A Historical Review on the Muscle of Cruveilhier

Authors

M. Ashraf Aziz[a]

Samuel S. Dunlap[b]

Janine M. Ziermann[a*]

Affiliations

[a] Howard University College of Medicine, Dept. Anatomy, 520 W St NW, Washington, DC, 20059, USA;

[b] 2062 Cobblestone Lane, Reston, VA, 20191, USA;

Corresponding author:

Janine M. Ziermann

Department of Anatomy, Howard University College of Medicine, Washington, DC, 20059, USA

Phone: +1 202 660 8447

Fax: +1 202 265 7055

Email: jziermann@yahoo.de

Abstract

Despite the fact that the human thumb has been investigated intensely with reference to its functional morphology, controversies remain; for example, regarding the muscle of Cruveilhier (deep head of the flexor pollicis brevis). Originally described in 1749, the human flexor pollicis brevis (FPB) only received special attention since Cruveilhier described it in 1834 as having a superficial and a deep head. Since then the existence of Cruveilhier's deep head has been debated. By 1920 five views existed: 1. The deep head is not part of FPB because of its nerve supply; 2. It became extinct and was replaced by a slip from the oblique adductor pollicis; 3. It is a part of the "composite" FPB and is synonymous with Henle's "interosseous volaris primus"; 4. The deep head received ontogenetically myofibrils from the primordial flexores breves medius and from the adductor (contrahentes) muscle plates; and 5. The deep head, "Henle's muscle", and oblique adductor pollicis are distinct muscles. In the 1960s Day and Napier revealed variations of the insertion and innervation of the deep head, but did not delineate their deep head from the "Henle's muscle" or the adductor pollicis. They hypothesized, that the shift of the deep head's insertion from ulnar to radial facilitated "true opposability" in anthropoids. We revealed that there are still new aspects to the story of this muscle, including new interpretations / conclusions regarding its development and evolution. The history of the investigations around this muscle is a fascinating story showing the next generation of anatomists the importance of detailed observation combined with the knowledge of several fields (anthropology, developmental biology, functional morphology, etc.). We discuss the muscles' functional significance for the evolution of the precision grip and why – with respect to surgery (replantation) - it is important to know the anatomical details of this muscle.

Keywords: flexor pollicis brevis; nerve-muscle specificity; precision grip;

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1 Introduction

Complexity and variability of the components and actions of the versatile thumb have played a crucial role during human evolution; this is indicated by the fact that modern humans have more muscles attached to the thumb than in most primates (e.g., *1; 2; 3*). Thumb opposition is the fundamental prerequisite to the origin and refinement of the two central grasping movements – i.e. the power and precision grips – of the hominoid hand (*4-13*). The emancipation of the hominid hand from locomotion following the adoption of habitual bipedalism occurred before 4.4 million years ago (Mya) in *Ardipithecus ramidus* (australopithecines). According to Lovejoy et al. (*14*) this hominid fossil demonstrates facultative bipedal locomotion and the hands compare favorably with those of *Homo*. The earliest known manufactured stone tools first appeared about 3.3 Mya (*15; 16*). Tool use and manufacturing facilitated the change from predominantly power to precision grasping movements, including their divergent forms (*13; 17-21*). In fact, the anatomy of whole hand underwent modifications of varying degrees to permit incrementally precise manipulation of objects; these constituted the essential attributes required for tool use and, in due course, tool manufacture (*22-24*). Furthermore, the individuation of finger control, and enhanced, variegated articulatory thumb movements, permitted early humans to engage not only in pulp-to-pulp opposition, but also in fine manipulation called "precision handling" (*25*). The latter involves pulp-to-tip and tip-to-tip pinch control of fine objects.

The hominid thumb underwent dramatic alterations and its evolution has been the subject of several targeted investigations and reviews (e.g., *1; 20; 21; 26; 27-29*). Once the fundamental epidermal, osteological, arthrological and myological characteristics – including their neurological controls – were in place, early hominids transitioned from tool use to tool manufacture phase – or a combination of these skills (*13; 18-20; 28*). Habitual tool-use then triggered a responsive change in pollical form and function leading to further enhancement and diversification of all categories of gripping movements, particularly the precision grip and/or handling (*9; 10; 13; 22; 30*). Yet, the hominid thumb is far from being an extra-refined appendage (see *30; 31*). It is a mosaic of primitive and derived features, reflecting stages in the hand evolution from support and locomotion on the ground to a grasping structure in the trees, and, eventually, the organ of manipulation (*20; 29*). Several specific locomotory specializations of the thumb were lost (*10; 32*) and their disappearance (or re-purposing) led to incremental "prehensile-tactile activities", i.e., exploratory behavior, facilitated by manipulation activities. With the gradual loss of locomotor anatomical constraints, the articulate human hand, with its versatile thumb, acquired a functional universe under the direct control of higher cortical centers. The evolution of an area of cortical processing might be the first step in design or abstraction as it implies that patterns that are not present in the environment can be internally processed as well (*10*).

All hominid hand attributes required for tool manufacture and manipulation involve complex sensory perceptions and versatile individual actions of the digits (and their segments). Key to the execution of this are tactile/kinesthetic thumb movements, especially opposition. The latter is a series of connected actions and has been defined by Tubiana (*2*, pp69-70) as a *"... combined movement involving all three segments of the*

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thumb: the metacarpal segment moves in anteposition, then in adduction, a movement that is accompanied by … longitudinal rotation into pronation. The proximal phalanx flexes, pronates, and radially deviates; the distal phalanx flexes to a variable degree and this flexion is accompanied by a slight pronation adapted to the requirements of the grip. There is, in fact, not one single opposition but a whole range of oppositions in a fixed conical section … which allows a huge variety of grips." (see also *33; 34*). These movements are essentially pivoted on the trapezio-metacarpal joint, but also include movements of the metacarpo-phalangeal and the interphalangeal thumb joints which are activated by a large number of extrinsic and intrinsic pollical muscles (*35-41*). The dynamic foci of the other digits are also their joints: carpo-metacarpal, metacarpo-phalangeal and interphalangeal joints (*10; 42; 43*). Joint actions of all digits are actuated by voluntary contractions of all or selected extrinsic and intrinsic muscles.

However, the thumb has the largest number of exclusive extrinsic and intrinsic muscles, including several unique named ones which facilitate the complex actions of its joints (*1; 2; 23; 41; 44-46*). One muscle has played an important role in the origin of sophisticated precision grip and its diversification: the deep head of the flexor pollicis brevis (FPB) (*20; 47-50*), hereafter named the "deep head of Cruveilhier" (see *46; 51; 52; 53*). Few human muscles have experienced as checkered a history as this one. First described 267 years ago by Albinus et al. (*54*) the FPB did not receive much attention until almost a hundred years later when it was described as having two heads (*47; 55*). Since then the FPB and in particular the deep head of Cruveilhier have been investigated and discussed in detail. Day and Napier (*48*, *49*) attempted to clarify the status of the deep head, but controversy has persisted (*56*) and even Day and Napier proposed equivocal, even contradictory views regarding its true nature. Disagreements involve issues relating to its form, function, innervation, development and phylogeny of the deep head of Cruveilhier.

We decided to further explore and elaborate on the deep head of Cruveilhier having initially observed a larger percentage of ulnarward inserting cases than had been reported by Day and Napier (*48*). The origin of the deep head of Cruveilhier is usually described as from the capitate (*48; 53; 57-69*) and additionally from the ligamentum carpi radiatum (*70: Fig. 94, p103*). While re-investigating the attachments and innervation of the deep head of FPB we discovered the long fascinating history of this muscle. However, many newer anatomical textbooks and atlases only describe the superficial head of the FPB, while the deep head is barely acknowledged as a distinct thenar compartment muscle and in diagnoses of nerve injuries (*71*), leading to confusion during education.

The deep head of Cruveilhier is a functionally and clinically significant muscle and medical students in particular should be aware of it and its contribution to the subtle movements of the thumb. Accurate anatomical information is required for surgeries as the re-attachments of severed digits or even wrist and hand are now possible using enhanced, fine surgical techniques – including robotic procedures. Therefore, our goals here are to (1) analyze the history of the investigation of the deep head of Cruveilhier to demonstrate the importance of taking all possible information from different specialties into account (e.g. comparative anatomy,

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anthropology, developmental biology, etc.); (2) document the variability of this muscle (attachments, innervation); and (3) discuss our results with respect to its development, evolution and functional significance for the origin and maintenance of various precision grips, therefore also providing information on its clinical importance.

2 Methods

For this investigation, we have studied human anatomy publications, focusing mainly on literature between 1833 and 2004 because those works included more details about human variations, ontogeny and evolutionary issues. More recent publications were included for the discussion on evolution and implications for surgery and medical education. In order to present the most common configuration we show here one dissected hand obtained from the Anatomy Department's "gross anatomy laboratory willed-body programs" at Howard University College of Medicine (Washington, DC) The dissection sequence generally followed instructions in Romanes (*72*).

3 Results

History of the deep head of FPB

The flexor pollicis brevis (FPB) was first described by Albinus et al. (*54*) and did not receive much attention until almost a century later (*47; 55*). Cruveilhier (*47*) was, to our knowledge, the first investigator who described the FPB as having a superficial and a deep head. He united the heads under *a single named* muscle largely based on the insertions of the heads. In the 1850s, Henle (*73*) discovered a deep-seated, slender muscle with its origin from the base of the pollical metacarpal and insertion onto the ulnar sesamoid along with both heads of the adductor pollicis. He named it the "interosseous primus volaris" (hereafter named the IPV of Henle) (syn. "pollical palmar interosseous muscle", "musculus adductor pollicis accessorius", "interosseous primus volaris of Henle" or "Henle's muscle", "TDAS-AD = thin, deep additional slip of adductor pollicis") (see *41; 74; 75-80*), and suggested that it might be the FPB's deep head. Bischoff (*81*), basing his research on the gibbon (*Hylobates leuciscus),* had independently suggested that the IPV of Henle might be the "true" deep head of the FPB and that the double-headed FPB might be a compound entity (*82; 83*).

The German ("Heidelberg") School of Anatomists led by Flemming (*84*, *85*) essentially viewed the FPB as single-headed muscle composed only of its superficial/external portion (*86; 87*) based on the application of the Gegenbaur-Fürbringer's nerve-muscle specificity test (see *88*). They concluded that only the superficial part which received the (recurrent) median nerve, was the true FPB; all other heads which were supplied by the (deep) ulnar nerve belonged to the adductor pollicis complex which is innervated by the deep ulnar nerve. However, Brooks (*82*) found that the superficial head was, in 19 out of 31 of cases, innervated by both the recurrent median and the deep ulnar nerve and in five cases only by the ulnar nerve. In five cases both nerves supplied both heads and in two cases the median nerve supplied both heads but the deep head also received supply from the ulnar nerve. (NB: Brooks' "inner head" was "Bischoff's true inner head" i.e., the IPV of Henle.) Cunningham (*89*) demonstrated that the nerve supply of

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Cruveilhier's deep head is variable and supported Brooks data in the sense that both – the superficial (Brooks) and the deep (Cunningham) – heads of the FPB receive variable innervation. Investigations by Brooks ad by Cunningham questioned the rigid application of Gegenbaur-Fürbringer hypothesis.

Clearly, additional information was required to elucidate the true nature of the FPB heads. One possibility was to study the derivation of specific (i.e., named) muscles from the primordial fundamental layers of the intrinsic palmar muscles of related classes of vertebrates (*86; 90; 91*). Cunningham performed a comparative anatomical analysis of the hand muscles of different classes of mammals organized as an evolving series. He suggested that ancestrally the FPB was a two-headed thumb muscle which was derived from the intermediate layer called the flexor brevis manus. He proposed that in humans the outer (radial) head of the thumb's flexor brevis manus has remained as the (superficial) FPB whereas the actual (phylogenetic) inner (ulnar, deep) became reduced as a result of the expanded development of the adductor pollicis (i.e. the contrahentes) complex (*89*). The IPV of Henle, a radial slip which had presumably differentiated from the oblique adductor pollicis, and which Bischoff (*81*) had called the "true deep head", had taken the role of the now extinct authentic (phylogenetic) deep head. This view was endorsed by Young (*92*) and by Schäfer and Thane (*93*) [see also the investigations of this muscle by Bello-Hellegouarch et al. (*79*) and Dunlap and Aziz (*41*)].

The French School of Anatomists accepted Cruveilhier's proposal of the two-headed FPB without independent tests to confirm the status of its constituents (*94-97*). However, during the 19th and early decades of the 20th century, the German and British anatomists continued to deny the existence of the Cruveilhier's deep head of the FPB; they regarded the IPV of Henle as the "true deep head" of this muscle (Table 1). During this period, the French, German and British anatomists disagreed on the actual named muscle elements in humans.

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Table 1: Slips of the Flexor pollicis brevis (FPB) in the literature of the past 267 years. A, B, C, and D refer to different slips of FPB. A – all insertion to radial sesamoid = true superficial FPB; B – insert onto ulnar sesamoid; C – separate slip; D – all insertion onto ulnar sesamoid = adductor pollicis. *Flemming (*85*) actually shows in his Figure on page 68 the FPB superficial head (A), and the split deep head of FPB (B & C). However, he himself considers B and C as slips of the adductor pollicis (B being more often present than C).

	Slips of FPB				
Investigator (Year)	**A**	**B**	**C**	**D**	**Note**
Albinus et al. (*54*)	x			x	
Cruveilhier (*47*)	x			x	All fibers which insert on radial sesamoid = FPB; All fibers on ulnar sesamoid = Adductor
Bischoff (*81*)	x	x	x	x	B: shown to insert on ulnar sesamoid; C: separate slip; Adductor oblique head
Henle (*120*)	x	x	x	x	A: Deep Abductor; B + C: two slip FPB, one on each sesamoid; D: Adductor
Gegenbaur (*121*)	x	x	x	?	A: actual FPB - inserts on radial sesamoid, + a slip which splits to insert on the two sesamoids; or B and C which insert on radial sesamoid
Flemming (*84*, *85*)*	x	x	x	x	C: Henle's Interosseus volaris primus
Cunningham (*89*)	x	x	x	x	Supports two headed FPB: inner head = muscle of Henle
Brooks (*82*, *83*, *100*)	x	x	x	x	D: Henle's muscle, supports two headed FPB but actually describes inner head Henle's muscle
McMurrich (*98*)	x	x	x	x	B+C+D: "Compound muscle, including Henle's muscle, related to Adductor pollicis
Wood Jones (*51*)	x	x	x	x	B: Deep head; C: Muscle of Henle
Lewis (*56*)	x	x	x	x	B: Deep head; C: Muscle of Henle
Day and Napier (*48*, *49*)	x	x			B: Deep head - may form one slip which goes either to radial or ulnar sesamoid exclusively, respectively, or splits to insert on both; may even be absent; C: Muscle of Henle; D: Adductor pollicis oblique head

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At the dawn of the 20th century, McMurrich (*98*) synthesized a large body of earlier comparative anatomical data of the palmar musculature in various vertebrates and enlarged the tripartite schemes of the primordial muscle plates of the hand proposed by Cunningham (*90*, *91*) and Young (*92*) and divided the palmar muscle layers into five developmental laminae. The additional laminae were subdivisions of the earlier three layers initially proposed by Cunningham (*91*). McMurrich disagreed with Cunningham's (*91*) derivation of the superficial head of FPB from the immediate layer and suggested that this head derives instead from the pollical component of his "flexores breves superficialis" layer. He also endorsed the view that the IPV of Henle – a derivative of the adductor pollicis (oblique head) – was the actual deep head of FPB. It should be noted that McMurrich employed the nerve-muscle specificity hypothesis although it had been seriously questioned (see above; *82; 89*). He concluded that the FPB was a compound structure, with elements derived from three different layers namely, the superficialis, the deep stratum of the medius and the profundus (*98*). Cunningham (*89*) viewed the thenar compartment and its immediate environment as a territory contested by parts of the ancestral FPB of the thumb and the adductor/contrahentes muscles. The same territory was viewed by Brooks (*82*) as being actively sought-after by the median and ulnar nerves, respectively. According to Brooks, the ulnar nerve was encroaching upon the myological domain of the median nerve and he proposed that muscle slips could be conduits of the expansion of a particular nerve into the domain of a neighboring nerve. Therefore, it was logical for McMurrich (*98*) to regard the FPB as a "compound structure" similar to the digastric muscle located in the floor of the oral cavity.

It is important to observe that Cunningham, Young, Brooks, Schaffer and Thane, and McMurrich were writing about the deep head of FPB which was *not* the actual deep head proposed by Cruveilhier (*55*), i.e., the slip arising from the trapezoid, capitate and the adjoining palmar intercarpal ligament and crossing deep to the flexor pollicis longus tendon to join the superficial head of FPB to insert on the radial sesamoid and adjoining area. The former authors were referring to the IPV of Henle as the flexor's deep head (Table 2). Flemming (*84*, *85*) and Cunningham (*89*) actually do show the deep head of Cruveilhier in several figures; however, they failed to appreciate its true identity. Brooks (*82*, pp642-3) took special note of this muscle as follows: *"… a fasciculus from the inner head, which crosses the deep surface of the long flexor tendon to join the more superficial part at its insertion; it is the latter portion that one would naturally expect to receive an ulnar nerve-supply, but in every case both parts of the outer head received twigs."* He assumed that the muscle band regarded by Cruveilhier as the deep head was only an odd slip (Flemming's, Cunningham's, and Brook's *"slip B"* – note their illustrations; Table 1) which had shifted its insertion from the ulnar to the radial sesamoid to join the superficial head's insertion tendon. Brooks (*82*, pp642) explanation as to how the FPB acquired its double nerve supply (recurrent median and deep ulnar nerves) is as follows: *"I am inclined to think that the fasciculus of fibers from the deep to the superficial head has acted as a bridge, and, as it were, dragged the branch of the ulnar nerve across."* Brooks' *"fasciculus of fibers from the deep to*

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the superficial head", i.e. *"slip B"* was none other than Cruveilhier's deep head of FPB.

Table 2: Historical overview of the description of the deep head of the flexor pollicis brevis (FPBd, Deep head of Cruveilhier). Most of the authors did not describe the deep head of Cruveilhier but the interosseous primus volaris (IPV) of Henle. Abbreviations: a – Tendon on sheath flexor I radialis; add. pol. oblique – oblique head of adductor pollicis brevis; Distal palm lig = distal palmar ligaments = distal row of carpal ligaments. *Flemming (*85*) actually describes the deep head of FPB but does not acknowledge it as independent head; instead, he claims it is part of the oblique head of the adductor pollicis. [x]Brooks (*100*) doesn't name the deep head of FPB but describes it properly including the origin from the annular ligament and the two heads to be present in *Hylobates*.

Author (Year)	**Origin**						**Insertion**					
	Trapezoid	**Capitate**	**Trapezium**	**Distal palm lig**	**retinaculum**	**Metacarpal**	**Radial sesamoid**	**Ulnar sesamoid**	**P1 base**	**M1 head**	**Tendon**	**Joint capsule**
Thomson et al. (*64*)		x	x		a	II & III						
Brooks (*82, 83*)	calls it deep head, but describes IPV of Henle											
Flemming (*85*)*	describes no deep head											
Brooks (*100*)[x]	calls it deep head, but describes IPV of Henle											
Gerrish (*122*)	is IPV of Henle, with origin from metacarpal I											
Robinson (*61*)	x	x	blended with lateral part of add. pol. oblique									
Huber (*99*)	calls it deep head, but describes IPV of Henle, with origin from metacarpal I											
Robinson (*62*)	x	x	x		a	II, III, IV						
Wood Jones (*53*)	x	x					x		x			
Jamieson (*123*)	calls it deep head, but describes IPV of Henle											
Hollinshead (*60*)	x	x		x			x		x			
Goss (*124*)	calls it deep head, but describes IPV of Henle											

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Lockhart et al. (*125*)	? IPV of Henle?											
Day and Napier (*48*, p125)	x	x		x			x		x			
Zuckerman (*126*)	calls it deep head, but describes IPV of Henle											
McFarlane (*127*)	no information on deep head											
Day and Napier (*49*)	x	x		x			x		x			
Kaplan (*39*)	x	x		x			x				x	
Anson (*57*)	x	x					x					
Romanes (*72*)	not much information											
Warwick and Williams (*104*)	x	x		x			x					
Gardner et al. (*59*)	x	x		x		II	arises with add. pol. oblique					
Landsmeer (*103*)				x			x	x			x?	
O'Rahilly (*68*, p96)	variously present "arises in common with oblique head" (add. pol. oblique)											
Crafts (*128*)	calls it deep head, but describes IPV of Henle											
Fahrer (*46*)				?			x					
Clemente (*58*)	x	x					x		x		x	
Stern (*63*)	x	x					x	x				
Woodburne and Burkel (*67*)	x	x					x		x			
Linscheid (*12*)	?	?	?				x					x
Jan and Rooze (*129*)	x	x	x	x	x		x	x	x			
Schmidt and Lanz (*105*)	x	x		x			x	x	x		x	x
Standring (*130*)	x	x		x			x		x			
Drake et al. (*119*)	no information											
Moore et al. (*131*)	no information											

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Wood Jones (*51*) undertook a systematic review of the hand muscles, including the status of the human FPB components. He described four distinct muscle slips which were inserted on either the radial or the ulnar metacarpo-phalangeal sesamoids and argued in favor of regarding the portion B (in his Fig. 89, p199) as constituting Cruveilhier's deep head of the FPB (Table 1). However, a major textbook, *Piersol's Human Anatomy* (*99*), followed the German anatomists' proposal to deny the existence of a deep head altogether. This book provides some additional information of the various positions of other anatomists and illustrating the interosseous palmaris I of Henle (*99: Fig. 588, p609*). Huber (*99*) shows in is Fig. 588 the deep head of the FPB but names it as a slip of the oblique head of the adductor pollicis.

Studies by Brooks (*82*) and Highet (*71*) showed that in 80% and 77%, respectively, of the cases studied the median and ulnar nerves caused complete paralysis of all the intrinsic hand muscles including the thenar muscles. Highet (*71*) observed that paralysis and atrophy of the FPB was not surprising in those cases where the ulnar nerve had been transected, because this muscle usually gets innervated by both the median and ulnar nerves. However, even Highet (*71*) did not include the actual deep head of Cruveilhier in his work although he described the muscle correctly (p227 of his study). This variable innervation of the FPB and the deep head of Cruveilhier made it difficult to delineate the status of the FPB heads. Anatomists continued to dread entering the myological depths of our *"twenty-four-carat thumb"* (*23*) and contend with the *"quagmire of obstructive terms"* used to describe those muscles (*53; 100*) (see also Table 3).

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Table 3: Studies of the Flexor pollicis brevis superficial head (FPBs) during the last 150 years. None of the studies reported an insertion of the FPBs onto the ulnar sesamoid. Abbreviations: DR – distal retinaculum; FPLt = Flexor pollicis longus tendon; FCR = Flexor carpi radialis; lig. = ligament; P1 = Phalanx 1; TS - Tendon sheath flexor carpi radialis

Author	**Origin**						**Insertion**			
	Volar carpal lig.	**Metacarpal I base**	**Trapezium crest**	**Radial side of FPLt**	**Anterior carpal lig.**	**FCR Tunnel**	**Radial sesamoid**	**P1 base**	**tendon**	**Metacarpal 1**
Thomson et al. (*64*)	DR									
Brooks (*82*)	x		x				?	?		
Brooks (*83*)	x	x	x				x			
Flemming (*85*)	x		x				x	x		
Brooks (*100*)	x		x				x			
Gerrish (*122*)	DR		x							
Robinson (*61*)	DR		X							
Huber (*99*)	x, DR							x		
Robinson (*62*)	DR		x							
Wood Jones (*53*)	x		x	x			x	x		
Jamieson (*123*)	DR		x							
Hollinshead (*60*)	x		±				x	x		
Goss (*124*)	x	x	x	x						
Lockhart et al. (*125*)	DR		x							
Day and Napier (*48*, p125)	x		x				x	x		
Zuckerman (*126*)			x							
McFarlane (*127*)	x							x	x	MP + joint

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Day and Napier (*49*)	x		x				x	x		
Kaplan (*39*)	x	x	x	x	x	x	x	x	x	
Anson (*57*)	x		x			x, TS	x	x	x	
Romanes (*72*)	x		x ±				x	x		
Warwick and Williams (*104*)	x		x				x	x		
Gardner et al. (*59*)	x		x							
Landsmeer (*103*)	x						x			
O'Rahilly (*68*, p96)	x		x							
Crafts (*128*)	x		x				x	x		
Fahrer (*46*)	x	x	x				x		x	
Clemente (*58*)	x	x	x				x	x		
Stern (*63*)	x						x	x		
Woodburne and Burkel (*67*)	x		x	x			x	x		
Linscheid (*12*)	x		x						x	
Jan and Rooze (*129*)	x		x		x		x	x		x
Schmidt and Lanz (*105*)	x	x		x		x	x		x	
Standring (*130*)	x		x	x			x	x		
Drake et al. (*119*)	x				x	x				
Moore et al. (*131*)	x		x				x	x		M1 + scaphoid

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Variability of the deep head of FPB

The FPB is the only commonly occurring bicipital thenar muscle; the adductor pollicis which also has two heads is located in the midpalmar space. The superficial (external) head of FPB originates from the distal, lateral part of the flexor retinaculum and the tubercle of the trapezium; it inserts onto the radial sesamoid of the metacarpo-phalangeal joint, the glenoid surface of this joint, and the radial aspect of the thumb's proximal phalanx (see Table 3). The deep head of Cruveilhier is commonly described as originating from the trapezoid, the capitate and neighboring parts of the distal palmar ligament (Table 2). Additionally, ligamentum carpi radiatum is an important landmark for the origin of the deep head (*70: p103*, *Fig. 94*). This distinct and invariable ligament is a vital aid in recognizing variations of origins in both heads of FPB and the oblique adductor pollicis. Zancolli and Cozzi (*101*: p19, Fig. 6-3D and pp474-5, Fig. 6-14A) and Ross and Lamperti (*102*: p247, Fig. 1.2B) showed very similar figures of this ligament.

In normal thumb posture, i.e., in its abducted position, the deep head is directed away from the palmar plane and, after passing deep to the flexor pollicis longus tendon, it, too, inserts in the same manner as the superficial head (Fig. 1) – this insertion is said to be the common form in humans amidst several other notable variations (*39; 46; 48; 49; 52*).

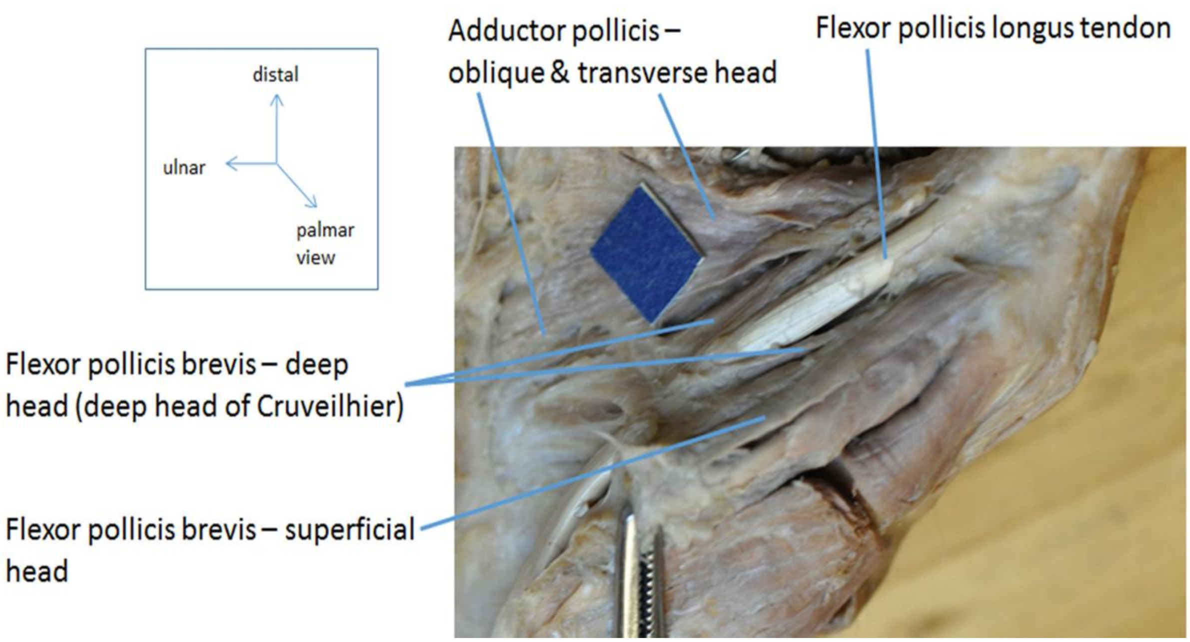

Fig. 1: Example of a male, right hand, palmar view. Deep head of Cruveilhier split and inserting ulnar- and radial-ward on proximal phalanx I. Scale = 1 cm.

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Day and Napier (*48*) carried out the first ever systematic study of "The two heads of flexor pollicis brevis" using a larger sample of hands. After summarizing and evaluating many early investigations that concurred with Wood Jones' (*51; 53*) view that the muscle did indeed have a deep head which was the same slip described by Cruveilhier (*47*). For the first time they described the variable forms of this head. Day and Napier (*48*, see their Fig. 1) differentiated Cruveilhier's deep head from all other muscle slips with which it had been associated or confused: IPV of Henle and the oblique head of the adductor pollicis (*82; 83; 98; 100*). Day and Napier's (*48*) study is an observational test of various views regarding the status of the digastric flexor pollicis brevis. They reported on its attachments, configuration, varieties and relationships to other contiguous muscles and the nerve supply of the two heads. Their sample size (65 total specimens) permitted only preliminary – though illuminating – quantitative analysis. One major drawback of the Day and Napier (*48*) investigation involves the precise relationships of the deep head of Cruveilhier with the two neighboring muscles with which it was and still is frequently confused: the oblique head of the adductor pollicis and the IPV of Henle. They showed both of these muscles in their illustrations and described their role in the intriguing history of the FPB (especially the deep head) (Fig. 1 in *48*). However, they presented no evidence to show that, in their dissections, they had individually separated these muscles and differentiated out the deep head of Cruveilhier from them. Dunlap and Aziz (*41*) showed that the muscle "interosseous palmaris I of Henle" is constantly present and is independent from the deep head of Cruveilhier (see also *79*). Essentially Day and Napier strove to settle the question of the true identity of Cruveilhier's deep head (*48*) and to elucidate its phylogenetic history (*49*) – especially in relation to the origin and refinement of various precision grips facilitate by the opposing actions of the thumb. They had found that Cruveilhier's deep head was present in 62 out of 65 hands (*48*). Day & Napier (*48*, see their Fig. 2) also discovered that the deep had of the FPB was variable: a single head inserting exclusively onto the radial sesamoid (53 out of 65 hands) in the manner stipulated by Cruveilhier (*47*); splitting into two insertion tendons (8 out of 65 hands) which were attached to the radial and ulnar sesamoid, respectively; and a single head inserting exclusively onto the ulnar sesamoid (1 out of 65).

Day and Napier (*48*) also studied the innervation of the FPB heads and concluded that variation of nerve supply was a common condition even though in most cases the superficial head received the median nerve while the deep head received the ulnar nerve, respectively. Day and Napier (*48*, p125) describe the origin of the deep head of FPB as *"… from the trapezoid and capitate bones and the palmar ligaments of the distal row of carpal bones."* Although they do not discuss it in their narrative, the two figures (on pp124-5) suggest that the origin of the deep head is superficial to the oblique head of the adductor pollicis. A similar figure is also found in their later paper (*49*). Even after Day and Napier's studies the deep head of Cruveilhier continued to be the center of various interpretations.

Lewis (*56*) clearly describes the tough, fibrous, distal extension of the carpal tunnel wall on the radial side along which passes the large tendon of flexor pollicis longus which

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separates the two heads of the FPB. According to Lewis (*56*, pp104-6, 164) the parts that arise adjacent to the margin of the carpal tunnel comprise the FPB and the deepest part, which is closely associated with the origin of the first palmar interosseous, is the deep head of the FPB. Lewis (*56*, his Fig. 9.8.C, p162) showed a most radialward portion of the oblique adductor pollicis head contributing to the deep head of Cruveilhier. However, after analyzing 80 hands in the present study we conclude that this portion is a part of the deep head because it lies superficial to the oblique head as shown in Lewis' figure (*56*: Fig. 9.8C, p162).

We found that the origin of the deep head of Cruveilhier always lies superficial to the oblique adductor pollicis head (Figs. 1, 3B, C); this was not described in previous work acknowledging the presence of the deep head (*2; 48; 51; 57-68; 99; 103-105*). However, this relationship was shown in ten illustrations (*2; 48; 57; 58; 64-67; 70; 103*) and in three publications its origin was described as being blended or in common with the oblique head (*59; 61; 68*).

Having confirmed the presence and clear delineation of the deep head of Cruveilhier, the muscle of Henle and the oblique adductor pollicis in each hand, we also confirmed all variations of insertions described by Day and Napier (*48*).

4 Discussion

History

Brooks (*100*) and Cunningham (*89*) based their explanation of the formation of the bicipital FPB from their own observations and those of Flemming (*84*, *85*). All those studies proposed that a slip of the adductor (contrahentes) complex may have shifted its insertion radialward to form the dual-headed ("composite") FPB. However, none of them analyzed actual the *variation* of this muscle in order to support their hypothesis. Cunningham (*89*) suggested that the shift illustrated the hypertrophy of the adductor (contrahens) pollicis at the cost of the ulnar head of the FPB. In contrast, Brooks (*82*, *83*) interpreted this shift as mechanism by which the ulnar nerve extended its domain into the territory of the median nerve. The muscle slips supplied by the ulnar nerve shifted, according to Brooks, their insertion radialward and functioned as "bridges" to enable the deep ulnar nerve to reach the median innervated muscle region. He proposed that this was the mechanism by which some thenar muscles acquired their dual innervation.

Day and Napier (*48*, *49*) used several methods to elucidate the true nature of the FPB heads; this is the detailed description of attachments and nerve supply, and two additional, independent tests which include: phylogeny and kinesiology. They succinctly addressed observational and experimental tests which invalidated the nerve-muscle specificity theory as an exclusive basis for computing phylogenetic relationships of any muscle. They concluded that the different nerve supply of the superficial head (most frequently from the median nerve) and that of the deep head (most frequently from the deep ulnar nerve) did not exclude their classification as a single anatomical and functional unit.

Even after the detailed studies of Day and Napier (*48*, *49*) discussions regarding the origin and true nature of the FPB and its two heads continued. Day & Napier (*48*, *49*) made

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following propositions (our conclusions added):

The human FPB is constituted of a superficial and a deep head as originally postulated by Cruveilhier (*55*). Our data support this.

The deep head of FPB / Cruveilhier has a distinct and fairly constant origin from the trapezoid, capitate and their contiguous deep carpal ligaments. Our study supports this and we add the ligamentum carpi radiatum as an important origin.

Its insertion is variable as follows: (A) onto the ulnar sesamoid, (B) onto the ulnar and radial sesamoids, and (C) onto the radial sesamoid (also the insertion point of the superficial head), the latter insertion being the most common. Our data support this.

The deep head is usually innervated by the deep ulnar nerve, although it might, on rare occasions, also receive a branch of the median nerve which may supply it exclusively or in association with the deep ulnar nerve.

We found that the radial slip/head is usually innervated by the median nerve and the ulnar slip/head by the deep ulnar nerve. However, we only analyzed the innervation in 11 hands and more detailed dissections on fresh material is needed to clarify this discrepancy.

The deep head is phylogenetically "… derived from the contrahentes layer of the mammalian palmar muscles by radial migration …" (i.e., the FPB is, like the cephalic digastric, a compound muscle) (*106: p132*). FPB heads are derived from the dual-headed flexores breves profundi layer of the mammalian palmar muscles (see for example *80*).

The evolution of the deep head was associated with the origin and perfection of "true opposability" of the thumb (i.e., the precision grip) in most (Old World) catarrhine primates. The distribution of the presence/absence of the flexor brevis profundus 2 in primates indicates that the deep head of FPB is present in the last common ancestor of primates and was lost or fused with its immediate neighbors in New World monkeys (see for example *80*).

Development, Evolution, Medical student education

Cunningham (*90*, *91*) was the earliest investigator to suggest, that the flexores brevis profundi are the true progenitors of the entire bicipital FPB complex. McMurrich (*98*) concluded that the FPB is a compound muscle whose heads derived (phylogenetically) from different layers of intrinsic hand muscles. The superficial head was proposed to derive from the flexores brevis superficialis (innervated by the median nerve) and the deep head and the oblique head of the adductor pollicis from the contrahentes/adductor layer (*98*). Based on their analysis Day and Napier (*48*) first assumed that the deep head of Cruveilhier is part of the superficial FPB, but later contradicted themselves stating that the deep head is actually part of the adductor pollicis (*49*).

In the early 70's Cihak (*106*) wrote his voluminous summary of over a decade's worth of investigations of the myological, osteological, and arthrological aspects of the human hand and foot (see also *107*). Cihak (1972, p134) stressed that the blastema complex which gives rise to both FPB heads *"… does not include the adductor pollicis, which is derived from the contrahentes layer,*

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...” Furthermore, he suggested that the myoblasts from the contrahentes layer were probably also involved in the development of the interossei. Those observations and those of the Japanese morphologists (*108-110*) argue that during the morphogenesis of hand muscles it is not uncommon for exchanges of myocytes between neighboring embryonic muscle layers (see also *106*). Thus, it is possible that the muscle slips of the deep FPB seen by Day and Napier (*48*) are the odd slips of the developing oblique adductor pollicis (contrahentes-derivative layer) which fused with the true deep FPB (i.e., Cruveilheir’s deep head; flexores breves profundi layer). In other words, Day and Napier’s (48, p125) illustration does not necessarily lead to the conclusion that the deep head, a contrahentes-derived slip, shifted its insertion to the radial sesamoid. The ulnar slips of the deep FPB may just be an odd vagrant fellow traveler picked up from the blastema of the neighboring oblique adductor by the specific developing flexor brevis profundus of the thumb.

The re-investigation of the evolutionary myology of the hand muscles has very significant implication for the accurate diagnosis and treatment of nerve injuries of the hand (*71*), muscle and tendon injuries of the hand (*111*), replantation microsurgical repair (*112*), and the design of human hand prosthesis (*113*). The role of insufficient and/or incorrect information regarding the innervation of the thenar muscles in clinical misdiagnosis is discussed by Highet (*71*).

Various forms of precision grips also influenced other joints of the hand such as the trapeziometacarpal joint, which is flattened in the ulnar aspect, which in turn enables opposition of the third, fourth and fifth finger to the thumb what is required also in the three- and five-jawed grips (*29*). The use of tools was formerly associated with the estimated brain size in hominoids, but a closer look at the anatomical details of the thumb showed that the form of the metacarpophalangeal joint of the thumb gives more reliable information about the ability to achieve various precision grasps and ultimately to make tools (e.g., *6; 20*).

Clearly, the origin and diversification of the precision grip needs to be reviewed to examine the cause and effect of tool use versus variations of thumb (joints, muscle slips, muscle attachments, and innervation). The power and precision grips were established after the morphology was in place (*29*). Therefore, the observed variability supports the view that selection operated on the myological variation of the deep thenar muscles to give rise to more refined and variable opposition. Here, we showed the variability of the deep head of Cruveilhier with respect to number of slips (Fig. 3; see also *114*), and attachments (e.g., Fig. 3), characters that underlie selection. The form of the metacarpophalangeal joint combined with the variability of pollical muscles enabled a range of movements beneficial for tool use; in turn tool use influenced the anatomy. Selection on the variability enabled a better movement of the thumb, which allowed incremental tool use facilitating tool making and finer movements of the thumb.

Of all the manual digits, the thumb is unique in the architecture of its joints. This is especially true for the saddle-shaped trapezio-metacarpal and the metacarpophalangeal joint, which divide the thumb into two functional compartments resulting in increased mobility of its distal segment. Furthermore, the thumb has several unique muscles (flexor pollicis longus muscle;

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Henle's "interosseus primus volaris"; the anatomically complex first dorsal interosseous; the long and short extrinsic extensors) which are supplied by several nerves (median and ulnar nerves supplying the intrinsic muscles; the radial nerve supplying the extrinsic muscles). Furthermore, the thumb is richly vascularized (princeps pollicis artery) and it exclusively contains an untethered distal metacarpal head, because the connecting band of the transverse metacarpal ligaments is absent (*29*)

Despite Books' (*100*) caution that the deep thenar muscles constitute a number of distinct fascicles which challenged easy and definitive identification, expert anatomists continued to argue regarding slips which were the actual deep head of Cruveilhier; Henle's "interosseous primus volaris"; and the oblique adductor pollicis. Until the mid-20th century the deep thenar muscles were incorrectly (certainly inadequately) classified (*48; 49*). The variability of the nerve supply and insufficient developmental and phylogenetic data added to the challenge of reliable classification of some thumb muscles. The fact that electrophysiological (EMG) studies of the deep thenar muscles were nearly impossible due to the phenomenon of electrical "cross talk" between neighboring contracting muscles posed further difficulties evaluating their precise role in thumb movements.

It is baffling that from 1850 to 1960 no systematic investigation of the myological variation of thenar muscles were performed. Day and Napier (*48*, *49*) showed that the deep head of Cruveilhier was a distinct entity with several recognizable variants. Our investigations have confirmed and expanded the sample size of the variants of the deep head described by Day and Napier (*48*).

Furthermore, Kuhlmann and Guerin-Surville (*115*), Simard and Roberge (*116*), Perkins and Hast (*117*), and Van Sint Jan and Rooze (*114*) provide additional data on the variations/fascicles (including information on the nerve supply) of thumb muscles. The evolutionary significance of these variations is obvious. However, this data has clinical application. Surgeons equipped with knowledge of additional (supernumerary) muscle slips attached to the thumb may recruit them for reconstructive repair of injured thumb.

Highet (*71*) regretted the proclivity of anatomy education to overly simplify the innervation of the thenar muscles (exclusively by the recurrent branch of the median nerve). Despite clear demonstration of the complex dual nerve supply [by median and deep ulnar nerves see Day and Napier (*48*)], highly abbreviated textbooks (e.g., *118; 119*) designed for time-challenged contemporary anatomy programs do not sufficiently prepare students for the clinical experience (see comments by *71*). It is essential for students to appreciate the actual complexity of neuromuscular anatomy of the deep thenar space in advance of clinical experience, in which correct diagnosis leads to satisfactory treatment.

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Author Contributions

MAA, SSD, and JMZ envisioned and designed this project, collected the hands, dissected the muscles of the thenar compartment, analyzed the data, and wrote the manuscript. JMZ photographed the dissections and made the figure plates. MAA tabulated in detail the early literature regarding the heads of FPB.

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