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EVOLUTIONARY DEVELOPMENTAL BIOLOGY (R DIOGO AND E BOYLE, SECTION EDITORS)

Muscles Lost in Our Adult Primate Ancestors Still Imprint in Us: on Muscle Evolution, Development, Variations, and Pathologies

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Abstract

The study of evolutionary developmental pathologies (Evo-Devo-Path) is an emergent field that relies on comparative anatomy to inform our understanding of the development and evolution of normal and abnormal structures in different groups of organisms, with a special focus on humans. Previous research has demonstrated that some muscles that have been lost in our ancestors well before the evolution of anatomically modern humans occasionally appear as variations in adults within the normal human population or as anomalies in individuals with congenital malformations. Here, we provide the first review of fourteen atavistic muscles/groups of muscles that are only present as variations or anomalies in modern humans but are commonly present in other primate species. Muscles within the head and neck and pectoral girdle and upper limb region include platysma cervicale, mandibulo-auricularis, rhomboideus occipitalis, levator claviculae, dorsoepitrochlearis, panniculus carnosus, epitrochleoanconeus, and contrahentes digitorum manus. Within the lower limb, they include scansorius, ischiofemoralis, contrahentes digitorum pedis, opponens hallucis, abductor metatarsi quinti, and opponens digiti minimi. For each muscle, we describe their synonyms, comparative anatomy among primates, embryonic development, presentation and prevalence as a variation, and presentation and prevalence as an anomaly. Research on the embryonic origins of six of these muscles has demonstrated that they appear early on in normal human development but usually disappear before birth. Among the eight muscles in the upper half of the body, mandibulo-auricularis is, to our knowledge, present in humans only as a variation, while the other seven muscles can be present as either a variation or an anomaly. All six muscles of the lower limb are present only as variations, and to our knowledge have not been described in anomalous individuals. Interestingly, although these muscles conform to most definitions of what constitutes an atavism—i.e., they were lost in our adult ancestors and now appear in some adult humans—some of them are seemingly present in more than 2% of the normal population. Therefore, they might actually constitute polymorphisms rather than variations. The research summarized here therefore emphasizes the need of future studies of the evolution, development, and prevalence of soft tissue variations and anomalies in humans, not only for the understanding of our evolutionary history but also of our phenotype and pathologies.

Keywords Primate evolution · Muscles · Soft tissues · Variations · Polymorphisms · Anomalies

Introduction

The description of muscular variations in adults within the normal human population and muscular anomalies in humans with congenital malformations has been a significant focus of the medical and anatomical literature since the nineteenth century [1–9]. Attempts to better understand the human musculoskeletal system as it compares with those of other mammals, particularly our closest living relatives (the apes), have a similarly long history [10–15]. Recent technological advances in studying human development, such as whole-mount immunostaining, have made it possible to better understand the ontogenetic origins of variable and anomalous muscles in humans and compare them with what we know about musculoskeletal development in other species [16–19]. The study of evolutionary developmental pathologies (Evo-Devo-Path) is an emergent field that formally integrates these approaches to study the links between anatomical variations, anomalies,

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development, and evolution, focusing in particular on human anatomy and the anatomical consequences of birth defects within an evo-devo framework [20–30].

Evo-Devo-Path provides a particularly useful lens for evaluating previously suggested hypotheses for how and why atavistic muscles—ancestral muscles that reappear in a species after evolutionary loss in previous generations—persist in both adults within the normal human population and humans with congenital anomalies [20, 31]. Haeckel, an early theorist in comparative embryology, proposed that ontogeny recapitulated phylogeny, i.e., that the ontogeny of embryo recapitulates the adult stages of its ancestors [20, 32]. Haeckel's recapitulation is no longer considered valid, in part due to the work of von Baer, who argued that the ontogeny of an embryo mainly goes from a more general, e.g., tetrapod, embryonic configuration to a more specific, e.g., human, configuration, that is, some of the similarities between for instance humans and salamanders or mice mainly refer to the embryonic, not the adult stage [20, 33].

Recent studies have confirmed, using more modern visualization techniques, that in early developmental stages, some of the muscles of human embryos do resemble those of the embryos of other animals, particularly our closest living relatives, the nonhuman primates [19]. In particular, researchers have demonstrated that several muscles that were lost in our adult ancestors—some of them more than 250 million years ago—do usually develop in early human ontogenetic stages only to be reabsorbed or fused with other structures in later stages, before birth, in most humans [19, 20, 34]. That is, these observations indicate that the developmental pathways related to the formation of such complex structures persist over the evolution of various taxa even when they are absent in the adult normal phenotype of those taxa [20, 35, 36].

While the persistence of developmental pathways is the ultimate cause for why muscles that were phylogenetically lost in our adult ancestors' evolution still "imprint" us, the proximate causes of how these muscles persist are not clear. The persistence of certain atavistic muscles in some adult humans could be due to developmental delay/arrested development, by which lingering muscle slips are present in later ontogenetic stages due to the delay of muscle reabsorptions/fusions that should normally occur in earlier stages [21, 37]. Specifically, it has been suggested that decreased apoptosis in skeletal muscles could be the mechanism leading to the presence of several supernumerary muscles and non-differentiated muscles observed in individuals with Trisomy 13, 18, and 21 [20, 21].

There is some controversy on whether such muscles should be appropriately designated as atavistic or not, within our species. According to Hall [35], an atavism can be characterized by four features including the persistence of the structure into adult life, absence of the structure in parents or recent ancestors, presence in only one or a few individuals within a population, and close resemblance to a character possessed by all members of an ancestral population. However, authors such as Diogo et al. [19] would not strictly apply some of the criteria of Hall [35] to designate structures that are usually present in human embryos such as a tail or the muscles dorsometacarpales of the hand, as atavisms of embryos, even if they will disappear before birth and are present in all embryos. This is precisely because they want to avoid adult-centric views of evolution. That is, within this view, the tail present in humans, be it in all human embryos or in adults with congenital malformations, is always seen as atavistic because the crucial criterion is that it was lost in the evolution of our adult ancestors. Another main complication concerns the fact that some of the muscles might eventually be present in more than 2% of the normal population, that is, they should be designated as polymorphic traits and not as variations because per definition, variations are present in less than 2% of the population [20]. So, an important distinction needs to be made. If the muscle was present in our direct adult ancestors and is now present as an adult polymorphism in our species, as it is the case with the palmaris longus (present only in about 85%) of humans, this constitutes an adult non-atavistic polymorphism. But if the muscle was lost at some point in the evolution of our adult ancestors and is now present as an adult polymorphism in our species, then in phylogenetic terms, it would be considered an evolutionary reversion [36].

To provide a stronger foundation for discussing these key issues, we rely on primate comparative anatomy and developmental research in humans to undertake a comprehensive review of fourteen atavistic muscles/groups of muscles (using Diogo et al.'s [20] less strict definition of atavism) that are present in adult humans either as variations—or polymorphisms, if prevalence if higher than 2%—or as pathological anomalies. For each muscle, we describe their presentation as a variation/potential polymorphism and/or anomaly, their presentation in nonhuman primates, data on prevalence in humans, and what we know, if anything, about their development in early human ontogenic stages. By doing this, our goal is to not only provide a review for evolutionary developmental biologists but also include information relevant for comparative anatomists, functional morphologists, and biological anthropologists, as well as to clinicians, as atavistic muscles are often misdiagnosed in medical studies, can compress or displace adjacent structures, and can be related to exercise-induced pain [38].

Nonhuman Primate Muscles that Imprint in Humans

Descriptions of presentation, prevalence, development, and comparative anatomy for fourteen muscles are described below and summarized in Table 1.

Table 1 Summary of muscles. Muscles with text in italics present as both variations and anomalies in humans. Muscles with text in bold present only as variations in humans, to our knowledge

Muscle	Anatomical Region	To our knowledge, is it present early in normal human ontogeny?	Present as a variation	Variation prevalence (but caution: see text)	Present as anomaly	Anomaly prevalence
Platysma cervicale	Head and neck	Yes	*Yes*	*25–60%*	*Yes*	*25–100%*
Mandibulo-auricularis	Head and neck	NA	**Yes**	**NA**	**No**	**NA**
Rhomboideus occipitalis	Pectoral girdle & arm	NA	*Yes*	*NA*	*Yes*	*4–31%*
Levator claviculae	Pectoral girdle & arm	NA	*Yes*	*2–3%*	*Yes*	*20%*
Dorsoepitrochlearis	Pectoral girdle & arm	Yes	*Yes*	*1.9–5%*	*Yes*	*5–15%*
Panniculus carnosus	Pectoral girdle & arm	No	*Yes (as extra muscular slips)*	*NA*	*Yes*	*4–14%*
Epitrochleoanconeus	Pectoral girdle & arm	Yes	*Yes*	*13–25%*	*Yes*	*7%*
Contrahentes digitorum	Hand	Yes	*Yes*	*NA*	*Yes*	*4–15%*
Scansorius	Posterior leg	NA	**Yes**	**12.5–80%**	**No**	**NA**
Ischiofemoralis	Posterior leg	NA	**Yes**	**NA**	**No**	**NA**
Abductor metatarsi quinti	Foot	NA	**Yes**	**43–45%**	**No**	**NA**
Contrahentes pedis	Foot	Yes	**Yes**	**NA**	**No**	**NA**
Opponens hallucis	Foot	No	**Yes**	**NA**	**No**	**NA**
Opponens digiti minimi	Foot	Yes	**Yes**	**NA**	**No**	**NA**

NA no available information

Platysma Cervicale

Synonyms

This muscle is also referred to as occipital platysma [37], occipitalis minor, the occipital transverse muscle [39], or the querer Halsmuskel [40]. A diminutive platysma cervicale is often referred to as the transversus nuchae muscle [41, 42].

Comparative Anatomy

Platysma cervicale is often present in adult nonhuman mammals [21]. Among adult nonhuman apes, platysma cervicale is only usually present as a distinct muscle in *Hylobates* (hylobatids/gibbons) and *Pongo* (orangutans), being often absent in adult *Gorilla* (gorillas), and typically absent in adult *Pan* (common chimpanzees and bonobos). When the muscle is present in *Pan* and *Gorilla*, it is often small and resembles the condition of diminutive platysma cervicale "transversus nuchae" of some adult humans [43–48]. Since it is typically present in orangutans and gibbons and often absent in the African great apes, platysma cervicale therefore was seemingly lost in the steps leading to the adult common ancestor of African apes and humans [49].

Embryonic Development

Platysma cervicale is present in normal human development, as the occipital lamina that gives rise to this muscle is established during the sixth week of embryonic growth [42, 50]. It typically disappears in early embryonic developmental stages and is therefore often absent in normal adult humans [21, 37, 41, 42]. Gasser [37] notes that between CR58 mm and CR80 mm (crown rump length of 58 mm to 80 mm), "occipital platysma" is present as a distinct band that runs between the main platysma mass and the occipital region, but this muscle was not identified in a CR 142 mm fetus. Gasser [37] also observes the occasional presence of a diminutive platysma cervicale "transversus nuchae" laying dorsal to auricularis posterior in the lower occipital or upper cervical region between CR58 mm and CR80 mm. Later, this diminutive muscle was still observed in 210 mm and 270 fetuses and was blended with the auricularis posterior [37].

Presentation as a Variation

When present in adults of the normal human population, platysma cervicale originates from the region of auricularis posterior to insert onto the external occipital protuberance or the superior nuchal line (Fig. 1) [39, 40, 52]. Its presentation

can also resemble the condition seen in anomalous cases (see below), in which the muscle can originate from near the mouth or parotid fascia to insert onto the occipital protuberance [39, 40, 53, 54]. Auricularis posterior, auricularis superior, or sternocleidomastoid may be connected to or fused with this muscle [39, 40, 52]. Lei et al. [54] observed fibers extending to the zygomatic region. Watanabe et al. [55] observed that this muscle extended from the external occipital protuberance to insert onto the mastoid process (about 43% of cases in which it is present) or originated from the external occipital protuberance and curved around the mastoid process to join with platysma (about 58% of cases in which it is present). Platysma cervicale can sometimes have two bellies [53, 54].

Variation Prevalence

A well-developed platysma cervicale is almost never present in adults of the normal human population. Concerning the diminutive platysma cervicale "transversus nuchae," Standring [52] suggests that it is present in 25% of individuals. Bergman et al. [39] cite studies that state that "occipitalis minor" is present frequently in Malaysian individuals, present in 56% of Black individuals, present in 50% of Japanese individuals, present in 36% of European individuals, and typically absent in Khoisan peoples and Melanesians. It is however important to keep in mind, when we refer to such so-called "racial anatomical studies" in the present paper, that most of them were plagued by racist views and often included errors that reinforced such racist ideas, either in purpose or unconsciously due to the prevalent biases of that era [56, 57]. That is, we will provide the numbers used in those studies, as they are part of the very few studies that referred to the prevalence of such muscles in humans, but these numbers should be taken with enormous caution. Lei et al. [54] found "transversus nuchae" on twelve out of twenty sides (60%) from a total sample ten cadavers (seven male and three female). The muscle was absent in the females. Watanabe et al. [55] found "transversus nuchae" in forty out of 124 sides (32.2%) from a total sample of 62 cadavers (present in 26 cadavers, bilaterally in 14, and unilaterally in 12).

Anomalous Presentation

Platysma cervicale is frequently present as an anomaly in trisomic individuals, often presenting as a discrete bundle of the platysma complex that extends from the mouth to the nuchal region [21]. It can either originate from the posterior part of the platysma myoides and insert with sternocleidomastoideus onto the mastoid process or it can originate from the corner of the mouth and insert with trapezius onto the occipital bone (Fig. 1) [21].

Anomalous Prevalence

In their literature review, Smith et al. [21] found that platysma cervicale was present in five out of twenty neonates/fetuses with Trisomy 13 (25%), thirteen out of seventeen neonates/fetuses with Trisomy 18 (about 76.5%), and five out of five individuals with Trisomy 21 (100%).

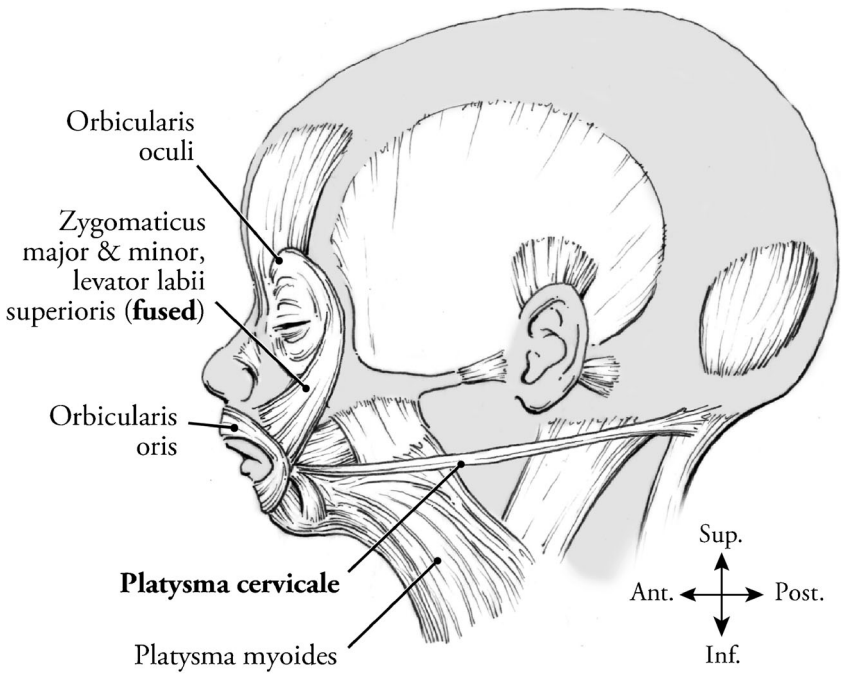

Fig. 1 From Smith et al. [21] illustration based on common presentations of the muscles in fetuses and infants with trisomies 13, 18, and 21. Lateral view of the head and neck. Fusion of the zygomaticus major and minor and levator labii superioris in a thin sheet originating at the corner of the orbicularis oculi. Platysma cervicale originating from corner of mouth with no risorius, inserting with the trapezius onto the occipital bone. Anomalies labeled in bold. Modified from Bersu and Optiz [51]

Mandibulo-Auricularis

Synonyms

This muscle is also sometimes referred to as auricularis inferior [15, 58, 59].

Comparative Anatomy

Mandibulo-auricularis is present in many non-primate mammals [60] and disappeared in adult primates as a distinct fleshy muscle in the lineage leading to anthropoid primates [49]. It probably gave rise to the anthropoid stylomandibular ligament, except in rare cases where it is present as a distinct fleshy muscle, such as in some *Pan* and *Homo* [49, 58, 61]. According to Standring [52], the stylomandibular ligament is a thick band of deep cervical fascia that extends from the styloid process to the angle and posterior border of the mandible.

Embryonic Development

There is currently a poor understanding of how and when mandibulo-auricularis develops in primate embryos.

Presentation as a Variation

Mandibulo-auricularis is rare in adults within the normal human population [39]. Le Double [15] describes an "auricularis inferior" in just one case, which was subcutaneous and extended from the parotid fascia to the base of the concha auris. Hussey and O'Sullivan [62] also describe the presence of a similar "auricularis inferior" in one individual, which extended from the parotid fascia to the conchal cartilage inferior to the tragus.

Variation Prevalence

There is currently a poor understanding of how prevalent mandibulo-auricularis is among adults within the normal human population.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Rhomboideus Occipitalis

Synonyms

This muscle is also referred to as occipitoscapularis, omo-occipitalis, rhomboideus capitis, levator scapulae minor vel posterior, or levator anguli scapulae minor [5, 6, 63–66].

Comparative Anatomy

Rhomboideus occipitalis is usually present in adult non-hominoid primates [49]. Among the apes, only in adult orangutans it is often present, therefore not being clear if it disappeared in the hominoid lineage as a whole and was independently regained by adult orangutans, or if it disappeared twice, in adult hylobatids and the adult common ancestor of African apes plus humans [46, 49].

Embryonic Development

It is unclear whether this muscle appears during normal muscle formation and then disappears before birth. However, Jelev and Landzhov [67] suggest that variation in the rhomboid muscles may happen in the embryo when the rhomboid mass migrates to its usual position after its formation at CR14 mm (crown-rump length of 14 mm).

Presentation as a Variation

Rhomboideus occipitalis is present in adults within the normal human population as an extremely rare variation [21, 68]. Wood [5] provided a description of the rhomboideus occipitalis as an adult human variation and noted that this muscle passes from the superior nuchal line on the occipital bone to attach to the medial border of the scapula at the level of the scapular spine. As noted by Patten [64], Zağyapan et al. [69], and Stanchev et al. [70], this muscle can also originate from the superior angle of the scapula between the origins of rhomboideus minor and levator scapulae (Fig. 2). In the case described by Patten [64], rhomboideus occipitalis sent slips to the fascia of serratus posterior superior. In the cadaver examined by Rogawski [68], there were three other muscular variations on the left side of the body, including a third head of biceps brachii, absence of plantaris, and insertion of the tertius onto the distal phalanx of the fifth digit. Stanchev et al. [70] describe a bilateral presentation of rhomboideus occipitalis that appeared to be comprised of an inferior oblique and superior oblique part on the left side and an inferior oblique, middle straight, and superior oblique part on the right side.

Variation Prevalence

There is currently a poor understanding of how prevalent rhomboideus occipitalis is among adults within the normal human population.

Anomalous Presentation

The anomalous presentation of rhomboideus occipitalis is similar to the above. When present, rhomboideus occipitalis passes between rhomboideus minor and levator scapulae and

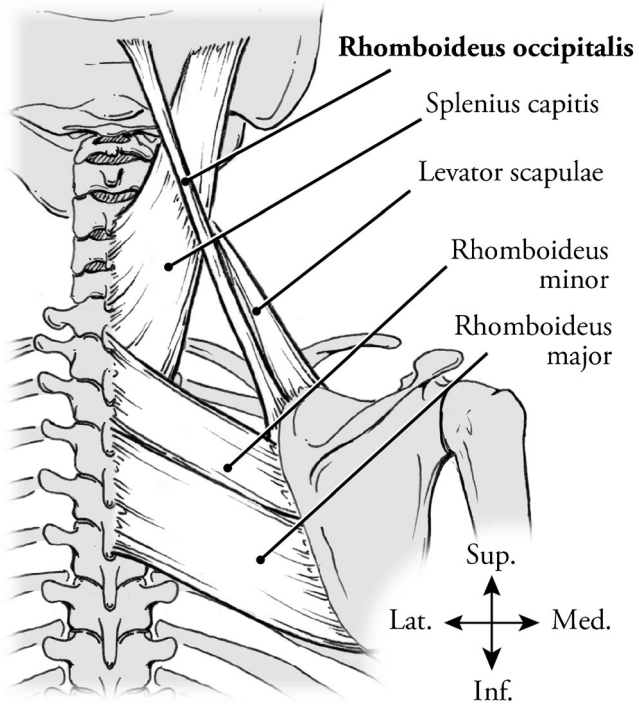

Fig. 2 From Smith et al. [21] illustration based on common presentations of the muscles in fetuses and infants with trisomies 13, 18, and 21. Posterior view of the back. The rhomboideus occipitalis spans from the superior angle of the scapula between the rhomboideus minor and levator scapulae to the occipital region of the skull. Anomalies labeled in bold. Modified from Aziz [66]

extends from the superior angle of the scapula to the occipital region of the skull (Fig. 2) [21]. Smith et al. [21] illustrate two presentations of this muscle, one in which rhomboideus occipitalis is associated with normal presentations of the rhomboid major and minor muscles and of the levator scapulae, and another in which this muscle is associated with a hypotrophied levator scapulae and rhomboideus minor. In a Trisomy 18 cyclopic fetus dissected by these authors, they found that rhomboideus occipitalis was part of a complex with trapezius and a broad sternocleidomastoideus [21]. Rhomboideus occipitalis was also present in a fetus with craniorachischisis dissected by Alghamdi et al. [28]. In an otocephalic fetus examined by Lawrence and Bersu [71], rhomboideus occipitalis extended from the spinous processes of the fourth and fifth cervical vertebrae to the medial border of the scapular, inserting just above the level of the scapular spine.

Anomalous Prevalence

In the literature review conducted by Smith et al. [21], they found that rhomboideus occipitalis was present in one out of twenty-four neonates/fetuses with Trisomy 13 (about 4%) and eight out of twenty-six neonates/fetuses with Trisomy 18 (about 31%). This muscle was not present in seven individuals with Trisomy 21.

Levator Claviculae

Synonyms

Levator claviculae is also referred to as omocervicalis, levator scapulae anticus, or levator scapulae ventralis [72] or the cleidocervical muscle [73].

Comparative Anatomy

In all major groups of nonhuman primates, adults normally have a levator claviculae, so it is normally present as a separate muscle in adult hylobatids, *Pan*, *Pongo*, and *Gorilla* (Fig. 3) [43–48]. Therefore, this muscle stopped appearing in adults in human evolution.

Embryonic Development

Early in development, specifically between CR9 mm (crown-rump length of 9 mm) and CR10.5 mm, the axial pectoral muscles resemble those of adult humans as subclavius is present but levator claviculae is absent [74]. Though closely associated with and considered a variant of levator scapulae [75, 76], levator claviculae has been argued to have embryological origins from scalenus anterior [77], sternocleidomastoid [11], trapezius [78], longus colli [79], or the ventrolateral muscle primordia of the [73]. In their review, Odate et al. [76] arrive to the conclusion that levator scapulae shares a common embryological origin with levator scapulae (i.e., arise from the same myotome), based on the work of McKenzie [80] and shared characteristics between these two muscles, including similar innervation and origin/insertion. This idea is reinforced by a detailed study of the comparative myology of tetrapods [72].

Presentation as a Variation

When present in adult humans, it extends from the transverse processes of various cervical vertebrae (rarely from the first, but commonly from the second to sixth cervical vertebrae) and attaches onto the middle third or lateral end of the clavicle and the acromion [39, 73, 75, 76, 81]. This muscle can also insert onto the sternocleidomastoid or serratus anterior muscles [82, 83]. Levator claviculae can be misidentified as various pathologies. It can resemble a neck mass, cyst, lymphadenopathy or cervical adenopathy, metastasis, neurofriboma, arterial aneurysm, or thrombosed vein or can be identified as an abnormal levator scapulae or sternocleidomastoid [76, 81, 83–86]. The presence of this muscle can also contribute to thoracic outlet syndrome [87].

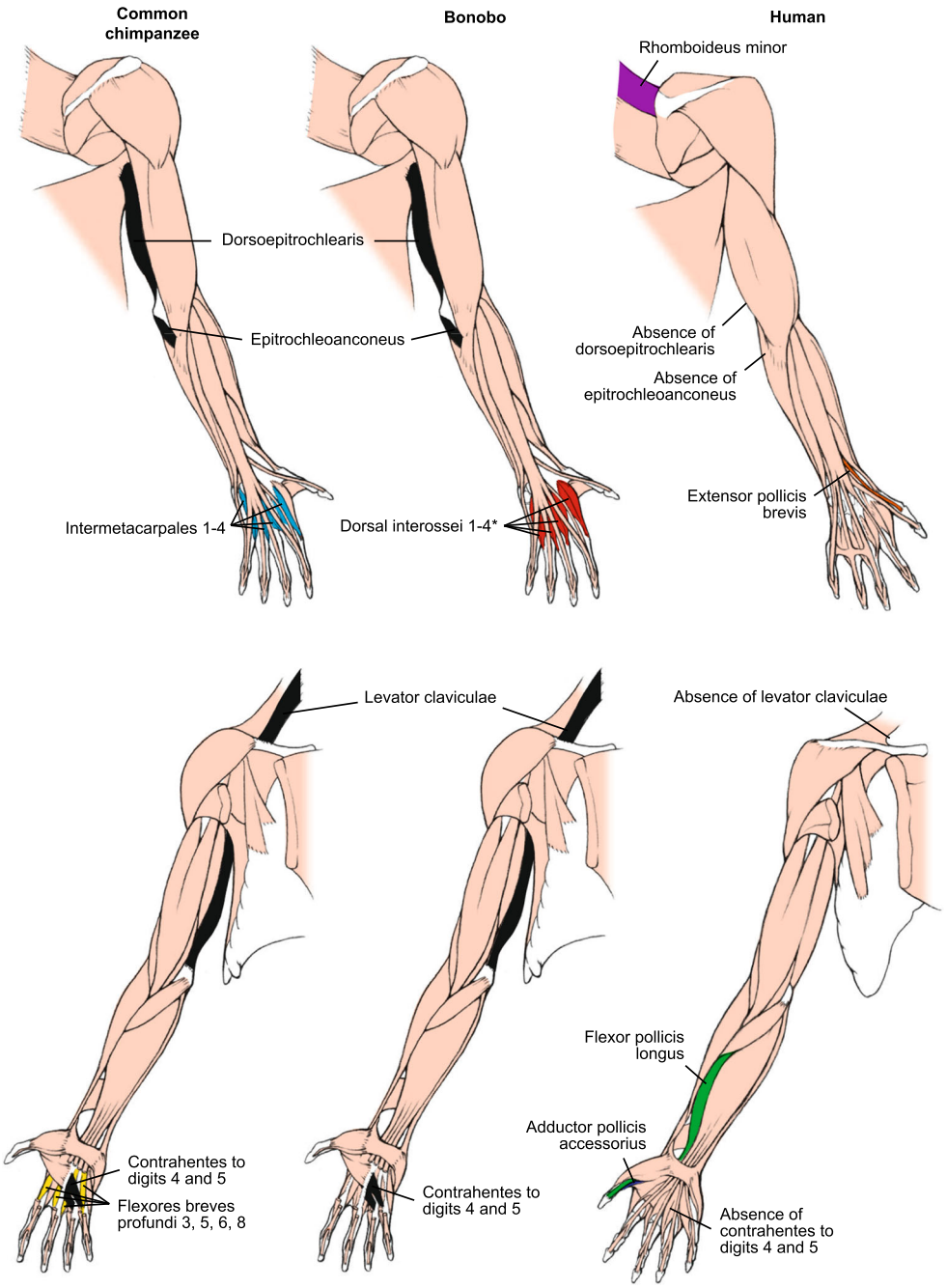

Fig. 3 From Diogo et al. [48]. Upper limbs seen in posterior (top panel) and anterior (bottom panel) views, showing differences between the typical adult presentation of upper limb muscles of common chimpanzees (left), bonobos (middle), and modern humans (right). Muscles shown here that are typically present in adult common chimpanzees and bonobos that appear in adult humans as variations—or eventually as polymorphisms (see text)—or anomalies include dorsoepitrochlearis (the muscle inserting onto medial epicondyle of the humerus), levator claviculae, and contrahentes digitorum manus, all shown in black on the common chimpanzee and bonobo schemes. Note: adult muscle differences typically seen between adult common chimpanzees and bonobos are shown in yellow, while adult muscles usually present in adult humans but not in adult common chimpanzees or bonobos are shown in green

Variation Prevalence

Wood [11] observed that levator claviculae is present in only four out of 202 humans (about 2%). Loukas et al. [75] observed levator claviculae in only two out of 2000 cadavers (0.0001%). Based on CT scans of 300 individuals, Rubinstein et al. [85] noted seven instances of the muscle (one bilateral case, five unilateral cases) in six individuals (2% of 300 individuals). Review articles [73, 76, 81, 85] report a prevalence of 2–3%.

Anomalous Presentation

Anomalous presentation is similar to the above. Smith et al. [21] note that this muscle passes from the base of the occipital bone to the clavicle.

Anomalous Prevalence

In the literature review conducted by Smith et al. [21], they found that levator claviculae was present in one out of five

individuals with Trisomy 21 (20%). This muscle was not present in twenty neonates/fetuses with Trisomy 13, nor in seventeen neonates/fetuses with Trisomy 18.

Dorsoepitrochlearis

Synonyms

Alternative names for this muscle include latissimo-condylus or latissimo-epitrochlearis [12], latissimo-condyloideus [14, 63, 88–99], latissimo-tricipitalis [100–103], appendix of latissimus dorsi [10], accessorium tricipitis [39], and tensor fasciae antebrachii, anconeus accessorius, acessorius latissimus dorsi, dorso-antebrachialis, anconeus quintus, anconeus longus, or extensor cubiti sensu Jouffroy [65].

Comparative Anatomy

While typically absent in adult humans, dorsoepitrochlearis is commonly present in nonhuman primates [31, 49]. According to the literature reviews and dissections done by Diogo et al. [43–48], this muscle is present in hylobatids, *Pongo*, *Gorilla*, and *Pan* (Fig. 3). Therefore, this muscle was lost in adults during human evolution. The presentation of this muscle in adult apes is similar to that in the few adult humans in which it is present, but dorsoepitrochlearis in nonhuman apes is said to be innervated by the radial nerve while it is said to be innervated by the thoracodorsal nerve in humans [43–48, 72, 104].

Embryonic Development

Dorsoepitrochlearis is typically only present in the early stages of human development, usually present in human embryos from CR15 mm (crump-round length of 15 mm) to CR18 mm [104]. However, Diogo et al. [19] state that since all other arm muscles are differentiated much earlier, CR10.5 mm, further research is needed to reveal if dorsoepitrochlearis is also differentiated earlier than CR15 mm.

Presentation as a Variation

When present in human adults, dorsoepitrochlearis originates from latissimus dorsi near the tendon of insertion, passes through the axilla, and inserts onto the medial epicondyle of the humerus (Fig. 4) [104]. Bergman et al. [39] list other possible insertions including the brachial and forearm fascia, the humerus, the lateral epicondyle and olecranon, and the long head of triceps.

Variation Prevalence

Haninec et al. [104] observe the presence of this muscle in 4 out of 209 adults examined in Prague, three men and one woman (1.9%). Bergman et al. [39] note this muscle is present in 5% of bodies.

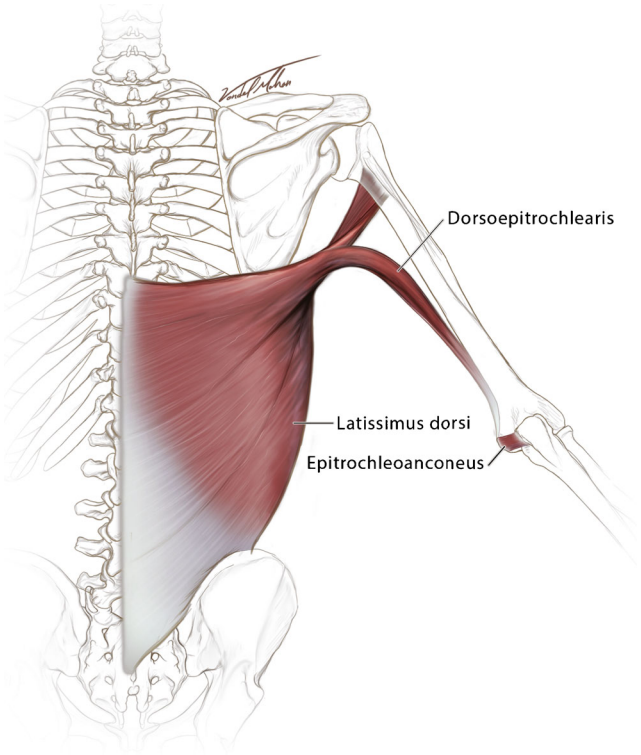

Fig. 4 Torso and upper right limb in posterior view. Dorsoepitrochlearis extends from latissimus dorsi near the tendon of insertion, passes through the axilla, and inserts onto the medial epicondyle of the humerus. Epitrochleoanconeus extends from the medial epicondyle of the humerus to the medial side of the olecranon process of the ulna

Anomalous Presentation

An anomalous dorsoepitrochlearis muscle may connect latissimus dorsi to pectoralis major or to the long head of the triceps [9, 21, 28]. Alghamdi et al. [28] note that in a fetus with craniorachischisis, dorsoepitrochlearis was fused to the inner side of the inferior band (costohumeralis) of pectoralis major. Alghamdi et al. [28] note that this muscle is similar in presentation to dorsoepitrochlearis found on the right side of one female fetus with anencephaly by Windle [9].

Anomalous Prevalence

Testut [14] and Aziz [66] suggest that this muscle is present in about 5% of anomalous humans. Barash et al. [105] state that this muscle is present in an infant with Trisomy 18, and Aziz [66, 106] note the presence of dorsoepitrochlearis in two Trisomy 18 neonates, but not in three Trisomy 13 neonates. In the literature review conducted by Smith et al. [21], they noted the presence of this muscle in four out of twenty-six neonates/fetuses with Trisomy 18 (about 15%). This muscle

was not present in twenty-four neonates/fetuses with Trisomy 13, nor in seven individuals with Trisomy 21.

Panniculus Carnosus

Synonyms

According to the review by Naldaiz-Gastesi et al. [107], alternative names for this muscle include cutaneous trunci, musculus cutaneous, cutaneous maximus muscle, subcutaneous muscle, and superficial fascia system.

Comparative Anatomy

Panniculus carnosus derives from the pectoralis muscle of amphibians and reptiles and is present in many mammals including basal primates and several species of monkeys [49, 72]. It has been described as vestigial in adult *Gorilla* [65]; dissections by Sommer [96], Raven [108] and Diogo et al. [43] did not find this muscle in adult gorillas. Panniculus carnosus likely disappeared in adult primates along the lineage leading to apes, that is, to hominoids [49].

Embryonic Development

As far as we know, panniculus carnosus is not present in early developmental stages in humans [19].

Presentation as a Variation

Bergman et al. [39] state that panniculus carnosus is represented only by vestigial remnants in some adult humans, which present as extra muscular slips near pectoralis major and minor. These slips can be found between the abdominal aponeurosis and the rectus sheath or are attached to the fascia covering serratus anterior [39]. Other bundles from these remnants may arise below pectoralis major and insert into the axillary fascia, the pectoral ridge of the humerus, the fascia between coracobrachialis and pectoralis minor, or the coracoid process [39]. Several muscles in adult humans are considered to be remnants of panniculus carnosus, including the pectorodorsalis or sternalis, and potentially several other striated muscles in the upper limb, pectoral region, and trunk [107].

Variation Prevalence

As panniculus carnosus is only present as a variation in adult humans in the form of extra muscular slips, there is no information on the possible presence of the whole muscle in human adults.

Anomalous Presentation

In anomalous human cases, panniculus carnosus is a cutaneous muscle sheet arising from the pectoral muscle mass and covering various trunk regions [21].

Anomalous Prevalence

In the literature review conducted by Smith et al. [21], they found that remnants of the panniculus carnosus were reported in one out of twenty-six Trisomy 18 neonates/fetuses (about 4%) and one out of seven individuals with Trisomy 21 (about 14%). This muscle was not observed in twenty-four neonates/fetuses with Trisomy 13.

Epitrochleoanconeus

Synonyms

Alternative names for this muscle include flexor antebrachii ulnaris [102], epitrochleo-olecranonis, accessory anconeus, ulnaris internis, and cubital anterieur [109], as well as anconeus quartus, anconeus medialis, anconeus sextus, anconeus parvus, and tensor fasciae antebrachii [65].

Comparative Anatomy

While typically absent in adult humans, epitrochleoanconeus is present often in most adult primates, including chimpanzees and bonobos (Fig. 3) [31, 45, 47–49,]. As it is usually not present as a distinct muscle in hylobatids, *Pongo* and *Gorilla* [43, 44, 46], the most parsimonious phylogenetic hypothesis is that it stopped appearing in adult primates along the hominoid lineage and then became present as a reversion in the genus *Pan* [49].

Embryonic Development

Epitrochleoanconeus derives from the primordium that also gives rise to flexor carpi ulnaris [19]. This muscle is typically only present in early stages of human development, being present as a distinct muscle at CR25 mm (crown-rump length of 25 mm) and persisting until at least CR33.5 mm [19].

Presentation as a Variation

When present as a distinct muscle in human adults, epitrochleoanconeus extends from the medial epicondyle of the humerus to the medial side of the olecranon process of the ulna (Fig. 4) [21, 65, 110, 111]. It may sometimes be fused with anconeus [39]. Wilson et al. [109] suggest that the presence of this muscle may protect against the development of cubital tunnel syndrome as it may decrease the rigidity of the

entrance into the cubital tunnel, replacing Osborne's ligament as the roof of this tunnel.

Variation Prevalence

Galton [110] suggests that the epitrochleoanconeus is found in about 53 out of 200 human upper limbs (about 25%). In a study of 218 Brazilian adults, Nascimento and Ruiz [112] found that this muscle was present in 29 cases (about 13%).

Anomalous Presentation

Anomalous presentation is same as above.

Anomalous Prevalence

In the literature review conducted by Smith et al. [21], they found that epitrochleoanconeus was reported in two out of twenty-six Trisomy 18 neonates/fetuses (about 7%). This muscle was not observed in twenty-four neonates/fetuses with Trisomy 13, nor seven individuals with Trisomy 21 [21].

Contrahentes Digitorum Manus

Synonyms

Another name for this group of muscles is transversus manus [14].

Comparative Anatomy

The contrahentes are "adductor" muscles of the digits. In the normal phenotype of the adult human hand, only the thumb receives such muscles, the so-called adductor pollicis of human anatomy. However, the contrahentes digitorum manus are often present as adductors of at least some other hand digits in most adult primates, including adult hylobatids and *Pan* within apes (Fig. 3) [31, 44, 49]. They are however rarely present in adult *Pongo* [45–48] and not described in adult *Gorilla* [43]. Therefore, the hand contrahentes, to digits other than the thumb, likely stopped appearing in adults along the lineage leading to great apes plus humans and became secondarily present as a reversion in adult *Pan* [49].

Embryonic Development

Contrahentes of the hand to digits other than the thumb, such as contrahentes 3, 4, and/or 5, are typically only present in the early stages of human development and then disappear later in ontogeny (Fig. 5) [19, 34]. According to Cihák [34], contrahentes 1 and 2 form the adductor pollicis by gestational week 8, or CR20 mm, but it is not clear if the adductor pollicis does include embryologically contrahentes 1 and 2 or just contrahens 1. Contrahentes 3, 4, and 5 persist in the embryo until CR36 mm (crown-rump length of 36 mm) and then start diffusing or fuse with the interossei [19].

Presentation as a Variation

Hand contrahentes other than the adductor pollicis are very rare in adults of the normal human population. When present as distinct muscles, such contrahentes originate from the carpals, or the bases of the metacarpal bones, and can have separate insertions into the metacarpals and phalanges of digits four and five [114] The presence of hand contrahentes has been associated with problems including cramping of the hand [115] or potentially compression of the median nerve [114]. Stark et al. [115] described the presence of contrahentes in three children, and in each case the muscle was only present unilaterally and was associated with an accessory palmaris brevis in all cases.

Variation Prevalence

There is currently a poor understanding of how prevalent the contrahentes digitorum of the hand other than the adductor pollicis are among adults within the normal human population.

Anomalous Presentation

Anomalous presentation of the contrahentes of the hand other than the adductor pollicis is similar to that described above as variations.

Anomalous Prevalence

In the literature review conducted by Smith et al. [21], they found contrahentes of the hand, other than adductor pollicis, in Trisomy 18 individuals: contrahens to digit two was present in four out of twenty-six (~15%) cases, contrahens to digit four was present in one out of twenty-six (~4%) of cases, and contrahens to digit five was present in two out of twenty-six cases (~8%). Hand contrahentes other than the adductor pollicis were not observed in twenty-four individuals with Trisomy 13, nor seven individuals with Trisomy 21 [21].

Scansorius

Synonyms

This muscle is also referred to as gluteus quartus [39].

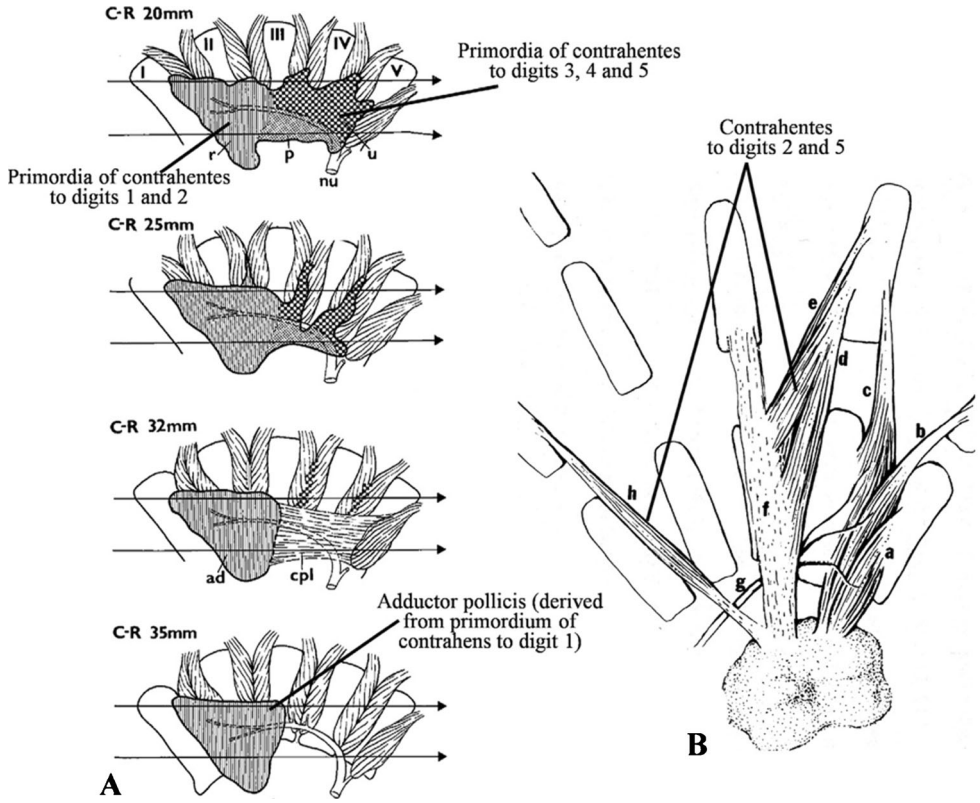

Fig. 5 From Smith et al. [21]. **a** Ontogeny of the contrahentes digitorum manus in the hand of a karyotypically normal human embryos showing how the contrahentes to digits other than digit 1 are usually lost (reabsorbed) early in human development (modified from Cihák [34]). Part of the interossei primordia (i.e., the flexores breves profundi layer) are shown between the metacarpals. r, u, p: radial, proximal, and ulnar parts of contrahentes layer; nu: ulnar nerve; ad: adductor pollicis; cpl: contrahens plate; I-V: metacarpals I-V; CR: crown-rump length of the embryos. **b** Deep left hand musculature of a trisomy 18 human neonate (100 days old, female) showing the abnormal presence of contrahentes to digits 2 and 5 at later stages of development (the more superficial muscles, as well as the adductor pollicis, are now shown; modified from Dunlap et al. [113]. (a) Opponens pollicis; (b) "interosseous palmaris of Henle"; (c) interosseous dorsalis 1; (d) contrahens to digit 2; (e) interosseous palmaris 1; (f): contrahens fascia/medial raphe; (g) deep branch of ulnar nerve; (h) contrahens to digit 5

Comparative Anatomy

Scansorius is commonly present in adult *Pongo*, occasionally present in adult hylobatids and *Gorilla*, and commonly absent in adult common chimpanzees but usually present in adult bonobos (Fig. 6) [43–48, 116, 117]. Until a detailed phylogenetic study of the primate lower limb muscles is done, it is therefore difficult to discern if the scansorius was lost multiple times within adult hominoids, or instead was lost as part of the normal adult phenotype in hominoids and then as a reversion became again present as the normal adult phenotype in bonobos and orangutans.

Embryonic Development

In mice, the scansorius is present in 12- and 13-day-old embryos, developing from the anlage of the iliopsoas and then fusing with the gluteus minimus, which is thus divided at its origin by the passage of the nerve to the tensor fasciae latae into a gluteus minimus proper originating from the posterior part of the gluteal fossa and into a scansorius head originating from the lateral crest of the ilium and the iliac fossa [118]. However, there is currently a poor understanding of the development of the scansorius in primates.

Presentation as a Variation

When the scansorius is present as a variation in adults of the normal human population, it is represented by a bundle that extends from the anterior margin of gluteus minimus, or from between gluteus minimus and gluteus medius, to insert onto the anterior border or tip of the greater trochanter [39, 116].

Variation Prevalence

Beck et al. [119] noted the presence of scansorius in two out of 16 cadaveric hips (about 12.5%). Woyski et al. [120] report a higher prevalence for scansorius in humans. Based on examination of 45 cadaveric hips (29 female, 16 male), these

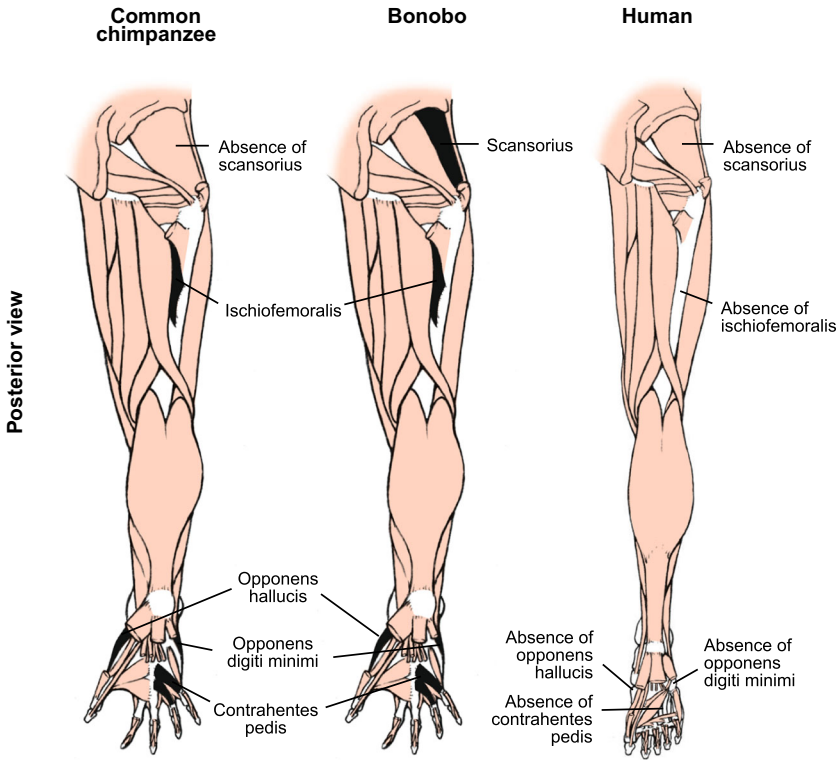

Fig. 6 Adapted from Diogo et al. [48]. Lower limb in the posterior view. Differences between the typical adult presentation of the lower limb muscles of common chimpanzees (left), bonobos (middle), and modern humans (right). Muscles that are typically present in adult common chimpanzees and/or bonobos that appear in adult humans as variations—or eventually as polymorphisms (see text)—include scansorius, ischiofemoralis, contrahentes digitorum pedis, opponens hallucis, and opponens digiti minimi, all shown in black on the common chimpanzee and bonobo schemes

authors find fibers corresponding to scansorius in 41% of female specimens and 44% of male specimens. Scansorius was present as a distinct bundle in 50% of males and 31% of females. The overall prevalence of scansorius was 80% [120]. However, one should keep in mind that such a high prevalence might be due to the fact that some authors use different definitions of what is truly a variant muscle, for instance they might code a bundle of the gluteus minimus as the scansorius, even if that bundle does not truly represents a distinct scansorius as that found in adult bonobos or orangutans and many other adult non-hominoid tetrapods.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Ischiofemoralis

Synonyms

N/A

Comparative Anatomy

Ischiofemoralis is commonly present as a distinct muscle in adult *Pongo* and is commonly present but frequently blended with gluteus maximus in hylobatids, *Pan* and *Gorilla* [43–48, 117]. This muscle therefore disappeared in adults within human evolution. In apes, the muscle typically originates from the ischial tuberosity and inserts on the lateral aspect of the femoral shaft and the aponeurosis of vastus lateralis (Fig. 6) [43–48, 117].

Embryonic Development

It is possible that the ischiofemoralis found as a variation in some adult humans derives from the embryonic muscle that Tichý and Grim [121] refer to as "coccygeofemoralis," a muscle that originates from the coccyx and inserts onto the femur near the distal margin of gluteus maximus and is innervated by a branch of the inferior gluteal nerve. This muscle persists as a distinct structure until CR40–45 mm (crown-rump length of 40 to 45 mm), and then fuses with gluteus maximus [121]. As noted by Morimoto [122], the presence of both gluteus maximus and "coccygeofemoralis" is similar to the configuration seen in adult apes, in which gluteus maximus consists of a proximal portion (gluteus maximus proprius) and a distal portion (ischiofemoralis). However, Tichý and Grim [121] suggest that there is little evidence that the "coccygeofemoralis" corresponds to any muscle found in adult humans, even as a variation. They note that Testut [13] described a "coccy-femoralis muscle" and Le Double [15] described a "femoro-coccygeus" muscle. Testut [13] suggests "coccy-femoralis" is homologous to "caudofemoralis" in other mammals, and Tichý and Grim [121] argue that their

"coccygeofemoralis" corresponds to this structure in adults that had incomplete fusion of this muscle and gluteus maximus.

Presentation as a Variation

Ischiofemoralis is normally absent in normal adult humans [117] When present as a variation, ischiofemoralis is commonly considered to be a variation of gluteus maximus, as it can present as an independent bundle that originates from the lumbar aponeurosis or the ischial tuberosity [39].

Variation Prevalence

There is currently a poor understanding of how prevalent ischiofemoralis is among adults within the normal human population.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Contrahentes Digitorum Pedis

Synonyms

N/A

Comparative Anatomy

In humans, the only contrahentes digitorum pedis commonly present in the adult normal population is the adductor hallucis. Descriptions of contrahentes digitorum pedis of the feet, other than the adductor hallucis, are often neglected within the primate comparative anatomy literature, but Diogo et al. [47, 48] observe the presence of contrahentes running to digits four and/or five of the foot in most *Pan paniscus* (bonobo) specimens dissected by them (Fig. 6). As noted by these authors, it is likely that contrahentes of the foot other than the adductor hallucis are also commonly present in adults of at least some other ape, and non-hominoid primate, species but further comparative studies are needed in order to confirm if this is really the case.

Embryonic Development

Contrahentes of the foot (contrahentes 3, 4, 5) are typically only present in the early stages of human development and then disappear completely later in ontogeny [19, 34]. The adductor hallucis, present as part of the normal adult human phenotype, seemingly includes only the contrahens 1 [114]. Contrahentes 3, 4, and 5 persist in the embryo until CR25–35 mm (crown-rump length of 25 to 35 mm), but as noted above then become usually absent as distinct muscles, before birth [19, 34].

Presentation as a Variation

Contrahentes of the foot other than the adductor hallucis are very rare in human adults. Hirsch and Vekkos [123] describe two presentations of this muscle based on two specimens. In one case, the muscle inserted onto the metatarsophalangeal joint capsules of digits one and two. In the second case, the muscle inserted onto the metatarsophalangeal joint capsules of digits two through five.

Variation Prevalence

There is currently a poor understanding of how prevalent contrahentes digitorum pedis are among adults within the normal human population.

Anomalous Presentation and Prevalence

To our knowledge, these muscles were not described as anomalies in humans with congenital malformations.

Opponens Hallucis

Synonyms

N/A

Comparative Anatomy

Among nonhuman apes, opponens hallucis is only commonly present in adult orangutans, originating from the medial cuneiform and inserting onto the first metatarsal, sometimes being fused with flexor hallucis brevis [46]. The opponens hallucis has been described as a variant in adult hylobatids and *Pan* (Fig. 6), but as noted by Diogo et al. [47, 48], this muscle is actually often present in at least adult bonobos and, likely, commonly chimpanzees, but has been confusingly designated in those taxa under other names. Therefore, more studies are needed to discern the actual taxonomic distribution of this muscle within primates.

Embryonic Development

Opponens hallucis appears to be absent at all stages of normal human ontogeny [19, 34].

Presentation as a Variation

Opponens hallucis has been described as either a variable slip of adductor hallucis [52] or of flexor hallucis brevis [39] that attaches to the first metatarsal. Kafka et al. [124] state that opponens hallucis describes a slip originating from either the oblique or transverse head of adductor hallucis that inserts onto the first proximal phalanx, but this slip actually seems to correspond instead to the adductor hallucis accessorius, which is in fact often present in adult humans [47, 48, 72].

Variation Prevalence

There is currently a poor understanding of how prevalent opponens hallucis is among adults within the normal human population.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Abductor Metatarsi Quinti

Synonyms

This muscle is also referred to as abductor ossis metatarsi digiti quinti [39, 52, 108] or abductor os metatarsi digiti minimi or abductor ossis metatarsi quinti [116].

Comparative Anatomy

Abductor metatarsi quinti is frequently present in adult *Gorilla*, *Pan*, and *Pongo* and sometimes present in adult hylobatids [43–48, 125]. It seems to correspond to part of the abductor digiti minimi of humans [47] and therefore seems to have disappeared in adults within human evolution. When present in apes, it inserts onto either the tuberosity of the fifth metatarsal, like it often does in adult human variations, or onto the proximal phalanx of the fifth digit [125].

Embryonic Development

There is currently a poor understanding of the development of this muscle in primates. However, Kopuz et al. [126] note that variable slips associated with abductor digiti minimi, such as abductor metatarsi quinti, may arise during phase 3 of Cihák's [34] four fundamental phases of human muscle development.

Presentation as a Variation

When present in adults of the normal human population, abductor metatarsi quinti is a variation related to the abductor digiti minimi [127], being thus a supernumerary muscle originating from the lateral plantar process of the calcaneus and inserting onto the tip of the tuberosity at the base of the fifth metatarsal [39, 52]. Bergman et al. [39] note that it may be fused with abductor digiti minimi and may attach to the midsection or the anterior aspect of the fifth metatarsal.

Variation Prevalence

Le Double [15] reports a prevalence of 43% (from examinations of 65 adult feet) and of 45% (from examinations of 40 adult feet). Bergman et al. [39] state that more distal attachments of abductor metatarsi quinti along the fifth metatarsal occur in over 40% of cases. However, once again, this might be a case where a high prevalence is related to the fact that the authors are referring to a bundle, or just some fibers, of the abductor digiti minimi going to metatarsal 5, rather than to a whole, distinct muscle as that often present in adult apes.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Opponens Digiti Minimi

Synonyms

This muscle is also referred to as opponens digiti quinti [108, 116].

Comparative Anatomy

While typically absent in adult humans, opponens digiti minimi is commonly present in adult hylobatids, *Pongo*, *Gorilla*, and *Pan* [43–48]. Therefore, it likely stopped appearing in adults along human evolution. When present in nonhuman primates, opponens digiti minimi has the configuration as when it is found in human adults as a variation, originating from the base of the fifth metatarsal and extending to the lateral border of this bone, or to the base of the proximal phalanx of digit five (Fig. 6) [43–48].

Embryonic Development

Opponens digiti minimi is typically only present in the early stages of human development, then disappears later in gestation. Bardeen [128] states that the blastema of opponens digiti minimi and flexor digiti minimi brevis appears at CR12 mm, and then the muscles differentiate at CR18 mm. Cihák [34] suggests that this muscle appears at CR20 mm (crown-rump length of 20 mm) and differentiates from flexor digiti minimi brevis at CR40 mm. Diogo et al. [19] found that opponens

digiti minimi is well-differentiated from flexor digiti minimi brevis at CR 36 mm and persists until at least CR51 mm or gestational week 11.5.

Presentation as a Variation

When present in adults of the normal human population, this muscle originates from the base of the fifth metatarsal and extends to the lateral part of the distal half of the fifth metatarsal, being often blended with flexor digiti minimi brevis [52]. Another presentation in an adult male cadaver was noted by Rana and Das [129], where this muscle had the typical origin but inserted onto the distal phalanx of the fifth digit.

Variation Prevalence

There is currently a poor understanding of how prevalent opponens digiti minimi is among adults within the normal human population.

Anomalous Presentation and Prevalence

To our knowledge, this muscle was not described as an anomaly in humans with congenital malformations.

Discussion

Perhaps the most striking conclusion that results from examining these fourteen atavistic muscles/groups of muscles, particularly when referring to Table 1, is the disparity in muscular presentations between the upper and lower halves of the body. Among the atavistic muscles/groups of muscles present in the upper half of the body, mandibulo-auricularis has been reported in adult humans only as a variation, while the other seven muscles have been reported either as a variation or as an anomaly. In the lower limb, the six muscles/groups of muscles have been reported only as variations and to our knowledge have not been described in individuals with congenital disorders. On the one hand, our review seemingly supports observations made by previous studies that both muscular variations [5, 130] and muscular anomalies [20, 131] are more common in the upper limb than in the lower limb. It also seemingly corroborates the statement by Diogo et al. [132] that the upper limbs of normal humans and humans with trisomy 18 are more different from one another than are the lower limbs of these groups. However, on the other hand, it has been suggested that lower limb anomalies are underreported in the literature [133], which calls into question whether or not a disparity in anomaly prevalence is a true anatomical difference between the upper and lower halves of the body or just a result of a bias toward research on upper limb variations and anomalies [132]. But in the case of this review, as lower limb variations in normal humans appear to be similarly infrequent as lower limb anomalies, it is likely that this is not just an artifact of reporting bias.

This review also demonstrates that there remains much to learn about how these fourteen muscles/groups of muscles develop in humans. Research on the embryonic origins of six of them—platysma cervicale [37, 41, 42], dorsoepitrochlearis [19, 104], epitrochleoanconeus [19], contrahentes digitorum [19, 34], contrahentes pedis [19, 34], and opponens digiti minimi [19, 34, 128]—has revealed that they appear early in normal human development and usually disappear before birth. Therefore, their occasional presence in adults of the normal human population or as an anomaly in individuals with congenital disorders could be due to developmental delay or arrest [20]. The developmental processes that lead to the manifestation of the other eight muscles/muscle groups is unclear. At least two of them—the opponens hallucis and panniculus carnosus—seem to be absent as distinct muscles in all stages of normal human development [19, 34], so their occasional presence in some adults of the normal human population is particularly puzzling. Future research not only on the ontogeny of human embryos but also on the development of muscles in nonhuman primate embryos and fetuses would shed light on how atavistic muscles develop are formed in these puzzling cases [122].

Also interesting is the relatively high prevalence rates reported by some authors in adults of the normal human population for at least some of these 14 atavistic muscles/muscle groups, such as the platysma cervicale, levator claviculae, dorsoepitrochlearis, epitrochleoanconeus, scansorius, and abductor metatarsi quinti. Such a high prevalence call into question their status as variations, accepted in the vast majority of the medical and comparative anatomy literature, because in at least some studies each of these muscles have been reported as present in more than 2% of adults of the normal human population, which would qualify them as polymorphisms and not as variations. However, as noted above, such a high prevalence might be due to the fact that some authors might consider what is just an undifferentiated bundle of fibers, or a small remnant of the original muscle, as the presence of that muscle. For instance, the platysma cervicale has been reported as present in up to 56% or 60% in some human populations, but clearly such studies refer to the presence of a small remnant of that muscle, the "transversus nuchae" [39, 54]. A true platysma cervicale, such as that commonly found in most mammals, is clearly absent in the vast majority of adult humans [72]. The same applies to the scansorius, which as noted above was reported to be present by Woyski et al. [120], as fibers in 44% of males and 41% of females, and as a muscular bundle in 50% of males and 31% of females, yielding an overall prevalence of 80%. That is, such cases mainly refer to undifferentiated bundles or even just a few fibers, not to the presence of a true, distinct scansorius as that

commonly present in adults of many tetrapod taxa. Similarly, the very high prevalence for the abductor metatarsi quinti reported by Le Double [15]—43% based on dissections of 65 feet and a prevalence rate of 45% based on dissections of 40 feet—clearly seems to be due to the fact that he is referring simply to a bundle of the abductor digiti minimi of the foot, and not to the whole, distinct muscle abductor metatarsi quinti commonly found in adult apes.

However, it is indeed possible that some of these atavistic muscles—such as the epitrochleoanconeus, reported in up to 25% of the adult normal cases by some authors as noted above—may be truly present as distinct, well-formed muscles in more than 2% of human adults, i.e., as true adult polymorphisms. More studies are therefore clearly needed to confirm if some atavistic muscles are truly present as polymorphisms in humans, as well as to analyze if in such cases of phylogenetic reversions normally there is a sequence between a muscle being/appearing as an adult variation, then as an adult polymorphism, and then eventually as the adult normal phenotype within a taxon. Or are there cases in which an atavistic muscle that is absent in the vast majority of adults of a taxon can become suddenly part of the normal phenotype of that taxon, without passing through polymorphic state, thus providing an example of saltational evolution, rather than gradualistic evolution. Future studies should also address questions on the broader links between evolutionary, development, variations, and pathologies, such as: are atavistic muscles that are present as polymorphisms in the adult normal population more likely to be also present within pathological conditions than if they are just present as variations in normal adults? What would be the developmental mechanisms involved in such a pattern, if that was the case? This review therefore not only highlights the importance of further research into the normal and abnormal development and pathological vs non-pathological prevalence of atavistic muscles in humans but also stresses the necessity for detailed comparative myological research in nonhuman primates and other animals.

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