Evolutionary Consequences of the Structure-Function Relationship of Ankle Joints in the Pinnipeds during their Secondary Adaptation to Life in Water

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Secondary adaptation to life in water is an evolutionary event that returns to aquatic life, which had arisen at various times (from the early Mesozoic to the present day) and in various vertebrates (i. e., the reptiles, the aves, and the mammals). Secondary adaptation is a major evolutionary shift, as it demands wholesale changes to an animal's body plan and a transition of niche in the aquatic ecosystem. In particular, the limbs change into fins for swimming. In the mammals, the sirenians (dugongs and manatees) and the cetaceans (whales, dolphins, and porpoises) represent a full-aquatic style losing the hindlimb: the loss of walking ability. This evolutionary process can be roughly divided into three phases: terrestrial, semi-aquatic, and full-aquatic. Analysis of individual cases of evolutionary transition of morphology and function from walking to swimming can help clarify this mechanism in adaptive evolution: secondary adaptation to life in water. There are some previous studies for the semi-aquatic stages. However, the study for the transitional process and the consequence of the ankle joint possessing a role of supporting the body weight is not enough. Moreover, while many studies on secondary aquatic adaptation focus on the acquisition of swimming ability, and the study considering dual locomotion (i. e., walking and swimming) is also not enough. In the semi-aquatic stage, an animal's body is required to have an adaptive morphology for both locomotions: walking on land and swimming in water. Accordingly, a revelation of functional requirements from dual locomotion in morphologies of semi-aquatic animals leads to reveal a balance of dual structure-function relationships for walking and swimming during this evolutionary event. An animal, which contributes to reveal this subject, is the pinnipeds.

In this study, I focus on morphologies of ankle bones (i.e., the astragalus and calcaneum) in a body of pinnipeds, because these bones have highly functional importance. The main roles of these bones as the ankle joint are bearing of animal's own body weight, a keeping of animal's balance and a generating of thrust during walking on land. In addition to these roles, because these bones are related to maneuvering and generating of thrust during swimming in water in the pinnipeds, these bones are much more important. To reveal the structure-function relationship of the pinniped ankle joint during secondary adaptation to life in water, I dissect extant pinnipeds and describe the astragali and calcanei of extinct and extant pinnipeds. Then, I carry out the tracing character change, which traces character changes on the fixed phylogenetic tree based mainly on my own analysis, of the astragalus and calcaneum using the data matrix based also on my own observations by dissections and descriptions.

To reveal evolutionary consequences of the structure-function relationship of ankle joints (the astragalus and the calcaneum) in the pinnipeds during their secondary adaptation to life in water, I carried on the tracing character change with the use of 45 species (38 species described in this study and seven species from references) and 30 characters based on this study and previous studies.

In the otariids, the astragalus and the calcaneum possess the greatest number of primitive characters in the crown pinnipeds, suggesting that they do not have a requirement from a function of swimming locomotion using only forelimbs. The morphologies and functions of the ankle joints between the Odobeninae (specially *Odobenus rosmarus*) of the Odobenidae and *Allodesmus* spp. of the Desmatophocidae show many similarities, thus my study supported that *O. rosmarus* and *Allodesmus* spp. share the same swimming style suggested previous studies. Some previous studies suggested the correlation between prosperity of derived odobenids (i.e., Dusignathinae + Odobeninae) and decline of *Allodesmus* spp. during Tortonian (mid–late Miocene).

Considering the functional importance of the ankle joint for dual locomotion (i.e., walking and swimming) in the pinnipeds, my study suggests that the possibility of the correlation between a replacement of their niche and an inferred similarity of their ankle joints.

The phocids have the specialized ankle joint, which possess totally 14 unique characters. Several characters (e.g., the laterally developed and warped lateral malleolar facet; the peroneal tubercle is plantarly located in talocalcaneal view) represent that an arrangement between the astragalus and the calcaneum changes from up-and-down as other pinnipeds, to side-to-side; in other words, considering the hind limbs of the phocids fixed in a caudally directed position, the plantar surface of the phocids actually is nearly vertical to the ground because of the "twisted" ankle. It means that the phocid ankle joint does not have a role during a movement on land; on the other hand, it is adaptive for their swimming: pelvic lateral oscillation, because a direction of the plantar flexion changes from plantar to mediolateral by the "twisted" ankle. This fact is the functional trade-off for dual locomotion; in other words, it is the functional dichotomy of the ankle joints during their adaptive evolution (i.e., secondary adaptation to life in water).

Finally, I discussed comparisons with the species diversity, the distributional area, and the feeding diversity in three groups (i. e., *Odobenus rosmarus* of the Odobenidae, *Allodesmus* spp. of the Desmatophocidae, and the phocids) of the pinnipeds possessing the same swimming style: pelvic laterally oscillation (hindlimb swimming). At all points of these comparisons, the phocids indicate the most diverse. Considering the importance of the swimming ability for their foraging and migration, I suggested that phocid's acquisition of the specific ankle led to their divergence in the pinnipeds of the same swimming style during their secondary adaption to life in water.