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“Pollical Palmar Interosseous Muscle” (*Musculus Adductor Pollicis Accessorius*): Attachments, Innervation, Variations, Phylogeny, and Implications for Human Evolution and Medicine

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ABSTRACT Most atlases and textbooks dealing with human anatomy do not refer to the “pollical palmar interosseous” (PPI) muscle of Henle. In order to undertake a fresh and detailed study of this muscle and to thus better understand human comparative anatomy and evolution, we: 1) analyze the frequency of the PPI in a large sample of human hands; 2) describe the attachments, innervation and varieties of the PPI in these hands; 3) compare the data obtained with the information available in the literature; and 4) discuss the phylogenetic origin of the PPI and the implications of our observations and comparisons for medicine and for the understanding of human evolutionary history. Within the 72 hands dissected by us, the PPI is present in 67 hands (93%), commonly having a single muscular branch, originating from the medial side of the base of metacarpal I only, inserting onto the medial side of the base of the pollical proximal phalanx and/or surrounding structures (e.g., ulnar sesamoid bone, wing tendon of extensor apparatus), and passing at least partially, and usually mainly, medial to the princeps pollicis artery. A careful study of the human PPI, as well as a detailed comparison with other mammals, strongly suggest that the muscle is evolutionarily derived from the adductor pollicis, and namely from its oblique head. Therefore, we propose that PPI should be designated by the name *musculus adductor pollicis accessorius*, which indicates that the muscle is most likely a *de novo* structure derived from the adductor pollicis. *J. Morphol.* 000:000–000, 2012. © 2012 Wiley Periodicals, Inc.

KEY WORDS: thumb muscles; primates; hand; adductor pollicis accessorius; flexor brevis profundus 2; pollical palmar interosseous

INTRODUCTION

In his extended “meditation on the human hand,” the neurologist and musician Wilson (1998) stated that a remarkable unique feature of modern humans is having “eight (sometimes nine) muscles attached to the thumb” (Wilson, 1998; our emphasis). The eight “uncontested” muscles to which Wilson was referring are the extrinsic muscles

flexor pollicis longus, abductor pollicis longus, extensor pollicis brevis, and extensor pollicis longus, and the hand intrinsic muscles abductor pollicis brevis, opponens pollicis, flexor pollicis brevis and adductor pollicis. It should be noted that there is actually another “uncontested” intrinsic muscle that can promote the movement of the thumb, namely its adduction: the first dorsal interosseous. However, the ninth muscle to which Wilson was referring is instead the so-called “pollical palmar interosseous” (PPI) of Henle (e.g., Susman et al., 1999; Morrison and Hill, 2011), which was designated by Henle (1858) as the “interosseus volaris primus.” Other names that have been used to designate this muscle are, among others, the “interosseus palmaris des Daumens” (Frohse and Frankel, 1908), “first volar interosseous” (Robinson, 1923), “first palmar interosseous” (e.g., Huber, 1930; Abramowitz, 1955), “premier interosseus palmaire” (Kapandji, 1980), “palmar interosseous muscle of the thumb” (Yamamoto et al., 1987), “palmar interosseous of Henle” (Stern, 1988), “ligamentum metacarpale pollicis” (Henkel-Kopleck and Schmidt, 2000), “internal interosseous muscle” (Smith and Lanz, 2004) and “thin

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TABLE 1. Frequency of the “pollical palmar interosseous” in modern humans according to relevant research reports

Author/Authors	Hands studied	Hands with muscle	Percentage
Abramowitz (1955)	58	58	100
Fahrer (1981)	5	4	80
Perkins and Hast (1993)	80	68	85
Susman et al. (1999)	20	17	86
Witthaut and Leclercq (1999)	20	16	80
Henkel-Kopleck and Schmidt (2000)	81	47	58
Morrison and Hill (2011)	45	41	91

dorsal additional slip of the adductor pollicis, or TDAS-AD” (Diogo et al., 2009; Diogo and Abdala, 2010; Diogo and Wood, 2011, 2012).

The most detailed research reports that have focused specifically on the occurrence of the PPI in adult modern humans have shown that the muscle constitutes a persistent part of the normal modern human phenotype (Table 1). In addition, the ontogenetic studies of the human hand by Cihak (1968, 1969, 1972, 1977) suggested that the PPI is usually already developed and differentiated in early developmental stages of modern humans (but see Discussion below). According to these research reports the PPI is often a small, thin muscle that usually runs from the base of metacarpal I to the

base of the proximal phalanx of the thumb, although it may originate and insert also/instead from/onto other structures (Table 2; see also Table 3). Most authors of the research reports listed in Tables 1 and 2 consider that the PPI is either the remnant of an original, plesiomorphic palmar interosseous going to digit 1 (thence the use of the name “PPI” or of similar names), or a de novo structure originated from the adductor pollicis (see, e.g., Diogo and Wood, 2011, 2012; see also Discussion below).

It is therefore remarkable that despite the fact that most research reports clearly indicate that the PPI is usually found in modern humans, most atlases and textbooks dealing with human anatomy have suggested, and continue to suggest, that the PPI is usually, or even always, absent in our species (Table 4; see also Table 1 of Morrison and Hill, 2011). A detailed examination of these textbooks and atlases shows that only a handful of works—including a few recent books—attempt to analyze and organize muscles based on their ontogenetic and phylogenetic relationships (e.g., Schäfer and Thane, 1894; Huber, 1930; Cartmill et al., 1987; Stern, 1988). In fact, many of these atlases and textbooks refer to the muscles on a more teleological and/or functional context. For example, Last (1978, p. 100) stated that “the palmar interossei adduct the fingers; the thumb requires no palmar interosseous, already possessing its own

TABLE 2. The attachment of the “pollical palmar interosseous” in modern humans according to relevant research reports

Author	Origin						Insertion		
	Capitate	Trapezoid	Trapezium	M I	M II	M III	Ulnar sesamoid	BPPP	Extensor expansion
Brooks (1887)				+			+		
McMurrich (1903)				+				+	
Abramowitz (1955)									
Type 1	+			+	+	+	+	+	
Type 2	+	+	?	+			+	+	
Type 3				+			+	+	
Lewis (1965)				+			+		+
Fahrer (1981)				+			+		
Kaplan (1981)				?			+	+	+
Valentin (1981)				+					+
Yamamoto et al. (1987)	+	+	?	+				+	
Yamamoto et al. (1988)		+			+		?	+	
Susman (1994)				+				+	
Van Sint Jan and Rooze (1994)			+	+				+	
Susman et al. (1999)				+				+	+
Witthaut and Leclercq (1999)			+	+				+	+
Henkel-Kopleck and Schmidt (2000)									
Type 1				+			+[1]		
Type 2				+			+[2]		
Type 3				+			+		
Type 4				+				+	
Type 5				+				[3]	
								+[4]	

MI, metacarpal I; MII, metacarpal II; MIII, metacarpal III; BPPP, base of proximal phalanx of pollex; [1], inserts between the radial and the ulnar sesamoids of the thumb; [2], inserts on both sesamoids; [3], sends a tendon to the radial sesamoid; [4], also sends a tendon to the radial sesamoid; + means yes, while ? means the original author/authors was/were not clear about this specific item in their descriptions.

TABLE 3. The attachment of the “ollical palmar interosseous” in modern humans according to some leading anatomy textbooks

Author	Origin			Insertion		
	Trapezium	M I	M II	Ulnar sesamoid of the thumb	BPPP	Extensor expansion
Henle (1858)	±	+	±		+	
Jackson (1921)	+	+			+	+
Robinson (1923)		+			+	
Huber (1930)		+			+	
Schaeffer (1942)	+	+			+	+
Wood Jones (1949)		+		+	+	
Brash (1958)		+			+	
Goss (1959)		+			+	
Lockhart et al. (1959)		+				+
Zuckerman (1963)		+			+	
Gardner et al. (1975)		+				+
Craft (1979)		+			+	
Clemente (1985)		+			+	
Cartmill et al. (1987)		+			+	
Standring (2008)		+		+	+	

MI, metacarpal I; MII, metacarpal II; BPPP, base of proximal phalanx of pollex; + means yes, while ± means sometimes.

powerful adductor pollicis muscle.” Such purely functional and/or clinical considerations of manual myology—pollical myology included—fail to see the human thumb as a rich repository of both plesiomorphic and derived muscular components (Marzke, 1992, 1999).

There are various reasons why it is particularly relevant to undertake a fresh, detailed study of the PPI. One reason is that the study of this muscle has important implications for the understanding of human evolution. For instance, Susman (1994) and Susman et al. (1999) suggested that the PPI is uniquely found in humans, probably due to the significance of tool use in human evolution, and this idea has been followed by most anthropologists and primatologists since then. However, as explained in the recent studies of Diogo and Wood (2011, 2012), their dissections, comparisons and review of the literature clearly indicate that the PPI may be found in at least some nonhuman primates such as gorillas and chimpanzees, although the muscle does seem to be more frequently found

in modern humans than in those primate taxa. Fundamental questions such as “what is the function of the PPI?,” “did this muscle really play an important role in human evolution?,” and “what is the phylogenetic origin of this muscle?,” which are crucial for the study of human evolution, still remain unanswered.

Another reason for such a reexamination is that the vast majority of medical students study human anatomy from atlases and textbooks and not from research reports. Therefore, it is crucial to check if the information provided in these atlases and textbooks does reflect the real frequency of occurrence of the PPI among modern humans. For example, books such as “US Surgeon General” (e.g., 1918, 2004) do not refer to the PPI. So one wonders if the numerous reconstructive surgeries undertaken in the United States are effective in reconstructing the normal hand phenotype of modern humans. Of course, to address these and other medical questions one has to have an informed idea about the frequency of the PPI and of its relationships with

TABLE 4. Presence/absence of the “pollical palmar interosseous” in modern humans according to leading atlases and textbooks

Vesalius (1543): P ; Albinus (1734): A; Gray (1858): A; Henle (1858): P ; Humphry (1872): P ; Thomson et al. (1887): A; Ellis and Ford (1882): A; Testut (1896): A; Cruveilhier (1843): P ; Gerrish (1902): A; Frohse and Frankel (1908): A; Poirier and Charpy (1909): P ; US Surgeon General (1918): A; Jackson (1921): A; Robinson (1923): P ; Spalteholz (1927): A; Huber (1930): P ; Schaeffer (1942): P ; Toldt (1942): A; Grant (1943): P ; Rouvière (1943): P ; Bunnell (1948): A; Wood Jones (1949): A; Brash (1858): P ; Hollinshead (1958): A; Goss (1959): A; Lockhart et al. (1959): P ; Zuckerman (1963): P ; Romanes (1965): P ; Kaplan (1965): A; Anson (1966): P ; Healey (1969): A; Warwick and Williams (1973): P ; Gardner et al. (1975): P ; (Landsmeer) (1976): P ; Langman and Woerdeman (1978): A; Last (1978): A; Craft (1979): P ; Rouvière and Delmas (1984): P ; Clemente (1985): A; Gosling et al. (1985): A; Hall-Craggs (1985): A; Cartmill et al. (1987): P ; Basmajian and Slonecker (1989): A; Rogers (1992): P ; Zancolli (1992): A; Colborn and Skandalakis (1993): A; Lumley et al. (1995): P ; Williams (1995): P ; Snell (1995): P ; Ger et al. (1996): A; Mathers et al. (1996): P ; Putz and Pabst (1997): A; Stern (1997): P ; Netter (2003): A; Morton et al. (2004): A; Smith and Lanz (2004): P ; US Surgeon General (2004): A; Moses et al. (2005): A; Palastanga et al. (2006): P ; Clemente (2007): A; Drake et al. (2008): P ; Nessen et al. (2008): A; Olson and Pawlina (2008): A; Standring (2008): P ; Agur and Dalley (2009): A; Tank (2009): A; Tank and Gest (2009): A; Moore et al. (2010): A; Drake et al. (2010): P ; Rohen et al. (2011): A.
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A, absent; P, present, in bold.

other neighboring structures in modern humans. The main aims of the present paper are therefore: 1) to analyze the frequency of the PPI in a large sample of modern human hands; 2) to describe the attachments, innervation and varieties of this muscle in the dissected hands; 3) to discuss its phylogenetic origin, based on its topographical relationships and nerve supply and on the ontogenetic and comparative data available in the literature; 4) to discuss the implications of our observations, comparisons and review of the literature for the understanding of human evolution. To our knowledge, this is the first study to provide detailed descriptions of not only the attachments, but also the innervation and varieties, of this muscle in such a large sample of human hands (see below).

MATERIALS AND METHODS

We dissected 72 hands of 39 adult modern humans that were being studied by Howard University College of Medicine and Howard University College of Dentistry (HU) students (22 hands) as well as by the University of Maryland (Baltimore) School of Medicine (UMB) students (50 hands) during their gross anatomy courses (Table 5). The hands were dissected by the authors after these courses were finished; the variation found among the hands dissected will be described in the text and Table 5. Each of the muscles associated to the thumbs of most hands, as well as the nerves and arteries associated to these muscles, were photographed using a Nikon-D90 camera. Regarding the soft and hard tissues structures surrounding and/or in contact with the PPI, we use the same taxonomic nomenclature as Diogo and Wood (2011, 2012). Apart from the modern humans dissected for this study, we have dissected, in the past, specimens from all the major groups of nonhuman primate and nonprimate vertebrates. As explained above, to our knowledge this is the first study to provide detailed descriptions of the attachments and importantly also the innervation and varieties of the "PPI muscle" in such a large sample of human hands. A list of the dissected nonprimate vertebrate specimens is given in Diogo and Abdala (2010); a list of the dissected primate specimens is given in Diogo and Wood (2011, 2012). Discussions of the evolutionary changes occurring during primate and human evolution are based on the phylogenetic results of Diogo and Wood (2011).

RESULTS

The results obtained are shown in Table 5 and also in Figures 1–7; therefore in the text below we will only provide a brief summary of our observations. Within the 72 hands dissected by us the PPI is present in 67 hands (e.g., Figs. 1–7), that is, in 93% of the cases. We observed its origin in 66 of the 67 hands with a PPI, and the configurations found, from most common to most rare, are: origin from metacarpal I only (25 hands, i.e., 37.9% of the cases; in almost all of them the origin being from the base of this bone: e.g., Fig. 1); from metacarpal I plus a common origin with the dorsal interosseous 1 (seven hands, i.e., 10.6%; e.g., Fig. 3); from carpal bones/ligaments only (seven hands, i.e., 10.6%; e.g., Fig. 7); from metacarpal I and

carpal bones/ligaments (seven hands, i.e., 10.6%); from a thin membrane associated to the dorsal interosseous, only (four hands, i.e., 6.1%); directly from the dorsal interosseous, only (four hands, i.e., 6.1%); from metacarpal I plus a common origin with the oblique head of the adductor pollicis (four hands, i.e., 6.1%); from metacarpal I and the thin membrane associated to the dorsal interosseous 1 (three hands, i.e., 4.5%); from metacarpals I and II (two hands, i.e., 3.0%); from metacarpal I, carpal bones/ligaments and the thin membrane associated to the dorsal interosseous (one hand, i.e., 1.5%; e.g., Fig. 2); from carpal bones/ligaments and the thin membrane associated to the dorsal interosseous (one hand, i.e., 1.5%; e.g., Figs. 5 and 6); and from this membrane and both metacarpals I and II (one hand, i.e., 1.5%). In total, the origin of the PPI is associated to the dorsal interosseous, either directly (in 11 hands) or indirectly (through the thin membrane associated to this latter muscle, in 10 hands) in 21 (31.8%) of these 66 hands, while it is associated to the adductor pollicis in four (6.1%) of these 66 hands.

We observed the insertion of the PPI in 66 of the 67 hands that exhibit this muscle, and the configurations found are: insertion onto the pollical proximal phalanx only (34 hands, i.e., 51.5% of the cases, which include attachments onto the wing tendon of the extensor apparatus of the thumb and/or onto the radial/ulnar sesamoids of this digit: e.g., Figs. 1, 2, 5, and 6); onto the proximal phalanx of thumb plus a common insertion with the oblique head of the adductor pollicis (18 hands, i.e., 27.3%; e.g., Fig. 3); onto the metacarpal I and the proximal phalanx of the thumb (five hands, i.e., 7.6%; e.g., Fig. 7); onto the distal portion of metacarpal I only (three hands, i.e., 4.5%); onto the distal portion of metacarpal I plus common insertion with the oblique head of the adductor pollicis (three hands, i.e., 4.5%); distal fusion and thus common insertion with the oblique head of adductor pollicis (two hands, i.e., 3.0%); and onto the distal portion of metacarpal I, proximal phalanx of the thumb, and a common insertion with the oblique head of the adductor pollicis (one hand, i.e., 1.5%). In total, the insertion of the PPI is associated to the dorsal interosseous 1 in 0 (0.0%) of these 66 hands, while it is associated to the adductor pollicis in 24 (36.4%) of these 66 hands.

We observed the PPI's innervation in 51 hands, and in all of them the muscle is innervated by a lateral (radial) prolongation of those branches of the deep branch of the ulnar nerve that run mainly laterally to innervate the adductor pollicis, and namely its oblique head (and not of the branches of the deep branch of the ulnar nerve that run instead mainly distally to innervate the dorsal and palmar interossei: e.g., Figs. 4 and 5).

In all the 66 hands in which we could observe the relation between the PPI and the princeps

TABLE 5. Presence / absence of the "pollical palmar interosseous" and its attachments, innervation and relation to the princeps pollicis artery in the modern humans hands dissected by us

Hand #	Origin	Insertion	Relation to PP artery	Innervation	Notes
HU D43, RH, FE	MEMB	Medial side of BPPP	Dorsal and medial to PP	Branches of DBUN that innervate OHAP	
HU D43, LH, FE	Medial side of base of MI and fascia of ID1	Medial side of BPPP and fascia of OHAP inserting at medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	PPI has two muscular bundles
HU D41, RH, MA	Medial side of MI and origin of ID1	Medial side of BPPP and insertion of OHAP at medial side of BPPP	Dorsal and medial to PP	Branches of DBUN that innervate OHAP	
HU D6A, LH, S?	MEMB	Medial side of diaphysis of MI and medial side of BPPP	Medial and dorsal to PP	?	PPI is mainly tendinous but has a few muscular fibers
HU D6A RH, S?	Medial side of base of MI and MEMB	Medial side of diaphysis of MI and medial side of BPPP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP	
UMB 11, LH, FE	Lateral bundle from medial side of base of MI; medial bundle from lateral side of base of MII	Medial side of BPPP	PP passes between the two bundles of PPI and then distally passes laterally to them	Branches of DBUN that innervate OHAP	
UMB 11, RH, FE	-	-	-	-	PPI absent
UMB 10, LH, MA	Between palmar and medial sides of base of MI	Insertion of OHAP at medial side of BPPP	PP passes between PPI and OHAP and then distally passes laterally to PPI	Branches of DBUN that innervate OHAP	PPI is thin with just a few muscular fibers
UMB 10, RH, MA	Between palmar and medial sides of base of MI	Palmar side of MI and then medial side of BPPP together with insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	PPI is thin at origin and fan-like at insertion
UMB 0A, LH, MA	-	-	-	-	PPI is absent
UMB 0A, RH, MA	-	-	-	-	PPI is absent
UMB 24, LH, FE	Medial side of base of M1 and fascia of ID1	Medial side of BPPP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP	
UMB 24, RH, FE	Medial side (almost palmar) of base of M1	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 21, LH, FE	One bundle from medial side of base of MI and origin of OHAP; other bundle from medial side of MI only	Medial side (almost palmar) of BPPP	Proximally the two bundles are separated by the PP, but then join and pass medially to PP	Branches of DBUN that innervate OHAP	
UMB 21, RH, FE	Medial side of base of MI	Medial side (almost palmar) of BPPP	Dorsal and medial to PP	Branches of DBUN that innervate OHAP	PPI is remarkably broad
UMB 22, LH, MA	Medial and palmar side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 33, LH, FE	Medial side of ligaments between trapezium and MI	Medial side of BPPP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP	
UMB 33, RH, FE	MEMB	Medial side of BPPP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP	
UMB 31, LH, MA	Medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 31, RH, MA	Medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 30, LH, MA	Medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 30, RH, MA	Medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	

TABLE 5. (Continued.)

Hand #	Origin	Insertion	Relation to PP artery	Innervation	Notes
UMB 28, RH, S?	MEMB and medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 5A, RH, FE	One bundle from MEMB; other bundle from bases of MI and MII	Medial side of distal portion of MI and medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 5A, LH, FE	One bundle from base of MII; other bundle from base of MI	Medial side of BPPP	Lateral bundle is lateral to PP; medial bundle passes between two branches of PP	Branches of DBUN that innervate OHAP	PP divides into two branches at the origin of PPI
UMB 4, LH, FE	PPI has one belly with three origin sites, the major one from medial side of MI, other site from fascia of OHAP, and the other from base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 4, RH, FE	PPI has one belly with two origin sites, both from medial side of base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 8, LH, MA	PPI has one belly with two origin sites, one from medial side of MI, other from fascia of OHAP	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	PPI is deeply blended with bundles of OHAP
UMB 8, RH, MA	Medial side of MI	One belly to medial side of BPPP; the other to insertion of OHAP at medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	PPI has two bellies
UMB 13, RH, FE	Base of MI	Ulnar sesamoid with insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 13, LH, FE	Base of MI	Head of MI and ulnar sesamoid with insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 15, RH, MA	Tendinous bundle from MI; muscular bundle from OHAP	?	PP passes between two bundles of PPI	?	
UMB 15 LH, MA	?	Ulnar sesamoid and head of MI	PP runs between medial bundle and two lateral bundles of PPI	Branches of DBUN that innervate OHAP	PPI has a medial muscular bundle and two lateral tendinous bundles
UMB 16 RH, MA	Base of MI	Ulnar sesamoid	Medial to PP	?	PPI has a very narrow fibrous band and a thin muscular belly
UMB 16, LH, MA	Base of MI	Ulnar sesamoid	Medial to PP	?	PPI has a very narrow fibrous band and a thin muscular belly
UMB 2, RH, MA	Base of MI and seemingly trapezium	Head of MI	Medial to PP	?	
UMB 2, LH, MA	Base of MI and seemingly trapezium	Head of MI	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 12 RH, FE	Base of MI	Ulnar sesamoid	Medial to PP	Branches of DBUN that innervate OHAP	PPI has muscular fibers
UMB 12 LH, FE	Base of MI	Head of MI	?	?	PPI has muscular fibers
UMB 1, RH, FE	Trapezium and carpal ligaments	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	

TABLE 5. (Continued.)

Hand #	Origin	Insertion	Relation to PP artery	Innervation	Notes
UMB 1, LH, FE	Trapezium and carpal ligaments	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 3A, RH, MA	Base of MI	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 3A, LH, MA	Trapezium and base of MI	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 6, RH, FE	Base of MI	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP ?	
UMB 6, LH, FE	Trapezium and carpal ligaments	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 7, RH, MA	Trapezium and base of MI	Ulnar sesamoid	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 7, LH, MA	Trapezium and carpal ligaments	Ulnar sesamoid and insertion of OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 9, RH, MA	Base of MI	Ulnar sesamoid with OHAP	Medial to PP	Branches of DBUN that innervate OHAP	PPI is slender fleshy slip
UMB 9, LH, MA	Trapezium and MI	Ulnar sesamoid with OHAP	Medial to PP	Branches of DBUN that innervate OHAP	PPI is slender fleshy slip
UMB 20, RH, FE	ID1	BPPP with OHAP	Medial to PP	Branches of DBUN that innervate OHAP	
UMB 20, LH, FE	ID1	Distal MI and BPPP	Mainly dorsal to PP	Branches of DBUN that innervate OHAP	
UMB 3B, RH, FE	Whole medial side of MI	OHAP	Mainly dorsal to PP	Branches of DBUN that innervate OHAP ?	
UMB 3B, LH, FE	Base of MI	Medial side of BPPP and insertion of OHAP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP ?	
UMB 5B RH, S?	ID1 and MI	Distal MI and OHAP	Mainly dorsal to PP	Branches of DBUN that innervate OHAP ?	
UMB 5B, LH, S?	ID1 and base of MI	Distal MI, medial side of BPPP and insertion of OHAP	Mainly dorsal to PP	Branches of DBUN that innervate OHAP ?	PPI has two slips
HU D6B, RH, FE	Medial side of base of MI and MEMB	Medial side of BPPP	Medial and dorsal to PP	Branches of DBUN that innervate OHAP	
HU D6B, LH, FE	The more dorsal belly from medial side of base of MI; the other two bellies from lateral side of trapezium	Two bellies to medial side of BPPP; the other belly to medial collateral ligament of metacarpo-phalangeal joint	Mainly medial to PP	Branches of DBUN that innervate OHAP	
HU D2, LH, MA	Fascia of ID1	Medial side of BPPP	Mainly medial to PP	Branches of DBUN that innervate OHAP	
HU D45, RH, S?	Base of MI	Medial side of BPPP	Medial to PP	Branches of DBUN that innervate OHAP	
HU D30, LH, S?	MEMB	Medial side of BPPP with insertion of OHAP	Mainly medial to PP	Branches of DBUN that innervate OHAP ?	
HU D30, RH, S?	ID1 and distal MI	Medial side of BPPP with insertion of OHAP	Mainly medial to PP	Branches of DBUN that innervate OHAP	Additional fibers of PPI running from deep palmar fascia (with OHAP) to palmar side of BPPP (with FPB)
HU D20, LH, S?	-	-	-	-	PPI is absent

TABLE 5. (Continued.)

Hand #	Origin	Insertion	Relation to PP artery	Innervation	Notes
HU D20, RH, S? HU D27, LH, Sex?	- ID1	Medial side of BPPPP with insertion of OHAP	Mainly dorsal to PP	Branches of DBUN that innervate OHAP, but possible also from branches of DBUN innervating ID1	PPI is absent The PPI has several thin muscular bundles
HU D27, LH, S? HU D33, RH, FE	Carpal bones Medial side of base of MI, medial and distal sides of trapezium, and MEMB	Medial side of BPP Medial side of BPPPP	Mainly medial to PP Medial and dorsal to PP	Branches of DBUN that innervate OHAP	PPI has several muscular bundles
HU D33, LH, FE	Medial and distal sides of trapezium and MEMB	Medial side of BPPPP	Medial and palmar to PP	Branches of DBUN that innervate OHAP	PPI has several muscular bundles
HU D2, RH, MA	Tendinous head from base of MI; thin muscular head from ID1	Ulnar sesamoid and BPPPP	Tendinous head is mainly palmar to PP; muscular is dorsal and medial to PP	?	PPI has a thin tendon and a thin muscular bundle
HU M18, LH, FE	Mainly from carpal bones/ ligaments	BPPPP	Mainly palmar to PP	?	PPI is just a thin tendon
HU M18, RH, FE	Mainly from carpal bones/ ligaments	BPPPP	Palmar and medial to PP	?	PPI has a thin tendon and a thin muscular bundle
HU M14, RH, MA	Base of MI	Distal MI and medial side of BPPPP and associated wing tendon	Medial to PP	Branches of DBUN that innervate OHAP	PPI has a well-developed muscular bundle, which is in contact with an additional bundle of the OAAP
HU M14, LH, MA	Base of MI	Medial side of BPPPP	Medial to PP	Branches of DBUN that innervate OHAP	PPI has three well-developed muscular bundles

BPPPP, base of proximal phalanx of pollex; DBUN, deep branch of ulnar nerve; FPB, flexor pollicis brevis; FE, female; ID1, interosseous dorsalis 1; LH, lateral hand; MI, metacarpal I; MA, male; MEMB, thin membrane associated to interosseous dorsalis 1; OHAP, oblique head of adductor pollicis; PP, princeps pollicis artery; RH, right hand; UMB, University of Maryland, School of Medicine at Baltimore; HU D, Howard University College of Dentistry; HU M, Howard University College of Medicine; S?, sex is undetermined because hands were cut.

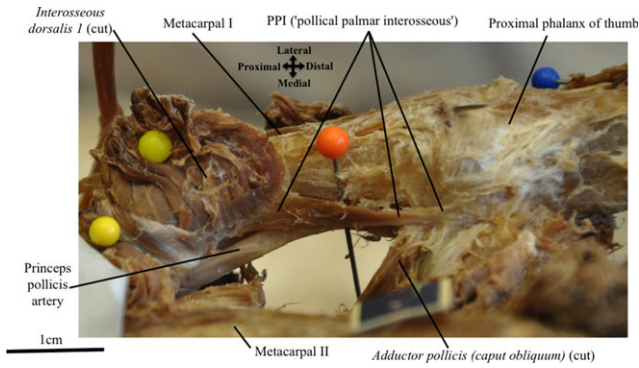


Fig. 1. *Homo sapiens* (HU D41, adult male): dorsal view of the right hand showing a PPI that exhibits the most common attachments (origin from the medial side of the base of metacarpal I near the origin of the dorsal interosseous 1; insertion mainly onto the medial side of the base of the proximal phalanx of the thumb and surrounding structures, e.g. the wing tendon of the extensor apparatus, near the insertion of the oblique head of the adductor pollicis), relationship with the princeps pollicis artery (distally the muscle passes mainly medial to the artery), and overall configuration (PPI formed by a single, muscular belly), found in the hands dissected by us (N.B., this hand also has the most common innervation of the PPI, i.e. by a lateral prolongation of the deep branches of the deep branch of the ulnar nerve that innervate the adductor pollicis, and namely its oblique head: not shown). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

pollicis artery, the muscle is always at least partially, and usually mainly, ulnar (medial) to the artery (e.g., Figs. 5 and 7). Out of the 66 hands in which we could analyze the number of bundles of the PPI, the muscle usually has a single, muscular bundle in 38 (57.6%; e.g., Fig. 1); in 10 (15.2%) it has two muscular bundles (e.g., Fig. 3), in 10 (15.2%) it has more than two muscular bundles

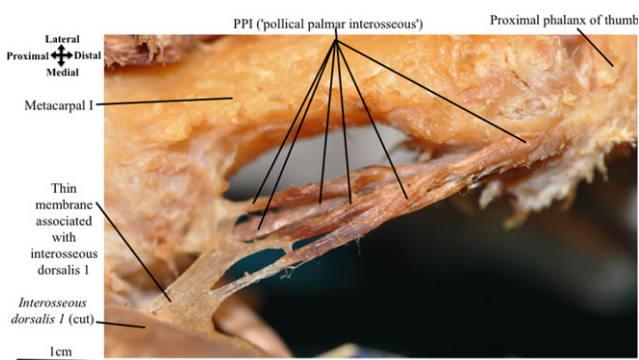


Fig. 2. *Homo sapiens* (HU D33, adult female): dorsal view of the right hand showing a case in which the PPI has several bundles and in which it originates from a thin membrane that is associated to the interosseous dorsalis 1 (as well as from the trapezium and the medial surface of the base of metacarpal I); such a connection between the PPI and this membrane can be used as an argument to support the idea, defended by many authors, that the PPI forms part of the interossei muscles (but see Discussion). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

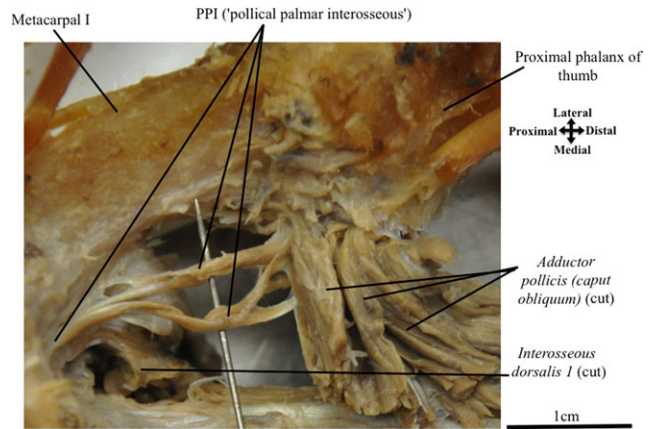


Fig. 3. *Homo sapiens* (HU D43, adult female): ventral view of the left hand, showing a case in which the insertion of the PPI is closely associated to that of the oblique head of the adductor pollicis and in which this latter head is divided into various bundles; such a configuration can be used as an argument to support the idea, defended by some authors and by us, that the PPI actually corresponds to an additional bundle of the oblique head of the adductor pollicis that became further differentiated from the adductor pollicis, forming a distinct structure (see Fig. 8 and Discussion). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

(e.g., Figs. 2, 5, and 6), in five (7.6%) it is a single, very thin tendon with no apparent muscular fibers, and in three (4.5%) it has a muscular bundle and a tendinous bundle.

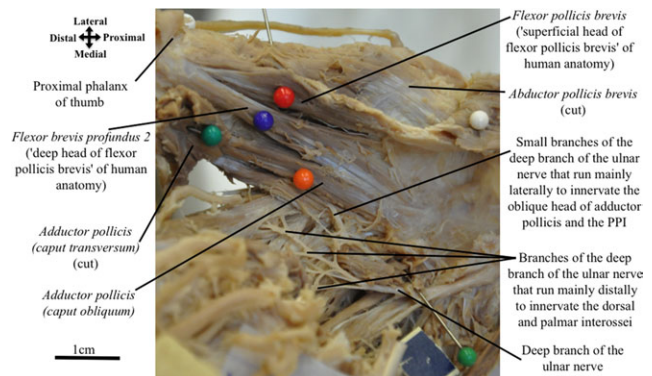


Fig. 4. *Homo sapiens* HU (D43, adult female): ventral view of the right hand, showing that some branches of the deep branch of the ulnar nerve run mainly distally to innervate the dorsal and palmar interossei (N.B., other branches run mainly laterally to innervate the oblique head of the adductor pollicis and then the PPI: not shown, but see Fig. 5 and text). Note that in this hand, as well as in all the other hands dissected exhibiting a PPI, the oblique head of the adductor pollicis, the so-called ‘deep head of the flexor pollicis brevis’ (flexor brevis profundus 2 sensu the present work) and the PPI are all present, so the PPI should clearly not be confused with the so-called ‘deep head of the flexor pollicis brevis’, as it is sometimes done in the literature (see also Discussion). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

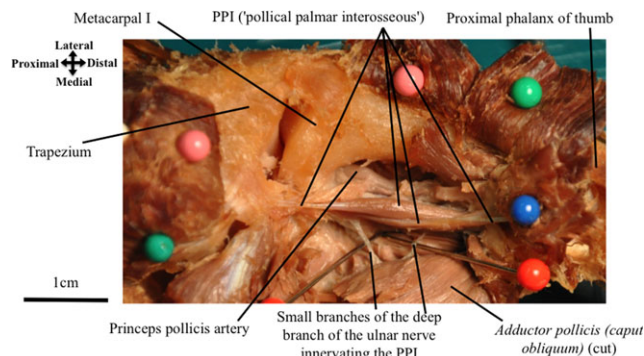


Fig. 5. *Homo sapiens* (HU D33, adult female): ventral view of the left hand, showing that the branches of the deep branch of the ulnar nerve that run mainly laterally to innervate the adductor pollicis, and namely its oblique head (Fig. 4), then continue to run laterally to innervate the PPI (two bellies of the PPI are visible in this ventral view; the other bellies can only be seen in a dorsal view: see Fig. 6). This pattern of innervation can be used as an argument to support the idea, defended by some authors and by us, that the PPI actually corresponds to one or more additional bundles of the oblique head of the adductor pollicis that became further differentiated from the adductor pollicis, forming a distinct structure (see Fig. 8 and Discussion). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

DISCUSSION

As a summary of the results above, within the 72 hands dissected the PPI is present in 93% of the cases, its most common origin being the base of metacarpal I only (37.9%), its most common insertion being the base of the proximal phalanx of the thumb and surrounding structures (e.g., sesa-

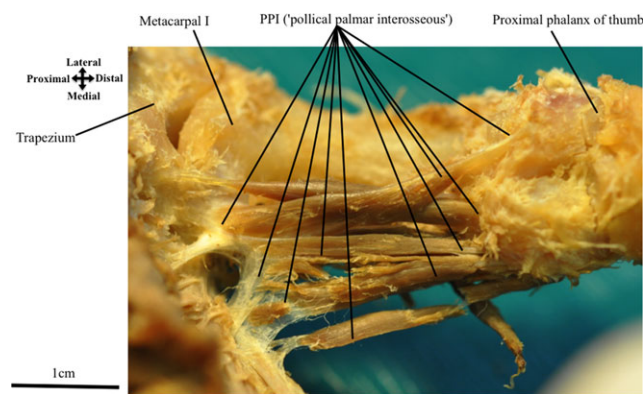


Fig. 6. *Homo sapiens* (HU D33, adult female): ventral view of the left hand, showing a PPI with several muscular bundles running from the trapezium and the thin membrane associated to the dorsal interosseous 1 to the medial side of the base of the pollical proximal phalanx. The remarkable variation of the PPI, from cases where the muscle is completely absent to cases where it is a robust muscle with several muscular bundles, as seen in this picture, can be used as an argument to support the idea, defended by some authors and by us, that the PPI has probably not been the subject of strong selective process (see Discussion). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

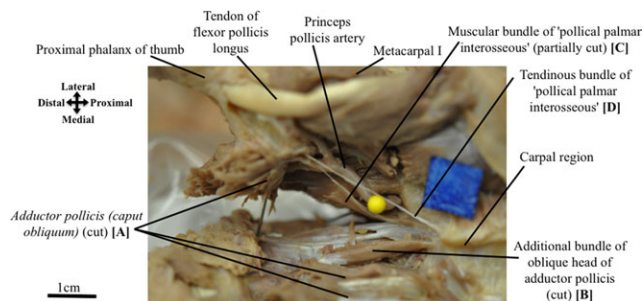


Fig. 7. *Homo sapiens* (HU M18, adult male): ventral view of the right hand, showing a configuration that might provide clues about the evolution of the PPI, according to our hypothesis: [A] mainly undivided oblique head of the adductor pollicis; [B] additional bundle of the oblique head of the adductor pollicis that has an origin separated from the main body of this head but still a common insertion together with that main body; [C] muscle bundle of the PPI; [D] more lateral and tendinous bundle of the PPI (see evolutionary scheme of Fig. 8). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

moid bones and wing tendon: 51.5%); commonly the muscle has a single muscular bundle (57.5%). As these numbers show, there is substantial variation regarding the attachments and overall configuration of the PPI (e.g., Table 5; Figs. 1–7). However, there is less variation regarding its innervation and relation to the princeps pollicis artery, because in 100% of the hands in which we could analyze these features in detail the muscle receives innervation by those branches of the deep branch of the ulnar nerve that innervate the oblique head of the adductor pollicis, and runs at least partially medial to the princeps pollicis (Table 5; Figs. 4, 5, and 7). Based on our observations and comparisons as well as on an extensive review of the literature, in the sections below we will provide an updated overview of the historical discussions about the PPI, of its function and of its evolution.

History: The PPI in Research Reports

The first comprehensive description of the PPI was done by Henle (1858), who designated this muscle as “interosseous primus volaris,” thus suggesting that the muscle is a fourth palmar interosseus. In the subsequent years there was a dispute regarding the existence of this muscle. For instance, Cunningham (e.g., 1878, 1882, 1906), a pioneer investigator of the comparative morphology of the mammalian hand, initially doubted its existence, but later conceded that the muscle is “invariably” present in modern humans although its presence is often “observed” by its close relations with the oblique head of the oblique head of the adductor pollicis. It should be noted that Cunningham (1878) originally derived all palmar interossei from the contrahentes; however, he later

decided that the flexores breves profundi layer (i.e., his intermediate muscle plate) of the hand (including the PPI's according to him) was the true source of the palmar interossei. Although Windle (1883) initially considered the PPI as being the so-called “deep head of the flexor pollicis brevis” (see below), his pioneering study of the ontogeny of the mammalian hand musculature convinced him that the PPI had its own unique identity; authors such as Le Double (1897: p. 195) also suggested that the PPI has a “distinct nerve supply.” In order to locate this muscle, Windle (1883: p. 237) recommended “that the proper way to arrive at it in a dissection is to work from the dorsal surface towards the palm, when on removing the superficial tissue and first dorsal interosseous, it is brought into view.” Observations by Macalister and Wood, renowned British anatomists, also led to a reaffirmation of Henle's claims that the PPI is a separate muscle (see, e.g., Macalister, 1867, 1875; Le Double, 1897; Forster, 1917). Forster (1917) reviewed the late 19th century works on the interossei and concluded that the palmar interossei (also including the PPI according to him) were derived from the flexores breves profundi.

However, various anatomists did not agree with the idea that the PPI constitutes a separate muscle. To be sure, most of those anatomists who explored the lower depths of the first metacarpal space encountered a perplexing array of muscle slips, which were not always easy to classify into named intrinsic thumb muscles. But they often considered the PPI as a part of other muscles. Brooks (1887) was amongst the first to attempt to bring order to the so-called “flexor pollicis” complex (which most probably included the PPI). His description and analysis were one of the first efforts to sort through the “quagmire of obstructive terms” which challenged comprehension; however, Brooks chose to accept von Bischoff's (1870a,b, 1894) assertion that the PPI was “the true, or inner head of the flexor pollicis brevis,” creating still more confusion.

The next comprehensive attempt to bring order to the system of short muscles of the thumb was done by Wood Jones (1949). He argued in favor of classifying the “deep head of the flexor pollicis brevis” as the “first palmar interosseus” (i.e., the PPI). Abramowitz (1955) wrote that the PPI is nearly universally present in modern humans. Day and Napier (1961, 1963) revisited the topic, with additional dissections of the deeper thenar musculature, and supported the idea that the so-called “superficial and deep heads of the flexor pollicis brevis” (see below), the oblique and transverse heads of the adductor pollicis, and the PPI are distinct, separate muscles.

An important contribution for the understanding of the human hand and the homology of its muscles was made by Lewis (1965), and particu-

larly by Lewis (1989). Based on fresh comparative myological studies of not only modern humans and numerous other primates but also of other mammalian and nonmammalian tetrapods, Lewis stated that a first palmar interosseous is usually separately identifiable in the modern human hand, corresponding to the flexor brevis profundus 2 of other mammals. However, there is some ambiguity in Lewis' works about the homology of the PPI, that is, in some cases he seems to suggest that the PPI corresponds to the flexor brevis 2 of other mammals, while in other cases he seems to point out that this is not the case (Diogo and Wood, 2012). The studies of Lewis have been meticulously analyzed by the most recent attempts to provide a comprehensive review about the identity and evolution of the hand and other upper limb muscles of modern humans, which were published by Diogo and colleagues in a series of papers and monographs where they compared modern humans with all other major groups of vertebrates (e.g., Diogo et al., 2009; Diogo and Abdala, 2010; Diogo and Wood, 2011, 2012). We will discuss the works of Lewis and of Diogo and colleagues in more detail below, in the section that will focus on the phylogeny and evolution of the PPI.

Since the publication of Lewis' (1965) paper, authors such as Mannerfelt (1966), Kuhlmann and Guerinsurville (1985), Simard and Roberge (1988), and Perkins and Hast (1993) have found additional variations in the muscles associated to the thumb movements; these observations have contributed to a fresher appreciation of the variability and complexity of the muscle slips in the deep thenar region. The latter investigators have also discovered additional subdivisions of each distinct pollical muscle based on fibromuscular partitions and distinct parts receiving distinct branches of the median and the ulnar nerves (e.g., Simard and Roberge 1988). Perkins and Hast (1993: p. 230) stated that “the thumb has a palmar interosseous muscle distinct and separate from surrounding muscles.” Van Sint Jan and Rooze (1994) discovered a very significant factor, which has a direct bearing on the reliable identification of the slips of the deep pollical musculature. Their work found that the embalming process itself allows an easier separation of the muscular fascicles from each other; thus, the degree of freshness of the specimens, and the duration of the embalming process lead to the appearance of additional muscle slips in the area. Therefore, the degree of preservation of muscles affects the separation of muscle slips. Although Van Sint Jan and Rooze (1994) nowhere in their work refer to the PPI as a named entity, it is very much present as a described fascicle of their “adductor pollicis complex.”

Susman et al. (1999) wrote that the PPI is present in the majority (>85%) of human thumbs, and proposed a very strict definition of this muscle,

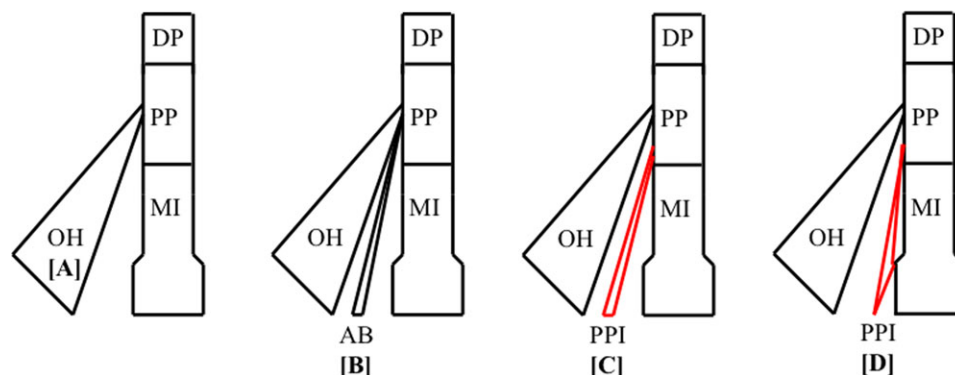


Fig. 8. Simplified scheme showing how the configuration seen in Fig. 7 might provide clues about the evolution of the PPI, according to our hypothesis: [A] First stage of evolution, with a mainly undivided oblique head of the adductor pollicis (OH); [B] Second, hypothetical stage of evolution, with the oblique head plus an additional bundle (AB) that has an origin separated from the main body of this head but still a common insertion together with that main body; [C] Third, hypothetical stage of evolution, in which the insertion of the additional bundle is also somewhat separated from the main body of the adductor pollicis, forming an almost completely differentiated PPI; [D] Fourth, hypothetical stage of evolution, showing a PPI that is even more lateral (radial) and thus even more separated from the main body of the oblique head of the adductor pollicis, resembling a PPI configuration that is commonly found in modern humans (DP, distal phalanx of digit 1; MI, metacarpal I; PP, proximal phalanx of digit 1). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

based on the characteristic features of a “typical palmar interosseous”: 1) the PPI is constituted by a single belly that originates on metacarpal I and inserts onto the same digit; 2) its insertion is essentially onto the wing tendon of the extensor expansion of that digit; 3) it should be found in the layer “anterior” (palmar sensu the present work) to the dorsal interossei. A clear definition of each named muscle, or any other trait, is obviously very important in the description of the modern human phenotype. However, the entire human phenotype is precisely constituted of variable traits, so a correct definition must also include its variations in nature, which are the raw material of organic evolution by natural selection (e.g., Bergman et al., 1988). Therefore, Susman et al.’s (1999) very narrow definition of the PPI cannot be sustained, as most investigators who have conducted dissections of numerous hand specimens (e.g., Abramowitz, 1955; Perkins and Hast, 1993; Witthaut and Leclercq, 1999; Henkel-Kopleck and Schmidt, 2000), as well as ourselves, have found the PPI to be a remarkably variable entity. This is clearly illustrated in the textual description of our Results, as well as in the complementary Figs. 1–7 and Table 5, and also in Tables 2 and 3, which summarize some of the variations found by other authors. Therefore, any definition of the PPI should acknowledge that the muscle often runs from the medial side of the base of metacarpal I to the medial side of the base of the proximal pollical phalanx and associated structures (e.g., sesamoids, wing tendon) and receives its innervation by those branches of the deep branch of the ulnar nerve that innervate the oblique head of the adductor pollicis. But it should also acknowledge that the PPI displays a wide range of variations, as shown

in Tables 2, 3, and 5. Some authors have reported additional landmarks to define the PPI; for instance Murakami (1969) and Murakami et al. (1987), Yamamoto et al. (1987, 1988), and Henkel-Kopleck and Schmidt (2000) pointed out that the palmar articular nerve (branch of the deep ulnar nerve) and the princeps pollicis artery may provide significant landmarks to distinguish the PPI from the oblique head of the adductor pollicis. However, as shown in the description of our Results and in Table 5 and, e.g., Figure 7, and as will also be stressed in the Discussion below, there are cases where it is not so easy to distinguish between the oblique head of the adductor pollicis and the PPI because of the remarkable variation of the PPI and particularly the fact that the PPI is very likely a derivative of the adductor pollicis, to which it often remains connected (see, Figs. 7 and 8, and below). For a thorough and thoughtful work on muscles that discusses similar subjects from a different perspective (namely, by studying turtle anatomy) and that introduces some suggestions for a protocol that may be helpful to appropriately address these subjects, please see Werneburg (2011).

The PPI in Anatomical Atlases and Textbooks

After reviewing some of the most relevant research reports focused on the PPI, and showing that these reports consistently provide convincing evidence that the PPI is usually present in modern humans (Table 1), as corroborated in the present study (Table 5), one has to address the question: why is it that most atlases and textbooks about human anatomy thus fail to report/identify

the PPI or have chosen to reduce it to a nameless variation?

Atlases and textbooks (Table 4) and current medical education have tended to highlight only the principal thenar muscles (abductor pollicis brevis; flexor pollicis brevis and the opponens pollicis) and the adductor pollicis. Attenuation of the anatomy sector of contemporary medical education only permits emphasis on the boldest, “clinically relevant” material (e.g., Collins et al., 1994; Drake, 1998). Recently, a user friendly, easily digestible, hyper-graphic, and “clinically relevant” version of Grey’s Anatomy for medical students has been published (Drake et al., 2010). We do not wish to berate this excellent textbook; however, the book is a logical response to a highly abbreviated anatomy curriculum. Even a cursory examination of any present-day human anatomy dissection guide reveals a bare-bones program (e.g., Morton et al., 2004; Tank, 2009). Faculty are actively encouraged by their supervisors to delete “irrelevant” or “medically inconsequential details”; a discussion of the distinct, and clearly separate “heads of the flexor pollicis brevis” (which actually seem to represent two distinct and evolutionarily different muscles: e.g., Diogo and Wood 2011, 2012: see below) and of the two heads of the adductor pollicis is regarded as being not “test worthy” even though the actions of these structures lead to the production of different thumb movements. Moreover, oddly, contemporary medical textbooks are no longer rooted in the Darwinian paradigm; there is a tendency to classify muscles in a “clinically oriented,” pragmatic scheme. For instance, the deletion of the PPI has been justified on the grounds that it is a “nearly obsolete adductor” (e.g., Lockhart et al., 1959). Mardel and Underwood (1991) also exemplify this expedient approach to the status of the PPI. Side-stepping substantial ontogenetic and phylogenetic (i.e., Darwinian) data altogether, they propose that the adductor pollicis “should be considered” as the first palmar interosseus and that this view “simplifies” the teaching of hand anatomy. They did identify the PPI, however they saw a need to avoid the “paradox” of the thumb having a palmar interosseus far smaller than the remaining digits. Since they saw the thumb as a magnified digit, only the large muscle mass constituted of the adductor pollicis heads plus the PPI could rightly be considered consonant with its stature.

Furthermore, contemporary medical school authorities have started to question the value of actual cadaver dissection itself, seeing it to be an excessively time—and labor-consuming activity (for a review, and criticism of this idea, see, e.g., Aziz and McKenzie, 1999; Aziz et al., 2002). Anatomy departments are asked to consider the digital media and prosected material as shortcuts to the Part I of the United States Medical Licensing Examination. These trends are not conducive to a

search for or analyses of a muscle such as the PPI, let alone the undeniable complexities of the human form. However, these complexities are of enormous significance to understand human anatomy, human evolution, and human medicine, and are also crucial in clinical practice (e.g., Bergman et al., 1988; Diogo and Wood, 2012).

Function of the PPI

Several—many as yet untested—hypotheses have been proposed regarding the functions/actions of, and/or medical/evolutionary implications of having, the PPI. One hypothesis is that the hypertrophy and cleavage of the adductor pollicis has usurped PPI’s supposed main function (i.e., adduction), thus contributing to its near extinction. This view is, for instance, expressed by Standring (2008: p. 885), who wrote that the PPI “is often very rudimentary because the thumb has its own powerful adductor (the adductor pollicis).”

Another view is that the presence of two sets of adductor muscles of the manual digits (including the thumb) facilitated “powerful syndactylous adduction” of the digits of the arboreal and brachiating ancestors of the hominoids (Abramowitz, 1955). According to this view incremental bipedalism in hominoids such as gorillas and humans led to the loss of all contrahentes except the first (i.e., adductor pollicis; N.B., other contrahentes are usually present in chimpanzees); evolution of the precision grip (and its distinct refinements; see, e.g., Marzke 1992) fostered the retention of two distinct adductors of the thumb. According to Abramowitz (1955) the adductor pollicis and the PPI mainly facilitate ulnar and palmar adduction, respectively.

Warwick and Williams (1973: p. 558) have proposed another hypothesis, that is, that the PPI flexes and adducts the pollical proximal phalanx during precision grip, being a synergist of the adductor pollicis and the so-called two heads of the “flexor pollicis brevis” (see below); all these structures facilitate the “endlessly variable application of manipulatory skills” which are promoted by “any of the possible permutations” of the actions of the muscles involved in opposition. According to this hypothesis the PPI has been selected to facilitate the evolving complexity of the variegated precision grips as a synergist of two key muscles of opposition.

Susman et al. (1999) proposed that the PPI is a human myological novelty (in addition to the individualized flexor pollicis longus and extensor pollicis brevis), which was selected in association with evolving tool behavior of the early hominids. They suggest that it was derived either from the oblique head of the adductor pollicis or from the “flexor pollicis brevis.” Another alternative hypothesis proposed by Susman et al. (1999) is that the diminutive PPI is a synergist of other prominent

thumb muscles forming a “parallel muscle combination.” In such a myological association the smaller, yet spindle-rich muscle, helps to “serve an important sensory feedback role” (e.g., Peck et al., 1984). According to Peck et al. (1984) a muscle—such as the PPI—may serve as a part of a set of “kinesiographical monitors” which play a critical role during the control of the precision grip; however, their investigation also showed that whereas the intrinsic thumb muscles had high mean density of spindles (11–29), the “interossei” had a mean density of only 4 (it is not clear whether this measurement included the PPI or not).

Another hypothesis is related to the fact that the saddle-shaped trapezo-metacarpal (first carpo-metacarpal) joint is amongst the most mobile joints of the entire upper limb. According to Standring (2008: p. 875) “significant forces pass across and compress this joint compared to the remaining CMCJs (carpo-metacarpal joints).” Witthaut and Leclercq (1999) thus proposed that the PPI provides added stability to the pliant trapezo-metacarpal joint during its complex actions.

Weathersby et al.’s (1963) and Forrest and Basmajian’s (1965) electromyographic studies of the muscles of the thumb provide physiological support for the idea that the diversity of the precision grip was facilitated by the intricate choreography of the thenar muscles as well as of the other muscles attaching onto the thumb. According to authors such as Marzke (1992, 1999) and Wilson (1998), without the three principal classes of the precision grip and their endless combinations, it is difficult to imagine the rise of exponentially complex tool manufacture and use; complex movements of the hands may also have played a role in the incrementally complex body language that probably preceded/complemented symbolic language.

However, Diogo and colleagues have recently criticized the often “exaggerated” adaptationist and even somewhat teleologist views of evolution that lead to some of these functional and evolutionary hypotheses. Following the view that constraints probably also play a substantial role (both positive and negative) in evolution (e.g., Gould, 2002), these authors argue that not all the structures that are found in modern humans were necessarily adaptations (e.g., Diogo and Wood, 2011, 2012). That is, some structures may be present due to ontogenetic constraints (e.g., the facial muscle *platysma cervicale* is formed in most human embryos to disappear just some weeks after) while others may be present because they are mainly neutral or at least not highly detrimental (e.g., polymorphisms) (Diogo and Wood, 2012). In this regard, the remarkable variation concerning the origin, insertions, and particularly the number of bundles of the PPI found in the modern human hands dissected by us (see above, and also Table 5

and Figs. 1–7) seem to indicate that this muscle has not been the subject of a strong selective process. This view is in line with the recent work of Morrison and Hill (2011), who stated that it is unlikely that even markedly large PPIs confer significant biomechanical advantage across the joints of the thumb. That is, the muscle may be functionally insignificant as noted by Stern (1997), or even potentially prejudicial if it gets so broad that it might obstruct the *princeps pollicis* artery that usually passes between it and the thumb bones. Of course, as stressed by Morrison and Hill (2011), electromyographic studies and more detailed histological analyses, as well as detailed analyses of full medical records of individuals in which the PPI was either completely absent or abnormally developed (as discovered in gross anatomical dissections), are needed to test these hypotheses.

Also, it should be noted that, as explained in the Introduction, although the PPI does seem to be more frequently found in modern humans than in other primates, the observations and review of the literature done by Diogo and Wood (2011, 2012) have shown that the muscle is present in at least some nonhuman primates such as gorillas and chimpanzees. Therefore, contrary to what is suggested by most of the evolutionary/functional hypotheses listed above, the PPI is neither a *de novo* structure that is uniquely found in modern humans nor, very likely, the “vestige” of a very ancient structure that is found in most other taxa, because so far there is no clear, sound evidence of a PPI in nonhominoid primates (Diogo and Wood, 2012).

Phylogeny and Evolution of the PPI

In order to fully understand the phylogenetic origin and evolution of the PPI, one has to consider the hand muscles as a whole, and particularly to also pay attention to the phylogenetic origin and evolution of the so-called “deep head of the flexor pollicis brevis.” The comparative context of these and other hand muscles has been elegantly set out by Lewis (1989). Lewis embraced the hypothesis of Forster (1917) who suggested that the plesiomorphic condition for placental mammals is to have 10 flexores breves profundi, each inserting onto the lateral and medial sides of each digit, and four intermetacarpales connecting the adjacent metacarpal bones. In primates the plesiomorphic condition is the same, but two of the 14 muscles have differentiated to form new muscles: the flexor pollicis brevis and the opponens pollicis come from the flexor brevis profundus 1, while the flexor digiti minimi brevis and the opponens digiti minimi come from the flexor brevis profundus 10 (Diogo and Wood, 2011). In hominoids other than chimpanzees, as well as in New World monkeys, the flexores breves profundi 3, 5, 6, and 8 usually fuse

with the intermetacarpales 1, 2, 3, and 4 to form the dorsal interossei 1, 2, 3, and 4, respectively, whereas the palmar interossei 1, 2, and 3 are derived directly from the flexores breves profundi 4, 7, and 9, respectively (Diogo and Wood, 2011). Lewis (1989) model thus explains why the dorsal interossei muscles are usually bipennate, whereas the palmar interossei are usually unipennate, and is mainly supported by the developmental studies of authors such as Cihak (1972), which point out that at least some flexores breves profundi effectively become ontogenetically fused with the most dorsal intrinsic muscles of the hand (the intermetacarpales) in modern humans, forming the dorsal interossei of adults (N.B., it should be noted that Cihak 1972 suggested that “residua” of the contrahentes may also join the interossei during human ontogeny, a view followed by Murakami et al., 1987, and Yamamoto et al., 1988). Lewis’ proposition has been supported by authors such as Witthaut and Leclercq (1999), who point out that the dorsal interossei are effectively formed by both the flexores breves profundi and the intermetacarpales.

Chimpanzees have undergone a secondary reversion to the plesiomorphic state, probably because their flexores breves profundi do not fuse with the intermetacarpales during ontogeny to form the dorsal interossei (Diogo and Wood, 2011). Interestingly, chimpanzees also display a secondary reversion of a synapomorphy of the Hominidae in that adult chimpanzees have two contrahentes digitorum in addition to the adductor pollicis, one going to digit 4 and the other to digit 5 (in other adult hominids there is usually none: Diogo and Wood, 2011). Because the studies of Cihak (1972) suggest that in at least modern humans the contrahentes are lost (i.e., “reabsorbed”) during ontogeny, the presence of intermetacarpales and of contrahentes in chimpanzees is very likely due to a prolonged or delayed development of the hand musculature of these apes, that is, in this particular case extant chimpanzees are seemingly more neotenic than modern humans (Diogo and Wood, 2012).

The main controversy concerning the evolution and taxonomic distribution of the so-called “deep head of the flexor pollicis brevis” and of the PPI mainly concerns the identity of one of the flexores breves profundi, that is, number 2 (which plesiomorphically in mammals goes to the ulnar side of digit 1). As explained above, most authors consider that the PPI corresponds to a “vestigial” flexor brevis profundus 2, that is, that it is a fourth (and most radial) palmar interosseous. We want to stress that our results revealed an aspect that could be used to defend that the PPI is derived from the interossei: as explained above, the origin of the PPI is associated to the dorsal interosseous, either directly (in 11 hands) or indirectly (through

the thin membrane associated to this latter muscle, in 10 hands) in 21 (31.8%) of the 66 hands dissected by us where we observed the origin of the PPI, while the origin of this muscle is associated to the adductor pollicis in only 4 (6.1%) of these 66 hands. However, the insertion of the PPI is associated to the dorsal interosseous 1 in 0 (0.0%) of these 66 hands, while it is associated to the adductor pollicis in 24 (36.4%) of these 66 hands. So, even if we would only take into account its blending with other soft tissues, the overall numbers would still favor a closer affinity with the adductor pollicis. Another point that could be used to defend that the PPI corresponds to an ancient, true flexor brevis profundus 2 is that Cihak (1972) suggested that his ontogenetic studies of the human hand revealed that the PPI is one of the first thumb muscles to be differentiated, early in development. But it should be noted that Cihak’s interpretations of his own ontogenetic studies have been strongly criticized by authors such as Lewis (1989), who accused Cihak of often following a very simplistic, and pretty much out-dated, “recapitulatory” view of evolution without taking into consideration the fact, now well-known and documented, that heterochronic events frequently play a crucial role, and are actually very frequent in biological evolution. That is, the appearance of a structure in the early development of a particular biological organism does not necessarily mean that the structure surely also had a very early evolutionary origin. Perhaps even more important in this specific case, there are some doubts about whether the structure that Cihak (1972) identified as PPI really corresponds to the PPI *sensu* the present work (see, e.g., Diogo and Wood, 2012).

In fact, our observations and comparisons, as well as the phylogenetic analysis of Diogo and Wood (2011), strongly suggest that the PPI muscle was derived instead from a thin, deep additional slip of the adductor pollicis (hence the name *TDAS-AD* proposed by Diogo and Wood, 2011). As explained just above, and shown in Table 5, the PPI is often deeply blended with the adductor pollicis distally (e.g., Fig. 3), and even proximally and, at least in modern humans usually, or always, innervated by the branches of the deep branch of the ulnar nerve that innervate the oblique head of the adductor pollicis (and not by the branches of the deep branch of this nerve that innervate the dorsal and palmar interossei: Figs. 4 and 5). Furthermore, many of the hands dissected by us have, apart from the PPI, various additional bundles of the adductor pollicis, which might originate or insert near or in association with the PPI (e.g., Fig. 7). In this sense, we consider that the right hand of the HU M18 adult male shown in Figure 7 is particularly illustrative of what might have occurred during the evolution of the PPI. As it is well-known, the study of anatomical variations

often helps to better understand the evolutionary history of taxa (e.g., Bergman et al., 1988; Diogo et al., 2012). This particular hand has a remarkable mix of features that not only strongly supports, as does a detailed analysis of other features seen in other hands, that the PPI derives from the oblique head of the adductor pollicis, but also provides clues, in a single case study, about four hypothetical, but highly likely, evolutionary stages, which are schematized in Figure 8: **[A]** First stage of evolution, with a mainly undivided oblique head of the adductor pollicis; **[B]** Second hypothetical stage of evolution, with the oblique head plus an additional bundle that has an origin separated from the main body of this head but still a common insertion together with that main body; **[C]** Third hypothetical stage of evolution, in which the insertion of the additional bundle also becomes somewhat separated from the main body of the adductor pollicis, forming an almost completely differentiated PPI; **[D]** Fourth, hypothetical stage of evolution, showing a PPI that is even more lateral and thus even more separated from the main body of the oblique head of the adductor pollicis, resembling a PPI configuration that is commonly found in modern humans.

Another crucial argument in favor of our hypothesis is that, contrary to the statements of Susman (1994), the comparative and phylogenetic analyses of Diogo and Wood (2011, 2012) revealed that the so-called “deep head of the flexor pollicis brevis” of human anatomy is actually present in the vast majority of primates and that it corresponds to the flexor brevis profundus 2 of other mammals. For example, the structure designated as the flexor brevis profundus 2 in rats is the same structure that is designated as “deep head of the flexor pollicis brevis” of modern humans. Such a structure is effectively found in the vast majority of non-human primates, except for the New World monkeys in which this structure is either missing or, more likely, has fused with the flexor brevis profundus 1 component of the so-called “superficial head of the flexor pollicis brevis” of these monkeys (Diogo and Wood, 2011, 2012). As Diogo and Wood (2011) explain, most authors have found a flexor brevis profundus 2 in the nonhuman and nonplatyrrhine primates, but many have erroneously designated this structure either a component of the adductor pollicis or they have referred to it as the “interosseous volaris primus of Henle.” In fact, it is now well-known that in modern humans the so-called “deep head of the flexor pollicis brevis” is likely the flexor brevis profundus 2 and is usually mainly innervated by the deep branch of the ulnar nerve, while the so-called “superficial head of the flexor pollicis brevis” is usually mainly innervated by the median nerve (Diogo and Wood, 2012).

GENERAL REMARKS

Our observations, comparisons and review of the literature point out that the PPI, or “interosseous volaris primus” sensu Henle, of modern humans does not correspond to the flexor brevis profundus 2 of other mammals, that is, it is not a true palmar interosseous, being instead very likely derived from the adductor pollicis. The phylogenetic data available reveals that the muscle is a *de novo* structure that was very likely already present, as a polymorphism, in at least the last common ancestor of humans, chimpanzees and gorillas. Then, for some reason that is still not clear, but that may well have something to do with the evolution of the human thumb and thus with tool fabrication and use (as it had with other structures that are almost uniquely found in humans, for example, the extensor pollicis brevis and flexor pollicis longus), the PPI become more frequently found in humans than in gorillas and chimpanzees (Diogo and Wood, 2011). So this seems to have occurred after the split between chimpanzees and humans. Interestingly, the PPI has apparently not been the subject of a strong selective process in the recent evolutionary history of the human lineage, as indicated by its remarkable variation within modern humans. One reason for this could be that the initial strong selective force related to stone tool fabrication and use lessened when humans from different world regions then started to independently discover and employ other techniques to fabricate and use other types of tools. We thus propose that, from now on, the PPI is designated by the name *musculus adductor pollicis accessorius*, because this name indicates that the evidence available strongly supports the idea that the muscle is a *de novo* structure derived from the adductor pollicis. That is, this name refers to the evolutionary origin of the muscle, instead of referring to its attachments, which are variable, or to its function, which is still not completely clear, as explained above.

The true flexor brevis profundus 2 has been present and has basically kept the same anatomical configuration from the last common ancestor of placental mammals to *Homo sapiens* where it forms the so-called “deep head of the flexor pollicis brevis,” being thus a very ancient structure. The names “deep head of the flexor pollicis brevis” and “superficial head of the flexor pollicis brevis” are thus also inappropriate and in our opinion should be abandoned, because the former corresponds directly to the flexor brevis profundus 2 of other mammals while the latter derives from the flexor brevis profundus 1 (the opponens pollicis being also derived from the flexor brevis profundus 1: see above). We thus also propose that the “deep head of the flexor pollicis brevis” and “superficial head of the flexor pollicis brevis” are therefore

designated as *musculus flexor brevis profundus 2* and as *musculus flexor pollicis brevis*, respectively (see, e.g., Fig. 4).

The adoption and consistent use of these names is thus not a mere nomenclatural detail: it is a return to an old, and Darwinian, tradition in which it is also important to understand the phylogeny and homology of each and every anatomical structure. It is also a way to stress that modern humans usually have 11 muscles attached to metacarpal I and the pollical phalanges, and not 9 as it often stated in atlases and textbooks: the *abductor pollicis longus*, *extensor pollicis brevis*, *extensor pollicis longus*, *flexor pollicis longus*, *abductor pollicis brevis*, *flexor pollicis brevis*, *opponens pollicis*, *adductor pollicis*, *dorsal interosseous 1*, *adductor pollicis accessorius*, and *flexor brevis profundus 2*.

We hope that this article will call the attention of the authors of human anatomy atlases and textbooks to this fact and will thus contribute to the inclusion, in these atlases and textbooks, of information about the frequency, attachments, innervation and variations of the *musculus adductor pollicis accessorius*, so this information can be easily accessed and used by medical students, physicians and surgeons, among others. Contemporary advances in microsurgery now permit the repair, reattachment and/or transplantation of the hand, including each of its digits (e.g., Amer et al., 2011). The reconstruction of the opposable thumb which Bunnell (1948) regarded as man’s “great asset” requires a thorough knowledge of the detailed anatomy of the pollex and all its muscles (Smith and Lanz, 2004; Nessen et al., 2008). Only the knowledge of the existence, and importantly of not only the common attachments and bundles and innervation, but also of the different variants, of each of the 11 muscles attaching onto the thumb can allow the medical students and physicians to fully understand the human hand and surgeons to appropriately reconstruct a completely functional thumb.

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