Muscles of Facial Expression in *Otolemur*, With a Comparison to Lemuroidea

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ABSTRACT

Gross and histologic aspects of facial expression muscles are presented here for *Otolemur* spp. (suborder Prosimii, family Lorisidae) and are compared with those of lemuroids. Muscles of facial expression are involved in social signaling among primates, and are a primary means by which close-proximity nonverbal communication is achieved. These muscles have been well described in catarrhines and many of the lemuroids; however, their arrangement is not well known in the lorisids. In the present study we examined muscles of facial expression in *Otolemur* by dissecting preserved faces. The arrangement and appearance of the muscles were noted, and samples were gathered from each muscle for histologic processing. The results showed 17 muscles of facial expression in *Otolemur*, as compared to seven reported in previous studies. Histologically, muscles of the ear region were arranged in tight, dense fascicles, while muscles of the orbital region were arranged more loosely. Grossly, the facial expression muscles in *Otolemur* were very similar in morphology and attachments to those in the lemuroids, with some differences in the ear region. *Otolemur garnettii* had several muscles that appeared to be more robust than in the larger *O. crassicaudatus*. This may be due to dietary and/or social differences between the species. In previous studies it was concluded that, relative to lemuroids, *Otolemur* has a primitive arrangement of facial expression muscles. The current results do not support that conclusion, and in fact support a far greater similarity between *Otolemur* and lemuroids in general. These results underscore the need for a reexamination of facial musculature in prosimians in general, and may have taxonomic value as regards the position of *Otolemur* with lemuroids and other galagos. Anat Rec Part A 274A:827–836, 2003. © 2003 Wiley-Liss, Inc.

Key words: muscles of facial expression; otolemur; galago; bushbaby; prosimian

Muscles of facial expression are skeletal muscles that are found in all vertebrate orders and are derived from the hyoid branchiomeric arch. As such, they are distinguished from other cranial musculature by their innervation via the seventh cranial nerve (Young, 1962; Carlson, 1981; Walker and Liem, 1994). In the vertebrate orders below Mammalia, these muscles are restricted to the gill region (in fish), the neck, and the mandibular region, and aid in constricting the openings associated with these areas (Huber, 1930a; Walker and Liem, 1994). In mammals, including monotremes and marsupials, the facial expression musculature has become highly derived and differentiated relative to more primitive vertebrates (Huber, 1930a,b, 1931). The muscles extend into the facial region, where they connect to the skin and are used to transform the shape of the face and the orbital, nasal, and oral openings. Thus, they give the face mobility and enable voluntary control over movement of the vibrissae. The basic developmental portions of this musculature are the undifferen-
tiated platysma and the sphincter colli profundus sheets. From the undifferentiated platysma sheet arises the platysma muscle, which is restricted to the cervical, shoulder, and mandibular regions, and the postauriculo-occipital muscles (including muscles of the extrinsic ear). The sphincter colli profundus sheet gives rise to the other superficial facial muscles innervated by the facial nerve (Huber, 1930a; Carlson, 1981).

Although muscles of facial expression are involved in various activities, such as mastication, vision, and respiration, their major role is in nonverbal communication, such as close-proximity social signaling and mate recognition (Darwin, 1872; van Hooff, 1962; Andrew, 1963; Bearder et al., 1995; Schmidt and Cohn, 2001). This role is especially obvious in the Primate order, where close-range social signaling and communication among individuals reach a high level relative to most other mammals. Much social signaling and communication among individuals of other mammalian orders is achieved via long-range mechanisms, such as olfaction, pheromones, and auditory signals. Within the Primate order, however, binocular vision, increased visual acuity, and convergence are so well developed that close-range visual cues, such as facial expressions, take on special importance in social interactions (Darwin, 1872; van Hooff, 1962; Schultz, 1969; Ankel-Simons, 2000; Schmidt and Cohn, 2001).

Many of our current concepts regarding primate facial expression and its corresponding musculature are based upon a phylogenetic perspective: as the phylogenetic scale progresses from prosimians to humans, the complexity of these muscles and their corresponding actions increases (e.g., van Hooff, 1962; Schultz, 1969). In this schema, it has been suggested that the relatively undifferentiated large muscular sheets in prosimians break up into smaller, more discrete individual muscles in the progression toward Homo (Huber, 1931; Schultz, 1969). Indeed, it is in the catarrhines that we find the most thorough descriptions of primate facial expression and its morphological correlates. Outstanding studies on the muscular anatomy of the face and facial displays have been performed on various members of the Catarrhini, including the rhesus macaque (Huber, 1933; Hinde and Rowell, 1962), gorilla (Raven, 1950), and orangutan (Lightoller, 1928). In addition, most systematic studies of primate facial expression and its evolution have been based solely upon the catarrhines (Chevalier-Skolnikoff, 1973; Preuschoft and van Hooff, 1995; Preuschoft, 2000; Schmidt and Cohn, 2001). While the form and function of the facial musculature have been well described in the catarrhines, they are relatively poorly understood in the prosimians. Members of Lemuroidea, especially the lemurs and indris, have been most commonly studied in terms of soft-tissue anatomy and behavioral repertoire. Most notably, Ruge (1885) described facial expression musculature for members of Lemur, Varecia, Avahi, Lepilemur, Propithecus, and Daubentonia (referred to therein as Cheiromys). Murie and Mivart (1872) reported on the facial expression musculature for Otolemur (referred to therein as Galago). They described only seven muscles (grouping the muscles associated with the nasal region into one broad category): the occipitofrontalis m., atellens aurem m., attrahens aurem m., retrahens aurem m., orbicularis palpebrum m., orbicularis oris m., and “nasal region” mm. Aside from these original studies, morphological descriptions of the prosimians are generally lacking, as are descriptions of their facial displays (see, however, Huber (1931)).

Andrew (1963) described scant facial expressions for a variety of prosimians. In O. crassicaudatus he specifically described (in males) a folding of the external ear during courtship, and (in both sexes) a drawing back of the skin when grooming was solicited. Jolly (1966) described a facial grin in Lemur catta and Propithecus verreauxi during aggressive/submissive encounters, and Pereira and Kappeler (1997) observed a variety of oral and external ear movements in L. catta during aggressive/submissive encounters. Doyle (1974), citing Andersson (unpublished results), reported a variety of facial expressions in Galago senegalensis emanating from the mouth, eyes, and external ears. Tandy (1974) and Charles-Dominique (1977) described an open-mouth gesture with teeth bared in the agonistic postures of several lorisids, as well as various movements of the external ears for a variety of situations. These studies also noted a few facial expressions in prosimians, but our knowledge of facial expression and its associated musculature in prosimians remains sparse. To enhance our understanding of prosimian muscles of facial expression, and to further advance our understanding of the chronological correlates, we present the described musculature in the present study we examined the detailed gross muscular anatomy of the facial expression muscles (i.e., those muscles innervated by the seventh cranial nerve) in the greater bushbabies, O. crassicaudatus and O. garnettii.

Otolemur (according to Olson, 1979, 1986) comprises the greater galagos or bushbabies, O. crassicaudatus (large-eared bushbaby) and O. garnettii (small-eared bushbaby). These species fall within the subfamily Galaginae of the Lorisidae family and are the largest of the galagos. As are all galagos, Otolemur spp. are nocturnal (Charles-Dominique, 1977; Sussman, 1994). Both species are arboreal; however, whereas O. crassicaudatus occurs most frequently in the dense forests, open savanna woodlands, and plantations of sub-Saharan Africa, and prefers the upper levels of the trees, O. garnettii tends to inhabit only forests and prefers the lower levels of trees (Nash et al., 1989). Previous observations suggest that O. crassicaudatus occurs singly or in groups of up to six (Bearder and Doyle, 1974; Harcourt, 1980; Harcourt and Nash, 1986), while O. garnettii groups more commonly in smaller numbers and is more territorial than O. crassicaudatus (Harcourt, 1980; Harcourt and Nash, 1986). Other than the 1872 account by Murie and Mivart, descriptions of the facial musculature of Otolemur are lacking. They have been simply described as possessing a primitive arrangement of muscles (Ruge, 1885; Huber, 1931). In the current study we used freshly preserved specimens to outline the gross anatomy of facial expression musculature in Otolemur and provide a histologic account of these muscles. We discuss our findings relative to the position of Otolemur in the Prosimii, and to catarrhines in general.

MATERIALS AND METHODS

The preserved heads of 18 adult Otolemur (10 from O. crassicaudatus and eight from O. garnettii; see Table I for sex and age distributions) were used in this study. The heads were preserved in 10% buffered formalin. All specimens were obtained from the Duke University Medical Center. The brains and calvariae had been removed in previous experiments. From the skin flap where the calvaria had been removed, a midline incision was made over the nasal and oral regions down into the neck, so that the
left and right portions of the face were separated. All skin, superficial fascia, superficial facial musculature, and deep fascia were dissected away from the deeper masticatory musculature, the buccinator muscle, and bone using a #12 scalpel blade and microdissection tools. Care was taken to remove as much superficial facial musculature as possible and 3)

Muscle Descriptions and Attachments (Figs. 2 and 3)

**Occipitofrontalis muscle.** This is a very thin, sheet-like muscle composed of horizontal fibers that becomes thickened inferiorly, giving rise to the attrahens aurem and atollens aurem muscles. Anteriorly it is attached to the skin superior to the superciliary region of the orbit, superior to the attachment of the orbitoauricularis muscle. Here this muscle is exceptionally thin. Posteriorly it travels to the level of the superior concha1 before giving rise to the thicker fibers of the attrahens aurem and atollens aurem muscles.

**Attrahens aurem muscle.** The attrahens aurem is a posteroinferior thickening of the occipitofrontalis muscle that is composed of horizontal to oblique fibers that attach to the posterosuperior concha. These fibers tend to be much thicker and more obvious than those of the atollens aurem muscle.

1The term “concha” is used here to delineate the central part of the external ear that is attached directly to the skull. See Schultz (1969) and Ankel-Simons (2000) for full descriptions.
**Atollens aurem muscle.** This muscle is composed of vertical to oblique fibers, and is an anteroinferior thickening of the occipitofrontalis muscle. It is attached inferiorly to the tragus just posterior to the orbitoauricularis muscle. While it is an obvious extension of the occipitofrontalis muscle, it is not as thick or large as the attrahens aurem muscle.

**Retrahens aurem muscle.** In all of the specimens the central attachment of this muscle was gone, as all calvariae had been removed for previous studies. However, the peripheral attachments were visible in all of the specimens. In 11 of the 18 specimens (64.7%), this muscle presented as three distinct slips that passed to various aspects of the concha. Here there was a large inferior slip that attached to the inferior concha, a smaller posterior slip that attached to the posterior concha, and a fairly large anterior slip that attached to the anterior concha. In three specimens (two *O. crassicaudatus* and one *O. garnettii*) only two slips noted: a small posterior band and a large anterior band in two of the specimens, and equal-sized anterior and inferior bands in one specimen. In one specimen (*O. garnettii*) there was only one large superior slip.

**Depressor helicis muscle.** This muscle consists of a distinct, thin, gracile band of oblique to vertical fibers immediately posterior to the mandibuloauricularis muscle and at the point of attachment for the orbitoauricularis muscle. It is attached to the tragus and the base of the...
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**Mandibuloauricularis muscle.** In general this muscle consists of a short, wide set of vertical fibers just anterior to the tragus located in the gap between the orbitoauricularis and inferior auriculolabialis muscles. It is attached to the skin anterior to the concha and the tragus, immediately anterior to the depressor helicis muscle. It was absent in two specimens (one of each species).

**Platysma muscle.** This is a broad, flat muscle with horizontal fibers that extends from the commissure of the mouth to the region posterior to the ear. Superoinferiorly, it extends from the region of the zygomatic arch to slightly inferior to the lower lip, with some fibers stretching into the ventral neck. Superiorly, it gives rise to the inferior auriculolabialis muscle. The platysma muscle lies superficial to the sphincter colli muscle, and its muscle fibers are typically most dense in the cheek region.

**Sphincter colli muscle.** This muscle is relatively thin and gracile, but is clearly distinguishable from the superficial platysma muscle. Its fibers are vertical and are easily divided into a small, thick, posterior portion and a large, thin, anterior region. Anteriorly, where the muscle is thinnest, there is a generous quantity of fascia mixed in with the muscle. Superiorly, it is attached to the skin over the zygomatic arch region (reaching superior to the platysma muscle), extending inferiorly past the inferior border of the platysma muscle and attaching into the skin over the ventral neck. Posteriorly, it attaches into the skin anterior to the ear region. The scant anterior fibers attach to the skin posterior to the oral commissure. The sphincter colli muscle is usually thicker and more robust in *O. garnetti*.

**Orbicularis oris muscle.** This is a dense set of thick, sphincter-like muscle fibers surrounding the oral opening. Its deep surface is covered by a thick buccal mucosa. Superiorly, the fibers are more horizontal and looser, while inferiorly the fibers are much more oblique and denser. Posteriorly, the fibers are quite thick and densely organized. Occasionally the superior portion is attached to the inferior extent of the levator labii muscle.

**Mentalis muscle.** This is typically a small muscle with a few oblique fibers. In two specimens (one *O. crassicaudatus* and one *O. garnetti*) it could not be located. In some cases the fibers were horizontal rather than oblique, but they were always attached to the skin inferior to the lower lip and to the skin of the midline of the mandibular region.

**Maxillolabialis muscle.** This is a fleeting set of oblique fibers superficial to the orbicularis occuli and levator labii muscles, which passes posteroinferiorly from the skin of the midface to the skin superior to the upper lip. These fibers were occasionally attached directly to the orbicularis occuli muscle fibers. This muscle was absent in four specimens (two of each species).

**Levator labii muscle.** Most often this muscle was composed of oblique fibers arranged in a wide, dense, single band; however, in six specimens (35%) it was a two-pronged muscle. When present as a wide, single mus-
cle, it passed from the skin of the midface near the inferior margin of the orbicularis oculi muscle anteroinferiorly to the skin just superior to the upper lip. Occasionally it was attached superiorly to fibers of the orbicularis oculi muscle. When present as a two-pronged muscle, it passed from the same superior and inferior attachments as previously described, but with a second set of oblique fibers diverging posteroinferiorly to the skin just superior to the upper lip. In five of the six two-pronged cases it was seen in \textit{O. crassicaudatus}.

\textbf{Nasalis muscle.} This muscle is typically a thick, wide set of oblique fibers passing from the skin associated with the bridge of the nose to the skin associated with the nares and mysticial vibrissae. There is also a considerable attachment to the nasal bone itself. Occasionally there is an attachment as far inferior as the skin associated with the upper lip. In two specimens of \textit{O. crassicaudatus} it was absent. This muscle is usually more robust in \textit{O. garnetti}.

\textbf{DISCUSSION}

In this study we found no histological differences between species in muscles of facial expression. However, histologic examinations revealed marked differences between muscles more closely related to the ear and those more closely related to the eye. Muscles of facial expression tied more closely to the ear tended to have relatively
few muscle fibers in each fascicle, and there was little perimysium among the fascicles. Each fascicle was fairly small but densely packed, and tended to have a block-like shape. In contrast, muscles of facial expression more closely associated with the orbit tended to have a large number of fibers in each fascicle, and a great quantity of perimysium among the fascicles. These fascicles were long and slender, and tended to taper at one end. For example, the retrahens aurem muscle (Fig. 1) presented as a number of fibers per fascicle and little perimysium separating each fascicle. The orbicularis occuli muscle appeared as a number of long, densely packed fascicles separated from each other by large quantities of perimysium. This orientation of fibers and fascicles may indicate functional correlates. It has long been noted that the force a muscle can potentially generate is partially dependent upon the spatial arrangement of muscle fibers within the muscle (Gans, 1982; Herring et al., 1984; Otten 1988; van Eijden et al., 1996). This is commonly measured with respect to fiber length, which reflects the number of sarcomeres and the maximal force a muscle can produce. However, the number of sarcomeres in parallel, their spatial orientation, and position of the fibers are also measures of potential interest. Densely packed fibers with little space taken up by perimysium may provide more muscle force (van Eijden et al., 1996; Antón, 1999). The notion that the ear muscles have potentially greater force

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Attachments</th>
<th>Proposed function</th>
</tr>
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<tbody>
<tr>
<td>Occipitofrontalis</td>
<td>Attached to scalp as far anterior as frontal region, as far posterior as lambdoidal region, and as far lateral as superior portion of concha; attached posteriorly to atrahens aurem and atollens aurem muscles</td>
<td>Movement of the scalp and elevation of brows</td>
</tr>
<tr>
<td>Attrahens aurem</td>
<td>These fibers are the thickened postero inferior portion of occipitofrontalis m. and are attached to the posterosuperior concha</td>
<td>Drawing the external ear posterosuperiorly</td>
</tr>
<tr>
<td>Atollens aurem</td>
<td>These fibers are the thickened antero inferior portion of occipitofrontalis m. and are attached to the tragus</td>
<td>Drawing the external ear antero inferi orily</td>
</tr>
<tr>
<td>Retrahens aurem</td>
<td>Three slips: inferior slip attached to the inferior concha; posterior slip attached to the posterior concha; anterior slip attached to the anterosuperior concha</td>
<td>Drawing the external ear inferiorly, posteriorly, and anterosuperiorly</td>
</tr>
<tr>
<td>Depressor helicis</td>
<td>Attached to the tragus and the anteroinferior concha</td>
<td>Drawing the external ear inferiorly</td>
</tr>
<tr>
<td>Orbitoauricularis</td>
<td>Attached to the skin immediately superior to upper eyelid, the skin of the supracylari region, and to the tragus</td>
<td>Drawing the skin of the upper eyelid postero inferi orily and drawing the external ear anter osuperiorly</td>
</tr>
<tr>
<td>Orbicularis occuli</td>
<td>Sphincter-like fibers attached to the skin around eye, the supracylari region of the frontal bone and the nasal and maxilla bones</td>
<td>Squeezing the eyelids shut</td>
</tr>
<tr>
<td>Superior auriculolabialis</td>
<td>Attached to the inferior portion of the orbicularis occuli m. and to the skin over the anter osuperior concha</td>
<td>Drawing the external ear superanter iorly</td>
</tr>
<tr>
<td>Inferior auriculolabialis</td>
<td>Attached to the superior portion of the platysma midway between the mouth and ear region and to the tragus</td>
<td>Drawing the external ear anteriorly infero an teri orily</td>
</tr>
<tr>
<td>Mandibuloauricularis</td>
<td>Attached to the skin anterior to the concha and to the skin anterior to the tragus</td>
<td>Approximating the superior and inferior borders of the external ear opening</td>
</tr>
<tr>
<td>Platysma</td>
<td>Attached to the oral commissure and to the skin over the ventral neck and posterior to the ear region</td>
<td>Drawing the oral commissure postero inferi orily and elevating the skin of the neck</td>
</tr>
<tr>
<td>Sphincter colli</td>
<td>Attached to the skin over the zygomatic arch and to the skin over the ventral neck</td>
<td>Drawing the skin over the ventral neck postero inferi orily</td>
</tr>
<tr>
<td>Orbicularis oris</td>
<td>Oblique sphincter-like fibers surrounding the skin over the oral region</td>
<td>Squeezing the oral opening shut</td>
</tr>
<tr>
<td>Mentalis</td>
<td>Attached to the skin inferior to the lower lip and the skin near the mandibular midline</td>
<td>Raises and elevates the lower lip</td>
</tr>
<tr>
<td>Maxillolabialis</td>
<td>Attached to the skin associated with the midfacial region and to the skin associated with the upper lip</td>
<td>Draws the upper lip posterosuperiorly</td>
</tr>
<tr>
<td>Levator labii</td>
<td>Attached to skin of the midface and to the skin around the upper lip</td>
<td>Elevates the angle of the mouth and enlarges nasal aperture</td>
</tr>
<tr>
<td>Nasalis</td>
<td>Attached to the nasal bone, the skin associated with the bridge of the nose and the skin associated with the mystacial vibrissae</td>
<td>Wrinkles and elevates the skin associated with the snout, enlarges nasal aperture, and moves the mystacial vibrissae</td>
</tr>
</tbody>
</table>

*As Murie and Mivart (1872) did not discuss muscle functions, the Proposed Functions are drawn from studies on lemurs (Huber, 1931), macaques (Huber, 1933), and humans, chimpanzees, and baboons (Swindler and Wood, 1982).

*Where information from any source is lacking, such as for the mandibuloauricularis m., the authors have proposed functions based upon the attachments of the muscle.

*bSince specimens did not have calvariae, it was not possible to evaluate the central attachments of this muscle. However, its central attachments are reported to be the lateral portion of the occipital bone (Murie and Mivart, 1872).
in *Otolemur* may correspond with numerous observations that the external ear is highly mobile (e.g., Charles-Dominique, 1977). Finally, no appreciable variation in fiber diameter was noted among any of the muscles in either species. This is in contrast to results gleaned from studies of human facial expression musculature (Stål, 1994). However, great variation in muscle fiber shape was noted between muscles associated more closely with the ear and those associated more closely with the eye. In muscles associated with the ear, a triangular to quadrilateral shape was noted, while a round shape was noted in muscles associated with the eye. The triangular shape may be an artifact related to fibers being packed together, compressing adjacent sarcolemmæ, or it may be caused by differential shrinkage of muscle fibers during the histologic processing. In fibers of the orbicularis occuli muscle, which contains large amounts of perimysium, there may be less compression of adjacent fibers. This would yield a rounder shape than that found in the ear muscles, where there is relatively scant perimysium.

**Muscle Findings**

In examining the gross aspects of *Otolemur* facial expression musculature, we found a far greater number of individual muscles than were previously reported. In their direct dissections of *Otolemur garnettii* and *O. crassicaudatus*, Murie and Mivart (1872) identified only seven muscles of facial expression: the occipitofrontalis muscle, atrahens aurem muscle, atollens aurem muscle, retrahens aurem muscle, orbicularis occuli (palpebrum) muscle, orbicularis oris muscle, and the "nasal" muscles. Aside from that account, and a few generic descriptions of prosimians (Ruge, 1885; Huber, 1931), information about *Otolemur* facial expression musculature is lacking. The data from the present study indicate that *Otolemur* facial expression musculature is far more complex than was previously described. The table below compares the gross results from this study with previous descriptions of facial expression musculature in the lemuroids as presented in Ruge (1885) and Huber (1931). The number and arrangement of muscles found here closely resembles the condition found in *Lemur*.

### Muscle Findings

#### Table 3. Comparison of results of present study to those of Murie and Mivart (1872) and muscles reported in lemuroids

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Murie and Mivart (1872)</th>
<th>Lemuroids*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occipitofrontalis</td>
<td>Similar</td>
<td>Grouped in to “postauriculo-occipital group” with several slips diverging and attaching into ear cartilage (Huber, 1931) which may represent the atollens aurem and atrahens aurem of <em>Otolemur</em> spp.; referred to as the auriculo-occipital group by Ruge (1885)</td>
</tr>
<tr>
<td>Atrahens aurem</td>
<td>Report attachment to the anterior concha</td>
<td>Not reported; most likely included in with the postauriculo-occipital group (Huber, 1931) or auriculo-occipital group (Ruge, 1885)</td>
</tr>
<tr>
<td>Atollens aurem</td>
<td>Similar</td>
<td>Not reported; may be included in with the postauriculo-occipital group (Huber, 1931) or auriculo-occipital group (Ruge, 1885)</td>
</tr>
<tr>
<td>Retrahens aurem</td>
<td>Similar</td>
<td>Not reported in Huber (1931) but appears to be represented by the auricularis group of muscles (multiple slips) in <em>Daubentonia</em> (Ruge, 1885, referred to therein as <em>Cheiromys</em>)</td>
</tr>
<tr>
<td>Depressor helicis</td>
<td>Not reported</td>
<td>Not reported by Huber (1931) but similar to Ruge (1885) for <em>Lemur</em> spp.</td>
</tr>
<tr>
<td>Orbitalauricularis</td>
<td>Not reported</td>
<td>Not reported by Huber (1931) but similar to Ruge (1885) for <em>Lemur</em> spp.</td>
</tr>
<tr>
<td>Orbicularis occuli</td>
<td>Similar</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Superior auriculolabialis</td>
<td>Not reported</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Inferior auriculolabialis</td>
<td>Not reported</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Mandibuloauricularis</td>
<td>Not reported</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Platysma</td>
<td>Similar</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Sphincter colli</td>
<td>Not reported</td>
<td>Similar but neither Huber (1931) nor Ruge (1885) report any differences between the anterior and posterior extents of this muscle</td>
</tr>
<tr>
<td>Orbicularis oris</td>
<td>Similar, but reported to be more closely connected to fibers of “cheek and nasal muscles”</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Mentalis</td>
<td>Not reported</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Maxillolabialis</td>
<td>Not reported</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Levator labii</td>
<td>Not reported; may have been included with “nasolabial musculature”</td>
<td>Similar in all accounts</td>
</tr>
<tr>
<td>Nasalis</td>
<td>Not reported; may have been included with “nasal musculature”</td>
<td>Similar in all accounts</td>
</tr>
</tbody>
</table>

*Ruge (1885) and Huber (1931).
sp., Varecia, and the indrids in general (Ruge, 1885). It is readily apparent that Otolemur cannot be regarded as having a more primitive arrangement than any of the members of Lemuroidea (see Table 3).

While a number of muscles were reported for the first time in the present study, several muscles previously described for Lemur spp., Varecia, and the indrids (Ruge, 1885) were not located (i.e., the caninus muscle, tragoantitragus muscle, and helicis muscle). It is especially curious that two muscles associated with the ear in the lemuroids—the tragoantitragus and helicis muscles—were not found in the present study, since Otolemur is particularly noted for their large, mobile ears (e.g., Charles-Dominique, 1977; Ankel-Simons, 2000).

Few gross differences were noted between Otolemur crassicaudatus and O. garnetti in the present study, but in several cases O. garnetti appeared to have a more robust musculature, specifically in the orbitoauricularis, nasalis, and sphincter colli muscles. The orbitoauricularis muscle, which is attached to the ear region and supraorbital region, presumably moves the ear complex and elevates the skin over the supraorbital region, while the nasalis muscle presumably moves the skin associated with the nares and mystical vibrissae. These functions may be associated with hearing, vision, olfaction, and/or tactile functions, in addition to social signaling. In the light of the higher degree of territoriality in O. garnetti (Harcourt, 1986; Harcourt and Nash, 1986), the greater apparent robustness of these muscles may reflect greater usage in territorial displays. However, in the absence of detailed descriptions of any territorial displays, it is not possible to make definitive statements regarding this potential function. In addition, the diet of Otolemur garnetti is composed of half insects and half fruits (Harcourt and Nash, 1986), while that of O. crassicaudatus primarily consists of gums (Harcourt, 1986). Any increased robustness in muscles that move the pinna and the nares may provide an advantage to O. garnetti in localizing prey.

Phylogenetic Aspects

In comparing the muscles of facial expression located in the present study to those in lemuroids, it is apparent that Otolemur is very similar to the lemuroids. The most notable differences were observed in the ear region. While Murie and Mivart (1872) recognized the occipitofrontalis, atollens aurem, and atrahens auren muscles as three distinct entities, this was not recognized for lemuroids (see Ruge, 1885). In the lemuroids, the occipitofrontalis (referred to as the auriculo-occipitalis) has only a brief connection to the external ear, which is very unlike the situation in Otolemur.

Whereas the Otolemur have a three-banded retrahens auren muscle, the lemuroids have instead the superior and anterior auricularis muscles (which exist as a number of bands), running from the cranium to the concha. The auricularis muscles of lemuroids are very similar in their attachments to the retrahens auren, and may not represent a significant departure. However, the apparent reduction of the attachment of the occipitofrontalis/attrahens auren/atollens auren grouping to the ear seen in the lemuroids may be viewed as a noteworthy alteration. Previous authors have described complex movements of the external ear in Otolemur social interactions (Andrew, 1963; Tandy, 1974; Charles-Dominique, 1977), while similar descriptions for lemuroids are lacking. In these species expressions involving the mouth are more common (Andrew, 1963; Jolly, 1966; Pereira and Kappeler, 1997). Since this is the only notable difference between the results of the present study and those reported by Ruge (1885) and Huber (1931) for lemuroids, it may be inappropriate to describe the muscles of facial expression in Otolemur as being primitive compared to those in lemuroids, or as being significantly different.

Huber (1930a,b, 1931) noted that significant taxonomic information can be extracted from muscles of facial expression and their arrangements in species. Considering the far greater number of muscles found in Otolemur, and their similar arrangement relative to lemuroids, the current results may be useful in the ongoing research into the taxonomic relationships between the lorisoids and lemuroids, and the position of Otolemur relative to other Galaginae. Our findings underscore the need to investigate the facial expression musculature in all prosimians. However, these results should not be interpreted by themselves as evidence that Otolemur is more closely related to the lemuroids than to the lorisoids.

LITERATURE CITED


