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The Head and Neck Muscles of the Serval and Tiger: Homologies, Evolution, and Proposal of a Mammalian and a Veterinary Muscle Ontology

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ABSTRACT

Here we describe the head and neck muscles of members of the two extant felid subfamilies (*Leptailurus serval*: Felinae; *Panthera tigris*: Pantherinae) and compare these muscles with those of other felids, other carnivorans (e.g., domestic dogs), other eutherian mammals (e.g., rats, treeshrews and modern humans), and noneutherian mammals including monotremes. Another major goal of the article is to discuss and help clarify nomenclatural discrepancies found in the Nomina Anatomica Veterinaria and in veterinary atlases and textbooks that use cats and dogs as models to understand the anatomy of domestic mammals and to stress differences with modern humans. We propose a unifying nomenclature that is expanded to all the head and neck muscles and to all mammalian taxa in order to help build veterinary and mammalian muscle ontologies. Our observations and comparisons and the specific use of this nomenclature point out that felids such as tigers and servals and other carnivorans such as dogs have more facial muscle structures related to the mobility of both the auricular and orbital regions than numerous other mammals, including modern humans, which might be the result of an ancient adaptation related to the remarkable predatory capacities of carnivorans. Interestingly, the skeletal differences, mainly concerning the hyoid apparatus, pharynx, and larynx, that are likely associated with the different types of vocalizations seen in the Felinae (mainly purring) and Pantherinae (mainly roaring) are not accompanied by clear differences in the musculature connected to these structures in the feline *L. serval* and the pantherine *P. tigris*. Anat Rec, 00:000–000, 2012. © 2012 Wiley Periodicals, Inc.

Key words: anatomy; evolution; felids; head and neck muscles; homologies; ontology; mammals; serval and tiger

INTRODUCTION

This study considers the head and neck myology of two felids, the serval (*Leptailurus serval*; Felinae) and the Sumatran tiger (*Panthera tigris sumatrae*; Pantherinae). The serval is a small-bodied felid, with males weighing 9–18 kg and females weighing 9–13 kg (Nowell and Jackson, 1996). Servals occupy grassland habitats in sub-Saharan Africa, Morocco, and Algeria (Cuzin, 2003; Clement et al., 2007; Macdonald et al., 2010). While classified as Least Concern for most of its range, populations in North Africa are considered Critically Endangered (Breitenmoser-Wursten et al., 2008). The serval is a small prey specialist, with rodents dominating the diet, followed by small birds, lizards, snakes, insects, and frogs (Geertsema, 1976, 1985; Bowland and Perrin, 1993; Skinner and Chimimba, 2010). Servals are characterized by long, slender limbs, and large ears, which they utilize to detect prey in tall grass (Geertsema, 1976). When hunting, the serval pounces on its prey, leaping into the air, and striking with its forepaws (Geertsema, 1976). A pounce may be over a meter high and can span 1-4 meters (Geertsema, 1976, 1985; Nowell and Jackson, 1996). Tigers occupy a wide range of habitats, from snow-covered mountain slopes to tropical rainforests and mangrove swamps (Sunquist and Sunquist, 2002; Macdonald et al., 2010). Their range has decreased dramatically in the past century, with populations now restricted to Russia, China, Southeast Asia, and the Indian subcontinent (Linkie et al., 2008; Macdonald et al., 2010). Tigers specialize in hunting medium to large-bodied ungulates, particularly cervids and wild boar (Seidensticker and McDougal, 1993; Sunquist et al., 1999; Sunquist and Sunquist, 2002; Hayward et al., 2012). Methods of prey capture are very plastic and tigers use a variety of bites (e.g., nape, throat) in concert with forepaw manipulation and other movements to subdue prey (Seidensticker and McDougal, 1993). The Sumatran tiger (*Panthera tigris sumatrae*), currently classified as Critically Endangered (Linkie et al., 2008), is the smallest of the living subspecies, with females weighing 75–110 kg and males weighing 100–140 kg (Mazák, 1981).

Very little is known about the soft tissues and particularly the head and neck muscles of the serval and tiger. For instance, authors such as Windle and Parsons (1897), Edgeworth (1935), Kunzel (1964), Saban (1968), Sasaki et al. (2000), and Anton et al. (2004) provided descriptions of a few muscles in tigers, but these mainly focused on the muscles of mastication and/or on some superficial neck muscles (e.g., trapezius, sternomastoid, and/or cleidomastoid); the facial muscles, and almost all pharyngeal and laryngeal muscles, were not described. Weissengruber et al. (2002) did provide some data about a few pharyngeal and laryngeal muscles from two tiger dissections in their analysis of the hyoid apparatus and pharynx, but they mainly focused on the attachments onto the hyoid apparatus. The lack of knowledge about the head and neck musculature of these felids raises difficulties for the discussion of not only the functional morphology and the evolution of these two taxa, but also the origin, evolution, functional morphology, and phylogenetic relationships of felids as a whole. Determing the phylogenetic relationships of felids has proven challenging due to the relatively recent radiation of the Felidae,

their conserved morphology, and poor fossil record. However, recent phylogenetic analyses indicate that the serval is closely related, and basal to, the caracal and African golden cat, diverging from a common ancestor around 6 Ma (Johnson et al., 2006; O'Brien and Johnson, 2007; Werdelin et al., 2010). Tigers, on the other hand, belong to the *Panthera* lineage (including the genera *Neofelis* and *Panthera*), which arose around 10.8 Ma, with members of the genus *Panthera* (i.e., lion, tiger, jaguar, leopard, and snow leopard) radiating more recently, in the last 4 million years (Johnson et al., 2006; O'Brien and Johnson, 2007; Davis et al., 2010; Werdelin et al., 2010). Davis and colleagues highlight the lack of consensus regarding relationships within *Panthera*, illustrating 13 conflicting phylogenetic hypotheses that have been supported by various morphological and molecular analyses (see Fig. 1 of Davis et al., 2010). A recently published supertree (Nyakatura and Bininda-Emonds, 2012) proposes older divergence times compared to the studies cited above, largely due to a heavily weighted basal calibration (Boreoeutheria, see Bininda-Emonds et al., 2007). Unfortunately, no calibrations within Felidae were utilized in the analysis by Nyakatura and Bininda-Emonds (2012); as a result, we consider the more recent divergence times to be better supported (e.g., Johnson et al., 2006).

In recent articles (Diogo, 2008, 2009; Diogo et al., 2009; Diogo and Wood, 2011) and monographs (Diogo, 2007; Diogo and Abdala, 2010; Diogo and Wood, 2012), Diogo et al. have reported the results of their long-term dissection-based study of the comparative anatomy, homologies and evolution of the head and neck muscles of all major groups of vertebrates. Recently, Diogo and Wood (2011, 2012) combined data from these dissections with carefully validated information from the literature to undertake the first comprehensive parsimony and Bayesian cladistic analyses of the order Primates and some other mammalian groups (e.g., tree-shrews, dermopterans, and rodents) based on myological data. These recent studies, together with previous phylogenetic studies of the relationships of various nonmammalian vertebrate groups based also on myological data (for a review, see Diogo, 2007; Diogo and Abdala, 2010), show that muscle characters are particularly useful for phylogenetic reconstructions. Importantly, these previous studies have also stressed that in order to do sound, broad phylogenetic and functional works on mammalian and nonmammalian taxa, one first needs to do a broad comparative study of those taxa and of the homologies and evolution of their muscles, as well as a very careful review and clarification of the literature and particularly of the nomenclature being used by different authors and in different textbooks and atlases. A major long-term goal is therefore to establish homologies and to propose a unifying nomenclature for muscles in mammals and other vertebrates in order to provide the comparative context for more detailed functional, physiological, phylogenetic, evolutionary, and taxon-based analyses.

Because the monograph of Diogo and Abdala (2010) included members of each major clade of vertebrates, it was not possible to include all the subgroups of each clade. In particular, it was not possible to provide detailed data for and comparisons with carnivorans and other mammalian taxa that include domestic animals, which are particularly relevant for veterinarians and
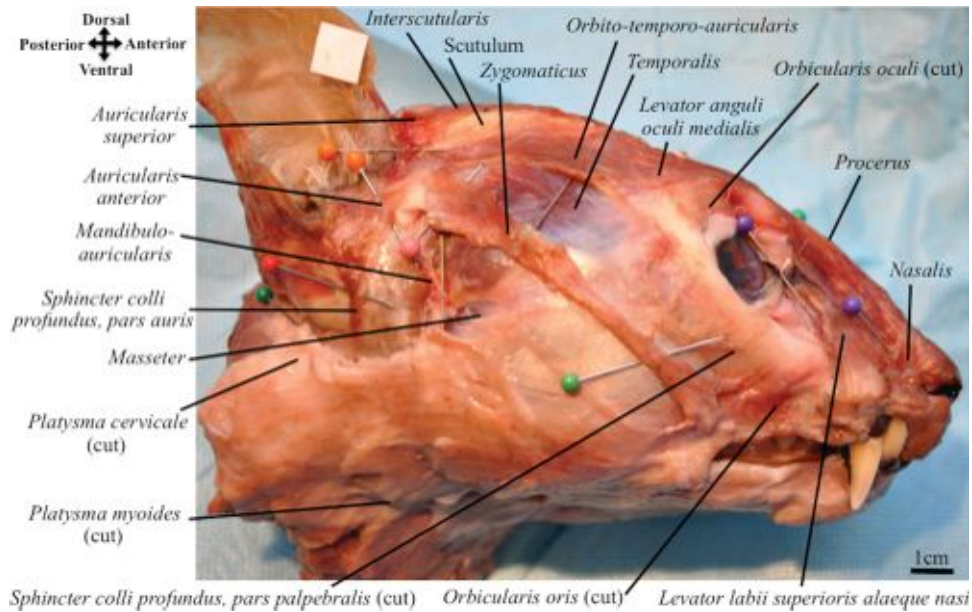
Fig. 1. *L. serval*: lateral view of the left (horizontal flip done with Photoshop) facial muscles; the masseter and temporalis are also shown.

extremely important for mammalogists, zoologists, functional morphologists and anatomists in general. In the present paper we therefore describe the head and neck muscles of the feline *L. serval* and the pantherine *P. tigris* and compare these muscles with those of other carnivorans and other mammals, including rats, treeshrews and modern humans, as well as the phylogenetically plesiomorphic monotremes. In addition to describing the muscles of these two felid taxa and analyzing the homologies and evolution of these muscles, one of the main goals of the present paper is to discuss and help clarify nomenclatural discrepancies found in the Nomina Anatomica Veterinaria and in veterinary atlases and textbooks that use cats and dogs as models to understand the anatomy of domestic mammals and to stress differences with modern humans. Because we have previously dissected members of all the major vertebrate groups we can better understand the descriptions of authors that use different nomenclatures for these muscles and this allows us to clarify the nomenclatural confusion involved in those descriptions. By including in our Tables and taking into account in our discussions various taxa that fill the large phylogenetic gap existing between carnivorans such as felids and primates such as modern humans, we will be able to critically examine and discuss the accuracy of the homologies, evolutionary scenarios and muscle nomenclatures provided in previous publications. Therefore, within our comparisons (given in the text and Tables 1–4) we will particularly focus on two well described representatives of the subfamilies Felinae and Pantherinae, i.e. domestic cats (*Felis catus*) and lions (*Panthera leo*); on other carnivorans that are often used as a model in comparative and veterinary atlases and textbooks, i.e. domestic dogs (*Canis lupus familiaris*); on a so-called 'generalized mammal' that is well described and frequently used in comparative anatomical atlases and

that is, at the same time, a member of the clade – Glires – that is the extant sister-group of the Euarchonta, i.e. rats (*Rattus norvegicus*); on representatives of the two extant euarchontan sister-groups of Primates, i.e. the dermopteran *Cynocephalus volans* and the scandentian *Tupaia* sp.; and on our own species, *Homo sapiens*, taking also into account the recent studies of Diogo and colleagues in which the muscles of this species have been extensively compared with the muscles of all the other major groups of extant primates and of other vertebrate groups (see below). Based on our observations and comparisons, we will thus be able to propose a unifying nomenclature that is expanded to all the head and neck muscles and to mammalian taxa such as carnivorans, which will hopefully help build veterinarian and mammalian muscle ontologies that will be useful to students, educators, and researchers. An ontology serves as a formal model through which one can employ mathematical or computational logic to clarify and define concepts and relationships within a domain of interest; ontologies link, and therefore provide critical contexts for biological concepts. In particular, for the purpose of building muscle ontologies, it is crucial to first make sure that when one applies an anatomical term/name to designate a certain muscle/bundle in the animals across clades, we are effectively referring to the same structure. This facilitates communication among scientists and, importantly, the development and use of databases that would allow one to search for muscles/bundles by taxon, anatomical region or innervation, for instance.

MATERIALS AND METHODS

We dissected the muscles on the right and left sides of the head and neck of an adult male serval (*L. serval*; total body weight of 9.7 kg) and an adult female Sumatran tiger (*P. tigris sumatrae*; total body weight of 152.0

TABLE 1. Scheme illustrating the authors' hypotheses regarding the homologies of the mandibular muscles of the adult serval and adult tiger dissected and of adult representative members of other mammalian taxa

	Ornithorhynchus anatinus (9 muscles)	L. serval and P. tigris (8 muscles, if t.t. is present)	Rattus norvegicus (9 muscles)	Cynocephalus volans (8 muscles)	Tupaia sp. (9 muscles)	Homo sapiens (8 muscles)	Nomina Anatomica Veterinaria, names as they would apply to felids such as Felis catus
VENTRAL	Mylohyoideus	Mylohyoideus	Mylohyoideus	Mylohyoideus	Mylohyoideus	Mylohyoideus	Mylohyoideus
	Digastricus anterior	Digastricus anterior	Digastricus anterior	Digastricus anterior	Digastricus anterior	Digastricus anterior	Digastricus, venter rostralis
	–	–	Interm. anterior	–	Interm. anterior	–	–
ADDUCTOR MANDIBULAE	Masseter	Masseter	Masseter	Masseter	Masseter	Masseter	Masseter
	Detrahens man.	–	–	–	–	–	–
	Temporalis	Temporalis	Temporalis	Temporalis	Temporalis	Temporalis	Temporalis
	Pterygoideus lateralis	Pterygoideus lateralis	Pterygoideus lateralis	Pterygoideus lateralis	Pterygoideus lateralis	Pterygoideus lateralis	Pterygoideus lateralis
	Tensor tympani	Tensor tympani ?	Tensor tympani	Tensor tympani	Tensor tympani	Tensor tympani	Tensor tympani
	Tensor veli palatini	Tensor veli palatini	Tensor veli palatini	Tensor veli palatini	Tensor veli palatini	Tensor veli palatini	Tensor veli palatini
	Pterygoideus medialis	Pterygoideus medialis	Pterygoideus medialis	Pterygoideus medialis	Pterygoideus medialis	Pterygoideus medialis	Pterygoideus medialis

The nomenclature of the muscles follows that used in the text. Data compiled from evidence provided by our own dissections and comparisons and by a review of the literature. Each of the homology hypotheses shown in this table is based on a detailed analysis of all the lines of evidence available (e.g., relation with other muscles; relation with hard tissues; configuration/orientation of muscle fibers; development; function; phylogeny; innervation; etc.: see Diogo and Abdala 2010 and Diogo and Wood 2012 and also text). In the far right column, the differences between the muscle names we list for the felids *L. serval* and *P. tigris* and the muscle names provided in the Nomina Anatomica Veterinaria (2005) that would apply to felids such as *Felis catus*, are indicated in bold. VENTRAL, ADDUCTOR MANDIBULAE = Ventral and adductor mandibulae musculature sensu Edgeworth 1935.

TABLE 2. Scheme illustrating the authors' hypotheses regarding the homologies of the hyoid muscles of the adult serval and adult tiger dissected and of adult representative members of other mammalian taxa (see caption of Table 1)

	Ornithorhynchus anatinus (12 mus. - not ex. ear*)	*L. serval* and *P. tigris* (29 mus. - not ex. ear, if s., s.c.s., d.n. & r.a.o.l. present)	*Rattus norvegicus* (23 mus. - not ex. ear)	*Cynocephalus volans* (22 mus. - not ex. ear)	*Tupaia sp.* (25 mus. - not ex. ear)	*Homo sapiens* (27 mus. - not ex. ear)	Nomina Anatomica Veterinaria, names as they would apply to felids such as *Felis catus*
DORSO-MEDIAL HYOID MUS.	Stylohyoideus	Stylohyoideus	Stylohyoideus	—	Stylohyoideus	Stylohyoideus	Stylohyoideus
	—	Jugulohyoideus	—	Jugulohyoideus	Jugulohyoideus	—	Occipitohyoideus
	—	Digastricus posterior	Digastricus posterior	Digastricus posterior	Digastricus posterior	Digastricus posterior	Digastricus, venter caudalis
	Stapedius	Stapedius ?	Stapedius	Stapedius	Stapedius	Stapedius	Stapedius
	Platysma cervicale	Platysma cervicale	Platysma cervicale	Platysma cervicale	Platysma cervicale	—	Part of platysma
	Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides	Platysma myoides	Part of platysma
	—	Occipitalis (several bundles)	Occipitalis	Occipitalis	Occipitalis	Occipitalis	Occipitalis + Part of auriculares caudales
	—	Auricularis posterior	Auricularis posterior	Auricularis posterior	Auricularis posterior	Auricularis posterior	Part of auriculares caudales
	Ex. ear mus.*	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.	Ex. ear mus.*	Ex. ear mus.	Ex. ear mus.*
	—	Mandíbulo-auricularis	Mandíbulo-auricularis	—	Mandíbulo-auricularis	—	Styloauricularis
	—	—	—	—	—	Risorius	—
VENTRAL HYOID MUS.	Interhyoideus prof.	—	—	—	—	—	—
	Sphincter colli supe.	Sphincter colli supe.?	Sphincter colli supe.	—	Sphincter colli supe.	—	Sphincter colli superficialis
	—	Sternofacialis	—	—	—	—	—
	(colli prof. in Echidna)	Sphincter colli prof.	Sphincter colli prof.	Sphincter colli prof.	Sphincter colli prof.	—	Sphincter colli prof. + Malaris + Parotidoauricularis
	Cervicalis tra.	—	—	—	—	—	—
	—	Interscutularis	Interscutularis	—	—	—	Interscutularis + Scutuloauriculares
	—	Zygomaticus	Zygomaticus major	Zygomaticus major	Zygomaticus major*	Zygomaticus major	Zygomaticus
	—	Zygomaticus minor	Zygomaticus minor	Zygomaticus minor*	Zygomaticus minor		
	—	Orbito-temporo-auricularis	Orbito-temporo-auricularis	Frontalis	Frontalis	Frontalis	Frontalis + Part of auriculares rostrales
	—	—	—	Auriculo-orbitalis	Auriculo-orbitalis	Temporoparietalis	—
	—	Auricularis anterior	—	—	—	Auricularis anterior	Part of auriculares rostrales
	—	Auricularis superior	—	Auricularis superior	Auricularis superior	Auricularis superior	Part of auriculares dorsales
	—	Le. anguli oculi medialis	—	—	—	—	Le. anguli oculi medialis
	—	Re. anguli oculi lateralis?	—	—	—	—	Re. anguli oculi lateralis
	Orbicularis oculi	Orbicularis oculi	Orbicularis oculi	Orbicularis oculi	Orbicularis oculi	Orbicularis oculi	Orbicularis oculi
	—	—	—	Zygomatico-orbicularis	Zygomatico-orbicularis	—	—
	—	—	—	—	—	Depressor supercili	—
	—	Corrugator supercili	—	Corrugator supercili	Corrugator supercili	Corrugator supercili	— (should be listed)
	Naso-labialis	Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup. al. nasi	Le. labii sup.	Levator nasolabialis
	—	Procerus	Procerus	—	—	Procerus	— (should be listed)
	Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius	Buccinatorius	Buccinator
	—	Dilatator nasi?	Dilatator nasi	—	—	—	Dilatator naris apicalis
	—	Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii sup.	Le. labii superioris
	—	Nasalis	Nasalis	Nasalis	Nasalis	Nasalis	Lateralis nasi
	—	—	—	—	—	Depressor septi nasi	—
	—	Le. anguli oris facialis	Le. anguli oris facialis	Le. anguli oris facialis	Le. anguli oris facialis	Le. anguli oris facialis	Caninus
	Orbicularis oris	Orbicularis oris	Orbicularis oris	Orbicularis oris	Orbicularis oris	Orbicularis oris	Orbicularis oris + Inc. superior + Inc. inferior
	—	—	—	—	—	Depressor labii inf.	Depressor labii inf.
	—	—	—	—	—	Depressor anguli oris	Depressor anguli oris
	Mentalis	Mentalis	—	Mentalis	Mentalis	Mentalis	Mentalis

The black arrows indicate the hypotheses that are most strongly supported by the evidence available; the gray arrows indicate alternative hypotheses that are supported by some of the data, but overall are not as strongly supported by the evidence available as are the hypotheses indicated by black arrows. al, alaeque; d.n., dilatator nasi; ex., extrinsic; inc., incisivus; inf., inferioris; le., levator; mus., muscles; prof., profundus; r.a.o.l., retractor anguli oris lateralis; s., stapedius; s.c.s., sphincter colli superficialis; sup., superioris; supe., superficialis; tra., transversus.

kg) that died of natural causes in the Bioparc Fuengirola and the Zoológico de Santillana, respectively, and were then fresh-frozen and stored at the Department of Anatomy of the University of Valladolid. At each stage of the dissection, muscles were documented with digital photographs, using a Nikon D90 camera. Origins, insertions and divisions of the muscles were recorded and their weights were measured immediately upon removal using a Sartorius 1219 MP 400g portable balance. Unless stated otherwise, the weights described in the text below refer to the weights of the muscles of the right side of the head and neck (t and s referring to tiger and serval, respectively). In order to weigh muscles that are partially or fully blended to each other, the fibers of each muscle were recognized by their orientation and separated, e.g. the fibers of the orbicularis are circular, surrounding the mouth, while the fibers of the levator labii superioris are vertical, i.e. run ventrodorsally, as explained below. This methodology is described in detail in Diogo and Abdala (2010; for more details, please refer

to this monograph). It should be noted that the weight percentages given for which muscle refer to the weight of the percentages of the total weight of the muscles from the respective group of muscles, e.g. the percentage given for the mentalis in the serval refers to the percentage regarding the total weight of the facial muscles (muscles innervated by the 7th cranial nerve) that could be weighted in this animal. Some of the neck muscles were cut prior to our dissections (e.g., in necropsy), so the respective weights could not be measured (these and other cases where the weights could not be determined are labeled as weight unmeasured (WU), in the descriptions below). We follow the taxonomic nomenclature of Diogo et al. (2008), Diogo and Abdala (2010) and Diogo and Wood (2011, 2012), and in Tables 1–4 we compare this nomenclature with that of the Nomina Anatomica Veterinaria (2005). It should be noted that apart from the serval and tiger, we have dissected, in the past, specimens from all the major groups of primates and of non-primate vertebrates. A list of the dissected non-

TABLE 3. Scheme illustrating the authors' hypotheses regarding the homologies of the branchial muscles of the adult serval and adult tiger dissected and of adult representative members of other mammalian taxa (see caption of Table 1)

		Ornithorhynchus anatinus (14 muscles)	L. serval and P. tigris (20 muscles)	Rattus norvegicus (19 muscles)	Cynocephalus volans (18 muscles)	Tupaia sp. (17 muscles)	Homo sapiens (16 muscles)	Nomina Anatomica Veterinaria, names as they would apply to felids such as Felis catus
TRUE BRANCHIAL MUS.	STRICTO	Stylopharyngeus	Stylopharyngeus	Stylopharyngeus	Stylopharyngeus	Stylopharyngeus	Stylopharyngeus	**Stylopharyngeus caudalis**
		Ceratohyoideus	Ceratohyoideus	Ceratohyoideus	Ceratohyoideus	Ceratohyoideus	—	Ceratohyoideus
		Subiculus rectis III						
	OTHER	Acromiotrapezius	Acromiotrapezius	Acromiotrapezius	Acromiotrapezius	Trapezius	Trapezius	**Trapezius, pars cervicalis**
		Spinotrapezius	Spinotrapezius	Spinotrapezius	Spinotrapezius	—	—	**Trapezius, pars thoracica**
		Dorsocutaneous						
		—	Cleido-occipitalis	Cleido-occipitalis	—	Cleido-occipitalis	—	**Cleidocephalicus, pars cervicalis**
		Cleidomastoideus	Cleidomastoideus	Cleidomastoideus	Cleidomastoideus	Cleidomastoideus	Sternocleidomastoideus	**Cleidocephalicus, pars mastoidea**
		Sternomastoideus	Sternomastoideus	Sternomastoideus	Sternomastoideus	Sternomastoideus		**Sternocephalicus, pars mast. & pars occip.**
PHARYNGEAL MUS.		Co. pharyngis	Co.pharyngis medius	Co.pharyngis medius	Co. pharyngis medius	Co. pharyngis medius	Co. pharyngis medius	**Hyopharyngeus**
		—	Co.pharyngis inferior	Co.pharyngis inferior	Co. pharyngis inferior	Co. pharyngis inferior	Co. pharyngis inferior	**Constrictores pharyngis caudales**
		Cricothyroid	Cricothyroideus	Cricothyroideus	Cricothyroideus	Cricothyroideus	Cricothyroideus	Cricothyroideus
		—	Co.pharyngis superior	Co.pharyngis superior	Co. pharyngis superior	Co. pharyngis superior	Co. pharyngis superior	**Part of constrictores pharyngis rostrales?**
		—	Pterygopharyngeus	Pterygopharyngeus	Pterygopharyngeus			Pterygopharyngeus
		Palatopharyngeus	Palatopharyngeus	Palatopharyngeus	Palatopharyngeus	Palatopharyngeus	Palatopharyngeus	Palatopharyngeus
		—	Uvulae (mod. veli palatini)				Uvulae	**Palatinus**
		—	Levator veli palatini	Levator veli palatini	Levator veli palatini	Levator veli palatini	Levator veli palatini	Levator veli palatini
		—	Salpingopharyngeus	Salpingopharyngeus	Salpingopharyngeus	Salpingopharyngeus	Salpingopharyngeus	**— (should be listed)**
LARYNGEAL MUS.		Thyroarytenoideus	Thyroarytenoideus	Thyroarytenoideus	Thyroarytenoideus	Thyroarytenoideus	Thyroarytenoideus	Thyroarytenoideus
		—	Cricoarytenoideus lateralis	Cricoarytenoideus lateralis	Cricoarytenoideus lateralis	Cricoarytenoideus lateralis	Cricoarytenoideus lateralis	Cricoarytenoideus lateralis
		Arytenoideus	Arytenoideus	Arytenoideus	Arytenoideus	Arytenoideus	Arytenoideus transversus	**Arytenoideus transversus**
							Arytenoideus obliquus	
		Cricoarytenoideus post.	Cricoarytenoideus post.	Cricoarytenoideus post.	Cricoarytenoideus post.	Cricoarytenoideus post.	Cricoarytenoideus post.	**Cricoarytenoideus dorsalis**

The black arrows indicate the hypotheses that are most strongly supported by the evidence available; the gray arrows indicate alternative hypotheses that are supported by some of the data, but overall are not as strongly supported by the evidence available as are the hypotheses indicated by black arrows. co., constrictor; occip., occipitalis; mast., mastoidea; mus., muscles; post., posterior.

TABLE 4. Scheme illustrating the authors' hypotheses regarding the homologies of the hypobranchial muscles of the adult serval and adult tiger dissected and of adult representative members of other mammalian taxa (see caption of Table 1)

		Ornithorhynchus anatinus (6 muscles not in. to.)	L. serval and P. tigris (7 muscles not in. to.)	Rattus norvegicus (7 muscles not in. to.)	Cynocephalus volans (7 muscles not in. to.)	Tupaia sp. (8 muscles not in. to.)	Homo sapiens (9 muscles not in. to.)	Nomina Anatomica Veterinaria, names as they would apply to felids such as Felis catus
GENIOHYOIDEUS		Geniohyoideus	Geniohyoideus	Geniohyoideus	Geniohyoideus	Geniohyoideus	Geniohyoideus	Geniohyoideus
		Genioglossus	Genioglossus	Genioglossus	Genioglossus	Genioglossus	Genioglossus	**Genioglossus + Hyoepiglotticus**
		Intrinsic mus. tongue	Intrinsic mus. tongue	Intrinsic mus. tongue	Intrinsic mus. tongue	Intrinsic mus. tongue	Intrinsic mus. tongue	Intrinsic mus. tongue
		Hyoglossus	Hyoglossus	Hyoglossus	Hyoglossus	Hyoglossus	Hyoglossus	Hyoglossus
		—	Styloglossus	Styloglossus	Styloglossus	Styloglossus	Styloglossus	Styloglossus
		—	—	—	Palatoglossus	—	Palatoglossus	—
RECTUS CERVICIS		Sternohyoideus	Sternohyoideus	Sternohyoideus	Sternohyoideus	Sternohyoideus	Sternohyoideus	Sternohyoideus
		Omohyoideus	—	Omohyoideus	—	Omohyoideus	Omohyoideus	Omohyoideus
		Sternothyroideus	Sternothyroideus	Sternothyroideus	Sternothyroideus	Sternothyroideus	Sternothyroideus	Sternothyroideus
		—	Thyrohyoideus	Thyrohyoideus	—	Thyrohyoideus	Thyrohyoideus	Thyrohyoideus

The black arrows indicate the hypotheses that are most strongly supported by the evidence available; the gray arrows indicate alternative hypotheses that are supported by some of the data, but overall are not as strongly supported by the evidence available as are the hypotheses indicated by black arrows. GENIOHYOIDEUS', 'RECTUS CERVICIS' = "geniohyoideus" and "rectus cervicis" groups sensu Edgeworth, 1935; in. to., intrinsic muscles of the tongue; mus., muscles.

primary vertebrate specimens is given in Diogo and Abdala (2010); a list of the dissected primate specimens is given in Diogo and Wood (2011, 2012), which are the main references for the comparisons with modern humans provided in the text below. When we refer to the anterior, posterior, dorsal and ventral regions of the body, we do so in the sense the terms are used for pronograde tetrapods (e.g., the forelimb is anterior to the hind limb, the sternum is ventral to the thoracic part of the vertebral column).

RESULTS

In this section we describe the mandibular, hyoid, branchial, pharyngeal, laryngeal and hypobranchial muscles of the serval specimen and the tiger specimen dissected by us. The descriptions apply to both specimens; in those cases in which the myology of the two specimens differs, these will be mentioned. The order in which the muscles are described mainly follows that used in Tables 1–4. When the muscles have tendinous attachments, these will be described; in all other cases, attachments are exclusively via fleshy fibers.

Mandibular Muscles

Although exceptions may occur (Table 1), the mandibular muscles sensu Edgeworth (1935) are considered to be derived from branchial arch 1 (mandibular arch) and generally innervated by the Vth cranial nerve. Seven
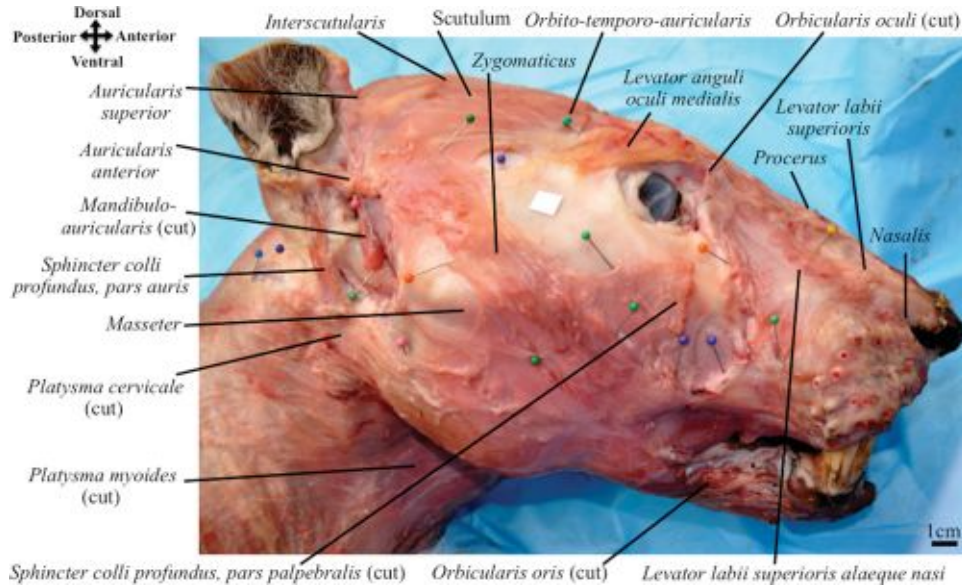
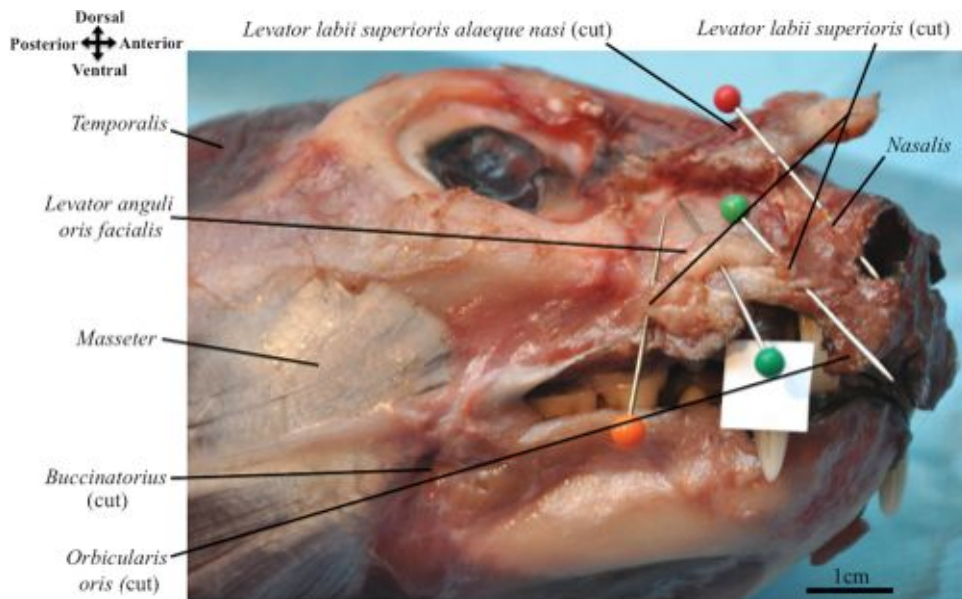Fig. 2. *P. tigris*: lateral view of the right facial muscles; the masseter is also shown.

Fig. 3. *L. serval*: anteroventrolateral view of the left (horizontal flip done with Photoshop) deep facial muscles; the masseter and temporalis are also shown.

mandibular muscles were dissected in the serval and tiger: the masseter, temporalis, mylohyoideus, digastricus anterior, pterygoideus medialis, pterygoideus lateralis, and tensor veli palatini. It was not possible to examine if the tensor tympani is present or not in these felids, as the skull was kept intact for curation in the osteology collection at the University of Valladolid.

The masseter (Figs. 1–6) originates from the zygomatic arch both tendinously and via fleshy fibers and inserts onto the mandible via tendons and fleshy fibers, being subdivided into a ventral bundle (3.35 g, i.e. 5.7%, s; 11.49 g, i.e. a superficial bundle (15.84 g, i.e.

27%, s; 176.84 g, i.e. 22%, t), and a deep bundle (2.32 g, i.e. 3.9%, s; 46.02 g, i.e. 5.6%, t). The ventral bundle is small and attaches to the ventral and also the ventromedial surfaces of the ramus of the mandible, its posterior fibers passing deep (medial) to the fibers of the superficial bundle and ventral to the angular part of the mandible. This ventral bundle is blended with the pterygoideus medialis posteriorly and with some fibers of the digastricus anterior anteriorly. The superficial bundle is the largest of the three bundles and inserts mainly onto the ventral and ventrolateral surface of the ramus of the mandible and also blends with the pterygoideus
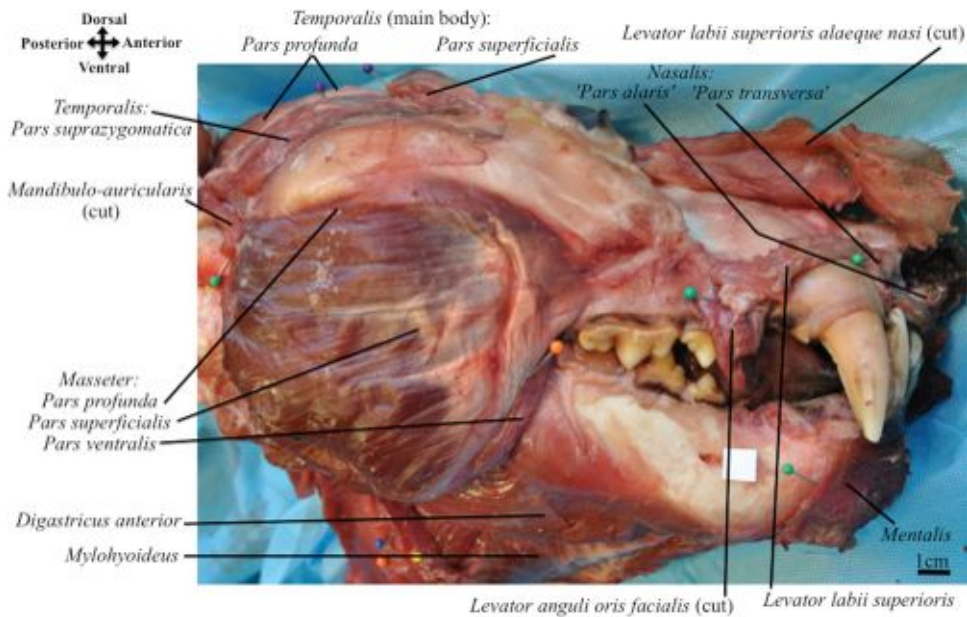
Fig. 4. *P. tigris*: ventrolateral view of the right mandibular and deep facial muscles.
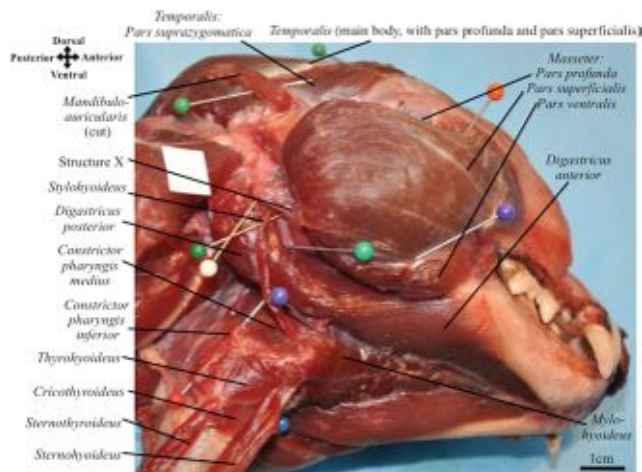

Fig. 5. *L. serval*: ventrolateral view of the right head and neck muscles after removing most of the facial muscles; the muscle bundle X seems to be an anomaly or variation, and might be a bundle of the stylohyoideus or of the styloglossus (see Discussion).
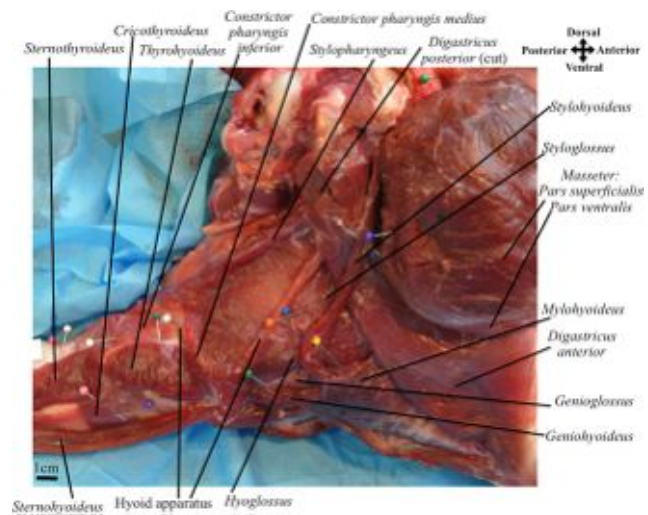

Fig. 6. *P. tigris*: ventrolateral view of the right head and neck muscles after removing most of the facial muscles.

medialis. The deep bundle probably includes the 'zygomatico-mandibularis' sensu Saban 1968 (we did not find a distinct muscle 'zygomatico-mandibularis'); it attaches to the lateral side of the ramus of the mandible, being deeply blended with the pars suprazygomatica of the temporalis and thus also inserts together with this latter structure onto part of the lateral surface of the coronoid process. The temporalis (Figs. 1, 3–5) has a more superficial pars suprazygomatica sensu Saban (1968) (5.55 g, i.e. 9.4%, s; 122.52 g, i.e. 15.1%, t) and a deeper main body, which is in turn subdivided into a superficial, anterior bundle (4.78 g, i.e. 8.1%, s; 70.07 g, i.e. 8.6%, t) and a deep, posterior bundle (21.22 g, i.e. 36.0%, s; 265.83 g, i.e. 32.7%, t). Both its origin and insertion are via tendons and fleshy fibers. The pars suprazygomatica runs from the posterodorsolateral margin of the skull and medial side of the zygomatic arch, reaching the lateral portion of the superior nuchal line posteriorly, to the lateral portion of the coronoid process. The superficial head of the main body of the temporalis runs from the dorsomedial margin of the skull and also from the orbital portion of the frontal (lying just posterior to the orbit) to the anterodorsal and anteromedial portion of the coronoid process. The deep head of the main body of the temporalis is the largest bundle of the muscle, running from the whole posterodorsal margin of the skull, reaching a well developed dorsomedial crest medially as well as the superior nuchal line posteriorly, to the medial and dorsal sides of the coronoid process.

The mylohyoideus (0.69 g, i.e. 1.2%, s; 14.82 g, i.e. 1.8%, t; Figs. 4–7) is a thin muscle running from the medial surface of the body of the mandible to a median raphe separating it from its counterpart; it does not reach the hyoid apparatus posteriorly. The posterior portion of the digastricus anterior (5.07g, i.e. 8.6%, s; 48.26g, i.e. 5.9%, t; Fig. 4–6) is connected to the digastricus posterior (a hyoid muscle: see below) by a short tendinous intersection. The anterior portion of the digastricus anterior attaches mainly to the medial side of the body of the mandible; in the tiger it also extends to a significant area of the lateral side of the body of the mandible. The digastricus anterior does not meet its counterpart at the midline, and both the digastricus anterior and digastricus posterior lie far from the hyoid apparatus. There is no distinct muscle intermandibularis anterior sensu Diogo and Abdala (2010).
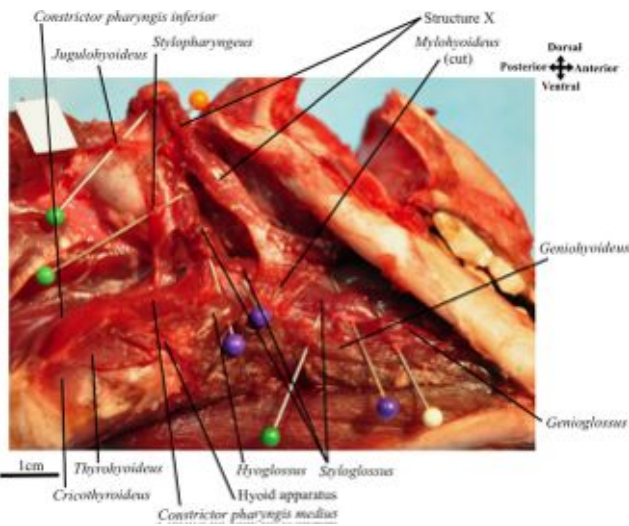

Fig. 7. *L. serval*: ventrolateral view of the right head and neck muscles after removing most of the mandibular and hyoid muscles and some hypobranchial muscles; the muscle bundle X seems to be an anomaly or variation, and might be a bundle of the stylohyoideus or of the styloglossus (see Discussion).

The pterygoideus medialis (WU s) is a broad muscle originating from the pterygopalatine fossa and adjacent regions of the skull and inserting tendinously and via fleshy fibers to the ventromedial margin of the ramus of the mandible, being blended with the masseter. The pterygoideus lateralis (WU s) is undivided and lies anteriorly to, and is deeply blended with, the pterygoideus medialis, originates from the subtemporal fossa and adjacent structures, and inserts tendinously and via fleshy fibers to the mandibular condyle and adjacent structures (total mass of pterygoideus medialis + pterygoideus lateralis in t = 56.48 g, i.e. 6.9%,). The tensor veli palatini (0.14 g, i.e. 0.2%, s; 1.07 g, i.e. 0.1%, t; Fig. 8) is a small muscle originating from the auditory region and passing anteriorly to the levator veli palatini (a branchial - pharyngeal - muscle: see below) to attach tendinously onto the soft palate and pterygoid hamulus.

Hyoid Muscles

The hyoid muscles sensu Edgeworth (1935) are considered to be derived from branchial arch 2 (hyoid arch) and usually innervated by the VIIth cranial nerve (Table 2). Apart from the extrinsic musculature of the ear (including facial muscles such as the tragicus, antitragicus or trago-helicinus), we found 25 hyoid muscles in the dissected serval and tiger: digastricus posterior, jugulohyoideus, stylohyoideus, platysma cervicale, platysma myoides, occipitalis, auricularis posterior, interscutularis, mandibulo-auricularis, sphincter colli profundus, zygomaticus, orbito-temporo-auricularis, levator anguli oculi medialis, auricularis anterior, auricularis superior, orbicularis oculi, corrugator supercilii, mentalis, orbicularis oris, levator labii superioris alaeque nasi, levator labii superioris, levator anguli oris facialis, buccinatorius, nasalis, and procerus. In addition, in the serval we found a structure that might correspond to the dilatator nasi of other mammals. As shown in Table 2 and explained below, we did not find a distinct sphincter colli superficialis nor a distinct retractor anguli oculi lateralis. It was not possible to examine if the stapedius is present or not in these felids as the skull was left intact for the osteology collection at the
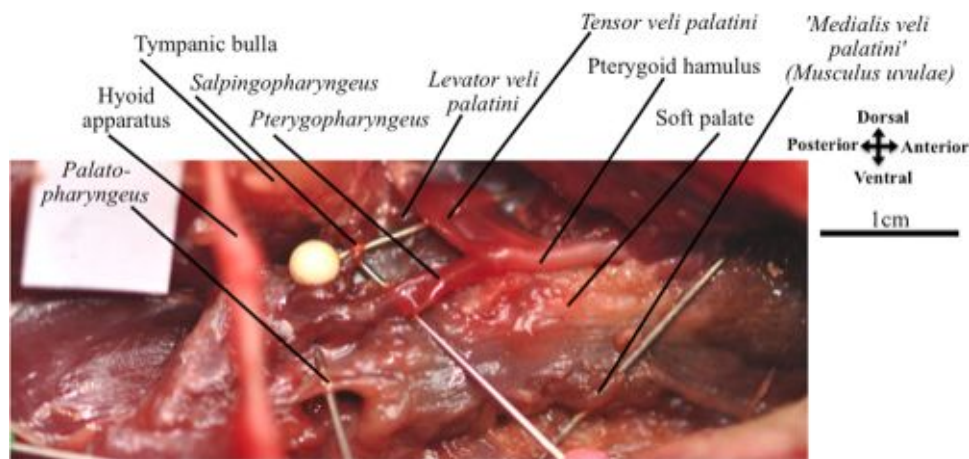

Fig. 8. *L. serval*: medial view of the left (horizontal flip done with Photoshop) deep pharyngeal muscles.
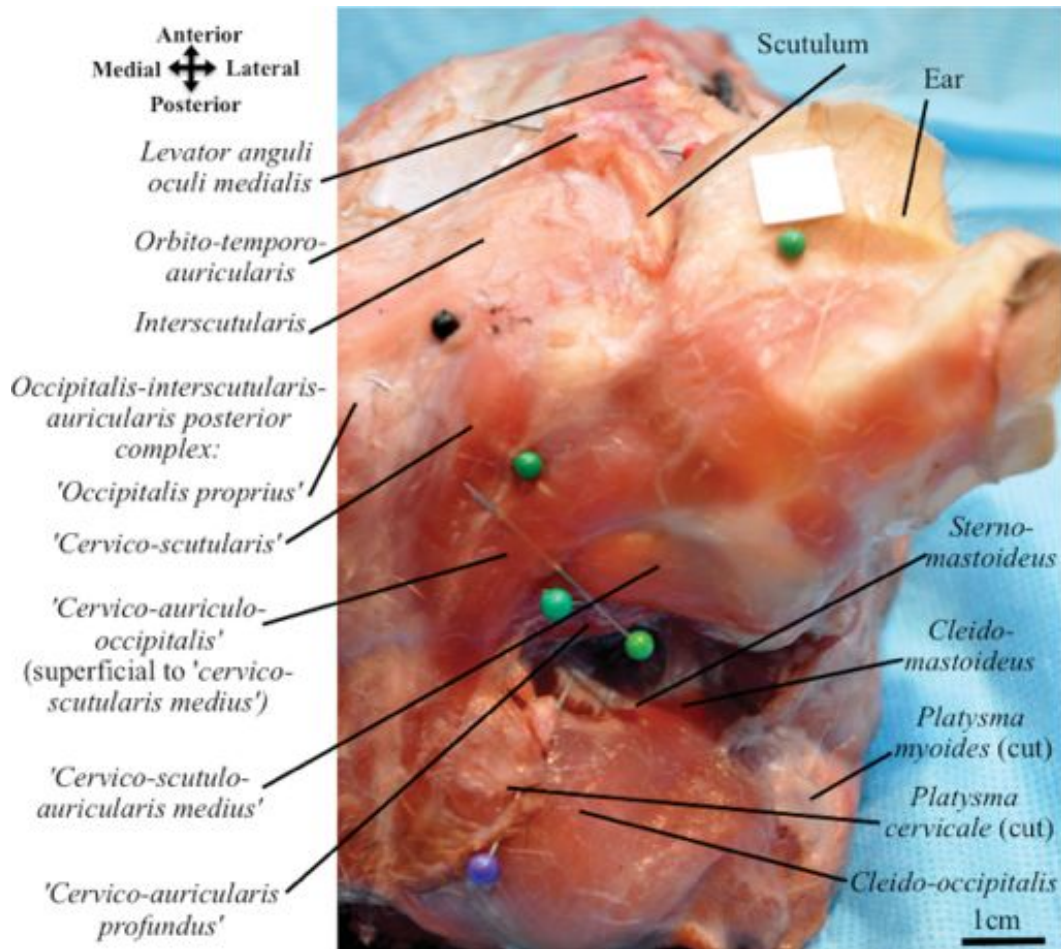
Fig. 9. *L. serval*: posterodorsomedial view of the right facial muscles associated with the ear and scutulum.

University of Valladolid; this muscle and the jugulohyoideus, stylohyoideus and digastricus posterior are the only hyoid muscles that are not facial muscles sensu, e.g., Huber (1930a,b, 1931) and Seiler (1971–1980).

The digastricus posterior (1.10 g, i.e. 8.3%, s; 11.10 g, i.e. 5.5%, t; Figs. 5 and 6) originates tendinously and via fleshy fibers from the mastoid region and is connected anteroventrally to the digastricus anterior (a mandibular muscle: see above) by a short tendinous intersection, being much shorter than the latter muscle. The jugulohyoideus (0.02 g, i.e. 0.2%, s; 0.38 g, i.e. 0.2%, t; Fig. 7) originates from the mastoid process, medial to the digastricus posterior, and inserts onto the proximal surface of the hyoid apparatus (including the tympanohyoideum sensu Weissengruber et al. (2002); in this paper the nomenclature of the other structures of the hyoid apparatus will also follow that of these authors). The stylohyoideus (0.09 g, i.e. 0.7%, s; 2.83 g, i.e. 1.4%, t; Figs. 5–6) originates from the auditory region, being in contact with the anterior potion of the jugulohyoideus. It inserts onto a strong aponeurosis that indirectly connects it to the hyoid apparatus, and in the serval it also has a very thin tendon that meets the thin tendon of its counterpart in the ventral midline. On the right side of the serval there is a structure X (0.32 g, i.e. 2.4%,; Figs.

5, 7), i.e. a muscle bundle running from the auditory region, just anterior to the stylohyoideus and somewhat lateral to it proximally, to the posterolateral margin of the mylohyoideus, to which it is completely fused distally (see Discussion). The platysma cervicale (WU s; Figs. 1–2, 9) runs from the nuchal region, meeting its counterpart in the dorsal midline, to the region of the mouth, passing deep (medial) to the zygomaticus. The platysma myoides (WU s; Figs. 1–2, 9) is blended with the platysma cervicale, running from the lateral and ventral regions of the neck to the region of the mouth, some of its fibers seemingly meeting those of its counterpart in the ventral midline (total weight of platysma cervicale and platysma myoides in $t = 78.39$ g, i.e. 38.7%,).

The occipitalis-auricularis posterior-interscutularis complex is divided into several structures, which are often designated as muscles in the veterinary literature (Saban, 1968). However, at least some of these structures clearly correspond to structures that are present in other mammals (e.g., rats, tree-shrews, flying lemurs, numerous primates) and that have been described, e.g., as bundles of the occipitalis muscle sensu Diogo et al. (2009), Diogo and Abdala (2010) and Diogo and Wood (2012). Therefore, following this nomenclature we will
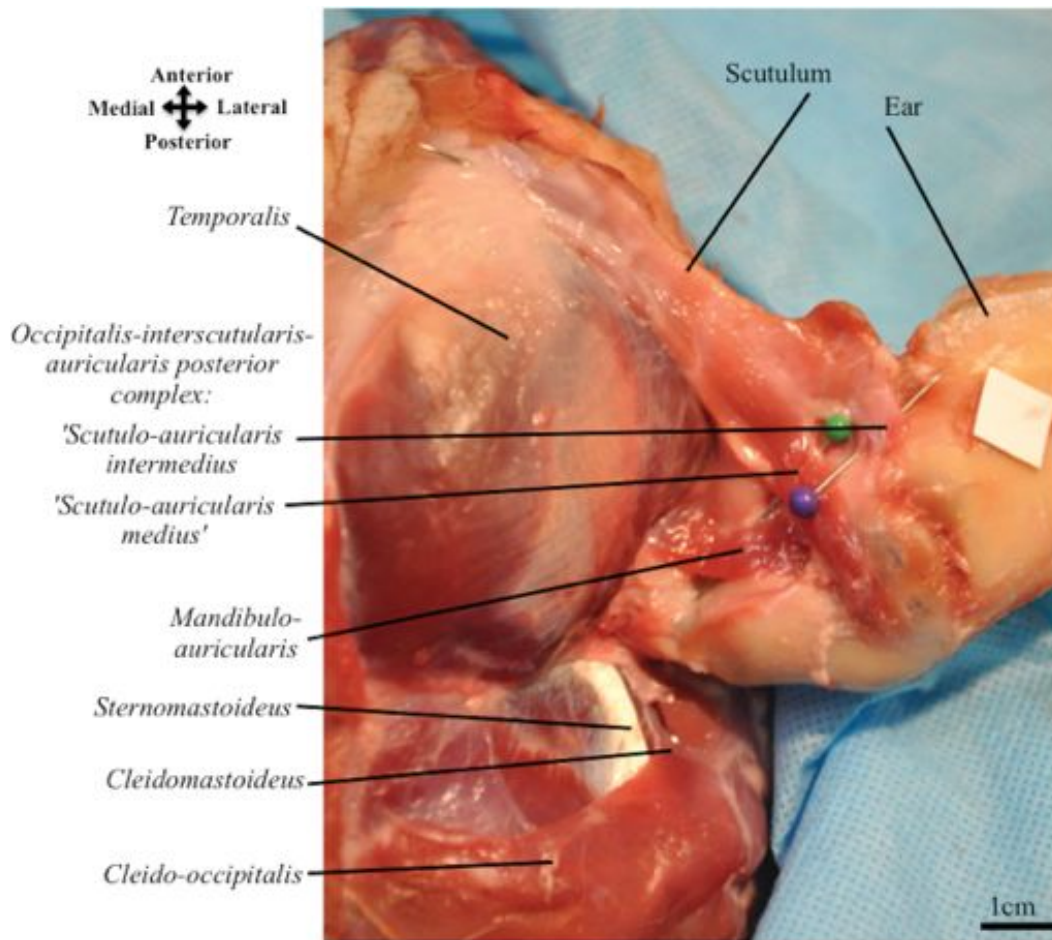
Fig. 10. *L. serval*: posterodorsal view of the right deeper facial muscles associated with the ear and scutulum.

designate these structures as bundles of the occipitalis-auricularis posterior-interscutularis complex, although we recognize that some adjustments probably need to be made in the future in order to recognize at least some of these structures as individual muscles (e.g., the "subscutulo-auricularis intermedius" sensu Jouffroy and Saban, 1971, and Evans, 1993, which is well differentiated and separated from the surrounding muscle structures); we will address this issue in future studies. The "cervico-auriculo-occipitalis" bundle (10.02 g, i.e. 4.9%, t; Figs. 9, 11) of the occipitalis sensu Diogo and Wood (2012) corresponds to the "cervico-auricularis" sensu Jouffroy and Saban (1971; e.g. their fig. 427), running from the dorsal midline of the nuchal region to the dorsomedial surface of the cartilaginous ear. Anterior to this bundle lies the "cervico-scutularis" (4.97 g, i.e. 2.4%, t; Figs. 9, 11) sensu Jouffroy and Saban (1971; e.g. his fig. 427), which runs from the dorsal midline to the scutulum (total weight of "cervico-auriculo-occipitalis" and "cervico-scutularis in s = 1.81 g, i.e. 13.6%). Ventral (deep) to the "cervico-auriculo-occipitalis" and "cervico-scutularis" lie two structures running from the dorsal midline to the ear/scutulum, the anterior one seemingly corresponding to the "cervico-scutularis medius" (0.70 g, i.e. 5.2%, s; 4.93 g, i.e. 2.4%, t; Fig. 11) and the posterior one seemingly corresponding to the "cervico-scutulo-auricularis medius" (0.40 g, i.e. 3.0%, s; 4.61 g, i.e. 2.3%, t; Figs. 9, 11), sensu Jouffroy and Saban (1971; e.g. their fig. 427). Ventral (deep) to the latter structure lies a structure running from its ventral surface to the posterior surface of the cartilaginous ear, which seemingly corresponds to "cervico-auricularis profundus" (0.42 g, i.e. 3.2%, s; 1.19 g, i.e. 5.9%, t; Figs. 9 and 11) sensu Jouffroy and Saban (1971; e.g. their Fig. 427). The auricularis posterior sensu Diogo and Wood (2012) probably corresponds to part or the totality of the "cervico-auricularis-profundus" or "cervico-scutulo-auricularis medius" of the serval and tiger, sensu Jouffroy and Saban (1971; see e.g. their Fig. 427; see Discussion). The "occipitalis proprius" bundle (0.97 g, i.e. 7.3%, s; 9.43 g, i.e. 4.6%, t: Figs. 9 and 11) of the occipitalis sensu Diogo and Wood (2012) corresponds to the "occipitalis" sensu Jouffroy and Saban (1971; e.g. their Fig. 427), running from the dorsal midline, posteriorly, to the orbito-temporo-auricularis, anteriorly. The interscutularis (Figs. 1, 2, 9, 11) sensu Diogo and Wood (2012) and sensu Jouffroy and Saban (1971; e.g. their Fig. 427) is a single, undivided, continuous muscle connecting the scutulum of the right side to the scutulum of the left side of the body (i.e., it has no medial raphe, aponeurosis or intersection; total weight of muscle divided
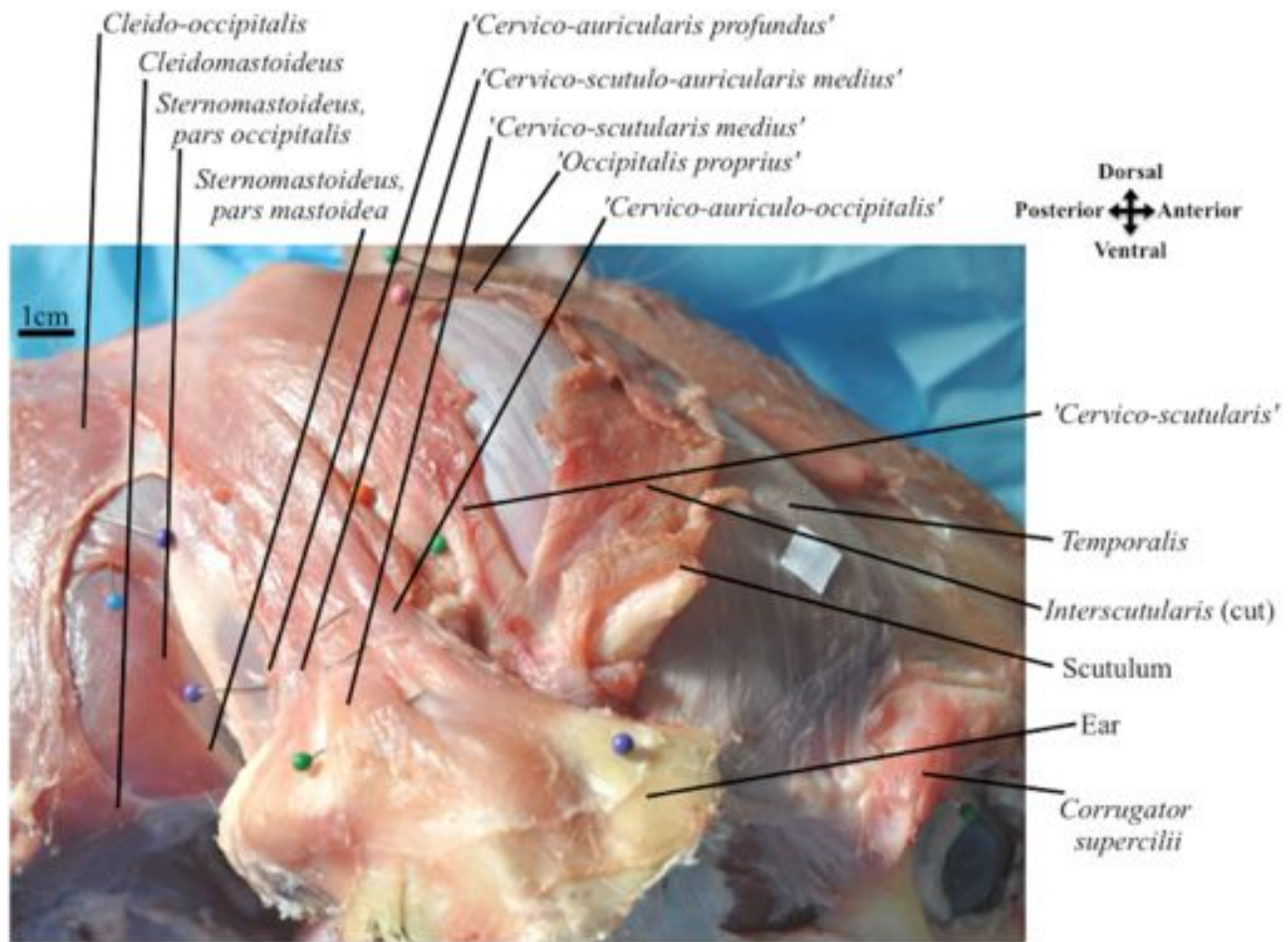
Fig. 11. *P. tigris*: dorsolateral view of the right facial muscles associated with the ear and scutulum.

in half = 1.02 g, i.e. 7.7%, s; 4.59 g, i.e. 2.3%, t:). Ventral (deep) to the interscutularis lies, on each side of the body, the "scutulo-auricularis intermedius" (0.46 g, i.e. 3.4%, s; 10.06 g, i.e. 5.0%, t; Fig. 10) sensu Jouffroy and Saban (1971; e.g. their Fig. 427), which connects the scutulum to the cartilaginous ear. Medial to the "scutulo-auricularis intermedius" lies a small bundle that also connects the scutulum to the cartilaginous ear, which might correspond to the "scutulo-auricularis medius" (0.16 g, i.e. 1.2%, s; 3.23 g, i.e. 1.6%, t; Fig. 10) sensu Jouffroy and Saban (1971; e.g. their Fig. 427).

The mandibulo-auricularis ("stylo-auricularis"; 0.49 g, i.e. 3.7%, s; 3,23 g, i.e. 1.6%, t; Figs. 1, 2, 4,5, 10) runs from the auricular region to the ramus of the mandible, passing lateral to the pterygoideus medialis. The sphincter colli profundus (WU s; WU t; Figs. 1 and 2) is deep to the platysma myoides and platysma cervicale, and has some well-differentiated bundles such as the pars auris, which attaches onto the cartilaginous ear, and the pars palpebralis, which goes to the orbital region (NB., these bundles are sometimes designated as distinct muscles, see Discussion). The zygomaticus ("auriculolabialis"; 0.68 g, i.e. 5.1%, s; 17.12 g, i.e. 8.4%, t; Figs. 1 and 2) is superficial to the platysma cervicale, running from the auricular region to the region of the mouth, where it blends with the orbicularis oris. The posterior

portion of the orbito-temporo-auricularis ("frontalis"; Figs. 1, 2, 9) is blended with the occipitalis and is associated with the scutulum and auricular region, while its anterior portion goes to the orbital region. The posteromedial portion of the levator anguli oculi medialis (Figs. 1, 2, 9) is blended with the posterior portion of the orbito-temporo-auricularis, but its anterolateral portion is well differentiated from it, inserting onto the frontal bone just posterior to the superciliary arch (combined weight of the orbito-temporo-auricularis plus levator anguli oculi medialis = 1.38 g, i.e. 10.4%, s; 11.47 g, i.e. 5.6%, t). The auricularis anterior ("zygomatico-auricularis"; 0.30 g, i.e. 2.2%, s; 1.29 g, i.e. 0.6%, t; Figs. 1 and 2) runs from the auricular region to the zygomatic arch and/or connective tissue associated with the posteroventral portion of the scutulum; it corresponds to the "auricularis anterior inferior" sensu Jouffroy and Saban (1971; NB: their suggestion that the "auricularis anterior inferior" does not correspond to the auricularis anterior of primates has been recently contradicted by Diogo and Wood, 2012). The auricularis superior ("auricularis anterior superior"; 0.16 g, i.e. 0.4%, s; 1.36 g, i.e. 6.7%, t; Figs. 1 and 2) originates from muscular fibers or connective tissue lying dorsomedial to the cartilaginous ear and runs ventrolaterally to attach onto the auricular region. The orbicularis oculi (WU s; WU t; Figs. 1 an 2)

is a broad muscle surrounding the eye that lies superficial to the corrugator supercilii (WU s; 2.31 g, i.e. 1.1%, t; Fig. 11), which is a well-developed muscle with a bony attachment onto the superciliary arch. There are a few fibers that lie just medial to the eye and that are associated with the glabella, which could correspond to the fibers of the depressor supercilii of primates such as modern humans; however, these fibers do not seem to form a well-defined, distinct muscle as is the case in those primates.

The mentalis (0.18 g, i.e. 1.4%, s; 3.99g, i.e. 2.0%, t; Fig. 4) lies deep to the broad orbicularis oris (WU s; WU t; Figs. 1 and 3) and to the platysma myoides, attaching onto the anteroventral surface of the body of the mandible; in the serval it is thin and seemingly does not meet its counterpart at the ventral midline, while in the tiger it is well developed and apparently has some fibers that meet the fibers of its counterpart. The levator labii superioris alaeque nasi ("nasolabialis"; 0.60 g, i.e. 4.5%, s; 11.85 g, i.e. 5.8%, t; Figs. 1–4) is a broad muscle that does not meet its counterpart at the dorsal midline; posterodorsomedially it originates from the orbital region and posterior region of the snout, running ventrolaterally to attach onto the upper lip. The levator labii superioris ("maxillo-naso-labialis"; 0.25 g, i.e. 1.9%, s; 4.97 g, i.e. 2.4%, t; Figs. 2–4) runs anterodorsally from the maxilla and upper lip to the anterolateral portion of the snout and adjacent structures, being superficial to, and somewhat blended with, the levator anguli oris facialis. The levator anguli oris facialis ("caninus" or "maxillo-labialis"; 0.28 g, i.e. 2.1%, s; 2.28 g, i.e. 1.1%, t; Figs. 3 and 4) is deep to the levator labii superioris, connecting the maxilla to the upper lip (following Diogo and Abdala, 2010, we use the name levator anguli oris facialis to distinguish this muscle from the levator anguli oris mandibularis of some non-mammalian tetrapods, which is a mandibular, and not a hyoid, muscle: Diogo, 2007, 2008). The buccinatorius (1.21 g, i.e. 9.1%, s; 3.21 g, i.e. 1.6%, t; Fig. 3) lies deep to the other facial muscles, being attached to both the ventrolateral surface of the maxilla and the dorsolateral surface of the mandible posteriorly and with the orbicularis oris anteriorly. The nasalis (part or totality of the 'naso-labialis profundus' sensu Jouffroy and Saban, 1971; Figs. 1–4) has two bundles that are fused ventrally but separated dorsally: one (0.08 g, i.e. 0.6%, s; 1.48 g, i.e. 0.7%, t) is somewhat similar to the pars alaris of modern humans, running from the upper lip (deep to the orbicularis oris) to the ventral surface of the nose; the other (0.03 g, i.e. 0.2%, s; 1.18 g, i.e. 0.6%, t) somewhat resembles the pars transversa of modern humans, running from the upper lip (also deep to the orbicularis oris) to the lateral surface of the nose. The procerus (part or totality of the 'naso-labialis superficialis' sensu some authors: see, e.g., Jouffroy and Saban, 1971; 0.11 g, i.e. 0.8%, s; 1.06 g, i.e. 0.5%, t; Figs. 1–2) runs from the glabellar region to the anterodorsal surface of the snout, being superficial to the levator labii superioris alaeque nasi and seemingly not meeting its counterpart in the midline. In the serval we found an additional thin muscle (0.09 g, i.e. 0.7%, s) that might correspond to the dilatator nasi of other mammals. It lies deep to the procerus and to the levator labii superioris alaeque nasi and runs anteroventrally from the orbital region to the dorsolateral region of the snout, being parallel to the procerus and perpendicular to the

levator labii superioris alaeque nasi, so it does not seem to be part of the latter muscle (see Discussion).

True Branchial, Pharyngeal, and Laryngeal Muscles (Table 3)

The branchial muscles sensu lato of Edgeworth (1935) may be divided into three main groups. The first group includes the "true" branchial muscles, which are subdivided into: A) the branchial muscles sensu stricto that are directly associated with the movements of the branchial arches and that in mammals are usually innervated by the glossopharyngeal nerve (CNIX) and represented by the subarcualis rectus III (found in adult extant monotremes), subarcualis rectus II (found in adult extant marsupials), and subarcualis rectus I (which corresponds to the ceratohyoideus and possibly to the stylopharyngeus of monotremes, marsupials and placentals: Smith, 1992; Noden and Francis-West, 2006; Diogo and Abdala, 2010); B) the branchial muscles that are instead often associated with the pectoral girdle and that in mammals are primarily innervated by the accessory nerve (CNXI) and represented by muscles such as the acromiotrapezius, spinotrapezius, trapezius, cleido-occipitalis, cleidomastoideus, sternomastoideus and/or sternocleidomastoideus (NB., recent studies are supporting the idea that these muscles might be at least partially derived from somites: e.g., Noden and Francis-West, 2006; Diogo and Abdala, 2010). The second group includes the pharyngeal muscles, which are only present as independent elements in extant mammals and are considered to be derived from arches 4-6 and are usually innervated by the vagus nerve (CNX; the mammalian stylopharyngeus, which is considered to be derived from the third arch and is primarily innervated by the glossopharyngeal nerve, is grouped here with the 'true' branchial muscles, and not with the pharyngeal muscles: see above). The third group includes the laryngeal muscles, which are considered to be derived from arches 4-6 and are usually innervated by the vagus nerve (CNX).

The serval and tiger have seven "true" branchial muscles sensu this work: the stylopharyngeus ceratohyoideus, acromiotrapezius, spinotrapezius, cleido-occipitalis, cleidomastoideus, and sternomastoideus. The stylopharyngeus (0.21 g, i.e. 0.8%, s; 1.60 g, i.e. 0.5%, t; Figs. 6 and 7) originates from the auditory region and the proximal surface of the hyoid apparatus (e.g., tympanohyoideum in the tiger and tympanohyoideum and stylohyoideum in the serval, sensu Weissengruber et al., 2002), most of its fibers attaching onto the pharyngeal wall. The ceratohyoideus (0.12 g, i.e. 0.4%, s; 1.29 g, i.e. 0.4%, t) lies deep (ventromedial) to the constrictor pharyngis medius and runs from the thyrohyoideum to the ceratohyoideum and the distal portion of the epihyoideum. The acromiotrapezius ("pars cervicalis of trapezius"; 13.36 g, i.e. 47.8%, s; 64.67 g, i.e. 19.6%, t-left side) originates, in the serval, via the ligamentum nuchae (at approximately the C3 level) and via an aponeurosis with no bony attachments that is attached to its counterpart at the dorsal midline (at approximately the C4 through T4 levels). In the tiger it originates from the aponeurosis (at approximately the C4 through T3 levels). In both animals the acromiotrapezius is partially fused with the omotransversarius and with the anterior

aspect of the spinotrapezius, and inserts via fleshy fibers onto the scapular spine; in the tiger, it also inserts onto the fascia of supraspinatus and infraspinatus. In both the serval and tiger the spinotrapezius ('pars thoracica of the trapezius'; 12.66 g, i.e. 45.3%, s; 99.04 g, i.e. 30.0%, t-left side) originates via fleshy fibers from the spinous processes of T3-T10, being partially overlapped by the aponeurosis of the acromiotrapezius, and inserts via fleshy fibers onto the scapular spine and via an aponeurosis onto the fascia of the infraspinatus and supraspinatus near the base of the scapular spine. The cleido-occipitalis ("pars cervicis of cleidocephalicus," or "cleidocervicalis"; WU s; Figs. 9–11) originates from the ligamentum nuchae (at approximately the C1-C3 level) and via a thin aponeurosis from the medial part of the superior nuchal line deep to the platysma cervicale and superficial to the rhomboideus capitis; it inserts via fleshy fibers onto the caudal aspect of the clavicle and onto the entire length of the intersectio clavicularis, the fibrous remnant of the lateral aspect of the clavicle. The cleidomastoideus ("pars mastoidea of cleidocephalicus"; WU s; Figs. 9–11) lies deep to the cleido-occipitalis and originates via an aponeurosis and fleshy fibers from the mastoid process in both the tiger and serval and also from the lateral portion of the superior nuchal line in the serval. In both animals, it inserts independently onto the caudal aspect of the clavicle and onto about half of the length of the intersectio clavicularis. The combined weight of the cleido-occipitalis plus the cleidomastoideus in the tiger is 126.62 g, i.e. 38.3% (left side). The sternomastoideus ('sternocephalicus'; WU s; WU t; Figs. 9–11) consists of a pars occipitalis and a pars mastoidea, which are partially fused. Both parts are mainly deep to the cleidomastoideus and attach posteriorly onto the cranial aspect of the manubrium, the pars mastoidea being fused with that of its counterpart across the ventral midline. Anteriorly the pars occipitalis and pars mastoidea attach tendinously and via fleshy fibers onto the superior nuchal line and onto the mastoid region, respectively.

The tiger and serval have nine pharyngeal muscles: constrictor pharyngis inferior, constrictor pharyngis medius, constrictor pharyngis superior, palatopharyngeus, salpingopharyngeus, levator veli palatini, pterygopharyngeus, musculus uvulae, and cricothyroideus (which is a pharyngeal muscle, and not a laryngeal muscle as it is sometimes erroneously suggested in the literature: see, e.g., Edgeworth, 1935; Saban, 1968; Diogo and Abdala, 2010). The constrictor pharyngis inferior ("thryropharyngeus plus cricopharyngeus"; 0.90 g, i.e. 3.2%, s; 9.65 g, i.e. 2.9%, t; Figs. 5–7) is poorly differentiated into a pars thyropharyngea running from the dorsal pharyngeal raphe to the thyroid cartilage and a pars cricopharyngea running from the dorsal pharyngeal raphe to the cricoid cartilage. The constrictor pharyngis medius ("hyopharyngeus"; 0.26 g, i.e. 0.9%, s; 10.48 g, i.e. 3.2%, t; Figs. 5–7) connects the dorsal pharyngeal raphe to the thyrohyoideum (pars chondropharyngea) and to the ceratohyoideum and adjacent structures (e.g., basihyoideum and/or epihyoideum; pars ceratopharyngea); the two parts of the muscle are blended with each other. There is seemingly a "glossopharyngeus" (part of constrictor pharyngis superior; WU s; WU t) in the serval, running from the tongue to the pharyngeal wall, but we could not discern if there are other parts

(e.g., buccopharyngeus) of the superior constrictor in this feline, or which parts of this muscle are present in the tiger.

The palatopharyngeus (0.04 g, i.e. 0.1%, s; 1.70 g, i.e. 0.5%, t; Fig. 8) is a small muscle running from the soft palate to the pharyngeal wall. The salpingopharyngeus (0.02 g, i.e. 0.1%, s; 2.16 g, i.e. 0.6%, t; Fig. 8) runs from the auditory region to the pharyngeal wall, being blended with the palatopharyngeus and pterygopharyngeus distally. The levator veli palatini (0.03 g, i.e. 0.1%, s; 1.01 g, i.e. 0.3%, t; Fig. 8) originates from the auditory region, posterior to the tensor veli palatini (a mandibular muscle: see above), attaching distally onto the soft palate. Ventral to these two muscles lies the pterygopharyngeus (0.09 g, i.e. 0.3%, s; 0.97 g, i.e. 0.3%, t; Fig. 8), which originates from the pterygoid hamulus and inserts onto the pharyngeal wall, blending with the palatopharyngeus and salpingopharyngeus. The "medialis veli palatine" ("palatinus") is a long muscle that is attached anteriorly to the hard palate and that runs posteriorly across the medial region of the soft palate; the musculus uvulae (WU s; WU t; Fig. 8) of mammals such as modern humans seemingly corresponds to part or the totality of this muscle (see Discussion). The cricothyroideus (0.06 g, i.e. 0.2%, s; 3.65 g, i.e. 1.1%, t; Figs. 5–7) is a undivided muscle connecting the cricoid and thyroid cartilages; it is well separated from its counterpart at the ventral midline below the larynx and does not reach the dorsal midline above the larynx.

Four laryngeal muscles are present as independent elements in the serval and tiger: thyroarytenoideus, cricothyroideus posterior, arytenoideus and cricoarytenoideus lateralis. The thyroarytenoideus (Fig. 12) connects the ventral portion of the thyroid cartilage to the arytenoid cartilage. It is divided into a posterior, medial pars inferior (0.05 g, i.e. 0.2%, s; 1.56 g, i.e. 0.5%, t), an anterior, lateral pars superior (0.04 g, i.e. 0.1%, s; 1.53 g, i.e. 0.5%, t), and a deeper pars profunda (0.01 g, i.e. 0.04%, s; 0.43 g, i.e. 0.1%, t; "musculus vocalis": see Discussion). The cricoarytenoideus posterior (0.06 g, i.e. 0.2%, s; 2.07 g, i.e. 0.6%, t; Fig. 12) runs from the dorsal surface of the cricoid cartilage, posteriorly, to the arytenoid cartilage, anteriorly; it does not meet its counterpart in the dorsal midline, above the larynx. The arytenoideus (Fig. 12) is a small, continuous muscle connecting the right and left arytenoid cartilages (total muscle divided in half = 0.03 g, i.e. 0.1%, s; 0.57 g, i.e. 0.2%, t). The cricoarytenoideus lateralis (0.04 g, i.e. 0.1%, s; 1.18 g, i.e. 0.4%, t; Fig. 12) lies ventral to the cricoarytenoideus posterior, running from the anterior margin of the cricoid cartilage to the arytenoid cartilage.

Hypobranchial Muscles

According to Edgeworth (1935: 189) the hypobranchial muscles are "developed from the anterior myotomes of the body" and thus "are intrusive elements of the head"; they "retain a spinal innervation" and may also be innervated by the XIth and XIIth nerves, but usually "do not receive any branches from the Vth, VIIth, IXth, and Xth nerves" (see Diogo and Abdala, 2010, for a recent review) (Table 4). Apart from the intrinsic musculature of the tongue (including hypobranchial muscles such as the longitudinalis superior, longitudinalis inferior, transversus linguae, and/or verticalis linguae), seven
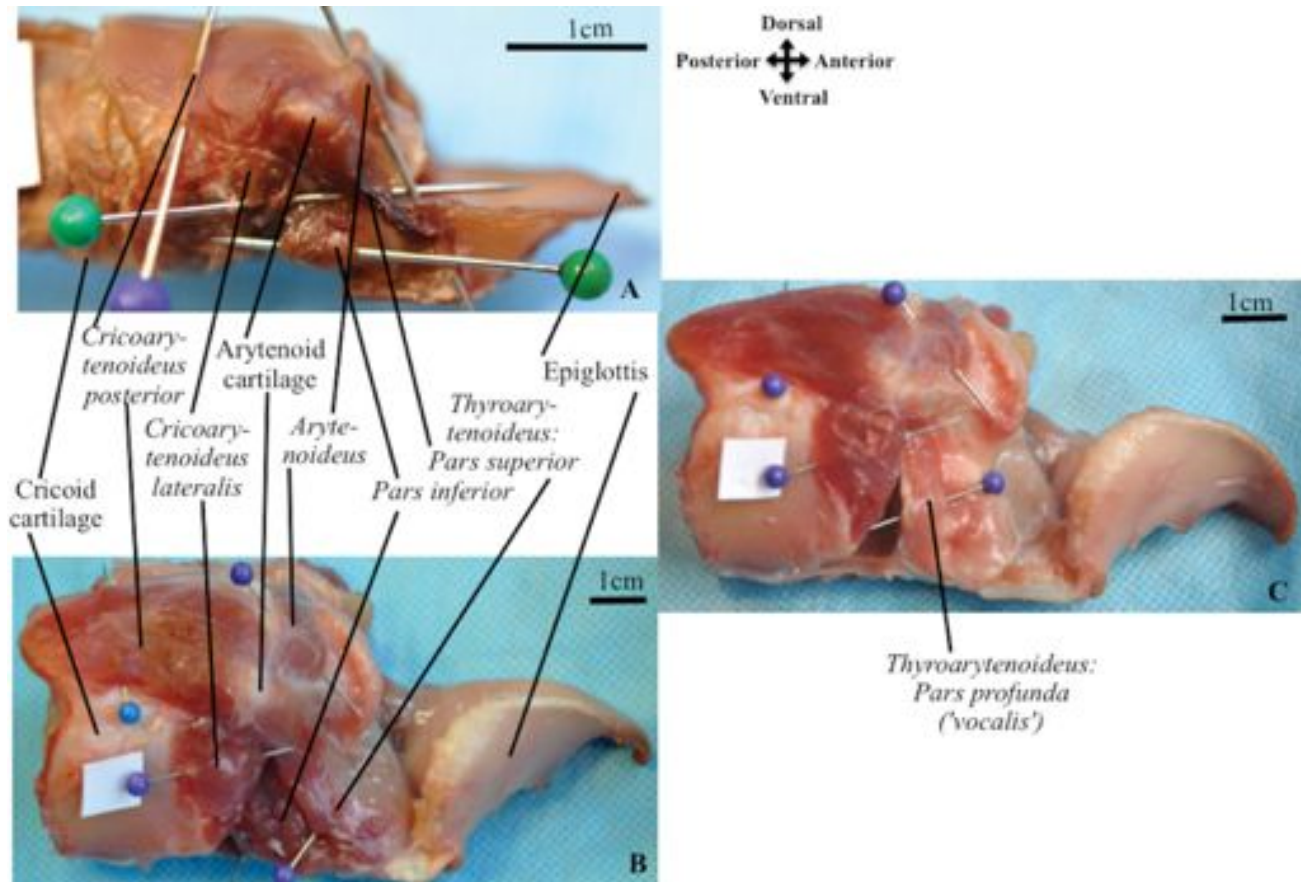
Fig. 12. **A**: *L. serval*: lateral view of the right laryngeal muscles after cutting the thyroid cartilage; **B** and **C**) *P. tigris*: lateral view of the right laryngeal muscles after cutting the thyroid cartilage (B) and then after removing the pars superior and the pars inferior of the thyroarytenoideus (C).

hypobranchial muscles are present as independent structures in the serval and tiger: geniohyoideus, genioglossus, hyoglossus, styloglossus, sternohyoideus, sternothyroideus, and thyrohyoideus.

The geniohyoideus (0.79 g, i.e. 22.7%, s; 7.74 g, i.e. 7.1%, t; Figs. 6 and 7) is attached posteriorly to the hyoid apparatus (basihyoideum only); anteriorly, it reaches the mandibular symphysis, inserting onto the mandible just ventral to genioglossus; it contacts its counterpart at the midline but is not deeply fused with it. The genioglossus (1.15 g, i.e. 33.0%, s; 24.06 g, i.e. 22.1%, t; Figs. 6 and 7) is a broad muscle that is well separated by fatty tissue from its counterpart at the ventral midline and that connects the mandible to the hyoid apparatus (basihyoideum and seemingly also ceratohyoideum), tongue, and epiglottis ("musculus epiglotticus or hyoepiglotticus": see Discussion). The hyoglossus (Figs. 6 and 7) is differentiated into two bundles: the "chondroglossus" (0.09 g, i.e. 2.6%, s; 3.70 g, i.e. 3.4%, t) is more superficial (lateral) and mainly runs from the basihyoideum, and other structures such as the ceratohyoideum and/or thyrohyoideum, to the tongue, passing superficial (lateral) to some fibers of the geniohyoideus and genioglossus and being blended with the styloglossus; the "ceratoglossus" (0.13 g, i.e. 3.4%, s; 5.53 g, i.e. 5.1%, t) is deep (medial) to this bundle and runs from the cerato-

hyoideus to the tongue. The styloglossus (0.86 g, i.e. 24.7%, s; 32.84 g, i.e. 30.1%, t; Figs. 6 and 7) is a long muscle running from the auditory region and proximal portion of the hyoid apparatus (e.g., tympanohyoideum and stylohyoideum) to the tongue. As noted in the description of the stylohyoideus (see above), on the right side of the serval there is a structure X (0.32 g, i.e. 9.1%; Figs. 5 and 7) that runs from the auditory region to the posterolateral margin of the mylohyoideus, its anterior portion lying just lateral to the styloglossus (see Discussion). The palatoglossus does not seem to be present as a distinct muscle. The sternohyoideus (WU s; 11.01 g, i.e. 10.1%, t; Figs. 5 and 6) originates from the pectoral region tendinously and trough fleshy fibers and inserts onto the basihyoideum, not having marked tendinous intersections; in the tiger it is deeply blended with its counterpart at the ventral midline. The sternothyroideus (WU s; 17.77 g, i.e. 16.3%, t; Figs. 5 and 6) originates from the pectoral region tendinously and via fleshy fibers and inserts onto the posterior margin of the thyroid cartilage, and also lacks marked tendinous intersections; in the tiger it has a main, lateral bundle and an additional medial bundle, which converges anteriorly to meet its counterpart at the ventral midline, just ventral to the cricothyroideus. The thyrohyoideus (0.14 g, i.e. 4.9%, s; 4.38 g, i.e. 4.0%, t; Figs. 5–7) connects the

thyroid cartilage to the thyrohyoideum, as well as to the basihyoideum in the tiger. The omohyoideus is absent in both animals.

DISCUSSION

Below we will compare the muscles of the serval and tiger with those of other mammals dissected by us and by other authors, focusing mainly on other felids in which the head muscles have been studied in detail such as lions and domestic cats, on other carnivorans with relevance for veterinary studies such as domestic dogs, and on our own species, *Homo sapiens*; the muscles of monotremes, rodents, dermopterans and scandentians have been recently described in detail by Diogo et al. (2008, 2009), Diogo (2009), and Diogo and Abdala (2010), and are listed in Tables 1–4, together with the muscles of the serval and tiger and of modern humans (see Introduction). To facilitate the comparisons and discussions and to avoid generalizations as well as confusions with animals dissected by other authors, we will refer to the tiger and serval dissected by us as "our tiger and serval".

Mandibular Muscles

The division of the masseter into a ventral bundle, a large superficial bundle and a deep bundle, found in felids such as our serval and tiger and the tigers dissected by Sazaki et al. (2010), as well as lions (e.g., Fig. 1 of Barone, 1967), is also found in some other mammals, including some marsupials (e.g., Fig. 190A of Saban, 1968; see also e.g. Edgeworth, 1935 and Schumacher, 1961). The posterior part of the ventral bundle of the masseter of our serval and tiger and the tigers dissected by Sazaki et al. (2010) that passes deep (medial) to the fibers of the superficial bundle of this muscle and ventral to the angular part of the mandible is often designated as the "pars reflexa"; it is often present in other carnivorans as well as other mammals such as rodents, lagomorphs and some primates (e.g., Adams, 1919; Edgeworth, 1935; Schumacher, 1961; Saban, 1968). In modern humans and most other mammals (e.g., Saban, 1968; Druzinsky et al., 2011), the masseter usually has a deep bundle and a superficial bundle, i.e. the ventral bundle of servals and tigers is not present as a distinct structure in modern humans.

According to Saban (1968) the pars suprazygomatica of the temporalis is often present in the Carnivora (including domestic cats; see also, e.g., Turnbull, 1970; Riley, 1985; Gorniak, 1986; Laison et al., 2001) and in other mammals such as rodents and some primates but not in modern humans; this structure is effectively well developed in our serval and tiger, being similar to that reported in *Puma* by Schumacher (1961). Regarding the division of the main body of the temporalis into a deep, posterior bundle and an anterior, superficial bundle, this is a feature commonly found in most groups of carnivorans (e.g., Windle and Parsons, 1897; Davis, 1964; Saban, 1968) and other mammals, being often present in modern humans (e.g., Schumacher, 1961; Saban, 1968). However, the broad attachment of the latter bundle onto a broad area of the orbital part of the frontal bone lying just posteriorly to the orbit, found in our serval and tiger, is a feature less commonly found within mammals,

being present in carnivorans and in a few other taxa such as bats and some primates but not in modern humans (Saban, 1968).

The descriptions of the ventral mandibular muscles of other felids, including domestic cats and lions, as well as of domestic dogs (see e.g., Fig. 212 of Saban, 1968; see e.g., also Edgeworth, 1935; Schumacher, 1961; Clair, 1975; Scapino, 1976), are similar to the condition found in our serval and tiger. That is, the intermandibularis anterior is often not present as a distinct muscle and the digastricus anterior is connected to the digastricus posterior by a tendinous intersection and not by a true tendon as seen in a few mammals including modern humans (e.g., Edgeworth, 1935; Diogo and Abdala, 2010). Regarding the mylohyoideus, Gilbert (1968) reported that in domestic cats this muscle attaches onto the hyoid apparatus, but the descriptions and illustrations of these felines provided by other authors indicate that the muscle is usually not directly inserted onto this apparatus, being instead connected to it indirectly via a strong aponeurosis, as found in our serval and tiger as well as in other felids (e.g., lions: e.g., Barone, 1967).

There has been some controversy about the presence/absence of a pterygoideus lateralis in carnivorans, some authors defending that the muscle is usually completely missing in these mammals, others defending that it is present but displays a peculiar fusion with the pterygoideus medialis, and still others that the two muscles are actually completely separable (for a review, see e.g. Saban, 1968). Our observations of the serval and tiger revealed that the pterygoideus lateralis and the pterygoideus medialis are effectively deeply blended, and that the former muscle is undivided, as found in other felids such as domestic cats (e.g., Kawawura et al., 1968; Saban, 1968); i.e. it is not differentiated into distinct superior and inferior heads as is often the case in various mammalian taxa, including modern humans (e.g., Jablonski, 1986; Birou et al., 1991; Aziz et al., 1998; Diogo and Wood, 2012). Windle and Parsons (1897) stated that the deep blending between the pterygoideus lateralis and the pterygoideus medialis is a feature seen in all major carnivoran groups. Regarding the tensor veli palatini, its configuration in our serval and tiger is similar to that usually found in other felids and in domestic dogs (e.g., Saban, 1968). As explained above, we were not able to discern if the tensor tympani is present in our serval and tiger, but this muscle is almost always present in mammals and is present in other felids, including domestic cats (e.g., Fig. 274 of Saban, 1968), so it is likely present in these two taxa as well; both the tensor veli palatini and the tensor tympani are present in modern humans (Table 1).

Hyoid Muscles

The stylohyoideus of other felids such as lions and jaguars is similar to that of our tiger, i.e., the muscle originates from the skull, jugulohyoideus and/or proximal part of the hyoid apparatus and attaches onto a strong aponeurosis that indirectly connects it to the hyoid apparatus (see e.g., Fig. 212 of Saban, 1968; see e.g., Weissengruber et al., 2002). The condition found in our serval is different in the sense that the stylohyoideus has a very thin tendon that meets the thin tendon of its counterpart at the ventral midline. According to

Weissengruber et al. (2002), in cheetah and domestic cats the muscle usually inserts directly onto the hyoid apparatus, namely onto the basihyoideum. In domestic dogs, the muscle is highly variable, e.g., it may attach onto an aponeurosis, directly onto the hyoid apparatus, or onto the digastricus posterior, or be completely missing (e.g., Huber, 1930a, 1931; Saban, 1968; Evans, 1993). In modern humans and various other primates the stylohyoideus originates from the styloid process and splits around the intermediate digastric tendon to insert onto the body of the hyoid bone. The jugulohyoideus is often designated as "mastoideostyloideus" because it usually runs from the mastoid region to the proximal portion of the hyoid apparatus, as it does in our serval and tiger. It is present in other felids such as domestic cats, in domestic dogs and in most other carnivorans (e.g., Windle and Parsons, 1893; Scapino, 1976; Evans, 1993; Weissengruber et al., 2002; Fig. 271 of Saban, 1968), as well as in various other mammals including cetaceans, artiodactyls, elephants, rodents (but not rats), treeshrews, flying lemurs, and nonanthropoid primates (Table 2; e.g., Saban, 1968). As explained above, we were unable to discern if the stapedius is present in our serval and tiger, but this muscle is almost always present in mammals and is present in felids such as domestic cats (e.g., Blevins, 1963, 1964), so it is likely present in servals and tigers as well.

The various divisions of the sphincter colli profundus found in our serval and tiger (e.g., pars auricularis and pars palpebralis) are also usually found in other carnivorans such as lions, domestic cats and dogs (e.g., Fig. 9C of Huber, 1930a; see also Fig. 50-1 of Clair, 1975, who designates the pars palpebralis as "musculus malaris"; the pars auris is often designated as "musculus parotidoauricularis": see Table 2). These carnivorans also have a sphincter colli superficialis (e.g., Fig. 9A of Huber, 1930a), as do numerous other mammals (e.g., Boas and Paulli, 1908), but we could not find this muscle in our serval and tiger, perhaps because the neck region was partially damaged prior to our dissections. In lions, which are closely related to tigers, the muscle is very thin and small (Barone, 1967; *contra* Jouffroy and Saban, 1971 who stated that previous authors had reported a remarkably well developed muscle in lions). We could also not find the muscle "retractor anguli oris lateralis," which is often described in felids such as domestic cats, and also in domestic dogs (see, e.g., Figs. 50–1 and 50–17 of Clair, 1975). As shown in Table 4 of Jouffroy and Saban (1971), some veterinarians have named this latter muscle the "corrugator supercilii lateralis," thus suggesting that it might correspond to part or the totality of the corrugator supercilii ("superciliaris") of modern humans. Because we found a well-developed corrugator supercilii in our tiger and serval but did not find a "retractor anguli oris lateralis," and because the corrugator supercilii is not even listed in the Nomina Anatomica Veterinaria (2005), we could be inclined to agree with this suggestion. However, as clearly shown in Figs. 405 and 442 of Jouffroy and Saban (1971), both these muscles are found in domestic dogs, and they are actually very different from each other: the corrugator supercilii lies on the superciliary arch and is deep to the orbicularis oculi, while the retractor anguli oris lateralis lies superficial to the posterolateral margin of the orbicularis oculi. Other authors have suggested that it is instead the "levator anguli oculi medialis" that corresponds to the corrugator supercilii of humans (e.g., Clair, 1975); however, we found both muscles in our serval and tiger, and these muscles also very different from each other, because the former muscle is a superficial muscle that lies dorsal (superficial) to the orbicularis oculi and to the frontalis.

We did find a distinct muscle levator anguli oculi medialis in our tiger and serval, which clearly seems to derive from the frontalis, being accordingly often designated as "frontalis pars orbitalis" (e.g., Fig. 2 of Windle and Parsons, 1897; Fig. 1 of Barone, 1967; Fig. 459 of Jouffroy and Saban, 1971). We also found, in the serval, a structure that might correspond to the dilatator nasi of other mammals (Table 2); this muscle is found in carnivorans such as domestic dogs, but authors such as Jouffroy and Saban (1971) do not refer to the presence of this muscle in felids. In both the tiger and serval we also found a single zygomaticus, a nasalis, a levator labii superioris alaeque nasi ("nasolabialis"), a platysma cervicale, a platysma myoides, a levator labii superioris ("levator labii maxillaries") and a levator anguli oris facialis ("caninus"), as usually found in other felids, e.g. domestic cats and lions, and in domestic dogs (see, e.g., Figs. 50–1, 50–2, 50–3, and 50–17 of Clair, 1975). It should be noted that many mammals, including rodents, ungulates, primates, and chiropterans, have an "auriculo-labialis superior" and an "auriculo-labialis inferior," which clearly seem to correspond to the zygomaticus minor and zygomaticus major of modern humans, respectively (Table 2; Diogo and Wood, 2012). Examples of other differences between modern humans and our serval and tiger is that in the former the sphincter colli profundus, interscutularis, levator anguli oculi medialis, retractor anguli oculi lateralis, platysma cervicale, and sphincter colli superficialis are usually not present, and the depressor supercilii, depressor septi nasi, depressor labii inferioris and depressor anguli oris are usually present, as distinct muscles (Table 2; Diogo and Wood, 2012).

Gilbert (1968) stated that in domestic cats there are six facial muscles that connect different parts of the ear ("extrinsic musculature of the ear") and 15 facial muscles that connect the ear to the skull. We did not recognize 15 distinct muscles connecting these two latter structures in our serval and tiger, because many of the structures designated as muscles by this and other authors in felids such as domestic cats clearly correspond to bundles of the occipitalis, auricularis posterior and/or interscutularis sensu Diogo et al. (2009), Diogo and Abdala (2010), and Diogo and Wood (2012) (see also Fig. 424 of Jouffroy and Saban, 1971). However, it is clear that, as in domestic cats, our tiger and serval have more facial muscle structures associated with the mobility of the auricular region than do modern humans and most other primates, which usually only have three mainly undivided facial muscles connecting the ear to the skull, i.e., the auricularis anterior, auricularis superior and auricularis posterior (Table 2; e.g., Gasset, 1967; Gibbs, 1999; Burrows, 2008; Diogo and Wood, 2011, 2012). In our serval and tiger these three muscles are also present, corresponding to part or the totality of the structures designated as "auriculares rostrales," "auriculares dorsales," and "auriculares caudales" by Clair (1975), respectively (N.B., the "auriculares

ventrales" sensu this author corresponds to/includes the "sphincter colli profundus pars auris" sensu Jouffroy and Saban, 1971). In addition various bundles of the occipitalis, as well as muscles such as the interscutularis, orbito-temporo-auricularis, and mandibulo-auricularis, also connect the ear and scutulum to the skull. The structure that is often designated as auricularis posterior in mammals such as primates probably corresponds to part or the totality of the "cervico-auricularis-profundus" and/or "cervico-scutulo-auricularis medius" of our serval and tiger (sensu Jouffroy and Saban, 1971; see e.g. their Figs. 424 and 427). As explained in the Results, some adjustments probably need to be made in the future in order to recognize at least some of the structures of the occipitalis-auricularis posterior-interscutularis complex as individual muscles, and we plan to undertake a study specifically focused on these structures, their variations, their homologies and their nomenclature.

Branchial Muscles

The configuration of the stylopharyngeus and ceratohyoideus seen in our serval and tiger is similar to that found in domestic cats, lions and jaguars as well as in domestic dogs (e.g., Clair, 1975; Weissengruber et al., 2002; NB., these authors designate the stylopharyngeus as "stylopharyngeus caudalis"). Modern humans and other primates have a similar stylopharyngeus, but various primates, including modern humans, lack a ceratohyoideus (e.g., Diogo and Wood, 2012).

As is the case in domestic cats, dogs and lions, and various other mammals, e.g., numerous ungulates, in our serval and tiger and the tigers dissected by Anton et al. (2004) the cleido-occipitalis and cleidomastoideus are usually grouped into a functional complex "brachiocephalicus" (e.g., Barone, 1967; Gilbert, 1968; Jouffroy, 1971; Clair, 1975; Anton et al., 2004). This complex also includes the upper limb muscle "cleidobrachialis," which is actually part of the deltoideus complex and usually connects the clavicle and the intersectio clavicularis to the upper limb. It is often said that the "clavotrapezius," or "pars cervicis of the cleidocephalicus," of domestic cats and dogs corresponds to part of the trapezius of modern humans (e.g., Gilbert, 1968: p. 21; see also Gilbert, 2000). However, the "clavotrapezius" of these carnivorans is clearly similar to the "clavotrapezius" of mammals such as rats (e.g., Parsons, 1898; Greene, 1935; Walker and Homberger, 1998), which is in turn homologous with the cleido-occipitalis of other mammals including some primates; in modern humans the cleido-occipitalis is usually not present as a distinct muscle (e.g., Diogo and Abdala, 2012; Diogo and Wood, 2012). The cleido-occipitalis of our serval and tiger and the tigers dissected by Anton et al. (2004) is similar to that of domestic cats, which usually runs from the dorsal midline of the neck and superior nuchal line to the clavicle and intersectio clavicularis (e.g., Gilbert, 1968). The sternomastoideus and cleidomastoideus (often designated, respectively, as "sternocephalicus" and as "pars mastoidea of the cleidocephalicus" in felids) of our tiger are similar to those of other felids such as domestic cats, in which the former runs from the sternum to the mastoid process and superior nuchal line and the latter runs from the clavicle and intersectio clavicularis to the mastoid process (e.g.,

Gilbert, 1968). In the tigers dissected by Anton et al. (2004) the sternomastoideus originates exclusively from the mastoid process and mastoid crest. Contrary to our tiger, in which the cleidomastoideus only originates from the mastoid process, in our serval, the muscle originates from both this process and the superior nuchal line. The acromiotrapezius and spinotrapezius (often designated, respectively, as 'pars cervicalis and pars thoracica of the trapezius' in felids and other carnivorans) of our serval and tiger are also similar to those of domestic cats and dogs, in which there is also no direct bony attachment onto the skull (e.g., Gilbert, 1968; Clair, 1975). In modern humans and various other primates, the sternocleidomastoideus and the cleidomastoideus are fused and form the muscle sternocleidomastoideus, while the acromiotrapezius and spinotrapezius are also used fused and form the muscle trapezius, which does attach onto the skull (Table 3; Diogo and Wood, 2012).

According to Weissengruber et al. (2002), in lions, jaguars, cheetah and domestic cats the constrictor pharyngis medius is attached onto the ceratohyoideum, basiohyoideum and thyrohyoideum, i.e. it has a pars ceratopharyngea (going mainly to the ceratohyoideum) and a pars chondropharyngea (going mainly to the thyrohyoideum; NB., these authors designated the constrictor pharyngis medius as "hyopharyngeus"). These two parts are also present in domestic dogs (e.g., Fig. 2 of Dyce, 1957; Clair, 1975; Himmelreich, 1977). In modern humans and various other primates this muscle has a pars ceratopharyngea and a pars chondropharyngea attaching mainly onto the greater and lesser horns of the hyoid bone, respectively (e.g., Diogo and Wood, 2012). As in our tiger and serval, in the lion, tiger, cheetah, and domestic cat dissected by Weissengruber et al. (2002), as well as the domestic dogs dissected by other authors (e.g., Dyce, 1957), the levator veli palatini, palatopharyngeus, and pterygopharyngeus were present as distinct muscles, the palatoglossus was missing, the constrictor pharyngis inferior had a pars cricopharyngea and a pars thyropharyngea going respectively to the cricoid and thyroid cartilages, and the "medialis veli palatine" (or "palatinus") connected the hard palate to the velum. According to Weissengruber et al. (2002) a small, uvula-like projection could be observed in the tiger dissected by them, supporting the idea that the muscle musculus uvulae of modern humans corresponds to part or the totality of the structure. In our tiger and serval, the cricothyroideus is undivided and we were able to recognize what seems to be a pars glossopharyngea of the superior constrictor in the serval. We could not discern which other parts of this latter muscle were present in this feline or which parts were present in the tiger, but other carnivorans such as domestic dogs do have other parts (e.g., pars buccopharyngea and pars oropharyngea: e.g., Saban, 1968). As in felids, domestic dogs also have a distinct muscle pterygopharyngeus, as well as a levator veli palatini, a "medialis veli palatine," a palatopharyngeus and an undivided cricothyroideus (e.g. Figs. 2, 3 of Clair, 1975; Himmelreich, 1977). Clair (1975) did not describe a salpingopharyngeus in domestic dogs or cats, but Himmelreich (1977; Figs. 2, 3) shows a muscle "azygos pharynges" running from the auditory region to the pharyngeal wall in domestic dogs, which seems to correspond to the salpingopharyngeus sensu the present work (see Fig. 8). However, Saban

(1968) stated that the "azygos pharynges," or "solitarius pharynges," is only present as a supernumerary muscle in modern humans, thus suggesting that it does not correspond to the salpingopharyngeus, which is usually found in modern humans.

Regarding the laryngeal muscles, as explained above, the most medial of the three sections of the thyroarytenoideus in our serval and tiger seems to be related to the vocal cords, and thus to correspond to the structure that is often designated as "musculus vocalis" in modern humans. The laryngeal muscles of domestic dogs are remarkably similar to the laryngeal muscles of our serval and tiger, but various authors reported two muscle structures that lie deep to the main body of the thyroarytenoideus in canids, instead of one as seen in our felids: a "musculus vocalis" lying near the vocal fold and ligament and a "musculus vestibularis, or ventricularis" lying near the vestibular ligament and running from the cuneiform process to the interarytenoid cartilage (e.g., Clair, 1975). However, Pierdard (1963) did a careful study of domestic dogs and stated that the so-called "musculus ventricularis" of these canids is actually merely a superficial bundle of the arytenoideus. Weissengruber et al. (2002) reviewed the literature and discussed the production of sounds in felids, and noted that a "musculus vocalis" is effectively often present in felids such as domestic cats, the characteristic purring of these animals being caused by extremely rapid twitching of this muscle structure. These authors argue that skeletal differences, mainly concerning the hyoid apparatus, pharynx and larynx, between members of the subfamily Pantherinae such as lions, jaguars, and tigers and members of the subfamily Felinae such as domestic cats and cheetah have an influence on specific structural differences of their vocalizations (e.g., importance of roaring in the Pantherinae vs. of purring in the Felinae). These skeletal differences do not seem to be directly associated with clear changes of the overall configuration, divisions, and/or attachments of muscles, because the musculature that is connected to these structures is remarkably similar in our serval and tiger (see Results and above). Modern humans have a cricoarytenoideus posterior, a cricoarytenoideus lateralis, a thyroarytenoideus that is divided into various structures (including a "musculus vocalis" and a "musculus ventricularis") and two arytenoid muscles, instead of one as seen in our serval and tiger and most other mammals: an arytenoideus transversus, which is similar to the arytenoideus of our serval and tiger, and an arytenoideus obliquus, which mainly runs obliquely from the arytenoid cartilage to the contralateral arytenoid cartilage, often extending into the aryepiglottic fold (e.g., Diogo and Wood, 2012).

Hypobranchial Muscles

At least some of the fibers that run anteriorly from the anterior surface of the epiglottis in domestic cats, lions, jaguars, and cheetah (e.g., Gilbert, 1968; Weissengruber et al., 2002) and other carnivorans such as domestic dogs (e.g., Fig. 67 of Saban, 1968), as well as in many other eutherians and also in marsupials (e.g., Edgeworth, 1935; Saban, 1968), seem to correspond to the fibers of the genioglossus that in our serval and tiger extend posteriorly to attach onto the epiglottis. Authors such as Edgeworth (1935) consider that the fibers of the genioglossus that go to the hyoid apparatus and/or epiglottis in many eutherians and marsupials form muscles such as the "geniohyoglossus" (from mandible directly to hyoid apparatus), the "genioepiglotticus" (from mandible directly to epiglottis), the "geniohyoepiglotticus" (from mandible directly to hyoid apparatus and epiglottis), the "glossoepiglotticus" (from tongue to epiglottis), and the "hyoepiglotticus" (from hyoid apparatus to epiglottis). Weissengruber et al. (2002) described a "hyoepiglotticus" in the lion, jaguar, tiger, cheetah, and domestic cat dissected by them, as well as a "thyroglossus" running from the thyrohyoideum to the tongue between the hyoglossus and genioglossus, in the lion, tiger, and jaguar they examined. However, in our serval and tiger, none of these six muscles seems to be present as distinct muscles; these six muscles are usually not present as distinct structures in modern humans. The structure X shown in Figs. 5 and 7 seems to be an anomaly or a variation, because this muscle bundle was only found on the right side of the serval. It can for instance be an additional bundle of the stylohyoideus because it originates near the origin of this muscle and is blended distally with the mylohyoideus, as the stylohyoideus usually is. Alternatively, it can be an additional bundle of the styloglossus, as seen for example in other felids and carnivorans, e.g. jaguars and domestic dogs, as well as in numerous other mammals (e.g., fig. 291 of Saban, 1968; see also Weissengruber et al., 2002), because it passes just medial to this muscle, deep to the digastricus posterior. Weissengruber et al. (2002) report that in the lion, tiger and jaguar dissected by them the main body of the styloglossus originates only from the proximal portion of the hyoid apparatus, but in our tiger, as well as in our serval, the muscle also originates from the skull (see Results). The hyoglossus is partially attached onto the thyrohyoideum in the lion, jaguar, cheetah, domestic cat and tiger dissected by Weissengruber et al. (2002), and is attached onto the thyrohyoideum and the basihyoideum in the domestic dogs reported by Clair (1975). Himmelreich (1977; figs. 2, 3) shows a hyoglossus that seems to be mainly undivided in domestic dogs (see also, e.g., fig. 7 of Smith, 1992), and the palatoglossus is usually missing in these and other carnivorans as well as in most other mammals (e.g., Saban, 1968), as it is in our serval and tiger. Modern humans and various other primates do have a distinct palatoglossus (Table 4), and have a hyoglossus divided into a "ceratoglossus" and a "chondroglossus" attaching mainly onto the greater horn and on the lesser horn of the hyoid bone, respectively (e.g., Diogo and Wood, 2012).

The geniohyoideus in lions and domestic cats and dogs is similar to that of our serval and tiger (e.g., Barone, 1967; Clair, 1975). Interestingly, in domestic cats and dogs the sternohyoideus and sternothryroideus often originate from the first costal rib (e.g., Gilbert, 1968; Saban, 1968), and not exclusively from the sternum as is usually the case in other felids such as lions (e.g., Barone, 1967) and in numerous other mammals, including modern humans (Diogo and Wood, 2012). Lions have two bundles of the sternothyroideus (e.g., Barone, 1967) that are similar to the two bundles found in our tiger, which are not present in our serval. The omohyoideus, missing in our tiger and serval, is also lacking in domestic cats and lions (e.g., Barone, 1967), as well as in domestic dogs (e.g., Clair, 1975) and many other mammals (e.g.,

Saban, 1968). Apart from the sternohyoideus, sterno-thyroideus and geniohyoideus, modern humans do usually have a well developed omohyoideus (Table 4), which is divided into a superior head and an inferior head (e.g., Diogo and Wood, 2012).

GENERAL COMMENTS

Felids such as our tiger and serval have more facial muscles than many other mammals, including modern humans, being the taxa listed in Table 2 with the largest number of hyoid muscles (29 excluding the extrinsic facial musculature of the ear, if the stapedius, sphincter colli superficialis and retractor anguli oculi lateralis are present, as they usually are in other felids and other carnivorans; vs . 27 in modern humans). As explained above, they have more facial muscle structures related to the mobility of the auricular region, but they also have other peculiar, derived facial muscles that are instead related to the mobility of the orbital region, e.g. the levator anguli oculi medialis (and, in at least some other felids and non-felid carnivorans, the retractor anguli oculi lateralis: see above). The presence of peculiar, derived muscles and muscle bundles related to the mobility of both the auricular and orbital regions in felids but also in distantly related carnivorans such as canids might be related to an ancient adaptation related to the remarkable predatory capacities of carnivorans, e.g. enhancing the detection of movements, and then the capture, of the animals they prey through sounds and visual cues. Our serval and tiger also have more branchial muscles than the other taxa listed in Table 3, including modern humans (20 vs. 16), but this is mainly because they did not loose any of the muscles that constitute the Bauplan of eutherian mammals, while the other taxa did. They have 8 mandibular muscles, as modern humans do, because they lack an intermandibularis anterior, which is found in a few eutherian mammals, e.g. rats and tupaias (Table 1). They have less hypobranchial muscles than modern humans (7 vs. 9, excluding the intrinsic tongue muscles) because they do not have a palatoglossus and an omohyoideus.

Comparisons such as the ones just made above have been difficult due to the huge discrepancies between the muscle nomenclature used in e.g. veterinary textbooks vs. in human anatomy atlases (e.g., Netter 2006) and in the Terminologia Anatomica (1998). As explained above, various atlases and textbooks use domestic cats and dogs as a comparative model to understand the anatomy of domestic mammals and to stress the differences and similarities between these mammals and modern humans (e.g., Clair, 1975; Gilbert, 1968). One of the problems of such atlases and textbooks is that they often compare domestic cats/dogs directly with modern humans, without really taking into account or at least stating the condition found in other animals that would help to decrease the huge phylogenetic gap between these domestic animals and *Homo sapiens*. A clear example of this is the book "*Outline of cat anatomy, with reference to the Human*", which is otherwise an excellent publication, including detailed and valuable descriptions and superb drawings of the musculoskeletal system, nervous system and internal organs, among others (Gilbert, 2000). After having dissected representative members of all the major groups of non-human primates

as well as colugos, tree-shrews and Glires and members of various other mammalian groups (Diogo, 2008; Diogo et al., 2008, 2009; Diogo and Abdala, 2010), our idea was thus to provide a more comprehensive assessment of the homology/evolutionary hypotheses advanced in these atlases and textbooks. For instance, in both Gilbert's 1968 and 2000 books it is for instance stated that the 'clavotrapezius' of domestic cats and dogs corresponds to part of the trapezius of modern humans, but the 'clavotrapezius' of these carnivorans is exactly similar to the 'clavotrapezius' of taxa such as rats, which is in turn clearly homologous with the cleido-occipitalis of other mammals such as tree-shrews and non-human primates (see above). The cleido-occipitalis is usually not present as a distinct muscle in modern humans, being only found in a few cases, as a variation (Wood, 1866–1870); the trapezius of modern humans is therefore very likely formed by the fusion of the spinotrapezius and acromiotrapezius (and not of the so-called "clavotrapezius") of other mammals (Table 3; e.g. Diogo and Wood, 2012).

In this respect, our observations and comparisons point out that there are effectively various problems with those publications as well as in nomenclatural publications such as the Nomina Anatomica Veterinaria (2005; NAV). For instance, in this latter book the groupings of the muscles are highly problematic, because they do not take into account information about the phylogeny, ontogeny, innervation, or even the function or attachments of the grouped muscles. An illustrative example concerns the "musculi hyoidei" group, which includes hypobranchial muscles that are not even attached to the hyoid apparatus (e.g. sternothyroideus), branchial muscles (e.g., ceratohyoideus), hyoid muscles (e.g., stylohyoideus) and mandibular muscles (e.g., mylohyoideus). The names provided for individual muscles in the NAV are also problematic. For instance, although it well known that the muscles digastricus anterior and digastricus posterior have a different phylogenetic and ontogenetic origin and are usually innervated by different nerves (V and VII, respectively), they are named as bundles of a single muscle in this book ('musculus digastricus venter rostralis' and 'musculus digastricus venter caudalis', respectively). We consider that there is no reason to continue following such incorrect designations and to continue using discrepant nomenclatures such as those found in human and veterinary anatomy textbooks. As can be seen in Tables 1–4, these discrepant nomenclatures are particularly seen in hyoid and branchial muscles, and are thus clearly related to the historical controversies and confusion regarding the homologies of these muscles (the homologies between the individual mandibular and hypobranchial muscles of different mammalian taxa have been much less problematic: e.g., Diogo and Abdala, 2010). However, a series of recent studies have provided a comprehensive and updated survey of the ontogeny, phylogeny and homologies of the vertebrate muscles, thus setting the basis for a unifying nomenclature and ontology for the mammalian muscles (e.g., Diogo, 2008; Diogo et al., 2008, 2009; Diogo and Abdala, 2010; Diogo and Wood, 2012).

As explained in the Introduction, apart from describing the head and neck muscles of two poorly studied felid taxa and providing notes about the homologies and evolution of these muscles, one of the main goals of this article is precisely to eradicate such nomenclatural

errors and discrepancies. In particular, we hope that our proposition of a unifying nomenclature that is expanded to all the head and neck muscles and to mammalian taxa such as carnivorans will help build veterinarian and mammalian muscle ontologies and be useful for students, educators, comparative anatomists, zoologists, mammalogists, and ontologists as well as to the human and veterinary medical communities.

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