

Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean

D.P. Domning*

Laboratory of Evolutionary Biology, Department of Anatomy, Howard University, Washington, DC 20059, USA

Received 19 May 1999; accepted for publication 20 January 2000

Abstract

The Western Atlantic–Caribbean region preserves the longest (some 50 million years) and most diverse fossil record of the mammalian order Sirenia in the world. Sirenians are aquatic herbivores; in marine waters, they eat mainly seagrasses (Hydrocharitaceae and Potamogetonaceae). Though the fossil record of seagrasses and other marine macrophytes is meager, we can use it together with that of sirenians to frame interesting hypotheses about marine plant evolution, and speculate about the nature and dynamics of the Caribbean seagrass ecosystem during the ages when (unlike today) it was dominated by diverse large mammalian herbivores. In this synthesis, I define the aquatic megaherbivore adaptive zone, and identify those of its ecological dimensions that are likely to have been most critical in feeding-niche partitioning among fossil sirenians. Possible morphological indicators of such partitioning are specified for each of these dimensions, using data on functional anatomy and ecology of living sirenians. Faunal lists of Caribbean sirenians (including unpublished taxonomic and morphological data) show what suites of species have occurred sympatrically at different times during the Cenozoic. Based on cranial morphology, I suggest how these herbivores most probably partitioned their resources. This makes it possible to follow the history of individual feeding niches within the sirenian guild through geological time, and, in turn, to speculatively reconstruct gross aspects of Caribbean seagrass communities and their changes through time. Eocene Caribbean sirenian faunas included prorastomids, protosirenids, and early dugongids. These were diverse in both locomotor and feeding adaptations, ranging from amphibious to fully aquatic forms and from selective browsers to incipiently indiscriminate grazers. Eocene Caribbean seagrass communities were already essentially modern in aspect, but included a greater diversity of species with mid-sized to large rhizomes. Oligocene faunas comprised as many as six apparently sympatric species. These included only dugongids, but were differentiated into halitheriines (generalized feeders on seagrass leaves and smaller rhizomes, or specialists on leaves) and dugongines (specialists on larger rhizomes). Miocene faunas of marine sirenians continued the Oligocene pattern. In freshwater habitats of South America, trichechids appeared in the record and adapted to an increase in abundance of fibrous, abrasive aquatic grasses (Gramineae). Pliocene marine sirenian faunas in the Caribbean consist only of dugongine dugongids, plus a trichechid species which evidently extended its range to North America. The dugongines most specialized for eating large rhizomes apparently died out during this epoch. Pleistocene and Recent faunas comprise only trichechids (manatees). Large-tusked dugongines probably acted as “keystone species”, disrupting climax seagrass communities and thereby increasing their productivity and diversity (including sirenian diversity). Under these conditions (which prevailed up to about 2–3 Ma), most primary productivity was presumably consumed by herbivores, in contrast to the detritus-based seagrass ecosystems of today, which include few if any large herbivores. Pliocene oceanographic changes following closure of the Central American Seaway probably led to the collapse of this diverse system, causing extinction of several large, “climax” seagrass species and producing

* Fax: +1-202-265-7055.

E-mail address: ddomning@fac.howard.edu (D.P. Domning).

the florally and faunally depauperate seagrass communities of the present-day Caribbean. The resulting “vacuum” in marine sirenian niches may have enabled manatees to spread from South America into the Caribbean and North America, as well as West Africa. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Angiosperms; Caribbean region; Cenozoic; Marine environment; Paleocology; Sirenia

1. Introduction

The mammalian order Sirenia comprises the only herbivorous marine mammals living today, and most of those that have existed in the past. Although sirenians are thought to have arisen in the Old World together with the closely related orders Proboscidea, Desmostylia, Embrithopoda, and Hyracoidea, they seem to have spread quickly to the New World end of the Tethys Seaway, where their actual fossil record begins in the late Early Eocene of Jamaica. They have inhabited the Caribbean-western Atlantic region continuously throughout the subsequent 50 million years, and all four sirenian families (Prorastomidae, Protosirenidae, Dugongidae, and Trichechidae) are recognized in deposits of this region. Indeed, in no other part of the world are sirenians known in every epoch from Eocene to Recent.

Sirenians as a group are one of the less diverse mammalian orders, but fossil sirenian diversity, in the Caribbean as elsewhere, is far from being fully sampled. In the past decade or two, new genera or species have been discovered almost every year, and several remain undescribed at this writing. However, the overall phylogenetic framework of the order is fairly well understood (Domning, 1994b), and the time is ripe to begin a discussion of the role that sirenians have played in the Cenozoic ecosystems of the Caribbean. Given that for most of the last 50 Ma, the region has been inhabited by sizable populations of these large herbivores (with body masses ranging from under 100 kg to more than 1000 kg), and with three or more sympatric species often present at any one time, this role cannot have been negligible.

2. Caribbean–West Atlantic sirenians and their fossil record

The following synopsis of known sirenian diver-

sity in the West Atlantic–Caribbean region shows that this region has always been important in sirenian history, and implies a corresponding importance of sirenians to the paleoecology of these waters. Except where otherwise noted, all of these species are endemic to the region, and the dugongine adaptive radiation in particular seems to have had the Caribbean as its center of origin. This synopsis draws on both published and unpublished material under study; hence some of the taxonomy used below is still tentative.

2.1. Eocene

Late Early Eocene, Jamaica (Stettin Member, Chapelton Formation): *Prorastomus sirenoides* Owen, the earliest and most primitive sirenian known (Savage et al., 1994).

(*Florentinoameghinia mystica* Simpson, 1932a from the Early Eocene of Patagonia, referred to the Sirenia by Sereno (1982), is here considered *Mammalia incertae sedis*.)

Late Early or early Middle Eocene, Jamaica (Guys Hill Member, Chapelton Formation): two new genera and species of Prorastomidae (Domning et al., 1995, 1996).

Middle Eocene, Florida and North Carolina (Avon Park, Inglis, and Castle Hayne formations): sirenians reported by Domning et al. (1982); these now seem to include cf. *Protosiren* sp., a new genus and species of protosirenid, and probably a primitive dugongid as well. A prorastomid also occurs in the Inglis Formation in Florida (Savage et al., 1994).

Late Eocene, Florida (Crystal River Formation): A prorastomid, perhaps the same one noted in the Inglis Formation (Savage et al., 1994).

Unidentified Middle and Late Eocene sirenians are also known from Mexico (Chiapas), Texas, Alabama, Georgia, and South Carolina (Domning et al., 1982).

2.2. Oligocene

Early or Middle Oligocene, Mississippi, Alabama, Florida, and North Carolina (Vicksburg, Byram, Bucatunna, Suwannee, and River Bend formations): one or more unidentified dugongids (Whetstone and Martin, 1979, and unpublished records).

Early to Late Oligocene, Puerto Rico (Juana Díaz and San Sebastián formations): two halitheriine dugongids, ?*Halitherium antillense* Matthew (1916) and *Caribosiren turneri* Reinhart (1959). MacPhee and Wyss (1990) regard ?*H. antillense* as Early Oligocene in a two-fold division of the Oligocene, and regard *Caribosiren* as “probably latest Oligocene in age.”

Late Oligocene (and/or earliest Miocene), Mississippi, Alabama, Florida, South Carolina, and North Carolina (Chickasawhay, Parachucla, Ashley, Chandler Bridge, and Belgrade formations): two to four probable halitheriines (*Halitherium alleni* Simpson, 1932b; possibly *Caribosiren* sp., *Metaxytherium* sp. (which may or may not be synonymous with *H. alleni*), and a new genus and species, all unpublished), and at least two dugongines (*Crenatosiren olseni* (Reinhart) and *Dioplotherium manigaulti* Cope; see Domning, 1989a, 1997a). Since the *Corystosiren-Rytiodus* clade is the sister group of the clade containing *Dioplotherium* (Domning, 1994b, 1997a) and is thus of equal antiquity, a representative of the former could have been present also; a primitive *Corystosiren* from the South Carolina phosphate beds (listed below under Early or Middle Miocene) may alternatively have come from Late Oligocene deposits.

Indeterminate Oligocene sirenian fossils have also been found in Mississippi (Arata and Jackson, 1965), Cuba (Trelles-Duelo, 1936), and Jamaica (Domning, 1999). *Lophiodolodus chaparralensis* Stirton (1947) from Colombia, referred to the Sirenia by McKenna (1956), is here considered *Mammalia incertae sedis*, possibly Sirenia.

2.3. Miocene

Early Miocene, Brazil (Pirabas Formation): two dugongines (*Dioplotherium*, cf. *D. allisoni*; cf. *Rytiodus*) and a halitheriine (cf. *Metaxytherium*) (de Toledo and Domning, 1991). *Sirenotherium pirabense* de Paula Couto (1967) is a *nomen dubium*.

Early and Middle Miocene, Cuba, Puerto Rico,

Florida, Georgia, South Carolina, North Carolina, Virginia, Maryland, and New Jersey (Guines, Cibao, Torrey, Hawthorn, Statenville, Edisto, Pungo River, Calvert, and Kirkwood formations): *Metaxytherium crataegense* Simpson (1932b) (= *M. calvertense* Kellogg, 1966; = *M. riveroi* Varona, 1972); *Dioplotherium*, cf. *D. allisoni*; an unnamed primitive species of *Corystosiren*; one or two unnamed small dugongids, probably dugongines. The Puerto Rican “*Metaxytherium*, cf. *M. calvertense*” of MacPhee and Wyss (1990) may instead be a dugongine, but cannot yet be associated with one of the established taxa.

Middle Miocene, Colombia (Honda Group): *Potamosiren magdalenensis* Reinhart (= “*Metaxytherium ortegense* Kellogg), the earliest and most primitive known trichechine trichechid or true manatee (Domning, 1997b).

Middle Miocene, Argentina (Parana Formation): cf. *Dioplotherium* Reinhart, 1976 (“*Metaxytherium* sp. indet.”).

Middle and Late Miocene, Florida (lower Bone Valley and Hawthorn formations): *Metaxytherium floridanum* Hay (see Domning, 1988).

2.4. Pliocene

Late Miocene or Early Pliocene, Yucatan (Carrillo Puerto Formation): the large-tusked dugongines *Xenosiren yucateca* and *Corystosiren varguezi* (Domning, 1989b, 1990).

Late Miocene or Early Pliocene, Argentina (“Mesopotamian” beds): the trichechine *Ribodon limbatus*. A single specimen referred to *Ribodon* sp. by Domning (1982), and possibly of correlative age, is known from North Carolina (formation undetermined).

Early Pliocene, Florida (upper Bone Valley Formation): *Corystosiren varguezi* (Domning, 1990), together with an undescribed genus and species of small dugongine.

Late Pliocene, Florida (Caloosahatchee Formation): an undescribed new genus and species of dugongine close to the living Indopacific *Dugong*. This is the latest dugongid known in the West Atlantic–Caribbean region.

2.5. Pleistocene

Early Pleistocene, Florida (Bermont Formation): *Trichechus manatus* from the Leisey Shell Pits (late

early Irvingtonian, 1.5–1.1 Ma; probably less than 1.3 Ma) (Hulbert and Morgan, 1989; Morgan and Hulbert, 1995). This is the earliest in situ trichechid occurrence in North America.

Late Pleistocene, Jamaica, Louisiana, Arkansas, Florida, South Carolina, North Carolina, Maryland, and New Jersey (Falmouth, Canepatch and undetermined formations; many from riverbed or beach localities with mixed faunas): *Trichechus manatus* Linnaeus. Late Rancholabrean (ca. 120,000–125,000 BP) manatees from the southeastern United States represent an unnamed subspecies of *T. manatus* (Domning, 1982 and in preparation).

2.6. Recent

The New World today is inhabited by two species of sirenians: the Amazonian manatee (*Trichechus inunguis* (Natterer)) in the Amazon basin, and the West Indian manatee (*T. manatus*) in coastal waters and rivers from the southeastern United States to southern Brazil. These two species are distributed parapatrically, with contact at the mouths of the Amazon River (Domning, 1981a). (A third manatee species, *T. senegalensis* Link, occurs in West Africa.) The Florida manatee is recognized as a subspecies (*T. m. latirostris* (Harlan)) distinct from the Antillean manatee (*T. m. manatus* Linnaeus), which occupies the species' range from Mexico and Cuba southward and displays considerable genetic diversity (Domning and Hayek, 1986; Garcia-Rodriguez et al., 1998).

3. Caribbean seagrasses and their fossil record

Seagrasses are a polyphyletic group of marine angiosperms belonging to the families Hydrocharitaceae and Potamogetonaceae. Like sirenians, they are species-poor, being represented today by only a dozen genera and about 50 species in the entire world. Nearly all of them inhabit shallow, sheltered, tropical and subtropical marine waters. They are mostly small plants, consisting of shoots and leaves that extend above the sea floor, and systems of roots and rhizomes (underground stems) that are buried in the substrate. The rhizomes store nutrients in the form of carbohydrates, and typically comprise half or more of the plant biomass in a seagrass bed. For this reason, the rhizomes tend to assume special importance in the

diets of any sirenians that can excavate and consume them (e.g. Packard, 1984; Erftemeijer et al., 1993).

As summarized by den Hartog (1970); Phillips and Meñez (1988), and Larkum and den Hartog (1989), the fossil record of seagrasses extends back to the late Cretaceous, but is very sparse. Interestingly, the fossil record they do have does not suggest a greater taxonomic diversity in the past: all of the Eocene and later fossils are referred to extant genera, and in many cases to living species. Whether this usage is taxonomically correct is not important for the present purpose; but it does testify to the fact that the gross forms and growth habits that characterized seagrasses throughout the evolutionary history of sirenians did not differ noticeably from those observed in seagrasses today.

The only reported occurrence of fossil seagrasses in the Caribbean region is in the late Middle Eocene Avon Park Formation of northern Florida (Lumbert et al., 1984; Ivany et al., 1990). This occurrence is most fortunate in that it nearly coincides in time and space with the earliest sirenian records (late Early and early Middle Eocene of the Caribbean), and establishes that seagrass habitats of modern aspect already existed close to the beginning of recorded sirenian history. In fact, fossil sirenians are directly associated with the seagrasses in the Avon Park Formation (Domning et al., 1982; Ivany et al., 1990).

The fossils from the Avon Park Formation demonstrate that Eocene seagrass communities in the region were much like those of the present-day Caribbean, except that they were more diverse. In addition to specimens referred to the modern genera *Thalassia* and possibly *Halodule*, this Eocene deposit has yielded (indeed, is dominated by) representatives of *Cymodocea* and *Thalassodendron*, genera which today occur only in the Old World. It is unknown at what time these latter taxa went extinct in the Caribbean; but, as recognized by Ivany et al. (1990) and as argued below, this could have occurred during the Pliocene, as a result of changing circulation patterns and cooling associated with closure of the Central American Seaway and/or onset of Plio-Pleistocene glaciation.

Possibly other Old World seagrasses such as *Posidonia* and *Enhalus* also occurred in the Caribbean before the Pliocene, though this is not documented. Den Hartog (1970, p. 29) considered it biogeographically problematic that *Enhalus*, *Cymodocea*, and

Thalassodendron are absent from the Caribbean today, and suggested that “The rather specialized *Enhalus* is probably one of the last evolved genera and for this reason may never have reached the Caribbean.” Since then, however, most of the problem has been solved by the discovery of *Cymodocea* and *Thalassodendron* in the Eocene of Florida (cf. Larkum and den Hartog, 1989), and fossil *Enhalus* may yet turn up in the New World as well. At any rate, it is premature to draw biogeographic conclusions from the supposed phylogeny of seagrasses when no rigorous phylogenetic analysis of these plants has yet been presented.

Caribbean seagrasses today comprise only four genera and six species: *Halophila engelmanni*, *Halophila decipiens*, *Halophila baillonis*, *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum* (den Hartog, 1970; Phillips and Meñez, 1988). “*Thalassia* dominates in terms of biomass and standing crop” (Thayer et al., 1984, p. 364).

For present purposes it will be useful to classify these plants into three size categories according to the maximum diameters of their rhizomes: “small”, with rhizomes less than 2 mm thick (*Halophila*, *Halodule*); “medium”, with rhizomes 2–3 mm thick (*Syringodium*, *Cymodocea*); and “large”, with rhizomes attaining thicknesses of 3–10 mm (*Thalassia*, *Thalassodendron*, *Posidonia*). At least one seagrass, *Enhalus*, would fall into a “very large” category with rhizomes up to 15 mm in diameter.

Although the dimensions of these rhizomes may seem unimpressive, it is in fact quite difficult to dig out the larger, typically more fibrous and more deeply buried ones — for example, rhizomes of *Thalassia* growing on a sand bottom. For this task, bare human hands (or the lips and vibrissae of a sirenian) are ill suited; use of a shovel or knife (or tusk) is advisable. Depending on bottom type and density of the rhizome mat, even *Halodule* rhizomes can require considerable force to extract (Anderson, 1998, p. 410).

The seagrass communities of today are notable for the low level of herbivory that generally takes place in them. Seagrasses are fed upon mainly by sea urchins, fish, waterfowl, sea turtles, and sirenians (Thayer et al., 1984; for a more comprehensive list see McRoy and Helfferich, 1980; Table 1). Nonetheless, most of the primary production of modern seagrass ecosystems ends up as detritus (McRoy and Helfferich,

1980; Klumpp et al., 1989). “The great bulk of material present in any seagrass meadow, in any single seagrass plant, at any time is destined for detritus” (McRoy and Helfferich, 1980, p. 310). “In coastal marine ecology, one elusive question continues to be why there are such relatively few grazers on the abundant and extensive seagrass meadows, especially on a global basis. These meadows would seem to be a vastly underutilized resource. This review supports earlier conclusions that only a small portion of the energy and nutrients in seagrasses is usually channeled through herbivores. In the Caribbean, which is noted for a relatively high number of seagrass herbivores, only 5–10% of the productivity of *Thalassia testudinum* is consumed by herbivores near the island of St. Croix” (Thayer et al., 1984, p. 352, 370).

It is therefore plausible that empty niche space for large herbivores exists in these communities today. I will argue that this niche space was occupied by a diversity of sirenians until quite recently in geological time.

4. Concepts and criteria for interpretation of sirenian paleoecology

In order to interpret with any confidence the feeding ecology of fossil sirenians, we must first outline the parameters of what may be called the aquatic mega-herbivore adaptive zone. This can be defined as the set of ecological niches for large animals (1–10 m long, with body masses from tens to thousands of kilograms) that live (or at least feed) entirely in water and eat plants (macrophytes). Such an adaptive zone is an ecological hyperspace defined by many physical, chemical, and biological dimensions: spatial location, climate, seasonality, water depth, salinity, turbidity, nutrient levels, taxonomic composition and diversity of potential food, et cetera.

Not all of these parameters, however, will necessarily be relevant to resource partitioning among any given set of sympatric species in a guild of potential competitors. In the special case of tropical marine habitats, the number of important variables is more manageable than may at first appear; many variables, in fact, are relatively constant and need not be considered. The analysis is also simplified by the fact that virtually all the sirenians we will consider are basically alike in gross structure and in most biological

parameters. Domning's (1977) ecological model of North Pacific sirenian evolution was explicitly based on such generalizations, in the form of postulates which included the following: Sirenians are, with few exceptions:

- (1) shallow-water, near-shore animals;
- (2) tropical or subtropical;
- (3) moderately vagile; and
- (4) opportunistic feeders that prefer angiosperms.
- (5) Seagrasses are likewise shallow-water, nearshore plants typically preferring protected tropical waters.

These postulates are equally valid in the Caribbean context, as will be elaborated on below.

This analysis also assumes that sirenian populations are food-limited, and that competition for food is therefore important in structuring sirenian communities. Direct tests of these assumptions are not possible under the present conditions of human-reduced sirenian population sizes.

Since the growth of marine angiosperms is sharply restricted by both light penetration and hydrostatic pressure, the habitats we need to consider are confined to shallow water and therefore to near-shore areas. Tropical marine plant communities include both algae and seagrasses, which (as noted above) are fed upon by several kinds of animals (Thayer et al., 1984). However, for the present purpose much of this diversity can also be ignored, and we can model the community as though it consisted simply of seagrasses and sirenians. Although green turtles (*Chelonia mydas*) are major consumers of seagrass leaves, they do not disturb the rhizomes, and they also eat large amounts of algae, in contrast to sirenians; they also use a much wider range of habitats (Heinsohn et al., 1977; McRoy and Helfferich, 1980; Thayer et al., 1984; Lanyon et al., 1989). Hence it is doubtful whether they would compete significantly with sirenians under the present conditions of reduced sirenian diversity, even if the numbers of both turtles and sirenians were not reduced by human-caused mortality (though in the more crowded megaherbivore guilds of the past, the chelonian presence may have been of greater consequence). Neither are any other tropical marine animals known to eat significant amounts of seagrass rhizomes; and since most of

the primary production of modern seagrass beds ends up as detritus, it would seem that consumption of the leaves is quantitatively insignificant also.

Sirenians, for their part, are almost exclusively consumers of angiosperms (Heinsohn et al., 1977; Hartman, 1979; Best, 1981; Marsh et al., 1982; Erftemeijer et al., 1993). They tend to avoid algae (Provanca and Hall, 1991; Preen, 1995a), eating them in significant amounts only when angiosperms are scarce — e.g. after storms (Spain and Heinsohn, 1973), in winter at the margins of their range (Lewis et al., 1984), or in the North Pacific range of the extinct Steller's sea cow (*Hydrodamalis*; Domning, 1978a) — and so far as is known, this has always been true. Sirenians also eat animals on occasion (Powell, 1978; Anderson, 1989; Preen, 1995a), but mainly on the subtropical and climatically stressful margins of their range, and never, so far as is known, as a major part of the diet. We therefore seem justified in regarding tropical marine sirenians, past and present: (1) as obligate seagrass consumers for all practical purposes; (2) as the only potential consumers of seagrass rhizomes; and (3) probably as the most important consumers of seagrass leaves. These conclusions apply in particular to the Dugongidae, which during the Holocene, and apparently throughout their history, have been exclusively marine and (except for hydrodamalines) tropical. Manatees are likewise tropical, and at least some species (including *Trichechus manatus*) pass easily and regularly between salt and fresh water; however, they cannot survive indefinitely in salt water without access to fresh water sources (Ortiz et al., 1998).

Thus we may, at least as a first approximation, focus on the seagrass–sirenian system in isolation, and consider the ways in which different sirenians might compete for seagrass resources. Unfortunately we cannot observe such competition in today's world, where no two sirenian species are sympatric (the closest approach to sympatry is the parapatric occurrence of Amazonian and West Indian manatees near the mouths of the Amazon River; Domning, 1981a). Therefore the conclusions of this study will constitute only hypotheses for which further tests must be sought.

In hypothesizing the feeding niches of extinct species, it should be remembered that competition

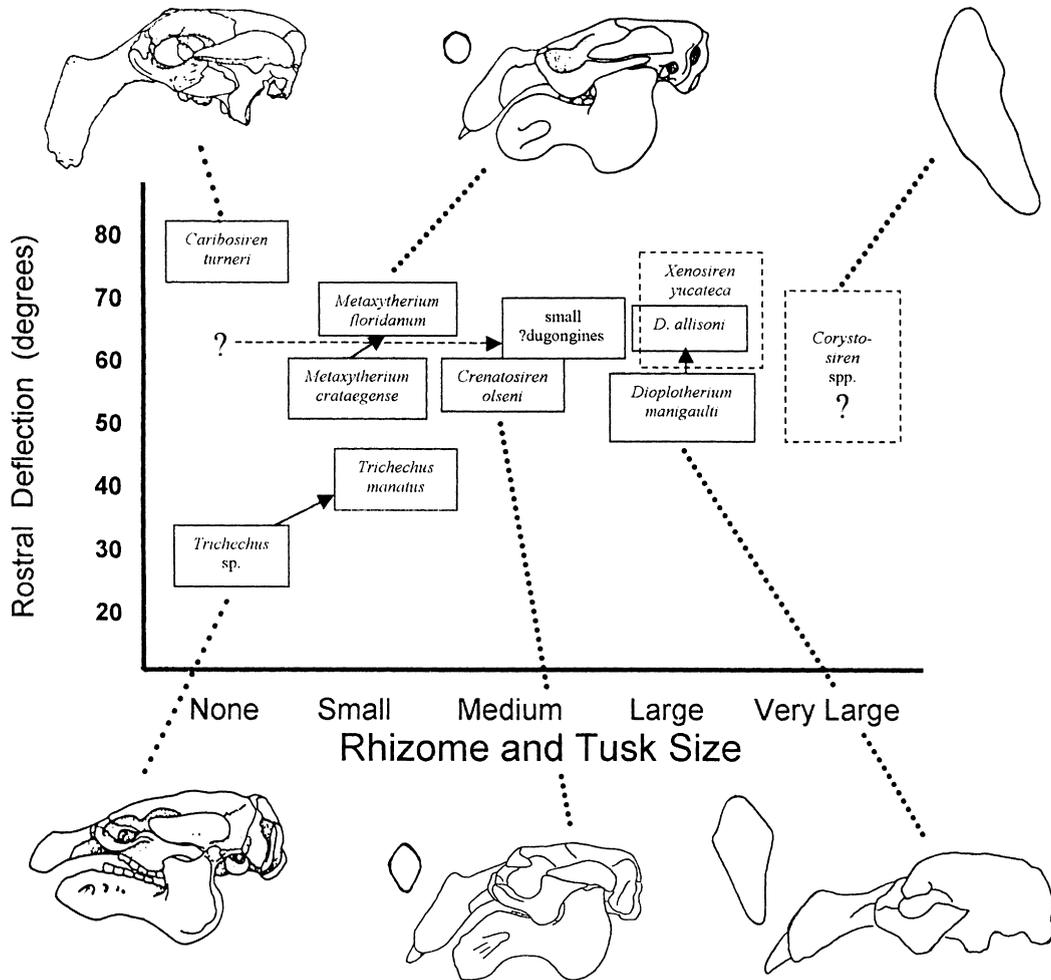
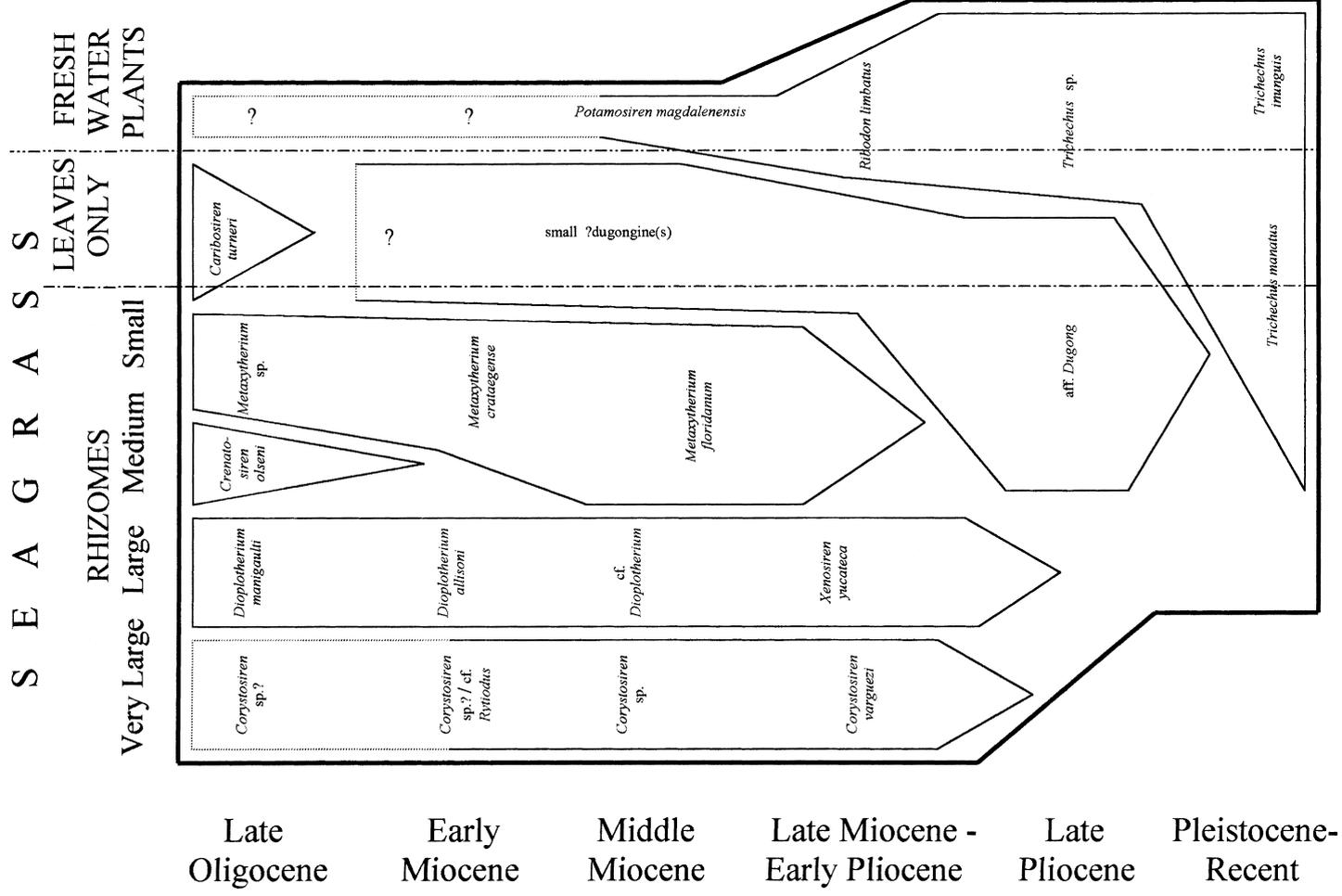


Fig. 1. Diagram representing the feeding niches of Caribbean sirenians in two dimensions, as represented by two ecomorphological features: rostral deflection and tusk size. The latter is assumed to correspond approximately to the size of seagrass rhizomes specialized upon (variable 3A), as in Fig. 2; paleoecological interpretation of rostral deflection is more complex, as explained in the text (variable 2). Boxes symbolize the two-dimensional feeding niche spaces occupied by the taxa. The “small ?dugongines” category includes the Late Pliocene aff. *Dugong*. Dashed borders of boxes denote uncertainty concerning rostral deflection. Arrows denote evolutionary trajectories; the initial rostral deflection and therefore the evolutionary trajectory of the “small ?dugongines” lineage is uncertain, as is its phyletic connection with Late Pliocene aff. *Dugong*. *Xenosiren* is considered a descendant of *Dioplotherium allisoni* (arrow denoting descent omitted). All *Trichechus* are tuskless; their evolutionary trajectory indicates shift of *T. manatus* to a diet including small and medium seagrass rhizomes. Geological time can be thought of as an axis perpendicular to the page; apparently overlapping boxes and evolutionary trajectories are actually separated along the time axis, as shown in Fig. 2, and thus do not imply simultaneous occupation of the same niche space. Five taxa (identified by dotted lines) are illustrated by left lateral views of skulls (not drawn to the same scale). Shapes shown just above the rostra of the three tusked forms are cross-sections of their tusks, enlarged relative to the skulls but drawn to a common scale. For *Corystosiren*, only the cross-section of the tusk is shown.

may be more severe during some years, or some seasons of the year, than others. Discussions of competition in this paper are meant to pertain to the circumstances, seasonal or otherwise, in which competition, and consequently selection for niche-

partitioning strategies, are most severe. Therefore, specifications of feeding niches (such as by the polygons in Figs. 1 and 2) are intended only to suggest the narrow zones in which each taxon could best have held its own in competition with others, and not to



indicate the full widths of these niches. Related to this is the idea that morphology of the feeding apparatus likely “will [not] usually reflect the average food of an animal; especially demanding constituents will probably have a disproportionate influence” (Fortelius, 1990, p. 216).

The ecological dimensions most obviously relevant in this simplified, tropical aquatic megaherbivore adaptive zone would seem to include the following:

1. *Habitat/salinity*: “where on the Earth” a sirenian species lives — in salt, brackish, and/or fresh water. Niche partitioning in this dimension might involve physiological adaptations for maintaining water balance (stenohaly, euryhaly).

A. Significant correlates of this parameter are *diversity of flora* and diversity of herbivores, both of which are inversely proportional to salinity: contrast, for example, the mere 50-odd species of marine angiosperms with the far greater diversity of freshwater species. Aquatic floras in general are species-poor relative to terrestrial ones. Niche partitioning here might involve morphological adaptations for greater or lesser selectivity of feeding: in terrestrial ungulates, narrow muzzles are correlated with selective browsing, wider muzzles with nonselective grazing (Janis and Ehrhardt, 1988).

2. *Location of food plants in the water column*:

“where (vertically) within its habitat” a species feeds. Domning (1977) stated the following postulates in addition to the five listed above:

- (6) Efficient forward locomotion while feeding requires a sirenian’s body to remain relatively horizontal (see also Domning, 1980, 1982; Domning and de Buffrénil, 1991); hence
- (7) specialization on plants of a particular growth habit can be achieved most economically by altering the position of the mouth opening while keeping the body axis horizontal, so
- (8) the degree of rostral deflection should be correlated with degree of specialization for bottom-feeding. (Extreme bottom-feeders such as *Dugong* have rostra deflected 65–75° from the palatal plane, and this causes the mouth to open straight downward when the horizontal semi-circular canals of the ear are in the horizontal plane; Fenart, 1963.) In the light of postulates 4 (sirenians prefer angiosperms but are opportunistic) and 7 (different growth habits call for different placements of the mouth), it follows that
- (9) plants of different growth habit offer sympatric sirenian species a resource-partitioning strategy that they can be expected to use; and postulates 8 and 9 together lead to the prediction that sympatric species should exhibit different rostral deflections.

Fig. 2. Diagram representing a model of the evolution of sirenian feeding niches in western Atlantic and Caribbean waters from the Late Oligocene to the present. The height of the large polygonal area (heavy outline) at any point represents the total aquatic angiosperm biomass available to sirenians at a given time; the portion of that height below or above the upper dashed horizontal line represents the proportion of that biomass made up of marine or freshwater angiosperms, respectively. The marine plants (seagrasses) are divided by rhizome size into small (*Halophila*, *Halodule*), medium (*Syringodium*, *Cymodocea*), large (*Thalassia*, *Thalassodendron*), and very large (e.g. *Enhalus*) categories; the presence of *Enhalus* or other very large forms is hypothetical. The freshwater plant biomass is assumed to have increased after the Middle Miocene due to the Andean orogeny in South America (Domning, 1982). *Cymodocea*, *Thalassodendron*, and any “very large” seagrasses that were present are hypothesized to have persisted in the Caribbean until the mid-Pliocene closure of the Central American Seaway; seagrass diversity and biomass are assumed to have diminished thereafter. Polygons inside the heavy border suggest “exclusive” feeding-niche spaces of sirenian lineages (i.e. the food categories in which each taxon was most competitive). However, any species capable of exploiting medium, large, or very large rhizomes could also have taken rhizomes of any smaller category, and all species could have eaten leaves of all seagrasses; these areas of niche overlap are not shown. In the Early Miocene, *Corystosiren* sp. and cf. *Rytiodus* are inferred to have been ecological vicars in North and South America, respectively. Portions of the lineage polygons enclosed by dotted lines denote an absence of fossil record. The exact phyletic and geographic origins of the “small ?dugongine(s)” are uncertain. Pointed terminations of these polygons represent extinction events. Note the vacated niche space in the large-rhizome category at the lower right corner of the diagram. This model is a crude first approximation, based mostly on a single niche dimension, plant form (variable 3A in text), and to a lesser degree on salinity (variable 1). Use of additional dimensions such as water depth (variable 2B) or location of food items as shown by rostral deflection (variable 2) would improve the ecological separation of some lineages (cf. Fig. 1).

These postulates, however, need to be supplemented by two related considerations:

A. *The extent to which sub-bottom food items are ingested*, especially the more resistant seagrass rhizomes. As explained below, the horizontal-body constraint (postulate 7) is relaxed when a sirenian has to stay in one spot to dig food out of the substrate, rather than simply grazing seagrass blades (and shallow, readily-uprooted rhizomes) off the surface of the sea floor while maintaining forward momentum. To the extent that such stationary digging is the rule in a species' feeding behavior, selection for strong rostral deflection should be relaxed or even reversed.

B. *The water depth* in which (bottom-) feeding occurs. For example, at least the modern sirenians have a minimum limit to their depth tolerance: unless food is scarce they prefer to avoid feeding in water depths much less than 1 m, especially in areas distant from (hence without ready access to) deeper water (Anderson and Birtles, 1978; Anderson, 1979, 1982; Hartman, 1979). Deeper water in such cases provides a refuge from stranding by falling tide, and possibly from terrestrial predators. On the other hand, frequent diving much below 10 m, where mammalian lungs begin to collapse, would push the envelope of sirenians' anatomical and physiological performance. Approaches to this limit might involve (among other changes) a reduction in skeletal ballast, as in the possible case of *Dugong dugon* (Domning and de Buffrénil, 1991).

3. *Mechanical properties of food plants*: "what the animal must do to ingest and masticate the plant." This can be broken down into several categories of properties, such as:

A. *Form of the plant, including robustness and accessibility of the desirable parts*. In the case of seagrasses, this would apply especially to size and depth of the rhizomes. Efficient harvest of thicker, more deeply buried rhizomes might require more specialized structures (e.g. larger, sharper tusks; skulls constructed to cope with greater and differently oriented stresses; adaptations of the soft parts of the feeding apparatus). As noted under variable 2A above, a greater proportion of resistant rhizomes in the diet might also be reflected in reduced snout deflection.

B. *Abrasiveness of the plant*; increased, for example, by siliceous phytoliths. These are lacking in seagrasses but present in true grasses (Gramineae). Where present, they typically necessitate dental adaptations to resist tooth wear, such as hypsodonty, complication of crown pattern, and/or (in manatees) horizontally replaced supernumerary teeth (Domning, 1982; Domning and Hayek, 1984). Abrasiveness of diet can also be increased to varying degrees by grit that is ingested along with the food; for example, quartz sand is more abrasive than coral sand, and may account for the extreme tooth wear observed in Florida manatees (Domning, 1982).

C. *Toughness of the plant*, or "chewiness": this is a function of fiber content, and is distinct from abrasiveness in its demands on the masticatory apparatus (Domning and Hayek, 1984). Lack of fibrousness in its algal diet may have allowed *Hydrodamalis* to dispense with teeth entirely (Domning, 1978a). Toughness also has implications for digestion as well as ingestion: in general, larger herbivores can digest tougher material (see below).

5. Application of concepts to morphological features of Caribbean Sirenia

With the above in mind as dimensional axes along which the sirenians of the Caribbean Tertiary might have partitioned their food resources, we can ask: What morphological indicators seen specifically in Caribbean sirenians might allow us to detect such partitioning?

Variable 1 (salinity) is of limited relevance, since most Caribbean sirenians are found in marine deposits and represent a marine group (Dugongidae). However, in addition to the euryhaline trichechids, the more or less amphibious prorastomids (and possibly protosirenids and early dugongids as well) are likely to have exploited at least some freshwater resources. This would help account for whatever species diversity we find in Eocene sirenian faunas (and perhaps even early Oligocene ones; see Domning et al., 1994, p. 106), as well as in late Tertiary faunas that include trichechids.

An important morphological indicator of diet in these early forms is *width of the rostrum and*

(especially) of the mandibular symphysis. These structures are narrow in prorastomids and early dugongids, and suggest selective feeding habits. This in turn suggests feeding to a large extent in fresh water, since very diverse plants mixed together in a small area characterize freshwater aquatic floras. In contrast, marine seagrass beds tend to be much more nearly homogeneous, and thus more suited to broad symphyses and less discriminate grazing (variable 1A). *Trichechus* spp. have broader mandibular symphyses than prorastomids or early dugongids and are generalized feeders, but have a high degree of prehensile ability thanks to their lips and vibrissae (Marshall et al., 1998). Sirenians with still broader cropping structures (both bony and soft-tissue), such as *Dugong*, “are generally prevented from feeding selectively at the individual plant level by their wide muzzles” (Preen, 1995b, p. 201). “Dugongs, although also [having] prehensile [lips], do not appear to have as high a degree of tactile discriminatory abilities as do manatees” (Marshall, 1997). Such differences in soft-part adaptations may have had a role in niche specialization even among later sirenians, but unfortunately are difficult or impossible to infer from fossils (cf. variable 3A).

Domning (1977) postulated that the *degree of rostral deflection* in a sirenian is directly correlated with its degree of specialization for bottom-feeding, and that sympatric sirenian species should tend to specialize on plants located at different levels in the water column (variable 2). Measurement of rostral deflection did, in fact, suffice to account for both niche partitioning in extinct North Pacific dugongids and feeding ecology of extant manatees (Domning, 1977, 1978a, 1982). In both these cases, the relevant food plants were distributed throughout the water column, making feasible the partitioning of resources along this axis.

In the case of sirenians inhabiting tropical marine waters, however, food resources are and presumably have always been more uniform: namely seagrasses, which grow only on the bottom, mostly in depths less than 10–15 m (though some species are found down to 90 m in clear water), and mostly rising less (usually much less) than 1 m above the bottom. Such plants apparently constituted the diets of all the salt-water sirenians that lived in the Caribbean region; this, at least, is the conservative assumption in the absence of

evidence that any of them had radically different diets. Thus I would predict that location of food in the water column might not suffice to distinguish the feeding niches of all sirenians that fed exclusively in Caribbean marine waters, since all of them are presumed to have been more or less “bottom-feeders”; and, as predicted, all of them do in fact display relatively strong snout deflections (50° or more; Fig. 1).

Hence characteristics of seagrasses other than their gross growth habits must also have played a part in sirenian niche partitioning. A possible alternative strategy for partitioning seagrass resources is by water depth (variable 2B). No Caribbean sirenian is yet known to display *reduction in skeletal mass* such as might, in theory, be correlated with habitual diving below 10 m. However, evidence from bryozoans and corals has been used to suggest that pre-Pliocene Caribbean seagrass beds may have been more abundant at depths of 20–30 m than they are today (Cheetham and Jackson, 1996; Budd et al., 1996), so such adaptations on the part of sirenians would not be unexpected.

Adaptations in the opposite direction are also possible: some undescribed Caribbean sirenians have the smallest estimated adult *body sizes* of any sirenians (total lengths as little as 2 m or possibly even less). One possible advantage of such small size is shallow draft: given that modern sirenians tend to avoid depths less than 1 m, small body size might raise a sirenian’s tolerance for shallow water (by reducing its chances of stranding) and give it access to shallow-water seagrasses that larger species hesitate to exploit.

Another obvious basis for resource partitioning is the relative size and robustness of different seagrasses, especially their nutritious rhizomes (variable 3A); and, as noted above, these can be divided into at least four size categories. I have suggested that the *size and morphology of sirenian tusks* indicate degrees of specialization for excavating these rhizomes, with the largest, most bladelike, self-sharpening tusks being adapted to harvesting the largest and toughest rhizomes (Domning, 1989a–c, 1994a; Fig. 1). Of course tusks can have other uses as well, particularly in Recent *Dugong dugon* where they are sexually dimorphic, used in social interactions, and have no apparent role in feeding (e.g. Preen, 1989; Domning, unpublished data). However, no other known sirenians

have sexually dimorphic tusks; and since tusks are, after all, teeth, whose original uses are in feeding, I regard any social role of sirenian tusks as secondary, and regard their exclusively social role in *Dugong* as exceptional.

A high proportion of large rhizomes in the diet might also have the paradoxical effect of *decreasing rostral deflection* (variables 2A and 3A). We can infer this from variations in the behavior of *Dugong dugon*, which mostly graze on seagrass leaves and small, non-resistant rhizomes and do not use their tusks in feeding (Marsh et al., 1982; Domning, unpublished data). When dugongs merely crop leaves, they can easily maintain forward momentum while feeding (Anderson, 1986). When they feed instead (as they more typically do) on both leaves and rhizomes of small seagrasses like *Halophila* and *Halodule*, they likewise maintain headway, keeping the body relatively horizontal, and make 1–3 linear feeding trails, each several meters long, on each dive (Heinsohn et al., 1977; Anderson and Birtles, 1978; Preen, 1995b; De Iongh et al., 1995, 1997; Anderson, 1998). Their strong rostral deflection (about 70°) seems adapted to these modes of feeding. However, the more resistance they encounter and the more digging they have to do, the shorter their feeding trails become: Anderson and Birtles (1978) reported that trail length was inversely proportional to density of the seagrass bed. In the extreme and atypical case, when dugongs feed on plants or invertebrates that are very resistant to excavation, they must remain in one spot during each dive, and hence make a pit rather than a linear trail. On such occasions the body is not kept horizontal; rather, it assumes a high angle to the bottom, and in shallow water the tail may even break the surface (Anderson, 1989, 1998).

We may conjecture that if this latter (pit-making) mode of feeding were to predominate in a sirenian species, its rostral deflection might be reduced from the extreme otherwise expected in a specialized bottom-feeder. In other words, we might expect to find that species which to a significant extent feed below the bottom (on resistant, deeply buried rhizomes) paradoxically have lesser rostral deflections than ones feeding mainly on or just above the bottom (on seagrass leaves). This conjecture is supported by the moderate rostral deflections of at least some large-tusked dugongines such as *Dioplotherium manigaulti* (50–55°; Domning,

1989a), *D. allisoni* (63°; de Toledo and Domning, 1991), and *Bharatisiren kachchensis* (30–40°; Bajpai and Domning, 1997), in contrast to deflections of 70° or more in some other dugongids (such as *Dugong* and *Caribosiren*). Another example is the aberrant large-tusked sirenian *Miosiren kocki* (41°), which was very likely molluscivorous (Sickenberg, 1934, p. 339) and therefore would have employed a pit-making mode of feeding if it fed on infaunal prey. Note that this argument only applies to tusked forms, because tusks would be involved only in feeding on the bottom; moderate snout deflection in sirenians lacking tusks (e.g. manatees, hydrodamalines) would presumably indicate a less than purely benthic diet, as previously proposed (variable 2; postulate 8).

To carry still further this conjecture about the pit-making mode of feeding, adaptations which increased the efficiency of rhizome harvesting (such as improvements in tusk design) would presumably allow an animal to maintain more headway while feeding and thus a more horizontal attitude; this should lead to an increase in rostral deflection. Such a scenario would account for the increase in deflection observed between *Dioplotherium manigaulti* and *D. allisoni* (Fig. 1), which coincides with the evolution of self-sharpening tusks in this lineage. A more perplexing feature of *D. allisoni* is a mandibular deflection some 15–20° greater than the rostral deflection (de Toledo and Domning, 1991). This built-in anterior gape may possibly be related to the mode of severing rhizomes suggested by Domning (1989b) for *Xenosiren*: with the mouth open, the front of the mandible was placed against the substrate, and the jaw-closing muscles (especially the masseter) were used to pull the tusks down and back through the substrate and against the buried rhizomes. Unfortunately, however, the mandible is not yet known for *Xenosiren* or for any of the other fossil taxa mentioned in the previous paragraph, so this idea cannot yet be tested by further comparisons.

Variable 3B (abrasiveness of food) is less promising for niche partitioning. There is no fossil evidence that Caribbean sirenians differed in degree of resistance to dental wear, except for manatees, which arrived late in marine waters after apparently evolving their horizontal tooth replacement in fresh water. The abrasiveness of ingested grit might be relevant, but more as a component of geographic (allopatric or

parapatric) separation based on bottom type than of sympatric partitioning of resources: siliciclastic substrates predominate in some parts of the Caribbean, carbonate sediments in other parts.

Processing of fibrous plant material once it is inside the mouth is a separate consideration (variable 3C), and differences in fibrousness of diet might be reflected in different *tooth morphology*, *skull architecture*, and/or *jaw muscle attachments*. More dietary fiber requires more intraoral processing, which might entail more lophodont teeth and a different arrangement of jaw muscles (as in *Trichechus*; Domning, 1978b, 1982). Less fiber, conversely, might be reflected in reduction of the same structures (as in *Hydrodamalis*; Domning, 1978a). Unfortunately, most Caribbean sirenians fall between these extremes and show little if any relevant variety.

Finally, of fundamental importance (and cutting across most of the above niche dimensions) is the general role of *body size* in niche partitioning. Marked differences in body mass can provide a means of niche separation even among species that seemingly differ in no other ecological dimension. The mechanism of separation in such cases, however, is not always clear (see Maiorana, 1990). In the case of sirenians in the equable tropics, differential adaptation to climatic fluctuations or extremes would not explain size differences (though the gigantism of *Hydrodamalis* seems to have been largely an adaptation to cold; Domning, 1978a). Divergent adaptations to predation are, in the near-absence of data, no more than a theoretical possibility, although predation has certainly been a part of sirenian biology (e.g. Anderson and Prince, 1985), perhaps especially where small sirenians have coexisted with very large sharks (Domning and Thomas, 1987). But a more plausible rationale for size-mediated niche separation among tropical sirenians involves ingestibility and digestibility of plant food (variables 3A and 3C): “Larger foliage-feeding mammals can digest older and tougher plant material more efficiently than smaller species can because the food stays in the intestinal tract for longer periods of time” (Maiorana, 1990, p. 82; cf. Owen-Smith, 1985). They could also use their greater size and strength to uproot larger rhizomes, and chew them more thoroughly with their more powerful jaws. Anderson (1998) suggested that pit-making by foraging dugongs may be a specialty of the largest and heaviest indi-

viduals. Smaller species, on the other hand, could be more selective feeders (due to smaller mouthparts; variable 1A) and could possibly beat larger ones to younger, more succulent vegetation; and as noted above, smaller sirenians may have access to vegetation in shallower water (variable 2B).

With this background, we can turn once more to the Caribbean fossil record, to see how the observed morphologies of sympatric sirenian species relate to the above niche-partitioning strategies. If and when two or more sympatric species seem not to differ in regard to any of these morphological indicators of feeding niche, then (and only then) we must search for other ecological axes along which their separation and coexistence might have been maintained.

6. Interpretation of sirenian evolutionary history and adaptations in the Caribbean region

6.1. Eocene

Prorastomids, the most primitive sirenians, were amphibious quadrupeds that resembled Paleocene and Eocene condylarths but had aquatic specializations such as retracted nasal openings, absence of paranasal air sinuses, and dense and swollen (pachyosteosclerotic) ribs. At least the most primitive ones known had adequate support of body weight through the sacroiliac joint to provide for terrestrial locomotion. Protosirenids, representing the next most primitive evolutionary grade, also retained well-developed (though reduced) hind limbs, but had weak sacroiliac joints; so they were mainly aquatic animals that probably spent little if any time on land. Early dugongids were fully aquatic, with vestigial hind limbs.

Prorastomids had almost straight (undeflected) rostra, whereas all later sirenians had more or less downturned snouts, respectively reflecting greater or lesser degrees of specialization for bottom-feeding. Prorastomids and the earliest dugongids had narrow rostra and mandibular symphyses and were probably selective browsers on aquatic plants, presumably to some degree in fresh water. *Protosiren*, in contrast, paralleled later dugongids and trichechids in evolving a broader snout (Domning and Gingerich, 1994), which was suited for less selective underwater “grazing”.

Unlike prorastomids, *Protosiren* and early dugongids are well known from the Old World, where only one possible prorastomid specimen has been found (Goodwin et al., 1998). Both prorastomids and protosirenids were evidently extinct by the end of the Eocene. Dugongids went on to become the most diverse and successful sirenians, and also may have given rise to the trichechids (Domning, 1994b).

Thanks to the rapid evolution and diversification which sirenians underwent during the Eocene, the known prorastomids, protosirenids, and early dugongids are already grossly different in locomotor and feeding adaptations. This is not surprising, as they were actively radiating into a relatively vacant adaptive zone.

6.2. Oligocene

Fragmentary Oligocene sirenian remains from the southeastern US and Puerto Rico were traditionally lumped into the well-known European dugongid genus *Halitherium*; for example, *H. alleni* and ?*H. antillense*. Although the validity of these New World species remains uncertain, they do seem to represent *Halitherium* or very similar creatures; i.e. halitheriine dugongids. However, at least some of the Late Oligocene South Carolina fossils seem referable to *Metaxytherium*, a halitheriine genus derived from *Halitherium* that became widely distributed in the Miocene and Pliocene. *Caribosiren* from Puerto Rico is also placed in the Halitheriinae.

Most members of the *Halitherium*–*Metaxytherium* lineage had rather strongly downturned snouts and small to mid-sized tusks, and seem to have been generalized consumers of seagrass blades and (presumably) the rhizomes of smaller seagrass species. *Caribosiren*, in contrast, had an extreme snout deflection (75°) and altogether lacked tusks (Fig. 1). Doubtless it could nonetheless have extracted small- and mid-sized rhizomes with high efficiency, like the tuskless manatees today. However, the small tusks of *Halitherium* and *Metaxytherium* would presumably have given them an edge in this regard. In view of its extreme rostral deflection (perhaps the greatest of any known sirenian), *Caribosiren* might best be seen as a specialist on seagrass leaves that normally ate only a few of the smallest rhizomes, if any. It may thus have occupied a feeding niche like

that toward which the modern *Dugong* (whose large tusks have apparently lost their former role in feeding) seems to be evolving.

A second dugongid subfamily, the Dugonginae, has been detected in the Caribbean fossil record only recently; but this region appears to be where this group first arose and diversified. Its most primitive known member is *Crenatosiren olseni*. This rather small species, however, inhabited the Caribbean contemporaneously with at least one other, much larger, and much more derived dugongine, *Dioplotherium manigaulti* (see Domning, 1989a,c, 1997a). Since still other, even more highly derived dugongines such as *Corystosiren* and *Rytiodus* appear in the Early Miocene and thereafter, it is likely that at least some of these lineages already existed in the Oligocene as well.

Dugongines as a group tended to evolve large, often bladelike tusks that were presumably used to dig up the nutritious rhizomes of the larger seagrasses, such as *Thalassia*. Among Oligocene dugongines, *Crenatosiren* has the smallest tusks, though they would rank as medium-sized in comparison with the small tusks of contemporary *Metaxytherium*; i.e. their sockets extend only about half the length of the premaxillary symphysis. In contrast, *Dioplotherium*, *Rytiodus*, and *Corystosiren* had “large” tusks that were not only as long as the symphysis but also flattened and bladelike (Fig. 1). In the latter two genera, the tusks were broader and flatter than in *Dioplotherium*; and they were also self-sharpening (with enamel on only one side). Later *Dioplotherium* independently developed self-sharpening tusks.

The sirenian family Trichechidae, which includes today’s manatees, was evidently in existence during the Oligocene and was probably found in South America at that time, although no Oligocene fossils of this family have yet been discovered in the New World.

From the Oligocene onward, sirenians in general were of a “modern” aspect, i.e. fully aquatic: by then the amphibious prorastomids and protosirenids were evidently extinct, and we are on slightly firmer ground in interpreting sirenian paleoecology by analogy with living forms. By the Late Oligocene, furthermore, we can identify and characterize multispecies sirenian communities in the Caribbean region. Beginning with the Late Oligocene, therefore,

I make here a first attempt at hypothesizing how these animals might have partitioned the available food resources.

In Figs. 1 and 2, *Metaxytherium* (with small tusks) is interpreted to have specialized on the smallest seagrass rhizomes; *Crenatosiren* (with intermediate-sized tusks), on middle-sized rhizomes; and *Dioplotherium* (with large tusks), on the large rhizomes. If a form with even more massive tusks (such as an early *Corystosiren* species) was present at this time, it would presumably have anchored the “large” end of the rhizome spectrum, forcing *Dioplotherium* into a more intermediate position unless “very large” seagrasses were also present, as conjecturally illustrated here. As argued above, the tuskless *Caribosiren* may have foraged exclusively on seagrass leaves. (NB: All sirenians had ready access to the leaves of all seagrasses, and even tuskless ones presumably could, like modern manatees, excavate small and medium-sized rhizomes. Again, the polygons in Figs. 1 and 2 are intended only to suggest the narrow zones in which each taxon was competitively superior, and not to indicate the full widths of their dietary niches.) The feeding ecology of the undescribed Late Oligocene halitheriine genus cannot yet be characterized; fitting it into this already-crowded picture may pose a problem. Primitive trichechids are likely to have inhabited South American brackish and/or freshwater habitats at this time, but are unrecorded.

6.3. Miocene

Described from the southeastern US, *Metaxytherium crataegense* is also reported from the eastern Pacific, where it gave rise to a new, endemic subfamily of dugongids, the Hydrodamalinae (Aranda-Manteca et al., 1994). In the Caribbean it apparently gave rise, with little change, to *M. floridanum*, which died out by the end of the Miocene (although other species of the genus survived into the Late Pliocene in the Mediterranean Sea; Domning and Thomas, 1987). The near-absence of morphological change in *Metaxytherium* from the Late Oligocene to the Late Miocene is the only known example of prolonged evolutionary stasis in the entire fossil record of the Sirenia. This may be attributable to this taxon’s general-

ized feeding habits compared with the more specialized large-tusked dugongids. A slight increase in body size and rostral deflection (though not tusk size) seen in the transition from *M. crataegense* to *M. floridanum* (Fig. 1) suggests some change in feeding ecology, possibly a broadening of the niche in response to the extinction of *Crenatosiren* and/or some other taxon (Fig. 2). Alternatively or simultaneously, increased body mass might have permitted maintenance of greater headway while foraging on the same small seagrasses, and thereby allowed an increase in snout deflection.

As for the dugongines, *Dioplotherium allisoni* (which is reported in the eastern Pacific as well as the western Atlantic; Domning, 1978a) is a more derived descendant of *D. manigaulti*, and *Rytiodus* is known from Early Miocene sites in France and Libya as well as (possibly) Brazil. *Corystosiren* is so far known only from the southeastern US and Yucatan; it and cf. *Rytiodus* may or may not have been sympatric. All these have large, bladelike, self-sharpening tusks; those of *Dioplotherium*, however, are more slender, so less robust rhizomes are allocated to it in Figs. 1 and 2.

Also apparently endemic to this faunal region, but of uncertain origin, are the small but inadequately known dugongids (dugongines?) that occur at several Miocene and Pliocene horizons; these seem to have had small tusks or none at all, so they cannot have been competing for the larger rhizomes. Their rostral deflection is also uncertain. Logically they would seem to have fed on the smallest plants, including *Halodule* and *Halophila*, some of which also happen to occur intertidally, in shallower water than other seagrasses (den Hartog, 1970). As suggested above, a shallower draft may have given these small dugongids access to shallow-water seagrass beds that the larger *Metaxytherium* avoided. They also may have competed with and/or replaced *Caribosiren*. If they had to subsist on leaves in competition with numerous other, more capable seagrass consumers, smaller size and consequently lesser food requirements would have been additionally advantageous.

Manatees (trichechines) at this time were perhaps confined to freshwater and possibly estuarine habitats

in South America; they have not been found in marine deposits of Miocene age. *Potamosiren*, which lacks supernumerary molars, evidently predates the proliferation of abrasive aquatic grasses in South America, which Domning (1982) attributed to the Late Tertiary Andean orogeny. Its thick molar enamel likewise can be interpreted as adapted to a diet of relatively soft and mostly nonabrasive aquatic plants; the enamel became thinner in the “throwaway” teeth of later trichechids (Domning, 1982, 1997b).

6.4. Pliocene

Halitheriines are not known to occur in the Caribbean after the Miocene; only dugongines are known from the region’s Pliocene deposits. *Corystosiren* is present in the Early Pliocene, and *Xenosiren* may have been contemporaneous with it. The skull architecture of *Xenosiren* hints at even more forceful digging with the tusks than in its putative ancestor *Dioplotherium*, although it is not clear whether the tusks themselves were larger (Domning, 1989b). This more forceful digging would seem to imply feeding on the largest and toughest rhizomes. However, the alveolar process of the maxilla is reduced in *Xenosiren*, providing less support for the molars and indicating less occlusal force in the molar region, hence presumably a less fibrous diet. Resolution of this paradox may require more complete material of this peculiar, inadequately known taxon. In Figs. 1 and 2, *Xenosiren* is provisionally assigned smaller rhizomes than *Corystosiren*, to maintain continuity with the niche position of its supposed ancestor *Dioplotherium* relative to that of *Corystosiren*.

The only Late Pliocene dugongid known in the region is a *Dugong*-like dugongine with large but not bladelike tusks. Its immediate ancestry is unclear, but it may have stemmed from one of the undescribed small dugongines mentioned above. It presumably did not feed on rhizomes of the larger seagrasses, many of which by then (following the closure of the Central American Seaway) are here assumed to have died out in the New World. In the apparent absence of sirenian competitors other than trichechids, it may have been a comparative generalist, consuming leaves and small to mid-sized rhizomes.

By the end of the Pliocene, dugongids seem to have died out in the western Atlantic altogether. Trichechids, however, in the form of *Ribodon*, known

from North Carolina, had apparently expanded their range outside South America by the Pliocene, and with the end of that epoch they became the only surviving western Atlantic–Caribbean sirenians.

Ribodon and its descendant *Trichechus* are characterized by supernumerary molars which continue to be replaced horizontally throughout the animal’s life; this is an adaptation to eating the abrasive true grasses (Gramineae) which constitute the principal diet of manatees in South American rivers, their ancestral home (Domning, 1982). Nutrient runoff from the rising Andes during the Late Tertiary is assumed to have greatly increased the abundance of these grasses and the biomass of freshwater plants in general (Fig. 2).

6.5. Pleistocene–Recent

Diversification of New World *Trichechus* into ancestors of the modern Amazonian and West Indian species, followed by dispersal of members of the latter stock to West Africa, probably occurred in the Late Pliocene to Pleistocene. *Trichechus inunguis* is specialized for exclusively freshwater habitats, whereas the euryhalic *T. manatus* ranges widely in coastal marine waters. Florida manatees have more downturned snouts than any other taxa of manatees, probably reflecting a greater proportion of benthic seagrasses in their diet (Domning, 1982). They can efficiently excavate both small and mid-sized rhizomes (Packard, 1984), and have thereby moved into at least parts of the former niches of the smaller-tusked dugongids (Figs. 1 and 2). Sometimes they manage to take even rhizomes of *Thalassia*, but only on very soft sediments (Zieman, 1982, p. 69). Their more wear-resistant cheek dentitions would have given them a competitive edge over dugongids, especially when rooting in abrasive sediment; and this competition from manatees, following a Late Pliocene reduction in seagrass diversity, may help to explain the final extinction of dugongids in the Caribbean (Domning, 1982).

6.6. Summary of Late Oligocene–Neogene sirenian lineages

From the Late Oligocene through most of the Neogene, at least six or seven sirenian lineages were simultaneously present in the Caribbean–West

Atlantic faunal province, and probably more. Most of these would have been sympatric at any given time. As diagrammed in Fig. 2, these were:

1. Trichechids, probably distributed (at least initially) mostly in brackish and/or fresh water. The freshwater portion of their niche expanded following the Late Tertiary Andean orogeny, to the ultimate benefit mainly of Amazonian manatees (*Trichechus inunguis*). After the end-Pliocene extinction of the last Caribbean dugongids, West Indian manatees (*T. manatus*) invaded the salt-water ecological vacuum, and the Recent Florida subspecies in particular has incorporated small and mid-sized seagrass rhizomes into its diet. The trichechids are the only Caribbean lineage to show clear evidence of branching (into the species of *Trichechus*) during the Late Oligocene–Recent interval.
2. *Caribosiren*, possibly specializing on seagrass leaves while taking only the smallest, most accessible rhizomes. It disappears from the record after the Oligocene.
3. One or two lineages of undescribed small dugongids/dugongines, which may have used their shallow draft to reach shallow-water beds of small seagrasses (*Halodule*, *Halophila*). They may have competed with and/or replaced *Caribosiren*. After the ?mid-Pliocene extinction of other Caribbean dugongids, their terminal member may have expanded its diet into a more *Metaxytherium*-like niche.
4. *Metaxytherium* spp., which probably ate leaves and rhizomes of small and mid-sized seagrasses in water deeper than 1 m. This niche may have broadened by the Middle Miocene to encompass resources made available by the extinction of *Crenatosiren* and/or other species.
5. *Crenatosiren*, with larger tusks than *Metaxytherium*, may have concentrated on leaves and mid-sized rhizomes prior to its extinction sometime after the latest Oligocene or earliest Miocene.
6. *Dioplotherium* spp.-*Xenosiren*, which specialized on the larger rhizomes, evolving self-sharpening tusks and, eventually, extreme modifications of skull architecture for coping with the stresses of digging with the snout and tusks. This lineage died out with the inferred Pliocene regional extinction of some large seagrasses.
7. *Corystosiren* spp., probably present though not yet

discovered in the Late Oligocene, and persisting thereafter up to the inferred Pliocene seagrass extinction. These animals, with the largest and most knife-like self-sharpening tusks, were the ones best equipped to excavate the largest rhizomes.

Left out of this reckoning are the undescribed Late Oligocene halitheriine mentioned above, which cannot yet be located on the resource spectrum, and cf. *Rytiodus* from the Early Miocene of Brazil, which was adaptively equivalent to the Caribbean *Corystosiren* and may have been parapatric with it. If a true *Halitherium* was present in the Late Oligocene together with the earliest *Metaxytherium*, this would raise the tally still higher; but this seems unlikely because of the close ecological similarity of these two forms.

In any case, it is evident that the niche space for Caribbean sirenians was well packed, to the point of straining to the limit the explanatory power of the resource axes I have proposed. Any further discoveries of new taxa would seem difficult to accommodate on these axes. However, as shown in Figs. 1 and 2, none of the known lineages overlap in “exclusive” feeding-niche space, even when using as few as one (Fig. 2) or two niche dimensions (Fig. 1; the apparent overlap of *Metaxytherium* with the conjectured evolutionary trajectory of the small ?dugongines disappears when the time dimension is added, as seen in Fig. 2). This suggests that a robust explanation of their coexistence may be almost within our grasp.

Further evidence that these lineages were not as crowded in multidimensional ecospace as they appear to be in one or two dimensions is offered by estimates of body size. Maiorana (1990) demonstrated that terrestrial herbivorous mammal guilds tend to show an approximately fourfold periodicity in body mass, corresponding to a periodicity of 1.6 in linear dimensions. She interpreted this amount of separation to reflect some degree of diffuse competition, in contrast to the Hutchinsonian periodicities of 2 in mass and 1.3 in linear dimensions often thought to be the minimum necessary for separation of potential competitors. The sirenian data approach a fourfold mass difference or a 1.6-fold linear difference only between the smallest and largest taxa: the skull lengths of *Caribosiren turneri* and of the small Bone Valley ?dugongine are estimated at close to 300 mm, whereas those of *Dioplotherium manigaulti* and *Metaxytherium*

floridanum are near 460 mm (a ratio of 1.53). The differences between the most similar sympatric species are even less than the Hutchinsonian minima. This confirms that these lineages had other strategies for avoiding competition in addition to difference in body size; so much so, in fact, that body-size difference as a partitioning strategy did not need to be resorted to in most cases.

It should also be kept in mind that not all of these taxa need have maintained equal, similar, or constant population sizes or biomasses. The specialized, large-tusked dugongines in particular, which putatively were the species most dependent on the relatively unproductive “climax” species of seagrasses, may well have been rare. This may be why their presence and diversity remained largely undetected until the last 20 years. Conversely, more generalized sirenians like *Metaxytherium*, which apparently exploited the more productive, early-successional “pioneer” seagrass species, could have maintained larger populations and enjoyed greater long-term niche stability. The abundance of *Metaxytherium* bones in, for example, the Bone Valley deposits of Florida certainly gives the impression of actual abundance of the living animals, though this could of course be misleading. However, the quantitative dominance of the sirenian fossil record by specimens of halitheriines such as *Halitherium* and *Metaxytherium* — a pattern which has persisted over nearly two centuries of collecting in Europe and eastern North America — may in fact be telling us something about the real abundance of these generalists in the seagrass communities of the past, at least in those regions. Furthermore, the morphological near-stasis observed in Miocene *Metaxytherium* also testifies to a stable niche, one which might be expected to lie well away from the extremes of the resource spectrum. This stasis and presumed niche stability contrast with the apparently more rapid evolution and taxonomic turnover of the dugongines.

These dynamic aspects of the system, on ecological as well as evolutionary timescales, may explain this system’s most puzzling feature: the apparent dependence of so many sympatric herbivore species on a comparable or possibly even smaller number of seagrass species. Unbalanced, or even inverted, ecological pyramids of this sort are not entirely without precedent, however; they may even be especially prone to develop in relatively simple ecosystems

like the sirenian–seagrass system. An example is the mammal fauna of Newfoundland, in which carnivore species outnumber the herbivore species (Bergerud, 1983). Bergerud emphasizes that in such a system, “any shift in the prey species can have strong reverberations; the damping of the effects that would take place in a more complex ecosystem is absent.” The inherent fragility and instability of such systems makes them prone to violent fluctuations in population sizes, even cyclic fluctuations such as the well-known lynx–hare–caribou cycles which Bergerud describes. Species that were periodically reduced to rarity under such conditions would obviously be in greater danger of chance extinction, which would further destabilize the community.

The sirenian–seagrass system in the Caribbean may well have followed such a pattern. Climax species of seagrass, and the large-tusked dugongines that were able to drastically reduce their dominance, may have exhibited boom-and-bust cycles analogous to those of hares and lynxes. In this kind of game the dugongines would have been under strong selective pressure for efficient foraging, and (with far fewer individuals per species than the seagrasses) in greater danger of extinction than their food plants. When oceanographic changes were also imposed on the system, however (possibly in the form of a restricted supply of nutrients, and/or in major sealevel cycles that greatly reduced shallow shelf areas more and more frequently during the late Tertiary) such cyclic instability might have become amplified, causing extinction of Caribbean dugongids and even loss of some seagrass species. Trichechids may have survived this upheaval by chance, by virtue of their more wear-resistant and competitively superior dentitions, and/or (probably most likely) by virtue of their ability to exploit freshwater plant resources in addition to seagrasses.

7. Implications for ecology and paleoecology of Caribbean seagrasses

The above hypotheses concerning sirenian evolutionary history and paleoecology depend on, and have implications for, hypotheses concerning seagrasses themselves. This has already been demonstrated on the grossest scale: contrary to foraminiferal evidence which seemed to indicate an absence of seagrasses

from Florida (or even the entire Caribbean) during the Eocene, sirenian fossils of that age provided evidence for their presence, which was confirmed by discovery in Florida of actual Eocene seagrasses (see Domning, 1981b). However, this far from exhausts the conclusions about seagrass history that can be drawn from the sirenian record.

To recapitulate the boundary assumptions made above: I have postulated that Caribbean seagrass communities at least from the Middle Eocene onward have had the same general structure, similar taxonomic makeup as today, and significantly greater diversity due to the presence of *Cymodocea* and *Thalassodendron* (Ivany et al., 1990) and conceivably other large seagrasses as well (such as *Posidonia* or *Enhalus*). I have also postulated that these additional genera went extinct in the New World during the mid- or late Pliocene rather than at some earlier time, coinciding with and in part explaining the extinction at that time of the last Caribbean dugongids.

This joint extinction of seagrasses and the sirenians that depended on them would in turn apparently have coincided with, and could easily have resulted from, the cooling and other paleoceanographic changes in the Caribbean around that time, as noted by Ivany et al. (1990). In particular, decline in upwelling and other changes in circulation patterns, resulting in reduced biological productivity, could have been important (Petuch, 1982; Jones and Hasson, 1985; Allmon et al., 1996). The Pliocene closure of the Central American Seaway (complete by ca. 3.1 Ma) coincided with significant environmental and faunal changes in the Caribbean as well as the eastern Pacific (Jackson et al., 1996); in particular, there was an extinction of shallow-water molluscs in the Caribbean and West Atlantic, apparently correlated with changes in salinity and circulation patterns (Vermeij, 1978; Stanley and Campbell, 1981; Keigwin, 1982; Petuch, 1982; Jones and Hasson, 1985; Duque-Caro, 1990). Allmon et al. (1996) also point out Late Pliocene changes in assemblages of calcareous algae and plankton, as well as regional extinctions among turritellid gastropods, seabirds, cetaceans, and pinnipeds, and extinction of the giant shark *Carcharodon megalodon*. Budd et al. (1996) estimated that 75% of the Early to early Late Pliocene reef coral species became extinct in the Caribbean. It is therefore plausible that this major upheaval in Caribbean marine ecology also

made itself felt among seagrasses and sirenians. In fact, the corals most affected by this turnover were precisely those associated with seagrasses, which showed extinction rates of 30–50% per million years (Budd et al., 1996). Likewise, seagrass-associated bryozoans (*Metrarabdotos* spp.) underwent dramatic extinction in the latest Miocene and the Pliocene (Cheetham and Jackson, 1996). Both these trends are interpreted by the respective authors as indicating decline of the seagrasses themselves.

Other implications of the present model for seagrass paleoecology have to do mainly with the fact that for most of the past 50 Ma, Caribbean seagrass communities have had to withstand heavy, sustained grazing pressure from several sympatric lineages of large mammalian herbivores. This factor is almost totally absent both from these communities today (wherein manatees are scarce or absent in most areas) and from the thinking of the aquatic botanists and marine ecologists who study these communities. Consequently, the long-established tenet that seagrass ecosystems are largely detritus-based (e.g. Fenchel, 1977; Klug, 1980) must be revised to recognize that the modern situation is anomalous, and that the “normal” pattern throughout most of tropical seagrass history has been that much (probably most) of the primary productivity has been channeled through the guts of herbivores, particularly sirenians. This would have even speeded up the detritus cycle itself and accelerated the recycling of nutrients (as has been shown for green turtles by Thayer et al., 1982), with possibly far-reaching impacts on the seagrass community as a whole. Of course, grazing by large herbivores can also modify community structure directly, at least over the short term: like turtles, dugongs and possibly manatees reportedly practice “cultivation grazing” to maximize their foraging efficiency and nutritional intake (Preen, 1995b; De Iongh et al., 1995; Lefebvre et al., 2000). Likewise, over the longer term, the overall community structure of terrestrial grasslands is also heavily influenced by their history of grazing pressure (Milchunas et al., 1988).

A further corollary of this model is that a significant portion of this herbivory has been concentrated on the larger species of seagrasses, which are viewed as “climax” species. I have shown above that several lineages of sirenians (the large-tusked dugongines) are likely to have specialized on these large seagrasses

and specifically on their rhizome systems. By disrupting beds of these climax seagrasses, it is likely in turn that these dugongines acted as “keystone species”, pushing seagrass communities away from climax stages and thus increasing their species diversity and biological productivity, as even Florida manatees and dugongs can accomplish to some extent (Packard, 1984; Preen, 1995b). This, in turn, would have opened up ecological niches for a more diverse array of herbivores, which helps to explain the long-maintained coexistence of so many different sirenians in the same general region.

This hypothesis may also help explain the collapse of this diversity which possibly coincided with extinction of the large-tusked forms; a similar “keystone” mechanism has been suggested for the Pleistocene extinctions of many land mammals when the large proboscideans were removed (Owen-Smith, 1987). Collapse of diversity among non-large-tusked sirenians might have resulted from loss of either the climax seagrasses or their disruptors. The survival of *Thalassia* shows that extinction of the disruptors was not caused by total loss of large-rhizome resources. However, if large seagrasses in general were once reduced to a point where the keystone sirenians would go extinct (as suggested in the previous section), perhaps *Thalassia* was the only one to recover, leaving an obviously vacant niche. In this connection, it is significant that the bulk of Caribbean seagrass biomass and standing crop today consists of the little-exploited climax species *Thalassia testudinum* (Thayer et al., 1984, p. 364) — a situation that would be ripe for harvest if any seacows capable of harvesting this (rhizome) resource were extant.

Sirenians may also provide a key to understanding present patterns of seagrass use by other herbivores. Ogden (1980) pointed out that herbivore diversity is greater in Caribbean than in any other seagrass communities, due largely to the number of fish and sea urchin species involved. Few of these, however, are obligate seagrass consumers, or even permanent residents of seagrass beds, and it may be wondered if much of this seagrass utilization has not begun only recently (geologically speaking), in response to the vacuum left by extinction of the Caribbean dugongids. If so, this would be consistent with Johnstone’s (1978) suggestion that evolution of other seagrass consumers was inhibited by competition from historically large

populations of turtles (and a fortiori, I would add, of sirenians).

The massive impact of past herbivory may also have left its mark on features of modern seagrass morphology, chemistry, reproduction, and dispersal mechanisms. Have seagrasses adapted their growth forms or life strategies to cope with, or even profit from, cropping by sirenians? On land, rhizomatous or stoloniferous grasses are more prevalent in grasslands with long evolutionary histories of grazing (Mack and Thompson, 1982). Chemical defenses are also to be expected; phenolic acids in seagrass may help to deter herbivores (Zieman, 1982, p. 73). However, tolerance rather than resistance to herbivory is an alternative strategy, and one that may actually promote stability in plant-herbivore relationships (Strauss and Agrawal, 1999). Seagrass reproduction today is predominantly asexual; would sexual reproduction have been more common under conditions of intense grazing? Even more speculatively, could sirenians have once played some role in seagrass dispersal or pollination? Relevant observations have just begun to be made. For example, Peterken and Conacher (1997, p. 338) report that “[a]s dugongs graze, they plough a furrow in the seagrass bed, which could bury *Z[ostera]. capricorni* seeds and also abrade the seed coat, promoting germination.... By increasing rates of nitrogen fixation the dugong grazing may also have enhanced the germination success and seedling development of *Z. capricorni*...”. Earlier, Phillips and Meñez (1988, p. 19) noted that “[i]n *Halodule* and *Cymodocea*, the one-seeded fruits are produced under the sediment surface. They apparently remain in the sediments until surface erosion occurs or until fish or skates disrupt the sediment. In this way they might roll along the sediment or be carried by a fish and deposited in another location.“ Here also there would seem to be a potential role for sirenians.

In conclusion, Caribbean (and, by implication, many other) seagrass floras, throughout most of their Cenozoic history, were probably: (a) more taxonomically diverse on both regional (bioprovincial) and local scales; (b) more subject to significant herbivory; and (c) generally kept farther away from “climax” by herbivory than they are today. This means that, from the perspective of evolutionary time, their present conditions are not “normal” (e.g. in terms of the relatively small role now played by herbivory and the

predominantly detritus-based nature of their energy pathways). This abnormality of the present may extend further, to such aspects of seagrass biology and evolution as life history, growth habit, community structure, reproduction, and dispersal. In the Caribbean, the shift from “normal” to the present “abnormal” conditions may have largely taken place in the Pliocene, and it likely coincided with the decline in biological productivity and other ecological changes thought to have accompanied the Late Pliocene closure of the Central American Seaway. Therefore, “climax” seagrass species and dugongid sirenians were probably among the victims of the Late Pliocene mass extinction that affected shallow-water Caribbean molluscs and other organisms.

Acknowledgements

I take special pleasure in dedicating this paper, a synthesis of some three decades of work, to Emily and Harold Vokes, who recruited me to come to Tulane University for my undergraduate studies and gave me my first formal instruction in geology and paleontology. Many colleagues have assisted in this study over the years; particularly relevant here are the material and intellectual contributions of P.K. Anderson, W.J. Kenworthy, L.W. Lefebvre, H. Marsh, R.W. Portell, J.A. Powell, Jr., A.R. Preen, and C.J. Terranova. J.A. Powell, Jr. and S.D. Webb provided formal reviews of the manuscript. My research on Caribbean and West Atlantic fossil sirenians has been supported by the National Science Foundation, the National Geographic Society, and Barbara and Reed Toomey.

References

- Allmon, W.D., Emslie, S.D., Jones, D.S., Morgan, G.S., 1996. Late Neogene oceanographic change along Florida's west coast: evidence and mechanisms. *Journal of Geology* 104, 143–162.
- Anderson, P.K., 1979. Dugong behavior: on being a marine mammalian grazer. *Biologist* 61 (4), 113–144.
- Anderson, P.K., 1982. Studies of dugongs at Shark Bay, Western Australia. I. Analysis of population size, composition, dispersion and habitat use on the basis of aerial survey. *Australian Wildlife Research* 9, 69–84.
- Anderson, P.K., 1986. Dugongs of Shark Bay, Australia — seasonal migration, water temperature, and forage. *National Geographic Research* 2, 473–490.
- Anderson, P.K., 1989. Deliberate foraging on macroinvertebrates by dugongs. *National Geographic Research* 5, 4–6.
- Anderson, P.K., 1998. Shark Bay dugongs (*Dugong dugon*) in summer. II: Foragers in a *Halodule*-dominated community. *Mammalia* 62, 409–425.
- Anderson, P.K., Birtles, A., 1978. Behaviour and ecology of the dugong, *Dugong dugon* (Sirenia): observations in Shoalwater and Cleveland Bays, Queensland. *Australian Wildlife Research* 5, 1–23.
- Anderson, P.K., Prince, R.I.T., 1985. Predation on dugongs: attacks by killer whales. *Journal of Mammalogy* 66, 554–556.
- Aranda-Manteca, F.J., Domning, D.P., Barnes, L.G., 1994. A new Middle Miocene sirenian of the genus *Metaxytherium* from Baja California and California: relationships and paleobiogeographic implications. *Proceedings of the San Diego Society of Natural History* 29, 191–204.
- Arata, A.A., Jackson Jr., C.G., 1965. Cenozoic vertebrates from the Gulf Coastal Plain — I. *Tulane Studies in Geology* 3 (3), 175–177.
- Bajpai, S., Domning, D.P., 1997. A new dugongine sirenian from the Early Miocene of India. *Journal of Vertebrate Paleontology* 17, 219–228.
- Bergerud, A.T., 1983. Prey switching in a simple ecosystem. *Scientific American* 249 (6), 130–141.
- Best, R.C., 1981. Foods and feeding habits of wild and captive Sirenia. *Mammal Review* 11, 3–29.
- Budd, A.F., Johnson, K.G., Stemmann, T.A., 1996. Plio-Pleistocene turnover and extinctions in the Caribbean reef-coral fauna. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. University of Chicago Press, Chicago, IL, pp. 168–204.
- Cheetham, A.H., Jackson, J.B.C., 1996. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary cheilostome Bryozoa of tropical America. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. University of Chicago Press, Chicago, IL, pp. 205–233.
- De Iongh, H.H., Wenno, B.J., Meelis, E., 1995. Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany* 50, 1–19.
- De Iongh, H.H., Bierhuizen, B., van Orden, B., 1997. Observations on the behaviour of the dugong (*Dugong dugon* Müller 1776) from waters of the Lease Islands, eastern Indonesia. *Contributions to Zoology (Amsterdam)* 67, 71–77.
- Domning, D.P., 1977. An ecological model for Late Tertiary sirenian evolution in the North Pacific Ocean. *Systematic Zoology* 25 (4), 352–362.
- Domning, D.P., 1978. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Science*, 118: xi + 176 pp.
- Domning, D.P., 1978b. The myology of the Amazonian manatee, *Trichechus inunguis* (Natterer) (Mammalia: Sirenia). *Acta Amazonica* 8 (2 Suppl. 1), 1–81.
- Domning, D.P., 1980. Feeding position preference in manatees (*Trichechus*). *Journal of Mammalogy* 61 (3), 544–547.
- Domning, D.P., 1981a. Distribution and status of manatees *Trichechus* spp. near the mouth of the Amazon River, Brazil. *Biological Conservation* 19 (2), 85–97.

- Domning, D.P., 1981b. Sea cows and sea grasses. *Paleobiology* 7 (4), 417–420.
- Domning, D.P., 1982. Evolution of manatees: a speculative history. *Journal of Paleontology* 56 (3), 599–619.
- Domning, D.P., 1988. Fossil Sirenia of the West Atlantic and Caribbean region. I. *Metaxytherium floridanum*. *Journal of Vertebrate Paleontology* 8, 395–426.
- Domning, D.P., 1989a. Fossil Sirenia of the West Atlantic and Caribbean region. II. *Dioplotherium manigaulti* Cope, 1883. *Journal of Vertebrate Paleontology* 9, 415–428.
- Domning, D.P., 1989b. Fossil Sirenia of the West Atlantic and Caribbean region. III. *Xenosiren yucateca*, gen. et sp. nov. *Journal of Vertebrate Paleontology* 9, 429–437.
- Domning, D.P., 1989c. Fossil sirenians from the Suwannee River, Florida and Georgia. In: Morgan, G.S. (Ed.). *Miocene Paleontology and Stratigraphy of the Suwannee River Basin of North Florida and South Georgia*. Southeastern Geological Society Guidebook, No. 30. Southeastern Geological Society, Tallahassee, FL, pp. 54–60.
- Domning, D.P., 1990. Fossil Sirenia of the West Atlantic and Caribbean region. IV. *Corystosiren varguezii*, gen. et sp. nov. *Journal of Vertebrate Paleontology* 10, 361–371.
- Domning, D.P., 1994a. West Indian tuskens. *Natural History* 103, 72–73.
- Domning, D.P., 1994b. A phylogenetic analysis of the Sirenia. *Proceedings of the San Diego Society of Natural History* 29, 177–189.
- Domning, D.P., 1997a. Fossil Sirenia of the West Atlantic and Caribbean region. VI. *Crenatosiren olseni* (Reinhart, 1976). *Journal of Vertebrate Paleontology* 17, 397–412.
- Domning, D.P., 1997b. Sirenia. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington, DC, pp. 383–391.
- Domning, D.P., 1999. Oligocene Sirenia of the Caribbean region. Appendix 1 (p. 29) in H.L. Dixon and S.K. Donovan, Report of a field meeting to the area around Browns Town, parish of St. Ann, north-central Jamaica, 21st February 1998. *Journal of the Geological Society of Jamaica* 33, 24–30.
- Domning, D.P., Hayek, L., 1984. Horizontal tooth replacement in the Amazonian manatee (*Trichechus inunguis*). *Mammalia* 48 (1), 105–127.
- Domning, D.P., Hayek, L., 1986. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). *Marine Mammal Science* 2 (2), 87–144.
- Domning, D.P., Thomas, H., 1987. *Metaxytherium serresii* (Mammalia: Sirenia) from the Lower Pliocene of Libya and France: a reevaluation of its morphology, phyletic position, and biostratigraphic and paleoecological significance. In: Boaz, N., El-Arnauti, A., Gaziry, A.W., de Heinzelin, J., Boaz, D.D. (Eds.), *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York, pp. 205–232.
- Domning, D.P., de Buffrénil, V., 1991. Hydrostasis in the Sirenia: quantitative data and functional interpretations. *Marine Mammal Science* 7 (4), 331–368.
- Domning, D.P., Gingerich, P.D., 1994. *Protosiren smithae*, new species (Mammalia, Sirenia), from the late Middle Eocene of Wadi Hitan, Egypt. *Contributions from the Museum of Paleontology, University of Michigan* 29 (3), 69–87.
- Domning, D.P., Morgan, G.S., Ray, C.E., 1982. North American Eocene sea cows (Mammalia: Sirenia). *Smithsonian Contributions to Paleobiology* 52 (iii + 69pp.).
- Domning, D.P., Gingerich, P.D., Simons, E.L., Ankel-Simons, F.A., 1994. A new Early Oligocene dugongid (Mammalia, Sirenia) from Fayum Province, Egypt. *Contributions from the Museum of Paleontology, University of Michigan* 29 (4), 89–108.
- Domning, D.P., Donovan, S.K., Dixon, H.L., Portell, R.W., Schindler, K., 1995. The world's most primitive seacow: a new sirenian site in western Jamaica. [Abstr.] *Geological Society of America, Abstracts with Programs*, vol. 27(6), p. A386.
- Domning, D.P., Donovan, S.K., Portell, R.W., Schindler, K., 1996. In search of the primitive seacow *Prorastomus* Owen (Mammalia, Sirenia): preliminary results from the 1996 expedition. [Abstr.] *Contributions to Geology, University of the West Indies, Mona*, No. 2, pp. 36–37.
- Duque-Caro, H., 1990. Neogene stratigraphy, paleoceanography and paleobiogeography in northwest South America and the evolution of the Panama Seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* 77, 203–234.
- Ertfemeijer, P.L.A., Djunarlin, Moka, W., 1993. Stomach content analysis of a dugong (*Dugong dugon*) from South Sulawesi, Indonesia. *Australian Journal of Marine and Freshwater Research* 44, 229–233.
- Fenart, R., 1963. Note sur l'étude du crâne de *Halicore Dugong* par la méthode vestibulaire. *Mammalia* 27 (1), 92–98.
- Fenchel, T., 1977. Aspects of the decomposition of seagrasses. In: McRoy, C.P., Helfferich, C. (Eds.), *Seagrass Ecosystems: A Scientific Perspective*. Marcel Dekker, New York, pp. 123–145.
- Fortelius, M., 1990. Problems with using fossil teeth to estimate body sizes of extinct mammals. In: Damuth, J., MacFadden, B.J. (Eds.), *Body Size in Mammalian Paleontology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, UK, pp. 207–228.
- García-Rodríguez, A.I., Bowen, B.W., Domning, D.P., Mignucci-Giannoni, A.A., Marmontel, M., Montoya-Ospina, R.A., Morales-Vela, B., Rudin, M., Bonde, R.K., McGuire, P.M., 1998. Phylogeography of the West Indian manatee (*Trichechus manatus*): how many populations and how many taxa?. *Molecular Ecology* 7 (9), 1137–1149.
- Goodwin, M.B., Domning, D.P., Lipps, J.H., Benjamini, C., 1998. The first record of an Eocene (Lutetian) marine mammal from Israel. *Journal of Vertebrate Paleontology* 18 (4), 813–815.
- Hartman, D.S., 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. *American Society of Mammalogists Special Publication* 5, viii + 153pp..
- den Hartog, C., 1970. The sea-grasses of the world. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde* 2, vol. 59(1), pp. 1–275.
- Heinsohn, G.E., Wake, J., Marsh, H., Spain, A.V., 1977. The dugong (*Dugong dugon* (Müller)) in the seagrass system. *Aquaculture* 12, 235–248.
- Hulbert, R.C., Jr., Morgan, G.S., 1989. Stratigraphy, paleoecology, and vertebrate fauna of the Leisey Shell Pit Local Fauna, early

- Pleistocene (Irvingtonian) of southwestern Florida. *Papers in Florida Paleontology*, No. 2, pp. 1–19.
- Ivany, L.C., Portell, R.W., Jones, D.S., 1990. Animal–plant relationships and paleobiogeography of an Eocene seagrass community from Florida. *Palaios* 5, 244–258.
- Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), 1996. *Evolution and Environment in Tropical America*. University of Chicago Press, Chicago, IL (425pp.).
- Janis, C.M., Ehrhardt, D., 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* 92, 267–284.
- Johnstone, I.M., 1978. The ecology and distribution of Papua New Guinea seagrasses. II. The Fly Islands and Raboin Island. *Aquatic Botany* 5, 235–243.
- Jones, D.S., Hasson, P.F., 1985. History and development of the marine invertebrate faunas separated by the Central American isthmus. In: Stehli, F.G., Webb, S.D. (Eds.), *The Great American Biotic Interchange*. Plenum Press, New York, pp. 325–355.
- Keigwin Jr, L.D., 1982. Isotopic paleoceanography of the Caribbean and East Pacific: role of Panama uplift in Late Neogene time. *Science* 217, 350–353.
- Kellogg, R., 1966. Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia. 3. New species of extinct Miocene Sirenia. *US National Museum Bulletin* 247, 65–98.
- Klug, M.J., 1980. Detritus–decomposition relationships. In: Phillips, R.C., McRoy, C.P. (Eds.), *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM Press, New York, pp. 225–245.
- Klumpp, D.W., Howard, R.K., Pollard, D.A., 1989. Trophodynamics and nutritional ecology of seagrass communities. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*. Elsevier, Amsterdam, pp. 394–457.
- Lanyon, J., Limpus, C.J., Marsh, H., 1989. Dugongs and turtles: grazers in the seagrass system. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*. Elsevier, Amsterdam, pp. 610–634.
- Larkum, A.W.D., den Harteg, C., 1989. Evolution and biogeography of seagrasses. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of Seagrasses*. Elsevier Science Publishers B.V., Amsterdam, pp. 112–156.
- Lefebvre, L.W., Reid, J.P., Kenworthy, W.J., Powell, J.A., 2000. Characterizing manatee grazing of seagrasses in Florida and Puerto Rico: implications for conservation and management. *Pacific Conservation Biology* (in press).
- Lewis III, R.R., Carlton, J.M., Lombardo, R., 1984. Algal consumption by the manatee (*Trichechus manatus* L.) in Tampa Bay, Florida. *Florida Scientist* 47 (3), 187–189.
- Lumbert, S.H., den Hartog, C., Phillips, R.C., Olsen, F.S., 1984. The occurrence of fossil seagrasses in the Avon Park Formation (late Middle Eocene), Levy County, Florida (USA). *Aquatic Botany* 20, 121–129.
- Mack, R.N., Thompson, J.N., 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119, 757–773.
- MacPhee, R.D.E., Wyss, A.R., 1990. Oligo-Miocene vertebrates from Puerto Rico, with a catalog of localities. *American Museum Novitates* 2965, 1–45.
- Maiorana, V.C., 1990. Evolutionary strategies and body size in a guild of mammals. In: Damuth, J., MacFadden, B.J. (Eds.), *Body Size in Mammalian Paleontology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, UK, pp. 69–102.
- Marsh, H., Channells, P.W., Heinsohn, G.E., Morrissey, J., 1982. Analysis of stomach contents of dugongs from Queensland. *Australian Wildlife Research* 9, 55–67.
- Marshall, C.D., 1997. The sirenian feeding apparatus: functional morphology of feeding involving perioral bristles and associated structures. PhD thesis, University of Florida.
- Marshall, C.D., Huth, G.D., Edmonds, V.M., Halin, D.L., Reep, R.L., 1998. Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). *Marine Mammal Science* 14, 274–289.
- Matthew, W.D., 1916. New sirenian from the Tertiary of Porto Rico, West Indies. *Annals of the New York Academy of Science* 27, 23–29.
- McKenna, M.C., 1956. Survival of primitive notoungulates and condylarths into the Miocene of Colombia. *American Journal of Science* 254, 736–743.
- McRoy, C.P., Helfferich, C., 1980. Applied aspects of seagrasses. In: Phillips, R.C., McRoy, C.P. (Eds.), *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM Press, New York, pp. 297–343.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132, 87–106.
- Morgan, G.S., Hulbert Jr, R.C., 1995. Overview of the geology and vertebrate biochronology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History* 37 (Part I), 1–92.
- Ogden, J.C., 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips, R.C., McRoy, C.P. (Eds.), *Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland STPM Press, New York, pp. 173–198.
- Ortiz, R.M., Worthy, G.A.J., MacKenzie, D.S., 1998. Osmoregulation in wild and captive West Indian manatees (*Trichechus manatus*). *Physiology and Zoology* 71 (4), 449–457.
- Owen-Smith, N., 1985. Niche separation among African ungulates. In: Vrba, E.S. (Ed.), *Species and Speciation*. Transvaal Museum Monograph No. 4, pp. 167–171.
- Owen-Smith, N., 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* 13 (3), 351–362.
- Packard, J.M., 1984. Impact of manatees *Trichechus manatus* on seagrass communities in eastern Florida. *Acta Zoologica Fennica* 172, 21–22.
- de Paula Couto, C., 1967. Contribuição à paleontologia do estado do Pará. Um sirênio na formação Pirabas, Atas do Simpósio sobre a Biotá Amazônica, Vol. 1 (Geociências), pp. 345–357.
- Peterken, C.J., Conacher, C.A., 1997. Seed germination and recolonisation of *Zostera capricorni* after grazing by dugongs. *Aquatic Botany* 59, 333–340.

- Petuch, E.J., 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37, 277–312.
- Phillips, R.C., Meñez, E.G., 1988. Seagrasses. *Smithsonian Contributions to the Marine Sciences*, vol. 34, vi + 104pp.
- Powell Jr., J.A., 1978. Evidence of carnivory in manatees (*Trichechus manatus*). *Journal of Mammalogy* 59, 442.
- Preen, A.R., 1989. Observations of mating behavior in dugongs (*Dugong dugon*). *Marine Mammal Science* 5, 382–387.
- Preen, A.R., 1995a. Diet of dugongs: are they omnivores? *Journal of Mammalogy* 76, 163–171.
- Preen, A.R., 1995b. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series* 124, 201–213.
- Provanca, J.A., Hall, C.R., 1991. Observations of associations between seagrass beds and manatees in east central Florida. *Florida Scientist* 54, 87–98.
- Reinhart, R.H., 1959. A review of the Sirenia and Desmostylia. *University of California Publications in Geological Sciences* 36, 1–146.
- Reinhart, R.H., 1976. Fossil sirenians and desmostylids from Florida and elsewhere. *Bulletin of the Florida State Museum, Biological Sciences* 20, 187–300.
- Savage, R.J.G., Domning, D.P., Thewissen, J.G.M., 1994. Fossil Sirenia of the West Atlantic and Caribbean region. V. The most primitive known sirenian, *Prorastomus sirenooides* Owen, 1855. *Journal of Vertebrate Paleontology* 14 (3), 427–449.
- Sereno, P.C., 1982. An Early Eocene sirenian from Patagonia (Mammalia, Sirenia). *American Museum Novitates* 2729, 1–10.
- Sickenberg, O., 1934. Beiträge zur Kenntnis tertiärer Sirenen. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, No. 63, pp. 1–352.
- Simpson, G.G., 1932a. The supposed association of dinosaurs with mammals of Tertiary type in Patagonia. *American Museum Novitates* 566, 1–21.
- Simpson, G.G., 1932b. Fossil Sirenia of Florida and the evolution of the Sirenia. *Bulletin of the American Museum of Natural History* 59 (8), 419–503.
- Spain, A.G., Heinsohn, G.E., 1973. Cyclone associated feeding changes in the dugong (Mammalia: Sirenia). *Mammalia* 37 (4), 678–680.
- Stanley, S.M., Campbell, L.D., 1981. Neogene mass extinction of Western Atlantic molluscs. *Nature* 293, 457–459.
- Stirton, R.A., 1947. The first Lower Oligocene vertebrate fauna from northern South America. *Compilacion de los Estudios Geologicos Oficiales en Colombia (Ministerio de Minas y Petroleos, Servicio Geologico Nacional)*, vol. 7, pp. 325–341.
- Strauss, S.Y., Agrawal, A.A., 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14 (5), 179–185.
- Thayer, G.W., Engel, D.W., Bjorndal, K.A., 1982. Evidence for short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonia mydas* L. *Journal of Experimental Marine Biology and Ecology* 62, 173–183.
- Thayer, G.W., Bjorndal, K.A., Ogden, J.C., Williams, S.L., Zieman, J.C., 1984. Role of larger herbivores in seagrass communities. *Estuaries* 7 (4A), 351–376.
- de Toledo, P.M., Domning, D.P., 1991. Fossil Sirenia (Mammalia: Dugongidae) from the Pirabas Formation (Early Miocene), northern Brazil. *Boletim do Museu Paraense Emílio Goeldi, Série Ciências da Terra* 1 (2), 119–146.
- Trelles-Duelo, L., 1936. Restos fosilizados de un manati extinguido del periodo oligoceno inferior. *Memorias de la Sociedad Cubana de Historia Natural* 9 (4), 269–270.
- Varona, L.S., 1972. Un dugongido del Mioceno de Cuba (Mammalia: Sirenia). *Memorias de la Sociedad de Ciencias Naturales La Salle* No. 91 Tomo 32, 5–19.
- Vermeij, G.J., 1978. *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press, Cambridge, MA.
- Whetstone, K., Martin, L.D., 1979. An Oligocene (Orellan) sirenian from the Bucatunna Formation of Alabama. *Tulane Studies in Geology and Paleontology* 14 (4), 161–163.
- Zieman, J.C., 1982. The ecology of the seagrasses of south Florida: a community profile. *US Fish and Wildlife Service, Office of Biological Services, Washington, DC FWS/OBS-82/25*, 158 pp.