論　文　の　内　容　の　要　旨

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論文題目　Adaptation for aquatic and terrestrial environments by locomotive trunk structure in Urodela
（両棲類有尾目の体幹部運動器形態による水陸環境適応）

In Devonian Period, early tetrapod stepped on to the land. They changed their locomotive mode and structure according to the landing event. In water, their bodies are buoyed up by the water, and viscosity of water occurs for them. By contrast, on land, they need to lift up their body by more developed limbs against gravity. The late Devonian tetrapod are thought to use their limbs more in swimming than walking, and their life is suggested to be still aquatic. *Pederpes* is the earliest-known tetrapod which is supposed to begin terrestrial locomotion in early Carboniferos Period. In the Permian Period, tetrapod is postulated to adapt to terrestrial life since they had robuster limbs and more massive skeleton than its early relatives. The locomotive mode of early tetrapod from the morphological transitions in aquatic life to terrestrial life has been roughly mentioned. To clarify the evolutional morphological changes of fish to tetrapod, surveying and comparing the structure of living Urodela which morphologically resemble the extinct early tetrapod are needed.

Urodela have species with various lifestyles such as aquatic, semi-aquatic and terrestrial. The more terrestrial species possessed more developed girdles and limbs than those of the more aquatic species. These features show that the living Urodela contribute to the postulation of the transition of locomotive mode in early tetrapod from water to land. Since they use their trunk undulatory both in swimming and walking, trunk of Urodela is a functionally important part of their locomotion. The structure of trunk of Urodela is supposed to vary according to their locomotion modes and habitats. The locomotive function is morphologically determined by the muscular and skeletal systems. The muscles produce locomotive power and help to support the body, and the axial skeleton forms the framework of the body and plays a role in the movement and support of the body. To mention the environmental adaptation in Urodela, ontogenetic changes should be morphologically examined in addition to phylogenetic comparisons since Urodela include the species which changes their habitats from water to ground by metamorphosis. The purpose of this study is clarifying the adaptive strategy of landing from water in early tetrapod by characterizing and quantifying morphological variations in trunk structure in Urodela of different ecotypes and different developmental stages. In this study, various species in different habitats (aquatic: *Siren intermedia*, *Amphiuma tridactylum*, *Necturus maculosus*, *Andrias japonicus*, semi-aquatic: *Cynops phyrrhogaster*, *Cynops ensicauda*, terrestrial: *Hynobius nigrescens*, *Hynobius lichenatus*, *Ambystoma tigrinum*) were used for comparative study.

In chapter 1, strategy of environmental adaptations for aquatic and terrestrial environments of trunk muscles in Urodela was studied. Trunk muscles of Urodela have been studied in the past studies because of the importance of usage of trunk muscle for locomotion both in water and ground. Though the groups of trunk muscles have been quantified by measuring cross-sectional area, to weight each trunk muscle is the best way for quantifying trunk muscles. Eight species of adult salamanders representing six families and three different habitats were used. The structure of trunk muscles was observed in cross-sections of mid-trunk and lateral view by using fixed specimens. Each trunk muscle was weighed and muscle weight ratio was calculated. Trunk muscles morphologically varied among species (Fig. 1). The aquatic species possessed thicker and larger lateral hypaxial muscles, and unseparated smaller *M. rectus abdominis*. By contrast, the more terrestrial species were equipped with thinner smaller lateral hypaxial muscles, larger dorsalis muscles, and separated larger *M. rectus abdominis*. It is suggested that the more aquatic species use their lateral hypaxial muscles for powerful lateral undulatory swimming, whereas developed larger dorsalis muscles and *M. rectus abdominis* play a role in keeping posture and sustain own weight against gravity in the more terrestrial species.

In chapter 2, the interspecific variations of structure of vertebra were revealed. Zygapophyseal angle of vertebra adjusts the direction of movement and the degree of movement, and may reflect the strength of vertebra. Though vertebral structure has been in the past studies, prezygapophyseal angle was not quantified among Urodela species. The aim of chapter 2 is to clarifying the relationship between prezygapophyseal angle of vertebral and habitats in Urodela. Prezygapophyseal angle in Urodela with different habitats was measured using images scanned by μ-CT. Prezygapophyseal angle was obviously different among species (Fig. 2). The more aquatic species possessed the more horizontal prezygapophyseal angle whereas the more terrestsial species had the more vertical prezygapophyseal angle. It is postulated that the more horizontal prezygapophyseal angle enables aquatic species to locomote undulatory and more flexiblely. The more terrestrial species were equipped with the more vertical prezygapophyseal angle to strengthen vertebral column against gravity and resisting torsion of walking.

In chapter 3, the environmental adaptive strategy of positional differences of trunk muscles was shown. Anguilliform swimmers swim by traveling wave along the body, in contrast, in terrestrial quadrupedal vertebrates with elongated body, stress differently occurs in each position of the trunk (Fig. 3). The positional differences are thought to vary among Urodela with different habitats since their usage of trunk is determined by habitats. The percentage of group of trunk muscle was obtained by measuring cross-sectional area in anterior, middle and posterior parts of trunk in Urodela representing different habitats. The smaller positional differences of trunk were shown in the more aquatic species. The more terrestrial species was equipped with larger dorsalis and abdominal muscles in the middle part than that of anterior and posterior parts. It is considerable that aquatic species had smaller positional differences since their anguilliform swimming mode is conducted by propagating undulatory waves along the body. In the more terrestrial species, dorsalis muscles and abdominal muscles may be larger in the middle part for sustaining own weight more effectively without the usage of limbs in the middle part.

In chapter 4, ontogenetic changes of trunk muscles in *Hynobius nigrescens* which transit habitats from water to ground by metamorphosis were surveyed. They develop from aquatic swimming larvae to terrestrial walking juvenile. According to the transition of habitats, they may change trunk muscle which acts as a main locomotive structure. Develomental changes of external figure in various Urodela species have been studied. The descriptive studies of trunk muscles have been conducted in *Hynobius nebulosus*. Despite these studies, developmental changes of trunk muscles have not been quantified. To clarify the adaptive way of the trunk muscles ontogenetically, quantifying and observing trunk muscles are needed. Egg batch of *H. nigrescens* were collected and reared up until they land by metamorphosis. Specimens were captured and fixed randomly in the six developmental stages. Trunk muscles were observed and the weight ratios of each trunk muscle group were calculated for comparison of the different developmental stages. Trunk muscles were changed according to growth (Fig 4). In the beginning of the development, lateral hypaxial muscle composed one thicker *M. ventralis,* whereas *M. rectus abdominis* did not appear.

They possessed larger lateral hypaxial muscles in the beginning of development than in the later stages. By contrast, *M. obliqqus externus* and *M. rectus abdominis* were shown after *M. transversus abdominis* was developed from *M. ventralis* by continued growth. The weight ratios of dorsalis and abdominal muscles increased according to growth. It is suggested that the single thicker and larger lateral hypaxial muscle is suitable for swimming in the beginning of development. Increasing and developing dorsalis and abdominal muscles are thought to be prepared for resisting gravity.

In this study, the adaptive way of aquatic and terrestrial environments by trunk structure in Urodela was revealed. The strategy of environmental adaptation of trunk muscles shown in the phylogenetic comparative study corresponds to that in the ontogenetic study in Urodela. The more aquatic species had larger and thicker lateral hypaxial muscles and unseparated *M. rectus abdominis* for powerful undulatory swimming. In contrast, the more terrestrial species possessed thicker lateral hypaxial muscles and larger dorsalis muscle and separated larger *M. rectus abdominis* for resisting gravity. In ontogenetic changes in *H. nigrescens*, swimming larvae had larger thicker lateral hypaxial muscles for swimming, whereas metamorphosed juveniles were equipped with larger dorsalis muscles and abdominal muscles against gravity. Therefore, the strategy of trunk muscles of Urodela that they needs larger and thicker lateral hypaxial muscles for swimming, and larger dorsalis and larger and separated abdominal muscles for terrestsial walking could be found.

In the phylogenetic comparative study, the *M. rectus abdominis* was not separated in aquatic species; by contrast it was separated in semi-aquatic and terrestrial species. In the ontogenetic changes, *M. rectus abdominis* appeared and increased in the later developmental stages for preparation of landing. The direction of *M. rectus abdominis* is longitudinal and *M. rectus abdominis* ran from the anterior edge on the pelvis to the sternal cartilage and covered ventral side of trunk. The muscle is thought to be suitable for keeping posture and sustaining own weight from ventral side by the fiber direction and position. Therefore, *M. rectus abdominis* may be necessary for terrestrial life.

The more aquatic species had more horizontal prezygapophyseal angle of vertebrae, whereas the more terrestrial species possessed more vertical prezygapophyseal angle of vertebrae in this study. The aquatic species had prezygapophyseal angle of 14.0° on average for lateral bending more flexibly and avoiding dislocating vertebral joint. Terrestrial species possessed prezygapophyseal angle of 19.5° on average. Though terrestrial species need to significantly resist gravity, they have to remain swimming ability for mating season. Therefore, the angle of prezygapophyseal vertebra may enable the terrestrial species to mainly resist gravity in addition to bend their trunk laterally for swimming. Prezygapophyseal angle was 17.5° on average in the semi-aquatic species for both lateral bending and resisnting gravity effectively.

In this study, the way of environmental adaptation of trunk structure in living Urodela was noted. It is suggested that early tetrapod may change the structure of trunk according to event of landing as living Urodela in this study. Early tetrapod may be equipped with larger hypaxial muscles with smaller positional differences of trunk and more horizontal prezygapophyseal angle of vertebrae in water, whereas they may obtain larger dorsalis and abdominal muscles with positional differences of trunk, and more vertical prezygapophyseal angle of vertebrae for landing.

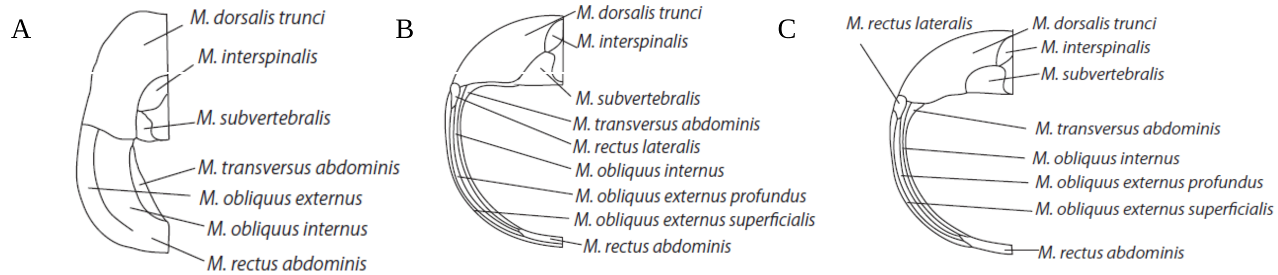

Figure 1. Cross-sectional areas of trunk muscles in A: *Siren intermedia* (aquatic), B: *Cynops pyrrhogaster* (semi-aquatic), C: *Ambystoma tigrinum* (terrestrial).

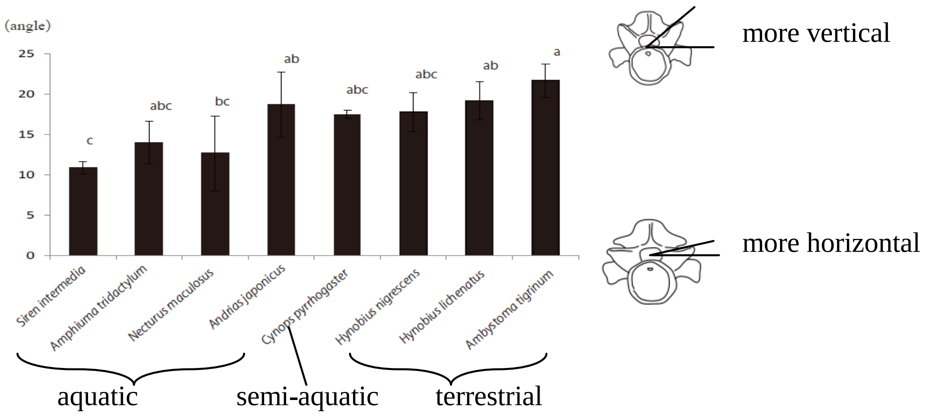

Figure 2. Prezygapophyseal angle of vertebra. Different superscript letters indicate significant differences.

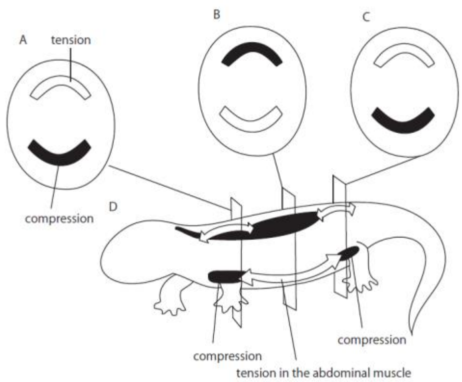

Figure 3. A: Cross-section of trunk in anterior part, B: Cross-section of trunk in middle part, C: Cross-section of trunk in posterior part, D: Resting quadrupedally on two paies of limbs, with distribution of stress derived from gravity. White arrows show tension. Brack destributions represent compression. Modified from Preuschoft et al. (2007).

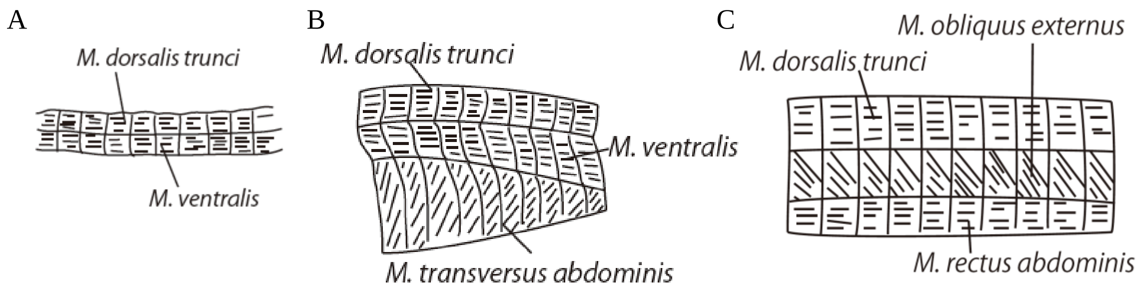

Figure 4. Ontogenetic changes of trunk muscle in lateral view in *Hynobius nigrescens*. A: st 38 in the beginning of development, B: st 50 in the midstream of development, C: st 68 in the compression of metamorphosis.