues proximally for a third of the muscle length. All of the heads reach by the individual tendons the distal quarter of the forearm length, and then they fuse into a common tendon, extending to the manus. Therein, the tendon divides into five branches inserting on all the nail phalanxes. The final tendon to the first digit is thin, and it originates from the common tendinous plate above the other tendons.

#### CONCLUSION

It is necessary to note that in Laonastes and Cteno*dactylus*, the m. trapezius is a single undifferentiated muscle, whereas in *Chinchilla*, the m. clavotrapezius is isolated muscle. On this evidence, Laonastes and *Ctenodactylus* are closer to each other. At the same time the representatives of Myomorpha (more than 30 species, investigated by us earlier) have three individual mm. trapezius: clavo-, acromio- and spinotrapezius. According to published before data on Myomorpha in this respect there have been also no exceptions (Howell 1926; Green 1935; Rinker 1954; Gambaryan 1960; Dzerzhinskyi 2005). Similarly, these three isolated muscles are present in more than 10 members of Sciuromorpha and 8 members of Hystricomorpha studied earlier that correlates with the literature data (Parsons 1894; Alezais 1901-1902; Bryant 1945; Olborth 1964). However, among investigated by us Hystricognathi, in one case (Hystrix) the m. trapezius was presented by a single muscle, and in three forms the m. clavotrapezius was not distinct. In this way in hystricognathous rodents, the structure of the m. trapezius can vary from undifferentiated state to three individual muscles.

On the assumption that a single undifferentiated state of the m. trapezius is indicative of its more archaic, close to the initial organisation, the particular structure of this muscle in *Laonastes* and *Ctenodactylus* is apparently the plesiomorphic trait.

*Laonastes* and *Ctenodactylus* are close to each other on such feature as the insertion of the m. trapezius on the metacromial process of the scapula: their acromial fibres are inserted over the attachment of the m. atlantoscapularis inferior. Another structure is observed in the majority of members of the suborders Sciuromorpha and Myomorpha, in which the m. atlantoscapularis inferior covers up the insertion of the m. acromiotrapezius (Howell 1926; Green 1935; Bryant 1945; Rinker 1954; Jouffroy 1971; Dzerzhinskyi 2005). In *Chinchilla*, the intermediate condition is observed since the insertion of the m. atlantoscapularis inferior envelops the attachment of the m. trapezius from the surface and from the dip. In some rodents of Hystricognathi the insertion of the m. acromiotrapezius onto the acromial process does not reach its extremity (Alezais 1901-1902; Gambaryan 1960; Olborth 1964). However, it is not difficult to imagine the possibility of such an extension onto the acromial process up to its distal end by the same manner, as in Laonastes and Ctenodactulus (i.e. over the insertion of the m. atlantoscapularis inferior) or in most rodents (i.e. deeper than the m. atlantoscapularis inferior).

In *Laonastes* and *Ctenodactylus*, the origin of the m. sternomastoideus on the basis of the mastoid process is muscular, while in *Chinchilla*, unlike the two previous forms, this muscle originates there by a strong tendon. For other forms of rodents, the detailed descriptions of this muscle have not been found.

Apparently, it is necessary to consider that the topography of the m. rhomboideus in Laonastes is more primitive than those in *Ctenodactylus* and *Chinchilla*. Primarily the m. rhomboideus originated only from the midline of the neck and, therefore, it was the m. rhomboideus cervicis. Then it began to expand in both cranial and caudal directions. The caudal bundles of the m. rhomboideus radically changed its functional nature. Initially this muscle provided the moving of the scapula forward and holding it in the parasagittal plane. The extension of its origin at the caudal direction caused the development of a new function: moving the vertebral edge of the scapula caudally. The appearance of this function soon led to the complete isolation of the caudal part of the m. rhomboideus and the formation of a new muscle - the m. rhomdoideus thoracitis. Its bundles were not only isolated but also inserted along the whole vertebral edge of the scapula, usually penetrating under the m. rhomboideus cervicis.

The distribution of the m. rhomboideus origin on the head also affected the work of the muscle, because the moving of the scapula forward was associated with a new function – the raising of the head. For many rodents and insectivores that was extremely important. To perform a new function, the displacement of the muscle insertion from the medial to the lateral side of the scapula has become useful. That happened parallel in the marsupials, insectivores and rodents. In *Laonostes*, the distribution of the initial bundles of the m. rhomboideus on the head is already observed, but the transition of the muscle insertion on the lateral surface of the scapula is not noticed. However, the m. rhomboideus thoracitis in all three considered species, like most rodents, has not yet formed.

In *Laonastes*, a quite unique insertion of the m. endopectoralis also takes place. We do not know any case of the transition of the muscle insertion to the clavicle. Usually in the rodents, the m. endopectoralis inserts on the crista tuberculi majoris of the humerus, not extending along it until the tuberculum itself, and certainly not reaching the scapular extremity of the clavicle. In *Laonastes*, the insertion of the m. endopectoralis is not only transferred to the clavicle, but also occupies more than half of its length.

There are many similar features in the origin and insertion of the m. latissimus dorsi in *Laonastes* and *Ctenodactylus*. The difference between them consists only in the fact that in the latter the whole wide origin along the spine is presented by an aponeurosis, while in *Laonastes*, the cranial part of the m. latissimus dorsi originates muscularly. In *Chinchilla*, the origin of the muscle is much narrower and is shifted caudally. At the same time in *Ctenodactylus* and *Chinchilla*, unlike the *Laonastes*, the muscular origins on the ribs are absent. The muscular attachment of the m. latissimus dorsi on the ribs in *Laonastes* is not unique feature and observed in some other rodents.

Usually in rodents, the m. dorsoepitrochlearis originates on the final tendon of the m. latissimus dorsi. In *Chinchilla* and some other members of Hystricognathi studied earlier, the m. dorsoepitrochlearis originates from the external fascia of the m. latissimus dorsi. However in *Laonastes* and *Ctenodactylus*, the m. dorsoepitrochlearis arises on the external fascia of the m. cutaneus trunci that is unique for the rodents and provides additional information to clarify the evolution of this muscle. The close relationship of the m. dorsoepitrochlearis with the m. cutaneus trunci is apparently archaic trait and undoubtedly shows that the idea of the origin of the m. dorsoepitrochlearis from the subcutaneous muscle is quite realistic. In *Laonastes* as well as in *Ctenodactylus*, the m. latissimus dorsi inserts more medially than the m. cutaneus trunci, and the m. dorsoepitrochlearis originates on the external fascia of the latter. At the same time the m. cutaneus trunci inserts by two tips (or tails). The first of them is the aponeurosis, throwing over the m. biceps brachii and inserting on the continuation line of the crista tuberculi majoris. The second tip of the m. cutaneus trunci with the insertions of the m. latissimus dorsi and m. teres major are inserted on the crista tuberculi minoris of the humerus (Figs. 5, 6).

In this way the specific features of the examined muscle complex, like the more primitive topography of the m. rhomboideus, the unusual insertion of the m. endopectoralis and absence of the m. flexor digitorum sublimis, were revealed in Laonastes. In addition, in *Laonastes* and *Ctenodactylus*, a number of common characters in the structure of the locomotor musculature were observed: a single undifferentiated m. trapezius and the features of its insertion on the metacromial process of the scapula; the muscular origin of the m. sternomastoideus; the unusual attachments of the m. latissimus dorsi and the unique origin of the m. dorsoepitrochlearis unnoted in other rodents. The majority of these features are probably indicative of more archaic organisation and the plesiomorphic traits of the examined muscle complex in Laonastes and Ctenodactylus. The similarity in the structure of the locomotor muscles in Laonastes and Ctenodactylus can be apparently considered as manifestation of their common ancestral condition. The obtained results support the hypothesis of the close affinity between Diatomyidae and Ctenodactylidae proposed on the basis of the molecular-genetic and some morphological data (Dawson et al. 2006; Huchon et al. 2007).

#### **ACKNOWLEDGEMENTS**

The authors would like to thank Dr. A.V. Abramov (ZIN) for the opportunity to examine the unique material on *Laonastes aenigmamus* collected in Laos. Special thanks to "American Journal Experts" for the correction of English. We are especially grateful to Dr. E.G. Potapova (Moscow) for reviewing the manuscript and constructive recommendations. The study was supported by the Ministry of Education and Science of the Russian Federation and Russian Foundation for Basic Research (grant No. 10-04-00973).

### REFERENCES

- Alezais H. 1901–1902. Étude anatomique du Cabaye (*Cavia cabaya*). Journal of Anatomy and Physiology, 37: 102–126; 38: 259–275; 624–648.
- Bryant M.D. 1945. Phylogeny of the Nearctic Sciuridae. American Midland Naturalist, 33(2): 257–390.
- Dawson M.R., Marivaux L., Li Ch., Beard K.Ch. and Métais G. 2006. *Laonastes* and the "Lazarus effect" in recent mammals. *Science*, 311: 1456–1458.
- Dieterlen F. 2005. Suborder Hystricomorpha. Infraorder Ctenodactylomorphi. In: D.E. Wilson and D.A.M. Reeder (Eds.). Mammal species of the World. A Taxonomic and Geographic Reference. Vol. 2. Johns Hopkins University Press, Baltimore: 1536–1537.
- Dzerzhinskyi F.Y. 2005. Sravnitel'naya anatomya pozvonochnych zhivotnych [Comparative anatomy of the vertebrate animals]. Aspekt Press, Moscow, 304 p. [In Russian]
- Gambaryan P.P. 1960. Prisposobitel'nye osobennosti organov dvizheniya royushchikh mlekopitayushchikh [Adaptive features of the locomotor organs in fossorial mammals]. Izdatel'stvo AN Armyanskoi SSR, Erevan, 195 p. [In Russian]
- Green E.C. 1935. Anatomy of the rat. Transactions of the American Philosophical Society, New Series, 27: 1–370.
- Hautier L. and Saksiri S. 2009. Masticatory muscle architecture in the Laotian rock rat *Laonastes aenigmamus* (Mammalia, Rodentia): new insights into the evolution of hystricognathy. *Journal of Anatomy*, 215: 401-410.

- Howell A.B. 1926. Anatomy of the wood rat. The Williams and Wilkins, Baltimore, 230 p.
- Huchon D., Chevret P., Jordan U., Kilpatrick C.W., Ranwez V., Jenkins P.D., Brosius J. and Schmitz J. 2007. Multiple molecular evidences for a living mammalian fossil. *Proceedings of the National Academy of Sciences of the USA*, 104: 7495–7499.
- Jenkins P.D., Kilpatrick C.W., Robinson M.F. and Timmins R.J. 2005. Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. Systematics Biodiversity, 2(4): 419–454.
- Jouffroy F.-K. 1971. Mammifères. Musculature des members. Traité de Zoologie. Anatomie, Systématique, Biologie, 16(3): 1–476.
- Olborth H. 1964. Die Anatomie des Bewegungapparates der *Chinchilla* (postcraniales Bereich). *Anatomische Anzeiger*, 114: 302–327.
- Parsons F.G. 1894. On the myology of the sciuromorphine and hystricomorphine rodents. *Proceedings of the Zoological Society, London*: 251–296.
- Rinker G.C. 1954. The comparative mycology of the mammalian genera *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyacus* (Cricetinae), with remarks of their intergeneric relationships. University of Michigan Press, 124 p.
- Woods C.A. and Kilpatrick C.W. 2005. Suborder Hystricomorpha. Infraorder Hystricognathi. In: D.E. Wilson and D.A.M. Reeder (Eds.). Mammal species of the World. A Taxonomic and Geographic Reference. Vol. 2. Johns Hopkins University Press, Baltimore: 1538–1600.

Submitted May 12, 2013; accepted September 2, 2013.