Degenerate dentition of the dugong (*Dugong dugon*), or why a grazer does not need teeth: morphology, occlusion and wear of mouthparts

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Abstract

The morphology and functional occlusion of the cheekteeth of 57 dugongs *Dugong dugon* of both sexes were examined using reflected light and scanning electron microscopy, radiography, hardness testing and skull manipulation. The functional morphology of the horny oral pads was also described. Mouthparts and body size allometry was examined for ontogenetic and gender-related trends. We found that the worn erupted cheekteeth of the dugong are simple flat pegs composed of soft degenerative dentine. During occlusion, the mandible moves in a mainly antero-lingual direction, with the possibility of mandibular retraction in some individuals. Anterior parts of the cheektooth row may become non-functional as a dugong ages. As a function of body size, dugong cheekteeth are extremely small compared with those of other mammalian herbivores, and with other hindgut fermenters in particular. The morphology, small size and occlusal variability of the cheekteeth suggest that there has not been strong selective pressure acting to maintain an effective dentition. In contrast, great development of the horny pads and associated skull parameters and their lower size variability suggest that the horny pads may have assumed the major role in food comminution.

Introduction

For a herbivore to access the cell wall or cell content fraction of its food, the plant material must undergo physical breakdown of the cell wall envelope and/or particle size reduction of the fibrous cell wall component. Reduction of food particle size increases the surface area for microbial attachment (Latham *et al.*, 1978) and may lead to increased rates of fermentation (Bjorndal, Bolten & Moore, 1990) and enzymatic digestion (Sanson, 1990). Thus, initial mechanical preparation of food affects the capacity of the gut for enzymatic digestion and digestibility (Spalinger, Robbins & Hanley, 1986). Mechanical breakdown of the plant material by the dentition is usually the first step in digestion preparatory to chemical digestion in mammalian herbivores.

The teeth of hindgut-fermenting herbivores usually play an important role in food breakdown. There are energetic advantages in a hindgut fermenter maximizing cell rupture so that cell contents are released before the small intestine and can be absorbed directly by the animal in an unfermented form (Hintz, Schryver & Stevens, 1978). Hindgut fermenters usually attempt to maximize cell rupture through development of large and/or complex dentitions and many are capable of dealing with high fibre (Fortelius, 1985). The premolars may be molarized (Butler, 1972) and there may be increased complexity of the crown surface topography to increase occlusal efficiency (Sanson, 1977, 1990). The masticatory muscle mass is often increased (Fortelius, 1985), so that greater masticatory forces are applied during chewing.

The dugong *Dugong dugon* is a hindgut fermenter (Murray *et al.*, 1977) as are its closest living relatives, the manatees *Trichechus* spp. (Burn, 1986). Manatees show dental adaptations consistent with a hindgut fermenter's strategy to maximize cell content release. The three species of manatee all have a large number of enamelled bilophodont teeth (Sanson, 1977; Domning, 1982) and the molars are replaced sequentially throughout life via molar progression (Domning & Hayek, 1984). Dugongs are almost exclusively herbivorous throughout their range, grazing selectively on only a few seagrass species (Lanyon, Limpus & Marsh, 1989; Preen, 1993). Surprisingly, the dugong has a small and fixed number of simple peg-like cheekteeth (Owen, 1838; Heuvelmans, 1941) that appear to lose surface enamel before or shortly after eruption (Fernand, 1953; Marsh, 1980), suggesting poor occlusal performance.

The dugong has greatly developed accessory mouthparts in the form of an expanded rostral disc externally (Marshall *et al.*, 2003) and internal opposing horny pads. The high digestibility of the diet (Murray *et al.*, 1977) and the finely ground nature of particulate matter in dugong stomach

contents (Marsh, Heinsohn & Spain, 1977; Marsh, Beck & Vargo, 1999) indicate that some mechanical breakdown of seagrasses probably occurs in the anterior part of the digestive tract, presumably by the mouthparts. If the dugong uses a strategy similar to that of other hindgut fermenters, it is likely that these mouthparts play an important role in obtaining nutrients, particularly from the contents of plant cells. This paper investigates the functional morphology of the mouthparts of the dugong to determine if dugongs fit the dental paradigm of other hindgut-fermenting mammalian herbivores.

Materials and methods

Dental morphology and occlusion

Cheekteeth morphologies of 57 dead, stranded dugongs from tropical north Queensland were examined. This collection of prepared skulls included dugongs of both sexes over a broad range of estimated ages, based on dentinal growth layer group counts (Marsh, 1980). The precise occlusal relationships of dugong cheekteeth were examined by several complementary techniques described by Sanson (1980). Each specimen was examined under a Nikon (Japan) V12 profile projector at $5 \times$ magnification and with reflected light to trace the distribution of crown surface features, including topography (Mills, 1967), wear facets, striae distribution and orientation (Butler, 1952; Rensberger, 1978), crown depressions and areas of hard plaque-like calculus that builds up on non-occluding areas (Sanson, 1980). Because there were no obvious differences between right and left tooth rows, upper and lower tooth rows from the right side only were examined. The tracings of the lower tooth rows were inverted and placed in their correct relative positions over tracings of the upper rows. By sliding the lower tooth row over the upper in the path indicated by the orientation of striae, we could elucidate relative movements and potential contacts of opposing teeth during the power stroke of the occlusal cycle (Mills, 1967; Sanson, 1980). Manipulation of three fresh dugong skulls indicated that preparation of the dried skulls had not significantly distorted the bone or altered the spatial relations of teeth. Relative positions of the upper and lower anterior horny pads were also recorded during reconstructed occlusal cycles.

To investigate microwear, the crown surfaces of the entire upper right tooth rows of seven dugongs aged between 19 and 45 years were sectioned and examined with an Hitachi (Japan) S570 scanning electron microscope (SEM) at magnifications of between 25 and 1200. Wear facet features, including abrasion and attrition striae (Butler, 1952; Rensberger, 1978) and pits and gouges (Gordon, 1982), were recorded. The direction of occlusion was determined by asymmetry of the leading versus trailing edge contours (Greaves, 1973), form of striae (Ryan, 1979), positions of embedded sand grains and examination of tooth surface profiles. For each upper and lower right M3, a series of four surface profiles, running across the crown from buccal to lingual sides, was constructed using a Reflex microscope

(Reflex Measurement Ltd., Somerset, England). Crown profiles were produced by determining the three-dimensional coordinates, $200 \mu m$ apart, along a line running parallel to the occlusal striae. M3 was selected because its central dentine basin was most pronounced. For each tooth profile, a frequency distribution was plotted as depth of dentine lost (y) (from a reference line across the top of the basin, representing the path of travel of the opposing tooth), against distance across the central basin or depression (x). The mode (i.e. the point of deepest dentinal excavation) was compared with the midpoint of the range (i.e. midway along the central depression) to examine the symmetry (skewness) of the crown basin. Based on Greaves' (1973) theory, the leading slope of the basin should be gradual and continuous while the trailing slope is stepped or steeper. Further, the lateral tooth margin on the leading side should be sharp whilst the trailing edge is rounded (Greaves, 1973). In the dugong, the wear facets extend across the crown surface so that the edge of the facet is also the margin of the tooth.

Hardness tests were carried out on the 21 erupted cheekteeth from the upper right tooth rows of these seven adults. Tooth stumps from 2 mm below the crown (remaining after SEM) were embedded in polyester resin, lapped on a high-speed diamond lap until flat, and then hand-lapped using silicon carbide 600 grit and 1200 grit wet-dry polishing paper. Tooth hardness was measured on a Matsuzawa Seiki (Japan) 1982 hardness testing unit using a Vicker's $136°$ diamond pyramid under a load of 300–500 g for 12 s. Hardness was calculated from the dimensions of the indentations formed in the exposed tooth surface and was expressed as Vicker's microhardness units (H_v) (Lysaght, 1960). Hardness measurements were taken at several points along two perpendicular transects on each tooth, one running along the longitudinal tooth axis. Mean H_v for each concentric zone was calculated. To examine differences in hardness between tooth types, a one-way ANOVA was performed with homologous teeth from different individuals as replicates. Three-way ANOVAs could not be performed (i.e. with individual dugongs included as a factor) as dugong teeth erupt in a monophyodont series with individual erupted dental formulae varying between individuals and dentinal layer number varying even between homologous teeth. For those specimens in which individual dentinal layers were distinguishable (all except one juvenile), two-way ANOVAs were performed with tooth hardness as the dependent variable and tooth type (PM2–M3) and layers (1–5) as the fixed factors. Tooth row (i.e. all erupted teeth) was also considered as a single functional unit. Lingual and buccal sides of the tooth row were also compared, with the two central dentinal layers excluded. A two-way ANOVA was performed with hardness of the tooth row as the dependent variable and dugong specimen and tooth side as the independent variables. A one-way ANOVA examined differences between dugongs in terms of hardness of the entire tooth row.

Lateral radiographs of the lower cheekteeth of 26 skulls of various ages were examined for the angle of root deflection and to determine if alteration in molar surface

area after eruption could be accounted for by vertical wear of the existing tooth.

Relative growth of skull and teeth

To investigate the possibilities of mesial drift, molar progression or ontogenetic growth of skull parts to account for successive replacement and movement of teeth, the relative positions of the teeth and skull features were compared for 20 female specimens over a wide age range. Skull length (condylo-premaxillary length, Spain & Heinsohn, 1974) was measured and then skulls were photographed from a constant ventral aspect and printed to a constant length. Eleven bony reference points were chosen at intervals along the ventral longitudinal axis of the skull (Fig. 1). Osteological identification and nomenclature followed Spain & Heinsohn (1974), James (1974) and Spain & Marsh (1981).

The positions of each of the bony reference points for each specimen were traced from the photographs. When there was some slight asymmetry in reference point positions between the left and right sides of the skull (also found by Spain & Heinsohn, 1974), the point recorded was that falling midway between the two sides. The anterior and posterior margins of the tooth row and positions of individual teeth were superimposed over the skull reference points. Tooth row was defined as the posterior edge of the most posterior socket containing an erupted tooth, to the anterior edge of the most anterior socket. Posterior sockets containing unerupted teeth were excluded, but anterior sockets that contained wizened or partially resorbed teeth, or were empty were included. Tooth position was defined as the point midway along the length of the tooth, in line with the longitudinal axis of the skull.

Tooth size–body size relationships were examined for specimens representing both sexes and from a wide age range (<1 year to 46 years; dugongs <1 year were given an age of 0.5 year) for which intact skulls were available ($n = 54$). Tooth size was expressed as a function of metabolic body weight ($kg^{0.75}$). As actual body weights were available for only 11 of the 54 specimens, two successive regression equations were used to estimate body weight from skull length: Equation (1) relates condylo-premaxillary (skull) length to body length: $y = 54.214 + 1.650x + 0.110x^2$, where y = body length (cm) and x = skull length (cm) (Spain & Heinsohn, 1974).

Equation (2) relates body length (as derived above) to body weight: $y = (-34.251) - 14.976x + 55.218x^2$, where y = body weight (kg) and x = body length (m) (Spain & Heinsohn, 1975).

We also used the 11 specimens of known body weight to derive a single and direct regression equation of body weight against head length. The best equation relating these variables was achieved with a log transformation of each variable, $\log(\text{body weight kg}) = -7.39 + 3.89 * \log(\text{head length mm})$ and was significant ($F = 132.98$; d.f. $= 1$, 9; $P < 0.001$; adj. $R^2 = 0.94$). The range of head lengths included in this regression spans the specimens in this study. Body weight was converted to metabolic body weight ($kg^{0.75}$), because the function that best fits the discrepancy between energy metabolism and size is the three-fourth power of body weight or $kg^{0.75}$ (Tyndale-Biscoe, 1973). This estimate of metabolic body weight is based on the assumption that metabolic body rate in dugongs scales to $BM^{0.75}$.

Crown surface area is probably an appropriate index of the functional part of the tooth (see Results). Furthermore, because dugongs chew on one side of the jaw at a time (see Results), the functional surface area is the combined surface areas of teeth in one jaw quadrant. Because differences between quadrants within an individual were negligible, measurements were made on the upper right tooth rows only. The surface area of each erupted cheektooth was digitized in planar view from tracings. These measurements were considered representative because dugong teeth wear relatively flat with age. Two variables representing tooth size
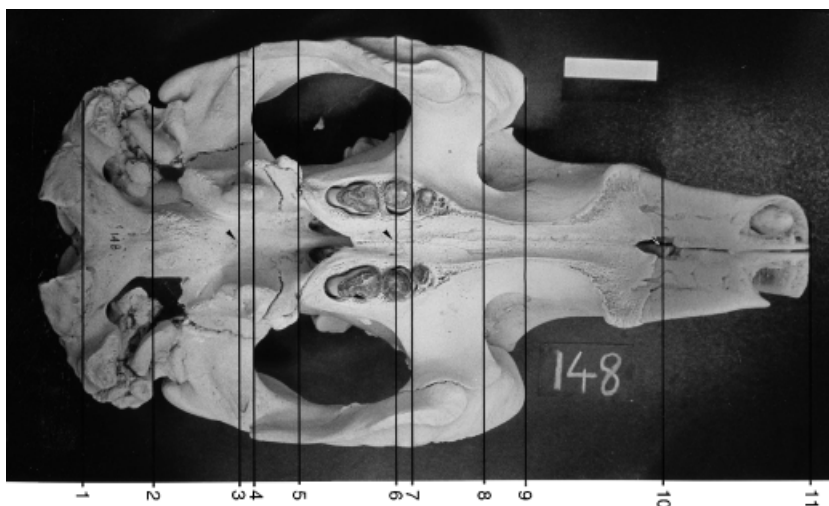

Figure 1 Ventral longitudinal aspect of the skull and cheektooth row of an adult dugong *Dugong dugon* (specimen mm 148), showing 11 bony reference points used in skull allometry studies. This diagram allows tracking of skull areas and migration of cheekteeth in relation to these reference points. Scale bar = 5 cm. 1. Ventral edge of foramen magnum. 2. Antero-lateral rounded edge of post-tympanic process of squamosal bone. 3. Anterior edge of basioccipital in midline. 4. Posterior edge of temporal fossa. 5. Anterior edge of ventromedial process of pterygoid. 6. Anterior edge of palatine, at junction with maxillary, in midline. 7. Anterior edge of temporal fossa. 8. Most posterior part of anterior edge of malar process (=zygomatic–orbital bridge) of maxillary (indicated on skull's left side). 9. Anterior edge of jugal. 10. Anterior-most edge of maxillary, at junction of premaxillary. 11. Anterior tip of premaxillae.
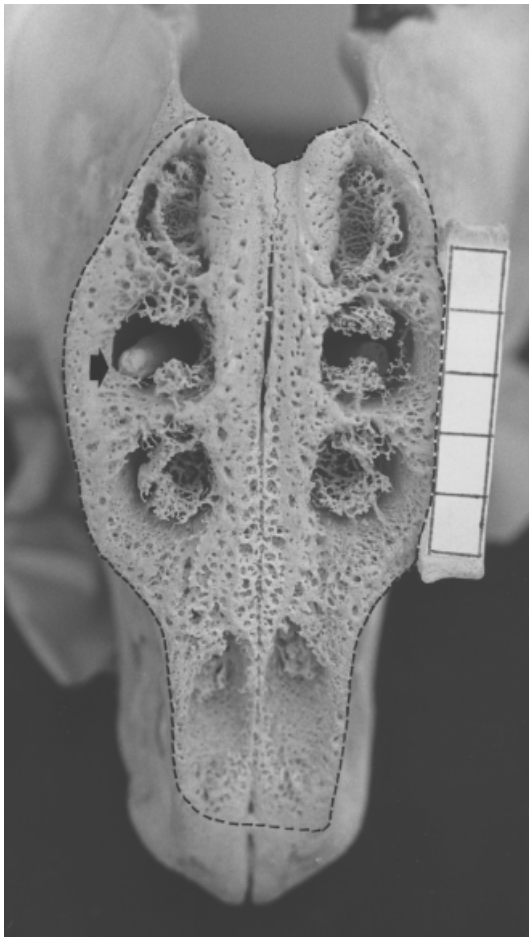
Figure 2 Anterior view of the downturned mandibular symphysis mandible showing vestigial incisor and canine sockets. A vestigial incisor sits in the third right socket (arrowed). Dashed line indicates perimeter of lower horny pad attachment area. Scale bar = 5 cm.

were expressed as a function of body size: (1) total crown surface area of cheekteeth and (2) occlusal or functional surface area. The latter was estimated by subtracting non-functional tooth areas (i.e. those coated with calculus, partially erupted or non-occluding teeth (Sanson, 1980)) from the total tooth surface area.

The oral horny pads were dissected away from the mandible and premaxilla in three fresh dugongs, to examine the relationship between the surface area of the pad and the underlying bone. The surface area of the lower horny pad attachment area on the symphysial part of the mandible was a good approximation of the surface area of the overlying pad (Fig. 2). The anterior edge of the horny pad was defined as running along the edge of the most anterior incisor socket, and the posterior edge along the dorsal margin of the deflected portion of the dentary, i.e. the posterior end of the lower incisor socket row. Surface area, maximum length and maximum width perpendicular to the long axis of each traced pad ($n = 57$) were measured digitally on an image analyser.

The coefficients of variation (standard error/mean) (Bader, 1955; Gingerich, 1974; Gould, 1975) in cheektooth surface areas were calculated for each tooth type for all specimens, and then for adult specimens only (i.e. dugongs 11 years with erupted molars and no premolars). Variation in the two measures of tooth size was determined for each tooth type. Variation in size of the lower horny pad was also assessed.

Regressions were performed on tooth size versus body size. Huxley's (1932) allometric power function may be expressed as $y = bx^a$. On a log–log plot, a = slope and n = intercept on the y-axis. For an allometric comparison of an area (L^2) e.g. tooth surface area (mm^2), and a volume (L^3), e.g. body mass ($kg^{0.75}$), a slope of $a = 0.67$ represents isometry. For a comparison of an area (L^2), and a length (L), a slope of $a = 2$ represents isometry (Huxley, 1932). Regressions of tooth size:body size against gender were compared using ANCOVA (Wilkinson, 1988). In those cases where a significant sex difference occurred, Johnson–Neyman tests (Wilcox, 1987) were performed to establish at which age or body size, the difference first occurred.

Feeding observations

A 113 min video recording was made of two captive dugongs feeding at Jaya Ancol Oceanarium, Jakarta, Indonesia. These dugongs were fed fresh seagrass leaves, mostly *Syringodium isoetifolium* with small amounts of *Cymodocea serrulata* and *Enhalus acoroides*. Seagrass was usually thrown onto the water surface at feeding time; however, the dugongs were also hand-fed. The footage was observed at regular speed and in slow motion, to elucidate gross movement of the mandible relative to the maxilla during food ingestion and handling, and to confirm the orientation and directionality of mandibular movement as suggested by microwear features.

Results

As configuration and morphology of dugong dentition have been described previously (Owen, 1838; Heuvelmans, 1941; Fernand, 1953), only a brief review is given here to facilitate an understanding of the occlusal relationships of the cheekteeth. With the exception of Fernand's (1953) brief comment, there is no previous detailed description of the mechanism of occlusion.

Morphology of cheekteeth

The cheekteeth are positioned towards the rear of the buccal cavity (Fig. 1). Heuvelman's (1941) dental formula, which recognizes functional teeth as I_0^1; C_0^0; PM_3^3; M_3^3, is followed here. This description excludes the vestigial lower incisors and upper deciduous first incisor. Three premolars (presumably the posterior three deciduous premolars) are erupted at birth. The molars progressively erupt posteriorly during growth, whereas the premolars progressively fall out or are partially resorbed (Fernand, 1953; Mitchell, 1973), the sockets filling with bone, until usually only M2 and M3

(occasionally M1) are present in each quadrant in old animals. Thus the cheekteeth are never simultaneously all erupted and in wear (Mitchell, 1973) (Fig. 3).

Dugong cheekteeth have tuberculated crowns initially, and these have been described as vestiges of the typical dugongid cusp pattern (Domning, 1982). A thin uneven veneer of true enamel is present on the crown surface of unerupted cheekteeth and for only a short time on the erupted teeth of young animals (Fernand, 1953). The original crown surface features are rapidly worn away. Consequently, the following morphological descriptions are of both unworn and variously worn cheekteeth. Cheekteeth in the post-occlusal stages are not described here; these become wizened and undergo resorption. Each tooth description fits both upper and lower teeth.

PM2 is small, monocuspid and roughly cylindrical in cross section (Fig. 3a). The single cusp is roughly conical, rising to a blunt apex. Small grooves run along the sides of the cusp from apex to base. This cusp is worn rapidly to a flat peg. PM3, PM4, M1 and M2 are all bicuspid initially (Fig. 3a and b). Anterior and posterior cusp(s) are divided by a central fissure running linguo-buccally. Wear facets originally appear on the more lingual faces of the cusps and then expand and coalesce until a single flat wear facet is formed (Fig. 3b–d). Cusps of unworn teeth widen from their apices to their bases; hence with initial tooth wear the facets and crown surface increase in size. The worn cross-sectional shape of these teeth varies between wear stages and individuals, from subterete or cylindrical to rectangular. Unworn M3 is initially cuspid (Fig. 3b); however, the worn tooth has a unique morphology (Fig. 3c and d). During the course of its development, the tooth becomes extended antero-posteriorly (with a length:width ratio of 1.7 or more; Mitchell, 1973) and contracted in the middle so that it appears shoe-shaped (Owen, 1838; Mitchell, 1973, 1978; James, 1974). Regions on the surface of each of the cheekteeth may be differentially eroded, particularly in M3, where a central depression forms. In addition, the surface of an individual cheektooth and the entire tooth row may undulate slightly, particularly parallel to the long axis of the tooth row.

Morphology of the horny pads

The opposing cornified horny pads are situated on the anterior downturned part of the rostrum (Figs 1 and 2). The morphology of the pads has been described in detail by Gudernatsch (1908), Petit (1955) and particularly by Gohar (1957). Each pad can be divided into different morphological regions. The upper pad has areas of raised 'warts' and protuberances (Fig. 4a) and, at the flexure of the jaw, 'claw-like protuberances' (described by Gohar, 1957). The upper pad continues into the palatal region (Fig. 4a). The palatal ridges have been described by Marsh & Eisentraut (1984).

The lower pad is beset by short dense bristles that are angled posteriorly (Fig. 4b). Underneath the lower pad, in the anterior and deflected symphysial portion of
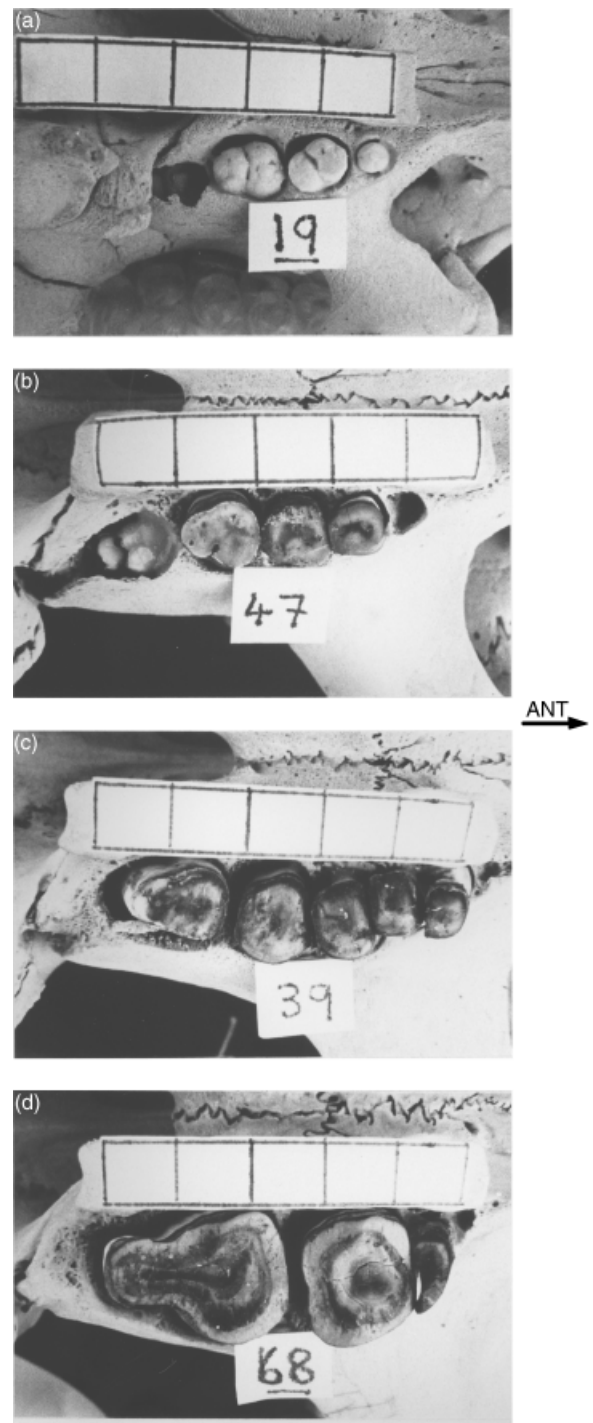

Figure 3 Series of upper cheektooth rows showing the ageing/wear sequence of erupted teeth. (a) Neonate (0.5 year) with erupted PM2, PM3, PM4 (specimen mm 19), unerupted M1; (b) juvenile (2 years +) with erupted PM4, M1, M2, unerupted M3 (mm 47); (c) juvenile (7 years +) with erupted with erupted PM3, PM4, M1, M2, M3 (mm 39); (d) adult (31 years +) with erupted M1, M2, M3 (mm 68). Scale bars = 5 cm.
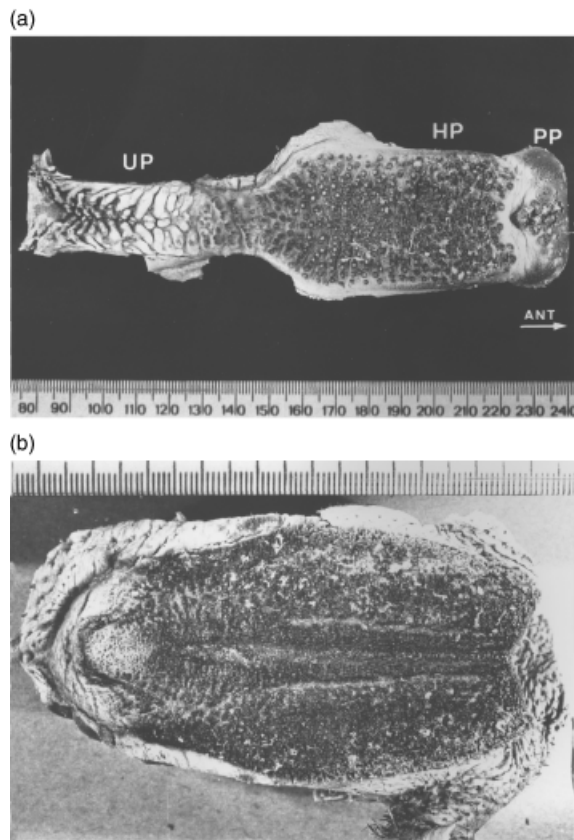
Figure 4 Gross morphology of the surface of dissected oral horny pads. (a) Upper palate (UP) and horny pad (HP) with surface callosities. Note the palatal process (PP) at the anterior of the horny pad, and the gradation of surface features between the upper palate and the horny pad; (b) lower pad with short bristles.

the mandible, is a series of vestigial tooth sockets sometimes containing vestigial incisors (Owen, 1838; Lyman, 1939; Fernand, 1953; J. M. Lanyon, pers. obs.) (Fig. 2). Each socket is filled with a tract of fibro-vascular tissue that attaches the pad to the underlying bone (Owen, 1838; Fernand, 1953; Gohar, 1957).

Occlusion of cheekteeth

General features

The cheekteeth are the only teeth that are functional during mastication. In lateral view, the tooth row is straight so that once erupted, all cheekteeth along a quadrant may potentially occlude. From a dorso-ventral view, the buccal borders of the tooth row are straight except for the anterior part, which curves medially, and the lingual borders are curved slightly (Fig. 1). From an anterior–posterior perspective, crown surfaces of both the worn upper and lower cheekteeth incline the same way: from dorsal and lingual to ventral and buccal, cf. Fernand (1953) who suggested that the lower teeth sloped from lingual to buccal in this manner but with the reverse occurring in the upper teeth.

Dugongs are functionally anisognathous, i.e. teeth contact on only one side of the jaw during occlusion. Evidence for this is provided by teeth on either side of the jaw not lining up in centric occlusion at the same time, and opposite striae orientation on left and right cheekteeth. Observations of feeding dugongs indicate alternation of the chewing side and a marked vertical or orthal component at least at the front of the jaw in the vicinity of the horny pads, during the recovery stroke. Such orthal movement of the mandible, as indicated by opening and closing the mouth, could presumably serve to aid ingestion by moving the seagrass into the mouth (see below).

Unworn cheekteeth are cuspid for less than 1 year after eruption. With repeated occlusal contacts, the thin enamel cap is rapidly worn so that the underlying softer dentine is exposed right across the crown surface. Worn adult teeth are essentially flat pegs that lack identifiable topographic features. However, irregular and variable crown undulations may occur along a tooth row, and across individual teeth. In juvenile animals, surface undulations in opposing teeth are complementary so that when they occlude, their surface topographies compel them to move relative to each other in a restricted way. In adults, the fit of the opposing molars is less precise.

The state of tooth eruption is similar on both sides of the jaw so that homologous premolars and molars occlude, i.e. upper M2 directly opposes lower M2. A rare exception was found in one specimen (mm 19) in which the anterior part of lower M2 opposed upper M1 and the posterior part of lower M2 opposed the anterior part of upper M2 so that lower right M3 had erupted ahead of upper M3. This exceptional condition, of development in the upper jaw lagging behind that in the lower jaw, has been documented previously (Mitchell, 1973; Marsh, 1980).

The power stroke

Orientation of striae indicates that the jaw is hinged on the contralateral side, with rotation around the balancing side condyle (Fig. 5). This directly contradicts the ipsilateral mode of jaw hinging suggested by Domning (1977). Antero-lingually orientated striae suggest that relative tooth movements are mainly lateral but have an anterior–posterior component (Fig. 5). However, the variability in distribution of wear facets and striae type both within and between individual dugongs suggests that occlusal contacts during the power stroke are not uniform or tightly controlled.

There is a range of striae types on individual wear facets, from highly polished areas with few or no striae to areas of shallow multidirectional abrasion striae (Fig. 6a) to deeper attrition striae (Fig. 6b). There is also marked variation in striae type along a tooth row, but no consistent difference in striae orientation between anterior and posterior parts of the tooth row. Variation in wear patterns is not directly attributable to differences in tooth type, structure or hardness (see below). Pits and gouges also occur frequently on the tooth surface (Fig. 6c) with no obvious differences in
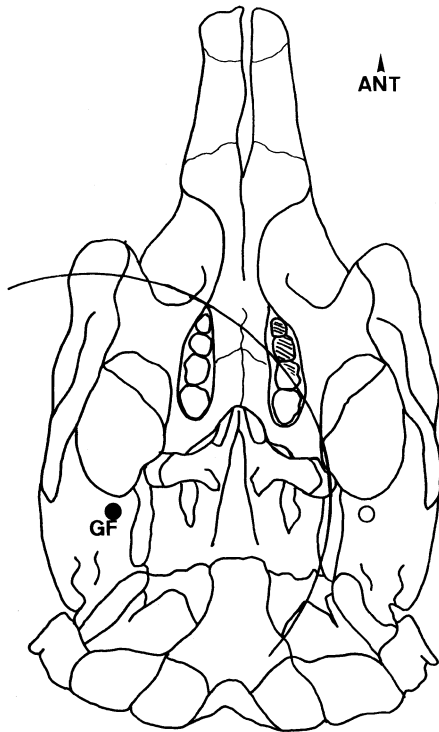
Figure 5 Ventral aspect of adult dugong *Dugong dugon* skull showing arc of rotation of mandible about the glenoid fossa (GF). The sector of the circle with its centre at the fulcrum represents the path of travel of the mandible. The orientations of occlusal striae on the active side are indicated by parallel lines.

frequency of pitting between lingual and buccal sides (according to Gordon, 1982).

Calculus is generally absent from erupted premolars (Figs 3 and 7). In juvenile dugongs, it first appears in non-occluding cracks and grooves of erupted molars. As central dentine areas develop into concave depressions, calculus deposits increase (Fig. 7b–e). Generally, anterior molars have more extensive calculus areas than posterior molars (Fig. 7b and c), suggesting that there are fewer occlusal contacts between anterior teeth. In some cases, the entire crown surfaces of some or all cheekteeth become coated (Fig. 7e), indicating a significantly reduced occlusal area or at least occlusal forces that are insufficient to remove the calculus. Significantly, variation in calculus distribution is not age-specific so that while some old dugongs retain highly polished teeth with little or no calculus, the teeth of some younger adult dugongs may be almost entirely coated by calculus.

Directionality

Representative M3 crown profiles of the youngest (19 years) and oldest (45 years) dugongs examined are shown in Fig. 8. The mode and midpoint of each M3 profile are given in Table 1. In all specimens examined, leading and trailing
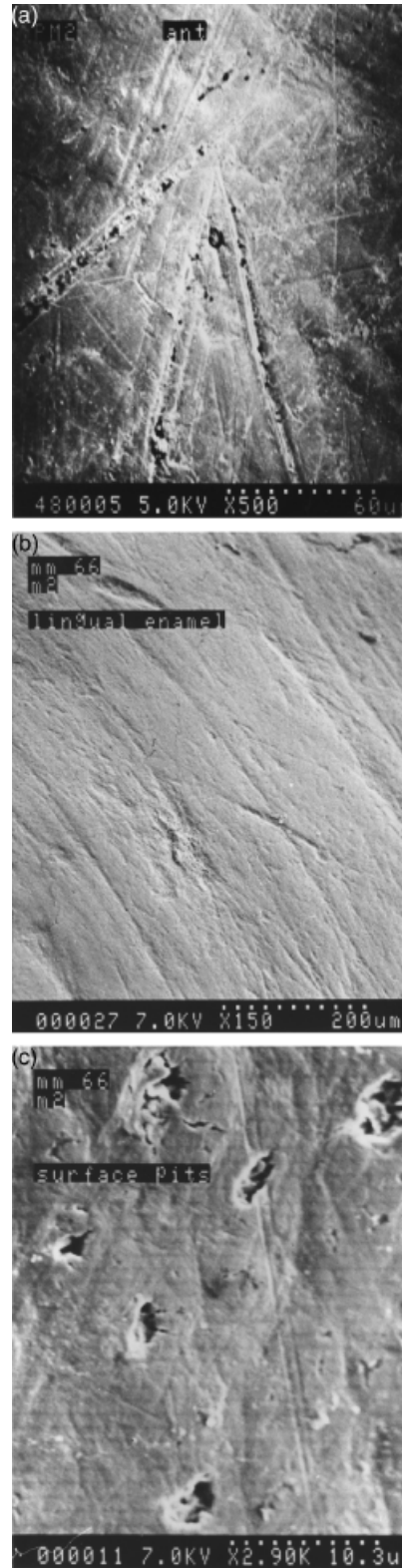

Figure 6 Scanning electron micrographs of striae types found on the crown surface of dugong *Dugong dugon* cheekteeth. (a) Abrasion striae (magnification × 500 times), (b) attrition striae (× 150 times), (c) pits and gouges (× 2900 times).
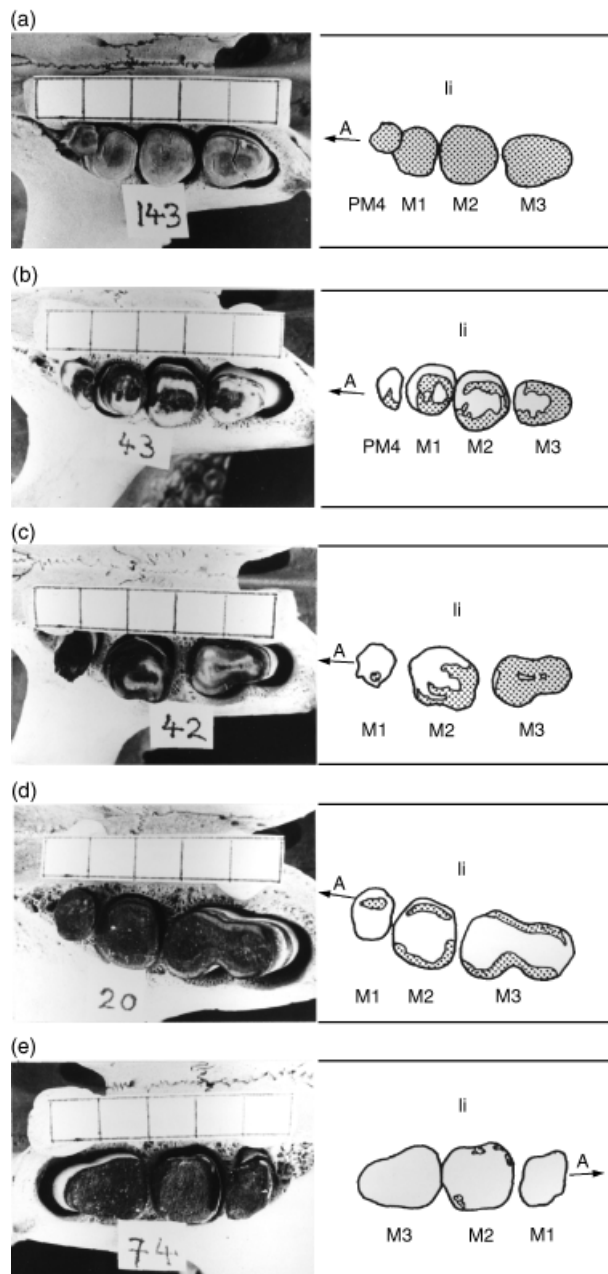
Figure 7 Distribution of calculus deposits on cheekteeth of dugongs *Dugong dugon* of various ages. On drawings, stippled areas are occlusal (functional) and clear areas are calculus. (a) Juvenile (8 years); (b) juvenile (11 years); (c) young adult (13 years); (d) adult (27 years); (e) adult (17 years). Scale bars = 5 cm.

edges were consistently reversed for opposing teeth, confirming that the tooth profiles were attributable to occlusion. For five of the 12 (41%) specimens, the buccal side of upper M3 was the leading edge (LE), and, conversely, the lingual side of the lower tooth (Table 1; Fig. 8a). This indicates forward movement of the mandible during the occlusal stroke, assuming an antero-lingually orientated

power stroke. One specimen (mm 100) indicated an occlusal stroke in the opposite direction, i.e. mandibular retraction. In contrast, in the remaining six specimens (50% of the sample), the more posterior profiles indicated forward mandibular movement whereas the anterior profiles indicated mandibular retraction (Fig. 8b). This pattern of mandibular retraction was pronounced on dugongs aged >36 years. One explanation is that the anterior parts of M3 do not occlude in older animals, but are subject to abrasion by food. The gape of the dugong is small, so that when handling relatively large volumes, food may pass over the teeth in a reverse direction during the recovery stroke. Alternatively, occlusal contacts or food passage may occur in either direction in older dugongs.

Examination by light microscopy of cheekteeth from another 50 skulls supported this directionality. Twenty of the 50 specimens (40%) had profiles and margins consistent with forward movement of the mandible. In the remaining specimens, examination by light microscopy alone was insufficient to determine directionality. Although the asymmetrical profiles were pronounced on M3, they also occurred on other cheekteeth. These results indicate that forward movement of the mandible during the power stroke is probably normal, but retraction of the mandible may occur in some dugongs.

Horny pad occlusion

The fit between upper and lower horny pads is very precise. The opposing morphologies of the pads appear to regulate pad occlusion, in much the same way that tooth crown morphology may regulate relative tooth movements (Maynard-Smith & Savage, 1959). The fit of opposing pads indicates that during contact they move relative to each other with a largely lateral component, but with some room for either anterior or posterior movement. The lower pad has backwardly directed bristles so that orthal movement plus retraction of the mandible would appear to move ingested seagrass up the symphysial part of the mandible and posterior towards the teeth. This phenomenon was examined by manipulating seagrass and pieces of paper in fresh dissected dugong jaws, but was not quantified. One cycle of mandibular retraction was generally sufficient to move seagrass along the entire length of the upper pad and into the horizontal palatal region of the mouth. Further, because of the geometry of the jaw system, the pads occlude when the cheekteeth do, regardless of the direction of occlusal movement. Thus, there is a single occlusal stroke for the two systems.

Tooth wear

Description

In juvenile dugongs, the first wear facets are small (Fig. 3a) and form on the slopes of the posterior cusps of both upper and lower teeth. With further wear, the facets expand and coalesce so that in animals with teeth that are worn flat,
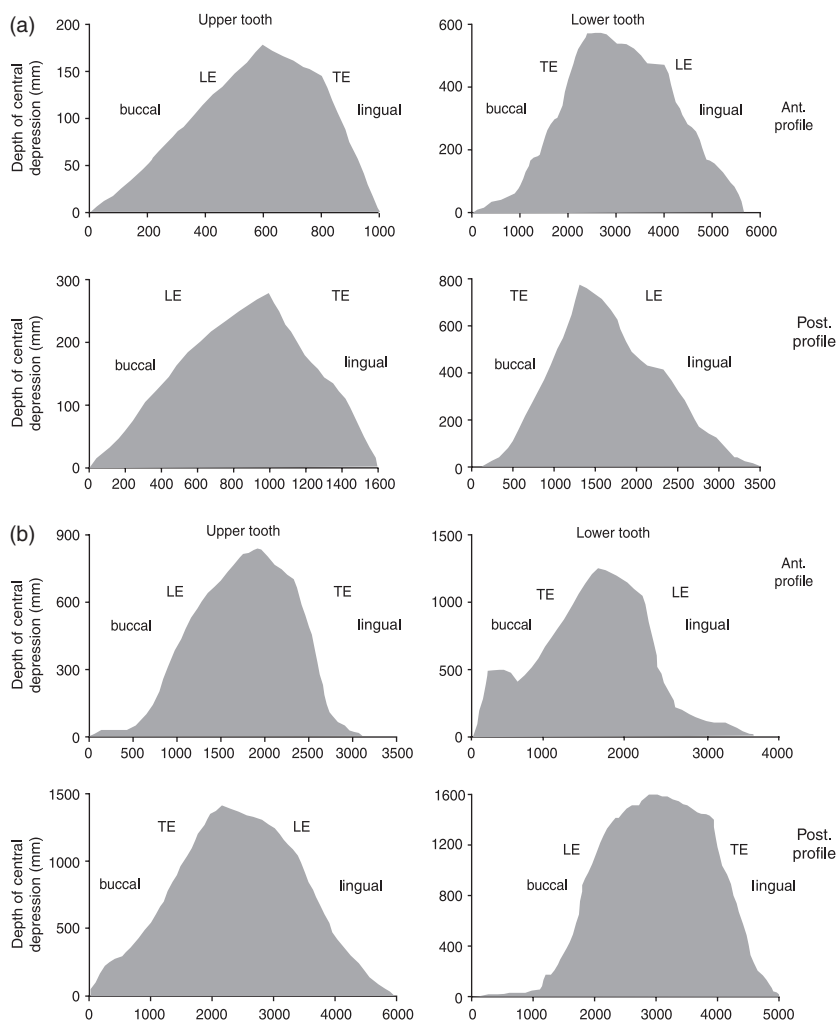
Figure 8 Tooth profiles across upper M3 of (a) 19-year-old dugong *Dugong dugon* (mm 148) and (b) 45-year-old dugong (mm 66). Two profiles are shown: one anterior and one posterior. The leading edge (LE) and trailing edge (TE) are consistent between anterior and posterior profiles for (a); LE and TE edges are reversed between anterior and posterior profiles for (b). Note: profiles have been inverted and graphed as frequency (depth) distribution curves, so that the stippled region represents the excavated dentine area. LE and TE edges were identified by comparing midpoint to mode of deepest point of excavation to determine skewness of the basin. As the actual profiles are very shallow, the horizontal axes have been contracted for clarification.

wear facets are distributed across the entire crown surface (Fig. 3b–d), except in areas of calculus deposits. There is considerable variation in size and extent of wear facets along a tooth row and even across individual teeth. Further, opposing teeth may not move entirely past each other so that wear is uneven across the tooth from lingual to buccal, especially in older animals.

Uneven wear along individual teeth suggests uneven occlusal pressures. Uneven wear across upper M3 frequently results in the anterior–buccal part of the tooth being higher. This is generally not so marked in lower M3. This differential height suggests that there is reduced frequency of contacts on the anterior raised area and/or that occlusal forces are greater towards the rear of the tooth row. The angle of elevation and relative height of this area appear to increase with age. Thus, there is development of a 'tertiary morphology' of teeth past a certain wear state (age > 36 years). In most specimens in which M2 is fully erupted, calculus deposits form anteriorly, then more posteriorly and buccally, indicating that only the posterior part of the tooth row remains fully functional.

Tooth hardness

Worn cheekteeth of the dugong are soft (Table 2). Individual hardness measurements of exposed dentine ranged from 16.3 to $59.7H_v$ units with a mean ($\pm$ SE) of 33.93 ± 0.4 ($n = 275$) and a (low) coefficient of variation of 19.75. Mean hardness of individual teeth ranged from $23.8 \pm 2.6H_v$ (PM2) to $37.5 \pm 2.5H_v$ units (M1) (Table 2). However, tooth type did not differ significantly in hardness ($F = 2.78$; d.f. = 5, 15; $P = 0.057$).

In adult teeth, five concentric dentinal growth layer groups were discernible in cross section in erupted molars M1–3 (Fig. 9). Fewer layers (2–4) were distinguishable in premolars and M1 of juveniles, and in anterior adult teeth that were externally worn and/or undergoing resorption. Hardness zones were consistent with the concentric dentinal layering visible on the crown surface. For those specimens in which individual layers were distinguishable (i.e. all specimens except the youngest, mm 24), there were no significant interactions between erupted tooth type and dentine layer (Table 3) so that differences between layers were similar for

Table 1 Symmetry of the crown profiles across the central dentine basins from buccal to lingual sides of the upper and lower third molars (M3)

Specimen	Age (years)	Profile	Upper M3			Lower M3		
			Mode	Midpoint	LE	Mode	Midpoint	LE
mm 148	19	1	600	500	Buccal	2400	2800	Lingual
		2	1000	800	Buccal	1200	1700	Lingual
		3	3800	3200	Buccal	1200	1600	Lingual
		4	3600	3300	Buccal	2200	2900	Lingual
mm 136	21	1	5600	3750	Buccal	2000	2300	Lingual
		2	5600	3950	Buccal	1400	1800	Lingual
		3	1200	1033	Buccal	3800	3000	Buccal
		4	1400	1000	Buccal	3000	2100	Buccal
mm 005	24	1	No data			3000	2300	Buccal
		2				2200	2200	No skew
		3				1200	1400	Lingual
		4				1000	1300	Lingual
mm 003	26	1	3500	3000	Buccal	1600	2500	Lingual
		2	4600	3500	Buccal	2200	2500	Lingual
		3	1400	1300	Buccal	4200	4300	Lingual
		4	1200	1300	Lingual	4000	4000	No skew
mm 102	34	1	2000	1750	Buccal			
		2	1650	1275	Buccal		No data	
		3	3000	2700	Buccal			
		4	4000	3100	Buccal			
mm 100	36	1	2000	1520	Buccal	2400	2000	Buccal
		2	1600	1700	Lingual	2600	2100	Buccal
		3	2400	3500	Lingual	4200	4100	Buccal
		4	3000	3400	Lingual	6000	4300	Buccal
mm 66	45	1	2000	1600	Buccal	1600	1800	Lingual
		2	1100	1450	Lingual	1800	1950	Lingual
		3	2000	2400	Lingual	2800	2490	Buccal
		4	2200	2500	Lingual	2800	2400	Buccal

Profiles are numbered 1 to 4 from the posterior to the anterior part of each tooth. Mode and midpoint values are expressed as distance (μm) from the buccal edge. LE, leading edge of the tooth during occlusion as inferred from a comparison of mode and midpoint values.

each of the tooth types. There were no significant differences in the hardness of individual teeth within dugongs, except in one animal (mm 148) where M2 was significantly softer than the other teeth ($F = 3.92$; d.f. $= 2, 31$; $P = 0.030$). All adult animals, except one (mm 18), showed significant differences in the hardness of the five growth layer groups (Table 3) so that the outer perimetric layer (layer 5) was harder than the inner layers for each of the molars M1–M3.

Because all erupted teeth potentially occlude at once, the hardness of the entire tooth row should probably be considered as a single unit. There was no significant interaction between dugong and buccal or lingual side of the tooth row ($F = 1.03$; d.f. $= 5, 95$; $P = 0.404$). There was no significant difference in hardness between buccal and lingual sides of the erupted tooth row ($F = 0.07$; d.f. $= 1, 95$; $P = 0.787$) which translates to no difference in hardness between leading and trailing edges. There were significant differences in mean hardness of entire tooth rows of dugongs ($F = 2.64$; d.f. $= 5, 95$; $P = 0.028$), but these differences did not correlate with age or gender.

Sub-surface regions of the teeth are frequently darkly stained to a depth of up to 2 mm. This stain appears to be associated with calculus and may cause sponginess of the dentine. We also found a hypermineralized area some 2 mm below the tooth surface in some specimens, which was birefringent under the polarizing microscope. Such a hypermineralized layer under plaque or calculus may be a precursor to decay (W. G. Young, pers. comm.).

Radiography

Initial widening and then tapering of M1 is reflected in an increase and then decrease in crown surface area with wear. The roots of M2 and particularly M3 widen out anteroposteriorly within the tooth socket (Fig. 10). The pulp cavities of M2 and M3 appear to remain open throughout life, with continual deposition of dentine as reported by Marsh (1980).

The direction of deflection of cheekteeth roots for individual tooth types varies. There is also variation among

Table 2 Hardness (H_v units) of tooth layers, individual teeth and total tooth row in dugongs *Dugong dugon*; mean $\pm$ SE (*n*)

Specimen	Tooth	Layer 1	Layer 2	Layer 3	Layer 4	Layer 5	Whole tooth	Tooth row
mm 24	PM2	–	–	–	–	31.6 ± 1.8 (3)	31.6 ± 1.8 (3)	31.5 ± 0.8 (13)
	PM3	–	–	–	–	31.9 ± 3.2 (3)	31.9 ± 3.2 (3)	
	PM4	–	–	–	31.7 ± 1.1 (3)	31.0 ± 1.1 (4)	31.3 ± 0.7 (7)	
mm 48	PM2	16.3 ± 0 (1)	–	–	–	26.3 ± 0.7 (3)	23.8 ± 5.6 (4)	29.5 ± 1.2 (31)
	PM3	33.5 ± 1.5 (3)	–	23.4 ± 1.8 (4)	–	31.0 ± 4.4 (4)	28.9 ± 2.1 (11)	
	PM4	33.1 ± 8.4 (2)	–	33.3 ± 1.0 (4)	–	30.6 ± 5.1 (4)	32.2 ± 2.3 (10)	
	M1	–	–	–	30.4 ± 1.6 (3)	29.1 ± 3.1 (3)	29.7 ± 1.6 (6)	
mm 22	M1	31.5 ± 0.7 (2)	34.1 ± 0.9 (4)	36.0 ± 0.9 (4)	23.9 ± 1.9 (4)	41.6 ± 3.1 (4)	33.6 ± 1.6	35.5 ± 0.9 (60)
	M2	38.0 ± 0.4 (2)	33.7 ± 1.0 (4)	34.8 ± 1.0 (4)	30.1 ± 4.0 (4)	41.0 ± 7.1 (4)	35.3 ± 1.9 (18)	
	M3	33.9 ± 0 (1)	38.6 ± 0.4 (2)	40.8 ± 0.7 (8)	26.1 ± 1.2 (5)	40.5 ± 1.2 (8)	37.3 ± 1.3 (24)	
mm 148	M1	34.7 ± 4.2 (2)	35.3 ± 0.7 (4)	30.5 ± 0 (1)	–	–	34.4 ± 1.2 (7)	33.8 ± 0.8 (48)
	M2	27.1 ± 0 (1)	27.7 ± 3.0 (4)	29.6 ± 3.4 (4)	–	38.8 ± 5.0 (3)	31.1 ± 2.2 (12)	
	M3	30.9 ± 1.1 (6)	34.4 ± 0.9 (8)	34.2 ± 1.0 (3)	32.8 ± 0.7 (6)	41.7 ± 1.6 (6)	34.8 ± 0.8 (29)	
mm 102	M1	34.0 ± 0 (1)	36.7 ± 2.5 (3)	37.4 ± 3.1 (4)	40.6 ± 13.4 (2)	–	37.5 ± 2.5 (10)	36.0 ± 1.0 (52)
	M2	29.1 ± 1.1 (7)	32.2 ± 1.9 (4)	34.7 ± 2.0 (4)	39.1 ± 3.8 (4)	53.2 ± 2.9 (4)	36.5 ± 2.0 (23)	
	M3	32.9 ± 1.7 (3)	30.9 ± 2.5 (4)	35.2 ± 1.1 (4)	36.3 ± 2.0 (4)	36.7 ± 1.5 (4)	34.5 ± 0.9 (19)	
mm 18	M2	29.3 ± 0 (1)	32.4 ± 1.0 (3)	34.8 ± 1.5 (4)	29.5 ± 6.3 (3)	32.6 ± 2.4 (4)	32.5 ± 1.5 (15)	32.4 ± 1.1 (30)
	M3	34.7 ± 3.9 (3)	31.8 ± 1.1 (4)	29.5 ± 3.4 (4)	–	34.1 ± 4.5 (4)	32.2 ± 1.6 (15)	
mm 66	M1	32.3 ± 2.6 (2)	–	33.3 ± 1.5 (4)	–	45.9 ± 3.1 (3)	37.2 ± 2.5 (9)	34.6 ± 0.9 (41)
	M2	32.8 ± 2.3 (3)	–	34.7 ± 1.7 (4)	–	32.3 ± 5.4 (4)	33.3 ± 2.0 (11)	
	M3	31.4 ± 0 (1)	33.1 ± 1.4 (5)	31.6 ± 0.4 (7)	37.9 ± 1.3 (4)	37.0 ± 2.7 (4)	34.2 ± 0.8 (21)	
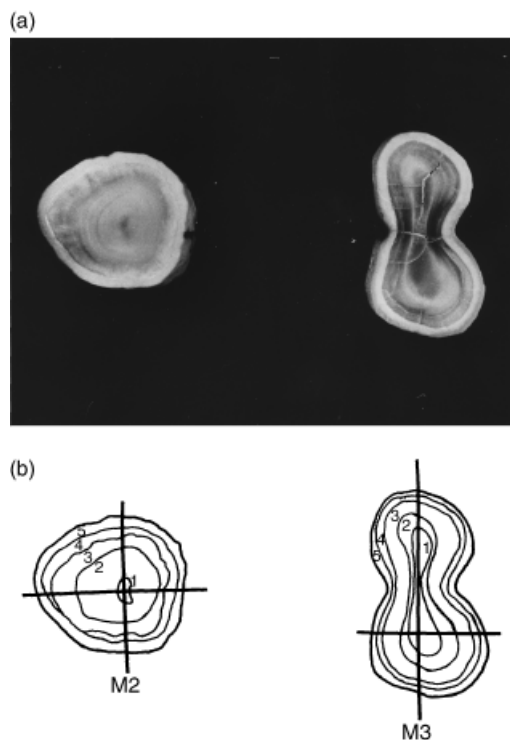
Figure 9 Transverse sections through dugong *Dugong dugon* cheek-teeth M2 and M3 showing (a) concentric dentinal layers 1–5, and (b) perpendicular transects across teeth to measure hardness.

homologous teeth, so that root deflection appears to relate to the tooth's position in the ramus with respect to other erupted and erupting teeth. When the premolars and first molars are erupted, the roots descend straight into the mandible. During resorption of the most anterior teeth, their roots tend to incline anteriorly (e.g. PM4 in Fig. 10a). As M2 and then M3 erupt, there is commonly posterior deflection of the roots of M1 (Fig. 10a and b). Frequently there is also posterior deflection of the roots of M2 as the elongated M3 erupts into the occlusal plane (Fig. 10b). There was no posterior deflection of the roots of M3 in the specimens examined.

Relative growth of skull and teeth

A plot of skull reference position against skull length is shown in Fig. 11. Parallel reference lines indicate isometric growth of the area contained within. Divergent lines with increasing skull size indicate positive allometry. There is an increase (positive allometry) in the anterior part of the skull (i.e. from the anterior of the skull back to reference point 3) as skull length increases. There is isometric or even slightly negative allometric growth of the posterior part of the skull (i.e. the neurocranium).

The ramus or tooth bearing area (erupted teeth) lies between reference points 5 and 8, and the cheekteeth as a unit remain within this area. There is slight positive allometry in the length of the erupted tooth row. There is some sort of molar progression occurring in that some of the cheekteeth (i.e. PM3–M2) move forward crossing two bony reference points 6 and 7 on the skull (Fig. 11). This indicates that the inferred forward movement of these teeth does not result merely from growth of individual teeth after eruption or during ontogeny. PM2 and M3 do not migrate past skull reference lines.

Table 3 Results from two-way ANOVAs examining differences in hardness (H_v) between tooth types (PM2 to M3) and dentinal layers within individual dugongs *Dugong dugon*

Dugong	Differences between teeth				Differences between layers				Teeth * layer interaction			
	MS	F	d.f.	P	MS	F	d.f.	P	MS	F	d.f.	P
mm 24	0.35	0.03	2, 10	0.97	–	–	–	–	–	–	–	–
mm 48	98	1.53	2, 11	0.26	0	0	1, 11	0.999	47	0.74	2, 11	0.501
mm 22	66.1	2.62	2, 45	0.08	383	15.2	4, 45	<0.001*	27.3	1.08	8, 45	0.393
mm 148	78.7	3.92	2, 31	0.038*	202	10.1	3, 31	<0.001*	9.95	0.5	6, 31	0.806
mm 102	36.2	0.96	2, 40	0.39	335	8.87	3, 40	<0.001*	56.8	1.5	6, 40	0.201
mm 18	0.03	0	1, 22	0.98	2.16	0.06	3, 22	0.982	36.7	0.95	3, 22	0.433
mm 66	47.8	1.81	2, 23	0.19	93.9	3.55	2, 23	0.045*	62.4	2.36	4, 23	0.083

*Significant result at the $P=0.05$ significance level.
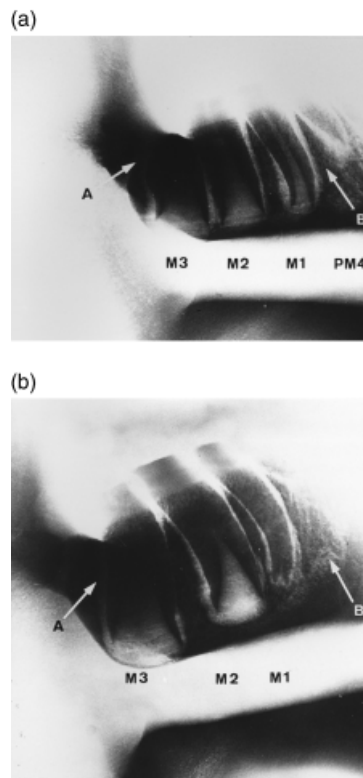MS, mean squares; *F*, *F* value; d.f., degrees of freedom.

Figure 10 Lateral radiographs of cheekteeth of two dugongs *Dugong dugon*. A, dense bone at rear of tooth row; B, less dense bone at front of tooth row. (a) Juvenile dentition (6 years) (specimen mm 75): erupted PM4, M1, M2 and unerupted M3. Note the relatively straight roots of M1 and M2. (b) Young adult (11 years) (mm 43) erupted M1, M2 and M3. Note the strong posterior root deflection of M1 and M2.

Ontogenetic allometry in mouthparts

The total tooth crown surface area increased from the most anterior (PM2: $7.75 \pm 2.3 \, \text{mm}^2$) to the most posterior tooth (M3: $202.87 \pm 15.4 \, \text{mm}^2$). The occlusal surface areas of both individual teeth and entire tooth rows were lower than total surface areas. The surface areas of most of the mouthparts measured (i.e. crown surfaces of individual teeth PM4–M3
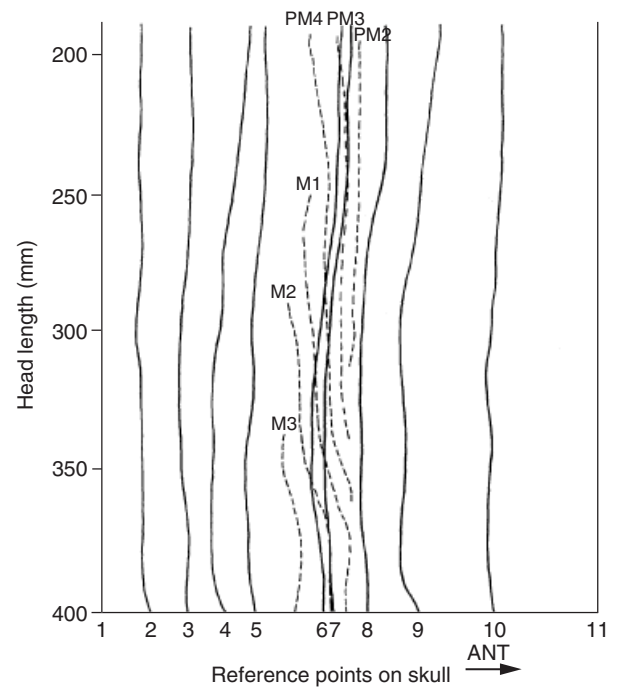

Figure 11 Ontogenetic relationships between each of the 11 skull reference points (see Fig. 1) and the positions of the cheekteeth for dugongs *Dugong dugon* of increasing skull length. The ontogenetic trajectory of the midpoint of each tooth's occlusal surcae is indicated by a dashed line. PM, premolar; M, molar; ANT, anterior.

with the exceptions of PM2 and PM3, total tooth row and functional tooth row, surface area of lower horny pad) were all significantly regressed with body size (Table 4).

Erupted PM4, M2 and especially M3 continue to increase in size throughout life, whereas M1 grows isometrically with respect to body size (Table 4). Surface area of the total tooth row grows in a positively allometric fashion with respect to body size (Table 4). In contrast, occlusal or functional surface area of the tooth row increases isometrically with respect to body size (Table 4). Further, occlusal surface area was less than and more variable than total surface area of cheekteeth, indicating that a significant proportion of the

erupted tooth row (as much as 30% in adults) may be non-functional during occlusion. ANCOVA comparing regressions of these tooth parameters against metabolic body weight indicated that the slopes were not significantly different from each other ($F = 2.44$; d.f. = 1, 110; $P = 0.121$) but that the intercepts were different ($F = 13.853$; d.f. = 1, 112; $P < 0.001$). This probably results from the fact that occlusal area drops off in relation to total surface area because of increasing deposition of calculus with age.

The total surface area of the lower horny pad ranged from 900 mm^2 in juvenile dugongs up to 6280 mm^2 in the largest adults (mean 4933 ± 109 mm^2 for adults). The coefficient of variation (CV) (SE/m) for the adult horny pad surface areas was 12.73, which is considerably lower than the CV for total tooth row surface area (CV = 23.08) and for occlusal surface area (CV = 35.05). The absolute surface area of the horny pad provides a much greater surface against which to comminute food than the crown surface area of the cheekteeth. There is positive allometric growth of the horny pad during ontogeny.

Intersexual allometry

Metabolic body weight (kg$^{0.75}$) was significantly regressed against estimated age (log-transformed) (years) for both sexes (males: $F = 160.01$; d.f. = 1, 23; $P < 0.001$; females: $F = 130.78$; d.f. = 1, 28; $P < 0.001$). There was no difference in metabolic body weight against age (log) for males and females (H_0 = equal slopes $F = 0.186$; d.f. = 1, 53; $P = 0.668$; H_0 = equal intercepts $F = 0.003$; d.f. = 1, 55; $P = 0.955$), nor in skull length against age (H_0 = equal slopes $F = 0.372$; d.f. = 1, 50; $P = 0.544$; H_0 = equal intercepts $F = 1.362$; d.f. = 1, 52; $P = 0.249$). This indicates that animals of similar age (range 0–35 years) have similar body sizes, regardless of gender. Estimated ages of adult males were minima because some wear of erupted tusks may have occurred. If male ages were greater than estimated, this would imply that for a given age, adult females may have greater body weight.

Surface areas of all mouthparts measured for each sex separately (i.e. total surface area of tooth row, functional tooth row, maximum width, length and surface area of horny pad) were significantly regressed with body size (Table 4). Males have greater total tooth surface area per body size than females ($F = 8.232$; d.f. = 1, 51; $P = 0.006$) at metabolic body weights greater than 51.18 kg$^{0.75}$ (which corresponds to age > 6.3 years and skull length > 310.5 mm). For both sexes, total surface area of tooth row increased with positive allometry through ontogeny. In contrast, there was no significant difference between the sexes with respect to occlusal surface area against metabolic body weight

Table 4 Regression equations of surface area of various mouthparts relative to metabolic body weight

	Linear regression	Log–log slope + 95% confidence limit	Growth	
Sexes combined				
PM4	$F = 12.95$; d.f. = 1, 19; $P = 0.002$	1.15 ± 0.43	Positive allometry	
M1	$F = 4.69$; d.f. = 1, 31; $P = 0.04$	0.58 ± 0.41	Isometry	
M2	$F = 32.20$; d.f. = 1, 45; $P < 0.001$	1.26 ± 0.42	Positive allometry	
M3	$F = 14.15$; d.f. = 1, 36; $P = 0.001$	2.09 ± 1.05	Positive allometry	
Total tooth row	$F = 92.01$; d.f. = 1, 53; $P < 0.001$	1.27 ± 0.16	Positive allometry	
Occlusal tooth row	$F = 21.79$; d.f. = 1, 53; $P < 0.001$	0.84 ± 0.67	Isometry	
Lower horny pad	$F = 739.69$; d.f. = 1, 53; $P < 0.001$	0.92 ± 0.04	Positive allometry	
				Significant difference between sexes?
Separate sexes				
Total tooth row				Highly significant
Males	$F = 55.00$; d.f. = 1, 23; $P < 0.001$	1.13 ± 0.17	Positive allometry	
Females	$F = 87.97$; d.f. = 1, 28; $P < 0.001$	1.35 ± 0.16	Positive allometry	
Occlusal tooth row				No
Males	$F = 8.58$; d.f. = 1, 21; $P = 0.008$			
Females	$F = 16.72$; d.f. = 1, 31; $P < 0.001$			
Horny pad				No
Males	$F = 508.80$; d.f. = 1, 22; $P < 0.001$			
Females	$F = 344.86$; d.f. = 1, 29; $P < 0.001$			
Maximum width pad				Significant
Males	$F = 395.58$; d.f. = 1, 22; $P < 0.001$	0.49 ± 0.05	Positive allometry	
Females	$F = 121.81$; d.f. = 1, 29; $P < 0.001$	0.40 ± 0.06	Positive allometry	
Maximum length pad				No
Males	$F = 566.70$; d.f. = 1, 23; $P < 0.001$	0.50 ± 0.03	Positive allometry	
Females	$F = 191.56$; d.f. = 1, 28; $P < 0.001$	0.47 ± 0.04	Positive allometry	

All mouthparts are surface areas unless otherwise stated. Slope refers to log–log plots of size of mouthpart versus body size. Geometric slope for isometry = 0.67. A slope greater than 0.67 denotes positive allometry. Note that PM2 and PM3 are not significantly regressed with body weight, so are not included here.

$(H_0 =$ equal slopes $F = 0.332$; d.f. $= 1$, 51; $P = 0.567$; $H_0 =$ equal intercepts $F = 0.095$; d.f. $= 1$, 53; $P = 0.759$).

Males have significantly wider horny pads than females ($H_0 =$ equal slopes $F = 6.266$; d.f. $= 1$, 51; $P = 0.016$) at metabolic body weights greater than $59.3 \, kg^{0.75}$ (which corresponds to age > 10.8 years and skull length $> 330 \, mm$). Pad width (mm) grew in a positively allometric fashion in both sexes (Table 3). In contrast, there was no significant difference in maximum length of horny pad between sexes ($H_0 =$ equal slopes $F = 0.746$; d.f. $= 1$, 51; $P = 0.392$; $H_0 =$ equal intercepts $F = 1.997$; d.f. $= 1$, 53; $P = 0.164$). Pad length (mm) continued to grow in both sexes. There was no significant difference in horny pad surface area between the sexes ($H_0 =$ equal slopes $F = 3.025$; d.f. $= 1$, 51; $P = 0.088$; $H_0 =$ equal intercepts $F = 0.827$; d.f. $= 1$, 53; $P = 0.367$) despite the sexual dimorphism in maximum pad width.

Discussion

Cheektooth morphology

The soft cheekteeth of the dugong are particularly vulnerable to wear. Enamel is present as a thin cap on the three erupted cheekteeth of the newborn but is completely worn through before the dugong is weaned, probably at age 18–24 months (Marsh, 1980). Once the initial tuberculate crowns are lost, the teeth are rapidly worn to simple cylindrical flat pegs comprising orthodentine and/or vasodentine (Fernand, 1953; Petit, 1955) with large interglobular spaces (P. P. Phakey, pers. comm.). Dentine of a similar structure has also been found in manatee teeth (Widdowson, 1946). Erupted and worn adult dugong cheekteeth have a dentinal hardness (mean of $34H_v$) that is around half that measured in other herbivores (e.g. Sanson, 1977; Molina, 1981) and much less than more wear-resistant enamel with a Vickers hardness of $263H_v$ to over $400H_v$ units (Sanson, 1977; Palamara *et al.*, 1984). Bradford (1967) was correct when he described the dentine of dugongs as being 'degenerate'. The outer dentinal layer of each tooth is slightly harder than the central zones, and this may serve to help maintain tooth shape, in the face of tooth wear.

The lack of crown features has prompted such descriptions of dugong cheekteeth as 'reduced' (Sanson, 1977) or even 'degenerative' (Sickenberg, 1934): these descriptions are probably accurate. Owen (1838) compared dugong molars, with their wide conical pulp, to those of Edentata, which have extremely reduced molar teeth including nearly complete loss of enamel. Lack of hard enamel edges means that the crown morphology of the dugong is not maintained. Further, small changes in abrasion may result in altered crown morphologies and, consequently, altered occlusal action. This phenomenon may account for the variability in tooth surface morphology and occlusion within and between individuals. In herbivores with more wear-resistant dentitions of enamel, tooth morphology and occlusion are more tightly controlled.

Occlusion

The mechanism of dental occlusion is not tightly controlled in dugongs. Dental features such as the relatively flat occlusal surfaces, absence of cutting edges, frequency of striae and pitting, and large areas of abrasion striae all combine to suggest that the dugong grinds its food, probably initially with some orthal movement producing a crushing component and then with a largely lateral mandibular movement. Striations and pits present on the same facets suggest that grinding and crushing occur on the same surface.

The high incidence of multidirectional striae suggests that significant tooth wear may be caused by large volumes of food moving past the teeth rather than by direct tooth–tooth contact (Weijs & Dantuma, 1981). This may be exacerbated by abrasive inclusions in seagrass (e.g. high ash content, Lanyon, 1991) or associated with seagrass (e.g. epiphytic siliceous diatoms or sand). In a bottom feeder such as the dugong, one might expect some geophagia. However, several workers have remarked on the conspicuous absence of sediment in the gut (Annandale, 1905; Petit, 1924; Prater, 1928; this study). If sediment is ingested, it is likely to contribute substantially to tooth wear, being orders of magnitude harder than the tooth material (according to Peters, 1982). In this study, sand grains were found embedded deeply in the tooth surface of individual cheekteeth, and a number of deep pits and gouges may have been caused by the same. In light of the probable abrasive nature of the ingested material, it is surprising that these very soft teeth are not more heavily striated if they are functionally important. Further, striae type and distribution vary greatly between individuals, suggesting that the mechanism of dental occlusion is not tightly regulated.

When they do occur, attrition striae are orientated antero-lingually across the tooth surface, indicating a large lateral component to the occlusal stroke. These results contradict those of Annandale (1905), who suggested that the jaw had very little if any lateral movement, but concur with those of others (Prater, 1928; Fernand, 1953; Domning, 1977), who acknowledged the possibility of lateral movement. Striae orientation indicates that the lower teeth move either antero-lingually or postero-buccally relative to the uppers. Determining directionality was difficult given the paucity of surface features on the cheekteeth and the inapplicability of conventional techniques such as videoradiography. Tooth profiles, based on Greaves' (1973) model, suggest that antero-lingual movement of the mandible is most likely to occur during the power stroke. However, variation in crown profiles between individual dugongs, and at times even along teeth of the same individual, suggests that mandibular retraction may occur at least sometimes in some dugongs. If true, this makes the dugong unique in its being the only extant mammal recorded as having mandibular movement with a posterior component. Mammals commonly have a lingual or antero-lingual (= antero-mediad) component to the power stroke (Fortelius, 1985). In fact, Hiiemäe (1978) suggested that the power stroke is, without exception, from buccal to lingual. Since then,

however, some extinct mammals (e.g. the Palaeocene multi-tuberculate, *Ptilodus* and possibly some haramiyids) have been recorded as having mandibular retraction (palinal movement) (Krause, 1982). Due to the rarity of this condition, a more likely explanation may be that parts of the tooth row are non-functional, so that profiles across these areas are not really indicative of true occlusal movement but rather of food flow across the teeth.

If the dugong mandible moves antero-lingually, the preparatory stroke (Hiiemäe, 1978) would likely begin with orthal movement as the opposing teeth on the active side move into centric occlusion. The power stroke would then move the lower teeth laterally and slightly anteriorly. The point at which the power stroke terminates is unclear but the distribution of wear facets right across the crown surface would suggest movement of the whole surface of lower teeth across the whole surface of uppers, at least along part of the tooth row. This movement would account for the smaller amount of wear on the antero-buccal parts of the upper tooth row in older specimens.

Tooth wear

Effect on occlusion

As a dugong ages, tooth morphology changes so that the cheekteeth become flat and the anterior-most teeth (PM2–M1) eventually move out of occlusion and wizen. Heavy calculus deposits indicate that less of the tooth row is fully functional in older animals than in younger ones, and in some extreme cases the entire tooth row may be non-functional as indicated by a continuous calculus coating. However, generally in animals with erupted M2 and M3 remaining, there is some evidence of continuing wear at least on M3. The maintenance of M3 and its continual growth provides a grinding area at the rear of the tooth row. As axial molar load is likely to be greatest on the tooth closest to the condyle (Mansour, 1977), it may be mechanically advantageous to have the largest functioning tooth here.

Dugong cheekteeth are hypselodont (open-rooted) so that the teeth form continually as they erupt (Marsh, 1980; Domning, 1982). After initial wearing of the crowns, the cheekteeth (mainly M2 and M3) consist of structures that correspond to the roots of normal teeth. This is generally accepted as an evolutionary response to increased dental wear in herbivores (Fortelius, 1985). Such continually growing teeth require a certain amount of wear to maintain the erupted crown height at an appropriate level for efficient occlusion and to prevent over-eruption with consequent incapacity to close the mouth. For example, lack of normal tooth wear in a captive dugong in the early 1980s (Toba Aquarium, Japan) was found to markedly affect tooth crown height above the gingiva. The deformed elongate cheekteeth rendered normal occlusion of the cheekteeth and horny pads impossible, so that the result was fatal malnutrition (J.M. Lanyon, pers. obs.). Domning (1982) has suggested that the primitive brachyodont crown of the dugong cheektooth has been written off by selection as

unsalvageable and functionally replaced by the hypertrophied root. An alternative explanation could be that loss of enamel may be advantageous in continually growing and non-functional teeth. Maintenance of enamel in the dugong tooth may have exacerbated the requirements for tooth wear because enamel is more wear-resistant than dentine. Soft dentine, on the other hand, may wear even in the absence of direct occlusal pressures.

Molar replacement

Dugongs do not have *in situ* replacement of milk dentitions (Nishiwaki & Marsh, 1985). Rather, their cheekteeth, of which there is a finite number, erupt sequentially in a monophyodont series (Petit, 1955). Dugong cheekteeth have been reported to undergo some forward migration (Mitchell, 1973; Sanson, 1977). Some authors have suggested that this migration may constitute molar progression (e.g. Sanson, 1977), whereas others have suggested that it may be more similar to mesial drift (Domning & Hayek, 1984). Molar progression is considered here to be an accelerated form of mesial drift where teeth drift towards the midline and fill gaps generated by interstitial wear. Molar progression is more obvious when a diastema is present and teeth drift or progress beyond individual tooth lengths. Cheekteeth PM3–M2 do show molar progression, with movement of M3 being less pronounced. Because each of these migrating teeth move past fixed skull reference points in their entirety, this migration cannot be accounted for solely by eruption and growth of the teeth, contrary to the views of Heuvelmans (1941) and Petit (1955). Nor can it be accounted for by growth of the surrounding jaw (according to Aichel, cited in Heuvelmans, 1941). With the exceptions of M2 and M3, each migrating tooth is eventually lost anteriorly. Further, the posteriorly deflected roots of PM3–M2 are characteristic of molar progression (e.g. in manatees, Sanson, 1977) and there is evidence of interstitial wear between the cheekteeth. In contrast, PM2 does not show this. PM2 erupts at the anterior of the tooth row and is shed from this position. Dugong teeth appear to move forward only enough to allow the more posterior teeth to move into the occlusal area. This process permits successive eruption in a short jaw. Further, if the more posterior teeth are largely non-functional as we suggest, then there is no conversion of the occlusal vector to forward movement of these.

Growth of the mouthparts

The coefficient of variation has been used successfully as a measure of variability in the size of teeth (Bader, 1955; Gingerich, 1974). Variability in crown surface area of homologous teeth within a sample of adult dugongs is high, when compared with the teeth of other mammal groups (see Gingerich, 1974). Further, there does not appear to be a marked difference in variability between individual tooth type. High variability in the size of individual teeth is thought to reflect low selection pressure on tooth maintenance (Bader, 1955). In contrast to the cheekteeth,

variability in the size of the horny pads is low, suggesting relatively greater selection pressures.

Tooth size–body size allometry

The allometric relationship between tooth size and body size has been suggested as a useful index in determining whether or not teeth fulfil an important role in the masticatory process. Since an animal's energy comes from its food thereby driving metabolism, and because the teeth are usually the major mechanical food processing organs, Gould (1975) suggested that the occlusal area of the cheekteeth of herbivorous mammals should scale according to the metabolic requirements of the animal, i.e. body weight to the power of 0.75 (Kleiber, 1947). In an interspecific comparison of herbivorous mammals of 'fairly similar design', Gould (1975, p. 358) found evidence for positive allometry for the scaling of postcanine tooth area. In contrast, Fortelius (1985) has found that isometry may be more common.

Most mammalian teeth do not continue to grow throughout life (Gingerich, 1977). The cheekteeth of dugongs are a rare exception. In addition to cheekteeth PM4–M3 increasing in size from anterior to posterior, they continue to grow axially and radially after eruption. Individual cheekteeth, with the exception of M1, scaled with positive allometry to metabolic body size, so that as body size increased, total tooth size increased relatively more. In particular M3 and then M2 increased in size substantially after eruption. M3 increased more in length than in width. This increase in size is accounted for by tooth wear, because from the radiographs of the socketed roots, it could be seen that the roots flare out. The overall isometric growth of M1 may be explained by continual growth early on, followed by subsequent wizening.

The combined surface areas of all cheekteeth increased with positive allometry with respect to metabolic body weight and presumably increased nutritional requirements. However, this assumes that the entire tooth row constitutes a functional occlusal surface. In reality, within a tooth row there may be whole teeth that do not contribute to the occlusal surface (e.g. anterior teeth in some cases) and even areas within an occluding tooth that are non-functional (e.g. central basins of calculus). When only the occlusal surface area of the cheekteeth is considered (i.e. minus calculus areas, Sanson, 1980; Lanyon & Sanson, 1986), the growth is close to isometric. This would imply lower selection pressures on actual occlusal area than on total tooth surface area so that dugongs may not be making the most of their tooth surface area. Greater deposition of calculus on the teeth of older animals, with increased variability in occlusal area between dugongs, implies altered functional efficiency with age.

There is an increase in the size of the anterior parts of the skull during ontogeny in dugongs, as in mammals in general. This confirms Spain & Heinsohn's (1974) findings that characters of the anterior part of the skull show positive allometry whereas more posterior features exhibit isometry or even negative allometry. Therefore, brain size is established early on, but there is growth of the snout with increasing body size. Growth of the anterior skull region is reflected in continual growth of the horny pad apparatus; this result is hardly surprising given an animal's increasing absolute energetic requirements with increasing metabolic body size.

In addition, there were sexual differences in ontogenetic development of skull parameters, particularly those associated with the jaws and feeding apparatus. Although we did not find any difference in body size and age relationships between the sexes in this study, the age range over which data were available was limited. Also, the estimated ages of adult male dugongs were likely to be minimum ages (due to wear of dentinal growth layer groups (*sensu* Marsh, 1980) on the erupted part of the tusk). Based on a larger sample size, Marsh (1980) reported that the estimated asymptotic body length of females (from Townsville) is slightly larger than that of males. Spain & Marsh (1981) found no difference in skull length between the sexes. However, there does appear to be sexual dimorphism in relation to jaw parameters.

Adult male dugongs had significantly greater total tooth surface area than females, the difference occurring at about 6 years of age, i.e. before puberty at around 9–10 years (Marsh, 1980). If the teeth are important, this result is a little surprising given that there are likely to be generally greater nutritional loads placed on the female throughout her life. Lucas (1980) suggested that male mammals may have higher metabolic rates for weight than females, which might be invoked as an explanation for this observation. However, the higher metabolic rates of female mammals during reproduction, and particularly lactation (e.g. Crowley, 1989), lead us to question this generality. These types of data are unavailable for dugongs at the present time.

Males also have significantly wider snouts (at the anterior end of the premaxillae) than females (Mitchell, 1973; Spain & Heinsohn, 1974). It has been suggested that this sexual difference results from eruption and development of the males' tusks at the onset of puberty (Spain & Heinsohn, 1974; Nishiwaki & Marsh, 1985). As the horny pad is closely associated with the bony structure of the snout, we may expect this width differential to be reflected in pad width. Indeed, there was a difference in pad width so that males had wider pads, from the age of puberty. This sexual difference in pad width did not lead to an overall increase in pad surface area for males over females. As females did not have significantly longer pads than males to compensate for narrower pads, it is possible that there are more subtle differences in pad shape. This was not investigated here. Other studies have found that female dugongs have longer snouts, longer mandibles, greater anterior mandible depth, wider chins and deeper crania than males (Spain *et al.*, 1976). Sexual dimorphism in these parameters suggests differential growth of the feeding apparatus in females. These differences were not reflected in the dimensions of horny pad or tooth size measured here. But it is possible that some of the parameters are associated with muscles of food processing organs, because greater anterior skull size may lead to larger jaw muscles to manipulate the anterior parts. Weijs & Dantuma (1981) suggest that some animals (e.g.

rodents) have increased muscle mass to compensate for lack of tooth specialization. Perhaps dugongs have employed a similar strategy. In this case, the masticatory muscles may be associated with pad occlusion. If the masticatory muscles work the anterior pads, this would be consistent with the theory of females having greater nutritional requirements than males, particularly related to breeding. If the teeth are not functionally important, as would be suggested by their form, variability and size, males having greater tooth surface area may not be relevant.

The surface area of the erupted tooth row in the dugong is absolutely small for body size when compared with other mammal species, and in particular to other hindgut-fermenting herbivores such as the elephant and horse (Fig. 12). Creighton (1980) found that for several groups of mammals, the larger animals have smaller teeth relative to their body size than smaller mammals, which may be consistent with a larger animal's relatively lower metabolic requirements. Even comparing the dugong with other large mammals, its tooth size was $>60\%$ smaller than the mean. It is possible that the dugong's small tooth size relative to body size may reflect a low metabolic rate, as suggested by its phylogeny. However, unpublished data suggest that dugongs do not follow the manatee's low basal metabolic rate, because water turnover rates in the dugong ($282.8 \, \mathrm{ml \, kg^{-1} \, day^{-1}}$) are almost twice the highest rates measured in captive West Indian manatees *Trichechus manatus* ($145 \pm 12 \, \mathrm{ml \, kg^{-1} \, day^{-1}}$) (Ortiz, Worthy & Byers, 1999). If dugongs do not have a particularly low metabolic rate relative to other mammals, then their small functional tooth size makes the allometric growth of the cheekteeth
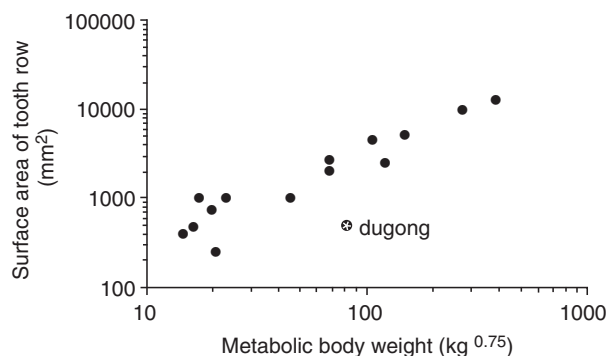

Figure 12 Size of dugong *Dugong dugon* cheekteeth compared with other herbivorous mammals. Creighton's (1980) graph is adapted here to include the dugong, whose adult M1 has a surface area of $59.25 \pm 4.22 \, \mathrm{mm^2}$ (mean $\pm$ SE). The dugong lies well outside the 95% confidence limits pertaining to the other 288 species of mammals. Data are from Gould (1975) and Sanson (1977). Species code: 1, elephant *Loxodonta africanus*; 2, hippopotamus *Hippopotamus amphibius*; 3, moose *Alces alces*; 4, horse *Equus caballus*; 5, cow *Bos primigenius*; 6, pygmy hippopotamus *Choeropsis liberiensis*; 7, boar *Sus scrofa*; 8, gorilla *Gorilla gorilla*; 9, capybara *Hydrochoerus hydrochaeris*; 10, peccary *Tayassu tajacu*; 11, sheep *Ovis aries*; 12, chimpanzee *Pan troglodytes*; 13, pygmy chimpanzee *Pan paniscus*; 14, red kangaroo *Macropus rufus*.

through ontogeny irrelevant, for no matter how large a size they attain through development, they still present a highly conservative occlusal surface.

In contrast, the horny pads represent a large abrasive surface, and although the functions of the horny pads and teeth may not be directly comparable, the dugong may have increased occlusal area by substantial development of these. The surface area of the horny pads increases with positive allometry with respect to metabolic body weight, so that like the tooth row surface area, pad area is maintained or even increased as the dugong ages. If the pads have assumed the primary function of food maceration and have been favoured by selection, then scaling of the pads or snout may have resulted in a similar scaling of the cheekteeth by default, through selection towards a larger head. Following the arguments of Gould (1974) to explain the positive allometry of Irish elk *Megaloceros giganteus* antler size, if selection acted to increase the size of the horny pad in adult dugongs and consequently skull size to accommodate a required increase in masticatory musculature, relatively large teeth in adults may have resulted merely as a consequence of correlation.

Function of the horny pads

Qualitative experiments during this study indicated that the horny pads are capable of comminuting seagrass into fine particles during opposition, even when relatively little pressure is applied. The horny pads occlude simultaneously with the cheekteeth. Lateral tooth occlusion with slight forward movement of the mandible occurs in concert with lateral occlusion of the pad, with a slight posterior and orthal component to one side. Application of such posterior action to the lower pad serves to move intervening food material towards the back of the pad. Thus it is not inconceivable that mandibular movement imparts another function to the horny pads, i.e. that of food transportation over the long distance between the mouth opening and the tongue and up the steep rostral angle. It is difficult to interpret the abrasive cycle of the horny pads. Feeding observations indicate a vertical component to the recovery stroke, culminating in food ingestion and/or movement of food up the pad.

The surface area of the horny pads is absolutely greater than that of the tooth row, and the entire surface appears capable of occlusion as indicated by the green staining by seagrass across the pads. Unlike the tooth row, the horny pad has no areas that are obviously non-functional. Further, several features of the dugong skull suggest that the dugong may be able to direct and maximize occlusal forces towards the anterior of the mandible in the region of the horny pads. First, there is strong development of the superficial masseter muscle (Domning, 1977), with anteriorly directed muscle fibres (J.M. Lanyon, pers. obs.). The origin of the masseter is on the well-developed descending process of the zygoma, and there is an extremely large insertion area on the mandible. In a number of mammal groups with propalinal occlusion (e.g. elephant, macropodid marsupials), the

superficial masseter is responsible for the forward thrust of the mandible (Sanson, 1977). As bite force is dependent, to some extent, on the size of the masticatory muscles (Lucas, 1982), and muscular force is proportional to cross-sectional muscular area (Turnbull, 1970), it is likely that the masseter directs considerable force towards the horny pads. Second, Domning (1977) has suggested that the massive pterygoid processes may reflect the importance of the external pterygoid as an additional mandibular protractor. The mechanism by which mandibular retraction could result, should it really occur, is also a matter of speculation at this stage. However, as Domning (1977) pointed out, the lowered origin and shortening of the digastric muscle may facilitate retraction of the mandible. It is possible that occlusal action is mainly directed towards operation of the horny pads, and that occlusion of the teeth is an incidental consequence.

Relative contribution of the mouthparts to mastication

Annandale (1905, p. 241) recorded the 'unbruised and perfect condition of seagrass' in the stomach of the dugong, and consequently suggested that the teeth were not important. Fernand (1953, p. 144) also reported on the 'uncrushed' appearance of the stomach contents, and Petit (1924) suggested that the plants were swallowed whole. The validity of these observations is doubtful because stomach content analysis indicates that most seagrass is well macerated by the mouthparts (Marsh *et al*., 1982, 1999; Lanyon, 1991).

It is impossible to quantify the relative contributions of the mouthparts to the process of mastication. However, based on the evidence available it appears that there may not have been great selection pressures acting on maintenance of an effective dentition in the dugong. As a result, the teeth appear to be poorly adapted in terms of structural composition, morphology, resistance to wear and occlusal surface area in relation to body size. Furthermore, occlusion of the teeth is highly variable between individual animals. In contrast, there has been great development of the horny pads, and overall development in the anterior part of the skull and snout region and its associated muscles. This evidence combines to suggest that although the dentition may have been useful in the past, the horny pads may now be more important food processing organs as suggested by Gohar (1957). A possible analogy may be made with some cricetine rodents where the anterior incisors have assumed the entire dental function and the cheekteeth have atrophied to degeneracy and nearly functionless simple cylindrical pegs (Hershkovitz, 1962).

In conclusion, in terms of its functional dental morphology, the dugong would appear to fall somewhere between the two extremes of the well-developed, complex and durable dentition of the manatees and the edentate condition of the dugong's once closest living relative (the giant extinct Steller's sea cow *Hydrodamalis gigas*) (Domning, 1982). Further, compared to other hindgut fermenters, the dugong would appear to be poorly equipped in terms of dental

adaptation. However, the great development of the horny pads and associated skull parameters permit a level of food comminution comparable to that found in other hindgut fermenting herbivores (Marsh *et al*., 1999; J.M. Lanyon & G.D. Sanson, unpubl. data).

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