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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 $\delta^{13}C$ value of tooth enamel can be used as a proxy for diet. *Desmostylus* had much higher $\delta^{13}C$ 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 $\delta^{18}O$ values than terrestrial mammals. Both fossil marine mammals and *Desmostylus* exhibited low $\delta^{18}O$ 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.

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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,

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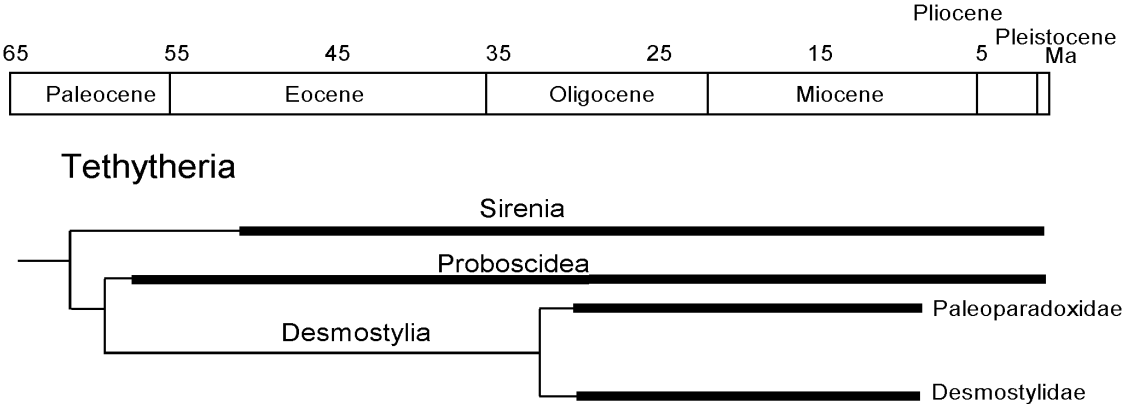

FIGURE 1. Proposed cladogram for the mirorder Tethytheria modified after Inuzuka et al. 1995.

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 sirenians 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.

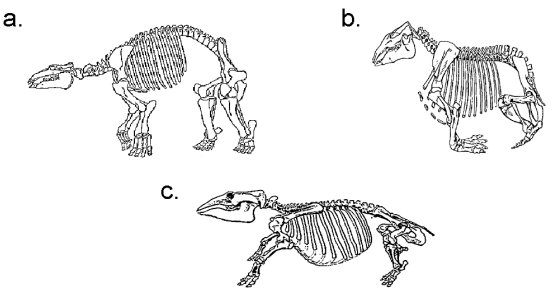

FIGURE 2. Three different skeletal reconstructions of desmostylians based on morphological data and proposed lifestyle. A, Cole and Domning (1998) proposed that *Paleoparadoxia* exhibited a posture and joint mechanics similar to those of extinct ground sloths and the extant hippopotamus. B, Repenning's (1965) reconstruction of *Desmostylus*, with a posture similar to that of modern otariid pinnipeds, was based on interpreting the fore- and hindlimbs as modified into flippers. C, Inuzuka (1984) proposed a completely new style of posture for *Desmostylus*, termed herpetiform, which was thought to enhance stability in high-wave-energy environments.

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 terrestrial mammals have challenged this idea. Cole and Domning (1998) argued that desmostylian postcranial elements were most 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 mammals, which hold their limbs directly under the body, Inuzaka'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 Schwarcz 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 $\delta^{13}C$ value[1] of carbonate in tooth enamel apatite is labeled by the $\delta^{13}C$ of an animal's diet. For ungulate herbivores, enamel $\delta^{13}C$ values are controlled by the $\delta^{13}C$ value of the vegetation the animal consumes with a small physiological fractionation of $\sim+12$–$14.1‰$ for wild populations (Lee-Thorp et al. 1989; Cerling and Harris 1999).

The $\delta^{13}C$ 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 $\delta^{13}C$ values ($-13 \pm 2‰$) for plants using C4 photosynthesis (e.g., warm-climate grasses), low $\delta^{13}C$ values ($-27 \pm 3‰$) for C3 photosynthesizers (e.g., trees, most shrubs, herbs, and cool-climate grasses), and $\delta^{13}C$ values that can be anywhere between these extremes for plants using CAM photosynthesis (e.g., most succulents). In aquatic systems, environmental conditions (dissolved $[CO_2]$, mixing of the water column, nutrient supply, etc.) have a stronger influence on primary-producer $\delta^{13}C$ values, creating differences in mean $\delta^{13}C$ values for kelp ($-17 \pm 4‰$), seagrass ($-10 \pm 3‰$), nearshore and offshore marine phytoplankton ($-20 \pm 2‰$, $-23 \pm 2‰$, respectively), and freshwater vegetation ($-26 \pm 7‰$) (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 $\delta^{13}C$ 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 $\delta^{13}C$ values typically increase toward shore, with the highest $\delta^{13}C$ values reported for consumers within kelp or seagrass beds. Onshore, consumer $\delta^{13}C$ values vary among C4 grazers (high $\delta^{13}C$), C3 browsers and grazers (low $\delta^{13}C$), and freshwater foragers (very low $\delta^{13}C$ values). Overall, enamel $\delta^{13}C$ 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 $\delta^{18}O$ value of biogenic apatite in bones and teeth is a function of the $\delta^{18}O$ 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 $\delta^{18}O$ value. Physi-

[1] $\delta^{13}C = [(^{13}C/^{12}C_{sample} \div {}^{13}C/^{12}C_{standard}) - 1) * 1000]$, where the standard is V−PDB. $\delta^{18}O$ follows the same conventions, where the ratios are $^{18}O/^{16}O$ and the standard is V−SMOW. Units are parts per thousand (‰).

TABLE 1. Mean $\delta^{13}C$ and $\delta^{18}O$ values for modern taxa collected from central California and Amboseli Park in Kenya. Values are reported $\pm$ 1σ.

	Taxon	*n*	Feeding zone	% Aquatic	Mean $\delta^{13}C \pm 1\sigma$	Mean $\delta^{18}O \pm 1\sigma$
Pinnipedia	Northern elephant seal*	10	Offshore	>50%	−14.1 ± 1.7	26.6 ± 0.4
	California sea lion*	6	Nearshore	>50%	−11.3 ± 1.0	26.1 ± 0.3
	Harbor seal*	11	Nearshore	>50%	−9.2 ± 1.6	26.5 ± 0.3
Cetacea	Pilot whale*	7	Nearshore	100%	−9.7 ± 1.2	28.1 ± 0.2
	Harbor porpoise*	11	Nearshore	100%	−9.9 ± 0.4	28.5 ± 0.2
	Bottlenose dolphin*	9	Nearshore	100%	−10.1 ± 0.6	27.8 ± 0.2
Sirenia	Dugong	12	Nearshore	100%	0.5 ± 1.0	29.3 ± 0.5
	Manatee	17	Rivers/nearshore	100%	−3.3 ± 4.2	29.3 ± 0.8
Carnivora	Sea otter*	5	Kelp bed	>50%	−6.1 ± 0.9	27.3 ± 0.6
	River otter*	10	Estuary	~33%	−8.1 ± 3.0	25.8 ± 0.9
	River otter*	7	Rivers/lakes	~33%	−17.3 ± 4.3	23.0 ± 0.3
	Coyote*	5	Terrestrial	<5%	−10.4± 3.4	27.4 ± 3.4
Artiodactyla	Black-tailed deer*	47	Terrestrial	<5%	−11.8 ± 1.7	29.8 ± 1.3
	Grant's gazelle‡	6	Terrestrial	<5%	−9.2 ± 1.4	33.8 ± 1.7
	Common wildebeest‡	8	Terrestrial	<5%	1.1 ± 1.0	32.7 ± 1.9
	Hippopotamus‡	3	Rivers/lakes	>50%	−3.0 ± 0.2	26.0 ± 1.4
Perissodactyla	Plains zebra‡	7	Terrestrial	<5%	−0.1 ± 1.1	31.5 ± 1.9
	Black rhinoceros‡	5	Terrestrial	<5%	−9.3 ± 1.2	29.4 ± 1.5
Proboscidea	African elephant‡	13	Terrestrial	5%	−7.7 ± 2.5	29.6 ± 0.6

* 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.

ology affects body water $\delta^{18}O$ values by controlling the magnitude of oxygen fluxes and isotopic fractionation that occurs as oxygen passes into and out of the body (Luz and Kolodny 1985; Bryant and Froelich 1995; Kohn 1996). The $\delta^{18}O$ values of environmental oxygen sources provide the baseline from which mammalian body water $\delta^{18}O$ values can deviate via physiological effects.

The mean $\delta^{18}O$ 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 $\delta^{18}O$ 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 $\delta^{18}O$ 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 $\delta^{18}O$ values.

Fully aquatic and semiaquatic species typically yield $\delta^{18}O$ 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 $\delta^{18}O$ 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 $\delta^{18}O$ values should show less variability among individuals (Amboseli elephants; Table 1). Likewise, for animals living in humid environments with low evaporative water loss, $\delta^{18}O$ values within a population may be less variable. Among aquatic species, differences in variability can result from $\delta^{18}O$ 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 $\delta^{18}O$ values (e.g., terrestrial, ^{18}O-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 1σ $\delta^{18}O$ values $\leq 0.5‰$, 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 ^{87}Sr to ^{86}Sr 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 $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ ratio similar to that of the ocean, and if rainfall is significant, it can dominate the $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ ratios show long timescale fluctuations due to shifts in these fluxes (Armstrong 1971; Capo and DePaolo 1990).

The $^{87}Sr/^{86}Sr$ 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 $^{87}Sr/^{86}Sr$ ratio with salinity, but differences in [Sr] cause the marine $^{87}Sr/^{86}Sr$ signal to dominate (Bryant et al. 1995).

Modern animals foraging in marine systems have $^{87}Sr/^{86}Sr$ ratios that closely match those of seawater (Schmitz et al. 1997; Vennemann 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 $^{87}Sr/^{86}Sr$ 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 $\delta^{18}O$ 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

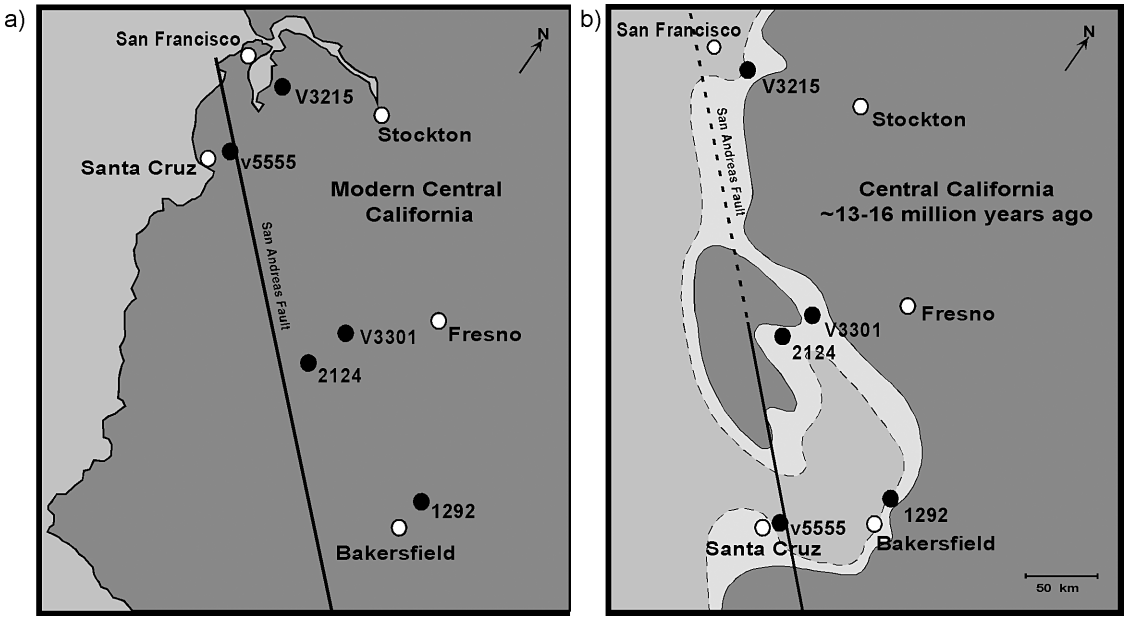

FIGURE 3. A, Map of modern-day central California highlighting the location of sampling sites included in this project. B, Central California as it appeared at ~13–16 Ma, during the time that our fossil specimens were deposited (modified from Bartow 1987).

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-

TABLE 2. Mean $\delta^{13}C$ and $\delta^{18}O$, and Sr isotope values for taxa from each site. All values are reported ± 1σ.

Locality	Taxon	*n*	Mean $\delta^{13}C \pm 1\sigma$	Mean $\delta^{18}O \pm 1\sigma$	Mean $^{87}Sr/^{86}Sr \pm 1\sigma$
1292	*Desmostylus*	6 (3)	−5.6 ± 1.6	27.8 ± 0.5	0.70850 ± 0.00044
1292	*Allodesmus*	7 (5)	−9.5 ± 0.8	27.1 ± 0.5	0.70861 ± 0.00004
1292	Odontocete, large	4 (4)	−7.4 ± 1.9	28.2 ± 0.3	0.70857 ± 0.00015
1292	Odontocete, small	6 (2)	−7.7 ± 0.3	27.5 ± 0.4	0.70833
2124	*Desmostylus*	5 (4)	−7.0 ± 2.5	27.2 ± 0.2	0.70781 ± 0.00070
2124	*Gomphotherium*	10 (4)	−9.6 ± 0.6	27.6 ± 0.8	0.70763 ± 0.00077
2124	*Merychippus*	15 (4)	−8.7 ± 0.7	29.0 ± 1.5	0.70781 ± 0.00077
V5555	*Desmostylus*	21 (6)	−5.5 ± 1.5	28.1 ± 0.7	0.70850 ± 0.00022
V5555	*Hipparion*	5 (5)	−11.5 ± 0.3	27.4 ± 1.2	0.70789 ± 0.00058
V5555	*Allodesmus*	3 (2)	−7.1 ± 1.1	28.1 ± 0.8	0.70853
V5555	Odontocete, small	2 (0)	−8.0 ± 1.0	27.5 ± 0.1	N/A
V3301	*Desmostylus*	8 (4)	−3.5 ± 1.0	27.6 ± 0.2	0.70808 ± 0.00051
V3215	*Desmostylus*	4 (0)	−3.0 ± 0.2	26.5 ± 0.3	N/A

cromass Optima gas source mass spectrometer in the Deptartments of Earth and Ocean Sciences, University of California, Santa Cruz. Samples were dissolved in 100% phosphoric acid at 90°C, with concurrent cryogenic trapping of CO_2 and H_2O. The CO_2 was then admitted to the mass spectrometer for analysis. The standards used in this study were Carrera Marble and NBS 19 and values are reported relative to V-PDB (for carbon) and V-SMOW (for oxygen). Precision, determined by repeated concurrent analysis ($n = 19$) of a modern elephant enamel standard, was 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{18}O$.

For $^{87}Sr/^{86}Sr$ analysis, ~1 mg of powder was collected from each sample, soaked in 0.5 ml of 1 N acetic acid for 20 minutes, rinsed in distilled water, and then repeated four more times. Samples were then dissolved overnight in 2.5 N HCl, dried down, redissolved in 0.5 ml of 2.5 N HCl, and injected onto a column filled with a cation exchange resin to isolate Sr. After washing with 20 ml of 2.5 N HCl, an additional 7 ml of 2.5 N HCl was passed through the column and collected for analysis. Samples were dried down overnight then dissolved in 1 μl of 10% nitric acid and placed on rhenium filaments. To conduct the isotope analyses we used the VG 354 Thermal Ionization Mass Spectrometer located in the Deptartment of Earth Sciences at the University of California, Santa Cruz. Precision, determined by repeated measurement of the NBS 987 Sr standard, was ± 0.00003.

Data Analysis.—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 $\delta^{13}C$ value ($\pm 1\sigma$) (−5.2 ± 1.9‰), followed by marine mammals (−8.1 ± 1.4‰), then terrestrial mammals (−9.5 ± 1.2‰) (Table 2, Fig. 4A). Median $\delta^{13}C$ values differed significantly among groups (Kruskal-

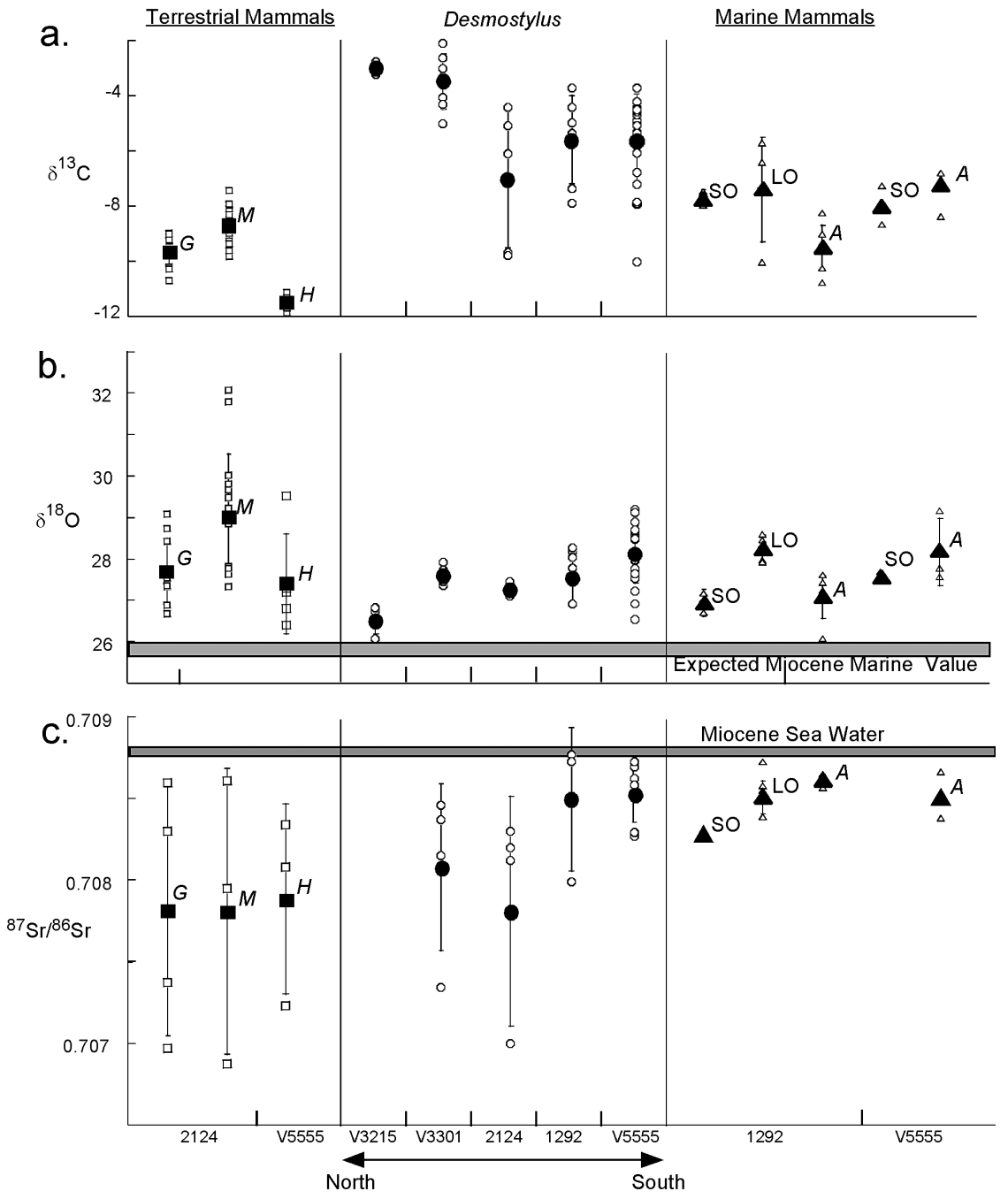

FIGURE 4. Carbon (a), oxygen (b), and strontium (c) isotope data collected for all taxa. Along the horizontal axis, terrestrial (squares) and marine (triangles) faunas are grouped on either side of the data for *Desmostylus* (circles) from all five sites. A = *Allodesmus*; G = *Gomphotherium*; H = *Hipparion*; 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 $^{87}Sr/^{86}Sr$ 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 $\delta^{13}C$ 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 ± 1.4‰) was higher than for either marine mammals (27.6 ± 0.6‰) or *Desmostylus* (27.7 ± 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 ± 0.00014), intermediate for *Desmostylus* (0.70826 ± 0.00048), and lowest for terrestrial mammals (0.70783 ± 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: $F = 6.09$, $p < 0.05$) 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 ≤0.5‰, significantly lower than the values for fossil fully terrestrial mammal populations ($1\sigma \geq 0.8$‰) (Table 2). The 1σ 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 differences 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 1σ 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 1σ 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 1σ 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 1σ 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 1σ 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 endmembers 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 *Allodesmus* 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 ~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 ~−11‰ (Hemminga and Mateo 1996). Another potential resource would be marine algae, which also can have high $\delta^{13}C$ values (Ravens 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 ~−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

estuaries and can tolerate low salinity conditions (>20 ppt). Also, seagrasses growing in low-salinity environments often exhibit extremely low $\delta^{13}C$ 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 $\delta^{13}C$ values. If *Desmostylus* was consuming a mixture of freshwater and estuarine vegetation or foraging on other consumers within these food webs, then the $\delta^{13}C$ and $^{87}Sr/^{86}Sr$ 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 $\delta^{13}C$ 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.

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