

Evolution of the Muscles of Facial Expression in a Monogamous Ape: Evaluating the Relative Influences of Ecological and Phylogenetic Factors in Hylobatids

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ABSTRACT

Facial expression is a communication mode produced by facial (mimetic) musculature. Hylobatids (gibbons and siamangs) have a poorly documented facial display repertoire and little is known about their facial musculature. These lesser apes represent an opportunity to test hypotheses related to the evolution of primate facial musculature as they are the only hominoid with a monogamous social structure, and thus live in very small groups. Primate species living in large groups with numerous social relationships, such as chimpanzees and rhesus macaques, have been shown to have a complex facial display repertoire and a high number of discrete facial muscles. The present study was designed to examine the relative influence of social structure and phylogeny on facial musculature evolution by comparing facial musculature complexity among hylobatids, chimpanzees, and rhesus macaques. Four faces were dissected from four hylobatid species. Morphology, attachments, three-dimensional relationships, and variation among specimens were noted and compared to rhesus macaques and chimpanzees. Microanatomical characteristics of the orbicularis oris muscle were also compared. Facial muscles of hylobatids were generally gracile and less complex than both the rhesus macaque and chimpanzee. Microanatomically, the orbicularis oris muscle of hylobatids was relatively loosely packed with muscle fibers. These results indicate that environmental and social factors may have been important in determining morphology and complexity of facial musculature in the less social hylobatids and that they may not have experienced as strong selection pressure for mimetic muscle complexity as other, more social primates. *Anat Rec*, 294:645–663, 2011. © 2011 Wiley-Liss, Inc.

Key words: communication; mimetic muscle; gibbon; siamang; facial muscle

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Hylobatids, the gibbons and siamangs [Primates: Hominoidea: Hylobatidae (Groves, 2005)], are small, arboreal, and territorial lesser apes found throughout the evergreen forests of southeast Asia including Indonesia, Eastern India, Vietnam, Laos, Cambodia, and Southern China (Rowe, 1996; Bartlett, 2008). Together with humans and the great apes (chimpanzees, bonobos, gorillas, and orangutans) they comprise the superfamily Hominoidea (Groves, 2001, 2005). All species are currently classified as endangered or critically endangered making insights into their behavior, ecology, and evolutionary morphology imperative (Cunningham and Mootnick, 2009; IUCN Red Book, 2010; Thinh et al., 2010).

During evolution of the hominoids, hylobatids were the first to branch off, around 17 million years ago (Fleagle, 1984; Pilbeam, 1996; Cunningham and Mootnick, 2009). Although it is clear that hylobatids form a monophyletic clade to the exclusion of the great apes, there is no clear consensus about the phylogenetic and taxonomic relationships among the family Hylobatidae with no definitive number of species or number of genera (Prouty et al., 1983; Hall et al., 1998; Groves, 2001, 2005; Roos and Geissmann, 2001; Mootnick and Groves, 2005; Takacs et al., 2005; Cunningham and Mootnick, 2009; Thinh et al., 2010). Currently, four genera are recognized by most authors: the small-bodied (around 5 kg) *Hylobates* (including *H. agilis*, *H. albibarbis*, *H. klossii*, *H. lar*, *H. moloch*, *H. muelleri*, and *H. pileatus*), *Nomascus* (including *N. concolor*, *N. gabriellae*, *N. hainanus*, *N. siki*, and *N. leucogenys*), and *Bunopithecus* (*B. hoolock*), and the larger-bodied (around 10 kg) *Symphalangus* (*S. syndactylus*). The genera *Hylobates*, *Nomascus*, and *Bunopithecus* are gibbons, in contrast with *Symphalangus*, which is the only extant member of the siamangs. Species are grouped into these genera primarily based upon differences in chromosome number (Cunningham and Mootnick, 2009).

Unlike the great apes (Hominidae), hylobatids show remarkable behavioral, ecological, and morphological uniformity. All hylobatids are brachiators with long upper limbs and digits (Leighton, 1987; Fleagle, 1999). They live in densely foliated trees, are primarily frugivorous (except for *S. syndactylus*, which eats primarily young leaves), and are characterized by loud, long-distance vocalizations (Raemaekers, 1984; Leighton, 1987; Bartlett, 2007; Cunningham and Mootnick, 2009). Hylobatids are especially remarkable in that they are the only monogamous ape and group size is drastically smaller than chimpanzees, bonobos, and gorillas, averaging only four individuals: a mated male and female with their infant and a sub-adult offspring (Carpenter, 1940; Chivers, 1984; MacKinnon and MacKinnon, 1984). Although there are reports of multi-male and multi-female groups, mated monogamous male/female pairs is by and large a characteristic trait across all hylobatid genera (Leighton, 1987; Bartlett, 2007). Although there is a dominance hierarchy in chimpanzees and gorillas with one male generally monopolizing access to the reproductive-aged females, dominance hierarchies seem to be absent in hylobatids (Kleiman, 1977; Gittins and Raemaekers, 1980; Palombit, 1996; Bartlett, 2007, 2008).

All hylobatids are highly territorial and they typically forage together as a "family" group (Raemaekers, 1984; Leighton, 1987; Bartlett, 2007). Although chimpanzee and bonobo populations sometimes fission into smaller

foraging parties that later re-group (Goodall, 1986; de Waal, 1997; Stumpf, 2007), hylobatid groups typically do not fission (Leighton, 1987; Bartlett, 2007). Territorial defense is common between and within hylobatid taxa and seems to be one of the functions of the loud vocalization known as "duetting," a stereotyped long-distance song performed by a mated pair. There is compelling evidence that these duets are species-specific and gender-specific (Carpenter, 1940; Mitani, 1988; Geissmann, 2002; Fan et al., 2009).

Outside of interactions with family members and regular morning duetting to defend territory, hylobatids lead a relatively subdued social life when compared to the African hominids (chimpanzees, bonobos, and gorillas) and spend very little time socializing with conspecifics in general. Unlike chimpanzees, who spend up to 20% of their daily activity budget socializing, hylobatids spend less than 5% of their daily activity budget socializing, presumably due to a lack of social partners and necessity for social bonding (Leighton, 1987; Dunbar, 1993). Despite the fact that hylobatids socialize less, their daily activity patterns are highly synchronized, probably coordinated through observation of the other group members, but not by communicating with them. Their limited communicative repertoire may result from this lack of necessity (Chivers, 1976).

All primates communicate with conspecifics using a variety of modalities including visual communication. One close-proximity method of visual communication used by many primates is facial expression, the production, and neural processing of facial movements (Darwin, 1872; Burrows, 2008). They serve, in a communicative setting, to signal the sender's emotional/motivational intent and territorial intentions, they are used in mate/kin recognition, and/or function in agonistic and conciliatory displays (Darwin, 1872; Andrew, 1963; van Hooff, 1972; Schmidt and Cohn, 2001; Burrows, 2008). Primate facial expressions are movements of the cartilage of the external ear and the alar cartilages of the nose, the skin of the face, the vibrissae, and the lips, eyelids, and nares. These facial movements are produced by the facial musculature, or the mimetic musculature, which is possessed by all mammals. This musculature is derived from the second (hyoid) pharyngeal arch, is innervated by the facial nerve/seventh cranial nerve, and is unique among all other skeletal muscle in attaching directly into the dermis of the face/neck (Young, 1957; Gasser, 1967).

Our conceptualization of primate facial musculature morphology and evolution is traditionally rooted in the organization of the phylogeny of primates. Generally, the lower primates, such as lorises, galagos, lemurs, and tarsiers, have been thought to possess a small number of relatively simple, undifferentiated muscles with little complexity (complexity is defined here as number and size of muscles and how interconnected they are with one another, so that a high number of small muscles with discrete attachment sites equals great complexity and a lower number of larger muscles with interconnected attachments equals lower complexity). On the other hand, monkeys, apes, and humans, have been conceptualized as having an increasing number of small, discrete facial muscles and greater muscle complexity in a linear, step-wise fashion as the primate phylogenetic scale is ascended toward humans.

Recent studies of primate facial musculature, facial expressions, and the neurobiology of facial movement have shown that this linear, phylogenetic concept is too simplistic and that factors such as group size, mating system, dietary niche, environment, and rigidity of dominance hierarchies are strongly associated with facial musculature morphology and complexity (Burrows and Smith, 2003; Sherwood, 2005; Sherwood et al., 2005; Burrows et al., 2006, 2009; Burrows, 2008; Dobson, 2009; Dobson and Sherwood, 2011). These findings have challenged the previous paradigm that phylogenetic position is the primary factor influencing complexity and morphology of primate facial musculature and facial displays (Ruge, 1885; Gregory, 1929; Huber, 1930a,b, 1931; Schultz, 1969).

HYPOTHESES

As the only group of monogamous apes and one of the few to live in very small groups (the other being orangutans), hylobatids represent an ideal group in which to evaluate hypotheses related to the evolution of primate facial musculature, facial displays, and social behavior. Although surprisingly little is known about hylobatid communication via facial expressions, previous studies have indicated that they may have a more limited repertoire than primate species living in large groups such as rhesus macaques (*Macaca mulatta*), chimpanzees (*Pan troglodytes*), and humans (Chivers, 1974; Gittins, 1979; Liebal et al., 2004).

The hylobatids live in a densely foliated arboreal environment in much smaller groups than rhesus macaques and chimpanzees, both of whom live in more open, less densely foliated environments. These factors likely limit opportunities for close-proximity visual communication by way of facial expressions in hylobatids. Rhesus macaques, *M. mulatta* [Cercopithecoidea: Cercopithecidae: Cercopithecinae, (Groves, 2005)], live in large multi-male/multi-female groups with a rigid, "despotic" dominance hierarchy in a more open, less densely foliated environment than hylobatids. As would be expected based upon these factors, rhesus macaques use a large number of facial displays in close-proximity communication with conspecifics (Maestriperi, 1999; Aureli and Schino, 2004; Parr et al., 2010). The facial musculature of *M. mulatta* has been shown to reflect the frequent use of specific, graded facial displays and is very similar in morphology and complexity to that of the distantly related chimpanzees, *P. troglodytes* [Hominoidea: Hominoidea: Homininae (Groves, 2005)]. Chimpanzees also live in large multi-male/multi-female social groups with dominance hierarchies in relatively open environments making opportunities for close-proximity interaction with conspecifics great. Recent studies have shown that chimpanzees have a well-developed, graded, and complex facial display repertoire (Parr et al., 1998; Parr and de Waal, 1999; Parr, 2003; Parr and Waller, 2006; Vick et al., 2007) with facial musculature very similar to that of the rhesus macaque (Burrows et al., 2006; Burrows, 2008).

The present study was designed to test the following hypotheses related to the evolution of hylobatid facial musculature: (1) If ecological variables such as environment (foliation, arboreal vs. terrestrial) and social factors, such as social group size, and organization are

influential in evolution of the morphology and complexity of facial musculature in hylobatids, then we expect to see relatively low complexity compared to the closely related chimpanzee and the distantly related rhesus macaque (hylobatids < *M. mulatta* = *P. troglodytes*); (2) If, instead, phylogenetic position is more influential in evolution of the morphology and complexity of facial musculature in hylobatids, we expect to see greater complexity than in the distantly related rhesus macaque but less complexity than in the closely related chimpanzee (*M. mulatta* < hylobatids < *P. troglodytes*), reflecting the phylogenetic position of hylobatids between rhesus macaques and chimpanzees.

MATERIALS AND METHODS

Faces from four hylobatids were used in the present study: one adult male *H. lar*, one adult male *H. muelleri*, one adult female *S. syndactylus*, and one juvenile male *Nomascus gabriellae*. The *H. muelleri* and *S. syndactylus* specimens were obtained from the Cleveland Metro-Parks Zoo (Cleveland, OH) as heads that had been separated from the cervical portion of the spine following necropsy. The *H. lar* specimen was housed in the comparative anatomy collection at Howard University (Washington, DC) and the *N. gabriellae* specimen was located at Valladolid University (Valladolid, Spain). Both of these specimens were full cadavers and were obtained following natural deaths in zoos (The National Zoological Park, Washington, DC and Valwo Zoo in Valladolid). All specimens were immersed and preserved in 10% buffered formalin following necropsies at the zoos except for the *N. gabriellae* specimen which was fresh.

In the *H. muelleri* and *S. syndactylus* specimens, the brains had already been removed at necropsy prior to preservation. A midline incision was thus made during dissection of the faces starting at the frontal and nasal regions, continuing over both lips, and over the mental region in order to separate the left and right sides of the face. The loose skin flap on the right side made during removal of the brain was continued inferiorly and caudally to complete removal of the right side of the face from the skull (see also Burrows and Smith, 2003; Burrows et al., 2006, 2009). The left side remained intact on the skull. All skin, superficial fasciae, and facial musculature were separated from the more deeply located musculature of the skull (the buccinatorius and masseter muscles) and the bone itself using No. 11, 12, and 21 scalpel blades and a variety of dissection tools. These dissections were done by a single investigator (AMB). Care was taken to remove as much of the facial musculature as possible with the skin and superficial fasciae, leaving behind only the bony attachments. The external ear was removed with the skin. This process created a "facial mask" that was separate from the skull and held all of the facial muscles (except for the buccinatorius muscle which was left behind with the skull).

In the *N. gabriellae* and *H. lar* specimens, both the right and left sides of the face were dissected by a single investigator (RD) using similar tools. Brains of these specimens had not been removed during necropsy and were still inside the cranial cavity during dissection. Thus, midline incisions were made from the bregmatic region down over the glabellar region, continuing over the nasal region, both lips, and over the mental region.

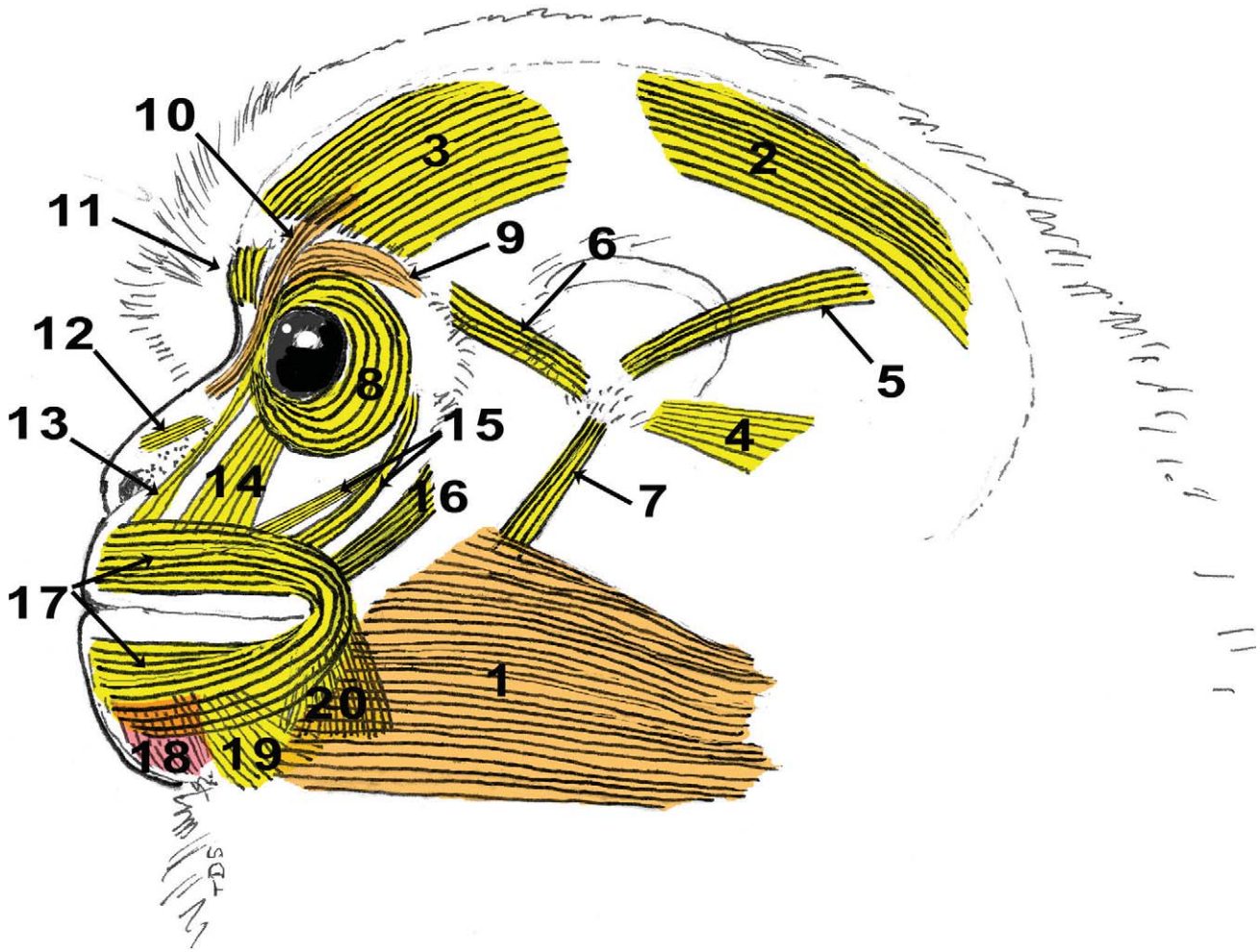


Fig. 1. Abstract of facial expression (mimetic) musculature in a representative hylobatid in lateral view. In this figure, yellow represents muscles that are on the most superficial level of the face, red represents muscles that are the most deeply located, and orange represents muscles that are intermediate in depth. 1—platysma muscle (cervicale and myoides), 2—occipitalis muscle, 3—frontalis muscle, 4—auricularis posterior muscle, 5—auricularis superior muscle, 6—auriculo-orbitalis muscle, 7—depressor helicis muscle, 8—orbicularis oculi muscle, 9—corrugator supercilli muscle, 10—depressor supercilli

muscle, 11—procerus muscle, 12—nasalis muscle, 13—levator labii superioris alaeque nasi muscle, 14—levator labii superioris muscle, 15—zygomaticus minor muscle, 16—zygomaticus major muscle, 17—orbicularis oris muscle, 18—mentalis muscle, 19—depressor labii inferioris muscle, 20—depressor anguli oris muscle. Not shown in this diagram: depressor septi nasi muscle, levator anguli oris facialis muscle, and buccinatorius muscle. See text in Results section and Table 1 for descriptions of these muscles.

Similar cuts were made caudally starting at the bregmatic region extending over the dorsal surface onto the neck. The skin and superficial fasciae were reflected away from the facial musculature which was kept with the skull. These specimens, then, had the facial musculature preserved on the bony skull. These two differing dissection methodologies allowed for a complete picture of the facial musculature among the specimens, their three-dimensional relationships to one another, and to the skull.

The facial masks created in the *H. muelleri* and *S. syndactylus* specimens were allowed to air dry for 30–45 min to produce the best possible differentiation among muscle, fasciae, and other connective tissue. All connective tissue was then removed from the musculature using microdissection tools so that each facial muscle and its borders on the mask were discernible from other

surrounding muscles and fasciae (see Burrows and Smith, 2003; Burrows et al., 2006, 2009).

In all four specimens, the musculature was examined for presence/absence, attachments to skin, bone, cartilage, and to one another, their three-dimensional relationships to one another and to the skull, and for variation among specimens. Muscles were classified with reference to a variety of sources (Burrows et al., 2006, 2009; Diogo et al., 2009). All muscles and their attachments were recorded, digitally photographed, and images were stored on a personal computer.

Microanatomical features of muscles may provide salient information on functional aspects of a muscle (e.g., Gans, 1982; van Eijden et al., 1996; Burrows and Smith, 2003; van Wassenbergh et al., 2007; Organ et al., 2009; Rogers et al., 2009; Vinyard and Taylor, 2010). To examine

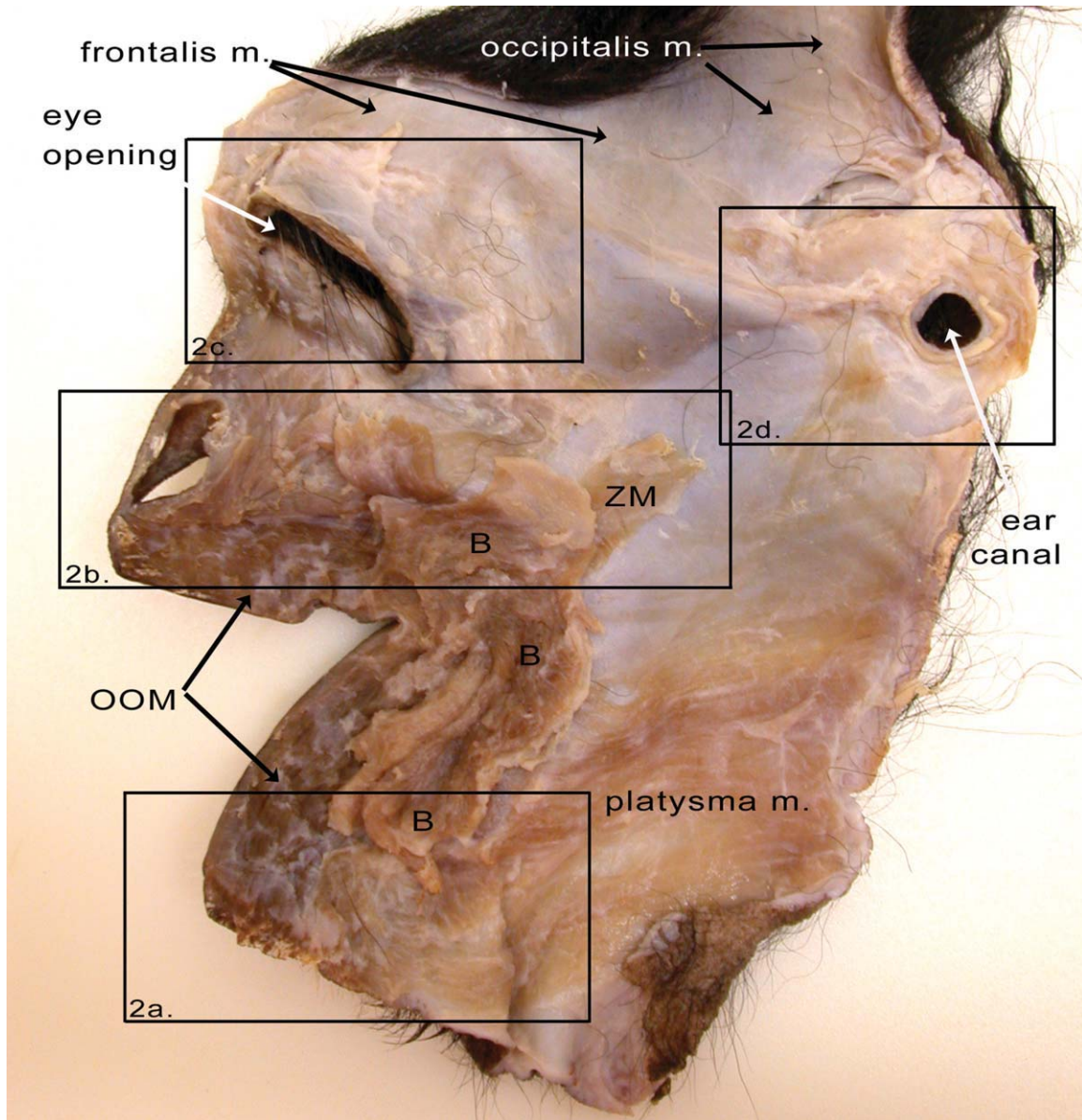


Fig. 2. Right side of facial mask from *H. muelleri*. This is a view of the deep surface of the facial mask. Boxes with numerals and letters refer the reader to close-up views of the selected regions in the following figures. ZM, zygomaticus major muscle; B, buccinatorius muscle; OOM, orbicularis oris muscle.

the microanatomical arrangement of facial muscle fibers in hylobatids, the present study gathered samples from the orbicularis oris muscle of the *H. muelleri* sample after dissection for histologic processing. This muscle was chosen because it is relatively large and easy to process histologically and has functional significance in producing facial expressions in many primate species (Liebal et al., 2004; Vick et al., 2007; Parr et al., 2010). A sample from the right upper fibers of the orbicularis oris muscle was taken ($\sim 2 \text{ cm} \times 1 \text{ cm}$) from the region directly inferior to the right nares. This location provided the most isolated portion of the orbicularis oris muscle, free from attachments of other muscles associated with the upper lip. This muscle sample was embedded in paraffin, sectioned at $10 \mu\text{m}$, and stained with Gomori trichrome (see Burrows and

Smith, 2003; Rogers et al., 2009). All stained sections were viewed under a light microscope for muscle fiber appearance, general appearance of the pars marginalis and pars peripheralis portions of the orbicularis oris muscle, and appearance of the connective tissue.

To test the hypotheses, results from the present study were compared to results from previous studies of *M. mulatta* (Burrows et al., 2009) and *P. troglodytes* (Pellett, 1979; Burrows et al., 2006).

RESULTS

Gross Musculature

Figures 1 and 2 show the hylobatid musculature in place on an abstraction of the facial mask and the facial

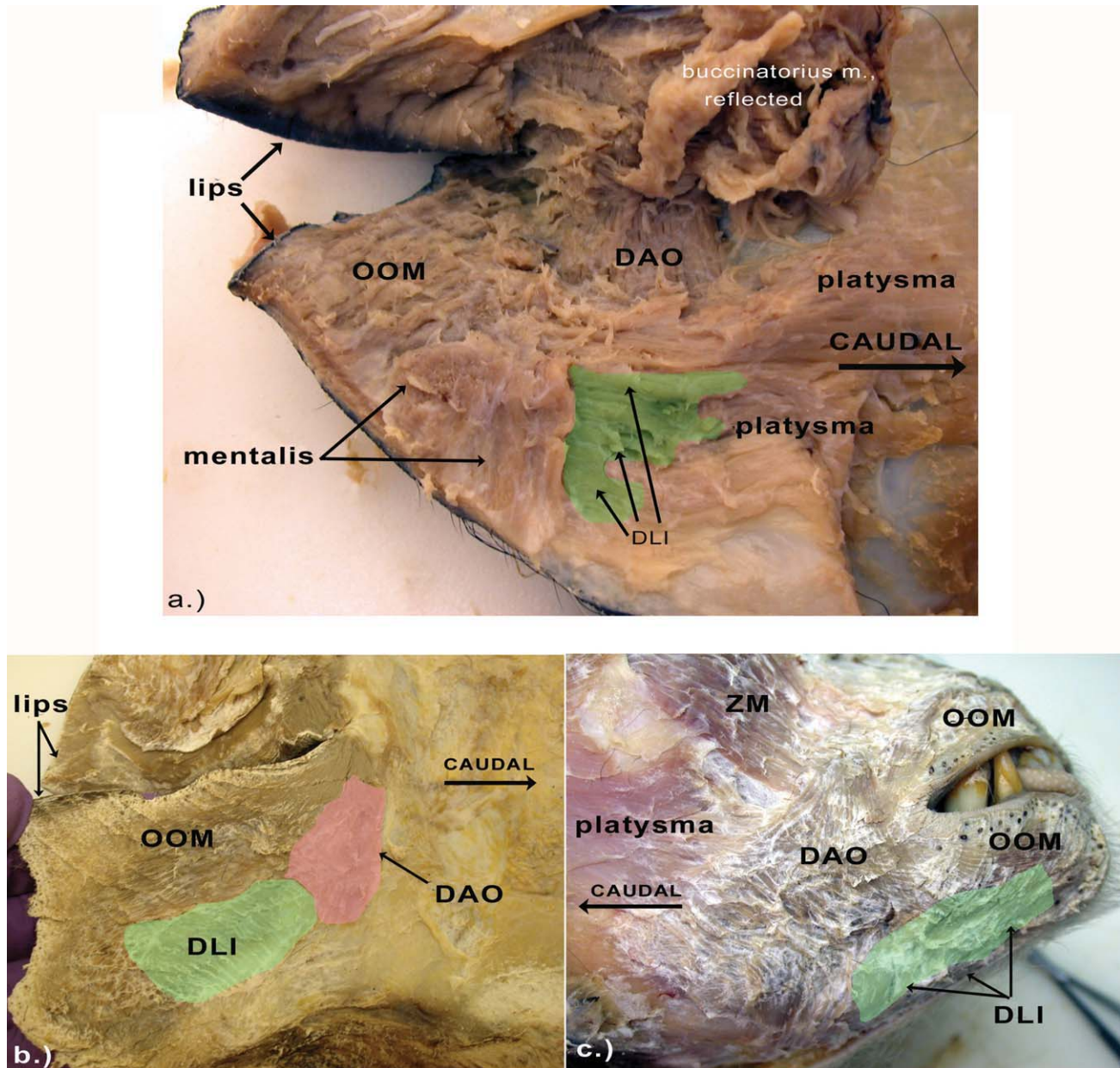


Fig. 2a. Close-up views of the lower lip/mental region from the indicated area of the facial mask from Fig. 2 in (a) *Symphalangus syndactylus* (right side of facial mask), (b) *Pan troglodytes* (right side of facial mask), and (c) *Macaca mulatta* (right side of face with musculature attached to skull). OOM, orbicularis oris muscle; DLI, depressor labii

inferioris muscle; DAO, depressor anguli oris muscle; ZM, zygomaticus major muscle. The different colors in these images are used to show the borders of muscles where it is not especially clear. Note the especially gracile nature of the DLI muscle in the *S. syndactylus* specimen compared to the others.

mask itself. Table 1 describes muscles located in the hylobatids of the present study along with their detailed attachments and Table 2 shows the musculature in comparison to those of rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*). Gross observation of the facial musculature from the four species in the present study revealed minimal variation in presence/absence of muscles (see Table 1 and text below); thus, all specimens are treated here together. Compared to previ-

ous work on chimpanzees, there was relatively little fascia interspersed among the muscles of the face (Burrows et al., 2006). As seen in chimpanzees and rhesus macaques, but unlike the case for humans, there was exceptionally little adipose in any region of the hylobatid faces (Standring, 2004; Burrows et al., 2006, 2009). Many muscles were intimately adherent to the superficial fasciae, such as the musculature associated with the upper lip and the superciliary region.

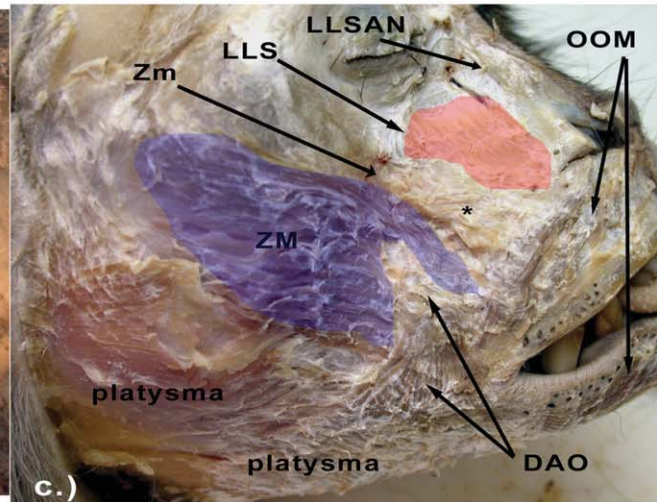
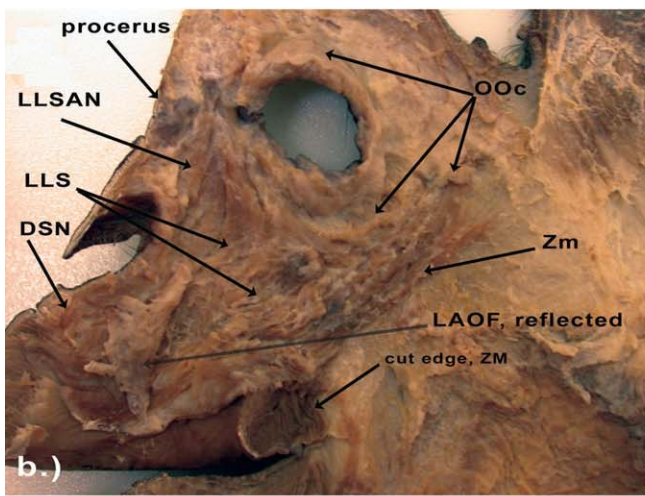
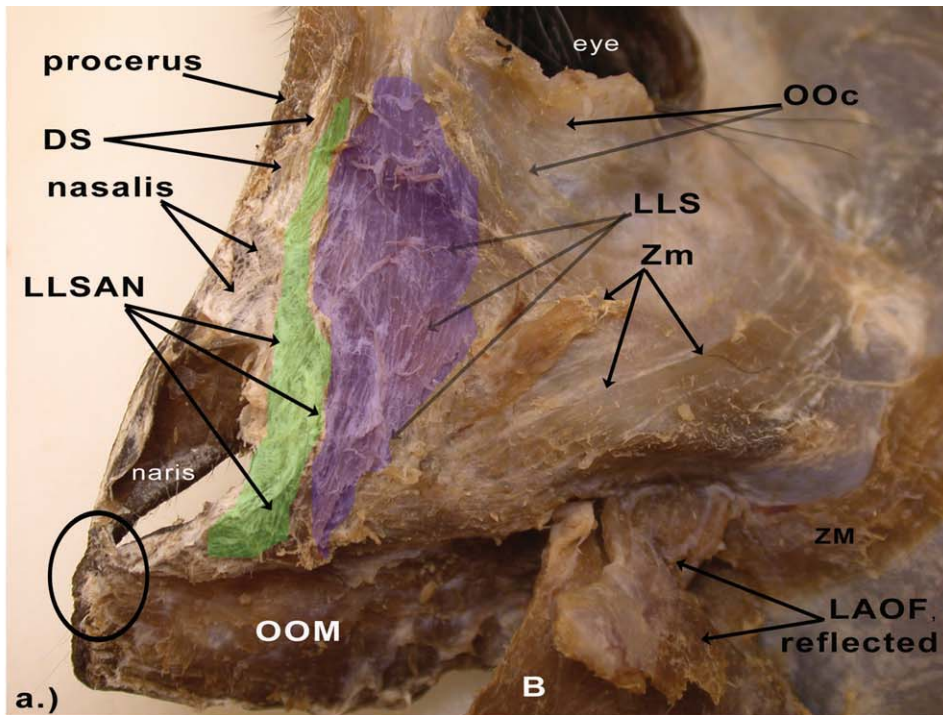


Fig. 2b. Close-up views of the midfacial region in facial masks from the indicated area of Fig. 2 for (a) *H. muelleri* and (b) *P. troglodytes*. Panel c is the right side of the skull of *M. mulatta* with the midfacial muscles adherent to the skull. DS, depressor supercilli muscle; LLSAN, levator labii superioris alaeque nasi muscle; OOM, orbicularis oris muscle; B, buccinatorius muscle; LAO, levator anguli oris facialis muscle; ZM, zygomaticus major muscle; Zm, zygomaticus minor muscle; LLS, levator labii superioris muscle; DSN, depressor septi nasi

muscle; OOc, orbicularis oculi muscle; DAO, depressor anguli oris muscle. The empty circle represents the area where the depressor septi nasi muscle was located in the *Nomascus gabriellae* and the *H. lar* specimens in the present study. Note the relatively gracile nature of the OOM in the *H. muelleri* relative to the *P. troglodytes* and *M. mulatta* specimens but the relatively robust, complex zygomaticus minor muscle in *H. muelleri*. The different colors in these images are used to show the borders of muscles where it is not especially clear.

Platysma muscle (cervicale and myoides portions). Figures 1, 2a–d, 3, 4 and 5 show the form of the platysma muscle and its attachments. A description of this muscle is given in Table 1. Interestingly, the platysma muscle attached to the walls of the air sac in the *S. syndactylus* specimen. In general form and appearance, this muscle was overall similar to that of rhesus macaques and chimpanzees. In chimpanzees (as well as

in humans and gorillas), the platysma usually has no nuchal origin, that is, there is no platysma cervicale (see Table 2).

Occipitalis muscle. The occipitalis muscle in hylobatids was connected to the auriculo-orbitalis muscle by a thick sheet of fascia and poorly differentiated from this muscle (Figs. 1, 2d; Table 1). In the rhesus macaque

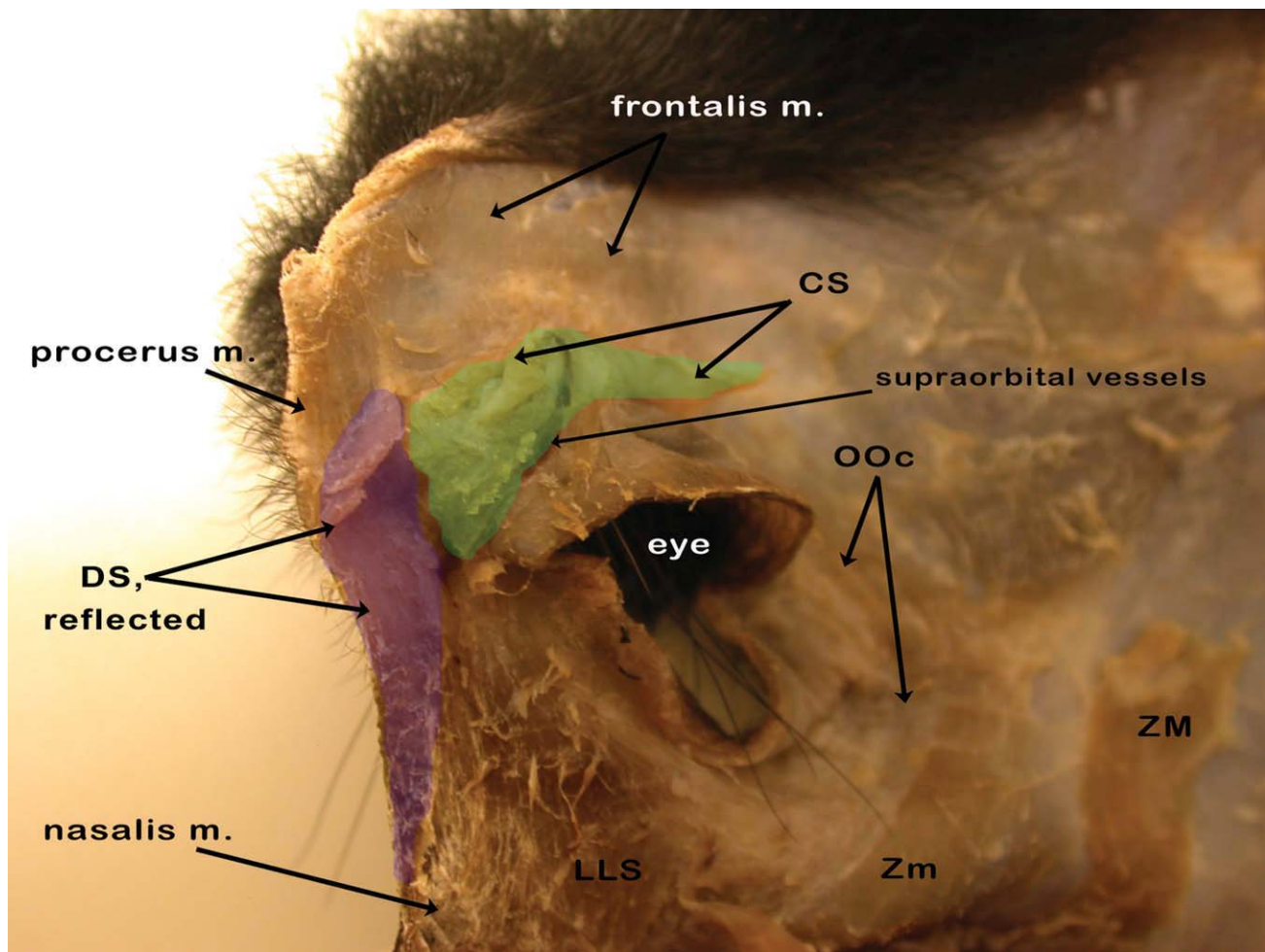


Fig. 2c. Right side close-up of the orbital/superciliary region in the facial mask from the indicated area of Fig. 2 using the same specimen. DS, depressor supercilli muscle; LLS, levator labii superioris muscle; Zm, zygomatic minor muscle; ZM, zygomatic major muscle; OOc, orbicularis oculi muscle; CS, corrugator supercilli muscle.

The green color represents the borders of the corrugator supercilli muscle and the blue color represents the borders of the depressor supercilli muscle. Comparative specimens for *P. troglodytes* and *M. mulatta* are not included here because there were not particular differences in the superciliary/orbital muscles among the three species.

and chimpanzee, the occipitalis muscle has no connections to any other muscle such as its connection here to the auriculo-orbitalis muscle.

Frontalis muscle. The frontalis muscle in hylobatids was also connected to the auriculo-orbitalis muscle via a broad fascial sheet (Figs. 1, 2c,d, 5; Table 1). Other than this attachment, the frontalis muscle in hylobatids was very similar to that of the rhesus macaque and the chimpanzee (Burrows et al., 2006, 2009).

Auricularis posterior muscle. This muscle in hylobatids was very robust and different from that of the rhesus macaque (where it is a two-headed muscle), but was similar to the auricularis posterior muscle of chimpanzees (Burrows et al., 2006, 2009) (Fig. 1; Table 1).

Auricularis superior muscle. Relative to the rhesus macaque, this muscle is quite small but is similar in

appearance to that in chimpanzees (Burrows et al., 2006, 2009) (Figs. 1, 2d, 5; Table 1).

Auriculo-orbitalis muscle. This muscle was referred to in the rhesus macaque and the chimpanzee as the “anterior auricularis muscle” but is termed “auriculo-orbitalis” here based upon Diogo et al. (2009) (Figs. 1, 2d; Table 1). This muscle is poorly separated from the frontalis and the occipitalis muscles, presenting as a relatively undifferentiated sheet of muscle fibers. This is very unlike the morphology seen in the rhesus macaque and the chimpanzee (Burrows et al., 2006, 2009) where it was well-defined and fully independent from all surrounding muscles.

Depressor helicis muscle. This muscle in the rhesus macaque was referred to as the “inferior auricularis” but is termed here “depressor helicis” in accordance with Diogo et al. (2009; see also Seiler, 1976) (Figs. 1, 2d, 5; Table 1). This muscle in hylobatids was robust and

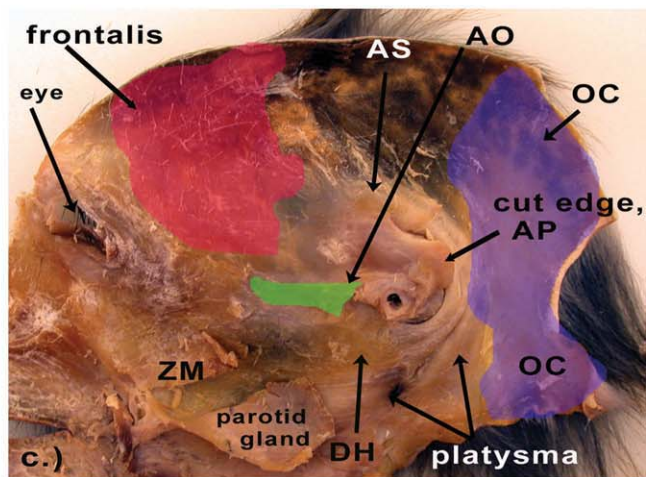
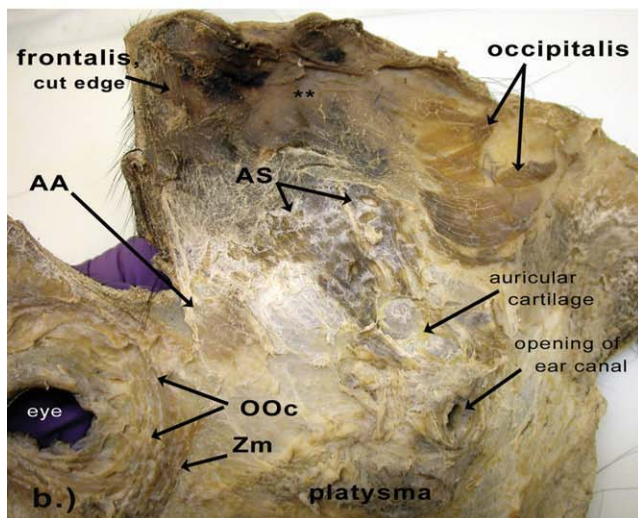
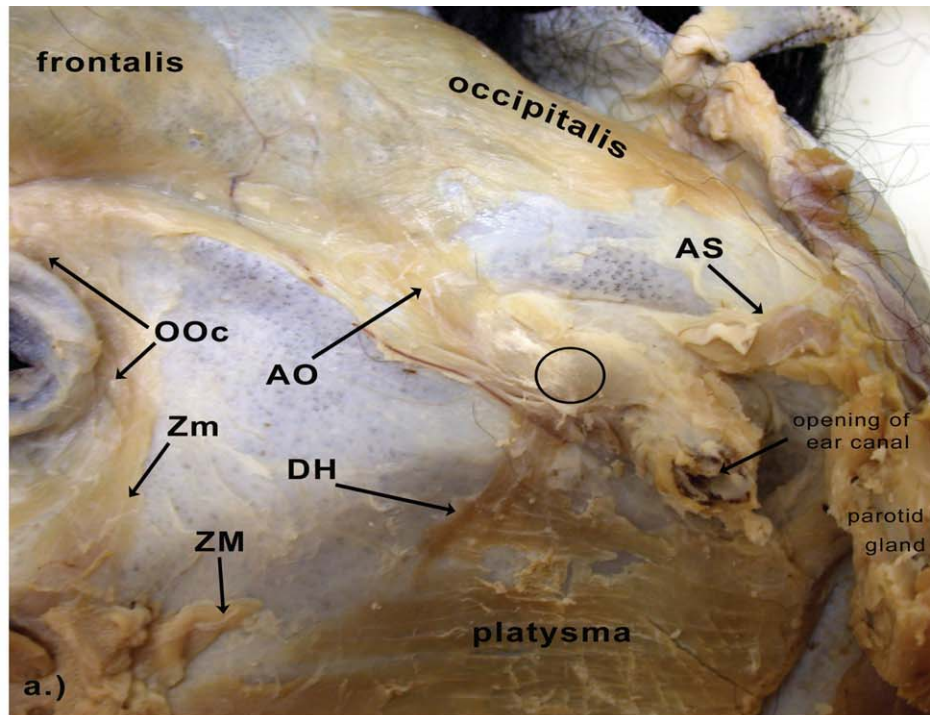


Fig. 2d. Close-up views of the region of the external ear in the indicated area of Fig. 2 using (a) *H. muelleri* (right side of the face mask), (b) *P. troglodytes* (right side of the face mask), and (c) *M. mulatta* (right side of the face mask). AS, auricularis superior muscle; AA, auricularis anterior; AO, auriculo-orbitalis muscle; DH, depressor helicis muscle; ZM, zygomaticus major muscle; Zm, zygomaticus minor muscle; OOc, orbicularis oculi muscle; OC, occipitalis muscle. The empty circle indi-

similar to that of the rhesus macaque (Burrows et al., 2009). The depressor helicis muscle was not noted in the chimpanzee (Sontag, 1923; Pellatt, 1979; Burrows et al., 2006).

Orbicularis oculi muscle. Compared to rhesus macaques and chimpanzees, the orbicularis oculi muscle in the hylobatids was much thinner and more difficult to differentiate from surrounding skin and fasciae (Figs. 1, 2b–d, 3, 4; Table 1). It was so gracile that the inferior

cates the position of the tragus in panel a. The different colors in these images are used to show the borders of muscles where it is not especially clear. Note in panel a that the auriculo-orbitalis muscle of *H. muelleri* is physically connected to both the frontalis and occipitalis muscles via a fascial band. This connection is absent in both *P. troglodytes* (b) and *M. mulatta* (c).

fibers failed to cover the superior parts of the levator labii superioris and zygomaticus muscles as they do in many other anthropoid primates (Standring, 2004; Burrows et al., 2006, 2009).

Corrugator supercilii muscle. The corrugator supercilii muscle in hylobatids was very similar to that of rhesus macaques and chimpanzees (Burrows et al., 2006, 2009) (Figs. 1, 2c, 3; Table 1).

TABLE 1. Facial musculature in hylobatids

Muscle	Attachments
Platysma	robust, flat, superficially located muscle attached to skin over lateral aspect of face superiorly near level of ear canal, inferiorly to level of neck, extending caudally to nuchal region (this portion represents the platysma cervicale); attachments also to walls of air sac and to skin over the clavicular region (this portion represents the platysma myoides); rostrally it is attached to the level of depressor labii inferioris and depressor anguli oris muscles, and to the upper and lower fibers of orbicularis oris muscle, as well as to the modiolus region (this represents the platysma cervicale plus the platysma myoides); superficial to depressor helcis muscle
occipitalis	flat, superficial, wide muscle as a single belly; attached to fascia near the nuchal region and the region of bregma; connected to auriculo-orbitalis muscle via fascia
frontalis	flat, wide, robust muscle attached caudally to the fascia near the rostral border of occipitalis muscle; attached rostrally to fascia near superciliary region and corrugator supercilii muscle; blends with superior edge of procerus muscle; connected to auriculo-orbitalis muscle via fascia
auricularis posterior	plump, robust, single-headed muscle attached rostrally to the cartilage of the external ear near the root of the posterior antihelix and to the fascia associated with the caudal and lateral portion of the calvaria
auricularis superior	small muscle attached to fascia near lateral edge of occipitalis muscle and to superior edge of helix
auriculo-orbitalis	flat, narrow sheet of muscle fibers attached to tragus and lateral border of frontalis and occipitalis muscles via fascia
depressor helcis	flat, robust set of fibers attached superiorly to tragus and inferiorly to platysma cervicale muscle and the fascia near it
orbicularis oculi	exceptionally gracile, thin, sphincter fibers attached to skin of eyelid and superciliary region; attached medially to frontal and maxilla bones at the medial palpebral region; very thin fibers over maxillary and superciliary regions; separate from zygomaticus minor muscle heads but blends with inferior fibers of corrugator supercilii muscle
corrugator supercilii	thick, robust, rope-like bundles of fan-shaped muscle bands attached to skin of medial palpebral region and laterally to skin of superciliary region; lateral and deep to procerus muscle; lateral to depressor supercilii muscle
depressor supercilii	robust, flat set of longitudinally oriented fibers located deep to procerus muscle and medial to corrugator supercilii muscle; attached to skin near medial palpebral region all the way down to the nasal region and to skin over medial aspect of superciliary region
procerus	flat and wide set of longitudinally oriented fibers superficial to depressor supercilii muscle and medial to corrugator supercilii muscle; attached to frontalis muscle via a fascial sheet and to the skin over nasal bone
nasalis	robust, flat set of obliquely oriented fibers located medial to LLSAN ^a muscle; attached to skin over lateral aspect of nasal region and the superior border of the nares
levator labii alaeque nasi	flat set of robust fibers lateral to nasalis muscle and medial to levator labii superioris muscle; attached to skin near superioris medial palpebral region, the lateral border of the skin of the nares, and to upper fibers of orbicularis oris muscle; also attached to superior aspect of maxilla near medial palpebral region
levator labii	wide, flat set of fibers lateral to LLSAN muscle and medial to zygomaticus minor muscle; attached to skin over medial palpebral region and to upper fibers of orbicularis oris muscle; also attached to maxilla near the inferior border of the orbicularis oculi muscle and to inferolateral edge of skin of nares
zygomaticus minor	robust, two-headed muscle composed of obliquely oriented fibers; both heads arise from upper fibers of orbicularis oris muscle; the smaller medial head is attached to the maxilla near infra-orbital foramen; the larger lateral head is attached to the skin near the caudal border of the orbicularis oculi muscle
zygomaticus major	relatively gracile set of fibers attached to the modiolus and to the rostrrolateral edge of the zygomatic arch
levator anguli	robust set of obliquely oriented fibers situated deep to the zygomaticus major muscle; attached to the modiolus, the skin near the inferior border of the orbicularis oculi muscle, and to the maxilla lateral to the attachment for the zygomaticus minor muscle
orbicularis oris	relatively gracile set of sphincter-like fibers surrounding the opening of the oral cavity; upper fibers attached to LLSAN, levator labii superioris, and zygomaticus muscles and to the corresponding skin; lower fibers attached to mentalis, depressor labii inferioris, and depressor anguli oris muscles and to the corresponding skin; both sets of fibers attached to alveolar margins of maxilla and mandible; connected to buccinatorius muscle at the modiolus
depressor septi nasi	variable; present in <i>H. lar</i> and <i>N. gabriellae</i> ; attached to inferior aspect of nasal septum and to the medial aspect of the upper fibers of the orbicularis oris muscle
mentalis	deeply located muscle composed of robust, obliquely oriented fibers; attached to skin over mental region and to the lower fibers of orbicularis oris muscle
depressor	very gracile, fleeting set of obliquely oriented fibers superficial and lateral to mentalis muscle; attached to inferior border of the mandible and to the lower fibers of the orbicularis oris muscle inferioris

TABLE 1. Facial musculature in hylobatids (continued)

Muscle	Attachments
depressor anguli oris	large, wide, and robust set of fibers superficial to the platysma (cervicale plus myoides) muscle and lateral to depressor labii inferioris muscle; attached to the lower fibers of the orbicularis oris muscle near modiolus and to the inferior border of the mandible
buccinatorius	flat wide sheet attached to alveolar margins of the maxillary and mandibular premolars and molars and to the modiolus

“*” Indicates that these muscles were not completely present in the specimens as their attachments to the dorsal region of the neck were removed when the head was disarticulated from the cervical portion of the spinal column.

^aLLSAN, levator labii superioris alaeque nasi muscle.

TABLE 2. Comparison of facial muscles among *Macaca mulatta*, hylobatids, and *Pan troglodytes*

Muscle	<i>M. mulatta</i>	Hylobatids	<i>P. troglodytes</i>
	P/A	P/A	P/A
Platysma ^a	P	P	P
Occipitalis	P	P	P ^b
Frontalis	P	P	P
Auricularis posterior	P	P	P
Auricularis superior	P	P	P
Auriculo-orbitalis	V	P	P
Depressor helicis	V	P	A
Tragicus	P	A	P
Antitragus	P	A	A
Orbicularis oculi	P	P	P
Corrugator supercilii	P	P	P
Depressor supercilii	V	P	P
Procerus	P	P	P
Nasalis	P	P	V
LLSAN	V	P	P
Levator labii superioris	P	P	P
Zygomaticus major	P	P	P ^c
Zygomaticus minor	V	P ^d	P
Levator anguli oris facialis	P	P	P
Orbicularis oris	P	P	P
Mentalis	P	P	P
Depressor septi nasi	P/V	P/V	P/V
Risorius	A	A	P
Depressor labii inferioris	P	P	P
Depressor anguli oris	P	P	P/V
Buccinatorius	P	P	P

“P,” present; “A,” absent; “V,” variable; “LLSAN,” levator labii superioris alaeque nasi muscle.

^aThis includes platysma cervicale and platysma myoides in *M. mulatta* and hylobatids, and usually only a platysma myoides in *P. troglodytes*.

^bThe occipitalis muscle in chimpanzees has a superficial head and a deep head (Pellatt, 1979; Burrows et al., 2006).

^cThe zygomaticus major muscle in chimpanzees has a deep head and a superficial head (Burrows et al., 2006).

^dThe zygomaticus minor muscle in hylobatids from the present study has a deep head and a superficial head (see Table 1 and Figs. 1, 2b).

Depressor supercilii muscle. The depressor supercilii muscle was similar to that of the rhesus macaque and the chimpanzee (Burrows et al., 2006, 2009) (Figs. 1, 2b,c, 3; Table 1).

Procerus muscle. The procerus muscle in hylobatids was imperfectly separated from the frontalis muscle by an irregular fascial connection (Figs. 1, 2b,c, 3; Table 1). It was similar to that of rhesus macaques and chimpanzees but it maintained a stronger fascial connection to the frontalis muscle not seen in the rhesus macaque

or the chimpanzee (Burrows et al., 2006, 2009) and was relatively poorly differentiated from the frontalis muscle.

Nasalis muscle. This muscle was similar to the nasalis muscle of the rhesus macaque (Huber, 1933) (Figs. 1, 2b,c; Table 1). The nasalis muscle was not described in chimpanzees by Sonntag (1923), Pellatt (1979), or Burrows et al. (2006) but it was reported by Gratiolet and Alix (1866), MacAlister (1871), Miller (1952), Seiler (1976), and Diogo et al. (2009).

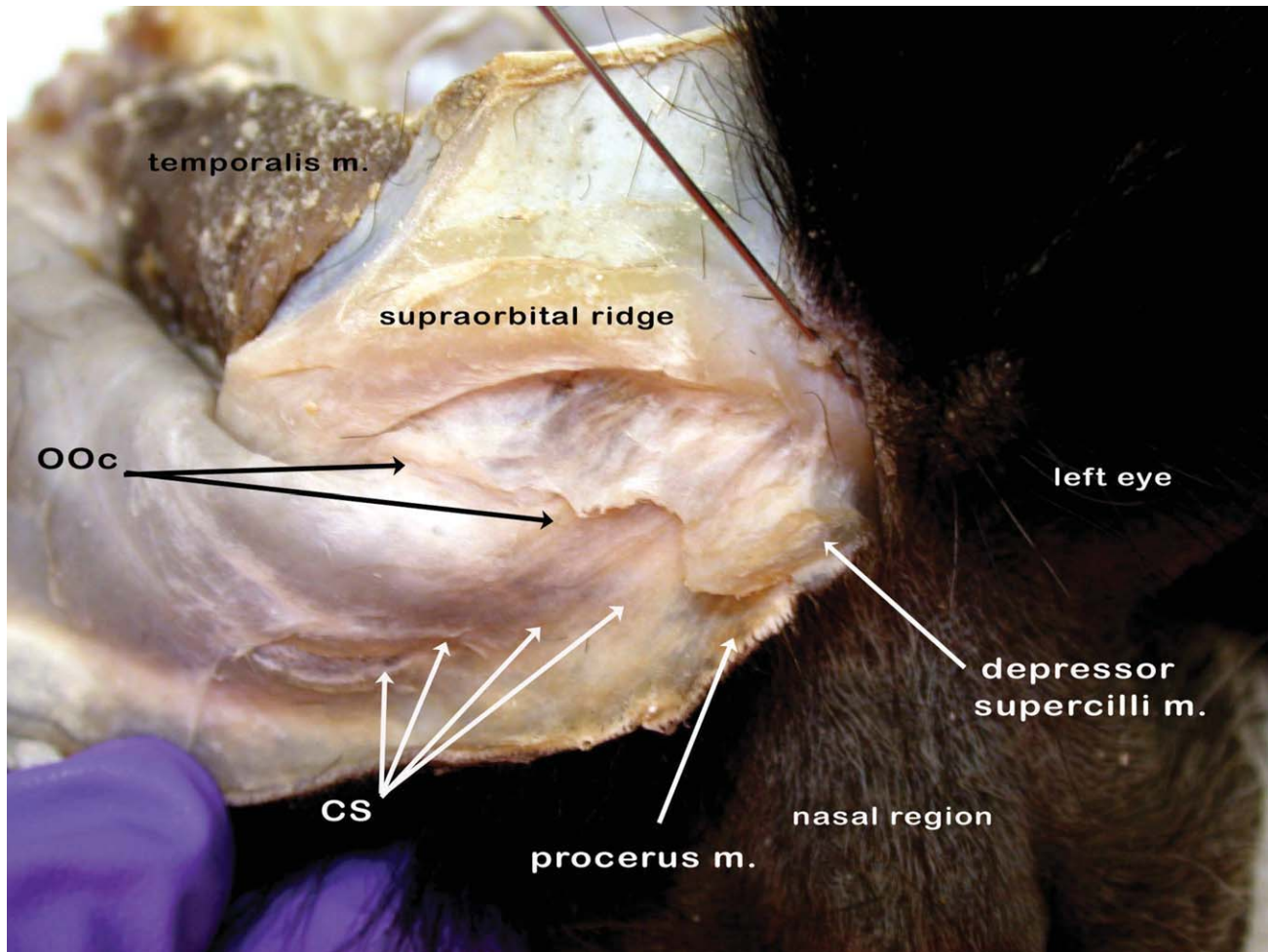


Fig. 3. Close-up of the right side of the superciliary/orbital region of the *S. syndactylus* specimen during dissection showing the relationship of the corrugator supercillii muscle (CS), depressor supercillii muscle, and the procerus muscle to one another. OOc, orbicularis oculi muscle. Note the greater robusticity of the depressor supercillii muscle relative to the corrugator supercillii muscle.

Levator labii superioris alaeque nasi muscle.

This muscle, abbreviated from this point forward as LLSAN, was generally similar to that of the rhesus macaques and chimpanzees but appeared to be relatively more robust in hylobatids than in rhesus macaques and chimpanzees (Burrows et al., 2006, 2009) (Figs. 1, 2b; Table 1).

Levator labii superioris muscle. The levator labii superioris muscle in hylobatids was similar to that of rhesus macaques and chimpanzees (Burrows et al., 2006, 2009) (Figs. 1, 2b,c; Table 1). In the *N. gabriellae* and *H. lar* specimens, the fibers of the levator labii superioris muscle were more horizontal than in *H. muelleri* and *S. syndactylus*, running from the infraorbital region (the more posterior and lateral portion of the muscle) to the nasal region (the more anterior and medial portion of the muscle) as shown in Diogo et al. (2009; Figs. 6 and 7). In this respect, the levator labii superioris muscle of these hylobatid specimens resembles the horizontal (postero-anteriorly oriented) arrangement of non-

primate mammals and non-catarrhine primates than the mainly vertical (supero-inferiorly oriented) arrangement of other extant catarrhines, as previously noted by authors such as Deniker (1885), Ruge (1911), Seiler (1976), and Diogo et al. (2009).

Zygomaticus minor muscle. This muscle was robust and two-headed, with both heads attached to the upper fibers of the orbicularis oris muscle, lateral to the levator labii superioris muscle (Figs. 1, 2b–d, 4; Table 1). Although both the rhesus macaque and the chimpanzee have a zygomaticus minor muscle (Burrows et al., 2006, 2009) they exist as a single-headed, relatively gracile muscle. Therefore, we describe the hylobatid zygomaticus minor muscle as being relatively complex in comparison.

Zygomaticus major muscle. This muscle was relatively gracile in hylobatids compared to the rhesus macaque, a smaller species, and the chimpanzee (Burrows et al., 2006, 2009) (Figs. 1, 2b–d, 4, 5; Table 1). Unlike

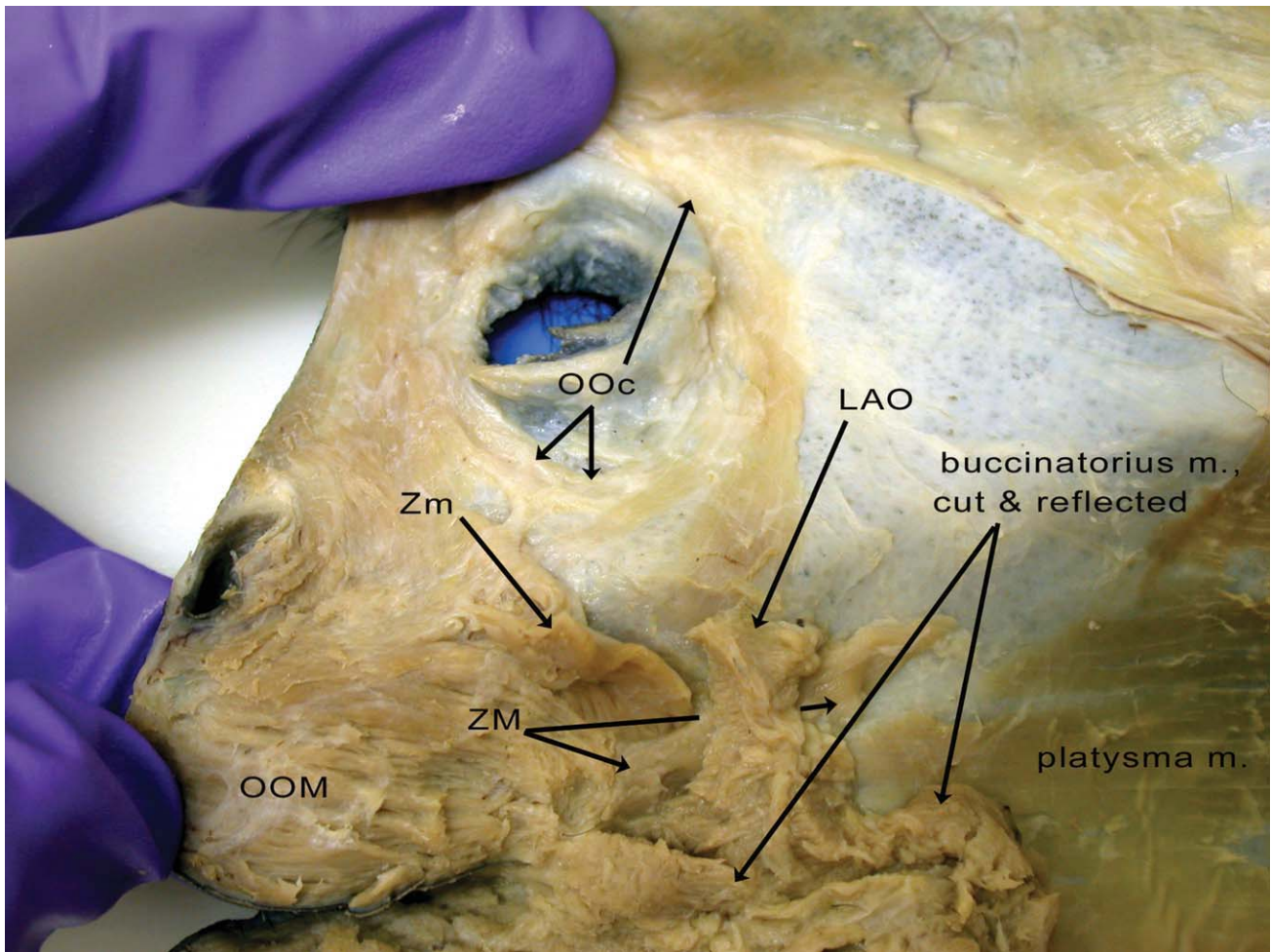


Fig. 4. Close-up of the right side of the midfacial region of the *H. muelleri* specimen showing the three-dimensional relationships of the muscles clustered around the lateral edge of the lips. OOC, orbicularis oculi muscle; ZM, zygomaticus major muscle; Zm, zygomaticus minor muscle; LAO, levator anguli oris facialis muscle; OOM, orbicularis oris

muscle. Note that the levator anguli oris facialis muscle is at a greater depth than the zygomaticus major muscle and the greatly reduced size of the zygomaticus major muscle relative to the zygomaticus minor muscle.

those species, the zygomaticus major muscles in hylobatids was found to be approximately the same size as the zygomaticus minor muscle. It is worth noting that the zygomaticus major muscle in chimpanzees exists as a two-headed, large muscle while it is a single headed muscle in the rhesus macaque.

Levator anguli oris facialis muscle. This muscle was referred to as “caninus” for the rhesus macaque (Burrows et al., 2009) and the chimpanzee (Burrows et al., 2006) but is termed “levator anguli oris facialis muscle” here in accordance with Diogo et al. (2009) (Figs. 2b, 4; Table 1). Like the rhesus macaque and chimpanzee, the hylobatids had a robust obliquely oriented set of fibers situated mainly deep to the zygomaticus major muscle.

Orbicularis oris muscle. This sphincter-like muscle was similar in the hylobatids to that in rhesus macaques and chimpanzees except for its relatively gracile

nature in the hylobatids (Burrows et al., 2006, 2009) (Fig. 1, 2a–c, 4; Table 1).

Depressor septi nasi muscle. This muscle was described in the rhesus macaque (Burrows et al., 2009) and the chimpanzee (Burrows et al., 2006) as the “depressor septi” muscle but is termed “depressor septi nasi” here in accordance with Diogo et al. (2009) (Fig. 2b; Table 1). This muscle was found in two of the four specimens (*N. gabriellae* and *H. lar*) of the present study, variation which is similar to that reported for other hylobatids by Seiler (1976). Its attachments (see Table 1) are similar to those described for humans and chimpanzees (Standring, 2004; Burrows et al., 2006). However, the depressor septi nasi muscle of humans is highly variable in both presence and in form (e.g., Latham and Deaton, 1976; Mooney et al., 1988; Rohrich et al., 2000). Thus, the variable appearance of the depressor septi nasi muscle in the hylobatids may be due to variation as in humans.

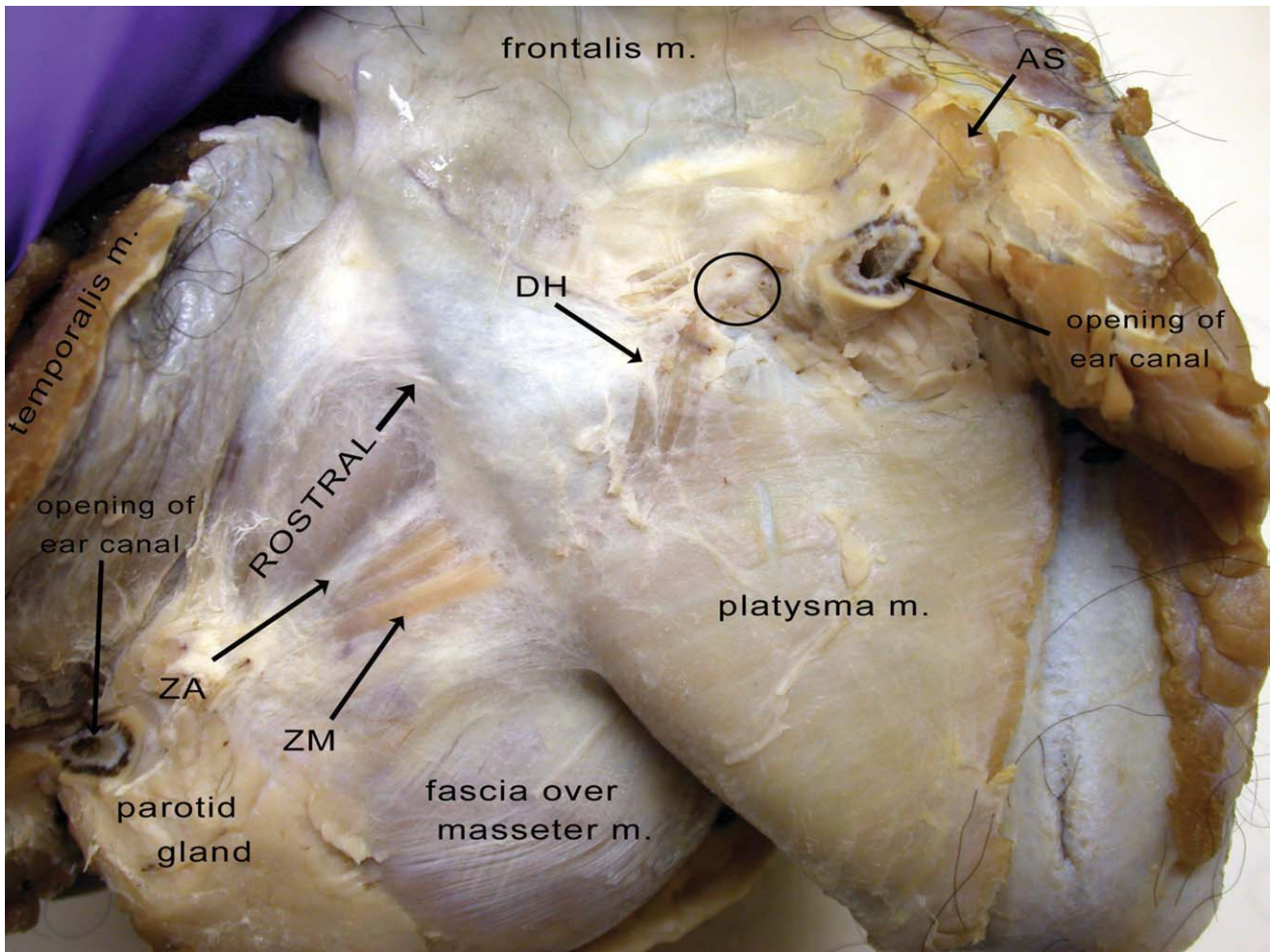


Fig. 5. Close-up of the right side of the zygomatic region of the *S. syndactylus* specimen during dissection showing the origin of the zygomaticus major muscle (ZM) and the three-dimensional arrangement of the some of the muscles related to the external ear. AS, auric-

ularis superior muscle; DH, depressor helicis muscle; ZA, zygomatic arch. Note the relatively thin, gracile nature of the zygomaticus major muscle at its attachment to the zygomatic arch.

Mentalis muscle. The mentalis muscle of hylobatids was similar to that of the rhesus macaque and the chimpanzee in terms of morphology and attachments (Burrows et al., 2006, 2009) (Figs. 1, 2a; Table 1).

Depressor labii inferioris muscle. Although it was similar to the rhesus macaque and chimpanzee, the depressor labii inferioris muscle of hylobatids was much more gracile than in either of the other species (Burrows et al., 2006, 2009) (Figs. 1, 2a; Table 1).

Depressor anguli oris muscle. The depressor anguli oris muscle of hylobatids was similar to that of rhesus macaques and chimpanzees (Burrows et al., 2006, 2009) (Figs. 1, 2a; Table 1).

Buccinatorius muscle. The buccinatorius muscle is not strictly a muscle of facial expression (as it is used in feeding) but is described here due to its innervation by the seventh cranial nerve (Figs. 2a,b, 4; Table 1). Its attachments were as those for all other primates

described (Lightoller, 1928; Swindler and Wood, 1982; Standring, 2004).

Microanatomical Results

Figure 6 shows representative transverse sections through the upper lip (containing the upper fibers of the orbicularis oris muscle) of *H. muelleri*, *M. mulatta*, and *P. troglodytes*, with corresponding images of the upper lips in facial masks from each species. The upper lip of the *H. muelleri* specimen is remarkable for the especially scant muscle content of the upper fibers of the orbicularis oris muscle (OOM). There is a relatively great representation of connective tissue in the hylobatid upper lip in comparison to the muscle fibers. While the orbicularis oris muscle of both humans and chimpanzees has been described as having two distinct sections, a deeply located pars peripheralis layer and a superficially located pars marginalis layer (Standring, 2004; Rogers et al., 2009), the hylobatid OOM does not appear to have this distinction. The OOM in the hylobatid sample appears to consist of a single muscular band.

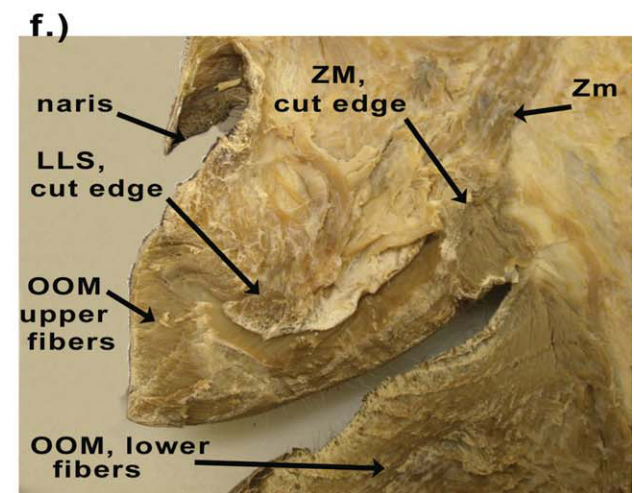
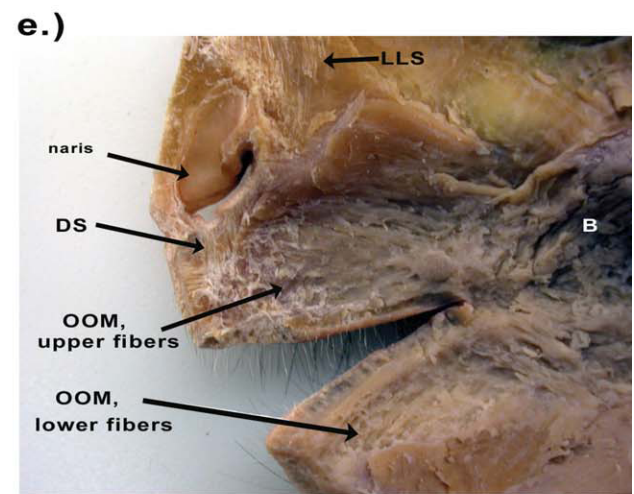
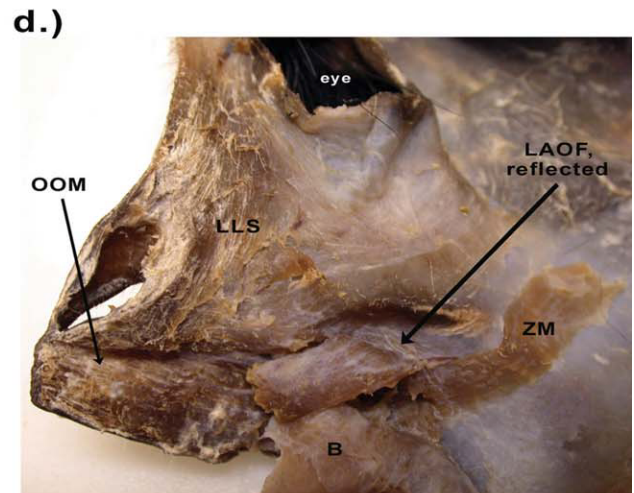
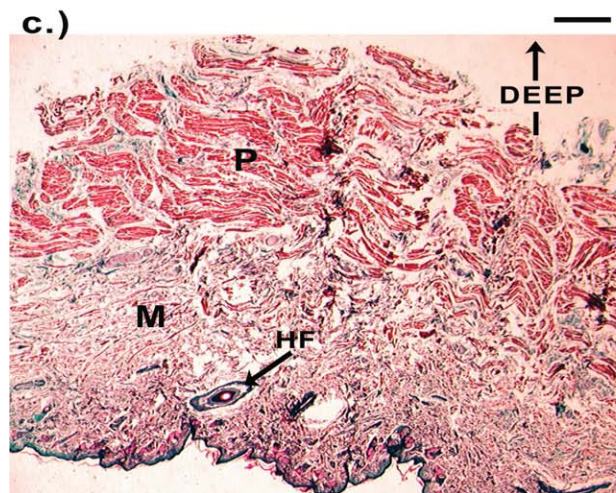
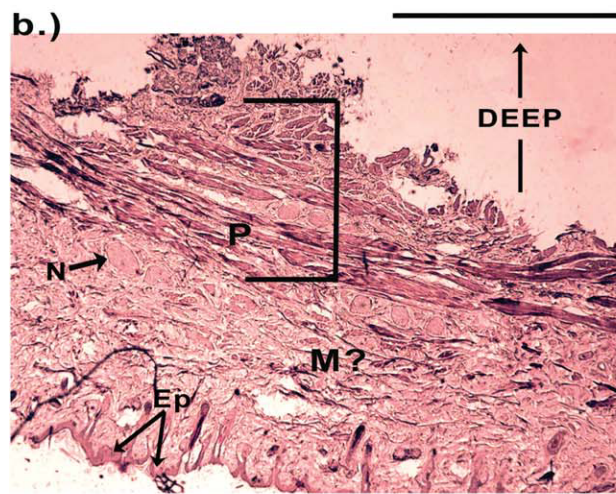
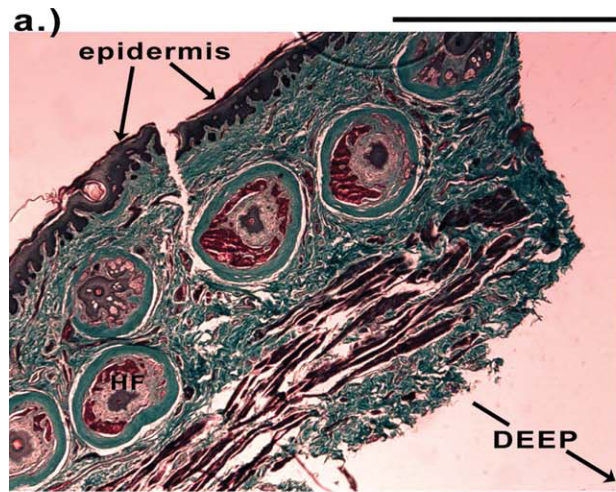


Fig. 6. Left side: representative microimages of the upper fibers of the orbicularis oris muscle in transverse section in (a) *H. muelleri* (stained with Gomori trichrome), (b) *Macaca mulatta* (stained with hematoxylin and eosin), and (c) *Pan troglodytes* (stained with Gomori trichrome). Scale bars represent 500 μm . The surface labeled "epidermis" is the skin of the lip. In panel a, teal color represents connective tissue. In panel b, the muscular layer of the lip is indicated by the open box located near the deep surface. In panel c, the muscular layer is the bright red area located near the deep surface. Note that the muscular portion of the upper lip in the hylobatid sample takes up

far less than half of the sample while the muscle fibers in the chimpanzee sample take up at least half of the sample. Ep, epidermis (representing the skin of the lip); N, nerve; HF, hair follicle; P, pars peripheralis layer; M, pars marginalis layer. Right side: images of the midfacial region in (d) *H. muelleri*, (e) *M. mulatta*, and (f) *P. troglodytes* showing the upper fibers of the orbicularis oris muscle approximating the region where it was sampled. OOM, orbicularis oris muscle; LLS, levator labii superioris muscle; ZM, zygomaticus major muscle; LAOF, levator anguli oris facialis muscle; B, buccinatorius muscle; DS, depressor septi nasalis muscle; Zm, zygomaticus minor muscle.

The upper lip of the rhesus macaque in Fig. 6b is more densely packed with muscle fibers than the hylobatid sample and the section of the upper lip occupied by OOM fibers appears to be greater than in the hylobatid. There is no clear presence of pars marginalis and pars peripheralis layers as in humans and chimpanzees, but there is some representation of muscle fibers in the general area where a pars marginalis layer may be expected.

The microanatomical form of the upper fibers of the orbicularis oris muscle in the chimpanzee has been described previously in detail (Rogers et al., 2009). In the present study, the chimpanzee upper lip section (Fig. 6c) appears to be similar to the rhesus macaque in terms of densely packed muscle fibers and proportion of the sample occupied by OOM muscle fiber relative to connective tissue. Both rhesus macaques and chimpanzees have qualitatively greater orbicularis oris muscle fiber density relative to connective tissue than the hylobatid in the present study. Unlike *H. muelleri* and the rhesus macaque, there is a distinct, deeply located pars peripheralis layer and a distinct, superficially located pars marginalis layer as in humans.

DISCUSSION

The present study provides the first detailed account of the facial musculature of hylobatids using a relatively large sample size. A total of 22 muscles (not counting the buccinatorius muscle, which is not typically involved in facial expressions) were found. Only one of those muscles, the depressor septi nasi muscle, was variable being found in two of the four specimens (the *Nomascus gabriellae* and the *H. lar* specimens). The hylobatids, the phylogenetically distant rhesus macaque, and the more closely related chimpanzee have roughly the same number of mimetic muscles (Burrows et al., 2006, 2009). Although the depressor helicis muscle was found in the present study and in *M. mulatta*, it has not been found in chimpanzees (Seiler, 1976; Burrows et al., 2006). Seiler (1976) found an antitragicus muscle in hylobatids, *M. mulatta*, and chimpanzees, but it was not located in the present study nor was it located in chimpanzees from Burrows et al. (2006). According to our observations, one of the main differences among these three taxa is that the risorius muscle is only consistently present in chimpanzees (as it is in humans and gorillas: Diogo et al., 2010), and not in hylobatids and rhesus macaques (see comments of Diogo et al., 2009 about the "risorius" muscle described by Seiler, 1976 in some hylobatids).

Of special note in the *Symphalangus syndactylus* (siamang) specimen was the attachment of the platysma muscle to the walls of the air sac. This attachment may reveal a previously unknown function of the platysma muscle in siamangs. Siamangs are characterized in part by overt inflation of the air sacs during loud vocalizations and this inflation may be aided by contraction of the platysma muscle.

Complexity of facial musculature in hylobatids in the present study was mixed. In the musculature of the external ear, hylobatids had poor separation of these muscles from the occipitalis, frontalis, and auriculo-orbitalis muscles by way of intersecting fascial connections. This series of connections would, by definition, decrease

complexity of the musculature and possibly the ability to move the external ear independently from the scalp. The procerus muscle was poorly separated from the frontalis muscle in hylobatids which may decrease the ability to move the skin over the external nose separately from the skin of the superciliary region. In addition, the zygomaticus major and depressor labii inferioris muscles were exceptionally gracile relative to both the chimpanzee and rhesus macaque. However, the present study documented a two-headed zygomaticus minor muscle in hylobatids which may be viewed as having great complexity relative to the chimpanzee and rhesus macaque.

Previous studies of hylobatid facial displays indicated a limited repertoire with all of the displays focused on movements of the lips with no movements of the nares, superciliary region, or external ears (Gittins, 1979; Liebal et al., 2004). Liebal et al. (2004) described four facial displays in the siamang, *Symphalangus syndactylus*: the "grin" (mouth slightly open with corners of the mouth withdrawn), "mouth-open half" (slightly open mouth), "mouth-open full" (mouth fully open with canine teeth exposed), and "pull a face" (lips slightly open and protruded). These movements would involve minimal muscle action and would presumably use the platysma muscle to withdraw the corners of the mouth, the zygomaticus major and minor, the levator anguli oris facialis, and the levator labii superioris muscles to expose the canine teeth, and the orbicularis oris muscle to protrude the lips. None of these facial movements would (presumably) involve action of the lower lip muscles, the nasal region muscles, the muscles of the superciliary region, or the muscles associated with the external ear. Morphological results of the present study support these behavioral studies (Gittins, 1979; Liebal et al., 2004). The small muscles of the external ear, the tragus and anti-tragus muscles, were not seen in hylobatids in the present study. They were, however, located in the rhesus macaque (Burrows et al., 2006, 2009). Rhesus macaques use movements of the external ear in visual communications of facial expression with relatively great frequency (Parr et al., 2010). Gibbons and siamangs are not reported to use movements of the external ear in facial displays and results of the present study support those observations (Liebal et al., 2004). However, it should be noted that without the benefit of detailed, muscular based coding systems such as ChimpFACS (Vick et al., 2007) and MaqFACS (Parr et al., 2010), subtle communicative movements may have been previously overlooked. Development of a similar system in hylobatids may reveal additional communicative movements during social interaction.

Findings on the limited facial display repertoire of hylobatids are especially startling in comparison to chimpanzees and rhesus macaques that have a well-documented facial display repertoire that includes over 20 movements (Parr et al., 2007; Vick et al., 2007; Parr et al., 2010). Both chimpanzees and rhesus macaques live in large groups, presenting a high number of potential social partners. They also live in open, less densely foliated environments than hylobatids, which would present relatively high numbers of opportunities for close-proximity visual communication with conspecifics.

Microanatomical characteristics of the orbicularis oris muscle and the upper lip in general support these observations as well. The hylobatid upper lip used in the

present study was found to be arranged with approximately even distributions of connective tissue and muscle fibers, unlike the chimpanzee and rhesus macaque which had relatively densely packed muscle fibers and very little connective tissue (see Rogers et al., 2009). There was no indication of separate pars marginalis and pars peripheralis layers in the hylobatid orbicularis oris muscle in the present study, also in contrast with the chimpanzee. Chimpanzees are reported to use their lips not only in facial displays and vocalizations but as a prehensile tool and in powerful actions involved with feeding (see Rogers et al., 2009). There are no reports of hylobatids using their lips in anything aside from facial displays and as an aid in the production of vocalizations (Gittins, 1979; Liebal et al., 2004). Thus, it may be expected that the microanatomical arrangement of the connective tissue and orbicularis oris muscle fibers would differ from those of the chimpanzee. Rhesus macaques are reported to make a high number of facial movements that involve upper lip movement (Parr et al., 2010) but they are not reported to use the lips in the prehensile fashion of chimpanzees.

Overall, both gross and microanatomical results of the present study support the first hypothesis that environmental and social variables are influential in the evolution of morphology and complexity of facial musculature in hylobatids. Muscles described in the present study were relatively flat, gracile, and, in some cases, of low complexity compared to the closely related chimpanzee and the distantly related rhesus macaque. If phylogenetic factors were the only factor responsible for determining morphology and complexity of hylobatid facial musculature we should have seen results intermediate to rhesus macaques and chimpanzees, reflecting the position of hylobatids between rhesus macaques (cercopithecoidea) and chimpanzees (hominoids).

Hylobatids are monogamous primates living in a densely foliated arboreal environment which would limit opportunities for close-proximity visual interactions such as facial displays. They also live in very small, relatively fixed groups and have limited numbers of social partners. Outside of that group the only opportunity for interactions with conspecifics is in territorial displays/disputes. The format of most territorial interactions is duetting, the long-distance stereotyped vocalizations produced by a mated pair. Although some territorial disputes escalate into a resident male chasing an interloping male, there are no reports of facial displays occurring during these chases (Brockelman and Srikosamatara, 1984; Leighton, 1987).

Duetting (and loud vocalizations in general) is one of the key characteristics defining hylobatids and seems to be the primary mechanism of communicating with conspecifics outside of the small "family" group (Mitani, 1988; Geissmann, 2002; Fan et al., 2009). It carries salient information on territorial limits, resources, reproductive status, gender, and is species-specific (MacKinnon and MacKinnon, 1977; Gittins, 1979; Mitani, 1985; Cowlishaw, 1992; Geissmann, 1999). Duetting is hypothesized to have originated from a single ancestral pattern not shared with monkeys or other apes (Geissmann, 2002). Chimpanzees, bonobos, gorillas, and orangutans all vocalize, sometimes very loudly, but do not possess this well-developed stereotyped form of vocal communication with conspecifics. The process and evolutionary mechanisms of

hylobatid duetting would possibly have decreased selection pressure on development of facial displays and facial musculature complexity relative to both the distantly related rhesus macaque and the closely related chimpanzee. Support for this possibility comes from studies on the facial motor nucleus volume in the midbrain of primates. Using a broad phylogenetic sample of primates, Sherwood et al. (2005) found that gibbons (*H. lar*) had relatively lower volume of the facial nerve nucleus than expected based upon body size, lower than both rhesus macaques and chimpanzees. In a similar study Sherwood (2005) found that *H. lar* had relatively far fewer neurons in the facial motor nucleus than the other hominoids, falling into the range occupied by some of the nocturnal strepsirrhines and small-bodied platyrrhines.

Clearly, more work on hylobatid facial displays, social interactions, and the neurobiological correlates of their facial movements is necessary to fully understand the evolutionary morphology of their facial musculature and the evolution of hylobatid social systems. In particular, the role of subtle facial movement in close social interaction as opposed to large group interactions needs to be investigated. However, results of the present study lend support to the notion that they communicate less via facial expression than other hominoids and that their facial musculature and facial expressions have most likely evolved in response to their environment and social system.

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