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The Anatomy and Ontogeny of the Head, Neck, Pectoral, and Upper Limb Muscles of *Lemur catta* and *Propithecus coquereli* (Primates): Discussion on the Parallelism Between Ontogeny and Phylogeny and Implications for Evolutionary and Developmental Biology

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ABSTRACT

Most anatomical studies of primates focus on skeletal tissues, but muscular anatomy can provide valuable information about phylogeny, functional specializations, and evolution. Herein, we present the first detailed description of the head, neck, pectoral, and upper limb muscles of the fetal lemuriforms *Lemur catta* (Lemuridae) and *Propithecus coquereli* (Indriidae). These two species belong to the suborder Strepsirrhini, which is often presumed to possess some plesiomorphic anatomical features within primates. We compare the muscular anatomy of the fetuses with that of infants and adults and discuss the evolutionary and developmental implications. The fetal anatomy reflects a phylogenetically more plesiomorphic condition in nine of the muscles we studied and a more derived condition in only two, supporting a parallel between ontogeny and phylogeny. The derived exceptions concern muscles with additional insertions in the fetus which are lost in adults of the same species, that is, flexor carpi radialis inserts on metacarpal III and levator claviculae inserts on the clavicle. Interestingly, these two muscles are involved in movements of the pectoral girdle and upper limb, which are mainly important for activities in later stages of life, such as locomotion and prey capture, rather than activities in fetal life. Accordingly, our findings suggest that some exceptions to the "ontogeny parallels phylogeny" rule are probably driven more by ontogenetic constraints than by adaptive plasticity. Anat Rec, 00:000–000, 2014.   © 2014 Wiley Periodicals, Inc.

Key words: development; head and neck; morphology; muscles; upper limb; primates; strepsirrhines

Most studies of the gross morphology of primates focus on hard tissues, and those that focus on soft tissues generally refer to the adult anatomy (for a review, see, e.g., Gibbs, 1999; Gibbs et al., 2000, 2002; Diogo and Wood, 2012a). However, recent studies have shown that muscular anatomy is particularly useful for phylogenetic studies (e.g., Diogo and Wood, 2011, 2012a,b). Moreover, including data from non-adult specimens can add valuable information to the discussion of functional specializations (e.g., Raichlen, 2005; Atzeva et al., 2007) and evolutionary topics such reversions and developmental constraints (e.g., Diogo and Wood, 2011, 2012a,b). Using postnatal samples, Diogo and Wood (2012a) presented a detailed analysis of head, neck, pectoral, and forelimb myology in each of the major primate higher taxa (strepsirrhines, tarsiers, new world monkeys, old world monkeys, and hominoids), and we have now embarked on a second study that focuses on the muscles of the trunk, pelvis and lower limb. These publications provide a broad phylogenetic and evolutionary basis for further, more specific analyses of certain primate taxa, anatomical regions, and/or developmental stages.

In this publication, we provide the first detailed description of the head, neck, pectoral, and upper limb muscles of fetal representatives of the lemuriform families Lemuridae (*Lemur catta*) and Indriidae (*Propithecus coquereli*) of the suborder Strepsirrhini. These descriptions are based on dissections and histological analysis of microscope slide series. The muscle anatomy will be compared with that of older specimens (infants and adults) of these species, dissected by us and by other authors, as well as with that of other primates. This comparison will allow us to explore and discuss the evolutionary and developmental implications of our anatomical observations, particularly their relevance to the notion that "ontogeny parallels phylogeny."

In Ontogeny and Phylogeny, Gould (1977) argues that researchers often use Haeckel's (refuted) hypothesis that the ontogeny of one organism recapitulates the adult stages of its ancestors (i.e., recapitulation) as a "strawman" to deny the existence of a parallel between otogeny and phylogeny. According to Gould, such a parallel nonetheless usually exists, probably driven more by phylogenetic/ontogenetic constraints than by adaptive plasticity. Our recent studies of human and non-human primate muscles support Gould's ideas (Diogo and Wood, 2012b). For instance, in karyotypically "normal" modern human ontogeny, the intermetacarpales are present as distinct muscles, and there are multiple contrahentes muscles in addition to the one inserting on Digit 1 (i.e., the adductor pollicis), but these muscles are lost or become indistinct later in ontogeny. This sequence parallels the evolutionary history of primates, in which these muscles were plesiomorphically present and then were lost in humans (Diogo and Wood, 2011). This parallel is not recapitulation in the Haeckelian sense: the contrahentes digitorum and the intermetacarpales of karyotypically 'normal' human embryos do not correspond to the muscles of adult primates such as chimpanzees, but instead to muscles in the embryos of the latter taxa. Even after several millions of years, the developmental pathways that produce these muscles have not been completely lost in modern humans, probably because they are related to pathways involved in the development of structures that are present and functional in modern human adults.

As we now have detailed data about the ontogeny of the head and neck muscles in many tetrapod taxa and the phylogeny and evolution of these muscles within vertebrates (Diogo and Abdala, 2010), we can compare the order in which the muscles appear in ontogeny with the order in which they evolved. For instance, our previous works show a parallel between ontogeny and phylogeny in zebrafish head muscles, with only a few exceptions; for example, the early ontogenetic appearance of muscles that evolved late in phylogeny but play a particularly important role in the feeding mechanisms of both adults and embryos (Diogo et al., 2008). A very similar pattern was found in axolotls (Ziermann and Diogo, 2013). However, these results do not necessarily accord with the commonly accepted view that muscles tend to differentiate (and not de-differentiate) during ontogeny. The order in which muscles appear in ontogeny is usually similar to the order in which they appear in phylogeny, but muscles are often lost/reabsorbed later in ontogeny. For instance, in neotenic salamander species such as axolotls that do not undergo full metamorphosis, some muscles become completely indistinct during ontogeny; for example, the pseudotemporalis profundus and the levator hyoideus become completely integrated in the pseudotemporalis superficialis and in the depressor mandibulae, respectively (Ziermann and Diogo, 2013). Parallels between ontogeny and phylogeny will be further discussed in the light of the results of this study.

MATERIALS AND METHODS

We dissected one side of the head, neck, pectoral, and upper limb muscles of a female *Lemur catta* fetus (Duke Lemur Center specimen number 6888, fixed in 10% buffered formalin) and of a male *Propithecus coquereli* fetus (Duke Lemur Center specimen number P6154, fixed in 10% buffered formalin). The contralateral side of the head was also available in a microscope slide series. Each half was paraffin embedded, serially sectioned (10 μm thick), and stained with hematoxylin and eosin or trichrome procedures. Because facial skin was present in the oronasal region of the slides series, some facial muscles were available for analysis.

The musculature of these two fetuses was compared with that of an adult male *Lemur catta* (GWUANT LC1; fresh), an adult female *P. coquereli* (GWUANT PV1; fresh), and an infant female *P. coquereli* (GWUANT PV2; fresh). These specimens had been dissected and described previously (Diogo and Wood, 2012a) and were retrieved from fixative for direct comparison with the fetal specimens. We also compared the musculature with that of additional specimens of these two species dissected by other authors (e.g., Meckel, 1820–1838; Cuvier and Laurillard, 1849; Murie and Mivart, 1872; Milne-Edwards and Grandidider, 1875; Ruge, 1878, 1885; Parsons, 1898a,b; Tschachmachtschjan, 1912; Kollmann and Papin, 1914; Lander, 1918; Loth, 1931; Edgeworth, 1935; Straus, 1942a,b; Miller, 1943; Hill, 1953; Starck and Schneider, 1960; Jouffroy, 1960a,b, 1962, 1971; Ashton and Oxnard, 1963; Kladetsky and Kobold, 1966; Saban, 1968; Kaneff and Cihak, 1970; Seiler, 1976; Lewis, 1989; Maier, 2008) as well as numerous other primate species dissected by other authors (for a recent review, see Diogo and Wood, 2012a). The head, neck, pectoral, and upper limb muscles of the *Lemur* and *Propithecus* fetuses were

dissected and photographed using a Nikon SMZ-1500 Zoom stereo-microscope equipped with a Nikon DS Fi1 5 Megapixel Color Camera Head.

The nomenclature for the head, neck, pectoral, and upper limb muscles follows that of Diogo and Abdala (2010) and Diogo and Wood (2012a). The pectoral and upper limb muscles are divided into five subgroups: pectoral, arm, ventral forearm, dorsal forearm, and hand. We focused on four main sub-groups of head and neck muscles: (1) mandibular muscles—generally innervated by cranial nerve V (e.g., the muscles of mastication and one of the middle ear muscles, the tensor tympani); (2) hyoid muscles—usually innervated by cranial nerve VII (e.g., muscles of facial expression and the other middle ear muscle, the stapedius); (3) branchial muscles—usually innervated by cranial nerves IX and X (e.g., the majority of the intrinsic laryngeal muscles), although the trapezius and sternocleidomastoideus are mainly innervated by cranial nerve XI; (4) hypobranchial muscles—according to Edgeworth (1935), these muscles develop from the anterior myotomes of the body and migrate into the head (e.g., infrahyoid muscles); although they retain their main innervation from spinal nerves, they may also be innervated by cranial nerves XI and XII, but they usually do not receive any branches from cranial nerves V, VII, IX, or X. Head and neck muscles not included in this study are the epibranchial muscles *sensu* Edgeworth (1935), which are absent in extant osteichthyans and therefore are not present in primates or other mammals, and the internal and external ocular muscles *sensu* Edgeworth (1935), which are usually innervated by the cranial nerves III, IV, and/or VI. In the sections below, we use the terms anterior, posterior, dorsal, and ventral as they apply to pronograde tetrapods.

RESULTS

The textual and visual (Figs. 1–10) descriptions refer to our observations of both the *L. catta* and *P. coquereli* fetuses. Major differences between these two specimens (and/or specimens of the same species dissected by ourselves or by other authors) will be mentioned in the text below.

Mandibular Muscles

The mylohyoideus (Figs. 3A, 9A) runs from the mandible to the ventral midline of the neck and to the body of the hyoid bone. In the *L. catta* fetus, the digastricus anterior (Figs. 3A, 8A) is well separated from its counterpart and runs from the digastric intermediate tendon and the hyoid bone to the medial margin of the mandible. This configuration was also found in the adult *L. catta* and adult *P. coquereli* we dissected. A similar configuration was found in the *P. coquereli* fetus, except that the digastricus anterior did not originate from the hyoid bone. We could not examine the tensor tympani because this region was too delicate. According to Maier (2008), this muscle is usually present in adults of both genera, and the chorda tympani passes below the muscle (hypotensoric configuration). The tensor veli palatini runs from the region near the external acoustic meatus to the soft palate, surrounding the pterygoid hamulus, and its orientation is more horizontal than in modern

humans. The masseter (Figs. 1B, 8B) runs from the zygomatic arch and zygoma to the angle, lower border, and ramus of mandible. The pars superficialis and pars profunda seem to be less differentiated than in adults of these two species (e.g., Hill, 1953; Diogo and Wood, 2012a) (the "zygomatico-mandibularis" not present as a distinct structure). In the *L. catta* fetus, the main body of the temporalis (Figs. 1B, 8B) is undivided and originates primarily from the lateral superior surface of the skull. A well-defined pars suprazygomatica (which was almost completely covered laterally by the zygomatic arch) originates from the inner margin of the zygomatic arch and inserts on the lateral margin of the coronoid process, while the main body of the temporalis inserts on the medial margin of the coronoid process. This configuration was also found in the adult *L. catta* and adult *P. coquereli* we dissected and is similar to the one found in the *P. coquereli* fetus, but in the latter specimen the pars suprazygomatica is less differentiated from the main body of the muscle. The pterygoideus lateralis originates from the pterygoid lamina and adjacent regions of the skull. In the *L. catta* fetus, there is a caput superius, which is thinner and inserts on the temporomandibular joint, and a caput inferius, which is broader and inserts on the condyloid process of the mandible. The two heads are well separated anteriorly by structures including the buccal nerve, but they blend into each other posteriorly. We could not discern whether the two heads of the pterygoideus lateralis are also separated in the *P. coquereli* fetus, and they were not described by Murie and Mivart (1872) in the adult *Lemur*. On one side of our adult *L. catta* GWUANT LC1 specimen, the two heads are not differentiated, but on the other side they are slightly differentiated and have a similar configuration to the *L. catta* fetus. Similarly, poor differentiation was present bilaterally in our adult *P. coquereli* GWUANT PV1 specimen. The pterygoideus medialis (Fig. 9A) is a single, undivided mass running from the fossa between the two wings of the pterygoid process to the inner surface of the angle of the jaw.

Hyoid Muscles

In the *L. catta* fetus, the stylohyoideus runs from the tympanic bulla and the most proximal (and non-ossified) portion of the hyoid apparatus and to the hyoid bone. It passes superficial to the digastricus tendon, without being pierced by it, and almost reaches its counterpart in the midline; that is, its insertion onto the hyoid bone is peculiarly extended in a medial direction (100%). The stylohyoideus is also directly connected to the mylohyoideus and/or to the aponeurosis connecting the mylohyoideus to the hyoid bone. The configuration of this muscle is similar between the *L. catta* fetus, the *P. coquereli* fetus and the adults of these two species except for the connection to the mylohyoideus, which we only observed in the *L. catta* fetus. The digastricus posterior (Figs. 3A, 8A) runs from the mastoid region to the long, well-defined intermediate tendon. In the *L. catta* fetus, the jugulohyoideus is well-developed, running from the mastoid region (deep to the digastricus posterior) to the connective tissue between the skull and the stylohyal ligament, as it usually does in adults of this species. However, unlike in the adult specimen we dissected, the jugulohyoideus also inserts directly onto the proximal
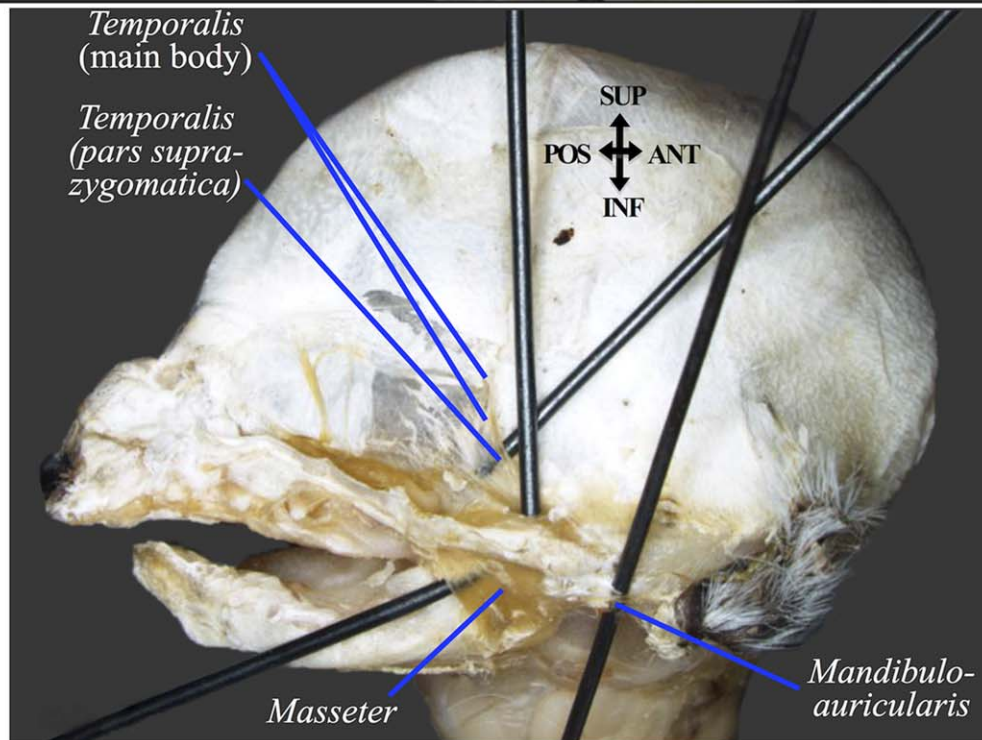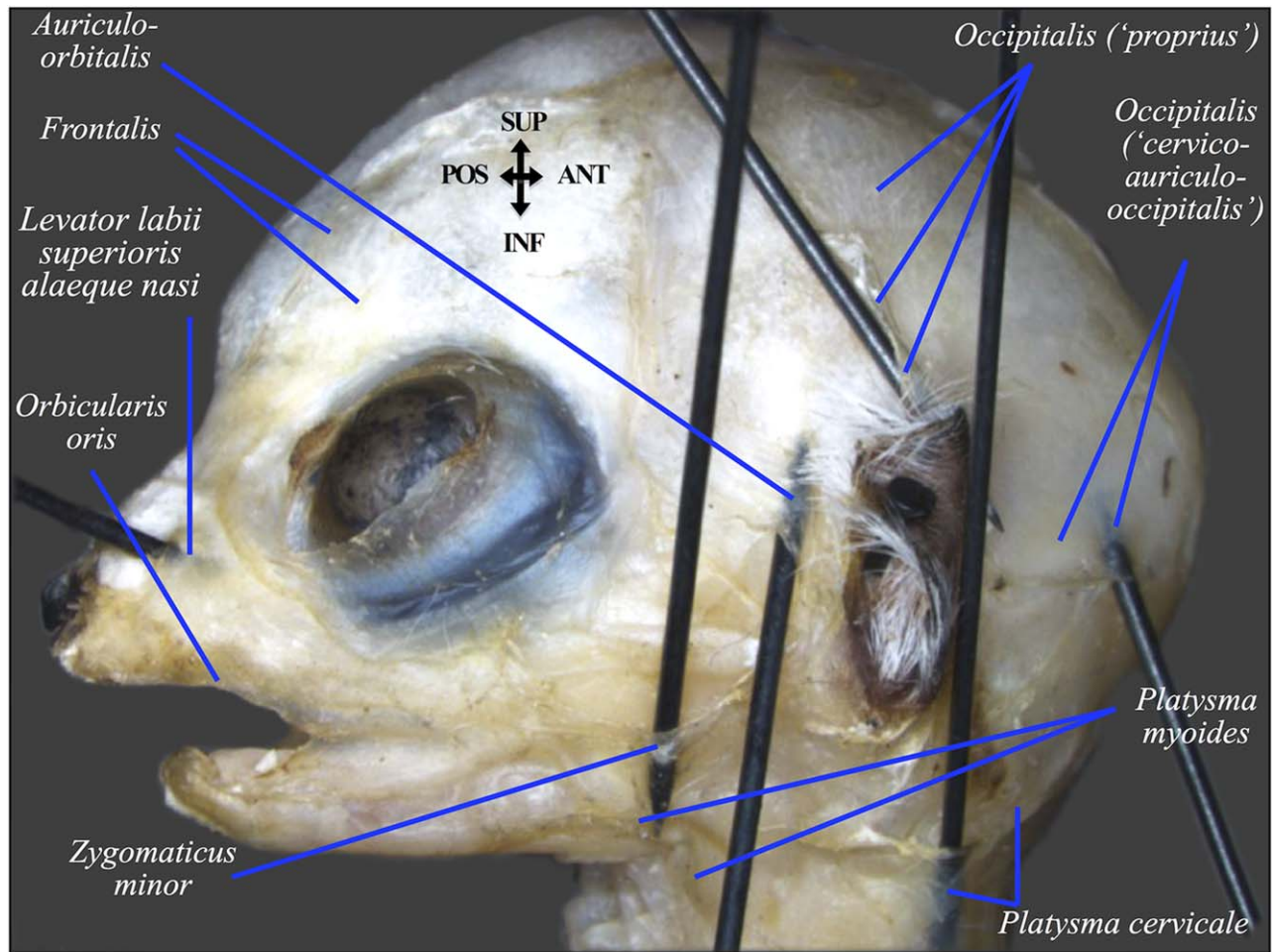
Fig. 1. *Lemur catta* (female fetus 6888). (**A**) Lateral view of the facial muscles. (**B**) Lateral view of the mandibular muscles and the facial muscle mandibulo-auricularis. In this and the other figures, the names of the muscles are in italics, and SUP, INF, ANT, POS, MED, LAT, VEN, DOR, PRO and DIS refer to superior, inferior, anterior, posterior, medial, lateral, ventral, dorsal, proximal, and distal, respectively (N.B., in the sense that the terms are used for pronograde tetrapods: see text for more details).
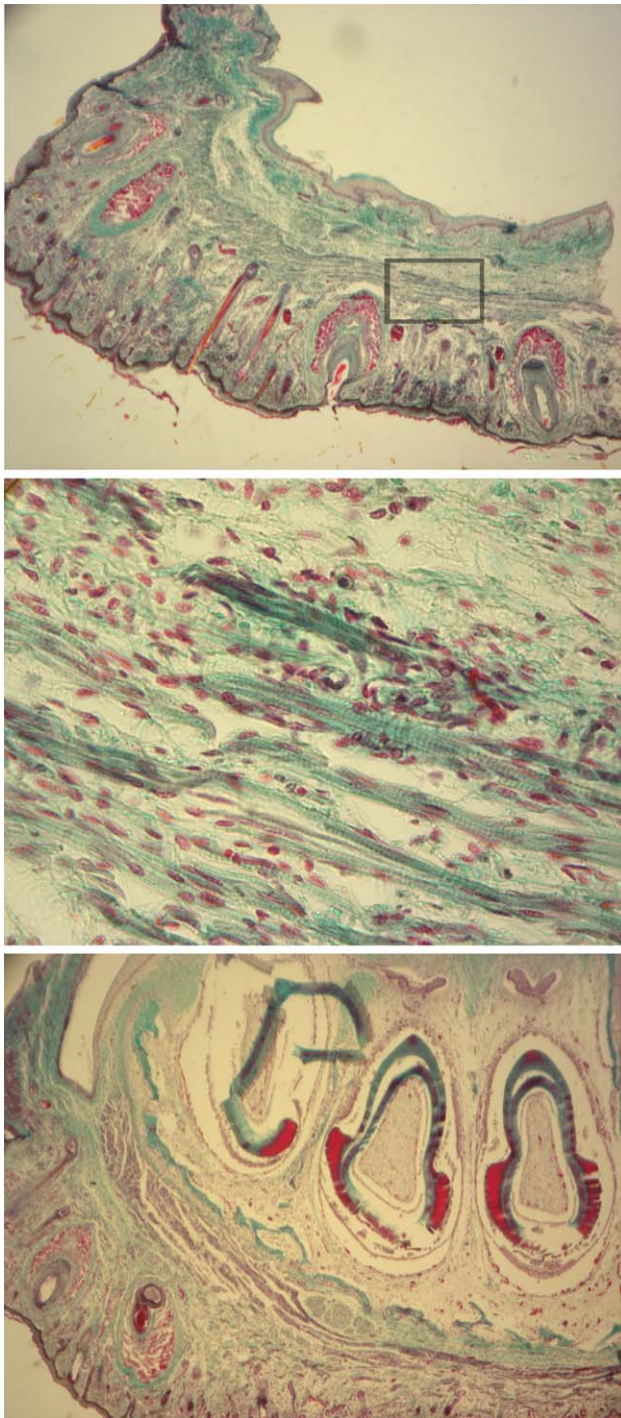
Fig. 2. *Lemur catta* (female fetus 6888, contralateral side to Fig. 1). (**A**) Serially sectioned skin of mandible, anterior to symphysis. (**B**) enlargement of boxed area in Fig. 2A, showing striated fibers (arrows) of mentalis projecting toward the midline. (**C**) The fibers originate from the body of the mandible near the roots of the deciduous incisors (and see Burrows and Smith, 2003, for gross description of this muscle in a prosimian). Scale bars: A, 0.5 mm, B, 40 μm.

portion (i.e., closer to the neurocranium) of the hyoid apparatus. In the *P. coquereli* fetus, the jugulohyoideus is much more developed than it is in adult strepsirrhi-

nids. As in adults of this species, it originates from the mastoid region and inserts on the connective tissue between the skull and the proximal portion of the hyoid apparatus, and it is deep to the digastricus posterior. Unlike in the adults, it also inserts directly onto the proximal portion of the hyoid apparatus, and it is somewhat blended with the digastricus posterior. Its size, position and blending with the digastricus posterior strongly suggest that the jugulohyoideus is actually derived from the digastricus posterior and that it is more developed in early stages than in later stages. Because the jugulohyoideus usually is not present in adult anthropoid primates, its ontogeny appears to parallel its evolution. We could not examine the stapedius in any of the specimens we dissected.

We could not analyze the muscles of facial expression in the *P. coquereli* fetus because the area was too delicate in this specimen; however, we were able to observe some oronasal muscles via histology. Most descriptions in this paragraph refer to the *L. catta* fetus. The platysma cervicale (Fig. 1A) originates from the nuchal region (its fleshy portion reaching the dorsal midline) and inserts on the region of the mouth. The platysma myoides (Fig. 1A) runs from the neck and chest to the region of the mouth and the mandible. The "cervico-auriculo-occipitalis" part of the occipitalis (Fig. 1A) runs from the occipital region to the external ear, passing laterally to join the occipitalis proprius part of the muscle, which runs from the occipital region (contacting its counterpart in the dorsal midline) to the galea aponeurotica. There is no distinct muscle interscutularis, but the anterior part of the occipitalis (which inserts directly on the ear) lies somewhat anterior to the ear, thus occupying the space where the interscutularis lies in other mammals (a similar condition was found in the adult *L. catta* shown in Fig. A2 of Diogo and Wood, 2012a). The auricularis posterior blends with the occipitalis and runs from the occipital region to the posterior surface of the ear. We could not examine the small muscles of the ear in detail nor discern whether the sphincter colli profundus was present. The mandibulo-auricularis (Fig. 1B) is a fleshy muscle running from the anterior region of the ear to the back of the mandible. The zygomaticus major ("auriculolabialis inferior") is undivided and, unlike the case in the adult *L. catta*, is deeply blended with the zygomaticus minor (Fig. 1A) ("auriculolabialis superior"), supporting the idea that these muscles derive from the same anlage. The combined mass formed by the two muscles runs from the anterior and inferoanterior margin of the external ear to the angle of the mouth and blends with the platysma cervicale, which lies on the same level. The frontalis (Fig. 1A) runs from the galea aponeurotica to the region of the eye. The auriculo-orbitalis (Fig. 1A) runs from the anterior portion of the ear to the region of the eye and blends with the frontalis; the auricularis anterior is not present as a distinct muscle. The auricularis superior runs from the superior margin of the ear to the galea aponeurotica. The orbicularis oculi is present and surrounds the eye, but we could not discern whether the depressor supercilii, nasalis, and corrugator supercilii were present as distinct muscles. The levator labii superioris alaeque nasi (Fig. 1A) runs from the region of the glabella to the nose and upper lip. It is broader than in hominoids and blends more completely with the frontalis and the orbicularis
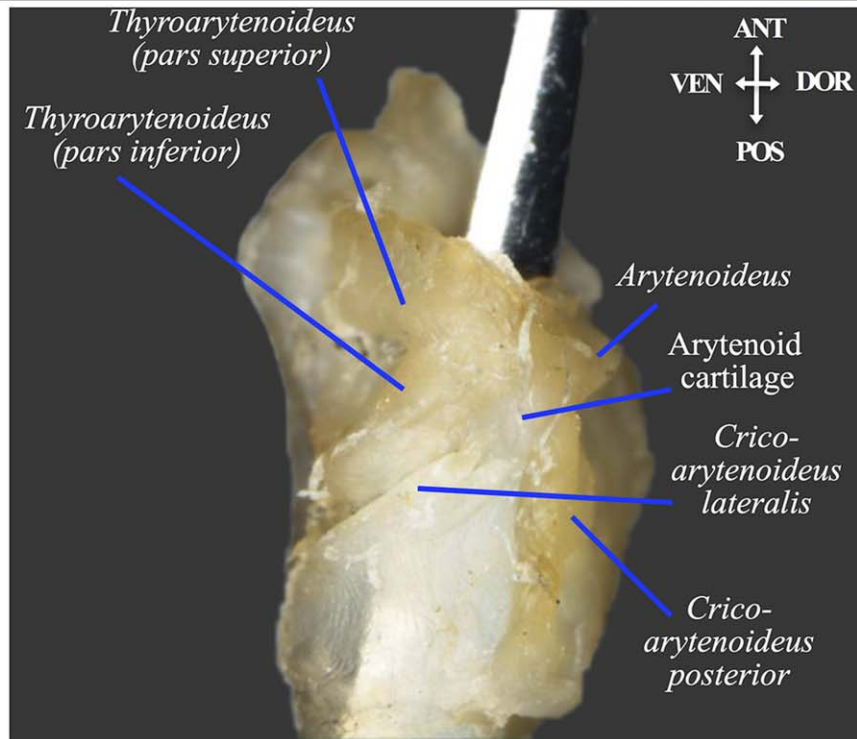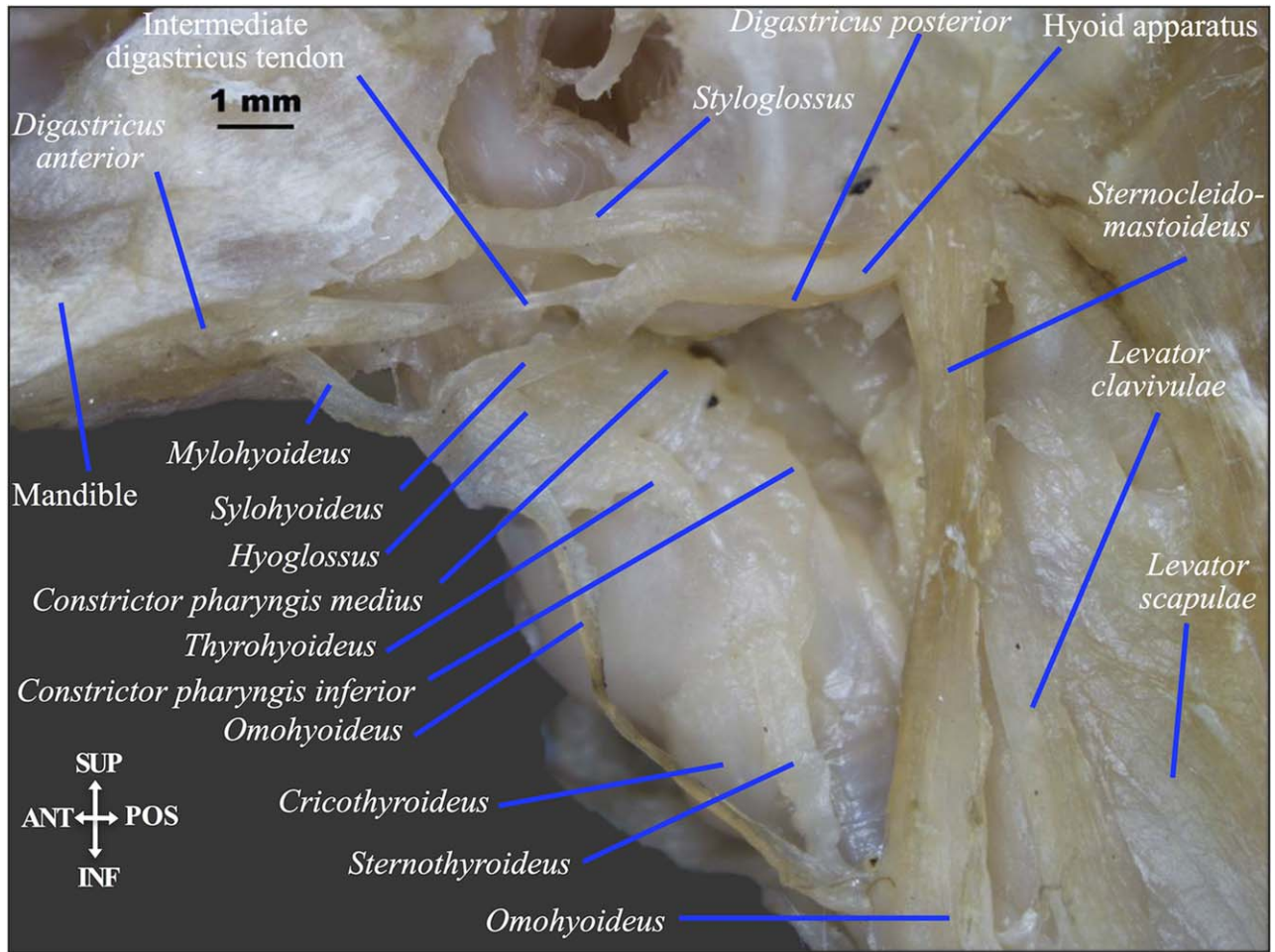
Fig. 3. *Lemur catta* (female fetus 6888). (**A**) Lateral view of the muscles lying in the auricular and neck regions and attaching to the mandible. (**B**) Lateral view of the laryngeal musculature.
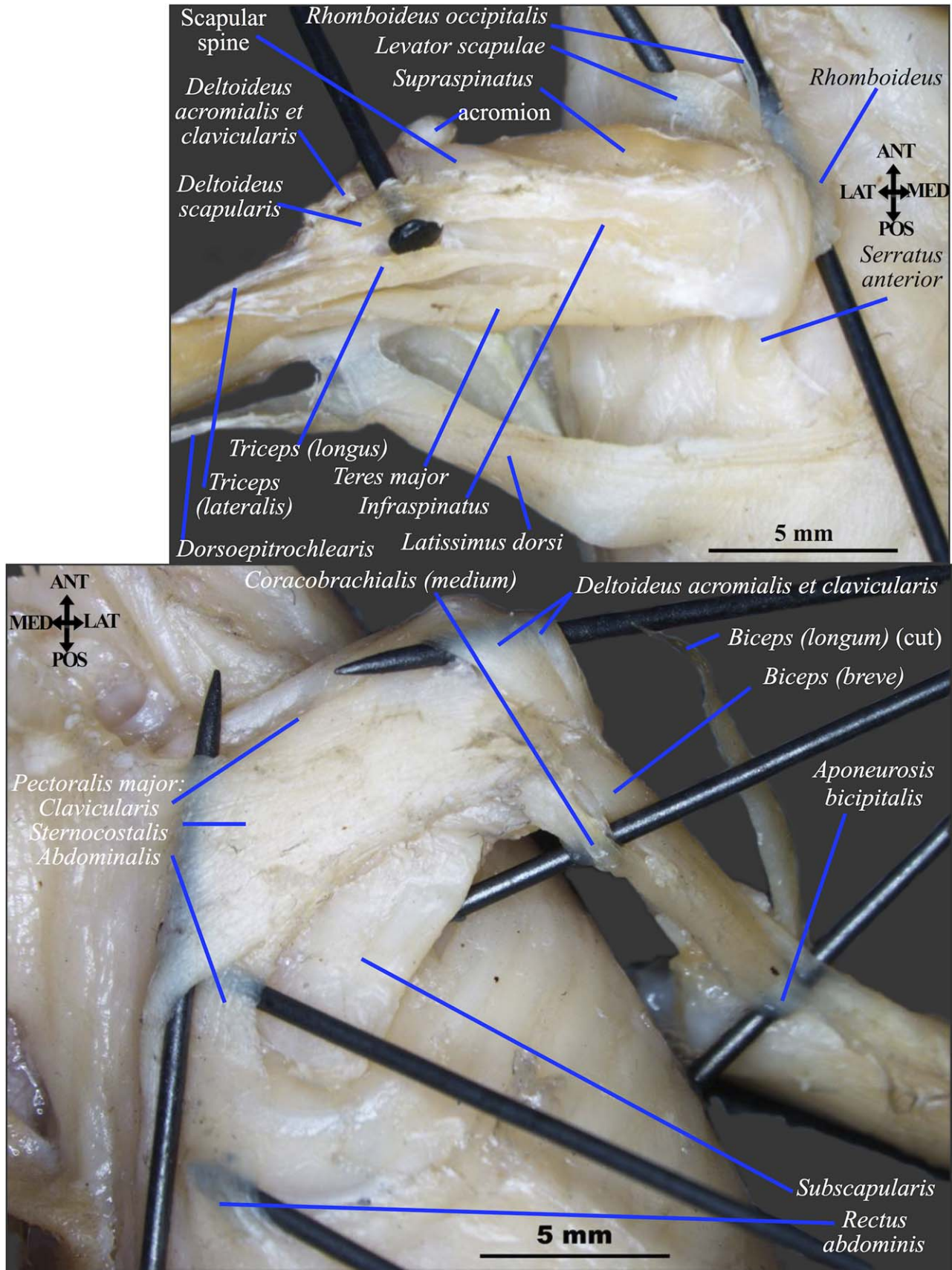
Fig. 4. *Lemur catta* (female fetus 6888). (**A**) Dorsal view of the pectoral girdle and arm musculature. (**B**) Ventral view of the pectoral girdle and arm musculature.
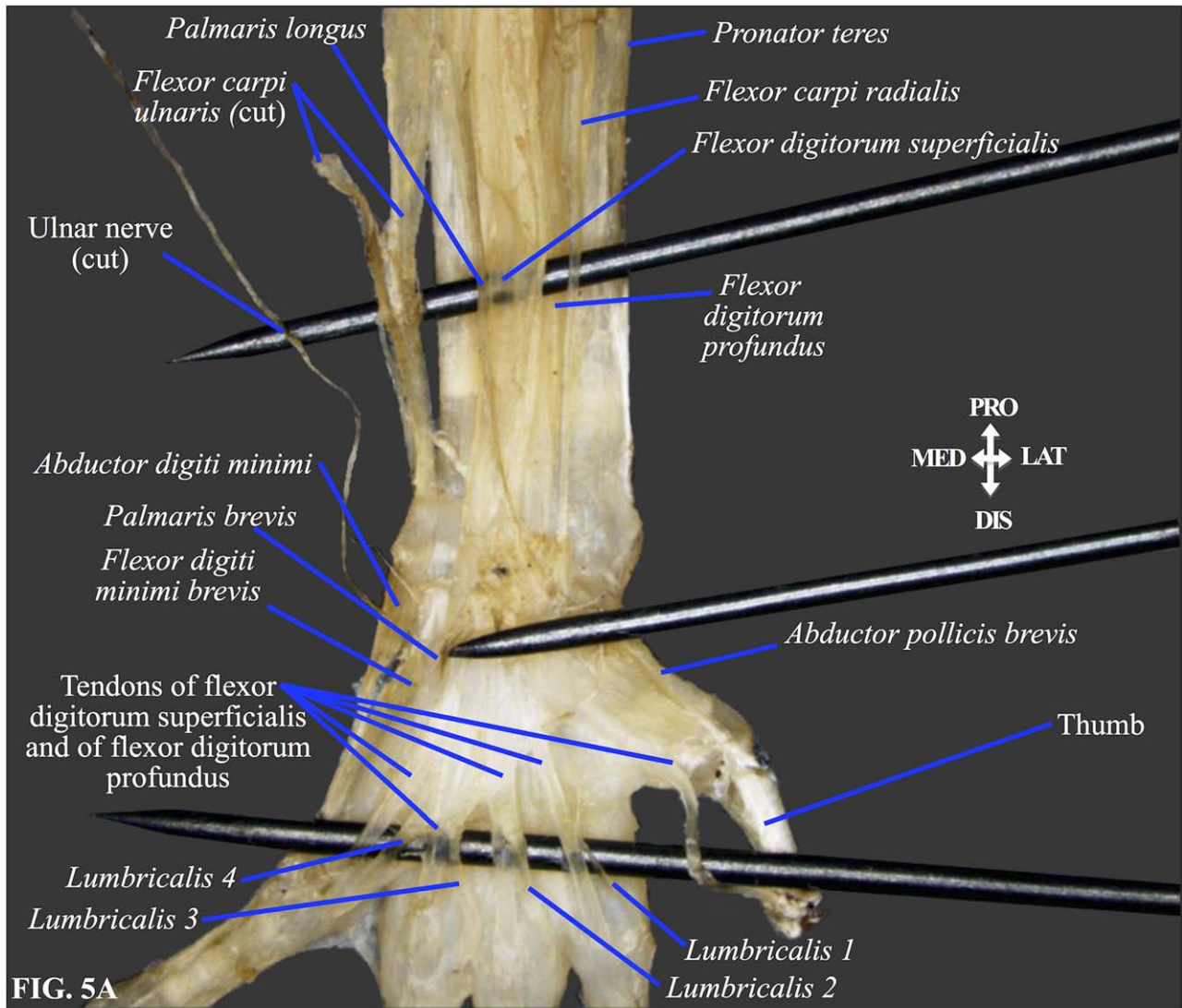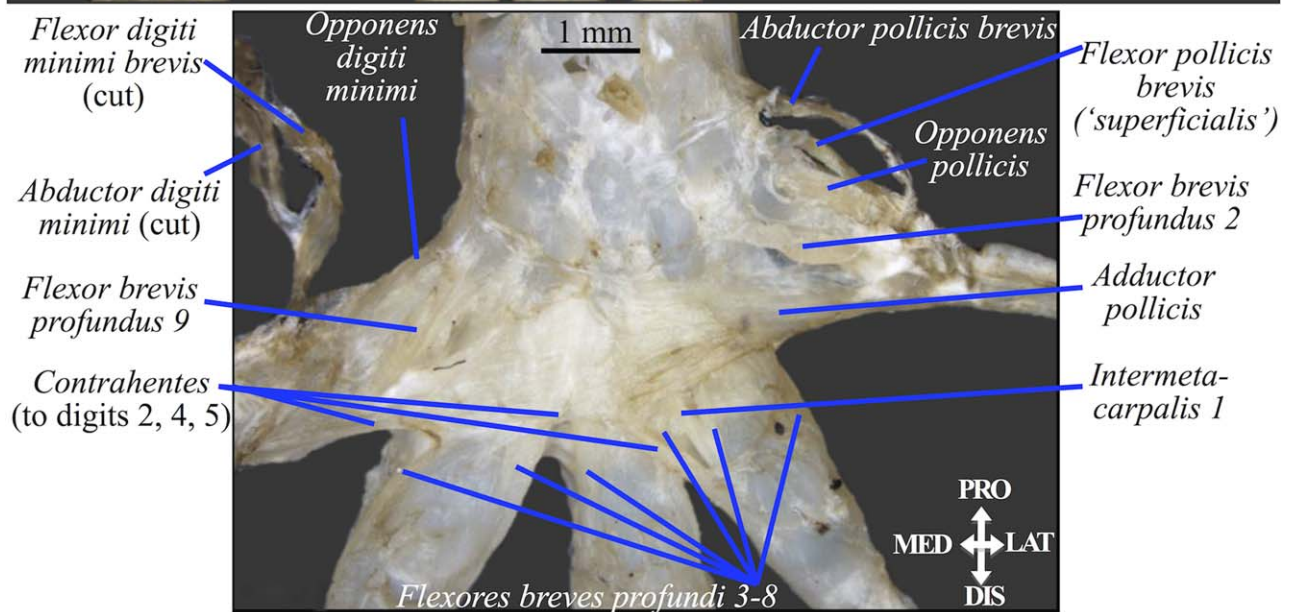
Fig. 5. *Lemur catta* (female fetus 6888). (**A**) Ventral view of the forearm and hand musculature. (**B**) Ventral view of the deeper hand musculature.
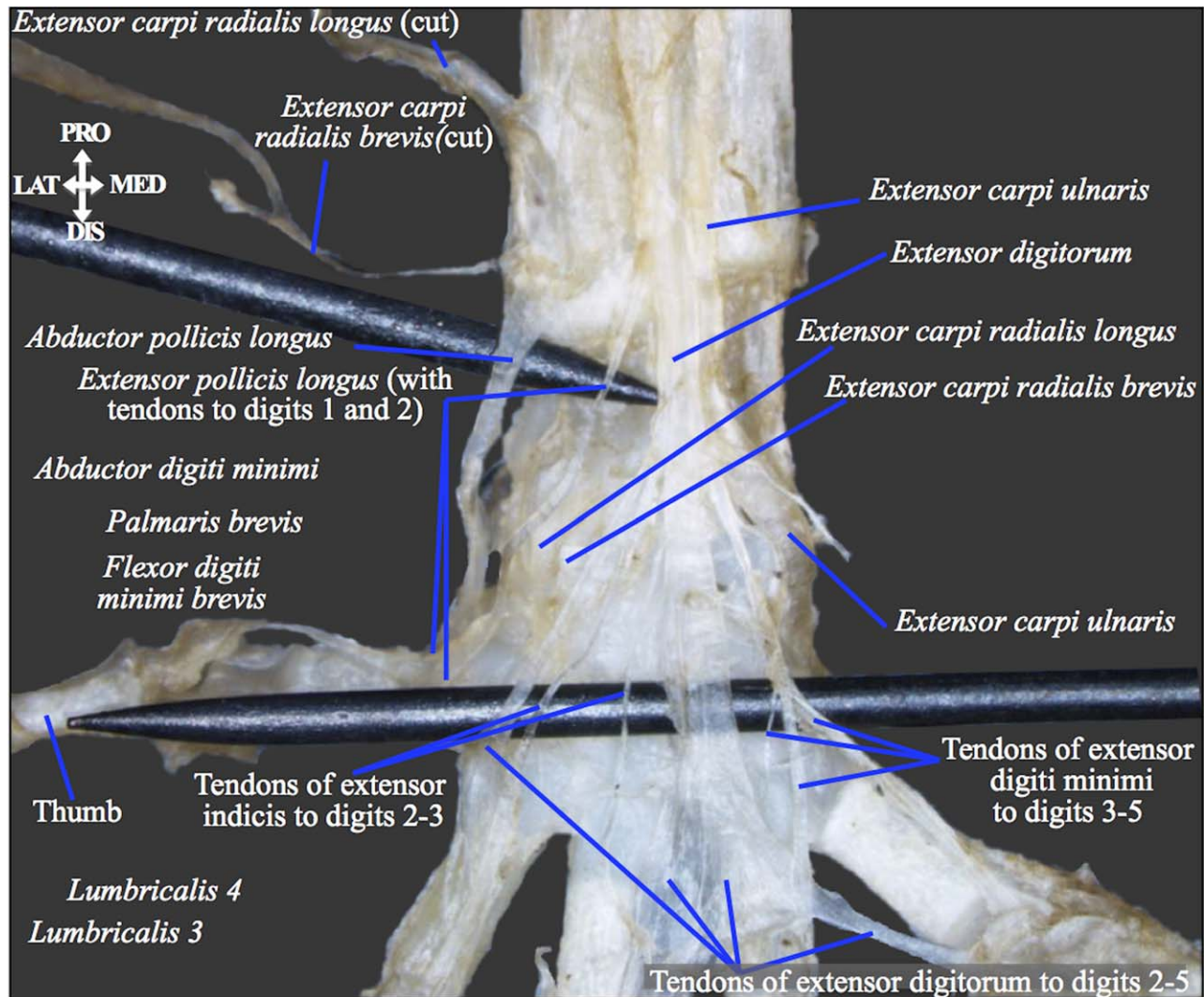
Fig. 6. *Lemur catta* (female fetus 6888). Dorsal view of the forearm and hand musculature.

oculi than in adult lemurs. The procerus is not present as a distinct muscle. The buccinatorius runs from the pterygomandibular raphe to the maxilla, mandible and orbicularis oris. The levator labii superioris ("maxillo-naso-labialis") is an approximately horizontal muscle running posteroanteriorly from the infraorbital region to the region of the nose and upper lip, deep (medial) to the levator labii superioris alaeque nasi. The levator anguli oris facialis runs from the maxilla to the angle of the mouth, deep to the levator labii superioris. The orbicularis oris (Fig. 1A) is present and normal, but, contrary to the case in adult lemurs, it is partially blended posterosuperiorly with some fibers of the orbicularis oculi due to the large size of the eye and its proximity to the mouth. The depressor labii inferioris and the depressor anguli oris are not present as distinct muscles.

Serial sections of the oronasal regions reveal that the mentalis is present in both fetuses (Figs. 2A,B, 7A,B), with fibers attaching laterally to the mandibular body adjacent to the deciduous canine and the roots of the deciduous incisors (Figs. 2C, 7C). The mentalis merges obliquely with its counterpart near the midline, anterior to the mandibular symphysis.

Branchial Muscles

In the *P. coquereli* fetus, the stylopharyngeus (Fig. 9A) runs from the auditory bulla and proximal portion of the stylohyal ligament to the pharyngeal wall (not inserting onto the hyoid bone), passing superior to the middle constrictor and inferior to the superior constrictor. This configuration is found in adult lemurs and adult *P. coquereli*, but in the *L. catta* fetus the stylopharyngeus does not originate directly from the skull. We could not discern whether the petropharyngeus was present as a distinct muscle. The ceratohyoideus connects the thyrohyal (greater horn of the hyoid bone), hypohyal and distal portion of the ceratohyal, lying deep (dorsal) to the insertions of the middle constrictor and the stylopharyngeus. The trapezius runs from the
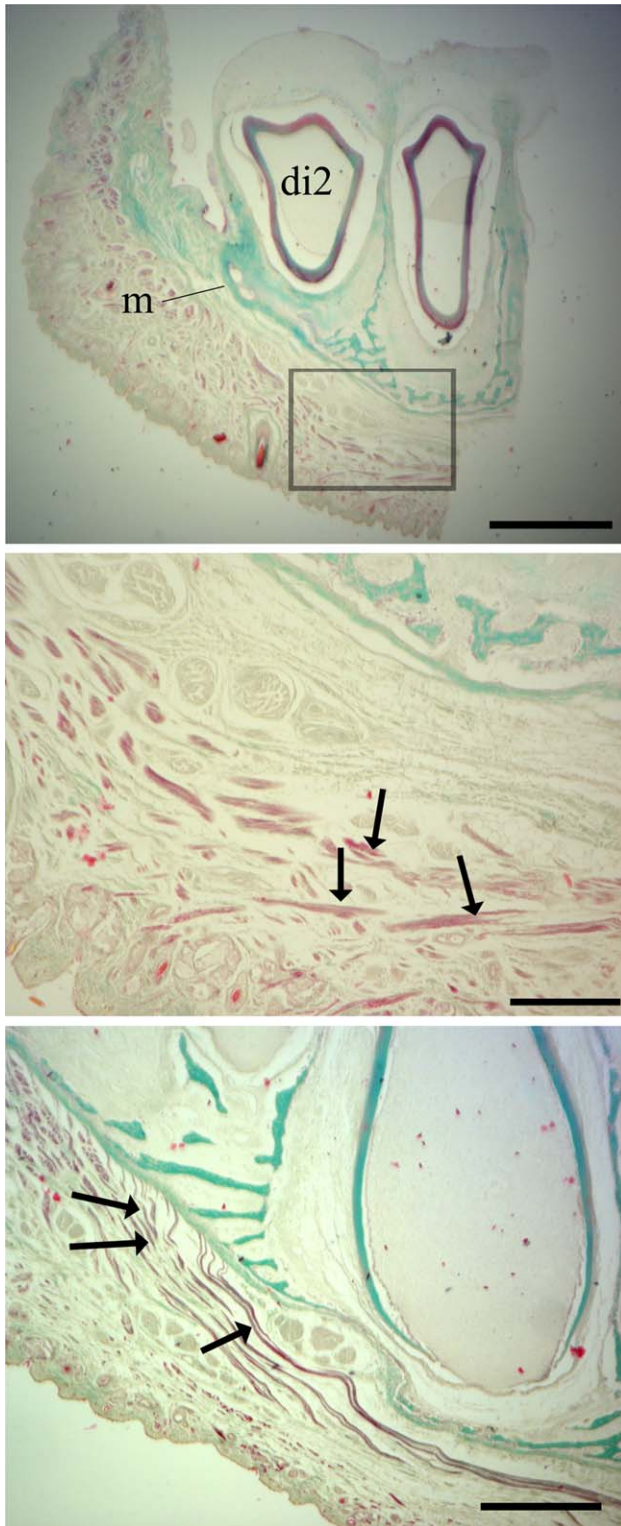
Fig. 7. *Propithecus coquereli* (male fetus P6154, contralateral side to Fig. 9). (**A–C**) Serially sectioned skin of mandible, showing anterior fibers of the mentalis muscle (arrows) passing horizontally toward the midline (B is an enlarged view of the boxed area in A). The fibers originate from the body of the mandible near the roots of the deciduous incisors (C). Scale bars: A, 1 mm; B, 250 µm; C, 0.5 mm.

ligamentum nuchae and vertebrae (not from the cranium) to the scapular spine and acromion (not to the clavicle), inserting deep (ventral) to the insertion of the levator claviculae. The cleido-occipitalis is not present as a distinct muscle. The sternocleidomastoideus (Fig. 3A) has a superficial caput sternomastoideum running from the sternum (not the sternal end of the clavicle as it often does in adults of the two species) to the mastoid process in the *L. catta* fetus, and also to the occipital region in the *P. coquereli* fetus. The deeper caput cleido-mastoideum runs from the clavicle to the mastoid region. The constrictor pharyngis medius (Fig. 3A) runs from the dorsal midline raphe to the thyrohyal (lesser horn of the hyoid bone; pars ceratopharyngea), the hypohyal and, perhaps, to the ceratohyal (if it does, this would constitute a pars chondropharyngea). The constrictor pharyngis inferior (Figs. 3A, 9A) runs from the dorsal midline raphe, which is associated with the cranium, to the thyroid (pars thyropharyngea) and cricoid (pars cricopharyngea) cartilages. The cricothyroideus (Figs. 3A, 9A,B) is only slightly differentiated into pars recta, pars obliquua and pars interna (seemingly less so than in adults). It runs from the cricoid cartilage to the thyroid cartilage and does not contact its counterpart in the ventral midline or have a broad insertion onto the inferior horn of the thyroid cartilage. The constrictor pharyngis superior runs from the midline raphe to the palate (pars pterygopharyngea), the tongue (pars glossopharyngea), and seemingly to the pterygomandibular raphe (pars buccopharyngea); we could not discern whether there is a pars mylopharyngea. The palatopharyngeus runs from the soft palate to the pharyngeal wall; we could not discern whether it reaches the thyroid cartilage or if there is a distinct muscle uvulae. The levator veli palatini runs from the region near the ear to the soft palate and is more horizontal than in humans. The thyroarytenoideus (Figs. 3B, 9B) connects the thyroid and arytenoid cartilages. It consists of a pars superior (more anterior and somewhat more lateral) and a pars inferior (which corresponds to the "pars intermedia" *sensu* Starck and Schneider, 1960). We could not find any other divisions of the muscle. The cricoarytenoideus lateralis (Figs. 3B, 9B) connects the cricoid and arytenoid cartilages. The arytenoideus (Figs. 3B, 9B) connects the two arytenoid cartilages; there is no median raphe or distinct muscle arytenoideus obliquus. The cricoarytenoideus posterior (Figs. 3B, 9B) connects the cricoid and arytenoid cartilages. It does not insert on the inferior horn of the thyroid cartilage but contacts its counterpart in the dorsal midline.

Hypobranchial Muscles

The geniohyoideus (Figs. 8A, 9A) originates from the mandible inserts on the hyoid bone. The genioglossus (Fig. 9A) runs from the mandible to the tongue. We did not examine the intrinsic muscles of the tongue in detail. In the *P. coquereli* fetus, the hyoglossus (Figs. 3A, 8A) has a thinner chondroglossus part originating from the body of the hyoid bone (basihyal) and a broader ceratoglossus part originating from the greater horn of the hyoid bone (thyrohyal) and inserts on the inferolateral surface of the tongue. In the *L. catta* fetus, the ceratoglossus part runs from the thyrohyal to the tongue, but

Fig. 8. *Propithecus coquereli* (male fetus P6154). (**A**) Lateral view of the head musculature. (**B**) Lateral view of the masticatory muscles and styloglossus.
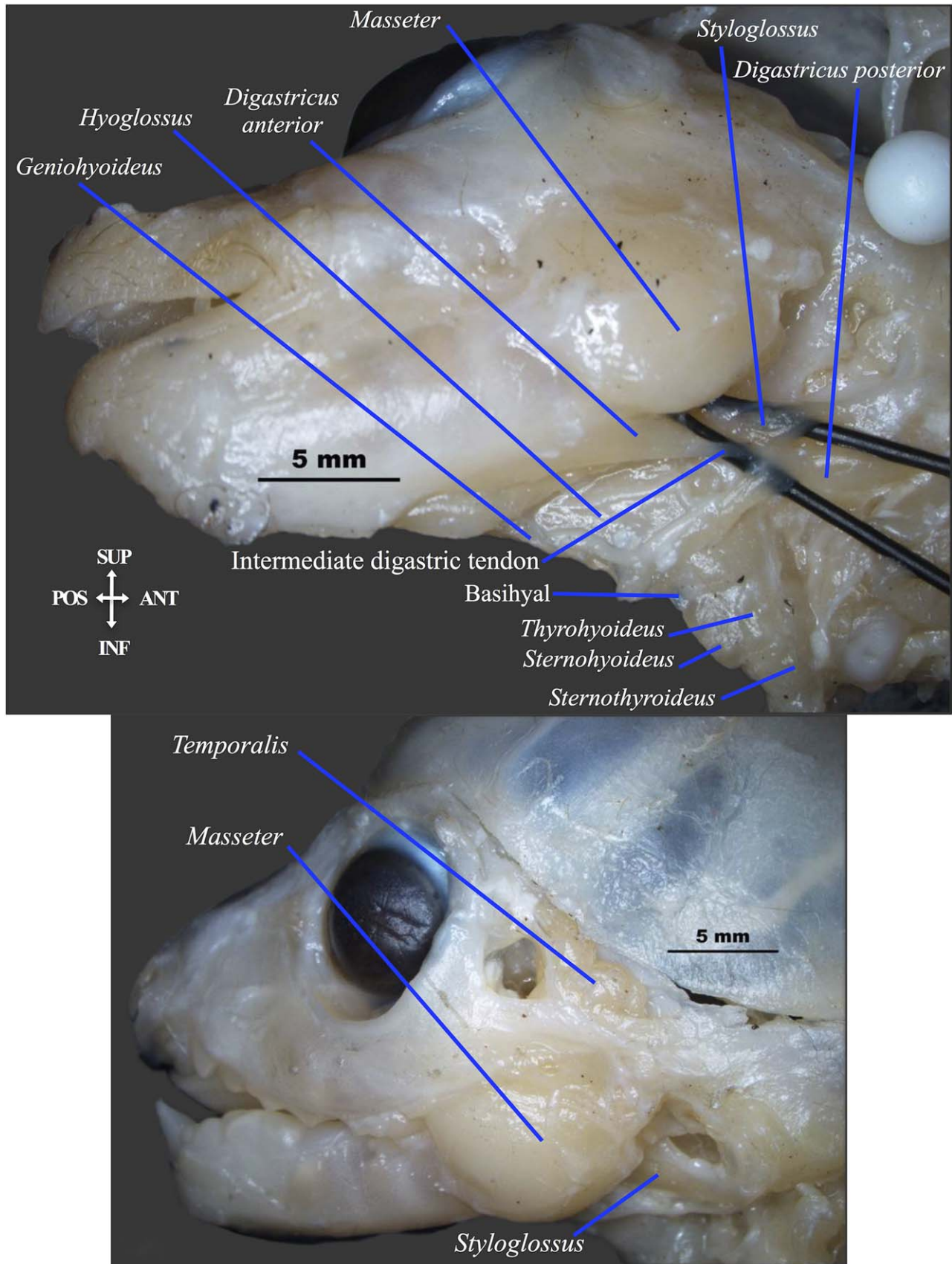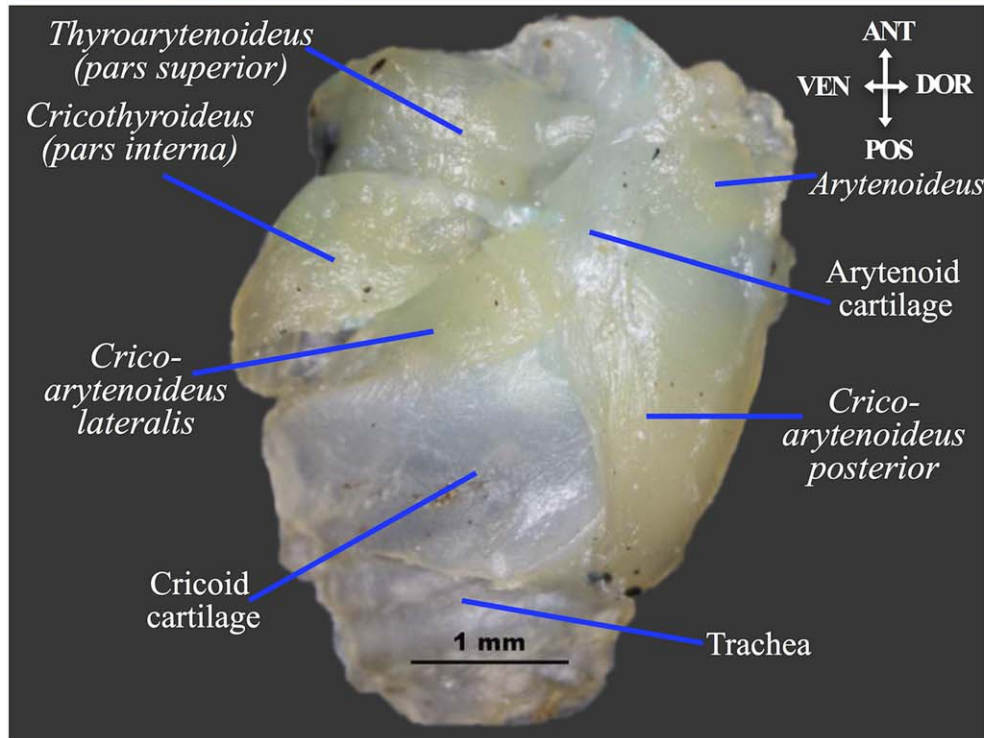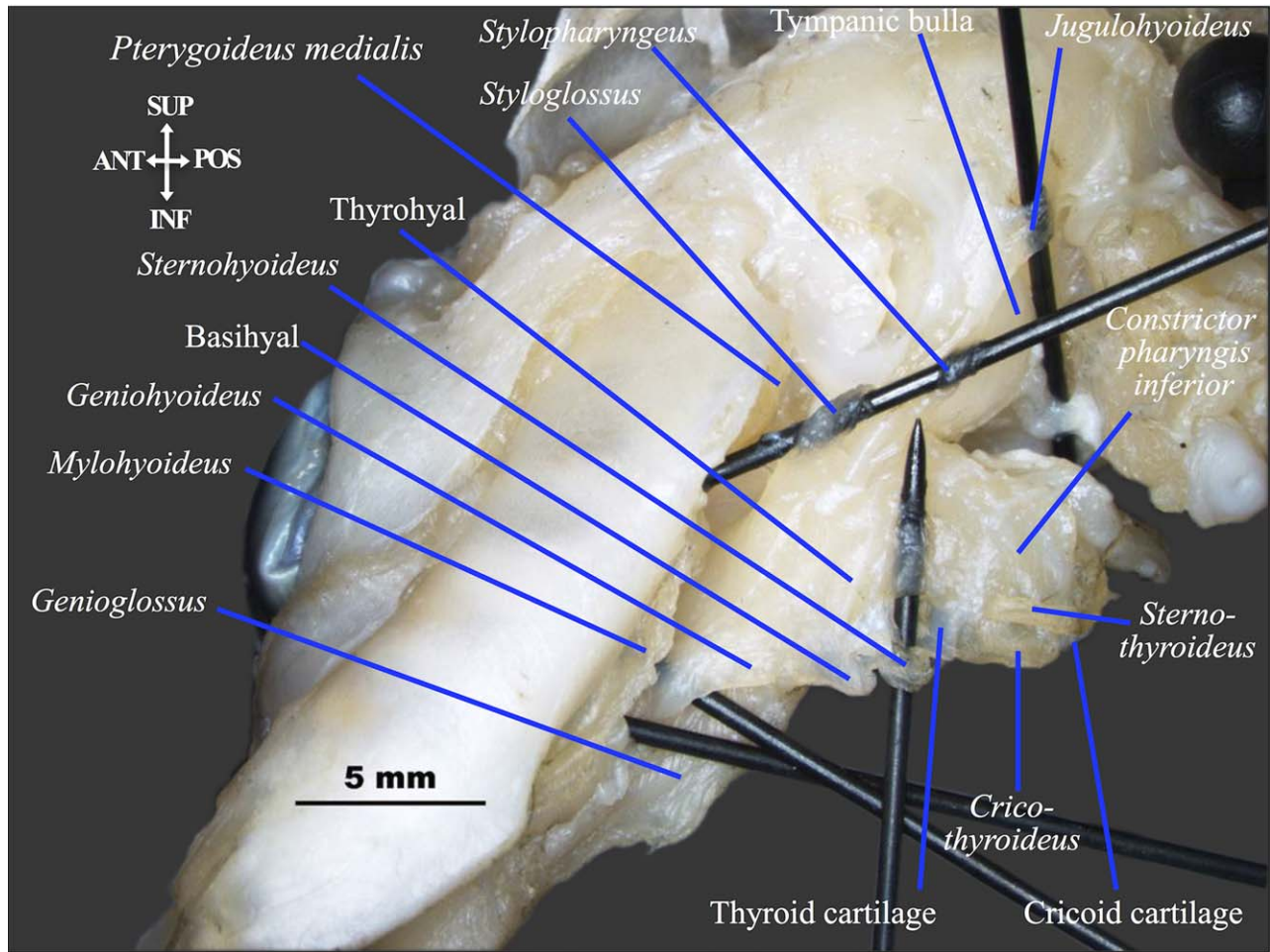
Fig. 9. *Propithecus coquereli* (male fetus P6154). (**A**) Ventrolateral view of the head musculature. (**B**) Lateral view of the laryngeal musculature.
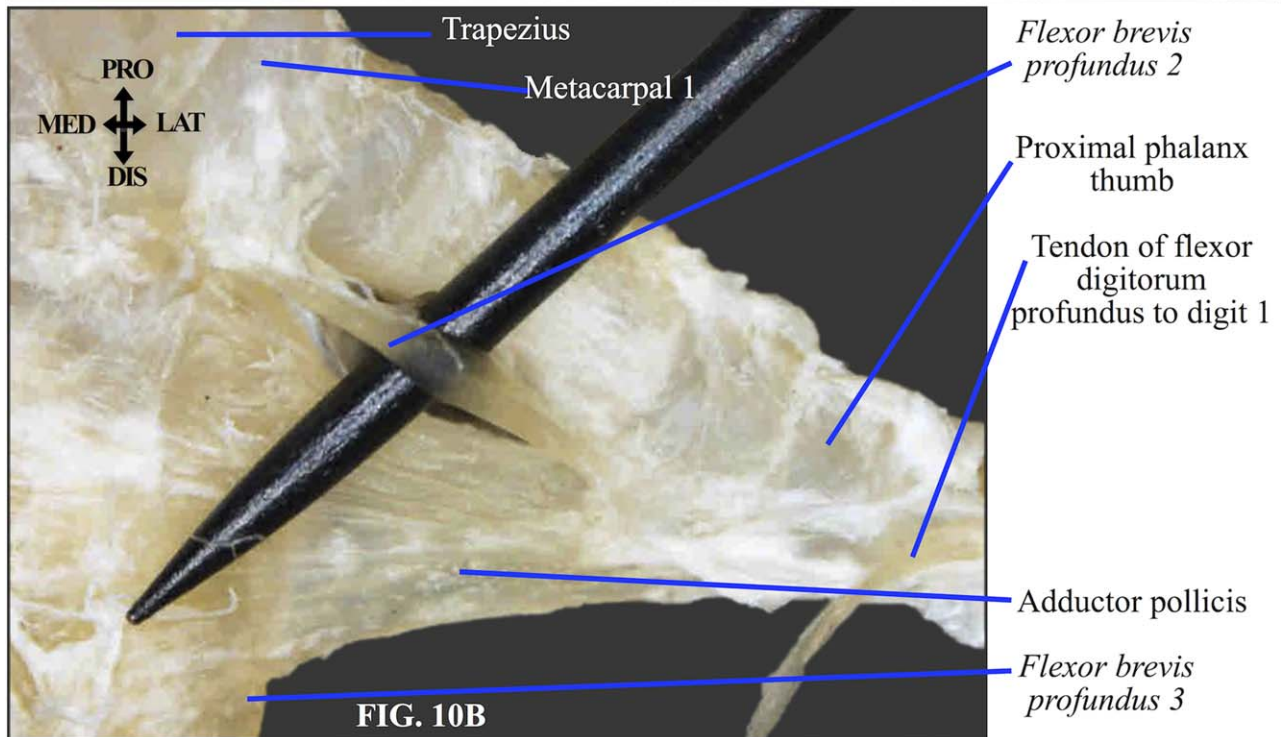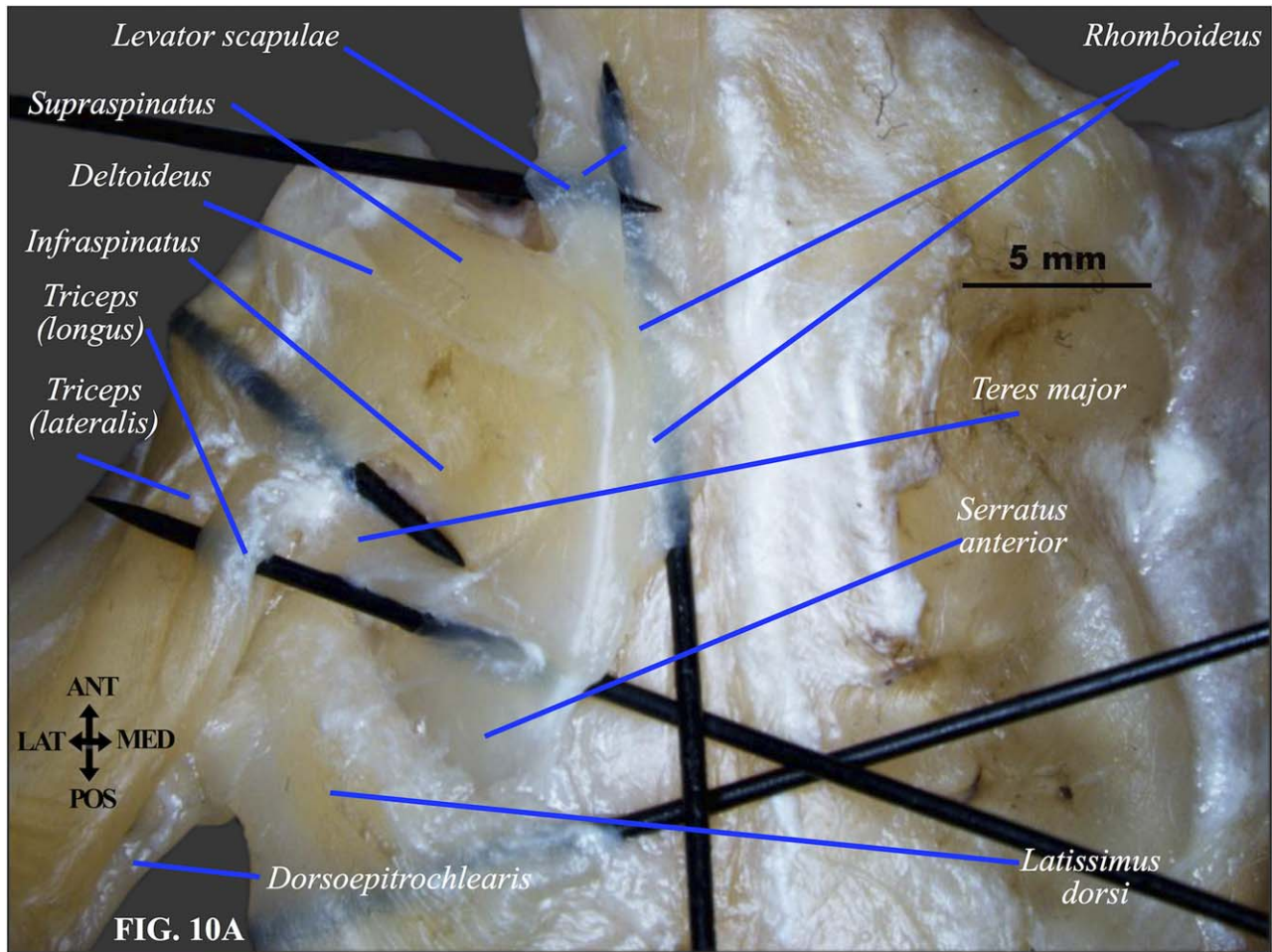
Fig. 10. *Propithecus coquereli* (male fetus P6154). (**A**) Dorsal view of the muscles of the pectoral girdle and arm. (**B**) Ventral view of some hand muscles.

we could not detect fibers from the basihyal; if they existed, the chondroglossus part is very thin. The styloglossus (Figs. 3A, 8A,B, 9A) runs from the proximal region of the hyoid arch (in the *L. catta* fetus and seemingly also in the *P. coquereli* fetus) and from the auricular region of the skull (only in the *P. coquereli* fetus) to the tongue. The palatoglossus is not present as a distinct muscle. The sternohyoideus (Figs. 8A, 9A) runs from the sternum to the hyoid bone, remains in contact with its counterpart for most of its length and has no well-defined tendinous intersection. In the *P. coquereli* fetus, the omohyoideus (Fig. 3A) runs from the scapula to the hyoid bone; it is deep to the sternocleidomastoideus and has no intermediate tendon. The configuration is similar in the *L. catta* fetus, except that the muscle seems to have a tendinous intersection at about half of its length. The sternothyroideus (Figs. 3A, 8A, 9A) runs from the sternum to the thyroid cartilage, inserting posteriorly to the origin of the thyrohyoideus with no tendinous intersection. The thyrohyoideus (Figs. 3A, 8A) connects the thyroid cartilage to the hyoid bone and is not blended with the hyoglossus or the sternothyroideus.

Pectoral Muscles

The serratus anterior (Figs. 4A, 10A) runs from the ribs to the medial side of the scapula and is being deeply blended with the levator scapulae. The rhomboideus (Figs. 4A, 10A) is a continuous muscle (i.e., not subdivided into rhomboideus major and minor) running from cervical and thoracic vertebrae to the medial surface of the scapula, as is usually the case in adults of both species. However, the rhomboideus and rhomboideus occipitalis in the fetuses are more deeply blended with the serratus anterior and the levator scapulae than in adults. The rhomboideus occipitalis (Fig. 4A) is a very thin muscle running from the cranium to the scapula. It is usually present in adult lemurs and may or may not be present in adult *Propithecus*: Jouffroy (1962) states that the rhomboideus occipitalis is missing in adult *Propithecus verreauxi* and *Propithecus deckenii*; this condition was also found by Milne-Edwards and Grandidier (1875); however, Ashton and Oxnard (1963) state that in the *Propithecus* sp. specimen they dissected there was an attachment of the rhomboid complex to the occipital region and that such a condition was also described in this genus by Milne-Edwards and Grandidier (1875), contradicting Jouffroy (1962). Because the muscle is missing in the adult *P. coquereli* GWUANT PV1 specimen, it is clear that the muscle is missing in at least some adult specimens of this species. In the fetuses of both species and in *P. coquereli* adults, the levator scapulae (Figs. 2A, 3A, 10A) runs from C2–C7 to the superior angle of the scapula, while in adult lemurs it usually attaches to C1 as well. There is no distinct muscle atlantoscapularis posticus. In the *P. coquereli* fetus, the levator claviculae (Fig. 3A) runs from C1 to the acromion and scapular spine, passing superficial (dorsal) to the trapezius, as it does in adults of this species and in adult lemurs (e.g., Murie and Mivart, 1872; Jouffroy, 1962; Diogo and Wood, 2012a). In the *L. catta* fetus, the levator scapulae also inserts on the lateral extremity of the clavicle. In the *L. catta* fetus, the subclavius runs from Rib 1 to the clavicle, but in the *P. coquereli* fetus a few fibers also run to the region of the scapula, specifically the proximal portion of the coracoid process. This division of the muscle could be interpreted as a remnant of the plesiomorphic costocoracoideus muscle, which is usually not present in the adults of either species.

The pars clavicularis of pectoralis major (Fig. 4B) originates from the medial portion of the clavicle and from the sternum and inserts on the proximal humerus, superficial and distal to the insertion of the pars sternocostalis, which originates from the sternum and ribs. The pars abdominalis is deep to the two other heads and blended distally with the pectoralis minor, originating from the abdominal muscles and some ribs and inserting on the humerus, proximal to the insertion of the two other heads. The pectoralis major contacts its counterpart in the midline. The pectoralis minor runs from the sternum and ribs to the proximal humerus. The panniculus carnosus is present in the *L. catta* fetus; the pars humerodorsalis inserts on the greater tuberosity of the humerus and blends somewhat with the distal portions of the pars abdominalis of the pectoralis major, among other muscles. We could not discern whether the panniculus carnosus was present in the *P. coquereli* fetus. The infraspinatus (Figs. 4A, 10A) and the supraspinatus (Figs. 4A, 10A) originate from the infraspinatous and supraspinatous fossae, respectively, and insert on the greater tuberosity of the humerus. In the *L. catta* fetus, the deltoid complex is differentiated into a pars clavicularis (from the clavicle) and a pars acromialis (from the acromion), which are blended with each other to form the deltoideus acromialis et clavicularis and well separated from the pars spinalis and deltoideus scapularis (from scapular spine and infraspinatous fascia) (Fig. 4A,B), as is usually the case in adult lemurs. In the *P. coquereli* fetus, the deltoideus (Fig. 10A) was only slightly differentiated into a pars clavicularis, a pars acromialis and a pars spinalis that lies just beside the two other parts, as is the case in adults of this species. The teres minor runs from the lateral 1/3 (in the lemur fetus and adults) or 1/2 (in the *P. coquereli* fetus and adults) of the lateral border of the scapula to the greater tuberosity of the humerus. In neither fetus does the insertion of the muscle extend distal to this tuberosity. The subscapularis (Fig. 4B) is an undivided muscle running from the subscapular fossa to the lesser tuberosity of the humerus and the capsule of the shoulder joint. The teres major (Figs. 4A, 10A) runs from the lateral border of the scapula to the proximal portion of the humerus, blends with the subscapularis and passes dorsally to (without blending with) the tendon of the latissimus dorsi. In the *L. catta* fetus, however, a very thin tendinous slip connects the two tendons at the level of the axilla, just proximal to their insertion onto the humerus. The latissimus dorsi (Figs. 4A, 10A) is somewhat blended with the trapezius in the *P. coquereli* fetus but not in the lemur fetus. In both fetuses, the latissimus dorsi does not insert directly on the scapula but runs from the dorsolumbar fascia, vertebrae, and/or ribs to the humerus.

Arm Muscles

The dorsoepitrochlearis (Figs. 4A, 10A) originates from the latissimus dorsi and inserts onto the olecranon process and proximal portion of the shaft of the ulna and onto the fascia superficial to the medial epicondyle

of the humerus (but is not directly attached to the epicondyle). The triceps brachii (Figs. 4A, 10A) has a long head (from the lateral border of the scapula), a lateral head (from the surgical neck), a medial head (from the surgical neck in the lemur fetus and adults, but from the humeral shaft in *P. coquereli* fetus and adults), and a posterior head (from the distal portion of the humerus). The posterior head appears to be derived from the medial head because its origin is noticeably proximal to, and clearly distinct from, the proximal origin of the epitrochleoanconeus. The four heads insert on the olecranon process of the ulna. A major difference between the lemur fetus and all the other specimens (i.e., the lemur adults plus the *P. coquereli* fetus and adults) is that in the former the posterior and medial heads of the triceps brachii are profoundly blended with each other. The brachialis is an undivided muscle running from the humerus to the coronoid process of the ulna. It does not appear to reach the surgical neck of the humerus in the *P. coquereli* fetus, and we could not discern this feature in the lemur fetus. The long head of the biceps brachii (Fig. 4B) originates from the infraglenoid tubercle of the scapula, while the short head originates from the coracoid process of the scapula. The two heads are completely blended distally and insert on the bicipital tubercle of the radius, where the tendon connects to a strong, distinct 'lacertus fibrosus' (aponeurosis bicipitalis). The coracobrachialis (Fig. 4B) originates from the coracoid process of the scapula, its caput medium inserting on the distal 1/2 of the humerus (including the medial epicondyle) and its caput profundum inserting on the proximal portion of the humerus. In the *P. coquereli* fetus, the musculocutaneous nerve passes between these two heads, as it usually does in adults of the two species, but we could not discern whether this was also the case in the lemur fetus.

Ventral Forearm Muscles

The pronator quadratus originates from the distal ulna and inserts on the distal radius. The flexor digitorum profundus (Figs. 5A, 10B) runs from the ulna, interosseous membrane, medial epicondyle of the humerus and radius to the distal phalanges of Digits 1–5. There is no distinct flexor pollicis longus: the tendon to Digit 1 is no thinner than the tendons to Digits 2–5, nor does it have a distinct fleshy belly. The flexor digitorum superficialis (Fig. 5A) is less developed than the flexor digitorum profundus, with which it is partially blended; it runs from the medial epicondyle of the humerus to the middle phalanges of Digits 2–5. The palmaris longus (Fig. 5A) runs from the medial epicondyle of the humerus to the palmar aponeurosis of the hand. The flexor carpi ulnaris (Fig. 5A) originates from the medial epicondyle of the humerus and the ulna and inserts both on the pisiform and on the base of metacarpal V. The epitrochleoanconeus runs from the medial epicondyle of the humerus to the olecranon process of the ulna. Contrary to the case in adults of both species and the *P. coquereli* fetus, in the lemur fetus the epitrochleoanconeus is deeply blended with the flexor carpi ulnaris. The flexor carpi radialis (Fig. 5A) runs from the medial epicondyle of the humerus to the bases of metacarpals III and II in both fetuses, rather than exclusively to metacarpal II as it usually does in adults of these species

(Diogo and Wood, 2012a). The pronator teres (Fig. 5A) runs from the medial epicondyle of the humerus to the radius, passing superficial (ventral) to the median nerve.

Hand Muscles

In the lemur fetus, the palmaris brevis (Figs. 5A, 6) is a short, thin muscle running from the fascia of the pisiform and flexor retinaculum to the hypothenar skin and palmar aponeurosis. We could not discern whether this muscle was present in the *P. coquereli* fetus; it was probably removed with the skin. The lumbricales (Figs. 5A, 6) 1, 2, 3, and 4 attach to the radial sides of the proximal phalanx and extensor expansion of Digits 2–5, respectively. In the *P. coquereli* fetus, there are only two fleshy, broad contrahentes: the more superficial one attaching to the radial side of Digit 5, and the deeper one attaching to the ulnar side of Digit 2. Both extend proximally to the carpal bones, originating from the carpals and metacarpals. The contrahentes are ventral (palmar) to the deep branch of the ulnar nerve, while the flexores breves profundi are dorsal to this branch. The lemur fetus has a similar configuration, but it also possesses a third contrahentes muscle series (Fig. 5B) attaching to the ulnar side of Digit 4. We found only contrahentes to Digits 2 and 5 in the adults of the two species we dissected, but authors such as Jouffroy (1962) reported a contrahentes to Digit 4 in adults of these species, as we found in our lemur fetus. The adductor pollicis (Figs. 5B, 10B) is undivided, and there is no distinct adductor pollicis accessorius (see Diogo and Wood, 2012b). The adductor pollicis originates from metacarpal III and the contrahens fascia and inserts on the ulnar side of the metacarpophalangeal joint and the base of the proximal phalanx of the thumb. In the *P. coquereli* fetus, there is no well-defined tendon to the distal phalanx of the thumb; such a tendon is usually not present in adults of either species, but it seems to be present in the lemur fetus. All flexores breves profundi (Figs. 5B, 10B) are present: the first corresponds to the "superficial head of the flexor pollicis brevis" plus the opponens pollicis; the second corresponds to the "oblique head of the adductor pollicis" *sensu* Jouffroy (1962) and to the "deep head of the flexor pollicis brevis" in human anatomy and inserts on the ulnar margin of the base of the proximal phalanx of Digit 1; the third, fourth, fifth, sixth, seventh, and eighth insert on the radial and ulnar sides of the proximal phalanges of Digits 2, 3, and 4, respectively; the ninth inserts on the radial side of the proximal phalanx of Digit 5; the 10th corresponds to the flexor digiti minimi brevis and part or all of the opponens digiti minimi. The flexores breves profundi pass superficial to the transverse laminae of the digits, while the intermetacarpales insert on the laminae or pass deep to them. There are four intermetacarpales (Fig. 5B), which are well separated from, and dorsal to, the flexores breves profundi. They insert onto the radial sides of the proximal phalanges of Digits 2 (intermetacarpalis 1, originating from metacarpals I and II), 3 (intermetacarpalis 2, originating from intermacarpales II and III), and 4 (intermetacarpalis 3, originating from metacarpals III and IV) and onto the ulnar margin of the proximal phalanx of Digit 4 (intermetacarpalis 4, originating from metacarpals IV and V). Therefore, Digit 4 is the functional axis of the hand. The flexor pollicis brevis (Fig. 5B) corresponds to

the "superficial head of the flexor pollicis brevis" in human anatomy and is well separated from the flexor brevis profundus 2 (which corresponds to the "deep head of the flexor pollicis brevis" in human anatomy). It originates from the trapezium and flexor retinaculum and inserts on the radial sesamoid of the interphalangeal joint and the base of the proximal phalanx of the thumb, together with the abductor pollicis brevis, radial to the tendon of the flexor digitorum profundus to Digit 1 (the insertion of the flexor brevis profundus 2 is ulnar to the tendon of the flexor digitorum profundus to Digit 1). More so than in adults of these two species, the configuration in the fetuses indicates that both the opponens pollicis and the flexor pollicis brevis ("superficial head" in human anatomy) derive from the flexor brevis profundus 1, because the two former muscles are clearly blended with each other. The opponens pollicis (Fig. 5B) is a thin muscle that runs from the trapezius to metacarpal I and also to the radial sesamoid of the interphalangeal joint. The flexor digiti minimi brevis (Figs. 5A,B, 6) originates from the hamate and flexor retinaculum and inserts on the ulnar side of the proximal phalanx of Digit 5, together with the abductor digiti minimi. The opponens digiti minimi (Fig. 5B) originates from the hamate and flexor retinaculum and inserts along the entire length of metacarpal V, completely dorsal (deep) to the deep branch of the ulnar nerve. The adductor pollicis brevis (Fig. 5A,B) originates from the sesamoid bone associated with the trapezium and from the flexor retinaculum and inserts on the radial side of the base of the proximal phalanx of Digit 1. The adductor digiti minimi (Figs. 5A,B, 6) originates from the pisiform and inserts on the ulnar side of the base of the proximal phalanx of Digit 5. The flexor digiti minimi brevis, opponens digiti minimi, adductor pollicis brevis and adductor digiti minimi are all undivided muscles.

Dorsal Forearm Muscles

The extensor carpi radialis longus (Fig. 6) runs from the lateral supracondylar ridge of the humerus, just distal to the origin of the brachioradialis, to the base of metacarpal II. The extensor carpi radialis brevis (Fig. 6) runs from the lateral ridge and epicondyle of the humerus to the base of metacarpal III. The brachioradialis runs from the distal portion of the humerus to the radius, reaching the styloid process distally. The supinator originates from the lateral epicondyle of the humerus, annular ligament and proximal portion of the radius and inserts on the shaft of the radius. The extensor carpi ulnaris (Fig. 6) runs from the lateral epicondyle of the humerus (caput humerale) and ulna (caput ulnare) to the base of metacarpal V. In the *P. coquereli* fetus, the anconeus runs from the lateral epicondyle of the humerus to the olecranon process of the ulna and is partially blended with the triceps brachii, as is usually the case in adults of the two species. We could not discern whether the anconeus was present as a distinct muscle in the lemur fetus. The extensor digitorum (Fig. 6) runs from the lateral epicondyle of the humerus to Digits 2–5. In the *P. coquereli* fetus, the equivalent of the extensor digiti minimi runs from the lateral epicondyle of the humerus to Digits 4–5, as is usually the case in adults of the two species. However, in the lemur fetus it also sends a very thin tendon to Digit 3, supporting

the idea that some tendons of the extensor indicis and/or extensor digiti minimi are lost during ontogeny (e.g., Kaneff and Cihak, 1970; see Discussion below). In the lemur fetus, the extensor indicis (Fig. 6) runs from the ulna and interosseous membrane to Digits 2 and 3, while in the *P. coquereli* fetus it also inserts on Digit 4. The adult configuration of this muscle is ambiguous: an insertion onto Digits 2–4 in *Lemur* was described by Barnard (1875), Kaneff and Cihak (1970) and Murie and Mivart (1872), while an insertion onto Digits 2–3 was described by Jouffroy (1962) and Kaneff (1980) and observed in the GWUANT LC1 specimen we dissected. Likewise, an insertion onto Digits 2–4 in *Propithecus* was reported in two cases by Jouffroy (1962), while an insertion onto Digits 2–3 was reported in two cases by Jouffroy (1962) and observed in our GWUANT PV 1 specimen. In the *P. coquereli* fetus, the extensor pollicis longus runs from the ulna and interosseous membrane to the distal phalanx of Digit 1, as is usually the case in adults of this species. In the lemur fetus, the extensor pollicis longus (Fig. 6) inserts on both Digits 1 and 2, as reported in some (e.g., Kaneff and Cihak, 1970) but not all (e.g., Murie and Mivart, 1872; our GWUANT LC1 specimen) lemur adults. In the lemur fetus, the abductor pollicis longus (Fig. 6) originates from the radius, interosseous membrane and ulna and sends an undivided tendon to the base of metacarpal I and to the trapezium and/or associated sesamoid bone. In the *P. coquereli* fetus, the origin is similar but the muscle has two tendons, one inserting onto the base of metacarpal I and the other inserting onto the trapezium and/or sesamoid bone.

DISCUSSION

As explained in the Introduction, our recent studies of the muscles of humans, non-human primates, zebrafish, and salamanders support Gould's idea of a parallel between ontogeny and phylogeny. The evolutionary and developmental implications of our data on fetal primates are best understood in comparison with other anatomical studies. In particular, we will examine whether intraspecific differences in muscular anatomy between fetuses, infants and adults reveal a more plesiomorphic phylogenetic condition in the fetus (as expected from the "ontogeny parallels phylogeny" hypothesis), or a derived condition already present in the earliest developmental stages. This part of the text is divided into two main sections, the first concerning characters specifically described and used by Diogo and Wood's (2011) myological phylogenetic analysis of primates, and the second concerning characters that were not used specifically by these authors but can easily be polarized. Each feature summarized below is described in detail in the Results section. The abbreviations PLESIO and DERIVED refer to phylogenetically more plesiomorphic/derived conditions, respectively, of the fetus compared with older ontogenetic stages in members of the same species.

Finally, we would like to address two points that bear on the results of this paper: sample size and anatomical variation. We performed dissections and histological analyses of two fetuses, one specimen of *L. catta* and one specimen of *P. coquereli*. As explained above, this study is the first to describe the muscles of fetuses of these species in detail. With small sample sizes, the extent of

intraspecific variation can be a concern. However, we have found in our previous research on the musculoskeletal structure of various non-human primates, including data from dissection and from the literature for numerous adult specimens (in some cases, more than 50) (e.g., Diogo and Wood, 2012a,b), that the features discussed here (e.g., attachments of muscles) vary little between members of the same species at the same developmental stage. Therefore, we assume that the fetuses of *P. coquereli* and *L. catta* we dissected are reasonable representatives of the normal fetal configuration for each species. We plan to undertake future works to test this prediction and to further study myological intraspecific variation within primates.

Characters from Diogo and Wood (2011)

- PLESIO: In the *P. coquereli* fetus, the pars suprazygomatica appears to be less differentiated from the main body of the muscle than in adults of this species. This configuration resembles the plesiomorphic adult condition reported by Diogo and Wood (2011; char. 8).
- PLESIO: In the *L. catta* and *P. coquereli* fetuses, the rhomboideus occipitalis was present as a distinct muscle, as is the case in adult lemurs, but the muscle is clearly missing in at least some adult *P. coquereli* specimens. Because the muscle tends to disappear in adults of more derived primate taxa (e.g., all hominoids except orangutans), the condition found in the *P. coquereli* fetus is a plesiomorphic one (Diogo and Wood, 2011; char. 70).
- DERIVED: In the *L. catta* fetus, the levator claviculae inserts on the scapular spine and acromion, as it does in adult lemurs, but unlike in adult lemurs it also inserts on the lateral extremity of the clavicle, as it does in adults of phylogenetically more derived taxa such as apes (Diogo and Wood, 2011; char. 74).
- PLESIO: Unlike the case in both the lemur adults and the *P. coquereli* fetus and adults, the posterior and medial heads of the triceps brachii are deeply blended with each other in the lemur fetus. The complex formed by these structures clearly corresponds to the two heads in the adult, but the posterior head is not clearly separated from the medial head in the fetus; this configuration is plesiomorphic for mammals (Diogo and Wood, 2011; char. 96).
- DERIVED: In the *L. catta* and *P. coquereli* fetuses, the flexor carpi radialis runs from the medial epicondyle of the humerus to the bases of metacarpals II and III, while in adults of both species the muscle usually goes to metacarpal II, as reported by Murie and Mivart (1872), Miller (1943) and Jouffroy (1962, 1971), and as found in our dissections. According to the phylogenetic analysis of Diogo and Wood (2011; char. 121), exclusive attachment to metacarpal II represents the plesiomorphic condition in adult primates.

Additional Characters that are Easily Polarized

- PLESIO: In the *L. catta* and *P. coquereli* fetuses, the pars superficialis and pars profunda of the masseter seem to be less differentiated than in adults of these two species. The fetal condition is similar to more phylogenetically plesiomorphic adult vertebrates in which the adductors of the mandible are less differentiated (Diogo and Abdala, 2010).
- PLESIO: In the *P. coquereli* fetus, the jugulohyoideus is relatively much larger than it is in adult strepsirrhines, and, unlike in adults, it is somewhat blended with the digastricus posterior. Its size, position and association with the digastricus posterior strongly suggest that the jugulohyoideus is actually derived from the digastricus posterior and is more developed in early stages than in later stages. This muscle is usually missing in adult anthropoids (whose morphology is presumably more derived); therefore, the ontogeny of the jugulohyoideus seems to parallel its evolution.
- PLESIO: Contrary to the condition in adults of the species, in the *L. catta* fetus the zygomaticus major is deeply blended with the zygomaticus minor, supporting the idea that these muscles derive from the same anlage and resembling the adult plesiomorphic mammalian configuration, in which these two muscles are not present as differentiated structures (Diogo and Abdala, 2010).
- PLESIO: In the *L. catta* and *P. coquereli* fetuses, the rhomboideus and rhomboideus occipitalis are much more deeply blended with the serratus anterior and with the levator scapulae than in the adults of the two species, reinforcing the idea that these muscles develop from the same anlage. Together with the levator claviculae and subclavius, these muscles constitute the axial pectoral muscles *sensu* Diogo and Abdala, 2010, which are similarly poorly differentiated in phylogenetically more plesiomorphic tetrapods such as salamanders.
- PLESIO: In addition to its insertion onto the clavicle, a few fibers of the subclavius also run to the proximal portion of the coracoid process of the scapula in the *P. coquereli* fetus. This portion could be interpreted as a remnant of the plesiomorphic costocoracoideus muscle, which is usually not present in the adults of either species but is present in monotremes and reptiles (Diogo and Abdala, 2010).
- PLESIO: Unlike its configuration in adults of both species and the *P. coquereli* fetus, the epitrochleoanconeus in the lemur fetus is deeply blended with the flexor carpi ulnaris. These two muscles derive from the same embryonic anlage and are profoundly blended or completely undifferentiated from each other in phylogenetically plesiomorphic tetrapods (e.g., many salamanders) (Diogo and Abdala, 2010).

There is another clear difference between the fetal and adult members of one species, but whether it represents the plesiomorphic or derived condition is ambiguous. As explained above, the equivalent of the extensor digiti minimi runs from the lateral epicondyle of the humerus to Digits 4–5 in the *P. coquereli* fetus, as is usually the case in adults of the two species. However, in the lemur fetus, this muscle also sends a very thin tendon to Digit 3, supporting the idea that some of the tendons of the extensor indicis and/or extensor digiti minimi are lost during ontogeny (e.g., Kaneff and Cihak, 1970). However, this character is not easy to polarize because the extensor indices inserts on Digits 3–5 in some primate outgroups and Digits 4–5 in others (see Diogo and Wood, 2011; char. 159).

Among the 11 cases listed above that are easily polarized, the fetal condition reflects the more plesiomorphic phylogenetic condition in nine and the more derived condition in only two, supporting the argument for a parallel between ontogeny and phylogeny among strepsirrhinids. Both exceptions concern fetal muscles that insert on additional bones, that is insertion of the flexor carpi radialis onto metacarpal III (in addition to metacarpal II, where it inserts in adults) and levator claviculae onto the clavicle (in addition to the scapula, where it inserts in adults). Interestingly, these two exceptions do not appear to relate to fetal demands because they involve muscles that move the pectoral girdle and upper limb, which are primarily important in later stages of life (e.g., locomotion/prey capture). These examples suggest that some exceptions to the "ontogeny parallels phylogeny" hypothesis are driven more by ontogenetic constraints than by adaptive plasticity. On the contrary, the few exceptions to this rule we have found in, e.g., zebrafish concern traits that play a particularly important role in feeding mechanisms in early developmental stages (Diogo et al., 2008). However, further developmental and functional studies are needed to clarify whether or not the exceptions found in strepsirrhines play a role in early developmental stages of these primates. One of the main aims of this work is to stimulate and pave the way for more developmental studies of primate musculature—which has been neglected so far—in a broader phylogenetic, evolutionary, and functional context.

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