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PRELIMINARY REPORT ON THE EVOLUTION OF AQUATIC ADAPTATION IN DESMOSTYLIANS (MAMMALIA, TETHYTHERIA)

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Abstract : Forty nine trends indicating aquatic adaptation are recognized based on the distribution of osteological characters in 16 species of four living mammalian taxa. Among them, 39 trends are also found in desmostylians. In the present paper their distribution is examined in four genera of Desmostylia, for which skeletons are known, *i.e.* *Behemotops* and *Paleoparadoxia* (family Paleoparadoxiidae), and *Ashoroa* and *Desmostylus* (family Desmostylidae). Characters inserted on the phylogenetic tree elucidate the evolution of aquatic adaptation within the order Desmostylia. The present paper introduces preliminary results: although the phylogenetic divergence of the two families shows no relation to aquatic adaptation, the Desmostylidae became more adapted to aquatic life than did the Paleoparadoxiidae, with *Desmostylus* representing the highest level of aquatic specialization on present fossil evidence.

Key words: Desmostylia, aquatic adaptation, comparative morphology, functional morphology

Observations préliminaires sur l'évolution vers l'adaptation au mode de vie aquatique chez les Desmostyliens (Mammalia, Tethytheria)

Résumé : Quarante-neuf tendances indiquant une adaptation à la vie aquatique sont reconnues grâce à la distribution de caractères ostéologiques chez 16 espèces appartenant à quatre taxons différents de mammifères actuels. Parmi ces caractères, 39 sont également présents chez les desmostyliens. Le présent article examine la distribution de ces caractères chez quatre genres de Desmostylia pour lesquels des squelettes sont connus : *Behemotops* et *Paleoparadoxia* (famille Paleoparadoxiidae), et *Ashoroa* et *Desmostylus* (famille Desmostylidae). Le placement des caractères sur un arbre phylogénétique indique les modalités de l'évolution vers un mode de vie aquatique à l'intérieur de l'ordre des Desmostylia. Des résultats préliminaires sont présentés ici : bien que la divergence des deux familles ne soit pas liée à l'adaptation au mode de vie aquatique, les Desmostylidae deviennent mieux adaptés à la vie aquatique que les Paleoparadoxiidae, *Desmostylus* représentant la plus forte adaptation au milieu aquatique sur la base des restes fossiles disponibles.

Mots clés : Desmostylia, adaptation aquatique, morphologie comparative, morphologie fonctionnelle

INTRODUCTION

Members of the extinct mammalian order Desmostylia inhabited the northern Pacific coasts and are found in Japan, Sakhalin and Kamchatka as well as in western North America from the Late Oligocene to the late Middle Miocene (Inuzuka *et al.*, 1994). Among living mammals, the Desmostylia are closely related to the terrestrial Proboscidea and the purely aquatic Sirenia, together constituting the Tethytheria (McKenna, 1975; Domning *et al.*, 1986). Questions concerning the ecological adaptation of the dentition and body form of the desmostylians have been dealt with by, *i.a.*, Inuzuka (1984; 2000a), but remain unresolved.

Osteological characters that indicate aquatic adapatation of the desmostylians (Inuzuka, 2000b) are studied in the four genera of Desmostylidae and Paleoparadoxiidae for which larger parts of the skeleton are known. The aim is to demonstrate differences in the manifestation of aquatic adaptation within the two families, and in the progression of the adaptation within each family. The aquatic adaptation trends are sorted into seven categories by distribution pattern and are, finally, mapped onto a simplified phylogenetic tree *sensu* Inuzuka (2000c).

As a result, it was proved that : morphological differences between Paleoparadoxiidae and Desmostylidae are mostly not related to aquatic adaptation; the differences of degree of adaptation in each body part between the two families are slight; portions more adapted for aquatic life are more numerous in the family Desmostylidae, namely in the evolutionary process from *Ashoroa* to *Desmostylus*, than in the Paleoparadoxiidae; and the most highly adapted animal for aquatic life was *Desmostylus*.

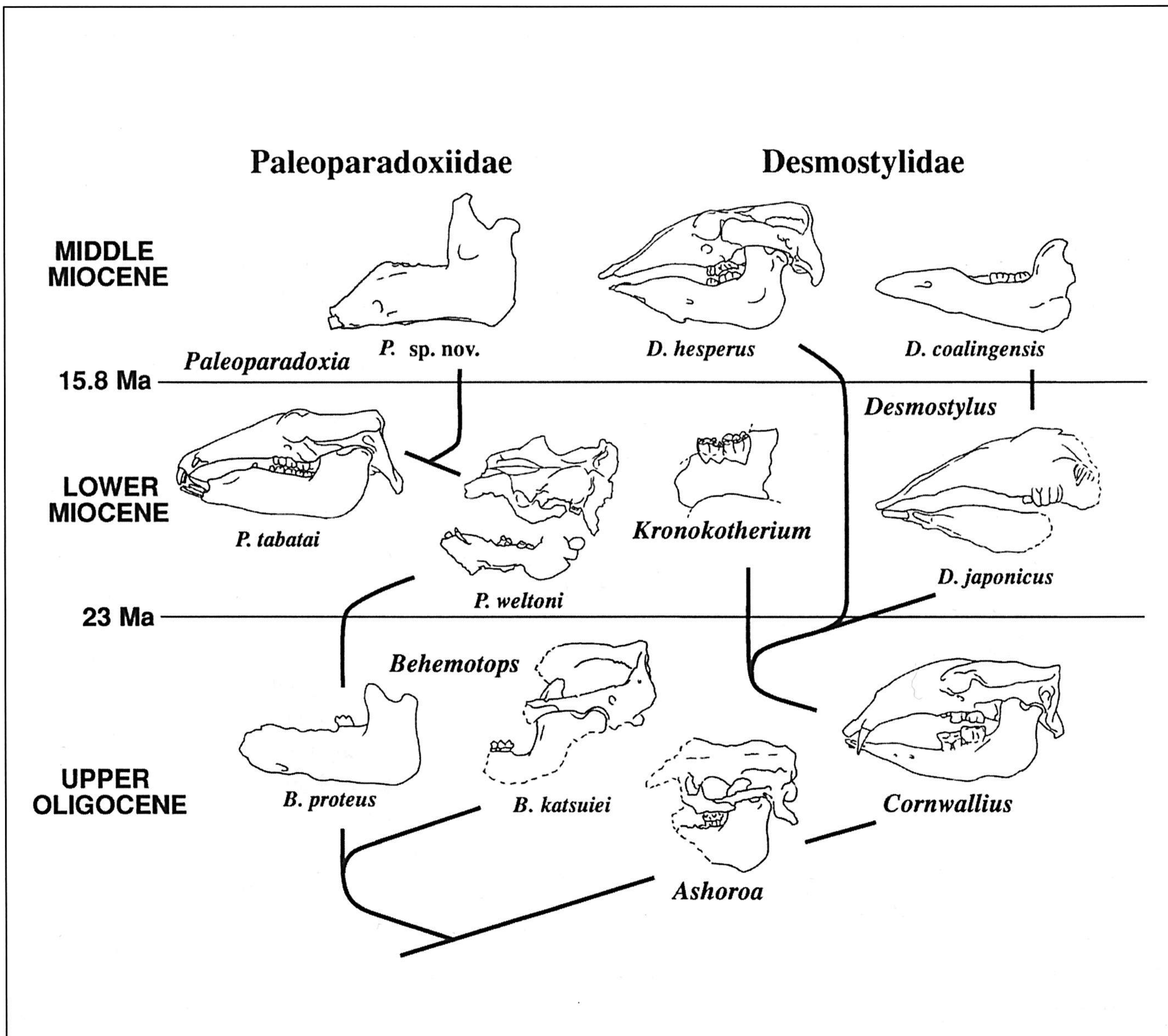
Institutional abbreviations: AMP, Ashoro Museum of Paleontology, Japan; UCMP, University of California Museum of Paleontology, Berkeley; NSM-PV, National Science Museum, Paleontology, Vertebrate, Tokyo, Japan; UHR, University of Hokkaido, Rigakubu, Sapporo, Japan; GSJ-F, Geological Survey of Japan, Fossil, Tsukuba, Japan.

SOME PREVIOUS STUDIES ON ADAPTATION AND RELATIONSHIP

VanderHoof (1937) suggested that "*Desmostylus* and *Cornwallius* are aquatic because: (a) their remains are always found in formations known to be marine; (b) certain characters in the skull, such as the absence of a lacrymal foramen, appear to be aquatic adaptations; (c) the structure of the forefoot is like that of the larger pinnipeds and of the Sirenia". When a complete skeleton was discovered in Saghalien, Japan in 1933, however, it differed in many ways from that of the Sirenia, such as by the presence of stout limb bones like those of the hippopotamus, and the animal was regarded to be amphibious (Nagao, 1941). Shikama (1957) assumed that desmostylians dived in water like a tapir or a hippopotamus, and that they inhabited shallow seas, lagoons or estuaries, and were not purely aquatic like the sea cow. Reinhart (1959) noted that "... evidence from newly described desmostylids suggests that there are forms, transitional in locomotion and habitat, which may have ranged from terrestrial to amphibious to completely aquatic habit ... all members of this group were chiefly amphibious." He also speculated that "*Paleoparadoxia* may have been more terrestrial in its habits than the other desmostylids" because its lower incisors are close-set. From the standpoint of comparative craniology, Ijiri & Kamei (1961) considered both desmostylids and paleoparadoxiids to be marine mammals, more adapted for aquatic life than the hippopotamus or tapir, with fur like seals and more or less webbed skin between digits. Shikama (1966) surmised that the desmostylians were amphibious to semiaquatic coast dwellers similar to the pinnipeds, since no remains had been found in terrestrial deposits. Inuzuka (2000b), through comparative functional morphology of extant mammals, corroborated that osteology shows desmostylians to be adapted for aquatic life at least more than *Hippopotamus amphibius*.

In 1996, when the first symposium on "Secondary Adaptation to Life in Water" was held in Poitiers, France, the desmostylians were believed to constitute a single, monophyletic evolutionary line (Domning *et al.*, 1986). This was based on *Behemotops*, *Paleoparadoxia* and *Desmostylus*. Subsequently, Inuzuka (2000c) described a new, primitive desmostylian, *Ashoroa*, found together with a new species of *Behemotops* in Ashoro, Hokkaido, Japan. The new generic name, *Ashoroa*, corresponds to the first Ashoro specimen referred by Inuzuka (2000b). Phylogenetic analysis of eleven species in six genera made Inuzuka (2000c) divide Desmostylia into two families, Paleoparadoxiidae and Desmostylidae, of which the former includes *Behemotops* and *Paleoparadoxia* and the latter includes *Ashoroa, Cornwallius, Kronokotherium* and *Desmostylus* (Fig. 1). The Paleoparadoxiidae are characterized by an extremely long dental root and relatively steep medial inclination of the calcaneal tuber, whereas the Desmostylidae is distinguished by a relatively reduced molar cingulum, a well-expanded braincase, a relatively recurved coronoid process, thirteen thoracic vertebrae, elongation and originating from the lower level of the thoracic transverse processes, and steep backward inclination of the thoracic vertebral spinous processes. Because advanced stylodont teeth evolved independently from primitive bunodont teeth in both families, the presence of stylodont cheek teeth which was previously used to define the Desmostylia is a parallel character within this order.

Figure 1. Phylogenetic tree of eleven species in the Desmostylia (after Inuzuka, 2000c).



MATERIALS AND METHODS

The fossil remains of seven individuals pertaining to five species were examined: *Behemotops katsuiei* (AMP 22), *Paleoparadoxia* sp. (Stanford specimen: UCMP 81302), and *P. tabatai* (Izumi specimen: NSM-PV 05601 and the Tsuyama specimen) representing Paleoparadoxiidae; and *Ashoroa laticosta* (AMP 21), and *Desmostylus hesperus* (Keton specimen: UHR 18466 and Utanobori specimen: GSJ-F 7743) representing Desmostylidae.

In a previous study 49 characters or trends of aquatic adaptation were recognized based on comparative and functional morphological analyses of sixteen species in four living mammalian taxa, and 39 of these trends were chosen on the basis that each trend was recognized in three to four of the extant orders or families, was present also in the Desmostylia, and was not affected by size (Inuzuka, 2000b). For the present study, for each trend, presence or absence is noted in each of the four genera of the Desmostylia, as well as degree of development, if any. Furthermore, some of the trends are grouped according to distribution pattern and by inserting the categories on a simplified phylogenetic tree it is speculated at which stage of evolution the trends were acquired. For instance, trends for which *Behemotops* and *Paleoparadoxia* show one distribution and *Ashoroa* and *Desmostylus* show another are differences at the family level, and it is surmised that the differentiation took place at an early stage in desmostylian evolution. In cases where *Paleoparadoxia* and *Desmostylus* share the same characteristics or trends, or characteristics of *Paleoparadoxia* compared to *Behemotops* and those of *Desmostylus* to *Ashoroa* indicate the same tendency, these are considered parallelisms.

RESULTS

Table 1 lists characters and trends of aquatic adaptation in desmostylians. Some of the features are divided into the following seven categories, which are mutually exclusive, to serve the purpose of evolutionary description.

[1] Common aquatic adaptation trend confirmed in all four genera of the order.

[2] Trend occurred in the evolutionary process from *Behemotops* to *Paleoparadoxia* in the Paleoparadoxiidae (unknown in Desmostylidae).

[3] Trend occurred in the evolutionary process from *Ashoroa* to *Desmostylus* in the Desmostylidae (unknown or did not change in Paleoparadoxiidae).

[4] Trends observed in *Ashoroa* and in a more pronounced state in *Desmostylus*.

[5] Trend evolved in both families in parallel.

[6] Trend is seen only in genus *Paleoparadoxia*.

[7] Trend is seen only in genus *Desmostylus*.

Figure 2 shows a simplified phylogenetic tree of only four genera of the order, and the numbers in brackets refer to the seven distribution categories listed above.

Common aquatic adaptation trends observed in all four desmostylian genera [1] include: shortening of the lumbar vertebral bodies, horizontal projection of lumbar vertebral transverse processes, reduction of the ischial tuberosity, and widening and thinning of all the femoral epiphyses. No adaptive character was seen in only the two genera of either Paleoparadoxiidae or Desmostylidae. The trend producing an evolutionary sequence from *Behemotops* to *Paleoparadoxia* observed in the family Paleoparadoxiidae but unknown in Desmostylidae [2] was only shallowing of the trochlea tali groove (Inuzuka, 2000b: fig.8). Four trends were observed in the Desmostylidae from *Ashoroa* to *Desmostylus* [3] : reduction of the scapular coracoid process, widening of the radioulnar epiphyses, lengthening of the olecranon, and shallowing of the acetabulum. Seven characters already observed in *Ashoroa* increased in degree of aquatic adaptation in *Desmostylus* [4] : weakening of the occipital condyle transverse ridges, widening of the axis, shortening and steeper inclination of the mid-thoracic vertebral spinous processes, shallowing of the scapular glenoid cavity, thickening of the radioulnar shaft, and enlargement of the femoral head. Three trends evolved in parallel in the two families [5] : shallowing of the atlantal fossa, enlargement of the sacral foramina, and dorsoventral flattening of the femoral shaft. Adaptations observed in *Paleoparadoxia* only [6] is a relatively gentle inclination of the lumbar vertebral articular surfaces, and in *Desmostylus* only [7] is an increase of the cervical lordosis.

Trends [Adaptation category #]	Paleopara doxiidae		Desmos tylidae	
	Behemotops	*Paleoparadoxia*	*Ashoroa*	*Desmostylus*
Widening of cranium		+		+
Regression of nasal bones		+		+
Rise of orbit	+	+		+
Weakening of ridge of occipital condyles [4]		+	+	++
Shortening of cervical vertebrae		+	+	+
Strengthening of cervical lordosis [7]		-		+
Shortening of vertebral bodies		+	+	+
Shallowing of atlantal fossa [5]	-	+	-	+
Widening of axis [4]		+	+	++
Enlargement of dens of axis		+		+
Shortening of spinous process of thoracic v. [4]		+	+	++
Steeper inclination of spine in midthoracic v. [4]		+	+	++
Shortening of lumbar vertebral body [1]	+	+	+	+
Increase in distance between zygapophyses	+	+	++	++
Gentler inclination of articular surfaces [6]	-	+	-	-
Horizontal projection of transverse processes [1]	+	+	+	+
Enlargement of sacral foramina [5]	-	++	-	+
Shortening of spinous process in sacrum		+	+	+
Reduction of coracoid process [3]			-	+
Shallowing of glenoid cavity [4]		++	+	++
Thickening of humeral shaft		+	+	+
Lowering of capitulum below trochlea		+	+	+
Widening of antebrachial epiphyses [3]	+	+	-	+
Thickening of antebrachial shaft [4]		+	+	++
Extension of olecranon [3]		+	-	+
Reduction of sacroiliac angle		+		
Shallowing of acetabulum [3]		+	-	+
Advance of acetabulum		+		+
Extension of pubis		+		+
Reduction of ischial tuberosity [1]	+	+	+	+
Reduction of horizontal angle of pelvic symphysis		+		+
Shortening of femur	+	+		+
Widening and thinning of femoral epiphyses [1]	+	+	+	+
Enlargement of femoral head [4]	+	+	+	++
Flattening of femoral shaft [5]	+	++	+	++
Shallowing of patellar surface of femur	+	+		+
Widening of patellar surface of femur	+	+		+
Widening of tibial epiphyses	+	+		+
Shallowing of trochlea tali groove [2]	-	+		+

Table 1. Characters and trends of aquatic adaptation in the Desmostylia +, ++ indicate absence, presence, or conspicuous presence, respectively, of the adaptive character or trend. Blank indicates no fossil evidence.

For many features observed in *Paleoparadoxia* and *Desmostylus* the evolutionary stage at which they were acquired cannot be suggested, because the same bones are not preserved in *Behemotops* and *Ashoroa*. Also, these assigned categories may be newly set or changed with future fossil discoveries.

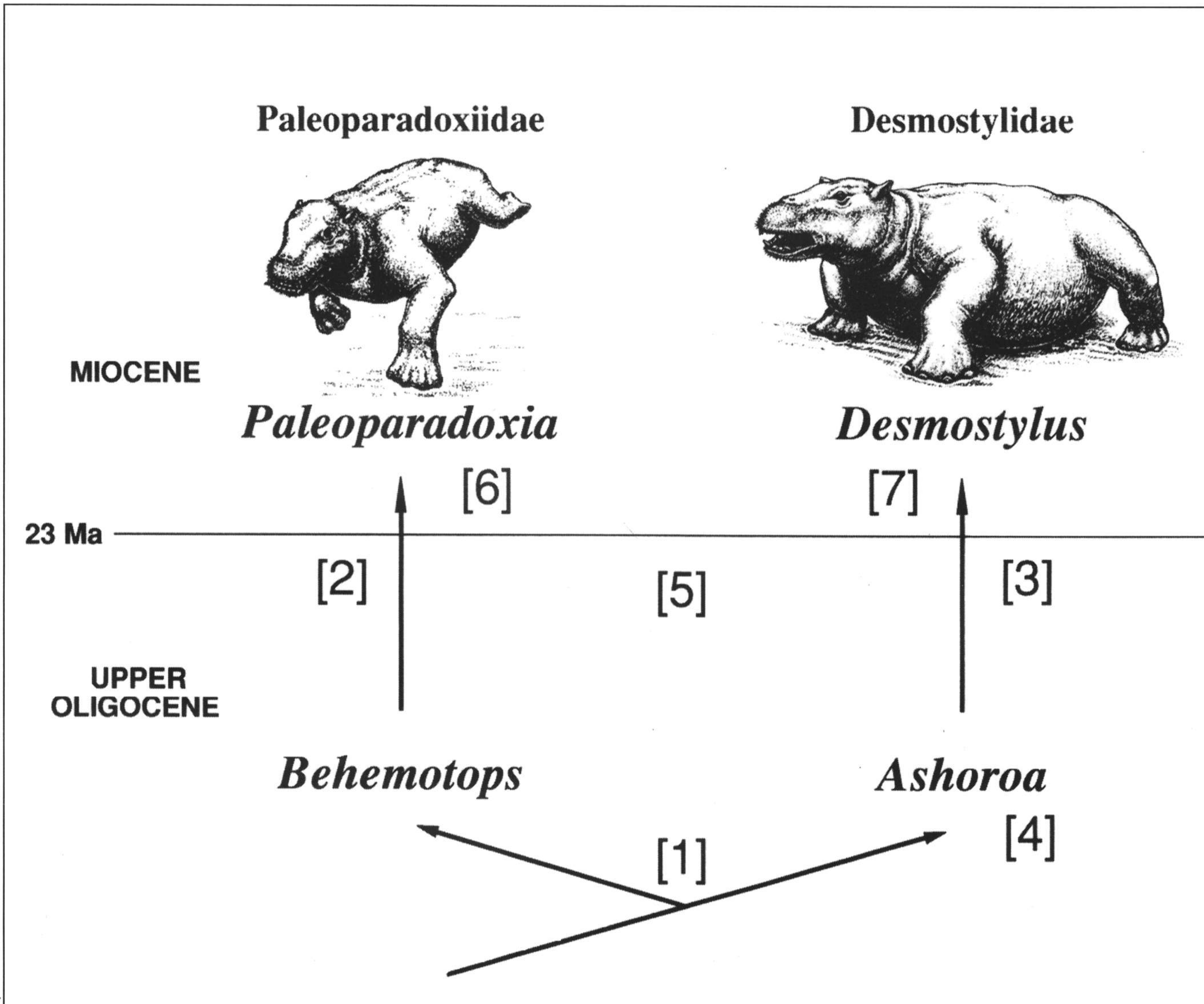


Figure 2. Simplified phylogenetic tree of four desmostylian genera. Illustrated life restorations are after Ijiri & Inuzuka (1989).

DISCUSSION AND CONCLUSION

Because there are so few specimens to work with, the significance of the quantitative comparison of adaptation characteristics is not strong. Therefore, it will be attempted here to assign functional significance to the adaptive characters based on joint kinesiology, functional morphology of the musculoskeletal system, and comparative morphology of living mammals. The change from ventrolateral to horizontal projection of the lumbar vertebral transverse processes suggests increased development of the psoas major which, when accompanied by proper dorsal muscles, would probably be the primary muscle for dorso-ventral movement of the trunk. Widening and thinning of the distofemoral epiphyses may imply not only flexion and extension but also some rotation in the knee joint.

Shallowing of the trochlea tali groove may indicate a capacity for rotation in the ankle joint. Since the scapular coracoid process in desmostylians joins the anterior margin of the glenoid cavity, a reduction of the process means a shallowing of the glenoid cavity and increased freedom of movement in the shoulder joint. Lengthening of the olecranon changes the lever ratio of the triceps brachii muscle, thus may strengthen elbow joint extension. Shallowing of the acetabulum increases freedom of movement in the hip joint. Weakening of the occipital condyle transverse ridges makes dorso-ventral movement possible at the atlantooccipital joint, which correlates with a shortening of the cervical region, as observed in whales and elephants. Short and steeply inclined spinous processes of the mid-thoracic vertebrae flatten the outline of the back at its highest point and may add to a streamlining of the trunk. Shallowing of the atlantal fossa would relate to an increased dorso-ventral movement of the head, as does the weakening of the occipital condyle ridges. Enlargement of the sacral foramina reduces the weight of the sacrum, and may signify a reduced role in bodily support due to the buoyancy of water. Increased cervical lordosis means that the head is held higher than the trunk, which correlates with a floating posture at the surface of the water. The functional significance of the other morphological changes remains unclear.

Many characters that distinguish the Desmostylidae from the Paleoparadoxiidae or *Desmostylus* from *Paleoparadoxia* are observed in the dentition and crania, and neither these nor most postcranial features are regarded to be related to aquatic adaptation. Therefore, it is assumed that the divergence of the two families was not primarily caused by factors connected with aquatic habitats. Differences between these families in degree of adaptation in each body part are slight. It appears that the Paleoparadoxiidae increased rotational function of the ankle, whereas the Desmostylidae increased freedom of movement in the fore- and hindlimbs and in the power of elbow extension. Adaptations for aquatic life are more numerous in the family Desmostylidae, i.e., in the evolutionary process from *Ashoroa* to *Desmostylus,* than in the Paleoparadoxiidae. For instance, the desmostylids could swim more effectively than paleoparadoxiids, because the back became flatter. Moreover, *Desmostylus* probably rested more easily on the surface of the water owing to the strong cervical lordosis. Therefore, among the Desmostylia, *Desmostylus* was the animal most adapted for aquatic life.

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