Proceedings of the Zoological Institute RAS
Vol. 316, No. 3, 2012, pp. 273–281

УДК 599.324;591.324;591.485

THE AURICLE MUSCLES IN THE RELICT RODENT *LAONASTES AENIGMAMUS* (RODENTIA: DIATOMYIDAE)

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ABSTRACT

The facial muscle complex responsible for auricle mobility in the recently described relict rodent *Laonastes aenigmamus* Jenkins et al., 2005 (Diatomyidae) was studied for the first time. The members of other high-level rodent taxa that could be closely related to this species according to various hypotheses were also included in the morphological analysis for comparative purposes: *Ctenodactylus gundi* (Ctenodactylomorphi: Ctenodactylidae) and *Chinchilla lanigera* (Hystricognathi: Chinchillidae). The results of the study demonstrated the origin of the m. cervico-occipitalis and the mm. cervico-auriculares on the occipital crest and the unusual structure of the m. platysma cervicale, all distinctive features of the examined muscle complex in *Laonastes*. In *Laonastes* and *Ctenodactylus*, a number of common characters in the structure of the auricle muscles were also observed: the topography, interaction and areas of the insertion of the m. interscutularis and the m. cervico-occipitalis; the two-layer condition of the mm. cervico-auriculares. The obtained results do not contradict the available morphological and molecular data supporting the close affinity between Diatomyidae and Ctenodactylidae.

Key words: facial musculature, *Laonastes aenigmamus*, mobility of auricle, rodents

УШНЫЕ МЫШЦЫ РЕЛИКТОВОГО ГРЫЗУНА *LAONASTES AENIGMAMUS* (RODENTIA: DIATOMYIDAE)

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РЕЗЮМЕ

Впервые проведено изучение комплекса лицевых мышц, обеспечивающих подвижность ушной раковины, у недавно описанного реликтового грызуна *Laonastes aenigmamus* Jenkins et al., 2005 (Diatomyidae). В сравнительный морфологический анализ включены также представители других крупных таксонов грызунов, которые, согласно разным гипотезам, могли быть в близком родстве с этим видом: *Ctenodactylus gundi* (Ctenodactylomorphi: Ctenodactylidae) и *Chinchilla lanigera* (Hystricognathi: Chinchillidae). Результаты исследования показали все отличительные особенности изучаемого комплекса мышц у *Laonastes*: начальное прикрепление m. cervico-occipitalis и mm. cervico-auriculares на затылочном гребне; необычное строение m. platysma cervicale. У *Laonastes* and *Ctenodactylus* наблюдался также ряд общих особенностей в строении ушных мышц: топография, взаимодействие и области прикрепления m. interscutularis и m. cervico-occipitalis; двухслойное состояние mm. cervico-auriculares. Полученные результаты не противоречат имеющимся морфологическим и молекулярным данным в пользу близкого родства Diatomyidae и Ctenodactylidae.

Ключевые слова: лицевая мускулатура, *Laonastes aenigmamus*, подвижность ушной раковины, грызуны

INTRODUCTION

Laonastes aenigmamus Jenkins et al., 2005 (hereafter *Laonastes*) is a recently described new species and genus of rock rats from Laos. *Laonastes* is a rat-like rodent with an elongated head and squirrel-like tail. Originally, a standard taxonomic analysis of this form revealed a variety of features different from those of all other recent rodents (Jenkins et al. 2005). The skull structure of the new species showed a unique combination of sciurognathous and hystricognathous characters. As a result, *Laonastes* was classified on the basis of the comparative analysis of morphological and molecular data in a new rodent family, Laonastidae (Jenkins et al. 2005), within the suborder Hystricognatha (currently classified as the infraorder Hystricognathi: see Woods and Kilpatrick 2005). Later, an integrated analysis of morphological and palaeontological characters indicated that *Laonastes* was almost identical to *Diatomys*, a Miocene representative of the fossil family Diatomyidae, based on the unusual combination of external and craniodental features found in the new form (Dawson et al. 2006). Currently, *Laonastes* is included in the family Diatomyidae. Together with its sister group, the family Ctenodactylidae, the family Diatomyidae is placed outside Hystricognathi but within the common clade Ctenochystrica (Huchon et al. 2007). Moreover, the Diatomyidae obviously represent the beginning of a broad zoogeographical and adaptive radiation of hystricognath rodents (Huchon et al. 2007). The examination of the masticatory apparatus of *Laonastes* produced results consistent with those of previous studies. These results revealed a unique combination of sciurognathous and hystricognathous characters (Hautier and Saksiri 2009).

The investigation of subcutaneous muscle (m. cutaneus trunci) in *Laonastes* is of special interest for the elucidation of the affinities of the species because the structure of this muscle in Hystricognathi, with only a few exceptions, is characterised by surprising uniformity and complexity (Woods 1972; Woods and Howland 1977). The first results of the comparative analysis of subcutaneous muscle in *Laonastes* demonstrated that its general structure is similar to that of several members of Sciuromorpha (Zherebtsova and Davidova 2011). The same structure of this muscle is also characteristic of many other (primarily weakly specialised) rodents (Myomorpha, Sciuromorpha), insectivores and carnivores (Meinertz 1941; Nozdrachev 1973; Woods and Howland 1977; Gambaryan and Zherebtsova 1988). In addition, the m. cutaneus trunci in *Laonastes* also shares some common features with the corresponding muscles of hystricognath rodents (members of Hystricognathi). In this study, the terms sciuromorph (Sciuromorpha) and hystricognath (Hystricognathi) rodents, will be used only in the context of the taxonomic status of the animals. The structure of the masticatory apparatus will be ignored.

Both the facial musculature and the subcutaneous musculature are closely connected with the skin, but the first of them differs from the m. cutaneus trunci in origin and innervation (the facial musculature is innervated by the facial but not by the thoracic nerve: Woods and Howland 1977; Gambarjan 1989). It is known that the facial muscles in mammals are derivatives of three muscular layers: the m. platysma, m. sphincter colli superficialis and m. sphincter colli profundus (Huber 1930; Gambarjan 1989). The m. platysma originates on the dorsal surface of the neck and passes cranially and ventrally to the dorsal and lateral surfaces of the head. In the course of evolution, the m. platysma has differentiated into two layers: the superficial layer, the m. platysma myoides, and the deep layer, the m. platysma cervicale (Gambarjan 1989). The m. platysma myoides pulls the integuments of the buccal region and the cervical region in caudal and cranial directions, respectively. The caudoventral expansion of the origin of the m. platysma myoides creates the best possibilities for longitudinal action, whereas the m. platysma cervicale produces traction in a transverse direction, preventing the ventral displacement of the m. platysma myoides under the influence of the m. sphincter colli profundus.

With the development of the auricle in mammals, the terminations of the cranial fibres of the m. platysma transfer to the surface of the concha and also to the space between the ears, forming the complex of the mm. cervico-auriculares and the m. cervico-occipitalis (Huber 1930; Meinertz 1941). The former member of this complex supports the vital function of the mobility of the auricles, whereas the latter supplies the longitudinal tension of the skin between the ears. Although the m. platysma cervicale does not insert on the auricle, it is closely associated with the cervico-aural muscles and can be placed in the same group (Gambarjan 1989). Another part of the facial muscles extends to the auricle in the front and represents derivatives of the m. sphincter colli pro-

fundus: the m. fronto-auricularis, the m. auricularis anterior superior, and the m. interscutularis. These muscles act primarily as antagonists of the mm. cervico-auriculares and the m. cervico-occipitalis (Gambarjan 1989).

The structure of the facial muscles mentioned above has specific features in rodents of various suborders. A comparative examination of the auricle muscles in *Laonastes aenigmamus* and in two representatives of the suborder Hystricomorpha (Dieterlen 2005; Woods and Kilpatrick 2005), *Ctenodactylus gundi* Rothmann, 1776 (Ctenodactylidae) (hereafter *Ctenodactylus*) and *Chinchilla lanigera* Bennett, 1829 (Chinchillidae) (hereafter *Chinchilla*), was conducted in this study. The data in the literature on the morphology of these muscles in other members of Hystricomorpha and also of Sciuromorpha and Myomorpha are few in number and were also considered. 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. A comparative analysis can also serve as a basis for the better understanding of the evolutionary histories of sciuromorph and hystricomorph rodents within Rodentia. 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 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 ($n = 2$; № 99491, 99496); the gundi, *Ctenodactylus gundi* Rothmann, 1776 ($n = 1$; № 6641); and the long-tailed chinchilla, *Chinchilla lanigera* Bennett, 1829 ($n = 2$; № 576 a, b). The adult specimens were preserved in 70% ethanol or 5% formalin. The facial muscles, which are responsible for moving the auricle, were examined using the total preparations. For determination of the general arrangement of these muscles and the details of their relationships a specific stain for myosin (i.e., water solution of Cresil-fast-Violet) was applied. The stain was dropped on the surface of the muscles and washed away after 10–15 minutes under a strong water stream. Subsequently, the stained muscle fibres were examined with a binocular stereomicroscope *Leica* MZ6.

RESULTS

M. fronto-auricularis. In *Laonastes aenigmamus*, the muscle arises on the lateral (orbital) edge of the os frontale deeper than the m. orbicularis oculi and passes caudolaterally, widening slightly and terminating in a thin aponeurosis on the upper anterior edge of the concha (Fig. 1A). In *Ctenodactylus gundi*, this muscle has a similar structure but is more weakly developed, arising by a thin aponeurosis on the orbital edge of the os frontale and inserting on the upper anterior edge of the concha (Fig. 1B). In *Chinchilla lanigera*, the well-developed muscle also originates on the os frontale but does so more caudomedially than in *Laonastes* (Fig. 1C). Its fibres insert on the anterior half of the back surface of the concha.

M. auricularis anterior superior. Among the three forms studied, this small muscle was found only in *Laonastes*. It arises by a thin aponeurosis on the level of the os squamosum, runs caudolaterally, gradually narrowing, and inserts on the anterior part of the back surface of the concha, above the attachment of the m. interscutularis (Fig. 1A).

M. interscutularis. This muscle is observed only in *Laonastes* and *Ctenodactylus* (Fig. 1A, B). In both forms, it has a very similar structure, extending perpendicular to the dorsal midline in the inter-ear space and inserting on the anterior parts of the back surface of the auricles. Its cranial fibres gradually deviate craniomedially and interdigitate on the midline.

M. cervico-occipitalis. *Laonastes aenigmamus* (Fig. 1A). This rather thin, flat muscle is situated in the inter-ear space. It originates on a small area of the occipital crest very near the dorsal midline. From there, the muscular fibres extend craniolaterally, forming a fan-like pattern and inserting primarily on the internal fascia of the m. interscutularis. The medial fibres of the m. cervico-occipitalis are near the midline only at their cranial ends. A small portion of the lateral fibres extend to the anterior part of the back surface of the concha, partially intertwining with the fibres of the m. interscutularis attached there.

Ctenodactylus gundi (Fig. 1B). The muscle has a very similar structure and is well developed as in *Laonastes*, but it originates rather narrowly on the dorsal midline of the head in the inter-ear space, and

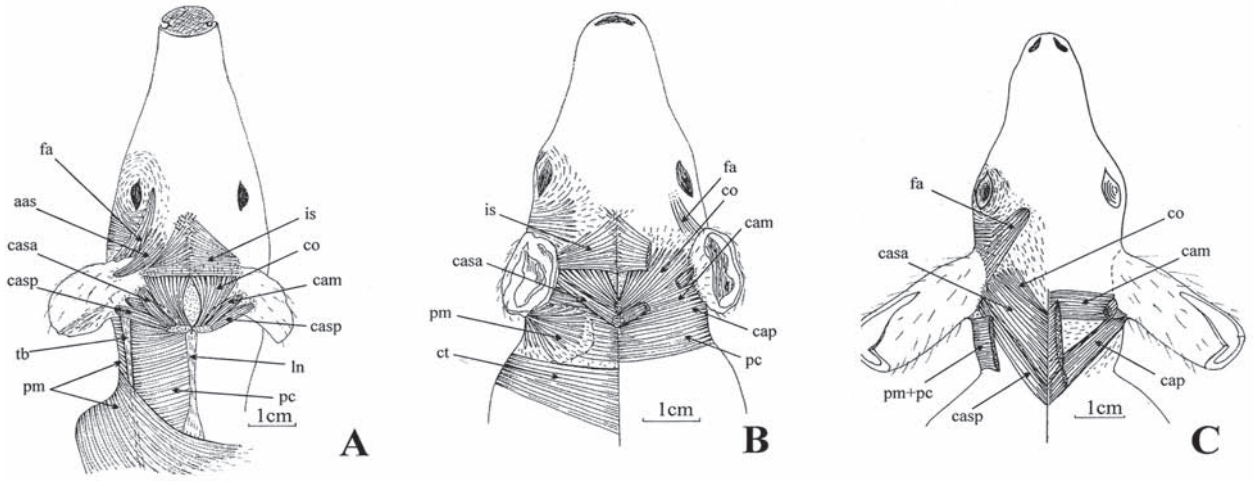

Fig. 1. Complex of the facial muscles responsible for auricle mobility in rodents (view from above): A – *Laonastes aenigmamus*; B – *Ctenodactylus gundi*; C – *Chinchilla lanigera*. *Abbreviations*: aas – m. auricularis anterior superior; cam – m. cervico-auricularis medius; cap – m. cervico-auricularis profundus; casa – m. cervico-auricularis superficialis anterior; casp – m. cervico-auricularis superficialis posterior; co – m. cervico-occipitalis; fa – m. fronto-auricularis; is – m. interscutularis; ln – ligamentum nuchae; pc – m. platysma cervicale; pm – m. platysma myoides; tb – tendinous bridge.

only its deep fibres have a muscular-tendinous insertion on the occipital crest. The muscle passes craniolaterally, forming a fan-like widening, and inserts on the inner fascia of the m. interscutularis but also on the anterior part of the back surface of the auricle.

Chinchilla lanigera (Fig. 1C). Only a small bunch of the fan-like diverging fibres is present, originating from the dorsal midline approximately at the level of the posterior quarter of the back surface of the concha. The m. cervico-occipitalis passes craniolaterally, as is usually the case, and terminates in a thin aponeurosis in the inter-ear space at the level of the anterior third of the back surface of the concha. This superficial aponeurosis approaches the medial edge of the strongly developed m. fronto-auricularis.

Mm. cervico-auriculares. *Laonastes aenigmamus* (Fig. 1A). This complex of muscles has a two-layer structure. The superficial part consists of two muscles: the m. cervico-auricularis superficialis anterior and the m. cervico-auricularis superficialis posterior. The first of these muscles is rather weakly differentiated from the m. cervico-occipitalis and originates laterally to it on the occipital crest. This narrow flat muscle also passes craniolaterally, inserting on the back surface of the concha immediately behind the m. cervicooccipitalis. The m. cervico-auricularis superficialis posterior begins on the occipital crest close to the m. cervico-auricularis superficialis anterior but caudally to it. It runs almost perpendicularly to the dorsal midline of the head, with a small cranial component, and it inserts on the posterior part of the back surface of the auricle.

The second layer of the mm. cervico-auriculares is formed by only one muscle, the m. cervico-auricularis medius, which also originates on the occipital crest but is deeper than the m. cervico-occipitalis and the m. cervico-auricularis superficialis anterior. It passes almost parallel to the m. cervico-auricularis superficialis posterior and terminates in front of it on the back surface of the concha. Thus, the insertion of this muscle is located between the ends of the two superficial muscles.

Ctenodactylus gundi (Fig. 1B). The complex of the mm. cervico-auriculares is characterised by a two-layer structure similar to that found in *Laonastes*. The superficial part, m. cervico-auricularis superficialis, intimately adjoins the caudal edge of the m. cervico-occipitalis. This ribbon-like muscle has a tendinous origin on the dorsal midline of the head immediately behind the attachment of the cervico-occipital muscle. Its fibres have a similar craniolateral direction and are inserted on the anterior half of the back surface of the concha.

The second layer of the complex is weakly differentiated. Its fibres originate from the dorsal midline of the neck, deeper than the m. cervico-auricularis

superficialis, and are almost perpendicular to the dorsal midline, with a small cranial deviation. The most anterior part of the fibres can be considered the m. cervico-auricularis medius in this case, not differentiated into the pars anterior and pars posterior. The m. cervico-auricularis medius terminates on the back surface of the auricle. Moreover, a few of the caudal fibres of the second layer are almost perpendicular to the dorsal midline of the head and extend down on the lateral surface of the neck, then passing around the auricle and inserting on its caudoventral part. Given its topography and insertion, it is obvious that this portion should be considered a rudimentary m. cervico-auricularis profundus.

Chinchilla lanigera (Fig. 1C). In this species, the complex of the mm. cervico-auriculares has a three-layered structure. The superficial part of the complex forms a single layer with the m. cervico-occipitalis, originating immediately behind it on the dorsal midline of the neck in the inter-ear space. In addition, the m. cervico-auricularis superficialis has two parts: the larger anterior part and the narrower posterior part.

The fibres of the m. cervico-auricularis superficialis anterior originate rather broadly along the entire dorsal midline of the neck. The muscle extends craniolaterally, as is usually the case, and attaches primarily to the middle third of the back surface of the concha, partially penetrating into the fibres of the well-developed m. fronto-auricularis, which inserts at the same place but more cranially. The m. cervico-auricularis superficialis posterior differs in this species by its narrower insertion on the midline, immediately behind the pars anterior and almost in the interscapular region. The posterior portion of the superficial layer also passes craniolaterally and terminates in the same manner on the back surface of the concha, immediately caudally to the insertion of the anterior portion.

The second layer of the complex, the m. cervico-auricularis medius, is not divided into anterior and posterior parts. The muscle originates on the dorsal midline of the neck in front of the occipital crest, deeper and partially more cranially relative to the anterior fibres of the m. cervico-auricularis superficialis anterior. It passes almost perpendicular to the dorsal midline up to the insertion on the posterior half of the back surface of the auricle.

The third layer of the cervico-aural muscles, the m. cervico-auricularis profundus, originates on the dorsal midline of the neck, deeper than the caudal fibres of the m. cervico-auricularis superficialis anterior and the pars posterior. The muscle has a craniolateral direction similar to that of these fibres and inserts partially beneath the attachment of the middle layer of the mm. cervico-auriculares on the posterior part of the concha.

Platysma cervicale. *Laonastes aenigmamus* (Fig. 1A). A small portion of the cranial fibres of this muscle immediately adjoin the caudal edge of the m. cervico-auricularis superficialis posterior, originating similarly on the occipital crest but from its caudal side. In this region, the fibres gradually change their direction from the craniolateral to the caudolateral. The remainder of the m. platysma cervicale originates on the well-defined nuchal ligament, which is widely extends throughout the entire cervical and interscapular regions. The front part of the fibres passes on the neck, primarily caudolaterally, and gradually changes its direction to near-lateral in the interscapular region.

The m. platysma cervicale inserts on the tendinous bridge (crosspiece) running parallel to the nuchal ligament on the side of the neck and in the interscapular region. The fibres of the m. platysma myoides originate from the ventral side of the crosspiece. Moreover, a superficial portion of its fibres originate over the m. platysma cervicale in the cervical region and form a well-developed overlapping group of fibres over the extended nuchal ligament in the interscapular region. The superficial part of the m. platysma myoides merges with the deep part behind the ear and then extends cranioventrally on the lateral surface of the neck and head.

Ctenodactylus gundi (Fig. 1B). The m. platysma cervicale originates along the dorsal midline of the neck immediately caudal to the m. cervico-auricularis profundus, forming a united layer with it. The fibres of the muscle are also nearly perpendicular to the midline of the neck and, joining gradually with the m. platysma myoides behind the ear, extend over the side of the neck and up to the mental area. Here, the combined layer of the platysma terminates, partially inserting on the inner fascia of the m. sphincter colli profundus p. intermedia ventralis.

Chinchilla lanigera (Fig. 1C). The platysma cervicale with the platysma myoides forms one layer, the fibres of which extend along the side of the neck and head, inserting in the mental area, at the corner of the mouth and partly in the area of the vibrissae.

DISCUSSION

The structure of the facial muscles responsible for the mobility of the auricle exhibits many similarities in *Laonastes aenigmamus* and *Ctenodactylus gundi*. These similarities are especially evident for such muscles as the m. interscutularis, the m. cervico-occipitalis, and the mm. cervico-auriculares.

The common features in the structure of the m. interscutularis and the m. cervico-occipitalis in *Laonastes* and *Ctenodactylus* are evident in their topography, insertion and interaction (Fig. 1A, B). In *Laonastes*, however, the m. cervico-occipitalis originates entirely on the occipital crest, whereas it originates only partially on the occipital crest in *Ctenodactylus*, transferring superficially to the dorsal midline of the head. In *Chinchilla*, the m. interscutularis is absent. Moreover, the m. cervico-occipitalis is more weakly developed, originates only on the dorsal midline of the head, forming a common layer with the m. cervico-auricularis superficialis.

In other representatives of the Hystricognathi, the m. cervico-occipitalis is either an independent muscle, as in *Hydrochoerus* Brisson, 1762 and *Octodon* Bennett, 1832, or it forms a common layer with the m. cervico-auricularis superficialis, as in *Cavia* Pallas, 1766, *Hystrix* Linnaeus, 1758, *Abrocoma* Waterhouse, 1837, and *Thryonomys* Fitzinger, 1867 (Schreiber 1929; Meinertz 1932, 1941, 1944; Gambaryan 1989). In all these cases, the origin of the m. cervico-occipitalis on the occipital crest has never been described, but the insertion of the muscle on the anterior part of the auricle has been noted to different degrees.

These findings indicate that the principal feature of the m. cervico-occipitalis in *Laonastes aenigmamus* is its origin on the occipital crest. Similar examples can be found in several other groups of mammals (e.g., insectivores, primates, bats, hyraxes), although this feature has not previously been reported in rodents (Ruge 1886; Sullivan and Osgood 1925; Huber 1931; Schneider 1961; Seiler 1975; Gambaryan 1989; Zherebtsova 1990).

The structure of the mm. cervico-auriculares also shows many similarities in *Laonastes* and *Ctenodactylus*. These muscles are characterised by a two-layer condition in both forms, whereas a more advanced three-layer state of the complex is observed in *Chinchilla*. In other rodents, the structure of the mm. cervico-auriculares is usually three-layered. The two-layer state of these muscles is observed in certain members of the Sciuromorpha and Myomorpha (Schreiber 1929; Meinertz 1941, 1942, 1943). In these cases, the simplification of the cervico-aural complex is connected with the burrowing mode of life and reduction of the conchas (Gambaryan 1989). However, it is probable that the two-layer structure of the mm. cervico-auriculares represents a more primitive type of morphology in such rock-dwelling animals as *Laonastes* and *Ctenodactylus*, where it corresponds to an earlier stage of these muscles differentiation. Moreover, the occurrence of a three-layer state of the mm. cervico-auriculares in most forms of rodents can also indicate that the character of the stratification of these muscles is most likely independent of the size of the conchas. Analogous conclusions can be drawn for members of the family Dipodidae (Myomorpha) regarding the variation in the size of the conchas (Gambaryan 1989).

In *Chinchilla* and *Laonastes*, the superficial layer of the mm. cervico-auriculares is equally differentiated into anterior and posterior portions, whereas only the p. anterior occurs in *Ctenodactylus*. The second, middle layer of the mm. cervico-auriculares in all the forms considered in this study shows a similar state and is not divided into portions indicative of a more primitive organisation. In *Ctenodactylus*, the m. cervico-auricularis medius merges without a visible boundary with a portion, terminating on the caudoventral edge of the concha. The insertion of this part of the fibres corresponds to that of the m. cervico-auricularis profundus. However, because a third layer of the mm. cervico-auriculares is not present in *Ctenodactylus*, the state of the m. cervico-auricularis profundus in this species can be considered rudimentary.

Thus, in *Laonastes*, the m. cervico-auricularis profundus is absent. In contrast, this muscle is still a part of the second layer of the complex in *Ctenodactylus*, and it forms a separate third layer of the cervico-aural muscles in *Chinchilla*. In *Chinchilla*, however, the m. cervico-auricularis profundus still preserves the craniolateral direction inherent in the m. cervico-auricularis superficialis posterior. In addition, the pars profundus is inserted not on the caudoventral part of the concha in *Chinchilla*, as is usually observed in rodents, but on the caudodorsal part.

The comparative analysis of the mm. cervico-auriculares indicates that the principal feature of this complex in *Laonastes*, in contrast to that of *Ctenodactylus* and *Chinchilla,* is the origin of these

muscles on the occipital crest. Within Rodentia, similar morphological features are known mainly in certain representatives of Sciuromorpha: *Aplodontia rufa* Rafinesque, 1817 and *Sciurus vulgaris* Linnaeus, 1758 (Meinertz 1932, 1941, 1942, 1943; Gambaryan 1989). Among hystricognath rodents, the attachment of mm. cervico-auriculares on the os supraoccipitale was described in *Hydrochoerus*, but for other members of Hystricognathi, the detailed descriptions of the auricle muscles and their illustrations are absent (Shriber 1929; Meinertz 1944). Moreover, the origin of the mm. cervico-auriculares on the occipital crest and on certain other areas of the skull is observed in a variety of other mammals, including marsupials, insectivores and carnivores (Huber 1930, 1931; Gambaryan 1989). The attachment of these muscles on the skull is also characteristic of such specialized animals as bats (Shneider 1961; Medvedeva 1989). The fixed attachment of the m. cervico-occipitalis and mm. cervico-auriculares on the skull apparently allows them to function relatively more independently from their counterparts on the opposite side of the head (Gambaryan 1989). Thus, it is possible that the cited peculiarity of the m. cervico-occipitalis and the mm. cervico-auriculares in *Laonastes* is determined by their specific functional properties rather than their archaic organisation.

In *Chinchilla*, in contrast with *Laonastes* and *Ctenodactylus*, essential transformations are found in the organisation of the auricle muscles. Thus, instead of the m. interscutularis, the m. fronto-auricularis is especially strongly developed and inserts on the back surface of the concha, not on its anterior edge as in *Laonastes* and *Ctenodactylus*. The origin of the superficial and deep layers of the cervico-aural muscles is displaced caudally along the dorsal midline of the neck up to the interscapular region. In addition, a significant expansion of the origin and the insertion of the m. cervico-auricularis superficialis anterior is also noted. The characters of the facial muscles mentioned above are not typical of all representatives of Hystricognathi (Meinertz 1941, 1944) and can apparently be related to their functional load, which are determined by the large size of the conchas in *Chinchilla*.

The incomplete division of the m. platysma into the m. platysma myoides and the m. platysma cervicale in *Laonastes* and *Ctenodactylus* gives these species a close resemblance to *Chinchilla* and to other members of the Hystricognathi. The m. platysma is weakly stratified in the majority of the hystricognath rodents, whereas it is usually well-differentiated in rodents belonging to the Sciuromorpha and Myomorpha (Schreiber 1929; Meinertz 1932, 1941, 1942, 1944; Gambaryan 1989). The different stages of the stratification of the m. platysma are also observed in such groups of mammals as marsupials, insectivores, and bats (Shneider 1961; Gambaryan and Zherebtsova 1988; Gambaryan 1989; Medvedeva 1989).

However, the origin of the m. platysma cervicale on the wide nuchal ligament and its unusual insertion on the tendinous bridge, both observed in *Laonastes*, have not been described in other mammals. It is probable that these traits can be viewed as a special morphological features of the m. platysma. This special morphology, probably, demonstrates one of the modes of the initial differentiation of the m. platysma into two layers, the m. platysma cervicale and the m. platysma myoides. On the assumption that a weakly stratified state of the m. platysma in hystricognaths is indicative of its more archaic organisation, the particular structure of the m. platysma cervicale in *Laonastes* is apomorphic rather, than the plesiomorphic character of the examined facial muscles.

Based on the data obtained in this study, one of the hypothetical developmental paths shown by the muscles considered can be followed from primitive to more advanced states. Thus, in *Laonastes*, the m. cervico-occipitalis and the mm. cervico-auriculares have their origin on the occipital crest, and the mm. cervico-auriculares are two-layered. In *Ctenodactylus*, the cervico-occipital muscle originates on the occipital crest only partially and transfers primarily to the dorsal midline of the head. In this case, the mm. cervico-auriculares have their origin superficially near the occipital crest and are also two-layered. Moreover, the formation of the third layer is already manifested in *Ctenodactylus* through the presence of the rudimentary m. cervico-auricularis profundus. In *Chinchilla*, as in most other hystricognaths, the structure of the muscle complex mentioned above is three-layered. The origin of this muscle complex is only on the dorsal midline of the head and neck, and transfers farther posteriorly in *Chinchilla,* as compared to that in *Laonastes* and *Ctenodactylus*.

If a two-layer state of the mm. cervico-auriculares and their origin on the occipital crest are the plesiomorphic traits, then the similarity in the structure of the auricle muscles in *Laonastes* and *Ctenodactylus*

can be considered a manifestation of the ancestral condition. However, the results obtained do not contradict the available morphological and molecular data in favour of the affinity between Diatomyidae and Ctenodactylidae and support the hypothesis that the relict rodent belongs to one of the basal groups of a broad adaptive radiation of the hystricomorph rodents (Hystricomorpha) (Dawson et al. 2006; Huchon et al. 2007).

ACKNOWLEDGEMENTS

The author would like to thank Dr. A.V. Abramov (ZIN, Saint Petersburg) for the opportunity to examine the unique material on *Laonastes aenigmamus* collected in Laos. I am especially grateful to Dr. P.P. Gambaryan (ZIN) for his valuable consultations in the course of the work as well as Dr. A.N. Kuznetsov and Dr. E.G. Potapova (Moscow) for reviewing the manuscript and constructive recommendations. Special thanks to T.N. Platonova (ZIN) and "American Journal Experts" for the correction of the English. 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).

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Submitted December 20, 2011; accepted September 4, 2012.