Skeletal Restoration of the Desmostylians : Herpetiform Mammals

Inuzuka, Norihisa

Inuzuka, Norihisa. Skeletal Restoration of the Desmostylians : Herpetiform Mammals. Memoirs of the Faculty of Science, Kyoto University. Series of biology. New series 1984, 9(2): 157-253

ISSUE DATE:
1984-10

URL:
http://hdl.handle.net/2433/258864

MEMOIRS OF THE FACULTY OF SCIENCE, KYOTO UNIVERSITY, SERIES OF BIOLOGY
Vol. IX, pp. 157–253, October 1984

Skeletal Restoration of the Desmostylians: Herpetiform Mammals*

By

NORIHISA INUZUKA

Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Tokyo, 113 Japan

(Received March 31, 1984)

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

CONTENTS

---

* Doctoral dissertation submitted to the Faculty of Science, Kyoto University.

I. INTRODUCTION

Reconstruction of the life in the geological past is a major palaeontological subject, notably in vertebrate palaeontology where much attention has found on the graphic restoration of extinct large animals such as dinosaurs and mammoths, at both a popular and scientific level. However, since no suitable theoretical base has been established, any attempt to restore the form of these animals is immediately beset with many unresolved problems. In his famous publication, "Geschichte und Methode der Rekonstruktion vorzeitlicher Wirbeltiere", Abel (1925) stressed that imaginary restoration of extinct life should be avoided, and noted the important role of both morphological and biological bases in the restoration of fossil animals. Nevertheless, previous authors have questioned the various postures and shapes of restorations made of extinct animals. Usually, the more distant from living animals, the greater the variety of figures produced! Therefore, to reconstruct the true form of an extinct animal having no living descendant it is essential to examine the basic concept of restoration and reconstruction.

The present paper deals with the restoration problems of the desmostylian skeleton. The desmostylians were large mammals that inhabited the coastal areas of the circum-North Pacific during the mid-Tertiary period. Taxonomically, they belong to the order Desmostylia (Reinhart, 1953), and are considered by many workers to have a close affinity to either the order Proboscidea or Sirenia. However, the taxonomic position of the desmostylians has been disputed for nearly a century since the first discovery of the fossil, and has not yet been resolved (Table 1). For example, Simpson (1945) included the desmostylians in his superorder Paenungulata, while Romer (1966) placed them in the Subungulata group. Recently, McKenna (1975) proposed the mirorder Tethytheria composed of two living orders, the Sirenia and Proboscidea along with the extinct Desmostylia.

There have also been divergent views concerning the body shape, locomotion, feeding habit and habitat of the desmostylians (Merriam, 1906; VanderHoof, 1937; Ijiri, 1939; Nagao,

Table 1. Opinions on the taxonomic position of the Desmostylia.

Date	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

1941; Reinhart, 1959; Ijiri and Kamei, 1961; Mitchell, 1966; Shikama, 1966; Domning, 1977). Thus, many questions have been raised about the paleobiology of the desmostylians.

To solve such questions it is indispensable that the desmostylian skeletons are correctly restored in order to provide a morphological outline on which muscles and skins are entirely based. Accurate morphological restoration of the animal is essential in order to reconstruct its ecology and function, which is, in turn, essential for accurate assessment of the phylogeny of the animal. Well-preserved specimens of desmostylian skeletons have frequently been found in Japan, of which two complete skeletons of *Desmostylus* (Keton and Utanobori specimens), two of *Paleoparadoxia* (Izumi and Chichibuohnohara specimens), and one rather complete skull bone of *Desmostylus* (Togari specimen) are best preserved. The author had an opportunity to study the Keton specimen and performed mounting on the Utanobori and the Keton skeletons, and the present works is based upon these studies.

Although all materials dealt with are restricted to *Desmostylus*, it is widely accepted that there only slight morphological differences in the postcranial elements between *Desmostylus* and *Paleoparadoxia* (Shikama, 1966) and therefore the results obtained from this study may eventually be applied to the restoration of *Paleoparadoxia*. Thus previous works covering both genera are referred to and the problems of skeletal restoration not only of *Desmostylus* but also of the desmostylians in general are discussed.

The present paper attempts to develop the methodology applied in the restoration practice, with the objective of providing an insight into desmostylian paleobiology.

II. SCOPE OF THIS STUDY

The desmostylians have been regarded as a member of the sirenians ever since Marsh (1888) described the first fossil teeth and even after the cranial bones were found in Japan and Oregon early this century, the shape of these animals has been supposed to resemble the dugongs or manatees.

In 1933, an entire skeleton of *Desmostylus mirabilis* was found from south Sakhalin for the first time (Keton specimen). From this discovery it became clear that the animals had four stout legs, suggesting active locomotion in terrestrial life. Nagao (1941) who studied this specimen first mounted its skeleton as a quadrupedal mammal. This new-look restoration changed the old image of the desmostylians, but there remained some contradictions in the newly shaped restoration. Subsequently, more information of desmostylian skeletons has become available from new discoveries and many workers have tried to amend Nagao's restoration.

An entire 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 Stanford University, California in 1964 (Stanford specimen). Remarkably, the second complete skeleton of *Desmostylus* was discovered in Utanobori-cho, north Hokkaido in 1977 (Utanobori specimen).

Skeletal restoration of the desmostylians have been performed 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 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).

However due to a lack of general consensus on the normal body form of these animals, the figures shown of the desmostylians differ so markedly that they cannot be believed to represent a restoration of the same animal. In view of this, it is considered necessary to discuss the problem of variety of the desmostylian body shape.

Firstly, this may be due to inappropriate usage of the restoration method. Usually, a living species supposedly having a close phylogenetic and morphological relationship to the fossil is taken as a model for restoration (Thenius, 1973). The usage of this method is obviously prone to error if the fossil shape bears no close resemblance to the living. Furthermore, the precise phylogenetic position of the extinct form is usually somewhat ambiguous and hence crucial contradiction will arise in the correlation between the shape of fossil bone and the mounted skeleton posture based on the model (Inuzuka, 1981c).

In the case of the desmostylians, the sirenia were chosen as the preferred model by some students, while other workers adopted the proboscideans and other ungulates as restoration models. Due to such a wide diversity of models, mounted skeletons were forced to be variously postured and consequently, when restoring a fossil animal which has become extinct without descendants it is inadvisable to adopt living species as a model.

Secondly, it seems probable that previous workers did not pay due attention to the basic posture essential for the shape of the animal. When Marsh (1884) restored the skeleton of Dinocerata, he made no reference to the basic shape of the animal, but did give some notes on the poses of the animal for drawing or display. Probably, such traditional practice is based upon the assumption that the posture of all large animals is fundamentally similar. Actually, the most important factor for restoration is how to determine the basic body form of the animal and the choice of poses, e.g. whether standing, at rest, or walking, are only of secondary importance. For the desmostylians, many postures have been illustrated e.g., standing, walking, swimming and feeding, but nothing of its basic shape has yet been presented. Therefore, one of the main objectives of this work was to clarify the basic shape of the animal, regardless of the pose.

Thirdly, it is probable that, even now, the theoretical base for restoration is insufficient. Certainly, a restored skeleton of an animal may represent only a hypothesis of its form (Abel, 1925) and there other choices of different restorations are possible. However, any restoration made is meaningless unless its theoretical base is clear and within this context it should be noted that, for the desmostylians, only Shikama (1966, 1968) clearly presented his theoretical basis for restoration.

Osteology and myology will provide important information in constructing theoretical bases, while recent progress in paleobiology allows the consideration of anatomical and physiological features in the skeletal restoration (Ostrom, 1969; Radinsky, 1977, 1982). The current author described each skeletal element in detail adopting this approach (Inuzuka, 1980a, b; 1981a, b; 1982) and these descriptions are reviewed briefly in the Appendix. Based on such results, pertinent osteological features of the desmostylians of use in restoration are explained, and the theoretical basis for skeletal restoration discussed.

III. MATERIALS AND METHODS

A. Materials

Currently, there are five whole desmostylian skeletons known in the world, among which 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 adopted as the main study 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 at Keton, near Shisuka-machi (Poronaisk), south Sakhalin in 1933, and has been studied by several workers (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 1936 (Nagao's restoration), but thereafter, Kamei modified it in 1975 using its replicated skeleton (Kamei's restoration). Nagao's restoration is exhibited at the Osaka Museum of Natural History, and Kamei's restoration at both Hokkaido University and the Mizunami Fossil Museum.

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

Skull			UHRno. 18466–1	
Mandible			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	
	Lumbar	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

Costae		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
Forelimb	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?	UHRno. 18466-12	UHRno. 18466-11
		Capitatum	—	—
		Hamatum	—	UHRno. 18466-14
	Metacarpus	II	—	—
		III	—	—
		IV	—	—
		V	—	UHRno. 18466-106
Hindlimb	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.

Skull			GSJ–F7743–1		
Mandible			GSJ–F7743–2		
Basihyoideum			GSJ–F7743–3		
				Right	Left
Stylohyoideum				GSJ–F7743–4	GSJ–F7743–5
Thylohyoideum				GSJ–F7743–6	GSJ–F7732–7
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–F7732–23		
		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

				Right	Left
Presternum				——	
Mesosternum			I	——	——
			II	——	GSJ-F7743-66
			III	——	GSJ-F7743-67
			IV	——	——
Forelimb	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 phalanx		V	GSJ-F7743-84	——
Hindlimb	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

Table 4. Living mammalian species used for comparison.

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

NSM: National Science Museum, Tokyo; OM: Osaka Museum of Natural History; UH: Hokkaido University; UTA: University of Tokyo, Faculty of Agriculture; UTM: University of Tokyo, University Museum; YL: Yomiuri Land.

The Utanobori specimen is the most recently discovered material and was excavated at Kamitokushibetsu, Utanobori-cho, Esashi-gun, Hokkaido in 1977 (Yamaguchi et al., 1981) and is deposited in the Geological Museum, Geological Survey of Japan, Tsukuba (Table 3). The descriptive work on this specimen has not yet been completed, but its skeletal restoration has been made by the author using a theoretical basis derived from a redescriptive study of the Keton specimen (Inuzuka, 1981d).

Paleoparadoxia belongs to the same order as *Desmostylus* and currently three full fossil skeletons of this genus are known. In the present study, four restorations made from two of these three specimens are considered. 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, of which there are two restorations, Repenning's restoration (Romer, 1966), and Hasegawa's restoration (Hasegawa, 1977).

In order to perform a comparative osteological study, the skeletons of forty-six genera of living mammals (Table 4) were examined and the results obtained adopted to elucidate the general rules for the construction of mammalian skeletons. Since they have been generally considered to have close taxonomical relations with the desmostylians, particular, attention was paid to the skeletons of large ungulates and sirenians. Pinniped skeletons were studied with respect to their habitat similarities with the desmostylians.

B. Methods

In the present paper, the theoretical basis for the skeletal restoration of the desmostylians is stated. A thorough survey of the skeletal materials of the Keton specimen was made and the axial and appendicular skeletons described (Inuzuka, 1980a, b; 1981a, b; 1982). Prior to this work, the cranium of this specimen was studied by Ijiri and Kamei (1961), whereas, the limb bones and sternum were investigated by Shikama (1966). These latter descriptive works are summarized and a critical review from an anatomical viewpoint is given with brief descriptions of each bone.

Based upon the results obtained from the study of the Keton specimen, a practical mounting was made for each of the Utanobori and the Keton skeletons. Both the Keton and the Utanobori specimens belong to the same genus, *Desmostylus*, although they may represent different species, i.e. *D. mirabilis** and *D. japonicus** respectively. The Keton specimen is of a mature body, but the Utanobori specimen is that of an immature individual. The Keton specimen also lacks some main portions such as the cervical vertebrae and the cranial portion of the thoracic vertebrae. However, in spite of these differences, both specimens show some common desmostylid characteristics and it is therefore valid to apply the restoration procedure adopted on the Keton specimen to the mounting of the Utanobori specimen.

The present study may result in future desmostylian restorations being of a quite different nature to that formerly supposed. Former works usually rested on a model based on a supposed

---

* The taxonomic positions may be changed in future, as the specimens have not yet been studied from a taxonomical viewpoint.

relative, whereas the present study is based mainly on the skeletal anatomy including two different viewpoints, functional anatomy and comparative anatomy, i.e. the function of the musculo-skeletal system should be considered from two different viewpoints: support of standing posture and locomotion. The body weight of terrestrial mammals is supported not only by the skeleton but also by soft tissues, i.e. muscles and ligaments, and therefore, the mode of support presumed from the skeletal form must coincide with the direction or degree of muscle development as estimated from bone shapes.

Comparative anatomy may be applied to the restoration in two ways. One method entails a comparison of the shape of each bone, and is done in order to assess morphological features characterizing the fossil in question. The alternative method is a comparison among skeletons, the purpose of which is the abstraction of common characteristics or general rules for the skeletal construction of the taxon to which the fossil belongs. The majority of mammals ought to conform to the skeletal rules derived from such an approach and therefore the rules may be applied to the fossil in question. In this manner errors in which models which are selected based on only a partial resemblance, or cases where the body shape is based only on the morphological resemblance of a few bones may be avoided.

Unless the posture of a mounted skeleton can be reasonably anatomically related to the most distinct characteristics of each bone, the restoration cannot be justified as exact.

The relative accuracy of the restoration will increase if it is identical to that of the posture in which preserved specimens are found. The skeleton of the Utanobori specimen was well preserved in jointed condition and its mode of occurrence endorsed the theoretical basis for restoration adopted throughout this paper. Confirmation of such articulation was also made from other cases of desmostylian preserved specimens in situ.

IV. CRITICAL REVIEW OF PREVIOUS WORKS

In this chapter six previous skeletal restorations of the desmostylia are critically reviewed. The main characteristics of these restored skeletons are shown in Table 5.

A. **Nagao's restoration** (Plate IX, Fig. 1)

This restoration is mounted with the skeleton of the Keton specimen. As described below, except for a part of the atlas and some of anterior thoracic vertebrae, the cervical vertebrae are lacking and thus it is reasonable to suppose that those bones in the mounted skeleton were not restored using any sound theoretical basis. The vertebral column extends nearly horizontally and is straight from the neck to the base of the tail. The fore- and hindlimb bones are straightly jointed and extend downward under the body from the trunk, articulating with a slight bending. Although Nagao (1941) claimed that the animal was "semidigitigrade", the result of his skeletal restoration seems to be plantigrade. The five digits in the fore- and hindlimbs are pointing forward.

Nagao (1941) offered no theoretical basis for his restoration except for the setting of the 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 this animal (Nagao, 1941)".

Table 5. Comparison of selected features of restored skeletons.

Restoration	Vertebral column	Limb position	Toe direction	Foot posture	Degree of flexion in limb joints
Nagao (1936)	horizontal; neck, shoulder and pelvis on nearly same level	under body	cranial	plantigrade	slightly flexed
Repenning (1965)	vertical pelvis	under body	F: caudal H: cranial	on the back of hand unguligrade	slightly extended strongly flexed
Shikama (1966)	high in the middle; slightly vertical pelvis	under body	F: lateral H: medial	on the back of hand semi-plantigrade	fairly extended slightly flexed
British Museum (1975?)	vertical pelvis	F: under body H: lateral	craniolateral cranial	digitigrade plantigrade	extended flexed
Kamei (1975)	high in the shoulder; slightly vertical pelvis	under body	craniolateral	digitigrade or unguligrade	F: extended H: slightly flexed
Hasegawa (1977)	high in the middle; vertical pelvis	under body	F: craniolateral H: medial	unguligrade	strongly flexed slightly flexed
Inuzuka (1984)	low as a whole	lateral	cranial	unguligrade	flexed

F: forelimb; H: hindlimb.

From this statement his method of restoration may be deduced: first, based on the resemblance of bone morphology he chose an animal as the closest relative, and then mounted the skeleton in a similar posture to the relative. Close observation of Nagao's restoration reveals that the wrist joint is dislocated. Although it was apparently possible to arrange the wrist bones to give a correct articulation, an artificial torsion at a right angle between those bones was given. Consequently, his construction of the forelimbs resulted in an unconformity between the surfaces of two groups of bones. Nagao's restoration, however, faithfully followed the rules of mammlian skeletal construction, especially the general rules of ungulate construction as mentioned later, and therefore it is reasonable to assume that this skeletal restoration was made in reference to an ungulates skeleton like hippopotami, and not to the bone morphology of *Desmostylus* itself.

It is inappropriate to use certain types of living animals as a model for the animal of which the phylogeny and ecology are obscure. Even if the bones of the animal are similar in part to those of the model, they may differ markedly from the model in other parts, because the model is not a true relative of the animal. Formerly different animals were selected as models according to different views on certain morphological characteristics allegedly important in phylogenetic relationships or ecological affinities. Following the restoration of the skeleton of an unknown animal to the original state after the model on the basis of partial resemblance, discordances with the original bone construction become immediately apparent. Thus, the use of an animal as a model should be avoided, when attempting to restore an extinct animal of unknown phylogenical position.

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

This skeleton is based on the Stanford specimen of *Paleoparadoxia tabatai* found in the Stanford University campus in 1964. The skeletal construction seems to be peculiar to ungulate skeletons in general. The neck is too raised, the thoracic vertebrae are arranged horizontally, the lumbar vertebrae bend strongly downward, and the pelvis stands nearly vertically. The forelimbs (shoulder to wrist) extend downward and, in the hindlimbs, the femurs project horizontally for- and outward. Articulation of the forelimbs extends at the joints, but that of the hindlimbs is arranged for extreme flexion at the knee joints. Most curious is the mode of attachment of the 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 the digits point backward in the forelimbs, forward in the hindlimbs.

The theoretical basis of Repenning's restoration is known from his personal communication (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 an osteological approach. The posture of the fore- and hindlimbs are described precisely from osteological observations. The distinct feature of his restoration is his consideration of the possibility of dislocation deduced from the angle of articular surface and partly from application of the 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. These are very important to accurately restore the posture of an animal, because an animal's weight is supported not only by bones but also by soft tissues. In this respect the 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 positions of connections between the trunk and limbs and the similarity between fore- and hindlimbs were not considered.

Third, it may be said that his application of the general rules of skeletal construction to the skeleton is irrelevant i.e. only one of the rules was chosen and adopted for the restoration e.g. a short metatarsus usually indicates a plantigrade posture, but he regarded that rule is absolute. There are many rules in skeletal construction, but those rules have their own exceptions and it is therefore necessary to examine which rule in practice should be conformed to and which is an exception.

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

Shikama (1966) described the Keton specimen of *Desmostylus* and the Izumi specimen of *Paleoparadoxia*, but dealt mainly with the skeleton of the latter in the restoration. In this 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 levelling of the pelvis. The limb bones are situated under the trunk, the forelimbs stretching considerably, but the hindlimbs flexed slightly. In his paper he states that the manus and the pes are held in "semiplantigrade" position, but in 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 in his illustration both the manus and the pes point inward.

Shikama (1966) was the first worker to show the theoretical bases for the restoration. The curvature of the vertebral column was arrived at from its resemblance to rodents which have a similar pelvic shape to the desmostylians. The position of the manus and pes and the direction of their digit tips were decided after consideration of the morphology of each bone. What was apparently considered primarily in this case was that the limb bones were situated under the trunk; one of the general features of the mammalian skeleton. Shikama also drew the swimming posture and reconstructed a mode of locomotion whereby "*Paleoparadoxia* does a *Phacochoerus* locomotion on sea bottom". He interpreted the large flat sternum as being a useful tool in this mode of locomotion. It was his excellent idea that restoration of desmostylians should depend upon how to interpret 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.

However, there is a fault in common with Repenning's method: he disregarded the musculoskeletal system. Although the bones were compared with those of other animals, their morphological characteristics were assessed too crudely e.g. the similar pelvic shape to rodents is not an adequate reason to presume that the backbone curvature is similar to that of a rat. In addition, little attention was paid to the following points: comparison of pelvis by each morphological element, consideration of the correlation between the pelvis and vertebral column, comparison of the pelvis forms among rodents, etc.

Shikama (1968) drastically altered his previous restoration (Shikama, 1966) making the position of the long axis of the scapula parallel with the vertebral column and turning the lateral surface of the antebrachial skeleton cranially. A consequence of this modification was that the position of a flexed manus and medially pointing toes was abandoned, and a normal semiplantigrade position was adopted instead. Due to this revision, the direction of the scapula and femur were reasonably improved; but the skeleton still seems to be still imperfect, for it was based only on osteological features and not on general rules for mammalian skeletal construction.

D. **Restoration by the British Museum (N. H.)** (Plate X, Fig. 1)

This restoration was based on the Izumi specimen of *Paleoparadoxia* as was Shikama's (1966, 1968) restorations. The vertebral column has a slight curvature extending from the cervical to the thoracic vertebrae with a deep flexion between the thoracic and lumbar vertebrae. The lumbar vertebrae run straight toward the pelvis in a downward direction. The forelimbs are placed under the trunk and extended straightly, but the femur of the hindlimbs is positioned horizontally and laterally and attached to the vertical tibia. The manus has a digitigrade foot posture while the pes, plantigrade. The manus is pointing anterolaterally and the pes forward.

This skeleton is exhibited in the British Museum of Natural History and is referred 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 posutre. According to Croucher, the basis of the restoration is mainly on the shape of the articular surfaces of the bones e.g. as the articular surfaces of the ankle joint and metatarsal bones are broad, the pes is fairly movable, and as the metatarsals are flat, the pes is thus supposed to work as a paddle.

This skeleton appears to be a modification of Repenning's restoration. The 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 metatarsal bones. As a result of this change in limb position, the difference in height between the fore- and hindlimbs has become so great, that the unnatural flexion is mostly concentrated between the thoracic and lumbar vertebrae.

Restoration based only on the shape of the articular surface of the bones is limited in its application. Firstly, a joint consists not only of bone but also of soft tissue such as cartilage and ligament. Thus the extent of flexibility in the living joint differs from that assumed from only the extent, orientation and form of the articular surfaces of bones e.g. the shoulder joint has a shallow articular surface suggesting large mobility, but its movement is actually fairly restricted due to the presence of ligaments. Moreover, it is unknown where each bone contacts with its counterpart when the body is in a standing position. Consequently, it should be noted that, although the joint pattern and the extent of articular surface are valid features as a key for mounting, the basic shape of the animal should not be determined solely by these criteria.

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

This is the second 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. The limb bones extend downward from the trunk, but the hindlimbs somewhat outward. The forelimbs are almost extended, while the hindlimbs are more or less flexed. Both the fore- and hindlimbs are digitigrade or unguligrade in position. Every toe is pointed obliquely outward.

According to Kamei's personal communication, the restoration was first modeled on tapirs, based on the close similarity between the microstructure of the teeth and cranial characters seen between desmostylians and tapirs (Ijiri and Kamei, 1961). However, as it proved difficult to position the desmostylian skeleton in the posture of a tapir, he subsequently adopted the rhinoceros, a larger perissodactyl, as a model. Judging from the posture, it appears that some modifications were made to Nagao's original restoration, this being accomplished by faithfully following the form of each bone. The resultant skeleton has no dislocation of joints and has abandoned the plantigrade position of the manus and pes peculiar to ungulates in general. The anterior part of the body is higher than the posterior, the scapulae are separated from the thorax, and the knees project slightly outwards. This method is similar to Nagao's method in its utilization of a living species as a model.

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

There are several restorations of *Paleoparadoxia* by Hasegawa, based upon the Izumi specimen, the Chichibu-ohnohara specimen and the Stanford specimen, which are exhibited in several museums in Japan. This particular restoration was based on the Stanford specimen. The vertebral column is high in the middle and strongly bent, with the hip lowered. The limb bones are under the trunk, the forelimbs extend strongly without being flexed whereas the hindlimbs are flexed weakly. As the femur in the hip joint projects without flexion, the distance between both feet is wide and the toes point inward. Both fore- and hindlimbs are unguligrade. The toes of the manus point anterolaterally.

According to Hasegawa's personal communication, this restoration is based exclusively upon bone shape, and each joint is maximally flexed or extended. The curvature of the 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 the glenoid cavity has become more forward and the elbow joint flexed more strongly than in Shikama's restoration. It is noticeable that both manus and pes are restored so as to be clearly unguligrade as in ungulates in general. This method is common with the British Museum's method in being based upon features of the articular bone surfaces.

V. CHARACTERISTICS OF THE DESMOSTYLIAN SKELETON

A. **Comparison with other mammals**

In this section the results of a comparative study between desmostylian skeletal elements and those of 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 seen in the proboscideans, sirenians and cetaceans. In the long necked artiodactyls and perissodactyls, the transverse ridge on the occipital condyle prevents dorso-ventral rotation of the head at the head joint. The neck of *Desmostylus* was short, like the proboscideans and sirenians, and it is presumed that some dorso-ventral rotation in the head joint was possible.

The absence of the transverse foramen of the atlas (UHRno. 18466–55, Fig. 2, Plate I) in *Desmostylus* is in common with 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 to the ungulates in having low and wide bodies, in the form of the transverse process and the position

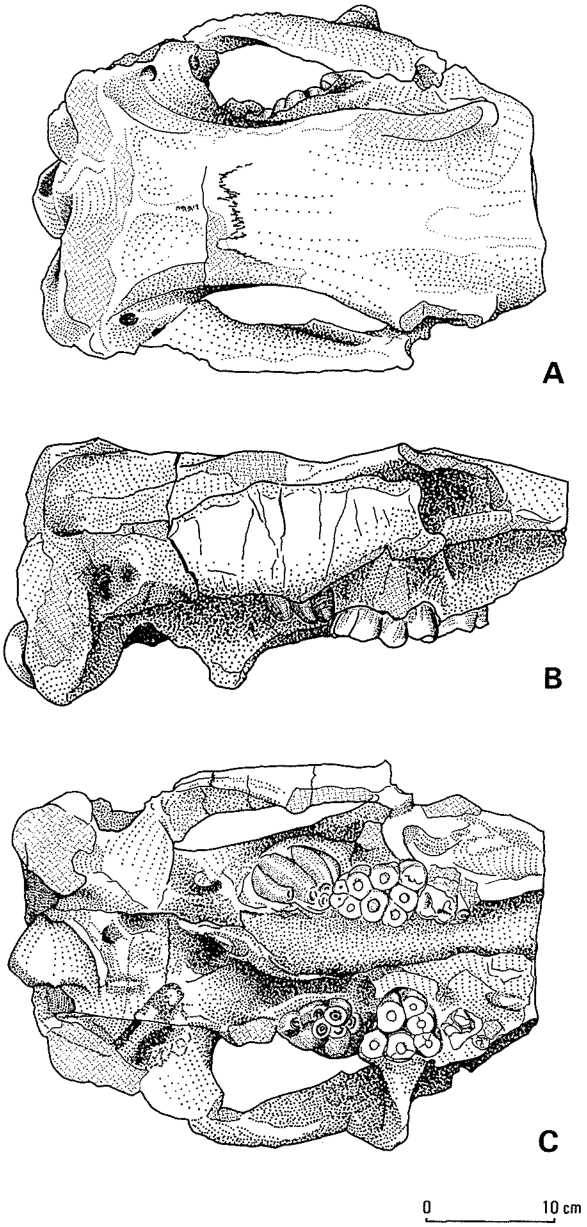


Fig. 1. Skull of *Desmostylus mirabilis* (UHRno. 18466–1). A: dorsal view. B: right lateral view, C: ventral view.

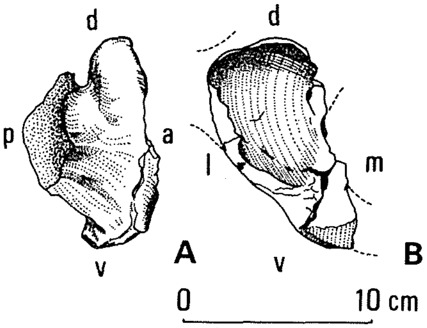


Fig. 2. Atlas of *Desmostylus mirabilis* (UHRno. 18466–55). A: right lateral view, B: cranial view. a: anterior side, p: posterior side, m: medial side, l: lateral side, d: dorsal side, v: ventral side.

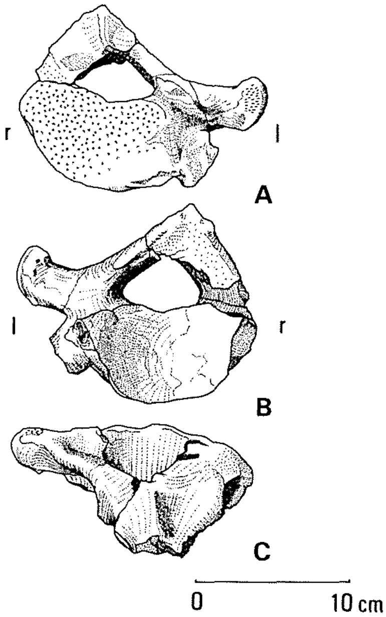


Fig. 3. ? Fourth thoracic vertebra of *Desmostylus mirabilis* (UHRno. 18466–56). A: cranial view, B: caudal view, C: dorsal view. r: right side, l: left side.

of the transverse foramen. Even if the vertebrae of *Desmostylus* bear a partial morphological resemblance other orders of mammals, they 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 a

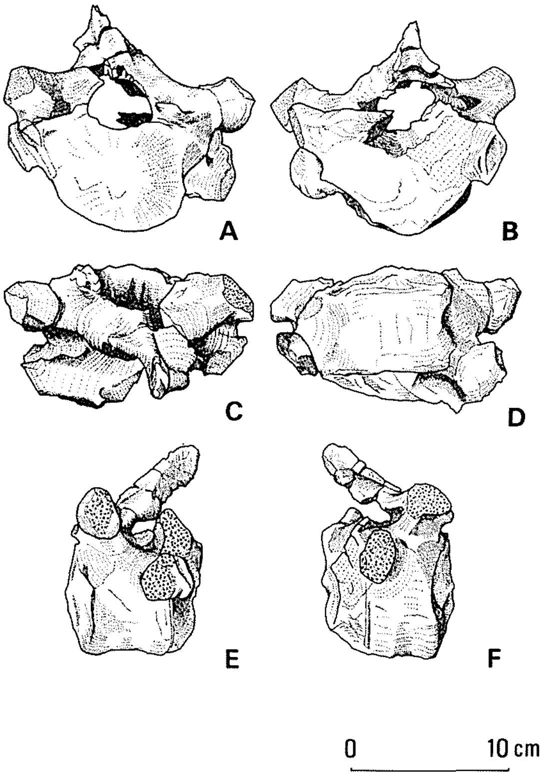


Fig. 4. ? Fifth thoracic vertebra of *Desmostylus mirabilis* (UHRno. 18466–57). A: cranial view, B: caudal view, C: dorsal view, D: ventral view, E: left lateral view, F: right lateral view.

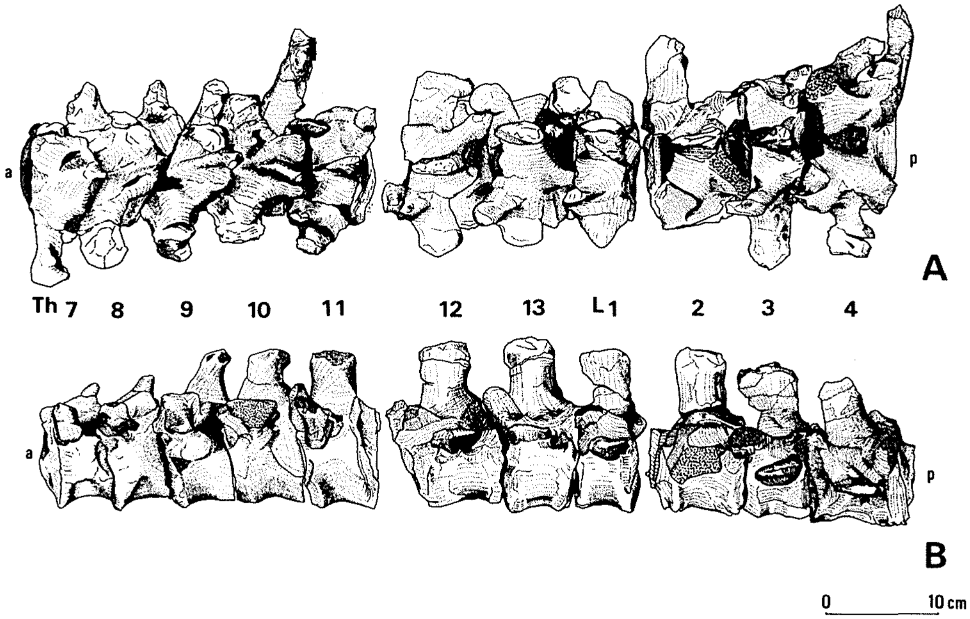


Fig. 5. Thoracic and lumbar vertebrae of *Desmostylus mirabilis* (UHRno. 18466–58—68). A: dorsal view, B: left lateral view. a: anterior side, p: posterior side.

deep posterior vertebral notch produced by an antero-posteriorly thin pedicle. The neural spines are similar to those of sirenians in their shortness, but the caudal inclination in the anterior and middle thoracic vertebrae is stronger than that of the spines of hippopotami. The cranial and caudal capitular facets have an obscure margin in every thoracic vertebra, but they are peculiar in their position in the middle thoracic vertebrae, being higher than the lower margin of the neural canal. In the posterior thoracic vertebrae it is peculiar that the accessory process projects backward from the caudal margin of the transverse process, and that the cranial articular process of succeeding vertebra tends to be placed 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 aspect and are unique in showing a parallelogrammic outline with its posteroventral corner pointed in lateral aspect. There is no median keel on the ventral surface. The transverse process originates at the level of the inferior margin of the neural canal as seen in the horse, but is peculiar in its shortness and in projecting horizontally and transversely. It is peculiar that the cranial articular process protrudes more anteriorly to the anterior surface of the body. The absence of the accessory process is in common with ungulates.

The form of the sacrum (UHRno. 18466–69, Fig. 6, Plate III) is also unique. Body width at the sacral base is three-fifths of the maximum width, much larger than in the perissodactyls or artiodactyls. The lateral part is dorso-ventrally flattened 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 a large body size. The sacrum is similar in shape to that of camels, in having a triangular outline, and to hippopotami in having a lower and vertical sacral crest.

The caudal vertebrae (UHRno. 18466–70—78, Fig. 7, Plate III) of *Desmostylus* differ most

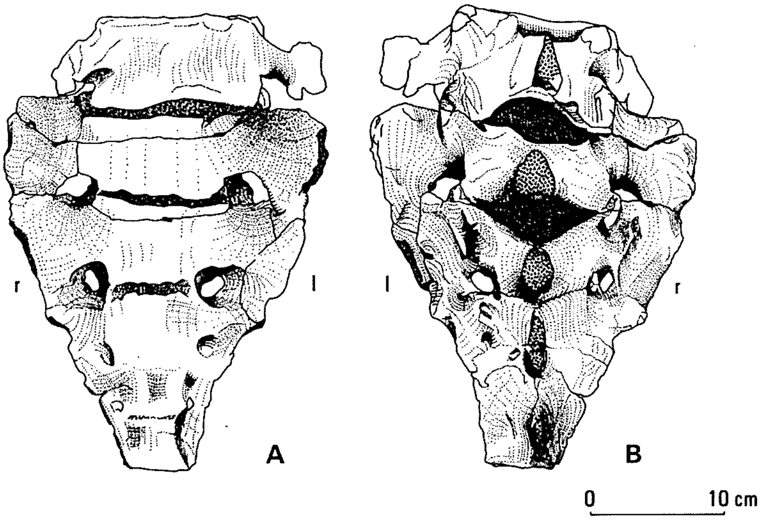


Fig. 6. Sacrum and fourth lumbar vertebra of *Desmostylus mirabilis* (UHRno. 18466–69, 68). A: ventral view, B: dorsal view. r: right side, l: left side.

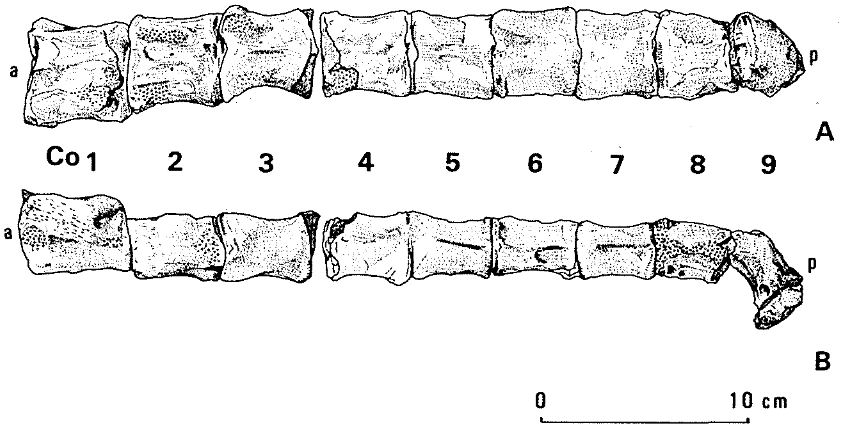


Fig. 7. Caudal vertebrae of *Desmostylus mirabilis* (UHRno. 18466–70—77). A: dorsal view, B: left lateral view. a: anterior side, p: posterior side.

from those of sirenians in the absence of the arch and transverse process, even in the first caudal vertebra.

The ribs (UHRno. 18466–79—103, Fig. 8, Plate IV) of *Desmostylus* are similar to those of tapirs or pigs in the shape of the costal head, while the degree of development of the dorsal muscle area is similar to that of perissodactyls. The shape of the sternal extremity is similar to that of the elephant or horse, being round in cross section, but not as stout as in the sirenians. The intercostal space is not so narrow as in some edentates.

The sternum (UHRno. 18466–46—54, Plate IV) of the desmostylian is similar to that of cetaceans or sirenians in its flat shape, but is characterized in being thicker and of paired form. It is broad in surface area, an adaptation for the attachment of 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 the infraspinous fossa. The tuberosity is little-developed in the facies serrata as also seen in the sirenians, contrasting with the condition, seen in many large terrestrial quadrupedal mammals (Fig. 10). The poor curvature of the dorsal margin is similar to that of giraffes while the thick caudal margin is a characteristic feature of graviportals such as rhinoceroses, hippopotami and buffalogs. The acromion is situated at a higher level than, and does not project as in the dugongs. It resembles that of the sirenians in that the scapula bends medially, particularly at the 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 the hippopotami, and the glenoid cavity is relatively large.

The humerus (UHRno. 18466–3, Fig. 11, Plate V) is stout disproportionately to the length as seen in rhinoceroses and hippopotami (Fig. 12). The epiphyses are large and the body is constricted in the middle as seen in the sea otters. The major tubercle is at a lower

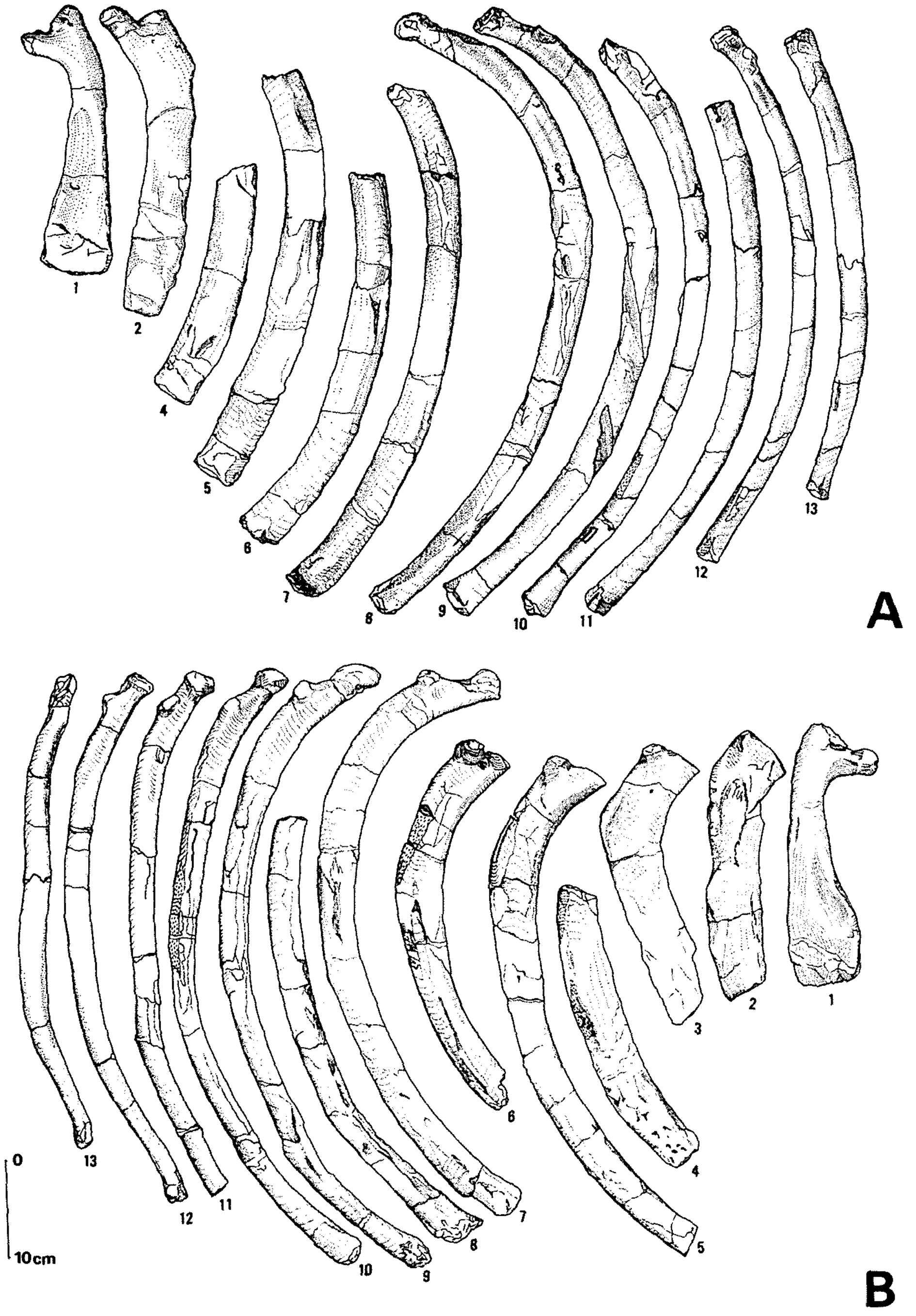


Fig. 8. Caudal view of ribs of *Desmostylus mirabilis* (UHRno. 18466–79—103). A: right ribs, B: left ribs. Numbers show rib positions.

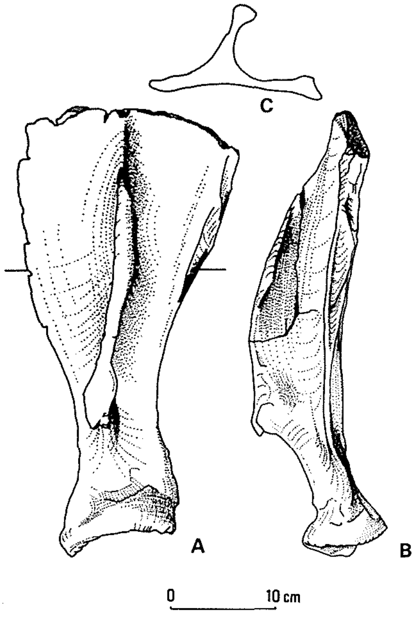


Fig. 9. Left scapula of *Desmostylus mirabilis* (UHRno. 18466–104). A: lateral view. B: caudal view, C: section seen from below.

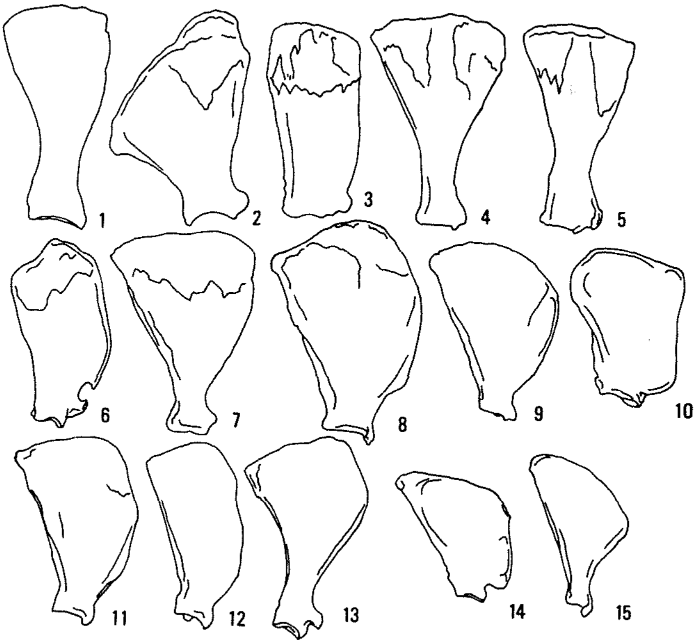


Fig. 10. Costal view of left scapula of *Desmostylus* in comparison with those of living mammals. Facies serrata, which is usually well-developed in large mammals, is indistinct in *Desmostylus*. 1: *Desmostylus*, 2: *Elephas*, 3: *Diceros*, 4: *Bos*, 5: *Equus*, 6: *Tapirus*, 7: *Sus*, 8: *Panthera*,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

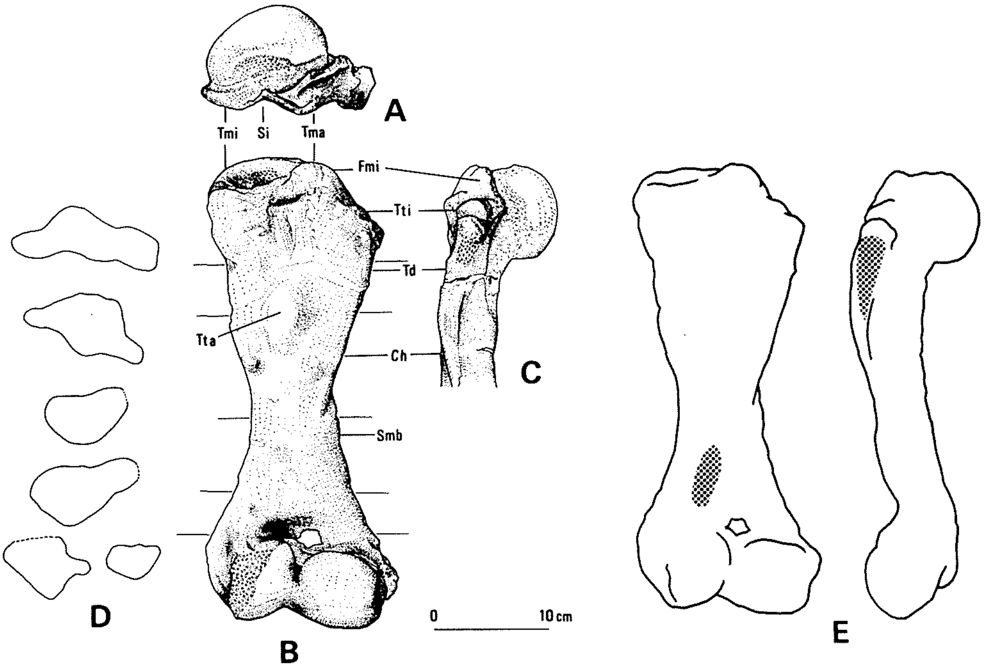


Fig. 11. Left humerus of *Desmostylus mirabilis* (UHRno. 18466–3). A: proximal view, B: cranial view, C: lateral view, D: sections seen from above, E: positions of rugged surface in cranial and lateral views. Ch: Crista humeri, Fmi: Facies musculi infraspinata, Si: Sulcus intertubercularis, Smb: Sulcus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

level than the head and projects feebly forward as in the camels and giraffes, however, *Desmostylus* is somewhat similar to the manatees in that the head faces posteriorly rather 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 the rhinoceroses or hippopotami (Fig. 14) and resembles that of the sirenians, pinnipeds and cetaceans in having a parallel arrangement of the radius and ulna. The olecranon is as large as that of pinnipeds, but is peculiar in bending markedly backwards. The ulna is similar to that of elephants and sirenians in being thickened, even in its distal end and also resembles that of sirenians in that the trochlear axis crosses with the long axis of the carpal articular surface at about right anlges. The 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 depressions. In sirenians and pinnipeds the metacarpus is proximally thick but distally thin. The metacarpus is longest along the hand axis (in the third and the fourth digit) in *Desmostylus*, but longest in the first digit in pinnipeds, and in the fourth or fifth digit in sirenians. In common with the dugongs, elephants and hip-

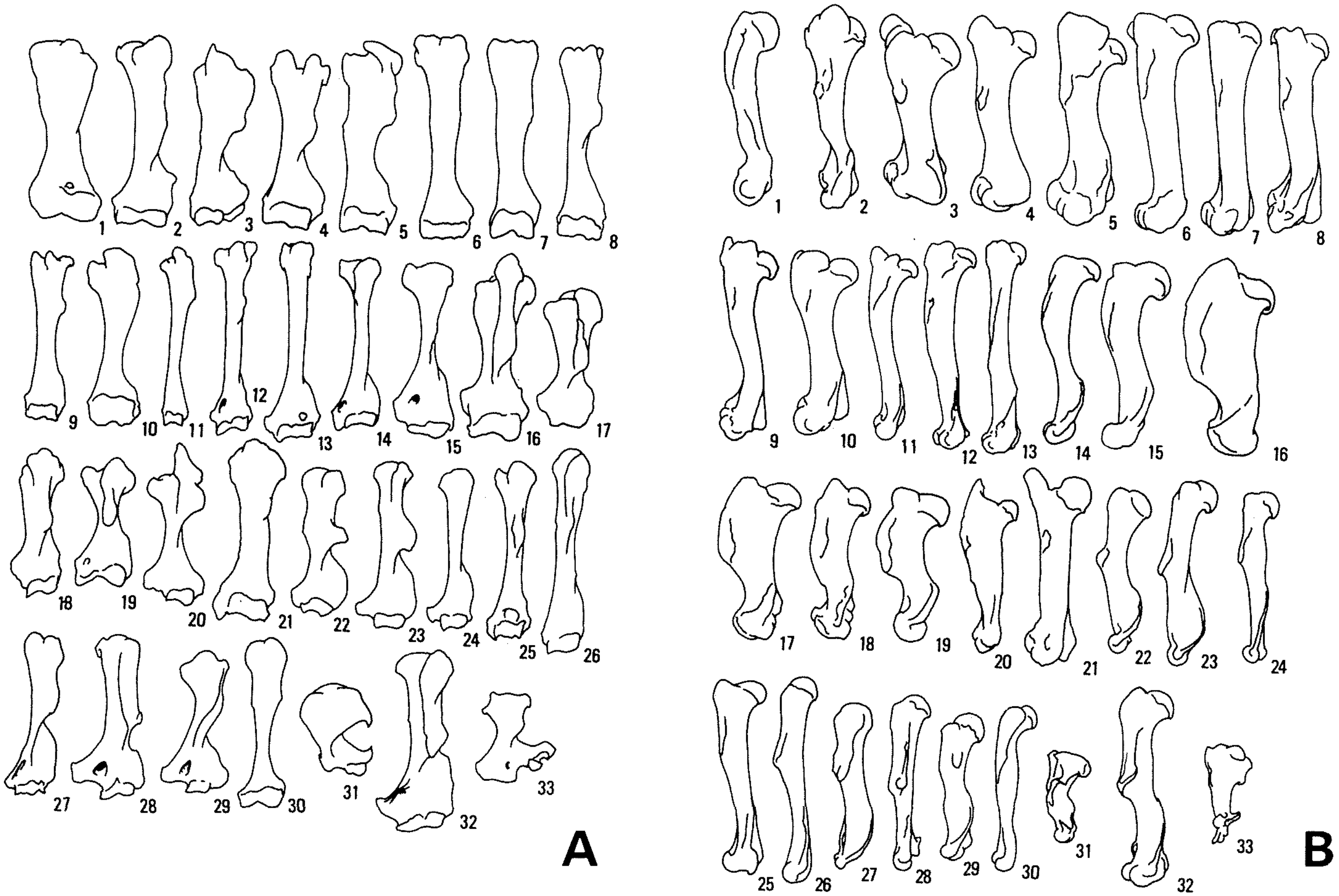


Fig. 12. Left humerus of *Desmostylus* in comparison with those of living mammals. Head of humerus faces backward and deltoid tuberosity is narrow and not protruded forward. Not drawn to scale. A: cranial view, B: lateral view. 1: *Desmostylus*, 2: *Elephas*, 3: *Diceros*, 4: *Hippopotamus*, 5: *Bubalus*, 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: *Erethizon*, 27: *Dasypus*, 28: *Myrmecophaga*, 29: *Manis*, 30: *Erinaceus*, 31: *Talpa*, 32: *Vombatus*, 33: *Tachyglossus*.

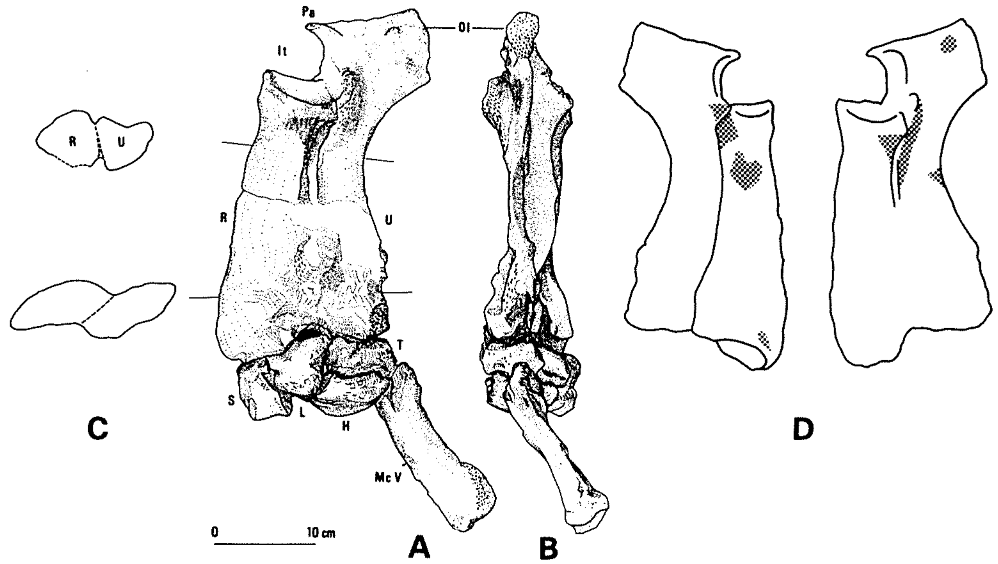


Fig. 13. Left skeleton antebrachii and skeleton manus of *Desmostylus mirabilis* (UHRno. 18466–4, 5, 6, 7, 8, 13, 106). A: lateral view (cranial view in manus), B: caudal view (lateral view), C: sections seen from above, D: positions of rugged surface in medial and lateral views. H: Os hamatum, It: Incisura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

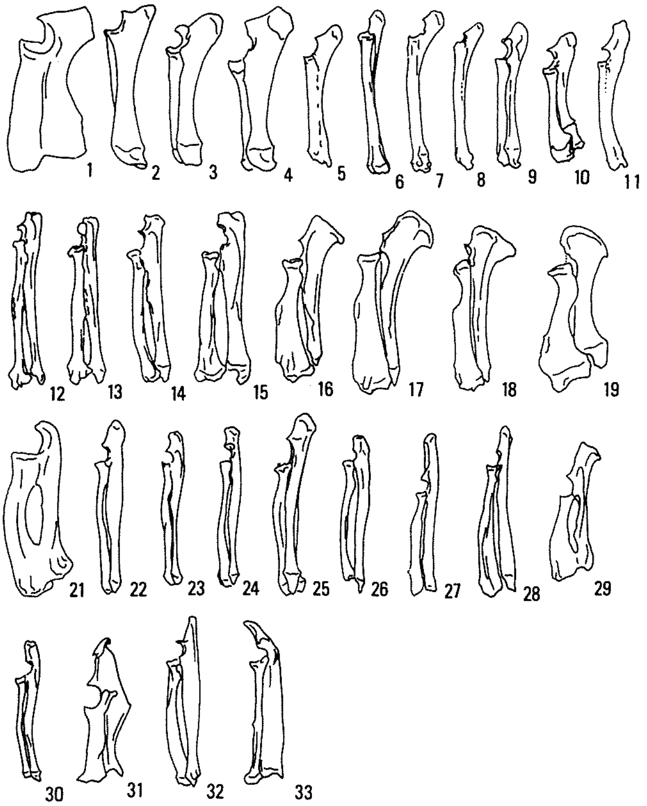


Fig. 14. Lateral view of left antebrachial skeleton of *Desmostylus* in comparison with those of living mammals. Ulna extends in parallel with radius and does not reduce in the distal part. Olecranon is well-developed. Not drawn to scale. Legend as in Fig. 12.

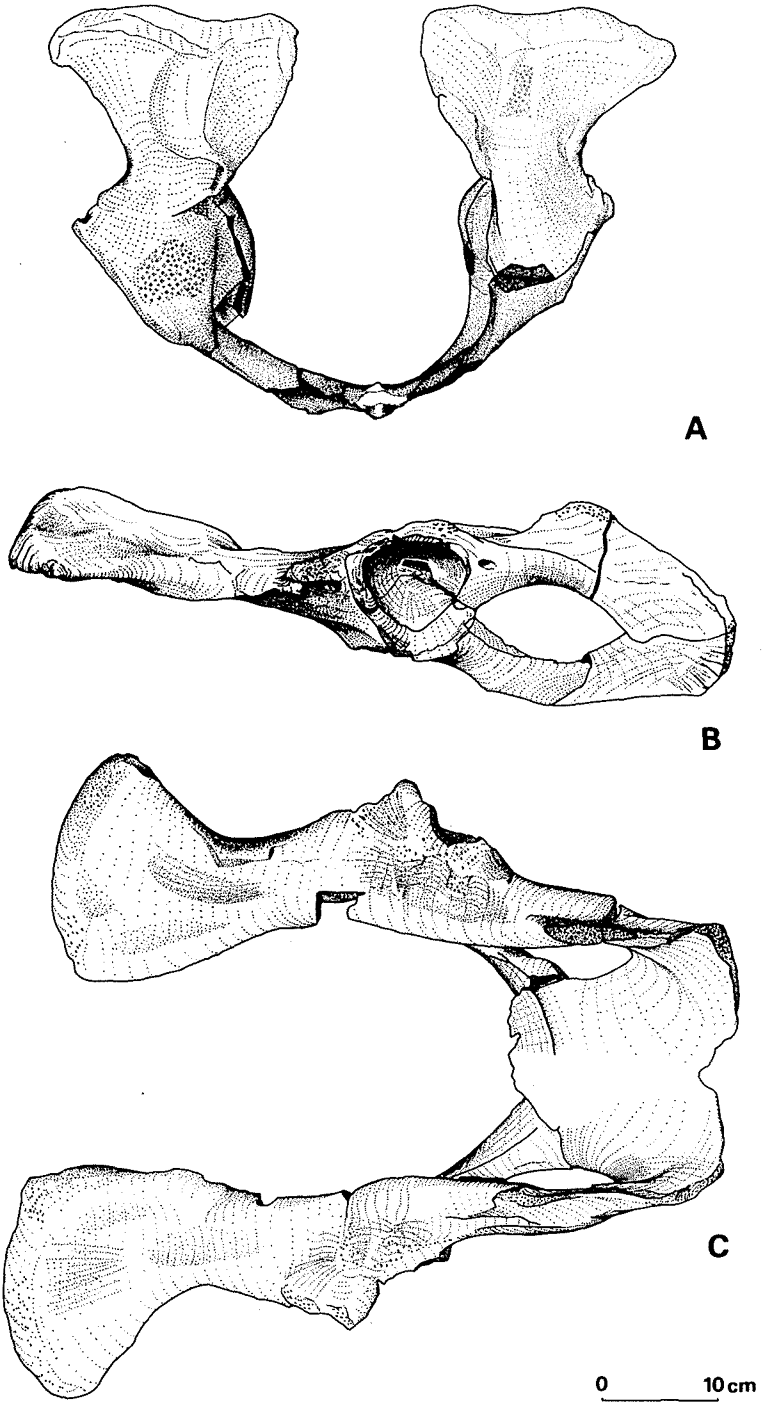


Fig. 15. Coxal bones of *Desmostylus mirabilis* (UHRno. 18466–105). A: cranial view, B: left lateral view, C: dorsal view.

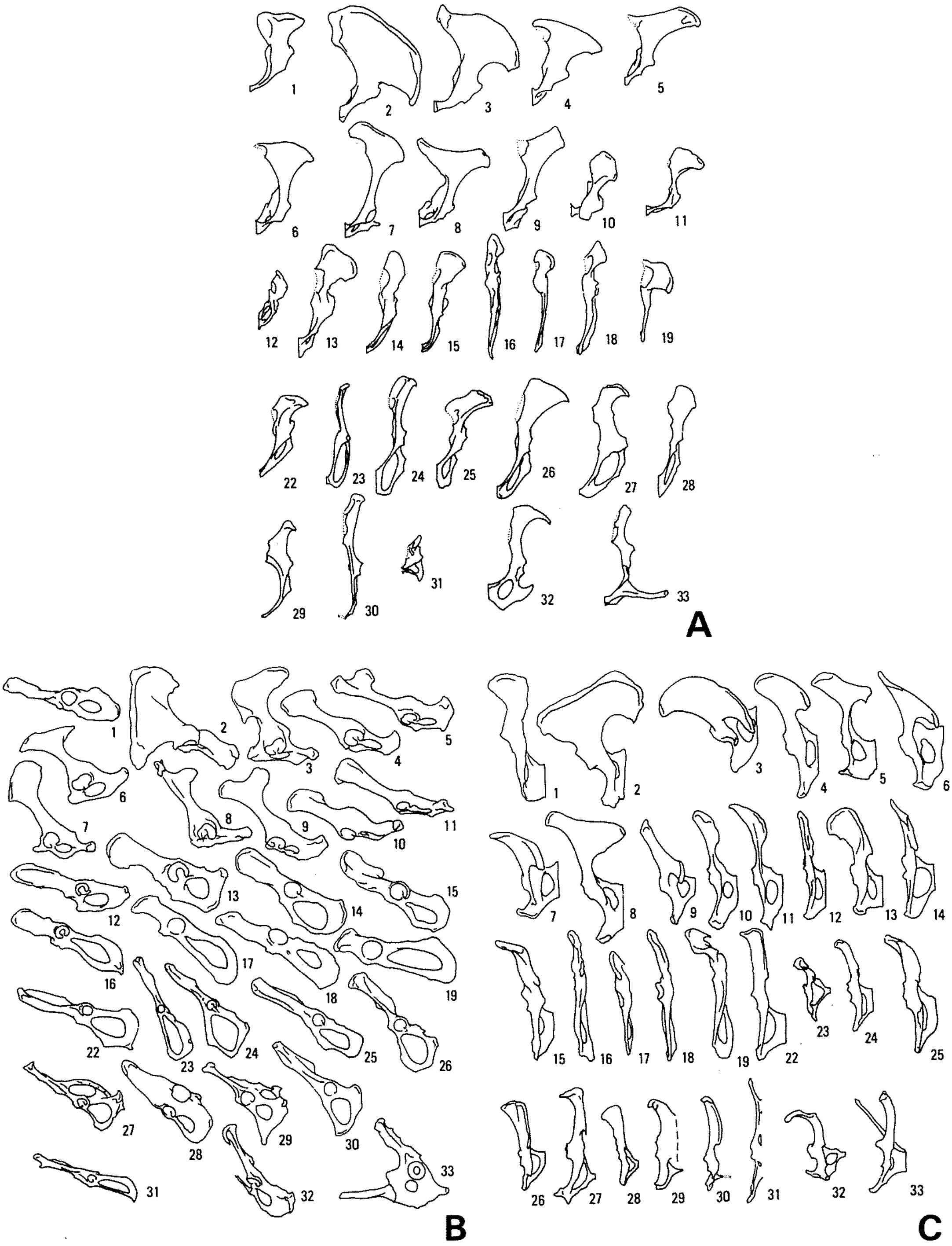


Fig. 16. Left coxal bone of *Desmostylus* in comparison with those of living mammals. Ilium is not so expanded as in a large mammal. Length of ilium is nearly equal with that of ischiopubis. Obturator foramem faces outward. Coxal bone of *Desmostylus* differs from those of rodents in spite of some resemblances. A: cranial view, B: lateral view, C: dorsal view. Not drawn to scale. Legend as in Fig. 12.

popotami the metacarpus is twice as long as the proximal phalanx, but this situation differs from that of dolphins, pinnipeds and perissodactyls.

The phalanx of *Desmostylus* is similar to that of the manatees, elephants, hippopotami and rhinoceroses in being short and wide and in frequently having torsion. It is, however, quite different from that of pinnipeds and cetaceans in which it forms an element of the fin.

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

The pelvic girdle (UHRno. 18466–105, Fig. 15, Plate VI) of *Desmostylus* is large but the wing of the ilium is only weakly expanded, thereby differing from that of elephants and 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 not directed as ventrally as in proboscideans and artiodactyls, being directed more posterolaterally. In contrast to ungulates, the obturator foramen faces laterally as in pinnipeds or rodents, but *Desmostylus* differs from them in having a broad area along the long pelvic symphysis. Although the shapes of the pubis and ischium in lateral view, and the ratio of pubic length differ from those of ungulates and resemble those of rodents, the angle of symphysis on the horizontal and frontal plane more closely resembles that of the ungulates rather than that of rodents.

The proportion of the femur (UHRno. 18466–28, 29, Fig. 17, Plate VII) of *Desmostylus*

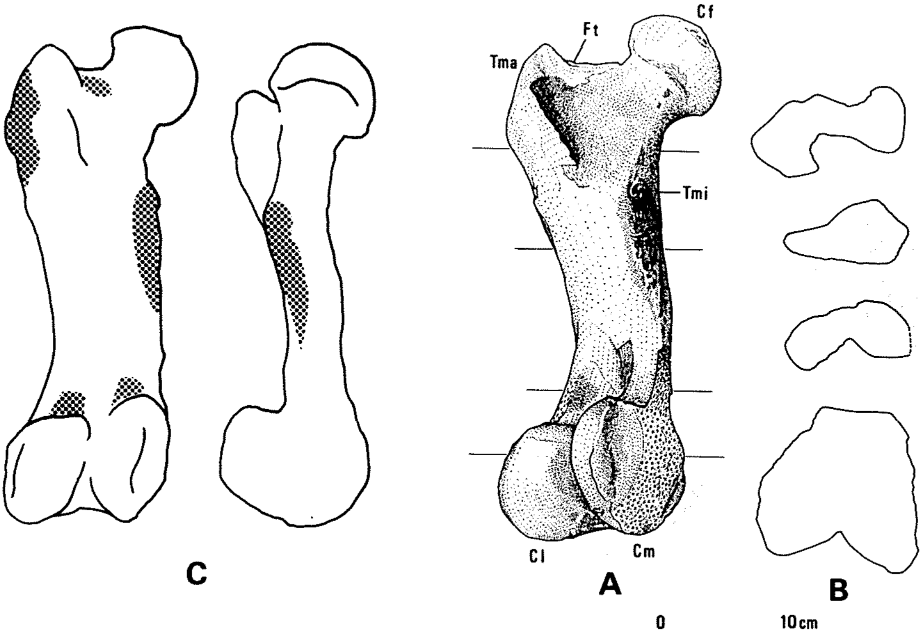


Fig. 17. Left femur of *Desmostylus mirabilis* (UHRno. 18466–29). A: posteromedial view, B: sections seen from above, C: positions of rugged surface in caudal and medial views. Cf: Caput ossis femoris, Cl: Condylus lateralis, Cm: Condylus medialis, Ft: Fossa trochanterica, Tma: Trochanter major, Tmi: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

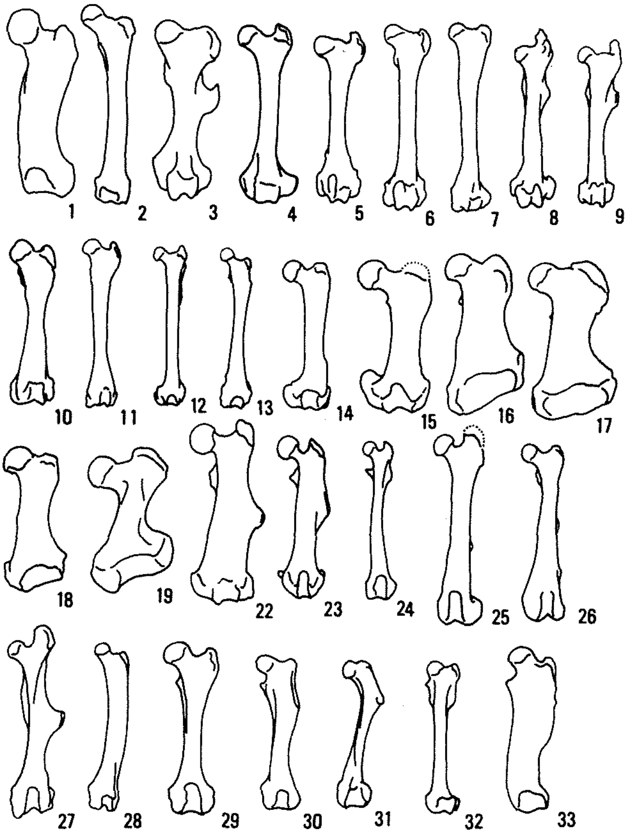


Fig. 18. cranial view of left femur of *Desmostylus* in comparison with those of living mammals. Not drawn to scale. Legend as in Fig. 12.

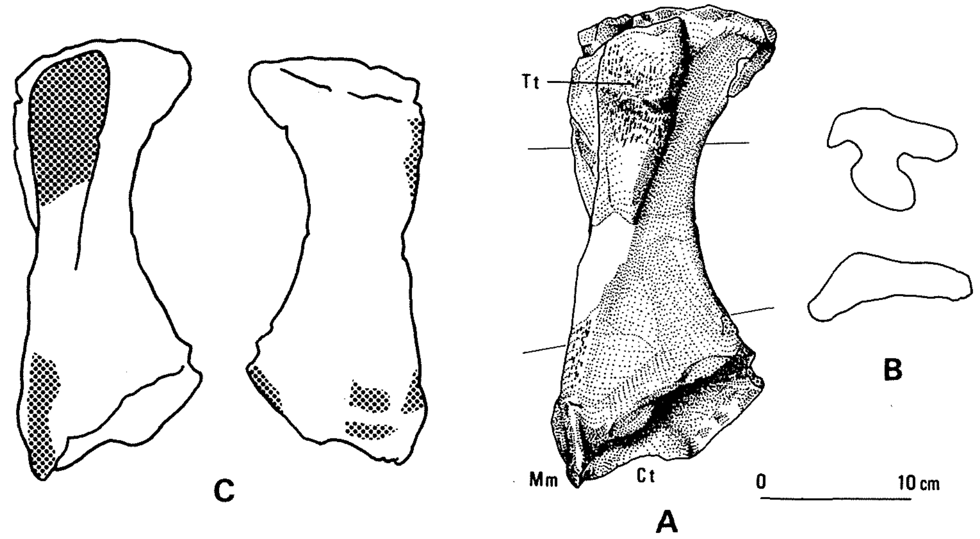


Fig. 19. Left tibia of *Desmostylus mirabilis* (UHRno. 18466–30). A: cranial view, B: sections seen from above, C: positions of rugged surface in cranial and caudal views. Ct: Cochlea tibiae, Mm: Malleolus medialis, Tt: Tuberositas tibiae.

resembles that of rhinoceroses, beavers and sea otters (Fig. 18). It is similar to elephants and pinnipeds in the shaft being flattened antero-posteriorly. *Desmostylus* is similar to rodents, but differs from ungulates in having the femoral neck constricted in all directions. It is similar to the rhinoceroses in that the major trochanter is at a lower level than the head, but this feature is more prominent in *Desmostylus*. The mode of distal expansion of the rugged surface in the minor trochanter is peculiar to *Desmostylus*. The laterally bending shaft resembles the pinnipeds and beavers, while the shallow trochlear groove is similar to that of the pinnipeds.

The proportion of the tibia (UHRno. 18466–30, Fig. 19, Plate VIII) of *Desmostylus* most closely resembles that of the hippopotami, but the epiphyses of the *Desmostylus* are more developed (Fig. 20). The tibia of *Desmostylus* is peculiar in the presence of a large and conspicuous laterally overhanging tibial crest, a medially twisted tibial shaft and an anterolaterally facing distal articular surface. *Desmostylus* is similar to pinnipeds in that the proximal articular surface slopes backwards.

The greatest peculiarity exhibited in the astragalus and calcaneum (UHRno. 18466–31, 32, Fig. 21, Plate VIII) that when both bones are articulated with the tibia the tuber calcis projects medially. This feature is peculiar to desmostylians. The desmostylid metatarsi are peculiar in that they are approximately the same length as the proximal phalanx and are much shorter than the metacarpi. It is probably also peculiar among mammals in that the length of

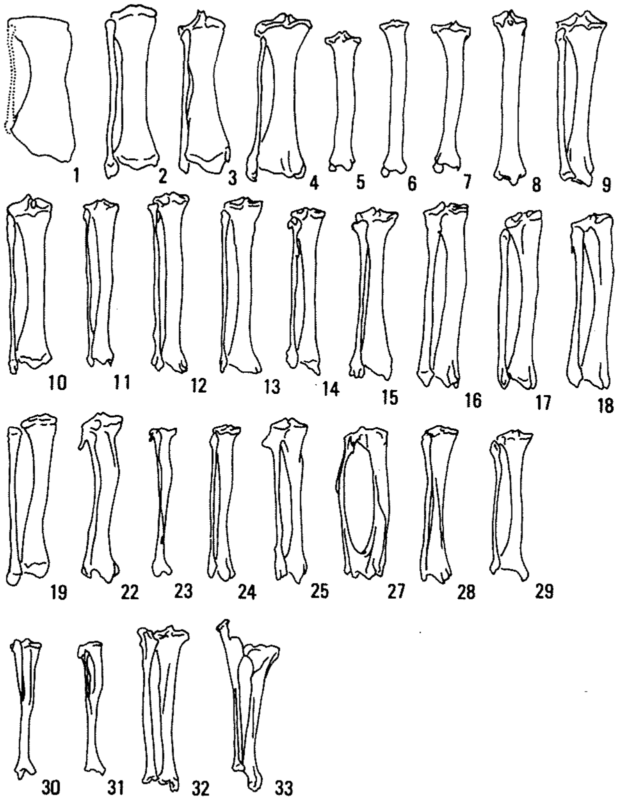


Fig. 20. Caudal view of left crural skeleton of *Desmostylus* in comparison with those of living mammals. Crural skeleton shows a marked medial twisting. Not drawn to scale. Legend as in Fig. 12.

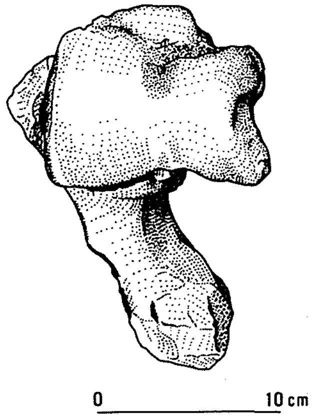


Fig. 21. Dorsal view of left astrag alus and clacaneum of *Desmostylus mirabilis* (UHRno. 18466–31, 32). When calcaneum is articulated with astragalus, tuber calcis declines much medially.

the metatarsi increases laterally from the second to the fifth metatarsi. The characteristics of the phalanges in the pes are the same as those in the manus.

Desmostylus most closely resembles to the rhinoceroses and hippopotami in having the same relative length ratio among the femur, tibia and pes.

B. Characteristics of the Desmostylian Skeletal Elements

In this section, the morphological characteristics of *Desmostylus* which are important for skeletal restoration are described briefly. Detailed descriptions and remarks are mentioned in the Appendix.

1. BONES OF THE AXIAL SKELETON

The general feature of the desmostylian's vertebral body is characterized by being antero-posteriorly short and low and wide in shape, with both short and stout transverse processes and short spinous process. The cervical vertebra is short, its vertebral body is low with a short spine and the ventral tubercle of the transverse process flat and projecting downwards. The costal facet of the transverse process of the thoracic vertebrae faces laterally. The lumber vertebra is wide and short, its costal processes short and projecting horizontally and perpendicular to the body axis, and the accessory processes are absent. The sacrum is triangular in outline, and flattened dorso-ventrally, with a low sacral crest. The caudal vertebra is short and has no neural or hemal arches.

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

The ribs increase markedly 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 ribs, and inclines more steeply in the anterior ribs, i.e. between the fifth and ninth ribs, the more anterior rib inclines more steeply due to each dorsal muscle area usually facing horizontally. The costal shaft is not flat in cross section except in the 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 in shape. As a whole the sternum widens towards the caudal end. The thorax is nearly circular in frontal section. It is estimated that the backward inclination of the sternum is fairly marked, 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 little-developed. The scapular spine is high and the acromion is situated at a higher level than the glenoid cavity.

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

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

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

The tibia is shorter than the femur, its proximal surface inclining 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 overhangs the lateral surface in the proximal region. The distal surface is inclined mediocaudally, facing craniolaterally. The fibula is much shorter than the tibia. It is jointed with the tibia at its posteroproximal and laterodistal surfaces—it lies as if winding round the posterolateral surface of the tibia.

When articulating the astragalus with the calcaneus, the 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

Although the body shape of the mammals varies greatly between species, it is also true that there are general rules in their skeletal composition. The rules themselves are useful not only for checking the adequacy of previously restored skeletons but also for the design of new restorations. Some rules obtained from observations on living mammalian skeletons are slightly tentative and they may be gradually improved by increased knowledge arising from further comparison with 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 bone and the whole skeleton, (3) the rules about the correlation among skeletal elements, and (4) the rules about the correlation between the form and function of bones. Each of these rules is explained and a comment on the exceptions among mammals, particularly ungulates is given, along with relevant examples.

A. Curvature of Vertebral Column

The outline of the back in life varies with the length and inclination of the spinous processes (Gergory, 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

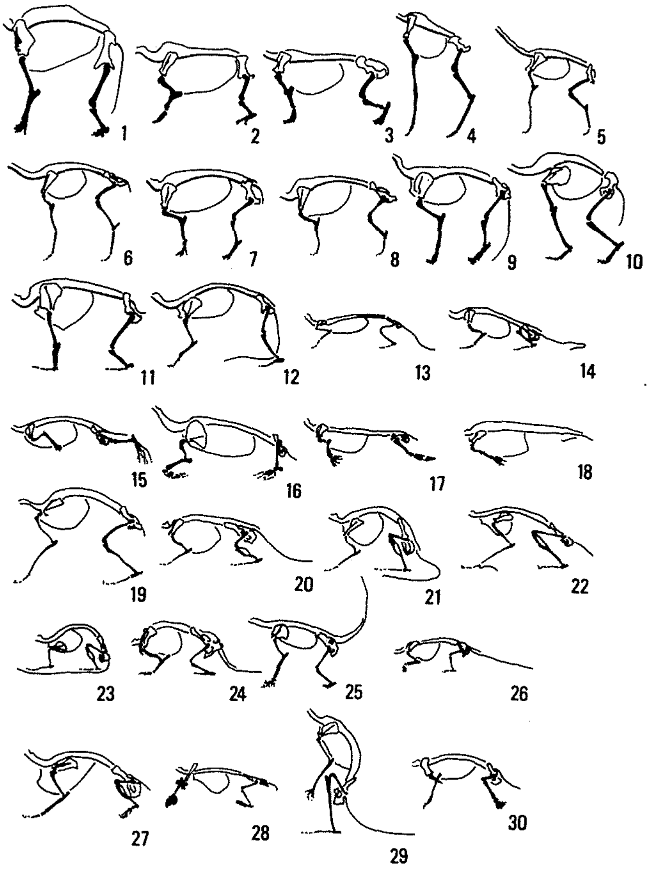


Fig. 22. Postcranial skeletons of living mammals. Curvature of vertebral column does not correlate with form of pelvis. Proximal segments of limbs are longer than other segments in graviportal type and are shorter in pinnipeds. Not drawn to scale. 1: *Elephas*, 2: *Diceros*, 3: *Hippopotamus*, 4: *Giraffa*, 5: *Lama*, 6: *Rangifer*, 7: *Tapirus*, 8: *Tayassu*, 9: *Panthera*, 10: ? *Crocuta*, 11: *Nasua*, 12: *Paguma*, 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*.

vertebral column curvature and pelvic shape (Fig. 22).

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

B. Neck Length and Shoulder Height

In terrestrial quadrupedal mammals the total length of the head and neck approximates to 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, or volant animals, or animals with anterior limbs used for various purposes other than supporting the body weight or walking on land. Thus, the rule may be applied in particular to large ungulates.

C. Form of Thorax in Cross Section

The major function of the 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 anterior ribs via the 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 circualr in frontal section.

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 and in terrestrial locomotion than the latter, and every case of large terrestrial mammal adjust themselves to the former state. Among mammals exceptions are monotremes, small insectivores, cetaceans, sirenians and bats.

E. Length of Limb Segments and Locomotive Function

The free limb bone is divided into proximal (stylopodium), middle (zygapodium) and distal segments (autopodium), and the ratio between the 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 the proximal segment is shorter than the middle segment in cursorial types, but longer in graviportal types (Gregory, 1912, 1941; Hildebrand, 1974). Aquatic mammals are apt to have a very short proximal segment and a long distal one (Romer and Parsons, 1977).

F. Limb Joints

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

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

The knee joint is regarded as a hinge joint. Restriction of movement is usually due to the presence of ligaments around the joint, although this is not reflected in the bone shape.

G. Foot Posture and Metapodials

The fundamental foot posture is plantigrade in terrestrial tetrapods, but it changes into digitigrade and unguligrade with the metapodials becoming longer, as the running speed increases. In general, the metapodials are as long as the proximal phalanges in the plantigrade but much longer in the unguligrade (Lessertisseur and Saban, 1967). The foot posture of artiodactyls or perissodactyls is exclusively unguligrade, and some of them have metapodials many times as long as the proximal phalanges (Fig. 23). This feature is especially conspicuous in the progressive types in which the digits are decreased in number. Exceptions include the

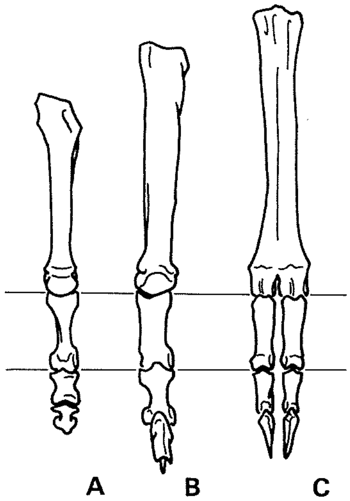


Fig. 23. Cranial view of the third left metatarsus and digit showing relationships between metapodials and foot postures. Not drawn to scale. A: *Homo* (plantigrade), B: *Panthera* (digitigrade), C: *Cervus* (unguligrade).

elephants, which have seeming become secondarily plantigrade by the presence of a fleshy pad, and bipedal saltators such as kangaroos.

H. Direction of Tips of Digits

Since mammals usually walk in a craniad fashion, it is convenient for the tips of the digits to point forwards during 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 the tips of the digits in the pes tends to be perpendicular to the body axis. Exceptions occur in such animals as anteaters with huge claws and great apes with knuckle-walking as well as aquatic and volant animals.

I. Similarity of Both Limbs

In quadrupeds the anterior and posterior limbs tend to take a similar shape and this is most noticeable in large ungulates which cannot utilize the forelimbs 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 attempting to articulate the bones faithfully to their shape, it will be realized that the restored skeleton cannot follow some of the rules in the foregoing section due to of bone characteristics of *Desmostylus* mentioned above. For example, with limbs stretching under the trunk, the tips of the digits in the manus should be directed either laterally, or medially, lying on the back of the manus on the ground, but were the limbs to extend outwards, then both the manus and the pes should be directed cranially. In this paper the latter mode of restoration is adopted, based on the following considerations.

A. Myology and Osteology of *Desmostylus*

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

1. FORELIMBS (Fig. 24)

In the desmostylians, the facies serrata of the scapula is less developed in comparison with ungulates in general, but the presence of a 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 forelimbs. In large ungulates these muscles differ in their direction; the serratus ventralis runs vertically while the pectoral muscles run horizontally. For this reason the serratus ventralis, which runs in the direction of gravitational force, mainly has a supporting function (Young, 1975).

However, to explain the rough nature of the facies serrata and the large surface area of the sternum in *Desmostylus*, it is more reasonable to assume that the major supporting function

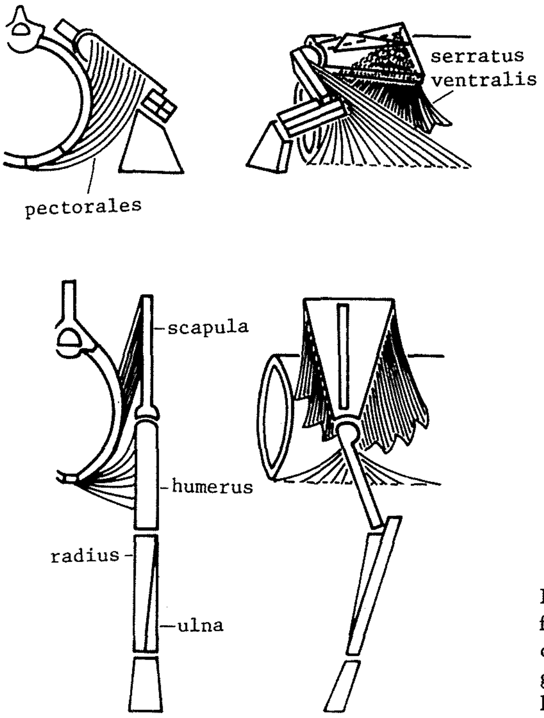


Fig. 24. Estimated mode of muscle attachment in forelimb of desmostylians in comparison with those of general mammals. Above:desmostylians, Below: general mammals, left: cranial view, right: left lateral view.

is performed 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 the fascicle of the pectoral muscles is rather perpendicular, because the relative position of the muscle insertion on the humerus to the sternum is higher in level than in other mammals. However, the direction of the serratus ventralis becomes fairly horizontal near the insertion, due to the scapula not being sagittal, but almost horizontal, in position with its glenoid cavity directed cranially, the spine directed dorsally and the dorsal margin is facing caudally.

Thus, the main muscles supporting the anterior body weight can be shifted from the serratus ventralis to the pectoral muscles simply by rotation of the scapula at a right angle to make the scapula and humerus lie in a nearly horizontal plane. Furthermore, this arrangement clearly conforms to the rules with respect 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 level and the deltoid crest is narrower than in other mammals. This is because the muscles that extend the shoulder joint attach to these areas, and play a less important role in transversal position than in a parasagittal position.

In *Desmostylus*, the pronation of the antebrachial skeleton seems to be impossible, for the radius and the ulna are parallel, being fixed to each other. As a result of the humerus being projected laterally and the elbow joint being flexed at a right angle, the distal portion of the forearm is directed forward, since the skeleton of the forearm is situated on the same plane as the scapula and humerus make. When the forelimbs stretch downward, the tips of the digits is not directed forward without the pronation of the forearm. However, in the transversal position, the tips of the digits point 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 a slight cranial dip, and both the humerus and the antebrachial skeleton on the same plane also incline 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 the carpal ligaments and antebrachial muscles, function to support the weight via the antebrachial skeleton which inclines backward, and the manus. As dorsal flexion of the wrist is impossible in this condition, a plantigrade position is impossible.

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 the antebrachial skeleton. This relation is related to the fact that the skeletal system from the shoulder to the manus inclines inwardly, not horizontally, 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 forelimbs, the bones of carpi hold more a horizontal position at the proximal part of the metacarpi.

An inevitable effect of stretching the limbs laterally is that the metacarpus is rather longer than the metatarsus. As it was necessary for *Desmostylus* to raise the belly from the gound when walking, the hindlimbs might provide the necessary height. The tibia should stand almost vertically, even if the femur is situated almost horizontally, whereas with a lateral projection of the humerus, the antebrachial skeleton must be inclined considerably. For this reason, some portion of the forelimbs distal to the wrist joint must be elongated in order to retain a height corresponding to the hindlimbs.

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

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

2. HINDLIMBS (Fig. 25)

Generally in mammals the posterior body weight is supported mainly by the femur in an adducted position, with the pull being exerted by the gluteus medius muscle inserted in the trochanter major. It is accepted that the fan-like expanded wing of the ilium in graviportal ungulates is to provide an increased attachment area of the gluteus medius muscle. However, in *Desmostylus* the ilium wing is not developed and the level of the trochanter major is lower, despite its large body size, similar to that of hippopotami. However, the regions lateral to the pelvic symphysis and between the obturator foramina, are exceptionally and disproportionately

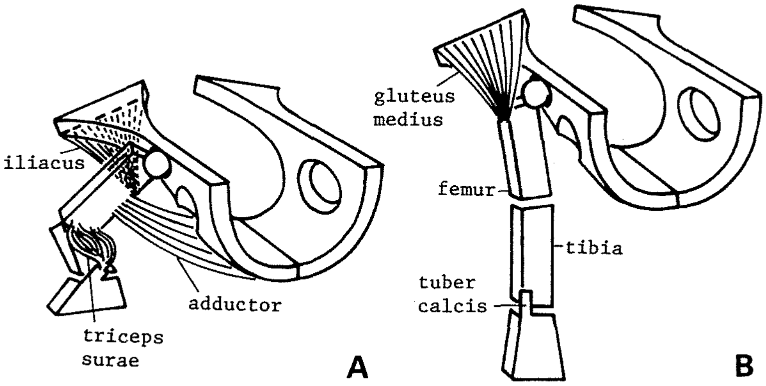


Fig. 25. Posterolateral view of estimated mode of muscle attachment in hindlimb of desmostylians in comparison with those of general mammals. A: desmostylians, B: general mammals.

wide. Besides them a rugged surface of the trochanter minor is well-developed and unusually expanded distally. Judging from these facts, it is estimated that in *Desmostylus*, both iliacus and adductor muscles that adduct the femur better developed than the gluteus medius, and probably mainly 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 to the following consequences; the femur is abducted; the hip joint is flexed; and the long axis of the femur is directed anterolaterally and nearly horizontally. As the femur is in a state extending laterally in this manner, circumduction of the femur becomes important in locomotion. This movement becomes more probable by the possession of the neck which is constricted in all directions.

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

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

Since both proximal and distal articular surfaces of the tibia incline posteriorly, the longitudinal axis of the tibia should be inclined slightly anteriorly. The balance of the hindlimbs is probably retained in this way.

When tibia, astragalus and calcaneus are articulated together, the tuber calcis usually to protrudes caudally, but in *Desmostylus* it inclines medially. This is understandable since the gastrocnemius muscle, originating 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 hindlimbs in *Desmostylus* differ from those of general mammals only in that of the femur, i.e. its anterior surface faces dorsally and the distal part craniolaterally.

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. Because the cranio-caudal diameter of each sternal segment is considerably longer than the intercostal spaces between the anterior ribs, the sternum would have been fairly low caudally.

It should be noted that the actual arrangement of the sternal segments differs from that described by Shikama (1966) and the name of each segment and its orientation is amended here (Table 7). As the anterior ribs decrease in length cranially, it is natural that the thorax becomes narrower cranially along with the sternum. Consequently, it will be appreciated that Shikama's arrangement is reverse with regard to the body axis. The lateral margin tends to be thinner in the anterior part of the first, second and third mesosterna. The orientation of the fourth mesosternum in Shikama's arrangement is discordant with this tendency, making it 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 diverge backward. Because embryologically each sternal segment is developed as paired cartilages which later fuse with one another at the mid-line and this process proceeds from front to back, the author's arrangement is suitable for *Desmostylus*, in which each segment of the sternum ossifies independently and is not adherent to 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 hindlimbs and to the flexion in their joints. In this case, the curvature of the vertebral column is gentle and it is not necessary to bend it strongly or to set up the pelvis nearly vertically, thus conforming to rule (A). The shoulder height is low owing to the lateral position of the anterior limbs, and thus this skeleton conforms well to rule (B) as seen in usual ungulates in spite of the shortness of the neck. The cross section of the thorax is circular as in aquatic mammals, although it is generally compressed in large ungulates with the anterior limbs in the parasagittal position. This probably reflects the transversal position of the anterior limbs in *Desmostylus*, and may possibly be the same as those of aquatic mammals (C).

Desmostylus, with its transversely positioned limbs, is an exception among large ungulates, which usually have parasagittally positioned limbs (D). The author's skeletal restoration was performed assuming *Desmostylus* was a quadrupedal graviportal mammal in which the proximal segments of the limbs are longer than the middle ones (E) i.e. it was assumed that the animal could walk without dragging its belly. Since both shoulder and knee joints were mounted faithfully according to the direction of the articular surface of the limbs, the limb position agrees with rule (F). On the basis of the forms of the metapodials and phalanges it is presumed that the foot posture is pseudounguligrade with the flesh pad in both fore- and hindlimbs, while the pes with its short metatarsi does not conform to rule (G) regarding the length of the metatarsi and phalanges. The direction of the digital tips is cranial in both manus and pes, and is consistent with rule (H).

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

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

Table 6. Conformability with general rules of mammalian skeletal construction in restored skeletons.

	Nagao (1936)	Repenning (1965)	Shikama (1966)	British Museum (1975?)	Kamei (1975)	Hasegawa (1977)	Inuzuka (1984)
Gentle curvature of vertebral column	○	×	×	×	○	×	○
Neck length and shoulder height	○	×	○	×	×	○	○
Similarity of fore- and hindlimbs	○	×	×	×	△	×	○
Under position of limbs	○	○	○	△	○	○	×
Toe pointed cranially	○	△	×	△	×	×	○
Interpretation of sternum	×	×	○	×	×	×	○

○: conformable, △: partly conformable, ×: incompatible. As to interpretation of sternum, ○: present, ×: absent.

C. Mode of Fossil Occurrences

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

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

The Utanobori specimen retains all the cervical vertbrae which are lacking in the Keton specimen. From this as the body of the cervical vertebrae is shorter cranio-caudally than that of other vertebrae, it has become clear that the neck region is short in proportion to body length. A longer neck is supposed in Nagao's restoration, but from this discovery the shoulder height must be changed to be even lower. Assuming the anterior limbs were situated under the trunk then the rostrum of this animal cannot reach the ground without flexing the limbs. Furthermore were the limbs situated under the trunk, the following facts are difficult to explain: (1) the neck is short, (2) each limb bone was found lying laterally, and (3) the longitudinal axis of the scapula was parallel to the vertebral axis.

The original buried posture of the Keton specimen is unknown as it was contained in nodules, but according to photos taken before preparation, the region from the thorax to the pelvis had remained articulated and the bone arrangement was the same as the Utanobori specimen found lying on its back.

Shikama (1966) showed a figure of the Izumi skeleton in the buried state which is the first whole skeleton of *Paleoparadoxia*. According to this figure, only the region from the posterior thoracic vertebrae to the pelvis remained in its original state, and the posture lying on the back was the same as that of the Utanobori and Keton specimens. Also in the Chichibu-tsuyagi

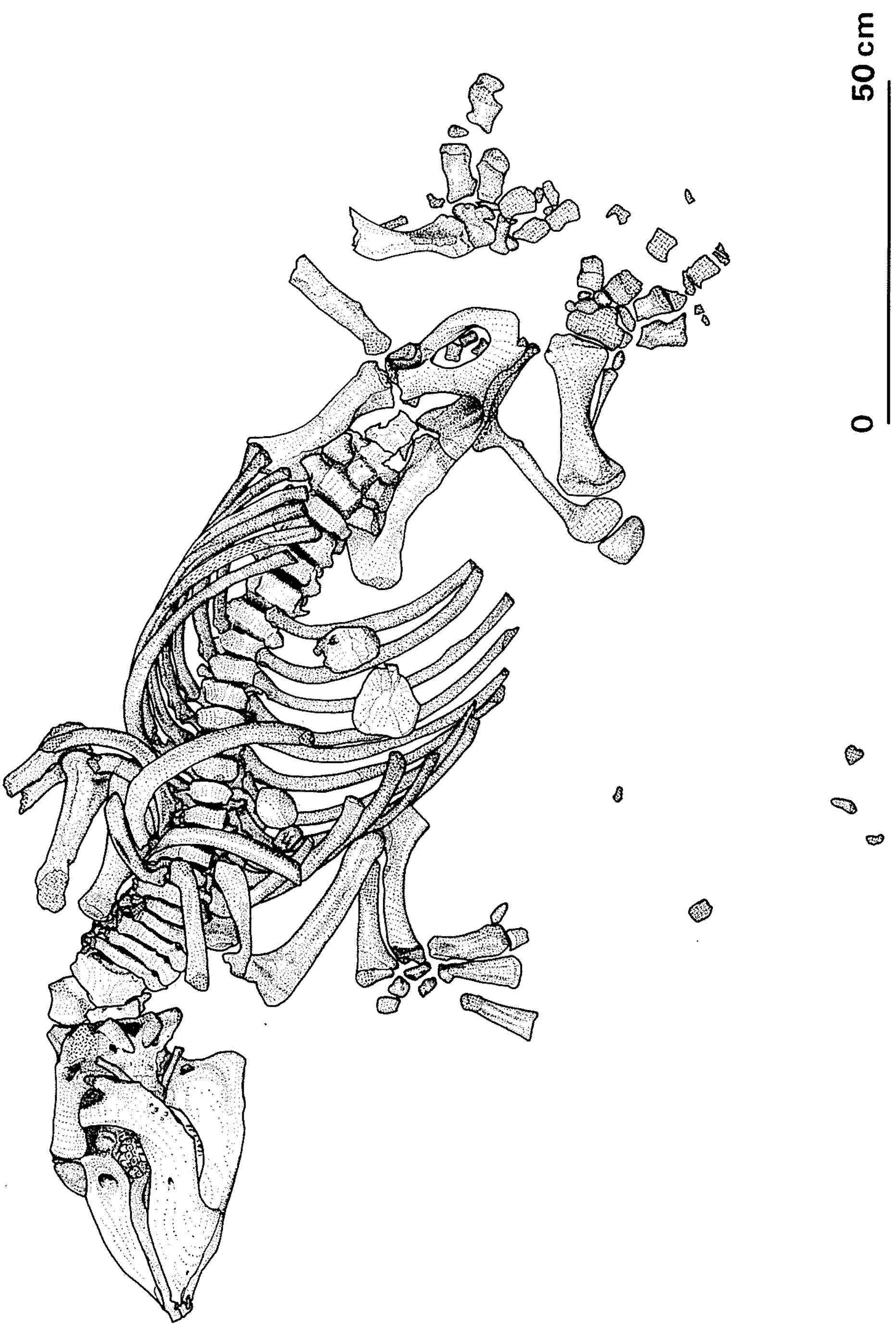


Fig. 26. Mode of fossil occurrence in the Utanobori specimen. The neck is short, longitudinal axis of scapula is parallel to the vertebral axis, and each femur lies on the opposite side.

specimen of *Paleoparadoxia*, it has been shown that the cadaver was deposited lying on its back, judging from the fact that the ribs of each side are situated on the right and left sides of the vertebral column respectively.

The modes of occurrence in the Keton, Izumi and Chichibu-tsuyagi specimens are common with the Utanobori specimen and thus, nothing contradictory to the author's restoration has been found in those data.

It may therefore be concluded that the desmostylians were unique mammals in having the limbs in the lateral position like amphibians or reptiles (Fig. 27, Plate XI).

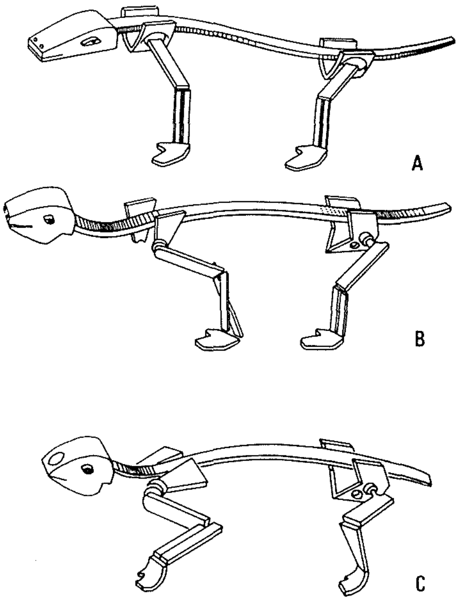


Fig. 27. Comparison of limb postures. A: Reptilia, B: Mammalia, C: Desmostylia. A and B after Lessertisseur and Saban (1967)

VIII. CONCLUSION

From comparative osteological and functional morphological studies, it has become clear that the desmostylians had a basic figure in which the limbs stretched laterally like amphibians or reptiles, quite exceptional among large terrestrial ungulates. This conclusion is mainly based on the examination of the Keton specimen, the holotype of *Desmostylus mirabilis* Nagao. The proposed restored body shape 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. Although the Keton specimen of *D. mirabilis* forms the basis of this work, the Utanobori specimen of *D. japonicus* was used to supplement important portions lacking in the Keton specimen. Forty-six species of living mammalian skeletons were compared with the bones of *Desmostylus*.

(2) The significance of this study is in its introduction of the methods of functional and comparative anatomy to skeletal restoration. The 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. General rules of skeletal construction in mammals, especially ungulates are sought, based on comparison among their skeletons.

(3) The current restoration differs most from those previously made in its transversal position of limbs: both the humerus and the femur extend laterally. Previous restorations have shown a more or less parasagittal position with the limbs extending under the trunk. In these cases, owing to the peculiar bone form of desmostylians, all are open to the critisism having an unnatural curvature of the vertebral column, as well as the direction of tips of digits, foot posture etc. In the present hypothesis, many points shown in these restorations are corrected; with respect to the limb directions the desmostylian represents the sole exception to the general rules of skeletal construction in ungulates.

(4) Because the important characteristics for the restoration of the postcranial skeletons are common to both *Desmostylus* and *Paleoparadoxia*, this conclusion is applicable to the skeletal restoration of all animals of the order Desmostylia, i.e. not only to the Desmostylidae but also to the Cornwalliidae. Moreover, the theoretical basis for this restoration was supported by the mode of fossil occurrence of both genera.

(5) Once the basic standing posture of the desmostylian skeleton has been resolved, the life restoration, the reconstruction of the locomotion, habitat etc. of these animals may be presumed with more secure foundation. The desmostylian posture with limbs stretching laterally seems to be inefficient for support of weight or terrestrial locomotion, but is however, extremely stable and should provide a key to understanding the ecological advantages of such a peculiar limb posture.

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). A few points pertinent to the author's restoration are 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 was estimated from data on the nearly perfect Utanobori specimen. It is 699 mm to 704 mm in length, the value varying with standard points taken for measurement.

B. Vertebrae

1. Descriptions

i) *CERVICAL VERTEBRAE*

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

Axis short, low and wide; dens stout and short, with articular surface in ventral half; anterior articular surface continuous with ventral articular surface of dens but not expanded ventrally; foramen transversarium small, penetrating transverse process from dorsal surface backward; no ventral spine present.

Other cervical vertebrae 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 plate-like and fused with ventral tubercle to broaden backward.

ii) *THORACIC VERTEBRAE* (UHRno. 18466–56—64, Fig. 3, 4, 5, Plate I, II)

Bodies short, low and wide, and tilted cranially in posterior thoracics; vertebral foramen narrower than body, low and wide transversally; pedicle wide and short antero-posteriorly; posterior notch deep and U-shaped; spinous process short and stout, and extremely retreating in anterior and middle thoracic vertebrae; transverse processes rather long, originating at the level of vertebral foramen and projecting dorsolaterally in anterior and middle thoracic vertebrae. In posterior thoracic vertebrae, 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; accessory and mammillary processes of posterior thoracic vertebrae developed; accessory processes depressed dorso-ventrally, situated above posterior notches and projecting from posterior margin of transverse processes; mammillary processes projecting upward and outward behind anterior articular processes, flat medio-laterally with triangular outline in lateral view.

iii) *LUMBAR VERTEBRAE* (UHRno. 18466–65—68, Fig. 5, Pl. II, III)

Bodies short, low and wide, parallelogram-shaped and lowering backward in lateral view; vertebral foramina low with triangular outline; pedicles wide and slightly tilted medially; lamina rather wide transversely, anterior margin with wide V-shaped notch reaching behind articular surface; anterior notch small, posterior notch deep; groove for spinal nerve running backward but slightly downward; spinous process short, projecting vertically and rectangular in lateral aspect, triangular in cross section, caudally thicker, and not expanded at top; transverse processes originate at level of inferior margin of vertebral foramen, project horizontally and transversely, short, depressed and tapering towards tip; anterior articular processes protrude strongly, 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)

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

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 length and height, but broaden in transverse diameter in posterior lumbar vertebrae. Vertebral canal rhombic in cross section up to seventh thoracic vertebra, spindle-shaped to elliptic from eighth thoracic to second lumbar, and depressed triangular from third lumbar, becoming smaller in posterior vertebrae. Direction of intervertebral foramina changes between anterior and middle thoracics, first dorso-ventral, then horizontal, finally ventro-dorsal, becoming more backward in the eighth and after. Posterior costal facets shift progressively to dorsal position, present up to twelfth thoracic vertebra.

Spinous processes gradually become thicker from anterior thoracics to posterior lumbar, inclined backward, most steeply at fifth thoracic vertebra, more gently up to tenth, almost vertical from eleventh thoracic to second lumbar, and inclined forward in last two lumbar. Transverse processes or costal processes thick and long to ninth thoracic and depressed in thirteenth thoracic to fourth lumbar. Originate at arch of middle vertebrae to ninth thoracic. The point of origin then lowers gradually until reaching body of thirteenth thoracic vertebra and following. Up to second lumbar vertebra they originate from the anterior half of body and from the middle in the last lumbar. They project somewhat forward up to the seventh thoracic vertebra, becoming perpendicular to vertebral axis between eighth and eleventh thoracic, and project somewhat backward from the twelfth. In the thoracic vertebrae they project slightly upward relative to the horizontal plane, but in the lumbar they lie in this plane. Posterior margin of arch between posterior articular processes gradually widens from tenth thoracic vertebra, and angle between posterior margins of processes becomes obtuse in posterior lumbar vertebrae. Articular surface of zygapophyseal junction directed horizontally, inclining slightly forward up to tenth thoracic, and nearly sagittally from eleventh thoracic.

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 (1959) description 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 generally accord with each other but the foramen alare in the Keton specimen is a notch and the shape of the vertebral foramen may also 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. This feature agrees closely 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 referring to the shape of the vertebral foramen, then it differs from that seen 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."

If it is one of the anterior or middle thoracic vertebrae then this specimen has many characteristics in common with the Japanese specimens. However, it differs from the first thoracic of the Utanobori specimen in the angle of the cranial articular process, the outline of the transverse process and the inclination of neural spine. Thus, it is unlikely that the specimen, U. C. M. P. no. 40863, is 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 89 mm; the vertical diameter of the anterior face is 90 mm, and its transverse diameter 107 mm." The position of this lumbar vertebra is unknown but it is much larger than those of the Keton specimen in length and vertical diameter despite a similar transverse diameter value. Because the ventromedian crest is not developed in the Keton specimen, the lumbar vertebra may belong to that of sirenians.

Nagao (1941) gave the vertebral formula of *Desmostylus* as "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, with one probably missing, there would have been thirteen pairs originally. The reason why the number was thought to be fourteen is that the left fifth metacarpus was misidentified as the left first rib.

Whether the number of lumbar vertebrae is four (Nagao, 1941) or six (Shikama, 1966) is determined from which vertebrae are articulated with the thirteen pairs of ribs. However, in the Keton specimen, such characters are not useful in distinguishing the lumbar vertebrae from the thoracic vertebrae, since the costal facet is obscure in the posterior thoracics and there is only a gradual transition from the transverse to the costal process of the lumbar vertebrae. Fortunately, the proximal portion of the right eleventh rib was attached in situ to the thoracic vertebra, and the relationship between the thoracic vertebrae and ribs was positively revealed, there being four lumbar vertebrae.

The probable presence of four sacral segments (Nagao, 1941; Shikama, 1966) may be inferred by the number of spines on the median sacral crest and the ventral sacral foramen.

This inference, however, is irrelevant, because it results in an unnaturally long "fourth sacral" which is situated caudal to the third ventral sacral foramen. The number of sacral segments 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. Although ten caudal vertebrae are remaining, the original number is unknown.

It can therefore be concluded that the vertebral formula of *Desmostylus* should be 7·13·4·5·10+, which does not contradict with the data from the Utanobori specimen. Comparison between this formula and that of living mammals (Flower, 1885) reveals it to be unique.

C. Thorax

1. DESCRIPTIONS

Curvature of the ribs (UHRno. 18466–79—103, Fig. 8, Plate IV) is strong in general, and particularly marked in the proximal one-third. There is a clockwise torsion in the proximal part of the left ribs. The costal neck is long, and the costal angle obscure. The costal body is only moderately flat in cross section and the sternal extremity is less expanded than the body. In the anterior ribs, the costal body is flat. In the anterior to the middle ribs, the dorsal muscle area is conspicuous. In the posterior ribs, the head and tubercle are united to form a short V-shaped proximal articular surface, and the costal body is wide for the length and thick for the width.

The sternum (UHRno. 18466–46—54, Plate IV) is broad, dorso-ventrally flattened, and composed of nine sternal segments (sternebrae). The thorax is subcircular in cross section even in the anterior section, 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). In reference to the ribs of the Keton specimen Nagao (1941) stated "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 described as: "Proximal third missing, spatulate, anterior surface flat; from a thin neck the lower half is broadly expanded; ventral border broadly rounded", while the other rib, "one of the posterior thoracic ribs", (U. C. M. P. no. 39998) is described: "Capitulum and tuberculum separated and estimated 47 mm, 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, the cranial surface is rather convex, the caudal surface flat or concave and the medial margin sharp at the sternal extremity. The posterior ribs are rather thick in the proximal region and taper steeply toward the distal extremity. Reinhart's observation on the close resemblance between the anterior ribs of desmostylids and proboscideans is confirmed.

Shikama (1966) described the sternum of Desmostylia in detail, but arranged and named each sternal segment incorrectly. 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 a somewhat similar sternum. It is wide like some of cetaceans and

Table 7. Points of difference in evaluation of characteristics between Shikama (1966) and present author.

Page(s)	Bone	Shikama's description (1966)
29	Humerus	In anterior view, distal border of inner trochlea more strongly projected than outer.
	Humerus	Perhaps major and outer tubercles were shifted from anterior to outer corners in deformation process.
35	Scaphoid	In outer view, bone subquadrate with much undulated and long aft margin; distal margin nearly straight and posterodistal corner projected; ...
38	Scaphoid	Textfig. 19–4, Outer side
42	Cueiform	Textfig. 23 –5, Outer side; –6, Inner side
43—4	Trapezoid	Left "trapezoid" Textfig. 25 –1—6
45—6	Magnum	Both "magnum" Textfig. 27 –1—11
47—8	Unciform	Right "unciform" Textfig. 29 –7—9
76	Femur	Small trochanter obsolete compared with that of Izumi, and very small.
	Femur	Crestlike inflation of small trochanter distinct in outer view.
81	Tibia	Textfig. 61 –2, Outer side; –4, Inner side
86	Astragalus	Textfig. 66 –4, Distal side (fore side is in lower)
90	Calcaneum	Textfig. 69 –1, Fore side; –2, Aft side; –5, Outer side; –6, Inner side; –3, –4, (fore 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.
122	Sternum	Praesternum
124	Sternum	Right
		Left bones
		Inner and fore portion
		Outer margin
		Inner margin
		Posterior margin
		Posterior inner corner
		31 mm in right and 26 mm in left, ...
125	Sternum	Aft margin
		Left bone
		Narrower
		Longer
		Right bone

Table 7. (Continued from the preceding page)

Present author's view
Distal border of outer trochlea projects more strongly than inner.
Even if major tubercle was compressed in deformation process, it would not be shifted from anterior to outer corners.
In outer view, ... and long fore margin; proximal margin nearly straight and anteroproximal corner projects; ...
Inverted
–5, Inner side; –6, Outer side
The identification is questionable because left "trapezoid" is not articulated with scaphoid and its distal surface to articulate with the second metacarpus is distinctly rough. It is probably the pisiform or the first metacarpus.
The identification is incorrect, because left "magnum" is not articulated with distal surface of lunar. It is probably the trapezoideum.
The identification is incorrect, because right "unciform" has many points discrodant with the description of the left bone and both are asymmetric in any situation. As it is similar to cuboid of *Paleoparadoxia* (Izumi specimen) and articulates with left astragalus and calcaneum, the bone may be the left cuboid.
Although small trochanter of Keton *Desmostylus* projects less than that of Izumi specimen, it is not obsolete, and is well-developed in area and development of rough surface.
Perhaps large trochanter distinct, for small trochanter not visible in outer view.
–2, Inner side; –4, Outer side
(fore side is in upper)
–1, Inner side; –2, Outer side; –5, Fore side; –6, Aft side; –3, –4, (Inner side is in upper)
It is not valid to assume that declining of tuber calcis is only due to deformation, because both astragalus and calcaneum have no trace of compression or depression; such declination must be primary.
Fourth Mesosternum
Left
Right bones
Fore and inner portion
Aft margin
Fore margin
Outer margin
Anterior outer corner
31 mm in left and 26 mm in right, ...
Outer margin
Right bone
Wider
Shorter
Left bone

Table 7. (Continued from page 206)

Page	Bone	Shikama's description (1966)
		Inner margin is more straight in right bone, ...
		Posterior inner corner
		Textfig. 105 -1
		-2
126	Sternum	First Mesosternum
		Right bone
		Fore portion
		Aft corner
		Left bone
		Posterior outer corner
		Anterior outer corner
		28 mm in right and 24 mm in left.
		In posterior view, ...
128	Sternum	Right bone
		Posterior outer corner
		In posterior view
		First Xiphisternum
		Posterior outer portion
130	Sternum	Posterior margin
		Anterior outer margin
		Posterior inner corner
		Posterior surface
		Second Xiphisternum

sirenians." Actually, there are nine sternal segments due to the presence of a small median segment in addition to the four pairs.

D. Forelimbs

1. DESCRIPTIONS

i) *SCAPULA* (UHRno. 18466–104, Fig. 9, Plate V)

From the cranial position of the tuber scapulae and the caudal position of the tuber spinae this specimen is judged to be the left scapula. It is in nearly perfect condition except for the broken cranial tips of the tuber scapulae and coronoid process.

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

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

Anterior border is anteriorly and inwardly concave in the ventral half, and anteriorly

Table 7. (Continued from the preceding page)

Present author's view
Fore margin is more straight than left bone, ...
Anterior outer corner
Rotate at a right angle in anticlockwise
Rotate at a right angle in clockwise
Third Mesosternum
Left bone
Aft portion
Fore corner
Right bone
Anterior outer corner
Posterior outer corner
28 mm in left and 24 mm in right.
In anterior view, ...
Left bone
Anterior outer corner
In anterior view
First Mesosternum
Anterior outer portion
Anterior margin
Posterior outer margin
Anterior inner corner
Anterior surface
Praesternum

convex in the dorsal half, thus being S-shaped as a whole in lateral and front view. Dorsal half of anterior border rather acute, the ventral half thicker and smooth.

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

On costal surface, facies serrata, to which serratus ventralis muscle attaches, is probably represented by area occupied with fine sparse lines radiating from posterior angle, lying within dorsal quarter and a caudal half of costal surface. A gentle rugged elevation to which subscapularis muscle attaches extends downward from vertebral border to center of surface. Costal surface hollows out slightly in the middle, reflecting presence of spine on lateral surface and is somewhat rugged in dorsal half due to the presence of fine lines converging towards neck, while rather smooth in ventral half.

Spine of scapula, to which deltoid and trapezius muscles attach, lies on the border between cranial one-third and caudal two-thirds of the neck. In lateral view, base of spine slightly convex anteriorly, while the free edge is convex posteriorly. In front view, spine shows an expanded wedge shape. The free edge highest at a point dorsal to acromion, the distance between them being about one-quarter of the total length of the scapula. Spine gradually decreases in height towards vertebral border. The free edge convex outward in its dorsal three-quarters, becoming smooth and gradually narrow in dorsal one-fifth, and concave outward in the part ventral to acromion. In dorsal view, spine inclines backwards, acromion projects forwards and tuber spinae backwards. Anterior lip of tuber does not overhang supraspinous fossa. Free edge widest at acromion, then wide next at tuber spinae and narrow between them. Tuber in middle of spine, extending within half its length. Rough surface developed between anterior and posterior lips of spine.

Supraspinous area of the blade, to which supraspinatus muscle attaches, trapezoidal in shape with its longest side bordered by spine, broaden only slightly in dorsal part. Ventral half smooth. Fossa in horizontal section long cranio-caudally in dorsal half, while medio-laterally in the ventral. Infraspinous area, to which infraspinatus muscle attaches, a dorso-ventrally long triangle, about 1.5 times as wide as supraspinous area. Dorsal half of infra-spinous fossa shallow and broad, but deeper in center.

Glenoid cavity elliptic, long cranio-caudally, shallow, but hollows in center, projecting slightly forward due to presence of tuber scapulae. Cavity large in proportion to short vertebral border. It inclines inward at about 10 degrees to the scapular long axis. Neck of scapula more constricted transversely. In horizontal section, triangular with angles cranial, caudal and lateral but slightly anterior. Only medial (costal) surface convex. Tuber on posterior border 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 being the left humerus, based on the cranial humeral condyle and lateral deltoid tuberosity. Dorsal part of head, anteromedial part of medial condyle and posterior surface of medial epicondyle 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, expanding slightly proximo-distally. Head larger, projecting caudally, condyles smaller, projecting cranially. In proximal view, anterior border protrudes at three points, posterior border semicircular and convex caudally, a process present in lateral part. In distal view, forming a flat parallelogram in outline with median sagittal groove running from anterolateral to posteromedial, lateral epicondyle protrudes at posterolateral corner.

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

Minor tubercle, to which the subscapularis muscle attaches, present anteromedial to head, projecting slightly medially, and much smaller than head. In proximal view, long mediolaterally, deformed and compressed antero-posteriorly.

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

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

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

Proximal portion of shaft has three margins, medial and anterolateral ones sharp, posterolateral one obtuse. In the middle of shaft anterolateral margin disappears, while medial and lateral margins remain. In distal, an anteromedial margin, arising from middle and running inward and downward to medial condyle, appears; there are also three margins with posteromedial and lateral margins.

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

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

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

Distal extremity projects at about 80 degrees to humeral axis. Medial condyle increases in diameter medially, but lateral one rather smaller and does not increase much in diameter laterally. The latter larger in transverse width. Articular surface reaches near distal end in lateral part of lateral condyle backward and downward, and olecranon fossa in medial part. In medial condyle, extent of articular surface unknown due to break of specimen.

Medial epicondyle, to which flexor carpi and digitorum muscles attach, rather flat. Lateral epicondyle, to which extensor carpi and digitorum muscles attach, protrudes markedly on trochlear axis, possibly deformed, its position appearing more caudal than the original. Diameter of lateral epicondyle about half that of lateral condyle in distal view. A smooth groove at anterior and inferior base of lateral epicondyle.

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

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

Head of humerus larger in both sagittal and transverse diameter, having a stronger curvature than glenoid cavity of scapula. Possible range of contact between head of humerus and glenoid fossa in shoulder joint about 50 degrees in sagittal plane, about 80 degrees in frontal plane.

Elbow joint probably deformed. Trochlear surface of condyles and semilunar notch nearly equal in both height and thickness. Range of contact in joint 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) and run parallel without torsion. In regard to orientation the following description will conform to that in general mammals, i.e. the radius fore and the ulna behind, thus the distal extremity of the antebrachial skeleton becomes long antero-posteriorly.

The side of the specimen is judged from the rather medial position of the radius in the distal. Except for the broken top of the olecranon and medial part of the radius head, and the lateral flattening deformity in the middle and distal portions, the specimen is preserved in nearly perfect condition.

The antebrachial skeleton has a huge olecranon, remarkably wide antero-posteriorly at the distal end. The space between the radius and ulna is filled with rock, but seems to be very narrow, if it exists.

Head of radius considerably wider shaft, expanding particularly outward. Concave surface of head representing lower part of articular surface for trochlea, being wide from side to side, with ridge running antero-posteriorly medial to its median line. The ridge appears straight in lateral view, and protrudes anteriorly to form coronoid process. Circumferentia articularis cannot be observed due to its adhesion with radial facet for ulna. Articular surface probably flat, preventing pronation of radius even prior to fusion. Distinct tuberosity, probably that of radius to which biceps brachii muscle attaches, about 30 mm in diameter, on posterior part of medial surface of head, and a very rough rise, to which 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 remarkably flat from side to side, anterior border becoming a sharp ridge from anteromedial corner of head to medial styloid process. In medial view, radius slightly constricted in neck, antero-posterior diameter in distal about twice that in proximal. In lateral view, antero-posterior diameter of head larger than in medial view; diameter in distal portion not so large as in medial view.

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

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

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

Beak sharply spatulate, proximo-distally flat, round in proximal view, protruding most forward medial to median part.

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

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

Many transversely running rough lines are found in the posterior part of lateral surface of distal end. Groove for tendon is obscure. Styloid process of ulna does not project. Carpal articular surface faces somewhat backward, and 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 radius. Articular surface a groove as a whole, running in a direction from anteromedial to posterolateral at an angle of 40 degrees to antero-posterior axis. Medial half of groove faces distally, lateral half posteromedially at an angle of about 45 degrees to medial surface. Posterior ulnar part has a width half of radial part, and is slender antero-posteriorly, its anterior two-thirds flat to convex, facing distally, while posterior one-third more or less convex, facing medioinferiorly and somewhat posteriorly.

Because the antebrachial skeleton has no twisting, the direction of the longitudinal axis of the carpal articular surface is perpendicular to the direction of axis of movement in the elbow joint. Consequently, articulation of the antebrachial skeleton with the 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 the triangular proximal articular surface and protruded lateral margin. Except for the lack of distal epiphysis, it is an almost perfectly preserved specimen, undeformed and repaired in the middle and proximal parts of the medial surface.

Shape a triangular prism with a surface facing medially in proximal half, a semicircular prism flat antero-posteriorly in distal. Bent outwards in proximal one-third in anterior view. Both extremities stout in lateral view.

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

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

Triangular in cross section in proximal, decreased in length in medial side towards distal to form isosceles triangle with sharp lateral angles being fusiform, elongate transversely, more convex dorsally in distal half.

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

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 particularly larger in sagittal diameter than middle phalanx of same digit. Proximal surface of proximal phalanx concave transversely and sagittally, but that of middle phalanx convex transversely due to presence of sagittal ridge in center. Bodies of proximal phalanges steeply decrease their thickness distally becoming nearly equal to those of middle phalanges in thickness in distal one-third portion. Both medial and lateral margins of proximal phalanges sharper than those of middle phalanges. Distal surface of both proximal and middle phalanges concave transversely, but in middle phalanx it is saddle-shaped and convex sagittally. Every distal phalanx has a flat plane on 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 (1941) first outlined the Keton specimen and Shikama (1966) described it in detail with a later revision (Shikama, 1968). It is not possible to refer to all descriptions and hence only differences in evaluation of data between Shikama and the author are shown (Table 7).

i) *SCAPULA*

Nagao (1941) reported 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"; agreeing with the author's obaservation.

The scapula which Khomenko (1928) regarded as that of *Desmostylus* sp. is huge, being 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 teil weise nach vorn gebogen ist. Das Collum hat einen eigenartigen Querschnitt." Among these features, both the large glenoid cavity and stout base of the spine are probably related to its size, but it differs from the scapula of the Keton specimen in the shape of the acromion and neck.

The scapula (U.C.M.P. no. 39986) of *Desmostylus* was also described by Reinhart (1959): "Blade elongate, lanceolate 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." Features differing from the Keton specimen are: "spine..., upper half with strong posterior curvature, ...well-developed coronoid process curves sharply medially". Making it probable that this specimen does not belong to *Desmostylus.*

According to Nagao, the outline of the scapula of *Desmostylus* is rather similar to that of ungulates except that the 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 a backward swing. Reinhart (1959) also pointed out differences from sirenians, pinnipeds, cetaceans and proboscideans.

ii) *HUMERUS*

VanderHoof (1937) described only 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 the "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". Thus it is possible that this specimen does not belong to *Desmostylus.*

---

* Corresponding to medial and lateral part of trochlea.

Nagao (1941) noted differences between *Desmostylus* and proboscideans and sirenians, and Reinhart (1959) between *Desmostylus* and sirenians.

iii) *ANTEBRACHIAL SKELETON*

The antebrachial skeleton (radius and ulna) of *Desmostylus* was described by VanderHoof (1937), Nagao (1941) and Reinhart (1959). The Keton specimen agrees with the description of 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 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 the proximal articular facet of this specimen (U.C.M.P. no. 39987) as being divided into two portions and provided with a central elevation. These facts and the "progressive increase in diameter toward distal end" also agree with the Keton specimen.

Nagao stated: "antebrachial skeleton is more massive than that of sirenians, different from that of proboscideans" while 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) and are very similar to those of *Paleoparadoxia* (Shikama, 1966). These genera resemble each other in the os hamatum decreasing in height laterally, this feature being peculiar among mammals.

The metapodials of *Desmostylus* have already been described by VanderHoof (1937), Nagao (1941), Reinhart (1959) and Shikama (1966), who discussed their identification. VanderHoof (1937) described for the first time three "right metacarpals" from California. Nagao (1941) identified "two right metacarpi" in the Keton specimen as "something except for the first and fifth", but he noted they are "quite different" from the three metacarpals described by

Table 8. Identification of the metapodials of *Desmostylus*.

	VanderHoof (1937)	Nagao (1941)	Reinhart (1959)	Shikama (1966)	Inuzuka (1981)
California specimen					
UCMP no. 32735–32737	*D. hesperus*		*D. hesperus* or *Vanderhoofius coalingensis*	*Desmostylus*	
	R. Mc. III, IV, V		Mc. or Mt.	L. Mc. III, IV, V	L. Mc. III, IV, V
UCMP no. 32041	Mc. I		entirely different animla 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

R: right, L: left, Mc: metacarpus, Mt: metatarsus.

VanderHoof. Reinhart (1959) did not conclude that the three bones were the metacarpi and suggested the possiblity that they were the metatarsi. Shikama (1966) 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*,".

Based on comparison with the Izumi specimen of *Paleoparadoxia tabatai* the bone that Nagao (1941) identified as the left first rib is actually the left fifth metacarpus. 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 the shortness of the bones as being due to the absence of the 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 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) described all phalanges in detail but made partly wrong identifications. Judging from the morphological characteristics mentioned above, the specimen UHRno. 18466–17, which was regarded as the second middle phalanx of the left manus is actually a proximal phalanx, while UHRno. 18466–37, designated as the second proximal phalanx of the left pes is a middle phalanx. Although there are many more questions regarding identification, they will be disregarded since they are not relevant to the restoration.

E. Hindlimbs

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 broken above and below obturator foramen, the ischium and pubis on both sides join at symphysis pelvis.

Body of ilium flat, long from dorsomedial to ventrolateral, triangular in frontal section in caudal part, having ilio-pectineal line on medioventral surface. The line becomes gradually obscure from cranial margin of pubis towards 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 medial surfaces of ilium meet at about right angles. A slight elevation, possibly the psoas tubercle, present in front of anterior margin of acetabulum on left ilio-pectineal line.

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

Crest of ilium, to which sartorius muscle attaches, convex forward in dorsolateral view;

in cranial view, flexed dorsally at a point a little medial to middle, where cranial margin of iliac fossa and sacropelvic face cross at an angle of 140 to 145 degrees. Dorsal lip of crest situated slightly posterior to the more accute ventral lip. Distance between both lips greatest at middle flexed part.

Tuber coxae, to which tensor fasciae latae muscle attaches, not bifurcated, bending somewhat ventrally. Tuber sacrale long cranio-caudally, concave laterally, thicker in front, its caudal end extending posterolaterally.

Gluteal surface, to which gluteus medius muscle attaches, directing more dorsally than laterally. Concave frontally and sagittally. Wing bears an oval, sagittally long depression slightly lateral to center, the medial margin of which seems to be gluteal line.

Articular part has a length of about one-third of total length of os coxae, scalene quadrilateral shaped with a longer cranial and shorter caudal border. Medial surface concave in frontal section. Outline of the auricular surface indistinct, but probably a ventrocaudal part of articular part.

Greater ischiatic notch deepest just behind tuber sacrale, becoming gradually narrower backward. Shaft flexed a little laterally at notch in dorsal view.

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

Body of ischium flat, its ventral surface, to which gracilis muscle and adductor muscles attach, transversely concave, becoming convex from caudal end of obturator foramen, as followed dorsolaterally to the acetabular branch. Tuber ischii, to which biceps femoris muscle attaches, a long ridge, situated at caudal end of ischium, not projecting laterally. Caudal end of ischium, to which semitendinous muscle and semimembranosus muscle attach, convex backward, ischial arch making an angle of about 105 degrees.

Ilio-pectineal eminence developed on medioventral part of body of pubis. Branch of pubis extends backward at an angle of about 40+ degrees ventral and about 35+ degrees medial to axis of ischium. As the branch is followed backward, it becomes gradually broad in posterior two-thirds, and flat and wide from anteromedial to posterolateral to join with the other branch. Branch has three crests, pecten ossis pubis in cranioventral portion, dorsal and caudal crest. Both anterior and posterior surfaces of dorsal crest incline more gently, when traced medially, the angle between them becoming obtuse. Branch a dorso-ventrally tall triangle in cross section with dorsal, ventral and posterolateral angles in cranial region, becoming depressed dorso-ventrally backward, due to the branch rotating clockwise, its cranial margin bending medially and caudal laterally in the left pubis. Dorsal crest runs a distance of about 40 mm to pecten ossis pubis, facing pelvic cavity, forming an convex backward arc with fellow of other side in medial part near anterior margin of obturator foramen. Pecten ossis pubis increases in thickness near median line to make pubic tubercle.

Symphysis pelvis situated rather posteriorly, its anterior end at about cranial one-third of obturator foramen. Median ventral margin of symphysis linear in lateral view, cranial margin V-shaped with an angle of about 120 degrees in cranial view.

Acetabulum nearly circular, although slightly depressed due to deformation. Sited almost in middle of whole hip bone, the distance from acetabulum to crest of ilium about equal to length of femur. Acetabulum directed backwards at an angle of about 70 degrees to axis of pelvis. Acetabular notch opens backward and is narrow. Acetabular fossa round, wider than acetabular notch.

Cranial margin of acetabulum protrudes laterally most, the caudal margin protrudes less, while dorsal margin protrudes laterally slightly more than ventral margin. Dorsal margin a sharp crest, ventral margin broad forming a tubercular surface broadening backward. Dorsal margin is straight with slight undulation, not hollowing out in middle.

Dorsal surface of acetabulum markedly rugged, raised and extending markedly inwards at cranial one-third and caudal one-third portion of acetabulum. Cranial margin of acetabulum tubercular on lateral surface.

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

Pelvis deformed, being depressed dorso-ventrally as a whole, axis inclining left at about 5 degrees, and dorsal side tilting right.

Inlet of pelvis square in shape, broadening slightly near medial part of acetabulum. Outlet of pelvis semicircular in the left half, depressed in the right half due to deformation.

Pelvis inclines backwards at about 30 degrees to long axis of sacrum, but this value is probably an underestimate due to deformation and depression. Pelvic cavity surrounded by broad symphysis on ventral side, obturator foramen in front and plate of ischium behind on lateral sides.

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

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

The side of the specimen may be identified by 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 left. Portions that differ considerably in shape between them may be caused by deformation due to compression in an antero-posterior direction. As a whole, the width of the femur is large for its length and cranio-caudal diameter is small. Epiphyses are well developed.

Head 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 transverse axis in proximal view. Surface smooth and fovea capitis indistinct.

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

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

Trochanteric fossa, to which obturator and gemelli muscles attach, a depression, a reversed triangle in outline, lying in proximal one quarter of shaft, its maximum width about one half of that of shaft. Depth of fossa corresponds to expansion of trochanter major in anterior surface, maximum depth about 30 mm from posterior surface in lateral.

Trochanter minor, to which iliopsoas muscle attaches, a round tubercle of proximal one-third about 25 mm in diameter in posterior part of medial margin of shaft. Conspicuous rough surfaced area along medial margin, to which pectineus and adductor muscles attach, maximum width 35 mm, length about 100 mm. It lies in 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 medial.

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

Each shaft differs in shape on account of deformation due to compression. Outline of shaft rectangular in anterior view, narrow in middle and bending laterally in distal. Shaft surface is smooth, rising in median line from neck.

Smooth posterior surface flatter than anterior surface, with no rough surface in middle. A number of rough lines run longitudinally in trochanter minor, its downward extension and lateral part of trochanteric ridge. A rough surface from which gastrocnemius muscle originates, present just above medial and lateral condyles.

Lateral margin runs obliquely, lying more anteriorly towards distal end. Sharp in upper half and obtuse in lower. Medial margin is more stout and obtuse than lateral, running sigmoidally as a whole, its middle one-third occupied by trochanter minor and its downward extension which forms a rough surface, running obliquely from proximocaudal to craniodistal.

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

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

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

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

Proximal articular surface unknown due to break and loss. Proximal portion kidney-shaped in cross section, long transversely, concave posteriorly. Tuberosity to which quadriceps femoris muscle attaches, markedly developed on crest of tibia, being 65 mm in width, triangular shaped with a sharp point upward, its surface very rough.

Medial surface flat, posterior surface concave, widening at both epiphyses. Medial surface smaller than posterior. Lateral surface concave both vertically and horizontally, being covered by anterior margin in proximomedial part. Each surface is smooth on shaft.

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

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

Medial malleolus a tubercle, ellipsoidal in shape, 66 mm in height and 45 mm in cranio-caudal diameter, having many rough lines running vertically on its surface. As it projects more distally than the distal end of anterior surface and the middle part of distal end of posterior surface is also projecting, the border around articular surface is undulated.

As articular surface is compressed antero-posteriorly, tibia cannot be articulated with talus. In case of flexion within range of contact of articular surfaces in tibio-tarsal articulation, the angle between directions of shaft of tibia and of longitudinal axis of tuber calcis ranges 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 smaller, differences in width between proximal and distal portions larger and depression of distal surface shallower and narrower than in fore phalanges. In middle phalanges, sloping angle of proximal surface 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 agreeing with the author's observations. Reinhart (1959) briefly described the 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"; while Reinhart (1959) stated: "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, the neck is shorter, the minor trochanter is neither "triangular" nor "conical" in shape, and distal end is not so "broadly expanded"; these specimens differ somewhat in outline and 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, i.e. "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 the 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 tendency for reduction in the 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 mammilo-articular processes to the caudal articular processes
2. Breadth across the transverse processes. In case of absence, one side beneath another side tip to the median plane was measured.
3. Breadth across cranial articular processes (prezygapophyses)
4. Breadth across caudal articular processes (postzygapophyses)
5. Breadth across base of pedicles
6. Breadth of vertebral foramen at cranial surface
7. Breadth of vertebral foramen at caudal surface
8. Height of vertebral foramen at cranial surface
9. Height of vertebral foramen at caudal surface
10. Breadth of cranial extremity. In thoracic vertebrae, facets for rib heads were excluded.
11. Height of cranial extremity
12. Breadth of caudal extremity
13. Height of caudal extremity
14. Maximum height
15. Length of body
16. Height of spinous process

Table 9. Measurement of thoracic and lumbar vertebrae. Specimen number: UHRno. 18466-56—68.

Vertebrae	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

Th: Thoracic, L: Lumbar, Measuring points: 1—16. —: impossible to measure, ( ): repaired, +: less than true value, −: more than true value, *: double value of half a side.

II. Sacrum

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

III. Caudal vertebrae (Table 10)

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

Table 10. Measurement of caudal vertebrae. Specimen number: UHRno. 18466-70—77 (C1—C9).

Caudal vertebrae	C1	C2	C3	C4	C5	C6	C7	C8	C9
UHR no. 18466-	70	71	72	73		74	75	76	77
				a	p				
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

a: anterior (C4), p: posterior (C5), Measuring points: 1—7. +: less than true value.

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 costal axis from the corner of the facet for articulation of the head to the center of sternal extremity (arc length)
3. Length from the center of the facet for articulation of the head to the center of sternal extremity
4. Length from medial end of costal head to lateral end of tubercle
5. Length from costal angle to lateral end of tubercle
6. Dorso-ventral diameter of facet for articulation of costal head
7. Cranio-caudal diameter of facet for articulation of costal head
8. Dorso-ventral diameter of costal neck
9. Cranio-caudal diameter of costal neck
10. Medio-lateral diameter of facet for articulation of costal tubercle
11. Cranio-caudal diameter of facet for articulation of costal tubercle
12. Longer (medio-lateral) diameter of costal shaft in middle
13. Shorter (cranio-caudal) diameter of costal shaft in middle
14. Maximum breadth of costal shaft
15. Thickness crosswise of maximum breadth of costal shaft
16. Longer (cranio-caudal) diameter of sternal extremity
17. Shorter (medio-lateral) diameter of sternal extremity

Table 11. Measurement of ribs. Rib position: I–XIII.

Ribs		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	26
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

R: right, L: left. Measuring points: 1—17. —: impossible to measure, +: less than true value.

V. Left scapula

		(mm)
1.	Maximum height parallel to the spine from ventral end of tuber scapulae to vertebral border	425
2.	Height of base of spine	374
3.	Height from dorsal end of base of spine to ventral end of acromion	315
4.	Minimum length from cranial angle to caudal border	203
5.	Maximum length of supraspinous fossa perpendicular to spine	88
6.	Smallest cranio-caudal length of neck of scapula	78
7.	Length from caudal end of glenoid cavity to lateral end of base of tuber scapulae	110
8.	Length of glenoid cavity	106
9.	Breadth of glenoid cavity	84
10.	Maximum thickness of surface of acromion perpendicular to spine	31
11.	Breadth from top of acromion surface to lateral surface	74
12.	Distance from medial margin of glenoid cavity to 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 shaft	71
8.	Cranio-caudal diameter of shaft in middle	47
9.	Maximum breadth of distal extremity	163
10.	Breadth of trochlea in distal end	125+
11.	Breadth of olecranon fossa	36+
12.	Maximum height of trochlea	77+
13.	Cranio-caudal diameter of medial condyle	78+
14.	Cranio-caudal diameter of lateral condyle	84+
15.	Breadth of supratrochlear foramen	24
16.	Height of supratrochlear foramen	14

VII. Antebrachial skeleton

LEFT RADIUS

		(mm)
1.	Maximum length	291
2.	Maximum breadth of proximal extremity	88+
3.	Maximum cranio-caudal diameter of proximal extremity	64
4.	Cranio-caudal diameter of neck	52
5.	Breadth of shaft in middle	27
6.	Cranio-caudal diameter of shaft in middle	66

7.	Maximum width of distal extremity	86
8.	Maximum cranio-caudal diameter of distal extremity	97
9.	Breadth of carpal articular surface	81
10.	Thickness of carpal articular surface	80
LEFT ULNA		
11.	Maximum length	331
12.	Cranio-caudal diameter of olecranon in beak	116
13.	Cranio-caudal diameter of olecranon in semilunar notch	73
14.	Cranio-caudal diameter of olecranon in coronoid process	71
15.	Cranio-caudal diameter of shaft in middle	55
16.	Maximum cranio-caudal diameter of distal extremity	82
17.	Breadth of olecranon	44
18.	Length of olecranon	112
19.	Minimum width of semilunar notch	42
20.	Length of semilunar notch	54
21.	Maximum width of semilunar notch	92
22.	Breadth of radial notch	88+

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

IX.	**Pelvis**	left	(mm) right
1.	Maximum length of one half	649	636
2.	Length from cranial end of iliac crest to cranial margin of acetabulum	311	326
3.	Length from cranial margin of acetabulum to lateral end of tuber ischii	310	315
4.	Length of symphysis	168	
5.	Width from tuber coxae to tuber sacrale	218	207
6.	Thickness of tuber sacrale	32	29
7.	Minimum height of shaft of ilium	37	40
8.	Minimum breadth of shaft of ilium	86	80
9.	Length of acetabulum	107	94
10.	Height of acetabulum	80	67+
11.	Minimum height of branch of ischium	46	37
12.	Thickness of branch of ischium at anterior end of ischiatic spine	43	52
13.	Maximum length of obturator foramen	136	131

14.	Maximum height of obturator foramen	69	66
15.	Minimum cranio-caudal diameter of branch of pubis	46	44
16.	Minimum dorso-ventral diameter of branch of pubis	28	29
17.	Minimum breadth from obturator foramen to symphysis	84	84
18.	Distance from cranial end of symphysis to medial margin of acetabulum	183+	210
19.	Distance from caudal margin of acetabulum to lateral end of tuber ischii	205	216
20.	Distance from caudal margin of acetabulum to caudal end of ischium	250	248
21.	Breadth from lateral end of tuber ischii to caudal end of symphysis pelvis	130	150
22.	Thickness of tuber ischii	15	17
23.	Length from caudal margin of obturator foramen to caudal margin of ischium	100	95
24.	Breadth across ischiatic spines	240	
25.	Breadth across auricular surfaces	190	
26.	Breadth across tubera coxarum	557	
27.	Breadth across acetabula	482	
28.	Breadth across deepest points acetabula	293	
29.	Breadth across tuber ischiadica	243	

X. Femur

			(mm)
		left	right
1.	Maximum length	404	410
2.	Maximum width of proximal extremity	152	142
3.	Length between trochanter major and minor	151	154
4.	Transverse diameter of head	84	87
5.	Cranio-caudal diameter of head	85	86
6.	Cranio-caudal diameter of trochanter major	76	74
7.	Length of neck	108	120
8.	Cranio-caudal diameter of shaft in middle	42	32
9.	Breadth of shaft in middle	85	84
10.	Maximum breadth of distal extremity	120	134
11.	Breadth of distal end	114	117
12.	Cranio-caudal diameter of medial condyle	121	111
13.	Cranio-caudal diameter of lateral condyle	114	99
14.	Breadth of trochlea	58+	58
15.	Height of trochlea	57	62
16.	Cranio-caudal diameter of intercondyloid fossa	92	83

XI. Left Tibia

		(mm)
1.	Maximum length	325
2.	Maximum cranio-caudal diameter of proximal extremity	90

3.	Maximum breadth of the proximal extremity	131+
4.	Cranio-caudal diameter of shaft in middle	48
5.	Breadth of shaft in middle	71
6.	Maximum breadth of distal extremity	151
7.	Maximum cranio-caudal diameter of distal extremity	84
8.	Length of articular surface of distal extremity	125+

Acknowledgements

I would like to acknowledge the assistance and encouragement of Dr. S. Ijiri and Dr. M. Minato in this work. I am also grateful to Prof. T. Kamei and Prof. M. Tasumi of Kyoto University, Prof. T. Yoro of the University of Tokyo, and Dr. Y. Kuwano of the National Science Museum, Tokyo, for continued guidance and critical reading of the manuscript. For examination of the Keton specimen I am deeply indebted to Dr. M. Akiyama, Prof. M. Kato, Dr. N. Minoura, Mr. S. Kumano, Mr. H. Nakaya, Mr. H. Nakai and Mr. N. Aida of Hokkaido University, and Dr. Y. Ujiie of Hirosaki University. For examination of the Utanobori specimen I was privileged to have the assistance of Dr. N. Kambe, Dr. M. Ishida and Dr. S. Yamaguchi of the Geological Survey of Japan and Mr. M. Kimura of the Sapporo College of Hokkaido University of Education. For comparative research of living mammalian skeletons I would like to express my grateful thanks to Prof. Y. Hasegawa of Yokohama National University, Prof. K. Mochizuki of the University of Tokyo, Dr. T. Ueno, Dr. N. Miyazaki, Dr. M. Yoshiyuki, Mr. K. Ono and Mr. Y. Tomida of the National Science Museum, Tokyo, Mr. H. Taruno of the Osaka Museum of Natural History and Mr. K. Takahashi of Nippon Dental University.

I am also indebted to Dr. A. W. Gentry, Dr. A. Currant and Mr. R. Croucher of the British Museum (Natural History) for providing information concerning the restoration of *Paleoparadoxia.*

It is a pleasure to acknowledge the conveniences given to me by the staff of the Department of Geology and Mineralogy, Faculty of Science, Hokkaido University. Thanks are also due to members of the Proboscidean Research Group, the Fossil Research Society of Japan, the Department of Anatomy, Faculty of Medicine, University of Tokyo, and the Paleontology Research Group in the Department of Geology and Mineralogy, Faculty of Science, Kyoto University for helpful suggestions and observations.

References

Abel, O. (1922) *Desmostylus*: Ein mariner Multituberculate aus dem Miozän der Nordpazifischen Küstenregion. Acta Zoologica 3: 361–394.

Abel, O. (1925) Geschichte und Methode der Rekonstruktion vorzeitlicher Wirbeltiere. Verlag von Gustav Fischer, Jena. 327 pp.

Domning, D. P. (1977) 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. Macmillan and Co., London. 382 pp.

Gregory, W. K. (1912) Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Ann. N. Y. Acad. Sc. 22: 267–294.

Gregory, W. K. (1941) Evolution Emerging, Vol. 1. Macmillan, New York. 736 pp.

Halstead, L. B. (1975) The Evolution and Ecology of the Dinosaurs. Peter Lowe, London. 116 pp.

Halstead, L. B. (1978) The Evolution of the Mammals. Peter Lowe, London. 116 pp.

Hasegawa, Y. (1977) A 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. John Wiley and Sons, New York. 710 pp.

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

Ijiri, S. and T. Kamei (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. Atals and thoracic vertebrae. Earth Science 34: 205–214 (in Japanese).

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

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

Inuzuka, N. (1981b) The skeleton of *Desmostylus mirabilis* from South Sakhalin IV. Metacarpus. Earth Science 35: 240–244 (in Japanese).

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

Inuzuka, N. (1981d) Newly restored *Desmostylus*. Geological News 327: 59–63 (in Japanese).

Inuzuka, N. (1982) The skeleton of *Desmostylus mirabilis* from South Sakhalin V. Limb bones. Earth Science 36: 117–127 (in Japanese).

Kamei, T. and Y. Okazaki (1975) Neogene desmostylid and proboscidean fossils from Japan. In: Atlas of Japanese Fossils (34). Edited by the Editorial Committee. Tsukiji Shokan Publishing Co. Ltd., Tokyo 24 pp. (in Japanese).

Kent, G. C. (1978) Comparative Anatomy of the Vertebrates, 4th ed. The C. V. Mosby Company, Saint Louis. 465 pp.

Khomenko, J. (1928) Neue Ergebnisse über die Familie der Desmostylidae. Zapiski Rossiiskogo Mineralogicheskogo Obshchestva 57(1): 140–147.

Kurtén, B. (1971) The Age of Mammals. Weidenfeld and Nicolson, London. 250 pp.

Lessertisseur, J. and R. Saban (1967) Squelette appendiculaire. In: Traité de zoologie. Edited by P. P. Grassé. 16 (1), 961–1078. Masson, Paris.

Marsh, O. C. (1884) Dinocerata: A monograph of an extinct order of gigantic mammals. United States Geological Survey 10: 1–191.

Marsh, O. C. (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: Phylogeny of the Primates. Edited by W. P. Luckett and F. S. Szalay. pp. 21–46. Plenum, New York.

Merriam, J. C. (1906) On the occurrence of *Desmostylus* Marsh. Science (n. s.) 24: 151–152.

Minato, M. and S. Ijiri (1976) Color Illustrations of Natural History. Tokyo Bunkyo Publishing Co. Ltd., Tokyo (in Japanese). 16 pp.

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.

Nagao, T. (1941) On the skeleton of *Desmostylus*. In: Jubilee Publication in the Commemoration of Prof. H. Yabe's 60th birthday. pp. 43–52 (in Japanese).

Nagao, T. and S. Oishi (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.

Radinsky, L. B. (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 Desmosytlia. Jour. Geol. 61(2): 187.

Reinhart, R. H. (1959) A review of the Sirenia and Desmostylia. Univ. California Publ. Geol. Sci. 36: 1–146.

Romer, A. S. (1966) Vertebrate Paleontology, 3rd ed. University of Chicago Press, Chicago. 468 pp.

Romer, A. S. and T. S. Parsons (1977) The Vertebrate Body. 5th ed. W. B. Saunders Co., Philadelphia. 624 pp.

Scheffer, V. B. (1976) A Natural History of Marine Mammals. Charles Scribner's Sons, New York. 157 pp.

Shikama, T. (1966) Postcranial skeletons of Japanese Desmostylia. Paleont. Soc. Japan, Special Papers 12: 1–202.

Shikama, T. (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.

Thenius, E. (1973) Fossils and the Life of the Past. Springer Verlag, New York. 194 pp.

Torrey, T. W. and A. Feduccia (1979) Morphogenesis of the Vertebrates, 4th ed. John Wiley and Sons, New York. 570 pp.

VanderHoof, V. L. (1937) A study of the Miocene sirenian *Desmostylus*. Univ. California Publ. Geol. Sci. 24(8): 169–262.

Vaughan, T. A. (1972) Mammalogy. W. B. Saunders Company, Philadelphia. 463 pp.

Wake, M. H. (ed.) (1979) Hyman's Comparative Vertebrate Anatomy, 3rd. ed. Univ. Chicago Press, Chicago. 788 pp.

Yamaguchi, S., N. Inuzuka, M. Matsui, M. Akiyama, N. Kambe, M. Ishida, T. Nemoto, and R. Tanitsu (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. Oxford University Press, New York. 525 pp.

Yoshiwara, S. and J. Iwasaki (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. Clarendon Press, Oxford. 528 pp.

EXPLANATION OF PLATES

All figures in Plates I–VIII are of the specimens (UHRno. 18466) of *Desmostylus mirabilis* Nagao from Keton, South Sakhalin. Scale bars indicate 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.

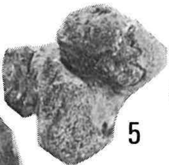
Fig. 31–36: Ninth thoracic vertebra (UHRno. 18466–60)
31: cranial view, 32: caudal view, 33: dorsal view, 34: ventral view, 35: right lateral view, 36: left lateral view.

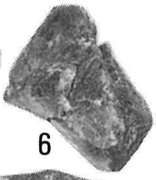

1


2


3

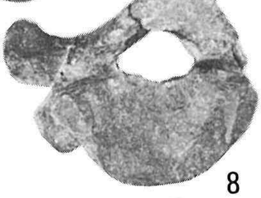

4

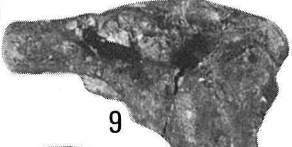

5


6


11

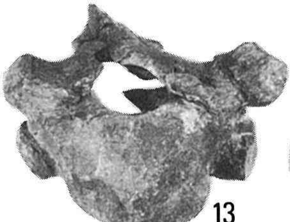

7


8

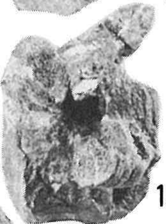

9


12

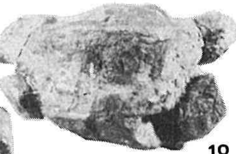

10

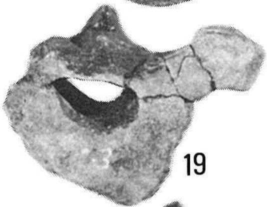

13

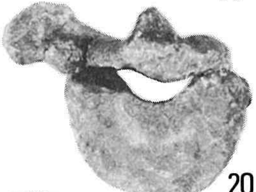

14


15


17


18

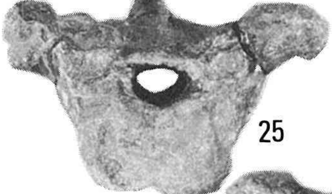

19

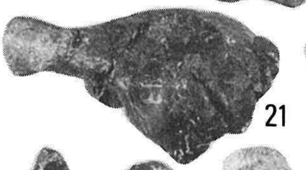

20

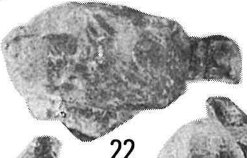

16

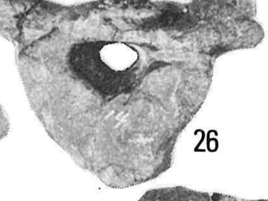

23


24


25

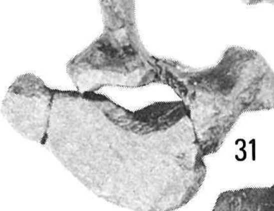

21


22

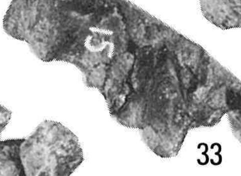

26

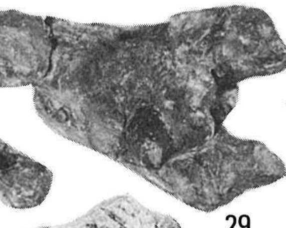

27

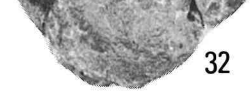

28


31


30


33


29


32


34


35


36

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: left lateral view, 30: right lateral view.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

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.

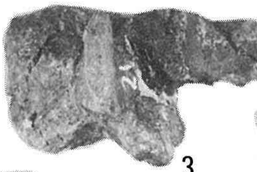
Fig. 13–18: Fourth lumbar vertebra (UHRno. 18466–68)
13: cranial view, 14: caudal view, 15: dorsal view, 16: ventral view, 17: left lateral view, 18: right lateral view.

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.


1

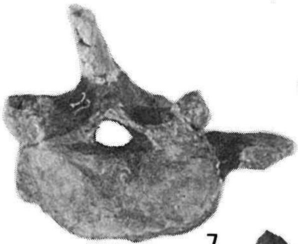

2


3

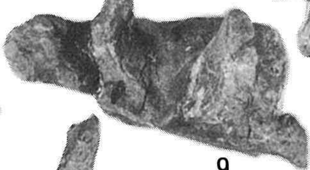

4

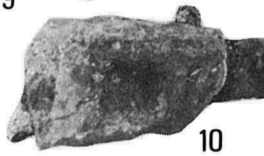

5


6


7


8

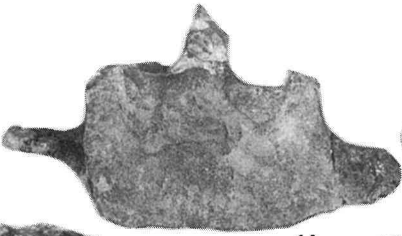

9

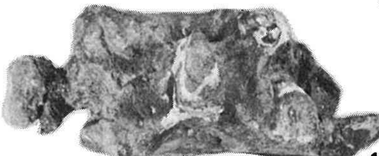

10


11


12


13

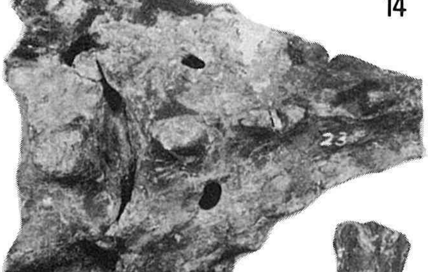

14

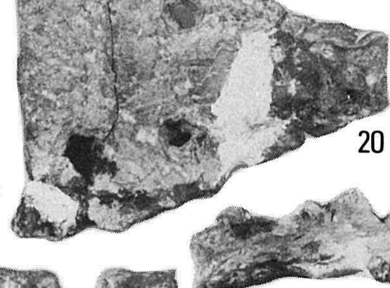

15

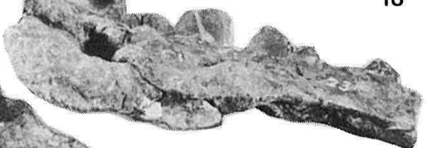

16

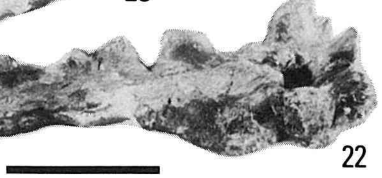

17


18


19


20

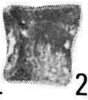

21


22


23


24


25


26


27


28

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 (UHRno. 18466–46—54)
27: dorsal view, 28: left lateral view, 29: ventral view.

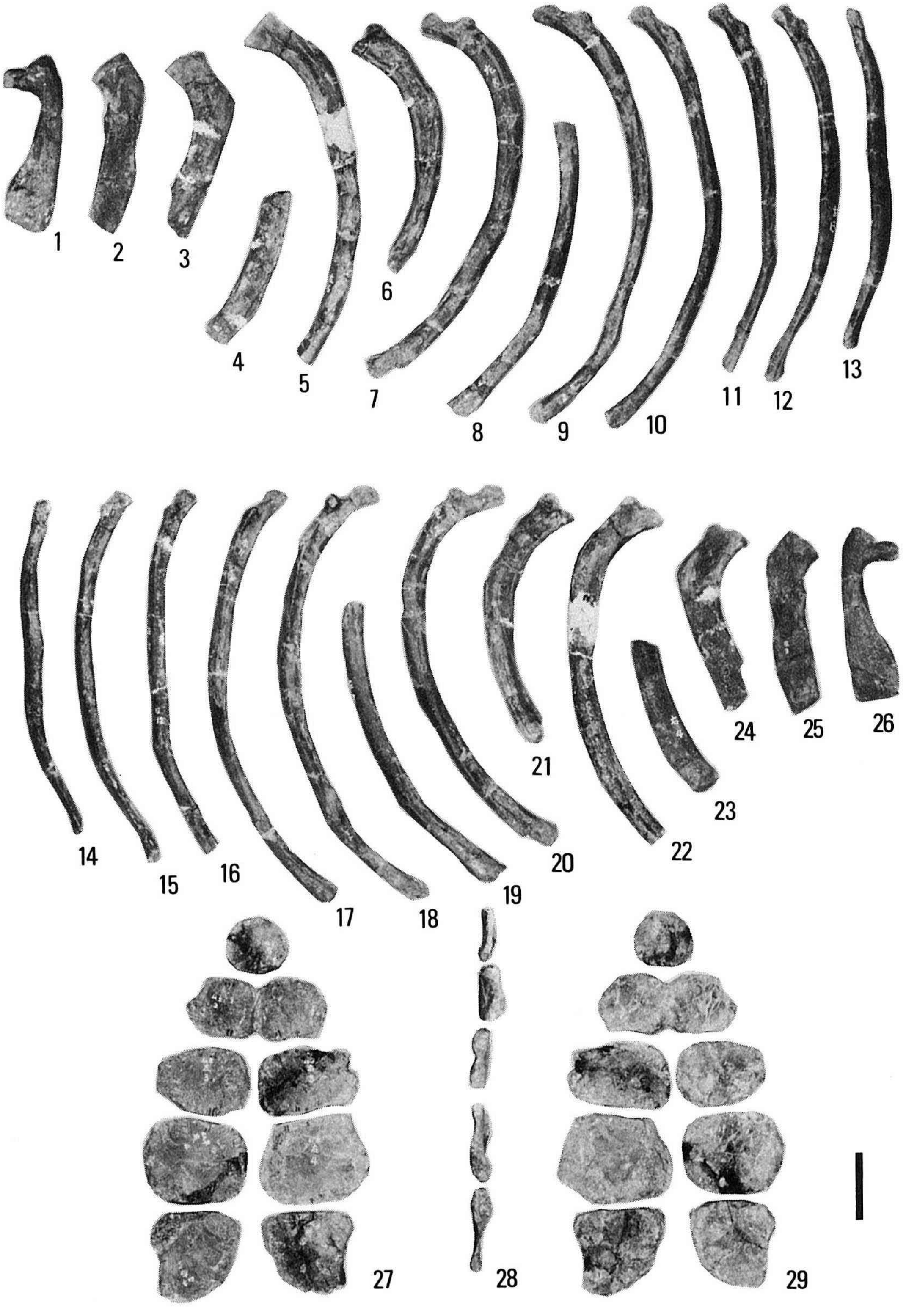

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

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.

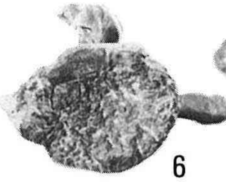

1

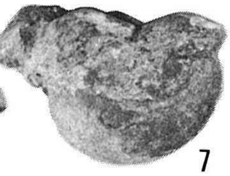

2

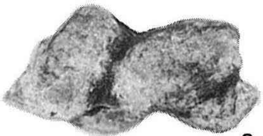

3


4


5


6


7


8


9


10


11


12

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.

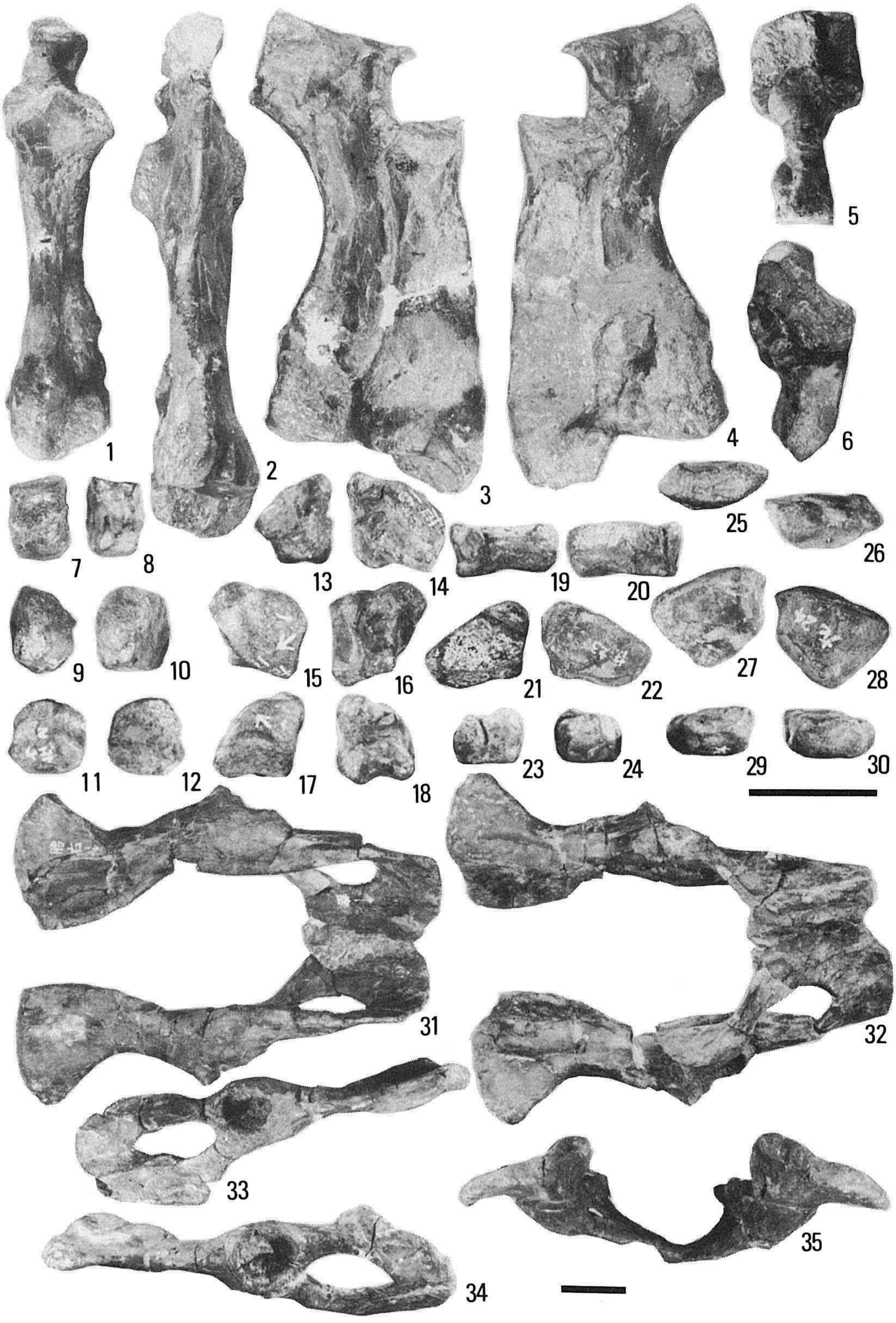

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

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.

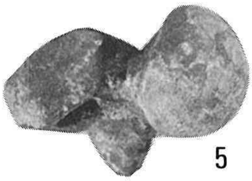
Fig. 7–12: Right femur (UHRno. 18466–28)
7: distal view, 8: proximal view, 9: cranial view, 10: caudal view, 11: medial view, 12: lateral view.

1

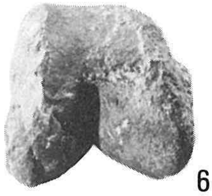
2

3

4



5



6

7

8

9

10

11

12

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.

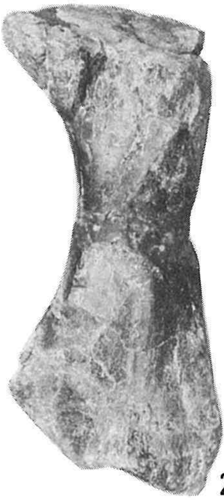
Fig. 25–30: Left second metatarsus (UHRno. 18466–15)
25: dorsal view, 26: plantar view, 27: medial view, 28: lateral view, 29: proximal view, 30: distal view.

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.

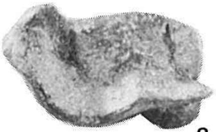

1

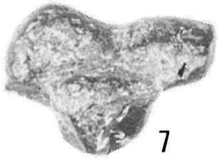

2

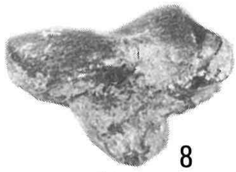

3


4


5

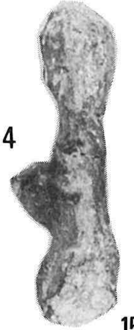

6

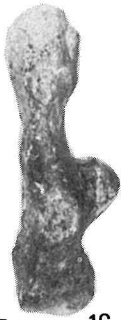

7

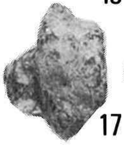

8

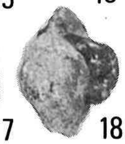

13


14


15

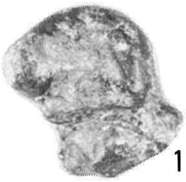

16

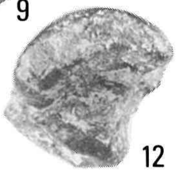

17


18

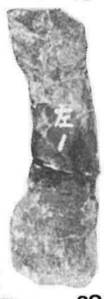

9


10


11


12

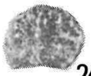

19


20

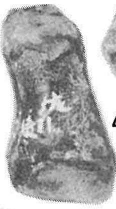

21

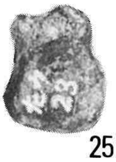

22

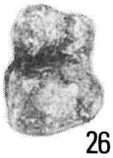

23


24


44

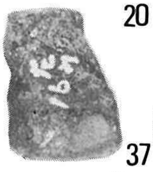

43


25


26


31


32

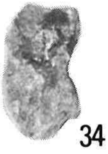

37


38


27

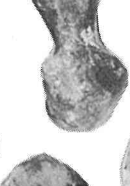

28

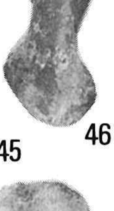

33


34


39


40


45


46

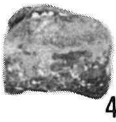

29


30


35


36


41


42


47

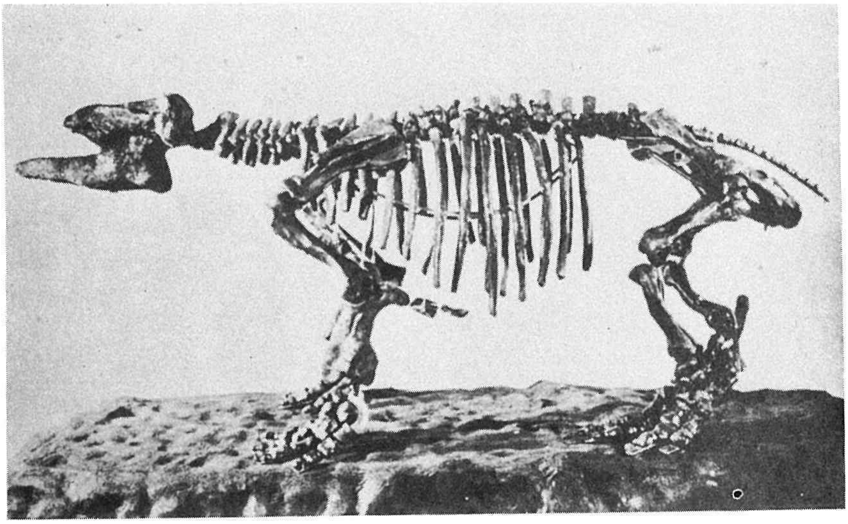

48

Plate IX

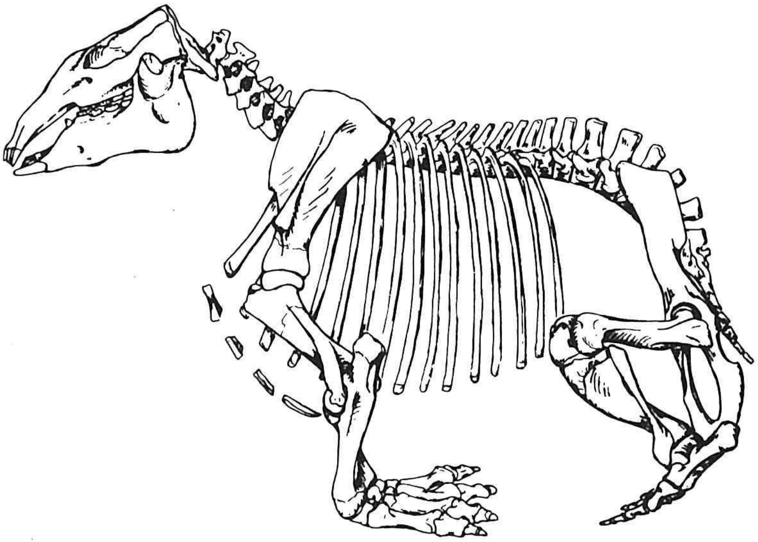
Fig. 1: Nagao's (1936) restoration of *Desmostylus*, previously displayed in Hokkaido University but currently in Osaka Museum of Natural History.

Fig. 2: Repenning's restoration of *Paleoparadoxia*, discovered in 1965. Figure from Romer (1966).

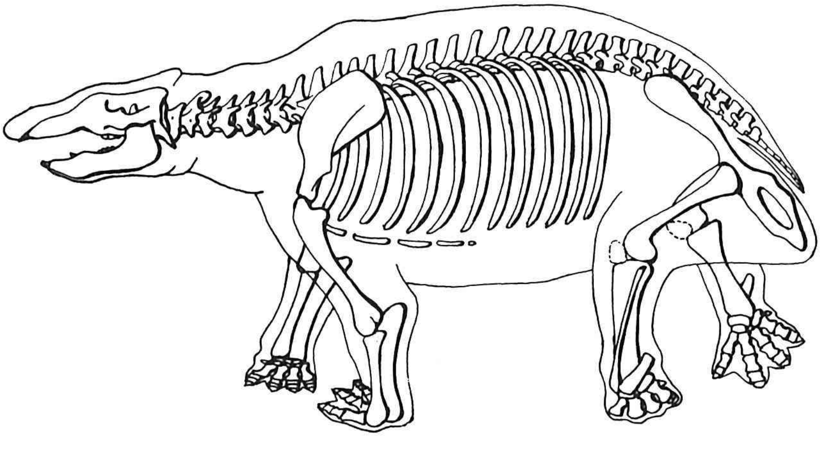
Fig. 3: Shikama's restoration of *Paleoparadoxia*, discovered in 1950. Figure from Shikama (1966).



1



2



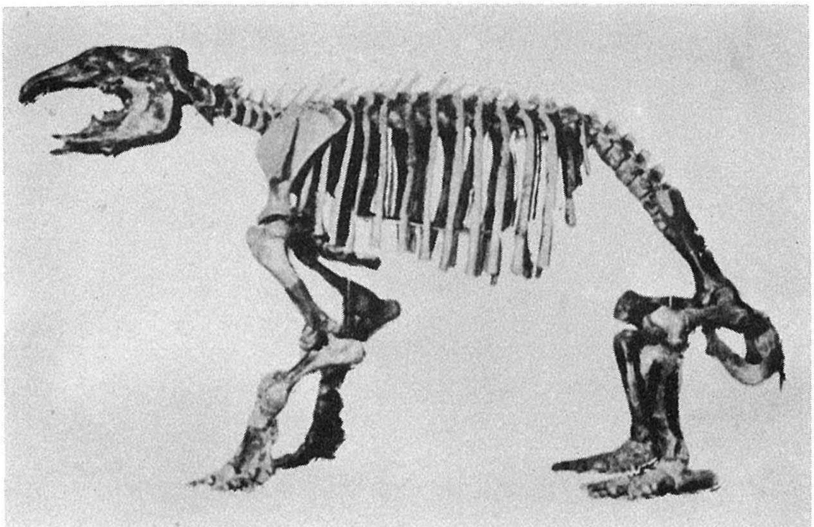
3

Plate X

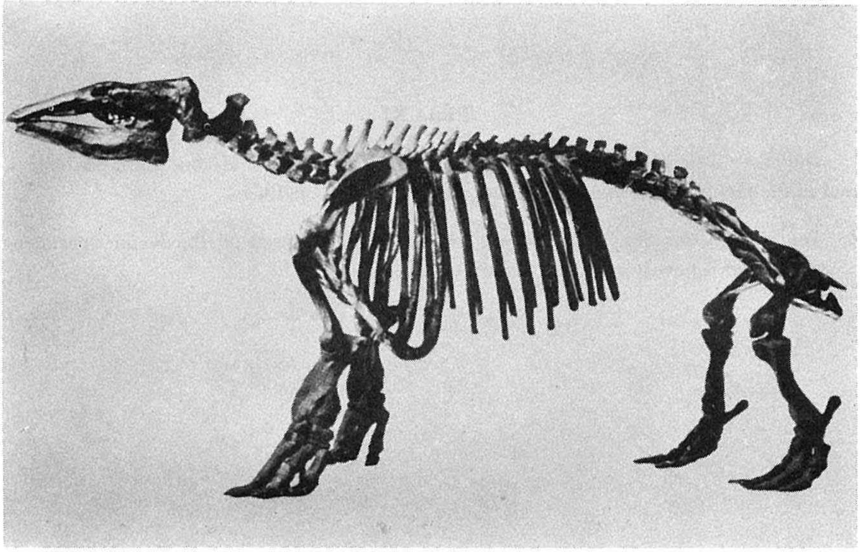
Fig. 1: The skeleton of *Paleoparadoxia* displayed in the British Museum. Photo from Halstead (1975).

Fig. 2: Kamei's restoration of *Desmostylus*, currently displayed in Hokkaido University and upon which the figure by Kamei and Okazaki (1975) is based.

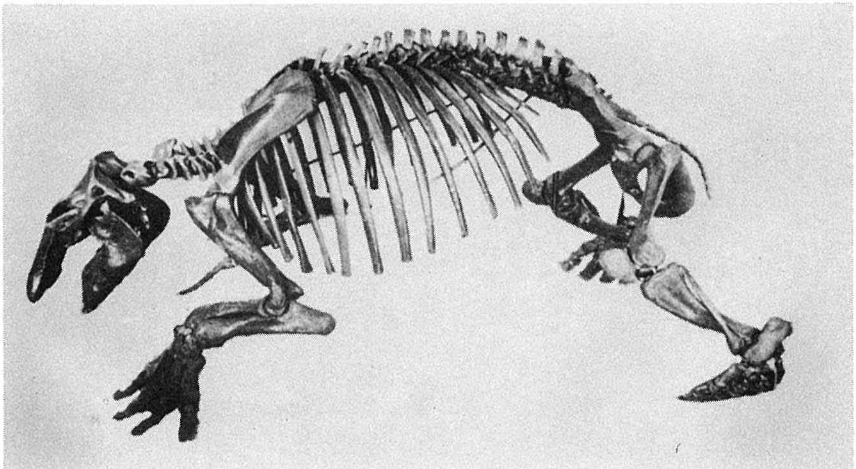
Fig. 3: Hasegawa's (1977) restoration of *Paleoparadoxia* displayed in the National Science Museum, Tokyo.



1



2

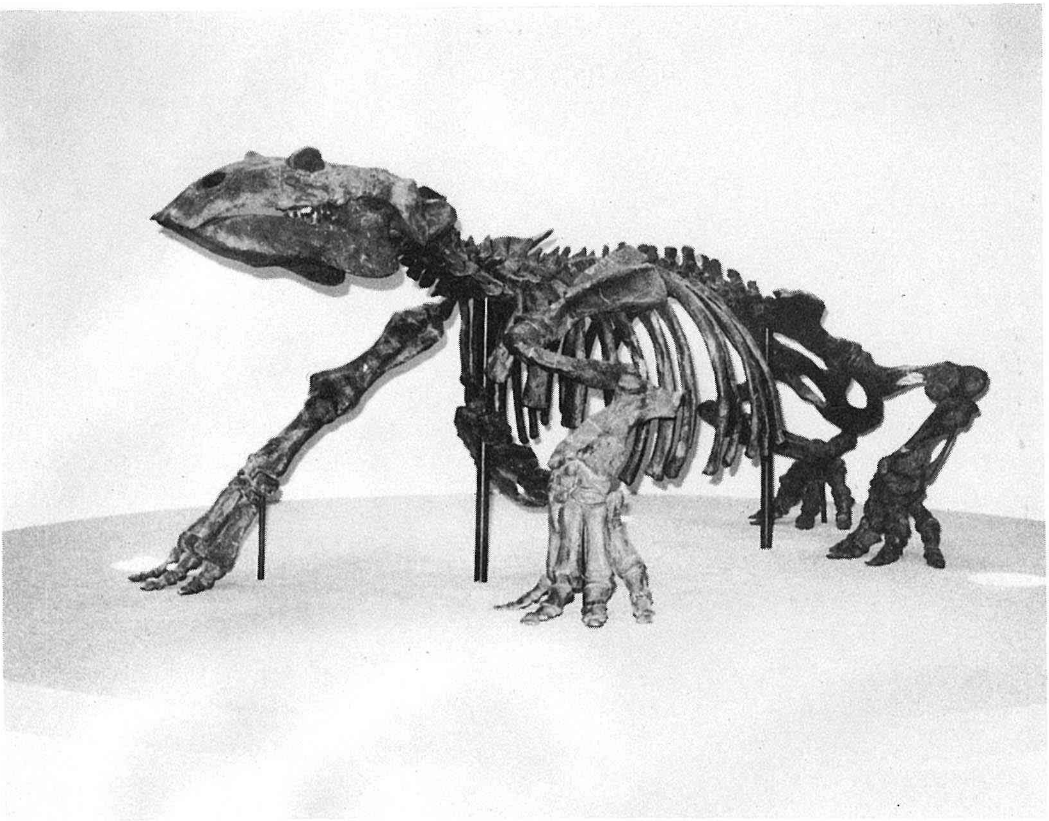


3

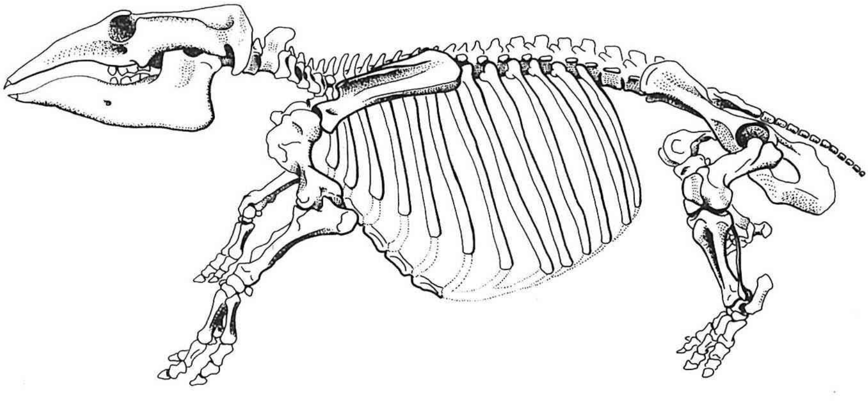
Plate XI

Fig. 1: Inuzuka's restoration of *Desmostylus*, which was discovered in Keton, south Sakhalin, and is mounted in the Hokumohken Kitami Culture Center, Kitami, in 1984.

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.



1



2