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Are "Herpetiform Mammals" Really Impossible? A Reply to Halstead's Discussion

By

NORIHISA INUZUKA

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I am very pleased to know that Dr. L. B. Halstead was interested in my work, "Skeletal Restoration of the Desmostylians: Herpetiform Mammals" (*Mem. Fac. Sci. Kyoto Univ., Ser. Biol.*, Vol. IX, No. 2, 1984) and that he had contributed his opinion to the *Memoirs* (Halstead, 1985). It is my duty and priveledge to reply to him in the same *Memoirs*. I believe that the discussion contributes greatly to the understanding of restorations of desmostylians, and also, of the desmostylian life, although there are some insuperable disparities between Dr. Halstead's refutation and my opinion. As for his opinion, I am able to enumerate the following as points of view divergent from my own.

1) There is little difficulty in a mammal taking up a reptilian type posture with the forelimbs. The forelimbs cannot be used to determine what was the habitual posture.

2) It is no longer possible to orient the hindlimbs in a normal reptilian manner. When the femur is placed in the acetabulum the femur is positioned vertically with the anterior surface facing forwards.

3) The herpetiform posture and gait do not allow the cruciate ligaments to function efficiently.

4) A large animal is not capable of supporting its body off the ground for long periods with limbs flexed.

5) The most important movement of the femur is a rotation of the shaft.

6) In order to postulate a new hypothesis, it seems necessary to show more sufficient credible evidence.

7) The comparison of desmostylians with animals of other mammalian Orders by bone-by-bone comparison reveals little more than that the *Desmostylus* possesses a typical mammalian skeleton.

8) A more rewarding approach would be one involving biomechanics.

9) The restorations by previous workers as Nagao, Shikama, Kamei and Hasegawa are fundamentally correct.

10) The scapulae in the Utanobori specimen can in no sense be considered in a natural position.

11) In the Utanobori specimen, the limbs are no longer in natural articulation.

I will state my answer to each item of his opinion in the same order.

1) Dr. Halstead stated "the forelimbs have a much greater freedom of movement than the hindlimbs". The difference between shoulder and pelvic girdles is generally explained by

the absence of a bony junction between the shoulder girdle and the axial skeleton. In my opinion, however, this account may not necessarily be applicable in the case of restoration of posture and gait of extinct animals. It is true that the forelimbs have great freedom of movement in comparison with the hindlimbs, but it is also true that the humeri of living dogs or horses cannot be abducted because of the restriction by muscles and ligaments. If "The forelimbs cannot be used to determine what was the habitual posture", as Dr. Halstead said is correct, we may be obliged to give up the posture restoration of forelimbs in the case of ungulates. But actually, there are many unique characteristics in desmostylian forelimb bones which reflect its peculiar posture.

2) In spite of the presence of a laterally facing femoral head as in normal mammals, one can assume a reptilian type posture with the hindlimbs. In the case of the elephant with typical parasagittal posture, the femoral head faces rather proximally than medially. On the other hand, in the monotremes and insectivores, which have laterally projected upper limbs (stylopodium in my paper), the femoral head faces laterally as in general mammals. Therefore, it is impossible to assert that an animal having a laterally facing femoral head could not hold the femur directed laterally. And, it is also impossible to define the femur orientation from the direction of articular surface alone, as in the case of the forelimbs. Finally, even if the femur is placed in the acetabulum, it would not always stand vertically with the anterior surface facing forwards.

3) Not only do I agree that "one of the advantages of an upright posture is that it is more efficient for supporting weight", but I am also in accord with Dr. Halstead's view that the normal cruciate ligament "can confidently be expected to have been present" in a desmostylian skeleton. However, it is needless to think that the cruciate ligaments were useful for supporting weight without the assistance of muscular force. "Upright posture" ("parasagittal position" in my paper) does not necessarily allow the cruciate ligaments to function effectively, except in the case of overextension in the knee joint. The knee joint is usually more or less flexed in normal large ungulates (ex. horse, ox, etc.). The exceptional case is rather of man in which the lock system works effectively.

The patellar ligaments play a greater role in supporting weight than the cruciate ligaments in the knee joints of most of living ungulates. So, in the desmostylians, where the limbs would have been fairly flexible in the knee joints, the patellar ligaments ought to have had greater importance than in normal ungulates. This is suggested by "the prominently developed patella", comparable to those of fully matured elephants in size, and "the conspicuously developed tibial crest".

4) Whether the upper limbs were projecting downwards or outwards, both the elbow and the knee joints are usually more or less flexed even in normal large animals. So, regardless of the direction of the upper limbs, holding the posture requires the muscles and the ligaments to extend the elbow or knee joint. There are some examples of large animals comparable to desmostylians in size with laterally directed stylopodium; *Eryops* and *Mastodonsaurus* in Amphibia, and *Cotylorhynchus* of Pelycosauria and *Jonkeria* of Therapsida in Reptilia; and with downward

directed stylopodium; *Hippopotamus* and *Rhinoceros* etc. in Mammalia. Throughout these large mammals, their body weight is supported off the ground for long periods with limbs more or less flexed.

5) The most important movement of the femur is a circumduction, rather than a rotation, of the shaft, as I explained to Dr. Halstead. These two movements, circumduction and rotation, are alike, but it is necessary to distinguish one from the other. A rotation is to revolve around the long axis of a bone, while in the case of circumduction, the long axis of a bone and a pivot form an angle. In other words, in rotation of the femur, the knee only revolves at one point. On the other hand, in circumduction of the femur, the position of the knee moves to generate the locus of an arc, producing the cranio-caudal components of the movement. In the case of desmostylians, in my view, the femur would have moved in a circumductive manner, making the long axis of the femoral neck a pivot (Fig. 1).

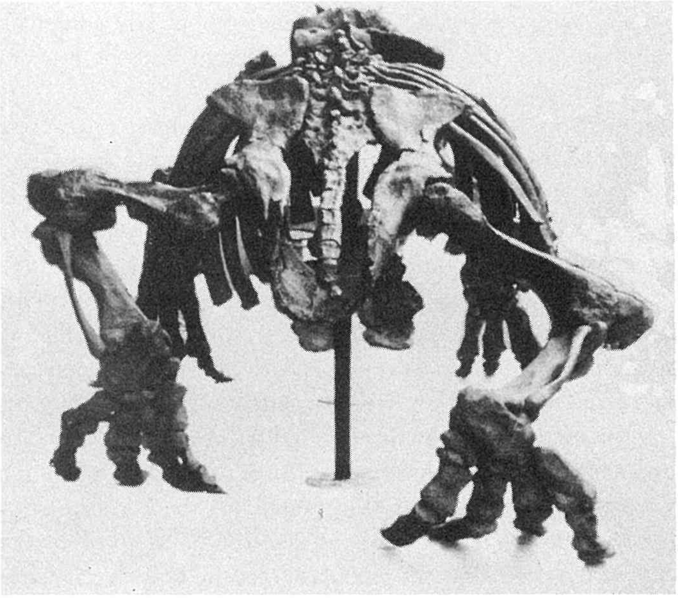

Fig. 1. The caudal aspect of the skeleton of *Desmostylus* reconstructed on the basis of Inuzuka's view. The different positions of the knee in each hindlimb are given.

6) I could not help but propose a fundamentally different type of posture because "a skeletal arrangement, of typical mammalian type" was not recognized in desmostylian bones. What would be considered "sufficient credible evidence to provide at least a *prima facie* case" in a skeletal restoration of extinct animals indicated? The best evidence is, in my opinion, inductive reasoning with anatomical rationality based on peculiar features in shape, which each fossil bone definitely indicates. Nevertheless, I am not neglecting efforts to assemble more credible evidence; actually, I am involved in preparations to write a thesis corresponding to it, conveniently entitled "Fossil footprints of desmostylians presumed from the restored skeleton". Writing the paper became possible when the skeleton was reasonably mounted on the basis of

reasoning from individual bones. Would it be advisable to postpone the reconstruction until actual fossil footprints are discovered, disregarding evidence in the present discovery of nearly complete bodies? Previsional character is one of the important elements in science. Which is preferable, a palaeontology with previsional character or a 'follow-up palaeontology', relying on sampling and description?

7) As *Desmostylus* is a mammal, it is natural that the pelvis and the femur show mammalian features rather than those of a reptile. But the *Desmostylus* also shows characteristics entirely different from animals of other mammalian Orders. This can be likened to that of a proboscidean bone which has both characteristics of general mammals and those which are distinct for proboscideans. In determining the distinctive characteristics of the Order Desmostylia, I carried out a comparison of bones between desmostylians and other mammalian Orders. If one intends to find only the characteristics of a mammal in the desmostylian bones, the characteristics peculiar to the Order will never become apparent. Reading the description of each bone of *Desmostylus* in my paper without preconception, any student should understand how singular, among mammals, the pelvic girdle, the femur and the other bones actually are.

8) I am in total agreement with the opinion that biomechanics is necessary in vertebrate palaeobiology. In fact, I also intend to begin the biomechanical approach as the second step in the study of *Desmostylus*. It is equally true, however, that the skeletal restoration of *Desmostylus* would have been impossible without applying a functional morphological approach for the skeletal system. Until completion of a reasonable skeletal restoration, an accurate restoration of the muscles of *Desmostylus* could not have been accomplished, and thus, estimation of the body weight should not have been possible. Application of biomechanics would be impossible without exact measurement data of skeleton and muscle power. Hence, it would seem that applying biomechanics to the reconstruction of an extinct animal is not so easy. I treated the fossil bones qualitatively at first. That is, I adopted the major premise that the animal could walk on the ground, judging from features such as stout limb bones, longer upper limbs and a broad attaching area of supporting muscle for the body weight. It would not be too late to determine whether or not the bulk of desmostylians could be "supported in air on dry land in such a posture", even after the calculation of the body weight, power of muscle and the lever ratio of the limbs of *Desmostylus*.

9) The restorations by previous workers in which Dr. Halstead expressed support are false in both result and methodology, as I have already criticized in detail. The only actual common point, in which these restorations "insist upon a basically mammalian posture", is having downward protruded upper limbs. Owing to this load, in my opinion, Nagao could not help but mount the skeleton in the condition of dislocated wrist bones, Shikama in the condition of the manus holding the ground with the back of its forelimbs as well as Repenning, Kamei in the condition of the toes pointed obliquely outward and Hasegawa of the toes inward. Could we regard their variety of models as "the minor differences"? I feel that the differences among them are so great that they are not supposedly the same desmostylian animal. The methods of previous workers are to adopt a model for an ungulate, as in the case of Nagao and Kamei,

to depend on bone form and the application of insufficient comparative anatomy, as in the case of Shikama, and to depend exclusively on the shape of articular surface, as in the case of Hasegawa.

On the other hand, I did the skeletal restoration in order to clarify the peculiar shape of each bone of *Desmostylus*, hitherto being a riddle; no riddle was left to be solved in previous restorations. For example, in regard to the flat, paired and large sternum of *Desmostylus*, entirely different from those of other mammals, what kind of interpretation would Dr. Halstead hope for? Any student of anatomy should be able to relate to my views.

10) With regard to the Utanobori specimen, the scapulae must be considered to be in a natural position. Just because "the scapulae are attached by muscles which rot rapidly", if further rotting had taken place in the corpse, the scapulae should have separated from the trunk, or at least to an asymmetrical position. And, indeed, since the scapulae have a tendency to "simply slide off to a natural position", it can be considered that the scapulae showing a fairly symmetrical arrangement had stayed in their original position in the Utanobori specimen (Fig. 2).

If the humeri of desmostylians project downward similarly as in most mammals, the scapulae should be in the sagittal position and the glenoid cavity faced ventrally, depending on the rule of the shoulder joint (VI; F in my paper, p. 191). In such a case, if the corpse is deposited on its back, the scapulae would lie with either their dorsal or cranial margins down, and finally, after further rotting, they would fall down either medially or laterally beside the thorax. It is scarcely possible to assume that the arrangement of scapulae in the Utanobori specimen occurred as a result of such a process.

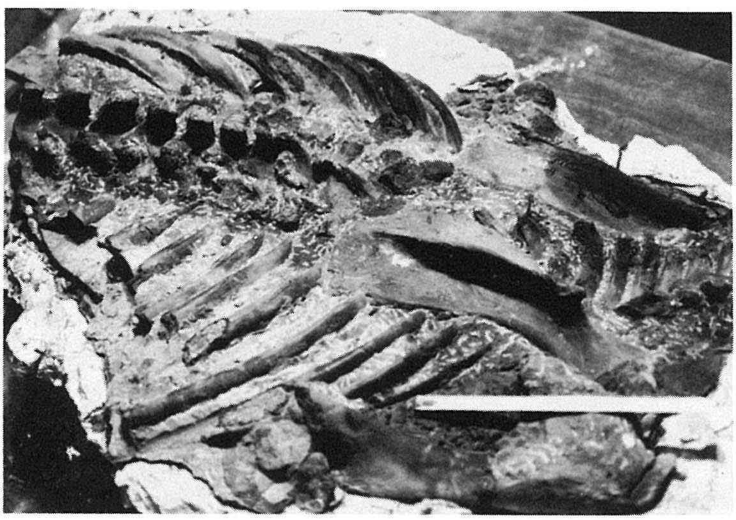

Fig. 2. The scapulae in the Utanobori specimen during the preparation. Note the scapular axis is parallel with the vertebral axis.

11) My image as to the deposition process of the Utanobori specimen is that the cadaver would have been buoyed by gases in the belly, and would have sunk with bursting of the gases to land

on its back. Observing the fossil occurrence in detail, surely the femora are not in natural articulation, because of the inner rotation at a right angle from the original position. But if the upper limbs of the animal had been projecting downward, when the body landed, the limbs would have normally fallen sideways, and not be extended to each side. And actually, the occurrence models of the fossil perissodactyls with downward projecting upper limbs are displayed showing all limbs fallen sideways in the British Museum (Natural History), London, and Muséum National d'Histoire Naturelle, Paris. Displayed occurrences of *Iguanodon*, a dinosaur with the downward projecting femora, in the Institut Royal des Sciences Naturelles de Belgique, depict them as almost always fallen sideways.

When further rotting takes place, the skeleton should show an irregularly dislocated condition, being put out of joint not only at the hip but also at the knee and the ankle joints. In general, *ceteris paribus*, the more distal articulations covered with less muscles, should rot and be scattered sooner. Actually, in the Utanobori specimen, many phalanges were missing. Therefore, it can be reasoned that the symmetrical arrangement of the hindlimbs in the Utanobori specimen resulted not by accident due to further rotting but from the high reflexion of the life posture.

The difference of limb direction between the fossil occurrence and the life posture is not caused by rotting but by compression of the bed. That is, the limb direction of the fossil results from the zygapodia being directed upwards when they sank, probably settling in a position parallel to the bedding plane when they were deposited. It seems that the femur rotated inwardly because the tibia and more distal bones fell down caudally at a time when the ligaments around the knee joints had not yet rotted.

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Reference

Halstead, L.B. (1985) On the posture of desmostylians: a discussion of Inuzuka's "herpetiform mammals". *Mem. Fac. Sci. Kyoto Univ., Ser. Biol.* X: 137–144.

Errata in Vol. IX, pp. 157–253

Page 186. Explanation of Fig. 18: For "cranial" read "Cranial".

page 229. Acknowledgements: For "Prof. T. Kamei and Prof. M. Tasumi" read "Professors T. Kamei, K. Nakazawa, J. Ikeda, and Dr. M. Tasumi".

Author's address: Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Bunkyo-ku, Tokyo, 113 Japan.