

Revision of the muscular anatomy of the paired fins of the living coelacanth *Latimeria chalumnae* (Sarcopterygii: Actinistia)

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As a sarcopterygian fish, the extant coelacanth *Latimeria* has muscular paired fins, different in their skeletal and muscular anatomy from the paired fins of actinopterygians. Although the muscular anatomy of the pectoral and pelvic fins of *Latimeria* has been described by several studies, a detailed functional description of the muscles and their architecture has never been performed. Our detailed functional description of the muscles of the paired fins shows a more complex organization than previously described. The pectoral and pelvic fins have a different organization of their muscular anatomy, and the pelvic fin shows a more plesiomorphic configuration of the muscles since most of them are poly-articular and run from the pelvic girdle to the fin rays, an organization typical of actinopterygians. We found that the pectoral fins are stronger than the pelvic fins which is likely to be associated with the greater contribution of the pectoral fins to locomotion and manoeuvring. Finally, the study of the joint mobility of the paired fins showed that the pectoral fins show greater mobility than the pelvic fins. The reduced mobility of the pelvic fin is possibly a consequence of the morphology of the mesomeres and the large pre-axial radials.

ADDITIONAL KEYWORDS: anatomical cross-section area – mobility – muscles – pectoral fin – pelvic fin – sarcopterygians.

INTRODUCTION

Most living vertebrates are bony fishes (Osteichthyes) whose evolutionary success is in part due to the morphological diversification of the paired appendages allowing their invasion of novel environments (Drucker & Lauder, 2002; Kardong, 2018). Based on the anatomical organization of pectoral and pelvic appendages, osteichthyan fishes are divided into two groups: the ray-finned fishes (Actinopterygii) grouping the vast majority of extant bony fishes and the sarcopterygians including lobe-finned fishes (extant coelacanths, lungfishes) and tetrapods (Diogo & Abdala, 2007; Amemiya *et al.*, 2013; Nelson *et al.*, 2016; Amaral & Schneider, 2018; Kardong, 2018).

The pectoral and pelvic fins of actinopterygian fishes are internally supported by bony spines (fin rays or lepidotrichia) that are directly attached to the body at the level of the pectoral and pelvic girdles by several basal skeletal elements (radials) connected to three basal cartilages (polybasal articulation). By contrast, the lepidotrichia of the paired fins of sarcopterygian fishes are connected to an endoskeleton composed of several adjacent elements (mesomeres) forming an axis (metapterygial axis) that is joined to the body by a single endoskeletal element (monobasal articulation), the first mesomere (Johanson *et al.*, 2007; Zhu & Yu, 2009; Kardong, 2018). In addition to endoskeletal differences, fin movements in actinopterygians are mainly controlled by relatively small abductor and adductor muscles located within the body, whereas these muscles are larger and located largely outside the body within the lobed fins in sarcopterygians

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(Millot & Anthony, 1958; Wilhelm *et al.*, 2015; Diogo *et al.*, 2016; Miyake *et al.*, 2016; Kardong, 2018).

Among sarcopterygians, coelacanths (Actinistia) include two extant species, i.e., the African coelacanth *Latimeria chalumnae* (Smith, 1939) and the Indonesian coelacanth *Latimeria menadoensis* (Erdmann *et al.*, 1998). However, fossil forms were extremely diverse from the Early Devonian to the Late Cretaceous and varied in shape, size and ecology (Agassiz, 1839; Erdmann *et al.*, 1998; Forey, 1998; Nulens *et al.*, 2011). Living coelacanths are large-bodied marine fishes, that measure up to 2 m in length and may weigh up to 105 kg (Nulens *et al.*, 2011). They are predatory fishes that live around deep-water caves and rugged terrain at depths between 110 and 400 m (Fricke *et al.*, 1987; Fricke & Hissmann, 1992; Hissmann *et al.*, 2006). The anatomy of the pectoral and pelvic fins of the African coelacanth *L. chalumnae* was extensively studied by Millot & Anthony (1958) and subsequently revised by many authors (Ahlberg, 1992; Diogo *et al.*, 2016; Miyake *et al.*, 2016). More recently, Miyake and co-authors (2016) studied the arrangement and function of the pectoral fin muscles.

Even though coelacanths are bottom dwelling, the hypothesis that these animals walk on substrate, similar to tetrapods, has been refuted by numerous observations in their natural environment (Fricke *et al.*, 1987, 1991; Fricke & Hissmann, 1992; Hissmann *et al.*, 2006). Coelacanths most often swim in a slow manner while maintaining a stiff and inflexible body. Propulsion is generated by the lobed, paired and unpaired fins (Fricke & Hissmann, 1992). The caudal fin is used mainly during accelerations. During slow continuous locomotion the second dorsal fin and anal fin as well as both pectoral fins typically show large amplitude movements whereas the amplitude of pelvic fins is lower (Fricke & Hissmann, 1992). Moreover, the paired fins are highly mobile and display atypical movements including figure of eight motions of the pectoral fin during forward swimming, or elliptical motions of the pelvic fins (Décamps *et al.*, 2017). Fricke & Hissmann (1992) hypothesized that the muscular part of the pelvic fin is shorter than that of the pectoral fin and that the mobility of the pelvic fin is limited compared to the pectoral fin; however, this remains to be tested.

Although the paired fins of the coelacanth are a derived condition in sarcopterygian fish, they are structurally comparable to the limbs of tetrapods and appear to develop in a similar way (Shubin & Alberch, 1986; Ahlberg, 1992; Diogo *et al.*, 2016). Compared to lungfish fins, the paired fins of coelacanths have been hypothesized to better reflect the ancestral sarcopterygian condition (Coates *et al.*, 2002; Friedman *et al.*, 2007). Consequently, coelacanths have been considered as one of the best

living models to infer the basal tetrapod condition in terms of anatomy, development and genetics (Ahlberg, 1992; Coates, 1994; Diogo & Abdala, 2007; Diogo *et al.*, 2016; Miyake *et al.*, 2016; Amaral & Schneider, 2018). Despite several studies describing the muscular anatomy of the pectoral and pelvic fins in coelacanths, little is known about the architecture of the musculoskeletal system of these paired appendages. However, an understanding of the muscle architecture is essential to understand the function and role of the different appendages during locomotion and the changes that occurred during the water-to-land transition.

The aim of the present study is to provide a detailed functional description of the muscular anatomy (i.e., muscle arrangement, muscle mass, anatomical cross-sectional area) of the paired fins of the living coelacanth *L. chalumnae*. Moreover, we provide data on the mobility of the endoskeletal axis (e.g., joint mobility) and compare it between the pectoral and pelvic fins. This will provide a better understanding of the functional role of the paired fins in the unique swimming mode of the extant coelacanth in addition to provide base-line data for future modelling studies.

MATERIAL AND METHODS

SPECIMENS STUDIED

Two specimens of the extant African coelacanth *L. chalumnae* were used for dissections: CCC 14 and CCC 27 (Nulens *et al.*, 2011). The specimen CCC 14 is an adult male specimen of 134 cm in total length (TL) and weighs 39 kg. It was captured in the region of Dzahadjou, Hambou, off the coast of Grande Comore Island in 1956. The specimen CCC 27 is an adult male specimen of 132 cm TL and weighs 38 kg, captured off the coast of Grande Comore Island in 1961. Both specimens are preserved in a 6–7% formaldehyde solution and stored in the collections of the Museum national d'Histoire naturelle (MNHN) in Paris, France, under the collection numbers MNHN-ZA-AC-2012-11 and MNHN-ZA-AC-2012-21, respectively. The isolated pectoral fin of a third specimen was used for the study of the joint mobility of the fins, specimen CCC 19 (MNHN-ZA-AC-2012-15; Nulens *et al.*, 2011). This specimen is a male of 140 cm TL and weighs 35 kg, captured in 1959 off the coast of Grande Comore Island. It was dissected and the pectoral fin is preserved in a 6–7% formaldehyde solution.

DISSECTIONS

The two specimens of *L. chalumnae* were immersed in water for 1 week before anatomical dissections in

order to remove the formaldehyde. The left pectoral fin of specimen CCC 14 and the left pelvic fin of specimen CCC 27 were dissected. The preservation of the specimens provided an exceptional preservation of the muscular tissues with no noticeable deterioration. The preservation of the specimens showed a slight retraction of the muscle tissues, allowing us to easily identify the muscle bundles during the dissections (Supporting Information, Fig. S1). For each fin, the origin and insertion sites of the muscle bundles were noted and muscle bundles were photographed, removed with care and classified into functional groups. Photographs were taken *in situ* at each stage of the dissection (Supporting Information, Fig. S2). After removal muscle bundles were directly placed in a 70% aqueous solution of ethanol. After the complete dissection of each fin, the length of all muscle bundles was measured using a ruler (± 1 mm), blotted dry and weighed using an analytical balance (Mettler AE100, ± 0.00001 g) or an electronic balance (Ohaus Scout Pro, ± 0.01 g). The total length of each muscle bundle was defined as the maximal distance between the origin and insertion of the muscle bundle (from the most proximal origin of the muscular part to the most distal insertion, excluding tendons or aponeuroses).

MUSCLE ARCHITECTURE

The mass and length of the muscles were used to quantify the anatomical cross-section area (ACSA) of each muscle bundle as an estimator of its force-generating capacity (Loeb & Gans, 1986). The ACSA is based on the bundle mass (m), a standard muscular density (ρ) and the muscle bundle length (L) using the following equation:

$$ACSA [\text{cm}^2] = m [\text{g}] / (\rho [\text{g} \cdot \text{cm}^{-3}] * L [\text{cm}])$$

Since the value of the muscular density of *L. chalumnae*, and more generally of lobe-finned fishes, remains unknown, we here used the values reported for fish ($1.06 \text{ g} \cdot \text{cm}^{-3}$) (Dabrowski, 1978).

JOINT MOBILITY

To compare the mobility of the different articulations of the pectoral and pelvic fins, we measured the mobility of each joint along the metapterygial axis after complete dissection but with the ligaments intact. We also had the opportunity to measure the joint mobility of the already dissected pectoral fin of CCC 19. To do so, we introduced two needles parallel to one another in the two bony elements involved in the joint (Moon, 1999). Then, the elements were moved maximally without damaging ligaments or joint capsules to estimate the degree of freedom of the joint for adduction/abduction, protraction/retraction and pronation/supination

movements (see below for definitions used here). For example, we introduced one needle on mesomere 1 and the other on mesomere 2 to determine the mobility of the joint between mesomere 1 and mesomere 2 and we photographed each maximum position. For each movement, five measures were taken, after returning the joint to the resting position of the fin. The resting position of each fin is defined in the *Results*. The angle formed by the needles was then determined using the software Fiji (v.ImageJ 1.52p, Java 1.8.0_172), and the mean maximal angle was calculated for each movement.

DATA AVAILABILITY

The data underlying the study are available in the main tables and in the Supporting Information.

RESULTS

The first anatomical description of the paired fins of *L. chalumnae* was done by Millot & Anthony (1958). The nomenclature used in the present study follows that of Diogo *et al.* (2016). The nomenclature used by Miyake *et al.* (2016) for the pectoral fin of the coelacanth is similar to that used by Diogo *et al.* (2016). The correspondence between the nomenclature used by Millot & Anthony (1958), Diogo *et al.* (2016) and the present work is shown in Tables 1 to 6. As previously described, both the pectoral and pelvic fin musculature is organized in three different layers: the superficial layer just beneath the scales, the middle layer, and the deep layer that overlaps the endoskeleton of the fin (Millot & Anthony, 1958; Diogo *et al.*, 2016; Miyake *et al.*, 2016).

OSTEOLOGICAL ANATOMY OF THE PAIRED FINS

We provide here a short description of the osteology of the pectoral and pelvic fins of *L. chalumnae* (Fig. 1). A more extensive description is available in the literature (see Millot & Anthony, 1958; Mansuit *et al.*, 2020a, b).

The pectoral girdle has an arc shape and is formed by four flattened dermal bones (the anocleithrum, cleithrum, extracleithrum and clavicle) and a massive endoskeletal scapulocoracoid element (Fig. 1A). The pelvic girdle is formed by a single endoskeletal bone containing a flat and curved lateral process, a short and triangular medial process, a rod-like cartilaginous anterior process and a small postero-superior process. The anterior part of the pelvic girdle presents a highly ossified surface and internal trabecular system (Fig. 1B).

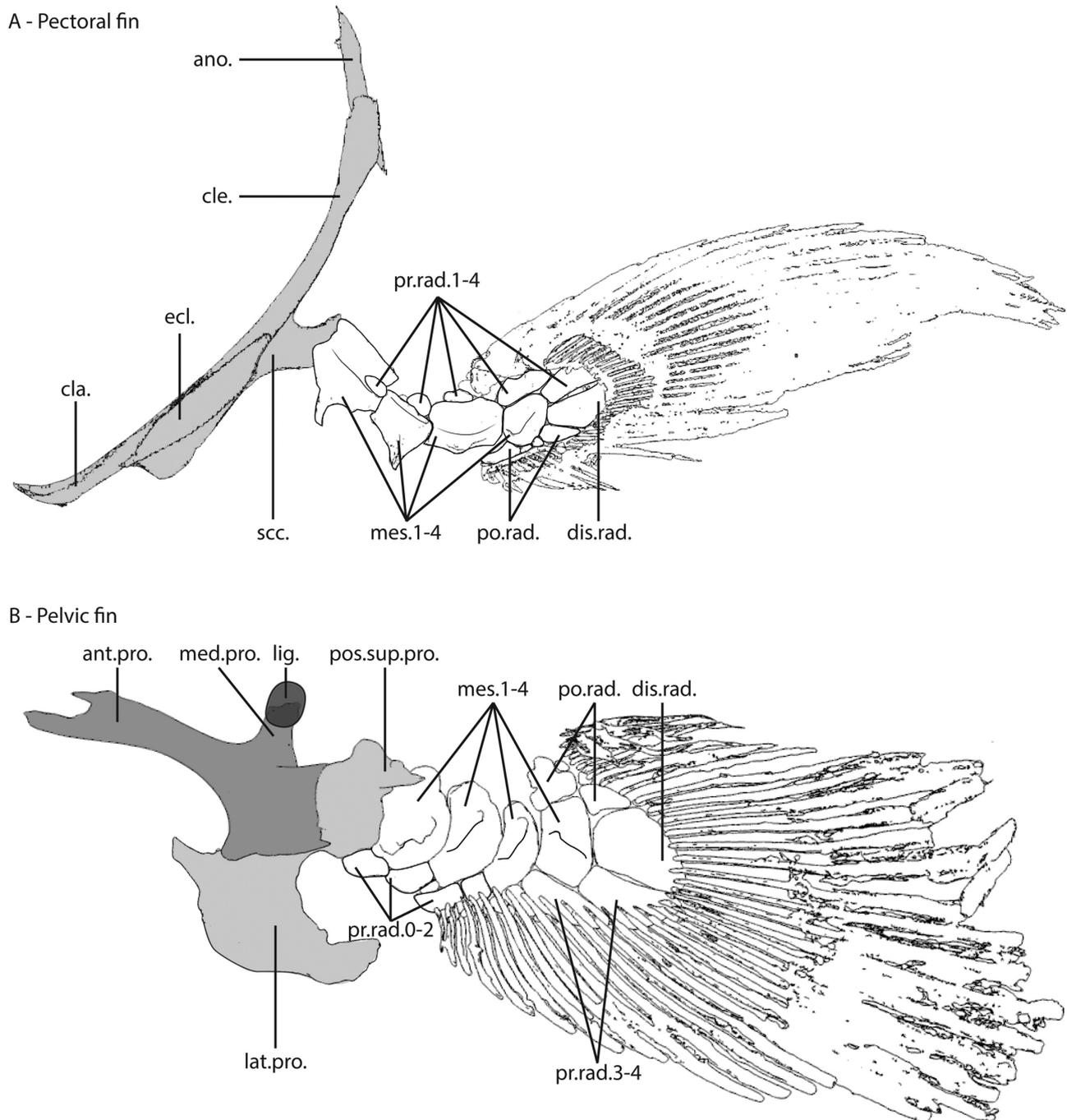


Figure 1. Comparison of the skeletal anatomy of the pectoral (A) and pelvic (B) fin of *L. chalumnae*. The shaded parts correspond to the pectoral (A) and pelvic (B) girdle. The dark grey part (B) corresponds to the dense ossification of the pelvic girdle associated with a trabecular system. ano.: anocleithrum; ant.pro.: anterior process; cla.: clavicle; cle.: cleithrum; dis.rad.: distal radial; ecl.: extracleithrum; lat.pro.: lateral process; lig.: “ligament-ball”; med.pro.: medial process; mes.: mesomere; pos.sup.pro.: postero-superior process; po.rad.: post-axial radial; pr.rad.: pre-axial radial; scc.: scapulocoracoid.

The left and right medial processes are linked to each other by a “ligament ball”.

The pectoral and pelvic fins have a similar organization, with the metapterygial axis formed by four

mesomeres associated with pre-axial radial elements and post-axial radial elements. The most proximal pre-axial radial elements are small and globular in shape, whereas the most distal pre-axial radials (pr.rad.3–4)

are elongated, trapezoidal in shape, and associated with dermal fin rays in both fins. The post-axial elements are formed by the post-axial radials and the distal radial (elongate and trapezoidal in shape), and are associated with dermal fin rays. The pelvic fin presents a supernumerary pre-axial radial, called pre-axial radial 0, associated with mesomere 1 and the pelvic girdle (Millot & Anthony, 1958; Mansuit *et al.*, 2020b).

PECTORAL MUSCLE ANATOMY

Eighty-six muscle bundles, organized into 13 functional groups, were identified in the pectoral fin of *L. chalumnae*. Similarly to Mansuit *et al.* (2020a), the resting position of the pectoral fin is considered as the fin positioned along the body with its leading edge oriented dorsally (Fig. 2). In this position, the muscles on the lateral side are abductor muscles protracting the fin and those on the medial side are the adductor muscles retracting the fin. Following this position, movements of the pectoral fin are defined as follows:

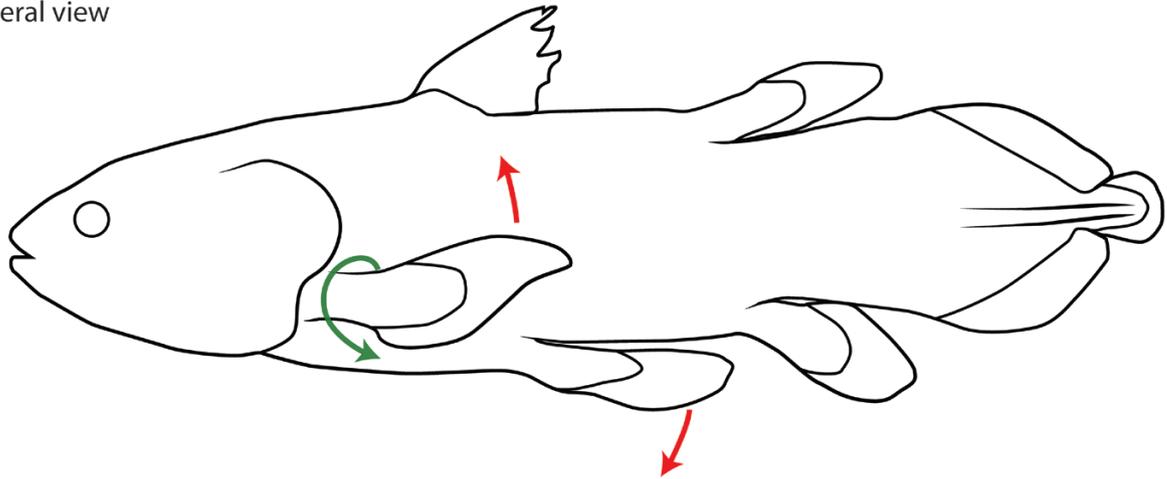
1. Protraction: the lateral side of the fin has a forward movement.
2. Retraction: the medial side of the fin has a backward movement.
3. Abduction: the pre-axial edge of the fin has an upward movement.
4. Adduction: the pre-axial edge of the fin has a downward movement.
5. Pronation: the lateral side of the fin has a downward pivoting movement around the axis of the fin.
6. Supination: the lateral side of the fin has an upward pivoting movement around the axis of the fin.

SUPERFICIAL LAYER

(TABLE 1)

The superficial layer of the pectoral fin is formed by two muscle masses: the abductor superficialis muscles on the lateral side and the adductor superficialis muscles on the medial side of the pectoral fin (Fig. 3).

A - Left lateral view



B - Ventral view

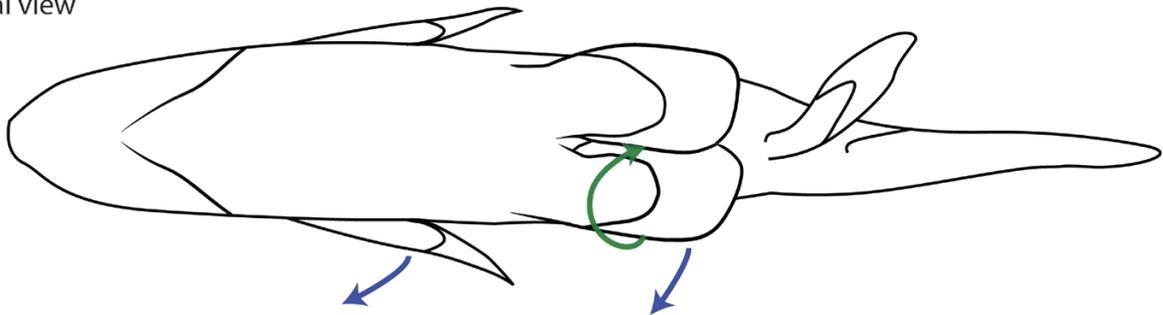


Figure 2. Pectoral and pelvic fins in their resting position in lateral (A) and ventral (B) views. The red arrows correspond to the abduction movement of the fins, the blue arrows to the protraction movement of the fins and the green arrows to the pronation movement of the fins, when fins are in their resting positions. The antagonist movements are not represented here.

Table 1. Muscles of the superficial layer of the pectoral fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Abductor superficialis 1	Abductor superficialis	“Adducteur superficiel”	Cleithrum: inner surface	Mesomere 1	Mono-articular	Abduction and protraction	9.000	4.25	1.998
	Abductor superficialis 2			Extracleithrum: posterior portion	Mesomere 1	Mono-articular	Adduction and protraction	3.653	5.00	0.689
	Abductor superficialis 3			Mesomere 1: distal part of dorsal edge; scapulocoracoid: glenoid process	Mesomere 2 and pre-axial radial 1	Mono-articular	Abduction and protraction	4.042	2.25	1.695
	Abductor superficialis 4			Mesomere 1: lateral edge	Mesomere 2	Mono-articular	Adduction and protraction	3.980	3.50	1.073
	Abductor superficialis 5			Mesomere 2: distal portion of the dorso-medial edge	Mesomere 3	Mono-articular	Abduction and protraction	2.899	2.00	1.367
	Abductor superficialis 6			Mesomere 2: dorso-lateral edge	Mesomere 3	Mono-articular	Protraction	2.423	2.75	0.831
	Abductor superficialis 7			Mesomere 3: lateral ridge	Fin rays 1–12	Poly-articular	Protraction	1.786	3.00	0.562
	Abductor superficialis 8			Mesomere 3: lateral ridge	Fin rays 13–33	Poly-articular	Protraction	2.732	4.50	0.573
	Medial	Adductor superficialis 1	Adductor superficialis	“Adducteur superficiel”	Scapulocoracoid	Mesomere 1	Mono-articular	Adduction and retraction	14.000	8.00
	Adductor superficialis 2			Cleithrum: anterior edge	Mesomeres 1–3	Poly-articular	Retraction	7.000	10.00	0.660
	Adductor superficialis 3			Cleithrum: anterior edge	Mesomeres 1–3	Poly-articular	Retraction	2.612	10.00	0.246
	Adductor superficialis 4			Mesomere 1: ventral ridge	Mesomere 2	Mono-articular	Adduction and retraction	2.838	4.50	0.595
	Adductor superficialis 5			Mesomere 1: ventral ridge	Mesomere 3 + fin rays 22–33	Poly-articular	Retraction	2.477	10.50	0.223
	Adductor superficialis 6			Mesomere 2: dorso-lateral edge	Mesomere 3	Mono-articular	Adduction and retraction	2.238	3.50	0.603
	Adductor superficialis 7			Mesomere 3: distal part of dorsal edge	Fin rays 1–21	Poly-articular	Retraction	2.265	2.50	0.855

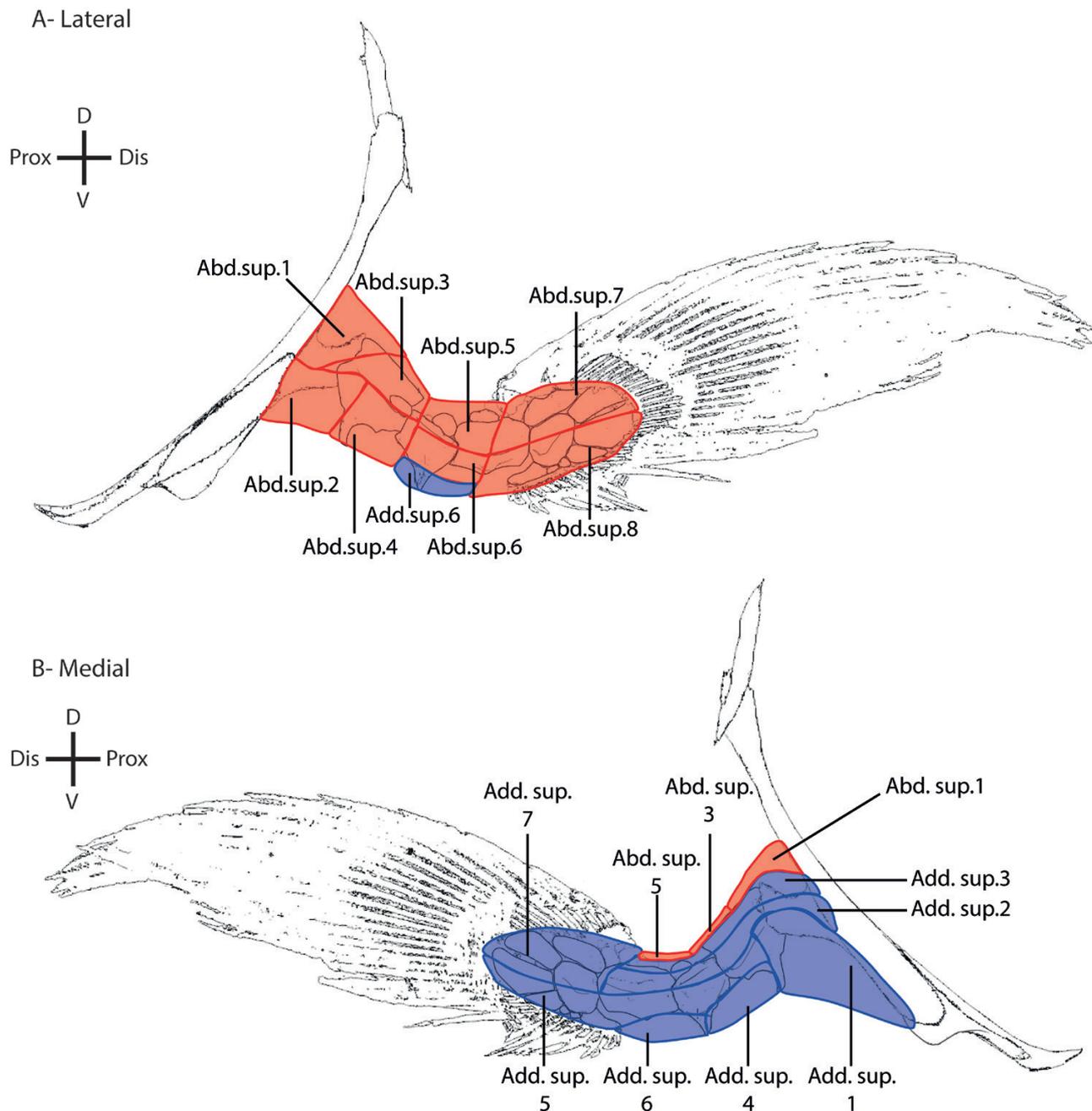


Figure 3. Superficial muscle layer of the pectoral fin of the coelacanth *L. chalumnae* in lateral (A) and medial (B) views. Blue: adductor superficialis; red: abductor superficialis. Abd.sup.: abductor superficialis; Add.sup.: adductor superficialis; D: dorsal; Dis: distal; Prox: proximal; V: ventral.

Abductor superficialis

The abductor superficialis muscle is formed by eight different muscle bundles having different origins and insertions (Table 1; Fig. 3A). Six bundles (abductor superficialis 1–6) are mono-articular, meaning they cross only one joint, and two other bundles (abductor

superficialis 7–8) are poly-articular, meaning they cross more than one joint.

Abductor superficialis 1: Originates on the lateral side of the fin, on the latero-posterior edge of the cleithrum dorsally to the extracleithrum. It inserts

on the proximal portion of the dorsal ridge and the dorso-lateral facet of mesomere 1. This muscle bundle permits the abduction and protraction of mesomere 1.

Abductor superficialis 2: Originates on the lateral edge of the extracleithrum. It inserts on the proximal portion of the ventro-lateral aspect of mesomere 1. It permits the adduction and protraction of mesomere 1.

Abductor superficialis 3: Originates on the dorso-lateral aspect of mesomere 1 and on its dorsal ridge, both on lateral and medial side of the fin. It inserts on the proximal portion of the dorsal part and dorso-medial ridge of mesomere 2. It permits the abduction and protraction of mesomere 2.

Abductor superficialis 4: Originates on the ventro-lateral aspect of mesomere 1. It inserts on the proximal portion of the ventral part of mesomere 2. It permits the adduction and protraction of mesomere 2.

Abductor superficialis 5: Originates on the dorsal part of mesomere 2, on its dorso-lateral and dorso-medial edge. It inserts on the dorso-lateral aspect of mesomere 3 and on its dorsal ridge, both on lateral and medial sides of the fin. It permits the abduction and protraction of mesomere 3.

Abductor superficialis 6: Originates on the proximal part of lateral aspect of mesomere 2. It inserts on the proximal portion of the ventro-lateral aspect of mesomere 3. It permits the protraction of mesomere 3.

Abductor superficialis 7: Originates on the distal portion of the dorso-lateral aspect of mesomere 3 and inserts at the base of fin rays 1 to 12 via an aponeurosis at the lateral side of the fin. It permits the protraction of the distal part of the fin and fin rays 1 to 12.

Abductor superficialis 8: Originates on the distal portion of the ventro-lateral aspect of mesomere 3 and inserts at the base of fin rays 13 to 33 via an insertion aponeurosis at the lateral side of the fin. It permits the protraction of the distal part of the fin and fin rays 13 to 33.

Adductor superficialis

The adductor superficialis muscle mass is formed by seven different muscle bundles having different origins and insertions (Table 1; Fig. 3B). Three bundles

(adductor superficialis 1, 4 and 6) are mono-articular and four bundles (adductor superficialis 2, 3, 5 and 7) are poly-articular.

Adductor superficialis 1: Originates on the ventro-medial edge of the cleithrum, the ventral side of the scapulocoracoid and the ventral edge of the extracleithrum. It inserts on the proximal portion of the ventro-medial aspect of mesomere 1 and on the large ventral ridge of this mesomere. It permits the adduction and retraction of mesomere 1.

Adductor superficialis 2–3: Originate from the anterior edge of the cleithrum, and insert on the distal portion of the medial aspect of mesomere 3. They are also attached to mesomeres 1 and 2 with strong fibrous connective tissue. Adductor superficialis 3 is dorsal to adductor superficialis 2. They permit the retraction of mesomeres 1 to 3.

Adductor superficialis 4: Originates on the distal portion of the ventral ridge of mesomere 1, on its medial side. It inserts on the proximal portion of the ventro-medial ridge of mesomere 2. It permits the adduction and retraction of mesomere 2.

Adductor superficialis 5: Originates on the proximal portion of the ventro-medial aspect of mesomere 1, just dorsal to the origin of the adductor superficialis 4. It inserts on the medial side of mesomere 3 and at the base of the fin rays 22 to 33 via an aponeurosis. It permits the retraction of mesomere 3 and fin rays 22 to 33.

Adductor superficialis 6: Originates on the medial and lateral sides of the fin, on the distal portion of the ventro-medial ridge of mesomere 2. It inserts on the ventral side of mesomere 3. It permits the adduction and retraction of mesomere 3.

Adductor superficialis 7: Originates on the distal portion of mesomere 3. It inserts at the base of fin rays 1 to 21 via an aponeurosis at the medial side of the fin. It permits the retraction of the distal part of the fin and fin rays 1 to 21.

MIDDLE LAYER

(TABLE 2)

The middle layer is also formed by two muscle masses: the abductor profundus on the lateral side and the adductor profundus on the medial side of the pectoral fin (Fig. 4).

Table 2. Muscles of the middle layer of the pectoral fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Abductor profundus 1	Abd. prof.	“Adducteur profond”	Cleithrum: inner surface	Mesomere 1: distal portion of the dorso-lateral facet	Mono-articular	Abduction and protraction	2.327	4.30	0.511
Lateral	Abductor profundus 2	Abd. prof.	“Adducteur profond”	Cleithrum: inner surface	Mesomere 1: distal portion of the dorso-lateral facet	Mono-articular	Abduction and protraction	1.545	4.00	0.364
Lateral	Abductor profundus 3	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 2–3 along the ventral edge (lateral face)	Poly-articular	Adduction and protraction	1.568	14.00	0.106
Lateral	Abductor profundus 4	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 3 along the ventral edge (lateral face)	Poly-articular	Adduction and protraction	7.000	18.00	0.367
Lateral	Abductor profundus 5	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 1–3 along the ventral edge (lateral face)	Poly-articular	Adduction and protraction	1.495	10.00	0.141
Lateral	Abductor profundus 6	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 1–3 (lateral face)	Poly-articular	Abduction and protraction	0.327	11.00	0.028
Lateral	Abductor profundus 7	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 1–3 (lateral face)	Poly-articular	Abduction and protraction	1.482	11.00	0.127
Lateral	Abductor profundus 8	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 1–2 along the ventral edge (lateral face)	Mono-articular	Adduction and protraction	1.642	10.50	0.148
Lateral	Abductor profundus 9	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomeres 1–2 along the ventral edge (lateral face)	Poly-articular	Adduction and protraction	1.032	8.00	0.122
Lateral	Abductor profundus 10	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1 along the ventral edge	Poly-articular	Adduction and protraction	0.219	6.00	0.034

Table 2. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Abductor profundus 11	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1 along the ventral edge	Mono-articular	Adduction and protraction	0.267	3.00	0.084
Lateral	Abductor profundus 12	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1 along the ventral edge	Mono-articular	Adduction and protraction	0.605	6.00	0.095
Lateral	Abductor profundus 13	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1 along the ventral edge	Mono-articular	Adduction and protraction	0.414	4.50	0.087
Lateral	Abductor profundus 14	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1 along the ventral edge	Mono-articular	Adduction and protraction	0.451	4.20	0.101
Lateral	Abductor profundus 15	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.247	4.50	0.052
Lateral	Abductor profundus 16	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.027	4.00	0.006
Lateral	Abductor profundus 17	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.140	4.20	0.031
Lateral	Abductor profundus 18	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.101	4.00	0.024
Lateral	Abductor profundus 19	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.014	3.70	0.003
Lateral	Abductor profundus 20	Abd. prof.	“Adducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.383	4.00	0.090

Table 2. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Abductor profundus 21	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.689	4.00	0.163
Lateral	Abductor profundus 22	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.046	4.00	0.011
Lateral	Abductor profundus 23	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.254	3.60	0.066
Lateral	Abductor profundus 24	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.035	3.10	0.011
Lateral	Abductor profundus 25	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.129	3.70	0.033
Lateral	Abductor profundus 26	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.247	3.80	0.061
Lateral	Abductor profundus 27	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.089	3.10	0.027
Lateral	Abductor profundus 28	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.194	4.00	0.046
Lateral	Abductor profundus 29	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	0.226	4.50	0.047
Lateral	Abductor profundus 30	Abd. prof.	“Adducteur profond”	Scapuloacoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	2.886	3.00	0.907

Table 2. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Abductor profundus 31	Abd. prof.	“Abducteur profond”	Scapulocoracoid: proximal portion of internal posterior surface	Mesomere 1: proximal edge (lateral face)	Mono-articular	Adduction and protraction	1.173	3.25	0.340
Medial	Adductor profundus 1	Adductor	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–3 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	0.869	8.30	0.099
Medial	Adductor profundus 2	Add. prof.	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–3 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	2.323	10.50	0.209
Medial	Adductor profundus 3	Add. prof.	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–3 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	3.253	12.60	0.244
Medial	Adductor profundus 4	Add. prof.	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–3 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	1.798	8.00	0.212
Medial	Adductor profundus 5	Add. prof.	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–2 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	0.694	5.50	0.119
Medial	Adductor profundus 6	Add. prof.	“Abducteur profund”	Cleithrum: medio-caudal edge of the superior portion	Mesomeres 1–2 along the dorsal edge (medial face)	Poly-articular	Abduction and retraction	0.134	3.50	0.036
Medial	Adductor profundus 7	Add. prof.	“Abducteur profund”	Scapulocoracoid: proximal portion of the ventral surface	Mesomeres 2–3 along the ventral edge (medial face)	Poly-articular	Adduction and retraction	1.948	10.50	0.175
Medial	Adductor profundus 8	Add. prof.	“Abducteur profund”	Scapulocoracoid: proximal portion of the ventral surface	Mesomeres 2–3 along the ventral edge (medial face)	Poly-articular	Adduction and retraction	2.460	12.50	0.186
Medial	Adductor profundus 9	Add. prof.	“Abducteur profund”	Scapulocoracoid: proximal portion of the ventral surface	Mesomeres 2–3 along the ventral edge (medial face)	Poly-articular	Adduction and retraction	2.028	13.00	0.147
Medial	Adductor profundus 10	Add. prof.	“Abducteur profund”	Scapulocoracoid: proximal portion of the ventral surface	Mesomeres 2–3 along the ventral edge (medial face)	Poly-articular	Adduction and retraction	1.228	14.50	0.080

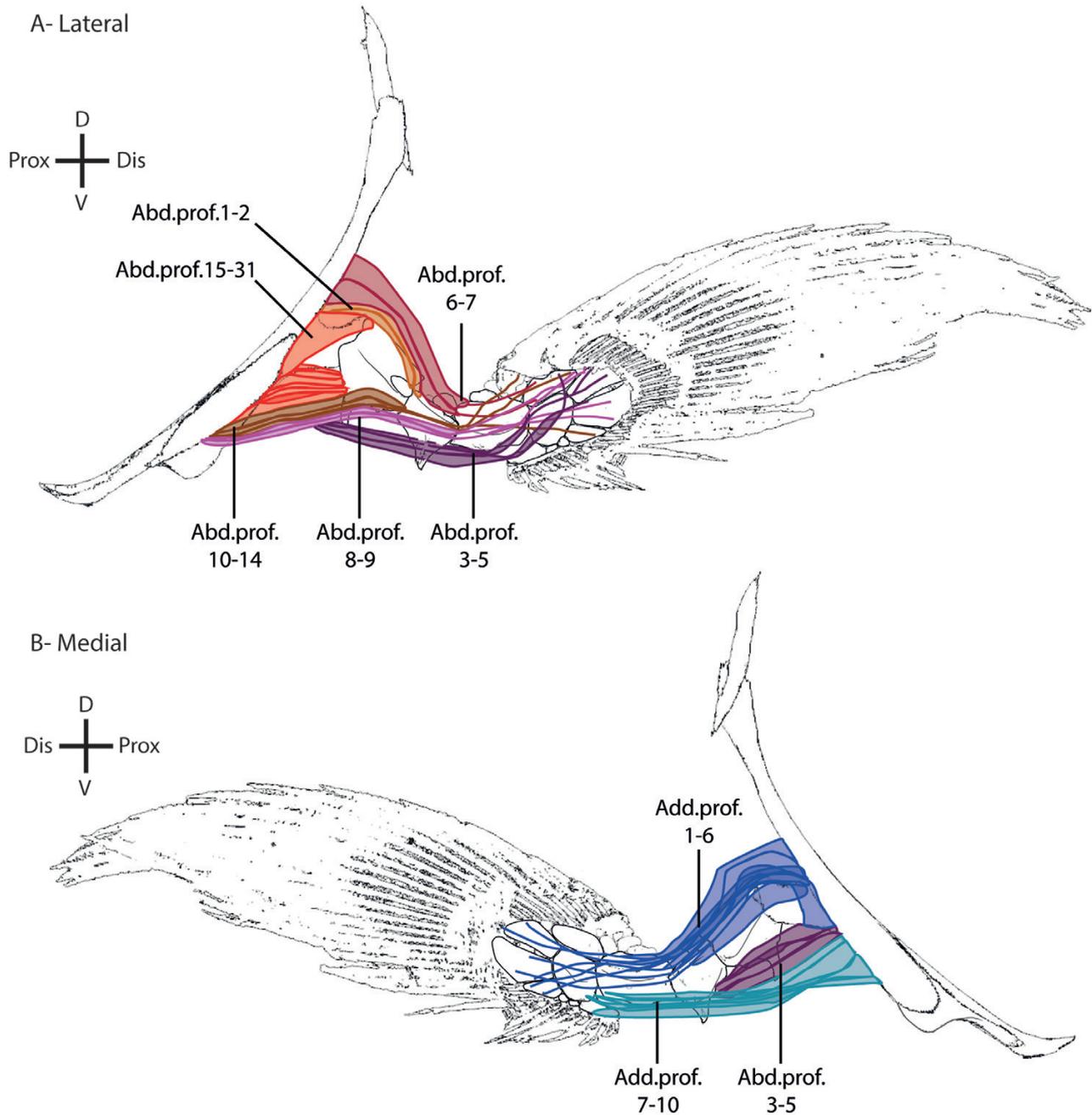


Figure 4. Middle muscle layer of the pectoral fin of the coelacanth *L. chalumnae* in lateral (A) and medial (B) views. Abd. prof.: abductor profundus; Add.prof.: adductor profundus; D: dorsal; Dis: distal; Prox: proximal; V: ventral.

Abductor profundus

The abductor profundus muscle is formed by 31 different muscle bundles (Fig. 4A). Among them, 24 bundles are mono-articular (abductor profundus 1–2, 8, 11–31) and seven are poly-articular (abductor profundus 3–7 and 9–10).

Abductor profundus 1–2: Originate on the medio-caudal edge of the superior part of the cleithrum (Table 2).

They insert on the distal part of the dorso-lateral aspect of mesomere 1. They permit the abduction and protraction of mesomere 1.

Abductor profundus 3–5: Originate on the ventral side of the scapulocoracoid. They follow the ventral edge of mesomeres 1 to 3 and insert on the lateral side of the fin via a long tendon. They permit the adduction and protraction of the fin.

Abductor profundi 6–7: Originate on the ventral side of the scapulocoracoid. They follow the dorsal edge of mesomeres 1 to 3 and insert on the lateral side of the fin via a long tendon. They permit the abduction and protraction of the fin.

Abductor profundi 8–9: Originate on the ventral side of the scapulocoracoid, near the edge of the extracleithrum. They follow the ventral edge of mesomeres 1 and 2 and insert on the lateral side of the fin via a long tendon. They permit the adduction and protraction of mesomeres 1 and 2.

Abductor profundi 10–14: Originate on the ventral side of the scapulocoracoid, near the edge of the extracleithrum on the lateral side of the girdle. They insert on the lateral side of mesomere 1 via a long tendon and follow the ventral edge of this mesomere. They permit the adduction and protraction of mesomere 1.

Abductor profundi 15–31: Originate on the ventral side of the fin, on the articular process of the scapulocoracoid. They insert on the proximal edge of mesomere 1 via a short tendon, on the lateral side of the fin. They permit the adduction and protraction of mesomere 1.

Adductor profundus

The adductor profundus muscle is formed by ten poly-articular muscle bundles that run under the surface of the abductor superficialis muscle (Fig. 4B).

Adductor profundi 1–6: Originate from the medio-caudal edge of the superior portion of the cleithrum (Table 2). They follow the dorsal edge of mesomeres 1 to 3 and insert via a long tendon to the medial side of the fin. They permit the abduction and retraction of the fin.

Adductor profundi 7–10: Originate on the ventral side of the scapulocoracoid (Table 2). They follow the ventral edge of mesomeres 2 and 3, and insert via a long tendon on the medial side of the fin. They permit the adduction and retraction of the fin.

DEEP LAYER

(TABLE 3)

Here, we refer to pronator and supinator muscles as the muscles of the deep layer that insert respectively on the lateral and medial sides of the pectoral fin (see Diogo *et al.*, 2016; Miyake *et al.*, 2016; Fig. 5). However, the exact role of each muscle can be different from what the name suggests, as indicated in Table 3.

The deep layer is composed of eight antagonistic pairs of pronator and supinator muscles that cover the entire endoskeletal axis of the pectoral fin and the proximal portion of dermal fin rays, and a post-axial muscle (pterygialis caudalis) (Fig. 5). In the deep layer, most of the muscles are mono-articular.

Pronator muscles

The pronator muscle group is formed by eight pronator muscles at the lateral side of the pectoral fin that run obliquely across the ventral margin of the fin (Fig. 5A). Pronator 1b is the only pronator bundle that originates and inserts on the medial side of the fin.

The pronator 1–4 muscles are mono-articular. Their numbers correspond to the mesomere they insert upon (or the previous pre-axial radial), and they originate from the previous element (scapulocoracoid or mesomere). They permit the pronation of the associated element and of the fin.

Pronators 5–8 insert on the proximal portion of the fin rays, and originate on mesomere 3 (pron. 5 and 7), mesomere 4 (pron. 6) and mesomere 2 (pron. 8). They permit the lateral flexion of the fin rays and the pronation (pron. 5, 6a) and supination of the fin (pron. 6b, 6c, 7, 8).

Supinator muscles

The supinator muscle group is formed by eight supinator muscles on the medial side of the pectoral fin (Fig. 5B–C). The organization of these muscles is quite similar to that of the pronator muscles. Supinators 1a, 2a and 2c insert on the lateral side of the fin.

Supinators 1–4 are mono-articular muscles. The number assigned to the muscles corresponds to the mesomere they insert upon (or the previous pre-axial radial). They originate from the previous element (scapulocoracoid or mesomere). These muscles permit the supination of the associated elements and of the fin.

Supinators 5–8 insert on the proximal portion of the fin rays at the medial side of the fin, and originate on mesomere 3 (sup. 5), mesomere 4 (sup. 6), mesomere 2 (sup. 7) and mesomere 1 (sup. 8). They are symmetrical to pronators 5–8 and permit their antagonistic movement (Table 3).

Pterygialis caudalis

The pterygialis caudalis follows the post-axial edge of the pectoral fin. It originates on the medial side of mesomere 1 and inserts at the base of fin ray 33. It permits the adduction of the fin.

Table 3. Muscles of the deep layer of the pectoral fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Lateral	Pronator 1a	Supinator 1	“Supinateur 1”	Scapulocoracoid: glenoid process (medial side)	Mesomere 1: proximal portion of the ventral ridge (lateral side)	Mono-articular	Pronation	6.000	5.00	1.132
	Pronator 1b	Supinator 1	“Supinateur 1”	Scapulocoracoid: proximal part of the inferior portion of the glenoid process (medial side)	Mesomere 1: ventro-medial face	Mono-articular	Pronation	5.411	3.50	1.458
	Pronator 2a	Supinator 1	“Supinateur 1”	Mesomere 1: proximal portion of ventral edge (lateral side)	Pre-axial radial 1 (lateral side)	Mono-articular	Pronation	0.312	3.00	0.098
	Pronator 2b	Supinator 1	“Supinateur 1”	Mesomere 1: ventral edge and ventral ridge (lateral side)	Pre-axial radial 1 (lateral side)	Mono-articular	Pronation	2.739	2.65	0.975
	Pronator 2c	Supinator 2	“Supinateur 2”	Mesomere 1: distal portion of ventral edge (medial side)	Mesomere 2: proximal portion of the dorsal edge	Mono-articular	Pronation	3.018	3.00	0.949
	Pronator 2d	Supinator 2	“Supinateur 2”	Mesomere 1: distal portion of ventral edge (medial side)	Mesomere 2: proximal portion of the ventro-lateral ridge	Mono-articular	Pronation	2.286	6.00	0.359
	Pronator 3a	Supinator 2	“Supinateur 2”	Mesomere 2: proximal portion of the ventro-lateral ridge	Pre-axial radial 2; mesomere 3: proximal portion of the dorsal edge (lateral face)	Mono-articular	Pronation	2.971	3.25	0.862
	Pronator 3b	Supinator 3	“Supinateur 3”	Mesomere 2: distal part of the ventro-lateral ridge	Mesomere 3: ventral side of the lateral ridge	Mono-articular	Pronation	2.200	3.50	0.593
	Pronator 4	Supinator 3	“Supinateur 3”	Mesomere 3: ventral ridge	Mesomere 4: proximal portion of lateral ridge	Mono-articular	Pronation	0.718	2.50	0.271
	Pronator 5	Supinator 3	“Supinateur 3”	Mesomere 3: ventral ridge (lateral side)	Proximal portion of fin rays 1–6	Mono-articular	Lateral flexion of fin rays and pronation	3.454	4.50	0.724
	Pronator 6a	Supinator 4	“Supinateur 4”	Mesomere 4: lateral edge	Proximal portion of fin rays 6–12	Mono-articular	Lateral flexion of fin rays and pronation	2.568	3.50	0.692

Table 3. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
	Pronator 6b	Supinator 4	“Supinateur 4”	Mesomere 4: distal portion of lateral edge	Proximal portion of fin rays 13–21	Mono-articular	Lateral flexion of fin rays and supination	1.356	2.75	0.465
	Pronator 6c	Supinator 4	“Supinateur 4”	Mesomere 4: lateral edge	Proximal portion of fin rays 21–33	Mono-articular	Lateral flexion of fin rays and supination	1.957	1.75	1.055
	Pronator 7	Pterygialis caudalis	“Supinateur 5”	Mesomere 3: ventral edge	Proximal portion of fin rays 28–33	Poly-articular	Lateral flexion of fin rays and supination	0.164	3.80	0.041
	Pronator 8	Pterygialis caudalis	“Supinateur 5”	Mesomere 2: distal portion of the dorso-lateral edge	Proximal portion of fin rays 28–33	Poly-articular	Lateral flexion of fin rays and supination	0.978	5.50	0.168
Medial	Supinator 1a	Pronator 1	“Pronateur 1”	Scapulocoracoid: superior portion of the glenoid process	Mesomere 1: proximal portion of the ventral ridge (lateral side)	Mono-articular	Supination	1.880	1.50	1.182
	Supinator 1b	Pronator 1	“Pronateur 1”	Scapulocoracoid: superior portion of the glenoid process	Mesomere 1: distal dorso-medial face	Mono-articular	Supination	5.140	3.50	1.385
	Supinator 2a	Pronator 1	“Pronateur 2”	Mesomere 1: proximal portion of the dorsal ridge (lateral side)	Pre-axial radial 1 (lateral side)	Mono-articular	Supination	1.244	1.50	0.782
	Supinator 2b	Pronator 2	“Pronateur 2”	Mesomere 1: distal portion of the medial edge	Mesomere 2: dorso-medial edge	Mono-articular	Supination	2.689	3.00	0.846
	Supinator 2c	Pronator 2	“Pronateur 2”	Mesomere 1: distal portion of the dorsal ridge (lateral side)	Pre-axial radial 2: proximal portion	Poly-articular	Supination	0.591	2.50	0.223
	Supinator 3a	Pronator 2	“Pronateur 3”	Mesomere 2: distal portion of the dorso-medial ridge	Pre-axial radial 2; proximal element of pre-axial accessory element	Mono-articular	Supination	1.875	2.00	0.884
	Supinator 3b	Pronator 3	“Pronateur 3”	Mesomere 2: distal portion of ventro-medial ridge	Mesomere 3: distal portion of the medial ridge	Mono-articular	Supination	1.699	4.00	0.401
	Supinator 4	Pronator 3	“Pronateur 3”	Mesomere 3: distal portion of the ventral ridge (medial side)	Mesomere 4: proximal portion of the ventral edge (medial side)	Mono-articular	Supination	0.663	2.75	0.227

Table 3. Continued

Fin side	Muscle	Dingo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	Bundle length (cm)	ACSA (cm ²)
Supinator 5	Pronator 3	"Pronateur 3"	Mesomere 3: distal portion of the dorsal ridge (medial side)	Proximal portion of fin rays 1–7	Mono-articular	Medial flexion of fin rays and supination	1.667	2.25	0.699	
Supinator 6a	Pronator 4	"Pronateur 4"	Mesomere 4: dorsal edge (medial side)	Proximal portion of fin rays 7–12	Mono-articular	Medial flexion of fin rays and supination	0.873	2.75	0.299	
Supinator 6b	Pronator 4	"Pronateur 4"	Mesomere 4: distal portion of the ventral edge (medial side)	Proximal portion of fin rays 13–23	Mono-articular	Medial flexion of fin rays and pronation	0.924	2.75	0.317	
Supinator 6c	Pronator 4	"Pronateur 4"	Mesomere 4: ventral edge (medial side)	Proximal portion of fin rays 23–33	Mono-articular	Medial flexion of fin rays and pronation	0.749	1.75	0.404	
Supinator 7	Pterygialis caudalis	"Pronateur 5"	Mesomere 2: distal portion of medial edge	Proximal portion of fin rays 28–33	Poly-articular	Medial flexion of fin rays and pronation	0.364	4.50	0.076	
Supinator 8	Pterygialis caudalis	"Pronateur 5"	Mesomere 1: ventro-lateral edge	Proximal portion of fin rays 28–33	Poly-articular	Medial flexion of fin rays and pronation	0.700	6.50	0.102	
Pterygialis caudalis	Pterygialis caudalis	<i>Undescribed</i>	Mesomere 1: distal portion of the medial edge	Proximal portion of fin ray 33	Poly-articular	Adduction	0.691	8.00	0.081	

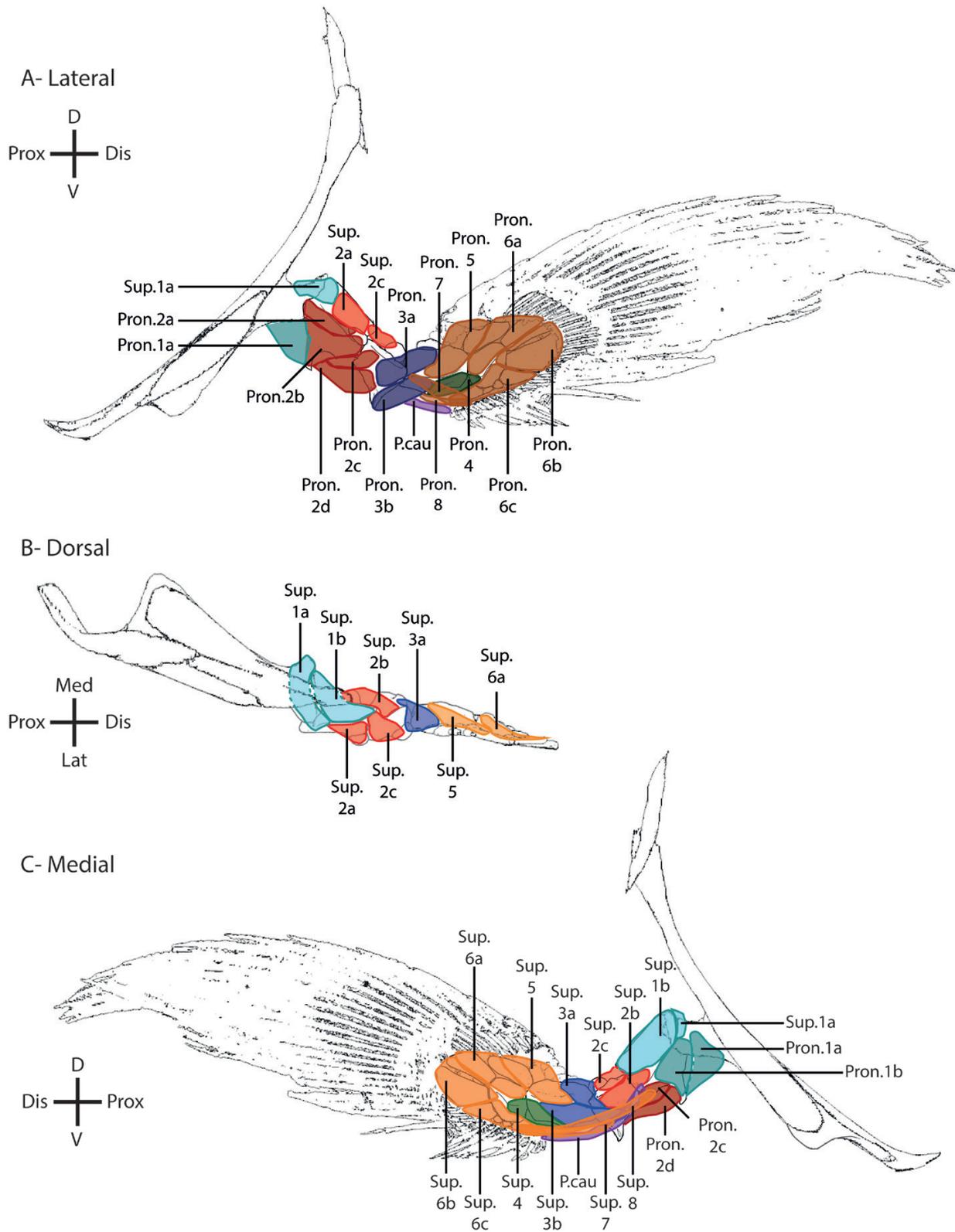


Figure 5. Deep muscle layer of the pectoral fin of the coelacanth *L. chalumnae* in lateral (A), dorsal (B) and medial (C) views. Different colors represent different muscles. P.cau: pterygialis caudalis; Pron.: pronator; Sup.: supinator; D: dorsal; Dis: distal; Lat: lateral; Med: medial; Prox: proximal; V: ventral.

PELVIC MUSCULATURE ANATOMY

Eighty-three muscle bundles, organized into 12 functional groups, were identified for the pelvic fin of *L. chalumnae*. Moreover, most of these muscle bundles were separated in several sub-bundles (Supporting Information, Table S1). The resting position of the pelvic fin was considered as the fin positioned along the ventral side of the body, with the leading edge directed laterally. Abductor muscles are on the ventral side of the fin, and adductor muscles are located on the dorsal side of the fin. Compared to the pectoral fin, most muscles of the pelvic fin are poly-articular and originate from the pelvic girdle and insert at the base of the fin rays. For the pelvic fin in its resting position, movements are defined as follows:

1. Protraction: the pre-axial edge of the fin has a forward movement.
2. Retraction: the pre-axial edge of the fin has a backward movement.
3. Abduction: the ventral side of the fin has a downward movement.
4. Adduction: the dorsal side of the fin has an upward movement.
5. Pronation: the ventral side of the fin has a medial pivoting movement around the axis of the fin.
6. Supination: the ventral side of the fin has a lateral pivoting movement around the axis of the fin.

Similar to the pectoral fin, the pelvic fin is not maintained in this reference position during swimming. The movements of the fin defined here thus refer to the resting position of the fin (Fig. 2). Since the pectoral and pelvic fins are oriented in different planes, the movements of the two fins are defined differently. Thus, the protraction movement of the pectoral fin corresponds to an abduction movement of the pelvic fin, and an abduction movement of the pectoral fin corresponds to a protraction movement of the pelvic fin.

SUPERFICIAL LAYER

(TABLE 4)

Since the muscle organization is simpler compare to that of the pectoral fin, we provide here a general description of the origin and insertion of the muscles of the superficial layer. The detailed origins and insertions of each muscle in the superficial layer are provided in Table 4.

The superficial layer of the pelvic fin is formed by four muscle masses: the adductor superficialis pelvicius on the dorsal side and the abductor superficialis pelvicius on the ventral side of the fin, as well as the pterygialis cranialis on the pre-axial side and the pterygialis

caudalis on the post-axial side of the fin (Fig. 6). All the muscles of the superficial layer are poly-articular.

Adductor superficialis pelvicius

The adductor superficialis pelvicius is composed of ten dorsal muscle bundles which are oriented proximally to distally and numbered from the pre-axial to post-axial side of the pelvic fin (Fig. 6A). These muscle bundles originate on: (i) the lateral process of the pelvic girdle (add. sup. pelvicius 1–7), onto both the dorsal and the ventral side; and (ii) on the fascia that separates the pelvic fin muscles from the abdominal muscles (add. sup. pelvicius 7–10; Table 4). They insert at the base of fin rays 1 to 27 on the dorsal side of the fin via short aponeuroses. Due to their origin onto the curved concave lateral process of the pelvic girdle, these muscle bundles cross each other (Fig. 6A). Add. sup. pelvicius 8 and 9 also insert respectively on the dorsal ridge of mesomere 3 and mesomere 2 by a strong fibrous connective tissue band. Add. sup. pelvicius 1 also inserts on the pre-axial radials 1 and 2. Add. sup. pelvicius 2–6 have a gutter-like shape and surround the adductor profundus pelvicius of the middle layer as follows. Add. sup. pelvicius 2 surrounds adductor profundus pelvicius 1,2, add. sup. pelvicius 3 surrounds add. prof. pelvicius 3,4, add. sup. pelvicius 4 surrounds add. prof. pelvicius 5,6,7,9, add. sup. pelvicius 5 surrounds add. prof. pelvicius 8,10 and add. sup. pelvicius 6 surrounds add. prof. pelvicius 11,12. All add. sup. pelvicius bundles permit the adduction of the fin rays. Add. sup. pelvicius 1 also permits the protraction of the fin.

Pterygialis caudalis

The pterygialis caudalis originates from the ventral side of the postero-superior process of the pelvic girdle and inserts at the base of pelvic fin rays 28–30 (Fig. 6A). Based on its origin and insertion, the role of the pterygialis caudalis is to adduct the pelvic fin.

Abductor superficialis pelvicius

The abductor superficialis pelvicius is composed of 15 ventral muscle bundles. As in the dorsal muscles, these muscles are numbered from pre-axial to post-axial, and are oriented from proximal to distal (Fig. 6B). They originate: (i) anteriorly on the lateral process of the pelvic girdle, on the adductor profundus pelvicius, via an aponeurosis; (ii) on the ventral side of the pelvic girdle; (iii) on the medial process of the pelvic girdle; and (iv) on the aponeurosis between the two pelvic fins from ventral to dorsal (Table 4). Abd. sup. 15 has the most dorsal origin on this aponeurosis.

Table 4. Muscles of the superficial layer of the pelvic fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Pterygialis cranialis	Pterygialis cranialis	“Abducteur de la nageoire”	Pelvic girdle: anterior side of the base of the lateral process, ventral side	Proximal portion of fin ray 1; pre-axial radial 2, lateral edge	Poly-articular	Protraction	2.280	0.341
Ventral	Abductor superficialis pelvicius 1	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis on adductor profundus	Pre-axial radials 1–2, proximal portion of fin rays 1–2	Poly-articular	Protraction and abduction	3.970	0.468
Ventral	Abductor superficialis pelvicius 2	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: lateral side of the base of the anterior process	Proximal portion of fin rays 3–7	Poly-articular	Abduction	4.350	0.363
Ventral	Abductor superficialis pelvicius 3	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: base of the medial process, ventral face	Proximal portion of fin ray 8	Poly-articular	Abduction	0.640	0.068
Ventral	Abductor superficialis pelvicius 4	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: base at the posterior edge of the medial process	Proximal portion of fin ray 9	Poly-articular	Abduction	0.520	0.060
Ventral	Abductor superficialis pelvicius 5	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process	Proximal portion of fin rays 10–11	Poly-articular	Abduction	0.620	0.065
Ventral	Abductor superficialis pelvicius 6	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process	Proximal portion of fin rays 11–14	Poly-articular	Abduction	1.140	0.111
Ventral	Abductor superficialis pelvicius 7	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process	Proximal portion of fin rays 14–17	Poly-articular	Abduction	1.470	0.127
Ventral	Abductor superficialis pelvicius 8	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process	Proximal portion of fin rays 17–18	Poly-articular	Abduction	1.550	0.137
Ventral	Abductor superficialis pelvicius 9	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process	Proximal portion of fin rays 19–20	Poly-articular	Abduction	0.700	0.062
Ventral	Abductor superficialis pelvicius 10	Abductor superficialis	“Abaisseur superficiel”	Pelvic girdle: posterior edge of the the medial process, on the ligament that linked the two medial processes	Proximal portion of fin rays 20–21	Poly-articular	Abduction	0.660	0.062

Table 4. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Abductor superficialis pelvicius 11	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis between the two fins (dorsal to Abd.sup.pelv.10)	Proximal portion of fin ray 22	Poly-articular	Abduction	0.540	0.067
Ventral	Abductor superficialis pelvicius 12	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis between the two fins (dorsal to Abd.sup.pelv.11)	Proximal portion of fin ray 23	Poly-articular	Abduction	0.560	0.064
Ventral	Abductor superficialis pelvicius 13	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis between the two fins (dorsal to Abd.sup.pelv.12)	Proximal portion of fin rays 23 and 24	Poly-articular	Abduction	0.440	0.055
Ventral	Abductor superficialis pelvicius 14	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis between the two fins (dorsal to Abd.sup.pelv.13)	Proximal portion of fin rays 25 and 26	Poly-articular	Abduction	1.810	0.211
Ventral	Abductor superficialis pelvicius 15	Abductor superficialis	“Abaisseur superficiel”	Aponeurosis between the two fins (dorsal to Abd.sup.pelv.14)	Proximal portion of fin rays 26 to 30	Poly-articular	Retraction and abduction	4.000	0.563
Dorsal	Pterygialis caudalis	Pterygialis caudalis	“Adducteur de la nageoire”	Pelvic girdle: posterior process, ventral side	Proximal portion of fin rays 28–30	Poly-articular	Adduction	1.000	0.201
Dorsal	Adductor superficialis pelvicius 1	Adductor superficialis	“Élévateur superficiel, faisceau secondaire”	Pelvic girdle: base of lateral process, ventral side	Pre-axial radials 1–2; proximal portion of fin rays 1–8	Poly-articular	Protraction and adduction	1.800	0.215
Dorsal	Adductor superficialis pelvicius 2	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Pelvic girdle: posterior edge of lateral process, dorsal and ventral side	Proximal portion of fin rays 8–11	Poly-articular	Adduction	0.738	0.084
Dorsal	Adductor superficialis pelvicius 3	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Pelvic girdle: posterior edge of the lateral process, dorsal side	Proximal portion of fin rays 12–15	Poly-articular	Adduction	0.910	0.095
Dorsal	Adductor superficialis pelvicius 4	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Pelvic girdle: lateral process, dorsal side	Proximal portion of fin rays 15–18	Poly-articular	Adduction	1.370	0.145
Dorsal	Adductor superficialis pelvicius 5	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Pelvic girdle: lateral process, dorsal side	Proximal portion of fin rays 18–20	Poly-articular	Adduction	1.400	0.139
Dorsal	Adductor superficialis pelvicius 6	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Pelvic girdle: antero-lateral edge of the lateral process, dorsal side	Proximal portion of fin ray 21	Poly-articular	Adduction	1.180	0.115

Table 4. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Dorsal	Adductor superficialis pelvificus 7	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Membrane between pelvic muscles and abdominal muscles; pelvic girdle: lateral process, dorsal side	Proximal portion of fin ray 22	Poly-articular	Adduction	3.330	0.291
Dorsal	Adductor superficialis pelvificus 8	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Membrane between pelvic muscles and abdominal muscles	Dorsal ridge of mesomere 3; proximal portion of fin rays 21–23	Poly-articular	Adduction	1.460	0.147
Dorsal	Adductor superficialis pelvificus 9	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Membrane between pelvic muscles and abdominal muscles	Dorsal ridge of mesomere 2; proximal portion of fin rays 23–25	Poly-articular	Adduction	0.540	0.088
Dorsal	Adductor superficialis pelvificus 10	Adductor superficialis	“Élévateur superficiel, faisceau principal”	Membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 26–27	Poly-articular	Adduction	0.350	0.066

The bundles of the abductor superficialis pelvificus insert on the ventral side of the fin, at the base of fin rays 1–30. Abd. sup. pelvificus 1 also inserts on the latero-ventral side of pre-axials 1 and 2. These bundles permit the abduction of the fin. Abd. sup. pelvificus 1 also permits the protraction of the fin, and abd. sup. pelvificus 15 the retraction of the fin, based on their origin and insertion.

Pterygialis cranialis

The pterygialis cranialis is a pre-axial muscle that originates on the ventral side of the lateral process of the pelvic girdle and inserts on the lateral side of pre-axial radial 2 and at the base of fin ray 1 (Fig. 6B). Based on its origin and insertion, the role of the pterygialis cranialis is to protract the pelvic fin.

MIDDLE LAYER

(TABLE 5)

The middle layer is formed by two muscle masses: the adductor profundus pelvificus on the dorsal side and the abductor profundus pelvificus on the ventral side of the pelvic fin (Fig. 7). As in the superficial layer, the muscle bundles are poly-articular. The exact origin and insertion of the muscle bundles of the middle layer are listed in Table 5, and detailed origins and insertions of each sub-bundle of the different muscles are listed in Supporting Information (Table S1).

Adductor profundus pelvificus

On the dorsal side of the pelvic fin, the middle layer is subdivided into 12 adductor profundus pelvificus muscle bundles. They originate: (i) from the anterior process of the pelvic girdle; (ii) on the fascia that separates the pelvic fin muscles from the abdominal muscles; and (iii) on the anterior part of the lateral process (Fig. 7A). These muscles overlap and intersect each other, and insert at the base of fin rays 6–21, and on mesomeres 1–4 (Table 5). Most of these bundles are separated into several sub-bundles (indicated by capital letters), that are also separated in different fasciculi (indicated by lowercase letters) (Table 5; Supporting Information, Fig. S3; Table S1). Unlike the bundles of the superficial layer, these muscle bundles insert onto the fin rays and mesomeres through long tendons (Fig. 7A). The role of the add. prof. pelvificus muscle bundles is mainly the adduction of the pelvic fin, but also the flexion of mesomere 1 (add. prof. pelvificus 8A), mesomere 2 (add. prof. pelvificus 10A), mesomere 3 (add. prof. pelvificus 4A,8B,9,10B) and mesomere 4 (add. prof. pelvificus 7C,8C,11).

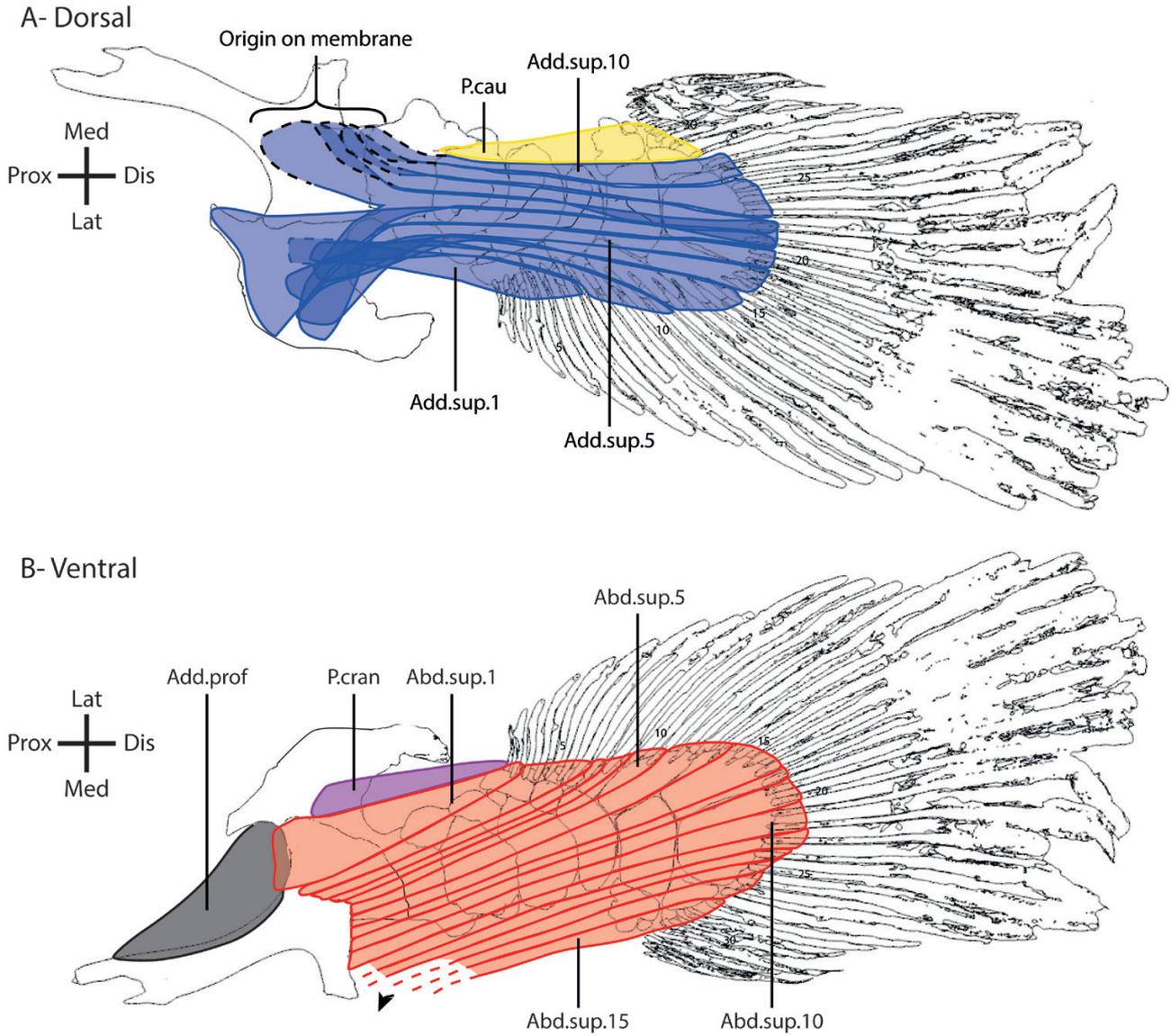


Figure 6. Superficial muscle layer of the pelvic fin of the coelacanth *L. chalumnae* in dorsal (A) and ventral (B) views. Different colors represent different muscles. Abd.prof: Abductor profundus, Abd.sup.: abductor superficialis; Add.sup.: adductor superficialis, P.cau: pterygialis caudalis, P.cran: pterygialis cranialis; Dis: distal; Lat: lateral; Med: medial; Prox: proximal. Origin on membrane indicates the membrane that separates the pelvic muscles from the abdominal muscles.

Abductor profundus pelvici

There are 14 abductor profundus pelvici muscle bundles on the ventral side of the pelvic fin that originate: (i) from the base of the lateral process (along the anterior edge); (ii) on the medial process; (iii) far anterior to the medial process, on the aponeurosis between the two pelvic girdles (dorsal to abd. sup. pelvici 15); and (iv) on the fascia that separates the pelvic muscles from the abdominal muscles (Fig. 7B). Abd. prof. pelvici 1–3 insert on pre-axial radial 1–2 and are protractor of the fin, abd. prof. pelvici 4–14 insert on fin rays 7–30 and

are abductor of the fin (Table 5). Abd. prof. pelvici 14 is also a retractor of the fin. As for the add. prof. pelvici, these muscle bundles insert on the fin rays through long tendons and are separated in several sub-bundles (Supporting Information, Table S1).

DEEP LAYER
(TABLE 6)

The deep layer is formed by pronator and flexor muscles on the dorsal side, and supinator muscles on the ventral

Table 5. Muscles of the middle layer of the pelvic fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Abductor profundus pelvicius 1	Abductor profundus	“Abaisseur profond”	Pelvic girdle: anterior edge of the base of the lateral process (ventral side), adjacent to the anterior process	Antero-lateral edge of pre-axial radial 2	Poly-articular	Protraction	0.160	0.039
Ventral	Abductor profundus pelvicius 2	Abductor profundus	“Abaisseur profond”	Pelvic girdle: anterior edge of the base of the lateral process (ventral side), adjacent to the anterior process	Lateral edge of pre-axial radial 1	Poly-articular	Protraction	0.210	0.051
Ventral	Abductor profundus pelvicius 3	Abductor profundus	“Abaisseur profond”	Pelvic girdle: anterior edge of the base of the lateral process (ventral side), adjacent to the anterior process	Pre-axial radial 1	Poly-articular	Protraction	0.150	0.046
Ventral	Abductor profundus pelvicius 4	Abductor profundus	“Abaisseur profond”	Pelvic girdle: base of the posterior side of the medial process, ventral side	Proximal portion of fin ray 7	Poly-articular	Abduction	0.220	0.027
Ventral	Abductor profundus pelvicius 5	Abductor profundus	“Abaisseur profond”	Pelvic girdle: base of the posterior side of the medial process, dorsal and ventral side	Proximal portion of fin rays 8–10	Poly-articular	Abduction	0.820	0.129
Ventral	Abductor profundus pelvicius 6	Abductor profundus	“Abaisseur profond”	Membrane between pelvic muscles and abdominal muscles; pelvic girdle: base of the posterior side of the medial process (ventral side); dorsal side of the medial process	Proximal portion of fin rays 10–11	Poly-articular	Abduction	1.340	0.267
Ventral	Abductor profundus pelvicius 7	Abductor profundus	“Abaisseur profond”	Pelvic girdle: dorsal side of the medial process	Proximal portion of fin ray 9 and fin rays 11 to 14	Poly-articular	Abduction	1.154	0.290

Table 5. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Abductor profundus pelvicius 8	Abductor profundus	“Abaisseur profond”	Pelvic girdle: dorsal side of the medial process; membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 11, 12 and 14	Poly-articular	Abduction	0.950	0.207
Ventral	Abductor profundus pelvicius 9	Abductor profundus	“Abaisseur profond”	Pelvic girdle: dorsal side of the medial process; membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 12–13 and 15–17	Poly-articular	Abduction	1.801	0.303
Ventral	Abductor profundus pelvicius 10	Abductor profundus	“Abaisseur profond”	Pelvic girdle: dorsal side of the medial process; membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 15, 17 and 19–21	Poly-articular	Abduction	3.960	0.532
Ventral	Abductor profundus pelvicius 11	Abductor profundus	“Abaisseur profond”	Pelvic girdle: dorsal side of the medial process; membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 21–22	Poly-articular	Abduction	2.060	0.200
Ventral	Abductor profundus pelvicius 12	Abductor profundus	“Abaisseur profond”	Membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 23–24	Poly-articular	Abduction	1.630	0.215
Ventral	Abductor profundus pelvicius 13	Abductor profundus	“Abaisseur profond”	Aponeurosis between the two pelvic fins	Proximal portion of fin rays 25–26	Poly-articular	Abduction	0.700	0.120
Ventral	Abductor profundus pelvicius 14	Abductor profundus	“Abaisseur profond”	Edge of the medial bud of mesomere 1; aponeurosis between the two fins	Proximal portion of fin rays 30–33	Poly-articular	Abduction and retraction	3.182	0.556
Dorsal	Adductor profundus pelvicius 1	Adductor profundus	“Élévateur profond”	Pelvic girdle: lateral edge of the base of the anterior stick, dorsal side	Proximal portion of fin ray 7	Poly-articular	Adduction	0.280	0.033
Dorsal	Adductor profundus pelvicius 2	Adductor profundus	“Élévateur profond”	Pelvic girdle: lateral edge of the anterior stick (ventral and dorsal side)	Proximal portion of fin rays 8 and 9	Poly-articular	Adduction	1.670	0.177

Table 5. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Dorsal	Adductor profundus pelvificus 3	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral process (dorsal side); laterak edge of the base of the anterior stick (ventral side)	Proximal portion of fin rays 12 to 15	Poly-articular	Adduction	1.275	0.133
Dorsal	Adductor profundus pelvificus 4A	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral edge of the base of the anterior stick, dorsal side	Dorsal ridge of mesomere 3	Poly-articular	Dorsal flexion of mesomere 3	0.711	0.128
Dorsal	Adductor profundus pelvificus 4B	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral edge of the base of the anterior stick, dorsal side	Proximal portion of fin rays 9 to 11 and fin ray 13	Poly-articular	Adduction	0.955	0.159
Dorsal	Adductor profundus pelvificus 5	Adductor profundus	“Elevateur profond”	Pelvic girdle: antero-lateral edge of the lateral process (dorsal side)	Proximal portion of fin rays 15 and 16	Poly-articular	Adduction	0.220	0.037
Dorsal	Adductor profundus pelvificus 6	Adductor profundus	“Elevateur profond”	Pelvic girdle: anterior edge of the lateral process (dorsal side)	Proximal portion of fin rays 17 and 18	Poly-articular	Adduction	1.570	0.260
Dorsal	Adductor profundus pelvificus 7A	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral edge of the anterior stick (ventral and dorsal side)	Proximal portion of fin rays 15 and 16	Poly-articular	Adduction	1.100	0.175
Dorsal	Adductor profundus pelvificus 7B	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral edge of the anterior stick (ventral and dorsal side)	Dorsal ridge of mesomere 4	Poly-articular	Dorsal flexion of mesomere 4	0.720	0.166
Dorsal	Adductor profundus pelvificus 8A	Adductor profundus	“Elevateur profond”	Pelvic girdle: medial edge of the base of the anterior stick (dorsal side)	Dorsal ridge of mesomere 1	Mono-articular	Dorsal flexion of mesomere 1	0.450	0.106
Dorsal	Adductor profundus pelvificus 8B	Adductor profundus	“Elevateur profond”	Membrane between pelvic muscles and abdominal muscles; pelvic girdle: medial edge of the anterior stick, anterior to add. prof.pelv.8a (dorsal side)	Dorsal ridge of mesomere 3	Poly-articular	Dorsal flexion of mesomere 3	1.390	0.299

Table 5. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Dorsal	Adductor profundus pelvicius 8C	Adductor profundus	“Elevateur profond”	Membrane between pelvic muscles and abdominal muscles; pelvic girdle: anterior side of the anterior process, dorsal and ventral side	Dorsal ridge of mesomere 4	Poly-articular	Dorsal flexion of mesomere 4	2.410	0.392
Dorsal	Adductor profundus pelvicius 8D	Adductor profundus	“Elevateur profond”	Pelvic girdle: anterior edge of the lateral process, dorsal side; pelvic girdle: anterior side of the anterior process, dorsal and ventral side	Proximal portion of fin rays 17 to 20	Poly-articular	Adduction	3.520	0.494
Dorsal	Adductor profundus pelvicius 9	Adductor profundus	“Elevateur profond”	Pelvic girdle: lateral edge of the anterior part of the anterior stick, ventral and dorsal side	Dorsal ridge of mesomere 3	Poly-articular	Dorsal flexion of mesomere 3	0.670	0.179
Dorsal	Adductor profundus pelvicius 10A	Adductor profundus	“Elevateur profond”	Pelvic girdle: anterior process, dorsal side	Dorsal ridge of mesomere 2	Poly-articular	Dorsal flexion of mesomere 2	0.420	0.104
Dorsal	Adductor profundus pelvicius 10B	Adductor profundus	“Elevateur profond”	Pelvic girdle: anterior process, dorsal side	Dorsal ridge of mesomere 3	Poly-articular	Dorsal flexion of mesomere 3	0.890	0.198
Dorsal	Adductor profundus pelvicius 11	Adductor profundus	“Elevateur profond”	Membrane between pelvic muscles and abdominal muscles; medial edge of the anterior stick	Mesomere 4	Poly-articular	Dorsal flexion of mesomere 4	2.430	0.523
Dorsal	Adductor profundus pelvicius 12	Adductor profundus	“Elevateur profond”	Pelvic girdle: anterior edge of the lateral process, dorsal side; lateral edge of the anterior stick; membrane between pelvic muscles and abdominal muscles	Proximal portion of fin rays 18 to 21	Poly-articular	Adduction	2.940	0.411

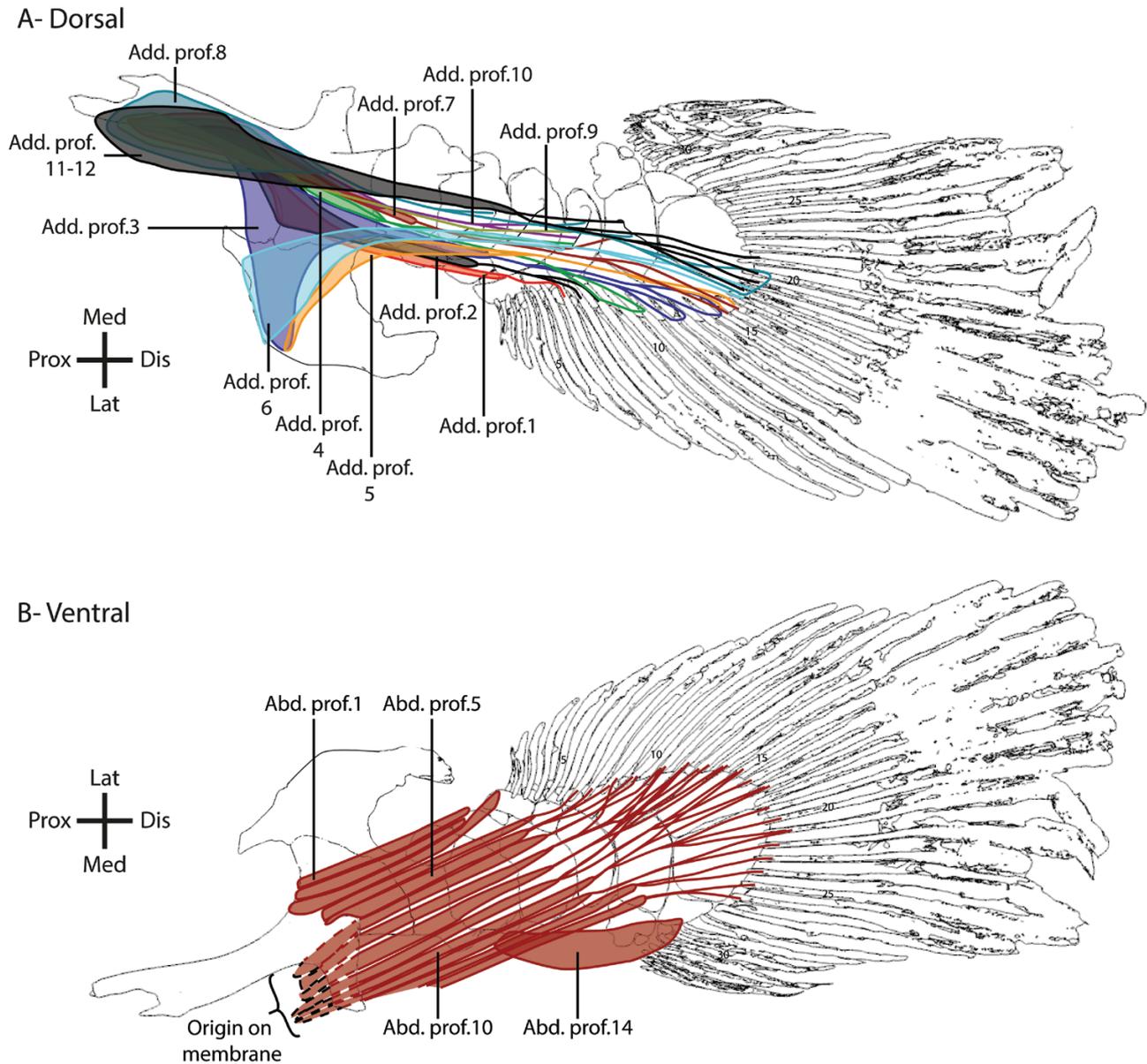


Figure 7. Middle muscle layer of the pelvic fin of the coelacanth *L. chalumnae* in dorsal (A) and ventral (B) views. Different colors represent different muscles. Abd.prof.: abductor profundus, Add.prof.: adductor profundus; Dis: distal; Lat: lateral; Med: medial; Prox: proximal. Origin on membrane indicates the membrane that separates the pelvic muscles from the abdominal muscles.

side of the pelvic fin. These muscles allow the rotation of the fin, based on their origins and insertions (Fig. 8). Except for the flexor muscles, the terminology used is based on Diogo *et al.* (2016). However, the function of the different pronator and supinator muscles is different from that suggested in previous studies. The detailed origins and insertions of each muscle of the deep layer are summarized in Table 6.

Pronator muscles

The pronator muscles are formed by eight muscles (Table 6), each muscle is itself separated into several muscle bundles (Fig. 8A; Supporting Information, Fig. S4; Table S1). The pronators are numbered from 1 to 8. Pronator 1 originates from the pelvic girdle and inserts on the pre-axial radials 0–2 and fin rays 1–5. Pronators 2–4 originate respectively from the

Table 6. Muscles of the deep layer of the pelvic fin of the coelacanth *L. chalumnae*

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Supinator 1	Supinator 1	“Supinateur”	Pelvic girdle: between lateral and medial processes (ventral face) and at the posterior edge of the base of the medial process (ventral face)	Anterior side of pre-axial radial 0	Poly-articular	Pronation	0.540	0.138
Ventral	Supinator 2	Supinator 1	“Supinateur”	Pelvic girdle: medial side of the girdle	Posterior side of pre-axial radial 0 and anterior side of pre-axial radial 1	Poly-articular	Pronation	1.310	0.272
Ventral	Supinator 3	Supinator 1	“Supinateur”	Membrane between pelvic muscles and abdominal muscles	Pre-axial radial 1; base of fin ray 1	Poly-articular	Pronation	1.344	0.219
Ventral	Supinator 4	Supinator 1	“Supinateur”	Membrane between pelvic muscles and abdominal muscles	Base of fin ray 2	Poly-articular	Pronation	1.392	0.146
Ventral	Supinator 5	Supinator 1	“Supinateur”	Membrane between pelvic muscles and abdominal muscles; medial edge of the girdle;	Pre-axial radial 2; base of fin rays 1 and 2	Poly-articular	Pronation	1.509	0.287
Ventral	Supinator 6	Supinator 2–4	“Supinateur”	proximo-medial edge of mesomere 1 Membrane between pelvic muscles and abdominal muscles; proximo-medial edge of mesomere 1	Base of fin rays 2, 3 and 5	Poly-articular	Pronation	1.873	0.283
Ventral	Supinator 7	Supinator 2–4	“Supinateur”	Medial edge of mesomere 1	Base of fin rays 3–4	Poly-articular	Pronation	0.464	0.111
Ventral	Supinator 8	Supinator 2–4	“Supinateur”	Membrane between pelvic muscles and abdominal muscles; postero-superior process;	Base of fin rays 4–6	Poly-articular	Pronation	1.377	0.216
Ventral	Supinator 9	Supinator 2–4	“Supinateur”	medial edge of mesomere 1 Membrane between pelvic muscles and abdominal muscles; aponeurosis between the two fins; proximo-medial edge of mesomere 2	Base of fin ray 7	Poly-articular	Pronation	1.676	0.267

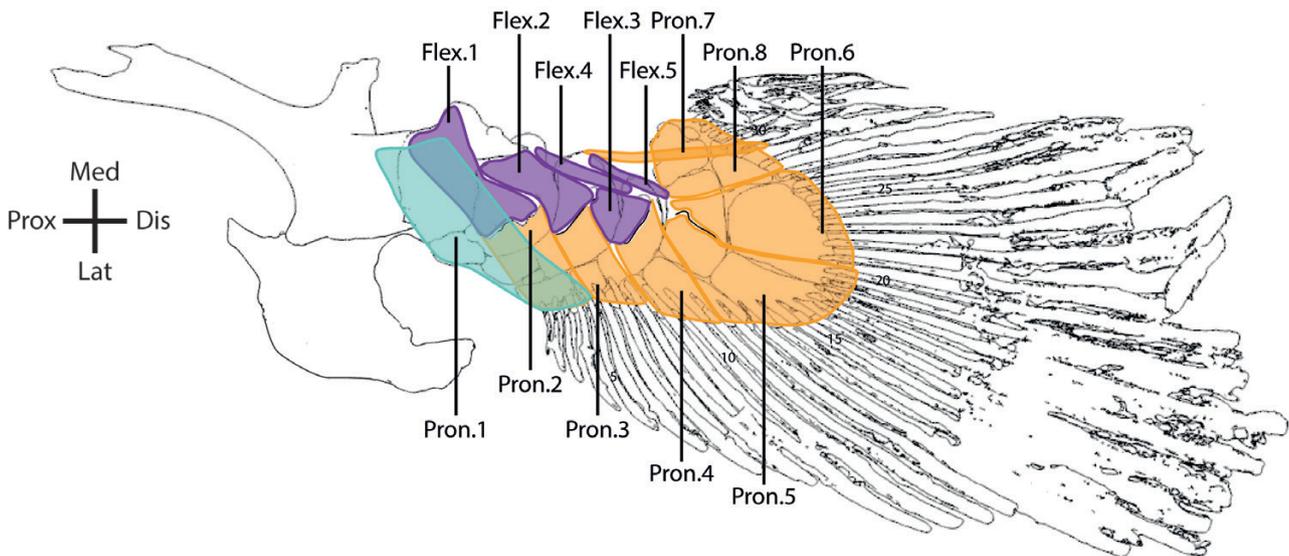
Table 6. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Ventral	Supinator 10	Supinator 2–4	“Supinateur”	Aponeurosis between the two fins; dorso-medial edge of mesomere 1; proximo-medial edge of mesomere 2	Base of fin ray 8	Poly-articular	Pronation	0.997	0.199
Ventral	Supinator 11	Supinator 2–4	“Supinateur”	Aponeurosis between the two fins; medial edge of mesomere 2	Base of fin ray 9	Poly-articular	Pronation	0.578	0.133
Ventral	Supinator 12	Supinator 2–4	“Supinateur”	Aponeurosis between the two fins; medial edge of mesomere 2; medial edge of mesomere 3	Base of fin ray 10	Poly-articular	Pronation	0.756	0.161
Ventral	Supinator 13	Supinator 2–4	“Supinateur”	Medial bud of mesomere 1; medial edge of mesomere 2; medial edge of mesomere 3	Base of fin ray 11	Poly-articular	Pronation	0.933	0.203
Ventral	Supinator 14	Supinator 2–4	“Supinateur”	Medial bud of mesomere 1; medial edge of mesomere 2; medial edge of mesomere 3	Base of fin rays 12–13	Poly-articular	Pronation	1.228	0.243
Ventral	Supinator 15	Supinator 2–4	Undescribed	Mesomere 4	Base of fin rays 12–17	Mono-articular	Pronation	0.700	0.425
Ventral	Supinator 16	Supinator 2–4	Undescribed	Proximo-medial edge of the distal radial	Base of fin rays 18–24	Mono-articular	Abduction	0.642	0.261
Ventral	Supinator 17	Supinator 2–4	Undescribed	Medial edge of mesomere 4; proximal edge of the post-axial radial	Base of fin rays 24–33	Mono-articular	Supination	1.164	0.598
Dorsal	Pronator 1	Pronator 1	“Pronateur 1–3”	Pelvic girdle, between the anterior stick and the posterior process, dorsal side	Pre-axial radials 0–2; proximal portion of fin rays 1 to 5	Poly-articular	Supination	3.490	0.962
Dorsal	Pronator 2	Pronator 1	“Pronateur 1–3”	Mesomere 1, dorsal ridge	Proximal portion of fin rays 1 to 5	Poly-articular	Supination	0.966	0.375
Dorsal	Pronator 3	Pronator 2	“Pronateur 1–3”	Mesomere 2, dorsal ridge	Proximal portion of fin rays 6 to 8	Mono-articular	Supination	0.680	0.256
Dorsal	Pronator 4	Pronator 3	“Pronateur 1–3”	Mesomere 3, dorsal ridge	Proximal portion of fin rays 9 to 11	Mono-articular	Supination	0.681	0.202
Dorsal	Pronator 5	Pronator 4	“Pronateur 4”	Mesomere 4, lateral edge of the dorsal ridge	Proximal portion of fin rays 12 to 20	Mono-articular	Supination and dorsal flexion of fin rays	0.617	0.241

Table 6. Continued

Fin side	Muscle	Diogo <i>et al.</i> (2016)	Millot & Anthony (1958)	Origin(s)	Insertion(s)	Articulation mode	Function	Mass (g)	ACSA (cm ²)
Dorsal	Pronator 6	Pronator 4	“Pronateur 5”	Mesomere 4, medial edge of the dorsal ridge	Proximal portion of fin rays 20 to 27	Mono-articular	Dorsal flexion of fin rays and pronation	1.671	0.634
Dorsal	Pronator 7	Undescribed	“Pronateur 5”	Mesomere 2, medial bud	Proximal portion of fin ray 29	Poly-articular	Dorsal flexion of fin rays	0.156	0.046
Dorsal	Pronator 8	Undescribed	“Pronateur 5”	Mesomere 4 proximo-medial edge and proximal edge of post-axial radial	Proximal portion of fin rays 28 to 32	Mono-articular	Pronation	1.066	0.503
Dorsal	Flexor 1	Undescribed	Undescribed	Pelvic girdle; postero-superior process (dorsal side)	Mesomere 1, proximal side of the dorsal ridge	Mono-articular	Dorsal flexion of mesomere 1	1.570	0.423
Dorsal	Flexor 2	Undescribed	Undescribed	Pelvic girdle; postero-superior process (ventral side) and mesomere 1 (dorsal side)	Mesomere 2, proximal side of the dorsal ridge	Mono-articular	Dorsal flexion of mesomere 2	1.058	0.370
Dorsal	Flexor 3	Undescribed	Undescribed	Mesomere 2, distal side of dorsal ridge	Mesomere 3, proximo-lateral side of the dorsal ridge	Mono-articular	Dorsal flexion of mesomere 3	0.116	0.109
Dorsal	Flexor 4	Undescribed	Undescribed	Mesomere 1, distal edge of the medial bud	Mesomere 3, proximo-medial side of the dorsal ridge	Poly-articular	Dorsal flexion of mesomere 3	0.340	0.139
Dorsal	Flexor 5	Undescribed	Undescribed	Mesomere 2, distal edge of the medial bud	Mesomere 4, proximo-medial edge	Poly-articular	Dorsal flexion of mesomere 4	0.437	0.187

A- Dorsal



B- Ventral

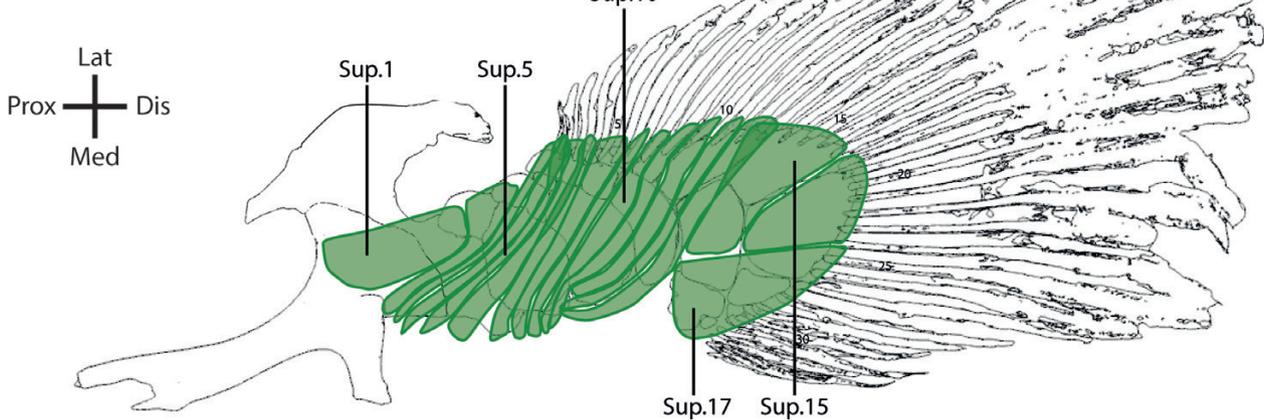


Figure 8. Deep muscle layer of the pelvic fin of the coelacanth *L. chalumnae* in dorsal (A) and ventral (B) views. Different colors represent different muscles. Flex.: flexor; Pron.: pronator; Sup.: supinator; Dis: distal; Lat: lateral; Med: medial; Prox: proximal.

dorsal ridge of mesomeres 1–3 and insert on fin rays 1–11. Pronator 5 and pronator 6 originate both on the dorsal ridge of mesomere 4, but pronator 5 from the lateral side of this ridge, and pronator 6 from the medial side of the ridge. Pronator 5 inserts on fin rays 12–19 and pronator 6 inserts on the fin rays from the post-axial side of the fin (20–27). Pronator 7 originates from the medial process of mesomere 2 and inserts at the base of fin ray 29, and pronator 8 originates from the proximal edge of mesomere

4 and inserts on fin rays 28 to 32. Although the muscles are called “pronator”, pronators 1–4 are supinators of the pelvic fin. Pronator 5 is involved in the flexion of pre-axial radial 4 and fin rays 12–20 and the supination of the fin. Pronator 6 is involved in the flexion of the distal radial and fin rays 20–27 and the pronation of the fin. Pronator 7 is involved in the flexion of fin ray 29 and pronator 8 in the pronation of the fin. Most of these pronator muscles are mono-articular (Table 6).

Flexor muscles

Flexor muscles originate and insert on two different mesomeres. Flexors 1–3 originate respectively on the pelvic girdle, mesomere 1 and mesomere 2, and insert respectively on the mesomere 1, mesomere 2 and mesomere 3 (Table 6; Fig. 8A). These muscles are mono-articular. Flexors 4–5 are bi-articular, they originate respectively on mesomeres 1 and 2, and insert on mesomeres 3 and 4. Flexor muscles permit the flexion of mesomeres 1–4.

Supinator muscles

The ventral side of the pelvic fin is formed by 17 supinator muscles (Table 6; Fig. 8B). Except for supinator 1, all these supinator muscles are subdivided in several bundles (Supporting Information, Table S1). Supinator 1 originates on the ventral side of the pelvic girdle and inserts on the anterior side of pre-axial radial 0. Supinators 2–14 have multiple origins and insertions since the smallest bundles of a muscle are covered by the longest bundles (Supporting Information, Table S1). They insert from pre-axial radial 0 to fin ray 12. Supinators 15–17 are also formed by several bundles; however, they are smaller and originate from mesomere 4 and the distal radial. Moreover, the different bundles are adjacent and insert on fin rays 12–33, similar in their arrangement to pronators 5–6 (Fig. 8B). Supinators 1–15 permit the pronation of the fin, supinator 16 permits the abduction of the fin, and supinator 17 permits the supination of the fin.

MUSCLE ARCHITECTURE

Muscle mass

The pectoral fin musculature of specimen CCC 14 weighs 165.8 g (0.43% of body mass). The size of the muscles of the lateral and medial sides of the pectoral

fin is different. Muscles of the lateral face weigh 93.9 g whereas muscles of the medial face weigh 71.9 g. Moreover, the distribution of the muscle mass is unequal among the different layers of the lateral side: the deep layer is the heaviest (36.1 g), then the superficial layer (30.5 g) and finally the middle layer (27.3 g). On the medial side, the distribution of the muscle mass is even more unequal, the superficial layer having the greatest mass (33.4 g), then the deep layer (21.7 g) and finally the middle layer (16.7 g) (Table 7).

The pelvic fin musculature of specimen CCC 27 weighs 112.6 g (0.30% body mass). Similar to the pectoral fin of CCC 14, the two sides (ventral and dorsal corresponding respectively to the lateral and medial sides of the pectoral fin) differ in the distribution of the muscle mass. The ventral side musculature (62.1 g) weighs more than that of the dorsal side (50.5 g). The distribution of the muscle masses along the three layers is also unequal, but more so on the dorsal side compared to the ventral side. On the dorsal side, the middle layer contributes around half of the total (23.6 g), whereas on the ventral side, the distribution of the mass is more similar across layers with the superficial layer being only slightly heavier than the other layers (25.3 g; Table 7).

Anatomical cross-section area

The anatomical cross-sectional area (ACSA) of the pectoral fin is 37.2 cm²; however, its distribution between the two sides of the fin is unequal. The ACSA of the lateral and medial side is 23.0 cm² and 14.2 cm², respectively. The distribution of the ACSA on the different layers for the lateral and medial sides of the fin is similar to the distribution of the muscle masses, the deep layer having an ACSA that is higher than that of the superficial and the middle layers (9.8 cm², 7.8 cm² and 4.2 cm² for the lateral side; 7.9 cm², 4.8 cm² and 1.5 cm² for the medial side). Of the 86 muscle bundles of the pectoral fin, 30 bundles are only involved in the articulation between

Table 7. Muscular properties of the different muscle layers of the pectoral and the pelvic fins of the coelacanth *L. chalumnae*

Pectoral fin	Layer	Mass (g)	ACSA (cm ²)	Pelvic fin	Layer	Mass (g)	ACSA (cm ²)
Lateral	Superficial	30.52	8.79	Ventral	Superficial	25.25	2.82
	Middle	27.25	4.23		Middle	18.34	2.98
	Deep	36.13	9.84		Deep	18.48	4.16
	Total	93.90	22.86		Total	62.07	9.96
Medial	Superficial	33.43	4.83	Dorsal	Superficial	14.08	1.59
	Middle	16.74	1.51		Middle	23.62	3.98
	Deep	21.75	7.91		Deep	12.85	4.45
	Total	71.92	14.25		Total	50.55	10.02

the pectoral girdle and the first mesomere (Tables 1–3). The total mass of these bundles is 57.8 g (35% total pectoral muscles mass), corresponding to an ACSA of 12.7 cm² (34% total pectoral ACSA).

The ACSA of the pelvic fin is 20.0 cm², and the distribution is similar for the dorsal and ventral sides (10.0 cm² and 10.0 cm²). The distribution of the ACSA across the different muscle layers shows that on the ventral side, the superficial and middle layers are similar (2.9 and 3.0 cm², respectively), whereas on the dorsal side they are different (1.6 and 4.0 cm², respectively). The deep layer of the ventral and dorsal sides is the most strongly developed (4.2 and 4.5 cm², respectively).

JOINT MOBILITY

Pectoral fin mobility

The pectoral fin of *L. chalumnae* shows a large degree of mobility in the three planes, defined as abduction/adduction, protraction/retraction and pronation/supination movements. The range of mobility is the highest for the joint between the pectoral girdle and the first mesomere (mean: 102° for abduction/adduction, 93° for protraction/retraction and 90° for pronation/supination) (Fig. 9). Mobility generally decreases along the metapterygial axis, and the distal joint is the least mobile in all planes (30° for abduction/adduction, 55° for protraction/retraction and 41° for pronation/supination for CCC 19, ligament damaged for CCC 14). The pectoral fins (CCC 14, CCC 19) show a similar joint mobility along the metapterygial axis. The large difference of mobility (Fig. 9) observed for the abduction/adduction of mesomere 1 with the girdle and mesomere 4 with mesomere 3, and the pronation/supination of mesomere 2 with mesomere 1 are possibly due to damaged ligaments on the CCC 19 specimen.

Pelvic fin mobility

Similar to the pectoral fin, the joint between the pelvic girdle and the first mesomere is the most mobile with a large range of motion for the abduction/adduction movement (50°). Antero-posterior and rotational movements have a reduced range of motion (32° and 29°, respectively). The measurements also show that the mobility decreases along the metapterygial axis, and that the distal joint is less mobile than the more proximal joints (Fig. 9). Overall, the mobility of the pelvic fin is lower than that of the pectoral fin.

DISCUSSION

THE MUSCULAR ANATOMY OF THE PAIRED FINS OF *L. CHALUMNAE*

In accordance with previous descriptions (Millot & Anthony, 1958; Diogo *et al.*, 2016; Miyake *et al.*, 2016)

our results show that the muscular anatomy of the pectoral and pelvic fins of the African coelacanth are arranged in three layers: superficial, middle and deep. However, both the pectoral and pelvic fins show a more complex muscular organization in terms of number of muscle bundles than previously described. Indeed, we observed 86 muscle bundles for the pectoral fin and 83 muscle bundles for the pelvic fin, whereas Millot & Anthony (1958) described only 40 muscle bundles for each fin. The more recent study of Miyake *et al.* (2016) described 48 muscles bundles for the pectoral fin, while that of Diogo *et al.* (2016) described a new elevator lateralis muscle at the dorsal side of the pelvic fin, originating on the abaxial musculature and inserting on the first mesomere. This muscle was subsequently reported in other studies (Molnar *et al.*, 2018, 2020). However, this muscle was never observed in our dissections, nor in the description of Millot & Anthony (1958). Moreover, the presence of a fascia that separates the pelvic muscles from the abdominal cavity precludes the presence of such a muscle in *Latimeria*.

The organization of the muscles along the metapterygial axis differs between the pectoral and pelvic fins. The pectoral fin shows a large number of mono-articular muscles on the lateral and medial sides of the fin (Figs 3–5) connecting adjacent elements, especially in the superficial and deep layers. Whereas the anatomy of the muscles on the lateral and medial sides of the fin appears visually symmetrical, the distribution of the mass is different between the two sides. Indeed, the lateral side of the pectoral fin contains more muscle mass than the medial side (93.9 g vs. 71.9 g; representing 57% and 43%, respectively, of the total pectoral mass). In the pelvic fin, the anatomy appears more asymmetrical (Figs 6–8). In the middle layer, the muscles of the dorsal side only insert on the pre-axial fin rays (fin rays 7–21) and only cover the lateral part of the dorsal side of the fin. In contrast, on the ventral side, the muscles insert on the pre-axial radial elements and on fin rays 7–33, and cover the entire ventral side of the fin. Moreover, in the deep layer, muscles are short and pronators join the mesomeres and the fin rays on the dorsal side. There are an additional five flexor muscles that connect the mesomeres. On the ventral side, however, most of the muscles are longer and originate dorsally on the membrane between the two fins. On the pelvic fin, the majority of muscles are poly-articular and insert directly on the fin rays. As in the pectoral fin, the distribution of the muscle mass is asymmetric. The ventral side of the fin has more mass than the dorsal side (63.1 g vs. 50.5 g; representing 56% and 44%, respectively, of the total pelvic muscle mass). In the pectoral fin, the more muscular side is involved in fin protraction. As the pectoral and pelvic fins have different orientations, in the pelvic fin, it

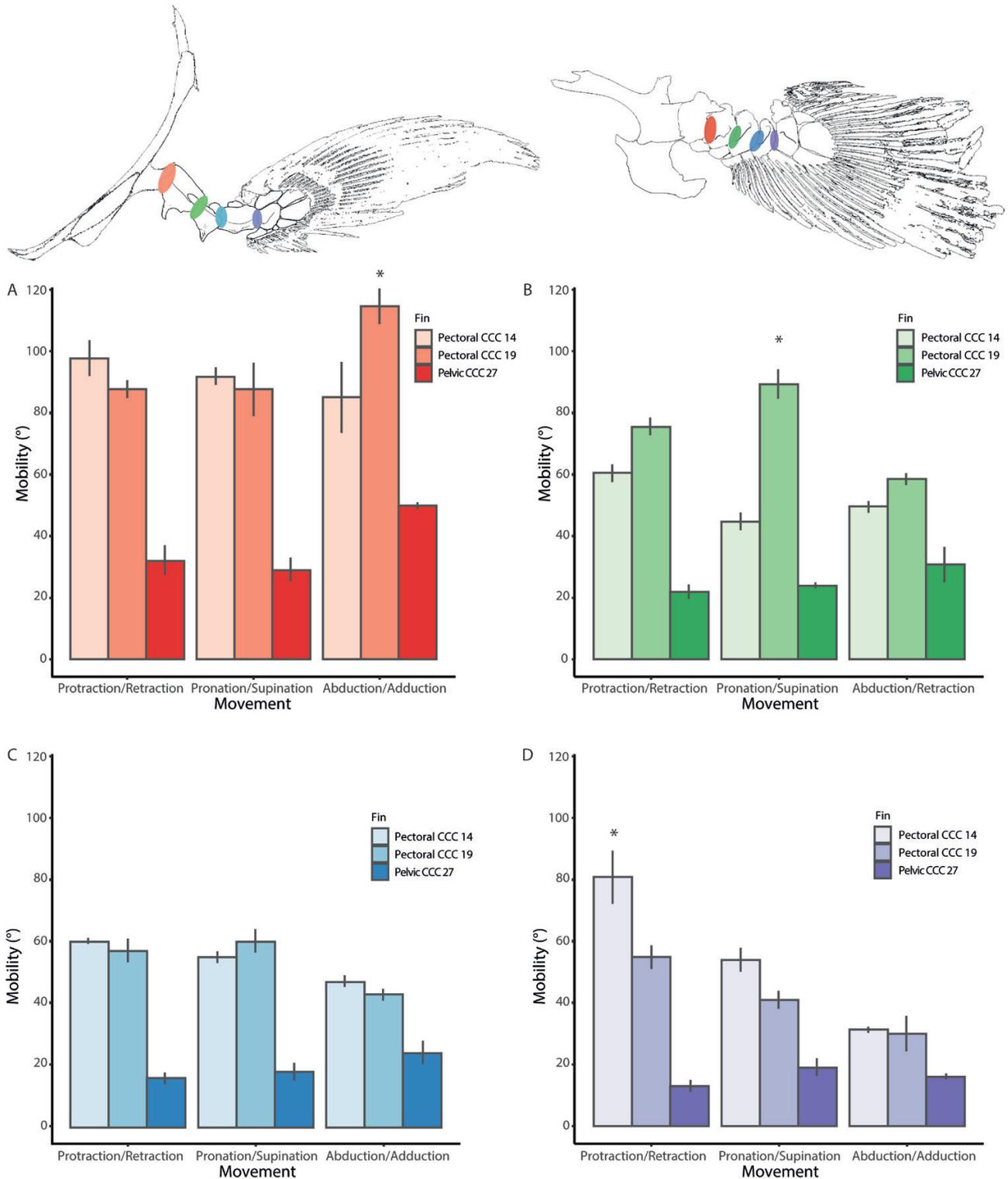


Figure 9. Range of mobility of the joints in the three planes along the metapterygial axis. A, joint mobility between the girdle and mesomere 1. B, joint mobility between mesomere 1 and mesomere 2. C, joint mobility between mesomere 2 and mesomere 3. D, joint mobility between mesomere 3 and mesomere 4. The * indicates a large difference of mobility between the two different pectoral fins. This difference either suggests a greater inter-individual variability of mobility, or more probably is due to a damaged ligament. The colors used in each panel correspond to the regions detailed on the pectoral and pelvic fins at the top of the figure.

is the side involved in the fin abduction that has the greatest muscular mass. However, whereas for the pectoral fin the ACSA on the lateral side of the fin is higher (Table 7), for the pelvic fin the ACSA on the ventral and dorsal sides is similar.

A smaller pelvic fin compared to the pectoral fin is common in actinopterygians and non-tetrapod sarcopterygians (Coates, 1995; Coates & Ruta, 2007; Shubin *et al.*, 2014). The coelacanth presents a similar muscular anatomy, since the pelvic fin is smaller in size and the muscle mass of the pectoral fin (166 g) is greater than that of the pelvic fin (113 g). However, the total masses of the pectoral and pelvic fins correspond only to 0.86% and 0.60% of the total body mass, respectively. The muscle architecture also differs between the pectoral and the pelvic fin. The ACSA of the pectoral fin is greater than that of the pelvic fins (Table 7). Since the ACSA is a proxy of the force that can be developed by muscles (Close, 1972), it appears that the pectoral fin can generate more force and is thus likely more involved in generating propulsion or in the stabilization of the coelacanth. This is in accordance with observations of Fricke & Hissmann (1992), who suggested that the pectoral fin is important in locomotion. In teleosts, the pectoral fins have an active role for a variety of manoeuvring behaviours and for low-speed swimming (Gibb *et al.*, 1994; Drucker & Lauder, 2003; Standen & Lauder, 2005; Don *et al.*, 2013). In teleosts, the pelvic fins help control the body position during manoeuvres and control stability (Lauder & Drucker, 2004; Standen, 2008; Don *et al.*, 2013). As in teleosts, the respective role of the pectoral and pelvic fins is likely different in the coelacanth, with the pectoral fins presumably having a more active role in contrast to the pelvic fins that likely have a function in body stabilization and manoeuvres (Fricke & Hissmann, 1992).

Whereas the two sides of the pelvic fin show an equal ACSA and should be able to develop the same force, in the pectoral fin the distribution is unequal. Indeed, the lateral side of the fin has a higher ACSA than the medial side (Table 7). This suggests that the lateral side of the pectoral fin (resulting in fin protraction) is stronger than the medial side (responsible for retraction). In the cod (*Gadus morhua*) and the saithe (*Gadus virens*), it has been shown that the abductor muscle mass of the pectoral fin is the same as the adductor muscle mass, whereas for the mackerel (*Scorpaenopsis scorpaenoides*), the abductor muscle mass is twice that of the adductor muscle mass (Geerlink, 1987). It appears that in the cod and the saithe, the pectoral fins have a more important role in the backward movements of the pectoral fin for braking than in the mackerel. During locomotion, Fricke & Hissmann (1992) showed that the lateral side of the pectoral fin (ventral face in their paper) pushes the water against the direction of

the motion suggesting that the muscles of this side are mainly involved in braking whereas the muscles from the medial side may be more important in generating propulsion.

The pelvic girdle of *L. chalumnae* has a superficial ossification around the anterior process and the medial process, associated with an internal trabecular system (Mansuit *et al.*, 2020b). It has been suggested that this ossification may reinforce these parts of the pelvic girdle to resist to the force developed by the muscles that insert there. The anterior process is long and thin, and even if the medial process is slightly more robust, the insertion area of the muscles is small such that high stresses may indeed be imposed on these processes. Based on our data it appears that the ACSA of the muscles inserting there is greater on the anterior (2.8 cm²) and medial processes (2.6 cm²) compared to other parts of the girdle (Supporting Information, Table S2). The robust part of the girdle with the articular head also is submitted to significant muscle forces (2.5 cm²). This part is not ossified, nor associated with a trabecular system. However, the robustness of this part of the girdle might explain why there is no need for such reinforcement to support the force developed by the muscles. The high value of ACSA of the muscle bundles inserting on the ossified part of the girdle supports the hypothesis of reinforcement of these parts to support the forces generated by the muscles during contraction. The ACSA of the muscle bundles on the lateral process is also large (2.0 cm²); however, since the surface of the lateral process is larger than the anterior or medial processes, the force produced by bundles is also distributed across a larger surface, likely reducing stress concentrations. The role of muscles in the ossification of bones during the development has been demonstrated for chickens and mice (Nowlan *et al.*, 2008, 2010), with muscle presence and its activity being essential in the ossification of the bones. When the muscle mass or the muscular activity is reduced, the ossification of the bone is reduced (Nowlan *et al.*, 2008).

As in all sarcopterygian fishes, the coelacanth *L. chalumnae* has lobed paired fins (e.g. Millot & Anthony, 1958), different in their anatomy from the fins of most actinopterygians. Different authors have pointed out that actinopterygians and sarcopterygians differ in the origin and insertion of fin muscles. In actinopterygians, muscles extend generally from the girdle to the fin rays, passing over the radials (e.g. Greene & Greene, 1914; Geerlink, 1979; Lauder & Drucker, 2004; Diogo & Abdala, 2007; Wilhelm *et al.*, 2015), even if the pre-axial and post-axial muscles can be inserted on the protopterygial or metapterygial elements in some species (Wilhelm *et al.*, 2015; Molnar *et al.*, 2017). In sarcopterygians, muscles present a more complex organization and most of the muscles

insert on the endoskeletal elements of the appendages in order to move the other skeletal elements of the fin or limb. The abductor and adductor superficialis of the coelacanth and lungfish are segmented and some bundles insert also on the fin rays (Boisvert *et al.*, 2013; Diogo *et al.*, 2016). In tetrapods, there is a functional regionalization of the metapterygial axis in stylo-, zeugo- and autopod, associated with the complex muscular organization of the limbs (Ashley-Ross, 1994; King & Hale, 2014). Associated with this functional regionalization of the limbs, tetrapods have an important proportion of mono-articular muscles and they have lost the abductor and adductor muscles (Miyake *et al.*, 2016). The functional regionalization found in the tetrapod limbs (stylo-, zeugo- and autopod) is not present in the paired fins of non-sarcopterygian fishes (Janvier, 1996; King & Hale, 2014) and there is no regionalization of muscles along the metapterygial axis. In sarcopterygian fishes, since there is no appendage-driven substrate locomotion, there is no need for such functional regionalization of the fin. However, the muscles of the pectoral and pelvic fins of *Latimeria* differ in their organization with more muscles inserting on the metapterygial axis of the pectoral fin than on the pelvic fin (e.g. abductor/adductor superficialis; supinator) (Figs 2, 4, 5, 7). On the pelvic fin of *L. chalumnae*, most muscles extend from the pelvic girdle to the fin rays. Only in the deep muscle layer can be observed some inter-mesomere muscles or muscles that originate from mesomeres and insert on the fin rays (flexor and pronator muscles). The muscular organization of the superficial and middle layers, as well as that of the majority of the bundles of the ventral deep layer, is similar to the muscular arrangement in actinopterygians, with muscles that originate on the girdle and insert at the base of the fin rays (Adriaens *et al.*, 1993; Lauder & Drucker, 2004; Molnar *et al.*, 2017). By contrast, in the pectoral fin, mono-articular inter-mesomere muscles allow the lateral or medial flexion of the different mesomeres. Thus, it can be considered that the pelvic fin has a more plesiomorphic organization of the muscles than the pectoral fin. The mesomeres of the fins are positioned in a single plane, different from the “Z-shape” organization of the tetrapod limbs. Moreover, the muscles on one side of the fin have a similar function. Consequently, although there is an anatomical regionalization of the muscles on the pectoral fin, there is no strict functional regionalization of the muscles along the metapterygial axis of the fin, which is different from what is observed in tetrapod limbs. Thus, it is the anatomical regionalization of the muscle that might be the driver of the subsequent functional regionalization of the muscles on the limbs. Indeed, there are an important number of mono-articular muscles that are involved only in the

mobility of the shoulder (i.e., the mobility of mesomere 1 on the pectoral girdle) of *L. chalumnae* (30 muscle bundles that corresponds to 35% of the pectoral muscle mass). The important number of muscles associated with this joint might be associated with the large stroke amplitude of the pectoral fin and the diversity and complexity of fin movements observed during swimming (Fricke & Hissmann, 1992; Décamps *et al.*, 2017). In tetrapods, rotational movements around the joint between the pelvic girdle and the femur are permitted by the coordinated activity of muscles associated with these elements (Wentink, 1976; Ashley-Ross, 1995; Aiello *et al.*, 2014). The presence of a large number of muscles associated with the first mesomere of the pectoral fin of *L. chalumnae* could underlie a similar functional mechanism allowing for the mobility of the pectoral fin.

JOINT MOBILITY ALONG THE METAPTERYGIAL AXIS OF THE FINS

Data on joint mobility demonstrated that the most proximal joint of the pectoral and pelvic fins (shoulder and hip) has the highest degree of mobility, and that the following joints along the metapterygial axis are less mobile. However, whereas the mobility of the pelvic fin follows the same general decreasing trends in mobility along its metapterygial axis as the pectoral fin, it is less mobile overall (Fig. 9). This difference in mobility was first documented *in vivo* during locomotion (Fricke & Hissmann, 1992), and was suggested to be due to the wide attachment of the pelvic fin to the body. The pectoral and pelvic fins have a similar organization of the endoskeleton except for the presence of pre-axial radial 0 on the pelvic fin (Millot & Anthony, 1958; Mansuit *et al.*, 2020b). It has been suggested previously that this element could reduce the mobility of this fin, and our measurements of the degree of mobility of this joint support this hypothesis. Moreover, the morphology of the mesomeres and pre-axial radial elements is different in the pectoral and pelvic fins (Fig. 1). The shape of the pelvic mesomeres may constrain the mobility of the elements, as the size of pelvic pre-axial radials is proportionally larger than those of the pectoral fin, and may consequently limit the lateral mobility of the elements.

Measurements made *in vivo* and during the first dissections confirm the mobility of the pectoral fin of *L. chalumnae*, since the pectoral fin is able to rotate a full 180° (Millot & Anthony, 1958; Fricke & Hissmann, 1992). However, this ‘rotation’ is greater than the shoulder joint allows, and is thus the consequence of the mobility of the different joints of the metapterygial axis. Similarly, the pectoral fin can be moved in the dorso-ventral and anteroposterior directions up to 120° *in vivo* (Fricke & Hissmann, 1992), an excursion

angle that is greater than the mobility of the shoulder joint for the abduction/adduction and the protraction/retraction movements, respectively. Here as well it is the combination of the mobility at successive joints that allows the large stroke amplitude of the pectoral fin. More detailed kinematic analyses of fin movements in 3D are clearly needed to be able to link joint mobility to overall fin movements.

The African lungfish *Protopterus annectens* also has a large mobility of the pelvic fin *in vivo*, possibly superior to that of the pelvic fin of *L. chalumnae* (King *et al.*, 2011; Aiello *et al.*, 2014). The joint mobility of the first mesomere with the body in *Protopterus* shows a larger mobility compared to that of the coelacanth. The long-axis rotational mobility was not calculated, nor the mobility of the different joints along the metapterygial axis; however, *in vivo* footage shows that the large mobility at the hip joint is present for the different joints along the entire metapterygial axis during 'walking' locomotion. This suggests that the joints between mesomeres of the paired fins of *P. annectens* are not constrained as observed for the pelvic fin of *L. chalumnae* (King *et al.*, 2011; Aiello *et al.*, 2014). The large mobility of the joints of these fins may thus be useful for the 'walking' locomotion of *P. annectens* in its aquatic environment (King *et al.*, 2011). Unlike the African lungfish, the coelacanth only uses its fins for the swimming. In cetaceans, the appendages are modified into flippers and mainly useful for manoeuvring and turning (e.g. Felts, 1966; Fish & Battle, 1995). In these animals, the shoulder joint presents a large mobility in three directions, whereas the elbow and wrist joint have a restricted mobility that turns the limb into a paddle-like structure. This large mobility at the shoulder and restricted mobility within the limb permits the production of thrust for locomotion and manoeuvring (Felts, 1966). Even if the joint mobility of the fins of the coelacanth is not as restricted as the elbow and wrist of cetaceans, the relatively rigid fins might allow thrust production, necessary for locomotion and manoeuvring.

CONCLUSION

As previously described, our dissections of the pectoral and pelvic fins of the African coelacanth *L. chalumnae* show that the muscles are organized in three different muscle layers, but with a more complex organization than previously known. The pectoral and pelvic fins show a different organization of the muscle bundles. The pectoral muscles are mostly mono-articular and insert on the different elements of the endoskeletal metapterygial axis of the fin, whereas almost all pelvic muscles are poly-articular and run from the pelvic girdle to the fin rays. Thus, the pelvic fin shows a more

plesiomorphic configuration of the muscles, similar to that of actinopterygians, whereas the pectoral fin shows a muscular anatomy closer to that of lungfishes and tetrapods. The ossification of part of the pelvic girdle may be associated with the stronger muscles that attach there as suggested by our data.

The pectoral and pelvic fins are different since the pectoral fin has a greater ACSA and can provide more force than the pelvic fin. A stronger pectoral fin can have a more important contribution in locomotion than the pelvic fin, in agreement with the observations of the locomotion of the coelacanth. Indeed, the pectoral fin seems more active than the pelvic fin during locomotion and manoeuvring.

Finally, the joint mobilities of the two fins are different, with the pelvic fin being less mobile than the pectoral fin. It is suggested here that the morphology of the mesomeres and the pre-axial radial of the pelvic fin may constrain the joints of the fin. Moreover, the presence of the supernumerary element pre-axial radial 0 at the base of the pelvic fin may further limit the mobility of the hip, whereas in the pectoral fin, the shoulder shows greater mobility in all directions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Organization of the muscle anatomy of the superficial layers of the pelvic fin of *Latimeria*, in ventral (A, B) and dorsal aspect (C). B, close-up of the ventral face of the superficial layer. The red muscle corresponds to the pterygialis cranialis (“abducteur de la nageoire”, Millot & Anthony, 1958) and the blue line corresponds to the “abaisseur superficiel” of Millot & Anthony (1958) (abductor superficialis in our description). This “abaisseur superficiel” is formed by several muscle bundles and some of them are represented in blue here. Similarly, on the dorsal side of the fin (C), the different bundles of the adductor superficialis are clearly identifiable on the fin.

Figure S2. Illustrations of the first steps of the dissection of the left pectoral fin in the coelacanth *L. chalumnae* in medial (A-C) and lateral view (D). A, fin before the dissection. B, dissection of the adductor superficialis 1 to show the adductor profundus below. C, separation of the different bundles of adductor profundus in medial view. D, separation of the different bundles of the abductor profundus in lateral view. D: dorsal, Dis: distal; Prox: proximal; V: ventral.

Figure S3. Muscular anatomy of the pelvic fin of *L. chalumnae* with focus on the adductor profundus 8 muscle bundle to illustrate the sub-bundles and fascicles. A, schematic illustration of the muscular organization of the dorsal middle layer of the pelvic fin, Add.prof.9–12 are not illustrated here. B, close-up of adductor profundus 8 *in situ* (numbered 39 during the dissections). C, the different sub-bundles and fascicles of Add.prof.8 are shown *in situ*; red point = insertion of the sub-bundle Add.prof.8B on mesomere 3; blue point = insertion of the sub-bundle Add.prof.8C on mesomere 4; purple point = insertion of the sub-bundle Add.prof.8D on the fin rays (39i corresponds to a sub-bundle of Add.prof.8D). Add.prof.8A and some fascicules of the sub-bundles of Add.prof.8C and 8D were removed before the photo was taken. Add. prof.: adductor profundus.

Figure S4. A, deep muscle layer of the pelvic fin of *L. chalumnae* in dorsal view illustrating the organization of the bundles of different pronator and flexor muscles. B, close-up of pronator 2 *in situ*. 76 corresponds to the pronator 2e muscle bundle. Flex.: flexor; Pron.: pronator.

Table S1. Details of the sub-division of the different muscle bundles of the pelvic fin of the extant coelacanth *L. chalumnae* and their properties.

Table S2. Distribution of the muscle masses and ACSA on the different parts of the pelvic girdle.