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On the Posture of Desmostylians: A Discussion of Inuzuka's "Herpetiform Mammals"

By

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Introduction

In 1984 there appeared a series of publications by N. Inuzuka on the restoration of the desmostylians (Inuzuka 1982, 1984a, b, c). Contrary to every previous attempt at restoration, he proposed that the upper limbs were held not vertically as in all other mammals, but rather they projected horizontally and laterally in a basically reptilian manner. This is such a novel interpretation, that there can be little doubt that Inuzuka will become the most widely quoted author of all time on the desmostylians. The novelty of his reconstruction will ensure that every author will be obliged to refer to his interpretation. The first comment on Inuzuka's restoration was by Urushido (1985) in a brief review in English of his book published in Japanese. My discussion is based on his paper 'Skeletal Restoration of the Desmostylians: Herpetiform Mammals', published in *Memoirs of the Faculty of Science, Kyoto University, Ser. Biol.*, Volume 9, pp. 157–253, (1984) the proofs of which I was kindly given by Dr. Inuzuka. I have examined various restorations mounted in museums, and have examined and photographed the major known specimens in Japan in Sapporo (Hokkaido), Tokyo, Yokohama, Mizunami, Kyoto and Osaka. I have also had the privilege of discussing Dr. Inuzuka's views directly with him and examining his own materials. Furthermore Dr. Inuzuka agreed to demonstrate the range of movement of the femur in its articulation with the acetabulum, as postulated by his new interpretation. As he performed this task I photographed the different stages so that I had an exact record of his interpretations.

In this short note I shall first outline some of the basic features of mammalian gait and posture to give a background, next I will deal with the salient points of Inuzuka's new interpretation and conclude by presenting my view of the evidence, which, in my opinion, effectively refutes Inuzuka's thesis.

Mammalian Posture

The characteristic feature of the posture of mammals is that the limbs are held vertically and in this, contrast with reptiles in which the humeri and femora project laterally and move through an horizontal anteroposterior arc. In primitive amphibians and reptiles the trunk itself describes a sinuous progress. Both the vertebral column, the proximal and distal parts of the limbs perform a crawling motion from which the name reptile itself is derived (from the

Latin verb *repere, reptilis* to crawl). In complete contrast to this pattern, in the mammals the vertebral column is severely restricted in its lateral plane and in some such as the ungulates, there is little flexuring of the column at all. In some carnivores, as in the classic example of the cheetah, the stride itself is increased by the flexuring of the entire vertebral column. The stride, which determines the maximum speed possible, is long in mammals because the movement is from the articulation with the limb girdles, whereas with reptiles and amphibians (such as salamanders and newts), it is essentially from the elbow and knee joints. However, the anteroposterior swinging of the humeri and femora does increase the stride length somewhat.

One of the fundamental differences in posture is reflected in the change in the morphology of the limb and girdle bones. Before discussing this in any detail, it is important to recognize the fundamental difference between the pectoral and pelvic girdles. The appendicular skeleton, anteriorly the pectoral girdle and forelimbs and posteriorly the pelvic girdle and hindlimbs, are attached to the axial skeleton in different ways. The pectoral girdle is attached to the ribs and vertebral column by muscles and tendons and this attachment is able to absorb the shock of impact when the animal lands when moving at speed. Although the glenoid faces downwards it is a very shallow cup-like articulation and although the head of the humerus is rounded, it does not have the nearly spherical geometry associated with the head of the femur. The forelimbs have a much greater freedom of movement than the hindlimbs and there is little difficulty in a mammal taking up a reptilian type posture with the forelimbs. One has only to think of the normal human mating position, where the definition of a gentleman is that he bears his weight on his arms, which in fact automatically take up a "herpetiform" stance. The variability and range of movement of the forelimbs, which are concerned with shock absorbing cannot be used to determine what was the habitual posture. The lateral head of the humerus would suggest that the limbs were normally held in a vertical position but there is no way of determining this with any exactitude from the articulations alone.

The pelvic girdle stands in dramatic contrast in that the articulation with the axial skeleton is rigid with direct joining of bone to bone by a fibrous collagenous joint. The hindlimbs are responsible for the initial thrust and lifting of the body. The appendicular skeleton must, therefore, have a firm and rigid attachment to the axial skeleton. In reptiles, the humeri and femora act as a kind of sling which supports the body and provides stability. The pelvic girdle comprises three bones: a dorsal ilium and ventrally the pubis anteriorly and the ischium posteriorly. If one takes a crocodile as a basic reptilian type, then there are three major areas of muscle attachment from which originate muscles which are primarily tonic or holding muscles rather than phasic or moving muscles. The main function is to hold the femora horizontally and projecting laterally. In the transition from reptile to mammal it can be discerned that with the change to the mammalian posture as illustrated during the evolution of the mammal-like reptiles or paramammals there are important changes in the proportions of the different elements of the pelvic girdle. Instead of the girdle having a tripartite form with three laterally facing plates for laterally directed muscles, the girdle has an anteriorly produced blade and a posteriorly directed one. The musculature is concerned not merely with holding but rather with drawing the limb forwards and upwards and backwards and down, the latter being the power stroke, the former the recovery stroke. The way in which the femur is held is also radically altered. The articular surface instead of being at the proximal termination becomes set

off from the main shaft at some 90 degrees. The presence of a lateral head to the femur is generally taken as evidence of an upright posture and gait. The head of the femur is virtually spherical but movement is restricted mainly to fore and aft direction. There is a considerable degree of variability of movement but it is no longer possible to orient the limb in a normal reptilian manner.

One of the advantages of an upright posture is that it is more efficient for supporting weight, as the force is transmitted via the bony skeleton. The knee joint with its cruciate ligaments is able to lock into position so that no muscular force is required for support. The effectiveness of this system can be readily tested by standing with ones knees slightly bent, so that one is supporting one's weight by muscular activity alone. One can stand for many hours with straightened limbs but only for about 20 minutes with limbs flexed. A large animal is not capable of supporting its body off the ground for long periods with limbs flexed, whether it is a mammal or a reptile.

Inuzuka's "Herpetiform Mammalian" Restoration

The critical evidence on which the basic posture and gait of a terrestrial vertebrate can be assessed must be in the nature of the pelvic girdle and the articulation of the hindlimbs with the girdle. The morphology of the pelvic girdle and femur must be the primary evidence from which one begins. The shape of the pelvic girdle and the femur have been well illustrated and one can do no better than reproduce Inuzuka's excellent sketches of them (Text-figures 1, 2). The morphology of the pelvic girdle is of the typical fore and aft mammalian pattern. Of all the specimens I have examined in both *Paleoparadoxia* and *Desmostylus* the articular head of the femur is positioned laterally and when the femur is placed in the acetabulum the femur is positioned vertically with the anterior surface facing forwards. The normal cruciate ligament locking of the knee joint of the normal mammalian type can confidently beexpected to have been present.

From such skeletal evidence of a typically mammalian nature Inuzuka has produced for the first time a radically different method of reconstructing the stance and gait of a mammal, as well as introducing the emotive neologism "herpetiform mammal". His description of the pelvis and femur is as follows:

"The pelvis is well developed. The wing of the ilium weakly expands laterally. Each side of the pelvic symphysis is wide. The obturator foramen faces rather more outward than downward. The acetabulum is situated in the middle and at a higher level than usual, facing posterolaterally. The femur is stout, particularly at the epiphyses and is flat cranio-caudally, bending outwards. The head is globular and the neck is clearly constricted in all directions. The major trochanter is present at a lower level than the head. The minor trochanter is well developed and its rugged surface is expanded distally. The third trochanter is absent. The trochlear groove is shallow and the patella is prominently developed."

He mentions the nature of the proximal portion of the limbs in mammals in the following terms:

"In quadrupedal mammals, the proximal segments of limbs extend under the trunk (parasagittal position; under position), which differs from amphibians or living reptiles (trans-

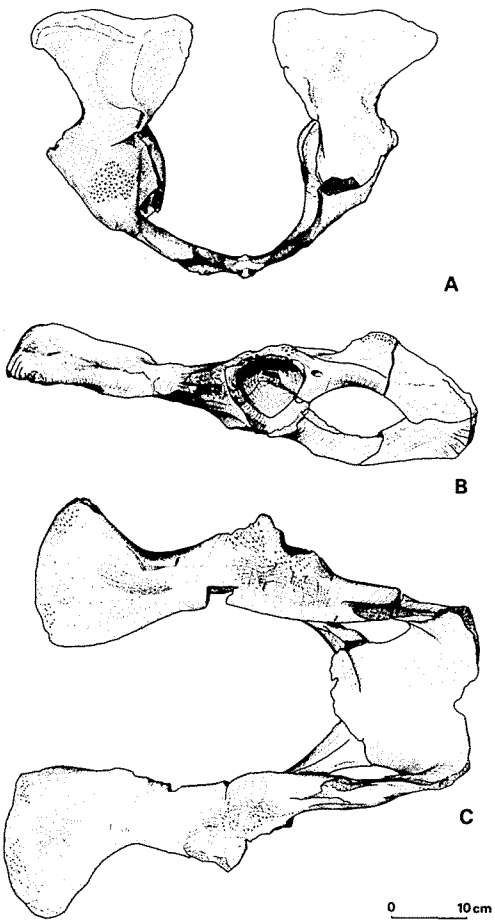

Fig. 1. The shape of the pelvic gurdle of *Desmostylus* illustrated by Inuzuka (1984c).

versal position; lateral position). The former state is more effective in supporting weight and in terrestrial locomotion than the latter, and every case of large terrestrial mammal adjust themselves to the former state. Among mammals exceptions are monotremes, small insectivores, cetaceans, sirenians and bats."

In discussing the femur he writes:

"As it is supposed that the adductor muscles mainly function as supporters of weight in the position of the femur, the posture corresponding to it leads to the following consequences; the femur is abducted; the hip joint is flexed; and the long axis of the femur is directed anterolaterally and nearly horizontally. As the femur is in a state extending laterally in this manner, circumduction of the femur becomes important in locomotion. This movement becomes more probable by the possession of the neck which is constricted in all directions . . .

Thus, the directions of bones in the hindlimbs in *Desmostylus* differ from those of general mammals only in that of the femur, i.e. its anterior surface faces dorsally and the distal part craniolaterally."

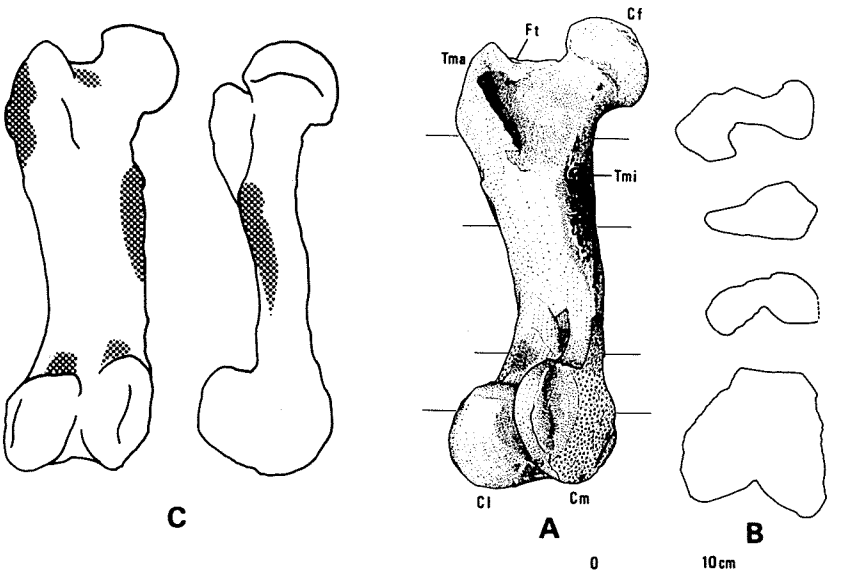

Fig. 2. The shape of the femur of *Desmostylus* illustrated by Inuzuka (1984c).

He emphasises that:

"*Desmostylus*, with its transversely positioned limbs, is an exception among large ungulates, which usually have parasagittally positioned limbs."

Finally as confirmatory evidence he cites the mode of occurrence of the Utanobori specimen which figures on the cover of his recent book (see Text-figure 3).

"The Utanobori specimen, the second entire specimen of *Desmostylus*, was found with most of the bones articulated in situ. It seems that the arrangement of these bones is not a result of dislocation due to putrefaction but the true life posture. The scapula, which does not have a direct connection with the thorax, remained almost in the original position.

Each scapula was situated with its longitudinal axis parallel to the body axis, and the glenoid cavity facing cranially. Assuming that the desmostylian skeleton follows the rules found in the shoulder joint, these facts indicate a lateral extension of the humerus. The posture in the buried state is extremely peculiar as an ungulate, with the body lying on its back except for the skull, which had fallen down sideways, and both fore- and hindlimbs extended laterally on each side. Were *Desmostylus* an animal in which the limbs were situated under the trunk, then all limbs would have fallen on the same side when the body sank to the sea bottom. Therefore, it is possible to infer that both the elbow and knee protruded outwards."

One of the problems I encountered was not being quite certain what exactly was the range of movement of the femur postulated by Inuzuka. Through the kindness of Dr. Inuzuka, I was able to examine the material in his laboratory. Dr. Inuzuka, at my request, placed the femur in the acetabulum and moved it in the manner that he has proposed. He allowed me to photograph this exercise and the three photographs below illustrate clearly that there is a very restricted anteroposterior movement possible when the femur is aligned in this lateral direction and that the most important movement is a rotation of the shaft (Text-figure 4).

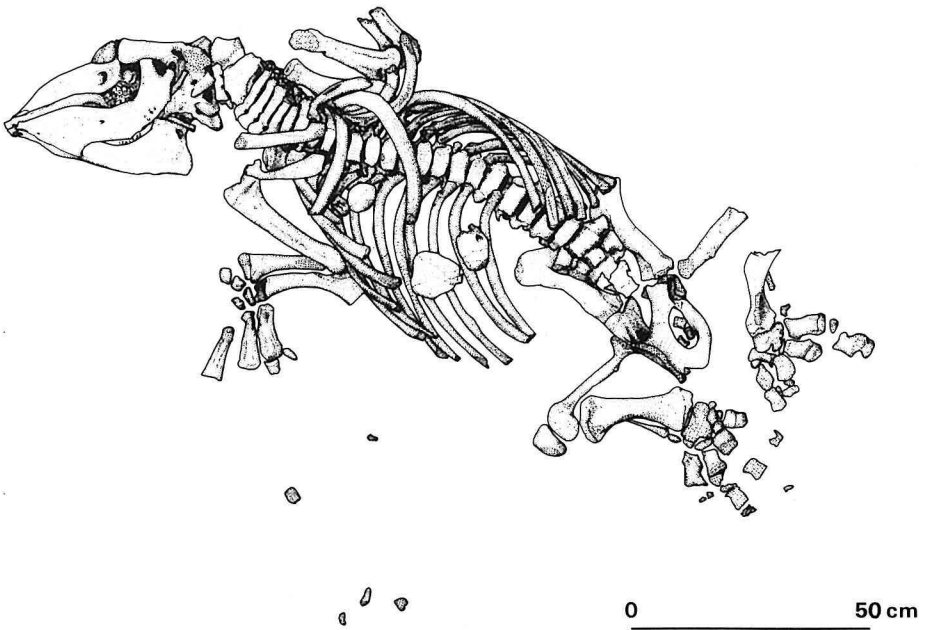

Fig. 3. The mode of occurrence of the Utanobori specimen illustrated by Inuzuka (1984c).

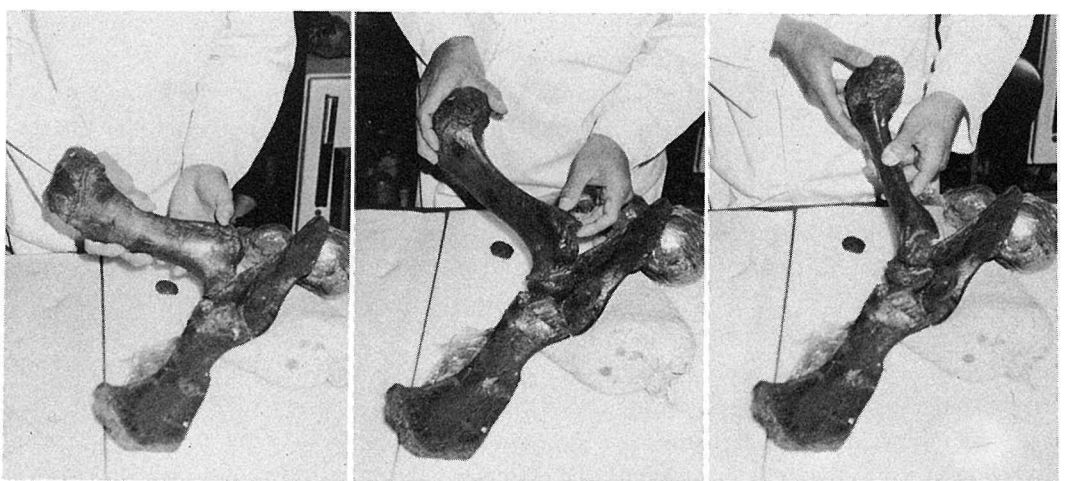

Fig. 4. The range of movement of the femur postulated by Inuzuka. This sequence of movement is demonstrated by himself.

I am satisfied that this sequence of movements and positions is a true reflection of the views of Dr. Inuzuka, because he himself so demonstrated it in my presence and I took the photographs myself. This information must therefore be an accurate account of Dr. Inuzuka's interpretation.

Discussion of Inuzuka's Model

In my opinion the restoration of skeletons of extinct tetrapods from amphibians, reptiles, birds and mammals is facilitated by the fundamental similarity of the muscular system. It is necessary only to dissect a reptile and a mammal to be made aware of this fact. The change in geometry of the bones is a simple reflection of changing forces of the musculature. As the pattern of muscles is fundamentally the same, it is not difficult to follow through evolutionary changes in function, from the 'herpetiform' posture and gait to the parasagittal one of dinosaurs, mammals and birds. I have already alluded to the basic mammalian pattern.

When a skeletal arrangement, of typical mammalian type, is recognized there seems to me to be no logical reason, beyond the search for novelty to postulate something radially different. This does not mean that there may not in fact be a fundamentally different type of posture. But if such is proposed then it becomes necessary to assemble sufficient credible evidence to provide at least a *prima facie* case. I do not think Inuzuka has yet done this. The comparison of desmostylians with other of mammals from proboscideans, ungulates, rodents, insectivores and carnivores in a bone by bone comparison reveals little more than the *Desmostylus* possesses a typical mammalian skeleton.

I would expect that a more rewarding approach would be one involving biomechanics. The physical size of an organism provides a number of fundamental constraints on the skeleton. Inuzuka has correctly noted in the concluding sentence of his paper:

"The desmostylian posture with limbs stretching laterally seems to be inefficient for support of weight or terrestrial locomotion, but is however, extemely stable."

The important point here is not merely that the reptilian posture is inefficient for the support of weight but in the case of *Desmostylus* the bulk of this animal could not be physically supported in air on dry land in such a posture. It is a simple matter of biomechanics. The nature of the femur, the position of the head, which is placed laterally with the shaft held vertically, has the anterior surface facing anteriorly. The parasagittal posture and gait allows the cruciate ligaments to function correctly. The muscles originating on the pelvic girdle permit the most effective antero-posterior action as is evidenced by the antero-posterior elongation of the pelvic girdle, in front of and behind the acetabulum. From the standpoint of comparative anatomy and biomechanics, there seems little doubt, in my opinion, that the restorations by previous workers Nagao, Shikama, Kamei and Hasegawa, for all the minor differences which Inuzuka enumerates, are fundamentally correct in insisting upon a basically mammalian posture.

There remains, to my mind, only one piece of evidence that merits serious discussion. This is the mode of occurrence of some of the articulated specimens. Although the taphonomy of these animals is currently being studied by Miss Takako Urushido, I think it is important to recognize what happens to a body when it sinks to the bottom of a body of water. With regard to the Utanobori specimen in particular, contrary to Inuzuka's assertion the scapulae can in no sense be considered in a natural position. The scapulae are attached by muscles which rot rapidly and the scapulae simply slide off to a natural position of rest. It may well be the case that long-legged artiodactyls often end up dead with all four limbs positioned on one side,

but when a corpse sinks through water particularly as a consequence of gasses bursting the cadaver in the gut region, the body will sink to land on its back, the upper hindlimbs will be extended and with the distal part trailing. When the corpse comes to rest on its back the limbs will fall sideways and when further rotting takes place will simply fall down as is clearly demonstrated in the Utanobori skeleton. The limbs are no longer in natural articulation. It is hoped that a detailed analysis of the form of preservation and the taphonomy of desmostylians will be concluded by Miss Urushido in the not too distant future.

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