# Skeletal Restoration of Desmostylians, the Herpetiform Mammals

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By

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Contents

# Abstract

There have been no standard hypotheses on the basic figure of Desmostylia (Mammalia). The author proposes an entirely new figure of Desmostylus on the basis of osteological examinations of D. mirabilis NAGAO. The resultant figure can be applied to all of desmostylians, considering the basic similarity of the shape of postcranial skeletal elements in Desmostylus and Paleoparadoxia. His method is based on comparative morphology of skeletal elements and functional anatomy of the musculoskeletal system. The desmostylian features which are supposed to be important for restoration are selected on the basis of comparison of skeletal elements in mammals, while general rules of skeletal construction were found out from comparison of living mammalian skeletons and applied to the skeletal restoration. The degree of muscle development deduced from the bone forms must be consistent with the supposed posture of restored skeleton. Only when the limb bones are situated in transversal position, the peculiar bone forms can be reasonably explained from anatomical viewpoint and the posture can conform to the skeletal rules. The posture can also be supported by the mode of occurrence of the second complete skeleton of Desmostylus from Hokkaido. Thus it can be concluded that proximal segments of limbs stretch laterally in desmostylians as in amphibians or reptiles.

# I Introduction

Restoration of the life in the geological past is one of the most important subjects in the realm of paleontology. In fact, especially in vertebrate paleontology, it is well-known that much attention has been paid for making graphic restoration of extinct large animals such as dinosaurs and mammoths, in both academic and popular levels. But any attempt to restore the form of these animals is immediately beset with many unresolved problems; there has been established no suitable theoretical base. In his famous publication Geschichte und Methode der Rekonstruktion vorzeitlicher Wirbeltiere, O. ABEL (1925) stressed reproving imaginary restoration of extinct life, and pointed out the important role of morphological and biological basis in restoration of fossil animals. Nevertheless, previous authors have puzzled about various form restorations made for extinct animals. Usually, the more distant they are from living animals, the more numerous figures are produced. Therefore, it is important and necessary to examine the basic concept of restoration and the reasonable method to reconstruct the real form of an extinct animal which has no living descendant.

In the present paper the problem on restoration of the desmostylian skeletons is dealt with. The desmostylians are large mammals that inhabited along the coasts of the circum-North Pacific during mid-Tertiary. Taxonomically,

they belong to the order Desmostylia (REINHART, 1953), and many students have considered them to have close affinity to either the order Proboscidea or Sirenia. On the other hand, however, it is also true that the taxonomical position of the desmostylians in higher categories has been disputed for nearly a century since the first discovery of the fossil, and not yet settled (Table 1). For example, SIMPSON (1945) included the desmostylians in his superorder Paenungulata, while ROMER (1966) denoted them under the Subungulata group. Recently, MCKENNA (1975) proposed the mirorder Tethytheria to which confined two living orders, Sirenia and Proboscidea, with the extinct Desmostylia.

Furthermore, there have been divergent views concerning the body shape, locomotion, feeding habit and habitat of the desmostylians (MERRIAM, 1906; VANDERHOOF, 1937; IJIRI, 1939; NAGAO, 1941; REINHART, 1959; IJIRI and KAMEI, 1961; MITCHELL, 1966; SHIKAMA, 1966; DOMNING, 1972, 1976). Thus, this raised many open questions to be solved about paleobiology of the desmostylians.

To solve those questions, it is indispensable that the desmostylian skeletons are correctly restored as far as possible. That will be given by a morphological outline on which muscles and skins are entirely based. As many researchers say, morphological restoration of the animals is essential for restoration of their ecology and function, which is, in turn, essential in controling precise consideration of phylogeny of the animals (HOPSON and

Table 1. Opinions on taxonomic position of desmostylians.

| | Sirenia | Proboscidea | Multituberculata | Marsupialia | Monotremata | Ungulates | Desmostylia |
|---|---|---|---|---|---|---|---|
| 1888 | MARSH | | | | | | |
| 1891 | FLOWER & LYDEKKER | | | | | | |
| 1902 | WATERHOUSE | OSBORN YOSHIWARA& IWASAKI | | | | | |
| 1904 | SCHLOSSER | | | | | | |
| 1905 | | OSBORN | | | | | |
| 1906 | MERRIAM | | | | | | |
| 1912 | | ABEL | | | | | |
| 1914 | YATSU | | | | | | |
| 1915 | HAY | | | | | | |
| 1916 | MATTHEW | | | | | | |
| 1918 | MATSUMOTO | | | | | | |
| 1919 | | | ABEL | | | | |
| 1920 | JOLEAUD | | | | | | |
| 1922 | | | | ABEL | | | |
| 1923 | HAY ZITTEL | | | | ABEL | | |
| 1924 | | | | ABEL | KISHIDA | | |
| 1925 | WOODWARD | | | | | | |
| 1927 | SONE | | | | HONDA | | |
| 1928 | DIETRICH | | | | WEBER | | |
| 1931 | SIMPSON | | | | | | |
| 1933 | | | | KISHIDA | | ROMER | |
| 1934 | DAVIES TOKUNAGA | | | | | | |
| 1937 | VANDERHOOF | | | | | | |
| 1939 | | | | | | IJIRI | |
| 1941 | | | | | | NAGAO | |
| 1944 | | NAORA | | | | | |
| 1945 | SIMPSON ROMER | | | | | | |
| 1951 | GREGORY | | | | | | |
| 1953 | | | | | | | REINHART |
| 1955 | | | | | | | COLBERT |
| 1958 | | | | | | | DECHASEAUX |
| 1961 | | | | | | IJIRI•KAMEI | |
| 1964 | | | | | | | MITCHELL |
| 1966 | | | | | | | SHIKAMA ROMER |
| 1968 | | | | | | | THENIUS |
| 1971 | OLSON | | | | | | KURTÉN |
| 1978 | | | | | | | STARCK |

RADINSKY, 1980; SZALAY, 1981; BOCK, 1981). Well-preserved specimens of the desmostylian skeletons have frequently been found in Japan: they are two complete skeletons of Desmostylus (Keton and Utanobori specimens), two of Paleoparadoxia (Izumi and Chichibu-ohnohara specimens), and one rather complete skull bone of Desmostylus (Togari specimen). The author had an opportunity to study the Keton specimen and performed mounting the Utanobori skeleton. These works are the bases of the present study.

All of the materials which he dealt with are restricted to those of Desmostylus, but it is widely accepted that there are less morphological differences in postcranial elements between Desmostylus and Paleoparadoxia (SHIKAMA, 1966). Accordingly it would be reasonable to apply the results obtained from the study on Desmostylus to the restoration of Paleoparadoxia eventually. By this reason, the author will refer to previous works covering both genera and discuss the problems of skeletal restoration not only of the Desmostylus but also of the desmostylians in general.

The present paper envisages to develop the methodology applied in the restoration practice and aims to contribute to solution of questions about desmostylian paleobiology.

## II Scope of this study

The desmostylians have long been regarded as a member of the sirenians since MARSH (1888) described the first fossil teeth. Even after the cranial bones were found in Japan and Oregon in the early stage of this century, the figure of these animals have been supposed to resemble the dugons or manatees.

In 1933, the entire skeleton of Desmostylus mirabilis was found from south Sakhalin for the first time (Keton specimen). By this discovery it became clear that the animals had four stout legs which suggest their active locomotion in terrestrial life. NAGAO (1941) who studied this fossil skeleton first mounted its skeleton as a quadrupedal mammal. This new-look restoration converted the old image of the desmostylians, but there remained some contradictions as to the form of restoration of those animals.

Thereafter, many workers have tried to emend NAGAO's restoration, because more information of desmostylian skeletons have become available by access to new discoveries. The whole skeleton of Paleoparadoxia tabatai was discovered in Toki-City, central Japan in 1950 (Izumi specimen), while another skeleton of Paleoparadoxia was found in the campus of the Stanford University, California in 1964 (Stanford specimen). It was remarkable that the second complete skeleton of Desmostylus was discovered in

Utanobori-cho, north Hokkaido in 1977 (Utanobori specimen).

Skeletal restorations of the desmostylians have been carried out on these materials by various workers: Paleoparadoxia by REPENNING (1965), SHIKAMA (1966) and HASEGAWA (1977); Desmostylus by KAMEI (1975) and INUZUKA (1981d). Apart from these skeletal restorations, varied forms of Desmostylus and Paleoparadoxia are seen in the illustrations of many books (MITCHELL, 1966; SHIKAMA, 1966; KURTÉN, 1971; SCHEFFER, 1976; MINATO and IJIRI, 1976; HASEGAWA, 1977; HALSTEAD, 1978).

The figures of the desmostylians shown in these trials were so various that none of them cannot be believed as a restoration of one and the same animal, and this is apparently due to lack of general consensus on the normal figure of the animals. In view of this, the author considered that it was necessary to discuss the problem of variety of the desmostylian figure.

First, it may happen due to irrelevant usage of the method for restoration. Usually, a living species supposed to have close relation phylogenetically and morphologically to the fossil form is used to be taken as a model for restoration (THENIUS, 1973). The method used here cannot help to lead to fault if the fossil form would have no close relation to the livings. Usually, the phylogenetical position of the extinct form has an ambiguity to some extent. If any model is taken for restoration, crucial contradiction will be brought about in correlation between

the shape of fossil bone and the mounted skeleton (INUZUKA, 1981c).

In the case of the desmostylians, the sirenian was esteemed as a preferable model by some students, but any of the proboscidean and other ungulates was also treated as a model for restoration by other workers. Corresponding to such diversity of model, it was natural that mounted skeletons were forced to be variously postured. Consequently, it is advisable to avoid adopting any model of living species for restoration of fossil animal which was extinguished without descendant.

Second, it seems probable that the previous workers have not paid due attention to basic figure essential for the form of animal. When MARSH (1884) restored the skeleton of Dinocerata, he did not take any reference to basic figure of the animal, while he gave some notes on the poses of the animal for drawing or display. Probably, such a traditional practice may stand on a tacit assumption that posture of large animals is fundamentally the same. Actually, what is the most important for restoration is how to determine basic figure of the animal. The choice of the poses, e.g. whether standing at rest or walking, is only a matter of subordinate problem. For the desmostylians, many forms have been figured at will, standing, walking, swimming and feeding, but nothing of its basic figure have been presented yet before us. Therefore, one of the main purposes in this work aims to clarify what is the basic

figure of the animal, not regarding the choice of the poses.

Third, it seems possible to say that the theoretical treatment for restoration is not sufficient even now. Certainly, a restored skeleton of an animal may represent only a hypothesis in nature (ABEL, 1925). There may be allowed to be existed other choice of different restorations. Even if any restoration is made, it will be meaningless unless its theoretical base is clear. It should be noted that, for the desmostylians, only SHIKAMA (1966, 1968) presented clearly his theoretical basis for restoration.

Osteology and myology will provide important information in constructing theoretical basis, and recent progress of paleobiology opens the way to take account anatomical and physiological views into the skeletal restoration (OSTROM, 1969; RADINSKY, 1977, 1982). Viewing from such points, the author described each skeletal elements in detail (INUZUKA, 1980a, b; 1981a, b; 1982). In this paper, those descriptions are reviewed briefly in Appendix. Based on those results, the present author will explain osteological facts of the desmostylians which are applicapable for restoration, and discuss about theoretical basis for skeletal restoration.

# III Materials and Methods

## A. Materials

For the desmostylians, there are five whole skeletons hitherto known in the world. Among them, two skeletons belong to the genus Desmostylus, and three to the genus Paleoparadoxia. In the present work, the Keton specimen and the Utanobori specimen of genus Desmostylus were treated as main materials.

The Keton specimen, the holotype specimen of Desmostylus mirabilis NAGAO, is kept in the Department of Geology and Mineralogy, Hokkaido University, Sapporo (Table 2). It was found from Keton, near Shisuka-machi (Poronaisk), south Sakhalin in 1933, and was studied by NAGAO and others (NAGAO and OISHI, 1934; NAGAO, 1935, 1941; IJIRI and KAMEI, 1961; SHIKAMA, 1966; INUZUKA, 1980a, b; 1981a, b; 1982). The skeleton was first mounted by NAGAO in 1938 (NAGAO's restoration), but thereafter, KAMEI modified it with its replicated skeleton in 1975 (KAMEI's restoration). NAGAO's restoration is exhibited at the Osaka Museum of Natural History, and KAMEI's restoration at both the Hokkaido University and the Mizunami Fossil Museum.

The Utanobori specimen is the newly found materials which was excavated at Kamitokushibetsu, Utanobori-cho, Esashi-gun, Hokkaido in 1977 (YAMAGUCHI et al., 1981). The materials are deposited in the Geological Museum, Geological Survey of Japan at Tsukuba (Table 3). The descriptive

Table 2. Denomination and analysis of each bone in the Keton specimen.

| | | | |
|---|---|---|---|
| Skull | | | UHRno.18466-1 |
| Lower jaw | | | UHRno.18466-2 |
| Vertebrae | Atlas | | UHRno.18466-55 |
| | Thoracic | IV? | UHRno.18466-56 |
| | | V? | UHRno.18466-57 |
| | | VII | UHRno.18466-58 |
| | | VIII | UHRno.18466-59 |
| | | IX | UHRno.18466-60 |
| | | X | UHRno.18466-61 |
| | | XI | UHRno.18466-62 |
| | | XII | UHRno.18466-63 |
| | | XIII | UHRno.18466-64 |
| | Lunbar | I | UHRno.18466-65 |
| | | II | UHRno.18466-66 |
| | | III | UHRno.18466-67 |
| | | IV | UHRno.18466-68 |
| | Sacrum | | UHRno.18466-69 |
| | Caudal | I | UHRno.18466-70 |
| | | II | UHRno.18466-71 |
| | | III | UHRno,18466-72 |
| | | IV+V | UHRno.18466-73 |
| | | VI | UHRno.18466-74 |
| | | VII | UHRno.18466-75 |
| | | VIII | UHRno.18466-76 |
| | | IX | UHRno.18466-77 |
| | | X? | UHRno.18466-78 |

| | | Right | Left |
|---|---|---|---|
| Costae | I | UHRno.18466-79 | UHRno.18466-80 |
| | II | UHRno.18466-81 | UHRno.18466-82 |
| | III | ——— | UHRno.18466-83 |
| | IV | UHRno.18466-84 | UHRno.18466-85 |
| | V | UHRno.18466-86 | UHRno.18466-87 |
| | VI | UHRno.18466-88 | UHRno.18466-89 |
| | VII | UHRno.18466-90 | UHRno.18466-91 |
| | VIII | UHRno.18466-92 | UHRno.18466-93 |
| | IX | UHRno.18466-94 | UHRno.18466-95 |
| | X | UHRno.18466-96 | UHRno.18466-97 |
| | XI | UHRno.18466-98 | UHRno.18466-99 |
| | XII | UHRno.18466-100 | UHRno.18466-101 |
| | XIII | UHRno.18466-102 | UHRno.18466-103 |

| | | | |
|---|---|---|---|
| Presternum | | UHRno.18466-54 | |
| Mesosternum | I | UHRno.18466-53 | UHRno.18466-52 |
| | II | UHRno.18466-51 | UHRno.18466-50 |
| | III | UHRno.18466-49 | UHRno.18466-48 |
| | IV | UHRno.18466-47 | UHRno.18466-46 |

| | | | Right | Left |
|---|---|---|---|---|
| Fore limb | Scapula | | ——— | UHRno.18466-104 |
| | Humerus | | ——— | UHRno.18466-3 |
| | Radius | | ——— | UHRno.18466-5 |
| | Ulna | | ——— | UHRno.18466-4 |
| | Carpus | Scaphoid | ——— | UHRno.18466-6 |
| | | Lunar | ——— | UHRno.18466-7 |
| | | Triquetrum | ——— | UHRno.18466-8 |
| | | Pisiform ? | UHRno.18466-9 | UHRno.18466-10 |
| | | Trapezium | ——— | ——— |
| | | Trapezoid | ——— | ——— |
| | | Capitatum | ——— | ——— |
| | | Hamatum | ——— | UHRno.18466-14 |
| | Metacarpus | II | ——— | ——— |
| | | III | ——— | ——— |
| | | IV | ——— | ——— |
| | | V | ——— | UHRno.18466-106 |
| Hind limb | Os coxae | | UHRno.18466-105 | |
| | Femur | | UHRno.18466-28 | UHRno.18466-29 |
| | Tibia | | ——— | UHRno.18466-30 |
| | Tarsus | Astragalus | ——— | UHRno.18466-31 |
| | | Calcaneum | ——— | UHRno.18466-32 |
| | | Navicular | ——— | ——— |
| | | Mesocneiform | ——— | ——— |
| | | Ectocneiform | ——— | ——— |
| | | Cuboid | ——— | UHRno.18466-13 |
| | Metatarsus | II | ——— | UHRno.18466-15 |
| | | III | ——— | UHRno.18466-16 |
| | | IV | ——— | UHRno.18466-35 |
| | | V | ——— | UHRno.18466-36 |

| | |
|---|---|
| Proximal phalanges | UHRno.18466-17,-18,-19,-38,-39,-40 |
| Middle phalanges | UHRno.18466-20,-21,-22,-23,-24,-37, -41,-42,-43,-44 |
| Distal phalanges | UHRno.18466-25,-26,-27,-45 |

Table 3. Denomination and analysis of each bone in the Utanobori specimen.

| | | | Right | Left |
|---|---|---|---|---|
| Skull | | | GSJ-F7743-1 | |
| Mandible | | | GSJ-F7743-2 | |
| Basihyoideum | | | GSJ-F7743-3 | |
| Stylohyoideum | | | GSJ-F7743-4 | GSJ-F7743-5 |
| Thylohyoideum | | | GSJ-F7743-6 | GSJ-F7743-7 |
| Vertebrae | Cervical | I | GSJ-F7743-8 | |
| | | II | GSJ-F7743-9 | |
| | | III | GSJ-F7743-10 | |
| | | IV | GSJ-F7743-11 | |
| | | V | GSJ-F7743-12 | |
| | | VI | GSJ-F7743-13 | |
| | | VII | GSJ-F7743-14 | |
| | Thoracic | I | GSJ-F7743-15 | |
| | | II | GSJ-F7743-16 | |
| | | III | GSJ-F7743-17 | |
| | | IV | GSJ-F7743-18 | |
| | | V | GSJ-F7743-19 | |
| | | VI | GSJ-F7743-20 | |
| | | VII | GSJ-F7743-21 | |
| | | VIII | GSJ-F7743-22 | |
| | | IX | GSJ-F7743-23 | |
| | | X | GSJ-F7743-24 | |
| | | XI | GSJ-F7743-25 | |
| | | XII | GSJ-F7743-26 | |
| | | XIII | GSJ-F7743-27 | |
| | Lumbar | I | GSJ-F7743-28 | |
| | | II | GSJ-F7743-29 | |
| | | III | GSJ-F7743-30 | |
| | | IV | GSJ-F7743-31 | |
| | Sacrum | | GSJ-F7743-32 | |
| | Caudal | I | GSJ-F7743-33 | |
| | | II | GSJ-F7743-34 | |
| | | III | GSJ-F7743-35 | |
| | | IV | GSJ-F7743-36 | |
| | | V | GSJ-F7743-37 | |
| | | VI | GSJ-F7743-38 | |
| | | VII | GSJ-F7743-39 | |
| Costae | | I | GSJ-F7743-40 | GSJ-F7743-41 |
| | | II | GSJ-F7743-42 | GSJ-F7743-43 |
| | | III | GSJ-F7743-44 | GSJ-F7743-45 |
| | | IV | GSJ-F7743-46 | GSJ-F7743-47 |
| | | V | GSJ-F7743-48 | GSJ-F7743-49 |
| | | VI | GSJ-F7743-50 | GSJ-F7743-51 |
| | | VII | GSJ-F7743-52 | GSJ-F7743-53 |
| | | VIII | GSJ-F7743-54 | GSJ-F7743-55 |
| | | IX | GSJ-F7743-56 | GSJ-F7743-57 |
| | | X | GSJ-F7743-58 | GSJ-F7743-59 |
| | | XI | GSJ-F7743-60 | GSJ-F7743-61 |
| | | XII | GSJ-F7743-62 | GSJ-F7743-63 |
| | | XIII | GSJ-F7743-64 | GSJ-F7743-65 |
| Presternum | | | ——— | |
| Mesosternum | | I | ——— | ——— |
| | | II | ——— | GSJ-F7743-66 |
| | | III | ——— | GSJ-F7743-67 |
| | | IV | ——— | ——— |
| Fore limb | Scapula | | GSJ-F7743-68 | GSJ-F7743-69 |
| | Humerus | | GSJ-F7743-70 | GSJ-F7743-71 |
| | Radius | | GSJ-F7743-72 | GSJ-F7743-73 |
| | Ulna | | GSJ-F7743-74 | GSJ-F7743-75 |
| | Carpus | Scaphoid | GSJ-F7743-76 | ——— |
| | | Lunar | GSJ-F7743-77 | ——— |
| | | Triquetrum | GSJ-F7743-78 | ——— |
| | | Pisiform | ——— | ——— |
| | | Trapezium | ——— | ——— |
| | | Trapezoid | ——— | ——— |
| | | Capitatum | GSJ-F7743-79 | ——— |
| | | Hamatum | GSJ-F7743-80 | ——— |
| | Metacarpus | II | ——— | ——— |
| | | III | GSJ-F7743-81 | ——— |
| | | IV | GSJ-F7743-82 | ——— |
| | | V | GSJ-F7743-83 | ——— |
| | Middle phalange | V | GSJ-F7743-84 | ——— |
| Hind limb | Os coxae | | GSJ-F7743-85 | GSJ-F7743-86 |
| | Femur | | GSJ-F7743-87 | GSJ-F7743-88 |
| | Patella | | GSJ-F7743-89 | ——— |
| | Tibia | | GSJ-F7743-90 | GSJ-F7743-91 |
| | Fibula | | GSJ-F7743-92 | GSJ-F7743-93 |
| | Tarsus | Astragalus | GSJ-F7743-94 | GSJ-F7743-95 |
| | | Calcaneum | GSJ-F7743-96 | GSJ-F7743-97 |
| | | Navicular | GSJ-F7743-98 | GSJ-F7743-99 |
| | | Mesocneiform | GSJ-F7743-100 | GSJ-F7743-101 |
| | | Ectocneiform | GSJ-F7743-102 | GSJ-F7743-103 |
| | | Cuboid | GSJ-F7743-104 | GSJ-F7743-105 |
| | Metatarsus | II | GSJ-F7743-106 | GSJ-F7743-107 |
| | | III | GSJ-F7743-108 | GSJ-F7743-109 |
| | | IV | GSJ-F7743-110 | GSJ-F7743-111 |
| | | V | GSJ-F7743-112 | GSJ-F7743-113 |
| | Proximal phalanges | II | ——— | GSJ-F7743-114 |
| | | III | GSJ-F7743-115 | GSJ-F7743-116 |
| | | IV | GSJ-F7743-117 | ——— |
| | | V | ——— | GSJ-F7743-118 |
| | Middle phalanges | II | GSJ-F7743-119 | GSJ-F7743-120 |
| | | III | ——— | ——— |
| | | IV | GSJ-F7743-121 | ——— |
| | | V | ——— | GSJ-F7743-122 |

works on this specimen is not yet completed, but the author made its skeletal restoration following his theoretical basis deduced from the redescriptive study of the Keton specimen (INUZUKA, 1981d).

Apart from Desmostylus, it is necessary to refer to the restoration of Paleoparadoxia belonging to the same order. Until now, the presence of three full skeletons of that fossil animal have been reported. In the present study, four restorations which were made from two of those three specimens are taken into consideration. SHIKAMA's restoration was based on the Izumi specimen of Paleoparadoxia tabatai (TOKUNAGA) which was found at Toki-shi, Gifu Prefecture in 1950 (IJIRI and KAMEI, 1961; SHIKAMA, 1966). The British Museum's restoration by CROUCHER and HOWIE is also based on the materials of the Izumi specimen (HALSTEAD, 1975). Another full skeleton of Paleoparadoxia is known as the Stanford specimen. There are two restorations made from this specimen. One is REPENNING's restoration (ROMER, 1966), and the other is HASEGAWA's restoration (HASEGAWA, 1977).

In order to carry out comparative osteological study, the skeletons of thirty six genera of the living mammals as listed in Table 4 were examined. Those results were adopted to elucidate the general rules for the construction of mammalian skeletons. In particular, the author paid much attention to the skeletons of large ungulates and sirenians, because they have been generally considered to have close

Table 4. Living mammalian species for comparison. NSM: National Science Museum, Tokyo, OM: Osaka Museum of Natural History, UH: Hokkaido University UTA: University of Tokyo, Faculty of Agricurture, UTM: University of Tokyo, University Museum, YL: Yomiuri Land.

| Specific name | Order | Storage |
|---|---|---|
| Elephas maximus | Proboscidea | UTM, NSM |
| Diceros bicornis | Perissodactyla | NSM, OM |
| Equus caballus | ibid. | UTA |
| Tapirus terrestris | ibid. | UTM, OM |
| Hippopotamus amphibius | Artiodactyla | NSM |
| Bubalus bubalis | ibid. | NSM |
| Giraffa camelopardalis | ibid. | NSM |
| Camelus dromedarius | ibid. | NSM |
| Lama glama | ibid. | NSM |
| Bos primigenius | ibid. | INUZUKA |
| Rangifer tarandus | ibid. | NSM |
| Sus scrofa | ibid. | INUZUKA |
| Tayassu angulatus | ibid. | NSM |
| Panthera leo | Carnivora | UTM, NSM |
| Felis catus | ibid. | INUZUKA |
| Crocuta crocuta ? | ibid. | UTM |
| Ursus arctos | ibid. | Dr.HASEGAWA |
| Nyctereutes procyonoides | ibid. | INUZUKA |
| Vulpes vulpes | ibid. | INUZUKA |
| Nasua narica | ibid. | NSM |
| Mustela itatsi | ibid. | NSM |
| Lutra lutra | ibid. | NSM |
| Enhydra lutris | ibid. | NSM |
| Eumetopias jubata | (Pinnipedia) | UH |
| Zalophus californianus | ibid. | NSM |
| Callorhinus ursinus | ibid. | NSM |
| Phoca richardi | ibid. | NSM |
| Dugong dugon | Sirenia | NSM, YL |
| Trichechus manatus | ibid. | YL |
| Lepus brachyurus | Lagomorpha | NSM |
| Pteromys momonga | Rodentia | NSM |
| Castor canadensis | ibid. | NSM |
| Ondatra zibethicus | ibid. | NSM |
| Marmota monax | ibid. | NSM |
| Rattus norvegicus | ibid. | INUZUKA |
| Hydrochoerus capibara | ibid. | NSM |
| Erithizon dorsatum | ibid. | NSM |
| Dasypus novemcinctus | Edentata | UTM, NSM |
| Myrmecophaga tridactyla | ibid. | NSM |
| Manis pentadactyla | Pholidota | NSM |
| Erinaceus europaeus | Insectivora | UTM |
| Talpa wogura | ibid. | UTM |
| Macropus giganteus | Marsupialia | NSM |
| Vombatus ursinus | ibid. | UTM, NSM |
| Tachyglossus aculeatus | Monotremata | UTM, NSM |

taxonomical relations with the desmostylians. The study on the skeletons of the pinnipeds was made regarding to their habitat resemblance with the desmostylians.

B. Methods

In the present paper, the author intends to state his theoretical basis for the skeletal restoration of the desmostylians. He made a survey throughout the skeletal materials of the Keton specimen, and described carefully axial and appendicular skeletons (INUZUKA, 1980a, b; 1981a, b; 1982). Prior to his works, the cranium of that specimen was precisely studied by IJIRI and KAMEI (1961), and on the other hand, the limb bones and the sternum were fully investigated by SHIKAMA (1966). Summarizing those descriptive works, the author will give critical review from anatomical view points with brief accounts on each bones.

Basing upon the results obtained from the study on the Keton specimen, the author made practically mounting for the Utanobori skeleton. Both the Keton and the Utanobori specimens belong together to the same genus Desmostylus, although those two may belong to different species, i.e. D. mirabilis and D. japonicus* respectively. The Keton specimen represents a skeleton of mature body, but the

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* Their taxonomical position may be changed in future, as the specimens have not yet been studied from taxonomical viewpoints by the author.

Utanobori specimen does that of immature individual. In addition, the Keton specimen lacks some main portions like as cervical vertebrae and cranial part of thoracic ones. In spite of their differences, both specimens have common characteristics as a desmostylid. Accordingly, it is correct that the conception of restoration procured from the study on the Keton specimen has been applied to the mounting of the Utanobori specimen.

The present study may result in to lead the desmostylian restoration to quite different form from those supposed formerly. The former works were usually relied on some model of supposed relatives, while the present study followed mainly to skeletal anatomy including two viewpoints, functional anatomy and comparative anatomy.

In other words, function of musculo-skeletal system should be considered from two different viewpoints: support of standing posture and locomotion. That is, body weight of terrestrial mammals is supported not only by the skeleton but by soft tissues, i.e. muscles and ligaments as well: therefore, the mode of supporting presumed by the skeletal form must coincide with direction or degree of development of muscle which may be estimated by bone shapes.

On the other hand, comparative anatomy should be applied to the restoration as follows: Two ways of comparison are necessary in the restoration. One is comparison of shape of each bone, and is done in order to find out morphological features characterized the fossil in

question. Another is comparison among skeletons, which purpose is abstraction of common characteristics or general rules for the skeletal construction of the taxon to which the fossil exactly belongs. Most of mammals or ungulates ought to conform to skeletal rules which found out in such a way; therefore the rules should be applied to the fossil in question. In this manner we can avoid errors which models are selected based on partial resemblance or only a part of figure is decided on morphological resemblance of a few bones.

Unless the figure of skeleton mounted in such a way can be reasonably related on anatomical basis to the most distinct characteristics of each bone, the restoration would not be justified as exact.

The method of restoration used in this paper are just mentioned above. Furthermore, reliability of restoration will increase, if there is no contradiction between the restored skeleton and the posture in the bed. The skeletons were well preserved in jointed state by the case of the Utanobori specimen. Therefore, its mode of occurrence resulted in the endorsement of theoretical basis for restoration. The confirmation to such articulation was also made for other cases of desmostylian mode of occurrences.

## IV Critical review of the previous works

In this chapter the author will take a review of six skeletal restoration of the desmostylian's formerly made and give criticism for them. Main characteristics of the restored skeletons mentioned below are arranged in Table 5.

### A. NAGAO's restoration (Plate IX, Fig.1)

This restoration is mounted with the skeleton of the Keton specimen. As will be described below, the cervical vertebrae are lacking except a part of the atlas and some of anterior thoracic vertebrae, so it is reasonable to say that those bones in the mounted skeleton were restored by imagination. The vertebral column extends nearly horizontally and is straight from the neck to the base of the tail. The fore and hind limb bones are jointed straightly under the body extending downward from the trunk, with articulation of slight bending. Although NAGAO (1941) claimed that the animal was "semidigitigrade", the result of his skeletal restoration seems to be plantigrade. Five digits in fore and hind limbs are pointing forward.

NAGAO (1941) did not offer any theoretical basis for his restoration except the reason for the setting of digital number. According to him, "Some resemblance with ungulates or with extinct orders, such as Taligrada (=Pantolambdidae, now included in the order Amblypoda), Amblypoda and Condylarthra, probably indicate a closer relationship of

Table 5. Comparison of characteristics of restored skeletons by previous authors.

| | Vertebral column | Limb position | Toe direction | Foot posture | Degree of flexion in joints of limbs |
|---|---|---|---|---|---|
| NAGAO (1938) | horizontal; neck, shoulder and pelvis on nearly same level | under | cranial | plantigrade | flexed slightly |
| REPENNING (1965) | vertical pelvis | under | F: caudal<br>H: cranial | by the back of hand<br>unguligrade | extended slightly<br>flexed strongly |
| SHIKAMA (1966) | high in the middle; slightly vertical pelvis | under | F: lateral<br>H: medial | by the back of hand<br>semi-plantigrade | extended fairly<br>flexed slightly |
| British Museum (1975?) | vertical pelvis | F: under<br>H: lateral | craniolateral<br>cranial | digitigrade<br>plantigrade | extended<br>flexed |
| KAMEI (1975) | high in the shoulder; slightly vertical pelvis | under | craniolateral | digitigrade or unguligrade | F: extended<br>H: flexed slightly |
| HASEGAWA (1977) | high in the middle; vertical pelvis | under | F: craniolateral<br>H: medial | unguligrade | flexed strongly<br>flexed slightly |
| INUZUKA (1984) | low as a whole | lateral | cranial | unguligrade | flexed |

this animal (NAGAO, 1941)". From his statement we can reason out his way of restoration: first he chose an animal as the closer relative from the resemblance of bone morphology, and then, he mounted the skeleton in similar posture to the relative. When we observe NAGAO's restoration precisely, everybody may notice that the wrist joint is dislocated. As it was apparently possible to settle those bones in the relation of correct articulation, he was forced to give an artificial torsion at a right angle between those bones. Consequently, skeletal construction of fore limbs resulted in contradiction to each of original bone shape. NAGAO's restoration, however, followed faithfully the rules of mammlian skeletal construction, especially to general rules of the ungulates construction as will be mentioned later. Thus, it is reasonable to assume that this skeletal restoration was made in reference to a certain skeleton of ungulates like hippopotami, and not to bone morphology of Desmostylus itself.

It is inappropriate, however, to use certain type of living animals as a model for the animal of which phylogeny and ecology are obscure. Even if the bones of the animal are similar in part to those of the model, they should be quite different from the model in other part, because the model is not a true relative of the animal. Different animals used to be selected as models according to different views on certain morphological characteristics supposed to be important in phylogenetic relationships or ecological

affinities. If students will restore the skeleton of unknown animal to the original state after the model on the basis of partial resemblance, some discordances with the original bone construction will become to be exposed in the parts imediately. Thus, the researcher should avoid to bring in an animal as a model, when he attempts to restore an extinct animal of unknown phylogenical position.

B. REPENNING's restoration (Plate IX, Fig.2)

This skeleton is drawn up on the Stanford specimen of Paleoparadoxia tabatai found in the Stanford University campus in 1964. The skeletal construction of it seems to be peculiar to ungulates skeleton in general. The neck is too much raised, the thoracic vertebrae are arranged horizontally, the lumbar vertebrae bending strongly downward, and the pelvis standing nearly vertical. The fore limbs (shoulder to wrist) extend downward, and in the hind limbs femurs project horizontally for- and outward. Articulation of the fore limbs is extending at joints, but that of the hind limbs is settled to be flexed extremely at knee joints. Most curious is the mode of attachment of manus to the ground; the wrist flexing backward deeply, with its back facing the ground. The pes is unguligrade landing with only distal phalanges. The tips of digits point backward in fore limbs, forward in hind limbs.

Theoretical basis of REPENNING's restoration is able to be known from his personal communication as follows

(SHIKAMA, 1966): "Ankylosis between the radius and the ulna was so great that there was no possibility of supination or pronation by rotation of the radius across the ulna. ••• hence propulsive swimming strokes by the manus were made with the manus held beneath the chest of the animal, the elbow turned outward." "Manus would also be held below the chest and the elbows pointing outward in terrestrial locomotion." "If the tibia is placed in a vertical position the plane of the pes is held 45° from horizontal, the weight of the handiquarter is placed entirely on the medial edge of the flat foot, and this weight is applied to the tibia-astragalus articulation at a very insecure angle which quite easily could cause dislocation." "Hence on land the animal had to support itself on flexed knees that pointed outward, with its feet beneath its belly, and its tibia held 45° from vertical." "I think the back feet, with their short metatarsals, had to function plantigrade on land. The front feet, with their longer metacarpals, might have been semi-plantigrade at times•••."

REPENNING's method is apparently based on osteology. The posture of the fore and the hind limbs are described precisely from osteological observations. The distinct feature of his restoration is in his consideration on the possibility of dislocation deduced from the angle of articular surface and partly in the application of skeletal rule, e.g. length of the metapodials and foot posture.

His method, however, seems to be insufficient in the

following three points. First, the relations of soft tissues such as ligaments and muscles to bones are not considered at all. Those are very important to restore the posture of an animal, because the weight of an animal is supported not only by bones but also by tissues. In this respect, possibility of dislocation is overestimated in his restoration. He considered only the direction of articular surfaces, but the central part of articular surfaces between limb bones need not always be horizontal. Second, each portion of the skeleton was examined individually, and the situation of connections between the trunk and limbs or the similarity between fore limbs and hind limbs were not considered. Third, it is possible to say that his application of the general rules of skeletal construction to the skeleton is irrelevant. That is to say, only one of the rules was chosen and adopted for the restoration: for instance, short metatarsus usually indicate plantigrade posture, but he regarded that rule is absolutely standing. As there are many rules in skeletal construction, but those rules have their own exceptions. It is necessary to examine which rule should be conformed and which is exception in practice.

C. SHIKAMA's restoration (Plate IX, Fig.3)

SHIKAMA (1966) described the Keton specimen of Desmostylus and the Izumi specimen of Paleoparadoxia, but he mainly dealt with the skeleton of the latter in the

restoration. In his skeleton, the vertebral column raises in the middle of the body and the curvature is stronger at the position of the lumbar vertebrae resulting in a lower leveling of the pelvis. The limb bones are situated under the trunk; the fore limbs stretching considerably, but the hind limbs flexed slightly. In his paper he states that the manus and the pes are held in "semiplantigrade" position, but in the figure of his plate, the manus is held with its back under and the pes is obscurely shown, for it differs on each side. He added, "manus is directed outward while pes is directed inward.", but both the manus and the pes point inward in his figure illustrated.

SHIKAMA (1966) was the first worker who restored the desmostylian skeleton with showing a reason for the restoration. The curvature of the vertebral column was settled by a resemblance to rodents which have similar shape of pelvis to the desmostylians. The position of the manus and the pes and the direction of their tips of digits were decided in consideration of morphology of each bone. It was the first that limb bones were situated under the trunk. It is one of the general rules of mammalian skeleton. SHIKAMA also drew the swimming posture and restored the locomotion in which "Paleoparadoxia does a Phacochoerus locomotion on sea bottom". He interpreted the large flat sternum as a quite useful tool in this locomotion. It was his excellent idea that restoration of desmostylians should depend upon how does it interpretate the uniquely

constructed sternum.

SHIKAMA's method of restoration was based on osteology and comparative anatomy. Important morphological characteristics were selected from each part of the body, and the posture was deduced from bone shape and comparative bases.

There is a fault common to REPENNING's method: he disregarded musculo-skeletal system. Although he compared the bones with those of other animals, he recognized their morphological characteristics too roughly. For example, the similar shape of pelvis to rodents is not an adequate reason to presume that the backbone curvature is similar to that of a rat. He did not pay attention to the following points: comparison of pelvis by every morphological element, consideration on the correlation between the pelvis and the vertebral column, comparison of the pelvis forms among rodents, and so on.

SHIKAMA (1968) drastically made correction of his previous restoration (SHIKAMA, 1966). He made a setting of the long axis of the scapula to parallel with the vertebral column and turned the lateral surface of antebrachial skeleton cranially. In consequence of this modification, such a position of flexed manus and medially pointing toes was abandoned, and normal semiplantigrade in position was adopted in stead. In this revision, direction of scapula and femur were improved fairly reasonably; but it seems to be still imperfect, for he relys only on osteological facts,

but not on general rules for mammalian skeletal construction.

D. Restoration of British Museum (N.H.) (Plate X, Fig.1)

This restoration is based on the Izumi specimen of Paleoparadoxia as same as in the case of SHIKAMA's restoration. The vertebral column has light curvature extending from the cervical to the thoracic vertebrae, and there is steep flexion between the thoracic and the lumbar ones. The lumbar vertebrae run straight toward the pelvis downwardly. Fore limbs are placed under the trunk and extended straightly, but in hind limbs the femur is positioned horizontally and laterally and attached to the vertical tibia. The manus has digitigrade foot posture while the pes plantigrade. The manus is pointing anterolaterally and pes forward.

This skeleton is exhibited in the British Museum of Natural History and is refered to by HALSTEAD (1975). Mr. R. CROUCHER and Mr. F. HOWIE of the Museum mounted it and Dr. R. J. G. SAVAGE agreed with the idea of the restored posture. According to CROUCHER, the basis of the restoration is mainly on the shape of articular surfaces of the bones. For example, as the articular surfaces of the ankle joint and the metatarsal bones are broad, the pes is fairly movable, and the metatarsals are flat, the pes is supposed to work as a paddle.

Seeing from the figure of the restored skeleton, it

osteological facts, but not on general rules for mammalian skeletal construction.

D. Restoration of British Museum (N.H.) (Pl.X, Fig.1)

This restoration is based on the Izumi specimen of Paleoparadoxia as same as in the case of the SHIKAMA's restoration. The vertebral column has light curvature extending from the cervical to the thoracic vertebrae, and there is steep flexion between the thoracic and the lumbar ones. The lumbar vertebrae run straight toward the pelvis downwardly. Fore limbs are placed under the trunk and extended straightly, but in hind limbs the femur is positioned horizontally and laterally and attached to the vertical tibia. The manus has digitigrade foot posture while the pes plantigrade. The manus is pointing anterolaterally and pes forward.

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Seeing from the posture of the restored skeleton, it

appears to be a modification of REPENNING's restoration. A peculiar direction of the manus is changed to the general position and the highly flexed knee joint is made to be less flexed. It seems that the digitigrade manus and the plantigrade pes are restored on the basis of the length of the metacarpal and the metatarsal bones. It appears that, as a result of this change in the limb position, difference in height between fore and hind limbs becomes so large, that the warp is concentrated mostly between thoracic and lumbar vertebrae.

The method of restoration depending on only the shape of articular surface of the bones is limited in its practical use. In the first place, the joint in the flesh consists not only of bones but also of soft tissues such as cartilages and ligaments, and the movable extent in the joint in living state differs from what is assumed based on only the extent, orientation and form of articular surface of bones. For example, the shoulder joint has a shallow articular surface suggesting large mobility, but its movement is fairly restricted in living state owing to the function of ligaments. Moreover, it is unknown where each bone contact with the counterpart within the extent, when the body is in standing state. Consequently, it should be noticed that though the joints pattern and the extent of articular surface are usable as the key for mounting, the basic figure of the animal is not determined only by these features.

E. KAMEI's restoration (Plate X, Fig.2)

This is the second attempt of the restoration of Desmostylus based on the Keton specimen. The vertebral column is most elevated at the shoulder region, the neck raised slightly up, and the hip somewhat down. Limb bones are extending downward from the trunk, but the hind limbs somewhat outward. The fore limbs are almost extended, while the hind limbs are more or less flexed. Both the fore and hind limbs are digitigrade or unguligrade in position. Every toe is pointed obliquely outward.

According to Dr. KAMEI's personal communication, the restoration was tried at first to take tapirs as a model. It is based on the study which the microstructure of teeth and cranial characters of the desmostylians suggest closest relation with those of tapirs in general (IJIRI and KAMEI, 1961). But, because it was difficult to mount the skeleton with the figure of tapirs using desmostylian bones, he adopted the rhinoceroses as a model which is a kind of perissodactyls same as tapirs. Judging from the figure, it appears that some modifications were made to NAGAO's restoration and restoration was accomplished, faithfully following the form of each bone. The resulted skeleton had no dislocation of joints, and abandoned the plantigrade position of the manus and the pes peculiar to ungulates in general. The anterior part of the body were higher than the posterior, the scapulae were separated from the thorax and

knees projected slightly outward. This method is common with NAGAO's method in utilizing a model of living species.

F. HASEGAWA's restoration (Plate X, Fig.3)

There are several restorations by HASEGAWA of Paleoparadoxia based on the Izumi specimen, the Chichibu-ohnohara specimen and the Stanford specimen, which are exhibited in several museums in Japan. This is one of them, which was based on the Stanford specimen. The vertebral column is high in the middle, strongly bent, and the hip down. Limb bones are under the trunk, the fore limbs strongly without flexed, the hind limbs flexed weakly. As the femur is projecting without flexion in hip joint, the distance between both feet is wide and toes pointing inward. Both fore and hind limbs are unguligrade. Toes of manus are pointing anterolaterally.

According to Dr. HASEGAWA's personal communication, this restoration is exclusively based on the shape of bones, and each joint is flexed or extended to the limit. The curvature of vertebral column agrees with that of SHIKAMA's restoration (SHIKAMA, 1966), since both are based on the vertebral column of rodents in which the pelvic shape is similar to that in the desmostylians. The direction of glenoid cavity becomes more forward, the elbow joint flexed more strongly than in SHIKAMA's restoration. It is noticeable that both manus and pes are restored to be clearly unguligrade as in ungulates in general. This method

is common with the British Museum's method in depending on articular surfaces.

# V. Characteristics of the desmostylian skeleton

## A. Comparison with other mammals

In this section the results of comparative study on skeletal elements of the desmostylian with those of the other mammals are enumerated to clarify the characteristics peculiar to the desmostylian.

### 1. Bones of the axial skeleton

The surface of the occipital condyles of the skull (UHRno.18466-1, Fig. 1) is smooth and convex, as same as in the cases of proboscideans, sirenians and cetaceans. In the case of long neck artiodactyls and perissodactyls the transverse ridge on occipital condyle prevents dorso-ventral rotation of the head at the head joint. The neck of Desmostylus was short like proboscideans and sirenians, and it is presumed that dorso-ventral rotation in the head joint was possible to a certain degree.

The absence of the transverse foramen of the atlas (UHRno.18466-55, Fig. 2, Plate I) in Desmostylus is common to artiodactyls, but the foramen in the axis of Desmostylus is peculiar in position. Thus, the feature of the axis differs from that of artiodactyls and perissodactyls in having no lateral vertebral foramen. The other cervical vertebrae are also peculiar in the ungulates in having low and wide bodies, the form of the transverse process and the position of the transverse foramen. Even if vertebrae of Desmostylus may have morphological resemblance partially to

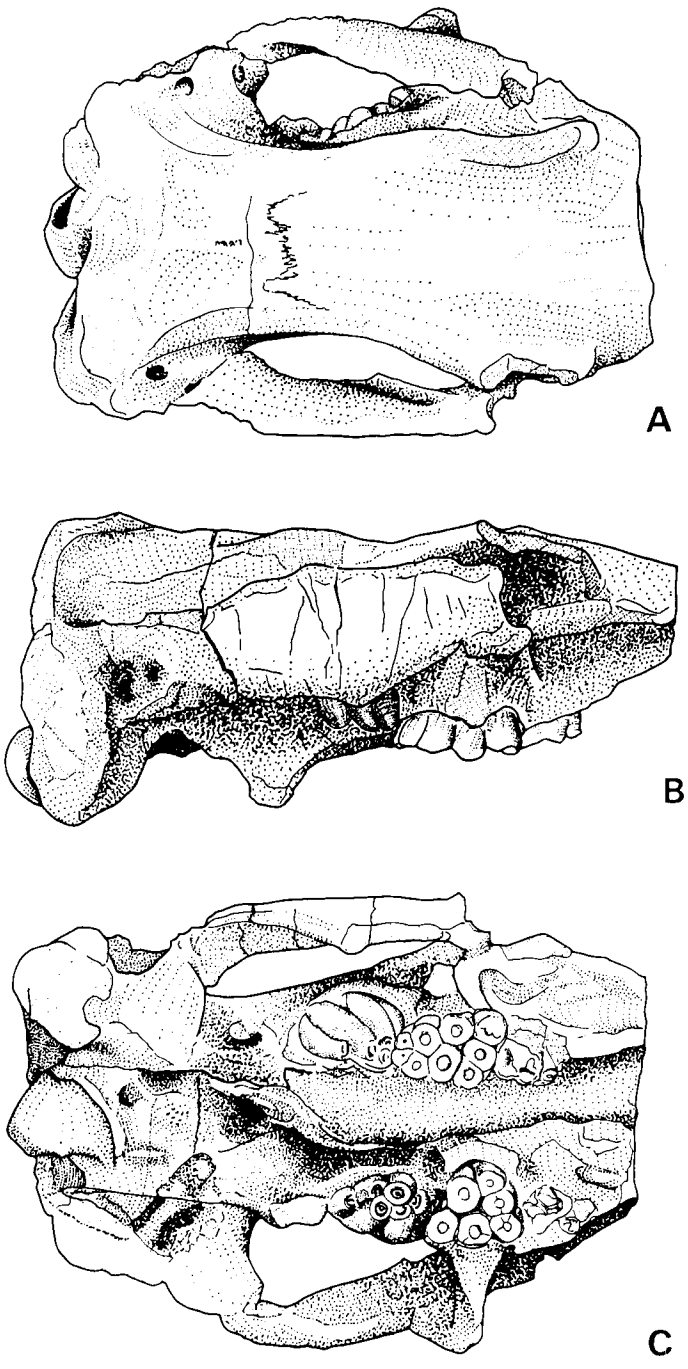



Fig. 1. Skull of Desmostylus mirabilis (UHRno. 18466-1)
A: dorsal view, B: right lateral view, C: ventral view

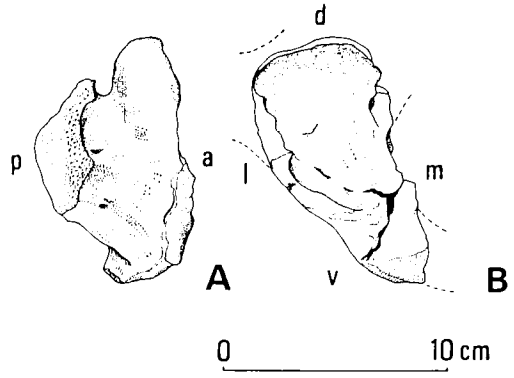



Fig. 2. Atlas of Desmostylus mirabilis (UHRno. 18466-55)
A: right lateral view, B: cranial view
a: anterior side, p: posterior side, m: medial side,
l: lateral side, d: dorsal side, v: ventral side

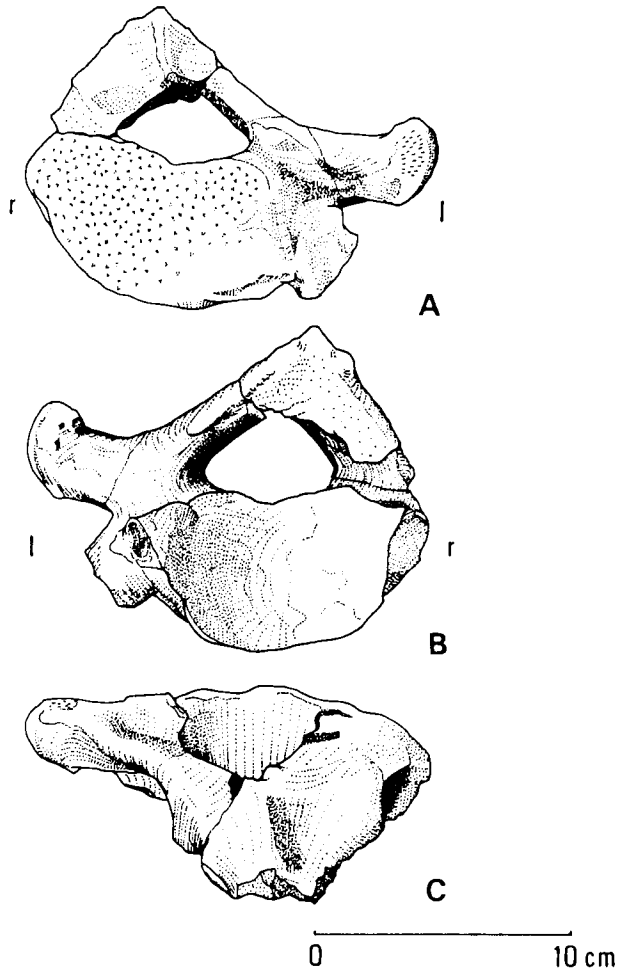



Fig. 3. ? Fourth thoracic vertebra of Desmostylus mirabilis (UHRno. 18466-56)
A: cranial view, B: caudal view, C: dorsal view
r: right side, l: left side

other orders of mammals, those are very unique as a whole.

The thoracic vertebrae (UHRno.18466-56—64, Fig.3, 4, 5, Plate I, II) of Desmostylus are similar to those of elephants or tapirs in their wide pedicle of arch, but are peculiar in having deep posterior vertebral notch produced by antero-posteriorly thin pedicle. The neural spines are similar to those of sirenians in their shortness, but caudal inclination is stronger than that of spines in hippopotami in the anterior and middle thoracic vertebrae. Cranial and caudal capitular facets have obscure margin in every thoracic vertebra, but they are peculiar in their position higher than lower margin of neural canal in the middle thoracic vertebrae. In the posterior thoracic vertebrae it is peculiar that the accessory process is projecting backward from caudal margin of the transverse process, and that the cranial articular process of succeeding vertebra tends to be put between the accessory process and the caudal articular process as observed in some edentates.

The lumbar vertebrae (UHRno.18466-65—68, Fig.5, Plate II, III) of Desmostylus are lower and wider than those of sirenians in anterior aspects and are unique in showing a parallelogrammic outline down backward in lateral aspects. There is no median keel on ventral surface. The transverse process is as same as that of horse in originating from the level of inferior margin of neural canal, but is peculiar in its shortness and in projecting horizontally and due transversely. It is peculiar that the cranial articular

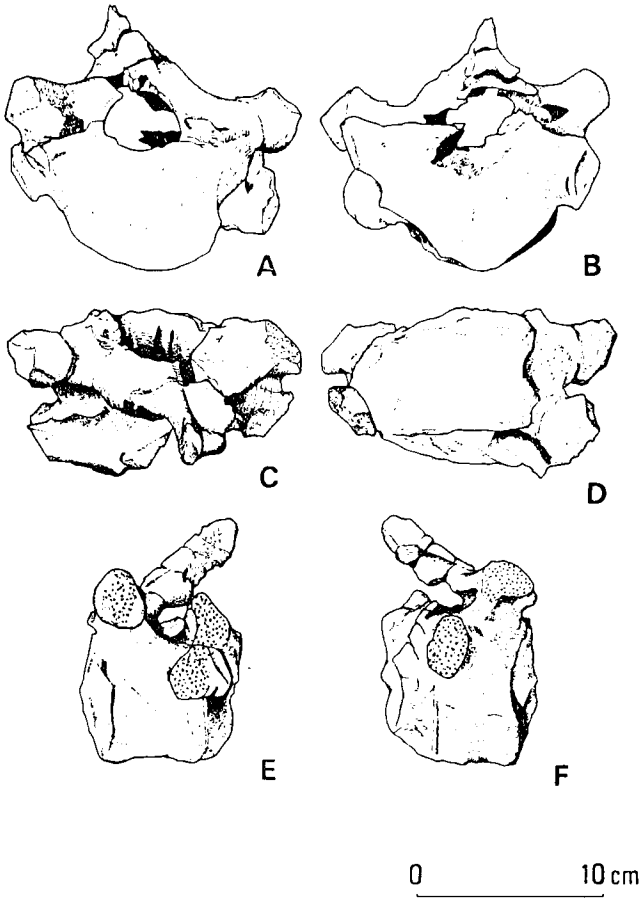



Fig. 4. ? Fifth thoracic vertebra of Desmostylus mirabilis (UHRno. 18466-57)
A: cranial view, B: caudal view, C: dorsal view, D: ventral view, E: left lateral view, F: right lateral view

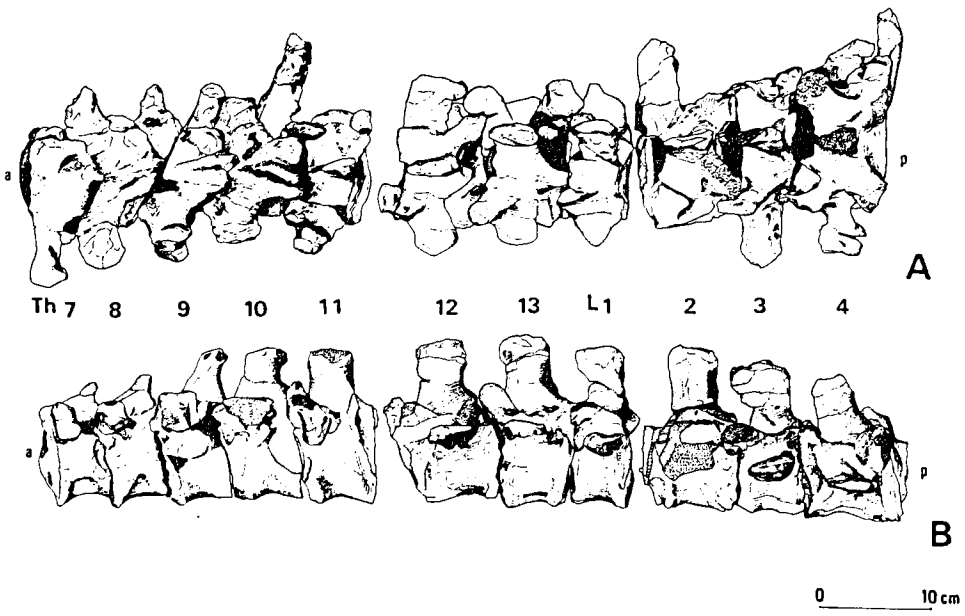



Fig. 5. Thoracic and lumbar vertebrae of Desmostylus mirabilis (UHRno. 18466-58—68)
A: dorsal view, B: left lateral view
a: anterior side, p: posterior side

process protrudes more anteriorly to the anterior surface of the body. The absence of the accessory process is common to ungulates.

The form of sacrum (UHRno.18466-69, Fig.6, Plate III) is also unique as a whole. Body width at sacral base is three-fifths of the maximum width, and is much larger than in perissodactyls or artiodactyls. The lateral part is dorso-ventrally flat as in perissodactyls, but no articular facet is present for the transverse processes of the last lumbar vertebra. It is strange that the auricular surface is improportionally small for big body size. Sacrum is similar in shape to camels in having triangular outline and to hippopotami in having lower and vertical sacral crest.

The caudal vertebrae (UHRno.18466-70—78, Fig.7, Plate III) of Desmostylus differ most from those of sirenians in having nothing of the arch and the transverse process even in the first one.

The ribs (UHRno.18466-79—103, Fig.8, Plate IV) of Desmostylus are similar to those of tapirs or pigs in the shape of costal head. To perissodactyls a degree of development of dorsal muscle area is alike. To elephant or horse the form of sternal extremity is same. They are round in cross section, but not so stout as in sirenians. The intercostal space is not so narrow as in a kind of edentates.

The sternum (UHRno.18466-46—54, Plate IV) of the desmostylian is similar to that of cetaceans or sirenians in

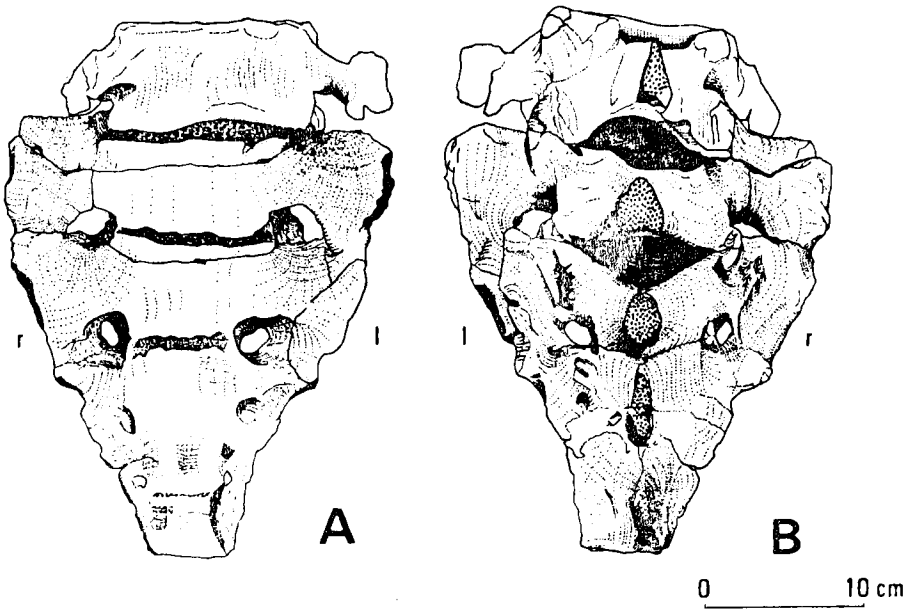



Fig. 6. Sacrum of Desmostylus mirabilis (UHRno. 18466-69)
A: ventral view, B: dorsal view
r: right side, l: left side

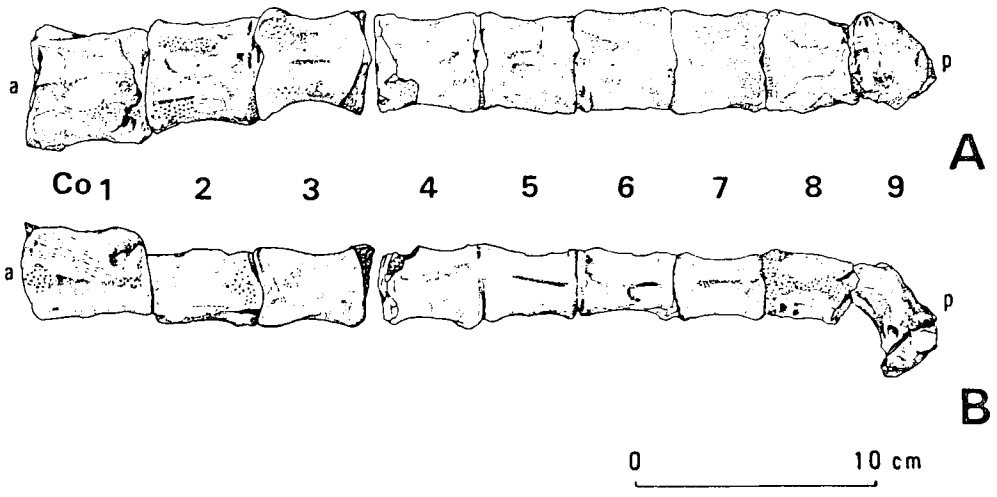



Fig. 7. Caudal vertebrae of Desmostylus mirabilis (UHRno. 18466-70—77)
A: dorsal view, B: left lateral view
a: anterior side, p: posterior side

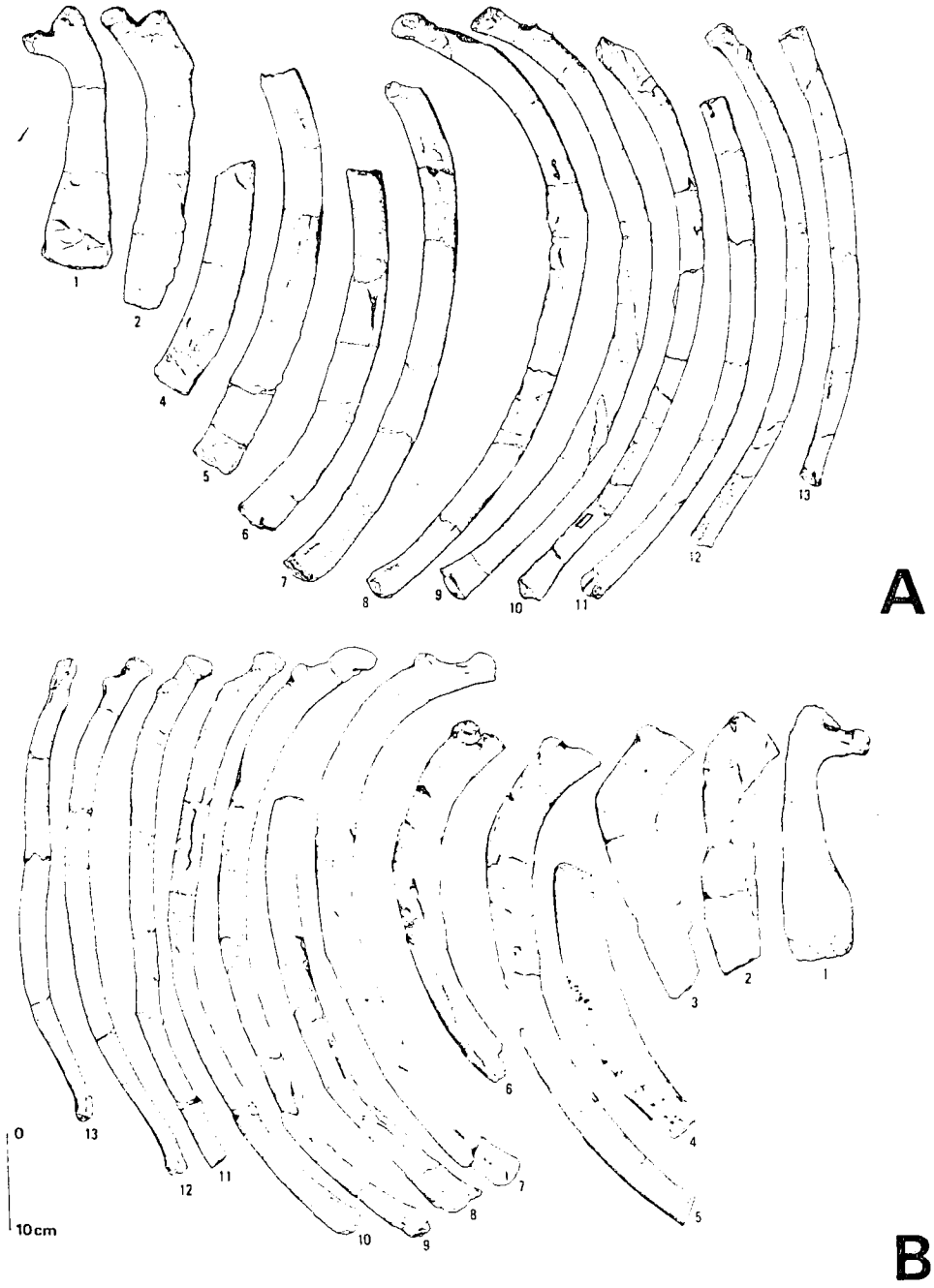



Fig. 8. Caudal view of ribs of Desmostylus mirabilis (UHRno. 18466-79—103)
A: right ribs, B: left ribs
Numbers show rib positions.

its flat shape, but is characteristic to be thicker and paired form. It is broad in surface area which adapts to attachment for many muscles. However, the mode of surface increment is entirely different from that of chiropterans or birds.

2. Bones of the appendicular skeleton

The scapula (UHRno.18466-104, Fig.9, Plate V) of the Keton specimen is elongated triangular in shape and closest in form to that of artiodactyls, particularly ruminants. However, the supraspinous fossa is larger in proportion to be compared with infraspinous fossa. The tuberosity is ill-developed in the facies serrata as same as in sirenians. This is in contrast with the state, seen in many large terrestrial quadrupedal mammals (Fig. 10). Poor curvature of dorsal margin reminds us that of giraffes. Thick caudal margin is one of characteristic features of graviportals like rhinoceroses, hippopotami and buffalos. The acromion is situated at a higher level and does not projected as same as in dugons. It is similar to sirenians in that the scapula bends medially, particularly at lower part, in cranial view. The so-called caudal swing is as strong as in tapirs, but less than in sirenians. The tuber spinae is well-developed similar to hippos, and glenoid cavity is relatively large.

The humerus (UHRno.18466-3, Fig.11, Plate V) is stout disproportionate to the length as seen in rhinos and hippos (Fig. 12). Epiphyses are big and body is constricted in the

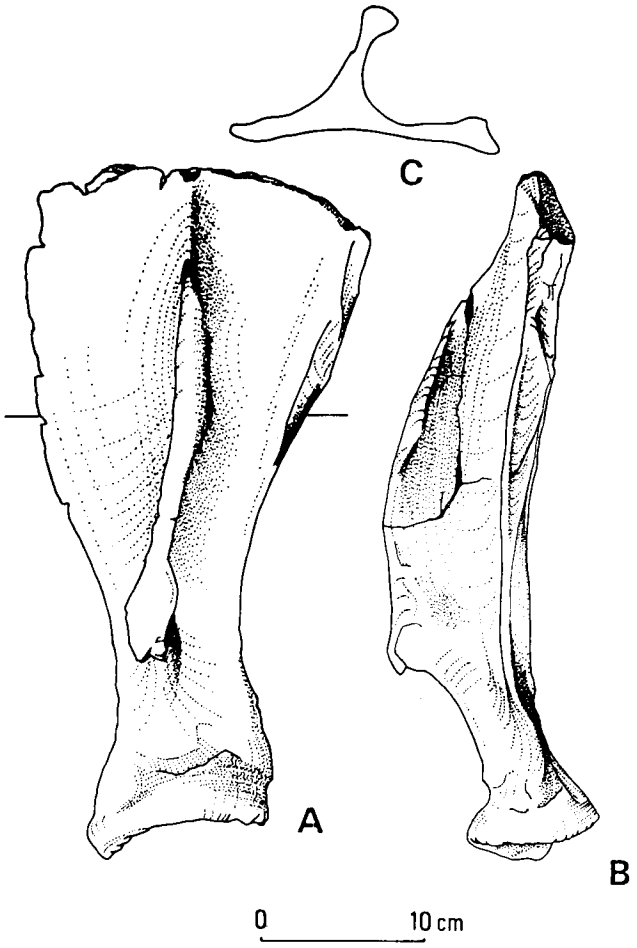



Fig. 9. Left scapula of Desmostylus mirabilis (UHRno. 18466 -104)
A: lateral view, B: caudal view, C: section seen from below

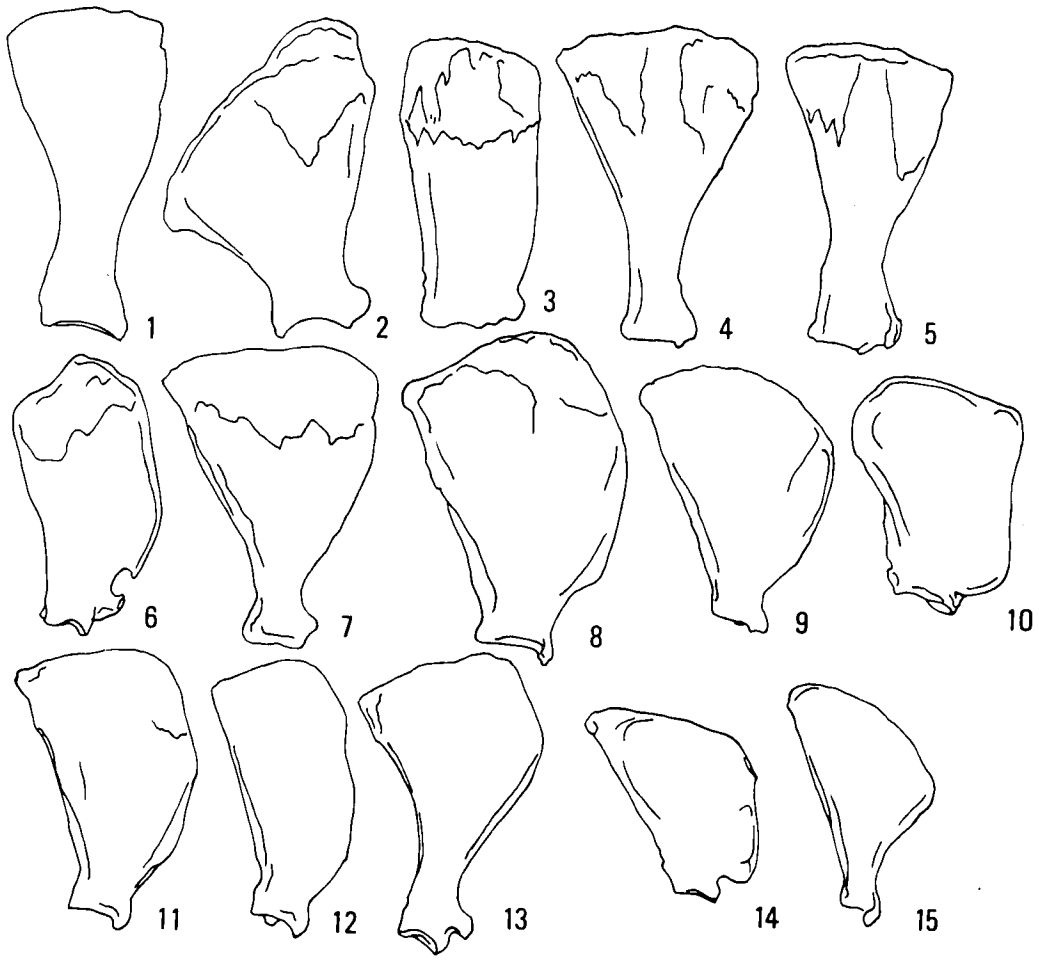



Fig. 10. Costal view of left scapula of Desmostylus in comparison with those of living mammals. Facies serrata which is usually well-developed in large mammals is indistinct in Desmostylus.
1: Desmostylus, 2: Elephas, 3: Diceros, 4: Bos, 5: Equus, 6: Tapirus, 7: Sus, 8: Panthera, 9: Felis, 10: Ursus, 11: Nyctereutes, 12: Vulpes, 13: Dugong, 14: Manis, 15: Rattus

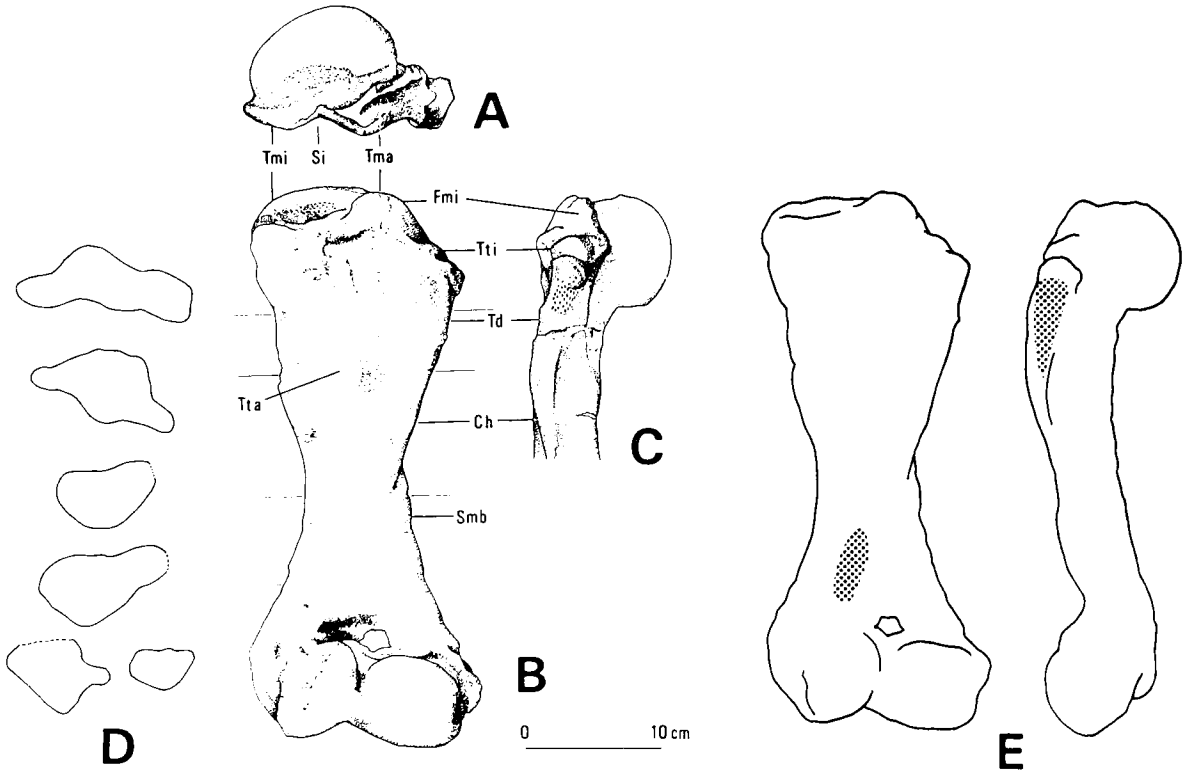



Fig. 11. Left humerus of Desmostylus mirabilis (UHRno. 18466-3)
A: proximal view, B: cranial view, C: lateral view
D: sections seen from above, E: positions of rugged surface in cranial and lateral views
Ch: Crista humeri, Fmi: Facies m. infraspinata, Si: Sulcus intertubercularis, Smb: Sulcus m. brachialis, Td: Tuberositas deltoidea, Tma: Tuberculum majus, Tmi: Tuberculum minus, Tta: Tuberositas teres major, Tti: Tuberositas teres minor

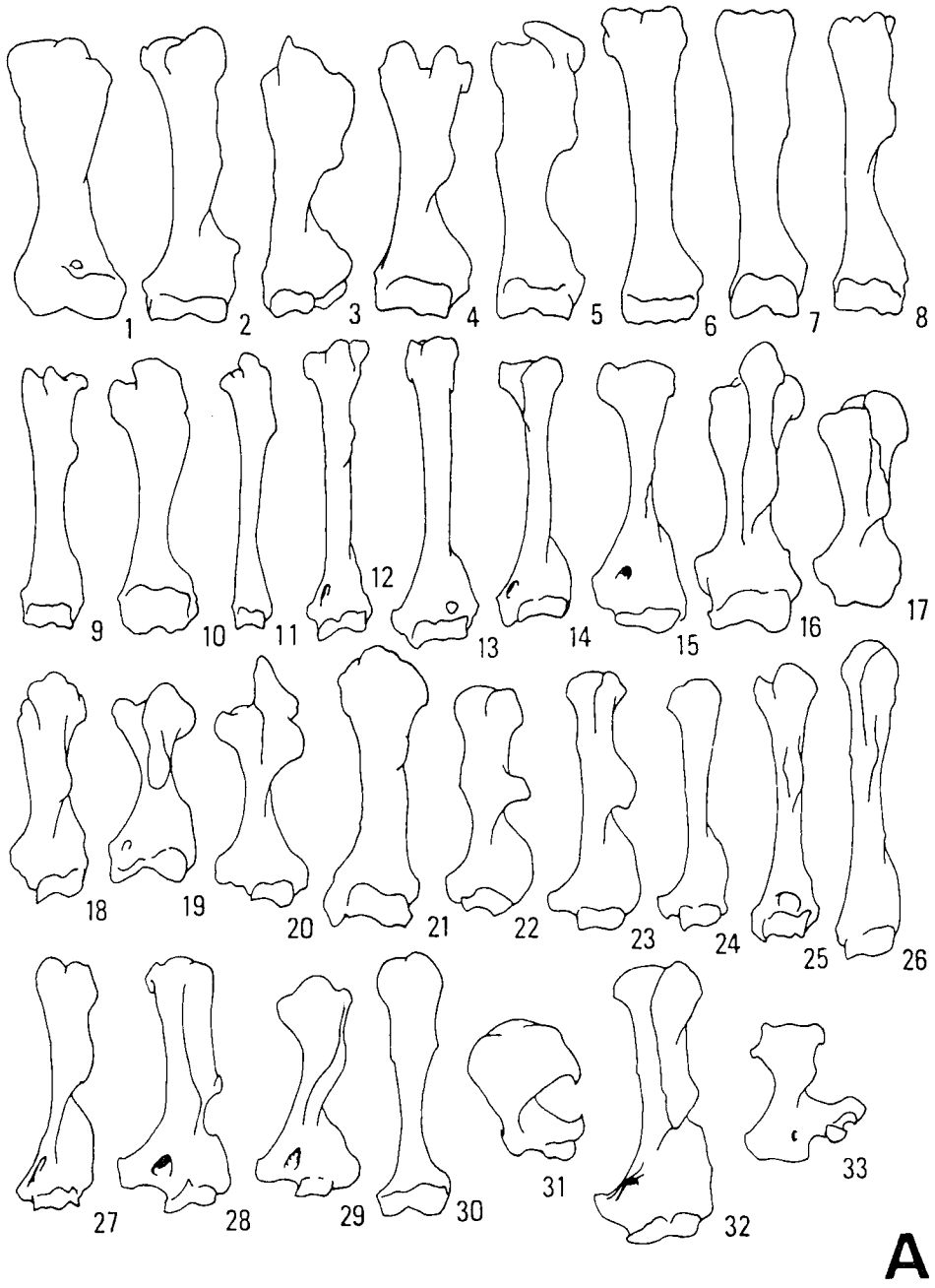
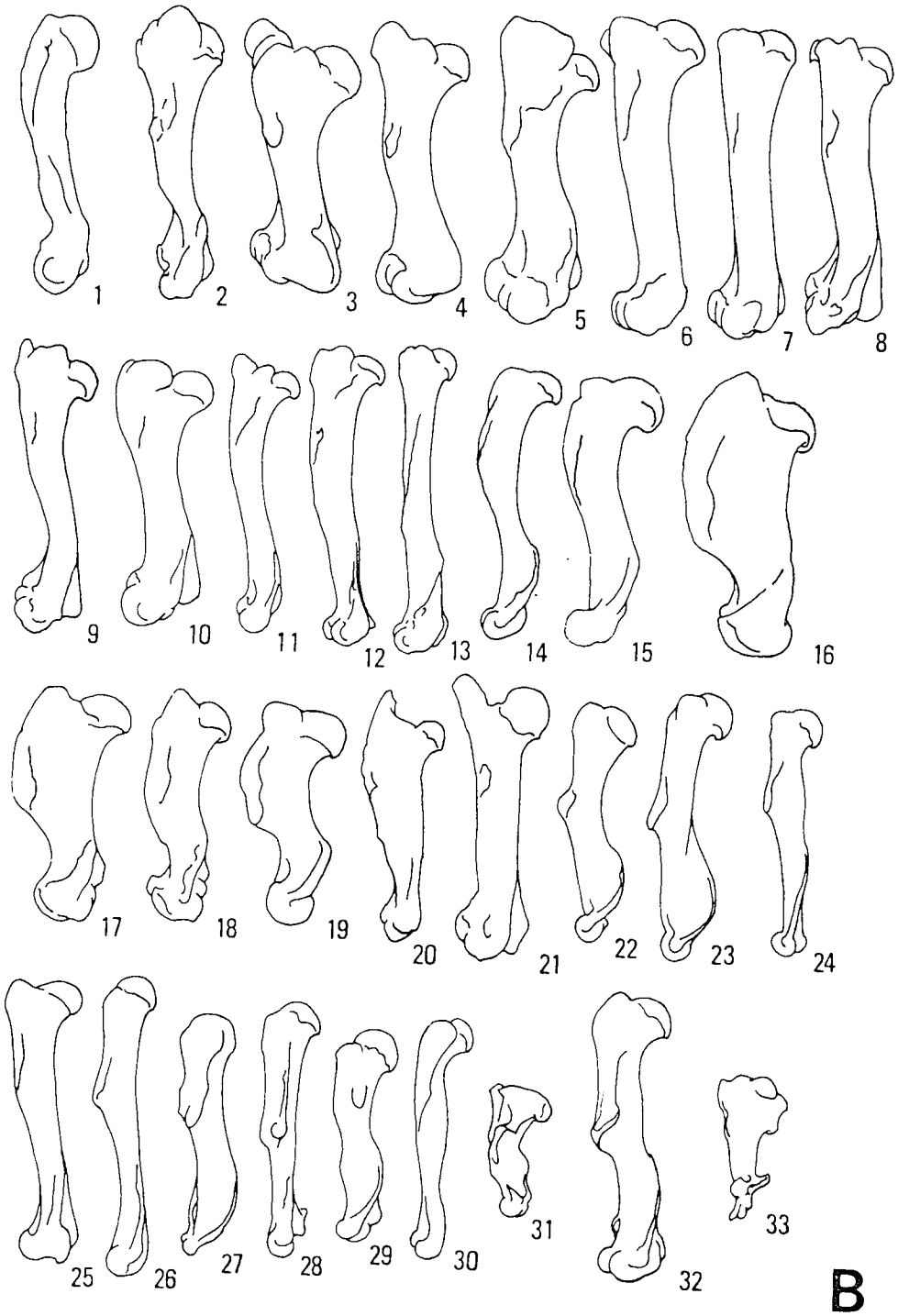



Fig. 12. Left humerus of Desmostylus in comparison with those of living mammals. Head of humerus faces backward and deltoid tuberosity is narrow and not protruded forward.
A: cranial view, B: lateral view
1: Desmostylus, 2: Elephas, 3: Diceros, 4: Hippopotamus, 5: Bubalus, 6: Giraffa, 7: Camelus, 8: Equus, 9: Tapirus, 10: Sus, 11: Tayassu, 12: Panthera, 13: Ursus, 14: Lutra, 15: Enhydra, 16: Eumetopias, 17: Zalophus, 18: Callorhinus, 19: Phoca, 20: Dugong, 21: Trichechus, 22: Castor, 23: Ondatra, 24: Marmota, 25: Hydrochoerus, 26: Erithizon, 27: Dasypus, 28: Myrmecophaga, 29: Manis, 30: Erinaceus, 31: Talpa, 32: Vombatus, 33: Tachyglossus
The regend is also applied in Fig. 14, 16, 18, 20.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middle as same as in sea otters. Major tubercle is in lower level than the head and feebly projects forward as same as in camels and giraffes, but Desmostylus is somewhat similar to manatees on the term that the head faces rather posteriorly than proximally. The small and laterally projecting deltoid tuberosity differs entirely from that of pinnipeds.

The antebrachial skeleton (UHRno.18466-4, 5, Fig.13, Plate VI) has graviportal characters; short and stout in proportion like rhinos or hippos (Fig. 14). It is similar to sirenians, pinnipeds and cetaceans in parallel arrangement of the radius and the ulna. Olecranon is as large as that of pinnipeds, but is peculiar in much bending backward. The ulna is similar to those of elephants, sirenians in thickening even in its distal end. It resembles that of sirenians since that trochlear axis crosses at about right angle with long axis of carpal articular surface. Carpal articular surface of Desmostylus is unique in inclining medially (palmarly in the manus).

The metacarpus (UHRno.18466-106, Fig.13, Plate VIII) of Desmostylus differs from that of cetaceans in having stout epiphyses without depression. In sirenians and pinnipeds metacarpus is proximally thick but distally thin. The metacarpus is the longest along the hand axis (in the third and the fourth) in Desmostylus; but the longest is the first in pinnipeds, and the fourth or the fifth in sirenians. Similar to dugons, elephants and hippos it is as twice as

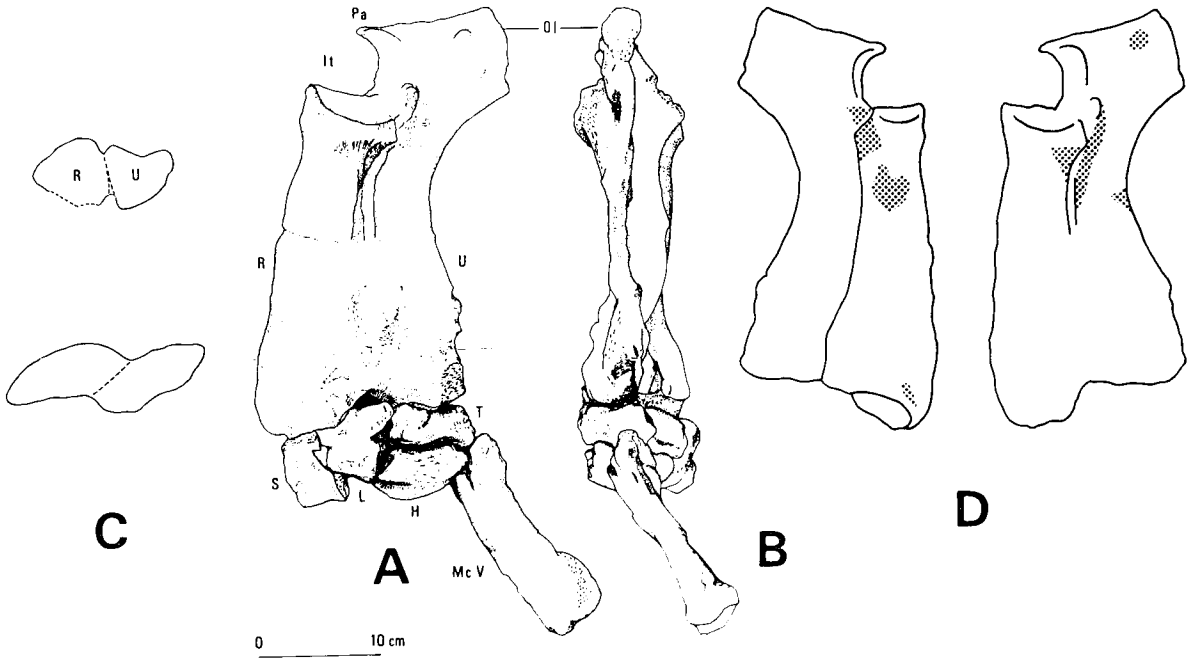



Fig. 13. Left skeleton antebrachii and skeleton manus of Desmostylus mirabilis (UHRno. 18466-4, 5, 6, 7, 8, 13, 106)
A: lateral view (cranial view in manus), B: caudal view (lateral view), C: sections seen from above, D: positions of rugged surface in medial and lateral views
H: Os hamatum, It: Incisura trochlearis, L: Os lunatum, McV: Os metacarpale V, Ol: Olecranon, Pa: Processus anconeus, R: Radius, S: Os scaphoideum, T: Os triquetrum, U: Ulna

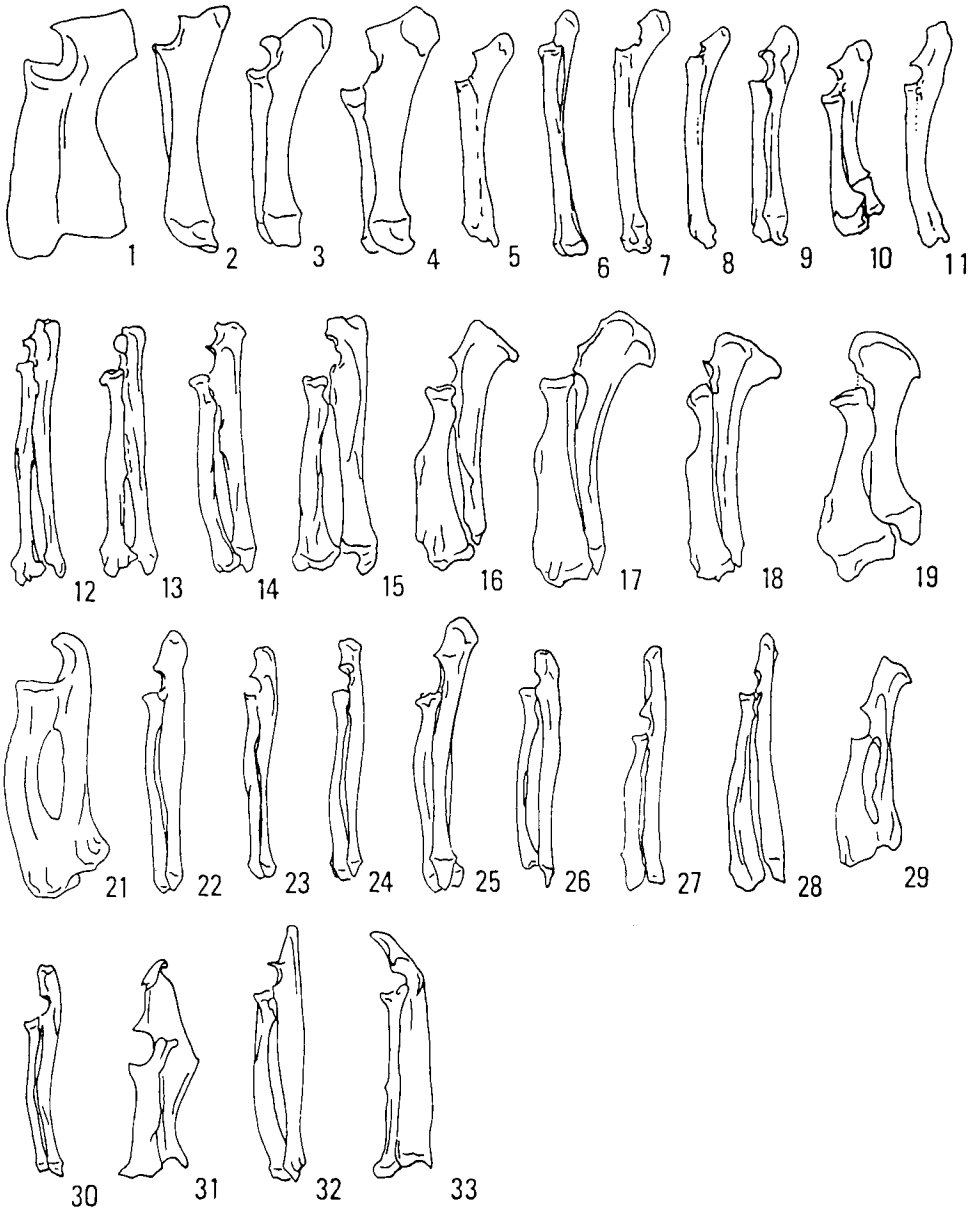



Fig. 14. Lateral view of left antebrachial skeleton of Desmostylus in comparison with those of living mammals. Ulna extends in parallel with radius and does not reduce in the distal part. Olecranon is well-developed.

long to proximal phalanx, but this situation differs from that of dolphins, pinnipeds and perissodactyls.

The phalanx of Desmostylus is similar to that of manatees, elephants, hippos and rhinos in short and wide shape and in having a torsion frequently. It is, however, quite different from that of pinnipeds and cetaceans which is an element of the fin.

Taking into consideration the length ratio of scapula, humerus, antebrachial skeleton and manus, that of Desmostylus is the nearest to that of hippos and otters, but differs from the value of pinnipeds.

The pelvic girdle (UHRno.18466-105, Fig.15, Plate VI) of Desmostylus is large but expansion of the wing of ilium is feeble. In this way, it differs from those of elephants or rhinoceroses (Fig. 16). The position of the acetabulum is more anterior than in proboscideans, artiodactyls, perissodactyls and rodents, and is as high as in pinnipeds and rodents. The acetabulum is directed not so ventrally as in proboscideans and artiodactyls, and is directed more posterolaterally. In contrast to ungulates, the obturator foramen faces laterally as in pinnipeds or rodents. However, Desmostylus differs from them in having broad area along long pelvic symphysis. Forms of the pubis and the ischium in lateral view and the ratio of pubic length differ from those of ungulates and resemble to those of rodents. But in angle of symphysis on the horizontal and frontal plane is nearer to that of ungulates rather than that of

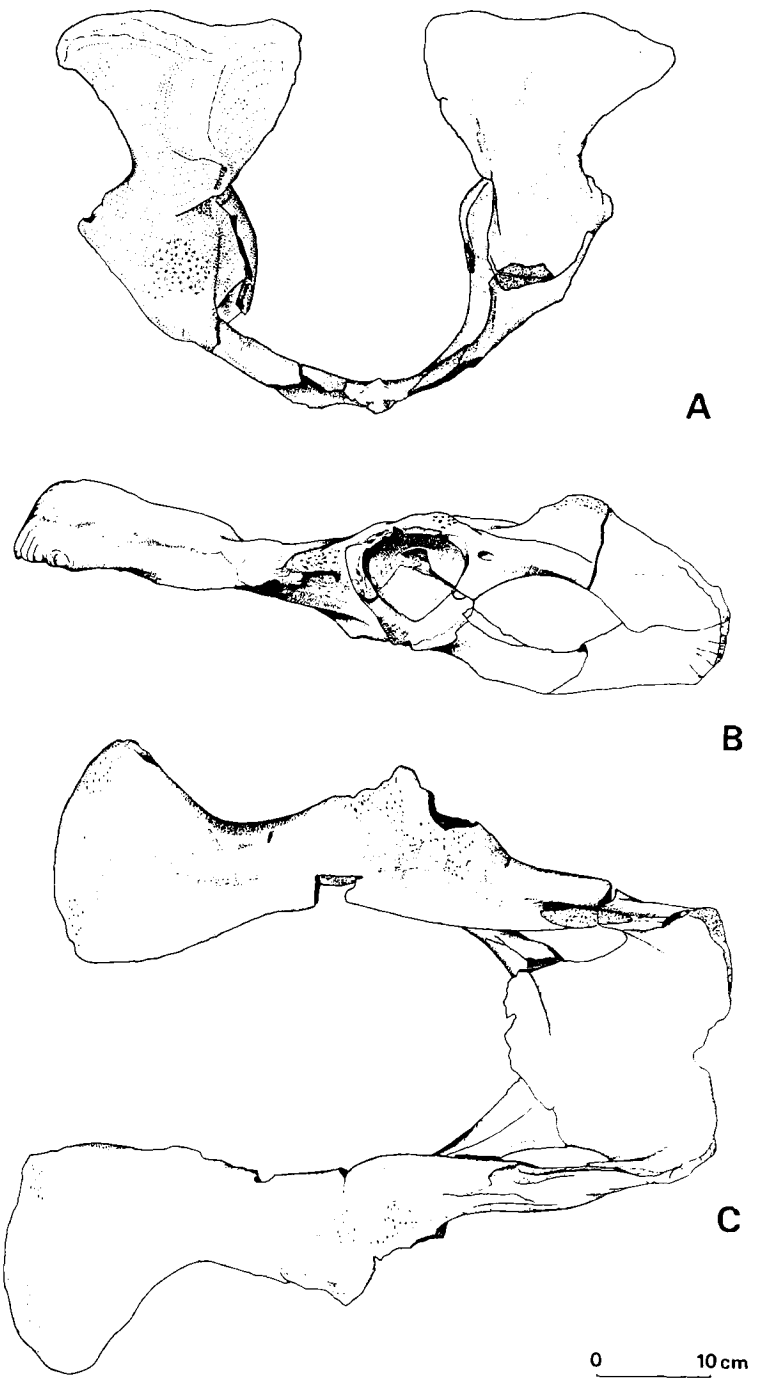



Fig. 15. Coxal bones of Desmostylus mirabilis (UHRno. 18466 -105)
A: cranial view, B: left lateral view, C: dorsal view

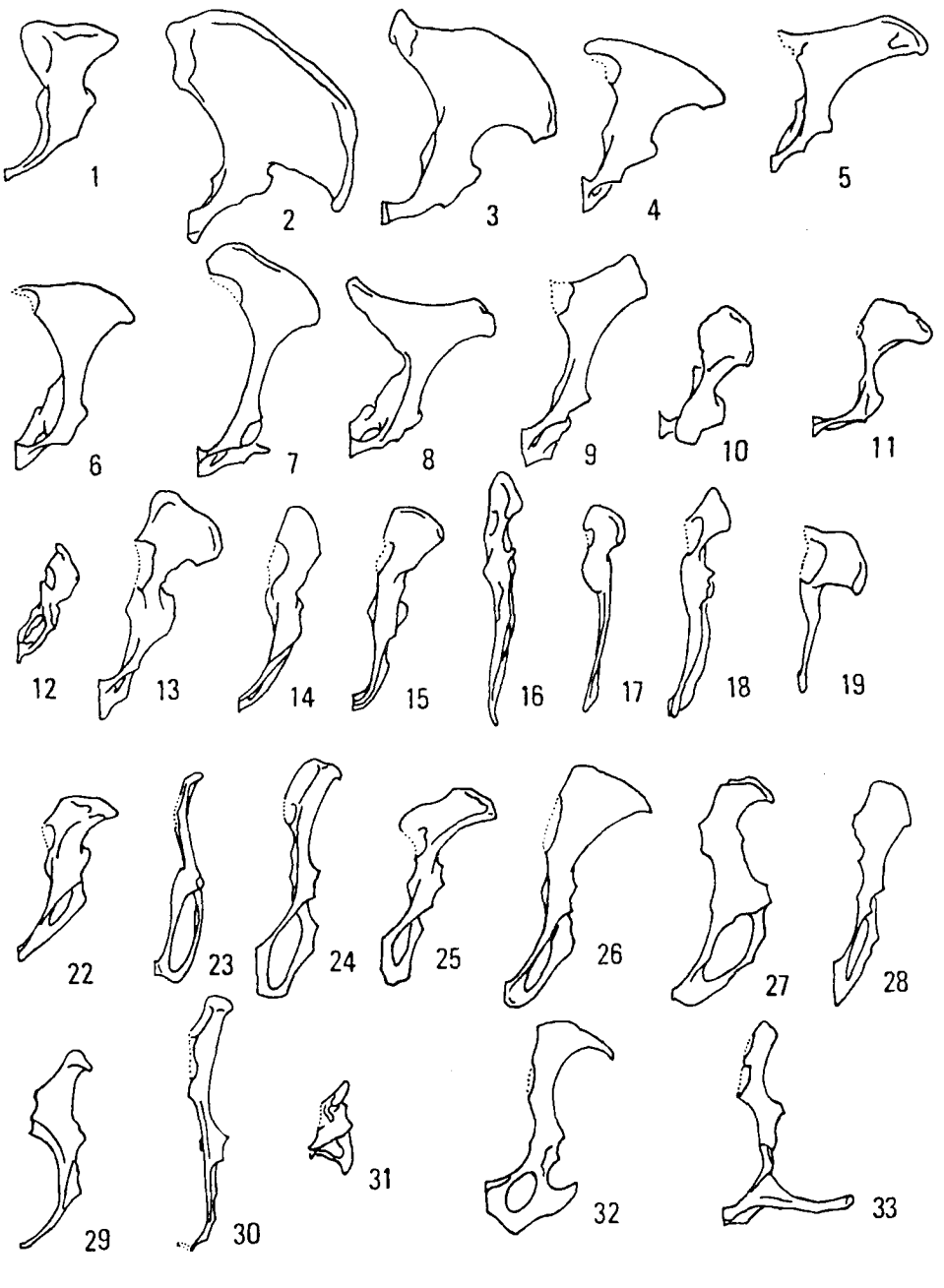
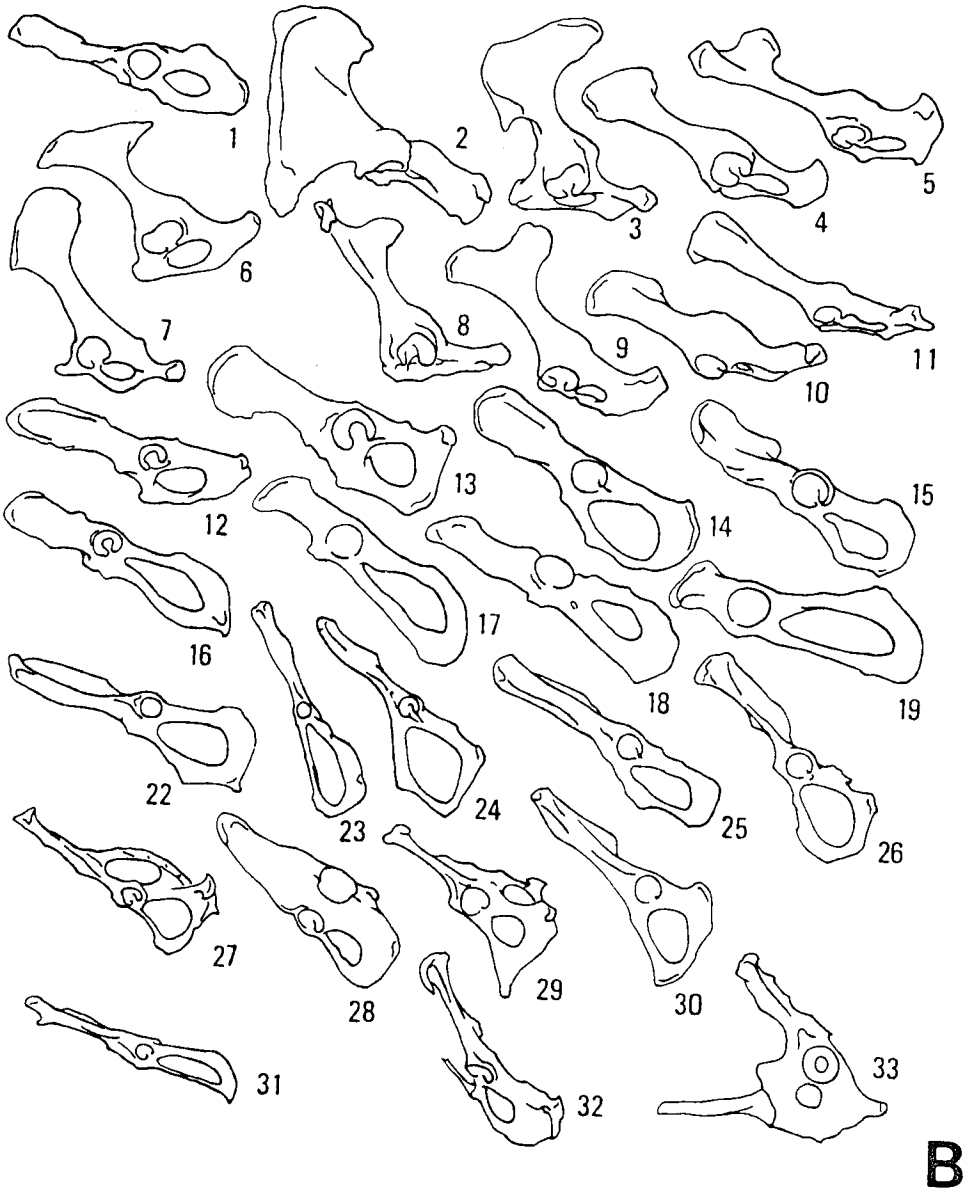



Fig. 16. Left coxal bone of Desmostylus in comparison with those of living mammals. Ilium is not so expanded as a large mammal. Length of ilium is nearly equal with that of ischiopubis. Obturator foramen faces outward. Coxal bone of Desmostylus differs from those of rodents in spite of some resemblances A: cranial view, B: lateral view, C: dorsal view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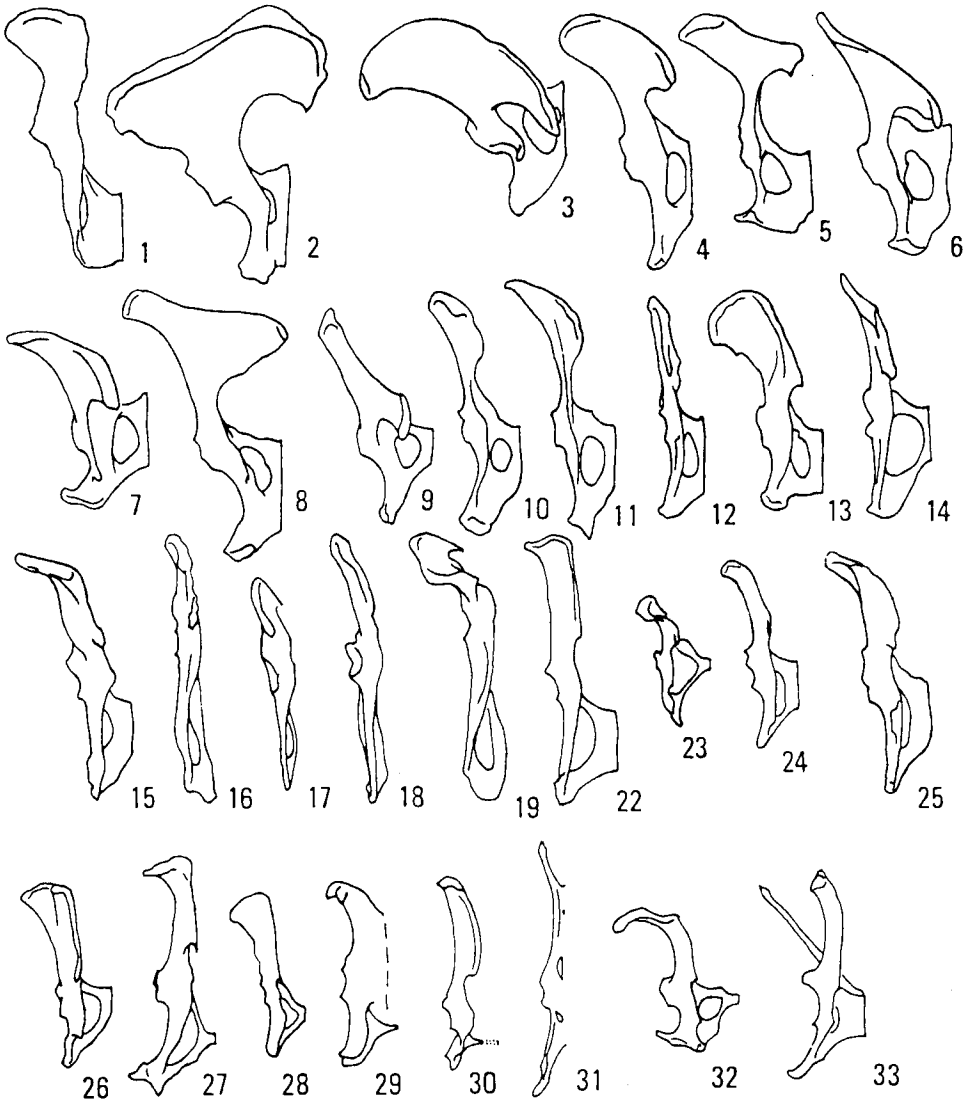
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The proportion of the femur (UHRno.18466-28,29, Fig.17, Plate VII) of Desmostylus resembles those of rhinos, beavers and sea otters (Fig. 18). It is similar to elephants and pinnipeds in the shaft flat antero-posteriorly. Desmostylus is similar to rodents, different from ungulates in having the constricted femoral neck in all directions. It is similar to rhinos in that the major trochanter is in lower level than the head, but this feature is revealed more remarkably in Desmostylus. The mode of distal expansion of rugged surface in the minor trochanter is peculiar to Desmostylus. It is similar to pinnipeds and beavers in that the shaft bends laterally, and is similar to pinnipeds in having shallow trochlear groove.

The proportion of the tibia (UHRno.18466-30, Fig.19, Plate VIII) of Desmostylus has the most close resemblance to that of hippos, but epiphyses of the former are more developed than those of the latter (Fig. 20). The tibia of Desmostylus is quite peculiar in the presence of large and conspicuous, laterally overhanging tibial crest, medially twisted tibial shaft and anterolaterally facing distal articular surface. Desmostylus is similar to pinnipeds in that proximal articular surface is sloping backward.

The greatest peculiarity in the astragalus and the calcaneum (UHRno.18466-31, 32, Fig.21, Plate VIII) is exhibited in that tuber calcis projects medially when both bones are articulated with the tibia. This feature is

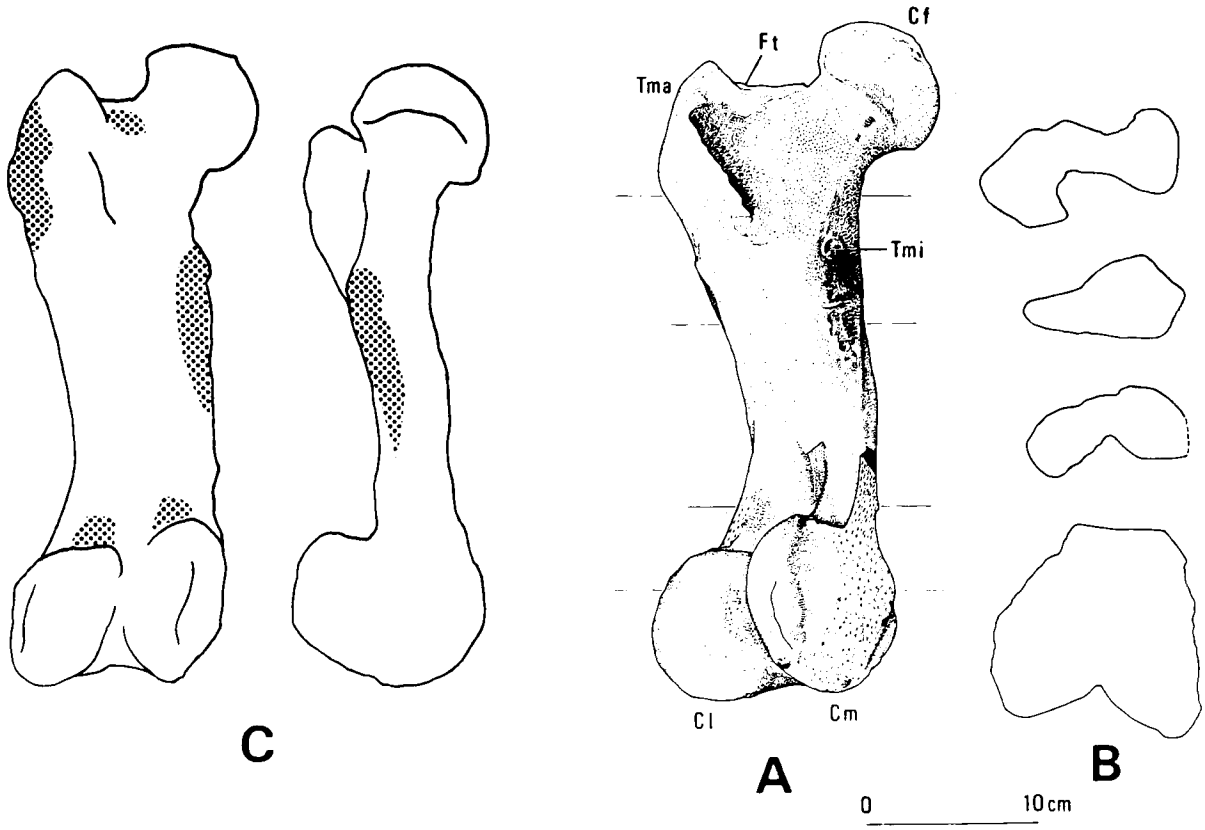


Fig. 17. Left femur of Desmostylus mirabilis (UHRno. 18466-29)
A: posteromedial view, B: sections seen from above, C: positions of rugged surface in caudal and medial views
Cf: Caput ossis femoris, Cl: Condylus lateralis, Cm: Condylus medialis, Ft: Fossa trochanterica, Tma: Trochanter major, Tmi: Trochanter minor

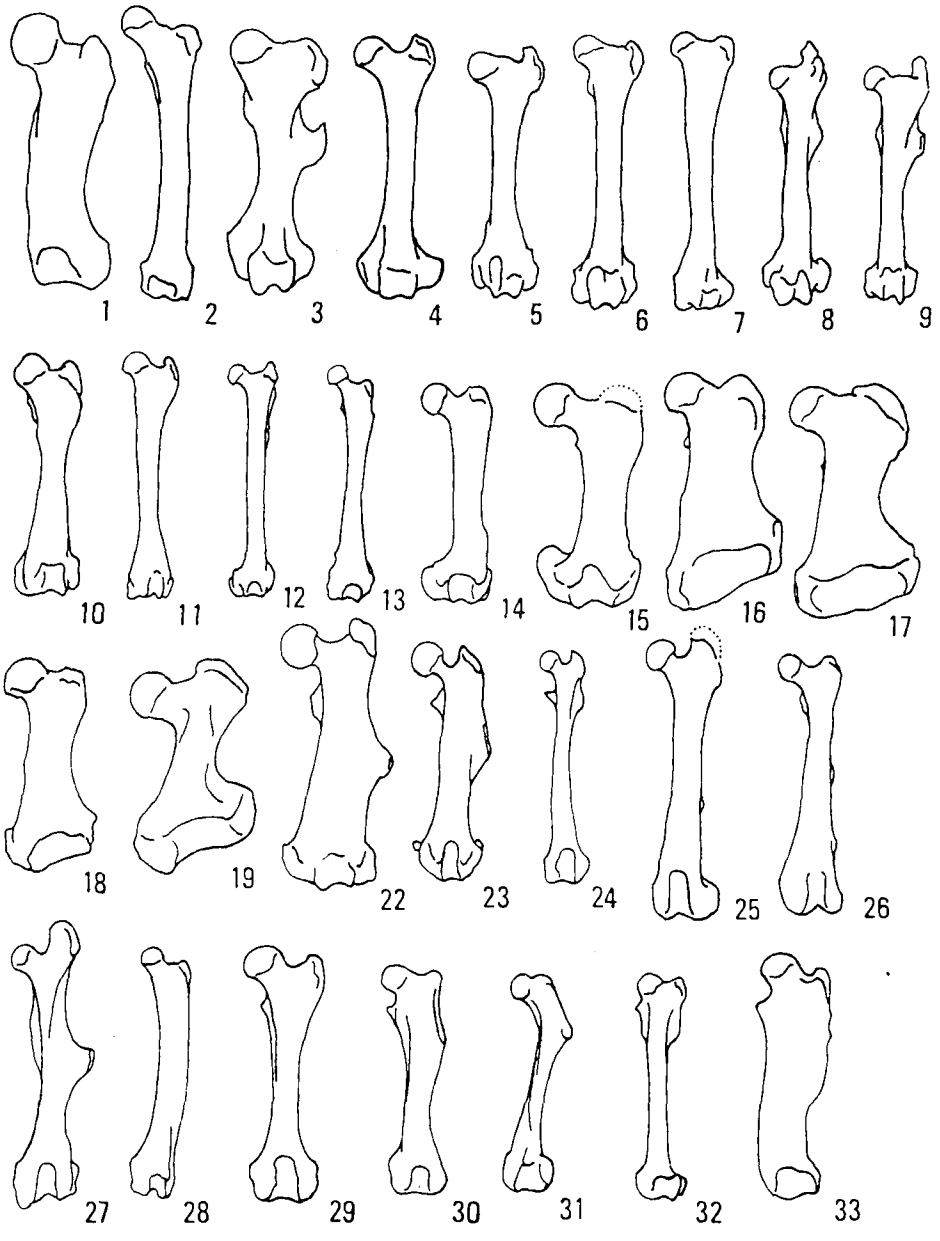


Fig. 18. cranial view of left femur of Desmostylus in comparison with those of living mammals.

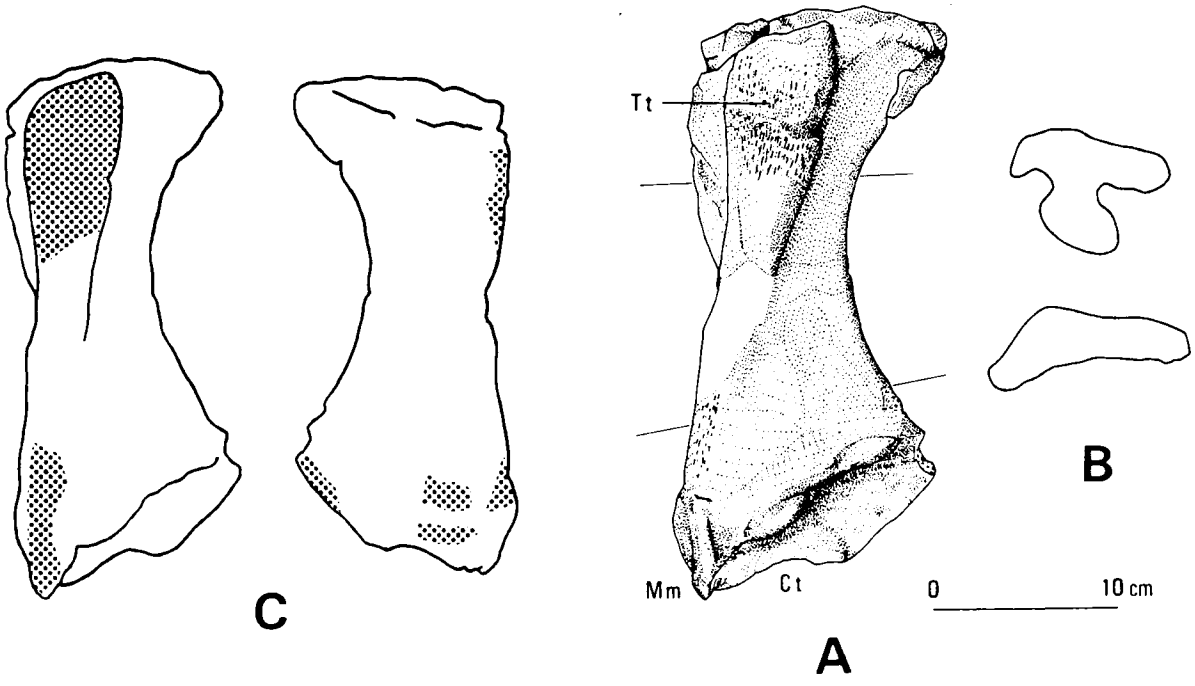


Fig. 19. Left tibia of Desmostylus mirabilis (UHRno. 18466-30)
A: cranial view, B: sections seen from above, C: positions of rugged surface in cranial and caudal views
Ct: Cochlea tibiae, Mm: Malleolus medialis, Tt: Tuberositas tibiae

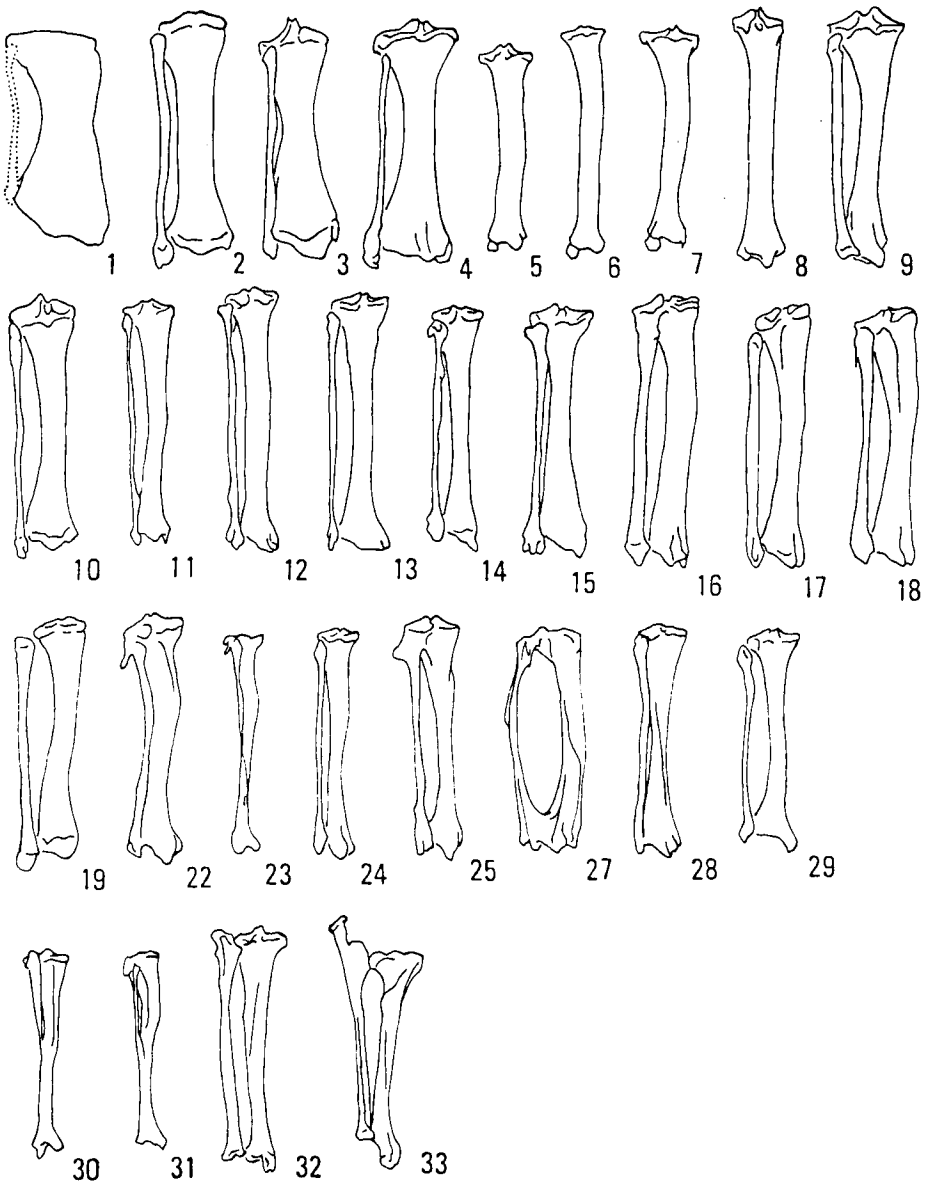


Fig. 20. Caudal view of left crural skeleton of Desmostylus in comparison with those of living mammals. Crural skeleton twists much medially.

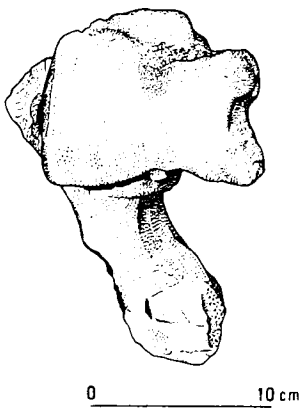


Fig. 21. Dorsal view of left astragalus and calcaneum of Desmostylus mirabilis (UHRno. 18466-31, 32) When calcaneum is articulated with astragalus, tuber calcis declines much medially.

desmostylians. The metatarsi of desmostylid are peculiar in that approximately same length to that of proximal phalanx and in that much shorter than that of the metacarpi. It is probably also peculiar among mammals that the length of the metatarsi increases laterally from the second to the fifth. Characteristics of the phalanges in the pes are the same as those in the manus.

Desmostylus has the closest resemblance to rhinos and hippos in having the same relative length ratio among femur, tibia and pes.

B. Characteristics of the desmostylian skeletal elements

In this section, the author describes morphological charateristics of Desmostylus which are important for the skeletal restoration. But detailed description and remarks are mentioned in the Appendix.

1. Bones of the axial skeleton

The general feature of the desmostylian's vertebral body is characteristic in having antero-posteriorly short, low and wide in form, with short and stout transverse processes and short spinous process. As for the cervical vertebra, it is short, the vertebral body is low, the spine is short, and the ventral tubercle of the transverse process is flat and projecting downward. Costal facet of the transverse process in thoracic vertebrae is facing laterally. The lumbar vertebra is wide and short, the costal processes are short and projecting horizontally and

perpendicular to the body axis, and the accessory processes are absent. The sacrum is triangular in outline, and flat dorso-ventrally, and the sacral crest is low. The caudal vertebra is short and has no neural and hemal arches.

The vertebral formula seems to be 7 · 13 · 4 · 5 · 10+. Cervical, lumbar and caudal portions are short relative to the total length of the body.

Ribs increase steeply in length from the anterior to the middle, and the curvature is strongest in the seventh. The dorsal muscle area is developed on the fifth to the ninth rib, and it inclines more steeply in anterior rib. That is to say, the rib inclines more steeply in more anterior rib within the fifth to the ninth, for every dorsal muscle area faces usually horizontal. Costal shaft is not flat in cross section except anterior ribs.

The sternum is broad in area and flat dorso-ventrally, and consists of nine sternal segments: one rounded presternum in the cranial end and four pairs of mesosternum, quadrilateral or a quarter round in shape. As a whole the sternum widens toward the caudal end. The thorax is nearly circular in frontal section. It is estimated that the backward inclination of sternum is fairly strong, because the sternebrae which ossify in every somite are much longer antero-posteriorly than the distance of the intercostal space.

2. Bones of the appendicular skeleton

The scapula is very long and triangular in outline.

The supraspinous fossa is narrower than the infraspinous fossa. The facies serrata is ill-developed. The spine of scapula is high. The acromion is situated at a higher level than the glenoid cavity.

The head of the humerus faces backward, the major tubercle is ill developed, the deltoid crest is narrow and facing outward, the shaft is flat and wide in epiphyses. The antebrachial skeleton is shorter than the humerus. The radius and the ulna run parallel with each other without torsion. The olecranon is developed remarkably, bending strongly backward. The articular surface for the carpi inclines inward as to the antebrachial skeleton (palmarly as to the manus).

The proximal surface of the carpi has such a composition that does not permit the manus to flex dorsally. The highest of the carpi is smaller in the lateral side than in the medial. The metacarpus is about twice as long as the metatarsus. There is a torsion along the bone axis in the proximal and the middle phalanges. The distal phalanges are flat and have planes in palmar surface.

The pelvis is well developed. The wing of ilium feebly expands laterally. Either side of the pelvic symphysis is wide. The obturator foramen faces rather outward than downward. The acetabulum is situated in the middle and in higher level than usual, facing posterolaterally. The femur is stout, particularly in epiphyses. It is flat cranio-caudally, bending outward. The head is globular and

the neck is clearly constricted in all directions. The major trochanter is present at 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. The patella is prominently developed.

The tibia is shorter than the femur. The proximal surface inclines posteriorly. The shaft twists medially and the anterior margin extends obliquely toward the medial malleolus. The tibial crest is conspicuously developed, the anterior margin leans laterally and its free margin is overhanging the lateral surface in the proximal region. The distal surface is inclined mediocaudally facing craniolaterally. The fibula is much shorter than the tibia and lies obliquely from the posterior side of tibia to the lateral toward the distal end.

When articulating the astragalus with the calcaneus, the author find that tuber calcis inclines more medially in regard to the direction perpendicular to the axis of motion of the tibio-tarsal articulation. Each lateral metatarsus is longer than the medial.

## VI. General rules for the skeletal construction of mammals

The body shape of the mammals is greatly varied from species to species, but it is also true that there are general rules in their skeletal composition. The rules themselves must be useful not only for the check of adequacy of restored skeletons previously made but also for the design of new restorations. But, of course, it is not to say to be impossible only by the rules in restoring the skeleton. Because, as some rules obtained from observations made for many living mammalian skeletons are tentative to a degree, they may be improved step by step by increasing knowledge as the results of further comparison to other specimens. Four kinds of rules are noted here: (1) the rules about common characteristics observable in many mammals, (2) the rules about the correlation between each single bone and the whole skeleton, (3) the rules about the correlation among skeletal elements, and (4) the rules about the correlation between form and function of bones. The author will explain each of those rules and give a comment for their exceptions among mammals, particularly ungulates, and show examples to which they are applicable.

### A. Curvature of vertebral column

The outline of the back in life varies with the length and inclination of spinous processes (GREGORY, 1941), and the contour of connected centra of the presacral vertebrae

is either gently arched dorsally or straight in most mammals. It seems that there is no correlation between curvature of vertebral column and shape of pelvis (Fig. 22).

Exceptions are some mammals including small ones like rats and mice with lesser influence of gravity, saltators like rabits and kangaroos with longer lumbar region, and hyaenids. The curvature itself is gentle in ungulates, though in some cases the anterior thoracic vertebrae lie in lower level than vertebrae posterior to them.

B. Neck length and shoulder height

In terrestrial quadrupedal mammals the total length of head and neck approximates to the shoulder height so that, in a standing position, the rostrum of the animal is able to reach the ground. This can never be applied to aquatic, arboreal, volant animals or the animals with anterior limbs used for various purposes other than supporting the body weight or walking on the land. Thus, the rule may be applied in particular to large ungulates.

C. Form of thorax in cross section

The important function of thorax in mammals is to support the weight of the anterior part of the body as well as to protect thoracic organs and support the diaphragm. Especially in large ungulates having no clavicula, the anterior region of thorax is extremely compressed from side to side to increase efficiency of transmission of power from

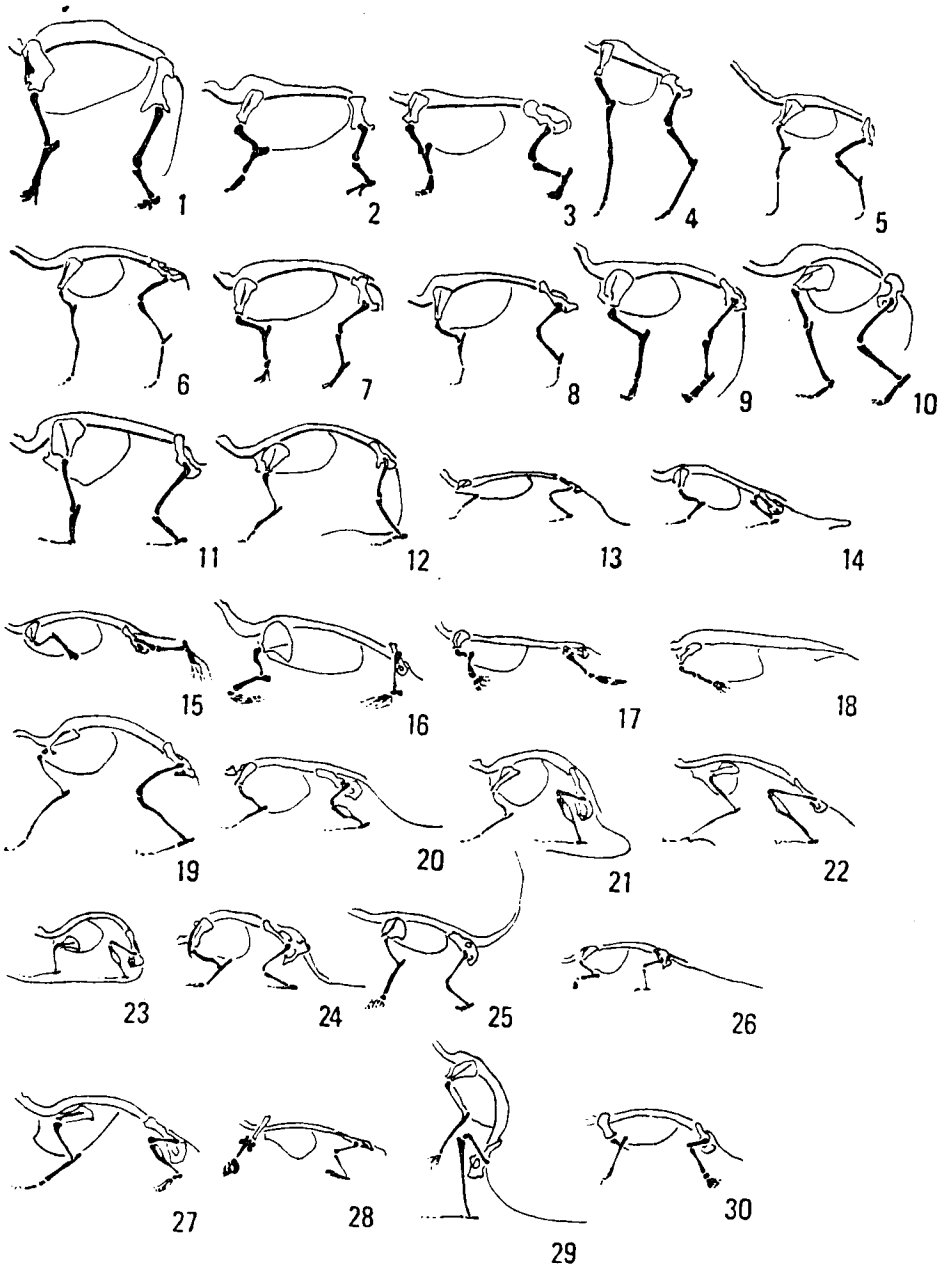


Fig. 22. Postcranial skeletons of living mammals. Curvature of vertebral column does not correlate with form of pelvis. Proximal segments of limbs are longer than other segments in graviportal type and are shorter in pinnipeds.
1: Elephas, 2: Diceros, 3: Hippopotamus, 4: Giraffa
5: Lama, 6: Rangifer, 7: Tapirus, 8: Tayassu,
9: Panthera, 10: ?Crocuta, 11: Nasua, 12: Pagma,
13: Mustela, 14: Lutra, 15: Enhydra, 16: Zalophus,
17: Phoca, 18: Dugong, 19: Lepus, 20: Castor,
21: Ondatra, 22: Pteromys, 23: Rattus, 24: Dasypus
25: Myrmecophaga, 26: Manis, 27: Erinaceus,
28: Talpa, 29: Macropus, 30: Tachyglossus

anterior ribs via serratus ventralis muscle to the scapula. Exceptions are aquatic mammals such as cetaceans, sirenians and pinnipeds, which are freed from supporting body weight and whose thorax is circular in frontal sections.

D. Directions of limbs

In quadrupedal mammals, the proximal segments of limbs extend under the trunk (parasagittal position; under position), which differs from amphibians or living reptiles (transversal position; lateral position)(LESSERTISSEUR and SABAN, 1967; VAUGHAN, 1972; YOUNG, 1975; KENT, 1978; WAKE, 1979; TORREY and FEDUCCIA, 1979). The former state is more effective in supporting weight or in terrestrial locomotion than the latter, and every case of large terrestrial mammal adjust themselve to the former state. Among mammals exceptions are monotremes, small insectivores, cetaceans, sirenians and bats.

E. Length of limb segments and locomotive function

The free limb bone is devided into proximal (stylopodium), middle (zygapodium) and distal segment (autopodium), and the ratio between lengths of these segments has a correlation with locomotive function (YAPP, 1965; LESSERTISSEUR and SABAN, 1967; WAKE, 1979). Terrestrial quadrupedal mammals include cursorial and graviportal types (YOUNG, 1975), and there is a tendency

that proximal segment is shorter than middle segment in cursorial type but longer in graviportal type (GREGORY, 1912, 1941; HILDEBRAND, 1974). Aquatic mammals are apt to have very short proximal segment and long distal one (ROMER and PARSONS, 1977).

F. Limb joints

The shoulder joint is a type of globular joint, and the humerus usually lies on the same plane as the costal surface of scapula (VAUGHAN, 1972) in normal position.

Directions of the head of humerus to its longitudinal axis varies with species, but that of the humeral shaft usually becomes nearly perpendicular in mammals with large body weight, and the head faces result upward. Thus in elephants, the head is on the direction of the bone axis.

The knee joint is regarded as a hinge joint. Restriction of movement is usually due to the function of ligaments around the joint, though it is not shown in the bone shape.

G. Foot posture and metapodials

The fundamental foot posture is plantigrade in terrestrial tetrapods, but it changes into digitigrade, unguligrade, and metapodials become long, as the running speed increases. In general, metapodials are as long as proximal phalanges in the plantigrade, much longer in the unguligrade (LESSERTISSEUR and SABAN, 1967). The foot

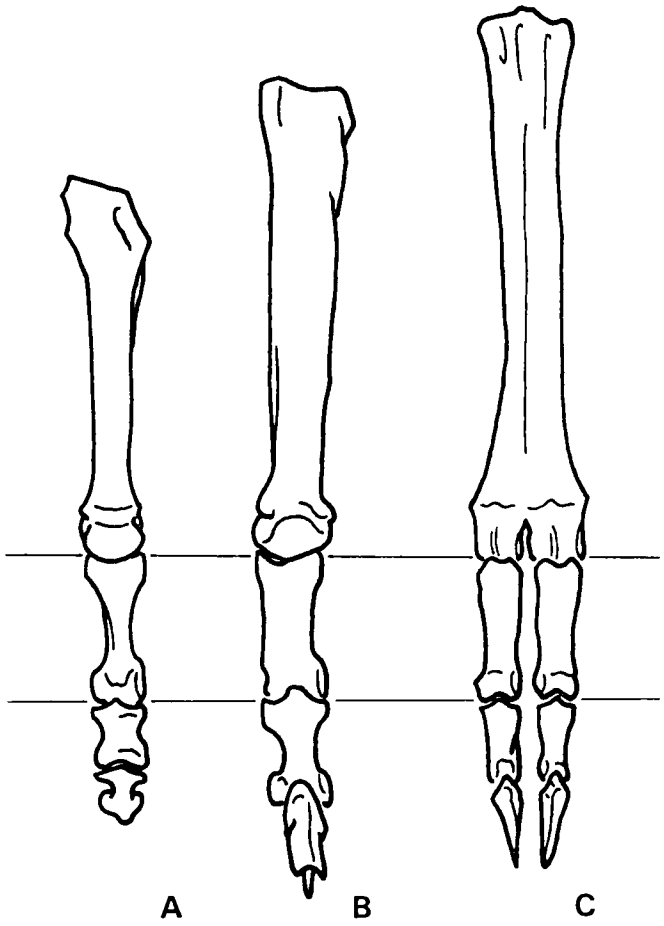


Fig. 23. Cranial view of the third left metatarsus and digit showing relationships between metapodials and foot postures.
A: Homo (plantigrade), B: Panthera (digitigrade), C: Cervus (unguligrade)

posture of artiodactyls or perissodactyls is exclusively unguligrade, and some of them have metapodials many times as long as proximal phalanges (Fig. 23). This feature is especially conspicuous in the progressive types in which digits are decreasing in number. Exceptions are elephants that become seeming plantigrade secondarily by the presence of flesh pad and bipedal saltators such as kangaroos.

H. Direction of tips of digits

Since mammals usually walk craniad, it is convenient that the tips of digits point forward in locomotion in terrestrial animals (VAUGHAN, 1972; YOUNG, 1975; ROMER and PARSONS, 1977). Even in some amphibians or reptiles with laterally positioned limbs, the line connecting tips of digits in the pes tends to be perpendicular to the body axis. Exceptions are known from the animals like anteaters with huge claws and great apes with knucle-walking as well as aquatic and volant animals.

I. Similarity of both limbs

Anterior and posterior limbs tend to take similar shape in quadrupeds. This tendency is expressed especially remarkably in large ungulates which cannot utilize fore limbs for functions other than support or locomotion. This rule applies mainly to ungulates, and not to aquatic, volant, arboreal and saltatorial mammals.

## VII. Bases for skeletal restoration of Desmostylus

When we attempt to articulate the bones faithfully to their shape, we can realize that the restored skeleton cannot follow some of the rules in foregoing section because of bone characteristics of Desmostylus as mentioned above. Supposed the limbs are stretching under the trunk, the tips of digits in the manus should be either directed laterally, or directed medially lying on the back of the manus on the ground. In case the limbs extend outward, to the contrary, both the manus and the pes should be directed cranially. The author would like to try to adopt the latter mode for the desmostylian restoration on the basis of the following considerations.

### A. Myology and osteology of Desmostylus

In the desmostylians the limb bones are usually thick and stout. The humerus and the femur are longer than the antebrachial and the crural skeletons respectively. The groove on the proximal articular surfaces of astragalus are shallow, and the phalanges are short and stout. Therefore, the desmostylians must have been a quadrupedal terrestrial mammal having fundamentally graviportal type of body construction.

#### 1. Fore limbs (Fig. 24)

In the desmostylians the facies serrata of the scapula is less developed in comparison with ungulates in general,

but the presence of flat and paired sternum is quite unique among mammals. Assuming that the muscle attachments are the same as in other mammals, the serratus ventralis muscles (the serratus anterior muscle in man) originating from the ribs attach to the facies serrata, and the superficial and the deep pectoral muscles (the pectoralis major and minor muscles in man) originate from the sternum. These muscles play an important role in supporting the body weight as they originate from the thorax and insert in the fore limbs. In large ungulates these muscles differ in their direction, and the serratus ventralis runs vertically while the pectoral muscles horizontally. For this reason the serratus ventralis which runs in the direction of gravitational force mainly works for supporting function (YOUNG, 1975).

To explain the rough nature of the facies serrata and the large surface area of the sternum in Desmostylus, however, it is more reasonable to assume that the major role of supporting function is held by the pectoral muscles rather than the serratus ventralis. The arrangement of the limb bones that satisfies such a condition can be deduced from a position in which the humerus extends outward from the trunk. In this posture, the direction of fascicle of the pectoral muscles is rather perpendicular; the relative position of the muscle insertion on the humerus to the sternum is higher in level than in other mammals. On the other hand, the direction of the serratus ventralis becomes fairly horizontal near the insertion, for the scapula is not

sagittal but almost horizontal in position and its glenoid cavity is directed cranially, the spine is directed dorsally and the dorsal margin is faced caudally.

Thus, the main muscles supporting the anterior body weight can be shifted from the serratus ventralis to the pectoral muscles simply with a flexion of the shoulder joint at a right angle to the place where the scapula and the humerus make nearly horizontal plane. Furthermore, this arrangement is clearly conformable to the rules in regard to the shoulder joint and the direction of the head of the humerus. Thus, the peculiar form of the sternum can be understood as an attachment surface essential for the muscles. This circumstance also agrees with the facts that the major tubercle is lower in the level and the deltoid crest is narrower than in other mammals. Because the muscles that extend the shoulder joint attach to these areas, and those play less important role in transversal position than in parasagittal position.

In case of Desmostylus the pronation of antebrachial skeleton seems to be impossible, for the radius and the ulna are parallel being fixed to each other. As the humerus is projected laterally and the elbow joint is flexed at a right angle, as a result, the distal portion of the forearm looks forward, since the skeleton of the forearm is situated on the same plane which the scapula and the humerus make. When the fore limbs stretch downward, the tips of digits do not look forward without the pronation of the forearm. But in

the transversal position the tips of digits look cranially without crossing the radius and the ulna, because flexing of the elbow and outward stretching of the humerus have an effect of the spination of the forearm. The dorsal surface of the anterior thorax on which the scapula is present forms somewhat cranial dip, and both the humerus and the antebrachial skeleton on the same plane also inclines caudally. Therefore, the manus approaches nearer to the ground. The distal, medially (palmarly in the manus) inclining articular surface of the radio-ulna becomes more horizontal due to the deepening of caudal inclination of the radio-ulna.

The dorsal flexion of the manus seems to be impossible, since the anterodorsal process of the lunar prevents the antebrachio-carpal joint from flexing, colliding with the anterior margin of the distal articular surface of the antebrachial skeleton. At the same time this cooperative process together with carpal ligaments and antebrachial muscles provide the function to support the weight by the antebrachial skeleton which inclines backward and the manus. As dorsal flexion of the wrist is impossible in this condition, there cannot be plantigrade position.

The articulated carpi as a whole lowers in proximo-distal height laterally, and the radius is longer than the ulna in the distal part of antebrachial skeleton. This relation is in connection to the fact that the skeletal system from the shoulder to the manus inclines inward, not

horizontal, owing to the lateral dip of the dorsal part of the thorax. As the distal articular surface of the antebrachial skeleton is higher more medially than laterally as a result of medial inclination of the fore limbs, those bones of carpi hold more horizontal position at the proximal part of the metacarpi.

It is also an inevitable effect of stretching the limbs laterally that the metacarpus is rather longer than the metatarsus. As it was necessary for Desmostylus to raise the belly from the ground in walking, the hind limbs might hold the necessary height. The tibia should stand almost vertically, even if the femur is situated almost horizontally. On the contrary, the antebrachial skeleton must be inclined considerably in the case of lateral projection of the humerus. For this reason, the fore limbs cannot help elongating anywhere in more distal portion for retaining height to be corresponded to the hind limbs.

It is presumed that the foot posture is unguligrade, for some of middle phalanges are twisted along its longitudinal axis. The twisting may result from that the digits along the radiated metacarpi are apt to twist inward and outward respectively in lateral and medial part of the manus. It increases the efficiency of stepping at the tips of the distal phalanges facing forward. If the foot posture is plantigrade or digitigrade, such twist would not be produced because there is no relation with the efficiency of the distal phalanges, even though the matacarpi are

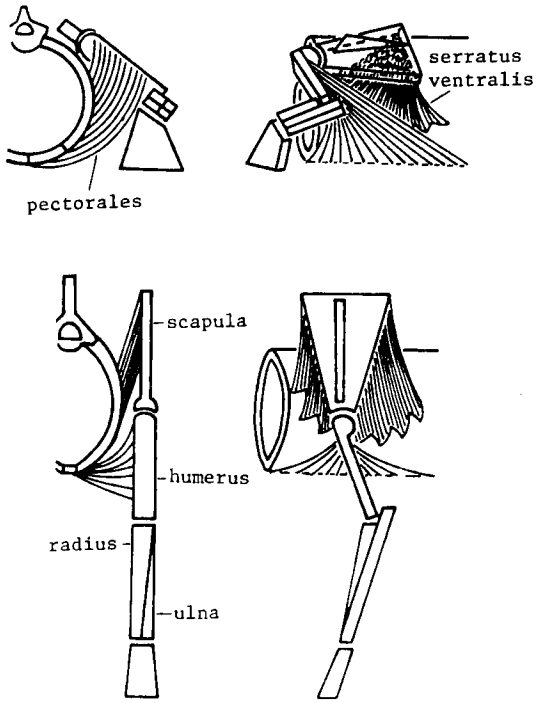


Fig. 24. Estimated mode of muscle attachment in fore limb of desmostylians in comparison with those of general mammals.
above: desmostylians, below: general mammals
left: cranial view, right: left lateral view

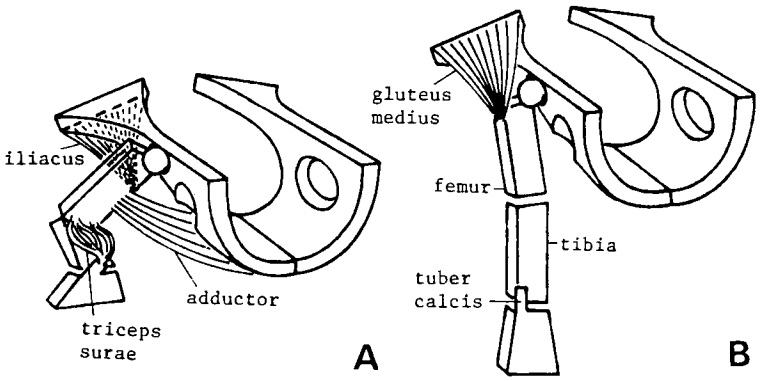


Fig. 25. Posterolateral view of estimated mode of muscle attachment in hind limb of desmostylians in comparison with those of general mammals.
A: desmostylians, B: general mammals

radiately arranged.

Thus, the arrangement of bones in the skeleton of the anterior limbs in Desmostylus is different from that in other mammals: the cranial margin of the scapula faces medially; the glenoid cavity turns cranially; the spine of scapula stands dorsolaterally; the medial margin of the humerus faces ventrally; the longitudinal axis of the humerus is directed medio-laterally; the head of humerus looks caudally; the radius runs through medial to the ulna; the lateral surface faces dorsocranially in the antebrachial skeleton.

2. Hind limbs (Fig. 25)

Generally in mammals the posterior body weight is supported mainly by the femur in adducted position with the pull by the gluteus medius muscle inserted in the trochanter major. It is accepted that fan-like expanded wing of the ilium in graviportal ungulates is caused by attachment area increasing of the gluteus medius muscle. On the other hand, the wing of ilium is not developed and the level of the trochanter major is lower in Desmostylus, despite of its larger body size like hippopotami. However, the regions, lateral to the pelvic symphysis and between obturator foramina, are exceptionally and disproportionately wide. Besides them a rugged surface of the trochanter minor is well-developed and unusually expanded distally. Judging from these facts, it is estimated in Desmostylus that both iliacus and adductor muscles that adduct the femur are

developed rather better than the gluteus medius, and probably mainly the former support the body weight.

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 the followings: 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.

When the femur extends horizontally, the knee joint must be always flexed at about a right angle, but it must be very useful for retaining this posture if the quadriceps femoris muscle is well-developed. Actually this is suggested by the wide tibial crest and the large patella.

It is assumed that both knee joint and tibio-tarsal joint are fundamentally hinge joints in Desmostylus too, but because of medial twist of the tibia itself, the tips of digits look forward in this posture. And yet it can be presumed that the rotation of the shank skeleton is possible to a certain extent, for the monaxonic nature in the knee joint is not so severe; the proximal articular surface of the tibia and the trochlear groove of the femur are flatter than in artiodactyls or perissodactyls.

Since both proximal and distal articular surfaces of

the tibia incline posteriorly, the longitudinal axis of the tibia should have inclined a little anteriorly. The balance of the hind limbs is probably retained in this way.

When tibia, astragalus and calcaneus are articulated together, the tuber calcis is used to protrude caudally. But it inclines so medially in Desmostylus. The reason is understandable that the gastrocnemius muscle, originated from the posterior distal part of the femur and inserted in the tuber calcis, is pulled toward its origin by both abduction of the femur and internal rotation of the shank skeleton itself.

Thus, the directions of bones in the hind limbs 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.

3. Trunk

Because of the short vertebral bodies and the presence of only four lumbar vertebrae, the length of the vertebral column from the thorax to the pelvis is estimated to be too short for strong bending of the back. The frontal section of the anterior thorax is nearly circular due to the effect of the short transverse process and its outward facing facet for the tubercle. The sternum should have been fairly lowered caudally, because cranio-caudal diameter of each sternal segment is considerably longer than the intercostal spaces between the anterior ribs.

It should be noted that the actual arrangement of the

sternal segments is different from that described by SHIKAMA (1966). The name of each segment and its orientation is emended here (Table 7). As the anterior ribs decreases in length cranially, it is natural that the thorax becomes narrower cranially and the sternum as well. Consequently, it will be define that SHIKAMA's arrangement is reversal in regard to the body axis. The lateral margin tends to be thinner in the anterior part in the first, second and third mesosterna. The orientation of the fourth mesosternum in SHIKAMA's arrangement is discordant with this tendency, so it is necessary to rotate the fourth mesosternum at a right angle in order to make its anterior part of the lateral margin to be thinnest. In the author's arrangement, the caudal margins of the fourth mesosternum on both sides are divergent backward. Because embryologically the cartilage of each sternal segment usually fuses with the fellow on the other side in the mid-line, and this process proceeds antero-posteriorly, the author's arrangement is rather natural for Desmostylus in which each segment of the sternum ossifies independently and is not adherent in the mid-line.

B. Conformity to the general rules

It is examined here how the restored skeleton conforms to the rules described in the preceding section.

The whole body is low owing to the lateral extension of both fore and hind limbs and to the flexion in their joints. In this case, the curvature of the vertebral column

is gentle and it is not at all necessary to bend it strongly or to set up the pelvis nearly vertically, so it conforms to the rule (A). The shoulder height is low owing to the lateral position of the anterior limbs, this skeleton conforms well to the rule (B) as in usual ungulates in spite of shortness of the neck. The cross section of the thorax is circular as same as in aquatic mammals, though it is generally compressed in large ungulates with the anterior limbs of the parasagittal position. This may probably reflect the transversal position of the anterior limbs in Desmostylus, and may be seemingly same as those of aquatic mammals (C).

Desmostylus with the transversely positioned limbs is the only exception among large ungulates with the parasagittal positioned limbs (D). The author's skeletal restoration is done as Desmostylus was a quadrupedal graviportal mammal in which the proximal segments of limbs are longer than the middle ones (E). That is to say, it is estimated that the animal could walk without dragging belly, and this is used as a presupposition of the restoration. Since both shoulder and knee joints were mounted faithfully to the direction of the articular surface of the limbs, the limb position agrees with the rule (F). It is presumed on the basis of forms of the metapodials and the phalanges that the foot posture is pseudounguligrade with the flesh pad in both fore and hind limbs, and the pes with the short metatarsi do not conform to the rule (G) about the length of

the metatarsi and the phalanges. The direction of the tips of digits is cranial in both manus and pes, and is consistent with the rule (H).

Similarity between anterior and posterior limbs exactly conforms to the rule (I). The proximal segments are longer than the middle ones in both limbs. They extend laterally from the body. Both the major tubercle of the humerus and the trochanter major of the femur are low in position. Both elbow and knee joints are flexed in a usual way. The olecranon of the ulna and the patella are well-developed. Both the carpal and the tarsal bones are low in their lateral portions. Both the manus and the pes are pseudounguligrade and the tips of digits look forward.

The relationships between the general rules and each restored skeleton are shown in Table 6.

C. Mode of fossil occurrences

The Utanobori specimen, the second specimen of whole skeleton of Desmostylus, was discovered with most of the bones articulated in situ. It seems that the arrangement of these bones is not the result of the dislocation due to putrefaction but the true posture in life itself. The scapula which does not have direct connection with the thorax was remained nearly to the original position (Fig. 26).

Each scapula was situated with its longitudinal axis parallel to the body axis, and the glenoid cavity facing

Table 6. Conformability with general rules of mammalian skeletal construction in restored skeletons.
○: comformable, △: partly conformable,
×: incompatible

| | NAGAO (1938) | REPENNING (1965) | SHIKAMA (1966) | British Museum (1975?) | KAMEI (1975) | HASEGAWA (1977) | INUZUKA (1984) |
|---|---|---|---|---|---|---|---|
| Gentle curvature of vertebral column | ○ | × | × | × | ○ | × | ○ |
| Neck length and shoulder height | ○ | × | ○ | × | × | ○ | ○ |
| Analogy of fore and hind limbs | ○ | × | × | × | △ | × | ○ |
| Under position of limbs | ○ | ○ | ○ | △ | ○ | ○ | × |
| Toe pointed cranially | ○ | △ | × | △ | × | × | ○ |
| Interpretation of sternum | × | × | ○ | × | × | × | ○ |

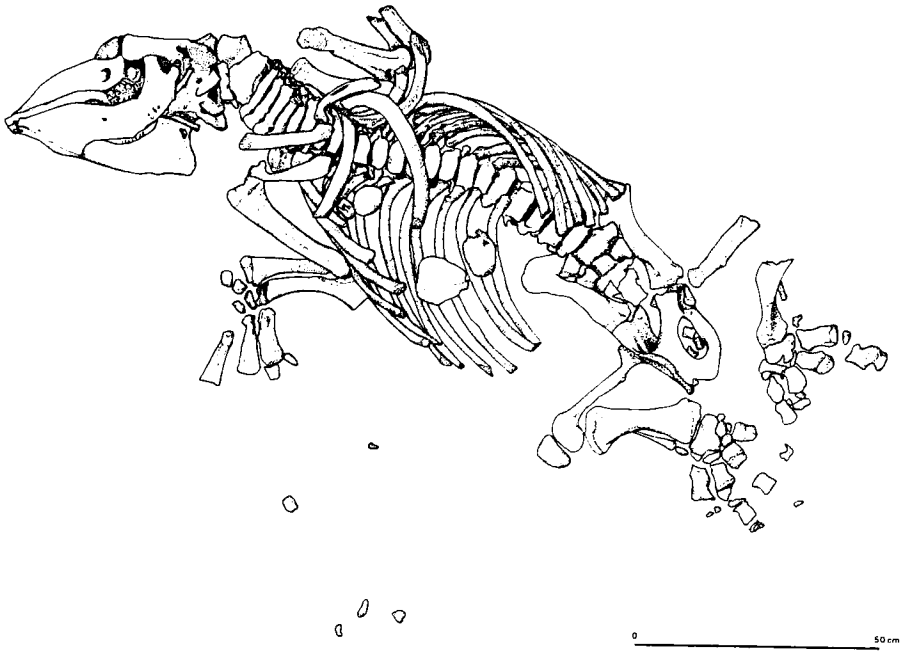


Fig. 26. Mode of fossil occurrence in the Utanobori specimen The neck is short, longitudinal axis of scapula is parallel to the vertebral axis, and each femur lies on the opposite side.

cranially. These facts indicate the lateral extension of the humerus on condition that desmostylian skeleton follows the rule found in the shoulder joint. The posture in the buried state is extremely peculiar as an ungulate, the body lied on the back except that the skull fell down sideways, and both fore and hind limbs were extended laterally on each side. If Desmostylus is an animal in which the limbs are situated under the trunk, all limbs would fall on the same side when the body sank and lay on the sea bottom. Therefore, it is possible to infer that both elbow and knee protruded outward.

The Utanobori specimen retains all the cervical vertbrae which are lacking in the Keton specimen. Then, it became clear that the neck region is short in proportion to the body length, as the body of the cervical vertebrae is shorter cranio-caudally than that of other vetebrae. A longer neck is supposed in NAGAO's restoration, but by this discovery the shoulder height must be changed to be still lower. The rostrum of this animal cannot reach the ground without flexing limbs in such a style as supposed anterior limbs lie under the trunk. When we suppose that limbs are under the trunk, the following facts are difficult to be explained: (1) the neck is short, (2) each limb bone lay laterally, and (3) the longitudinal axis of the scapula was parallel to the vertebral axis.

The primary buried posture of the Keton specimen is unknown; it was contained in nodules. But according to

photos before preparation, the region from the thorax to the pelvis had been remained articulated and the bone arrangement is the same as the Utanobori specimen lying on its back.

SHIKAMA (1966) showed a figure of the Izumi skeleton in buried state which is the first whole skeleton of Paleoparadoxia. According to the figure, only the region from the posterior thoracic vertebrae to pelvis had remained in original state, and the posture lying on the back was as same as that of the Utanobori and the Keton specimens. Also in the Chichibu-tsuyagi specimen of Paleoparadoxia, it is proved that the cadaver was deposited lying on the back, judging from that the ribs of each side are situated on the right and left sides of the vertebral column respectively.

Throughout the Keton, Izumi and Chichibu-tsuyagi specimens the mode of occurrences are common with the Utanobori specimen. Thus, nothing contradictory to the author's restoration has been found in those data.

Conclusively, it is definite that the desmostylians were unique mammals in having the limbs in the lateral position like amphibians or reptiles (Fig. 27, Plate XI).

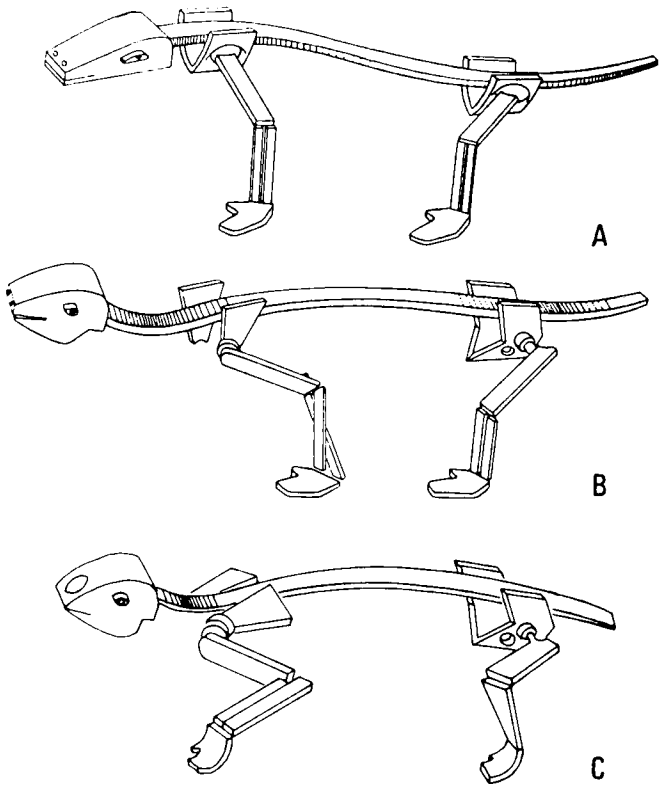


Fig. 27. Comparison of limb postures.
A: reptilians, B: mammals, C: desmostylians
A and B after LESSERTISSEUR and SABAN (1967)

# VIII. Conclusion

From comparative osteological and functional morphological studies, it has become clear that the desmostylians had a basic figure in which limbs stretch laterally like amphibians or reptiles, quite exceptionally among large terrestrial ungulates. This conclusion is mainly based on the examination of the Keton specimen, holotype of Desmostylus mirabilis NAGAO. The restored figure is supported by the mode of fossil occurrence. The essential points of the study can be enumerated as follows.

(1) Each skeletal element of D. mirabilis was described and reviewed osteologically in order to find out important characteristics for the restoration. The materials treated in the present paper are mainly the Keton specimen of the so-called "D. mirabilis", but the Utanobori specimen of D. japonicus supplements the restoration as to important portions which lack in the Keton. Forty-five species of living mamalian skeletons were compared with bones of Desmostylus.

(2) The significance of this study is in positive introduction of the method of functional and comparative anatomy to the skeletal restoration. Functional anatomical method is, in view of the function of support by bone-muscle association, applied to determine the "basic figure". The importance of distinction between the "basic figure" and the "pose for display" should be also stressed. The author

tries to find out general rules of skeletal construction in mammals, especially ungulates, based on comparison among their skeletons.

(3) In the author's restoration, the most different point from the previous restorations is in its transversal position of limbs: both the humerus and the femur extend laterally. The previous restorations have shown more or less their parasagittal position: the limbs extend under the trunk. In case of them, owing to the peculiar bone form of desmostylians, all of these figures are open to the critisism of being unnatural in the curvature of vertebral column, the direction of tips of digits, the foot posture and so on. In the present hypothesis, many points shown in these figures are corrected; the desmostylian cannot help being only one exception of general rules of skeletal construction in ungulates about the direction of the limbs instead.

(4) This conclusion is applicable to the skeletal restoration of the animals which belong to order Desmostylia, not only to Desmostylidae but also to Cornwalliidae. Because the important characteristics for the restoration of the postcranial skeletons is common in Desmostylus and Paleoparadoxia. Moreover, the theoretical bases for this restoration was supported by the mode of fossil occurrence of both genera.

(5) On the ground the basic figure of the desmostylian skeleton is settled, the life restoration, the

reconstruction of the locomotion, habitat and so on of these animals will be presumed with more secure foundation. The desmostylian figure stretching limbs laterally seems to be inefficient for support of weight or terrestrial locomotion, but it is excellently stable on the other hand. It should be a key to understand the ecology that desmostylians dared to show such a peculiar posture of limbs.

# Appendix I. Description of desmostylian skeleton

## A. Cranium

Characteristics of the cranium of Desmostylus have been documented on the Togari specimen of D. japonicus (YOSHIWARA and IWASAKI, 1902), the Oregon specimen of D. hesperus (HAY, 1915; ABEL, 1922; VANDERHOOF, 1937) and the Keton specimen of D. mirabilis (NAGAO, 1941; IJIRI and KAMEI, 1961). In this place a few points pertinent to the author's restoration will be described below.

As the anterior half of the skull (UHRno.18466-1, Fig. 1) is lacking in the Keton specimen, the total length of the skull is estimated from data on the nearly perfect Utanobori specimen. It is 699 mm to 704 mm, the value varying with standard points taken for measurements.

## B. Vertebrae

### 1. Descriptions

#### i) Cervical vertebrae

The atlas (UHRno.18466-55, Fig.2, Plate I) is short antero-posteriorly; wings are narrow in proportion to the width of lateral masses, cranio-caudally flat and ventrally expanded; foramen transversarium absent; foramen alare situated near the bone margin, showing incisura alaris in some cases; lateral vertebral foramen present; vertebral foramen constricted in the center and 8-shaped.

The axis is short, low and wide; dens is stout and

short, and articular surface lies in its ventral half; anterior articular surface is continuous with ventral articular surface of dens but not expanded ventrally; foramen transversarium is small, penetrates transverse process from dorsal surface backward; no ventral spine present.

The other cervical vertebrae are short antero-posteriorly, low dorso-ventrally and wide transversely; pedicle low and vertebral foramen triangular in outline; articular processes protrude weakly; foramen transversarium small and situated at lower level; transverse process is plate-like, fuses with ventral tubercle to broaden backward.

ii) Thoracic vertebrae (UHRno.18466-56—64, Fig.3,4,5, Plate I, II)

Bodies are short, low and wide, and titled cranially in the posterior thoracics; vertebral foramen narrower than body, low and wide transversally; pedicle is wide and short antero-posteriorly; posterior notch deep and U-shaped; spinous process short and stout, and extremely retreating in the anterior and the middle thoracic vertebrae; transverse processes rather long, originate at the level of vertebral foramen and project dorsolaterally in the anterior and the middle thoracic vertebrae, but in the posterior thoracic vertebrae they originate at lower level and project horizontally; facets for tubercles of transverse processes face outward; articular processes protrude strongly,

distance between right and left processes wide; lateral vertebral foramen absent and ventral spines less-developed; in the posterior thoracic vertebrae accessory and mammillary processes developed; accessory processes depressed dorso-ventrally, situated above posterior notches and projecting from the posterior margin of transverse processes; mammillary processes projecting upward and outward behind anterior articular processes, flat medio-laterally and triangular in outline in lateral view.

iii) Lumbar vertebrae (UHRno.18466-65—68, Fig.5, Pl.II,III)

Bodies are short, low and wide, and in lateral view, parallelogram-shaped and lowering backward; vertebral foramina low and triangular in outline; pedicles wide and slightly tilted medially; lamina rather wide transversely, anterior margin showing a wide V-shaped notch that reaches behind articular surface; anterior notch small, and posterior deep; groove for spinal nerve running backward but slightly downward; spinous process short, projecting vertically and rectangular in lateral aspect. They are triangular in cross section, caudally thicker, and not expanded at the top; transverse processes originate at the level of inferior margin of vertebral foramen, project horizontally and transversely, short and depressed and tapering toward the tip; anterior articular processes strongly protrude, their articular surfaces facing medially and dorsally, not rolled up; mammillary processes project upward with a crest extending mediocaudally from the

process; accessory process absent.

iv) Sacrum (UHRno.18466-69, Fig.6, Plate III) and caudal vertebrae (UHRno.18466-70—78, Fig.7, Plate III)

The sacrum is triangular in outline and slightly bends; lateral part depressed dorso-ventrally, wings not protruded; sacral foramina large in front and become smaller and narrower abruptly backward; sacral crests not developed; spines of the first and the second sacral segments separated, wide, low and vertical; broad interarcuate space present between the first and the second segments.

The caudal vertebrae short; vertebral arches and transverse processes not developed; hemal arch probably absent.

v) Vertebral column (Fig.5)

The cranio-caudal changes in shape and size of the dorsal vertebrae will be described below.

Bodies scarcely vary in both length and height, but broaden in transverse diameter in the posterior lumbar vertebrae. Vertebral canal is rhombic in cross section up to the seventh thracic vertebra, spindle-shaped to elliptic from the eighth thoracic to the second lumbar and depressed triangular from the third lumbar. It becomes smaller in the posterior vertebrae. The direction of intervertebral foramina changes from the anterior to the middle thoracics, first dorso-ventral, then horizontal and finally ventro-dorsal. It becomes more backward in the eighth and

the following. Posterior costal facets shift progressively to dorsal position and are present up to the twelfth thoracic vertebra.

Spinous processes gradually become thicker from the anterior thoracics to the posterior lumbar. They are inclined backward, most steeply at the fifth thoracic vertebra, more gently up to the tenth, are almost vertical from the eleventh thoracic to the second lumbar and inclined forward in the last two lumbar. Transverse processes or costal processes are thick and long to the ninth thoracic and depressed in the thirteenth thoracic to the fourth lumbar. They originate from the arch from the middle vertebrae to the ninth thoracic. Then the point of origin lowers gradually until it reaches the body in the thirteenth thoracic vertebra and the following. They originate from the anterior half of the body up to the second lumbar vertebra and from the middle in the last lumbar. They project somewhat forward up to the seventh thoracic vertebra, become perpendicular to the vertebral axis from the eighth to the eleventh thoracic and project somewhat backward in the twelfth and behind. In the thoracic vertebrae they project slightly upward in regard to the horizontal plane, but in the lumbar they lie in this plane. Posterior margin of the arch between posterior articular processes becomes gradually wide from the tenth thoracic vertebra, and the angle between posterior margins of the processes becomes obtuse in the posterior lumbar vertebrae.

The articular surface of zygapophyseal junction is directed horizontally, slightly inclining forward up to the tenth thoracic, and is nearly sagittaly from the eleventh thoracic and the following.

2. Remarks

The atlas, thoracic (REINHART, 1959) and a lumbar vertebra (MARSH, 1888) of Desmostylus have been described briefly, but it is not clear whether the specimen described by REINHART belongs to Desmostylus or Vanderhoofius.

According to REINHART's description (1959) of the atlas (U.C.M.P.no.39997), "Anterior cotyles transversely expanded, deeply concave; posterior cotyles flat, tear-shaped with point in a medial direction; neural canal large; arch for odontoid process of axis relatively small; neural spine present as a low cone-shaped boss; foramen for (vertebral) artery pierces anterior end of transverse processes, penetrates bone for short distance then passes through base of neural arch; transverse processes thin, winglike, rise dorsal in a broad curve, lateral borders terminate in this crest; ventral arch centered with low boss; no hyapophysis present."

As only a part of the atlas remains in the Keton specimen, REINHART's description can only be compared with data from the Utanobori specimen. Both will accord with each other in general. Foramen alare, however, is a notch in the Keton specimen. Shape of vertebral foramen may differ from that described by REINHART (see below).

REINHART's specimen has "a dorsally arched and less well-developed transverse process", which "differs greatly from both those of the sirenians and proboscideans" and is unique among mammals. The feature agree quite well with the Utanobori specimen. If his description, "less separation and differentiation between the arch for the neural canal and that for the odontoid process of the axis", is regarding the shape of vertebral foramen, it differs from the state in the Utanobori specimen.

As to the first thoracic vertebra (U.C.M.P.no.40863) REINHART described: "Ventral and lateral borders of centrum round, anterior and posterior borders vertically straight, ventromedian area of neural canal with slight indentation; prezygapophyses transversely straight, border of neural canal triangular with angles rounded; transverse processes with triangular outline, sharp anterior crest, rounded angles dorso- and ventroposteriorly; large elliptical facet for tuberculum of rib on ventrolateral surface, no capitular facet noted; base of neural arch with pronounced posterior expansion, top half of neural arch forms triangular spine; neural arch with pronounced posterior inclination, anteriorly convex, posteriorly concave; postzygapophyses, partly broken, are shallow oval indented facets on neural arch."

This specimen has many common characteristics with the Japanese specimens if it is one of the anterior or the middle thoracic verterbrae. However it differs from the

first thoracic of the Utanobori specimen in the angle of cranial articular process, the outline of transverse process and the inclination of neural spine. Thus, it is probable that the specimen, U.C.M.P.no.40863, is not the first thoracic vertebra.

MARSH's description (1888) of a lumbar vertebra of D. hesperus is as follows: "... a lumbar vertebra, which is noticeable for the extreme flatness of its articular surfaces. The sides of the centrum meet below, forming an obtuse median keel. The centrum of this vertebra has a length of 89mm; the vertical diameter of the anterior face is 90mm, and its transverse diameter 107mm." The position of this lumbar vertebra is unknown but it is much larger than those of the Keton specimen in length and vertical diameter inspite of similar value of transverse diameter. Because ventromedian crest is not developed in the Keton specimen, the lumbar vertebra may belong to that of sirenians.

After NAGAO (1941) vertebral formula of Desmostylus is: "cervical vertebra 7 · thoracic 14 (or 15) · lumbar 4 · sacral 4 · coccygeal 11 (or 12)", while SHIKAMA (1966) suggested it to be "7·14 · 6 · 4 · 11". As the number of the thoracic vertebrae is defined by the number of the ribs, it depends on identification of the ribs. Since twenty-five ribs remain in the Keton specimen and one probably missing, there should have been thirteen pairs originally. The reason why the number was thought to be fourteen is that the left

fifth metacarpus was misregarded as the left first rib.

Whether the number of the lumbar vertebrae is four (NAGAO, 1941) or six (SHIKAMA, 1966) is determined by the fact that which vertebrae are articulated with the thirteen pairs of the ribs. Because, these characters are not useful in distinguishing the lumbar vertebrae from the thoracic vertebrae, since costal facet is obscure in the posterior thoracics and transition from transverse process to costal process of lumbar vertebrae is gradual in the Keton specimen. Fortunately, proximal portion of the right eleventh rib was attached in situ to the thoracic vertebra. Thus, the relationship between thoracic vertebrae and ribs became clear, as a result, it could be decided that there are surely the four lumbars.

The presence of four sacral segments (NAGAO, 1941; SHIKAMA, 1966) may be probably inferred by the number of spines on median sacral crest and that of ventral sacral foramen. This inference, however, is irrelevant, because it results in the unnaturally long "fourth sacral" which is situated caudal to the third ventral sacral foramen. The number of the sacral segment is estimated to be five, judging from the position of the foramina, the presence of depressions on both sides of the fifth sacral and of the last (fourth) transverse line. Though ten caudal vertebrae are remaining, original number is not known.

As a result, it can be concluded that the vertebral formula of Desmostylus should be 7·13·4·5 · 10+, which does

not contradict with data from the Utanobori specimen. If I compare this with those of living mammals (FLOWER, 1885), I find that there is no such formula as this in other mammals.

C. Thorax

1. Descriptions

Curvature of the ribs (UHRno.18466-79—103, Fig.8, Plate IV) is strong in general and particularly remarkable in proximal one-third. There is clockwise torsion in the proximal part of the left ribs. Costal neck is long, and costal angle obscure. Costal body is not so flat in cross section. Sternal extremity is less expanded than the body. In the anterior ribs costal body is flat. In the anterior to the middle ribs dorsal muscle area is conspicuous. In the posterior ribs head and tubercle are united to make short V-shaped proximal articular surface, and costal body is wide for the length and thick for the width.

The sternum (UHRno.18466-46—54, Plate IV) is broad and dorso-ventrally flat, and is composed of nine sternal segments (sternebrae). The thorax is subcircular in cross section even in the anterior part, judging from the curvature of the ribs and the transverse width of the sternum.

2. Remarks

The ribs of Desmostylus have been described by NAGAO (1941) and REINHART (1959). NAGAO stated about ribs of the Keton specimen: "14 ribs have been obtained. The posterior

ones are thick, being subcircular or broadly oval in cross-section and differ from many terrestrial mammals." REINHART (1959) described two ribs from California, one of which (U.C.M.P.no.40864) is stated: "Proximal third missing, spatulate, anterior surface flat; from a thin neck the lower half is broadly expanded; ventral border broadly rounded." The other one, "one of the posterior thoracic ribs", (U.C.M.P.no.39998) is described: "Capitulum and tuberculum separated and estimated 47mm, partly broken; upper half anteroposteriorly flattened, dorsal, and ventral borders terminates in thin crest; lower half oval."

According to the author's view, there are thirteen pairs of ribs in Desmostylus. In the anterior ribs cranial surface is rather convex, caudal surface flat or concave and medial margin is sharp in sternal extremity. The posterior ribs are rather thick in proximal region and tapering steeply toward the distal extremity. REINHART's observation on the close resemblance of the anterior ribs between desmostylids and proboscideans is confirmed.

SHIKAMA (1966) has described the sternum of Desmostylia in detail, but he was wrong in arranging and naming each sternal segment. Corrected results are shown in Table 7. NAGAO (1941) stated: "(sternum) consists of 8 flat elements arranged in two longitudinal rows, ··· young Monodon is known to bear somewhat similar sternum. It is wide like some of cetaceans and sirenians." Actually there are nine sternal segments due to the presence of a small median

Table 7. Different points in evaluation of characteristics between SHIKAMA (1966) and present author.

| page | bone | SHIKAMA's description (1966) | present author's view |
|---|---|---|---|
| 29 | Humerus | In anterior view, Distal border of inner trochlea more strongly projected than outer. | Distal border of outer trochlea more strongly projects than inner. |
| | Humerus | Perhaps major and outer tubercles were shifted from anterior to outer corners in deformation process. | Even if major tubercle is compressed in deformation process, it will not be shifted from anterior to outer corners. |
| 35 | Scaphoid | In outer view, bone subquadrate with much undulated and long aft margin; distal margin nearly straight and posterodistal corner projected; | In outer view, and long fore margin; proximal margin nearly straight and anteroproximal corner projects; |
| 38 | Scaphoid | Textfig. 19-4, Outer side | upside down |
| 42 | Cuneiform | Textfig. 23 -5, Outer side; -6, Inner side | -5, Inner side; -6, Outer side |
| 43 4 | Trapezoid | left "Trapezoid" Textfig. 25 -1 6 | The identification is questionable, because left "Trapezoid" is not articulated with scaphoid and its distal surface to articulate with the second metacarpus is really rough. It is probably pisiform or the first metacarpus. |
| 45 6 | Magnum | both "Magnum" Textfig. 27 -1 11 | The identification is false, because left "Magnum" is not articulated with distal surface of lunar. It is probably one of the tarsal bones. |
| 47 8 | Unciform | right "Unciform" Textfig. 29 -7 9 | The identification is false, because right "Unciform" has many points discordant with the description upon the left bone and both are asymmetric in any situation. As it is similar to cuboid of Paleoparadoxia (Izumi specimen) and articulated with left astragalus and calcaneum, the bone may be left cuboid. |
| 76 | Femur | Small trochanter obsolete compared with that of Izumi, and very small. | Though small trochanter of Keton Desmostylus projects less than that of Izumi, it is not obsolete and well-developed in area and development of rough surface. |
| | Femur | Crestlike inflation of small trochanter distinct in outer view. | Perhaps large trochanter distinct, for small trochanter not observable in outer view. |
| 81 | Tibia | Textfig. 61 -2, Outer side; -4, Inner side | -2, Inner side; -4, Outer side |
| 86 | Astragalus | Textfig. 66 -4, Distal side (fore side is in lower) | (fore side is in upper) |
| 90 | Calcaneum | Textfig. 69 -1, Fore side; 2, Aft side; 5, Outer side; 6, Inner side; 3, 4, (fore side is in upper) | -1, Inner side; 2, Outer side; 5, Fore side; 6, Aft side; 3, 4, (Inner side is in upper) |
| | Calcaneum | When calcaneum is closely jointed with astragalus, it declines much inward; this may be due to deformation of astragalus and calcaneum. | It is not natural to assume that only declining of tuber calcis is due to deformation, because both astragalus and calcaneum have no trace of compression or depression. The declination must be primary. |
| 122 | Sternum | Praesternum | Fourth Mesosternum |
| 124 | | Right | Left |
| 124 | Sternum | left bones | right bones |
| | | inner and fore portion | fore and inner portion |
| | | outer margin | aft margin |
| | | inner margin | fore margin |
| | | posterior margin | outer margin |
| | | posterior inner corner | anterior outer corner |
| | | 31 mm in right and 26 mm in left, | 31 mm in left and 26 mm in right, |
| 125 | Sternum | aft margin | outer margin |
| | | Left bone | Right bone |
| | | narrower | wider |
| | | longer | shorter |
| | | right bone | left bone |
| | | Inner margin is more straight in right bone, | Fore margin is more straight than left bone, |
| | | posterior inner corner | anterior outer corner |
| | | Textfig. 105 -1 | rotate at a right angle in anticlockwise |
| | | -2 | rotate at a right angle in clockwise |
| 126 | Sternum | First Mesosternum | Third Mesosternum |
| | | Right bone | Left bone |
| | | fore portion | aft portion |
| | | aft corner | fore corner |
| | | left bone | right bone |
| | | Posterior outer corner | Anterior outer corner |
| | | anterior outer corner | posterior outer corner |
| | | 28 mm in right and 24mm in left. | 28 mm in left and 24 mm in right. |
| | | In posterior view, | In anterior view, |
| 128 | Sternum | Right bone | Left bone |
| | | posterior outer corner | anterior outer corner |
| | | In posterior view | In anterior view |
| | | First Xiphisternum | First Mesosternum |
| | | posterior outer portion | anterior outer portion |
| 130 | Sternum | posterior margin | anterior margin |
| | | anterior outer margin | posterior outer margin |
| | | posterior inner corner | anterior inner corner |
| | | posterior surface | anterior surface |
| | | Second Xiphisternum | Praesternum |

segment besides four pairs.

D. Fore limbs

1. Descriptions

i) Scapula (UHRno.18466-104, Fig.9, Plate V)

The specimen is judged as the left scapula from the cranial position of tuber scapulae and the caudal position of tuber spinae. It is nearly perfect except that the cranial tips of tuber scapulae and coronoid process are broken.

In outline it is triangular, dorso-ventrally long, and spine of scapula lies a little anterior to the middle of lateral surface. Neck bends slightly inward and spine leans backward. Costal surface is concave as a whole except the dorsal part. The bone is thick at the dorsal part of posterior border and at the caudal part of vertebral (dorsal) border, and is thin at the dorsal part of anterior border.

Vertebral border is convex upward and straight sagittally in dorsal view. The whole of the border is rugged, suggesting the presence of scapular cartilage. The border becomes thinner anteriorly in front of spine, is thin in the middle behind spine, but is thick at spine and posterior angle.

Anterior border is concave forward and inward in the ventral half, and is convex forward in the dorsal half, so it is S-shaped as a whole in lateral and front view

respectively. The dorsal half of anterior border is rather acute, the ventral half thicker and smooth.

Posterior border is linear in the dorsal one-fourth and concave backward in the ventral three-fourths. The lateral lip branches off medially from posterior border at a point a little ventral to the middle, ascends in parallel with the border to posterior angle. There is a surface of about 20 mm wide between posterior border and the lateral lip. The dorsal half to which the teres major muscle attaches is flat, and the ventral half to which the triceps brachii muscle attaches is a little concave. An oblique line runs from dorsolateral to medioventral between these two portions. Posterior border decreases in thickness ventrally, and slightly thickens against in its ventral end at tuber to which the teres minor muscle attaches.

In costal surface, facies serrata to which the serratus ventralis muscle attaches is probably represented by the area occupied with fine sparse lines radiated from posterior angle. The area lies within the dorsal one-fourth and a caudal half of costal surface. A gentle rugged elevation to which the subscapularis muscle attaches extends downward from vertebral border to the center of the surface. Costal surface hollows out slightly in the middle, reflecting the presence of spine on lateral surface. It is somewhat rugged in the dorsal half due to the presence of fine lines conversing toward neck, while rather smooth in the ventral half.

Spine of scapula to which the deltoid and the trapezius muscle attach lies on the border between cranial one-third and caudal two-thirds in neck. In lateral view, the base of spine is a little convex forward, while the free edge is convex backward. In front view, spine shows an expanded wedge shape. The free edge is highest at a point dorsal to acromion, and the distance between them is about one-fourth of the total length of the scapula. Spine decreases gradually in height toward vertebral border, and the free edge is convex outward in its dorsal three-fourths, becomes smooth and gradually narrow in the dorsal one-fifth, and is concave outward in the part ventral to acromion. In dorsal view, spine inclines backward, acromion projects forward and tuber spinae backward. The anterior lip of tuber does not overhang supraspinous fossa. The free edge is widest at acromion, then wide next at tuber spinae and narrow between them. Tuber is in the middle of spine, extends within a half of its length. A rough surface is developed between the anterior and the posterior lips of spine.

Shallow supraspinous fossa to which the supraspinatus muscle attaches is trapezoidal in shape with the long border at spine in shape and does not broaden much in the dorsal part. The ventral half is smooth. The fossa in horizontal section is long cranio-caudally in the dorsal half, while mediolaterally in the ventral. Infraspinous fossa to which the infraspinatus muscle attaches is a dorso-ventrally long triangle, and occupies about 150 per cent of the area of

spraspinous fossa. Its dorsal half is shallow and broad, but deeper in the center.

Glenoid cavity is elliptic, long cranio-caudally. It is shallow, but hollows in the center, and projects forward slightly due to the presence of tuber scapulae. The cavity is large in proportion to short vertebral border. It inclines inward at about 10 degrees to the scapular long axis. Neck of scapula is more constricted transversely. In horizontal section it is triangular with angles cranial, caudal and lateral but a little anterior. Only medial (costal) surface is convex. Tuber on posterior border is small, situated dorsocaudal to cavity, making ventral end of posterior border.

ii) Humerus (UHRno.18466-3, Fig.11, Plate V)

The specimen is judged as the left humerus from cranial humeral condyle and lateral deltoid tuberosity. Dorsal part of head, anteromedial part of medial condyle and posterior surface of medial epicondyle are broken. The specimen is deformed, antero-posteriorly, flat especially in the distal portion.

Shaft in lateral view straight, thinner than minimum width (in anterior view) of shaft, a little expanding proximo-distally. Head is larger and projects caudally, condyles smaller and projects cranially. In proximal view, anterior border protrudes at three points, posterior border semicircular and convex caudally, a process is present in lateral part. In distal view, it is a flat parallelogram in

outline with a sagittal groove in the middle running from anterolateral to posteromedial, lateral epicondyle protrudes at the posterolateral corner.

In posterior view, head is wide, about two-thirds of the maximum breadth of proximal extremity, and is a low ellipse in outline with the maximum breadth at higher level than the middle. Head in proximal view is a hemicircle in outline, facing inward about 10 degrees from the caudal axis. In lateral view curvature of head is a little larger than in proximal view. Head faces caudally at right angle to the bone axis. Major tubercle to which the supraspinatus muscle attaches lies anterolateral to head, much less developed than head. In proximal view major tubercle is flat antero-posteriorly, making a ridge running in anteromedial to posterolateral direction. In cranial view, major tubercle is present at somewhat higher level than minor tubercle, but not so high as head.

Minor tubercle to which the subscapularis muscle attaches is present anteromedial to head, projecting a little medially, and much smaller than head. In proximal view it is long medio-laterally and is deformed and compressed antero-posteriorly.

Intertuberal groove on which tendon of the biceps muscle passes is present in the middle of anterior surface of head, shallow and obtuse V-shaped in proximal view.

The portion corresponding to the surface for the infraspinatus muscle, anterolateral to major tubercle, is

somewhat elevated, semicircular and rough. A small rise inferolateral to the surface for the infraspinatus muscle, probably representing teres minor tuberosity, is a ridge long antero-posteriorly but round in lateral view. A smooth groove runs from anterodistal to posteroproximal in the medial part of this rise.

A ridge runs from the lateralmost point further distal to teres minor tuberosity toward the middle of shaft. Its upper half, a flat plane facing outward, corresponds to deltoid tuberosity, and the lower sharp ridge is humeral crest. Deltoid tuberosity is closely high rectangular in outline with the upper end projecting most laterally. Its long axis inclines backward slightly in lateral view. Humeral crest runs parallel to the long axis of shaft. Its anterior lip protrudes more than the posterior. Musculo-spinal groove (the brachialis muscle passes) behind humeral crest, is a flat plane facing laterally to shift anteriorly in the distal. The groove makes a right angle with posterior surface, though they actually make obtuse posterolateral margin in the proximal part. The length of the groove is about one-fourth of that of the humerus.

In its proximal portion, shaft has three margins, medial and anterolateral ones are sharp, posterolateral one obtuse. In the middle of shaft anterolateral margin disappears, while medial and lateral margins remain. In the distal, as anteromedial margin, arising from the middle and running inward and downward to the medial condyle, appears,

there are also three margins with posteromedial and lateral margins.

Anterior surface is rather flat above, rised in the median below. Large oval expansion is present in the center of the upper half, near proximal one-third of whole humerus, which is regarded as the teres tuberosity (Tuberositas teres major: the teres major muscle and the latissimus dorsi muscle attach) due to the presence of a number of rough lines running longitudinally on it. Median rise in the lower half is obtuse, becomes anteromedial margin in the distal.

In contrast to anterior surface, posterior surface is convex above, flat below. Upper median ridge is short, leading to the middle of the head. Posterolateral margin is continued in lateral margin distally. The lateral surface is a narrow space between anterolateral and posterolateral margins, forming musculo-spinal groove. A ridge in the medial runs obliquely from the proximal medial margin to the distal posteromedial.

The shape in cross section is tabular, slightly convex caudally just under the head, and is low trapezoidal with median rised base in the proximal one-third, semicircular and convex cranially in the middle, and triangular with angles anteromedial, posteromedial and lateral in the distal one-third.

Distal extremity projects at about 80 degrees with the humeral axis. Medial condyle increases in diameter

medially, but lateral one rather smaller and does not increase much in diameter laterally. The latter is larger in transverse width. The articular surface reaches near the distal end in lateral part of lateral condyle backward and downward, and olecranon fossa in medial part. In medial condyle the extent of articular surface is not known due to the break of the specimen.

Medial epicondyle to which the flexor carpi and digitorum muscles attach is rather flat. Lateral epicondyle to which the extensor carpi and digitorum muscles attach protrudes exceedingly, on the trochlear axis. It looks deformed and its position appears to be more caudal than the original. The diameter of the lateral epicondyle is about a half of that of the lateral condyle in distal view. There is a smooth groove at the anterior and inferior base of the lateral epicondyle.

Sharp lateral condyloid crest to which the brachioradialis muscle and the anconeus muscle attach runs along the lateral margin from lateral epicondyle, is continuous with obtuse posterolateral margin and disappears in the proximal quarter.

Olecranon fossa is an elliptic recess, transversely long and about 50 mm in width, with three definite margins, superior, medial and lateral, and inferior margin continues into synovial fossa. Coronoid fossa is a low triangle in outline, shallower, larger and more indistinct in general outline than olecranon fossa. Supratrochlear foramen

pierces the lateral part of olecranon fossa.

The head of humerus is larger in both sagittal and transverse diameter and has stronger curvature than glenoid cavity of the scapula. The possible range of contact between head of humerus and glenoid fossa in shoulder joint is about 50 degrees in sagittal plane, about 80 degrees in frontal plane.

The elbow joint is probably deformed. The trochlear surface of the condyles and semilunar notch are nearly equal in both height and thickness. The range of contact in the joint is about 80 degrees or less, based on measurement of articular surface.

iii) Antebrachial skeleton (UHRno.18466-4, 5, Fig.13, Pl.VI)

The left radius (UHRno.18466-5) is fused with the left ulna (UHRno.18466-4). The radius and the ulna run parallel without torsion. The following description will be done as in general mammlas in regard to the orientation, i.e. the radius fore and the ulna behind, so the distal extremity of antebrachial skeleton becomes long antero-posteriorly.

The side of the specimen is judged from rather medial position of the radius in the distal. The specimen is preserved nearly perfect except that top of olecranon and the medial part of head of the radius are broken, and deformed flat from side to side in the middle and distal portion.

The antebrachial skeleton has huge olecranon and as a whole remarkably wide antero-posteriorly at the distal end.

The space between radius and ulna is filled with country rock, but it seems to be very narrow, if it exists.

Head of radius is considerably wider than shaft, expands particularly outward. Concave surface of head represents lower part of the articular surface for trochlea. It is wide from side to side, and has a ridge running antero-posteriorly medial to its median line. The ridge looks straight in lateral view, and protrudes anteriorly to make coronoid process. Circumferentia articularis cannot be observed because of its adhesion with radial facet for the ulna. The articular surface is probably flat, so the radius cannot be pronated even before they are fused with each other. There is a remarkable tuberosity, probably that of the radius to which the biceps brachii muscle attaches, about 30 mm in diameter, on the posterior part of medial surface of head, and a very rough rise to which the flexor digitorum profundus muscle attaches, 40 or 50 mm in diameter, in proximal one-third to one-fourth of medial surface of shaft.

Shaft of radius is remarkably flat from side to side, and anterior border becomes a sharp ridge from anteromedial corner of head to medial styloid process. In medial view, the radius is constricted a little in neck and has the antero-posterior diameter in the distal is about twice that in the proximal. In lateral view, antero-posterior diameter of head is larger than in medial view, while the diameter in the distal portion is not so large as in medial view.

In cross section, shaft is convex medially and flat laterally. The distal part of medial surface is rough and elevated. Medial styloid process extends more distally than the distal border medial and posterior to anterior margin, to make lateral distal border by stretching outward and backward with a constant height. Outer surface of the process is rough, while inner one makes carpal articular surface.

Olecranon to which the triceps brachii muscle attaches bends extremely backward, its anterior margin to the beak bends at 75 degrees to the long axis of the ulna, posterior margin at about 45 degrees. In lateral view, olecranon decreases its width toward the tip, and the width at the base is nearly equal to sagittal diameter of antebrachial shaft at the level of neck. In posterior view, the tip of olecranon is thick, tapering toward posterior margin of shaft. In proximal view, olecranon protrudes backward and slightly inward. Olecranon is about half in width of semilunar notch.

Medial surface of olecranon is concave, lateral one convex and a tubercle, 20 or 30 mm in diameter, is present in apical one-third and upper one-third point, and a prominent rough expansion to which perhaps the anconeus muscle attaches is situated behind and below it.

Beak is sharply spatulated, proximo-distally flat, round in proximal view, and protrudes most forward medial to the median part.

The semilunar notch is parallelogram-shaped in outline in anterior view, with the proximal beak inclining outward. In lateral view, ulnar portion of semilunar notch is curved, composing upper and posterior part of articular surface. Rough lines to which the brachialis muscle may attach run perpendicular to the longitudinal axis of the ulna on the surface of lower end of medial margin of notch.

Shaft of ulna is a triangular prism, slightly flat from side to side with lateral, medial and posterior margins. Transverse width of shaft is largest at semilunar notch and decreases toward the distal. In contrast to the radius, lateral surface is convex, medial surface flat or convex. Medial surface is wider than lateral in the middle of shaft. There is a tubercle, about 50 mm in diameter, at the anterior part at a distance of a quarter of the total length from the distal end on lateral surface. Posterior margin is as sharp as anterior margin of the radius, somewhat undulated.

Many rough lines running transversely are found in the posterior part of lateral surface of the distal end. Groove for tendon is obscure. Styloid process of the ulna does not project at all. Carpal articular surface faces somewhat backward, and the border between radius and ulna is indistinct on it, but its anterior radial part is triangular in outline with angles posteromedial, posterolateral and anterior as shaft of the radius. The articular surface is a groove as a whole running in a direction from anteromedial

to posterolateral at an angle of 40 degrees to the antero-posterior axis. Medial half of the groove faces distally, lateral half posteromedially at an angle of about 45 degrees to medial surface. The posterior ulnar part has a half width of radial part, and is slender antero-posteriorly. Its anterior two-thirds are flat to convex, facing distal, while posterior one-third more or less convex, facing medioinferiorly and somewhat posteriorly.

Because the antebrachial skeleton has no twisting, the direction of longitudinal axis of carpal articular surface is perpendicular to the direction of axis of movement in elbow joint. Consequently, articulation of antebrachial skeleton with proximal three carpi produces discordance of 90 degrees in directional terms for the description (Fig. 13).

iv) Manus

[Carpi]

Concerning carpi (Fig.13, Plate VI), refer to Table 7.

[Metacarpus] (UHRno.18466-106, Fig.13, Plate VIII)

The specimen is identified as the left fifth metacarpus based on triangular proximal articular surface and protruded lateral margin. Except for lack of distal epiphysis, it is an almost perfectly preserved specimen, not deformed, repaired in the middle and the proximal part of medial surface.

The shape is a triangular prism with a surface facing

medially in the proximal half, a semicircular prism flat antero-posteriorly in the distal. It is bending outward in proximal one-third in anterior view. Both extremities are stout in lateral view.

Proximal surface is triangular in shape with anteromedial, posteromedial and lateral angles, inclining medially at an angle of 10 to 30 degrees to the plane perpendicular to the longitudinal axis of shaft. The surface medial to the median ridge running antero-posteriorly in proximal surface is inclined steeper, and seems to articulate with the distal surface of os hamatum.

The dorsal surface of the shaft increases in width distally. In the proximal half the dorsal surface inclines laterally at about 45 degrees and lateral margin to which the extensor carpi ulnaris muscle attaches becomes sharp. The outline in the proximal part of medial surface of the shaft in anterior view is straight and leans outward at about 20 degrees to the longitudinal axis of shaft. Palmar surface is less expanded in the middle than dorsal one. The medial margin is sharp and straight in the distal half, cranio-caudal diameter increases proximally in the proximal half. Medial surface is triangular and seems to be articular surface for the fourth metacarpus. Lateral margin is sharp, convex palmarly, expanded like a tubercle 15 mm wide, about 30 mm long in the distal portion.

It is triangular in cross section in the proximal,

decreased in length in the medial side toward the distal to become an isosceles triangle with sharp lateral angle, and is fusiform, elongate transversely, more convex dorsally in the distal half.

The distal portion of diaphysis is almost circular, somewhat concave palmarly, in outline. Distal surface is rough as a whole. In lateral view the distal portion is truncated to the direction perpendicular to the longitudinal axis of the bone, not showing the expansion like a head.

[Phalanges]

Proximal phalanges are generally longer than middle phalanges, but they differ in length to such a degree that it is not possible to distinguish proximal and middle ones only by their length. Proximal extremity of proximal phalanx is particularly larger in sagittal diameter than middle phalanx of the same digit. Proximal surface of proximal phalanx is concave transversely and sagittally, but that of middle phalanx is convex transversely due to the presence of a sagittal ridge in the center. Bodies of proximal phalanges steeply decrease their thickness distally and become nearly equal to those of middle phalanges in thickness in the distal one-third portion. Both medial and lateral margins of proximal phalanges are more sharp than those of middle phalanges. Distal surface of both proximal and middle phalanges are concave transversely, but in the middle phalalnx it is saddle-shaped and convex sagittally. Every distal phalanx has a flat plane in palmar or planter

side and shows broad surface area, but four specimens preserved vary in size and shape.

2. Remarks

Limb bones of the Desmostylia have already been described by VANDERHOOF (1937), NAGAO (1941), REINHART (1959) and SHIKAMA (1966). NAGAO first outlined the Keton specimen and SHIKAMA described it in detail with a later revision (SHIKAMA, 1968). The author cannot refer to all of them, so he shows here differences in evaluation of data between SHIKAMA and the author in Table 7.

i) Scapula

NAGAO (1941) reported about the scapula of the Keton specimen: "spine is tall; both supraspinous and infraspinous fossa are nearly the same in size; both cranial and caudal margins are straight; dorsal margin is not so expanded and not indicating "swing" backward"; this agrees with the author's observation.

The scapula which KHOMENKO (1928) regarded as that of Desmostylus sp. is huge, and 1,080 mm in estimated total length. He stated: "Cavitas glenoidalis zeichnet sich durch einen sehr massive Basis, die sich fast schon vom äusseren Rande der Cavitas glenoidalis kund tut. Die Crista ist hoch und schmal, mit einer mehr vorderen Position und leicht schräger Richtung nach unten nach vorn. Das Acromion stellt einen dünnen Kamm dar, welcher teilweise nach vorn gebogen ist. Das Collum hat einen eigenartigen Querschnitt." Among the features, both large glenoid cavity and stout base of

spine are probably related to its hugeness, but it differs from the scapula of the Keton specimen in the shape of acromion and neck.

The scapula (U.C.M.P.no.39986) of Desmostylus is also described by REINHART (1959): "Blade elongate, lanceorate in outline, upper border broken, greater part lies anterior to spine; spine well developed, upper half with strong posterior curvature, lower half almost vertical; depression centered behind spine on medial side of blade; well-developed coronoid process curves sharply medially; glenoid fossa shallow." Among them differences from the Keton specimen are: "spine ···, upper half with strong posterior curvature, ··· well-developed coronoid process curves sharply medially". It is probable that this specimen does not belong to Desmostylus.

According to NAGAO, the scapula of Desmostylus is rather similar to that of ungulates in outline except that acromion is situated at a higher level. It clearly differs from that of proboscideans and is also different from that of Moeritherium (ANDREWS, 1906) and sirenians in having backward swing. REINHART (1959) also pointed out differences from sirenians, pinnipeds, cetaceans and proboscideans.

ii) Humerus

VANDERHOOF (1937) described only about the distal extremity of the humerus, but the presence of "a strong trochlear groove" and supratrochlear foramen is common to

the Keton specimen. NAGAO (1941) pointed out: "(Humerus is) Much deformed; apparently expanded at both extremities, with a broad and thin shaft." The Keton specimen coincides with the specimen (U.C.M.P.no.39999) which REINHART (1959) regarded as the right humerus of Desmostylus or Vanderhoofius in "presence of a broad bicipital groove" and "anconeal fossa may be pierced by foramen", but differs from it in "a well developed external tuberosity", "deltoid crest on anterior surface extends length of shaft", "shaft transversely narrow, horizontally broad" and "trochlea and capitulum* smooth round half cylinders of equal size". So it is possible that this specimen does not belong to Desmostylus.

NAGAO noted differences between Desmostylus and proboscideans or sirenians, and REINHART between that and sirenians.

iii) Antebrachial skeleton

Antebrachial skeleton (radius and ulna) of Desmostylus was described by VANDERHOOF (1937), NAGAO (1941) and REINHART (1959). The Keton specimen agree with the description about the proximal extremity of the radius by VANDERHOOF: "From the appearance of the flattened and roughened posterior side of that bone, the ulna is thought to have been ankylosed with it. The anterior surface presents two glenoid fossae for the reception of the

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* Corresponding to medial and lateral part of trochlea.

condyles of the humerus."

NAGAO (1941) stated: "These bones (ulna and radius) are much flattened but deformed partly", and "apparently much expanded distally". But his statement "most of proximal particular surface occupied by radius" is too exaggerated. REINHART (1959) described about the specimen (U.C.M.P.no.39987) that the proximal articular facet is devided into two portions and provided with a central elevation. These facts and "progressive increase in diameter toward distal end " agree with the Keton specimen as well.

NAGAO stated: "antebrachial skeleton is more massive than that of sirenians, different from that of proboscideans." REINHART said: "In shape and proportions this radius is most similar to that of Hippopotamus."

iv) Manus

The carpi of Desmostylus have been examined only by SHIKAMA (1966). They are very similar to those of Paleoparadoxia (SHIKAMA, 1966). Both genera are common in the os hamatum decreasing in height laterally, and are peculiar among mammals.

The metapodials of Desmostylus have been already described by VANDERHOOF, NAGAO, REINHART and SHIKAMA, who discussed about their identifications. VANDERHOOF described for the first time three "right metacarpals" from California. NAGAO identified "two right metacarpi" in the Keton specimen as "something except for the first and

fifth", but he noted they are "quite different" from three metacarpals described by VANDERHOOF. REINHART did not conclude that three bones were the metacarpi and suggested the possibility that they were the metatarsi. SHIKAMA stated: "NAGAO designated two right bones (J and K) as the third and fourth metacarpi; they are distal end of the fourth (K) and fifth metacarpi (J)," and that three metacarpals from California belong to those of the left side, "Coalinga metacarpus may belong to Desmostylus, not to Paleoparadoxia,".

According to the author's observations, the bone that NAGAO identified as the left first rib is actually the left fifth metacarpus. The new identification is based on comparison with Izumi specimen of Paleoparadoxia tabatai. Moreover, two bones which have been hitherto identified as the metacarpi are the metatarsi. NAGAO's identification was perhaps based on the occurrence of fossil bones, and SHIKAMA interpreted shortness of the bones as missing of proximal part. However, their proximal articular surfaces are well preserved. Table 8 shows various views regarding identification of the metapodials mentioned above.

Characteristics of the metacarpus described by VANDERHOOF (1937) are: "The shaft is spatulate ··· . Metacarpal V is much the heaviest and has a decided offset just distal to the articular end." This agrees with the Keton specimen in the form of shaft and in the presence of "offset" in the proximal part. REINHART (1959) stated, "The

Table 8. Identifications of the metapodials of Desmostylus.
R: right, L: left, Mc: metacarpus, Mt: metatarsus

| | | VANDERHOOF (1937) | NAGAO (1941) | REINHART (1959) | SHIKAMA (1966) | INUZUKA (1981) |
|---|---|---|---|---|---|---|
| California specimen | UCMP no.32735-32737 | *D.hesperus* R. Mc. III,IV,V | | *D.h.* or *V.coalingensis* Mc. or Mt. | *Desmostylus* L. Mc. III,IV,V | L. Mc. III,IV,V |
| | UCMP no.32041 | Mc. I | | entirely different animal Mc. or Mt. | | |
| Keton specimen | UHR no.18466-15 (K) | | *D.mirabilis* R. Mc. IV | | *D.h.japonicus* R. Mc. IV | L. Mt. II |
| | UHR no.18466-16 (J) | | R. Mc. III | | R. Mc. V | L. Mt. III |
| | UHR no.18466-106 | | L. rib I | | L. rib I | L. Mc. V |

smooth articular surfaces of these bones is quite different from those of completely adapted aquatic animals".

According to NAGAO (1941), the phalanges of Desmostylus are "short and heavy, surface area of hand is short and wide." SHIKAMA (1966) has described all phalanges in detail but made partly wrong identifications. Judging from morphological characteristics mentioned above, the specimen UHRno.18466-17, which was regarded as the second middle phalanx of the left manus is a proximal phalanx, and UHRno.18466-37, designated as the second proximal phalanx of the left pes would be a middle phalanx. There are lots of questions regarding identification besides these, but they will be omitted since they are not important for restoration.

E. Hind limbs

1. Descriptions

i) Os coxae (UHRno.18466-105, Fig. 15, Plate VI)

The specimen is preserved almost perfectly, but is depressed and inclined to the right. Each side is broken above and below obturator foramen, and the ischium and the pubis on both sides join at symphysis pelvis.

Body of ilium is flat, long from dorsomedial to ventrolateral, triangular in frontal section in the caudal part, and has the ilio-pectineal line on the medioventral surface. The line becomes gradually obscure from the cranial margin of the pubis toward the ilium, but further

details are known due to the break near the acetabulum. More cranially it becomes a rounded ridge on which the ventral and the medial surfaces of the ilium meet at about a right angle. There is a slight elevation, possibly the psoas tubercle, in front of the anterior margin of the acetabulum on the left ilio-pectineal line.

The wing is triangular, widens and thickens forward to terminate at the thick iliac crest. It fans out laterally from the area between iliopectineal eminence and tuber coxae. Iliac fossa, the pelvic surface of wing, is raised in the medial one-third or a half, but is nearly flat in the lateral remainder. The surface twists clockwise on the right side at an angle of about 120 to 140 degrees to the dorsal surface of symphyseal branches of both pubis and ischium.

The crest of ilium to which the sartorius muscle attaches is convex forward in dorsolateral view. In cranial view it is flexed dorsally at a point a little medial to the middle, where the cranial margin of the iliac fossa and that of the sacropelvic face cross at an angle of 140 to 145 degrees. The dorsal lip of the crest is situated a little posterior to the ventral one, and the latter is more acute. The distance between both lips is biggest at the middle flexed part.

Tuber coxae to which the tensor fasciae latae muscle attaches is not bifurcated and bends somewhat ventrally. The tuber sacrale is long cranio-caudally, concave

laterally, and thicker in front. Its caudal end extends posterolaterally.

Gluteal surface to which the gluteus medius muscle attaches is directing rather dorsally than laterally. It is concave frontally and sagittally. The wing bears an oval, sagittally long depression in a little lateral to the center, the medial margin of which seems to be gluteal line.

The articular part has a length of about one-third of the total length of the os coxae, is in the shape of a scalene quadrilateral with a longer cranial and a shorter caudal border, and the medial surface is concave in frontal section. The outline of the auricular surface is indistinct, but it is probably a ventrocaudal part of the articular part.

Greater ischiatic notch is deepest just behind tuber sacrale, and becomes gradually narrower backward. In dorsal view, the shaft is flexed a little laterally at the notch.

The ischium is fairly long antero-posteriorly, and the section of the acetabular branch is almost a regular triangle with lateral, dorsal and ventral angles. Ischiatic spine is situated at the back of acetabulum and dorsal to the middle of obturator foramen, and the ischium is smaller in breadth there. In lateral view it raises tuberously and is not pointed. Lesser ischiatic notch is almost linear from the spine to tuber ischii, and does not hollow out.

The body of ischium is flat and its ventral surface to which the gracilis muscle and the adductor muscles attach is

transversely concave and becomes convex from the caudal end of obturator foramen, as followed dorsolaterally to the acetabular branch. Tuber ischii to which the biceps femoris muscle attaches is a long ridge, situated at the caudal end of the ischium and does not project laterally. The caudal end of the ischium to which the semitendinous muscle and the semimembranosus muscle attach is convex backward and ischial arch makes an angle of about 105 degrees.

Ilio-pectineal eminence develops on the medioventral part of the body of pubis. The branch of the pubis is extends backward at an angle of about 40+ degrees ventral and about 35+ degrees medial to the axis of the ischium. As the branch is followed backward, it becomes gradually broad in the posterior two-thirds of the branch, and flat and wide from anteromedial to posterolateral to join with the other branch. The branch has three crests, pecten ossis pubis in the cranioventral portion, the dorsal and the caudal crest. Both anterior and posterior surfaces of the dorsal crest incline more gently, as they are traced more medially, so the angle between them becomes obtuse. The branch in cross section is a dorso-ventrally tall triangle with dorsal, ventral and posterolateral angles, in cranial region, and it becomes depressed dorso-ventrally backward, for the branch rotates clockwise, as its cranial margin bends medially and the caudal one laterally in the left pubis. The dorsal crest runs a distance of about 40 mm to pecten ossis pubis, facing pelvic cavity, and forms an arc

convex backward with the fellow of the other side in the medial part near the anterior margin of obturator foramen. Pecten ossis pubis increases in thickness near the median line to make pubic tubercle.

Symphysis pelvis is situated rather behind, its anterior end is at about the cranial one-third of obturator foramen. The median ventral margin of symphysis is linear in lateral view, and the cranial margin is V-shaped with in angle of about 120 degrees in cranial view.

Acetabulum is nearly circular, though depressed slightly due to the deformation. It is situated almost in the middle of the whole hip bone, and the distance from acetabulum to the cresat of ilium is about same as the length of the femur. Acetabulum directs backward at an angle of about 70 degrees to the axis of the pelvis. Acetabular notch opens backward and is narrow. Acetabular fossa is round, wider than acetabular notch.

The cranial margin of the acetabulum protrudes laterally most and the caudal one protrudes less, and the dorsal margin protrudes laterally a little more than the ventral one. The dorsal margin is a sharp crest, but the ventral one is broad and makes a tubercular surface broadening backward. The dorsal margin is straight with a little undulation, and does not hollow out in the middle.

In the dorsal surface over acetabulum, rugged surface is well-developed, raises and extends particularly inward at the cranial one-third and caudal one-third portion of

acetabulum. The cranial margin of acetabulum is tubercular on the lateral surface.

Obturator foramen is in the shape of an antero-posteriorly long spindle. The cranial end of obturator foramen is situated posterior to acetabulum. The region medial to the foramen is so wide that obturator foramen faces rather outward than downward.

The pelvis is deformed so that it is depressed dorso-ventrally as a whole, the axis of the pelvis is inclining left at about 5 degrees, and the dorsal side tilting right.

The inlet of pelvis is square in shape and broadens slightly near the medial part of acetabulum. The outlet of pelvis is semicircular in shape in the left half and is depressed in the right half due to the deformation.

The pelvis inclines backward at about 30 degrees to the long axis of the sacrum, but probably the value is actually larger as the specimen is deformed and depressed. Pelvic cavity is surrounded by broad symphysis on ventral side, obturator foramen in front and the plate of ischium behind on lateral sides.

Sacro-ischiatic notch is U-shaped with an anterior apex in both dorsal and lateral view. The anterior end of the crest of ilium is situated at the level of the middle of body of the fourth lumbar vertebra. The medial region of the wing of ilium covers the first dorsal sacral foramen.

ii) Femur (UHRno.18466-28,29, Fig.17, Plate VII)

The side of the specimens is judged from condyles on the posterior surface and head on the medial. Each specimen is preserved almost perfectly, but the right one is more deformed than the other. Portions that differ considerably in shape between them may be caused by deformation due to compression in antero-posterior direction. As a whole width of the femur is large for the length, cranio-caudal diameter is small. Epiphyses are well developed.

Head is semispherical in shape, 87 and 88 mm in diameter. Its direction is nearly equal to that of neck. It makes an angle of 45 degrees medial to the shaft, 15 degrees cranial in medial view, and twisted at 10 to 20 degrees cranial to the transverse axis in proximal view. The surface is smooth and the fovea capitis is indistinct.

Neck is distinctly constricted in all directions, and has the minimum diameter 63 mm measured in anterior view, the minimum cranio-caudal diameter 47 to 49 mm in meidal, and the minimum diameter 32 to 33 mm in proximal.

Trochanter major to which the gluteus muscles attach is a huge tubercle of about 75 mm in antero-posterior diameter and 85 to 90 mm in dorso-ventral diameter. It is in the shape of reversed triangle in lateral view, projects forward and backward from neck in proximal view. Its top is situated obviously at a lower level than head.

Trochanteric fossa to which the obturator muscle and the gemelli muscles attach is a depression, a reversed triangle in outline, lying in proximal one quarter of the

shaft. Its maximum width is about one half of that of shaft. The depth of the fossa corresponds to expansion of trochanter major in anterior surface, and has it is about 30 mm deep at the deepest point from posterior surface in the lateral.

Trochanter minor to which the iliopsoas muscle attaches is a round tubercle of proximal one-third about 25 mm in diameter in posterior part of the medial margin of shaft. Along the medial margin a rough surfaced area to which the pectineus and the adductor muscles attach is conspicuous. Its maximum width is 35 mm and the length about 100 mm. It lies in the distal one-third of shaft below trochanter minor. The area is flat, long ellipsoid in outline as a whole, facing caudally at an angle of 35 degrees to the medial.

A small rough area on the lateral margin, about 60 mm distal to the lateral end of trochanter major, may be corresponding to trochanter tertius. Trochanteric ridge is overhanging on trochanteric fossa, running obliquely at angle of about 20 degrees to the longitudinal axis of the shaft from the proximolateral to the distal.

Each shaft is different in shape on account of deformation due to compression. The outline of shaft is rectangular in anterior view, narrow in the middle and bending laterally in the distal. Shaft surface is smooth, rise in the median line from the neck.

The smooth posterior surface is more flat than the

anterior one, and has no rough surface in the middle. A number of rough lines run longitudinally in trochanter minor, its downward extension and the lateral part of trochanteric ridge. A rough surface from which the gastrocnemius muscle originates is present just above medial and lateral condyles.

The lateral margin runs obliquely and lies more anteriorly toward the distal end. It is sharp in the upper half and obtuse in the lower. The medial margin is more stout and obtuse than the lateral, running sigmoidally as a whole, as its middle one-third is occupied by trochanter minor and its downward extension which makes a rough surface, and running obliquely from proximocaudal to craniodistal.

Intercondyloid fossa is a narrow groove due to the contact of both condyles. It may be caused by deformation. They run obliquely from superiomedial to inferolateral at an angle of 10 to 20 degrees to the longitudinal axis in posterior view. The direction is perpendicular to trochlear groove in the anterior surface in distal view.

Both medial and lateral epicondyles expands in the central portion and are about 50 mm in diameter. Medial epicondyle is broken in the left femur, and lateral in the right. Trochlea is smoothly convex in lateral view, not concave in transverse direction, does not rise in the margin, and its height and width are nearly equal.

Both left acetabulum and the head of femur are about 265 mm in circumferential length. In adduction and abduction, the range of contact in hip joint is 50 degrees with regard to the direction of the shaft of femur, from 30 to 80 degrees ventral to the horizontal plane, and in rotation, 70 degrees, from 10 degrees cranial to 60 degrees caudal to the frontal plane. The range of contact in knee joint is unknown due to the break and loss of the proximal articular surface of the tibia.

iii) Tibia (UHRno.18466-30, Fig.19, Plate VIII)

The specimen is judged as the left tibia, based upon the prominent crest and medial malleolus in the distal extremity. Excepting that the proximal articular surface is lacking due to a geological joint inclining backward, it is preserved almost perfectly, but is compressed antero-posteriorly as a whole, and flexed in the middle of the shaft due to the repair.

The tibia is wide from side to side, short as a whole and constricted in the middle. It is flat antero-posteriorly. Anterior margin projects in the proximal half. The direction of longitudinal axis of distal articular surface is twisted inward at the angle of 40 degrees to the medio-lateral axis of the proximal surface.

The proximal articular surface is not known due to the break and loss. The proximal portion is kidney-shaped in cross section, long transversely, concave posteriorly. The tuberosity to which the quadriceps femoris muscle attaches

is developed remarkably on the crest of tibia. It is 65 mm in width, in the shape of triangle with a sharp point upward, and its surface is very rough.

The medial surface is flat, and the posterior surface concave, widens in both epiphyses. The medial surface is smaller than the posterior. The lateral surface is concave in both vertical and horizontal directions, and is covered by the anterior margin in the proximomedial part. Each surface is smooth in shaft.

The medial margin runs straight vertically in distal half. The lateral margin is undulated sigmoidally and the proximal part is stout to make a tubercle to which the peroneus longus muscle attaches. Tibial crest runs obliquely from the proximal part of the anterior surface to the medial malleolus at about 25 degrees medial and 20 degrees caudal to the longitudinal axis of the tibia. Free margin of the crest inclines laterally in the proximal portion.

The articular surface of the distal extremity is concave sagittally with medial and lateral articular grooves and with an intermediate ridge. The distal border around the articular surface is inclining cranially and laterally, at an angle of about 25 degrees medial and 25 degrees posterior to the horizontal plane.

Medial malleolus is a tubercle, ellipsoidal in shape, 66 mm in height and 45 mm in cranio-caudal diameter. It has many rough lines running vertically on its surface. As it

projects more distally than the distal end of the anterior surface and the middle part of distal end of posterior surface is also projecting, the border around articular surface is undulated.

The tibia cannot be articulated with the talus, as the articualr surface is compressed antero-posteriorly. In case of flexsion within the range of contact of articular surfaces in the tibio-tarsal articulation, the angle between directions of the shaft of tibia and of longitudinal axis of the tuber calcis is ranging from 40 to 90 degrees.

iv) Pes

Concerning the tarsi (Fig.21, Plate VIII), refer to Table 7, and the metatarsi to Table 8.

Phalanges of the pes show features similar to those of the manus. In Desmostylus, they are dorso-ventrally thicker than the latter. In proximal phalanges, upward decrement in width of proximal surface is smaller, differences in width between proximal and distal portions larger and depression of distal surface shallower and narrower than in the fore phalanges. In the middle phalanges, sloping angle of proximal surface is smaller, distal surface wider.

2. Remarks

i) Pelvis

According to NAGAO's description, the os coxae of Desmostylus is: "Heavily built, with an expanded ilium, a deep acetabulum, a large obturator foramen and a well developed pubis"; this agrees with the author's

observations. REINHART (1959) outlined left fragment of the pelvis (U.C.M.P.no.40000) with the statement: "Neck of ilium forms half cylinder, flat laterally, round medially, anterior half expanded into broad blade, concave laterally, convex medially;crest and dorsal border of ilium broadly rounded, ventral border a thin crest; lunate depression midway on dorsomedial surface of ilium marks articular surface for contact with sacrum; acetabulum a deep hemispherical pocket, deeply emarginated posteriorly by a pit for the round ligament; flat medial surface behind acetabulum; fragment of ischium transversely flat, round borders, obturator foramen large."

In comparison with other animals, NAGAO (1941) states: "Pelvic girdle of Desmostylus is generally a little expanded in ilium compared with many graviportal forms like proboscideans, differs from that of completely aquatic forms like sirenians"; and REINHART (1959) as follows: "There are pelvic peculiarities, except in detail, separating it from the pelves of many terrestrial animals. It is more strongly developed than the pelvis of the earliest sirenian but is far less massive than the pelvic construction in proboscideans."

ii) Femur

NAGAO (1941) noted an important point concerning the femur: it is "with a well developed lesser trochanter (minor trochanter) and without a third trochanter." The Keton specimen agrees partly with the right femur

(U.C.M.P.no.39985) described by REINHART (1959): "Relatively short, stoutly developed; large bulbous head ··· ; constricted neck; lesser trochanter well developed, trochanteric fossa deep; shaft transversely broad, horizontally narrow;". In the Keton specimen, however, neck is shorter, minor trochanter is neither "triangular" nor "conical" in shape, distal end is not so "broadly expanded"; both specimens are fairly different in outline, thus, possibly REINHART's specimen does not belong to Desmostylus.

NAGAO mentioned: "This (femur) is relatively shorter compared with many proboscideans and is expanded remarkably in distal end". REINHART clarified "great differences" between desmostylids and sirenians or proboscideans, that is, "the femora of sirenians are elongate fusiform, greatly reduced in size," and "the femora of proboscideans are proportionally more elongate with less expanded extremities."

iii) Crural skeleton

NAGAO (1941) outlined the characteristics of the tibia of the Keton specimen: "It is much deformed, wide conspicuously; compared with proboscideans it is rather short and stout; distal end expanded; cnemial crest well developed; very different from that of Palaeomastodon."

The fibula and the patella of Desmostylus have not been described as yet. In the Utanobori specimen, the fibula is considerably shorter and thinner than tibia. The patella is large in proportion to the femur and has a flat articular

surface.

iv) Pes

NAGAO (1941) noted four kinds of the tarsi in the Keton specimen: "Both astragalus and calcaneum have peculiar features in form." All the six tarsi remaining in the Utanobori specimen have the same arrangement as Paleoparadoxia with a reductive tendency in medial bones. NAGAO has stated that the astragalus differs from those of proboscideans, perissodactyls and artiodactyls, and the calcaneum differs from that of proboscideans, but is close to that of some ungulates.

As for metatarsi, there are two bones in addition to the two which NAGAO designated as metacarpi.

# Appendix II. Measurements of bones

I. Dorsal vertebrae (Table 9)

1. maximum length parallel to the vertebral axis from the cranial articular or mammiloarticular processes to the caudal articular processes
2. Breadth across the transverse processes. In case of missing one side beneath another side tip to the median plane
3. Breadth across the cranial articular processes (prezygapophyses)
4. Breadth across the caudal articular processes (postzygapophyses)
5. Breadth across the base of the pedicles
6. Breadth of the vertebral foramen at the cranial surface
7. Breadth of the vertebral foramen at the caudal surface
8. Height of the vertebral foramen at the cranial surface
9. Height of the vertebral foramen at the caudal surface
10. Breadth of the cranial extremity. In thoracic vertebrae vertebrae, excluding the facets for the rib heads
11. Height of the cranial extremity
12. Breadth of the caudal extremity
13. Height of the caudal extremity
14. Maximum height
15. Length of the body
16. Height of the spinous process

Table 9. Measurement of thoracic and lumbar vertebrae.
Specimen number: UHRno. 18466-56—68
Measuring points: 1—14
—: impossible to measure, (): repaired, +: less than the true value, -: more than the true value, *: double value of a half side.

| Vert. dors. | Th4? | Th5? | Th7 | Th8 | Th9 | Th10 | Th11 | Th12 | Th13 | L1 | L2 | L3 | L4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UHR no.18466- | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 |
| 1 | 83+ | 103+ | (83) | (91) | — | 91 | 79 | 83 | 89 | 86 | 85+ | 78+ | 87+ |
| 2 | 155+ | 159+ | 140+ | 177 | 174* | 139+ | 143+ | 162+ | 139+ | 155+ | 168+ | 168+ | 200+ |
| 3 | 104+ | (73) | — | 96+ | — | — | (92) | 93+ | (117) | 114+ | 95+ | 110+ | 124 |
| 4 | 80 | 71+ | 70 | 69 | 66 | 56 | 65+ | — | — | — | 82+ | 90+ | 88+ |
| 5 | 50 | 44 | 50 | 51 | — | 40 | 44 | 44 | — | 46 | 38 | 57+ | — |
| 6 | 38 | 29 | 27 | 26 | — | 26 | 30 | 28 | 27 | 25 | 22 | 23 | 23 |
| 7 | 29 | — | — | — | 25+ | 21 | 29 | 25 | 28 | 23 | 19 | 25 | — |
| 8 | — | 80 | 88* | 84 | — | 85+ | 85 | 90 | 90 | 94 | — | 106 | 114 |
| 9 | 58+ | 66 | 49+ | 42 | — | 45 | 51 | — | 59 | 61 | 50 | 52 | 50 |
| 10 | 80 | — | 93 | — | 88 | — | 95+ | 111 | 108 | 95 | 106 | 99+ | — |
| 11 | 63 | — | 56 | — | 55 | 46 | 49 | 55 | 62 | 63 | 52 | 56 | — |
| 12 | 127+ | 138+ | (110) | (112) | 135 | 131 | 142 | 142 | 156 | 148 | 147 | 139 | 125+ |
| 13 | 43 | 63 | 56 | 60 | — | 53 | 56 | 63 | 56 | 54 | 56 | 57 | 63 |
| 14 | 34+ | 45+ | — | (40) | 61- | 58- | 64 | 66- | 72 | 64 | 73 | 66 | 48+ |
| 15 | | | | | | | | | | 46 | 51 | 56 | — |
| 16 | | | | | | | | | | 41 | 43 | 41 | 47 |

II. Sacrum (mm)

1. Maximum length parallel to vertebral axis from the cranial border of the wings to the caudal border of the body of the last segment 269
2. Maximum breadth across the wings 241
3. Breadth across the wings in the posterior end of the auricular surfaces 214
4. Breadth across the lateral borders in its posterior end 157
5. Breadth across the cranial articular processes of the first segment 133
6. Breadth across the caudal articular processes of the last segment 28
7. Width of the vertebral foramen at cranial surface 72
8. Height of the vertebral foramen at cranial surface 18
9. Breadth of the anterior extremity 130
10. Height of the anterior extremity 45
11. Breadth of the posterior extremity 49
12. Height of the posterior extremity 27
13. Vertical height from the ventral border of the body to the highest point of the spinous process 91
14. Body length between the ventral border of the anterior extremity and that of the posterior extremity 242
15. Vertical height from the median anterior margin of the arch to the highest point of the spinous process 27

III. Caudal vertebrae (Table 10)

Table 10. Measurement of caudal vertebrae.
Specimen number: UHRno. 18466-70—77
Measuring points: 1—7
+: less than the true value

| UHR no.18466-70 | 71 | 72 | 73 a | 73 p | 74 | 75 | 76 | 77 |
|---|---|---|---|---|---|---|---|---|
| 1 | 47 | 42 | 43 | 38 | 38 | 41 | 37 | 33+ | 29+ |
| 2 | 51 | 47 | 45 | 40 | 40 | 43 | 43 | 41 | 36 |
| 3 | 28 | 24 | 28 | 28 | 29 | 28 | 28 | 26 | 22 |
| 4 | 45 | 44 | 42 | 41 | 40 | 43 | 40 | 33 | 36 |
| 5 | 29 | 29 | 33 | 33 | 29 | 26 | 27 | 26 | 25 |
| 6 | 43 | 40 | 35 | 35 | 37 | 40 | 39 | 39 | 34 |
| 7 | 34 | 29 | 27 | 25 | 24 | 25 | 23 | 24 | 20 |

1. Maximum length of the caudal vertebra
2. Breadth of the anterior extremity
3. Height of the anterior extremity
4. Breadth of the posterior extremity
5. Height of the posterior extremity
6. Breadth of the body in the middle
7. Height of the body in the middle

IV. Ribs (Table 11)

1. Maximum length from the most sternal point of the sternal extremity to the dorsal end of the costal tubercle on the most vertebral point of the costal head (total length)
2. Length along the costal axis from the corner of the facet for articulation of the head to the center of the sternal extremity (arc length)
3. Length from the center of the facet for articulation of the head to the center of the sternal extremity
4. Length from the costal angle to the lateral end of the tubercle
5. Length from the costal angle to the lateral end of the tubercle
6. Dorso-ventral diameter of the facet for articulation of the costal head
7. Cranio-caudal diameter of the facet for articulation of the costal head
8. Dorso-ventral diameter of the costal neck
9. Cranio-caudal diameter of the costal neck

Table 11. Measurement of ribs.
Rib position: 1—13, R: right, L: left
Measuring points: 1—17
-: impossible to measure, +: less than the true value

| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I | R | 281 | 295 | 248 | 82 | 61 | 32 | 26 | 29 | 26 | 37 | 28 | 44 | 26 | 73 | 32 | 70 | 29 |
| | L | 271 | 285 | 229 | 82 | 38 | 31 | 25 | 28 | 26 | 41 | 29 | 45 | 22 | 76 | 21 | 56 | 34 |
| II | R | 317 | 345 | 321 | 78 | 62 | 34 | 31 | 30 | 22 | 25 | 27 | 46 | 18 | 56 | 16 | 37 | 17 |
| | L | 281+ | - | - | - | - | - | - | - | - | - | 30 | - | - | 58 | 17 | - | - |
| III | L | 291 | - | - | - | 83 | - | - | - | - | 25 | 25 | 53 | 17 | 68 | 22 | - | - |
| IV | R | 260+ | - | - | - | - | - | - | - | - | - | - | - | - | 49 | 16 | 48 | 21 |
| | L | 315+ | - | - | - | - | - | - | - | - | - | - | - | - | 51 | 20 | 41 | 19 |
| V | R | 439+ | - | - | - | - | - | - | - | - | - | - | - | - | 50 | 16 | 49 | 22 |
| | L | 535+ | - | - | - | - | - | - | - | - | 25 | 23 | - | - | - | - | - | - |
| VI | R | 404+ | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 47 | 22 |
| | L | 386+ | - | - | - | - | - | - | - | 16 | 30 | 26 | - | - | 49 | 24 | - | - |
| VII | R | 545+ | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 45 | 25 |
| | L | 573 | 700 | 548 | 90 | - | 41 | 41 | 28 | 36 | 25 | 25 | 40 | 28 | 45 | 28 | 39+ | 26 |
| VIII | R | - | 770 | 637 | - | - | 40 | 41 | 26 | 30 | - | - | 37 | 30 | 38 | 27 | 37 | 25 |
| | L | 478+ | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 41 | 16 |
| IX | R | 633+ | 755 | 622 | 91 | - | 40 | 43 | 26 | 30 | - | - | 38 | 28 | - | - | 43 | 23 |
| | L | 622 | 750 | 622+ | 95 | - | 45 | 36 | 30 | 25 | 24? | 23? | 42 | 25 | 43 | 26 | 37 | 33 |
| X | R | 614+ | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 35 | 28 |
| | L | 598 | 695 | 618 | 81 | - | 38 | 41 | 24 | 30 | 25 | 21 | 35 | 24 | 39 | 23 | 34 | 25 |
| XI | R | 563+ | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 29 | 32 |
| | L | 547+ | - | - | 71 | - | 36 | 44 | 24 | 30 | 28 | 19 | 34 | 25 | - | - | - | - |
| XII | R | 549 | 605 | 561 | 62 | - | 29 | 36 | 23 | 26 | 20 | 18 | 35 | 25 | 37 | 26 | 33 | 28 |
| | L | 533 | 575 | 539 | 58 | - | 32 | 38 | 25 | 32 | 23 | 18+ | 35 | 25 | - | - | 35 | 22 |
| XIII | R | 499 | 500 | 488 | - | - | 30 | 35 | - | - | - | - | 35 | 26 | 37 | 20 | 34 | 22 |
| | L | 491 | 500 | 488 | - | - | 22 | 33 | - | - | - | - | 33 | 26 | 37 | 24 | 31 | 19 |

10. Medio-lateral diameter of the facet for articulation of the costal tubercle
11. Cranio-caudal diameter of the facet for articulation of the costal tubercle
12. Longer (medio-lateral) diameter of the costal shaft in the middle
13. Shorter (cranio-caudal) diameter of the costal shaft in the middle
14. Maximum breadth of the costal shaft
15. Thickness crosswise of the maximum breadth of the costal shaft
16. Longer (cranio-caudal) diameter of the sternal extremity17. Shorter (medio-lateral) diameter of the sternal extremity

V. Left scapula (mm)

1. Maximum height parallel to the spine from the ventral end of the tuber scapulae to the vertebral border 425
2. Height of the base of spine 374
3. Height from the dorsal end of the base of spine to the ventral end of the acromion 315
4. Smallest length from the cranial angle to the caudal border 203
5. Maximum length of the supraspinous fossa perpendicular to the spine 88
6. Smallest cranio-caudal length of the neck of the scapula 78

| | |
|---|---|
| 7. Length from the caudal end of the glenoid cavity to the lateral end of the base of tuber scapulae | 110 |
| 8. Length of the glenoid cavity | 106 |
| 9. Breadth of the glenoid cavity | 84 |
| 10. Maximum thickness of the surface of acromion perpendicular to the spine | 31 |
| 11. Breadth from the top of the acromion surface to the lateral surface | 74 |
| 12. Distance from the medial margin of the glenoid cavity to the acromion | 158 |

| VI. Left humerus | (mm) |
|---|---|
| 1. Maximum length | 408 |
| 2. Maximum cranio-caudal diameter of proximal extremity | 98 |
| 3. Maximum width of proximal extremity | 152 |
| 4. Cranio-caudal diameter of head | 76 |
| 5. Breadth of head | 108 |
| 6. Height of major tubercle | 7.5 |
| 7. Minimum breadth of the shaft | 71 |
| 8. Cranio-caudal diameter of the shaft in the middle | 47 |
| 9. Maximum breadth of the distal extremity | 163 |
| 10. Breadth of the trochlea in the distal end | 125+ |
| 11. Breadth of olecranon fossa | 36+ |
| 12. Maximum height of the trochlea | 77+ |
| 13. Cranio-caudal diameter of the medial condyle | 78+ |
| 14. Cranio-caudal diameter of the lateral condyle | 84+ |
| 15. Breadth of the supratrochleal foramen | 24 |

16. Height of the supratrochleal foramen 14

VII. Antebrachial skeleton

[Left radius] (mm)

1. Maximum length 291
2. Maximum breadth of the proximal extremity 88+
3. Maximum cranio-caudal diameter of the proximal extremity 64
4. Cranio-caudal diameter of the neck 52
5. Breadth of the shaft in the middle 27
6. Cranio-caudal diameter of the shaft in the middle 66
7. Maximum width of the distal extremity 86
8. Maximum cranio-caudal diameter of the distal extremity 97
9. Breadth of the carpal articular surface 81
10. Thickness of the carpal articular surface 80

[Left ulna]

11. Maximum length 331
12. Cranio-caudal diameter of the olecranon in the beak 116
13. Cranio-caudal diameter of the olecranon in the semilunar notch 73
14. Cranio-caudal diameter of the olecranon in the coronoid process 71
15. Cranio-caudal diameter of the shaft in the middle 55
16. Maximum cranio-caudal diameter of the distal extremity 82

| | |
|---|---|
| 17. Breadth of the olecranon | 44 |
| 18. Length of the olecranon | 112 |
| 19. Minimum width of the semilunar notch | 42 |
| 20. Length of the semilunar notch | 54 |
| 21. Maximum width of the semilunar notch | 92 |
| 22. Breadth of the radial notch | 88+ |

| VIII. Left fifth metacarpus | (mm) |
|---|---|
| 1. Maximum length | 170 |
| 2. Cranio-caudal diameter of the shaft in the middle | 23 |
| 3. Transverse breadth of the shaft in the middle | 44 |
| 4. Cranio-caudal diameter of the shaft in the distal | 43+ |
| 5. Transverse breadth of the shaft in the distal | 54+ |
| 6. Cranio-caudal diameter of the medial surface in the proximal | 43 |
| 7. Transverse breadth of the shaft in the proximal | 46 |

| IX. Pelvis | left | right | (mm) |
|---|---|---|---|
| 1. Maximum length of one half | 649 | 636 | |
| 2. Length from the cranial end of the iliac crest to the cranial margin of the acetabulum | 311 | 326 | |
| 3. Length from the cranial margin of the acetabulum to the lateral end of the tuber ischii | 310 | 315 | |
| 4. Length of the symphysis | 168 | | |
| 5. Width from the tuber coxae to the tuber sacrale | 218 | 207 | |
| 6. Thickness of the tuber sacrale | 32 | 29 | |

| | | |
|---|---|---|
| 7. Minimum height of the shaft of ilium | 37 | 40 |
| 8. Minimum breadth of the shaft of ilium | 86 | 80 |
| 9. Length of the acetabulum | 107 | 94 |
| 10. Height of the acetabulum | 80 | 67+ |
| 11. Minimum height of the branch of ischium | 46 | 37 |
| 12. Thickness of the branch of ischium in the anterior end of the ischiatic spine | 43 | 52 |
| 13. Maximum length of the obturator foramen | 136 | 131 |
| 14. Maximum height of the obturator foramen | 69 | 66 |
| 15. Minimum cranio-caudal diameter of the branch of pubis | 46 | 44 |
| 16. Minimum dorso-ventral diameter of the branch of pubis | 28 | 29 |
| 17. Minimum breadth from the obturator foramen to the symphysis | 84 | 84 |
| 18. Distance from the cranial end of the symphysis to the medial margin of the acetabulum | 183+ | 210 |
| 19. Distance from the caudal margin of the acetabulum to the lateral end of the tuber ischii | 205 | 216 |
| 20. Distance from the caudal margin of the acetabulum to the caudal end of ischium | 250 | 248 |
| 21. Breadth from the lateral end of the tuber ischii to the caudal end of the symphysis pelvis | 130 | 150 |
| 22. thickness of the tuber ischii | 15 | 17 |
| 23. Length from the caudal margin of the obturator foramen to the caudal margin of the ischium | 100 | 95 |
| 24. Breadth across the ischiatic spines | 240 | |

| | |
|---|---|
| 25. Breadth across the auricular surfaces | 190 |
| 26. Breadth across the tubera coxarum | 557 |
| 27. Breadth across the acetabula | 482 |
| 28. Breadth across the deepest points of the acetabula | 293 |
| 29. Breadth across the tuber ischiadica | 243 |

| X. Femur | left | right | (mm) |
|---|---|---|---|
| 1. Maximum length | 404 | 410 | |
| 2. Maximum width of the proximal extremity | 152 | 142 | |
| 3. Length between the trochanter major and minor | 151 | 154 | |
| 4. Transverse diameter of the head | 84 | 87 | |
| 5. Cranio-caudal diameter of the head | 85 | 86 | |
| 6. Cranio-caudal diameter of the trochanter major | 76 | 74 | |
| 7. Length of the neck | 108 | 120 | |
| 8. Cranio-caudal diameter of the shaft in the middle | 42 | 32 | |
| 9. Breadth of the shaft in the middle | 85 | 84 | |
| 10. Maximum breadth of the distal extremity | 120 | 134 | |
| 11. Breadth of the distal end | 114 | 117 | |
| 12. Cranio-caudal diameter of the medial condyle | 121 | 111 | |
| 13. Cranio-caudal diameter of the lateral condyle | 114 | 99 | |
| 14. Breadth of the trochlea | 58+ | 58 | |

| | | |
|---|---|---|
| 15. Height of the trochlea | 57 | 62 |
| 16. Cranio-caudal diameter of the intercondyloid fossa | 92 | 83 |

| XI. Left tibia | (mm) |
|---|---|
| 1. Maximum length | 325 |
| 2. Maximum cranio-caudal diameter of the proximal extremity | 90 |
| 3. Maximum breadth of the proximal extremity | 131+ |
| 4. Cranio-caudal diameter of the shaft in the middle | 48 |
| 5. Breadth of the shaft in the middle | 71 |
| 6. Maximum breadth of the distal extremity | 151 |
| 7. Maximum cranio-caudal diameter of the distal extremity | 84 |
| 8. Length of the articular surface of the distal extremity | 125+ |

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# Literature

ABEL, O. (1922) Desmostylus: Ein mariner multituberculate aus dem Miozän der Nordpazifischen Küstenregion. Acta Zoologica. 3: 361-394

------- (1925) Geschichite und Methode der Rekonstruktion vorzeitlicher Wirbeltiere. Viii+327pp., Verlag von Gustav Fischer, Jena.

ANDREWS, C. W. (1906) A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. 319pp., British Museum (Nat. Hist.), London.

BOCK, W. J. (1981) Functional-adaptive analysis in evolutionary classification. Amer. Zool. 21: 5-20

DOMNING, D. P. (1976) An ecological model for late Tertiary sirenian evolution in the North Pacific ocean. Systematic Zoology. 25 (4): 352-362

FLOWER, W. H. (1885) An introduction to the osteology of the Mammalia. 3rd ed., Xi+382pp., Macmillan and co., London.

GREGORY, W. K. (1912) Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Annals N. Y. Acad. Sciences. 22: 267-294

------ (1941) Evolution emerging. Vol. 1, XXVi+736pp., Macmillan, New York.

HALSTEAD, L. B. (1975) The evolution and ecology of the dinosaurs. 116pp., Peter Lowe.

------ (1978), The evolution of the mammals. 116pp., Peter

Lowe.

HASEGAWA, Y. (1977) Queer mammal desmostylid was restored. Anima. 5 (12): 90-91 (in Japanese)

HAY, O. (1915) A contribution to the knowledge of the extinct sirenian Desmostylus hesperus MARSH. Proc. U. S. Nat. Mus. 49: 381-397

HILDEBRAND, M. (1974) Analysis of vertebrate structure. XV+ 710pp., John Wiley and Sons, New York.

HOPSON, J. A. and RADINSKY, L. B. (1980) Vertebrate paleontology: new approaches and new insights. Paleobiology. 6 (3): 250-270

IJIRI, S. (1939) Microscopic structure of a tooth of Desmostylus. Proc. Imp. Acad. 15 (5): 135-138

IJIRI, S. and KAMEI, T. (1961) On the skulls of Desmostylus mirabilis NAGAO from South Sakhalin and of Paleoparadoxia tabatai (TOKUNAGA) from Gifu Prefecture, Japan. Earth Science. 53: 1-27 (in Japanese)

INUZUKA, N. (1980a) The skeleton of Desmostylus mirabilis from South Sakhalin I. Atlas and thoracic vertebrae. Earth Science. 34: 205-214 (in Japanese)

------ (1980b) The skeleton of Desmostylus mirabilis from South Sakhalin II. Lumbar vertebrae, sacrum and coccygeal vertebrae. Earth Science. 34: 247-257 (in Japanese)

------ (1981a) The skeleton of Desmostylus mirabilis from South Sakhalin III. Ribs, scapula and os coxae. Earth Science. 35: 1-18 (in Japanese)

------ (1981b) The skeleton of Desmostylus mirabilis from

South Sakhalin IV. Metacarpus. Earth Science. 35: 240-244 (in Japanese)

------ (1981c) A trial method of the mounting —— Basis of the skeletal reconstruction of Desmostylus ——. Fossil Club Bulletin. 14: 1-7 (in Japanese)

------ (1981d) Newly restored Desmostylus. Geological News. 327: 59-63 (in Japanese)

------ (1982) The skeleton of Desmostylus mirabilis from South Sakhalin V. Limb bones. Earth Science. 36: 117-127 (in Japanese)

KAMEI, T. and OKAZAKI, Y. (1975) Neogene desmostylid and proboscidean fossils from Japan. In Editorial Committee published by Tsukiji Shokan Publishing Co. Ltd., (ed.), Atlas of Japanese fossils (34). Tsukiji Shokan Publishing Co. Ltd., Tokyo (in Japanese)

KENT, G. C. (1978) Comparative anatomy of the vertebrates. 4th ed., XiV+465pp., The C. V. Mosby Company, Saint Louis.

KHOMENKO, J. (1928) Neue Ergebnisse uber die Familie der Desmostylidae. Zapiski Rossiiskogo Mineralogicheskogo Obshchestva. 57 (1): 140-147

KURTÉN, B. (1971) The age of mammals. 250pp., Weidenfeld and Nicolson, London.

LESSERTISSEUR, J. and SABAN, R. (1967) Squelette appendiculaire. In GRASSÉ, P. P. (ed.) Traité de zoologie. 16 (1), 1162pp., Masson, Paris: pp. 709-1078

MARSH, O. C. (1884) Dinocerata a monograph of an extinct order of gigantic mammals. United States Geological

Survey. 10: 1-191

------ (1888) Notice of a new fossil sirenian, from California. Amer. Jour. Sci. ser. 3, 35: 94-96

MCKENNA, M. C. (1975) Toward a phylogenetic classification of the Mammalia. In LUCKETT, W. P. and SZALAY, F. S. (eds.) Phylogeny of the Primates. XVi+483pp., Plenum, New York: pp. 21-46.

MERRIAM, J. C. (1906) On the occurrence of Desmostylus MARSH. Science. (n.s.) 24: 151-152

MINATO, M. and IJIRI, S. (1976) Color illustrations of natural history. Tokyo Bunkyo Publishing Co. Ltd., Tokyo (in Japanese)

MITCHELL, E. (1966) Faunal succession of extinct north Pacific marine mammals. Norsk Hvalfangst-Tidende. 3: 47-60

NAGAO, T. (1935) desmostylus mirabilis nov. from Sakhalin. Jour. Geol. Soc. Jap. 42 (507): 822-824

----- (1941) On the skeleton of Desmostylus. Jubilee Publication in the Commemoration of Prof. H. YABE's 60th birthday. 43-52 (in Japanese)

NAGAO, T. and OISHI, S. (1934) Newly discovered Desmostylus remains in the frontier district of South Sakhalin. Jour. Geogr. Tokyo. 46: 103-111 (in Japanese)

OSTROM, J. H. (1969) Osteology of Deinonychus antirrhpus, an unusual theropod from the Lower Cretaceous of Montana. Peabody Museum of Natural History Yale University, Bull. 30: 1-165

RADINSKY, L. B. (1977) Early primate brains: facts and

fiction. J. Human Evolution. 6: 79-86

------ (1982) Evoluiton of skull shape in carnivores. 3. The origin and early radiation of the modern carnivore families. Paleobiology. 8: 177-195

REINHART, R.H. (1953) Diagnosis of the new mammlian order Desmostylia. Jour. Geol. 61 (2): 187

------ (1959) A review of the sirenia and desmostylia. Univ. California Publications in Geol. Sci. 36: 1-146

ROMER, A. S. (1966) Vertebrate paleontology. 3rd ed., 468pp., University Chicago Press, Chicago.

ROMER, A. S. and PARSONS T. S. (1977) The vertebrate body. 5th ed., 624pp., W. B. Saunders Co., Philadelphia.

SCHEFFER, V. B. (1976) A natural history of marine mammals. Xi+157pp., Charles Scribner's Sons, New York.

SHIKAMA, T. (1966) Postcranial skeletons of Japanese Desmostylia. Paleont. Soc. Japan, special papers. 12: 1-202

------ (1968) Additional notes on the postcranial skeletons of Japanese Desmostylia. Sci. Rep. Yokohama National Univ. sec. 2. 14: 21-26

SIMPSON, G. G. (1945) The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. 85: 1-350

SZALAY, F. S. (1981) Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. Amer. Zool. 21: 37-45

THENIUS, E. (1973) Fossils and the life of the past. 194pp.,

Springer Verlag, New York.

TORREY, T. W. and FEDUCCIA, A. (1979) Morphogenesis of the Vertebrates. 4th ed., Xii+570pp., John Wiley and Sons, New York.

VANDERHOOF, V. L. (1937) A study of the Miocene sirenian Desmostylus. Univ. California Pub. Geol. Sci. 24 (8): 169-262

VAUGHAN, T. A. (1972) Mammalogy. Viii+463pp., W. B. Saunders company, Philadelphia.

WAKE, M. H. (ed.) (1979) Hyman's comparative vertebrate anatomy. 3rd. ed., Xi+788pp., Univ. Chicago Press, Chicago

YAMAGUCHI, S., INUZUKA, N., MATSUI, M., AKIYAMA, M., KAMBE, N., ISHIDA, M., NEMOTO, T. and TANITSU, R. (1981) On the excavation and restoration of Desmostylus from Utanobori, Hokkaido. Bull. Geol. Surv. Japan. 32 (10): 527-543 (in Japanese)

YAPP, W. B. (1965) Vertebrates: Their structure and life. Vii+525pp., Oxford University Press, New York.

YOSHIWARA, S. and IWASAKI, J. (1902) Notes on a new fossil mammal. Jour. Coll. Sci., Imp. Univ. Tokyo, Japan. 16 (6): 1-13

YOUNG, J. Z. (1975) The life of mammals: Their anatomy and physiology. 2nd ed., XV+528pp., Clarendon Press, Oxford.

## Explanation of Plates

All figures in the Plates I—VIII are of the specimens (UHRno. 18466) of Desmostylus mirabilis NAGAO from Keton, South Sakhalin. Scale is 10 cm in all Plates.

### Plate I

Fig. 1—6 : Atlas (UHRno. 18466-55)
1: cranial view, 2: caudal view, 3: medial view, 4: lateral view, 5: dorsal view, 6: ventral view.

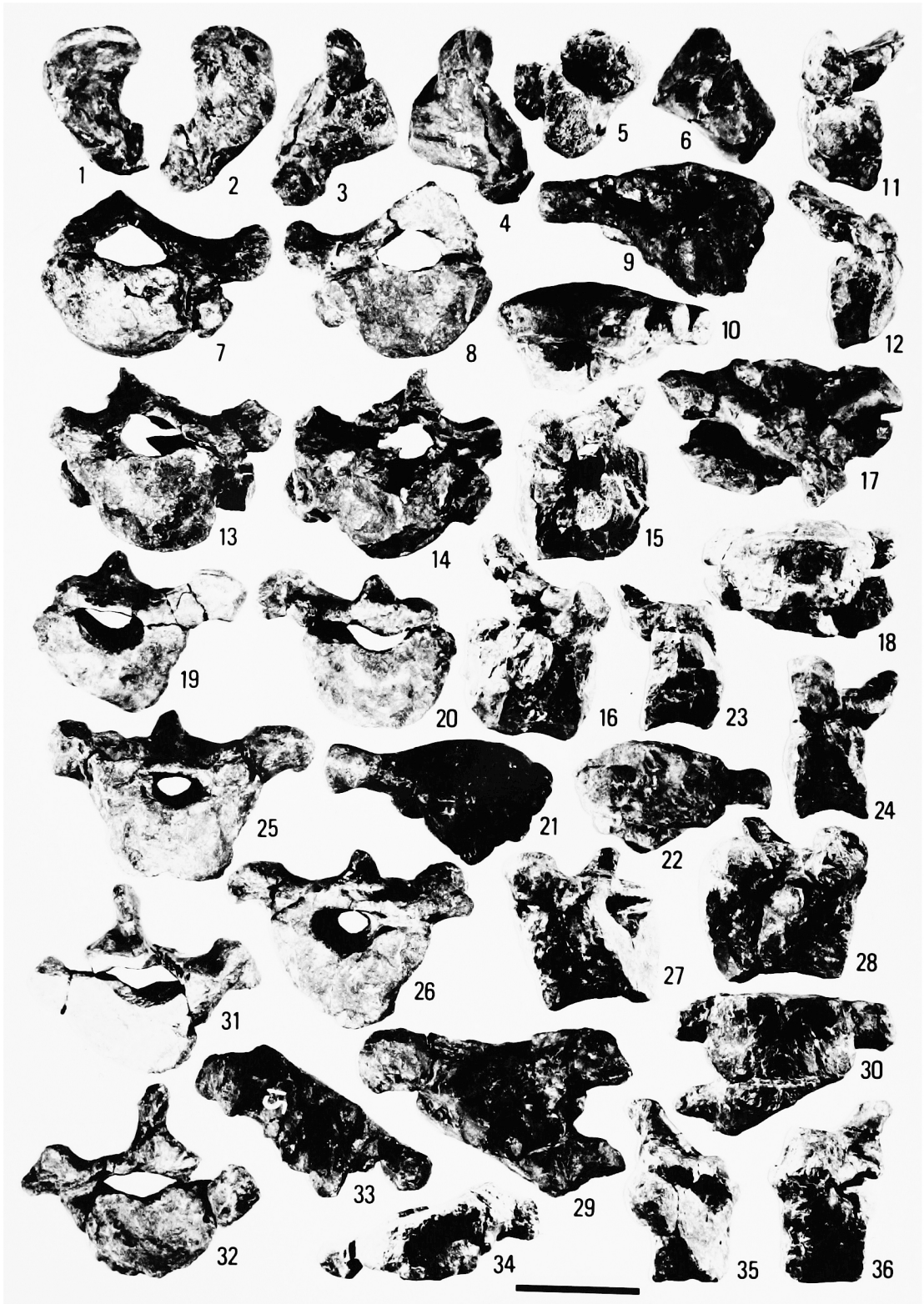
Fig. 7—12 : ?Fourth thoracic vertebra (UHRno. 18466-56)
7: cranial view, 8: caudal view, 9: dorsal view, 10: ventral view, 11: left lateral view, 12: right lateral view.

Fig. 13—18 : ?Fifth thoracic vertebra (UHRno. 18466-57)
13: cranial view, 14: caudal view, 15: left lateral view, 16: right lateral view, 17: dorsal view, 18: ventral view.

Fig. 19—24 : Seventh thoracic vertebra (UHRno. 18466-58)
19: cranial view, 20: caudal view, 21: dorsal view 22: ventral view, 23: right lateral view, 24: left lateral view.

Fig. 25—30 : Eighth thoracic vertebra (UHRno. 18466-59)
25: cranial view, 26: caudal view, 27: left lateral view, 28: right lateral view, 29: dorsal view, 30: ventral view.

Fig. 31—36 : Ninth thoracic vertebra (UHRno. 18466-60)
31: cranial view, 32: caudal view, 33: dorsal view 34: ventral view, 35; right lateral view, 36: left lateral view.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## Plate II

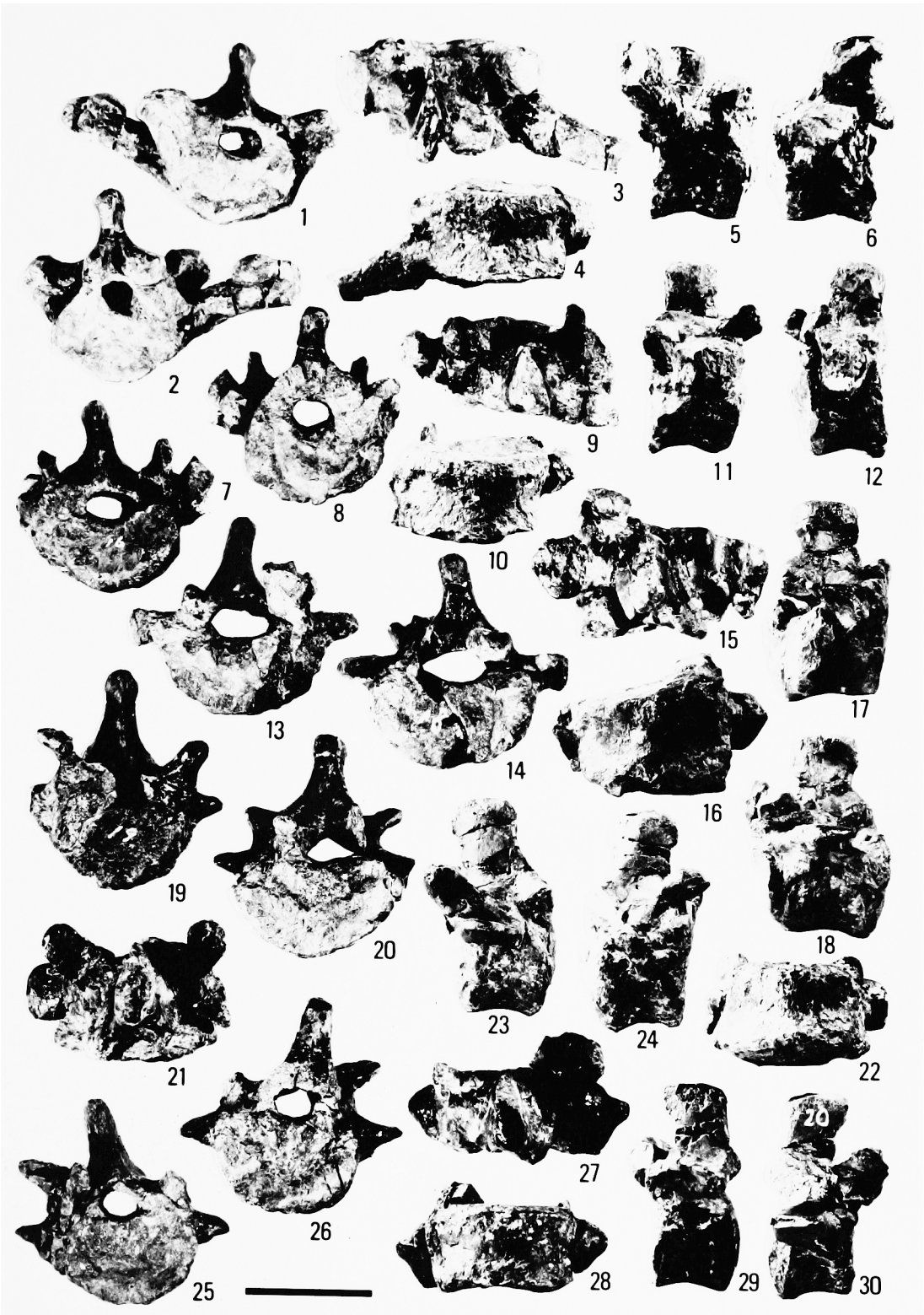
Fig. 1—6 : Tenth thoracic vertebra (UHRno. 18466-61)
1: cranial view, 2: caudal view, 3: dorsal view, 4: ventral view, 5: right lateral view, 6: left lateral view.

Fig. 7—12 : Eleventh thoracic vertebra (UHRno. 18466-62)
7: cranial view, 8: caudal view, 9: dorsal view, 10: ventral view, 11: right lateral view, 12: left lateral view.

Fig. 13—18 : Twelfth thoracic vertebra (UHRno. 18466-63)
13: cranial view, 14: caudal view, 15: dorsal view 16: ventral view, 17: right lateral view, 18: left lateral view.

Fig. 19—24 : Thirteenth thoracic vertebra (UHRno. 18466-64)
19: cranial view, 20: caudal view, 21: dorsal view 22: ventral view, 23: left lateral view, 24: right lateral view.

Fig. 25—30 : First lumbar vertebra (UHRno. 18466-65)
25: cranial view, 26: caudal view, 27: dorsal view 28: ventral view, 29: laft lateral view, 30: right lateral view.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## Plate III

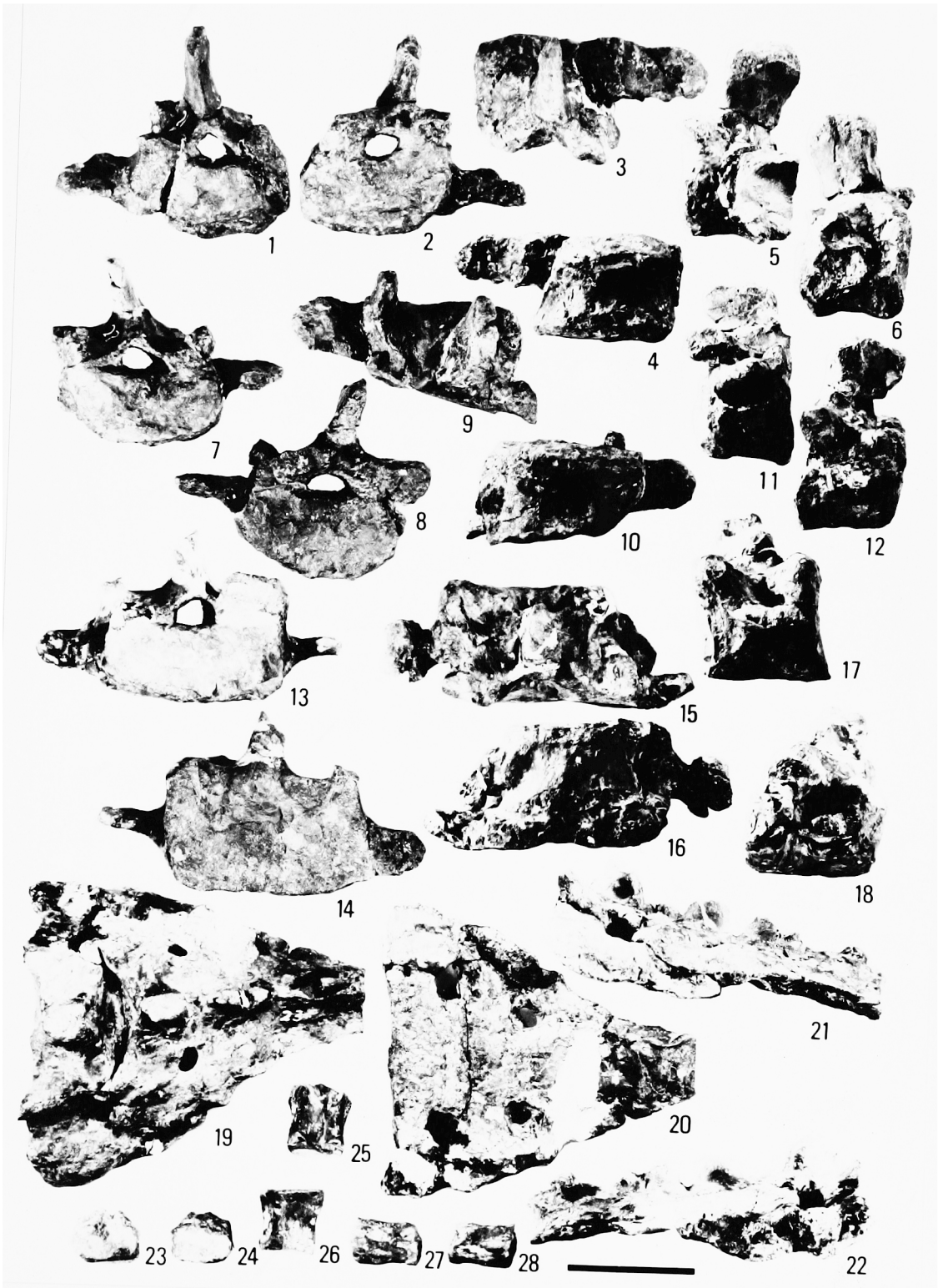
Fig. 1—6 : Second lumbar vertebra (UHRno. 18466-66)
1: cranial view, 2: caudal view, 3: dorsal view, 4: ventral view, 5: right lateral view, 6: left lateral view.

Fig. 7—12 : Third lumbar vertebra (UHRno. 18466-67)
7: cranial view, 8: caudal view, 9: dorsal view, 10: ventral view, 11: left lateral view, 12: right lateral view.

Fig. 13—18 : Fourth lumbar vertebra (UHRno. 18466-68)
13: cranial view, 14: caudal view, 15: dorsal view 16: ventral view, 17: left lateral view, 18: right lateral view.

Fig. 19—22 : Sacrum (UHRno. 18466-69)
19: dorsal view, 20: ventral view, 21: left lateral view, 22: right lateral view.

Fig. 23—28 : First caudal vertebra (UHRno. 18466-70)
23: cranial view, 24: caudal view, 25: dorsal view 26: ventral view, 27: left lateral view, 28: right lateral view.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## Plate IV

Fig. 1—13 : Cranial view of left ribs.
1: First rib (UHRno. 18466-80), 2: Second rib (UHRno. 18466-82), 3: Third rib (UHRno. 18466-83) 4: fourth rib (UHRno. 18466-85), 5: Fifth rib (UHRno. 18466-87), 6: Sixth rib (UHRno. 18466-89) 7: Seventh rib (UHRno. 18466-91), 8: Eighth rib (UHRno. 18466-93), 9: Ninth rib (UHRno. 18466-95) 10: Tenth rib (UHRno. 18466-97), 11: Eleventh rib (UHRno. 18466-99), 12: Twelfth rib (UHRno. 18466-101), 13: Thirteenth rib (UHRno. 18466-103).

Fig. 14—26 : Caudal view of left ribs.
14: Thirteenth rib, 15: Twelfth rib, 16: Eleventh rib, 17: Tenth rib, 18: Ninth rib, 19: Eighth rib, 20: Seventh rib, 21: Sixth rib, 22: Fifth rib, 23: Fourth rib, 24: Third rib, 25: Second rib, 26: First rib.

Fig. 27—29 : Sternum (UHR no. 18466-46—54)
27: dorsal view, 28: left lateral view, 29: ventral view.

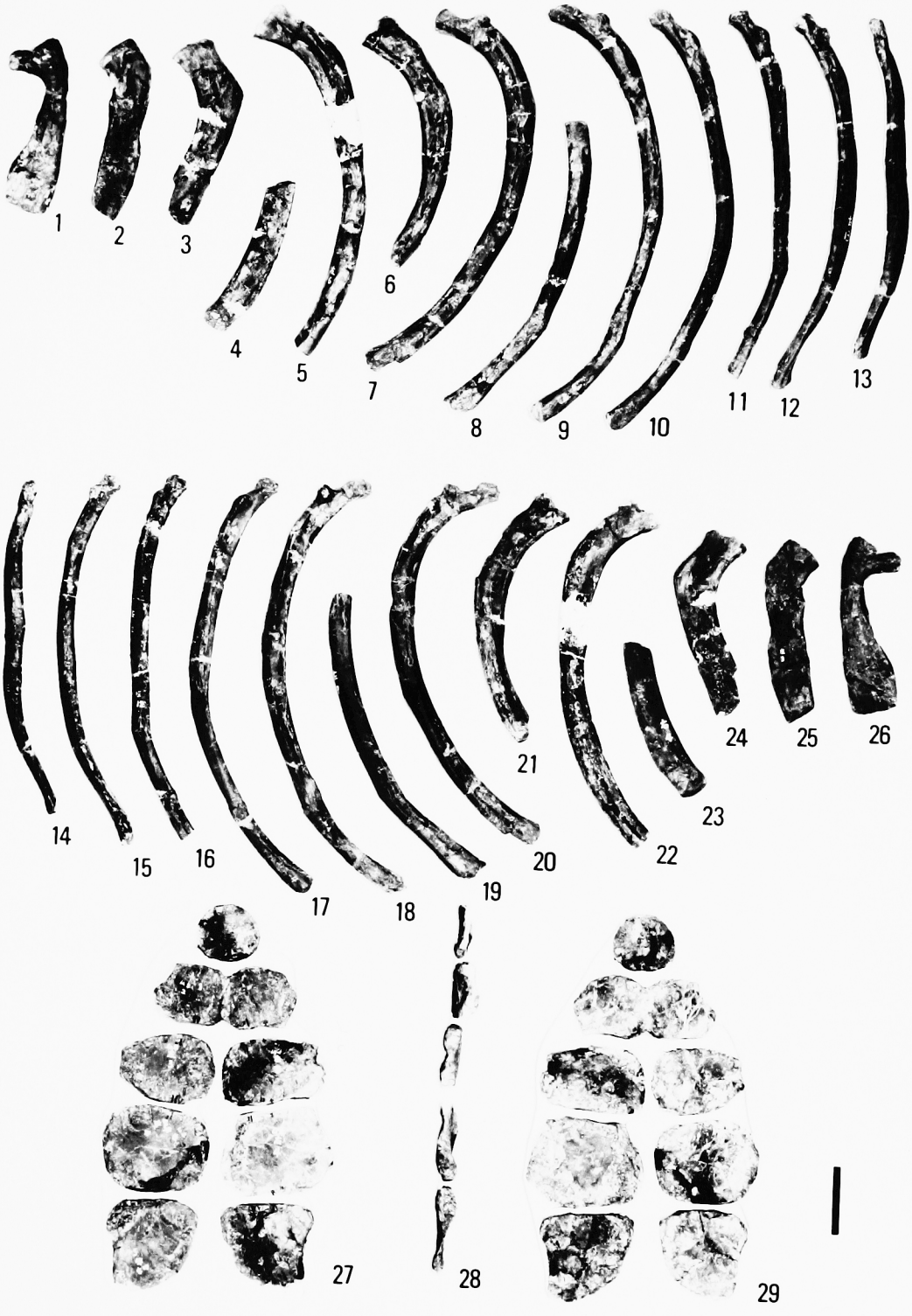
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Plate V

Fig. 1—6 : Left scapula (UHRno. 18466-104)
1: cranial view, 2: lateral view, 3: caudal view,
4: costal view, 5: dorsal view, 6: ventral view.

Fig. 7—12 : Left humerus (UHRno. 18466-3)
7: proximal view, 8: distal view, 9: cranial view
10: caudal view, 11: medial view, 12: lateral view


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Plate VI

Fig. 1—6 : Left radius and ulna (UHRno. 18466-4, 5)
1: cranial view, 2: caudal view, 3: medial view, 4: lateral view, 5: proximal view, 6: distal view

Fig. 7—12 : Left scaphoid (UHRno. 18466-6)
7: cranial view, 8: caudal view, 9: dorsal view, 10: ventral view, 11: medial view, 12: lateral view.

Fig. 13—18 : Left lunar (UHRno.18466-7)
13: cranial view, 14: caudal view, 15: dorsal view 16: ventral view, 17: medial view, 18: lateral view.

Fig. 19—24 : Left triquetrum (UHRno. 18466-8)
19: cranial view, 20: caudal view, 21: dorsal view 22: ventral view, 23: medial view, 24: lateral view.

Fig. 25—30 : Left hamatum (UHRno. 18466-13)
25: cranial view, 26: caudal view, 27: dorsal view 28: ventral view, 29: medial view, 30: lateral view.

Fig. 31—35 : Coxal bones (UHRno. 18466-105)
31: dorsal view, 32: ventral view, 33: right lateral view, 34: left lateral view, 35: cranial view.

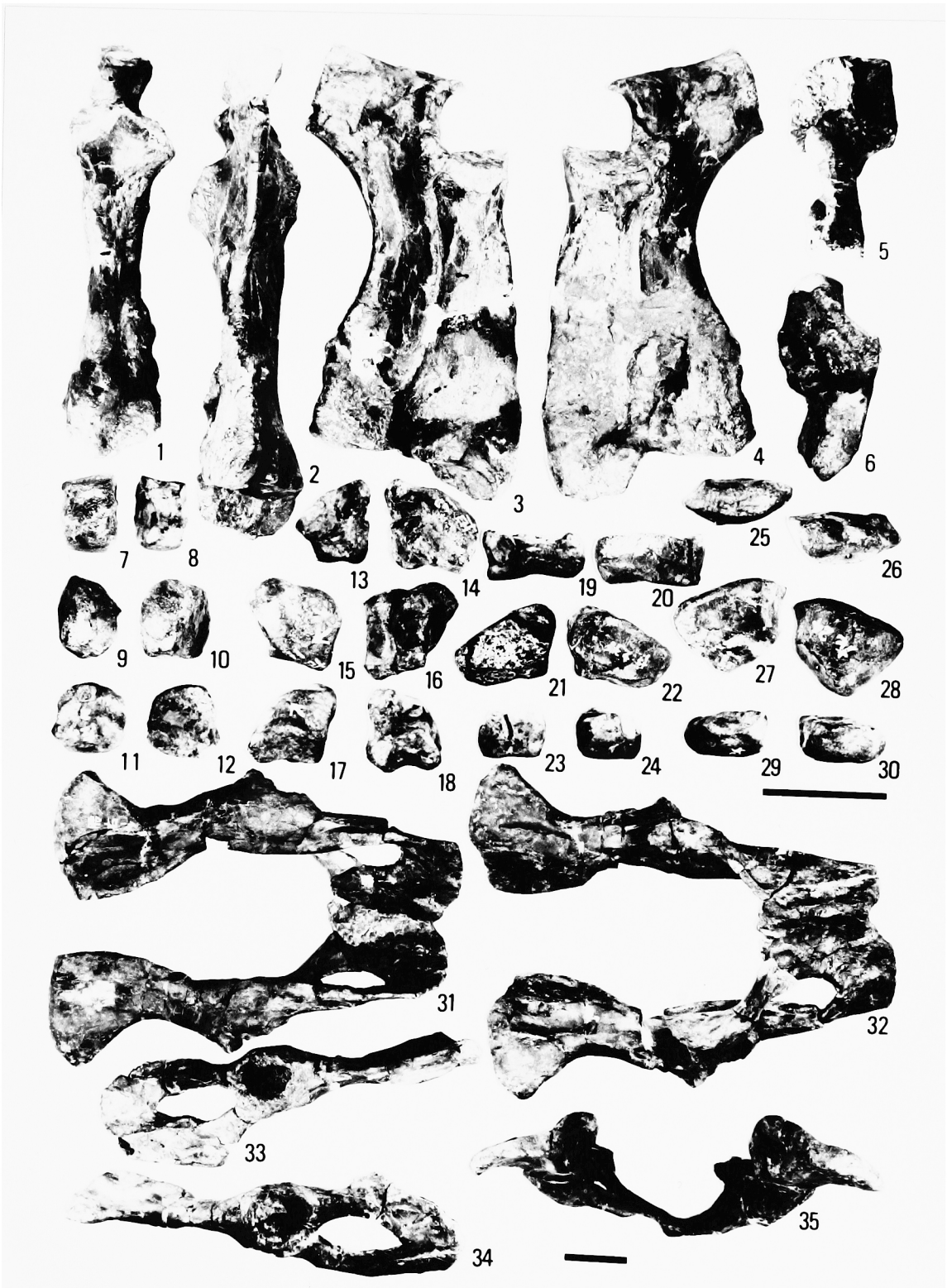
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Plate VII

Fig. 1—6 : Left femur (UHRno. 18466-29)
1: cranial view, 2: caudal view, 3: medial view,
4: lateral view, 5: proximal view, 6: distal view

Fig. 7—12 : Right femur (UHRAno. 18466-28)
7: distal view, 8: proximal view, 9: cranial view
10: caudal view, 11: medial view, 12: lateral view


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Plate VIII

Fig. 1—6 : Left tibia (UHRno. 18466-30)
1: cranial view, 2: caudal view, 3: medial view, 4: lateral view, 5: proximal view, 6: distal view

Fig. 7—12 : Left Astragalus (UHRno. 18466-31)
7: cranial view, 8: caudal view, 9: dorsal view, 10: ventral view, 11: medial view, 12: lateral view

Fig. 13—18 : Left Calcaneum UHRno. 18466-32)
13: medial view, 14: lateral view, 15: dorsal view 16: ventral view, 17: cranial view, 18: caudal view

Fig. 19—24 : Left fifth metacarpus (UHRno. 18466-106)
19: dorsal view, 20: palmar view, 21: medial view 22: lateral view, 23: proximal view, 24: distal view

Fig. 25—30 : Left second metatarsus (UHRno. 18466-15)
25: dorsal view, 26: plantar view, 27: medial view 28: lateral view, 29: proximal view, 30: distal view

Fig. 31—36 : Left third metatarsus (UHRno. 18466-16)
31: dorsal view, 32: plantar view, 33: medial view 34: lateral view, 35: proximal view, 36: distal view

Fig. 37—42 : Left fourth metatarsus (UHRno. 18466-35)
37: dorsal view, 38: plantar view, 39: medial view 40: lateral view, 41: proximal view, 42: distal view

Fig. 43—48 : Left fifth metatarsus (UHRno. 18466-36)
43: dorsal view, 44: plantar view, 45: medial view 46: lateral view, 47: proximal view, 48: distal view


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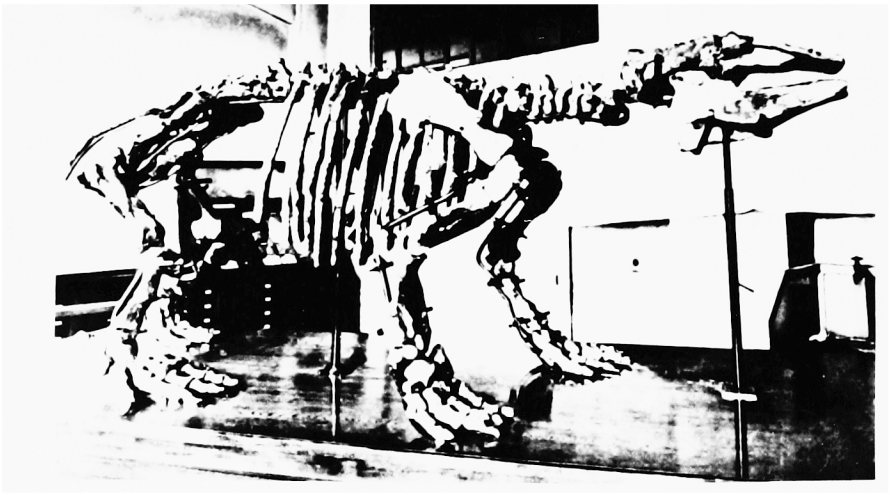
Plate IX

Fig. 1: NAGAO's restoration of Desmostylus, which was restored in 1938, and displayed in Hokkaido University before and is in Osaka Museum of Natural History now.

Fig. 2: REPENNING's restoration of Paleoparadoxia, which was found in 1965 and is drawn in "Vertebrate Paleontology" by ROMER (1966).

Fig. 3: SHIKAMA's restoration of Paleoparadoxia which was found in 1950, and is figured in SHIKAMA (1966).



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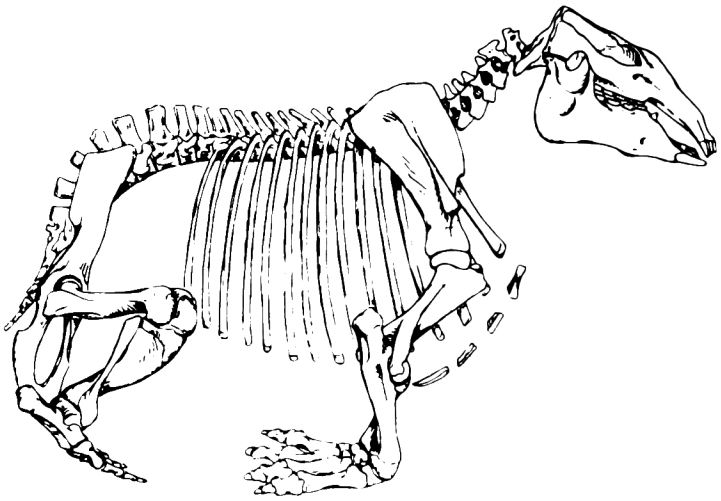

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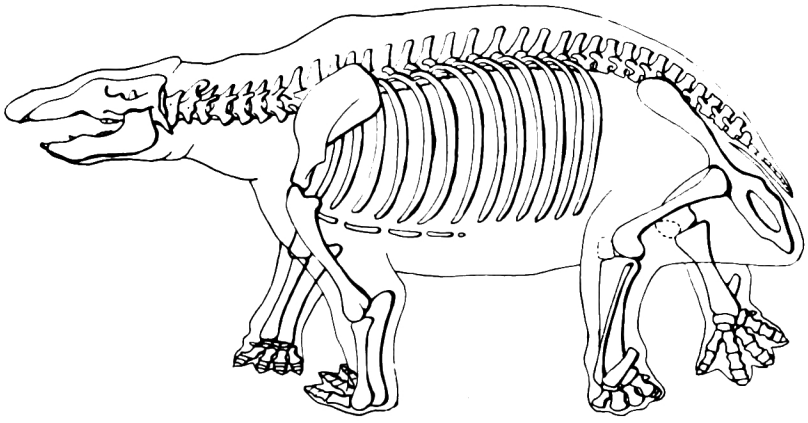

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Plate X

Fig. 1: The skeleton of Paleoparadoxia displayed in the British Museum, of which photo is adopted by HALSTEAD (1975).

Fig. 2: KAMEI's restoration of Desmostylus, which is displayed in Hokkaido University now and is figured by KAMEI and OKAZAKI (1975).

Fig. 3: HASEGAWA's restoration of Paleoparadoxia which is displayed in National Science Museum, Tokyo, and is noted by HASEGAWA (1977).

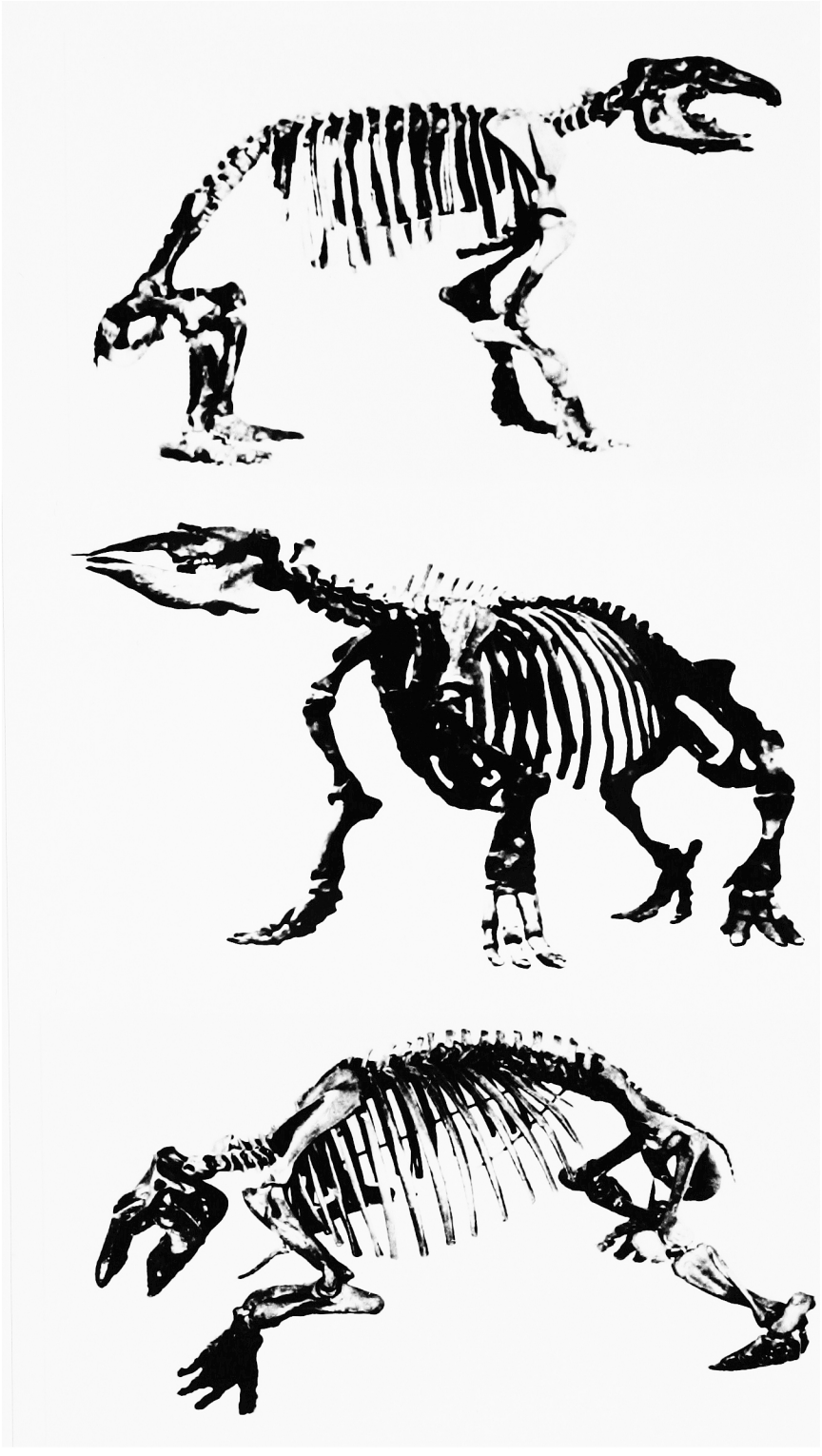

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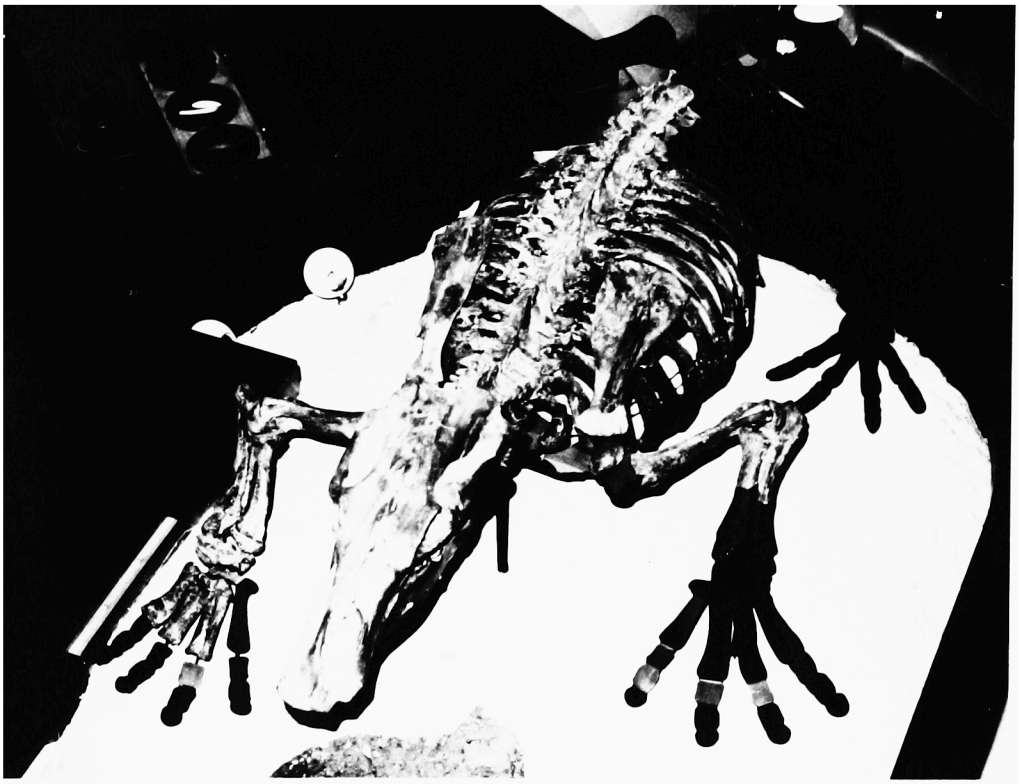
Plate XI

Fig. 1: INUZUKA's restoration of Desmostylus, which was discovered from Utanobori, Hokkaido, and is now displayed in Geological Survey of Japan.

Fig. 2: INUZUKA's restoration of Desmostylus, which is drawn based on the Keton specimen from south Sakhalin and is now stored in Hokkaido University.



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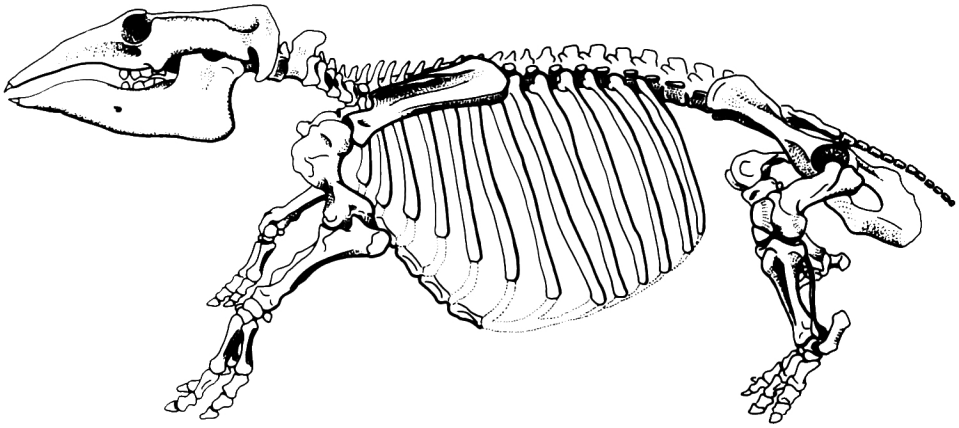

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