The Differences of the Functional-morphological Strategy between the First and Second Dorsal Fins of the Living Coelacanth (*Latimeria chalumnae*)

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(2011 年 5 月 15 日受領, 2011 年 10 月 31 日採択)

現生シーラカンス (*Latimeria chalumnae*) における第一・第二背鰭間の 機能形態学的戦略の相違

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ABSTRACT. The first and second dorsal fins of living coelacanths were studied using three-dimensional reconstructed images, while the sectional areas of the epaxial and hypaxial musculatures and the musculature related to the first and peculiar to the second dorsal fins were measured by image analyzing methods. The musculature related to the first dorsal fin was not enlarged to the lepidotrichia beyond the dorsal margin of the trunk; however, the fin rays consisting of lepidotrichia were supported by bone plate of the trunk. The two bones of the trunk supported the four bone elements of the second dorsal fin, in which the peculiar musculature was developed from the trunk area to the bone elements. The first dorsal fin may function as a passive stabilizer controlled by the relatively smaller musculature from the bone plate of the trunk and the mechanical articulation between the bone plate of the trunk and lepidotrichia. In contrast, the second dorsal fin represented an active generator of thrust during slow locomotion. We suggest that the active power generator of the sarcopterygian fin may be required in the second dorsal fin at the caudal region of the trunk, which possesses fewer epaxial and hypaxial muscles than the cranial region where the first dorsal fin is located.

Key words : Coelacanths, CT, Dorsal fin, *Latimeria*, Musculoskeletal system

Jpn. J. Zoo. Wildl. Med. 17(2) : 79-86, 2012

Two species of *Latimeria* belonging to the coelacanths have been considered as one of the living fossils. As the form of this taxon has not changed since the Cenozoic Era, the history of the discovery and records of *Latimeria chalumnae*, *L. menadoensis* and their related fossil species had great impacts on evolutionary biology [1-15]. Anatomical reviews of *L. chalumnae* have been published [16-18], since its description, especially pertaining to the origin of their four limbs, and the pectoral and pelvic fins have attracted the

attention of many evolutionary morphologists. The two pairs of fins [16, 19-22] and basicranial structure [23, 24] have been morphologically detailed after comparison with the fossils as one of the Crossopterygii, *Eustenopteron*, and the earliest amphibians as *Ichthyostega* and *Acanthostega*. However, because the locomotion mechanism of the two dorsal fins has not been shown to be associated with the origin of the four limbs, the first ray and second lobed dorsal fins have not been morphologically examined exhaustively. The reason for

the existence of two morphologically different dorsal fins in sarcopterygii fishes such as *Latimeria* remains unclear. In this study, therefore, using computed tomography (CT), the internal structure of the first and second dorsal fins and the epaxial and hypaxial musculatures were observed and quantitatively analyzed to determine the functional significance in the coelacanth during a specific evolutionary stage.

MATERIALS AND METHODS

One frozen specimen [CCC (Coelacanth Conservation Council, Grahamstown, South Africa) Individual No: 213] of the Comoran coelacanth (*L. chalumnae*) was used for CT examinations. The specimen was obtained from Tanzania and has been stored in Aquamarine Fukushima. The body of the specimen was axially sectioned by CT (Toshiba Aquilion16: Toshiba Medical Systems, Japan) at 2 mm thickness without gap at 120 kV and 200 mAs. Three-dimensional images were reconstructed from a series of CT sections by Voxel Transmission (Volume Rendering) techniques through an image analyzing system (AZE Virtual Place: AZE Corporation, Japan). Adequate thresholds were qualitatively selected and the axial, bilateral, and horizontal sections obtained from the three-dimensional reconstructed image were used to effectively visualize the regions of the dorsal fins and related axial musculatures. The software ImageJ (NIH, USA) was used to measure the sectional areas of the epaxial and hypaxial musculatures and muscles peculiar to the two dorsal fins. We used 43 serial axial sections of 10 mm interval including the regions of the first and second dorsal fins for measurements of the musculature areas.

RESULTS

The three-dimensional reconstructed images of the whole

Fig. 1 The three-dimensional reconstructed images of the whole body. A : left lateral aspect, B : dorso-lateral aspect, C : dorsal aspect.

body of the specimen were axially rotated (Fig. 1). The total body length was 1190 mm from the reconstructed data. The lateral sections of the region including the two dorsal fins are

Fig. 2 Parasagittal (A) and sagittal (B) sections of the body. The lepidotrichia (small arrow) with eight pairs of fin ray is seen. The bone plate (large arrow) related to the first dorsal fin, and the two bones (intermediate arrows) connected to the second dorsal fin are shown. N, Notochord. Cranial direction at the left.

Fig. 3 The axial sections of the area of the first dorsal fin. The sections are arranged from the cranial (A) to the caudal (F) region with the longitudinal interval of 20 mm. The musculature (large arrows) ran from the bone plate (intermediate arrow) to the lepidotrichia (small arrow). E, epaxial musculature. H, hypaxial musculature. N, notochord. Dorsal direction at the top.

shown (Fig. 2). The horizontal sections of the first (Fig. 3) and the second (Fig. 4) dorsal fins are arranged.

The first ray dorsal fin was equipped with the lepidotrichia, whereas the second lobed dorsal fin represented the sarcopterygian fin with substantial musculoskeletal elements (Fig. 2). The lepidotrichia of the first dorsal fin possessed eight pairs of fin ray. The first dorsal fin was supported by the bone plate along the sagittal plane (Fig. 2). Specialized attachment

between the bone plate and the lepidotrichia of the first dorsal fin were confirmed; however, peculiar musculature was not observed even in the fin itself (Fig. 3). The musculature related to the fin ran from the bone plate to the basal area of the lepidotrichia. Although the musculature was confirmed around the bone plate related to the first dorsal fin, it was not enlarged to the fin beyond the dorsal margin of the trunk. The musculature directly attached to the bone plate in the area

Fig. 4 The axial sections of the area of the second dorsal fin. The sections are arranged from the cranial (A) to the caudal (F) region with the longitudinal interval of 20 mm. The musculature (large arrows) peculiar to the fin originates from the two bone plates (intermediate arrows) of the trunk and runs to the bone element (small arrows). E, epaxial musculature. H, hypaxial musculature. N, notochord. Dorsal direction at the top.

of the first dorsal fin was clearly separated from the epaxial musculature (Fig. 3). The musculoskeletal mechanism of the second dorsal fin consisted of thick musculature peculiar to this fin (Fig. 4). The muscles arose from the two bones in the trunk and reached the distal area of the fin. The muscle bundle became thinner in the distal part of the fin; however connected each bone element to form an active locomotion apparatus.

Horizontal sections of the first dorsal fin are shown (Fig. 5). The lepidotrichia consisted of eight symmetrical fin rays in the first dorsal fin. Eight pairs of fin rays were bilaterally developed and dorso-caudally radiated. The lepidotrichia was articulated to the bone plate of the trunk. The musculature related to the first dorsal fin rose from the huge bone plate. It was adjacent to the dorso-medial surface of the epaxial musculature; however it

was not morphologically connected to the median neural spine and the notochord.

The hard parts of the second dorsal fin consisted of four bone elements supported by the two bones of the trunk (Figs. 2 and 6). The caudal bone of the trunk showed a thick post and thinner ventral plate (Fig. 6). The thick musculature enveloped the four bone elements of the second dorsal fin. The musculature was not substantially related to the median neural spine and notochord; however, it originated from the two bones of the trunk and ran to the four bone elements of the fin.

The data of the sectional area of the musculatures are arranged from the cranial to caudal regions of the body (Table 1 and Fig. 7). The enlarged areas of the musculature related to the first dorsal fin were 411-544 mm² in each side (Section

Fig. 5 The horizontal sections of the first dorsal fin. The sections are arranged from the dorsal (A) to the ventral (F) levels with the vertical interval of 20 mm. The eight fin rays (small arrows) of the lepidotrichia are observed, whereas the bone plate (large arrow) is discerned. Cranial direction at the top.

Nos. 9-13), in which the areas of the epaxial musculature were about 4000-4800 mm². Whereas the areas of the musculature peculiar to the second dorsal fin reached 423-739 mm² (Section Nos. 36-40), the epaxial musculature in each side were approximately 3000-4100 mm² in the same region (Table 1, Figs. 7 and 8). The total areas of the musculature related to the first dorsal fin were 3982 and 4025 mm², those peculiar to the second dorsal fin 4898 and 4113 mm² in each side. The largest sections of the epaxial and hypaxial musculature were in the

cranial region of the trunk; however, both axial musculatures rapidly decreased, as the sarcopterygian fin, such as the second dorsal fin, grew thicker (Table 1, Figs 3, 4, 7 and 8).

DISCUSSION

Since the enlarged musculature of the second dorsal fin originated from the two bone plates and attached to each bone element, this fin may have enabled the coelacanth to control the thrust from the caudal region of the body and to stabilize

Fig. 6 The horizontal sections of the second dorsal fin. The sections are arranged from the dorsal (A) to the ventral (F) levels with the vertical interval of 25 mm. The bone elements of the fin are observed in the sections of the fin (B, C, and D). The two bones support the bone elements from the trunk side (E and F). The caudal bone of the trunk consists of a thick post (large arrow) and thinner ventral plate (small arrow). Cranial direction at the top.

Table 1 Axial sectional area (mm²) of each musculature

	section No.															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
right epaxial	3968	4507	4399	4644	4642	4738	4447	4168	4108	4466	4304	4501	4073	4598	4466	
left epaxial	4044	4145	4278	4611	4982	4674	4576	4558	4431	4706	4710	4620	4700	4483	4806	
right hypaxial	4429	4528	4666	4319	4985	4419	4911	4582	4730	4640	4927	4922	4844	4979	4876	
left hypaxial	4554	4484	4690	4612	4554	4122	4307	4447	4264	4892	4595	4940	4916	4625	4580	
	section No.															
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
right epaxial	4529	4423	4597	4376	4452	4598	4537	4851	4380	4598	4505	4485	4452	4650	4294	
left epaxial	4810	4864	5033	4885	4430	4449	4721	4664	4370	4136	4374	4578	4343	4347	4212	
right hypaxial	4261	4396	4369	4276	4261	3989	4070	4258	4649	4833	4682	4977	5048	4601	4846	
left hypaxial	4505	4417	4521	4049	4392	4517	3952	3937	4046	4776	4583	4838	4690	4624	4507	
	section No.															
	31	32	33	34	35	36	37	38	39	40	41	42	43	total		
right epaxial	4281	4060	4118	4103	3908	4071	3703	3727	3086	3340	3331	3034	2486	181004		
left epaxial	4349	3972	3606	3646	3681	3513	3195	3406	3250	3019	3188	2913	2701	180979		
right hypaxial	4262	4296	4112	4352	4083	3820	3728	3858	3694	3247	3469	2885	3375	187454		
left hypaxial	4582	4273	4183	4318	4339	3683	3703	3686	3416	3337	3174	2999	2872	183501		
	section No.															
				8	9	10	11	12	13	14	15	16	17	total		
right side of the 1st dorsal fin				314	510	544	529	523	434	396	202	274	256	3982		
left side of the 1st dorsal fin				283	411	533	532	487	533	437	279	274	256	4025		
	section No.															
				31	32	33	34	35	36	37	38	39	40	41	42	total
right side of the 2nd dorsal fin				170	179	328	420	497	503	644	574	739	517	223	104	4898
left side of the 2nd dorsal fin				130	130	334	351	448	589	574	457	471	423	122	84	4113

the trunk during slow locomotion. The two dorsal fins have not been functional-morphologically detailed in *Latimeria*, although the field observation of the living *Latimeria* [25] and a comparative paleontological study [26] mainly dealt with the second dorsal fin. The second dorsal fin, together with the anal fin may help in generating thrust coordinated rotating movement around the long axis, and thus change the mode of slow locomotion [26]. Since the slow locomotion at least in *Latimeria* species is produced by flexible movement of the trunk and the sculling of the second dorsal and anal fins, the developments of the axial musculature and the second dorsal fin-related musculature are noteworthy.

On the musculatures related to the first and peculiar to the second dorsal fins, the axial sectional area was noticeable. The total areas were larger in the musculature peculiar to the second dorsal fin than that related to the first dorsal fin. It

indicated the strong power of the stroke of the second dorsal fin. As the region including the second dorsal fin had a smaller sectional area of axial musculatures than that of the first dorsal fin, we suggest that the musculature peculiar to the second dorsal fin may act as one of the important thrust generators in caudal region of the body.

In contrast, the musculature related to the first dorsal fin appeared relatively smaller than the thick axial musculature in cranial region. In addition, the musculature was not distally extended in the first dorsal fin. These findings suggest that the second dorsal fin may contribute to the slow locomotion of the coelacanths as one of the main active thrusters [25], whereas the first dorsal fin may act as an additional passive stabilizer [16, 27]. We suggest that the strong power generator of the sarcopterygian fin such as second dorsal and anal fins may be required in the caudal region of the trunk, which possesses

Fig. 7 Axial sectional areas of the axial musculatures. Horizontal axis, the section number from cranial to caudal region. Vertical axis, areas (square millimeter). Open circles, right epaxial musculature. Solid circles, left epaxial musculature. Open triangles, right hypaxial musculature. Solid triangles, left hypaxial musculature.

fewer quantity of the axial musculatures than in the cranial region in which the first dorsal fin is positioned. Considering, at least qualitatively, the sectional area of the axial musculatures, it was consistent that *Eustenopteron* possessed the second dorsal and anal fins in the portion of the trunk that rapidly thinned [19, 20].

Previously, the CT and/or MRI examinations of living *Latimeria* species have been published [21, 27]. The morphological relationships between external and internal structures can be easily observed in coelacanths; therefore quantitative analyses using CT data will have added importance in the functional-morphology of the coelacanths. In this study, the morphologically artifact might be caused because of freezing in a degree; however, the dorsal area including the two fins did not appear to have been artificially changed in this specimen.

Ecological and physiological studies have been published on Comoran *Latimeria* [25, 28-31]. We believe that the field observations and physiological approaches will help in elucidating the functional relationships between the dorsal fin structure and the slow locomotion characteristic of the coelacanths, in addition to the purely morphological observations. Since our team is collecting the movie data on

Fig. 8 Axial sectional areas of the musculature related to the first and peculiar to the second dorsal fins. Horizontal axis, the section number. Vertical axis, areas (square millimeter). Open circles, right musculature related to the first dorsal fin. Solid circles, left musculature related to the first dorsal fin. Open triangles, right musculature peculiar to the second dorsal fin. Solid triangles, left musculature peculiar to the second dorsal fin.

the action of the dorsal fins, the data will contribute to the functional analysis of the independent roles of each dorsal fin.

ACKNOWLEDGEMENTS

We thank the staff of Aquamarine Fukushima for their help and encouragement in this study. This study was financially supported by the Grant-in-Aids for Scientific Research nos. 21370033, 21658103, 22405002 from the Ministry of Education, Science and Culture, Japan.

要 約

現生シーラカンスの第一および第二背鰭を三次元復構画像を用いて検討し、軸上筋と軸下筋、第一背鰭に関連する筋肉、第二背鰭固有の筋肉の断面積を画像解析手法により計測した。第一背鰭に関連する筋肉は体幹の背側端を超えて鱗状鰭条まで伸長することはなかった。しかし、鱗状鰭条からなる放射した鰭は体幹部の骨性の板によって支持されていた。第二背鰭では、体幹部の2つの骨が鰭の4つの骨格要素を支持し、その4つの骨の周囲には、体幹部から固有の筋層が発達していた。第一背鰭は、体幹部の骨質の板から伸びる比較的小さな筋肉と、体幹部の骨質の板と鱗状鰭条の間の機械的な関節によって制御される、受動的な安定板として機能していると推察された。対照的に第二背鰭は、速度の遅い運動時に積極的な推進力を生み

出す装置となっていることが示唆された。第一背鰭が位置する体幹前方と比べて軸上筋と軸下筋が減少する体幹後方においては、肉鰭類の鰭による推進力の発生は、第二背鰭に要求される機能であることが推測された。

キーワード：シーラカンス, CT, 背鰭, *Latimeria*, 筋骨格系

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