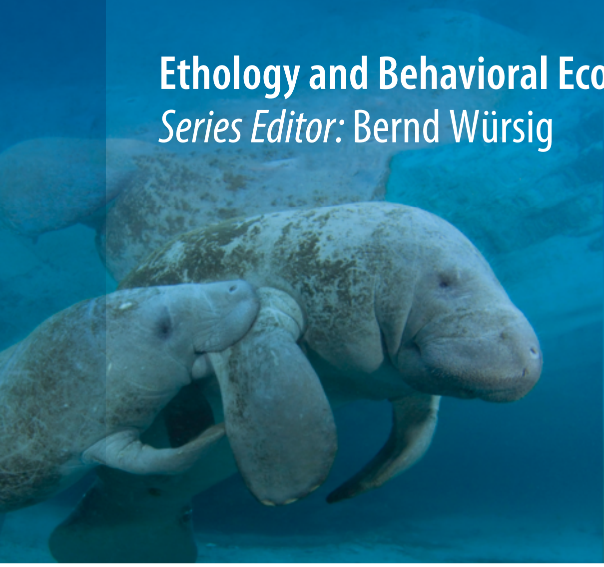
Ethology and Behavioral Ecology of Marine Mammals

Series Editor: Bernd Würsig



Helene Marsh *Editor*

Ethology and Behavioral Ecology of Sirenia

MOREMEDIA

Springer

Ethology and Behavioral Ecology of Marine Mammals

Series Editor

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The aim of this series is to provide the latest ethological information on the major groupings of marine mammals, in six separate books roughly organized in similar manner. These groupings are the 1) toothed whales and dolphins, 2) baleen whales, 3) eared seals and walrus, 4) true seals, 5) sea otter, marine otter and polar bear, and 6) manatees and dugong, the sirens. The scope shall present 1) general patterns of ethological ways of animals in their natural environments, with a strong bent towards modern behavioral ecology; and 2) examples of particularly well-studied species and species groups for which we have enough data. The scope shall be in the form of general and specific reviews for concepts and species, with an emphasis especially on data gathered in the past 15 years or so. A final 7th book was added since the beginning of this series, on "The Evolving Human Factor" to explore the effects that humans had, are having and will have (unless we change our ways) on these magnificent mammals of the seas. The editors and authors are all established scientists in their fields, even though some of them are quite young.

More information about this series at https://link.springer.com/bookseries/15983

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Ethology and Behavioral Ecology of Sirenia

Springer

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ISSN 2523-7500 ISSN 2523-7519 (electronic)
Ethology and Behavioral Ecology of Marine Mammals
ISBN 978-3-030-90741-9 ISBN 978-3-030-90742-6 (eBook)
https://doi.org/10.1007/978-3-030-90742-6

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Cover illustration: The close relationship between a mother and her calf is the most enduring feature of the social behavior of sirenians. On the left: A Florida manatee calf suckles from the left axillary teat of its mother. Photo by D.Schrichte/manateepics.com; On the right: Dugong mother and calf in Coral Bay, Western Australia. Photo by Samantha Lawrence.

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In his foreword to Marsh et al. (2011), John Robinson wrote: ‘On the surface of it, it seems preposterous to confuse mermaids and sirens with a 500 kg marine mammal with a face that only another sirenian might love’. Ten years later, this book confirms that the bond between a female sirenian and her nursing calf is long and strong and that the knowledge transmitted during the period of calf dependency is likely to be significant to individual survival. In future, deeper understanding of this knowledge may demonstrate the conservation significance of the mother love embodied in the mermaid legend and the ‘siren songs’ between mother and calf.

The top photograph of a Florida manatee and her calf is by David Schrichte. The bottom photograph of dugongs in Palau is by Mandy Etpison. Both are reproduced with permission. The reference is to Marsh H, O’Shea TJ, Reynolds JE III (2011) The ecology and conservation of Sirenia: dugongs and manatees. Cambridge University Press, 521pp.

Introduction to the Series

We—multiple topic editors and authors—are pleased to provide a series on ethology and behavioral ecology of marine mammals. We define ethology as "the science of animal behavior," and behavioral ecology as "the science of the evolutionary basis for animal behavior due to ecological pressures." Those ecological pressures include us, the humans. We determine, somewhat arbitrarily but with some background, that "marine mammals" habitually feed in the sea, but also include several mammals that went from saltwater oceans back into rivers, as see the chapter by Sutaria et al., first book on "Odontocetes." Polar bears represent a somewhat outlier "marine mammal," as they are quite at home in the sea, but can also feed on terrestrial mammals, birds, berries, lichens, and mosses.

In six books, we include toothed whales (the odontocetes); baleen whales (the mysticetes); sea lions and fur seals (the otariids) as well as the walrus; true seals (the phocids); the special cases of the sea otter and polar bear; and manatees and the dugong (the sirens). Each of our chosen editors and their chapter authors have their own schedules, so the series will not arrive in the order given above, but within the five years of 2019 through 2023, all six marine mammal books on "Ethology and Behavioral Ecology of Marine Mammals" will see light of day, and you, the readers, will be able to ascertain their worth and their promise, as to current knowledge and to accumulating data while our fields of science advance.

Since the first book on odontocetes came out in 2019, we added a seventh final book, on "The Human Factor," with chapters on past assaults on marine mammals, continuing assaults on the marine and other environments, dawning of awareness of assaults, and perhaps ways that we humans can and must do better. Several of us simply felt that to detail modern science of marine mammal ethology and behavioral ecology was not enough—we need to be aware of the amazingly destructive Anthropocene epoch in which we live, and try to improve, for all of nature (and therefore also for us). While topics of human influence run throughout each of the first six books, a concentration on human actions and potential solutions is needed.

Not all mammals that occur in marine waters are represented, nor all that have gone back to fresh water. Thus, there is nary a mention of marine-feeding bats, marine-feeding river otters, those aspects of beluga whales that foray way up into major rivers, seals living in land-locked lakes at times thousands of kilometers from the ocean, and other species that occasionally make the marine environment or—as generally accepted marine mammals—adjacent fresh water systems, their home. Such are the ways of a summary, and we apologize that we do not fully encompass all.

As series editor, I have been a science partner to all major taxonomic entities of this series, but this only because have been in the marine mammal field for about 50 years now, with over 65 graduate students who—in aggregate—have conducted research on all seven continents. In no manner do I pretend to have kept up with all aspects of diverse fields of modern enquiry. It is a special privilege (and delight) to have multiple up-to-date editors and their fine authors involved in this modern compilation, and I am extremely grateful (and humbled) for this. Still learning, and ever-so.

Each chapter is reviewed by the book editors, peer reviewed by other scientists as chosen by the editors and perused and commented on by me. If you learned something new and imparted that to your colleagues, students, or your own mentors, then the series and sections of it shall have been worthwhile.

Tortolita Desert, Arizona
December 2021

With respect and best wishes
Bernd Würsig

Preface

When series editor Bernd Würsig invited me to edit a book on the ethology and behavioral ecology of sirenians, I wondered whether there was enough material to justify a stand-alone volume on that topic. There are only four extant species of manatees and dugongs, and all are challenging to observe as they mostly occur in turbid waters and surface cryptically. All species are on the IUCN Red List of Threatened Species, mostly occur in developing countries and have "faces that only another sirenian might love".[1] Consequently, most research has been motivated by conservation concerns. Behavioral studies have rarely been a priority.

This book demonstrates that my concern was unjustified. There is a substantive body of research relevant to this topic, and the results were in urgent need of synthesis. I have certainly learned a lot through editing this volume and hope you will too as you read it.

From a biological perspective, sirenians are more different than most other marine mammals. As the only herbivorous mammals that spend all their lives in the water, they are grouped in a separate order in the clade Paenungulata. Thus, manatees and dugongs are more closely related to elephants and hyraxes than to other marine mammals. There are three recent genera: *Hydrodamalis* (one species), and the *Dugong* (one species) are in the Family Dugongidae; the three species of manatee, genus *Trichechus* in the family *Trichechidae. Hydrodamalis gigas*, (the giant Steller's sea cow), once ranged widely across the coastal waters of the North Pacific but was hunted to extinction within three decades after the relict population was discovered by "Western science" in the Commander Islands in the eighteenth century. The range of the dugong, *Dugong dugon*, spans some 40 Indo-West Pacific countries from east Africa to Vanuatu. Manatees occur on both sides of the Atlantic Ocean: the African manatee, *Trichechus senegalensis*, in 21 tropical countries in West Africa; the West Indian manatee, *Trichechus manatus*, mirrors this distribution on the other side of the Atlantic. The West Indian manatee has two sub-species: the Florida manatee, *Trichechus manatus latirostris,* which occurs in the southeastern USA and the Bahamas, and the Antillean manatee*, Trichechus manatus manatus*, with a range

[1] Quote from John Robinson's foreword to Marsh et al. (2011).

across 19 countries from Mexico to Brazil. The Amazonian manatee, *Trichechus inunguis*, exists in four countries in the Amazon basin.

Even though sirenian habitats are limited to relatively shallow waters where there is sufficient light to support the plant communities on which they depend for food, their habitats are diverse: The dugong is strictly marine, the West Indian and African manatees occur in coastal, riverine, and lake habitats, while the Amazonian manatee exists only in freshwater habitats. Unlike the extinct giant Steller's sea cow, all extant species are restricted to the sub-tropics and tropics due to their limited tolerance of colder water.

Although they are in separate families, manatees and dugongs look remarkably alike. The most obvious difference is in the shape of the tail: Manatees have a round tail like that of beavers (*Castor* sp.); the tail of a dugong somewhat resembles that of a cetacean. The build of a manatee is more robust than that of a dugong, the latter looks like a manatee that goes to the gym!

This book has eight chapters. Chapters 1 (Domning) and 2 (Marshall et al.) set the scene. The order Sirenia has a rich fossil record, and the three recent genera have adapted in radically different ways to environmental changes over the past 10 million years, especially with regard to their feeding adaptions. Chapter 1 explores what we can infer about the behavior of fossil sirenians from their skeletal remains. Chapter 2 explains the novel innovations of manatees and dugongs for life as aquatic herbivores. Their large body size confers thermal advantages and protection from predation. Their morphology also enables easy transitions from the benthic substrate, where their food is often located, to the surface where air is inhaled. Their perception of the aquatic environments is largely through somatosensation (touch and hydrodynamic reception) and hearing, although vision and taste (chemoreception) are also important to some degree. These morphological and sensory traits determine many aspects of sirenian ethology and behavioral ecology.

Chapters 3–6 describe the behaviors of manatees and dugongs: diving and feeding (Chap. 3: Keith-Diagne et al.), social and reproductive behaviors (Chap. 4: O'Shea et al.), and movements (Chaps. 5 and 6: Deutsch et al.). The diving achievements of all sirenians are modest, mostly reflecting the distributions of the food communities on which they depend. Although all sirenian diets are plant-based, it is likely that they all eat some animals as well. African manatees are arguably best described as omnivores. In contrast to dugongs, which apparently meet their water requirements from their food, all manatees like to drink fresh water. Sirenian social and reproductive behaviors lack much complexity or diversity and social groupings are transient, apart from the close relationship between a cow and her suckling calf. Home ranges overlap. Socially transmitted knowledge (tradition) is important to Florida manatees and perhaps all species, particularly when movements are necessary for survival.

The development and deployment of animal-borne GPS telemetry has enabled the movement behaviors of sirenians to be studied at a range of spatial scales, despite the difficulties of observing them directly. Consequently, Chip Deutsch and his collaborators required two chapters to synthesize knowledge of sirenian movement behaviors. Chapter 5 reviews sirenian movements across large spatial scales; Chapter 6 considers their movements and habitat use across diel and seasonal temporal scales.

Individual manatees and dugongs can be marathon swimmers, undertaking long-distance journeys over hundreds of kilometers. There is considerable variation in large-scale movement behaviors among and within individuals. The environments inhabited by manatees and dugongs are spatially heterogeneous and dynamic over a range of time scales. Sirenians must negotiate trade-offs among key activities within these fluctuating environments while minimizing exposure to predators including hunters and other anthropogenic threats.

In his Introduction to the Series, Bernd Würsig defines behavioral ecology as “the science of the evolutionary basis for animal behavior due to ecological pressures” and points out that these ecological pressures include us, the humans. We live in the Anthropocene, and human existence is now the biggest influence on the environment. Chapters 7 (Ponnampalam et al.) and 8 (Marsh et al.) consider the implications of current and future environments on the interactions between sirenians and people. Many sirenian habitats overlap with sites of high human use, and people have for millenia used knowledge of the predictability of sirenian habitat use and behaviors to capture them for their meat and other products. Manatees and dugongs nurse their calves over prolonged periods via axillary teats, fostering the widespread belief that sirenians are the basis of mermaid myths with associated folklore and magic. The cultural values of both dugongs and manatees are very high, especially for indigenous peoples. Dugongs and manatees are exposed to modern anthropogenic threats including habitat loss, vessel strike and the increased incidence of harmful algal blooms.

Climate change stressors are already affecting the subtropical and tropical coastal, estuarine, and riverine habitats of sirenians with consequential changes to their ethology and behavioral ecology. Climate stressors are predicted to increase over the coming decades and will be exacerbated by anthropogenic stressors, especially habitat loss and human food insecurity. The cumulative impacts on all sirenian habitats will be locally variable, but changes in habitat extent, continuity and food plants are likely to be widespread. Knowledge of how sirenians alter their behaviors in response to these changes will be central to designing strategies to increase their resilience to the climatic changes to their habitats.

Major questions remain. Do dugongs practice lek mating as well as scramble promiscuity, and if so is lek mating associated with “vocalization hotspots?” How great is the manatees’ physiological need for freshwater? What factors determine food quality for each species of sirenian? How do we determine the carrying capacity of sirenian habitats? How do sirenians navigate over large distances? How quickly can an individual update its cognitive environmental map, especially if it is no longer dependent on its mother? How do sirenians transmit information among conspecifics? The answers to these questions will determine capacity of sirenians to alter their behavior in response to climate change. I predict that knowledge of the behavioral ecology of sirenians will become central to future conservation efforts.

I am delighted to thank the many people who have assisted with this book, especially the 23 authors from seven countries and all major continents, a spread that fittingly represents the huge collective range of sirenians. The corresponding authors were remarkable in their persistence in “herding cats in a pandemic” and

their capacity to find photographers and artists that allowed us to reproduce their extraordinary works. Sirenians are notoriously difficult to photograph, and it is both wonderful and informative for this book to have such a fine spread of illustrations. I am extremely grateful to the reviewers and editors whose thoughtful comments improved the book, especially to Éva Lörinczi and her highly professional team at Springer. Series editor Bernd Würsig has been unfailingly supportive in gently and positively providing wise advice. Last but certainly not least, I thank my husband, Lachlan Marsh, for his unstinting love and support.

Townsville, Australia Helene Marsh
March 2022

All sirenians use their sensory hairs to obtain information about their environnment. These hairs occur all over the body but are most developed on the oral disk. In the top image, a dugong uses its oral disk to find sparse seagrass shoots (Photo by Ahmed Shawky). In the bottom image, two Florida manatees use their oral disks to explore the skin of a third (Photo by D.Schrichte/manateepics.com). Both images reproduced with permission.

Contents

Chapter 1
What Can We Infer About the Behavior of Extinct Sirenians?

Daryl P. Domning

Abstract Several aspects of the behavior of fossil sirenians can be inferred from their skeletal remains. Their transition from terrestrial walking to obligate swimming is relatively well documented by their postcranial skeletons. The salinity of their aquatic habitats, as well as their diets, is determinable from stable isotopes in their tooth enamel. Deflection and width of the front parts of their skulls, respectively, reflect where in the water column they fed, and how selective they were in feeding. Specializations of tusks and other teeth also offer hints about diet, intraoral food transport, and mastication. Sizes of the infraorbital and mental foramina may reflect the importance of their prehensile and tactile vibrissae. The three Recent sirenian genera have divergently adapted in radically different ways, especially in feeding adaptations, to environmental changes of the last 10 million years. Fossils shed little light on vision, chemical senses, or touch, apart from the facial vibrissae, but future study of their ear bones could reveal much about the evolution of sirenian hearing.

Keywords Ballast · Fossil sirenians · Habitat · Intraoral food transport · Locomotion · Mastication · Oripulation · Rostral deflection · Swimming · Teeth · Vibrissae

The fossil record of vertebrates is not usually considered to be a source of detailed behavioral data. Some broad generalizations, however, are possible, and specifically for the sea cows, there are several major categories of behavior on which fossil bones can shed at least dim light.

1.1 Habitat and Locomotion

As descendants of land mammals, sirenians obviously underwent a major transition to an aquatic lifestyle early in their history: so early, in fact, that no fully terrestrial ancestors have yet been identified. Proboscideans are generally considered their

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H. Marsh (ed.), *Ethology and Behavioral Ecology of Sirenia*, Ethology and Behavioral Ecology of Marine Mammals, https://doi.org/10.1007/978-3-030-90742-6_1

closest living relatives, although other Paenungulata, Afrotheria, or Tethytheria are possible candidates for their actual sister group (cf. Gheerbrant et al. 2005). This implies an Old World origin for the sirenia. A skull fragment of a very primitive, Early or Middle Eocene supposed sirenian has been reported from North Africa (Benoit et al. 2013); however, its postcranial skeleton and mode of locomotion are unknown. The next most primitive sirenian, *Prorastomus* (also known by just a skull; Savage et al. 1994; Table 1), from the early Middle Eocene of Jamaica (ca. 47 Ma), was aquatic enough to have at least followed the warm North Atlantic shoreline to the New World, if it did not actually swim the then-narrower low-latitude Atlantic Ocean (Fig. 1.1).

Somewhat later (late Middle Eocene, ca. 42 Ma), and also from Jamaica, is *Pezosiren* (Fig. 1.2*)*, the earliest sirenian known from fossils that adequately show the form of its body (Domning 2001a). It was a low-slung quadruped about 2.1 m long, with a relatively short neck, barrel-shaped trunk, short but strong legs, toes built for land rather than flippers, a firm sacroiliac joint that could support its weight on land, and a substantial (but not powerfully muscled) tail. The tall neural spines of its anterior thoracic vertebrae indicate a strong nuchal ligament that could support its heavy head and neck out of water. Although clearly amphibious, it bears distinct marks of having spent most of its time in the water (more so than a modern *Hippopotamus*, which rests in the water but forages on land): strongly retracted nasal openings, lack of paranasal air sinuses, and in particular some 20 pairs of swollen (pachyostotic)

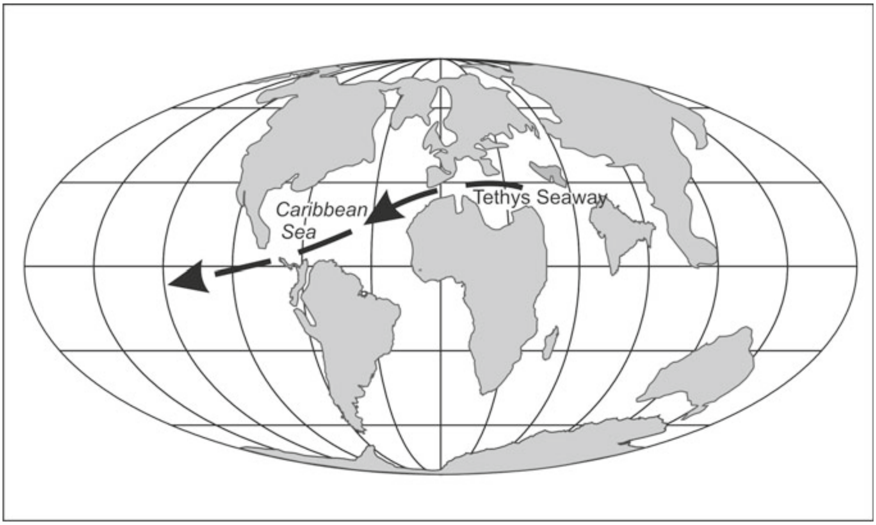

Fig. 1.1 Approximate positions of the major landmasses in the Middle Eocene. The Tethys Seaway (along the shores of which the early sirenians arose at an earlier time) was open at both ends, allowing dispersal of sirenians to the Caribbean via warm circumtropical currents (arrows). The Caribbean was also closer to the Tethys Sea in the Early Eocene than later in the earth's history, and warm waters extended above latitudes of the landmasses now known as Europe. (Map drawn by Adella Edwards, reprinted from Marsh et al. (2011) with permission)

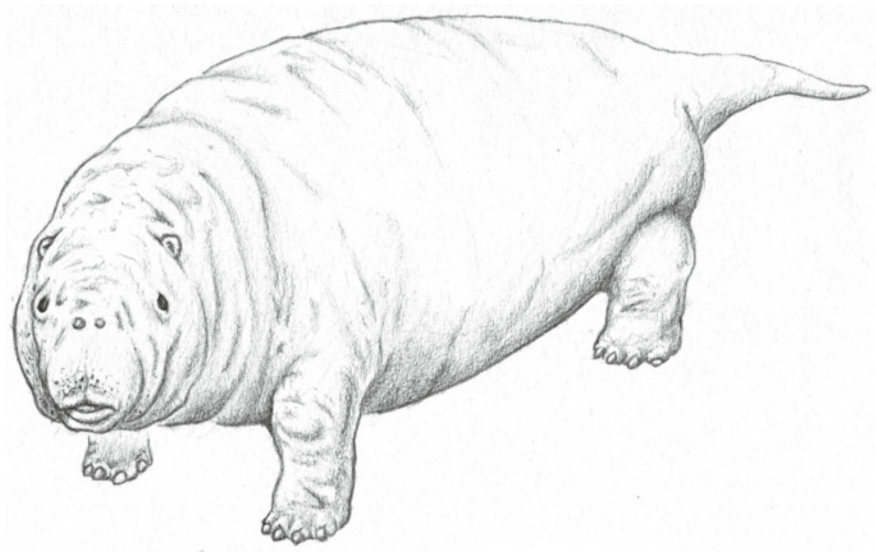

Fig. 1.2 Artist's model of possible appearance of *Pezosiren portelli*. (Model courtesy of locolobo.org, drawing by Gareth Wild, reproduced from Marsh et al. (2011) with permission)

ribs composed of bone nearly as dense (osteosclerotic) as those of modern sea cows (Buffrénil et al. 2010). These ribs serve as ballast, helping to provide neutral buoyancy, especially while feeding on bottom-growing plants (Domning and Buffrénil 1991). Judging from details of its vertebrae and hindquarters, *Pezosiren* swam by simultaneous pelvic paddling (kicking both hind legs backward together) along with dorsoventral pelvic undulation, foreshadowing the up-and-down tail propulsion of all later sea cows.

Corroborating the interpretation of aquatic habits based on sirenians' gross osteology is the evidence from stable isotopes in their tooth enamel, which show that these Eocene sea cows were already dwelling and feeding in saltwater, albeit of varying salinity (e.g., Clementz et al. 2009). Modern manatees (Trichechidae, Subfamily Trichechinae; Table 1) are euryhalic except for *Trichechus inunguis*, the most highly derived species, which is strictly freshwater. Although trichechines have a very limited fossil record (Domning 1982, 1997, 2005; Perini et al. 2020), the extinct trichechid subfamily Miosireninae was evidently marine, so the Family Trichechidae as a whole most likely was primitively marine as well. *T. inunguis* has fewer (14–16 pairs) and relatively slender ribs, while the other two living species (*T. manatus* and *T. senegalensis*) have more (respectively, 16–19 and 17–18 pairs) and broader and heavier ribs (especially *T. manatus*) (Domning and Hayek 1986), while the extinct *Miosiren* had 20 pairs of extremely massive ribs (Sickenberg 1934). This may reflect the freshwater habitat of *T. inunguis* and its consequent lesser need for ballast.

Sobrarbesiren (Middle Eocene of Spain; Diaz-Berenguer et al. 2018) and *Protosiren* (e.g., *P. smithae*, early Late Eocene of Egypt [ca. 37 Ma]; Domning and Gingerich 1994; Zalmout and Gingerich 2012) represent a diverse but poorly sampled Eocene adaptive radiation of amphibious sirenians that were more derived than *Pezosiren*. They show progressive weakening of the weight-bearing limbs, to the extent that *P. smithae* has been called "aquatic quadrupedal" rather than "amphibious quadrupedal" (Diaz-Berenguer et al. 2018). This trend continued with the development of propulsion using a powerful tail, followed by rapid loss of external hind limbs in the Late Eocene. Subsequent sirenians were all exclusively aquatic.

As part of their increasing efficiency at swimming, the Family Dugongidae (Table 1.1) had also evolved dolphin-like triangular flukes and a caudal-oscillation mode of propulsion, like cetaceans, by at latest the Early Oligocene. The flukes are indicated in fossil skeletons by widening of the caudal vertebrae posterior to the peduncle, as seen in the Recent *Dugong*. Manatees (*Trichechus*), in contrast, have retained a primitively beaver-like, rounded caudal fin in which the vertebrae steadily decrease in width toward the tip. Their mode of swimming is classified as caudal dorsoventral undulation, which is suited to a less active lifestyle than the dugong's (Kojeszewski and Fish 2007).

Steller's sea cow, *Hydrodamalis gigas*, was unique among sirenians in its great body size (clearly advantageous in its cold climate), but also unique among tetrapods in having lost entirely the phalanges of the front limb: its claw-like hand skeleton comprised only carpals and metacarpals, as observed and stated by Steller (1751).

Table 1.1 The families of Sirenia. References cited emphasize more recent literature and reviews. The online bibliography of Sirenia <http://sirendom.org/biblio> should be consulted for a more comprehensive listing of additional sources

Family	Time of occurrence	Distribution	References
Prorastomidae	Early middle to late Eocene	West Indies, North America, north and west Africa	Savage et al. (1994); Domning (2001a); Gheerbrant et al. (2005); Hautier et al. (2012); Benoit et al. (2013)
Protosirenidae	Early middle to late Eocene	Western Atlantic, Mediterranean, Indian Ocean regions	Domning and Gingerich (1994); Domning (2001b); Gheerbrant et al. (2005); Bajpai et al. (2009)
Dugongidae	Middle Eocene to recent	Mediterranean, Europe, North Africa, western Atlantic–Caribbean, Indian and Pacific oceans	Domning and Furusawa (1995); Domning (2001b); Gheerbrant et al. (2005)
Trichechidae	Oligocene to recent	Europe, South America, western Atlantic–Caribbean, North America, west Africa	Domning (1982, 2001b, 2005); Gheerbrant et al. (2005)

This reflected a major shift in uses of the flipper, from mainly steering and clasping food items or other animals, to harvesting seaweed and fending off from rocks. These inferences are corroborated by reconstructions of the forelimb muscles from their bony attachments (Domning 1978: 124–129). A Late Miocene ancestor of *Hydrodamalis*, *Dusisiren dewana*, displays an earlier stage in reduction of the phalanges (Takahashi et al. 1986). This feature corroborates Steller's account, which some later anatomists had difficulty believing, as evidenced by their attempts at reconstructing the animal's appearance (e.g., Kleinschmidt 1951). Even harder to accept has been the testimony of Steller and other eyewitnesses that *H. gigas* was so buoyant that it was never seen to entirely submerge. Although loss of diving ability has not been (and perhaps cannot be) confirmed from the *H. gigas* skeleton alone, it is actually reasonable to assume when neck muscle attachments, other anatomical and physiological considerations, and arguments from selective value are taken into account (Domning 1978: 129–132). Its body size increase compared to its ancestors, including a proportionately larger gut and possibly greater lung gas volume, meant that the bones made up proportionately less of the body, thereby having less capacity to act as an "inbuilt weight-belt." Keeping part of the back out of the water would reduce heat loss to the water. The thick blubber layer would have done the same, while further enhancing the animal's buoyancy. Floating would also have reduced wave drag while swimming at the surface, allowed access to shallower water to forage and elude predators, reduced skin area accessible to parasites, and permitted birds to remove them. On the other hand, obligate rather than facultative buoyancy would have diminished access to deeper-growing plants, exposed the back to subzero air temperatures, and exposed any open wounds to further damage by birds. On the whole, the adaptations of *Hydrodamalis* would seem to repay further analysis.

1.2 Interactions with Other Animals

1.2.1 Parturition and Care of Young

There is no direct indication of whether prorastomids or other amphibious sirenians gave birth on land or in the water. However, the extreme slenderness and fragility of a juvenile *Pezosiren* femur (105 mm long, with mid-shaft diameters of only 9 × 6 mm) casts doubt on the ability of juveniles to support their body weight on land until quite some time after birth. Whether born on land or in the water, therefore, they might have started to swim at an early age; but they must have rested on their bellies like seals whenever they hauled out, until the shafts of their long bones had thickened enough to support them in the manner of adults. Whatever provision the parents made in the meantime for care of their offspring and their protection from predators is open to speculation.

1.2.2 Mating Systems

Social arrangements of extinct sea cows also remain speculative beyond what we might extrapolate from observations on the living species, as Anderson (2002) has done in great detail. Judging from the Recent sirenians alone, these social systems may always have been quite diverse, as they are in terrestrial herbivores. The same goes for other aspects of natural history such as circadian behavior, movements, and migrations, which may lie forever beyond the reach of the paleontologist.

On the borderline between the extinct and extant realms are the few eyewitness reports of the behavior of *Hydrodamalis*. For example, in contrast to scramble promiscuity in manatees, and in some dugong populations, and alleged lek mating by dugongs in eastern Shark Bay in Western Australia, Anderson (2002) noted Steller's observations that it formed monogamous pair bonds and presented an ecological rationale supporting this mating system. Anderson's analyses are a rich source of testable hypotheses about mating in other prehistoric sirenians, if anyone is clever enough to devise suitable tests.

1.2.3 Agonistic Encounters

Anderson (2002) also emphasized the potential role of tusks in mating and other social interactions, a role which has also recently been documented in a study of scars inflicted on the skin of dugongs by the tusks of other dugongs (Lanyon et al. 2021). However, this behavior is unlikely to leave its mark in the fossil record. What are frequently observed on fossil sirenian (and other marine mammal) bones, are scars made by shark teeth, whether the result of predation or scavenging is unknown. An interesting question is the extent to which the sirenians might have actively defended themselves from sharks or other predators like killer whales or crocodilians. There are anecdotal reports of a bull dugong disemboweling a shark with its tusks to protect the calves in its herd (Promus 1937) or killing a crocodile by repeatedly jumping out of the water and landing on top of it (Sunter 1937), although, again, corroboration is lacking and fossil evidence still more so.

As for the tusks themselves, Anderson (2002) acknowledges their multifunctionality (for social functions, whether intra- or interspecific, and for use in foraging) and ponders which uses have been primary versus secondary in evolution. He argues (p. 78) that "[e]volution and retention of tusks exclusively, or even primarily, as foraging structures would be unique among mammalian herbivores." But then, no other mammalian herbivores have been exclusively aquatic. My own thinking is that tusks are teeth and teeth are primitively for feeding, but this function has never excluded simultaneous use for other purposes that may present themselves. This will be expanded upon below.

1.3 Feeding

1.3.1 Diet

We know from the living species that the sirenians have the collective capacity to feed on almost any plant types anywhere in the water columns of their marine or freshwater habitats. Occasionally, they even feed on plants close to, or overhanging, the water, even though individual species, especially the dugong, are more specialized (Chap. 3). Most fossil sirenians were tropical and marine, and thus (like modern dugongs) presumably fed on seagrasses in preference to algae (a supposition confirmed by stable isotopes; Clementz et al. 2009), though the cooler-water, kelp-eating hydrodamalines were an exception (Domning 1978).

1.3.2 Vibrissae

A more applicable generalization is that sirenians have always relied heavily on their muscular lips and vibrissae for sensing, grasping, and ingesting plants, which Reep et al. (2001) call "oripulation" (in effect, manipulation by mouth instead of hands; see Chap. 2). This is reflected in the fossil record by the increased size and/or number of the infraorbital and mental foramina: openings on the side of the snout and lower jaw, respectively, that carry branches of the trigeminal nerve, which transmit touch sensations from the vibrissae. Sirenians more derived than the Eocene prorastomids and protosirenids show marked enlargement of the infraorbital foramen in particular, suggesting that the array of vibrissae (and, implicitly, the facial muscles that move them, and the blood vessels that supply the muscles) had taken on greater importance in the animals' behavior.

1.3.3 Rostral Deflection

A still more direct and sensitive indicator of feeding behavior is the form of the rostrum, the enlarged bony snout that characterizes all sirenians. In the earliest known form, *Prorastomus* (Savage et al. 1994: Figs. 1, 6), this projects horizontally forward from the braincase as in land mammals. But in all later sea cows, the rostrum is turned down to varying degrees, so that its palatal surface forms a plane deflected from the occlusal plane of the cheek teeth. As explained in Chaps. 2 and 3, the angle of deflection correlates with the extent to which the extant manatees rely on bottom-growing plants for their diet: 15–40° (mean of 20 = 25.8°) in *Trichechus senegalensis*, which feeds on overhanging, shoreline, emergent and floating aquatic plants, as well as benthic ones; 25–36° (mean of 35 skulls = 30.4°) in *T. inunguis*, which feeds almost entirely on floating vegetation; and 24–52° (mean of 72 = 38.2°) in *T.*

manatus, which has as broad a dietary range as *T. senegalensis* but with more access (especially in Florida) to marine habitats with benthic seagrasses (Domning 1982; Marsh et al. 2011). In marked contrast, the exclusively bottom-feeding *Dugong* has rostral deflections in the neighborhood of 67–72° (in 3 *D. dugon*). The sirenian mouth is consequently subterminal, and where the deflection is as great as in *Dugong*, it opens nearly straight down (see Chap. 2), as is desirable for an essentially obligate bottom-feeder. The deflection is accordingly seen as a good indicator of where in the water column fossil sirenians fed.

1.3.4 Cropping Mechanism

Another relevant variable seen in the upper and lower jaws is the width of the masticating surfaces at the front of both jaws, particularly that of the mandible. In *Prorastomus*, the latter surface is extremely narrow, scarcely wider than the parallel left and right tooth rows borne by the very elongate mandibular symphysis (Savage et al. 1994: Figs. 6, 8). Together with the rostral masticating surface, which is also relatively narrow, this forms an almost forceps-like mechanism well suited for selective browsing amid diverse stands of floating as well as benthic plants. Later sirenians, in contrast, such as the modern dugong, which is a seagrass community specialist (Marsh et al. 2018), generally show mandibular surfaces that are proportionately much broader. An analogous contrast has been documented in terrestrial herbivores, between narrow-snouted browsers and broad-snouted grazers (Janis and Ehrhardt 1988).

1.3.5 Tusks

Most fossil sirenians had first upper incisors that were enlarged to various degrees to form tusks. These were primitively small and conical in most Eocene forms and do not show much potential as weapons of defense or offense. In most later dugongids the tusks came to be larger, with deep roots extending most, or all of the length of the premaxillary symphysis, and accordingly more likely to have had social uses along with more forceful application as digging tools. In a few specialized Oligocene and Miocene dugongines like *Rytiodus* and *Corystosiren*, the tusks became flattened and bladelike with a posterior, self-sharpening cutting edge held up by thin enamel that covers the medial surface (Fig. 1.3). These cutting tools (rather resembling a box-cutter, with a short cutting edge attached to a large handle embedded deep in the bone) are interpreted as having been used to sever the tough, fibrous rhizomes of large seagrasses like *Thalassia*, whereas rhizomes of the smallest seagrasses (e.g., *Halophila*) can be harvested efficiently even without tusks (Domning and Beatty 2007). The similarly self-sharpening tusks in *Dugong dugon*, however, are large but sexually dimorphic: developed in both sexes, but erupting only in males and

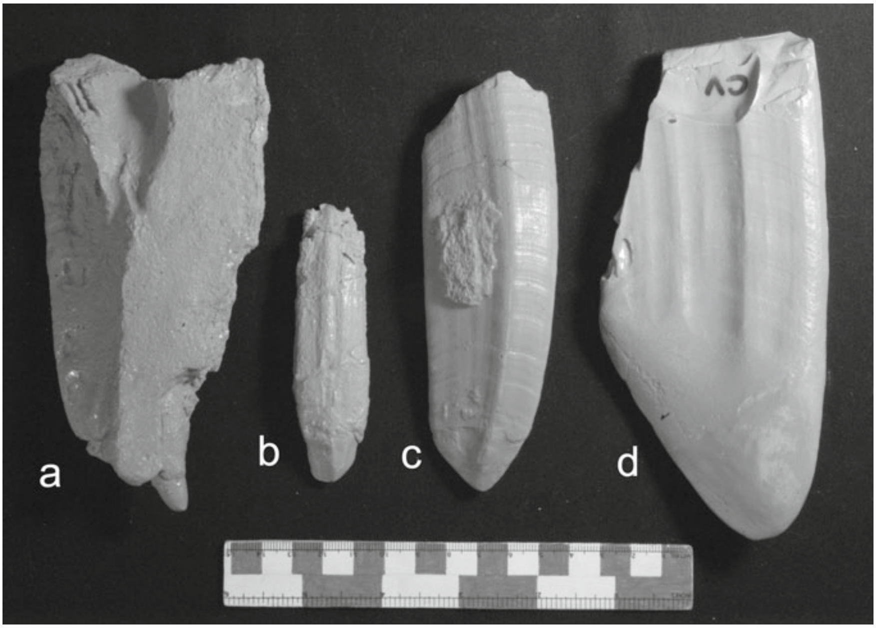

Fig. 1.3 Replicas of fossil sirenian tusks: **a** *Metaxytherium floridanum*, left tusk in premaxilla, medial view. **b** *Crenatosiren olseni*, right tusk, medial view. **c** *Dioplotherium manigaulti*, left tusk, medial view. **d** *Corystosiren varguezi*, distal part of right tusk, lateral view showing broad wear surface, partly restored. The tusks were self-sharpening because of the different thickness of the enamel on different sides of the tusk. Scale bar = 15 cm. Reproduced from Domning and Beatty (2007) with permission

post-reproductive females, and apparently no longer important in feeding but only in social interactions like fighting and mating (Marsh 1980; Domning and Beatty 2007; Lanyon et al. 2021; Chap. 4).

1.3.6 Intraoral Food Transport

Prorastomus retained full batteries of anterior teeth (incisors and canines) that lined the edges of the rostral and mandibular masticating surfaces. These more-or-less peg-like teeth, which evidently did not occlude with one another (only with the food), doubtless formed part of the cropping mechanism. But in addition, they (especially the more posterior ones, including most of the premolars) seem likely to have aided in intraoral food transport. The tongue is short in sirenians, not reaching to the front of the mouth, so these anterior teeth might have served like a ratchet to keep ingested vegetation moving toward the back of the mouth. This became all the more necessary as the rostral deflection became steeper.

But coincident with this development, something else occurred: In almost all sirenians, the incisors (excepting the first upper incisor tusk, if present) and the canines were steadily lost over the course of the Eocene and Early Oligocene, leaving the anterior masticating surfaces toothless, but covered with horny pads. While these pads are useful for grasping and crushing plant material, they also (at least in *Dugong*) form a surprisingly effective transport mechanism (Chap. 2). The surfaces of these pads are formed by short, closely packed bristles that are angled posteriorly (Lanyon and Sanson 2006a). When the upper and lower pads are rubbed together, leaves placed between them are moved steadily up the sloping surfaces toward the cheek teeth, as though on a conveyor belt. I suspect that this proved so efficient a means of intraoral transport that it rendered superfluous the much larger and clumsier incisors, canines, and anterior premolars.

1.3.7 Mastication

This brings us to the cheek dentition, which primitively in sirenians comprised five premolars and three molars in each jaw quadrant. Deciduous teeth occupied all the premolar positions (except possibly the first). These were replaced during growth, as in most mammals, and the permanent ones were more peg-like, like the more anterior teeth. Whether these five premolars (instead of the four found in typical placental mammals) represent a primitive condition retained from Mesozoic mammals, or a derived condition unique to sirenians, remains in doubt. What we do know, however, is that from almost their first appearance in the fossil record sirenians started *losing* teeth, beginning with the permanent fifth premolars. This loss resulted in that tooth's deciduous precursor (which resembled the true molars in having a low crown with two transverse ridges formed by distinct cusps) being retained into adulthood, thereby increasing the functional molariform battery from three to four. Thereafter, the more peg-like anterior teeth (all the permanent and most of the deciduous ones) were gradually eliminated in the course of evolution, starting at the front. By the Late Oligocene and continuing down through the Pliocene, a typical adult sirenian (of which nearly all the known ones were dugongids) had only a first upper incisor tusk on each side, separated by a long diastema (toothless gap) from the cheek tooth battery, which comprised the molariform fifth deciduous premolar followed by three molars (Domning 1982). These four teeth came into wear in sequence, so they display a strong front-to-back gradient of decreasing wear. By maturity, the fifth premolar is usually worn out and lost, followed by loss of one or more of the molars in old age.

What does all this tell us about behavior? First, that for most of the last 28 million years nearly all sirenians had settled on a tried-and-true oral mechanism for processing seagrass in a very stable tropical to subtropical marine ecological niche and there was no reason to experiment very much with this mechanism (except for the tusks, as discussed below). Thus in contrast to most fossil mammals, sirenian teeth are not particularly useful for distinguishing species or higher taxa: The molars mostly look pretty much alike, and identification and classification have to be based mainly on the structure of the skull itself.

But then, within the last 10 million years or even less, all sirenians with dentitions like those just described either went extinct or evolved into something quite different. This was doubtless due in various ways to the significant global cooling and other environmental changes that occurred during this period. In any case, all three of the lineages that survived into historic times evolved feeding adaptations drastically different from each other and from any that came before.

Hydrodamalis: In the North Pacific, climatic cooling, consequent marine floral shift from a tropical seagrass-dominated to a temperate kelp-dominated ecosystem, and (in North America) tectonic uplift and draining of coastal: embayments (e.g., the Central Valley of California), led to the evolution of a cool-adapted lineage culminating in Steller's sea cow (*H. gigas*) (Domning 1978; Takahashi et al. 1986; Domning and Furusawa 1995). This genus was characterized not only by large body size (for heat retention) and the loss of phalanges noted above (producing a boathook-like forelimb, useful for fending off from rocks on high-energy shorelines), but also total loss of teeth (permitted by a non-fibrous algal diet) and mastication performed solely with the horny rostral pads.

Trichechus: In South America, temporary conversion of the western Amazonian region into a closed basin with interior drainage appears to have isolated a population of Miocene trichechids, while also fertilizing the waters of this basin with runoff from the rising, rapidly-eroding Andes Mountain range. This nourished a freshwater ecosystem dominated by floating true grasses, which contained not only nutrients but also highly abrasive siliceous phytoliths that radically increased the rate of wear on the teeth of the sirenians. They adapted by evolving the endless horizontal replacement of small, cheap, disposable molars that characterizes *Trichechus*. Subsequent breakthrough of Amazonian drainage to the Atlantic allowed dispersal of these manatees to North America and West Africa, with subsequent speciation, and may even have equipped them to outcompete Caribbean dugongids having less wear-resistant teeth (Domning 1982, 1997, 2005; Domning and Hayek 1984).

Dugong: Probably the latest, the least dramatic, but certainly the most complex and mysterious of the evolutionary innovations for feeding seen in modern sea cows was the set of dental modifications found in the Indo-Pacific dugong:

1. Most conspicuously, the cheek tooth battery has degenerated by functional loss of the enamel crowns of the teeth, which initially form but are very thin and wear off quickly. In compensation, the last two molars in each quadrant retain open, ever-growing roots (root hypsodonty), so that at maturity the animal has only pegs of dentine with flat occlusal surfaces (Marsh 1980): teeth that seem only better than no teeth at all, and whose very functionality has even been questioned (Lanyon and Sanson 2006a, b).
2. In immature specimens, there is a tiny upper incisor that never erupts, lying *anterior* to the definitive (presumably first incisor) tusk (Marsh 1980). While this

seems most likely to be a deciduous first incisor, such a precursor to the permanent tusk has never been observed in any fossil sirenian.

3. Dugongs have four pairs of shallow empty pits on the mandibular masticating surface, which are assumed to be the vestigial alveoli of the lower incisors and canines. These are covered by the lower masticating horny pad. In many adult *D. dugon*, however, one or more of these pits are deep and contain vestigial teeth that never erupt (e.g., Lyman 1939; Lanyon and Sanson 2006b: Fig. 1.1). Similar deep pits containing unerupted teeth are never seen in fossil sirenians that have lost the erupted lower incisors and canines.
4. As noted above, the tusks in *D. dugon* are sexually dimorphic and apparently used only in males, and then only in social interactions like fighting and mating (Marsh 1980; Domning and Beatty 2007; Chap. 4). No such tusk dimorphism has been documented for any fossil sirenian (Sorbi et al. 2012).

All four of these features suggest that some heterochronic developmental process has been at work in the evolution of the dugong's dentition. The arrested development of the female tusk and the enamel crowns of the molars, the vestigial and non-erupting upper and lower incisors, and the persistently open roots of the posterior molars may have been achieved at least in part by a neotenic mechanism (Domning 1995).

All of these features together suggest the hypothesis (Domning 1995) that *Dugong* cheek teeth represent a desperate evolutionary attempt to salvage some chewing capacity under conditions of severely increased tooth wear that was beginning to cut into the animals' reproductive lifespan—a plausible explanation given that lack of food reduces dugong reproductive output today (Chap. 8). The only plausible cause of this in a marine environment over a huge area (the Indo-Pacific seas) would seem to be increased runoff of abrasive siliciclastic sediment into seagrass beds due to accelerated erosion resulting from global eustatic sea level drop during a glacial period. Faced with increased wear of its molar crowns, the dugong evidently resorted to root hypsodonty of molars 2 and 3 as an alternative to total loss of a functional cheek dentition. However, the resulting abandonment of molars having enamel cutting edges made the eating of fibrous material (i.e., large rhizomes) no longer energetically feasible, so the species shifted its diet to less fibrous seagrasses and possibly a nutritional strategy based more on cell contents than on cell walls.

The dugong's present preference for the most delicate, easily chewed and digestible seagrasses (in particular, *Halophila*) may also be reflected in one more skeletal feature. The ribs of *D. dugon*, while as dense (osteosclerotic) as those of other sirenians, are noticeably slenderer (less pachyostotic): in fact, among the slenderest ribs of known fully aquatic sirenians. This reduction in ballast could facilitate resurfacing from deep diving, and unlike other sirenians, dugongs may dive as deep as 36 m (Marsh et al. 2011:157; Chap. 3) in areas where large beds of *Halophila* (the deepest-growing seagrass; York et al. 2015) are found at that depth. The above hypothesis would imply that the dugong's dental degeneration occurred only after the beginning of the Pleistocene glaciations. Unfortunately, *D. dugon* itself has a negligible fossil record that might be used to test this idea. As it happens, however, it has a close sister taxon (arguably a congener; still undescribed because it is known only from one skull in a private collection) that dates from near the beginning of the Pleistocene, around 2 million years ago, and still has fully enameled molars, just as this hypothesis predicts. The most surprising thing about this specimen is that it was found not in the Indo-Pacific region, but in Florida—suggesting dispersal across the Atlantic and around the Cape of Good Hope, possibly at the same time manatees crossed to West Africa.

Lest the foregoing leave the impression that the dental adaptations of all the Sirenia are well understood, attention must be paid to *Miosiren*, a strange Miocene trichechid from Belgium and England. Its dentition is in itself only moderately surprising (large, conical upper tusks; retained permanent premolars 3 and 4; conventional-looking enameled molars except for a reduced, peg-like third molar). But its palate and the solid bony walls that support the palate are astonishingly thick (~4 cm) (Beatty et al. 2012: Fig. 1.3), suggesting that in comparison with any other sirenian, it generated enormous occlusal forces when chewing whatever it was that it ate. It certainly seems over-engineered for eating ordinary seagrass. A diet of molluscs has been suggested and not ruled out, but stable isotopes have not so far been able to shed light on its diet, whether vegetable or animal. Calcareous algae are a possibility, or the thickened skull bones may merely have served for ballast. In any case, there are still striking mysteries to be solved in sirenian paleontology.

1.4 Sensory Perception

Compared with the foregoing topics, there are few clues to sirenian sensory systems in the fossil record. There are no osteological signs of changes in sirenian vision over their evolutionary history. Neither, as far as we can tell, have the chemical senses of taste and smell changed very much. All sirenians retain cribriform plates (the sieve-like bony structures at the front of the braincase through which pass the olfactory nerves). This suggests that sirenians do have some sense of smell, which is more than can seemingly be said for modern cetaceans, in which the cribriform plate is greatly reduced (in baleen whales) or absent (in toothed whales). But the chemical senses have scarcely been studied even in the living sea cows (see Chap. 2). Florida manatees reportedly lack a vomeronasal organ, but retain taste buds, some olfactory epithelium and a rudimentary olfactory bulb (Mackay-Sim et al. 1985; Marriott et al. 2013; Barboza and Larkin 2020).

As described above and in Chap. 2, touch is an important sense in sirenians. Not only do they have well-developed tactile vibrissae on their snouts, but the sparse hairs all over their bodies are likewise sinus hairs, which seem to constitute an analog to the lateral-line systems of fishes (Reep et al. 2002; Gaspard et al. 2017; Chap. 2). Again, though, these have left no trace in the fossil record.

Although they do not echolocate, sirenians do have sensitive hearing (Chaps. 2, , 7). Indeed, the best chance of tracing the evolution of sirenian senses is offered by the bones of the ear, which are well represented throughout the history of the order, starting with the earliest, most primitive of them all: the Early or Middle Eocene sirenian reported by Benoit et al. (2013), which consists precisely of a petrosal bone. Unfortunately, the ears of fossil sea cows have hardly been studied from a functional viewpoint, but there is potential for future investigators. Even insights into underwater vocal communication may be conceivable.

1.5 Concluding Remarks

There are several clear ways forward to gain further insights into the "paleoethology" of sirenians, two in particular: collecting more complete specimens of species still inadequately known and employing new techniques of analyzing the fossils already in hand. Under the first heading comes traditional paleontological fieldwork to discover new forms of sirenians previously unknown (as is happening every year), and to recover better material of known taxa. An outstanding example of a specimen already in hand and needing basic description is the manus of Steller's sea cow: the first known skeleton that appears to preserve these bones was reportedly excavated in 2017 on Bering Island. It should have urgent priority for study by Russian morphologists. Under the second heading are studies of the inner ear by CT scanning; stable isotope and other forms of chemical analysis of teeth and bones, and biomechanical studies such as principal-components analyses of skull architecture to reconstruct the stresses caused by tusk use and mastication.

Beyond these, discoveries in the decades to come will be limited only by technology and the imagination of new generations of investigators. Such progress would include inferences from fossil endocasts of sirenian brains, which have been studied since Owen (1875), especially by Edinger (1933, 1975) and most recently by Kerber and Moraes (2021). Since I lack the knowledge of neuroanatomy needed to interpret behavior from such specimens, however, I must leave this study to others.

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