
Evolution of Facial Musculature

RUI DIOGO AND SHARLENE E. SANTANA

The face of humans and other mammals is a complex morphological structure (Figs. 8.1 and 8.2) in which both external and internal parts function in conveying information relevant for social interactions. Externally, facial features bear signals that allow recognition of conspecifics, individuals within the social group and potential mates. This information is encrypted in traits such as the shape of facial parts, and the complexity and hues of its color patterns (Fig. 8.1) (Setchell, 2005; Waite et al., 2003). Internally, the facial musculature (Fig. 8.2) and neural centers control how the external morphology is showcased to other individuals through the production of facial expressions, which are important in communicating behavioral intentions within a social context (e.g., bared teeth communicate the intent to withdraw from an agonistic encounter; Preuschoft & Van Hooff, 1997). Therefore, internal and external anatomical features of the face are not only in close physical proximity but are also tightly connected in their function.

Facial coloration patterns evolved in tandem with sociality and sympatry (when two species or populations exist in the same geographic area) in primates (Santana, Alfaro, Noonan, & Alfaro, 2013; Santana, Lynch Alfaro, & Alfaro, 2012). In most primate radiations, highly social and sympatric species evolved multicolored faces, while less social species tend to have less colorful faces. Complex facial patterns potentially enable higher interindividual

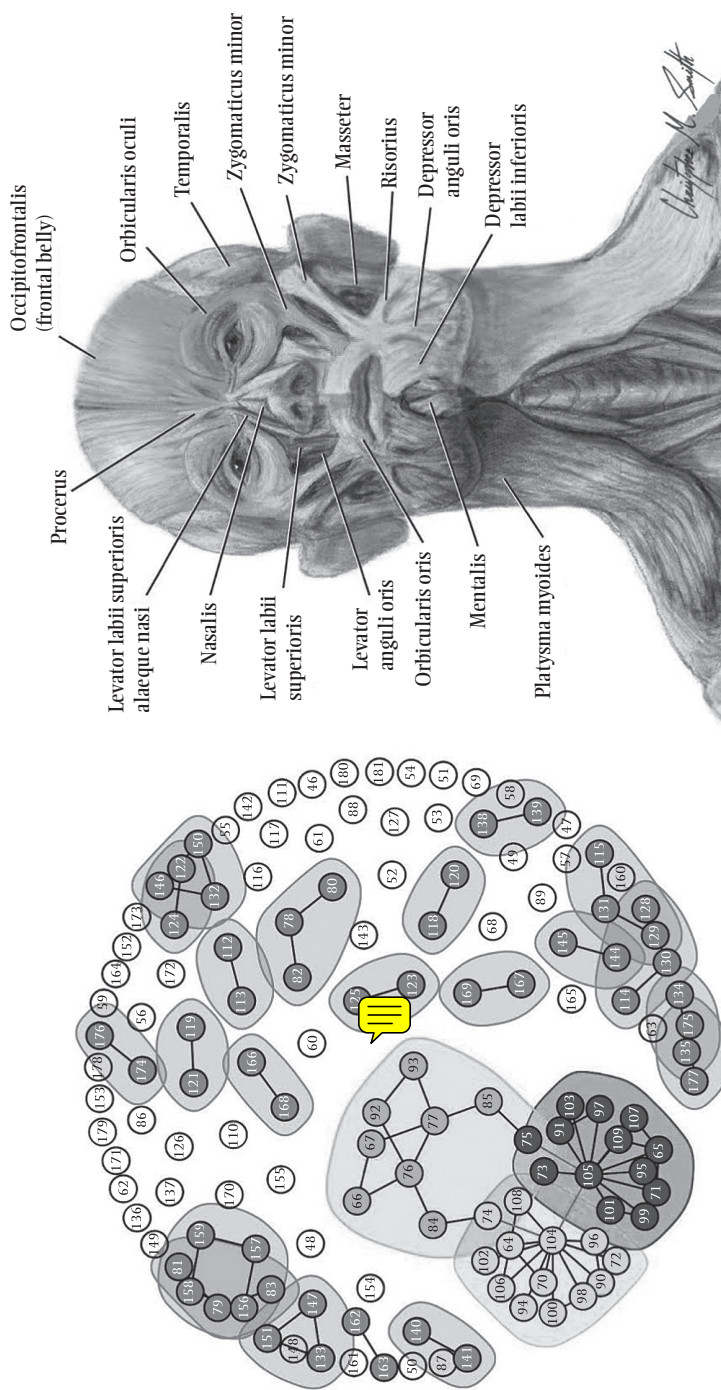


Figure 8.2 Muscle network modules of the normal adult head identified using anatomical networks: in yellow, the ocular/upper face module (66-67 Occipitalis left-right, 74-75 Zygomaticus minor left-right, 76-77 Frontalis left-right, 84-85 Orbicularis oculi left-right, 92-93 Procerus left-right); in light and dark blue, the left and right orofacial modules (64-65 Platsysma myoides left-right, 70-71 Risorius left-right, 72-73 Zygomaticus major left-right, 90-91 Levator labii superioris alaeque nasi left-right, 94-95 Buccinatorius left-right, 96-97 Levator labii superioris left-right, 98-99 Nasalis left-right, 100-101 Depressor septi nasi left-right, 102-103 Levator anguli oris facialis left-right, 104-105 Orbicularis oris left-right, 106-107 Depressor labii inferioris left-right, 108-109 Depressor anguli oris left-right); and in gray/white, the smaller muscle modules, which, in the absence of bones, are mostly disconnected to the three major muscle modules (©2015 Christopher Smith/HU; modified from Esteve-Altava et al. 2015, with permission)

variation within social groups and among species, facilitating recognition at either of these levels. Facial expressions are also linked to sociality; highly gregarious species produce a wider variety of facial movements, which may function in group cohesion by enhancing communication during conflict management and bonding (Dobson, 2009ab). Facial expressions result from the action of facial muscles that are controlled by neural pathways (facial nucleus of the pons—cranial nerve VII—and the primary motor cortex), and primate species with relatively large facial nuclei tend to have highly dexterous faces (Sherwood et al., 2005). The primate facial musculature is among the most complex across mammals (although not as complex as that of, e.g., elephants; Boas & Paulli, 1908, 1925), but it is unclear if and how it has evolved in response to functional demands associated with ecology and sociality (Burrows, 2008; R. Diogo, Wood, Aziz, & Burrows, 2009; Rui Diogo & Wood, 2012).

EVOLUTION OF THE MUSCLES OF FACIAL EXPRESSION

The first (mandibular), second (hyoid), and more posterior branchial arches are formed from bilateral swellings on either side of the pharynx. The muscles of facial expression (Fig. 8.2)—usually designated simply as “facial muscles”—are a subgroup of the hyoid (second arch) muscles and are innervated by the facial nerve (cranial nerve VII). This means that all other hyoid muscles (e.g., stapedius, stylohyoideus) are not designated as facial muscles, despite being also innervated by the facial nerve. Except for the buccinatorius (and the mandibulo-auricularis present in many nonhuman mammals), the facial muscles are mainly attached to the dermis of the skin and the elastic cartilage of the pinna. They are involved in generating facial expressions during social interactions among conspecifics, as well as in feeding, chemosensation, whisker motility, hearing, vocalization, and human speech. This section is mainly based on, and provides a short summary of, Diogo et al.’s (2009) overview on the evolution of primate facial muscles, which is complemented by Table 8.1; interested readers should refer to this publication for more details.

Evolution of Mammalian Facial Muscles and the Ancestral Condition for Primates

The facial muscles are only present in mammals, probably deriving from the ventral hyoid muscle interhyoideus, and likely also from at least some dorso-medial hyoid muscles (e.g., cervicomandibularis) of other tetrapods. Monotremes such as the platypus only have 10 distinct facial muscles (not

including the extrinsic muscles of the ear). Rodents, such as rats, have up to 24 facial muscles. The occipitalis + auricularis posterior, the procerus, and the dilatator nasi + levator labii superioris + levator anguli oris facialis of therian mammals (marsupials + placentals) probably correspond to part of the platysma cervicale (muscle connecting back of neck—nuchal region—to mouth, different from platysma myoides connecting front of neck and pectoral region to mouth: see also later discussion), of the levator labii superioris alaeque nasi, and of the orbicularis oris of monotremes, respectively. The sternofacialis, interscutularis, zygomaticus major, zygomaticus minor, and orbito-temporo-auricularis of therian mammals probably derive from the sphincter colli profundus, but it is possible that at least some of the former muscles derive from the platysma cervicale and/or platysma myoides. Colugos (Dermoptera or “flying lemurs”) and tree-shrews (Scandentia), the closest living relatives of primates (Fig. 8.1), have a similar facial musculature, but the former lack two muscles that are usually present in the latter, the sphincter colli superficialis and the mandibulo-auricularis. As both these muscles are found in rodents, as well as in tree-shrews and at least some primates, they were likely present in the last common ancestor (LCA) of Primates + Dermoptera + Scandentia. The frontalis, auriculo-orbitalis, and auricularis superior of this LCA very likely derived from the orbito-temporo-auricularis of other mammals, while the zygomatico-orbicularis and corrugator supercilii most likely derived from the orbicularis oculi.

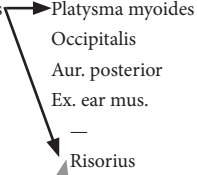
The facial musculature of the LCA of primates was probably very similar to that seen in the extant tree-shrew *Tupaia*. Muscles that have been described in the literature as peculiar to primates, for example, the zygomaticus major and zygomaticus minor, are now commonly accepted as homologues of muscles of other mammals (e.g., of the “auriculolabialis inferior” and “auriculolabialis superior”). The only muscle that is actually often present as a distinct structure in strepsirhines (primate group including extant members such as lemurs and lorises; Fig. 8.1), but not in tree-shrews or colugos, is the depressor supercilii, which derives from the orbicularis oris matrix. As the depressor supercilii is present in strepsirhine and nonstrepsirhine primates, it is likely that this muscle was present in the LCA of primates. In summary, the ancestral condition predicted for the LCA of primates is probably similar to that found in some extant strepsirhines (e.g., *Lepilemur*). Importantly, the number of facial muscles present in living strepsirhines is higher than that originally reported by authors in the 19th and first decades of the 20th century. For instance, Murie and Mivart (1869) reported only seven facial muscles in a lemur, grouping all the muscles associated with the nasal region into a single “nasolabial muscle mass.” The supposed lack of complexity seen in strepsirhines was consistent with the anthropocentric, “scalae naturae,” finalistic evolutionary paradigm subscribed to by

Table 8.1 SCHEME ILLUSTRATING THE AUTHORS' HYPOTHESES REGARDING THE HOMOLOGIES OF THE FACIAL MUSCLES OF ADULTS OF REPRESENTATIVE NONPRIMATE AND PRIMATE MAMMALIAN TAXA

<i>Ornithorhynchus anatinus</i> (10 mus. - not ex. ear)	<i>Rattus norvegicus</i> (24 mus. - not ex. ear)	<i>Tupaia</i> sp. (22 mus. - not ex. ear)	<i>Lepilemur ruficaudatus</i> (21 mus. - not ex. ear)	<i>Macaca mulatta</i> (23 mus. - not ex.ear)
Platysma cervicale	Platysma cervicale	Platysma cervicale	Platysma cervicale	Platysma cervicale
Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides
—	Occipitalis	Occipitalis	Occipitalis	Occipitalis
—	Aur. posterior	Aur. posterior	Aur. posterior	Aur. posterior
Ex. ear mus.	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.
—	Mandibulo-aur.	Mandibulo-aur.	Mandibulo-aur.	—
—	—	—	—	—
Interhyoideus prof.	—	—	—	—
Sphincter colli supe.	Sphincter colli supe.	Sphincter colli supe.	—	—
—(colli prof. in Echidna)	Sphincter colli prof.	Sphincter colli prof.	Sphincter colli prof.	—
—	Sternofacialis	—	—	—
Cervicalis tra.	—	—	—	—
—	Interscutularis	—	—	—
—	Zygomaticus major	Zygomaticus maj.	Zygomaticus maj.	Zygomaticus maj.
—	Zygomaticus minor	Zygomaticus min.	Zygomaticus min.	Zygomaticus min.
—	Orbito-temporo-aur.	Frontalis	Frontalis	Frontalis
—	—	Auriculo-orbitalis	Auriculo-orbitalis	Auriculo-orbitalis
—	—	—	—	—
—	—	Aur. superior	Aur. superior	Aur. superior
Orbic. oculi	Orbic. oculi	Orbic. oculi	Orbic. oculi	Orbic. oculi
—	—	Zygomatico-orbic.	—	—
—	—	Corru. supercilii	De. supercilii	De. supercilii
—	—	—	Corru. supercilii	Corru. supercilii
Naso-labialis	Le. labii sup. al.nasi	Le. labii sup. al.nasi	Le. labii sup. al.nasi	Le. labii sup. al.nasi
—	Procerus	—	—	Procerus
Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius
—	Dilatator nasi	—	—	—
—	Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii sup.
—	Nasalis	Nasalis	Nasalis	Nasalis
—	De. septi nasi	—	—	De. septi nasi
—	De. rhinarii	—	—	—
—	Le. rhinari	—	—	—
—	Le. anguli oris fac.	Le. anguli oris fac.	Le. anguli oris fac.	Le. anguli oris fac.
Orbic. oris	Orbic. oris	Orbic. oris	Orbic. oris	Orbic. oris
—	—	—	—	De. labii inf.
—	—	—	—	De. anguli oris
Mentalis	—	Mentalis	Mentalis	Mentalis

Data from evidence provided by our own dissections and comparisons and by a review of the literature. The black arrows indicate the hypotheses that are most strongly supported by the evidence available; the grey arrows indicate alternative hypotheses that are supported by some of the data, but overall they are not as strongly supported by the evidence available as are the hypotheses indicated by black arrows. al. = alaeque; aur. = auricularis; corru. = corrugator; fac. = facialis; de. = depressor; ex. = extrinsic; inf. = inferioris; lab. = labialis; le. = levator; maj. = major; min. = minor; mus. = muscles; orbic. = orbicularis; prof. = profundus; sup. = superioris; supe. = superficialis; tra. = transversus.

<i>Hylobates lar</i> (23 mus.- not ex. ear)	<i>Pongo pygmaeus</i> (21 mus.- not ex. ear)	<i>Gorilla gorilla</i> (24 mus.- not ex. ear)	<i>Pan troglodytes</i> (22 mus.- not ex. ear)	<i>Homo sapiens</i> (24 mus.- not ex. ear)
Platysma cervicale	—	Platysma cervicale	—	—
Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides
Occipitalis	Occipitalis	Occipitalis	Occipitalis	Occipitalis
Aur. posterior	—	Aur. posterior	Aur. posterior	Aur. posterior
Ex. ear mus.	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
—	—	—	—	—
Zygomaticus maj.	Zygomaticus maj.	Zygomaticus maj.	Zygomaticus maj.	Zygomaticus maj.
Zygomaticus min.	Zygomaticus min.	Zygomaticus min.	Zygomaticus min.	Zygomaticus min.
Frontalis	Frontalis	Frontalis	Frontalis	Frontalis
Auriculo-orbitalis	Auriculo-orbitalis	Temporoparietalis	Auriculo-orbitalis	Temporoparietalis
—	—	Aur. anterior	—	Aur. anterior
Aur. superior	Aur. superior	Aur. superior	Aur. superior	Aur. superior
Orbic. oculi	Orbic. oculi	Orbic. oculi	Orbic. oculi	Orbic. oculi
—	—	—	—	—
De. supercilii	De. supercilii	De. supercilii	De. supercilii	De. supercilii
Corru. supercilii	Corru. supercilii	Corru. supercilii	Corru. supercilii	Corru. supercilii
Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup. al. nasi
Procerus	Procerus	Procerus	Procerus	Procerus
Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius
—	—	—	—	—
Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii sup.
Nasalis	Nasalis	Nasalis	Nasalis	Nasalis
De. septi nasi	De. septi nasi	De. septi nasi	De. septi nasi	De. septi nasi
—	—	—	—	—
—	—	—	—	—
Le. anguli oris fac.	Le. anguli oris fac.	Le. anguli oris fac.	Le. anguli oris fac.	Le. anguli oris fac.
Orbic. oris	Orbic. oris	Orbic. oris	Orbic. oris	Orbic. oris
De. labii inf.	De. labii inf.	De. labii inf.	De. labii inf.	De. labii inf.
De. anguli oris	De. anguli oris	De. anguli oris	De. anguli oris	De. anguli oris
Mentalis	Mentalis	Mentalis	Mentalis	Mentalis



many anatomists at that time. However, it is now accepted that strepsirhines often have more than 20 facial muscles, and that although humans have more facial muscles than most primates, the difference is minimal in general. In fact, the total number of facial muscles found in humans is similar to that found in rats, as shown in Table 8.1, contradicting one of the major myths of human complexity and exceptionalism (see Diogo & Wood, 2012, 2013, and Diogo et al., 2015, for more details on this subject).

To give a functional context for these descriptions of the evolution and comparative anatomy of the primate facial muscles, here we provide a brief account of the general function of the facial muscles that are present in strepsirhines. Then, when we refer in the next section to a certain muscle that is not differentiated in strepsirhines but that is present in anthropoids (monkeys and apes, including humans), we will also briefly describe the general function of that muscle. The platysma myoides most likely draws the oral commissure posteroinferiorly, an action that may be used in social interactions as well as feeding, while the platysma cervicale most likely elevates the skin of the neck. The occipitalis draws the scalp posteriorly toward the nuchal region while the frontalis elevates the skin/brow over the superciliary region. The auriculo-orbitalis may be used to draw the lateral corner of the eyelid posteroinferiorly or the external ear anterosuperiorly. The corrugator supercilii and the depressor supercilii are used to draw the medial edge of the superciliary region inferomedially and inferiorly, respectively. The mandibulo-auricularis may be used to approximate the superior and inferior edges of the external ear, as well as the external ear and the mandible. The muscles clustered around the upper lip, including the zygomaticus major and zygomaticus minor muscles, may be used to draw the upper lip and the posterior region of the mouth posterosuperiorly, functions which may be used in both social interactions and in use of the vomeronasal organ. As their names indicate, the extrinsic muscles of the ear, as well as the auricularis posterior and auricularis superior, are mostly related to movement of the external ear, while the orbicularis oculi and orbicularis oris are primarily associated with movement of the eyes and of the lips, respectively. The buccinatorius mainly pulls the corner of the mouth laterally and presses the cheek against the teeth. The levator labii superioris alaeque nasi, levator labii superioris, and levator anguli oris facialis are most likely used together in drawing the upper lip and the posterior region of the mouth superiorly and medially, which most likely is used in social interactions and in feeding. The mentalis mainly elevates the skin ventral to the lower lip, while the sphincter colli profundus most likely draws the skin of the neck posterosuperiorly.

Evolution of the Facial Muscles Within Anthropoids

There are some notable differences between the ancestral condition described earlier for nonanthropoid primates such as *Lepilemur* and the condition found in New World and Old World monkeys. For example, the mandibulo-auricularis is usually not present as an independent, fleshy muscle in most anthropoids, although some of these primates have fleshy vestiges of this muscle as a rare variant. It likely corresponds to the stylo-mandibular ligament seen in hominoids (apes, including humans) and in some monkeys. The sphincter colli profundus is also normally absent in anthropoids, but fleshy vestiges of this muscle have been described in a few macaques as well. Anthropoids often have a depressor anguli oris and a depressor labii inferioris. These muscles are probably derived from the orbicularis oris matrix; some authors suggested that the depressor anguli oris might be the result of a ventral extension of the levator anguli oris. Generally, the depressor anguli oris and depressor labii inferioris function in anthropoids to draw the corner of the mouth posteroinferiorly and to draw the lower lip inferiorly, respectively. These movements are seen in some displays of facial expression and in some feeding contexts.

Within hominoids the platysma cervicale is usually present in hylobatids (lesser apes: gibbons and siamangs) and gorillas, but it is often highly reduced or absent in adult orangutans, chimpanzees, and humans. The transversus nuchae, found as a variant in the three latter taxa, is often considered to be a vestigial remain/bundle of the platysma cervicale. Interestingly, the platysma cervicale is present early in the development of humans, but it normally disappears as an independent structure in later stages of development. Contrary to the platysma cervicale, the platysma myoides is usually present as a separate structure in adult members of all the major five extant hominoid taxa. The occipitalis is also usually present in these five, but the auricularis posterior is normally not differentiated in orangutans, although it has been described in a few species.

In humans the risorius is usually—but not always—present, pulling the lip corners backward, stretching the lips—a function that is, interestingly, usually associated with the display of fear, being likely derived from the platysma myoides, although it cannot be discarded that it is partly, or even wholly, derived from the zygomaticus major. Among A “risorius” is sometimes found in some other hominoids (e.g., chimps), but it does not seem to be present in the fixed phenotype (i.e., > 50% of the cases) of any of the four major nonhuman hominoid taxa. Moreover, some structures that are often named “risorius” in these hominoids are probably not homologous to the human risorius, and even to each other, because some apparently derive from the platysma myoides, others from the depressor anguli oris, and others from muscles such as the zygomaticus

major. All the other facial muscles that are present in macaques are normally present in extant hominoids, but contrary to monkeys and to other hominoids, humans—and possibly also gorillas—usually also have an auricularis anterior and a temporoparietalis. Both of these muscles are derived from the auriculo-orbitalis, which, in other hominoids such as chimpanzees, has often been given the name “auricularis anterior,” although it actually corresponds to the auricularis anterior plus the temporoparietalis of humans and gorillas. When present, the temporoparietalis stabilizes the epicranial aponeurosis (a tough layer of dense fibrous tissue covering the upper part of the cranium), whereas the auricularis anterior draws the external ear superoanteriorly, closer to the orbit.

Before ending this section, it is interesting to note that each of the three nonprimate taxa listed in Table 8.1 has at least one derived, peculiar muscle that is not differentiated in any other taxa listed in this table. So, for instance, *Ornithorhynchus* has a cervicalis transversus, *Rattus* has a sternofacialis and an interscutularis, and *Tupaia* has a zygomatico-orbicularis. This is an excellent example illustrating that evolution is not directed “toward” a goal, and surely not “toward” primates and humans; each taxon has its own particular mix of conserved and derived anatomical structures, which is the result of its unique evolutionary history (Diogo & Wood, 2013). This is why we encourage the use of the term *correspond* to describe evolutionary relationships among facial muscles, because muscles such as the zygomatico-orbicularis are not “ancestral” to the muscles of primates. The zygomatico-orbicularis simply corresponds to a part of the orbicularis oculi that, in taxa such as *Tupaia*, became sufficiently differentiated to deserve being recognized as a separate muscle. Also, strepsirhines and monkeys have muscles that are usually not differentiated in some hominoid taxa, for example, the platysma cervicale (usually not differentiated in orangutans, chimps and humans) and the auricularis posterior (usually not differentiated in orangutans).

Humans, together with gorillas, have the greatest number of facial muscles within primates, and this is consistent with the important role played by facial expression in anthropoids in general, and in humans in particular, for communication. Nevertheless, the evidence presented in this chapter, as well as in recent works by Burrows and colleagues (e.g., Burrows, 2008; Burrows et al., 2014), shows that the difference between the number of facial muscles present in humans and in hominoids such as hylobatids, chimpanzees, and orangutans, and between the number of muscles seen in these latter hominoids and in strepsirhines, is not as marked as previously thought. In fact, as will be shown next, the display of complex facial expressions in a certain taxon is not only related with the number of facial muscles but also with their subdivisions, arrangements of fibers, topology, biochemistry, and microanatomical mechanical properties, as well as with the peculiar osteological and external features

(e.g., color) and specific social group and ecological features of the members of that taxon.

FACIAL PELAGE AND COLOR

From bright red to yellow, black, brown, and even blue, the faces of primates exhibit almost every possible hue in the spectrum of mammalian coloration. In many species, such as mandrills and guenons, facial skin and hair colors are combined to create remarkably complex patterns that are unique to the species. Is there a functional significance to these colors and their patterns? Recently, researchers have harnessed the tools of modern comparative methods and computer simulation to answer this question and investigate the factors underlying the evolution of facial color diversity across primate radiations.

Several lines of evidence suggest that facial colors are crucial to the ecology and social communication of primates. Variation in coloration within a species, such as the differences in brightness of red facial patches among male mandrills, appear to be used for assessment of overall health condition and potential mate quality (Setchell, Wickings, Knapp, & Jean Wickings, 2006; Setchell, 2005). At a broader scale, differences across species in facial color patterns are hypothesized to enable individuals of sympatric and closely related species to identify one another and avoid interbreeding. Phylogenetic comparative studies have demonstrated that social recognition explains trends in the evolution of primate facial color patterns. In the New World primate radiation (Platyrrhini), species that live in small social groups or are solitary (e.g., Owl monkeys, *Aotus*) have evolved more complexly patterned faces (Santana et al., 2012). In sharp contrast, diversity trends in Old World groups (Catarrhini) are the opposite, with highly gregarious species having more complexly patterned faces (Santana et al., 2013). These divergent trends may be explained by habitat differences and a higher reliance on facial expressions and displays for intra-specific communication in catarrhines (Dobson, 2009b; Mancini, Ferrari, & Palagi, 2013), in which facial colors may be further advertised through stereotyped head movements during courtship or appeasement behaviors (Kingdon, 1992, 2007).

Across all primates studied to date, the evolution of complexly patterned faces is also tightly linked to high levels of sympatry with closely related species (Santana et al., 2012, 2013). A face that is colorful may present features that are unique and more easily recognizable in the context of multiple sympatric species. Allen, Stevens, and Higham (2014) used computational face recognition algorithms to model primate face processing. Their results demonstrated that the evolution of facial color patterns in guenons fits models of selection to become more visually distinctive from other sympatric guenon species. This

indicates that facial color patterns function as signals for species recognition in primates, and they may promote and maintain reproductive isolation among species.

The degree of facial skin and hair pigmentation is also highly variable across primates, and comparative studies suggest that this diversity may illustrate adaptations to habitat. Darker, melanin-based colors in the face and body are characteristic of primate species that inhabit tropical, more densely forested regions (Kamilar & Bradley, 2011). It is hypothesized that these darker colors may reduce predation pressure by making individuals more cryptic to visually oriented predators (Stevens & Merilaita, 2009; Zinck, Duffield, & Ormsbee, 2004) and increase resistance against pathogens (Burt Jr & Ichida, 2004). Darker facial colors may also offer protection against high levels of UV radiation and solar glare (Caro, 2005) and aid in thermoregulation (Burt, 1986). However, the role of facial pigmentation in these functions remains unclear because primates may use behaviors to regulate their physiology (e.g., arboreal species can move from the upper canopy, which has the highest UV levels, to the middle and lower canopy, which are highly shaded). In catarrhines, ecological trends in facial pigmentation are only significant in African species (Santana et al., 2013), presumably because the African continent presents more distinct habitat gradients than South East Asia. In platyrrhines, darker faces are found in species that live in warmer and more humid areas, such as the Amazon, and darker eye masks are predominant in species that live closer to the equator. Eye masks likely function in glare reduction in habitats with high ultraviolet incidence, and similar trends in this facial feature have also been observed in carnivorans and birds (Burt, 1986; Ortolani, 1999).

The presence and length of facial hair are highly variable across primate species, but the role of facial hair in social communication, besides acting as a vehicle to display color, has not been broadly investigated. In platyrrhines, species that live in temperate regions have longer and denser facial hair (Santana et al., 2012), which could aid in thermoregulation (Rensch, 1938). Similar trends would be expected in other primate radiations.

COEVOLUTIONARY RELATIONSHIPS

To date, the evolutionary connections between external (coloration, facial shape) and internal (musculature) facial traits are poorly known. In a recent study (Santana et al., 2014), we contrasted two major hypotheses that could explain the evolution of primate facial diversity when these traits are integrated. First, if the evolution of facial displays has been primarily driven by social factors, highly gregarious primates would possess both complexly colored and highly expressive faces as two concurrent means for social

communication. Alternatively, if external facial features influence the ability of primates to perceive and identify facial expressions (Vick, Waller, Parr, Smith Pasqualini, & Bard, 2007), there would be a tradeoff in the evolution of facial mobility and facial color patterning, such that highly expressive faces would have simpler color patterns. We used phylogenetic comparative analyses integrating data on facial mobility, facial musculature, facial color pattern complexity, body size, and orofacial motor nuclei across 21 primate species to test these hypotheses.

The results from our study indicated a significant association between the evolution of facial color patterns and facial mobility in primates. Supporting the second hypothesis, primates evolved plainly colored faces in tandem with an enhanced ability for facial expressions. Thus, while complex facial color patterns may be beneficial for advertising identity (Allen et al., 2014; Santana et al., 2013), a highly “cluttered” face may mask the visibility of facial expressions used to convey behavioral intention. Why a species may rely more on facial color patterns versus facial expressions for communication is still unclear, but it is possible that these different modalities may be differentially selected across primate lineages based on the species’ habitat, social systems, or body size. Larger primates (e.g., apes), which have a larger facial nucleus, have more expressive faces than smaller species (e.g., marmosets; Dobson, 2009b), which in turn seem to use colorful facial patterns and head movements for communication. The evolution of larger bodies, potentially coupled with increased reliance on vision for other ecological tasks (e.g., finding food and avoiding predators) may have allowed a higher reliance on facial expressions, which was not possible at smaller body sizes due to physical constraints on the perception of facial movements. Smaller species are expected to have more difficulty discerning facial expressions because smaller mammalian eyes have lower visual acuity (Moynihan, 1967; Veilleux & Kirk, 2014).

Although the evolution of facial mobility is linked to facial coloration and body mass, we found that it is not directly related to the number of muscles that produce facial movements. The number of facial muscles is a slowly evolving trait that has strong phylogenetic inertia (Table 8.1; see Section 2 and also Diogo & Wood, 2012, 2013). Conversely, the size of the facial nucleus has evolved rapidly in the sample of primates studied. These results indicate that changes in facial mobility are likely to evolve first via changes in neurophysiology and body mass, instead of muscle morphology; that is, through motor control of muscles instead of the creation of new divisions of preexisting musculature. These patterns of evolution and potential tradeoffs give important insight into the simple organismal features, such as body mass, that have a strong relevance for which and how different types of facial cues evolve for social communication.

ADULT MODULARITY AND ASYMMETRICAL USE OF FACIAL EXPRESSIONS

Recent studies using a new quantitative and objective approach—anatomical networks—have revealed novel, and in some cases surprising, aspects about the modularity of the facial expression muscles of human adults and the developmental and evolutionary implications (Esteve-Altava, Diogo, Smith, Boughner, & Rasskin-Gutman, 2015). This method treats the skeletal, cartilaginous, and muscular units of the human head as the elements of a network (nodes), whose interactions at their physical contacts (links) determine the boundaries of the phenotypic modules of the head (Fig. 8.2). The use of this methodology revealed that the *muscular network* of the adult human head comprises 136 muscles sparsely connected at 78 contact points (fiber fusions and well-defined tendons), and it divides into three major modules (a single *ocular/upper face complex*, and *left and right orofacial complexes*) and 21 smaller blocks of 2–4 muscles each (Fig. 8.2). Remarkably, the three main muscular modules exclusively include muscles of facial expression. These results support the idea that the evolution of facial muscles has been crucial to human evolution and particularly for our unique abilities for verbal and visual communication.

Furthermore, these network analyses bring a new light to the debate on the symmetry/asymmetry of facial expression muscles in humans and primates. Recent developmental studies suggest that the left and right facial muscles separate from each other early in ontogeny; in fact, surprisingly, the left muscles are actually ontogenetically more closely related to the base of the pulmonary trunk, and the right ones to the base of the aorta, than they are to each other (R. Diogo et al., 2015; Lescroart et al., 2010). Also, functional studies in humans show that asymmetrical use of facial muscles is crucial to make complex facial expressions (Ahn, Gobron, Thalmann, & Boulic, 2013). Furthermore, functional and anatomical studies of human facial expressions have shown that asymmetrical use of facial muscles is less prominent, and that innervation patterns of muscles are more symmetric, in the upper face (muscles located above the upper brow) than in the mid-face and lower face (Rinn, 1984; Schmidt, Liu, & Cohn, 2006). Since human speech tends to involve symmetrical muscle contraction, asymmetrical use of facial muscles is likely related to nonverbal communication in our own species. The phenotypic modules identified in Figure 8.2 placed these developmental, functional, and anatomical observations in a completely new and quantitative context. That is, the existence of left and right orofacial muscle modules in the adult human head supports the ontogenetic separation of left and right facial muscles and the ability to asymmetrically contract or relax facial muscles, and thus strike more complex facial expressions in humans. In contrast, the single module including both the left

and right ocular/upper face facial muscles is in line with previous studies showing that innervations patterns and use of muscles are more symmetric in the upper face. As emphasized by Esteve-Altava et al. (2015), future anatomical network studies specifically about the muscles of facial expression among other primate and mammal species are needed to investigate which modules may be unique to humans and which others have deeper evolutionary origins.

DEVELOPMENT, BIRTH DEFECTS, MODULARITY, AND EVOLVABILITY

A further study also using anatomical networks, but to investigate the modularity of the head of human infants as well as of a trisomy-18 cyclopic human fetus (Fig. 8.3), supports the idea that facial expression had a crucial importance in primate/human evolution (Esteve-Altava et al., 2015). This is because, apart from being the three major muscle modules in the adult, the facial expression ocular/upper face and left and right orofacial modules are also already present in the newborn head, with exactly the same components. Facial expressions play a particularly important role in the first years of life: While vocalizations (e.g., crying) lack enough nuance to keep parents guessing at their meanings, already-complex (nonverbal) facial expressions help infants to mimic, read, and make facial expressions learned from and to communicate with their parents and other individuals, immediately from birth toward becoming socialized. This might explain why muscles of facial expression are already differentiated, functional, and competent to display recognizable facial expressions much before birth. For instance, a recent study using 4D ultrasound scans has suggested that some facial expressions, related to pain and distress, are recognizable as early as the second trimester of pregnancy (Reissland, Francis, & Mason, 2013). In other words, the developmental phenomena of differentiation, modularity, and integration assure that the form and function of the facial expression muscle complexes are “ready” well before the moment of delivery, due to the importance of facial expressions immediately after birth.

The facial expression muscles are also a good example of the increasing integration that occurs in human postnatal development between soft and hard tissues, leading to fewer musculoskeletal modules that also seem to be more coherent functionally later in life. This is because in the adult, the muscles of the three major functional facial expression muscle modules (ocular/upper face and left and right orofacial: Fig. 8.2) are essentially included in the corresponding mid/upper face and left and right oral/ocular musculoskeletal modules (Esteve-Altava et al., 2015). However, in the newborn there is a functionally less integrated, and more asymmetrical, configuration: The facial expression muscles are distributed into four musculoskeletal modules, the orbicularis

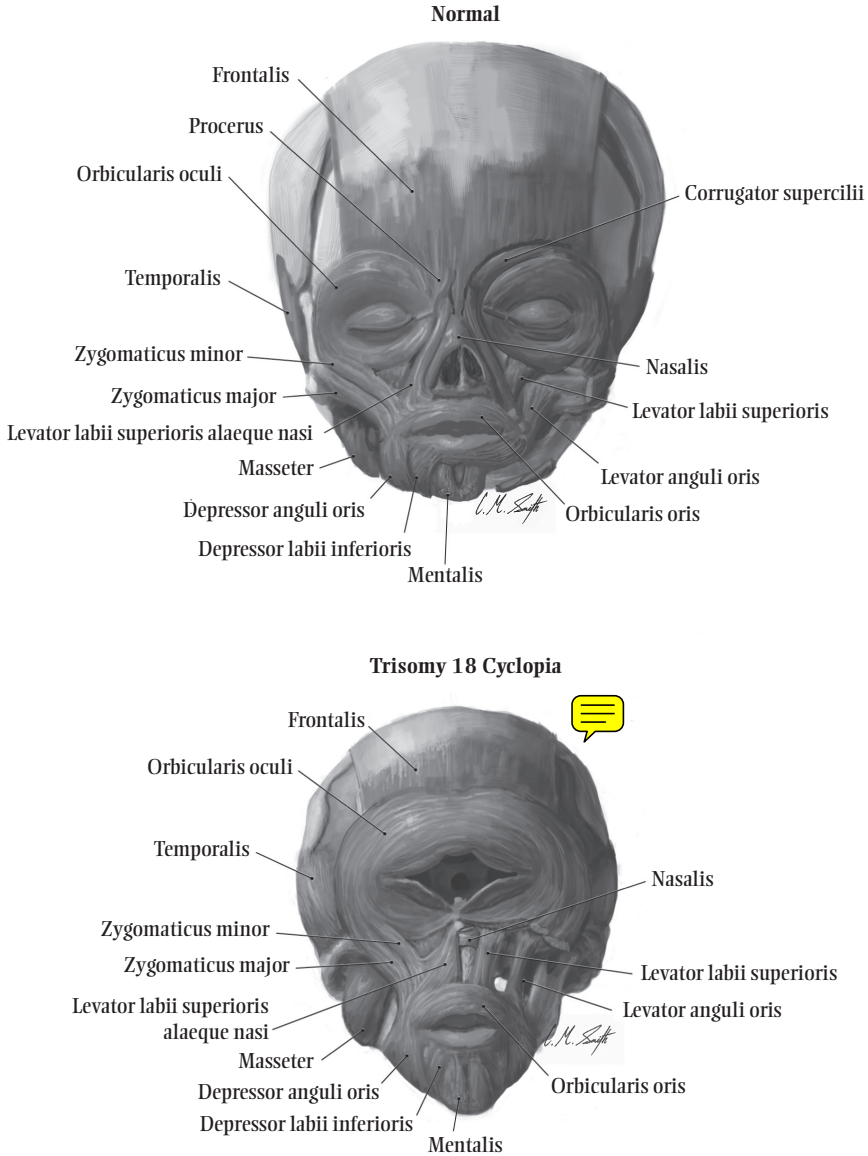


Figure 8.3 Comparison of anterior head musculature usually present in karyotypically normal infants and in a trisomy 18 cyclopic fetus. The platysma myoides, risorius, and buccal fat pad were removed; left side shows deep dissection (©2015 Christopher Smith/HU; modified from Esteve-Altava et al. 2015, with permission)

oculi forming a module with most orofacial muscles on the left side and with only a few facial muscles and some branchial and masticatory muscles on the right side (Diogo et al., in press). This does not seem so much the product of direct adaptive pressure on the newborn, but instead part of a process in which

the already well-defined muscle models are being properly integrated into the whole musculoskeletal modules.

It is particularly interesting to see that the independence of muscular and skeletal morphogenesis in early development still leads, later in development—and even in severe congenital malformations such as those seen in the trisomy 18 cyclopic fetus—to a recognizable general pattern of topological associations between the muscles of facial expression and the surrounding skeletal elements, despite the pronounced deformation of these elements (Diogo et al., in press; Smith et al., 2015). The findings of Smith et al. (2015) thus support the idea that the muscles of facial expression probably display a “nearest neighbor” pattern of muscle-skeletal associations (Diogo et al., in press): When subjected to developmental/evolutionary changes, facial muscles tend to insert onto bones that lie closer to their normal insertions, mostly ignoring the embryonic origin of these bones. Also interestingly, such a “nearest neighbor” model of muscle-skeleton connections is similar to that proposed for the limbs, but markedly different from models normally proposed for non-facial-expression head muscles, which seem to follow instead a “seek and find” model in which they usually attach in a very precise way to skeletal structures derived from their own arches. Developmental studies have shown that in some aspects the facial muscles do behave as limb and hypobranchial migratory muscles (i.e., tongue and infrahyoid muscles, which derive from somites and thus are not true head muscles), migrating far away from their primary origin, contrary to other head muscles (Prunotto et al., 2004). The developmental differences between the facial muscles and the other muscles of the head might help to explain why the attachments, overall configuration, and number of the muscles of facial expressions are particularly variable in mammals, including in primates and in our own species (Diogo et al., 2009; Diogo & Wood, 2012). In fact, these muscles are not only associated with the remarkably diverse facial expressions of mammals and particularly humans, but also with completely different functions, such as suckling or mastication in most mammals (e.g., buccinator muscle) and flying in mammals such as bats (e.g., occipito-pollicalis muscle: Tokita, Abe, & Suzuki, 2012).

CONCLUSIONS

We hope that this chapter emphasizes the remarkable diversity of primate facial structures and the fact that the number of facial muscles present in our species is actually not as high when compared to many other mammals as previously thought. A multitude of factors, from ecological traits to external features, such as facial pelage and color, also play a crucial role in the display—and perception by others—of facial expressions. Future studies should thus make an effort to combine as much data as possible—including information not included in

this chapter but included in this book as a whole, such as those from psychological studies—to have a better, more holistic understanding of the evolution and functional peculiarities of facial expressions. Importantly, the use of new tools, such as anatomical networks and phylogenetic analyses, should be further explored to compare the musculoskeletal and other features of humans across stages of development and with other animals. Such analyses will enable a better understanding of the links between the evolution of facial expressions, of their asymmetric use, and the evolvability of the face in general.

REFERENCES

- Ahn, J., Gobron, S., Thalmann, D., & Boulic, R. (2013). Asymmetric facial expressions: Revealing richer emotions for embodied conversational agents. *Computer Animation and Virtual Worlds*, *24*, 539–551. doi:10.1002/cav.1539
- Allen, W. L., Stevens, M., & Higham, J. P. (2014). Character displacement of Cercopithecini primate visual signals. *Nature Communications*, *5*(May 2014), 4266. doi:10.1038/ncomms5266
- Boas, J. E. V., & Paulli, S. (1908). *The elephant's head: Studies in the comparative anatomy of the organs of the head of the Indian elephant and other mammals. Part I*. Copenhagen: Folio, Gustav Fisher.
- Boas, J. E. V., & Paulli, S. (1925). *The elephant's head: Studies in the comparative anatomy of the organs of the head of the Indian elephant and other mammals. Part II*. Copenhagen: Folio, Gustav Fisher.
- Burrows, A. M. (2008). The facial expression musculature in primates and its evolutionary significance. *BioEssays*, *30*(3), 212–225.
- Burt, E. H. (1986). An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs*, *38*, 1–136.
- Burt Jr, E. H., & Ichida, J. M. (2004). Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. *The Condor*, *106*(3), 681–686.
- Caro, T. (2005). The adaptive significance of coloration in mammals. *Bioscience*, *55*(2), 125–136.
- Diogo, R., Kelly, R., Christian, L., Levine, M., Ziermann, J., Molnar, J., . . . Tzahor, E. (2015). The cardiopharyngeal field and vertebrate evolution: A new heart for a new head. *Nature*, *520*, 466–473.
- Diogo, R., & Wood, B. (2013). The broader evolutionary lessons to be learned from a comparative and phylogenetic analysis of primate muscle morphology. *Biological Reviews*, *88*, 988–1001. doi:10.1111/brv.12039
- Diogo, R., & Wood, B. A. (2012). *Comparative anatomy and phylogeny of primate muscles and human evolution*. Oxford (UK): CRC Press.
- Diogo, R., Wood, B. A., Aziz, M. A., & Burrows, A. (2009). On the origin, homologies and evolution of primate facial muscles, with a particular focus on hominoids and a suggested unifying nomenclature for the facial muscles of the Mammalia. *Journal of Anatomy*, *215*(3), 300–319. doi:10.1111/j.1469-7580.2009.01111.x
- Diogo, R., Smith, C., & Ziermann, J. M. (2015). Evolutionary developmental pathology and anthropology: A new area linking development, comparative anatomy, human

- evolution, morphological variations and defects, and medicine. *Developmental Dynamics*, 244(11), 13570–1374.
- Dobson, S. D. (2009a). Allometry of facial mobility in anthropoid primates: Implications for the evolution of facial expression. *American Journal of Physical Anthropology*, 138(1), 70–81.
- Dobson, S. D. (2009b). Socioecological correlates of facial mobility in nonhuman anthropoids. *American Journal of Physical Anthropology*, 139(3), 413–420.
- Esteve-Altava, B., Diogo, R., Smith, C., Boughner, J. C., & Rasskin-Gutman, D. (2015). Anatomical networks reveal the musculoskeletal modularity of the human head. *Scientific Reports*, 5, 8298. doi:10.1038/srep08298
- Kamilar, J. M., & Bradley, B. J. (2011). Interspecific variation in primate coat colour supports Gloger's rule. *Journal of Biogeography*, 38(12), 2270–2277. doi:10.1111/j.1365-2699.2011.02587.x
- Kingdon, J. (1992). Facial patterns as signals and masks. In S. Jones et al. (Eds.), *The Cambridge encyclopedia of human evolution* (pp. 161–165). Cambridge University Press: Cambridge.
- Kingdon, J. (2007). Primate visual signals in noisy environments. *Folia Primatologica*, 78(5-6), 389–404.
- Lescroart, F., Kelly, R. G., Le Garrec, J.-F., Nicolas, J.-F., Meilhac, S. M., & Buckingham, M. (2010). Clonal analysis reveals common lineage relationships between head muscles and second heart field derivatives in the mouse embryo. *Development*, 137(2010), 3269–3279. doi:10.1242/dev.050674
- Mancini, G., Ferrari, P. F., & Palagi, E. (2013). Rapid facial mimicry in Geladas. *Nature Scientific Reports*, 3(1527).
- Moynihan, M. (1967). *Comparative aspects of communication in New World primates* (D. Morris, Ed.). *Primate ethology*. Chicago, IL: Aldine.
- Murie, J., & Mivart, S. T. (1869). On the anatomy of the Lemuroidea. *The Transactions of the Zoological Society of London*, 7(1), 1–113.
- Ortolani, A. (1999). Spots, stripes, tail tips and dark eyes: Predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society*, 67(4), 433–476.
- Preuschoft, S., & Van Hooff, J. (1997). The social function of “smile” and “laughter”: Variations across primate species and societies. In U. Segerstrale & P. Molnar (Eds.), *Nonverbal communication: Where nature meets culture* (pp. 171–190). Hillsdale, NJ: Erlbaum.
- Prunotto, C., Crepaldi, T., Forni, P. E., Ieraci, A., Kelly, R. G., Tajbakhsh, S., . . . Ponzetto, C. (2004). Analysis of Mlc-lacZ Met mutants highlights the essential function of Met for migratory precursors of hypaxial muscles and reveals a role for Met in the development of hyoid arch-derived facial muscles. *Developmental Dynamics*, 231(3), 582–591.
- Reissland, N., Francis, B., & Mason, J. (2013). Can healthy fetuses show facial expressions of “pain” or “distress”? *PLoS ONE*, 8(June), 1–7. doi:10.1371/journal.pone.0065530
- Rensch, B. (1938). Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London*, 150, 275–285.
- Rinn, W. E. (1984). The neuropsychology of facial expression: A review of the neurological and psychological mechanisms for producing facial expressions. *Psychological Bulletin*, 95(1), 52.

- Santana, S. E., Alfaro, J. L., Noonan, A., & Alfaro, M. E. (2013). Adaptive response to sociality and ecology drives the diversification of facial colour patterns in catarrhines. *Nature Communications*, *4*(2765), 2765. doi:10.1038/ncomms3765
- Santana, S. E., Dobson, S. D., & Diogo, R. (2014). Plain faces are more expressive: Comparative study of facial colour, mobility and musculature in primates. *Biology Letters*, *10*(May 2014). doi:10.1098/rsbl.2014.0275
- Santana, S. E., Lynch Alfaro, J., & Alfaro, M. E. (2012). Adaptive evolution of facial colour patterns in Neotropical primates. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1736), 2204–2211. doi:10.1098/rspb.2011.2326
- Schmidt, K. L., Liu, Y., & Cohn, J. F. (2006). The role of structural facial asymmetry in asymmetry of peak facial expressions. *Laterality*, *11*(6), 540–561. doi:10.1080/13576500600832758
- Setchell, J. M. (2005). Do female mandrills prefer brightly colored males? *International Journal of Primatology*, *26*(4), 715–735. doi:10.1007/s10764-005-5305-7
- Setchell, J. M., Wickings, E. J., Knapp, L. a, & Jean Wickings, E. (2006). Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2395–2400. doi:10.1098/rspb.2006.3573
- Sherwood, C. C., Hof, P. R., Holloway, R. L., Semendeferi, K., Gannon, P. J., Frahm, H. D., & Zilles, K. (2005). Evolution of the brainstem orofacial motor system in primates: A comparative study of trigeminal, facial, and hypoglossal nuclei. *Journal of Human Evolution*, *48*(1), 45–84.
- Smith, C. M., Ziermann, J. M., Molnar, J. A., Gondre-Lewis, M. C., Sandone, C., Bersu, E. T., Aziz, M. A., & Diogo, R. (2015). *Muscular and skeletal anomalies in human trisomy in an evo-devo context: Description of a T18 cyclopic newborn and comparison between Edwards (T18), Patau (T13) and Down (T21) syndromes using 3-D imaging and anatomical illustrations*. Oxford, UK: Taylor & Francis.
- Stevens, M., & Merilaita, S. (2009). Animal camouflage: Current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1516), 423–427. doi:10.1098/rstb.2008.0217
- Tokita, M., Abe, T., & Suzuki, K. (2012). The developmental basis of bat wing muscle. *Nature Communications*, *3*, 1302.
- Veilleux, C. C., & Kirk, E. C. (2014). Visual acuity in mammals: Effects of eye size and ecology. *Brain, Behavior and Evolution*, *83*(1), 43–53. doi:10.1159/000357830
- Vick, S.-J. J., Waller, B. M., Parr, L. a, Smith Pasqualini, M. C., & Bard, K. A. (2007). A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). *Journal of Nonverbal Behavior*, *31*(1), 1–20. doi:10.1007/s10919-006-0017-z
- Waïtt, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M., & Perrett, D. I. (2003). Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(Suppl 2), S144–S146. doi:10.1098/rsbl.2003.0065
- Zinck, J. M., Duffield, D. A., & Ormsbee, P. C. (2004). Primers for identification and polymorphism assessment of Vespertilionid bats in the Pacific Northwest. *Molecular Ecology Notes*, *4*(2), 239–242. doi:10.1111/j.1471-8286.2004.00629.x