

The Terrestrial Posture of Desmostylians

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ABSTRACT

An attempt to reconstruct a skeleton of *Paleoparadoxia* Reinhart, 1959 (Mammalia, Desmostylia), suggests that desmostylian terrestrial posture deviated from that of typical ungulates much less than has been supposed by other authors. Desmostylians probably had a quadrupedal stance, with the body well off the ground and the limbs more or less under the body; a strongly arched spine and steeply inclined pelvis; slightly abducted elbows and more strongly abducted knees; and a digitigrade foot posture with an extended but not hyperextended wrist and hyperextended toes, the front toes pointing anterolaterad and the hind toes pointing forward. Most peculiarities of the skeleton have parallels in certain large, slow-moving terrestrial mammals, such as ground sloths and chalicotheres. The desmostylian skeleton was apparently well suited to supporting the body's weight on the hindquarters, perhaps while the animal clambered slowly over very uneven ground. This most likely occurred while it foraged for marine algae or sea grasses in rocky intertidal areas of the North Pacific shoreline, and while it crossed these areas en route to and from the water. Locomotion in the water probably resembled that of polar bears, with alternate pectoral paddling as the principal means of propulsion and the hind limbs used for steering. Surprisingly, desmostylian-like features of the tibia and ankle also are found in many other primitive ungulates and deserve closer study.

Introduction

Before and even since the discovery that desmostylians were quadrupedal, apparently amphibious marine mammals rather than wholly aquatic sirenians, their outward appearance and, in particular, their terrestrial posture have been controversial (see the remarkable collection of artists' reconstructions compiled by Inuzuka (1982)). Not even the more recent studies, based upon complete postcranial skeletons, have led to a consensus on this latter issue (cf. Repenning, 1965; Shikama, 1966, 1968; Inuzuka, 1984, 1985; Halstead, 1985; Repenning and Packard, 1990).

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In March 1986, I was asked to design a new mount of *Paleoparadoxia* Reinhart, 1959, in a terrestrial pose for a planned exhibit gallery at the National Museum of Natural History, Smithsonian Institution. (The mount was never actually constructed because of a change in the exhibit plan.) The specimen to be mounted was a cast of the neotype skeleton of *Paleoparadoxia tabatai* (Tokunaga, 1939), known in the literature as the Izumi specimen. Available for comparison were several other specimens and casts of various desmostylian genera and species (see below). Because some of these (notably the Stanford specimen) have not been formally described, most original specimens were not then accessible, and time and resources were limited, a thorough morphological or biomechanical study of the desmostylian skeleton was infeasible. Features critical for mounting the skeleton, however, were sufficiently clear from the available material, and the observations seemed worth recording as a contribution to the ongoing debate.

These conclusions were first presented at the Society of Vertebrate Paleontology annual meeting in Philadelphia in 1986. Subsequent discussions and collaboration with N. Inuzuka and others (see Inuzuka et al., 1995) have encouraged further refinement of these observations, which are offered herein for future testing as yet another alternative hypothesis on the fascinating subject of desmostylian locomotion.

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ABBREVIATIONS.—The following museum abbreviations are used:

PV	National Science Museum, Tokyo
UCMP	University of California Museum of Paleontology, Berkeley
USNM	Collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., which include the collections of the former United States National Museum

MATERIAL AND METHODS

1. Cast (USNM 26375) of nearly complete skeleton of subadult *Paleoparadoxia tabatai* (PV-05601; Izumi specimen) from Japan, partly described by Shikama (1966, 1968).

2. Cast (USNM 25899) of nearly complete skeleton of mature adult *Paleoparadoxia* sp. (UCMP 81302; Stanford specimen) from California.

3. Cast (USNM 24727) of nearly complete skeleton of adult *Desmostylus* Marsh, 1888 ("*D. mirabilis*" Nagao, 1935; Hokkaido University, Sapporo; Keton specimen), from Sakhalin, described by Shikama (1966) and Inuzuka (1980–1982).

4. Partial skeleton of immature *Desmostylus* (USNM 186891) from Oregon.

Also in existence are two partial skeletons possibly referable to *Behemotops* Domning, Ray, and McKenna, 1986 (the Ashoro specimens; Inuzuka, 1989); a well-preserved skeleton of *Desmostylus* (the Utanobori specimen, described in part by Inuzuka (1988)); two partial skeletons of *Paleoparadoxia tabatai* from the Chichibu Basin in the Saitama Prefectural Museum, Japan (Sakamoto, 1983); and the anterior one-half of an immature skeleton of *Paleoparadoxia weltoni* Clark, 1991 (UCMP 114285). The last three specimens do not appear to show any biomechanically significant postcranial differences from the Izumi specimen. *Behemotops*, *Paleoparadoxia*, and *Desmostylus* seem to have differed little, if at all, in their locomotor specializations (Shikama, 1966; Inuzuka et al., 1995), so observations made herein apply to all three genera unless otherwise stated.

I reached my conclusions mainly by manipulating the casts of the Stanford specimen, the well-preserved skeleton of a mature adult of the largest known species of *Paleoparadoxia*. Its joint surfaces are accordingly both fully developed and adapted to bear the maximum stresses that would have occurred in any known desmostylian. This makes the Stanford specimen the most sensitive indicator of the biomechanical constraints on desmostylian locomotion. The conclusions derived from this individual were then applied to the Izumi specimen, which is smaller, immature (judging from degree of epiphyseal fusion), less well preserved, and somewhat distorted, and which apparently represents a different species. No evidence was encountered, however, that would invalidate the assumption of biomechanical similarity.

The skeleton was built literally from the ground up, by assembling the feet in their most probable poses and then placing the limbs, girdles, and axial skeleton on top of them, with as little deviation as possible from a "normal" terrestrial ungulate or subungulate stance. Recent reconstructions that differed greatly from such a stance were not satisfactory. For example, Repenning's (1965) reconstruction, which was reproduced by Romer (1966, fig. 367), Barnes et al. (1985, fig. 3a), Inuzuka (1984, pl. 9: fig. 2), and others, placed the animal in a frog-like squatting pose with the dorsal surface of the manus against the ground. Inuzuka (1984, 1985) advocated a "herpetiform" posture with the limbs sprawled to the sides. In contrast, my work-

ing assumption, or null hypothesis, was that *Paleoparadoxia* did not differ essentially in posture from typical large land mammals such as hippopotamuses or rhinoceroses. (No single species of mammal, however, was used as a model.) When (as often happened) peculiarities of the joints demanded a departure from this assumption, other mammals provided analogies to demonstrate the mechanical feasibility of the posture. The aim of this study was to clarify the terrestrial posture of desmostylians and not their aquatic adaptations, so these examples were sought among land mammals; however, this is not meant to imply that desmostylians were other than largely aquatic in habits and habitat.

It is somewhat reassuring that this eclectic method, although applied separately to different parts of the skeleton, repeatedly led to comparisons with animals that share a similar habitus: heavy-bodied, presumably slow-moving quadrupedal forms resembling ground sloths. Perhaps *Paleoparadoxia* was not a paradox after all.

Results

PES.—The key observation of this study was made on the hind foot, which has always posed the most vexing problems for desmostylian functional anatomy. The axis of the ankle joint inclines ventromedially about 30°–40° from normal to the long axis of the tibia, and it slopes ventrolaterally about 10° from the plantar plane of the foot. If the foot is placed plantigrade on a horizontal surface, as it has been in some reconstructions (see Inuzuka, 1982), the tibia is thereby inclined about 40°–50° from the sagittal plane. Together with the torsion in the tibia itself (see below), this necessitates strong abduction of the knee, and awkward positions of other joints, in order to assume the plantigrade pose during the weight-bearing portion of the stride. This pose, however, is certainly incorrect, as is shown by the form of the metatarsals and, especially, the metatarso-phalangeal joints.

The pes as a whole is paddle-like; the tarsus-metatarsus is rigid and planar, rather than forming a half-cone as in an elephant. From digit II to digit V the metatarsals increase significantly in length, and the form of curvature of the phalangeal articular surface varies (Figure 1a–d). This surface lies on the dorsal side of the bone at its distal end and is nearly flat on metatarsal II, corresponding to the equally flat proximal surface of the proximal phalanx. The transition from this flat dorsal surface to the distal part of the articular surface is abrupt and much more strongly curved than the very slight proximal concavity of the phalanx. The latter can stably articulate with the metatarsal in either the maximally (about 75°) hyperextended position (the more stable position; Figure 1a) or the typical extended position, i.e., in line with the metatarsal. The metatarsal's palmar joint surface is slightly keeled and articulates with a pair of large sesamoids, so flexion of the phalanx onto this surface is impossible. The most likely terrestrial pose

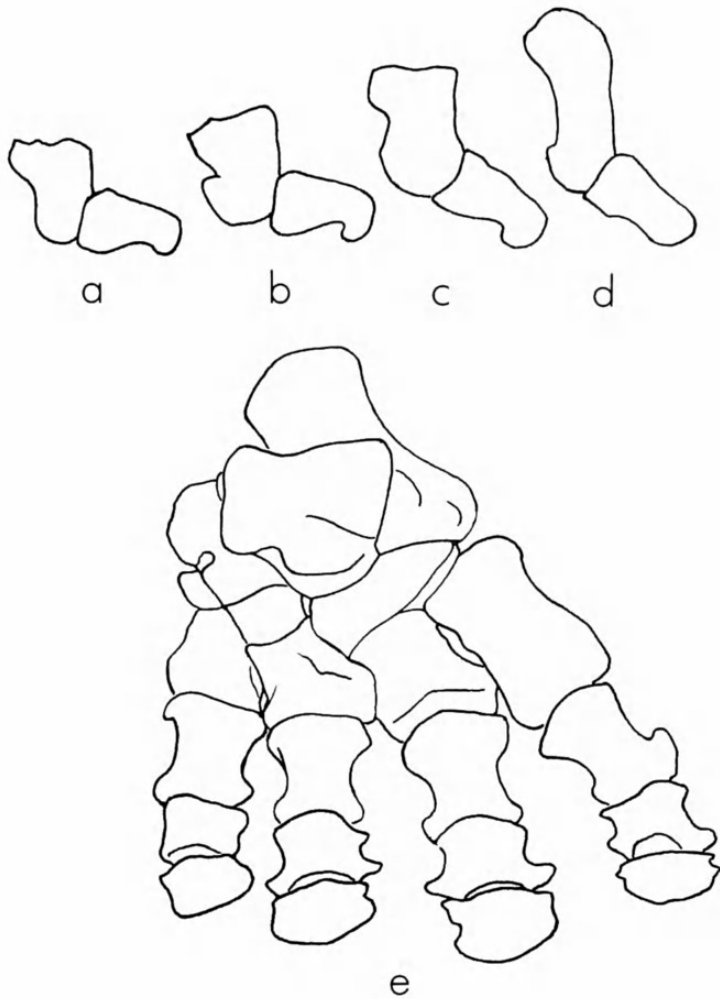


FIGURE 1.—*Paleoparadoxia* sp. (UCMP 81302), left pes: *a-d*, metatarsals and proximal phalanges of digits II–V, respectively, in medial views, each showing maximum degree of hyperextension possible; *e*, left pes in anterodorsal view. Note that the tibial-astragalar joint axis is horizontal, the metatarsals lie in a nearly vertical plane, the weight-bearing axis passes through digit III, and the toes are maximally hyperextended.

of the second digit is therefore the hyperextended one, with the phalanx nearly perpendicular to the metatarsal (Figure 1*a*).

The same observations hold for the more lateral toes to a progressively lesser extent. The dorsal-to-distal curvature of the metatarsal surface gradually becomes less abrupt, and the proximal articular concavity of the phalanx deepens. The degree of hyperextension required (or even possible) at these joints, after increasing slightly from digit II to III, correspondingly diminishes from about 80° on III to 60° on IV and 50° on V (Figure 1*b-d*).

This pattern becomes intelligible when the foot is placed in a digitigrade position, with the plane of the metatarsals at an angle to the ground and the phalanges flat on the substrate (Figure 1*e*). Then the short, almost cuboidal medial metatarsals (especially metatarsal III) support the body's weight on their flat distal ends and their sesamoids. The greater lengths of the more lateral metatarsals require them to extend distally and laterally at progressively greater angles to the sagittal plane. Conse-

quently they bear less weight; the end of metatarsal V may almost have been free of the ground, and not only is its digit the least hyperextended (Figure 1*d*), but its proximal phalanx has a canted distal articulation, causing the toe to curve medially and making the distal phalanges lie parallel to those of the other digits (Figure 1*e*).

When the metatarsals and phalanges are in this pose, one finds that, despite the peculiar shapes of the tarsals and metatarsals (1) the foot posture can be digitigrade during weight-bearing (i.e., when the hip is directly over the ankle) and would be within usual limits for a large land mammal; (2) both the axis of the ankle joint and the plane of the sole are nearly perpendicular to the sagittal plane; (3) the toes point forward; and (4) the axis of the ankle joint is horizontal (Figure 1*e*), so the ankle joint is not prone to dislocation by the body's weight. The calcaneal tuberosity does have a strong medial inclination (Figure 1*e*), but this can be seen as an adjustment to the torsion of the tibia (see below) and of the muscles of plantar flexion. A line from the apex of the calcaneal tuberosity perpendicular to the axis of the tibial-astragalar joint passes approximately through digit III, and therefore probably along the central weight-bearing axis of the foot. If the animal were to take a long stride, the hind foot might initially be placed in a plantigrade pose, becoming digitigrade only as the hip moved above it. Such a bulky animal as a desmostyliian may have habitually taken only short strides, however, throughout which the foot could have been digitigrade or nearly so.

On the whole, in view of its strange morphology, the posture of the hind foot is surprisingly normal. An elastic pad, such as exists in elephants, may have supported the foot in this digitigrade posture (although in elephants the foot bones surround the pad with a half-conical structure that is not seen in desmostyliians, and the posture of the digits themselves is actually unguligrade; Osborn, 1942:1336). Alternatively, desmostyliians may have managed without such a supporting pad because they were smaller than elephants, probably spent more time supported by water, and when hauled out probably took weight off their feet by squatting or lying on the ground as do sea lions. The modern *Hippopotamus*, for example, maintains a digitigrade posture on land without an elephant-like supporting pad in the foot.

TIBIA.—The tibia has two major peculiarities: lateral torsion of the proximal end about 45°–50° relative to the distal end, and mediolateral inclination of the distal joint surface about 30°–40° from normal to the long axis of the shaft. If the shaft is held vertically with its anteroposteriorly flattened distal portion perpendicular to a sagittal plane, the knee and femur must be strongly abducted and the sole of the foot must face both distally and laterally. Conversely, with the foot in the digitigrade position described above, the tibia is inclined outward from the ankle about 30°–40° from a sagittal plane. The abduction of the knee largely compensates for this, however, so that the ankle lies not far outboard of the parasagittal plane of the hip joint (Figure 2).



FIGURE 2.—*Paleoparadoxia tabatai* (Izumi specimen, cast, USNM 26375), skeleton partly assembled in sand-box in posterolateral view to show limb positions and spinal curvature postulated in this study. The three representative ribs shown are not in correct anatomical position; their ventral ends should be abducted much farther from the midline.

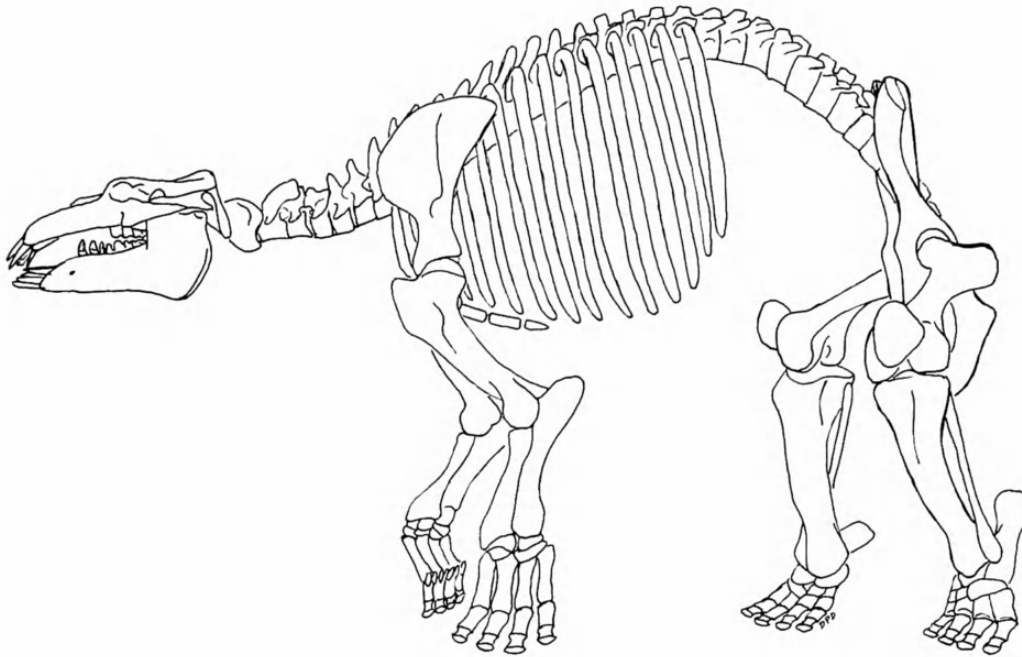


FIGURE 3.—*Paleoparadoxia tabatai* (Izumi specimen, PV-05601), reconstructed skeleton in lateral view, showing probable terrestrial posture. Note hyperextension and anterolateral direction of front toes, anterior direction of hind toes, and strong abduction of knees.

FEMUR.—The shaft of the femur is broad and greatly flattened anteroposteriorly. The neck protrudes anteromedially from the plane of flattening of the shaft. The head rises slightly above the level of the greater trochanter and lacks a fovea capitis. A line connecting the proximal and distal margins of the articular surface of the head forms an angle of about 50° – 65° with the femoral shaft. With the foot bones in the position described above, with the tibia inclined outward 30° – 40° from a sagittal plane and lying in a transverse plane inclined perpendicular to the sole of the foot, and with the knee joint bent at a right angle, the posterior (now ventral) edge of the femoral head lies barely inside the acetabulum; a 2–3 cm wide strip of the head's articular surface is exposed dorsally; and although the femur is laterally rotated, there remains clearance between the greater trochanter and the ischium (Figures 2, 3). This leg posture would seem to provide adequately for support and movement of the hindquarters. The medial condyle is somewhat larger than the lateral in the Izumi specimen and extends farther distally and posteriorly; in the Stanford specimen, probably representing a different species, they are more nearly equal in development. Court (1994:324) stated that “[i]n medial view, a line drawn from the posterior-most extent of the inner condyle to its anterior margin, when orientated in the horizontal plane, reflects the position of maximum articular congruence at the knee and the likely habitual posture of the femur.” By this criterion, the femur of *Paleoparadoxia* would have habitually inclined about 67° – 69° from the vertical. The crural index (lengths of tibia/femur $\times 100$) is 88 in the Izumi and 77 in the Stanford specimen. The ratios of lengths of meta-

tarsal III/femur $\times 100$ are 19 and 15, respectively. These differences might be ontogenetic, interspecific, or both.

INNOMINATE.—As others have noted, the innominate is primitive looking, even rodent-like, being very long and narrow for such a large mammal. The ilium in particular lacks the degree of lateral expansion typical of heavy ungulates. The vertical angle between innominate and sacrum is slight (about 10° – 15°), as in primitive mammals, and, given the length of the ilium, would seem to be disadvantageous for weight-bearing. The strong spinal curvature (see below), however, makes possible (indeed, necessitates) a very steep inclination of both sacrum and pelvis (Figures 2, 3). This accomplishes the same purpose as the short, almost vertical ilium of most other graviportal mammals, namely, to bring the hip joint nearly underneath the sacroiliac joint. In caudal view, the posterior part of the pelvis has a pronounced U-shape, with the pubes forming an almost flat floor of the pelvic canal and the ischia lying in almost parallel, parasagittal planes (cf. Inuzuka, 1985, fig. 1). The acetabulum is relatively wide and shallow. This is reflected in the extremely acute angle seen in ventral view between its superolateral and ventrolateral margins (cf. Jenkins and Camazine, 1977, fig. 7), which indicates that the superolateral margin does not extend very far laterally. Also, a line connecting the medial and lateral margins of the upper, weight-bearing articular surface of the acetabulum forms an angle of about 70° – 75° with the vertical, as nearly could be estimated for the disarticulated Izumi and Stanford skeletons.

VERTEBRAL COLUMN.—The desmostylian neck is short for an ungulate, and, although the head is fairly large, the anterior thoracic neural spines are normally inclined and not unusually

enlarged, so the nuchal ligament was evidently not relied upon much for cranial support. The cervical and anterior thoracic centra, largely missing from the Izumi specimen but restored by its preparators, give a distinct secondary (concave-dorsal) curvature to this region.

Fifteen thoracic and six lumbar vertebrae are present in the restored Izumi skeleton (although Shikama (1966) mentioned only 14 thoracics); the last 13 thoracics are preserved in the Stanford specimen. The posterior thoracics and lumbar have short, vertical spines, and there is no anticlinal vertebra. The fourth thoracic from the rear (?T12) in the Stanford specimen comes closest to being a diaphragmatic vertebra; the zygapophyseal articular planes shift from near-horizontal to near-vertical in the region of ?T11–13 but then return to an intermediate inclination in the lumbar region. This shift suggests more vertical flexibility in the posterior thorax than in the adjacent regions.

The most-posterior thoracic and most-anterior lumbar centra are distinctly wedge shaped, thicker dorsally, and thinner ventrally in both the Stanford and the Izumi *Paleoparadoxia* specimens (this, however, is not very evident in *Desmostylus*). This shape indicates a strong dorsal convexity of the spine in this region, with the summit of the backbone lying near the rear of the ribcage. From this point the lumbar and sacral vertebrae descend at a rather steep angle, with the pelvis in an almost vertical position (Figures 2, 3). The sacrum is fairly long and robust but is not fused to the pelvis, and sacral vertebrae 1 and 2 are not fused to one another, even in the Stanford adult (although sacra 2–5 are fused).

MANUS.—The metacarpals are about twice as long as the metatarsals. The metacarpo-phalangeal articulations are fairly uniform in shape and do not show a mediolateral gradient of change analogous to that seen in the hind foot. The long axis of the lunar articular surface lies at approximately a 65° angle to the plane of the palm. With the metacarpals vertical, the radius can easily be balanced upright on the lunar without any other support and with its shaft tilted backward some 15° from the vertical (Figure 3). The large radial styloid process thus would not have prevented wrist extension sufficient for digitigrade posture. In this position, the axis of the elbow joint is at about a 75° angle to the plane of the palm. Even with the elbow abducted 30° from the body, the front toes could not have pointed straight forward; at best the palm might have been “pronated” some 45° from a parasagittal plane when the animal stood on land. (True pronation and supination, however, were prevented by the firm articulation of the radius and ulna; this angle of “pronation” was controlled instead by movement at the shoulder joint.) The weight of the forequarters therefore appears to have been carried on metacarpals held essentially vertically, with the foot in a digitigrade stance; the toes presumably were hyperextended and pointed as much laterad as anterad, and the wrist joint was extended straight. From this position the wrist could have been flexed, but the very large styloid process of the radius would have prevented any significant hyperextension.

RADIUS AND ULNA.—As mentioned above, the radius and ulna are tightly articulated, although not fused, and the radius bears a massive styloid process that overlaps the anterior side of the wrist joint. The radius forms almost the entire distal part of the semilunar notch and is, therefore, the main weight-bearing bone. The ulna also bears considerable weight, however, and has an even thicker shaft than the radius. The olecranon is very long, equal to one-half the length of the radius (excluding the styloid process) in the Izumi specimen and to about two-thirds of the length of the radius in the Stanford specimen.

HUMERUS.—The humerus is long and slender in the Izumi specimen. The trochlea is deeply constricted at its middle, and a corresponding ridge on both radial and ulnar parts of the semilunar notch renders the elbow joint very stable. The notch, however, opens more anteriorly than proximally, so the elbow could not have been extended as straight as in graviportal forms such as elephants. The entepicondyle is short and stout, protruding more posterad than mediad. The trochlea is canted only about 80° to the long axis of the shaft, so the shafts of the humerus and radius are only 10° out of alignment when the elbow is extended. This alignment indicates a very slight degree of abduction of the elbow and nearly parasagittal forelimb movement in terrestrial locomotion (Jenkins, 1973). The supinator crest shows little or no expansion, but there is a long and fairly prominent deltopectoral crest reaching almost to the distal end of the shaft. The lesser tuberosity is weakly developed in the immature Izumi specimen, but the greater tuberosity is robust. The head is expanded anteromedially. The brachial index (lengths of radius/humerus $\times 100$) is 62 in the Izumi skeleton; the intermembral index (lengths of (humerus + radius)/(femur + tibia) $\times 100$) is 88; the ratio of lengths of metacarpal III/humerus $\times 100$ is 41; and the ratio of lengths of metacarpal III/radius $\times 100$ is 65 (64 in the Stanford skeleton).

SCAPULA.—The distal end of the scapula is not preserved in the Stanford specimen, and that of the Izumi specimen has the coracoid process detached; on the cast it has been restored as extending rather far anteriorly and distally. Although this prevents the humerus from being extended straight downward from the glenoid, such extension almost certainly would not have taken place. At maximum extension of the shoulder, the humerus would have made perhaps a 140° angle with the spine of the scapula. In a normal standing pose the angle would have been smaller, perhaps 120° – 130° (Figure 3).

Comparisons

PES.—The desmostylian hind foot has been thought to be completely without parallel, but it shows surprising resemblances to the pes of the perissodactyl *Chalicotherium* (Figure 4; Zapfe, 1979): the latter is digitigrade, the metatarsals increase markedly in length from medial to lateral, the calcaneal tuberosity has a strong medial inclination, and the toes point forward despite the strong abduction of the knee (see below). There are also differences from *Paleoparadoxia*: the axis of the



FIGURE 4.—*Chalicotherium grande*, left pes in anterior view, after Zapfe (1979).

astragalus is sloping rather than horizontal, and of course the feet have only three toes, which bear claws rather than the small hooves that desmostylians presumably possessed. Nonetheless, we see in *Chalicotherium* a large quadruped of unquestioned terrestrial habits that bore its weight mainly on the medial side of a hind foot that resembled in obvious ways the foot of *Paleoparadoxia*. The notoungulate *Homalodotherium* also has longer lateral than medial metatarsals, but the medial ones are thin rather than stout, and the animal evidently walked on the lateral rather than medial edge of its foot (Scott, 1930).

TIBIA.—Again, *Chalicotherium* approaches *Paleoparadoxia* in the torsion of the tibial shaft, although not in the tilt of the ankle joint. Even closer matches to *Paleoparadoxia* are found in the giant armadillo (*Priodontes*), the collared anteater (*Tamandua*), pangolins (*Manis*), various bears (including *Helarctos* and *Ursus spelaeus* Rosenmüller and Heinroth), and the giant panda (*Ailuropoda*). Indeed, one giant panda (USNM 258835, a wild-caught specimen) is identical to the Stanford

Paleoparadoxia in values of both variables (Domning, 2001). These two features (and especially the tilt of the ankle joint) also are seen to different degrees in a variety of other, extinct forms, including the most primitive sirenians (Prorastomidae; Domning, 2001) and proboscideans (*Numidotherium*; Court, 1994, and below), ground sloths (*Megalonyx*), *Coryphodon*, and “condylarths,” including *Hyopsodus* (Gazin, 1968) and *Meniscotherium* (Gazin, 1965; Williamson and Lucas, 1992; see also Domning, 2001). *Hyopsodus* and *Meniscotherium* belong to the group of primitive ungulates from which tethytheres or pantomesaxonians emerged (Thewissen and Domning, 1992), so these features of the tibia may well have been inherited from the ancestors of desmostylians. Their function is unclear, and their taxonomic distribution (or indeed, their very existence) within this group has attracted negligible attention. *Meniscotherium* (which exhibits much less tibial torsion but an even greater tilt of the ankle joint than *Paleoparadoxia*) has, however, been characterized as “adapted for ambulatory, habitual travel on an irregular terrestrial substrate” and as suited to negotiating “a rugged and obstacle-filled terrain” (Williamson and Lucas, 1992:32–33), as was also probably the case for desmostylians (see below). The desmostylians’ short tibia, relative to the femur, is characteristic of graviportal quadrupeds in general as well as the above-mentioned “condylarths.”

PATELLA.—Coombs (1983:38) suggested that a large patella (indicative of powerful knee extensors) was associated with body erection in *Chalicotherium*; this bone is proportionately much larger in the Stanford *Paleoparadoxia* than in chalicotheres.

FEMUR.—The flattened desmostylian femur is strikingly reminiscent of that of large ground sloths, but some flattening of the shaft is seen in most large land animals, including *Chalicotherium* and *Homalodotherium* as well as elephants, rhinoceroses, and sauropod dinosaurs. (This flattening is more pronounced in sauropods thought to have routinely used a bipedal posture; Wilson and Carrano, 1999.) The femur of *Paleoparadoxia*, like that of elephants and ground sloths, lacks a fovea capitis. The posture suggested herein for *Paleoparadoxia*, with the knees strongly abducted from the body, is likewise not unprecedented among large mammals, including the largest ground sloths and *Chalicotherium*. Bears adopt a similar pose when supporting themselves on their hind legs. Jenkins and Camazine (1977) described the form and kinematics of the hip joint in three other carnivores (raccoon, cat, and fox) that show progressively lesser degrees of hip abduction. The angle between the margin of the articular surface of the head and the femoral shaft is greater in desmostylians than in raccoons, in which it is about 50° (Jenkins and Camazine, 1977:363), suggesting a greater degree of femoral abduction in the former. When desmostylian bones are manipulated in the fashion advocated herein, the portions of the femoral articular surface enclosed within the acetabulum at each stage of the stride correspond well with the observations of Jenkins and Camazine (1977:359–360) on the raccoon, cat, and fox, indicating that the

present reconstruction does not involve a pattern of hip articulation unusual for terrestrial mammals.

INNOMINATE.—In most large terrestrial mammals, including *Chalicotherium*, *Homalodotherium*, and ground sloths, the ilium is much broader than in desmostylians. This broadening provides attachment area for enlarged gluteal muscles, which extend the hip against gravity. The absence of this graviportal adaptation in desmostylians may be because of their more amphibious habits; in any case, it does not rule out body erection. The long innominate and relatively narrow ilium of *Paleoparadoxia*, as noted above, resemble those of rodents, but they also strongly resemble those of the giant panda, *Ailuropoda* (see Davis, 1964). Desmostylians are probably the largest mammals to display this form of pelvis. Davis (1964:110) listed seven features that he believed to characterize the pelvis “in mammals in which forces parallel to the long axis of the pelvis predominate, i.e., those that stand erect and those that use their hind legs for bracing while digging.” Of these seven features (which do not include a broadened ilium), at least five are seen in desmostylians: the wings of the ilia tend to be shifted into the frontal plane; the corpus of the ilium is nearly circular in cross section; the pubo-ischiadic symphysis is reduced in its anterior part (i.e., the front of the symphysis lies posterior to the acetabulum); the number of sacral vertebrae is relatively high (five); and the tail is shortened. (Although Davis (1964:113) pointed out that *Ailuropoda* exhibits these features “to a far greater degree than any other carnivore,” he nonetheless believed that pandas do not stand erect more than bears and that the contrast in pelvic shape between these forms is due to nonadaptive factors. In any case, both bears and pandas frequently assume a bipedal posture, in contrast to most mammals.) Desmostylians also lack the noticeably enlarged ischial tuberosity that is typically seen in large ungulates, including *Chalicotherium* and *Homalodotherium*. In *Chalicotherium*, however, these tuberosities were thought by Zapfe (1979) to reflect the use of a sitting posture during feeding. The U-shape of the desmostylian pelvis in caudal view is outside the range of variation of the carnivores studied by Jenkins and Camazine (1977:368, fig. 7), but they generalized that “the ischial surface is approximately perpendicular to the middle of the range of abduction.” The nearly parasagittal ischial surface in desmostylians implies very pronounced abduction at the hip, as is agreed by most authors. The relatively shallow, open desmostylian acetabulum and the inclination of its upper articular surface likewise tend toward the end of the raccoon-to-fox spectrum that indicates relatively great hip abduction (Jenkins and Camazine, 1977:361–363, figs. 6, 7).

VERTEBRAL COLUMN AND BODY FORM.—The strongly curved backbone of *Paleoparadoxia* was explained above as an adjustment to supporting a heavy body by way of an elongate pelvis. A similar degree of spinal curvature and verticality of the pelvis can be observed in rodents as large as the giant beaver *Castoroides* (see Romer, 1966, fig. 442), which of course is still much smaller than *Paleoparadoxia*. A somewhat similar

overall body form (albeit with different osteological details) is seen in the giant panda, however (Davis, 1964, fig. 15), and even in some very heavy mammals, such as the notoungulate *Toxodon* and the edentate *Glyptodon* (Romer, 1966, figs. 374, 427). The last two forms share a bulky body, low forequarters, a high rump, and (as in nearly all graviportal mammals) a nearly vertical ilium, although they lack a pronounced lumbar curvature. Spinal curvatures more similar to that of *Paleoparadoxia*, as well as more equal limb lengths, occur in the sloth *Hapalops* and the marsupial *Diprotodon* (see Coombs, 1983, figs. 5a, 7e). *Chalicotherium* and *Homalodotherium*, on the other hand, have long front legs, low hindquarters, and straighter spines, although the schizotheriine chalicothere *Moropus* shows a distinct dorsal convexity of the spine at the front of the lumbar region (Coombs, 1983, fig. 7a).

MANUS.—Several large land mammals have longer metacarpals than metatarsals, including *Chalicotherium* and *Homalodotherium*. The latter used a digitigrade stance of the forefoot, but *Chalicotherium*, like anteaters, walked on the dorsal surfaces of the flexed and heavily clawed toes, with the palm in a parasagittal plane (an orientation also seen, to a lesser extent, in *Paleoparadoxia*).

RADIUS AND ULNA.—A strong radial styloid process (albeit not so strong as in *Paleoparadoxia*) is found in *Chalicotherium*; *Toxodon*; the smaller toxodont, *Nesodon* (Scott, 1912); and the polar bear, *Thalarctos* (as well as other ursids), in combination with digitigrade or even (in ursids) plantigrade posture. The olecranon is short in *Chalicotherium* and *Homalodotherium*; a closer match to that of *Paleoparadoxia* is seen in *Toxodon*, *Nesodon*, and *Glyptodon*, which used the forelimbs for support and not for pulling down tree limbs (see below).

HUMERUS.—The humerus of *Chalicotherium* is long, but with a more markedly tilted trochlea and a more expanded distal end than in *Paleoparadoxia*. Sloths, bears, and *Nesodon* also have relatively long and slender humeri.

STERNUM.—*Chalicotherium* shows a slight broadening and dorsoventral flattening of the sternbrae, but the double row of broad, flat plates forming the desmostylian sternum (Shikama, 1966) is unique. It is worth noting, however, that in large ground sloths, such as *Paramylodon* and *Eremotherium*, the costal cartilages are ossified. This arrangement and the desmostylian sternum both could be ways of providing a solid area of origin for massive pectoral muscles, used in ground sloths for pulling down branches and in desmostylians for swimming. This notion unfortunately is not readily testable, for such muscles generally have fleshy proximal attachments that leave no evidence in the form of distinct scars on the bones.

Discussion

TERRESTRIAL LOCOMOTION.—The foregoing is not intended to be an exhaustive catalog of the desmostylian-like features found among terrestrial mammals. Its purpose is merely to show that nothing in the present reconstruction is wholly un-

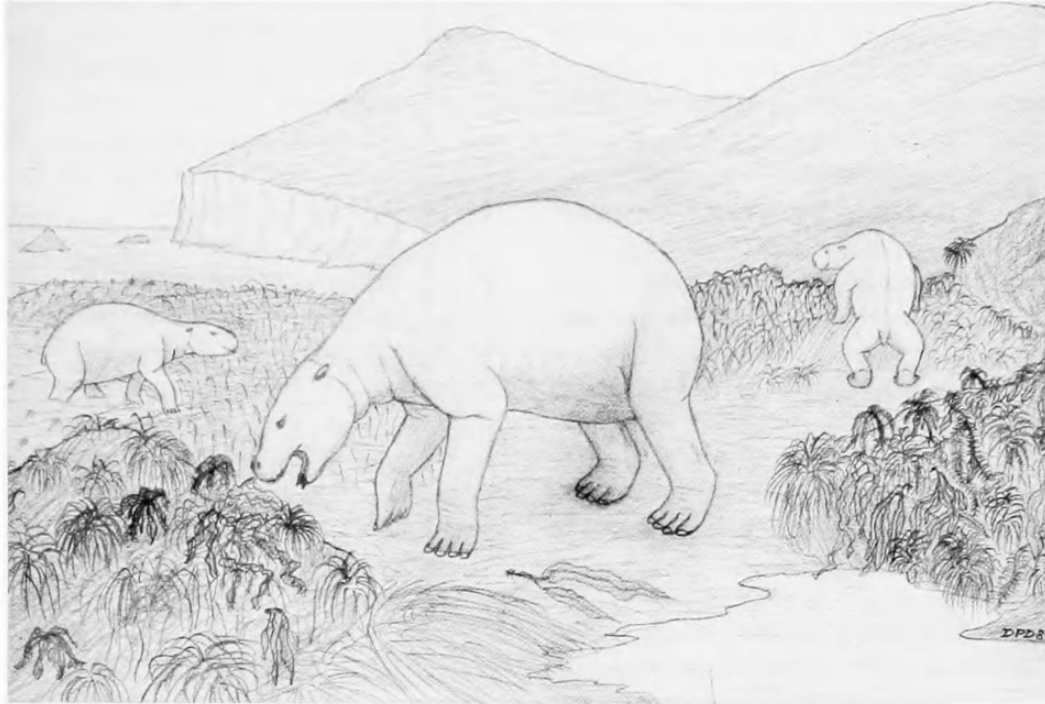


FIGURE 5.—Reconstruction of *Paleoparadoxia*, showing postures that it probably used while standing or traveling in the intertidal zone of North Pacific shorelines.

precedented among large land mammals. On the contrary, *Paleoparadoxia* presents a coherent suite of features that repeatedly appear in mammals believed to share a particular range of lifestyles: large, slow-moving herbivores that browsed (often bipedally) on leafy vegetation, in many cases by pulling it down from overhanging branches. These forms include ground sloths in addition to chalicotheres and *Homalodotherium*, both of which have been compared with sloths as well as with each other.

I do not suggest that desmostylians browsed on trees or even used their forelimbs to gather food. Apart from their marine habitat, their lack of claws and their non-elongated forelimbs, among other features, clearly rule this out. The sloth-like forms, however, are believed to have shared a less obvious trait, namely, the habit of supporting themselves on their hind legs while feeding. Large sloths had massive tails to help support them in this pose, but even the practically tailless *Chalicotherium* is thought to have behaved similarly (Zapfe, 1979). The essential requirement is a broad, stable base formed by the hind appendages. These forms all share an abducted posture of the knees (which steadies the upright body against falling sideways) and striking modifications of the hind feet—to support weight on the lateral edge of the foot in sloths and *Homalodotherium*, and on the medial side in *Chalicotherium* and desmostylians. The similarities in metatarsal, ankle, and tibial structure between the latter two seem too striking to reflect wholly different selective pressures.

Coombs (1983, figs. 3, 4, table 4) summarized in more detail the osteological features that appear to characterize diggers and bipedal browsers. The majority of these are features of the forelimbs, and judged on these alone, *Paleoparadoxia* resembles a digger more than a bipedal browser. This similarity, however, is surely due to its use of the forelimb for digging-like movements while swimming, because the front feet are not at all suited to efficient digging or food-gathering. Most features of the desmostylian hindlimb, in contrast, are consistent with the pattern Coombs described for semi-bipedal forms. These features—most of which also are well exemplified by humans—include a vertical ilium, a large acetabulum, a heavy femur, differing stance of manus and pes, a long calcaneal tuber, short metatarsals with rigid articulations, and splayed hind toes. Although Coombs's comparisons were designed to distinguish bipedal browsers from diggers and climbers rather than from swimmers or amphibious quadrupeds, and although they covered such a diversity of mammals that they are necessarily very generalized, these resemblances nonetheless show that the present interpretation of desmostylians is not without anatomical precedent.

Consequently, *Paleoparadoxia* likely was a slow, heavy, quadrupedal herbivore that often had to support much of its weight on its hindquarters when climbing over extremely uneven, rocky, slippery ground. This would have been especially true while it fed in the North Pacific intertidal zone, presumably on marine algae and sea grasses (see Domning et al., 1986:47–48; Figure 5), and while it traveled to and from the

water. Such a scenario fits well with Repenning and Packard's (1990) explanation for the bilateral hind-limb fractures seen in the Stanford skeleton, which also envisions a rocky seashore habitat.

Although it is possible that the peculiarities of the hind limbs were instead adaptations for swimming (see below), it is not necessary to look beyond the realm of purely terrestrial mammals to find detailed resemblances to the limbs of desmostylians. The latter, once envisioned as an aberrant group of sirenians or "sea cows," might more accurately be thought of as "sea sloths." (Interestingly, on the Pacific coast of Peru, where desmostylians apparently never occurred, *Thalassocnus natans* Muizon and McDonald, 1995, a newly discovered genus and species of megalonychid ground sloth, apparently filled an ecological niche much like that suggested herein for desmostylians.)

These parallels with semi-bipedal terrestrial browsers have been drawn from a diverse group of land mammals. The test, then, is whether the salient features of desmostylian osteology really fit together coherently. The hind feet and legs would provide stable support for most or all of the body's weight during slow, deliberate movements over rough ground. The almost vertical pelvis is appropriate for four-footed weight-bearing. The strongly arched back, although well suited for supporting a heavy trunk, is flexible enough for raising the forequarters without greatly changing the slope of the lumbosacral region. In quadrupedal stance, the base of the short neck is carried relatively low to the ground, which could easily be reached by the elongated rostrum. The scapula and forelimbs are in a normal ungulate pose, and the manus is peculiar only in its "semi-pronated" orientation. Although its gait was doubtless slow, nothing would seem to have prevented the animal from traveling with ease across dry, level ground.

A further and more rigorous test is to examine the moments of resistance against bending of the vertebral centra. Slijper (1946) and Coombs (1983) calculated these quantities by multiplying the width (b) of the caudal surface of the centrum by the square of the height (h^2). Calculated moments for each vertebra were graphed, as in Figure 6. A curve peaking in the lumbar region (Figure 6a) was interpreted to indicate use of an erect or semi-erect posture (cf. Coombs, 1983, fig. 2). Humans and bears (including *Ailuropoda*, Figure 6b) display this pattern. The results for the Stanford *Paleoparadoxia* (Figure 6c) agree for the most part with Slijper's theoretical curve for quadrupedal mammals (Figure 6d), but they also show bipedal tendencies in that the highest moments seen in the preserved portion of the vertebral column are relatively posterior, lying mostly in the lumbar region. Among the seven forms compared by Coombs (1983, fig. 2), this combination of a peak at the front of the thorax and one in the lumbar region is most closely matched by the chalicothere *Moropus*, the gerenuk (*Litocranius*), which often feeds in a bipedal pose (Figure 6e), and a goat (*Capra*) that was born without forelimbs and learned to walk bipedally. A normal goat did not show any lumbar or pos-

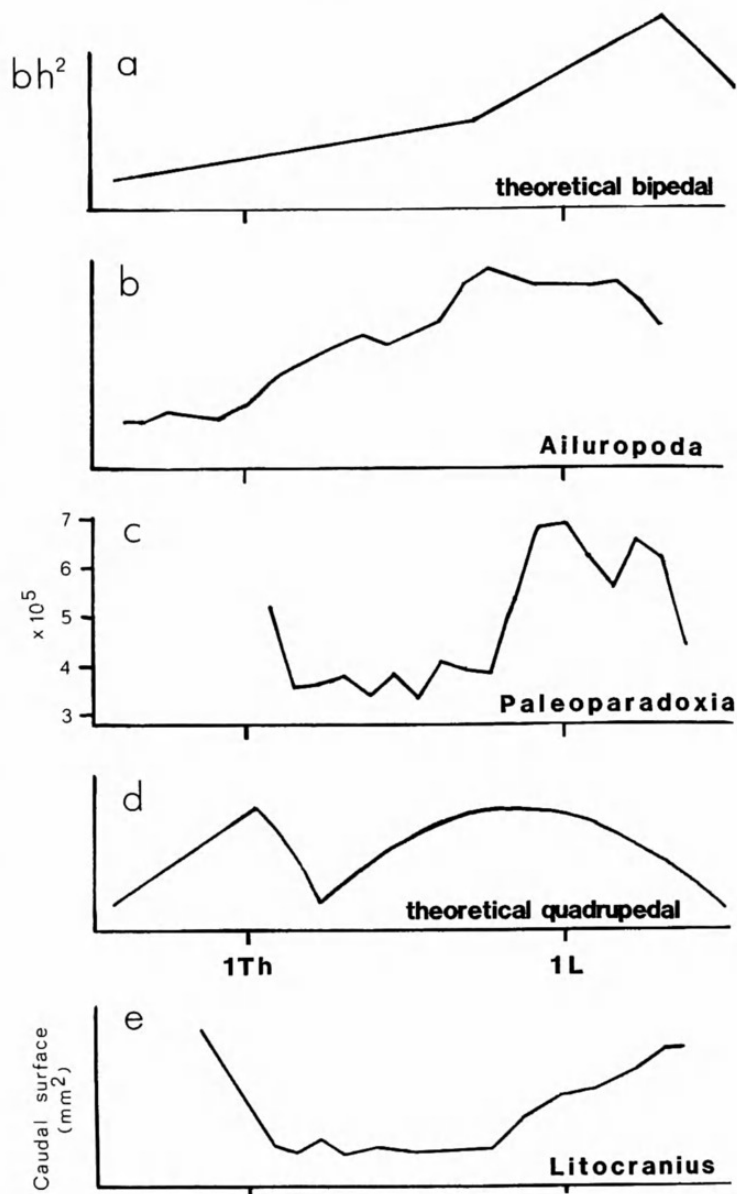


FIGURE 6.—a–d, Graphs of moments of resistance (bh^2 ; b =greatest caudal width of centrum in mm; h =greatest caudal height) against bending of vertebral centra, redrawn after Slijper (1946) and Coombs (1983): a, Slijper's theoretical curve for mammals with erect or semi-erect posture; b, curve for giant panda (*Ailuropoda*); c, curve for *Paleoparadoxia* sp. (Stanford specimen, UCMP 81302); d, Slijper's theoretical curve for quadrupedal mammals. e, Comparable curve for gerenuk (*Litocranius*), from Coombs (1983) after Richter; y-axis=caudal surface of centra, in mm^2 . For all curves, the x axis represents the vertebral series, with 1Th indicating first thoracic and 1L indicating first lumbar vertebra. Where scales are omitted, the y-axis just indicates lesser to greater.

terior thoracic peak. Although this evidence seems to support the concept of desmostylians as quadrupeds with semi-bipedal habits, it cannot be considered conclusive because patterns somewhat resembling that of *Paleoparadoxia* also are seen in *Hippopotamus* and even in horses and cows (Slijper, 1946, table 2). This body of data clearly needs to be analyzed in more detail.

Yet another possible test is to compare the limb and joint proportions of desmostylians with those of other large ungulates

and subungulates, in order to find phenetic resemblances that give clues to locomotor habits. An ongoing study will use multivariate ordination of dissimilarity (M. Cole, unpub. data) to assess patterns of overall similarity among taxa based upon relative joint size and limb shape. The study incorporates numerous osteological measurements from a variety of extinct and living taxa: *Desmostylus*, *Paleoparadoxia*, *Elephas*, *Loxodonta*, *Tapirus*, *Moropus*, *Dicerorhinus*, *Rhinoceros*, *Bos*, *Hippopotamus*, *Choeropsis*, *Eremotherium*, and *Paramylodon*.

Preliminary results of this principal coordinates analysis (M. Cole, pers. comm., 1999) show the two desmostylians linked together, then to the two ground sloths and to the pygmy hippopotamus and hippopotamus. The remaining taxa, in turn, are linked to the two hippos. Although the functional reasons for these linkages have yet to be interpreted, and the possible role of facultative bipedality remains unclear, it is interesting that the closest resemblances of desmostylians are with hippos on the one hand and ground sloths on the other. Although desmostylians have often been compared with hippos, no one has heretofore seen in desmostylians any resemblance to sloths. This independent result tends to corroborate my conclusion based upon the comparisons offered above.

AQUATIC LOCOMOTION.—Although *Paleoparadoxia*, like other desmostylians, seems to have been capable of fully terrestrial locomotion, it displays some features that seem best explained by, or at least consistent with, a partially aquatic mode of life. These include the retracted external nares, raised orbits, peculiar sternum, long, robust olecranon process, and unusual “semi-pronated” position of the manus. The toes are not obviously adapted for digging, so the powerful forelimb must have had other uses. *Toxodon* shows that weight-bearing alone might explain the large olecranon; this and large pectoral muscles also would have been of use in clambering over rocky ground. Nonetheless, the combination of characters cited also makes sense in the context of aquatic locomotion. Nothing in the desmostylian skeleton demands an aquatic interpretation, however, and aquatic habits might not have been postulated were desmostylian remains not found exclusively in marine deposits.

Repenning (in Shikama, 1966:145; Repenning and Packard, 1990, fig. 183) and Shikama (1966:148, fig. 114) visualized *Paleoparadoxia* as swimming with the broad, somewhat paddle-like forefeet while using the hind limbs as rudders. This swimming method (alternate pectoral paddling; Fish, 1996) is essentially the one used by polar bears (*Thalarctos*), which (although they do not possess a greatly enlarged olecranon or enlarged pectoral muscle attachments) have limb proportions similar to those of desmostylians (intermembral index of *Thalarctos*=87), are fully capable of both aquatic and terrestrial locomotion, and nonetheless show no obvious aquatic adaptations in the skeleton. This swimming method is entirely consistent with the comparatively short hind legs and metatarsals and powerfully developed forelimbs of a desmostylian, and it readily explains the features mentioned above. With the elbow strongly abducted, the manus could have been effectively re-

tracted underneath the trunk in a sweeping motion with the palm facing posteromedial, by means of movement at the shoulder permitted by the anteromedial expansion of the humeral head. Large pectoral muscles arising from the broad sternum and inserting on the long deltopectoral crest would have played an important role in this. With the elbow adducted against the ribcage, the manus, held almost parasagittally as in sirenians and other marine mammals, could have been feathered for the recovery stroke. The deeply grooved elbow joint would have resisted dislocation during the power stroke, with the huge olecranon enabling forceful extension of the elbow at the end of the stroke. The large radial styloid process would simultaneously have resisted hyperextension of the wrist. With their dorsoventrally flattened digits, whose lateral processes at the distal ends of the phalanges may have supported webbing (Figure 1e; Repenning and Packard, 1990), both front and hind feet would have been effective paddles.

Shikama (1966) described the desmostylians' probable mode of locomotion when feeding on the seafloor. The procumbent tusks would have been used for uprooting and raking in aquatic vegetation; the hind limbs, with the knees adducted and the soles directed posterolaterad against the substrate, would have driven the animal forward; and the forelimbs would have steadied and helped steer the body. The posterolaterad-directed hind feet might be likened to the anti-recoil spades of a split-trail field artillery carriage. The overall posture would have somewhat resembled that of a bottom-feeding walrus, although the hind limbs would have propelled the animal in a different manner.

Critique of Alternative Reconstructions

INUZUKA'S RECONSTRUCTION.—Inuzuka's “herpetiform mammal” reconstruction has been described several times in both Japanese and English, most recently and succinctly in Inuzuka et al. (1995). He defended his interpretation mainly on the basis of anatomical arguments, although the splayed-limb postmortem position of the Utanobori skeleton was also a factor (possibly the dominant one) in his original formulation of the idea.

Inuzuka postulated a highly unusual, horizontal orientation of the scapula, based only upon its position in the partly disarticulated, fossilized skeleton—a questionable source of information at best, and certainly not decisive. The broad sternum may well have served for the origin of large pectoral muscles, but a herpetiform stance is not needed to explain such muscles, as they also would be important in swimming. As evidence for a laterally extending humerus, he cites the semi-pronated position of the mutually immobile radius and ulna, on the assumption that the front toes would have had to point forward. As noted above, however, this latter constraint is sometimes relaxed—as in *Chalicotherium*—and it then becomes possible to bring the elbow and front feet much closer to the midline than Inuzuka shows.

As for the hind limb, the evidence Inuzuka cited for an abducted femur and strong adductor and quadriceps musculature

is equally consistent with a sloth-like pose, as is the inclination of the calcaneal tuber when the tibial torsion is taken into account. His reconstruction of the entire hind limb, including a digitigrade pes with the toes pointing forward, is basically in agreement with the interpretation presented herein for a semi-bipedal stance, although a normal walking stance would probably involve more extended hip and knee joints and less separation of the hind feet. The pelvis, however, should be more steeply inclined to accommodate a stronger dorsal convexity of the spine than he shows (e.g., Inuzuka, 1984, pl. 11: fig. 2). This also would bring the base of the neck closer to the ground.

In short, no feature of the skeleton demands a herpetiform posture; all features are at least equally explicable in the context of a sloth-like restoration, which has the major advantage for weight-bearing of keeping the feet (especially the front feet) much closer to the midline.

Also relevant to this discussion is *Numidotherium*, possibly the most primitive proboscidean (Court, 1994). Given that proboscideans have been proposed as the sister group of desmostylians (Domning et al., 1986), Court's (1994) conclusion that *Numidotherium* had a semisprawling posture might support Inuzuka's reconstruction. The resemblances between *Numidotherium* and desmostylians are relatively few, however: the femur was habitually abducted, laterally rotated, and posteriorly inclined; the cnemial crest is deflected laterally; the tibial shaft is twisted; and the talocrural joint surface of the tibia faces laterodistad. There are, on the other hand, many points of contrast: in desmostylians the lateral part of the humeral trochlea protrudes more distally; the spiral elbow joint is designed for forceful medial rotation of the humerus, as in most sirenians (cf. Domning, 1978:125–127, fig. 32c), and is dislocated by lateral rotation; the forefeet were evidently digitigrade rather than plantigrade; the head of the femur is nearly spherical and lacks a fovea, and its shaft is not bowed; the femoral condyles are much more nearly equal in size; the femur was habitually held in a more nearly horizontal position; the proximal tibia faced anterolaterad rather than anterad and lacks an interarticular eminence; movements of the talocrural joint do not seem to involve significant inversion/eversion or abduction/adduction; the calcaneal tuber is inclined; and a rugose plantar tubercle is present on the calcaneum, indicating strong plantar ligaments and possibly implying a digitigrade rather than a plantigrade pedal stance.

Numidotherium apparently was specialized in a direction rather different from that of desmostylians, a condition that provides no support for the idea of semisprawling posture in the latter. Furthermore, at least some of the few shared characters may merely reflect a common tethythere heritage, for example, the twisted tibial shaft and inclined talocrural joint surface, as discussed above.

REPENNING'S RECONSTRUCTION.—Repenning's (1965) "frog-like" or "sealion-like" reconstruction also can be reconciled with my own by means of a simple adjustment. Although *Paleoparadoxia* could doubtless have squatted in that position

when at rest, it would not necessarily have been confined to such a posture (with the belly "on or very close to the ground," Repenning and Packard, 1990:202) while moving about on land; again the key feature is the hind foot.

Repenning and Packard (1990) envisioned desmostylian terrestrial locomotion as resembling the "humping" or "hopping" gait of an otarioid pinniped, in which the front feet move in unison followed by the back feet moving in unison. This movement also would involve strong extension and flexion of the spine. They viewed the sole of the hind foot as being nearly vertical and the toes hyperextended against the substrate during this action. They further stated that lifting the body by greater extension of the hind-limb joints (i.e., so that the femur and tibia approached vertical, as in an elephant; C.A. Repenning, pers. comm., 1996) would result in "rotating the foot from a plantar position to one in which the plantar plane was approaching 45° from horizontal; ... concentrating the weight ... on the medial edge of the paddle-like foot, and ... rotating the tibial-astragalar articular surface toward the maximum of 45° from horizontal and toward possible dislocation" (Repenning and Packard, 1990:202–203).

The latter statement concerning ankle dislocation is true if the tibia is visualized in an elephant-like vertical position. There is, however, a less extreme possibility that also permits an alternating terrestrial gait. Repenning and Packard's interpretation overlooks the features of the metatarso-phalangeal joints described above, and the fact that the pes could adopt a digitigrade stance with the axis of the ankle joint level. This stance would allow the body's weight to be stably supported on moderately flexed hip, knee, and ankle joints and with abducted knees as shown in Figure 3. With the hip joint directly above the ankle, the weight would indeed fall on the medial side of the digitigrade foot, but this is just what the foot is built for. The hindquarters could thus have been lifted well off the ground, with the hind feet beneath the hip joint, and an alternating gait could have been used.

Repenning and Packard (1990) correctly noted the vertebral articulations allowing arching of the back, and they stated that the front legs "could be held vertically for support." Apparently, then, they did not regard as obligatory the front-limb posture shown by Repenning (1965), with the dorsum of the manus resting on the ground. In any case, the radial styloid process, although preventing hyperextension, does not prevent full extension of the wrist. Their anatomical interpretation and the present one therefore are essentially compatible, given the reinterpretation of the hind foot outlined above. Their conclusion that "*Paleoparadoxia* was well adapted to swimming and was as poorly adapted to terrestrial locomotion as are modern otarioid pinnipeds" (Repenning and Packard, 1990:203) appears incorrect, however. *Paleoparadoxia* was distinctly less aquatically specialized than otarioids: it swam more on a par with a polar bear, whereas it moved on level ground more like a typical ungulate or other terrestrial mammal than an otarioid, and most like a ground sloth.

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