A paleoecological paradox: the habitat and dietary preferences of the extinct tethythere Desmostylus, inferred from stable isotope analysis

Mark T. Clementz, Kathryn A. Hoppe, and Paul L. Koch

Abstract.—The Desmostylia, an extinct order of mammals related to sirenians and proboscideans, are known from the late Oligocene to late Miocene of the North Pacific. Though often categorized as marine mammals on the basis of fossil occurrences in nearshore deposits, reconstructions of desmostylian habitat and dietary preferences have been somewhat speculative because morphological and sedimentological information is limited. We analyzed the carbon, oxygen, and strontium isotope compositions of enamel from Desmostylus and co-occurring terrestrial and marine taxa from middle Miocene sites in California to address the debate surrounding desmostylian ecology. The δ13C value of tooth enamel can be used as a proxy for diet. Desmostylus had much higher δ13C values than coeval terrestrial or marine mammals, suggesting a unique diet that most likely consisted of aquatic vegetation. Modern aquatic mammals tend to exhibit lower variability in δ18O values than terrestrial mammals. Both fossil marine mammals and Desmostylus exhibited low δ18O variability, suggesting that Desmostylus spent a large amount of time in water. Finally, the Sr isotope composition of marine organisms reflects that of the ocean and is relatively invariant when compared with values for animals from land. Sr isotope values for Desmostylus were similar to those for terrestrial, rather than marine, mammals, suggesting Desmostylus was spending time in estuarine or freshwater environments. Together, isotopic data suggest that Desmostylus was an aquatic herbivore that spent a considerable portion of its life foraging in estuarine and freshwater ecosystems.

Introduction

Mammalian herbivores are a minor component of the total fauna in modern marine and coastal ecosystems, limited to just four sirenian species. Nonetheless, these herbivores are thought to play critical roles in structuring the species richness and productivity of these ecosystems (Bowen 1997; Peterken and Conacher 1997). These effects may have been even greater in the past, when the diversity of large-bodied, mammalian herbivores was higher (Domning and Furusawa 1992; Aranda-Manteca et al. 1994; Domning 2001). Other groups of mammals may have exploited the abundant vegetation in shallow coastal waters that were widespread from the Eocene through the Miocene, such as the Desmostylia, an extinct group of hippo-sized mammals related to sirenians. The coexistence of several species of large-bodied mammalian herbivores in coastal ecosystems has no modern analog, so the dynamics of ancient coastal ecosystems may have been very different from those today.

The feeding ecology and habitat preferences of desmostylians are not well understood, but before we can begin to explore what part, if any, desmostylians played in past coastal ecosystems, we need such basic autecological data. Here, we reconstruct the ecology of one genus, Desmostylus, through stable isotope analysis of tooth enamel. Using carbon isotopes, we assessed feeding preferences, exploring levels of dependence on terrestrial versus aquatic food sources. To assess the adaptation of Desmostylus to aquatic habitats, we used a method that relies on contrasts in oxygen isotope variability between terrestrial and aquatic species. Finally, we explored differences in habitation of marine, estuarine,
and terrestrial systems by identifying differences in strontium isotope composition among taxa.

**Background**

*The Desmostylia.*—Desmostylians are large, hippo-sized mammals known to have inhabited the Pacific coast of North America and Asia from the late Oligocene (~28 Ma) to late middle Miocene (~10 Ma) (Barnes et al. 1985; Inuzuka et al. 1995; Inuzuka 2000). Several characters of the skull suggest that desmostylians share a common ancestry with sireni-ans and proboscideans, which are classified with desmostylians in the mirorder Tethytheria (Domning et al. 1986; Novacek and Wyss 1987) (Fig. 1). The Desmostylia is composed of two families, the Paleoparadoxidae, which possessed low-crowned or bunodont molars, and the Desmostylidae, which had high-crowned or hypsodont molars (Inuzuka et al. 1995; Inuzuka 2000). Both families coexisted along the northern Pacific coast of Asia and North America until the late middle Miocene.

Desmostylian ecology is currently a mystery. Though most desmostylian fossils have been found in nearshore marine deposits, there are occasional reports of desmostylians associated with terrestrial mammals at sites where the depositional environment is unclear. Desmostylian morphology has also generated conflicting ecological interpretations. Early reconstructions portrayed desmostylians with a pinniped-like posture (Fig. 2A), suggesting they were fully aquatic swimmers (Repenning 1965), but recent studies comparing desmostylians with extant aquatic and terrestri-al mammals have challenged this idea. Cole and Domning (1998) argued that desmostylian postcranial elements were more similar to those of modern terrestrial ungulates or extinct ground sloths, and they suggested a mode of locomotion and a lifestyle similar to those of the semiaquatic hippopotamus. A more radical interpretation was suggested by Inuzuka (1984). Unlike other mamm-als, which hold their limbs directly under the body, Inuzuka’s reconstructed desmostylians had a “herpetiform” or sprawling posture similar to lizards, which would have pro-
vided a high degree of stability against lateral forces, such as those produced by waves in nearshore ecosystems. It is unclear which (if any) interpretation is correct.

Most interpretations imply some use of aquatic habitats by desmostylians, but the extent to which they foraged within these ecosystems is uncertain. Cranial and dental morphology, as well as their phylogenetic position, suggests that desmostylians were principally herbivores, though at least one study has proposed that they consumed mollusks (McLeod and Barnes 1984). Their northern geographical distribution and the depositional settings of their occurrences led Domning et al. (1986) to conclude that desmostylians primarily ate marine vegetation (e.g., macroalgae, seagrass) in cold, marginal marine environments. However, if desmostylians were capable of terrestrial locomotion (Cole and Domning 1998), they could have come ashore to feed on terrestrial plants, filling an ecological niche similar to that of the hippopotamus. Thus, even the dietary preferences of this extinct group of mammals are unresolved.

**Carbon Isotopes and Foraging Preferences.** Analysis of carbon isotopes in biogenic substrates (e.g., bone or enamel carbonate, collagen) has proven useful for paleodietary reconstructions (see reviews in Schwarz and Schoeninger 1991; Koch et al. 1995). Tooth enamel carbonate is the preferred substrate for reconstructions more than 100,000 years old because it is less susceptible to diagenetic alteration (Lee-Thorp 2000; Wang and Cerling 1994; Koch et al. 1997). The δ¹³C value of carbonate in tooth enamel apatite is labeled by the δ¹³C of an animal’s diet. For ungulate herbivores, enamel δ¹³C values are controlled by the δ¹³C value of the vegetation the animal consumes with a small physiological fractionation of ~+12–14.1‰ for wild populations (Lee-Thorp et al. 1989; Cerling and Harris 1999).

The δ¹³C values of primary producers at the base of food webs vary as a result of differences in photosynthetic physiology, sources of fixed carbon, and environmental conditions. In terrestrial ecosystems, differences are related to photosynthetic pathway (O’Leary 1988), resulting in relatively high δ¹³C values (~13 ± 2‰) for plants using C4 photosynthesis (e.g., warm-climate grasses), low δ¹³C values (~27 ± 3‰) for C3 photosynthesizers (e.g., trees, most shrubs, herbs, and cool-climate grasses), and δ¹³C values that can be anywhere between these extremes for plants using CAM photosynthesis (e.g., most succulents). In aquatic systems, environmental conditions (dissolved [CO₂], mixing of the water column, nutrient supply, etc.) have a stronger influence on primary-producer δ¹³C values, creating differences in mean δ¹³C values for kelp (~17 ± 4‰), seagrass (~10 ± 3‰), nearshore and offshore marine phytoplankton (~20 ± 2‰, ~23 ± 2‰, respectively), and freshwater vegetation (~26 ± 7‰) (Osmond et al. 1981; Boon and Bunn 1994; Hemminga and Mateo 1996; Rau et al. 2001; Ravens et al. 2002).

Many studies have exploited these differences in primary-producer δ¹³C values to trace the foraging habits of terrestrial and marine consumers (Cerling and Harris 1999; Clementz and Koch 2001) (see Table 1). Within marine habitats, consumer δ¹³C values typically increase toward shore, with the highest δ¹³C values reported for consumers within kelp or seagrass beds. Onshore, consumer δ¹³C values vary among C4 grazers (high δ¹³C), C3 browsers and grazers (low δ¹³C), and freshwater foragers (very low δ¹³C values). Overall, enamel δ¹³C values provide strong evidence about the types of food mammals consume and from which food webs that food came. We used this approach to determine the ecosystems in which Desmostylus foraged.

**Oxygen Isotopes and Aquatic Habitat Use.** The δ¹⁸O value of biogenic apatite in bones and teeth is a function of the δ¹⁸O of body water, plus a temperature-dependent fractionation that is constant in homeothermic mammals (Longinelli 1984; Luz et al. 1984). Unlike carbon in enamel, which has just one source (i.e., diet), body water has multiple sources of oxygen, and both environmental and physiological factors influence its δ¹⁸O value. Physi-
TABLE 1. Mean δ¹³C and δ¹⁸O values for modern taxa collected from central California and Amboseli Park in Kenya. Values are reported ± 1σ.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Feeding zone</th>
<th>% Aquatic</th>
<th>Mean δ¹³C ± 1σ</th>
<th>Mean δ¹⁸O ± 1σ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinnipedia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern elephant seal*</td>
<td>10</td>
<td>Offshore</td>
<td>&gt;50%</td>
<td>-14.1 ± 1.7</td>
<td>26.6 ± 0.4</td>
</tr>
<tr>
<td>California sea lion*</td>
<td>6</td>
<td>Nearshore</td>
<td>&gt;50%</td>
<td>-11.3 ± 1.0</td>
<td>26.1 ± 0.3</td>
</tr>
<tr>
<td>Harbor seal*</td>
<td>11</td>
<td>Nearshore</td>
<td>&gt;50%</td>
<td>-9.2 ± 1.6</td>
<td>26.5 ± 0.3</td>
</tr>
<tr>
<td>Cetacea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pilot whale*</td>
<td>7</td>
<td>Nearshore</td>
<td>100%</td>
<td>-9.7 ± 1.2</td>
<td>28.1 ± 0.2</td>
</tr>
<tr>
<td>Harbor porpoise*</td>
<td>11</td>
<td>Nearshore</td>
<td>100%</td>
<td>-9.9 ± 0.4</td>
<td>28.5 ± 0.2</td>
</tr>
<tr>
<td>Bottlenose dolphin*</td>
<td>9</td>
<td>Nearshore</td>
<td>100%</td>
<td>-10.1 ± 0.6</td>
<td>27.8 ± 0.2</td>
</tr>
<tr>
<td>Sirenidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dugong</td>
<td>12</td>
<td>Nearshore</td>
<td>100%</td>
<td>0.5 ± 1.0</td>
<td>29.3 ± 0.5</td>
</tr>
<tr>
<td>Manatee</td>
<td>17</td>
<td>Rivers/nearshore</td>
<td>100%</td>
<td>-3.3 ± 4.2</td>
<td>29.3 ± 0.8</td>
</tr>
<tr>
<td>Carnivora</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea otter*</td>
<td>5</td>
<td>Kelp bed</td>
<td>&gt;50%</td>
<td>-6.1 ± 0.9</td>
<td>27.3 ± 0.6</td>
</tr>
<tr>
<td>River otter*</td>
<td>10</td>
<td>Estuary</td>
<td>-33%</td>
<td>-8.1 ± 3.0</td>
<td>25.8 ± 0.9</td>
</tr>
<tr>
<td>Coyote*</td>
<td>7</td>
<td>Rivers/lakes</td>
<td>-33%</td>
<td>-173 ± 4.3</td>
<td>23.0 ± 0.3</td>
</tr>
<tr>
<td>Artiodactyla</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-tailed deer*</td>
<td>47</td>
<td>Terrestrial</td>
<td>&lt;5%</td>
<td>-118 ± 1.7</td>
<td>29.8 ± 1.3</td>
</tr>
<tr>
<td>Grant’s gazelle‡</td>
<td>6</td>
<td>Terrestrial</td>
<td>&lt;5%</td>
<td>-9.2 ± 1.4</td>
<td>33.8 ± 1.7</td>
</tr>
<tr>
<td>Common wildebeest‡</td>
<td>8</td>
<td>Terrestrial</td>
<td>&lt;5%</td>
<td>1.1 ± 1.0</td>
<td>32.7 ± 1.9</td>
</tr>
<tr>
<td>Hippopotamus‡</td>
<td>3</td>
<td>Rivers/lakes</td>
<td>&gt;50%</td>
<td>-3.0 ± 0.2</td>
<td>26.0 ± 1.4</td>
</tr>
<tr>
<td>Perissodactyla</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plains zebra‡</td>
<td>7</td>
<td>Terrestrial</td>
<td>&lt;5%</td>
<td>0.1 ± 1.1</td>
<td>31.5 ± 1.9</td>
</tr>
<tr>
<td>Black rhinoceros‡</td>
<td>5</td>
<td>Terrestrial</td>
<td>&lt;5%</td>
<td>-9.3 ± 1.2</td>
<td>29.4 ± 1.5</td>
</tr>
<tr>
<td>Proboscidea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>African elephant‡</td>
<td>13</td>
<td>Terrestrial</td>
<td>5%</td>
<td>-7.7 ± 2.5</td>
<td>29.6 ± 0.6</td>
</tr>
</tbody>
</table>

* Data from Clementz and Koch 2001. All collections are from geographically constrained modern populations, chiefly in central and southern California. Terrestrial plants in this region are dominantly C3. ‡ Data for populations from Amboseli Park, Kenya, discussed in Bocherens et al. 1996. Grasses in Amboseli are C4, whereas nearly all trees, shrubs, and herbs are C3. Grant’s gazelle and rhinoceros are browsers on C3 plants, wildebeest and zebra are grazers on C4 plants, and elephants are mixed feeders.

HABITAT AND DIETARY PREFERENCES OF THE EXTINCT TETHYTHERE DESMOSTYLUS

ology affects body water δ¹⁸O values by controlling the magnitude of oxygen fluxes and isotopic fractionation that occurs as oxygen passes into and out of the body (Luz and Koldy 1985; Bryant and Froelich 1995; Kohn 1996). The δ¹⁸O values of environmental oxygen sources provide the baseline from which mammalian body water δ¹⁸O values can deviate via physiological effects.

The mean δ¹³C value of mammalian tooth enamel has been proposed as a monitor of adaptation to freshwater or marine systems (Bocherens et al. 1996; Roe et al. 1998). However, mean δ¹³C values may not always be diagnostic of habitat preferences (Clementz and Koch 2001), because physiological differences among species also affect mean values. Differences in the population-level standard deviation of enamel δ¹³C values, on the other hand, can allow discrimination of aquatic/semiaquatic from terrestrial species (Table 1). Terrestrial mammals experience greater physiological and environmental variability than aquatic/semiaquatic mammals, resulting in higher variability in their body water and tooth enamel δ¹³C values.

Fully aquatic and semiaquatic species typically yield δ¹³C standard deviations of 0.5% or less, whereas terrestrial mammals typically have values >1% (Table 1). However, there are exceptions to this pattern. For terrestrial mammals, body size and environmental conditions may cause δ¹³C variation of populations to be lower than predicted. Large mammals (>1000 kg) obtain more of their oxygen from drinking water (~60%) than do smaller mammals (~20%) (Bryant and Froelich 1995). If drinking-water sources are isotopically homogeneous, large-mammal δ¹³C values should show less variability among individuals (Amboseli elephants; Table 1). Likewise, for animals living in humid environments with low evaporative water loss, δ¹³C values within a population may be less variable. Among aquatic species, differences in variability can result from δ¹³C variation of oxygen sources, either by movement between waters of different isotopic composition (e.g., marine vs. fresh water—sea otters, estuarine river otters, manatees) or by ingestion of other oxygen sources with distinct δ¹³C values (e.g., terrestrial, ¹³O-enriched plant water—Amboseli hippopotamus). Though these exceptions do generate overlap in 1σ values for aquatic
and terrestrial mammals, only fully aquatic, strictly marine (e.g., most pinnipeds and cetaceans), and semiaquatic mammals that forage aquatically (e.g., river otters) exhibit 1σδ¹⁸O values ≤0.5‰, providing a clear means of differentiating these habitat preferences from fully terrestrial populations. Here, we first test this approach on fossil taxa with known habitat preferences, and then use it to assess the extent of aquatic habitat use by Desmostylus.

Strontium Isotopes and Marine versus Terrestrial Ecosystems.—The ratio of ⁸⁷Sr to ⁸⁶Sr in biogenic materials has proven to be a valuable tool for extracting ecological information from modern and fossil organisms (Koch et al. 1992, 1995; Kennedy et al. 1997; Hoppe et al. 1999; Ingram and Weber 1999). Because strontium is not fractionated measurably when it is incorporated, the ⁸⁷Sr/⁸⁶Sr ratio of biogenic material is identical to that of the source of Sr and is passed up the food web without modification (Capo et al. 1998).

The Sr sources for an organism are the water it drinks or inhabits and the plant or animal food it ingests. On land, the ⁸⁷Sr/⁸⁶Sr ratios of rivers and plants are controlled by rock and soil compositions (Miller et al. 1993). Ratios of terrestrial rocks are highly variable and depend on rock type and age (Capo et al. 1998). River and soil ⁸⁷Sr/⁸⁶Sr ratios are controlled both by bedrock inputs and by atmospheric input of Sr as dust and precipitation (Capo et al. 1994; Kennedy et al. 1998). At coastal sites, precipitation has a ⁸⁷Sr/⁸⁶Sr ratio similar to that of the ocean, and if rainfall is significant, it can dominate the ⁸⁷Sr/⁸⁶Sr ratio of soils (Kennedy et al. 1998); dust inputs, however, can affect regional soil isotope compositions far from dust sources (Muhs et al. 1990).

Today, the ⁸⁷Sr/⁸⁶Sr ratio of seawater is homogeneous globally, because the residence time of oceanic Sr is several million years, orders of magnitude longer than the timescale for oceanic mixing (~1000 years). The ⁸⁷Sr/⁸⁶Sr ratio of seawater is controlled by the magnitude and isotopic ratios of Sr influxes, including weathering of terrestrial rocks and oceanic basalt alteration, and by Sr removal through deposition of marine carbonates. Seawater ⁸⁷Sr/⁸⁶Sr ratios show long timescale fluctuations due to shifts in these fluxes (Armstrong 1971; Capo and DePaolo 1990).

The ⁸⁷Sr/⁸⁶Sr ratio of water in estuaries is controlled by mixing. Freshwater has a much lower [Sr] (0.006–2.94 ppm) than seawater (8.0 ppm) (Capo et al. 1998). Mixing of fresh and marine water produces a correlation of ⁸⁷Sr/⁸⁶Sr ratio with salinity, but differences in [Sr] cause the marine ⁸⁷Sr/⁸⁶Sr signal to dominate (Bryant et al. 1995).

Modern animals foraging in marine systems have ⁸⁷Sr/⁸⁶Sr ratios that closely match those of seawater (Schmitz et al. 1997; Venne mann et al. 2001). Modern land and freshwater animals, in contrast, exhibit a greater range of ratios that depend on the geologically controlled differences at the base of the food web (Nelson et al. 1986; Koch et al. 1995; Ingram and Weber 1999). Animals foraging in estuaries have not received extensive study but would be expected to show a wide range in ⁸⁷Sr/⁸⁶Sr ratios among individuals in a population, depending on the salinity of the water they frequent. Sr isotope ratios will be our primary tool for determining whether Desmostylus inhabited marine, estuarine, or fully terrestrial ecosystems.

Diagenetic Monitoring via Control Taxa.—Prior work has shown that tooth enamel is resistant to diagenetic alteration of stable isotope ratios (Wang and Cerling 1994; Bocherens et al. 1996; Koch et al. 1997). Still, we will use control taxa to test for alteration whenever possible. For example, we expect population-level δ¹⁸O variability to be higher in obviously terrestrial animals (e.g., horses) than in obviously marine mammals (e.g., whales and dolphins). Because diagenetic alteration would tend to homogenize isotopic signals among specimens from a single locality, retention of consistent differences in mean and variability in control taxa provides support for the assumption that isotopic patterns in Desmostylus are preserved as well.

Materials and Methods

Locality and Specimen Information.—Specimens were obtained from five sites in central and southern California (Fig. 3). Four sites were in a restricted, shallow marine basin that
HABITAT AND DIETARY PREFERENCES OF THE EXTINCT TETYHERE DESMOSTYLUS

Figure 3. A, Map of modern-day central California highlighting the location of sampling sites included in this project. B, Central California as it appeared at ~13–16 Ma, during the time that our fossil specimens were deposited (modified from Bartow 1987).

inundated the interior of California during the Miocene; one site was exposed to open-marine conditions. Site 1292 is the famous Shark Tooth Hill deposit within the Round Mountain Silt Formation, which has an extensive accumulation of marine mammals, shark’s teeth, and rare terrestrial mammals deposited during the Barstovian Land Mammal Age (~13.5 to 15.9 Ma) (Barnes 1976). We obtained several Desmostylus molars and teeth from marine mammals, including the early pinniped Allodesmus and small and large odontocetes (toothed whales). At site 2124, Desmostylus teeth and isolated molars from the early horse Merychippus and the proboscidean Gomphotherium were obtained from the Temblor Formation, which is estimated to be coeval with the Shark Tooth Hill deposit. At site V5555, Desmostylus from the Santa Margarita Formation (late Miocene, Clarendonian Age, ~10 Ma) were found in association with marine (e.g., Allodesmus, small odontocetes, sirenians) and terrestrial mammals (e.g., the equid Hipparion). Site V3301 is from a reef bed deposit in the Temblor Formation, which has yielded a large number of Desmostylus molar fragments of Barstovian age, but no control taxa.

Control taxa were also absent at the open-marine site V3215, which was located north of the other sites in the Barstovian-aged Briones Formation.

Sampling Protocol and Analyses.—Stable isotope analysis was conducted on the carbonate within tooth enamel biological apatite. Approximately 5 to 10 mg of powder was drilled from each tooth after the surface had been abraded to remove possible contamination. Following the protocol in Koch et al. (1997), all powders were soaked for 24 hours in ~2% NaOCl to oxidize organic matter, rinsed five times with distilled water, soaked for 24 hours in 1 M calcium acetate-buffered/acetic acid to remove contaminating carbonate in non-lattice sites, rinsed five times with distilled water, and then freeze-dried. Because extended exposure time may alter enamel isotope values, all samples were treated for the same length of time (24 hours) to ensure the comparability of isotope values and reduce the risk of lab-induced variation in isotope values (Koch et al. 1997).

Approximately 1 mg of pretreated powder was analyzed using an Isocarb automated carbonate analysis system interfaced with a Mi-
We assessed the statistical significance of mean values by using a Student’s *t*-test for comparisons between two populations or a parametric, one-factor analysis of variance (ANOVA) for multiple populations. If a significant difference was detected among populations, we applied a pairwise comparison (post-hoc Tukey test) to identify populations that were statistically distinct. To use these tests, however, sample populations must be normally distributed and equivalent in variance. For sample populations that didn’t meet these criteria, we assessed statistically significant differences in median values using a nonparametric Kruskal-Wallis one-factor analysis of variance followed by pairwise comparison using the post-hoc Dunn’s method. We note which method of comparison was used in the “Results” section. For comparisons of variance between populations, a simple *F*-test was used. Spearman’s rank correlation method was used to assess significance of correlation of different isotopic values among samples. Either Sigmastat 2.03 or Microsoft Excel 2000 was used for all calculations.

**Results**

Samples were grouped into three categories for statistical comparisons: unambiguously marine mammals, unambiguously terrestrial mammals, and *Desmostylus*. *Desmostylus* had the highest mean δ¹³C value (±1σ) (−5.2 ± 1.9%), followed by marine mammals (−8.1 ± 1.4%), then terrestrial mammals (−9.5 ± 1.2%) (Table 2, Fig. 4A). Median δ³⁰S values differed significantly among groups (Kruskal-
HABITAT AND DIETARY PREFERENCES OF THE EXTINCT TETHYHERE DESMOSTYLUS

Figure 4. Carbon (a), oxygen (b), and strontium (c) isotope data collected for all taxa. Along the horizontal axis, terrestrial (squares) and marine (triangles) faunas are grouped on either side of the data for Desmostylus (circles) from all five sites. A = Allodesmus; G = Gomphotherium; H = Hipparion; LO = large odontocete; M = Merychippus; SO = small odontocete. Enlarged, closed symbols represent the mean value for each taxon or group, and all other values are plotted as open symbols. Vertical bars represent ±1σ. Estimated range in middle Miocene seawater ⁸⁷Sr/⁸⁶Sr values is based on Hodell et al. 1991.
Wallis: $H = 53.927, p < 0.01$). Pairwise comparisons revealed that *Desmostylus* was significantly different from both marine and terrestrial mammals, but that marine and terrestrial mammals were not different from each other (Dunn’s method). Differences in $\delta^{13}C$ variance among groups were only significant between *Desmostylus* and terrestrial mammals (F-test: $p < 0.01$). Within marine mammals, mean $\delta^{13}C$ values differed significantly between *Allodesmus* and all cetaceans (t-test: $t = 2.413$, d.f. = 20, $p = 0.026$). Mean $\delta^{18}C$ values also differed significantly among terrestrial mammals (one-factor ANOVA: $F = 39.591$, $p < 0.01$); pairwise comparison revealed statistically significant differences among all three groups (Tukey test: $p < 0.01$).

The mean $\delta^{18}O$ value for terrestrial mammals ($28.3 \pm 1.4\%$) was higher than for either marine mammals ($27.6 \pm 0.6\%$) or *Desmostylus* ($27.7 \pm 0.7\%$) (Table 2, Fig. 4B). Median $\delta^{18}O$ values did not differ among the three groups of mammals (Kruskal-Wallis: $H = 3.823$, $p = 0.148$). *Desmostylus* and marine mammals exhibited significant differences in $\delta^{18}O$ variance from terrestrial mammals (F-test: $p < 0.01$), but not between each other (F-test: $p = 0.496$). Within marine mammals, no significant difference was detected between means for *Allodesmus* and all cetaceans (t-test: $t = -1.029$, $p = 0.316$). Mean $\delta^{18}O$ values did differ significantly among terrestrial mammals (one-factor ANOVA: $F = 4.974$, $p = 0.014$); pairwise comparison revealed that only *Merychippus* and *Gomphotherium* were significantly different (Tukey test: $p = 0.031$).

Mean $^{87}Sr/^{86}Sr$ ratios were highest for marine mammals ($0.70854 \pm 0.00014$), intermediate for *Desmostylus* ($0.70826 \pm 0.00048$), and lowest for terrestrial mammals ($0.70783 \pm 0.00067$) (Table 2, Fig. 4C). Median $^{87}Sr/^{86}Sr$ values differed significantly among groups (Kruskal-Wallis: $H = 10.462$, $p < 0.01$), but pairwise comparison showed that only terrestrial and marine mammals were statistically distinct (Dunn’s method: $p < 0.05$). Differences in $^{87}Sr/^{86}Sr$ variance were statistically significant for *Desmostylus* versus marine mammals (F-test: $p < 0.01$) and marine mammals versus terrestrial mammals (F-test: $p < 0.01$), but not for *Desmostylus* versus terrestrial mammals (F-test: $p = 0.237$). Comparison of mean $^{87}Sr/^{86}Sr$ ratios among marine mammals (t-test: $t = 1.358$, $p = 0.202$) and terrestrial mammals (one-factor ANOVA: $F = 0.011$, $p = 0.989$) revealed no statistically significant differences.

*Desmostylus* is the only taxon that occurs at enough sites to warrant examination of geographic differences. Mean $\delta^{13}C$ values were significantly different among sites (one-factor ANOVA: $F = 5.69, p < 0.05$) with the highest values reported at northern sites V3301 and V3215. Mean $\delta^{18}O$ values were, likewise, significantly different among sites (one-factor ANOVA: $F = 7.73, p < 0.05$). Pairwise comparisons revealed that the mean for *Desmostylus* from site 3215 was significantly lower than mean $\delta^{18}O$ values from all other sites except site 2124, and that mean values for sites V5555 and 2124 were significantly different (Tukey test: $p < 0.05$). $\delta^{18}O$ variance at sites 1292 and V5555 were significantly different from variance at sites 2124 and V3301. No statistically significant differences were detected for mean $^{87}Sr/^{86}Sr$ values (Kruskal-Wallis: $H = 5.67, p = 0.129$).

**Discussion**

**How Committed Was Desmostylus to Aquatic Habitats?**—Most ecological interpretations for *Desmostylus* favor a connection with aquatic habitats, but the amount of time that this mammal actually spent in the water remains contested. Possible scenarios include that *Desmostylus* was fully aquatic, *Desmostylus* was semiaquatic and foraged onshore, or *Desmostylus* was semiaquatic and foraged in the water. Our proxy for extent of adaptation to aquatic life is population-level variability in $\delta^{18}O$ values, which we used after validation by analysis of fully aquatic and fully terrestrial fossil taxa.

As expected from studies of modern species, the standard deviation of $\delta^{18}O$ values for fossil fully aquatic mammal populations (of sufficient sample size, i.e., $n \geq 5$) was $\approx 0.5\%$, significantly lower than the values for fossil fully terrestrial mammal populations ($1\sigma \geq 0.8\%$) (Table 2). The $1\sigma$ values for fossil fully aquatic and fully terrestrial mammals were comparable to those for modern mammal
populations (Bocherens et al. 1996; Clementz and Koch 2001). We conclude that diagenetic alteration has not erased the in vivo differencesc in $\delta^{18}O$ values among mammals at these sites. Because Desmostylus has thicker enamel than any of the marine and terrestrial mammals, it is even less likely to be subject to diagenetic homogenization of $\delta^{18}O$ values.

Desmostylus populations had $1\sigma$ values ranging from 0.2‰ to 0.7‰ (Table 2, Fig. 4B). These values are lower than those for any of the fossil terrestrial mammals and for all but one of the modern terrestrial mammals (Table 1). Furthermore, these $1\sigma$ values are significantly lower than values for semiaquatic, terrestrial-foraging hippopotamus from Amboseli (Table 1), suggesting that though desmostylians and hippopotamids were similar in body size and basic morphology, the niches occupied by these taxa were quite distinct. Low $\delta^{18}O$ variability, particularly $1\sigma$ values near 0.2 or 0.3‰, provides strong support for the conclusion that Desmostylus was either a semiaquatic mammal feeding in water, or a fully aquatic mammal.

However, one population (V5555) had a $1\sigma$ value higher than that for modern fully terrestrial Amboseli elephants, which suggests that the low $\delta^{18}O$ variability in Desmostylus may simply be a result of large body size. This hypothesis is unlikely for two reasons. First, Gomphotherium is larger than Desmostylus, yet at the site where these two species co-occur, the difference in $\delta^{18}O$ variation is extreme (Table 2). An additional factor must be generating the low variability in Desmostylus. Furthermore no modern fully terrestrial mammal has yielded $\delta^{18}O$ variability as low as that reported for Desmostylus at the majority of sites. Thus, we stand by the conclusion that Desmostylus was either semiaquatic and feeding in water, or fully aquatic. The slightly higher $1\sigma$ value at site V5555 could therefore imply use of an estuary with significant $\delta^{18}O$ variability.

What Kinds of Aquatic Habitats Did Desmostylus Frequent?—Though the occurrence of Desmostylus remains in nearshore marine deposits suggests an affinity for marine ecosystems, the possibility of transport prior to deposition means that we can't rule out other aquatic environments (i.e., estuarine and freshwater ecosystems) as potential habitats. Patterns in mean and variability in $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ values can be useful for discriminating among these alternatives, even though we were unable to include clear isotopic end-members of freshwater and estuarine fossil aquatic mammals in our study. For $\delta^{18}O$ values, we would expect marine species to have high mean values and low variability, estuarine environments to have lower mean values and higher variability, and freshwater environments to yield the lowest mean values and low variability. For $^{87}Sr/^{86}Sr$ values, we would expect values for marine species to cluster near values calculated for middle Miocene seawater (Fig. 4C), whereas values for freshwater and estuarine species should be more variable.

However, mean $\delta^{18}O$ values in modern ecosystems were not always diagnostic of freshwater, let alone marine or estuarine, habitats (Table 1), and we observed a similar problem for our fossil samples (Table 2, Fig. 4B), which only yielded a 2‰ range in mean values for all taxa. In addition, the mean $\delta^{18}O$ values for marine mammals from our sample sites are higher than expected from estimated middle Miocene seawater $\delta^{18}O$ values (0.5‰ below modern seawater $\delta^{18}O$ (J. Zachos personal communication); Fig. 4B). However, the high $\delta^{18}O$ values we have reported for our marine mammals may reflect the regional hydrologic conditions of the basin in which these animals lived (Fig. 3). The fossils we sampled were all deposited within a restricted basin, which may have experienced significant evaporation and limited exchange with open-ocean waters. If so, $\delta^{18}O$ values for marine waters in this basin may have been enriched relative to mean seawater and could account for the high $\delta^{18}O$ values we have reported.

From the $^{87}Sr/^{86}Sr$ values of the tooth enamel, we were able to detect a clearer separation between terrestrial and marine mammals. Marine taxa had little variation in $^{87}Sr/^{86}Sr$ values ($1\sigma < 0.0002‰$) when compared with terrestrial mammals ($1\sigma > 0.0006‰$) (Table 2, Fig. 4A). As with the $\delta^{18}O$ data, the $^{87}Sr/^{86}Sr$ values we collected for marine mammals are not expected, according to the calculated range in $^{87}Sr/^{86}Sr$ values for seawater at this
time (0.70876 to 0.70877) (Hodell et al. 1991) (Fig. 4C). Again, the hydrology of the basin may explain these low $^{87}$Sr/$^{86}$Sr values. With restricted flow to and from the ocean, terrestrial inputs of $^{87}$Sr/$^{86}$Sr from rivers could have lowered the mean $^{87}$Sr/$^{86}$Sr value of waters within the basin.

Of most significance, however, is the large difference in range of values between terrestrial and marine mammals. Desmostylus $^{87}$Sr/$^{86}$Sr variation is greater than that calculated for any marine taxon and similar to the degree of variation observed for terrestrial taxa (Fig. 4C). High variation in $^{87}$Sr/$^{86}$Sr values would be unlikely if Desmostylus was foraging only within nearshore environments and suggests that it was spending a considerable amount of time in estuarine or freshwater environments.

What Did Desmostylus Eat?—From our previous analyses, we have concluded that Desmostylus was a fully aquatic or semiaquatic forager that was not restricted to marine habitats but foraged also in freshwater and estuarine habitats. Our next step is to identify the food webs within which Desmostylus was feeding—were they nearshore marine, kelp beds, seagrass beds, or freshwater food webs? To explore this question, we used mean $\delta^{13}$C values of tooth enamel as a proxy for dietary preferences, basing our interpretations on values from both modern and fossil taxa (Tables 1, 2, Fig. 4A).

Fossil terrestrial taxa have $\delta^{13}$C values similar to those reported for middle Miocene mammals that fed on C3 vegetation elsewhere in North and South America (MacFadden et al. 1994; MacFadden and Cerling 1996). Our marine species, including the early otariid Alloodesmus and two size classes of odontocetes, have been interpreted as nearshore, marine foragers on the basis of sedimentological and morphological criteria (Barnes 1972; Dupras 1985). As expected, mean $\delta^{13}$C values for these species were substantially more enriched in $^{13}$C than values for modern offshore foragers (Table 1), but they were also slightly more enriched than values for modern nearshore foragers (Table 1). This offset from modern nearshore foragers may reflect ocean $\delta^{13}$C values during the middle Miocene, which were $\sim 1.5\%$ higher than modern seawater values (Zachos et al. 2001). With known marine and terrestrial end-members, we can now determine the food webs contributing carbon to Desmostylus (Fig. 4A).

Mean $\delta^{13}$C values for Desmostylus are significantly higher than would be expected for a terrestrial C3 consumer and confirm that Desmostylus must have been foraging within other food webs (Fig. 4A), a conclusion supported by our $\delta^{18}$O and $^{87}$Sr/$^{86}$Sr evidence. Several aquatic habitats are possible alternatives: marine (nearshore, kelp, seagrass), estuarine (seagrass), and freshwater ecosystems. Isotope analysis of modern marine ecosystems has found that nearshore consumers often have higher $\delta^{13}$C values than consumers limited to terrestrial C3 resources (Hobson 1987; Bearhop et al. 1999). Seagrass, in particular, has $\delta^{13}$C values that are often higher than modern C4 vegetation, with a mean $\delta^{13}$C value of $\sim -11\%$ (Hemminga and Mateo 1996). Another potential resource would be marine algae, which also can have high $\delta^{13}$C values (Raven et al. 2002). In particular, the kelp group of marine algae (Family Laminaria), which is believed to have arisen along the Pacific Coast at this time (Estes and Steinberg 1988), yields mean $\delta^{13}$C values of $\sim -17\%$ (Raven et al. 2002).

Each of these marine resources could produce the high $\delta^{13}$C values observed in Desmostylus, either via direct consumption or indirectly via consumption of other consumers in these food webs. Incorporation of a multi-isotope analysis and inclusion of ecological control taxa limit the possible scenarios (Fig. 4B,C).

First, $\delta^{13}$C values for Desmostylus are typically higher than values reported for nearshore foraging marine mammals, suggesting that Desmostylus was not foraging within this ecosystem. This interpretation is also confirmed by the high $^{87}$Sr/$^{86}$Sr variation reported for Desmostylus, which suggests it was not spending much time in a strictly marine environment (Fig. 4C). The lack of a marine signal in $^{87}$Sr/$^{86}$Sr values for Desmostylus also allows us to exclude kelp beds as a potential dietary resource for Desmostylus, given that kelp is an exclusively marine macrophyte.

Seagrass, on the other hand, grows within
HABITAT AND DIETARY PREFERENCES OF THE EXTINCT TETHYHERE DESMOSTYLIUS

Estuaries and can tolerate low salinity conditions (>20 ppt). Also, seagrasses growing in low-salinity environments often exhibit extremely low δ13C values that are >1σ from the mean (<−11%). In these habitats, Desmostylus could also have foraged on other types of estuarine or marsh vegetation (including some species of macroalgae, such as Ulva), which can exhibit a large range in δ13C values. If Desmostylus was consuming a mixture of freshwater and estuarine vegetation or foraging on other consumers within these food webs, then the δ13C and 87Sr/86Sr values seem more reasonable.

Conclusion

By applying a multi-isotope approach, we have been able to identify significant ecological differences between Desmostylus and both terrestrial and marine mammals in terms of aquatic affinity and dietary preferences, respectively. The high δ13C values suggest that Desmostylus foraged on seagrasses, probably rooting up the vegetation to consume the carbohydrate-enriched rhizomes that would have formed dense mats within the shallow lagoons and estuaries along the Pacific coastline. In addition, Desmostylus was not limited to foraging on seagrasses but likely incorporated a wide range of freshwater and estuarine aquatic vegetation into its diet. In this way, the ecology of Desmostylus was most similar to that of modern manatees in Florida, which seasonally forage on aquatic vegetation in freshwater and marine ecosystems. Unlike manatees, Desmostylus was fully capable of terrestrial locomotion and was probably similar to the modern hippopotamus in terms of aquatic and terrestrial habits.

Thus, desmostylians were a unique group of mammals with no real modern analogs in terms of habitat preferences, diet, or locomotor capabilities. As the largest mammalian consumers of coastal aquatic vegetation at the time, their impact on coastal ecosystems must have been substantial. In addition, because they are believed to be the sister group to proboscideans, their aquatic preferences raise interesting evolutionary questions. Were the aquatic habits of this group characteristic of the basal members of the clade to which both desmostylians and proboscideans belong, or did desmostylians evolve aquatic habits shortly after their divergence? This issue may be addressed by applying similar techniques to samples of early proboscideans and basal tethytheres (e.g., anthracobunids).

Our results highlight the necessity of using multiple proxies to answer questions about the ecology of extinct taxa. If we had limited our interpretations to only one isotopic system, we would have generated substantially different conclusions about the ecology of Desmostylus. In future work, we will incorporate microwear analysis into studies of other desmostylian species to identify differences in foraging preferences among co-occurring taxa, and to develop a method for testing our interpretations of the trophic level of these extinct animals.

Acknowledgments

We would like to thank P. Holroyd at the University of California Museum of Paleontology, L. Barnes at the Natural History Museum of Los Angeles County, and T. Deméré at the San Diego Natural History Museum for providing access to specimens for analysis. A special thank you goes to P. Holden for assisting in analysis of Sr samples and to D. Domning for providing information on desmostylian phylogenetics. M.T.C. was supported by a National Science Foundation (NSF) Predoctoral Fellowship and Achievement Rewards for College Scientists Fellowship when much of this research was conducted. Analytical and travel costs were covered by NSF grants EAR-9725854 and 0087742.

Literature Cited


Barnes, L. G., D. P. Domning, and C. E. Ray. 1985. Status of stud-


HABITAT AND DIETARY PREFERENCES OF THE EXTINCT TETHYHERE DESMOSTYLUS


