

Orofacial morphology and feeding behaviour of the dugong, Amazonian, West African and Antillean manatees (Mammalia: Sirenia): functional morphology of the muscular-vibrissal complex

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Abstract

The external orofacial morphology, perioral bristle distribution and feeding behaviour of *Dugong dugon*, *Trichechus inunguis*, *T. senegalensis* and *T. manatus* are described. Despite their differing orofacial morphology, dugongs and trichechids possess six similar regions: the oral disk, orofacial ridge, supradisk, chin and upper and lower bristle (modified vibrissae) pads. All living sirenians possess six discrete fields of bristles: four on the upper lip (U1, U2, U3, and U4) and two on the lower lip (L1 and L2). The distribution of these fields is similar among all living sirenians with the exception of the U1 bristle fields in dugongs. Perioral bristle field boundaries are distinguished by distinct changes in their length-to-diameter ratios. Both dugongs and trichechids possess bristle-like hairs covering the oral disk, which possess length-to-diameter ratios intermediate between perioral bristles and postcranial hairs. Sirenians use elaborated facial musculature in conjunction with perioral bristles to acquire, manipulate and ingest aquatic vegetation. The U2 and L1 fields are the primary bristles used to ingest vegetation. The use of the L1 bristle fields is similar among all living sirenians. However, dugongs and trichechids are divergent in their use of the U1 and U2 bristle fields. Dugongs use the U2 bristles fields in a medial-to-lateral motion, while all trichechids use the U2 bristles in a prehensile, lateral-to-medial, grasping motion. These divergent behaviours presumably allow dugongs to exploit benthic foraging (i.e. consumption of rhizomes) to a greater degree than trichechids. Functional hypotheses of rhizome excavation are presented for both dugongs and trichechids.

Key words: feeding behaviour, perioral bristles, Sirenia, *Dugong*, *Trichechus*

INTRODUCTION

Sirenians are the only herbivorous 'marine mammals' in existence today. They are a relict group; only four species from two families are extant. The once diverse Dugongidae are represented by a single species, the dugong *Dugong dugon*. Dugongs are entirely marine and are benthic feeding specialists, consuming primarily the leaves and rhizomes of sea grasses (Potamogetonaceae and Hydrocharitaceae) (Kingdon, 1971; Heinsohn & Birch, 1972; Lipkin, 1975; Heinsohn *et al.*, 1977; Anderson & Birtles, 1978; Johnston & Hudson, 1981; Marsh *et al.*, 1982). Depending upon the species of sea grass being consumed, dugongs target either

the leaves alone (grazing) or uproot the entire plant (rooting) and consume leaves, roots and rhizomes. The excavation and consumption of rhizomes and roots is important to the dugong diet (Heinsohn & Birch, 1972; Marsh *et al.*, 1982; Preen, 1995b; Marsh *et al.*, 1999; Aragonés & Marsh, 2000), especially *Halodule* (Anderson, 1998) because it is high in digestible carbohydrates (Waldron, Baydon & Brett, 1989). Dugongs are also known occasionally to supplement their herbivorous diet with macro-invertebrates (Preen, 1995a). The Trichechidae are more generalist browsers and comprise three species, the West Indian manatee *Trichechus manatus*, Amazonian manatee *T. inunguis* and West African manatee *T. senegalensis*. West Indian manatees include two subspecies, the Florida manatee *T. m. latirostris* and the Antillean manatee *T. m. manatus* (Domning & Hayek, 1986; Garcia-Rodriguez *et al.*, 1998). West Indian manatees are widely distributed,

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exploit all available habitats (marine, estuarine and freshwater systems), and are known for their diverse feeding habits (Bertram & Bertram, 1973; Hartman, 1979; Best, 1981; Ledder, 1986; Lefebvre *et al.*, 1989; Marsh & Lefebvre, 1994). In contrast, Amazonian manatees are restricted to the freshwater rivers, lakes and floodplains of the Amazonian basin where they feed upon emergent grasses (Gramineae), inundated vegetation of the várzea and igapó, and 'floating meadows' (Bertram & Bertram, 1973; Husar, 1977; Best, 1981; Rosas, 1994). West African manatees are similar to West Indian manatees in that they move between marine, estuarine and freshwater habitats, and feed upon aquatic angiosperms in each system (Bertram & Bertram, 1973; Husar, 1978; Best, 1981; Marsh & Lefebvre, 1994). They are the least known sirenian and little is known about their trophic ecology. However, the habitat of the West African coast is not conducive to sea grasses and it is thought that they are not an important part of the West African manatee diet (Lawson, 1966; Domning, 1982; J. A. Powell, pers. comm.). Additionally, the murky water does not support extensive submerged aquatic vegetation, therefore *T. senegalensis* most likely relies upon natant and emergent aquatic and semi-aquatic vegetation.

Several morphological traits of the sirenian feeding apparatus influence their trophic ecology. One such trait is the degree of snout deflection, relative to the palatal plane. Snout deflection influences where in the water column sirenians feed and therefore the types of plants (benthic, mid-water or natant) consumed (Domning, 1976, 1978b, 1982). Of the four living sirenian species, *T. inunguis* and *T. senegalensis* have the least deflected snouts ($\sim 30^\circ$ and 26° , respectively) presumably an adaptation for feeding primarily upon natant vegetation. Dugongs possess the most deflected snout of the living sirenians ($\sim 70^\circ$). Their down-turned rostrum places the perioral region nearly parallel to the substrate (within 10° ; Anderson, 1979), an energetically advantageous position for a benthic forager. The snout deflection of West Indian manatees ($\sim 38^\circ$) is intermediate between those of the other trichechids and the dugong. This arrangement is best suited for its generalized foraging niche that includes benthic and surface feeding.

Another important relationship between sirenian morphology and trophic ecology is the use of a specialized muscular-vibrissal complex (elaborated facial musculature and vibrissae). Florida manatees use vibrissae in a prehensile motoric function, in addition to a sensory function, to manipulate vegetation and introduce it into the mouth (Marshall, Clark & Reep, 1998a; Marshall *et al.*, 1998b; Reep *et al.*, 1998; Bachteler & Denhardt, 1999; Reep *et al.*, 2001). This type of feeding is unique among mammals. Classically, vibrissae are used solely to pick up tactile cues during whisking or relatively passive behaviours. But is perioral bristle use in Florida manatees representative for all living sirenians, and are there differences in perioral bristle use between benthic specialists, dugongs and the more generalized trichechids? The objectives of this study are to describe the morphology of the muscular-vibrissal

Table 1. Abbreviations of sirenian orofacial morphology

cc	Central crease
chc	Chin crease
hp	Horny palate
lf	Lateral furrow
lfl	Lateral flaps
m	Mandible
mx	Maxilla
n	Nares
od	Oral disk
orf	Orofacial ridge
rc	Rostral crease
sd	Supradisk
t	Tusk

complex, the distribution of perioral bristles, and their use during functional feeding studies of the remaining living sirenians, dugongs, Amazonian, African and Antillean manatees. Functional hypotheses of rhizome excavation based on known orofacial myology, foraging behaviour and functional feeding experiments will be proposed for both dugongs and trichechids.

METHODS

Descriptions of dugong orofacial morphology are based on observations and measurements of 2 cadavers at the National Museum of Natural History (USNMNH specimen numbers 307610 and 307611), >100 hours of observation of 2 captive dugongs (Toba Aquarium, Mie Prefecture, Japan), necropsy photos and videos of free-ranging dugongs. Descriptions of *T. inunguis* and *T. m. manatus* orofacial morphology are based on ~ 100 hours of observation of captive individuals of each species ($n = 1$; Yomiuriland Marine Aquarium, Tokyo, Japan), and from observations of bottle-fed captive *T. inunguis* at the Instituto Nacional de Pesquisas da Amazonia ($n = 3$; INPA, Manaus, Brazil). Orofacial morphological descriptions of *T. senegalensis* are based on observations of 2 individuals also kept at the Toba Aquarium. A summary of the morphological abbreviations can be found in Table 1.

Functional feeding experiments were conducted with 2 dugongs, 2 West African manatees (Toba Aquarium), 1 Amazonian manatee and 1 Antillean manatee (Yomiuriland Aquarium). These controlled feeding trials involved the use of several versions of a plexiglass feeding platform that enabled close-up views of the perioral region during feeding. Plexiglass feeding platforms used were similar to that described by Marshall *et al.* (1998b). Feeding behaviours were also observed during hand-feeding and as part of their normal feeding regimes. The dugong feeding platform differed significantly from that of the other platforms in that the feeding surface was bent at a 90° angle and presented sea grasses to dugongs at a 45° angle when in position (Fig. 1). Based on the kinematic data, this compromise between the preferred video taping angle and the subject's preferred feeding angle did not appear to influence normal feeding

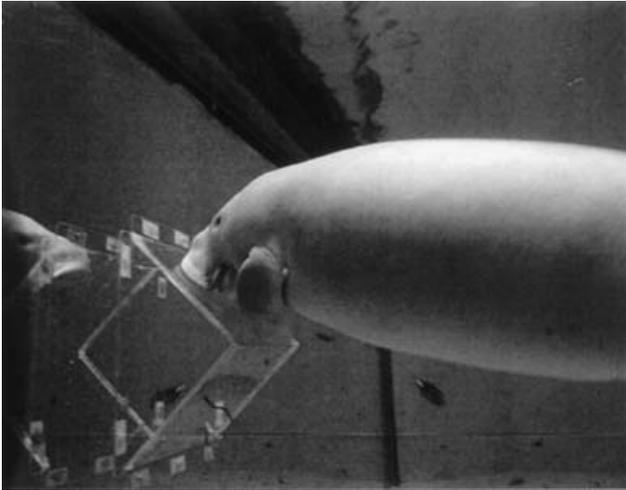


Fig. 1. Dugong feeding on plexiglass platform. After several days, captive dugongs learned to feed consistently from the platform. Leaves of *Zostera marina* were pushed into holes drilled through the plexiglass at approximately 10 cm intervals. The entire apparatus was held in place on the inside of the viewing window with suction cups.

behaviour and was indistinguishable from bottom feeding in captive dugongs. In addition, analysis of kinematic data of captive dugongs (either inclined or bottom) and videotapes of wild dugongs did not reveal any apparent differences in feeding behaviour despite the lack of sediment in the captive environment.

As part of their daily feeding regimen dugongs were fed an exclusive diet of *Zostera marina* and this was the only vegetation available for the study. Dugongs were presented with sea grasses (including roots) woven through a stainless steel mesh attached to a weighted PVC frame. This feeder was then carefully dropped into the tank where it sank and sat on the bottom, at which time the dugongs both grazed and attempted to uproot *Z. marina* similarly to wild dugongs. Observations of bottom feeding by captive dugongs were made from outside and inside the tank (using SCUBA) in close proximity to the snout (10–20 cm). Although *Z. marina* is not consumed by free ranging dugongs, most likely due to its northern distribution in both the Pacific and Atlantic oceans, they do feed on a shorter but morphologically similar species within the same genus, *Z. capricorni*. Both *Z. marina* and *Z. capricorni* exhibit similar leaf gross morphologies. *Zostera capricorni* leaves grow 7–50 cm long and 2–5 cm wide (Heinsohn & Birch, 1972; Phillips & Meñez, 1988). In contrast, *Z. marina* leaves grow only 1.5 to 12 mm wide but up to 2 m in length (Phillips & Meñez, 1988). The only substantial above-ground gross morphological difference between the 2 species is maximum height. Therefore we feel that a comparison of dugongs feeding upon *Z. marina* would yield comparable results to dugongs feeding on *Z. capricorni*; such comparisons between captive and free-ranging dugongs revealed no difference.

Videotapes of captive dugong, wild dugong and manatee feeding behaviour were analysed in real time, slow motion and frame-by-frame to determine the component movements of the lips, bristles, jaws and associated structures.

RESULTS

General description of the dugong snout

The dugong snout can be divided into five regions: (1) oral disk; (2) supradisk; (3) chin; (4) upper perioral bristle fields; (5) lower perioral bristle fields (Fig. 2). The oral disk (od) is the terminus of the dugong snout and is homologous with the oral disk of *T. m. latirostris*. When relaxed, the overall shape of the dugong oral disk resembles an arch or a horseshoe in shape (Figs 2a & b). The skin of the dorsal and lateral margins of the oral disk is thick and less pliable than the skin of the oral disk surface itself. This margin is homologous to the orofacial ridge (ofr) of *T. m. latirostris*. The orofacial ridge separates the oral disk from the supradisk (sd) region (Figs 2d & f). In contrast to Florida manatees, the ventral margin of the dugong oral disk is relatively straight and continuous from one side to the other (Figs 2b & d). The surface of the dugong oral disk is convex when relaxed (Figs 2a & 7e). It is marked by three creases, a shallow center crease (cc) and two deep furrows on each lateral side (lf) of the oral disk (Figs 2a & b). On the lateral side of the rostrum, a shallow crease (rc) can be observed near the border of the oral disk on each side (Fig. 2a). During feeding, or other oral behaviours, the lateral furrows of the oral disk open and are pushed out, which results in the expansion of the oral disk laterally and the extension of the lateral flaps (lfl) (Figs 2c, d & f). As the lateral flaps unfold and the lateral furrow disappears, the shape of the disk changes from arch-shaped to semicircular shaped and the disk surface becomes flat with only the central crease visible (Figs 2c, d & f). The concurrent unfolding of the lateral flaps and the flattening of the entire oral disk results in a substantial increase in its total surface area. A postnasal crease is only present when the longitudinal facial muscles contract. A chin crease (chc), running ventrally from one corner of the mouth to the other, marks the boundary of the chin region from the rest of the head and face (Fig. 2e). Modified vibrissae (perioral bristles) line the margins of the upper and lower lip.

Dugong perioral bristle distribution

Dugongs, like Florida manatees, possess six discrete fields of perioral bristles, four fields on the upper lip and two fields on the lower lip (Figs 3 & 4; Reep *et al.*, 1998). The ventral margin of the dugong oral disk is thick and muscular and can form a raised edge when active (Figs 3a & c). This region, most likely underlain by the superior portion of the *M. orbicularis oris*, is more developed than in Florida manatees. Within this ventral margin the U1 bristle fields extend from the mid-sagittal

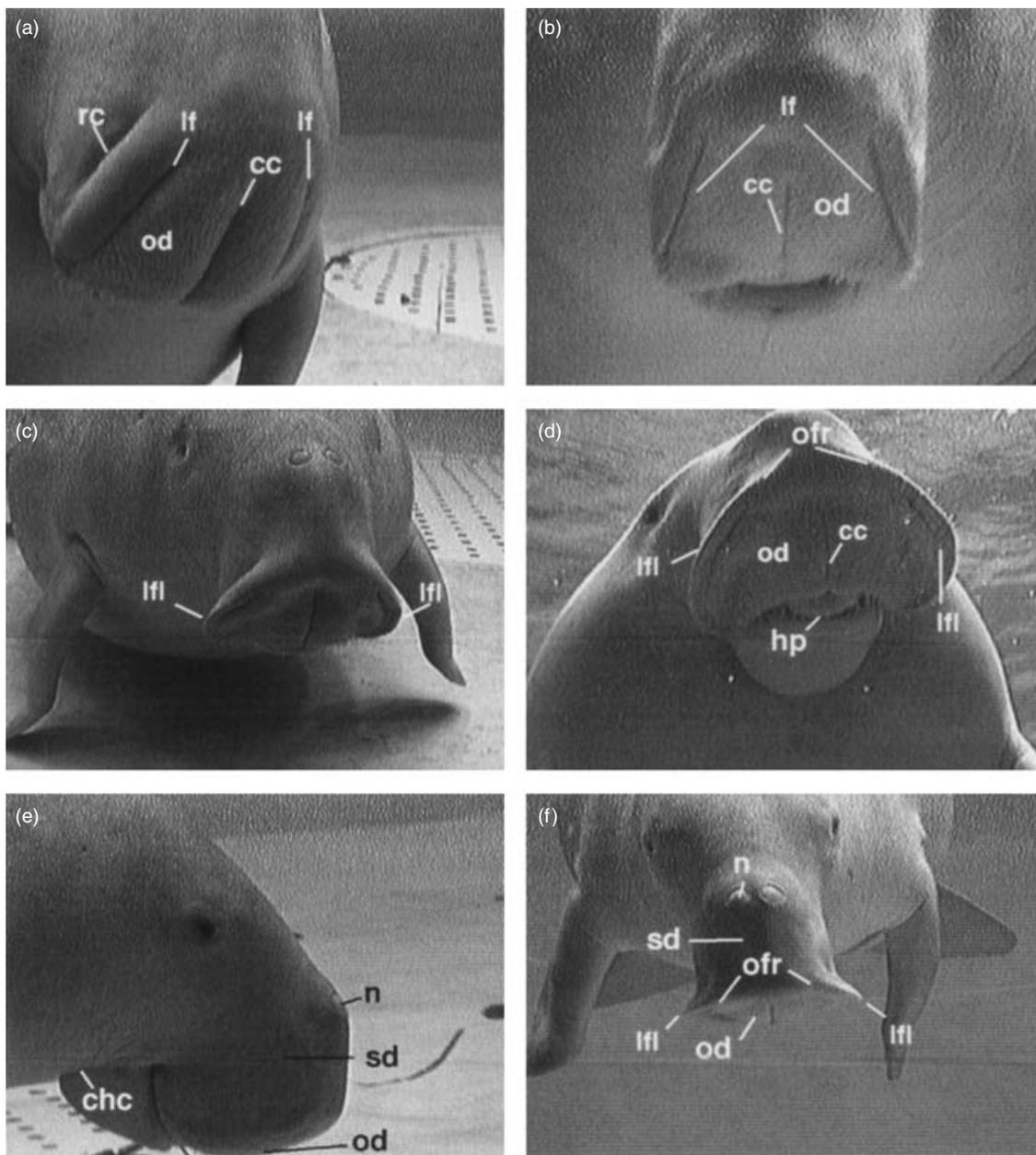


Fig. 2. External morphology of the dugong rostrum and snout. a, Frontolateral perspective of the relaxed oral disk (od) depicting the central crease (cc), lateral furrows (lf), and rostral crease (rc). b, Frontal perspective of the oral disk (od), lateral furrows (lf), and central crease (cc). c, Frontolateral perspective of the flared oral disk depicting the extended lateral flaps (lfl). d, Frontal perspective of the flared oral disk (od) in relation to the orofacial ridge (ofr), the lateral flaps (lfl), central crease (cc), and the upper horny palate (hp) are visible. e, Lateral perspective of the flared oral disk (od) in relation to the supradisk (sd) region and nares (n). Also visible is the chin crease (chc). f, Dorsofrontal perspective. Note the greater width of the oral disk (od) and extended lateral flaps (lfl) relative to the supradisk (sd) region. The orofacial ridge (ofr) is clearly seen separating the oral disk (od) from the supradisk region (sd) and nares (n).

Fig. 3. Dugong perioral bristles. a, Arrowheads indicate the location of the right U1 bristle field along the ventral margin of the oral disk (midline to the ventrolateral corner of the oral disk). The asterisk indicates the lateral flap in its relaxed state. Photo credit, D. Tikel. b, Arrowheads depict the location of the right U2 bristle field relative to the ventral margin. The asterisks indicate the simulation of the expansion of the lateral furrow in order to project the lateral flaps. Photo credit, D. Tikel. c, Protruding ventral margin of a relaxed oral disk (od) in a captive dugong, depicting the spatial relationship between the U1 and U2 bristle fields, and the upper horny palate (hp). d, Active oral disk of a feeding captive dugong while swimming inverted at the water's surface. Asterisks indicate the lateral margin of the left lateral flap. Note the large U1, U2, and L1 bristle fields and the upper horny palate (hp). e, Oral disk of a male dugong. Note the spatial relationship between the horny palate (hp), tusks (t), U1, and U2 bristle fields. Photo credit, Paul Anderson. f, USMNH specimen number 307610 illustrating the location of the U1, U2, and L1 bristle fields.

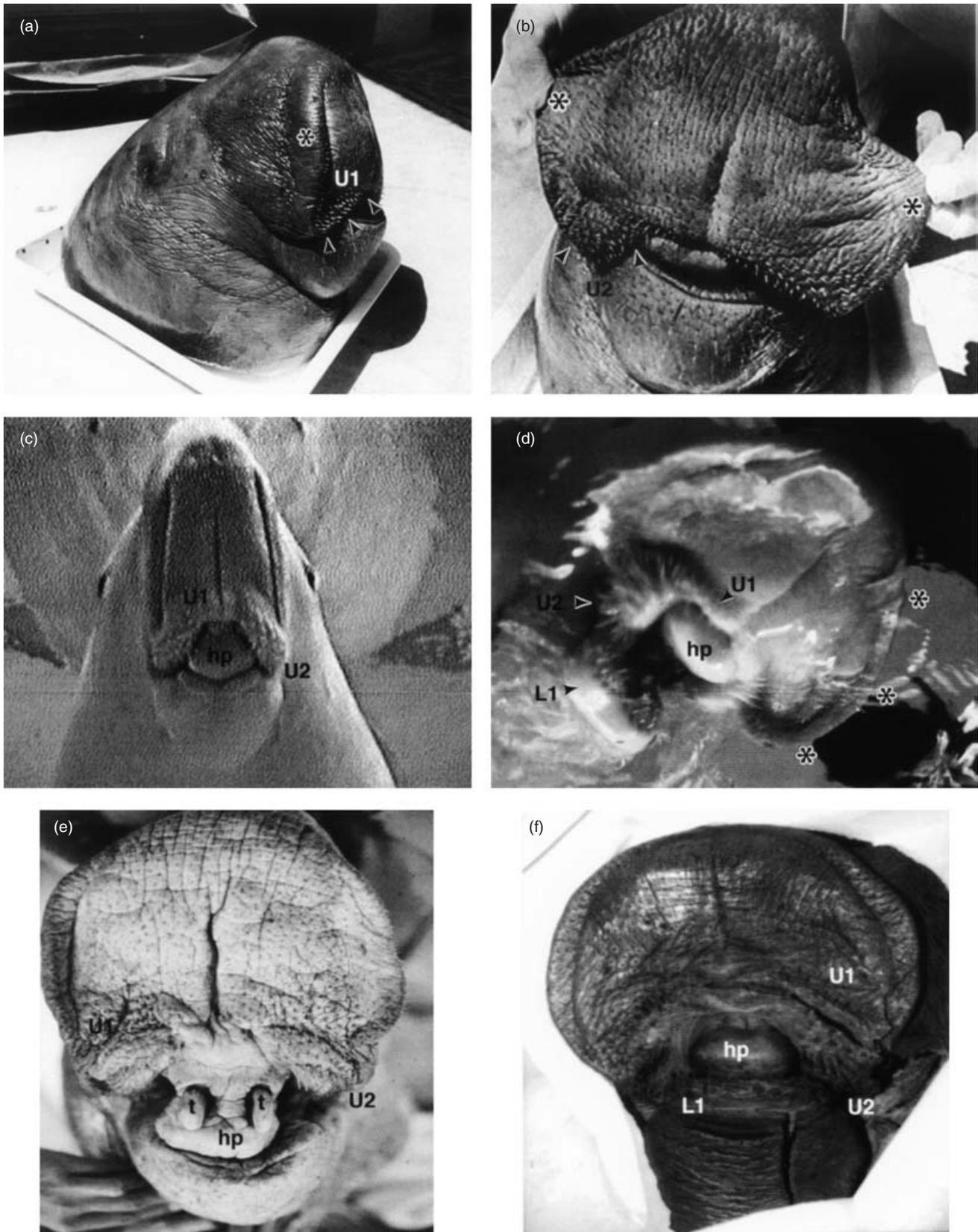


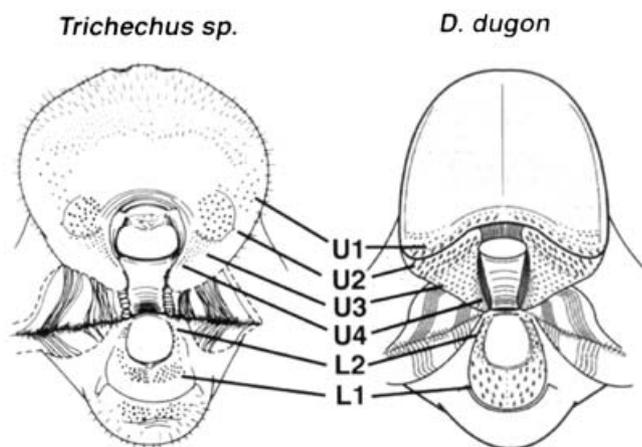
Fig. 3. For legend see facing page.

plane to the ventrolateral margins of the oral disk (Figs 3 & 4). The U2 bristle fields are located near the ventrolateral corners of the oral disk, deep to its

ventral margin, from the projecting upper horny palate (hp) medially, to the lateral border of the lip margin (Figs 3b-f & 4). The shafts of the bristles are recessed

Table 2. Characterization of dugong perioral bristles and bristle-like hairs (BLHs). Measurements were made on specimen USNMNH 307611. Values within parentheses are \pm SD

A. Upper Lip	U1	U2	U3	U4
Length (cm)	0.52 (0.11)	1.12 (0.22)	0.59 (0.23)	0.51 (0.12)
Diameter (cm)	0.04 (0.003)	0.13 (0.22)	0.03 (0.01)	0.017 (0.005)
Count	32.7 (2.25)	50.7 (2.16)	119.3 (2.19)	27.3 (0.67)
Length/Diameter ratio	13 (6.62)	8.61 (1.84)	19.67 (3.21)	30 (14.9)
B. Lower Lip	L1	L2	BLHs	
Length (cm)	0.38 (0.11)	0.20 (0.05)	0.12 (0.04)	
Diameter (cm)	0.103 (0.05)	0.017 (0.01)	0.02 (0.005)	
Count	19.5 (0.224)	25.8 (0.946)	40	
Length/Diameter ratio	3.69 (1.81)	11.8 (7.67)	6 (2.64)	

**Fig. 4.** Schematic of the distribution of perioral bristle fields in trichechids and the dugong. Trichechid figure reproduced from Reep *et al.* (1998) with permission. Note the similarity of the location of all the bristle field distributions with the exception of the dugong U1 bristle field.

in the soft tissue of the region. The ventral margin of the oral disk overhangs and conceals the U2 bristle fields from view when not active (Fig. 3a). Caudal to the U2 bristle fields are the U3 bristle fields (Fig. 4). The U3 bristle field is wider and more expansive than that found in *T. m. latirostris*. The hair shafts are oriented caudomedially, pointing into the mouth and are easily distinguished from the U2 bristles by their increased length-to-diameter ratio (Table 2). Further caudally, the U4 bristle fields extend from the U3 bristle field to the mouth corner (Fig. 4). As with the boundary between the U2 and U3 bristle fields, the U3 and U4 bristle field boundary is distinguished by an abrupt change in the length-to-diameter ratio (Table 2). The bristle distribution of the lower jaw includes the L1 and L2 fields (Figs 3d & f, Fig. 4). When relaxed, the L1 bristle fields are recessed

within a fleshy lower lip pad that lies rostral to the lower horny palatal pad. The diameter of these bristles is similar to those of the U2 bristles; both fields have diameters that exceed that of all other bristles by an order of magnitude. The L2 bristle fields are located between the lateral lower lip margin and the lower horny palate and extend caudally toward the lip commissure (Fig. 4). The L2 bristles are also distinguished from the L1 bristles by an abrupt change in their length-to-diameter ratio (Table 2). The mean number of dugong perioral bristles was 552 (SD \pm 5.29; $n = 2$). A seventh class of hairs, the so-called bristle-like hairs (BLHs), is sparsely distributed over the surface of the oral disk itself. These hairs were named due to their intermediate characteristics between the perioral bristles of the oral disk and the postcranial hairs in Florida manatees (Reep *et al.*, 1998). The postcranial body of dugongs is sparsely covered with long thin hairs.

Dugong feeding behaviour

The function of perioral bristles in dugongs is to acquire, manipulate and introduce vegetation into the mouth. Despite the homologous nature of their feeding apparatuses, the manner in which dugongs use perioral bristles is divergent from that of Florida manatees in two ways. First, the dugong U1 bristles participate in the manipulation of vegetation. Second, dugongs move their U2 bristle fields medial-to-lateral in a 'breast-stroke-like' manner that introduces vegetation into the sides of the mouth. This is in contrast to Florida manatees, which move their U2 bristle fields in a lateral-to-medial grasping action that is prehensile. Like Florida manatees, dugongs ingest vegetation through a series of cyclical manoeuvres that can be broken down into the following five events and is summarized in Fig. 5:

(A) Upon approaching the vegetation the oral disk is flared. This involves contraction of the snout along its

Fig. 5. Sirenian feeding sequences. a–e, Five major events during a single dugong feeding cycle. Note the medial-to-lateral movement pattern of the U2 bristle fields and the alternation of the U2 bristle fields with L1 bristle fields. See text for details. f–j, Five major events during a single trichechid feeding cycle. Note the lateral-to-medial movement pattern of the U2 bristle fields and the alternation of the U2 bristle fields with the L1 bristle fields in all three species.

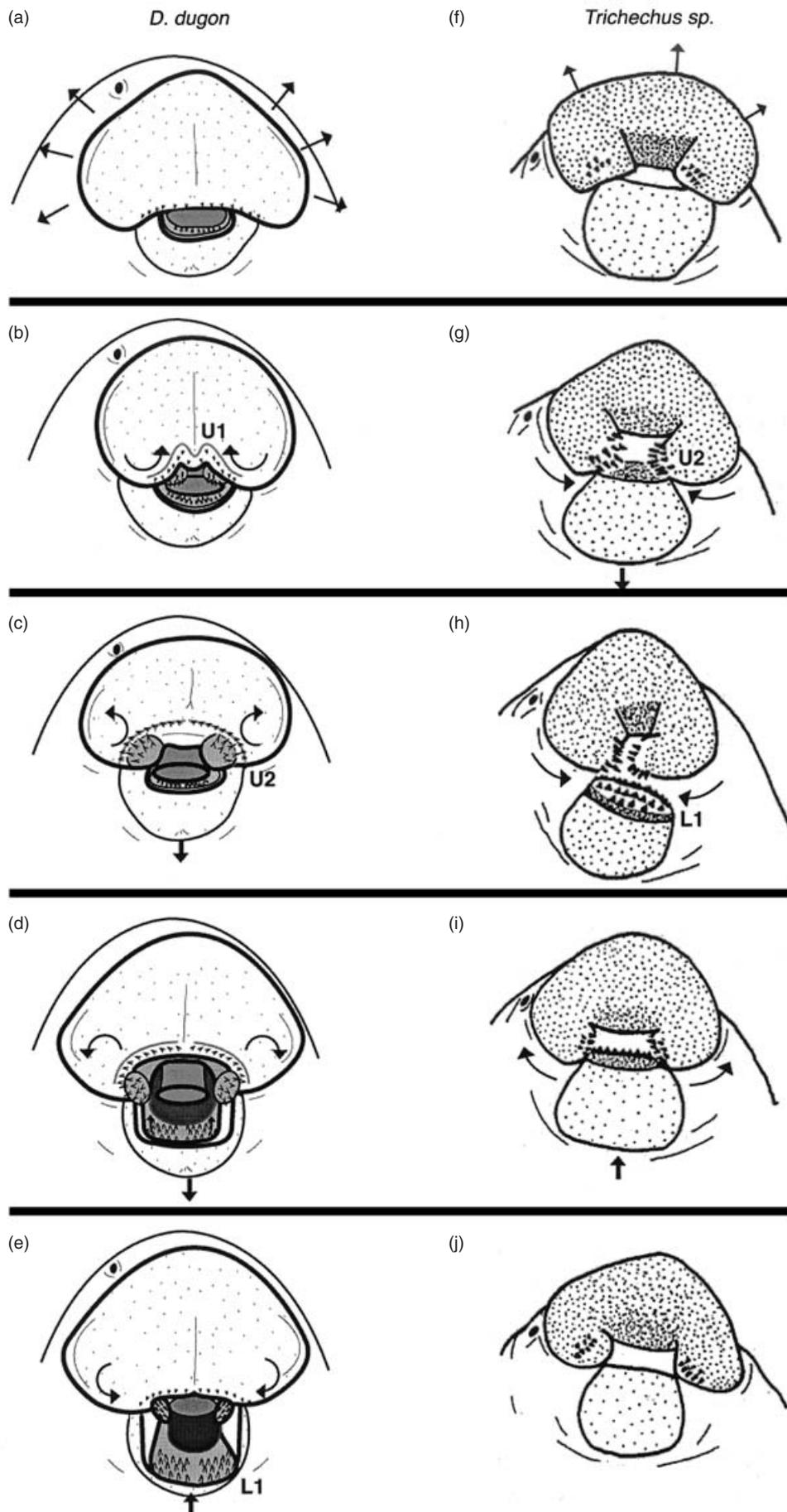


Fig. 5. For legend see facing page.

entire length, pulling the orofacial ridge dorsally and laterally. Simultaneously, the pair of lateral furrows open and expand, resulting in the extension of the lateral flaps and a shape change of the oral disk from arched and convex to semicircular and flat.

- (B) Perioral bristle movement (U1 and U2) begins near the midline, adjacent to the central crease. The upper lip (ventral margin of the oral disk) is lifted slightly to either side of the central crease of the oral disk to form a small, characteristic 'M' shape. The lip margin, where the U1 bristle fields are located, curls rostrally.
- (C) Both U2 bristle fields are maximally everted rostrally near the midline, and each field begins to move laterally. Simultaneously, the raised peaks of the upper lip travel laterally in a wave-like action. At this time the lower jaw begins to open.
- (D) At the ventrolateral corner of the oral disk the U2 bristle fields change directions and move caudally. During these events, the lower jaw continues to open and reaches its maximum gape. The L1 are everted to their full extent from the fleshy lower lip pad.
- (E) The U2 bristles move medially to complete a circular motion that sweeps vegetation into the side of the mouth, and then return to their original position (rostral). As the lower jaw closes, the L1 bristle fields sweep vegetation caudally into the oral cavity.

Events A–E describe a single dugong feeding cycle. This cycle was repeated as the dugongs skimmed the surface of the feeding platform consuming vegetation. The mean feeding cycle length was 791 ms (SD \pm 41.6, $n = 1$) and ranged from 738 ms to 899 ms.

During bottom feeding, the oral disk underwent the same characteristic flare behaviour. Flaring of the oral disk resulted in an oral disk shape change from convex and bulbous to flat and wide, and resulted in the protrusion of the lateral flaps. Perioral bristle use was similar to feeding on the plexiglass apparatus and functioned to introduce sea grass into the mouth. Additionally, both dugongs continually thrust their heads forward and backward as they worked their way across the bottom feeder. This action uses the oral disk as a wedge that pushes the leaves of sea grasses to the side, changing the blade orientation such that it facilitates the manipulation of the vegetation by the U1 and U2 bristle fields on the lateral–ventral region of the upper oral disk. During these feeding bouts both lateral flaps underwent an undulating wave-like motion that travelled rostrocaudally. Close-up observations of the oral disk from within the tank revealed no difference in perioral bristle movement compared to feeding on the plexiglass platform. Additionally, a hand placed between the oral disk and vegetation confirmed that perioral bristles were active and that feeding was occurring in the sequence described.

The down-turned rostrum of dugongs is a presumed adaptation for benthic feeding and indeed this was the primary mode of feeding for the subjects in this study. However, the female dugong also performed a surface feeding behaviour. During a normal bottom-feeding bout, it was inevitable that many loose strands of *Zostera* were

released to float, uneaten, within the tank. Over a period of time these leaves would gather at the surface. After consuming the vegetation in the bottom feeder, the female dugong repeatedly swam inverted, just below the water surface. While inverted, her oral disk was parallel to the water's surface and she was able to ingest individual leaves using the perioral bristles in the same manner as was observed from the feeding platform and during normal bottom feeding.

Exploration, tusk use and manipulative behaviours

Captive dugongs used their oral disk, tusks (male) and perioral bristles to explore their environment. The male dugong spent much time, outside of feeding, exploring the surfaces of the tank with both bristles and tusks. During these exploratory episodes the oral disk was flared but returned to the relaxed shape when the dugong ceased tactile exploration. Occasionally, when skimming across the surface of the viewing window, the male would stop and bob his head up and down (dorsal and ventral), and also forward and back, as if feeling some inconsistency in the texture of the window. During this type of behaviour the oral disk was pressed hard against the window, making an apparently tight seal over the region of interest. On other occasions the male often swam to the surface of the tank, placed his flattened oral disk on the surface of the viewing window and slowly sank, dragging the oral disk and tusks down the viewing window, scraping the surface. The viewing windows were lightly gouged in several regions due to this type of behaviour. During some of these behaviours, the male dugong would temporarily stop and gouge the window with the tusks with a greater and more focused effort. The tusks were also used when mounting and performing sexual behaviours with a semi-buoyant cylinder kept in the tank. Flippers were used to grasp the sides of the cylinder, spin it along its long axis, and pull it further underwater. During these behaviours the male would often repeatedly slap the flared oral disk and his entire head against the top surface of the tube. The tusks were used to repeatedly scrape and gouge the top of the cylinder. In addition to head butting and tusk gouging, the perioral bristles were very active during these behaviours, and used to feel and scrape the surface.

When presented with their normal bottom-feeding platform, both dugongs used their perioral bristles to touch and explore the surface of the feeding apparatus itself. This occurred during feeding bouts and when exploring for missed *Zostera* leaves. After the majority of the vegetation was consumed, occasionally the male dugong would interact with the apparatus itself. He repeatedly used the flattened oral disk as a wedge to get underneath the feeding apparatus, pick it up and drop it. Often, the whole head was pushed underneath the apparatus and the subject would then swim underneath the apparatus, letting it tumble down its back and onto the floor of the tank. Occasionally the flippers were also used to assist in the process. The male dugong displayed many surprising manipulative behaviours, using the snout and flippers, in

tumbling the apparatus in many directions throughout the tank.

Captive dugongs engaged in a behaviour that functioned to clear the perioral bristles of plant debris. As dugongs rested within the water column, the relaxed oral disk would undergo the characteristic flare. Then the U1 and U2 bristle fields would be everted followed by jaw opening and eversion of the L1 bristle fields. While the U2 bristle fields were maximally everted the subject moved these fields back-and-forth. Contraction of the orofacial musculature was indicated by the appearance of creases in the skin overlying the rostrum – this is the only time that a post-nasal crease was observed. This behaviour was repeated over and over, sometimes 20–30 times in a row for up to an hour. Often the flippers were brought up to the mouth and the subject appeared to attempt to remove pieces of vegetation stuck between individual bristles.

Trichechid orofacial morphology, perioral bristle distribution and feeding behaviour

The snouts of the Amazonian, African, and Antillean manatees in this study were remarkably similar to each other and to that described for Florida manatees (Reep *et al.*, 1998). These trichechids also possessed five facial regions (oral disk, supradisk, chin, upper and lower perioral bristle fields) and six perioral bristle fields, characteristics that they share with dugongs (Fig. 4). In *T. inunguis*, when the snout is relaxed, the BLHs at the upper (dorsal) edge of the od (i.e. at the ofr) terminate abruptly along a line separated from the ventromedial corners of the nostrils by 0.9–2.3 cm (in animals 80–246 cm in total straight line length, $n = 14$). In contrast, this distance in *T. m. latirostris* is significantly greater (corresponding to its greater rostral deflection), and the ofr is not marked by a sharp boundary to the BLH-bearing region; instead, this boundary is diffuse (D. P. Domning, pers. comm.). Although measurements of the same region were not taken in *T. senegalensis*, it appears that this distance is intermediate to *T. inunguis* and *T. manatus* (Fig. 6). Feeding behaviour among these species and Florida manatees was indistinguishable. All trichechids used U2 bristle fields to acquire, manipulate and introduce vegetation into the front of the mouth in a lateral-to-medial grasping motion. The L1 bristle fields alternate with the U2 bristle fields to sweep vegetation into the mouth in a circular rhythmic cycle (Fig. 5). The U1 bristle fields were passive and not involved in manipulation of vegetation. Numerous alternating cycles of U2 and L1 bristle movements moved vegetation effectively and quickly into the mouth. The manner in which the U2 bristle fields were used bestows all trichechids a prehensile ability. Based on a limited amount of data from a wide range of vegetation, the feeding cycle length of the Amazonian manatee at the Yomiuriland Marine Aquarium ranged from 770 to 830 ms.

The perioral bristles and bristle-like hairs of the trichechids in this study were also used for exploring surfaces of the feeding apparatus and other surfaces

around the tank. After a feeding trial, manatees would often scan the area using their bristles and bristle-like hairs, exploring for more vegetation. Upon approaching an item to be investigated, the oral disk would be flared, the U2 bristles would repeatedly touch the edges, and the subject would scan the item with bristle-like hairs on the oral disk. Amazonian manatees at INPA were observed using their flippers to manipulate food and introduce it to the mouth. These same individuals were also observed using their flippers to clean and dislodge plant matter from the perioral bristles and mouth.

DISCUSSION

Although portions of the orofacial morphology of the dugong have been described by several authors (Owen, 1838; Dexler & Freund, 1906; Gohar, 1957; Domning, 1976, 1977; Anderson & Birtles, 1978; Anderson, 1979), few have related form to function. The central crease and lateral furrows described for the dugong oral disk and rostrum are comparable with the central and lateral grooves of the rostral disk of Anderson (1979) and the ventral, posterior and lateral folds of Dexler & Freund (1906). Our observations agree with Anderson (1979), that the oral disk is compressed laterally when not feeding. However, we never observed an extension of the oral disk downward when flared. Instead the oral disk extended laterally due to the emergence of the lateral flaps. This lateral extension appears to be a result of flaring the oral disk that also flattens its surface and increases its surface area. The morphological landmarks and five orofacial regions described for Florida manatees (Reep *et al.*, 1998) can be extended to all extant sirenians. Each possesses an oral disk and supradisk region separated by an orofacial ridge. In each species the supradisk region and the chin are bounded caudally by the postnasal crease (except in *Dugong*) and the chin crease, respectively. The lateral furrows that open and expand to create the lateral flaps during the flare behaviour are absent in trichechids. Each possesses upper and lower bristle pads (bristle fields *in toto*) where six discrete bristle fields reside. The location and function of the U1 bristle fields in dugongs differs from trichechids in that the bristles are mobile and participate in manipulation of vegetation. In general the dugong bristle fields were more expansive, and contained 40% more bristles than in Florida manatees (Reep *et al.*, 1998). The expansion of the bristle fields and increased number of bristles is most notable at the U3 and L2 bristle fields. This expansion would presumably assist in holding and preventing vegetation from escaping from the sides of the mouth during bristle transport of vegetation. Descriptions of dugongs using perioral bristles as forceps to manipulate vegetation (Domning, 1977) were not substantiated by this study. In fact, we found the opposite to be true. The use of the word ‘forceps’ indicates a lateral-to-medial movement of U2 bristles that allows a prehensile ability. This behaviour would be similar to that exhibited by Florida manatees. Instead, the initial medial-to-lateral movements of the dugong U2 bristle fields result

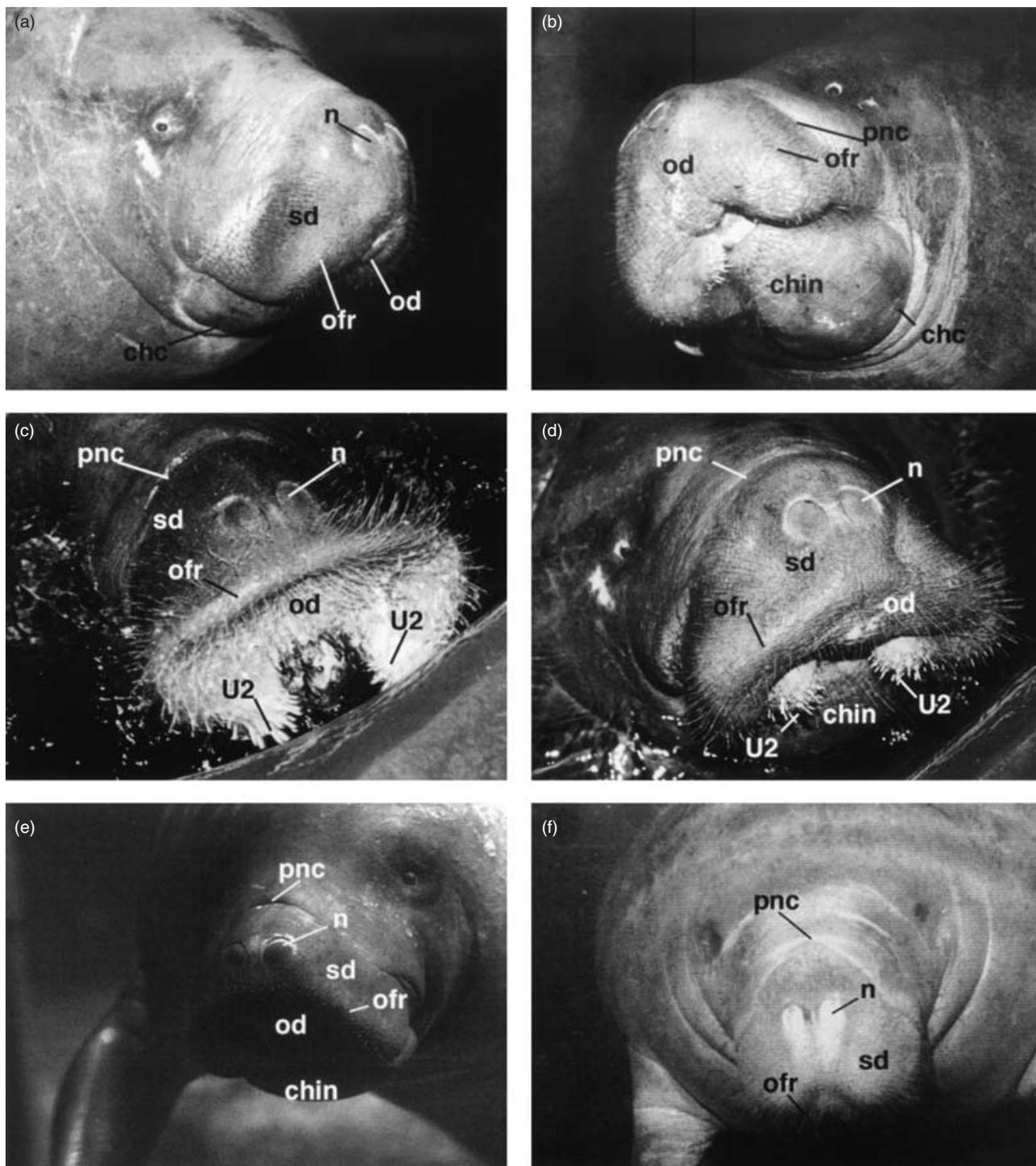


Fig. 6. External morphology of a trichechid snout (*T. senegalensis*). a, Frontolateral perspective depicting the oral disk (od), orofacial ridge (ofr), supradisk (sd) region, chin crease (chc), and nares (n). b, Frontoventral view. Note the location of the oral disk, the vague location of the orofacial ridge, supradisk, post-nasal crease (pnc), chin crease, and chin. c, Flared oral disk. Note the increased surface area and flattening of the oral disk and the now prominent orofacial ridge. The U2 bristle fields are everted; the post-nasal crease, supradisk, and nares are also visible. d, Oral disk at the end of a feeding cycle. Note the retraction of the U2 bristle fields and the less distinct condition of the orofacial ridge. Also visible are the chin, supradisk, nares, and post-nasal crease. e & f, External morphology of *T. inunguis*, and *T. m. latirostris*, respectively, depicting the oral disk, orofacial ridge, supradisk region, and post-nasal crease of each species.

in vegetation being swept into the sides of the mouth and do not invoke a prehensile ability. Unless the U2 bristle fields of dugongs are able to meet at the midline near

the end of their cycle, within the oral cavity, we must conclude that dugongs do not possess a prehensile ability, but are highly manipulative. However, Amazonian, West

African and Antillean manatees, like Florida manatees, do move their U2 bristle fields laterally-to-medially to grasp food and objects and therefore are prehensile. Thus, the pattern of perioral bristle use is similar among all living trichechids but divergent from dugongs.

In alluding to the introduction of sea grass laterally into the 'sides of the mouth' by dugongs, specifically we mean that vegetation is introduced between the upper and lower horny palatal pads. This occurs in manatees as well, but trichechids introduce food into the mouth from the rostral margin. Both trichechids and dugongs possess heavily cornified upper and lower palatal pads. These pads are located rostral to the cheek-teeth and are more robust and longer (rostrally) in dugongs than in trichechids (Marsh, Beck & Vargas, 1999). The increased length of the dugong palatal pads result in a potentially longer intraoral transport distance. Introduction of food into the side of the mouth could decrease this intraoral transport distance. The morphology of the horny pads in *D. dugon* is such that the protuberances on the upper pad occlude with the backward-oriented protuberances of the lower pad (Gohar, 1957). Lanyon (1991) demonstrated that the cheek-teeth occlude simultaneously with the horny pads and that the movement of sea grass up the vertical rostral mouth could be due to the rostral-lingual and caudal-buccal movement of the mandible during mastication (in addition to orthal movements). It is thought that sea grasses are broken down mechanically by these palatal pads during the transit to the cheek-teeth (Lanyon, 1991; Marsh *et al.*, 1999). Dugongs and West Indian manatees are able to mechanically process sea grasses of the genera *Thalassia* and *Halodule* equally well despite the relatively simple dentition of dugongs (Marsh *et al.*, 1999). Presumably, the horny pads of *Dugong* 'masticate' sea grasses in addition to, or in place of, cheek-teeth. The perioral bristles of dugongs, specifically the U1, U2, and L1 fields, function to collect and position sea grasses between the horny pad surfaces. The remaining bristle fields are passive but their caudomedial orientation into the mouth prevents movement of vegetation out of the mouth and maintains its position on the surface of the horny pads. Therefore the perioral bristles are one part of an efficient gathering, transport and mastication system of the dugong oral apparatus.

Anderson & Birtles (1978) report that dugongs can swim inverted and do so to rub their bodies against the substrate. This is similar to the surface feeding behaviour observed in this study and provides yet another glimpse into the apparently broad behavioural repertoire of dugongs. Like West Indian manatees, both captive and free-ranging dugongs were observed to 'walk' along the bottom using their flippers. Gohar (1957) and Jonklaas (1961) observed dugongs using their flippers to clean their mouths. The cleaning behaviour observed in captive dugongs (this study) has also been described in Florida manatees and is described as 'prominent among the self-care activities' (Hartman, 1979). These behaviours included cyclic grasping movements and the use of the flippers to dislodge material. Amazonian manatees at

INPA also used their flippers to remove debris from mouth-parts, as well as to introduce vegetation into the mouth. Although flipper use for feeding is well-known for Florida manatees (Hartman, 1979), little is known regarding the extent of flipper use in other trichechids and dugongs.

The use of the tusks and perioral bristles during sexual behaviour in the captive male dugong is consistent with observations on free-ranging dugongs (Anderson & Birtles, 1978; Preen, 1989; Anderson, 1995, 1997) and Florida manatees (Hartman, 1979). Exploration of the surfaces of the holding tank, including the presumed fascination by smooth surfaces of captive dugongs, and the dragging of the lower L1 bristle fields across the viewing window has been observed in Florida manatees (Marshall *et al.*, 1998b). Apparently, all sirenians have a repertoire of motoric and tactile behaviours involving the muscular-vibrissal complex that is used to manipulate and explore their environment under varying circumstances.

Current palaeoecological hypotheses of resource partitioning among Atlantic-Caribbean sirenians suggest that tusks have been important for rhizome excavation during sirenian, mostly dugongid, evolutionary history (Domning, 2001). Early dugongids were characterized by tusks and narrow premaxillary and mandibular symphyses. Such relative differences in rostra and incisor widths in terrestrial herbivores suggest a selective feeding niche (Janis & Ehrhardt, 1988) that may translate to dugongid aquatic herbivory (Domning, 2001). We suggest that the muscular-vibrissal complex is an efficient gathering apparatus that may also have been important early in sirenian evolution. If such an apparatus were present in basal tusked dugongids with narrow rostra transport of sea grasses, either grazed or uprooted, would by necessity be transported in a medial-to-lateral direction to avoid the medially oriented tusks. *Dugong dugon* is exceptional among the dugongid lineage in that their tusks are 'sexually dimorphic, used in social interactions, and have no apparent role in feeding' (Domning, 2001). However, the pleiomorphic medial-to-lateral motor pattern, relative to trichechids, may be have been conserved regardless of tusk morphology and use. This would explain the divergence in perioral bristle motor pattern by manatees, a group that never possessed tusks.

It is likely that the underlying myology and the muscle mechanics of all sirenian snouts is consistent with that of muscular hydrostats (Kier & Smith, 1985) as demonstrated for Florida manatees (Marshall *et al.*, 1998b). Such structures are capable of highly varied and intricate movements. In sirenians, this results in a diversity of snout conformations that span a spectrum from flared oral disks to flaccid depending upon the motivational state of the individual (Fig. 7).

Proposed mechanisms of rhizome excavation

Dugongs can feed by grazing the leaves of sea grasses or by rooting for rhizomes. Although recent evidence is

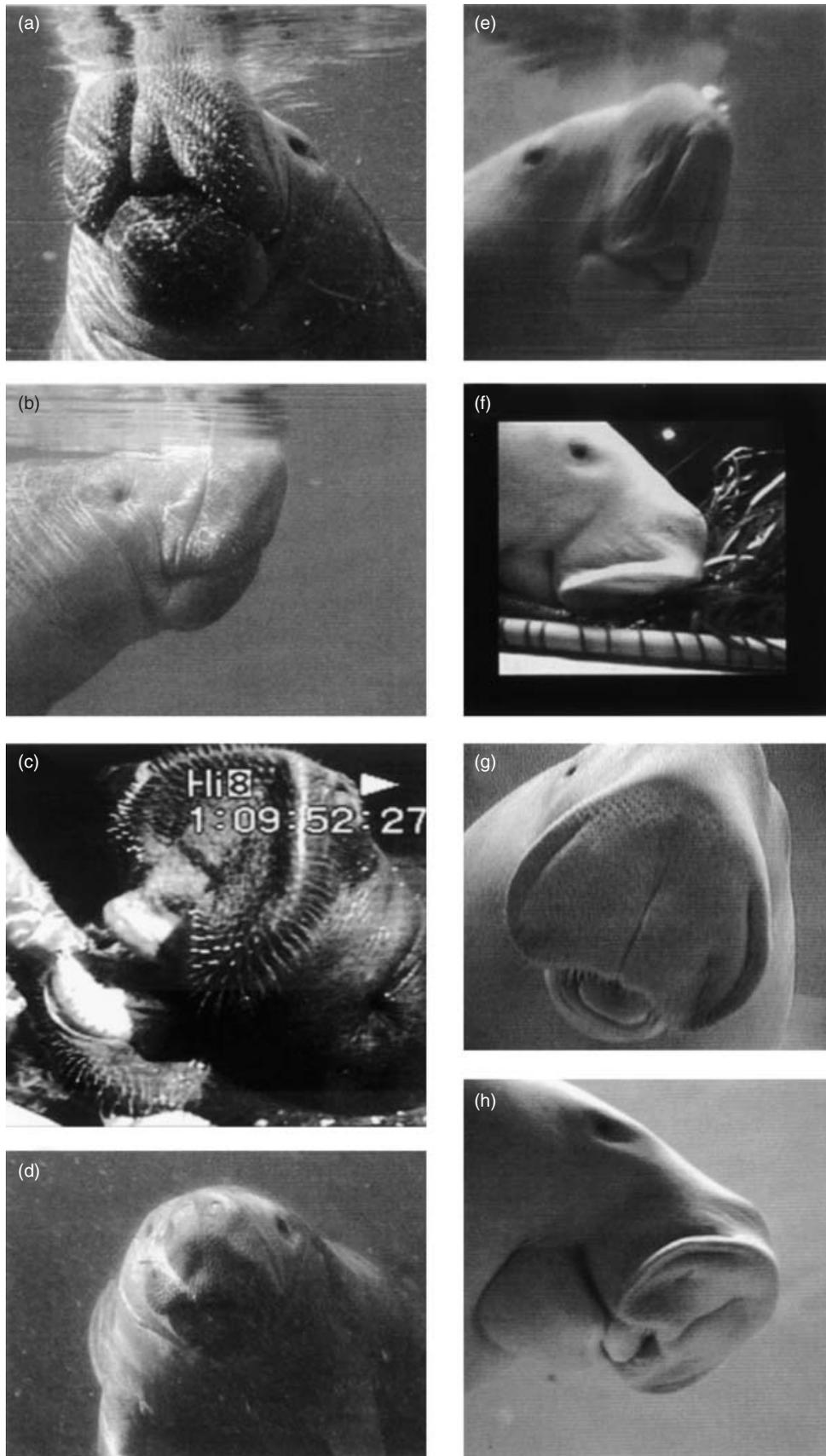


Fig. 7. For legend see facing page.

revealing greater complexity of dugong feeding behaviour (Aragones, 1994; Preen 1995*b*; De Iongh, Bierhuizen & van Orden, 1997; Aragones & Marsh, 2000), in general dugong rooting is characterized by repeated dives to the bottom and continuous forward movement during which small, delicate, low-fibre species of sea grasses are completely uprooted, including rhizomes, and ingested (Heinsohn *et al.*, 1977; Anderson & Birtles, 1978; Johnston & Hudson, 1981; Lanyon, 1991; Preen, 1993; Anderson, 1998). These feeding bouts leave trails through sea grass beds in which up to 95% of above-ground biomass and up to 71% below-ground biomass is removed (Heinsohn *et al.*, 1977; Preen, 1995*b*). Feeding trails can be up to 8 m long, 2–6 cm deep and 10–30 cm wide; the approximate width of the oral disk is also about 10–30 cm (Heinsohn *et al.*, 1977; Anderson & Birtles, 1978; Lanyon, 1991; Preen, 1993). The presumed objective is the excavation and consumption of rhizomes, which are rich in carbohydrates. Our knowledge of how dugongs excavate rhizomes is ‘hampered by the secretiveness of the animal, the often muddy water it inhabits, the ventral location of the mouth and the silty plumes produced by feeding activity’ (Lanyon, 1991). This is the first study to report a complete view of dugong feeding mechanics that have not been obscured by silt. Several authors have proposed methods of digging that involved tusks, protruding upper horny palatal pad and flippers (Gohar, 1957; Jarman, 1966; Domning, 1977, 1978*a*; Anderson & Birtles, 1978). We suggest that the feeding method used when grazing leaves is the same during rooting when rhizomes are excavated and consumed. Although wild dugongs do not co-occur with *Zostera marina*, they do feed on a shorter but morphologically similar species within the same genus, *Z. capricorni*. Dugongs usually consume only the leaves (grazing) of the sea grasses *Z. capricorni* and *Z. marina* (captive dugongs only). However, many aspects of captive feeding were consistent with observed rooting behaviour by free-ranging dugongs. Captive dugongs fed by grazing and attempted rooting. When attempting to root, they would place their oral disk directly above or on the ‘substrate’ (mesh of bottom feeder) and extract vegetation at the level at which sea grasses emerged from the mesh. Although this is not an observation of true rooting and sediment was not present, based on data from free-ranging dugongs we feel it is a reasonable approximation. We propose the following two hypotheses regarding the possible mechanisms involved in rooting that invoke the use of perioral bristles for excavation:

Hypothesis 1: Rhizome excavation by dugongs is accomplished by the U1 and U2 perioral bristle fields. The distribution of the U1 bristle fields transversely across the ventral margin of the oral disk is advantageous for

uprooting. The characteristic ‘M’ shape of the upper lip, its subsequent rostral curl and movement laterally may form an effective uprooting wedge when placed against the substrate. The eversion of the U2 bristle fields rostrally would result in a raking action of the U1 bristles by pushing the U1 bristles forward and then out of the way laterally. This action could begin to uproot the shallow root system within the soft sediment in which these sea grasses are found. After the U1 bristles move past plant material, the more robust and caudal U2 bristle fields would follow, finish the uprooting process, and move the plant material (leaves, roots, and rhizomes) laterally, caudally and then medially between the horny pads with the assistance of the L1 bristle fields. The relatively long distance of perioral transport would effectively remove sediment from the vegetation. The forces generated by these bristle fields are surprisingly powerful (pers. obs.). The continued and consistent forward movement of the animal and the thrusting movement of the head forward and back would facilitate the uprooting action of these perioral bristle fields. The cleaning behaviour of captive dugongs clearly demonstrated that the U2 bristles could be everted far beyond the rostral extent of the oral disk. The action of these bristle fields and the distance of bristle eversion are quite capable of creating a depression in soft substrate consistent with the measured depth (2–6 cm) of feeding trails created by free-ranging dugongs.

Hypothesis 2: Rhizome excavation by dugongs is accomplished by the L1 perioral bristle fields. The rostrocaudal sweeping motion of the L1 fields, and the lower jaw, could be used for digging up rhizomes by dragging the tip of the mandible through the substrate with the L1 bristles everted. The forward motion of the head and entire body, and the closing of the vertically oriented mandible could provide enough force to uproot small delicate sea grasses. The use of the L1 bristle fields in this manner may explain the thrusting motion of the head forward and backward as digging motions of the L1 bristle fields. Once uprooted, the plant material could be ‘handed-off’ to the U1 and U2 bristle fields, which would then deliver the vegetation to the horny palatal pads. Oral behaviours in which the L1 field is dragged along a substrate have been documented in captive manatees (Marshall *et al.*, 1998*b*). In this case manatees dragged L1 bristle fields along the surface of a plexiglass feeder to remove pieces of vegetation that it otherwise had difficulty removing.

Both hypothetical mechanisms could quickly remove and pass sea grass roots and rhizomes down a biological dis-assembly line in a methodical, rhythmic and efficient manner. It is possible that each method and some variation of the two are employed as part of a diverse behavioural repertoire that is used to deal with changing conditions of

Fig. 7. Variation in conformation of the muscular-vibrissal complex in trichechids (a–d, *T. m. latirostris*) and dugongs (e–h). a & b, Conformation of the snout during breathing. c, Maximal flaring of the oral disk (od). d, Minimal flare or contraction of the muscular snout (see Fig. 6 for complete flaccid states of the snout). e, Conformation of the snout during breathing. f, Maximal oral disk flare and extension of lateral flaps (lfl) during bottom feeding. g, Minimal flare or contraction of the snout. h, Maximal oral disk flare and extension of the lateral flaps during exploration behaviour. Photo credit (a, b & d) Doug Weaver.

sea grass density, substrate or other environmental factors. Anderson (1998) reported that perioral bristle movement 'flush[ed] softer sediment to the side' which presumably allowed bristles to pick up rhizomes. These observations support either of the two functional hypotheses we propose. However, based on the worn nature of perioral bristles of dugong cadavers, reported depth of feeding trails and the relatively fast forward movement while rooting, we suggest that the bristles are actually excavating and not merely fanning sediment away from the roots of sea grasses. Our observations do not support the hypothesis that the lateral perioral bristles (U3, U4 and L2) function analogously to baleen to prevent sediment from entering the oral cavity (Anderson, 1998). The density of these bristle fields is not high enough to perform this function. Still, even if these bristle fields were denser, it is doubtful that stiff, single shafted hairs could prevent the introduction of fine particular matter, as found in these soft sediments, from entering the buccal cavity. Instead, we offer the alternate hypothesis that the rostrocaudal undulations of the lateral flaps create a flow of water that 'pumps' sediment away from sea grass roots (and the mouth) and assists in plant excavation. Thus, the lateral flaps may function to remove sediment from plant roots. As mentioned previously, the long perioral transport of vegetation laterally then medially to the horny pads could also result in the removal of sediment. The sediment plumes observed from rooting, free-ranging dugongs appear to be pumped away from the oral disk and body at the trailing edges of these lateral flaps. The undulation of the lateral flaps appears to be passive and a direct consequence of the U2 bristle field movement pattern. These observations are similar to those of Anderson (1998), who reported 'Undulating movements of the disk margins were then apparent and sediment emerged from the lateral disk margins in pulses. Laterally directed puffs of sediment and *Halodule* leaf fragments emerged behind the disk as the head was lifted away from the substratum.'

The extent to which trichechids consume rhizomes is poorly known. Excavation of rhizomes is possibly limited to West Indian manatees. Amazonian and West African manatees feed primarily on natant and emergent vegetation (Best, 1981; J. A. Powell, pers. comm.). West Indian manatees are known to consume small, shallow rhizomes, especially those of *Halodule* and *Syringodium* (Packard, 1981, 1984; Zieman, 1982; Lefebvre *et al.*, 2000). When consuming rhizomes they leave irregular, circular patches or scars in which 93–96% of the biomass is removed (Packard, 1981, 1984). Rhizome excavation is possibly an energetic process and manatees would benefit from behavioural strategies that would allow them to reduce this cost. Such costs are likely higher for manatees than dugongs since many of the sea grasses they consume have deeper roots within a harder substrate than those which dugongs consume. We propose that *T. manatus* also excavates rhizomes using the U2 and L1 bristle fields. The pinching and grasping action of the U2 bristle fields would provide a superb tool for removing sea grass substrate. An initial depression is possibly created by these bristle fields. Once a depression is made, scraping away loose

substrate could be accomplished by dragging the L1 bristle fields across the substrate. Alternating the breaking up of hard substrate (U2 fields) with scraping away loose substrate (L1 fields) would quickly reveal the sea grass root system and rhizomes. The forces generated by the grasping action of the U2 bristle fields are surprisingly powerful (Marshall *et al.*, 1998b) and are likely greater in manatees than dugongs. A common interaction among captive manatees is to pinch a conspecific's back with the U2 bristles (Hartman, 1979; Marshall *et al.*, 1998b). The receiver of such a pinch was often observed to flinch suddenly and quickly swim away. Even after a few moments of inadvertent interaction during feeding trials with captive manatees, research assistants would complain that several grasping and pinching cycles of the perioral bristles would leave the skin superficially scratched and was an uncomfortable experience. If such attention were directed toward the substrate of sea grass beds, the manatee muscular-vibrissal apparatus would be effective for excavating rhizomes.

All living sirenians have modified both the morphology of their vibrissae and facial myology to create a muscular-vibrissal complex that endows vibrissae with a motoric function in addition to a sensory function that allows for the acquisition, manipulation and ingestion of vegetation. This apparatus is a departure from the classical mammalian function in which vibrissae are used solely to detect tactile cues. Even among modern sirenians, the use of perioral bristles by dugongs is unique. Such a structural complex is evolutionarily novel among mammals if not among all vertebrates. Differing snout morphologies and perioral bristle use among sirenians have resulted in divergent feeding behaviour and trophic ecologies between dugongs and trichechids. The arrangement of the dugong muscular-vibrissal complex as an adaptation for benthic foraging upon sea grasses and rhizomes results in a narrow ecological niche. In contrast, the arrangement of the trichechid muscular-vibrissal complex has provided a prehensile ability that (in addition to other adaptations) presumably allows manatees to obtain and consume a wide variety of vegetation and contributes to their generalist ecological niche. It is likely that snout morphology and perioral bristle use by trichechids (in addition to other morphological and behavioural traits) have been more advantageous than that in dugongs and may have contributed to the displacement of dugongids from the New World by trichechids.

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