

**Original Communication****Structural diversity of the vastus intermedius revealed by analysis of isolated muscle specimens**

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**Abbreviated title:** Structure of vastus intermedius

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1 **Structural diversity of the vastus intermedius origin revealed by**  
2 **analysis of isolated muscle specimens**

3

4 **Abstract**

5 **Introduction:** The (QF), a major extensor of the knee joint, plays an important role in  
6 human movement. However, descriptions of the three vastus muscles of QF remain  
7 confusing among anatomy textbooks. **Materials and Methods:** In the present study,  
8 we analyzed 33 QF with a newly invented methods employing isolated muscle  
9 specimens in order to clarify the origin structures of the vastus lateralis (VL), vastus  
10 medialis (VM), and vastus intermedius (VI). **Results:** The origins of the VL and VM  
11 were quite constant in shape and localization, whereas the VI exhibited structural  
12 diversity. In typical cases (23 of 33), the origin of the VI muscularly attached to the  
13 anterior and lateral surface of the femoral shaft. The origin of the VI adjoined that of  
14 the VL at the lateral lip of the linea aspera to form a common origin. In some cases  
15 (10 of 33), the muscle belly and origin of the VI were much smaller than those in the  
16 typical cases. The origin of the VI attached only to the anterior surface of the femur  
17 and did not contact the lateral lip. In addition, the muscle belly of the VI was narrow  
18 and almost corresponded to the width of the femoral shaft. **Conclusion:** The isolated  
19 muscle specimen is a useful tool to analyze individual muscle structure, which can be  
20 difficult to observe by routine dissection. By using this method, it became clear that  
21 the VI exhibits wide structural diversity in its origin compared with the VL and VM.

22 **Key Words:** quadriceps femoris; vastus intermedius; muscle origin; anatomic  
23 variation

24

## 1 Introduction

2 The quadriceps femoris (QF), a major extensor of the knee joint, plays a crucial role in  
3 human movement, such as standing, walking, and running (Bleck, 1979; Montgomery  
4 et al., 1994; Blazevich et al., 2006). The QF consists of four separate parts, the rectus  
5 femoris (RF), vastus medialis (VM), vastus lateralis (VL), and vastus intermedius (VI)  
6 (Willan et al., 2002) (**Fig. 1A**). The RF only originates from the small area of bony  
7 pelvis (the inferior anterior iliac spine). On the other hand, the VM, VL and VI arise  
8 from the femur, but not the pelvis. The VM mainly arises from the medial lip of the  
9 linea aspera. The VL arises from the lateral lip of the linea aspera and the anterior  
10 aspect of the lateral intermuscular septum (LIS) (**Fig. 1A**). The medial edge of LIS is  
11 attached to the lateral lip, therefore the two attachment regions of VL are continuous.

12 The descriptions on the origin of the RF, VL, and VM is consistent in the anatomy  
13 textbooks as described above. However, the description of the origin of the VI is  
14 different among the anatomy textbooks (as summarized in Table 1). Some textbooks  
15 described the VI originates from both from the shaft of femur and the LIS (Poirier,  
16 1893; Testut, 1899; Braus and Elze, 1954; Romanes, 1972; Moore, 1980; Hollinshead,  
17 1982; Williams, 1995), but others did not include the LIS as the attachment site of VI  
18 (Henle, 1855; Gegenbaur, 1890; Davis-Colley and Bardeen, 1907; Frohse and  
19 Fränkel, 1913; Staubesand, 1985).

20 Recent anatomical studies on the QF frequently have distinguished the  
21 longitudinal and oblique parts of the VL (Becker et al., 2009). However, because  
22 these two parts and their mutual relationship have not been clearly defined (Vieira,  
23 2011), the muscle belly found in the inferolateral part of the thigh has been regarded

1 as either the oblique part of the VL (Hallisey et al., 1987; Bevilaqua-Grossi et al.,  
2 2004) or the lateral part of the VI (Tomita et al., 2015).

3 In the present study, in order to clarify the origin structures of the three vastus  
4 muscles of the QF, in particular the VI, we analyzed isolated QF specimens. The  
5 isolated muscle specimen is a useful tool to individual muscle structure, which can be  
6 difficult to observe by routine dissection.

7

8



## 1 **Materials and Methods**

### 2 ***Cadaveric source***

3 All cadavers were from persons who donated their bodies for medical education and  
4 research to XXXXXX University School of Medicine. Prior to donation, written consent  
5 from persons and families was obtained. The protocol for the present research project  
6 was approved by the Ethics Committee of XXXXXX University School of Medicine  
7 (approval No. XXXXXX).

8 Thirty-three right lower extremities were collected from embalmed Japanese  
9 cadavers (21 males, 12 females; average age,  $79.2 \pm 10.9$  years), which were  
10 dissected by medical students in the gross anatomy course at XXXXXX University  
11 School of Medicine. In our dissection protocol for medical students, the left legs were  
12 dissected to observe the bones and ligaments, therefore the muscles, nerves, and  
13 vasculature were severely destroyed in the left legs. We thus used only the right legs,  
14 where the muscles remained without severe structural damage, in the present study.

15 We excluded the cadavers which exhibited the significant pathologic alteration in  
16 muscles (such as muscular dystrophy, fatty degeneration, and large intramuscular  
17 hematoma), the traumatic lesions, and the operative scars.

18

### 19 ***Isolation of muscle specimens***

20 The femoral muscles with fascia lata were exposed according to the routine  
21 procedures, and QF in the anterior fascial compartment was dissected out by  
22 removing the sartorius, hamstrings and adductor muscles. The isolated muscle  
23 specimens were prepared by detaching QF from the skeleton according to the  
24 following procedures (**Fig. 1B-D**). Firstly, the proximal end of RF was detached from

1 the pelvis, and the distal tendon of QF together with the articular capsule of knee joint  
2 was cut around the superior and lateral margins of patella and horizontally on the  
3 both sides of patella at the level of articular space. The distal end of QF was then  
4 lifted upwards and the proximal attachment of QF together with intermuscular septa  
5 on the femur was recorded, and then detached from the femur. The articularis genus  
6 on the deep surface was removed, and the deep surface of specimens was cleaned  
7 by removing soft connective tissue and fat.

8 The isolated QF specimens preserved the fundamental structure of QF *in situ*.  
9 The advantage of isolated specimens over the *in situ* specimens was found on its  
10 deep surface. The deep surface of specimens was divided into origin and non-origin  
11 domains depending on the surface texture. The origin domain was covered with  
12 either dense connective tissue of periosteum or stout fascial intermuscular septum,  
13 whereas the non-origin domain was covered by loose connective tissue and easily  
14 denuded to expose muscular fibers by blunt dissection.

15 The direction of muscle fibers of vastus muscles was clearly determined in the  
16 isolated muscle specimens. According to the direction of muscle fibers, we could  
17 identify the boundaries among the origin domains of vastus muscles.

## 1 Results

### 2 *The three vastus muscles in situ*

3 First, we removed the QF together with the femur and intermuscular septum and  
4 observed the superficial structure of the QF *in situ* (**Fig. 1B**). The QF was a massive  
5 muscle almost completely wrapping the femoral shaft (**Fig. 1B'**), except for the region  
6 between the lateral and medial lips of the linea aspera (**Fig. 1B'', C''**).

7 When viewed from the anterior side, the RF, VL, and VM were easily recognized  
8 (**Fig. 1B'**). As indicated by previous studies, the VL consisted of the main longitudinal  
9 part (VL-L) and the inferolateral oblique part (VL-O) (Hallisey et al., 1987;  
10 Bevilaqua-Grossi et al., 2004; Becker et al., 2009) (**Fig. 1D', D''**). The VI was almost  
11 completely covered by the RF and VL-L, but could be partially seen when the RF was  
12 removed (**Fig. 1B', D'**).

13 When viewed from the posterior side, the LIS was clearly recognized as a thick  
14 fibrous membrane (**Fig. 1B''**). The medial end of the LIS was attached to the lateral  
15 lip (**Fig. 1C''**), while the lateral end continued the iliotibial tract (data not shown).  
16 Unlike the LIS, the medial intermuscular septum was recognized as loose connective  
17 tissue that was easily removed by blunt dissection with tweezers. Instead of the  
18 medial intermuscular septum, the membranous tendon of origin of the VM attached to  
19 the medial lip (**Fig. 1B'', C''**).

20

### 21 *Origins of the three vastus muscles*

22 We could easily confirm that the RF originated from the inferior anterior iliac spine  
23 without observing the isolated muscle specimens, but to precisely examine the origin  
24 structures of the VL, VM, and VI, we needed to isolate the QF together with the LIS



1 from the femur (**Fig. 2**). The deep surface of the QF, which faced the femur and LIS,  
2 was subdivided into origin and non-origin domains. The origin domain arose directly  
3 from either the femur or the LIS, and was not easy to separate from these structures  
4 due to dense connection. On the other hand, the non-origin domain had indirect  
5 contact with the femur via loose connective tissue containing adipose tissue, and was  
6 easily detached from the femur. In all of the isolated specimens, we found the  
7 articularis genus on their deep surface and removed it from the vastus intermedius.

8

### 9 *Origins of VL and VM*

10 The VL possessed a stout membranous origin tendon on the superficial surface  
11 arising from the superior portion of femur including the greater trochanter (**Figs. 1C'**,  
12 **2A1–2**). On the deep surface of specimens, the origin domain of VL was found in the  
13 lateral region and divided into two subdomains, one for VL-L arising from both the  
14 femur and superior part of LIS, and the other for VL-O arising from the inferior part of  
15 LIS (**Fig. 2C1–3**). The origin domain of VL-L was further demarcated at its attachment  
16 to the lateral lip of the linea aspera into a superomedial part arising from the femur  
17 and an inferolateral part arising from LIS (arrowheads in **Fig. 2C1–3**). The  
18 superomedial part of VL-L origin domain arose from the superior portion of femur  
19 containing the anterior aspect of the greater trochanter, the small area of the gluteal  
20 tuberosity, and the superior one-fourth of the lateral lip (dark green area in **Fig. 2C2–**  
21 **3**). On the other hand, the inferolateral part of VL-L domain arose muscularly from the  
22 superior one-fourth of the anterior aspect of the LIS without tendon formation (light  
23 green area in **Fig. 2C2–3**). The origin domain of VL-O attached muscularly to the  
24 inferior three-fourths of the anterior aspect of the LIS also without tendon formation

1 (blue area in **Fig. 2C2–3**). In all of the specimens examined, the origin domains of the  
2 VL-L and VL-O were continuous to form a single domain which was almost constant  
3 in shape and location.

4 The VM possessed a narrow membranous origin tendon on the superficial surface  
5 arising from the posterior aspect of femur (solid circles in **Fig. 2A1–2**). On the deep  
6 surface of specimens, the origin domain of VM was found along the medial edge  
7 arising solely from the posterior region of femur containing the intertrochanteric line  
8 and the medial lip of linea aspera (purple area in **Figs. 1C2", 2C2–3**), and not from  
9 the intermuscular septum, since the medial part of intermuscular space was formed  
10 by loose connective tissue containing blood vessels and nerves practically lacking  
11 fascial intermuscular septum. In all of the specimens examined, the origin domain of  
12 the VM exhibited almost constant in shape and location (**Fig. 3**).

13

#### 14 *Origin of VI*

15 The VI typically arose muscularly from the anterior and lateral aspect of femur without  
16 origin tendon (**Figs. 1C', 2B1–2**). On the deep surface of specimens, the origin  
17 domain of VI was found in the superior two thirds of central region arising from the  
18 femur (**Fig. 2C1–2**). The shape and area of the origin domain of VI exhibited  
19 remarkable diversity compared with those of VL and VM (**Fig. 3**). In particular, the  
20 topographical variation of origin domain of the VI was remarkable in relation to the  
21 origin domain of VL, either contacting the lateral lip of linea aspera forming a  
22 continuous region with that of VL (**Figs. 3A1–23, 4A1–2**) or separated from it forming  
23 an isolated region (**Figs. 3B1–10, 4B1–2**). Thus, we classified the origin domain of



1 the VI into contacting and non-contacting types based on its positional relationship to  
2 the origin domain of the VL.

3 In the contacting type (23 of 33 cases), the origin domain of the VI muscularly  
4 attached to the anterior and lateral surface of the femoral shaft (**Fig. 4A1–2**). The  
5 muscle belly of the VI decreased in thickness from its anterior to lateral parts. The  
6 origin domain of the VI adjoined that of the VL-L at the lateral lip of the linea aspera to  
7 form a common origin domain.

8 In the non-contacting type (10 of 33 cases), the muscle belly and origin domain of  
9 the VI were much smaller than those in the contacting type (**Fig. 3**). The origin  
10 domain of the VI attached only to the anterior surface of the femur and did not contact  
11 the lateral lip of the linea aspera (**Fig. 4B1–2**). The muscle belly of the VI was narrow  
12 and almost corresponded to the width of the femoral shaft. The non-origin domain of  
13 the VL was seen between the origin domains of the VI and VL.

14

## 1 Discussion

2 Anatomical analysis of the three vastus muscles can be difficult due to their broad  
3 attachment to the femur, which makes them hardly manipulable in embalmed  
4 cadavers. In the present study, we analyzed isolated QF specimens, which allow for  
5 manipulation without restriction by the skeleton and direct observation of the deep  
6 surface of the muscles. By using this method, we precisely determined the origins of  
7 the three vastus muscles and found wide structural diversity of the VI.

8 The three-dimensional relation between muscles and skeletons is crucial to  
9 understand the muscle function, but this relation is completely disrupted in the  
10 isolated muscle specimens. The *in situ* muscle specimens that remain the attachment  
11 to the skeletons have an advantage in the anatomical analysis of muscle function.  
12 Therefore, to comprehensively understand the structure and function of muscles, it  
13 was needed to analyze both *in situ* and isolated muscle specimens.

14 In previous anatomy textbooks, the origin of the VI from the femur was  
15 consistently regarded as the anterior and lateral aspects of the femoral shaft (Table 1).  
16 However, the description of the origin of the VI from the LIS was controversial. Some  
17 textbooks described the VI as originating from the anterior aspect of the LIS with or  
18 without the VL (Poirier, 1893; Testut, 1899; Braus and Elze, 1954; Romanes, 1972;  
19 Moore, 1980; Hollinshead, 1982; Williams, 1995). Others did not mention the origin of  
20 the VI from the LIS (Henle, 1855; Gegenbaur, 1890; Davis-Colley and Bardeen, 1907;  
21 Frohse and Fränkel, 1913; Staubesand, 1985). Based on the present study using  
22 isolated muscle specimens, we confirmed that the VI originated only from the femoral  
23 shaft, and not from the LIS, as described by the latter group of textbooks.

24 In this study, we also revealed that the origin domains of the VL and VM were

1 relatively constant in shape and localization, but that the VI exhibited structural  
2 diversity, which has not been reported to the best of our knowledge. There are some  
3 reasons why the structural diversity of the VI has not been recognized. One is a  
4 methodologic reason. Previous anatomical studies were based on observation of  
5 skeletal muscles attached to the skeleton *in situ*. Although this ordinal method has the  
6 advantage of easy comprehension of muscle action on the skeleton, it is difficult to  
7 observe the deep attachment of the VI. Another reason is that the origin of the VI is  
8 not frequently treated during major surgical procedures on the hip joint.

9 The muscle fusion between the VL and VI has been reported in previous studies  
10 (Willan et al., 1990; Becker et al., 2009). In an extreme case, described that the VL  
11 and VI could not be distinguished, and, instead, that the extensor apparatus of the  
12 knee could be regarded to possess only three muscle heads (Frohse and Fränkel,  
13 1913). In the contacting type of VI, which was described here, the origin domains of  
14 the VL and VI were continuous. Thus, the QF associated with the contacting type of  
15 VI could be regarded as the “triceps femoris,” as mentioned by (Frohse and Fränkel,  
16 1913). However, the QF associated with the non-contacting type of VI clearly  
17 exhibited four separate muscle heads, as previously considered.

18 The structural diversity of the VI origin domain observed in the present study was  
19 simply correlated with the difference of muscle mass of VI. The muscle belly of the VI  
20 had constant location and morphology attaching to the anterior aspect of the femoral  
21 shaft, and decreasing thickness from the anterior to lateral parts. The contacting type  
22 of VI with larger origin domain would be explained by extensive development and  
23 lateral expansion of VI, while the non-contacting type with smaller origin domain  
24 would be resulted from poor development and limited mass of VI. We could not find



1 any sings of difference of developmental origin of VI from the muscle morphology,  
2 although we could not analyze the innervation of VI due to limitation of methods using  
3 the isolated muscle specimens.

4 The functional contribution of VI was estimated to be largest among the three  
5 vastus muscles of QF (Zhang et al., 2003). Recent investigators tried to measure the  
6 electromyographic activity of VI by surface and needle electrodes, on the assumption  
7 that the inferolateral part of QF would represent VI on the basis of MRI imaging  
8 (Watanabe and Akima, 2009; Saito and Akima, 2015; Tomita et al., 2015), but the  
9 present study revealed undoubtedly that this muscular part actually represented VL-O  
10 instead of VI. Furthermore in view of the conspicuous variation in the expansion of  
11 origin domain as well as muscle mass of VI, the feasibility of simple estimation of  
12 major functional role of VI in knee flexion appeared to be doubtful. Concerning the  
13 clinical aspects, VI did not became a specific site of traumatic injuries or objects of  
14 surgical intervention, except for rare cases such as VI tendon rupture (Thompson et  
15 al., 2008; Cetinkaya et al., 2015) or trans-VI transfer of pedicled thigh flap (Batdorf et  
16 al., 2013), because of its deep location in the thigh covered by the other vastus  
17 muscles.

18 As a future issue, we need to evaluate the morphology of the VI and to examine  
19 how the structural diversity of the VI influences the movement of the knee joint and  
20 the stability of the patellofemoral joint. Now we first challenges to evaluate the  
21 three-dimensional morphology of the three vastus muscles in healthy living  
22 individuals by using magnetic resonance imaging and reconstruction technique.

1        In conclusion, the isolated muscle specimen is a useful tool to analyze individual  
2 muscle structure. By using this method, it became clear that the VI exhibits wide  
3 structural diversity in its origin compared with the VL and VM.

4



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6

7 **Conflicts of interest**

8 The authors have no conflicts of interest to declare.

9

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1 **Figure Legends**

2 **Figure 1.** Process of isolation of quadriceps femoris (QF) is explained by schematic  
 3 drawings (A-D) and photographs (B'-D', B''-D''). (A) Un-dissected right thigh. Cross  
 4 section at the middle of thigh. The five parts of QF are depicted in green (longitudinal  
 5 part of the vastus lateralis [VL-L]), blue (oblique part of the vastus lateralis [VL-O]),  
 6 yellow (vastus intermedius [VI]), purple (vastus medialis [VM]), and gray (rectus  
 7 femoris [RF]). (B, B', B'') Isolated QF together with the femur and lateral  
 8 intermuscular septum (LIS) from the right thigh. The femur and QF are subsequently  
 9 separated by sharp dissection as indicated by a long double arrow. The RF is  
 10 reflected downward to expose the VI (B'). (C, C', C'') Isolated femur. The attachment  
 11 sites of the three vastus muscles on the femur are depicted in green (VL-L), blue  
 12 (VL-O), yellow (VI), and purple (VM). The VL-O and VM are attached to the lateral lip  
 13 (LL) and medial lip (ML) of the linea aspera. (D, D', D'') QF isolated from the femur.  
 14 The specimen is unfolded. The RF is reflected downward to expose the VI (D').  
 15 Asterisks in D', origin tendon of VL-L; Solid circles in D', origin tendon of VM;  
 16 Arrowhead in D'', attachment site to the lateral lip. (B', C') Anterior view. (B'', C'')  
 17 Posterior view. (D') Superficial surface view. (D'') Deep surface view. Abbreviations:  
 18 GT, greater trochanter.

19

20 **Figure 2.** Superficial and deep surfaces of isolated right QF. (A1, A2, B1, B2)  
 21 Superficial surface view of the three vastus muscles. The RF is reflected downward to  
 22 expose the VI. Membranous origin tendons are found at the VL-L (asterisks in A1,  
 23 A2) and the VM (solid circles in A1, A2). In B1 and B2, the VL-L is reflected to further  
 24 expose the VI. Membranous insertion tendons are found on the VL-L (asterisks in B1,



1 **B2**) and the VI (solid circles in **B1, B2**). (**C1, C2, C3**) Deep surface view of the three  
2 vastus muscles. The origin domains are depicted in yellow (VI), blue (VL-O), and  
3 purple (VM). The VI exhibits a contacting type of origin domain. The origin domain of  
4 the VL-L is subdivided into the superomedial and inferolateral parts by its attachment  
5 to the lateral lip (LL) of the linea aspera (arrowheads in **C2, C3**). The superomedial  
6 and inferolateral parts are depicted in dark and light green, respectively. (**C3**) The  
7 three vastus muscles separated by sharp dissection.

8

9 **Figure 3.** Schematic illustrations showing the origin domains of the three vastus  
10 muscles in all of the cases examined. The origin domains of the longitudinal part of  
11 the vastus lateralis (VL, green), oblique part of the VL (blue), and vastus medialis  
12 (purple) were quite constant in shape and localization, whereas the vastus  
13 intermedius (VI, yellow) exhibited wide structural diversity. The origin domain of the VI  
14 was subdivided into contacting and non-contacting types based on the positional  
15 relationship to the origin domain of the VL. In the contacting type (23 of 33 cases, **A1–**  
16 **A23**), the origin domain of the VI muscularly attached to the anterior and lateral  
17 surface of the femoral shaft. The origin domain of the VI adjoined that of the VL at the  
18 lateral lip of the linea aspera to form a common origin domain. A deep indentation was  
19 frequently found at the origin domain of the VI (arrows in **A6, A9, A10, A13–A16,**  
20 **A18–A20, and A23**). In the non-contacting type (10 of 33 cases, **B1–B10**), the  
21 muscle belly and origin domain of the VI were much smaller than those in the  
22 contacting type. The origin domain of the VI attached only to the anterior surface of  
23 the femur and did not contact the lateral lip. In addition, the muscle belly of the VI was  
24 narrow and almost corresponded to the width of the femoral shaft. Abbreviations: I,

1 vastus intermedius; L, longitudinal part of the vastus lateralis; M, vastus medialis; O,  
2 oblique part of the vastus lateralis.

3

4 **Figure 4.** Schematic illustrations showing the attachment sites of the VI on the femur  
5 in the cases of contacting type (**A1, A2**) and non-contacting type (**B1, B2**). The  
6 attachment sites are depicted in yellow (VI), green (VL-L), blue (VL-O), and purple  
7 (VM). (**A1, B1**) Anterior view. (**A2, B2**) Posterior view. GT, greater trochanter; LL,  
8 lateral lip; ML, medial lip.

9

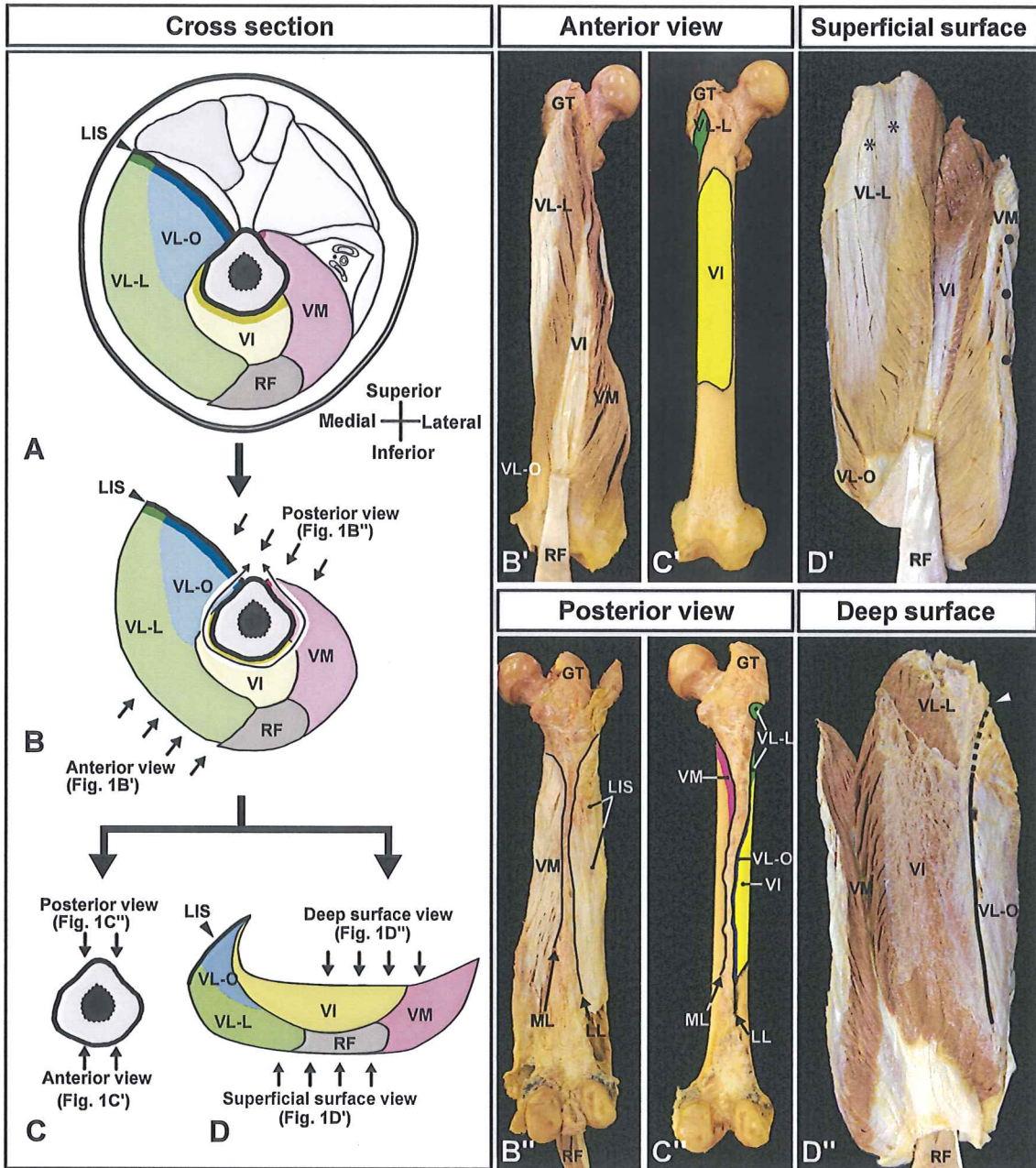
1 **Table 1.** Descriptions of the vastus muscles among anatomy textbooks

<b>Book title</b>	<b>Author(s) (year)</b>	<b>Vastus muscles originating from LIS</b>		<b>Origin of VI from femoral shaft</b>
Gray's Anatomy (38th ed.)	Williams (1995)	VL	VI	Anterior and lateral
Cunningham's Textbook of Anatomy (11th ed.)	Romanes (1972)	VL	VI	Anterior and lateral
Clinically Oriented Anatomy (1st ed.)	Moore (1980)	VL	VI	Anterior and lateral
Anatomy for Surgeons (3rd ed.)	Hollinshead (1982)	VL	VI	Anterior and lateral
Morris's Human Anatomy (4th ed.)	Davis-Colley and Bardeen (1907)	VL		Anterior and lateral
Handbuch der Muskellehre des Menschen (1st ed.)	Henle (1855)	VL		Anterior
Lehrbuch der Anatomie des Menschen (4th ed.)	Gegenbaur (1890)	VL		Anterior and lateral
Anatomie des Menschen (3rd ed.)	Braus and Elze (1954)		VI	Anterior and lateral
Benninghoff's Makroskopische und Mikroskopische Anatomie des Menschen (14th ed.)	Staubesand (1985)			Anterior and lateral
Handbuch der Anatomie des Menschen (1st ed.)	Frohse and Fränkel (1913)	VL		Anterior
Traité d'Anatomie Humaine (4th ed.)	Testut (1899)		VI	Anterior and lateral
Traite d'Anatomie Humaine (1st ed.)	Poirier (1893)	VL	VI	Anterior and lateral

2 Abbreviations: LIS, lateral intermuscular septum; VI, vastus intermedius; VL, vastus lateralis.

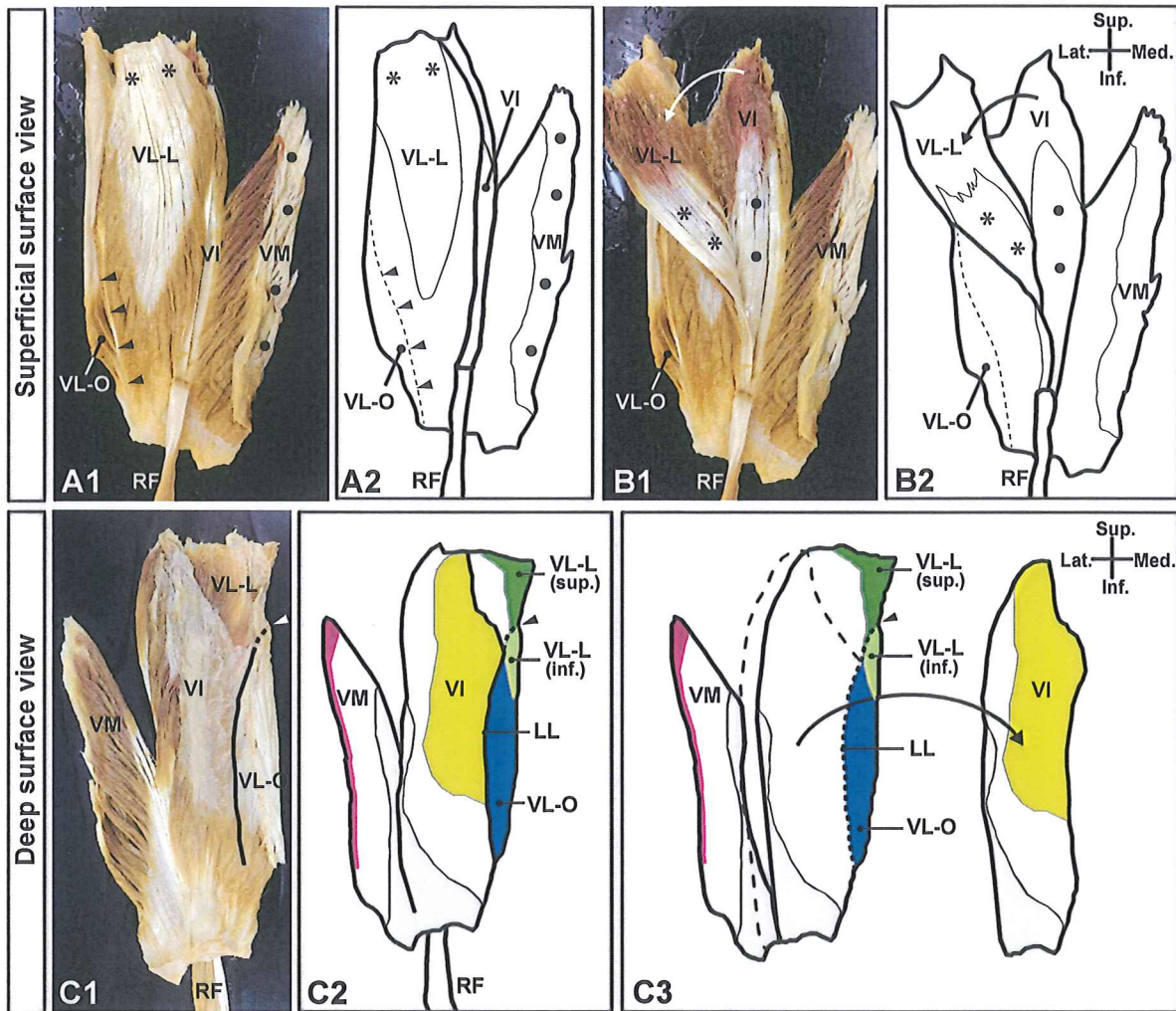
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**Figure 1**  
Yoshida et al.

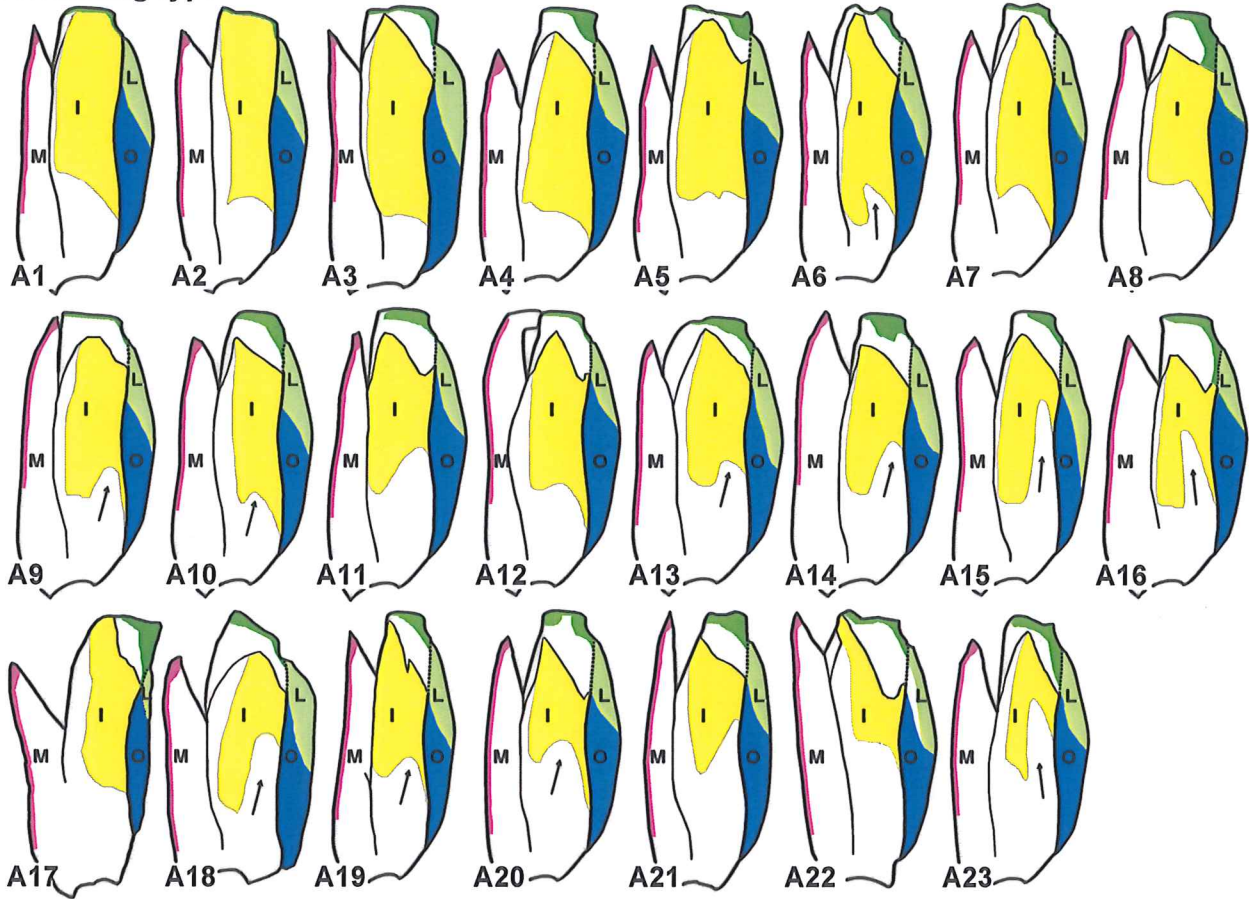




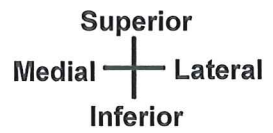
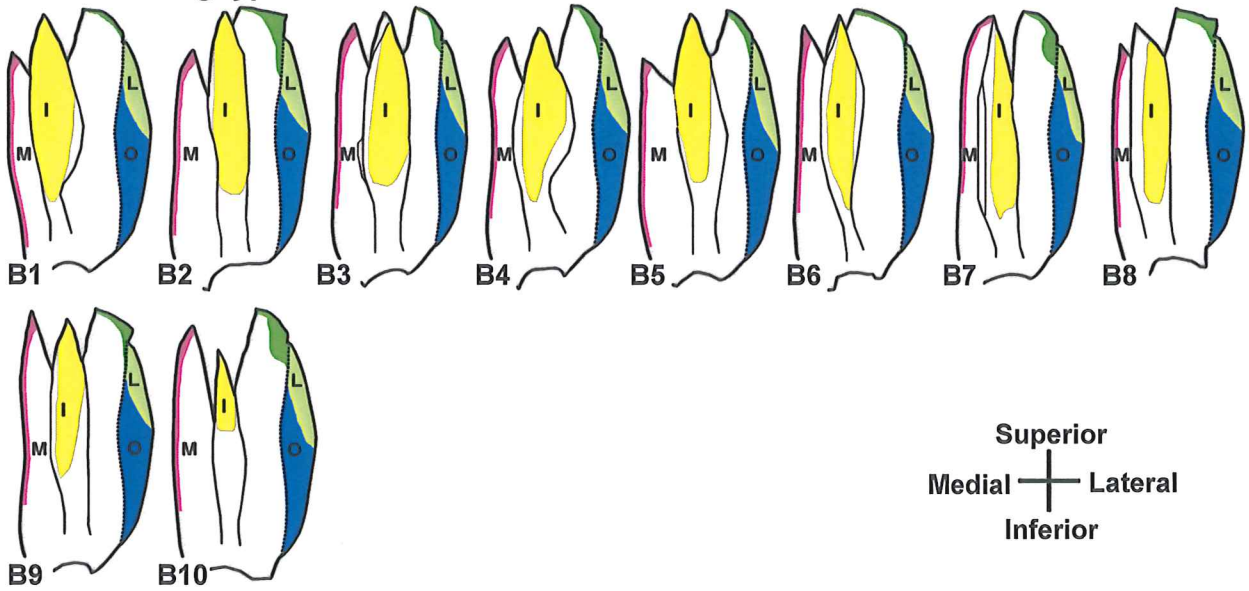
**Figure 2**  
Yoshida et al.



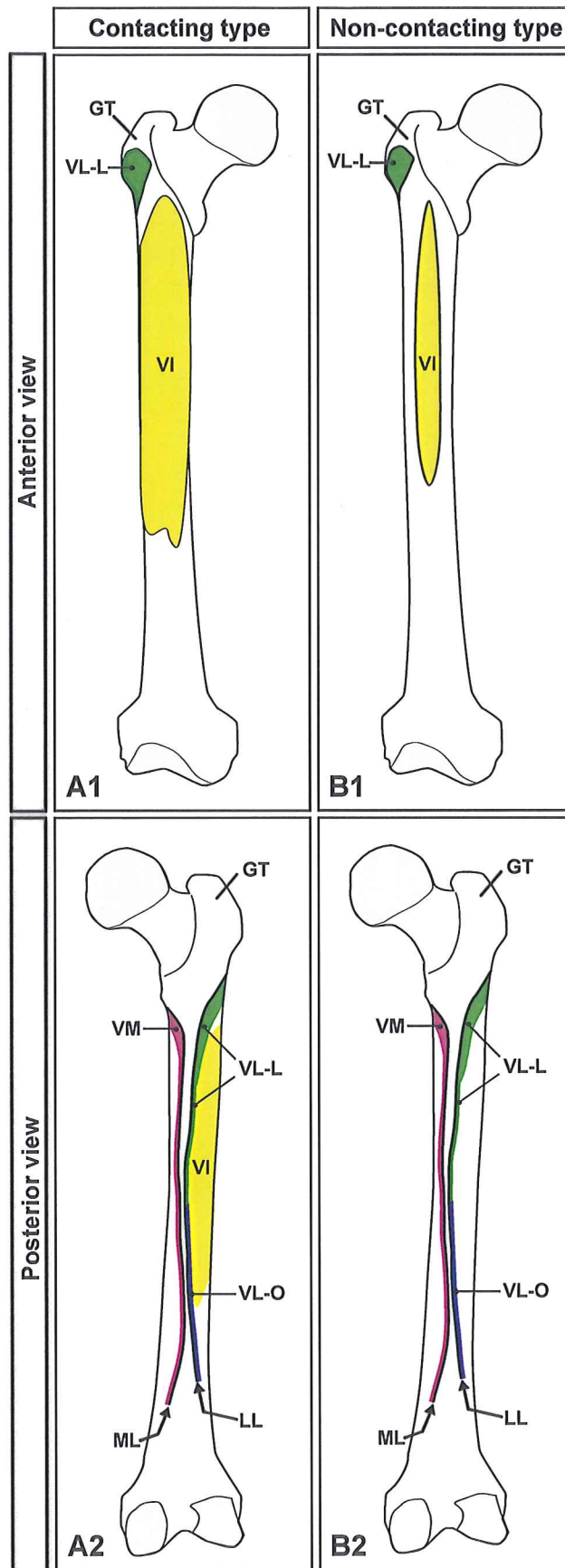
**Contacting type**



**Non-contacting type**



**Figure 3**  
Yoshida et al.



**Figure 4**  
Yoshida et al.