Quantitative analysis of aquatic adaptation in Desmostylia (Mammalia) based on cranial characteristics

（　頭骨形態を指標とした束柱類(哺乳類)の水棲適応の解明　）

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Desmostylia is one clade of extinct aquatic mammals with no close living relative. Its fossil records are known from the uppermost Eocene to Miocene marine strata in the North Pacific Rim. Many desmostylian fossils are known from Japan. However, their phylogenetic relationships, paleoecology and other aspects of their biology are still debated. For example, whereas Desmostylia has traditionally been considered as belonging to Tethytheria (Afrotheria) and closely related to sea cows (Sirenia) and elephants (Proboscidea), recent phylogenetic hypotheses placed Desmostylia in Perissodactyla (Laurasiatheria) or Paenangulatomorpha. In addition, many different hypotheses have been proposed on the interrelationship of Desmostylia. Traditionally, Desmostylia has been divided into two families, Desmostylidae and Paleoparadoxiidae. However, it is controversial whether the traditional Paleoparadoxiidae is monophyletic or paraphyletic. Paleoecology of desmostylians is equally debated. The post-cranial skeletal morphology suggests that they were analogous to large terrestrial ungulates or polar bears. Other studies, especially those on osteohistology, postulate demostylians as aquatic animals, with *Desmostylus* possibly showing a high degree of aquatic adaptation. Furthermore, the spatial and temporal distributions of desmostylian remains, one useful source of data for paleoecological inferences, have not been extensively analyzed.

In order to discuss paleoecology of Demostylia, especially the degree of their aquatic adaptation, I analyzed (1) phylogenetic interrelationship of Desmostylia, (2) spatial and temporal distributions of desmostylians and their relationship with global sea level changes and (3) the degree of their aquatic adaptation clearly. First of all, in Chapter 2, I created a new data matrix of Desmostylia by compiling and revising previous data matrixes and adding new characters. I used three taxa as outgroups that covered all hypotheses of desmostylian affinities in Mammalia and ran separate analyses using each of three taxa as the outgroup. Strict consensus trees obtained in all analyses supported monophyly of Desmostylidae and paraphyly of traditional Paleoparadoxiidae. Based on these results, I re-defined Desmostylidae and Paleoparadoxiidae as clades based on common ancestry.

Secondly, in Chapter 3, I reviewed previous reports of desmostylian occurrences based on the literature

and a database and mapped them by stage and taxon. The result showed that the temporal range of definite desmostylian records is from around the Eocene/Oligocene boundary through 10 mya. Furthermore, it was confirmed that Desmostylidae had a wider geographic distribution than Paleoparadoxiidae and was adapted to very cold environments. In addition, it was suggested that *Cornwallius,* a basally-diverging member of Desmostylidae, went extinct possibly through competition with more derived *Desmostylus*. The last desmostylian that survived into the late Miocene in the North Pacific Rim was *Desmostylus* spp. *Desmostylus* became completely extinct likely due to a rapid decrease of shallow marine areas associated with a major marine regression at around 10 Ma.

Thirdly, in Chapter 4, I analyzed quantitative characters of the skull and brain endocast in extant mammals and established correlations between these characters and the degree of aquatic adaptation. In this study, I focused on characters related to olfactory and optic senses because they are strongly correlated with modes of animal locomotion, functions and lifestyles. Based on CT scan data of extant mammalian skulls, the skull and brain endocast were digitally reconstructed as 3D models. Based on such 3D digital models, I measured the sizes of the olfactory bulb, orbit, and optic canal, which all have been considered as modified through aquatic adaptation based on qualitative studies. The result showed that the olfactory bulb and optic canal sizes are significantly different among different degrees of aquatic adaptation, with these sizes decreasing as the degree of aquatic adaptation increases. Accordingly, these characters can be used for making an inference on aquatic adaptation in fossil mammals. On the other hand, the orbital size did not show a clear trend of change corresponding to the degree of aquatic adaptation. Among aquatic and semiaquatic mammals, the orbital size showed a good correlation with their maximum diving depths. Therefore, this character may be used to infer the maximum diving depth of a taxon once it is identified as an aquatic or semiaquatic animal based on other evidence.

Finally, in Chapter 5, I reconstructed a brain endocast and obtained the same measurements as analyzed on extant mammals in the previous chapter for *Paleoparadoxia* based on a CT data set. The size of the olfactory bulb of *Paleoparadoxia* was intermediate between the means of the aquatic and semiaquatic species. The orbital size of *Paleoparadoxia* was similar to the means of the semiaquatic and nocturnal species whereas its optic canal size was close to the means of aquatic and full-aquatic species. These data suggested that *Paleoparadoxia* was likely a semiaquatic species, with its habitat limited to shallow marine areas.

In summary, the phylogenetic hypothesis presented in Chapter 2 and the spatial and temporal distribution patterns clarified in Chapter 3 have established frameworks for further analyzing paleoecology and evolution of Desmostylia in the future. By applying the results obtained in Chapter 4 and collecting data on more desmostylians as was done

for *Paleoparadoxia* in Chapter 5, a further understanding of aquatic adaptation in Demostylia will be achieved. An especially fruitful approach will be mapping of character values of various desmostylians on the tree proposed in Chapter 2 and conducting ancestral reconstruction to trace evolution of aquatic adaptation in Desmostylia.