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Age Determination of the Dugong (*Dugong dugon* (Müller)) in Northern Australia and its Biological Implications

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ABSTRACT

In the absence of known age material, incisor dentinal growth layer groups (GLGs) have been examined from 129 dugongs from northern Australia with a view to age estimation. Material was available from animals which died in all months of the year.

Each GLG consists of a thick zone of intermediate optical density followed by a thin zone consisting of one of three pairs of contiguous layers. One layer in each pair is opaque, the other translucent. The intensity of haematoxylin staining, the susceptibility to acid etching, and the radio-opacity of each layer mirror its degree of optical density.

Examination of the most recently deposited zone in teeth from 106 dugongs whose date of death was known suggests that one GLG is deposited each year, formation of the narrow zone generally occurring from July to October inclusive.

The permanent incisors erupt and become worn in adult males and occasionally in females, making a total GLG count impossible for these animals. Total GLG counts in unworn tusks of females suggest a life span of fifty years or more. The maximum number of GLGs in a worn tusk of a male was 34.5. Puberty in both males and females is estimated to occur at a minimum of about nine years of age in the Townsville population, but probably not until several years later in the Mornington Island population. The tusks erupt in male dugongs after puberty at about 12 years (Townsville population) or 14 years or later (Mornington Island population). A growth curve describing the age-length relationship, based on number of dentinal GLGs, has been developed for both males and females.

The ontogeny of the cheek teeth is described relative to the age estimates. The use of the pattern of cheek-tooth development as a means of estimating absolute age is described for animals estimated to be up to nine years old. Equations have been developed for the prediction of age from the size of molars 2 and 3 in animals from ten to thirty years of age.

INTRODUCTION

The dugong, *Dugong dugon* (Müller), is one of only four extant species of Sirenia or seacows. It is of particular interest as the only existing herbivorous mammal which is strictly marine.

Historically, the range of the dugong was broadly coincident with the tropical and subtropical Indo-Pacific distribution of the sea-grasses on which it feeds, but it is presently considered rare over most of its range (Bertram and Bertram, [illegible]) and is listed as a vulnerable species (IUCN Red Data Book, 1976).

Aerial surveys over the last four years have, however, established that sizable populations of dugongs still exist in the shallow seas around northern Australia (Heinsohn, [illegible] Ligon, 1976; Heinsohn *et al*, 1978; Marsh *et al*, in press) and a broadly-based programme of research has been established at James Cook University which aims to [illegible] effective conservation and management programmes [illegible] in this region.

[illegible] problem is that no definitive life history information [illegible] available for the dugong. There have been no [illegible] field studies of specific individuals over any time [illegible]. Dugongs have rarely been maintained in captivity and [illegible] never bred in captivity. Eleven-year growth records are, however, available for two captive male dugongs in India (Jones, 1967, 1976). Heinsohn (1972) used the body lengths [illegible] sexed dugongs accidentally drowned in nets throughout the year to distinguish four age classes. He estimated [illegible] maturity at approximately two years and constructed [illegible] hypothetical growth curve which described the increase [illegible] body length with age of northern Australian dugongs in their natural environment. His growth estimates suggest that dugongs grow much faster in the wild than Jones's observations on captive animals indicate.

Pocock (1940) used closure of cranial sutures and Mitchell (1973) a series of skulls and teeth to develop criteria for the determination of relative age in the dugong.

Several workers have counted dentinal growth layer groups (GLGs) in the tusks as an indicator of age (Scheffer, 1970; Mitchell, 1976, 1978; Kasuya and Nishiwaki, 1978). These studies were hampered by lack of biological information about all but a few of the dugongs from which the tusks were obtained, and it was not possible to establish the rate of deposition of the GLGs, especially as there is controversy over the deposition rate in tropical mammals (Klevezal' and Kleinenberg, 1967; Spinnage, 1973, 1976).

The present study is based on data records, skulls and reproductive tracts from 129 dugongs, the majority of which came from two locations in Queensland, northern Australia, and aims to estimate dugong life history parameters, such as maximum longevity and age at reproductive maturity, which are essential to the development of effective conservation strategies.

THE DENTITION OF THE DUGONG

Heuvelmans' (1941) classification of dugong teeth is followed in this paper.

Two pairs of upper incisors, neither of which is erupted, are present in all young and some older dugongs (Fig. 1). The anterior pair is referred to as the deciduous incisors. The posterior incisors, which are permanent, form the tusks and later erupt in males (Fig. 2) and occasionally in females.

The tusks are the only teeth present throughout life in all dugongs. Up to three pairs of vestigial incisors and one pair of canines may occur occasionally in the rudimentary sockets under the horny plate which covers the downturned symphysial portion of the lower jaw.

Apart from the erupted tusks, the only functional teeth are the cheek teeth. These teeth are difficult to classify since *in situ* replacement of the milk dentition does not occur. During the life of the animal there is a total of six pairs of cheek teeth in both jaws. These teeth are referred to as premolars 2, 3, 4 and molars 1, 2, 3.

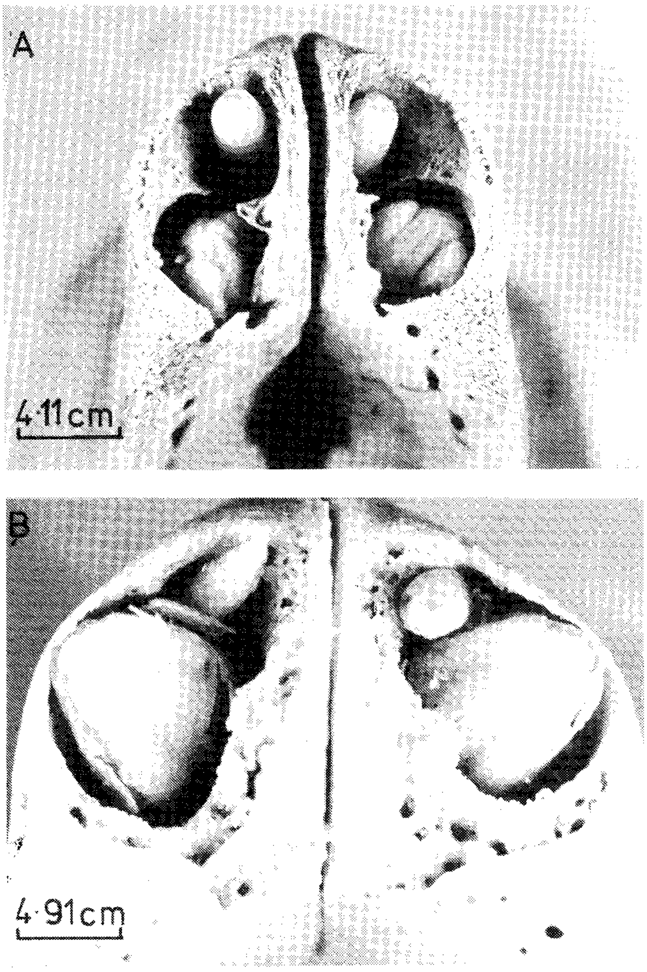


Fig. 1. Anterior ends of the premaxillae of two dugongs showing the unerupted deciduous incisors and tusks. (A) 2 year old 1.8-m-long male; (B) 28 year old 2.36-m-long female.

MATERIALS

Source of material

Specimen material was obtained between May 1969 and August 1978 as listed:

from 70 dugongs accidentally drowned in nets (usually shark nets set for swimmer protection) near Townsville (19°15′S; 146°15′E) within 2 h and 2.5 days of death (Heinsohn, 1972; Heinsohn and Spain, 1974);

from 39 dugongs speared and drowned for food by aboriginals in the Wellesley Islands (16°30′S; 139°30′E) within 0.5 h and 12 h of death (Marsh *et al,* in press);

from two dugongs similarly killed by Torres Strait islanders at Thursday Island (10°30′S; 142°3′E) within 0.5 h and 12 h of death; and

from one dugong caught off Cairns (16°55′S; 145°46′E) and held in captivity in the Cairns Oceanarium for several months prior to its death.

Four isolated dugong skulls, eleven isolated tusks and three isolated ribs collected from various northern Australian beaches are also included in this study.

Fig. 2. The head of a 2.7-m-long adult male dugong. There were 22.5 GLGs in each of the erupted and worn tusks.

Collection procedure

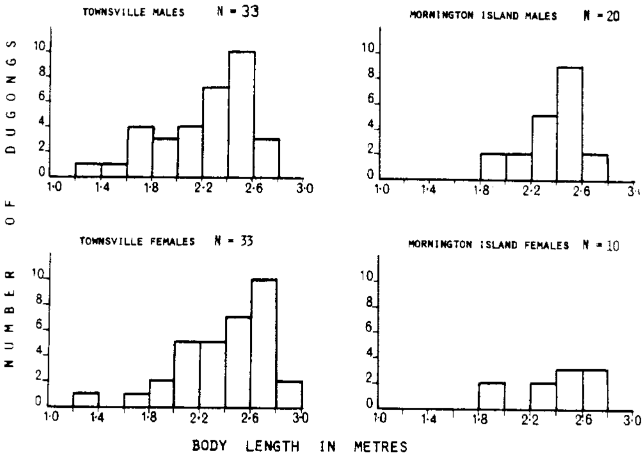
Unless very badly decomposed, each dugong carcass was sexed, measured and dissected to collect the stomach contents, skull and reproductive tracts. The entire reproductive tract was preserved by injection with, and immersion in, 10% sea water formalin (SWF). Small fetuses were preserved in the uterus. Larger fetuses were removed from the uterus and fixed in SWF. If time permitted, details of the ovarian follicles and corpora lutea of each female were recorded before fixation, and a sample of mammary gland was fixed in SWF. In the case of each male, a 1-cm cube from the centre of the right testis was removed and fixed in Cleland's solution (Rowley and Heller, 1966). The skull of each animal was collected and cleaned by boiling (Heinsohn, 1972; Heinshohn and Spain, 1974).

Description of material

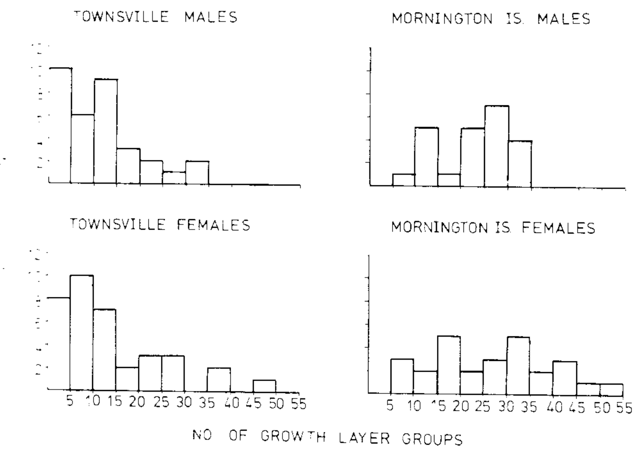
Body-length frequencies for the dugongs from Townsville and Mornington Island are illustrated (Fig. 3), arranged by sex and in 20-cm body-length classes for all animals for which these data were available.

The age-frequency distribution of the samples (Fig. 4) is reflected in these length-frequency histograms and indicates a paucity of young animals in the Mornington Island sample. No confirmed neonates were available, and only two females (both from Townsville) carrying near-term fetuses are presented.

The Townsville sample indicates that similar numbers of male and female dugongs drown in the shark nets. The total Mornington Island sample consisted of 23 males and 27 females and reflects the practice, adopted by at least some of the aboriginal hunters, of avoiding the capture of pregnant females as a conservation measure (Marsh *et al.* in press).



·ig. 3. Body-length frequency diagrams (by 0.2m classes) of the male and female dugongs collected from near Townsville and Mornington Island, 1969–1978.



.. 4. Frequency diagrams of 5-year age classes (determined by number of dentinal GLGs in the tusks) of dugongs and isolated dugong skulls collected from near Townsville and Mornington Island 1968–78. Males with erupted tusks have been assigned to the age class which corresponds to the number of GLGs present in their erupted tusks.

Seasonality of collection

.. monthly distribution of the dates of death of the speci-..s is shown in Figure 5. Specimens from Townsville were ..ained in all months of the year; the small number of ..als caught in June-July is a result of the removal of the ..k nets at that time (Heinsohn, 1972; Heinsohn and Spain, ..). The peak period of dugong hunting activity at ..ington Island is in July-August, the major period when ..server was on hand to collect specimens (Marsh *et al*, ..ess).

METHODS

T..th growth and succession

..ciduous incisors. If present, one deciduous incisor was ... ..ed from each skull with forceps. The pulp cavity was ... ..ded as open or closed and any tooth resorption or ..ternal growth layers were noted. The length was measured .. the nearest 0.1 mm using vernier calipers.

Tusks. Unerupted tusks were extracted from the skulls by removing a window from the premaxilla above the tusk using a small abrasive disc in a hand-held flexible drive. The length of each tusk was measured to the nearest millimetre

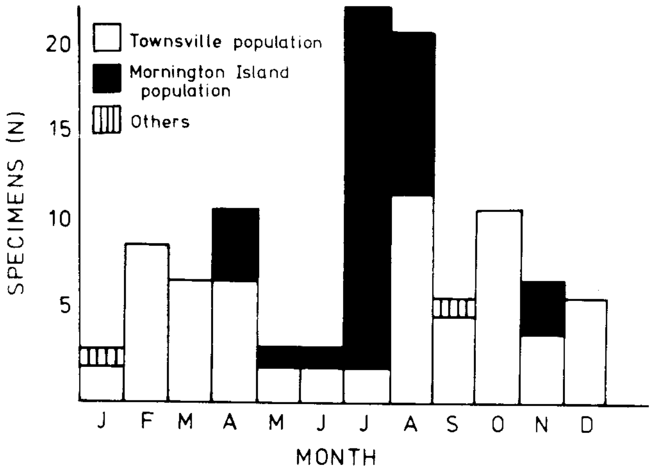


Fig. 5. Frequency distribution of the number of dugongs caught in each calendar month. All animals collected from 1969 to 1978 are included.

along the curvature in line with the centre of the tooth, using a flexible tape. The depth of the socket was measured using a set of vernier calipers as a probe. All tusks were examined for external evidence of growth layers.

Cheek teeth. All skulls in which molar 3 had not erupted were x-rayed using a *Toshiba* 4-valve, single-phase, x-ray generator with rotating anode tube with *Ilfex* 90, 18 × 24 cm, non-screen film. The mandibles were x-rayed from the right buccal surface at 42–60 kVP and 200 mAS; the crania were x-rayed obliquely from the ventral aspect at 65–77 kVP and 200 mAS.

The cheek dentition of each quadrant of each skull in the collection was recorded. Each tooth was listed as either: (1) unerupted; (2) partly erupted; (3) erupted and unworn; (4) erupted and in wear; (5) wizened (extensively resorbed); (6) broken (stump only in alveolus); (7) absent, alveolus empty; (8) absent, alveolus partly filled with spongy bone, or (9) absent, alveolus not visible.

A cheek-tooth index was calculated for each skull as a quantitative measure of the number and state of all the cheek teeth. A tooth in state (8) or (9) was scored 0; state (1), (2), (6) or (7) as 0.25; state (3) or (5) as 0.5 and state (4) as 1. The pulp cavity of each tooth was recorded as open, tapered at the base, or closed.

Estimates of the occlusal areas of molars 2 and 3 which were in wear in the lower right hand quadrant of each skull were obtained by tracing the outline of the crown surface of each molar. The tracing was then cut out and weighed correct to 1×10^{-5} g on a *Sauter* balance. Calibration was performed by weighing 1-cm squares of the same paper.

Estimates of the central cross-sectional areas of the same teeth, both including and excluding the pulp cavity, were obtained by placing each tooth buccal surface uppermost on the x-ray plate and x-raying at 60 kVP and 200 mAS. Two contact prints were made of each x-ray and the areas calculated by cutting out and weighing as above. The central cross-sectional area of the pulp cavity of each tooth was obtained by subtraction.

Preparation of teeth and bones to demonstrate growth layer groups

The tusk was the main tooth selected for this part of the age determination study. It is present throughout life, has a permanently open pulp cavity, and is unerupted and unworn in most females and juvenile males. One tusk was prepared from each animal unless there was a large difference in the size of the two tusks in which case both were prepared. One deciduous incisor was also examined provided that resorption had not commenced.

In the sections that follow, both 5% HCl in 70% ethanol, and 10% formic acid were used to etch or decalcify the teeth with equivalent results. There was also no substantial difference in the results obtained with the different haematoxylins used.

Etched half teeth. Each tusk was bisected longitudinally in the mesiodistal plane using a 10-inch diameter saw as follows: the cutting line was marked before each tusk was embedded in ice in the desired orientation prior to cutting; the optimum plane of section was maintained by holding the broad flat surface of the ice in contact with the movable carriage of the saw. Unresorbed deciduous incisors and tusks less than 4 cm long were mounted on chucks with dental impression compound and bisected using a 4-inch diamond saw. After the teeth were cut, the depth of the apex of the pulp cavity was measured along the curvature of the tooth using a flexible tape.

The cut surface of one half of each tooth was polished using progressively finer grades (150–600) of wet and dry sandpaper. This half tooth was then etched by immersing it in 5% HCl in 70% ethanol for 3 h at room temperature (25°C), washed and allowed to dry thoroughly with the cut surface uppermost. The resultant relief was emphasized by rubbing the surface with pencil. The tusks were usually examined without magnification.

Small tusks (less than 6 cm long) and deciduous incisors were stained with Mayer's haemalum after etching as above and examined under a binocular microscope (×8) using oblique light.

Thick sections. The unetched half of each tusk was cut transversely about 1 cm distal to the apex of the pulp cavity; tusks less than 6 cm long were processed without further cutting. The longitudinal cut face of the part of the tooth which included the pulp cavity was then polished using progressively finer grades of wet and dry sandpaper (150–1200) and glued on to a *perspex* slide with cyano-acrilate monomer glue. The tooth was then cut longitudinally on a diamond saw to produce a mounted section approximately 1 mm thick which was ground to a thickness of approximately 500 μm, etched in 5% HCl in 70% ethanol for 1 h, washed, stained with Mayer's haemalum, washed and mounted in glycerol. For two dugongs thick sections were also prepared of lower left molars 2 and 3.

Thin sections. One deciduous incisor and one tusk from each dugong less than 2 m long were mounted on chucks with dental impression compound and bisected longitudinally using a 4-inch diamond saw. The cut face of each half tooth was polished using whetstones (1200 and 4000 grit) and glued to a *perspex* slide. Sections 30 to 80 μm thick were prepared by grinding as above. One section from each tooth was then mounted in glycerol. The other section was decalcified in 10% formic acid for 2 h to 3 h, washed and stained for 3 min with Gill's haematoxylin (Lillie and Fullmer, 1976, p. 207), washed and mounted in glycerol.

Longitudinal and transverse sections from adult tusks and transverse sections from three ribs from uncatalogued dugongs, one tympanic bone and one malleus from each of two catalogued dugongs, one humerus from a catalogued dugong and one rib from another catalogued dugong were also prepared and stained as above.

Microradiographs. Four transverse sections (280–600 μm thick) were cut from one tusk, polished with whetstones without gluing to a slide, cleaned ultrasonically and microradiographed using a *Picker Mini Shot* (Model [illegible]) x-ray unit for 3 h at 13 kv and 1.5 mA. The source-to-film (*Kodak*, high resolution) distance was 20 cm. The microradiographs were examined with a compound microscope using transmitted light and photographed.

Determination of the pattern of the growth layer groups

An ontogenetic series was prepared of thin sections of one deciduous incisor and one tusk from one fetal (body length approximately 1 m) and 15 juvenile dugongs (body lengths 1.25 to 1.98 m).

The sections in this series were ranked in ascending order of body length and examined with transmitted light using both a binocular (×8) and a compound microscope (×63) to determine the nature and thickness of the prenatal dentine, the neonatal line and the pattern of GLG deposition.

Intercalibration of techniques

Polished and polished and etched half teeth. The dentinal layering seen in polished half teeth was intercalibrated with that seen in polished, etched and pencil-rubbed half teeth by masking a portion of the polished surface of one-half tooth with *Paraplast* before etching and pencil rubbing. The wax was removed with xylene prior to examination.

The effect of etching on the layers visible on the surface of the worn tip of an erupted male tusk was examined by masking half the worn area with wax before etching and pencil rubbing, etc., as above.

Untreated and decalcified and stained thin sections. The structures seen in undecalcified and unstained and in decalcified and stained sections were intercalibrated by masking part of several thin sections with dental wax prior to decalcification and staining. The sections were dehydrated in graded ethanols and the wax removed with xylene. The sections were then rehydrated, mounted in glycerol and examined as above.

Inter-calibration by performing several treatments successively on the same section. One face of the 600-μm section that was microradiographed (see above) was subsequently masked with dental wax before etching by immersion in 5% formic acid for 1.5 h. The wax was removed and the resulting relief on the face which had not been masked was then emphasized by rubbing with pencil. The section was then examined using both transmitted and reflected light. The pencil markings were removed and a 200Å-thick layer of carbon was evaporated onto the etched surface of the specimen, which was then photographed with reflected light. The section was then ground down to 90 μm by grinding both faces, mounted in glycerol, examined under a compound microscope (×63) and photographed with transmitted light. The section was then decalcified, stained with haematoxylin and examined and photographed with transmitted light. The inter-calibration was performed by comparing the photographs of each stage.

Scoring the tooth and bone preparations

Counting the layers. Each preparation was scored independently several times without reference to the biological information concerning the dugong from which it came. The GLGs in the etched tusks were counted without magnification, using oblique light. For old animals, scoring was

...itated by photographing the etched tusk and counting ...g the convex edge of the tusk in the photograph.

...etermination of the rate of deposition of growth layer ...roups. The nature and zone thickness of the dentine being ...d down at the time of death (i.e. adjacent to the pulp ...ity) was examined and plotted against date of death as ...direct evidence of the depositional rate of the GLGs. The ...k sections of tusks were all masked with random num...rs and examined under a binocular microscope (× 8) with ...flected light without knowledge of the date of death. ...ch section was examined independently by two people a ...al of six times before the slides were unmasked. For two ...ngs, thick sections of molars 2 and 3 were also exam...d.

...dications of cranial growth

... each skull the condylo-premaxillary length and the ...matic width (Spain and Heinsohn, 1974) were measured ...ct to 1 mm with vernier calipers. The basioccipital ...re (between the basioccipital and the basisphenoid), ...condyle sutures (between the basioccipital and the ...cipitals) and the basisphenoid suture (between the basi...henoid and the presphenoid) were examined and scored ...pen, partly fused (bony bridges present, suture line ...ible), or fused.

...easurement and histological preparation of reproductive materials

...ach fixed testis was trimmed of epididymis and fat and ...eighed correct to 0.1 g. The Cleland's-fixed specimen ...btained at autopsy was included with the remainder of ...he right testis. The length, width at mid-length and dorso-ventral thickness at mid-length were measured with vernier calipers. Tissue specimens were taken as follows: three from the centre along the longitudinal mid-line and two from along the transverse mid-line of each testis and one from each corpus and each cauda epididymis. These specimens were post-fixed in Bouin's fixative (Lillie and Fullmer, 1976, p. 61) and along with the Cleland's-fixed specimen dehydrated in ethanol, cleared in xylene, embedded in *Paraplast*, sectioned at 5 or 6 μm and stained with Mayer's haemalum and *Young's Eosin-Erythrosin*.

The preserved female material has not yet been measured and sectioned.

Data analysis

Computation was carried out either on the CSIRO *Cyber* 76 in Canberra or on the *PDP 10* computer at James Cook University of North Queensland. The Genstat System of programs was used for the multiple regression analyses. The Maximum Likelihood Program from Rothamsted and the Non-Linear Regression Program from IMSL (Anon, 1975) wêre used for the growth curves and Tustat II (Koh, 1973) for the t-tests.

RESULTS

Description of the structural components of the teeth used for age determination

Deciduous incisor. In the fetus and the juveniles with less than three GLGs the tip of the deciduous incisor (Fig. 6A) is covered with a layer of *enamel* approximately 100 μm to 130 μm thick; in older animals the tip is resorbed (Fig. 6C). The *prenatal dentine* appears reasonably homogeneous and is of intermediate optical density but generally less dense

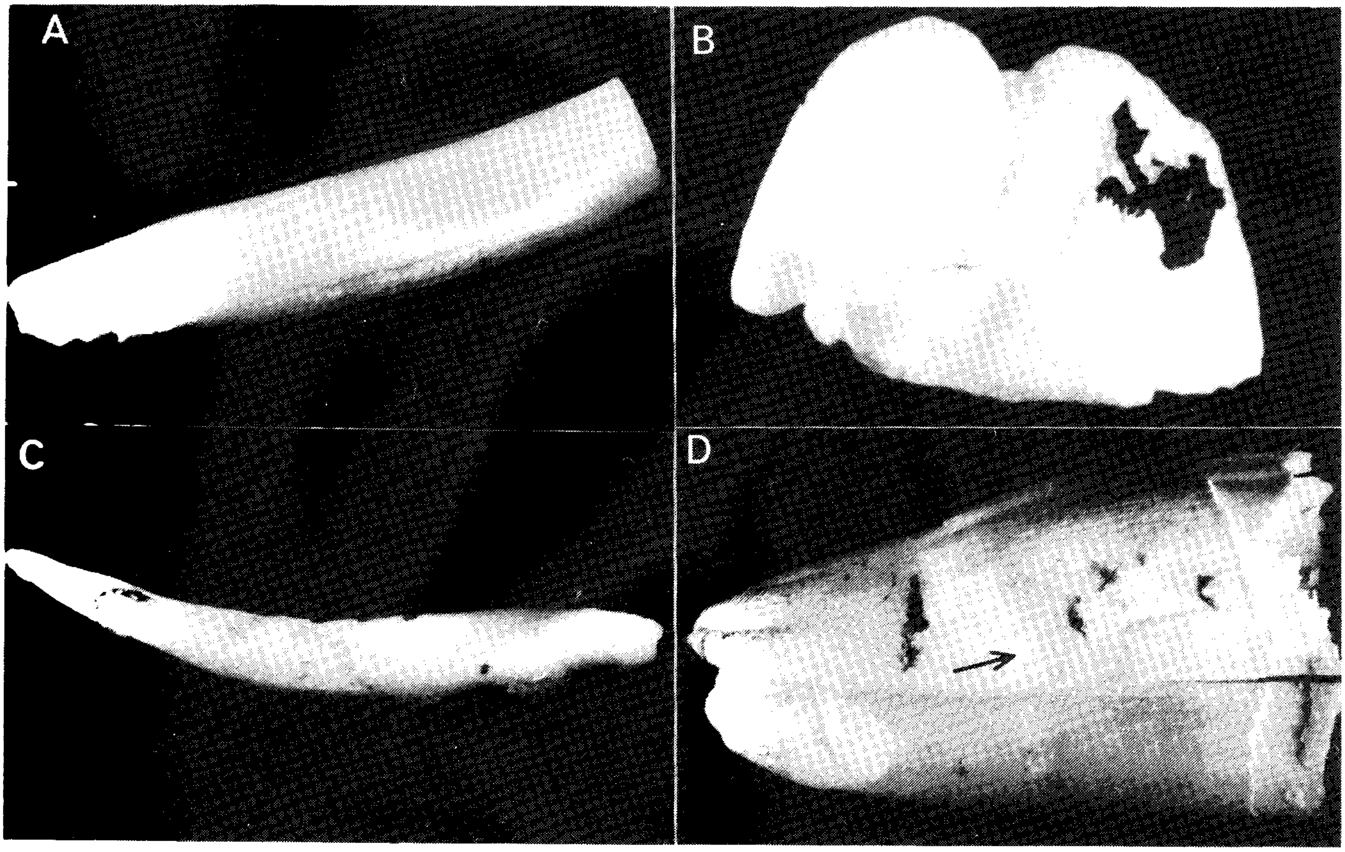


Fig. 6. The deciduous incisors and tusks from young dugongs. (A) 2.26-cm-long deciduous incisor and (B) 0.55-cm-long tusk from a 1.3-m-long male dugong less than three months old. (C) 4.18-cm-long deciduous incisor and (D) 2.4-cm-long tusk from a 1.8-m-long dugong with two GLGs in the tusk. An external growth layer is (D) arrowed.

than the postnatal dentine. It is about 5 mm thick at the tooth apex. The last-formed prenatal dentine is generally slightly more opaque than that formed earlier and stains more intensely with haematoxylin. The *neonatal line* (Fig. 7A) is a fine translucent unstainable layer about 40 μm thick. It lies between the opaque, intensely-stained edge of the prenatal dentine and another opaque (intensely stainable) line about 30 μm thick. This tripartite structure forms a groove in etched specimens, the stainable layers being at the sides of the groove.

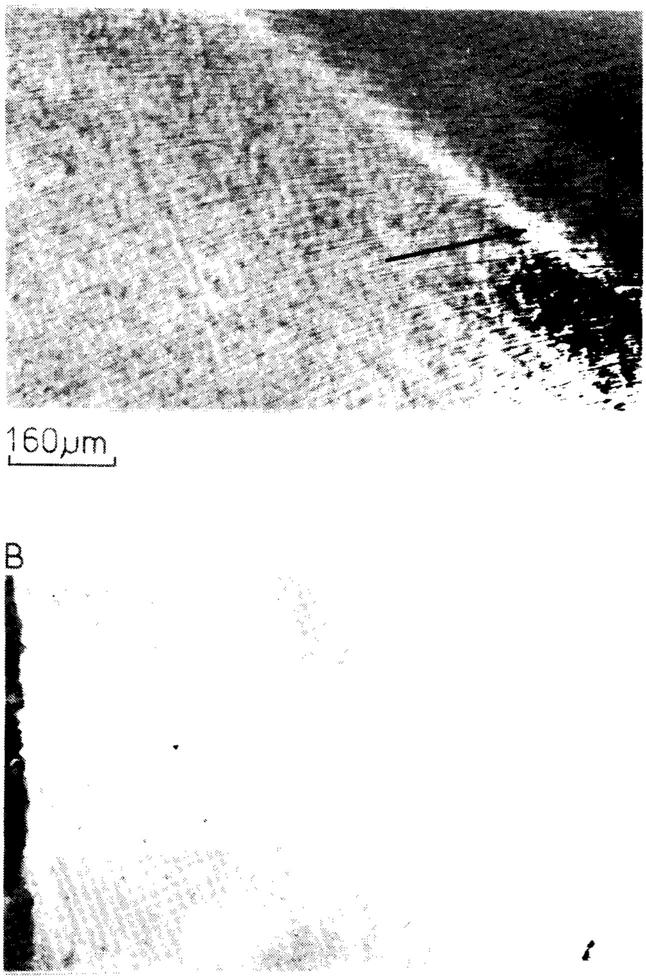


Fig. 7. (A) Decalcified and stained section of a deciduous incisor from a 1.5m-long male dugong estimated to be one year old showing the unstained neonatal line (arrowed). (B) Cementum layers in a decalcified and stained transverse section from the midlength of an erupted and worn tusk from a 2.65-m-long adult male dugong. Twenty layers can be seen in the cementum. 34 GLGs were counted in the tusk.

A GLG in the *postnatal dentine* consists of both fine and thicker accessory layers. The fine layers are opaque, stain strongly with haematoxylin, and are about 20 μm wide and separated by about 50 μm of intermediately staining dentine. About 12 fine layers are followed by one or more opaque (stainable) and thicker layers each about 60 μm wide and followed by translucent dentine. The combination of opaque and translucent thicker layers forms a groove in etched teeth. Because of the prominence of the fine accessory layering, the boundaries of GLGs may be difficult to distinguish in etched deciduous incisors.

The base of each deciduous incisor is coated with cementum 80 to 130 μm thick. In older animals, cementum covers almost the entire incisor except where resorption has taken place.

Tusk. The tip of the tusk consists of several cusps (Fig. 6B) which may be variably developed. Covering the tip is a layer of *enamel* up to about 330 μm thick. The enamel becomes thinner on the sides of the tusk and disappears altogether after the first four or five GLGs except on the ventromesial side, where a layer of enamel about 330 μm thick continues beneath the cementum to the base of the tusk in both males and females (Fig. 8A).

The thickness of the *prenatal dentine* varies according to the development of the cusps and may be up to 500 μm thick. It is generally less dense than the postnatal dentine both in stained and [illegible] preparations.

The *neonatal line* [illegible] translucent unstainable layer about 30 μm thick. [illegible] difficult to see at the center of the [illegible] the sides.

The [illegible] ranged series of coaxial [illegible] (Fig. 8) consists [illegible] density, referred to as Z [illegible] accessory layers, followed [illegible] B [illegible] which the access[illegible] B consists of [illegible], each followed [illegible] the opaque lay[illegible] identified as th[illegible] in some GL[illegible] particularly [illegible] lished [illegible] particularly [illegible] forms [illegible] Figs 8C, [illegible]

[illegible] first GLG [illegible] appeared as a crack. [illegible] stained sections, the [illegible] were more difficult [illegible] The mean [illegible] ages is given in Ta[illegible]

[illegible] with age [illegible] central axis [illegible] calipers

GLGs	[illegible]	SD (mm)
[illegible]	[illegible]	12.4
[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible].5
[illegible]	[illegible]	[illegible].1
[illegible]	[illegible]	5.4
[illegible]	[illegible]	4.9
[illegible]	[illegible]	4.2
[illegible]		
[illegible]	[illegible]	3.7
[illegible]	[illegible]	2.9
[illegible]	[illegible]	5.5
[illegible]	[illegible]	5.1

[illegible] been worn

Cementum covers almost the entire surface of the tusk in older animals but is absent from the tip of the tooth in young animals. The layering in the cementum (Fig. 7B) was not used to determine age. In many of the specimens studied, the cementum had been damaged, presumably by prolonged boiling.

External growth layers, where present, formed ridges on the surfaces of the tooth (Fig. 9B). They were found to correspond to Zone B.

Intercalibration of structures revealed by different techniques

Study of the masked teeth showed that the degree of optical density was mirrored by the degree of stainability (Fig. 8D). Examination of the tusk section which was subjected to a variety of treatments to demonstrate the GLGs (Figs. 8A to D) suggested that, for this animal at least, the degree of optical density corresponded to both the degree of radio-opacity and of staining capacity. However, this relationship did not hold for all dugong teeth. When the section was etched, pencil-rubbed, and examined under transmitted light the translucent component of Zone B was found to lie on the side of the groove. The opaque component was at the deepest part of the groove.

Growth layers are visible in the worn area at the tip of erupted tusks as poorly developed concentric ridges and grooves which presumably result from the differential abrasion of GLG components by the substrate as the dugong feeds. When half the worn tip was masked by wax before etching, it was evident that the more readily-abraded layer corresponded to the more readily-etched layer, i.e. Zone B. However, it was not possible to determine whether the opaque or translucent component of Zone B was the more abraded.

Scoring the number of dentinal growth layer groups

The first three or four dentinal layers were much more difficult to score than the layers formed subsequently. Hence, in young animals it was found to be necessary to use a range of preparations to determine age, i.e. both untreated and decalcified and stained sections of the deciduous incisors and the tusks; the external growth layers (Fig. 6D); and the half teeth.

The etched and pencil-rubbed half teeth (Fig. 9A) were used for counting GLGs in older animals. One ridge plus one groove was scored as one GLG; the ridge only, as half of a GLG. The layering in most teeth could be counted very easily, and there was usually complete agreement between repeat counts. Dentine deposition appeared to be occurring even in teeth with small pulp cavities. It was possible to count the layers in all teeth that were examined, although the nature of the zone next to the pulp cavity could not be ascertained with certainty in the teeth of six very old animals.

Counts ranged from zero to 51 in unerupted tusks. A maximum count of 34.5 was recorded for an erupted tusk from a male. The two erupted tusks from females had GLG counts of 37.5 and 45.5. When both tusks from the same animal were examined they were found to have the same number of GLGs despite any difference in size.

The external growth layers of older animals (Fig. 9B) were often difficult to see.

Rate of deposition of the growth layer groups

Uniformity of layer deposition in different teeth from the same animal. The zones being laid down at the time of death in the deciduous incisor, tusk, molar 2 and molar 3 in two animals and in the deciduous incisor and tusk of 13 animals were compared. They were found to be the same for all teeth examined from the same animal. The pulp cavity of each of the deciduous incisors and molars examined was open.

Seasonal pattern of layer deposition. When the nature of the zone being laid down at the time of death (Fig. 10) was tabulated against the date of death (Table 2), Zone B was seen to be almost always formed in the latter half of the year. These data were obtained from 106 animals, 57 of

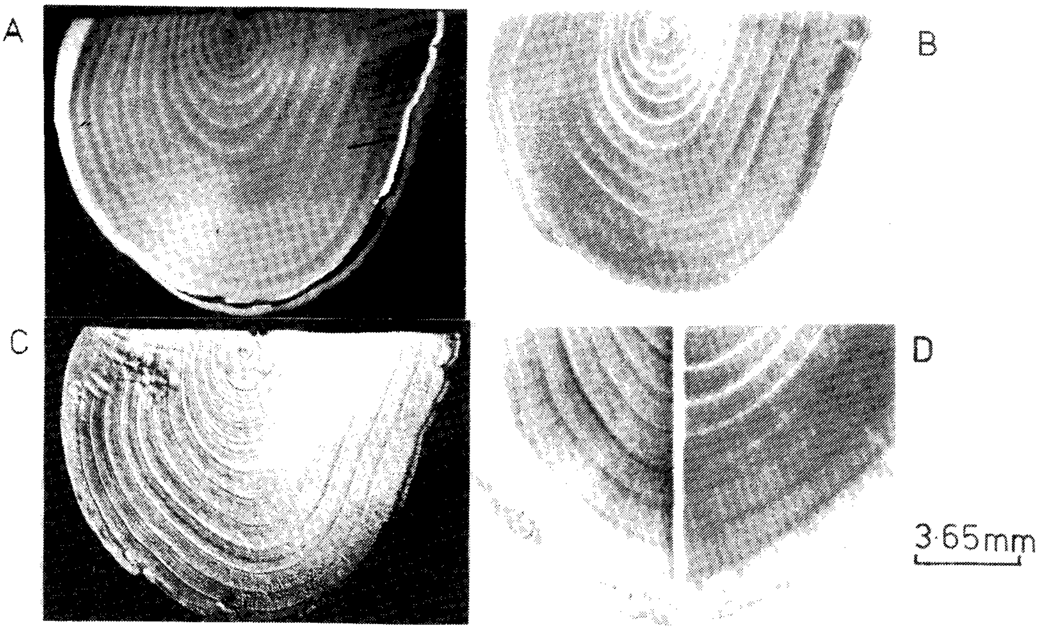


Fig. 8. Transverse sections from the midlength of the same tusk as the section in 7(B). (A) microradiograph of the ground section that is etched and coated with carbon and viewed with oblique light in (C), and that is viewed with transmitted light in (B). The section was 2 cm wide at the top. The enamel layer is arrowed in (A). (D) Adjacent section viewed with transmitted light. The right-hand portion of the section is untreated. The left-hand portion is decalcified and stained.

Table 2

Dugongs from northern Australia (1969–1978)
Distribution by month of the dentinal GLG zone in process of forma[illegible]
Data are numbers of animals recorded

Type of Zone being formed	Month											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Zone A (Haematoxylin +)	3	9	7	10	2	1	7	4	1	3	6	4
Zone B (Haematoxylin ++)	0	0	0	2	0	1	16	14	4	8	2	2

which died in the process of depositing Zone A and 49, Zone B. Only 15 of the 57 animals (26%) depositing Zone A died between July and October inclusive, while 42 of the 49 (86%) animals depositing Zone B died within this period ($P < 0.001$, χ^2 Heterogeneity Test). These data suggest that one GLG is usually deposited each year.

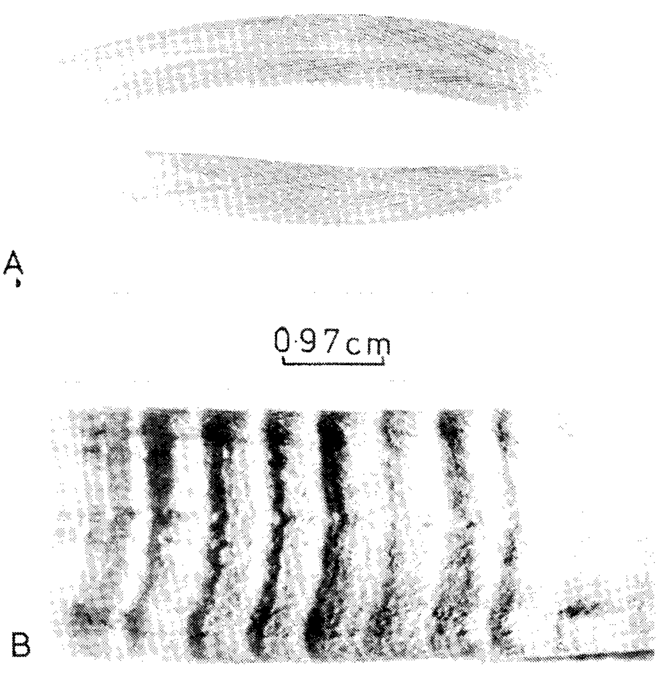


Fig. 9. (A) The etched and pencil-rubbed longitudinal surfaces of two dugong tusks. The top tusk is the erupted and worn 14.5-cm-long tusk from a 2.72-m-long male dugong showing 29.5 GLGs in the dentine. The 11.5-cm-long lower tusk is from a 2.5-m-long female dugong and has 17.5 GLGs. (B) The unusually clear external growth layers in the tusk of a 2.39-m-long adult male dugong.

The thickness of the Zone A next to the pulp cavity was recorded relative to that of the previous Zone A for all animals laying down Zone A at the time of death (Table 3 and Fig. 10). The zone was less than a third as wide as the penultimate Zone A in 11 animals, between one-third and two-thirds of the penultimate Zone A in 14 animals, and more than two-thirds as wide as the penultimate Zone A in 32 animals. The results indicated that the first third of Zone A was laid down between October and January, the second third between December and April and the last third between February and September, further supporting the thesis of a one-per-year GLG deposition rate.

In Tables 2 and 3, data from both sexes, all areas, and all years are combined. The data were also considered separately, but no differences from the general pattern were found. However, data from 31 dugongs killed in Townsville shark nets during 1972 considered separately are even more striking evidence of an annual deposition rate (Table 4). The only exception in this group was one animal, which appeared to be laying down a Zone B in April and had a score of two GLGs.

Layer deposition in sick or pregnant dugongs. Four animals collected from Mornington Island in July-August were described by the aboriginals as 'sick' and unfit to eat. These animals were observed to tire quickly, were easy to catch, and had an abnormally high parasite load (B. R. Gardner, pers. comm.). On the basis of pathological examination, R.S.F. Campbell (pers. comm.) reported that they had oedematous fat and muscle. The layer deposition pattern of these animals did not differ from that of the 12 apparently healthy dugongs caught at Mornington Island during the same period. The two females with large fetuses collected from Townsville, one in December, the other in July, were both laying down Zone B.

Relationship between changes in body length and the number of growth layer groups in the tusk

On the assumption that one GLG is deposited each year (see

Table 3

Dugongs with Zone A being formed at time of death
Distribution by month of thickness of Zone A relative to thickness of penultimate Zone A
Data are numbers of animals recorded

Thickness of Zone A being formed relative to thickness of penultimate Zone A	Month											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	[illegible]	Nov.	Dec.
Less than one-third	1										6	1
One-third to two-thirds	2	3	3	3								3
Greater than two-thirds		6	4	7	2	1	7	4				

Table 4

Dugongs killed in Townsville shark nets in 1972
Distribution by month of nature and thickness of dentinal GLG zone being formed at time of death

	Month											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Zone A : less than one-third												
Zone A : one-third to two-thirds	1	2	2	1								
Zone A : greater than two-thirds		6	3	3	1			2				
Zone B				1				1	3	3	1	1

section on GLG deposition rate), the relationship between body length (L) and age (A) (number of dentinal GLGs) was calculated using a standard single-phase asymptotic growth curve of the form

$$L_A = L_\infty + \beta\gamma^A$$

where L_A = length at age A
L_∞ = asymptotic length
and β and γ are constants.

This is algebraically equivalent to the von Bertalanffy Growth Equation (von Bertalanffy, 1938, 1957).

For the calculation of growth curves, dugongs were assigned ages that represented a mid-year point within their respective year classes. Thus, dugongs with less than one GLG were aged as 0.5 years, dugongs with one but less than two GLGs as 1.5 years, etc. This process takes account of the range of sizes within a year rather than at the beginning of a year, which was particularly important for dugongs with less than one GLG as the length at birth was not known with certainty.

Five growth curves were calculated for the Townsville population as follows: females; males (animals with unworn tusks only); all males (number of GLGs in worn tusks used as an estimate of age); males and females (unworn tusks only) (Fig. 11); all animals. As all but two of the females from Mornington Island were almost old enough for the asymptotic length to have been reached, separate analyses were not performed for males and females from this population but were restricted to age estimates based on unworn tusks and all tusks as above.

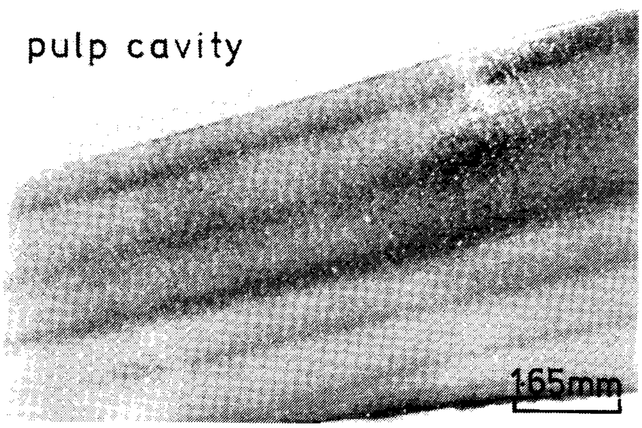


Fig. 10. Longitudinal tusk section used for determining the thickness and nature of the GLG adjacent to the pulp cavity.

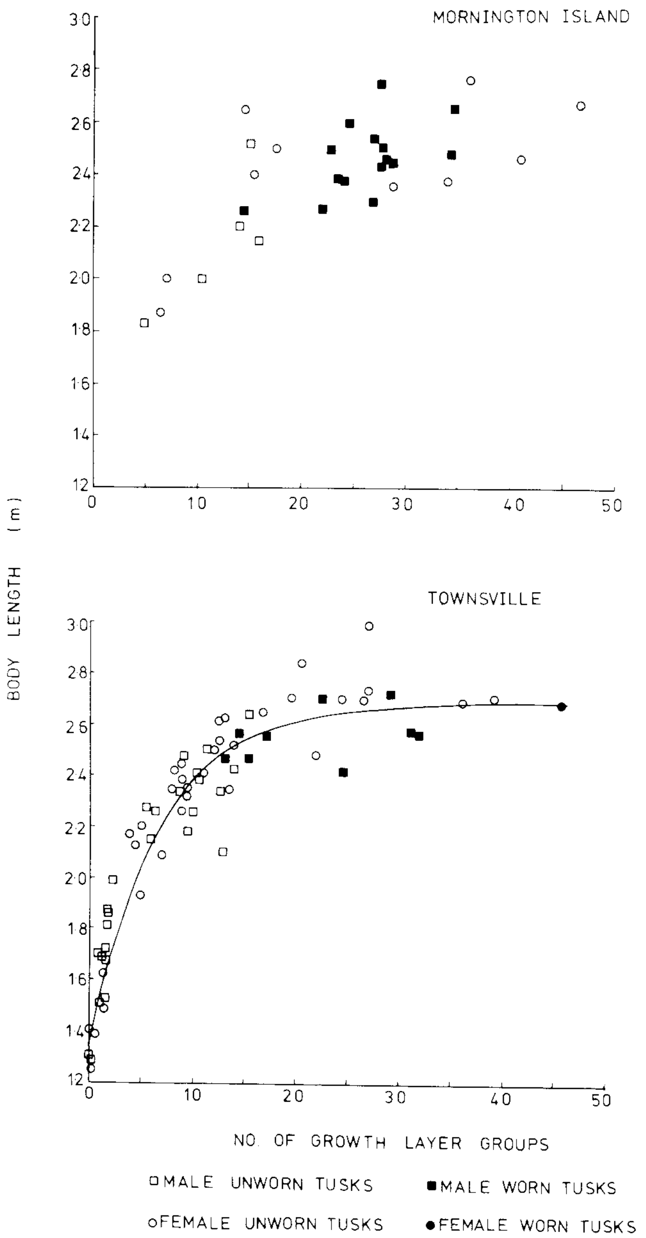


Fig. 11. Relationship between body length (L_A) in metres and age (A) in years (expressed by number of dentinal GLGs) for dugongs from Mornington Island and Townsville. The regression fitted to the Townsville data (unworn tusks only) is $L_A = 2.69 - 1.35\ (0.86)^A$.

Table 5

Estimates, including 95% confidence limits, of the asymptotic length (L_{∞}), birth length (L_0), and growth curve constants for dugong growth curves. The coefficient of determination (r^2) is also included

Sex	Condition of tusks	N	L_{∞} (95% CL)	L_0 (95% CL)	β (95% CL)	γ (95% CL)	r^2
Townsville population							
Female	Unworn	34	2.72 (2.63, 2.82)	1.31 (1.16, 1.45)	−1.41 (−1.57, −1.27)	0.86 (0.83, 0.89)	0.92
Male	Unworn	25	2.39 (2.30, 2.48)	1.10 (0.86, 1.35)	−1.29 (−1.51, −1.09)	0.70 (0.61, 0.80)	0.91
Male	Unworn + worn	34	2.53 (2.44, 2.62)	1.27 (1.10, 1.44)	−1.26 (−1.42, −1.10)	0.80 (0.74, 0.87)	0.91
Female + male	Unworn	59	2.69 (2.59, 2.79)	1.34 (1.24, 1.45)	−1.35 (−1.46, −1.23)	0.86 (0.83, 0.89)	0.91
Female + male	Unworn + worn	69	2.67 (2.60, 2.74)	1.35 (1.25, 1.45)	−1.32 (−1.43, −1.22)	0.86 (0.83, 0.88)	0.91
Mornington Island							
Female + male	Unworn	16	2.56 (2.37, 2.74)	0.93 (−0.33, 2.19)	−1.62 (−2.81, −0.44)	0.87 (0.77, 0.97)	0.71
Female + male	Unworn + worn	30	2.55 (2.43, 2.66)	1.05 (0.14, 1.96)	−1.49 (−2.34, −0.65)	0.88 (0.81, 0.95)	0.67

Estimates and 95% confidence intervals of the asymptotic lengths, birth lengths, and constants based on the above analyses are given in Table 5 with the coefficient of determination (r^2) for each curve. The estimates of L_{∞} and γ were all significantly different from zero at the 0.001 level. Those for β were significant at the 0.05 level or less.

The growth curves for Mornington Island dugongs (Table 5) are unsatisfactory as the confidence intervals for the birth lengths are too large to support the estimates of this parameter. This is not surprising as the youngest animal in the Mornington Island sample was estimated as five years old.

At a value of approximately 20 GLGs, all the curves approach an asymptote. The confidence intervals for the asymptotic lengths of the Townsville females and males, based on age estimates from both unworn tusks only and all tusks, do not overlap (Table 5), suggesting that the asymptotic length of the females is greater than that for the males. When the mean lengths of all Townsville females and males with 20 or more GLGs are compared using a t-test, the mean length for females is also found to be significantly larger ($0.025 < P < 0.05$).

A similar comparison between males and females from Mornington Island does not demonstrate any sex difference in asymptotic length at the $P = 0.05$ level, perhaps because the sample size is so small.

When the confidence intervals of the asymptotic lengths (both sexes combined) of the Townsville and Mornington Island populations are compared (Table 5), they overlap, possibly because of the comparatively small size of the Mornington Island sample. However, when the mean body lengths of all animals from the two populations with over 20 GLGs are compared using t-tests, the asymptotic length of the Townsville animals is found to be significantly greater ($P < 0.0005$; both sexes together). When the sexes are considered separately, the differences between the two populations are not significant. This may be related to the small sample sizes or may reflect the differences in the sex composition of the two samples.

The asymptotic length estimates of the Townsville dugongs produced by all the curves may be too low. In the case of the curve for males with unworn tusks only, this is obviously because animals with over 20 GLGs were not included in the analyses. Two females out of nine and two males out of five with more than 20 GLGs had body lengths greater than the upper limit of the 95% confidence interval for their respective asymptotic lengths.

Many mammals exhibit a 'growth spurt' at or around puberty (von Bertalanffy, 1957) and fitting a single curve obscures this feature and probably leads to the underestimation of asymptotic length. A two-stage growth curve could be fitted, but this would involve making an arbitrary decision concerning the starting point of the second section of the curve. In view of the limitations of the present data, a single curve seems to adequately describe the increase in body length relative to dentinal GLGs throughout life. The values of r^2 obtained for the curves fitted to the Townsville data were high (> 0.91) and the residuals from the fitted curves showed no systematic bias.

Relationship between puberty and the number of growth layer groups in the tusk

Males. Reproductive material from 52 male dugongs has been examined histologically. None of the 20 animals (13 of which had GLG counts over 10, 3 over 20) from Townsville and Mornington Island that died between November and April inclusive and only ten of the 32 animals from the same areas that died in the remainder of the year had sperm in their testes or epididymides. Included in these 32 animals were 12 with more than 20 GLGs which were collected from Mornington Island in July; only four of these had sperm in their testes and epididymides. These results suggest a seasonal cycle of reproductive activity in the male dugong in which not all males are in rut simultaneously.

Male dugongs have been classified as immature, mature active, or mature quiescent on the basis of testes weight, tubule diameter, state of tubule lumina, and the presence or absence of mature sperm. The oldest animal from Townsville classified as immature had six dentinal GLGs and the youngest with mature sperm in the testes and epididymides had nine. Corresponding figures for Mornington Island dugongs were 14.5 (oldest immature), 14 (youngest mature quiescent), 22.5 (youngest mature active). Although only six animals with between 10 and 20 GLGs have been examined from this population, these preliminary results suggest that male dugongs may be maturing later at Mornington Island than in the Townsville region.

Two 'mature active' males, one with nine and the other with 10.5 dentinal GLGs, had unerupted tusks. The tusks were just erupting in another with 12 GLGs. A 'mature quiescent' animal from Mornington Island had unerupted tusks and 14 GLGs. These results indicate that the tusks erupt after puberty.

Females. Examination of the female reproductive tracts has not proceeded sufficiently to enable any firm statements about the age of female reproductive maturity in the dugong. The reproductive tracts of 20 female dugongs from Townsville have, however, been examined at autopsy. The oldest which had no follicles visible on the surface of the ovaries had nine GLGs; the youngest with follicles had eight GLGs. The youngest dugong with corpora lutea had 13 GLGs and the youngest pregnant dugong had 16.5 Only seven female dugongs from Mornington Island have been examined and of these only three had less than 20 GLGs. The youngest with follicles had 14.5 dentinal GLGs. These results suggest that puberty does not occur before at least eight or nine GLGs are deposited.

Relationship between incisor growth and the number of growth layer groups in the tusk

Deciduous incisors. In the fetus (body length 1 m) 1.6 cm-long deciduous incisors were present. The deciduous incisors were 2.26 cm long (Fig. 6A) in the youngest juvenile, with a body length of 1.3 m and estimated to be less than three months old.

The growth of the deciduous incisors is summarized in Figure 12. The maximum length recorded for the deciduous incisors from a male dugong was 4.25 cm (6.5 GLGs) and for a female 5.72 cm (13 GLGs). After about 2.5 to 3 GLGs the pulp cavity of the incisor closes and the tooth starts to be resorbed (Fig. 6C). In males, the deciduous incisors are lost around the time of tusk eruption. The sockets of the deciduous incisors are lost as the tusks expand. In the female, small partially-resorbed incisors may persist until the tusk has laid down up to 30 GLGs (Fig. 1B).

Tusks. The tusks exhibit dramatic axial growth in both sexes (Fig. 13), making transverse sections useless for age determination based on dentinal layering (Fig. 9A). The 1.3 m juvenile had tusks 0.55 cm long (Fig. 6B). A maximum tusk length of 17.8 cm was recorded for two females, one with 36 GLGs (tusk unworn); the other 37.5 GLGs (tusk erupted and worn). The maximum tusk length recorded for a male was 15.8 cm. The tusk had 26.5 GLGs and was erupted and worn.

The growth of the tusks is similar in both sexes until about ten GLGs are laid down and the tusk is about 10 cm long (Fig. 12). The tusk grows posteriorly through the premaxilla, and, after the deposition of one or two GLGs, a hole appears in the lateral side of the premaxilla at the root of the tusk, enabling its state of growth to be seen. The increase in length of the tusk is generally accompanied by an increase in length in the pulp cavity, although the rate of increase in the size of the pulp cavity is less after the deposition of about five GLGs (Fig. 12).

The female tusk continues to grow posteriorly through the premaxilla. The increase in length of the tusk is accompanied by a corresponding increase in the length of the alveolus (Fig. 12) which continues to extend up the premaxilla, the hole in the premaxilla marking the base of the alveolus. In older animals, the width of the GLGs decreases (Table 1) and the pulp cavity decreases in length (Fig. 12). The inclination of the GLGs from the long axis of the tooth also increases with time, resulting in the later layers in very old teeth being almost perpendicular to the long axis of the tooth. In two females, with 45.5 and 38.5 GLGs, the tusks had erupted and worn, presumably because they had reached the base of the premaxilla and could not grow posteriorly any farther. Tusk eruption cannot therefore be considered to be diagnostic of male dugongs.

In the male, the tusks erupt (Fig. 2) after 12 to 15 GLGs have been laid down. The length of the tusk alveolus remains relatively constant thereafter and never reaches the base of the premaxilla. The premaxillary bones are much thicker than in the female and the hole in each premaxilla at the base of each tusk usually disappears around the time that the tusks erupt. The decrease in the width of the GLGs is

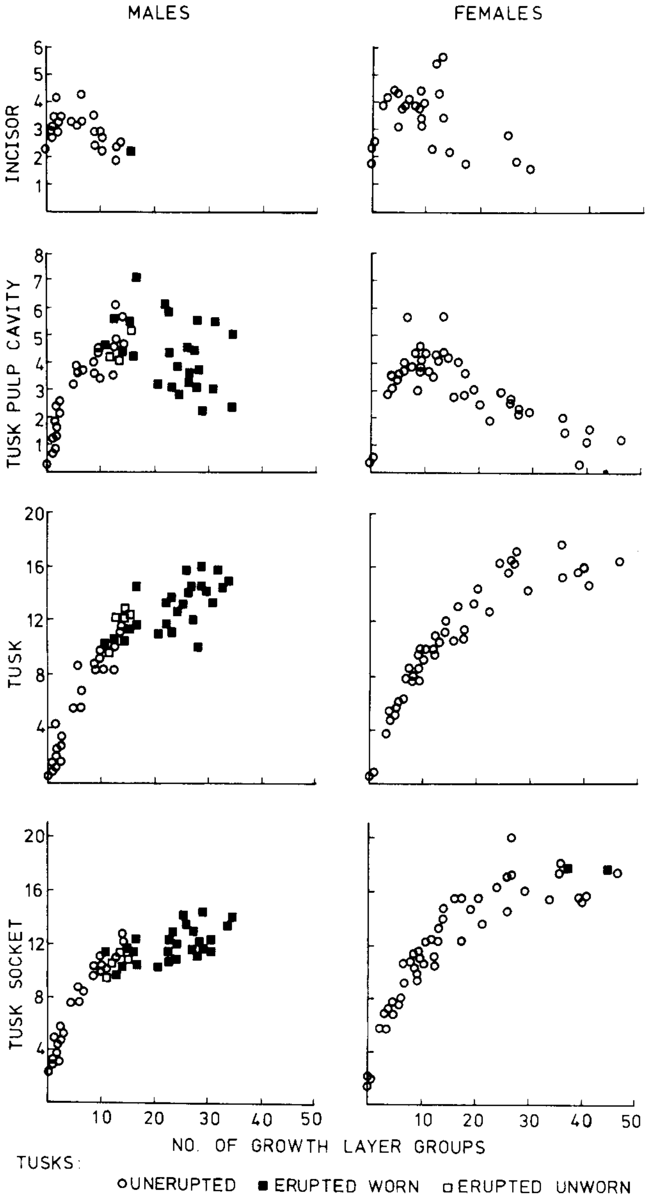


Fig. 12. Diagram showing the length (in cm) of the deciduous incisor, tusk pulp cavity, tusk, and the tusk socket at various ages (expressed as number of dentinal GLGs for male and female dugongs).

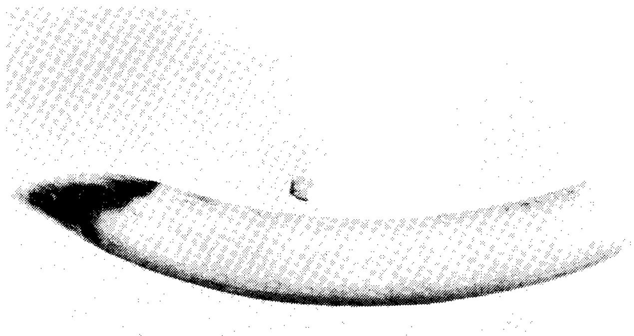


Fig. 13. The 0.55-cm-long tusk from a 1.28-m-long dugong and the 13.7-cm-long tusk from a 2.39-m-long male dugong.

not as great as in the female (Table 1). The inclination of the GLGs to the long axis of the tooth decreases in old animals. This causes the tusks of old males to taper at the base. However, the length of the pulp cavity decreases appreciably less than in females (Fig. 12).

The anterior erupted end of the tusk is worn into a chisel shape (Figs. 2, 9A), the cutting edge of which is reinforced by the enamel layer below the cementum (Fig. 8A) in this region.

Relationship between the ontogeny of the cheek teeth and the number of growth layer groups in the tusk

There was no instance of all six cheek teeth having been erupted and in wear at once in any one of the 107 skulls examined. Only one skull had all six cheek teeth present in each quadrant, molar 3 being unerupted. Any unerupted teeth always occurred at the posterior end of the tooth row. Teeth in which the roots were resorbed and which were wizened or broken always occurred at the anterior end. X-rays of the crania and mandibles did not reveal any unerupted teeth that were not visible from superficial examination. The enamel of all three premolars was usually present only in very young dugongs. Molars appeared to lose most of their enamel before or soon after eruption, as reported by Fernand (1953).

Usually the development state of the cheek teeth was similar in both jaws of any one skull. When differences existed, development in the upper jaw was found to be lagging behind that in the lower.

The development of each cheek tooth is considered separately below in relation to the number of GLGs in the tusk.

Premolar 2 (PM2): This tooth (Figs. 14A, B) is cylindrical and considerably smaller than the other teeth. It seems to be variably present, at least in the upper jaw, being absent both from the 1-m fetus and from another animal estimated to have been less than six months old. It was slightly worn in the youngest of the juvenile animals, and in wear in all other animals with less than two GLGs, except for two animals with one GLG, in which it was broken. The pulp cavity is open at birth but is occluded by the time the first GLG is deposited. The tooth is usually lost by the time the animal has laid down about five GLGs and all trace of the alveolus has disappeared by the time the animal has laid down eight or nine GLGs.

Premolar 3 (PM3): PM3 (Figs. 14A, B, C) was present and erupted in the 1-m fetus, erupted, but only slightly worn, in the youngest juvenile (1.3 m body length) and worn in all other animals in which it was present. As the tooth wears, it loses its original bilophodont shape and becomes peg-like. The pulp cavity is open at birth, starts to taper at the base by the time one GLG has been laid down and occludes by the time two GLGs have been laid down. After this, the tooth begins to erode. It is generally lost by the time six to ten GLGs have been laid down, all trace of the alveolus being lost by the time the animal has 14 GLGs in the tusk.

Premolar 4 (PM4): PM4 (Figs. 14A, B, C, D) was present and erupted in the fetus and in wear in all others except the youngest juvenile dugong, with resultant rapid loss of its originally bilophodont shape. The pulp cavity tapers at the base after about one GLG has been laid down and is generally closed by the time four GLGs have been laid down. The tooth is usually severely eroded (Fig. 14D) by the time the animal has eight GLGs in the tusk and may even be lost at this stage. In some animals it remains as a wizened stump for much longer (up to 16 GLGs). The alveolus is usually filled by the time the animal has 20 or 30 GLGs in the tusk.

Molar 1 (M1): M1 (Figs. 14A, B, C, D, E) is present but unerupted at birth. It erupts and comes into wear during the laying down of the second or third GLG. Its pulp cavity starts to taper at the base after about five GLGs have been deposited in the tusk and it closes at about 12 to 14 GLGs. M1 loses its bilophodont shape as it wears and becomes peg-like. It can persist for 45 or more GLGs but is usually lost by the time 25 GLGs have been deposited in the tusk.

Molar 2 (M2): The unerupted M2 was first seen in skulls from dugongs with one tusk GLG. It erupts and comes into wear during the time that the fourth GLG is laid down. The pulp cavity remains open throughout life although it is very reduced in old animals (Fig. 15A). M2 loses its initial bilophodont shape and wears down to a simple peg shape (Figs. 14C, D, E, F). It shows pronounced axial growth throughout life. In old animals M2 may be markedly curved to the front (Fig. 15A).

Molar 3 (M3): M3 (Figs. 14C, D, E, F) is first apparent as an unerupted tooth when the dugong has three to four tusk GLGs. It erupts and comes into wear at between seven and nine GLGs. Unlike the other teeth it retains its bilophodont shape, the crown having a characteristic keyhole outline (Figs. 14D, E, F). However, the occlusal surface wears flat as in the other teeth. The pulp cavity of M3 remains open throughout the life of the animal but becomes relatively smaller with age (Fig. 15B). M3 increases dramatically in size throughout life (Fig. 15B) as a result of prolonged axial and radial growth.

The ontogeny of each cheek tooth in relation to the number of GLGs in the tusk is summarized in Figure 16.

Relationship between relative growth criteria and the number of growth layer groups in the tusk

The age of young animals can be estimated from relative growth criteria, which become less reliable indicators of age as the animals get older.

The following age classes have been recognized by correlating changes in dentition characters, cranial sutures, body length, and cranial measurements with age, estimated as the number of dentinal GLGs in the tusk.

> ***0–1 year:*** PM2, PM3, PM4 present and come into wear soon after birth; [illegible] tusk. M1 unerupted; pulp cavities of all teeth [illegible] noid suture open; body length less than 1.5 [illegible] width less than 15 cm.

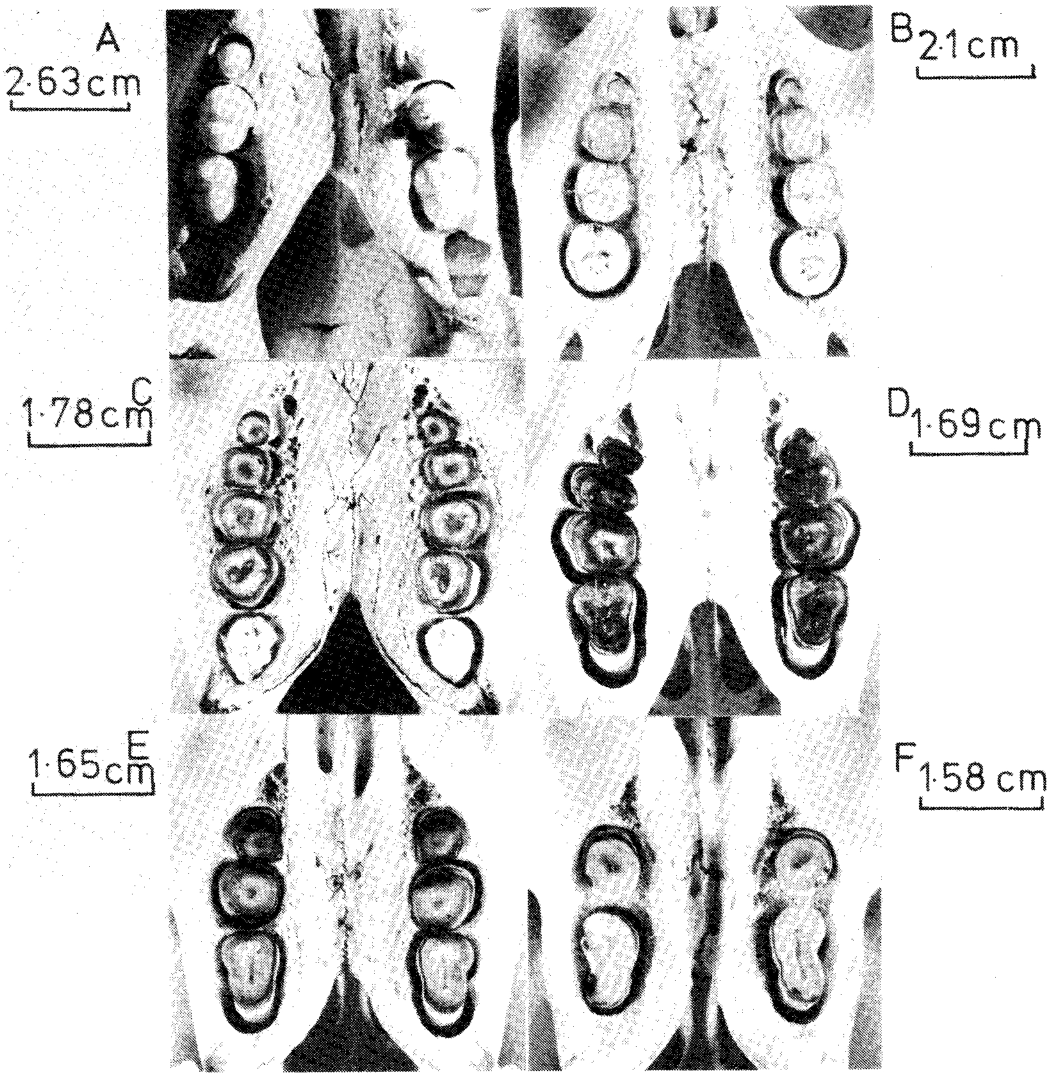


Fig. 14. The upper jaw cheek tooth dentition of dugongs of various ages. (A) presumed neonate; PM2, PM3, PM4 erupted, M1 unerupted. Wear can be seen on the crown surface of PM2. (B) 1.5 GLGs PM2, PM3, PM4, M1 erupted and in wear. (C) 6 GLGs; socket of PM2; PM3, PM4, M1, M2 in wear; M3 erupted and unworn. (D) 13 GLGs; socket of PM3; PM4 eroded; M1, M2, M3 in wear. (E) 16 GLGs (tusk worn); socket PM4, M1, M2, M3 in wear. (F) 29 GLGs (tusk worn); socket M1, M2, M3 in wear.

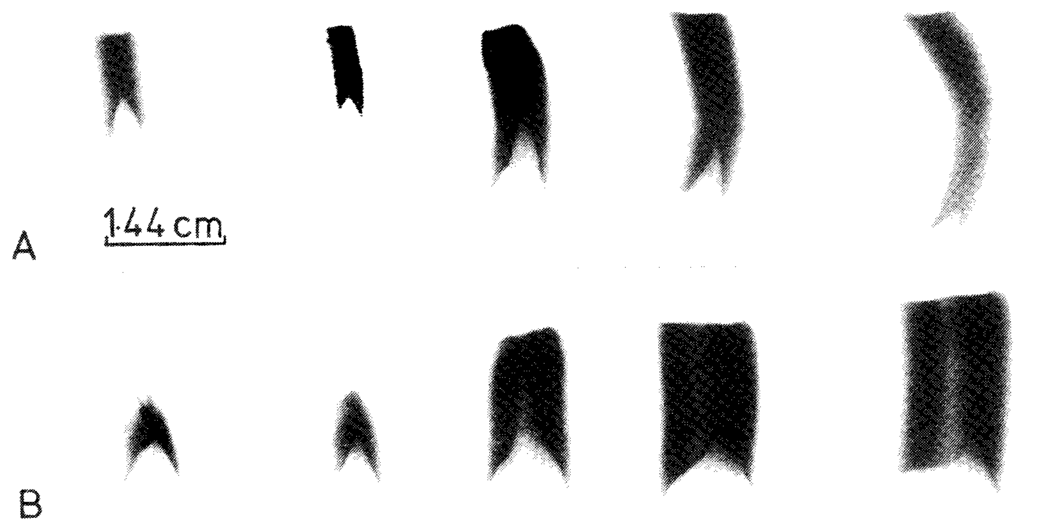


Fig. 15. X-rays showing the growth of M2 and M3 from the right hand side of the lower jaw. (A) M2 from dugongs with (left to right) 7 GLGs, 7-1/2 GLGs, 14 GLGs, 22 GLGs (tusk worn), 33 GLGs (tusk worn). (B) M3 from the same dugongs.

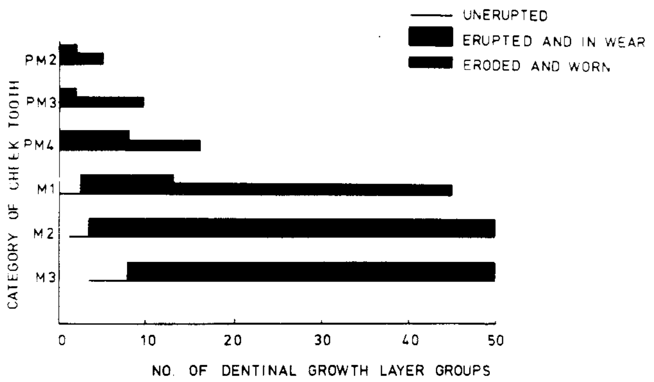


Fig. 16. Summary of the pattern of eruption and wear in dugong cheek teeth as related to age (number of dentinal GLGs in the tusks). The ages given for the persistence or eroded and worn teeth are the maximum observed. In many animals the teeth are lost before this.

1–2 years: M1 may be erupted; M2 unerupted; pulp cavity of PM2 closed; pulp cavities of PM3 and sometimes of PM4 tapered at base; basisphenoid suture closed; body length 1.5 to 1.75 m; zygomatic width 15 to 15.5 cm.

2–3 years: PM2 eroded, may be lost; M1 erupts and comes into wear; M2 unerupted; pulp cavity of deciduous incisor may be occluded; pulp cavity of PM3 occludes; zygomatic width 15.5 to 17.5 cm; body length 1.75 to 2 m.

3–4 years: PM2 usually lost; PM3 eroded; M2 erupts and comes into wear; M3 unerupted; pulp cavity of PM4 usually occluded.

4–6 years: PM3 eroded and may fall out; pulp cavity of PM4 occluded; pulp cavity of M1 tapered at base.

6–9 years: PM3 usually lost; PM4 eroded, may be lost; M3 erupts and comes into wear; condylar sutures may close.

After the eruption of M3, relative growth criteria become much less reliable. PM4 is variably lost between 8 and 16 years. Although the pulp cavity of M1 tapers and closes at 12 to 14 years, M1 may persist throughout life; however it is usually lost by 25 years. In males, the tusks erupt between 12 and 15 years and the deciduous incisors are usually lost around this stage. In females, the deciduous incisors may persist for 30 years. The condylar sutures close between 8 and 13 years, and the basioccipital usually, but not invariably, closes by 20 years.

Body length is a poor indicator of age except for young animals as the range of size at a given age is considerable (Fig. 11). The best non-linear regression that could be fitted between body length and age for animals in which M3 was erupted explained only 28% of the variance in body length with age.

Relationship between cheek-tooth parameters and the number of growth layer groups in the tusk

An attempt was made to describe the relationship between age and selected cheek-tooth parameters to see if they could be used as predictors of age.

Bivariate scatter diagrams were drawn on linear and logarithmic scales for all dugongs with molar 3 erupted and in wear to compare the number of GLGs used as an estimate of age (A) and the following cheek-tooth parameters: cheek-tooth index (T); crown area molar 2 (C_2); central cross-sectional area molar 2 (X_2); central cross-sectional area pulp cavity molar 2 (P_2); crown area molar 3 (C_3); central cross-sectional area molar 3 (X_3); central cross-sectional pulp cavity molar 3 (P_3).

Initially, data for males and for females and for the Townsville and Mornington Island populations were each analyzed separately, but as the analyses showed that there were no significant ($P < 0.05$) differences between the groups, the data were not separated for the subsequent analyses.

Scatter diagrams (Figs. 17A to D) are presented for the relationships between A and C_2, C_3, X_2, X_3 (Fig. 15) on linear scales. Each of the variables increases with age, particularly up to about 30 GLGs.

A similar plot of the relationship between T and A showed that T decreases with age (Fig. 18). Logarithmic transformations of both A and the independent variables were used to rectify the data and stabilize the residual variance in each case.

Least squares univariate linear regressions were computed for the logarithm of A and the logarithms of all the other variables. Data from animals with more than 30 GLGs were omitted from the analyses because the variance of the cheek-tooth parameters is so great after 30 GLGs have been reached. Two separate sets of analyses were performed. The first set included data from animals with unworn tusks only; the second set included data from all animals.

The resulting regression lines all explained a significant proportion of the variance in A ($P < 0.01$), except those for $\log_e P_2$, and $\log_e P_3$. Table 6 lists the estimates of the intercept a, the slope b and the coefficient of determination (r^2) for all significant regression lines. The estimate of the intercept a was significantly different from zero ($P < 0.001$) as was the estimated slope b ($P < 0.01$) (Table 6) of each of the significant regression lines.

A step-up multiple regression technique was used to compute the best relationship between the logarithm of age and the logarithms of the various cheek-tooth parameters.

The best relationship for the animals with unworn tusks for which estimates of the intercept and all the partial regression coefficients were significantly different from zero ($P < 0.05$) was:

$$\log_e A = 3.65 + 0.34 \log_e C_3 - 0.62 \log_e T + 0.38 \log_e X_3 - 0.32 \log_e C_2, \qquad R^2 = 0.83$$

$$\text{or } A = 38.47\, C_3^{0.34}\, T^{-0.62}\, X_3^{0.38}\, C_2^{-0.32}$$

and similarly for the animals with worn plus those with unworn tusks

$$\log_e A = 3.50 + 0.27 \log_e C_3 - 0.54 \log_e T + 0.57 \log_e X_3 - 0.34 \log_e X_2, \qquad R^2 = 0.89$$

$$\text{or } A = 33.12\, C_3^{0.27}\, T^{-0.54}\, X_3^{0.57}\, X_2^{-0.34}.$$

The same technique was used to compute the best significant relationship between $\log_e A$ and the $\log_e$ of those cheek-tooth parameters that could be obtained by x-raying a live animal, i.e. parameters excluding C_2 and C_3.

The best relationship for animals with unworn tusks was

$$\log_e A = 4.35 + 0.78 \log_e X_3 - 0.90 \log_e T - 0.44 \log_e X_2, \qquad R^2 = 0.82$$

$$\text{or } A = 77.48\, X_3^{0.78}\, T^{-0.90}\, X_2^{-0.44}$$

and for the animals with worn plus those with unworn tusks

$$\log_e A = 3.94 + 0.82 \log_e X_3 - [illegible] \log_e T - 0.43 \log_e X_2. \qquad R^2 = 0.87$$

$$\text{or } A = 51.42\, X_3^{0.82}\, T^{[illegible]}\, X_2^{-0.43}.$$

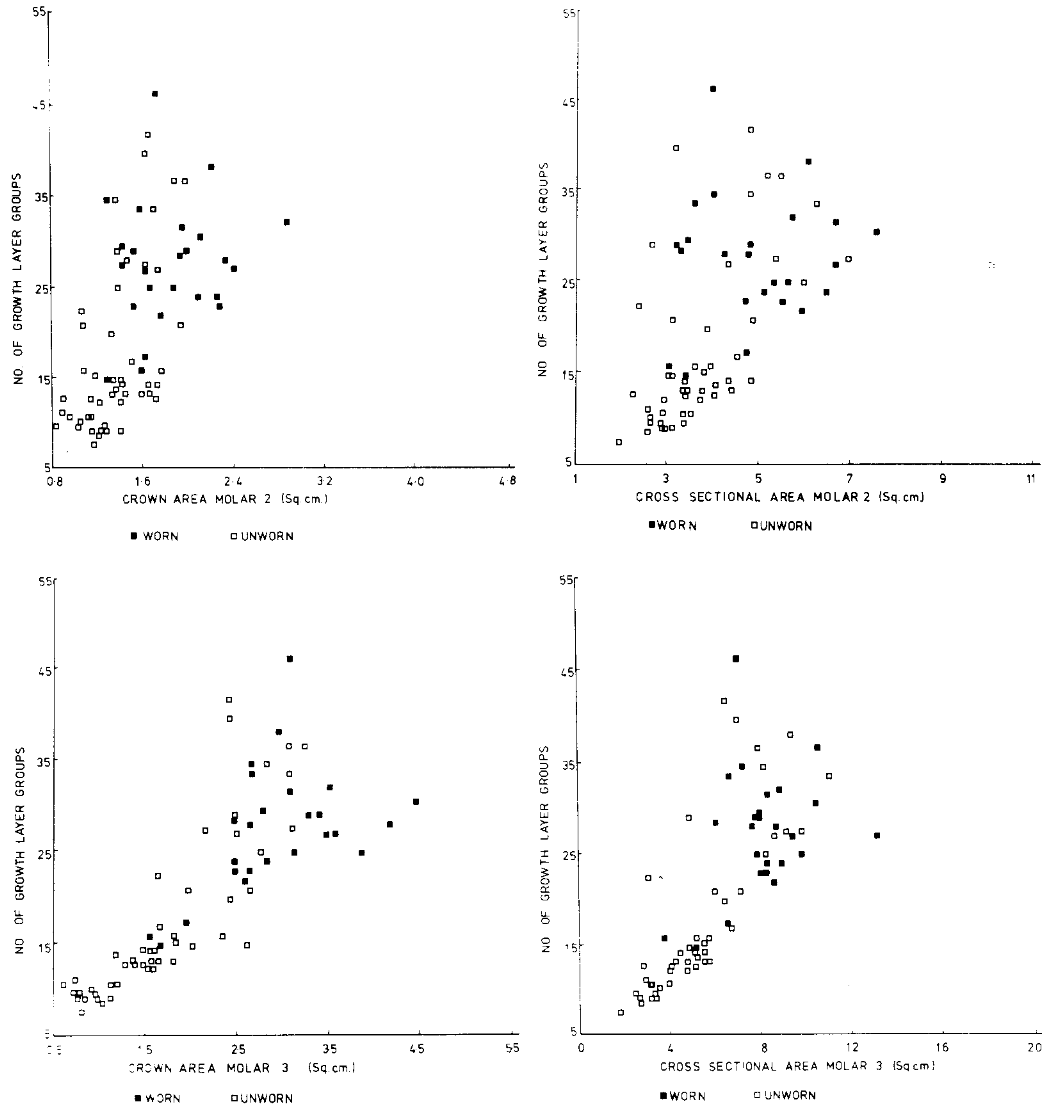


Fig. 17. Bivariate scatter plots showing the relationships between age (A) (the number of dentinal GLGs in the tusk) and the crown area (C) and central cross sectional area (X) of both M2 and M3 from the right hand lower jaw. Measurements are included from all animals in which M3 is erupted and in wear. Unworn and worn refer to the tusks.

F tests for all the above regression lines were significant ($P < 0.001$) as were all partial regression coefficients ($P < 0.05$).

Examination of other hard tissues

No GLGs were observed in the humerus or malleus. Layers were, however, clearly discernible in the tympanic bones and ribs. Twelve layers were counted in the tympanic bone of a dugong with 17 layers in its unworn tusk; 23 in a dugong with 33 layers in its erupted and unworn tusks. Eight layers were counted in the cross section of rib from a dugong with nine layers in its erupted and unworn tusk. The ribs from uncatalogued dugongs had six, seven, and at least 11 layers, respectively. The counting of layers in dugong ribs is difficult because of accessory layering and the orientation of the Haversian systems.

DISCUSSION

The sample

The collection of measurements, skulls and reproductive tracts from shark-netted dugongs from the Townsville area, acquired since 1969 by Heinsohn and his co-workers and used in this study, is the first substantial series of well-documented dugong material. In the absence of field studies, it is impossible to gauge how representative this sample of the Townsville dugong population is. When the distributions of sexes, sizes and estimated ages are considered (Figs. 3 and 4) there appear to be no major gaps. From the age determination viewpoint, it is fortunate that carcass material was collected in every month of the year. It would, however, have been desirable to have more individuals from certain age groups, particularly late fetal and neonatal animals.

Most of the material from Mornington Island dugongs was collected in July-August by somewhat selective hunting and no really young animals were obtained from the aboriginal hunters. This sample cannot, therefore, be considered representative of the Mornington Island dugong population.

Age determination using growth layer groups in the tusk

The tusks are ideal for age determination. They are present throughout life and do not erupt and wear except in post-pubertal males and occasionally in old females. Except in the case of some old females, the pulp cavity remains open and dentine appears to be deposited throughout life. The GLGs in the tusks of dugongs from the areas studied are

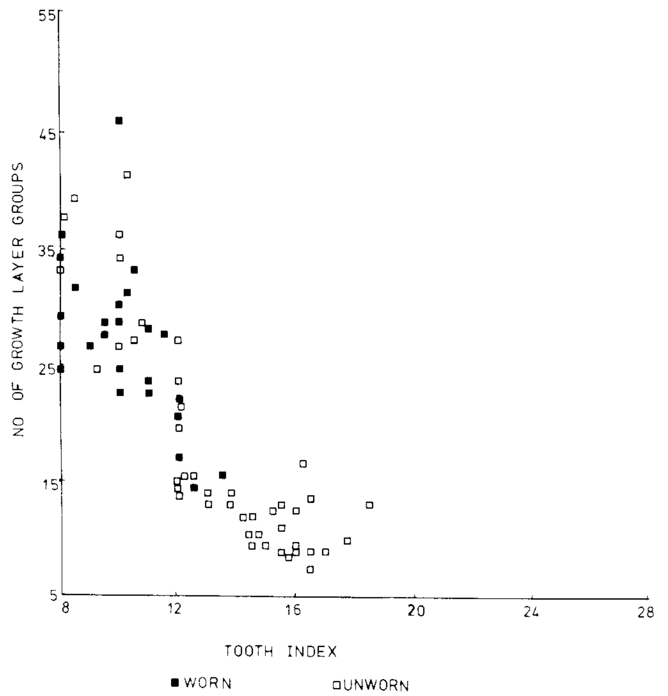


Fig. 18. Bivariate scatter plot of the relationship between age (A) (number of dentinal GLGs in the tusk) and the cheek tooth index (T) of all animals in which M3 is erupted and in wear. Unworn and worn refer to the tusks.

extremely clear and are usually easy to count, yielding highly repeatable results. Etched half teeth are ideal for this purpose (Fig. 9A), except in the case of young animals, where thin sections of both a deciduous incisor and a tusk should be used.

The description of the dentinal GLG in the tusk of the dugong is rather more complex in this paper than those of Kasuya and Nishiwaki (1978) and Mitchell (1978).

The arrangement of a broad zone of intermediate optical density followed by a narrow zone consisting of contiguous opaque and translucent layers is very similar to that described in the Ziphiidae (Report of the Ziphiid Group, published in this volume).

Intercalibration of different techniques used to demonstrate growth layer groups

In the masked specimens examined, the degree of optical opacity was mirrored by the intensity of haematoxylin staining (Fig. 8D). This has also been observed in dugongs by Kasuya and Nishiwaki (1978 and pers. comm. 1978). However, this relationship does not hold for all species examined (Kasuya, pers. comm. 1978). The neonatal line (Fig. 7A) seems to be always translucent and unstainable in all marine mammal species so far examined by Kasuya (pers. comm. 1978), including the dugong.

In the GLGs of the single specimen of dugong tusk studied in detail (Figs. 8A to D), the degree of optical density of the layers not only appeared to correspond to the degree of stainability, but also to the degree of radio-opacity (Fig. 8A) and etchability (Fig. 8C). This observation must be viewed with caution as the most and least optically opaque layers are both narrow and contiguous. It is similar to the observations by Hohn (published in this volume) of the properties of the components of the GLGs of *Tursiops truncatus* except that Hohn did not use stain. In contrast, in *Phocoena phocoena* the optically translucent zone was found to be more radio-opaque (Nielsen, 1972). However, Grue-Nielsen (pers. comm.) considers that this relationship may not remain constant with increasing age even within one specimen of this species.

Although the relationships between the layering demonstrated by various techniques are of interest, they are not very important to the practical problem of absolute age determination as the numbers of GLGs revealed by each method are clearly similar (Fig. 8).

Time scale represented by the layers

Zone B of the GLG was almost always formed between July and October (Table 2) and the thickness of Zone A increased from October to September (Table 3). Both these results suggest that one GLG is deposited per year.

Kasuya and Nishiwaki (1978) also reached this conclusion. Mitchell (1976 and 1978) suggested that the deposition rate was annual or biannual. The patterns of layer deposition observed by Mitchell (1978) in 11 dugongs from northern Australia and by Kasuya and Nishiwaki (1978) in two dug-

Table 6

Estimates of the intercept (a), slope (b), result of the significance test for b, and value of the coefficient of determination (r^2) for the significant univariate linear regression relationships between $\log_e$ age (A) and $\log_e$ of various cheek tooth parameters.
Separate analyses are presented for dugongs with unworn tusks only (U) and for those with unworn and worn tusks (U + W)

		a	b	Pb	r^2
Tooth index (T)	U	7.22	−1.76	≤ 0.001	0.65
	U + W	7.05	−1.68	≤ 0.001	0.75
Crown Area 2 (C_2)	U	2.41	0.76	≤ 0.01	0.16
	U + W	2.40	1.08	≤ 0.001	0.40
Central X-sectional Area 2 (X_2)	U	1.63	0.80	≤ 0.001	0.33
	U + W	1.68	0.83	≤ 0.001	0.42
Crown Area 3 (C_3)	U	2.35	0.71	≤ 0.001	0.73
	U + W	2.36	0.75	≤ 0.001	0.83
Central X-sectional Area 3 (X_3)	U	1.48	0.76	≤ 0.001	0.66
	U + W	1.43	0.82	≤ 0.001	0.76

ongs [illegible] dugong from Luzone (16°30′N) and tw[illegible] the Celebes (2°S), are the same as that [illegible] study. One dugong from northern Australia [illegible] Mitchell (1978) was exceptional in that it [illegible] completed Zone A in November. However, [illegible] death of this animal is questionable. It thus [illegible] assume a deposition rate of one GLG per [illegible]

Factors which may influence layer deposition

Attem[illegible] seasonality of layer deposition in other marine [illegible] tropics have so far been unsuccessful: [illegible] (1976), who studied offshore tropical populations [illegible] *Stenella attenuata*. Spinnage (1976) studied several [illegible] terrestrial mammals in tropical Africa. He observed [illegible] annual layer in the cementum of animals living in unimodal rainfall areas and two layers per year in animals living in areas of bimodal rainfall.

There is a unimodal drop in sea water temperature in the Townsville area which reaches a minimum in July (Fig. 19), the month in which the deposition of Zone B is thought to commence. Both Townsville and Mornington Island have one wet season per year, typically between December and April when Zone A is being deposited.

Not all the dugongs that died between July and October in any one year had commenced laying down Zone B. This suggests that layer deposition may not be cued by an external stimulus but may be controlled by an endogenous rhythm of growth starting from birth. The asynchrony may thus reflect the extended calving season thought to last from August to January.

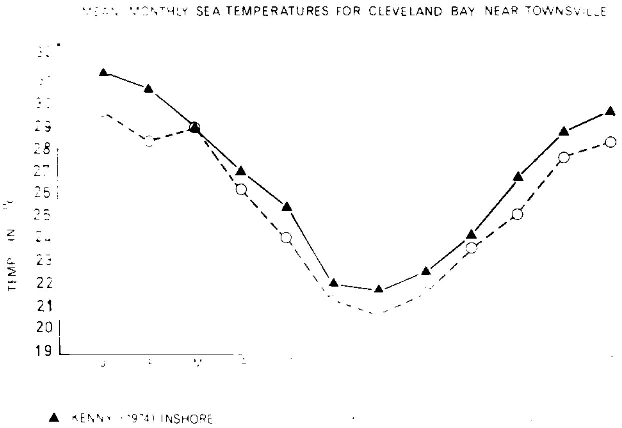


Fig. 19. Annual variation in sur[illegible] Bay near Townsville.

About 12 fine accessory [illegible] been observed in the deciduous incis[illegible] Kasuya and Nishiwaki (1978) observed 10 to 15 [illegible] per [illegible] in the dentine of the tusk. The[illegible] [illegible] lunar months or an endogen[illegible] observed in *Berardius bairdii*. [illegible] by the phases of the moon [illegible] [illegible]lators of dugong feeding [illegible] that the fine layers [illegible] may represent days and that the coarse layers may represent months. The seasonality of GLG (= coarse lay[illegible] suggested in this paper weakens his argument. [illegible] fine accessory layers can be shown to represent [illegible] they would be very useful in age determination [illegible] young animals.

Mitchell (1978) observed that tusks from the Torres Strait area (10°S) were difficult to read as they had more marked accessory layering than teeth from Townsville (19°S). This difference was not observed in the two specimens from Torres Strait included in this study, but the one specimen etched and examined from the oceanic island of Palau (7°30′N) had so many accessory layers that it was almost impossible to read using the standards and methods applied for the major part of this study. Kasuya and Nishiwaki (1978), however, successfully counted layers in the tusks of two dugongs from the Celebes (2°S). It seems likely that marked accessory layering may be a feature of the teeth of individual dugongs rather than of all dugongs living close to the equator.

Age determination in adult males

Although not critical to the conservation and management of the Australian dugong populations, the accurate estimation of the age of males with erupted and worn tusks is an unsolved problem as an unknown number of dentinal GLGs are lost from the anterior end of the tusk in these animals. Counts of GLGs ranged from 13 to 17 in newly-worn tusks and from 21.5 to 34.5 in tusks which had been substantially worn.

Cemental counts from near the tip of an unerupted tusk may be useful in dugong age determination (Kasuya and Nishiwaki, 1978), but the cementum from this region will, of course, be worn away as the tusk erupts and wears. Cementum counts are therefore unlikely to be useful for aging males with worn tusks (Fig. 7B).

Results obtained from counting GLGs in other hard tissues in the dugong do not appear particularly promising. No distinct layering was seen in sections of humerus or malleus. Mitchell (1978) found four layers in the periosteal zone of the ventral edge of the mandible of a dugong with 10.5 GLGs in the tusks. I counted 12 layers in the tympanic bone of one dugong which had 17 GLGs in the tusk; 23 GLGs in another which had 33 GLGs in the tusk which was worn. Eight layers were counted in the rib of a dugong which had nine layers in the tusk. Rib layering is, however, difficult to count. Kasuya has observed 11 to 14 layers in an uncatalogued dugong rib (pers. comm. 1979). Thus the number of layers seen in the mandible, rib and tympanic bone are lower than those in the tusk.

The number of layers in the ribs, tympanic bones and the tusks should be compared in a larger sample of dugongs from a range of ages. If the number of layers in the tympanic bones is found to be predictably lower than that in the tusk in dugongs, tympanic bone layer counts may also be useful in determining age in the manatee. Rib-layer counts may also prove to be useful in this regard (Domning and Myrick, 1980), although the layering was very indistinct in the one *Trichechus manatus* rib I have examined. Useful age estimates cannot be obtained from layer counts in manatee teeth as they are replaced at frequent intervals (Domning and Magor, 1977).

Age determination using cheek teeth

Attempts to obtain age estimates more accurate than those from erupted tusks, by using cheek teeth, have not been very successful. The equations that have been computed to describe the relationships between age and the cheek-tooth parameters of dugongs with unworn tusks only are not substantially different from those which include data from dugongs with worn tusks. Thus the use of cheek-tooth parameters for age determination would seem to be most valuable when it is not possible to count the dentinal GLGs in the tusk. The method should be applicable to captive dugongs, the teeth of which could be x-rayed.

The relative aging of young dugongs based on cheek-tooth succession that is reported in this paper, does not differ greatly from that of Mitchell (1973, 1978). Some of the differences may be attributable to the problems associated with counting the dentinal layers in the tusks of young animals, where, of course, accuracy is critical.

Growth of young dugongs

Kasuya and Nishiwaki (1978) and Mitchell (1978) appear to have had some uncertainties about the ages of the few young specimens that they studied. I share this uncertainty and regard the growth curves for young dugongs proposed from the Townsville data (Fig. 11B and Table 5) as tentative. They are comparable with the observed growth of a manatee born in captivity (Odell, in press).

The upper and lower limits of the 95% confidence intervals for the birth lengths calculated for the Townsville population ranged from 1.10 m to 1.45 m (excluding the curve based on unworn tusks only in which the confidence limits are very wide). Heinsohn (1972) recorded a near-term fetus that was 1.14 m long and a calf 1.09 m long, both from the Townsville population. Unfortunately, material from these animals was not available for this study. One female in the Townsville sample had the dentition of a neonate and a body length of 1.39 m, and the stump of the umbilical cord was still evident in a 1.23 m male examined recently. Thus the confidence intervals for the birth length estimated by the curves appear to be valid.

Attempts have been made to estimate dugong growth rates by observing captive animals. These estimates are probably less reliable than those obtained for manatees because of the considerable problems associated with feeding captive dugongs (personal observation) which eat sea-grasses, the collection of which is extremely labour-intensive.

A 1.4-m-long dugong was captured near Cairns, northern Australia, in March 1978 and maintained at the Cairns Oceanarium until it died in July 1978. It did not increase in body length during this period and it failed to regain the 10% loss in body weight that occurred in the first few weeks following its capture, despite its being bottle-fed milk and provided with more sea-grass than it could eat.

One of the two male dugongs, maintained in captivity at Mandapam Camp, India and fed sea-grass, increased in body length from 1.60 m to 2.05 m in nearly seven years and to 2.07 m after a further four years (Jones, 1967; 1976). This dugong may have been suckling at the time of capture and it is possible that the rapid and untimely weaning may have resulted in growth retardation.

In contrast, the body length of the other dugong (1.96 m long at capture) after 11 years in captivity was 2.26 m, which is comparable with that recorded for several dugongs from Mornington and Thursday Islands estimated to be more than 20 years old.

In view of the uncertainty of extrapolating the results of growth studies on captive dugongs to field situations, efforts should be made to monitor the growth of young marked dugongs in the wild over several years.

Life history parameters

Maximum longevity. The maximum number of GLGs counted in an unerupted female dugong tusk was 51. Mitchell (1978) scored four such tusks as over 50, the maximum being 57.5. Assuming that one GLG is laid down per year, I estimate the maximum longevity of female dugongs as 50 to 60 years. In view of the maximum male GLG counts, it seems likely that the figure for males is similar to that of females.

Puberty. On the same basis, puberty is estimated to occur at around nine years for Townsville males and possibly not until four or five years later at Mornington Island.

The fact that the tusks do not erupt until several years after mature sperm first appears in the testes and epididymides of Townsville dugongs, suggests that there may be a difference between puberty and sexual maturity in male dugongs parallel to that observed for sperm whales by Best (1969). The function of the erupted tusks has not been confirmed by direct observation, but parallel scars are often observed on the dorsal surface of both male and female dugongs. The distance between these scars corresponds with the distance between the tusks and it seems likely that the tusks are used to roll the female over for mating (Anderson and Birtles, 1978) and in fighting.

Information is insufficient to make a firm estimate of the age of sexual maturity in the female. Evidence so far accumulated in this study suggests that it is unlikely to be earlier than nine years. In addition an immature female with seven GLGs from the Celebes has been reported by Kasuya and Nishiwaki (1978). Mitchell (1978) reported that an immature female from north-eastern Australia had 9.5 GLGs in its tusk.

Heinsohn (1972), on the basis of examination of reproductive tracts of 14 dugongs drowned in Townsville shark nets from 1969 to 1971, suggested that sexual maturity in both males and females occurred at a body length of approximately 2.4 m. He constructed an hypothetical growth curve based on the body lengths and dates of death of 73 dugongs and concluded that a body length of 2.4 m could be reached at about two years of age. Spain and Heinsohn (1974) showed that a body length of 2.4 m corresponded to a condylo-premaxillary length of about 34 cm. Mitchell (1978) showed that this corresponded to a dentinal GLG count of nine to ten and concluded that sexual maturity occurred at an age of about ten years providing that one GLG is deposited annually.

The above estimates of sexual maturity are all based directly or indirectly on the results of the examination of reproductive tracts. There is other evidence that sexual maturity occurs at about ten GLGs. Kasuya and Nishiwaki (1978) reported that after the deposition of an average of ten GLGs, the layering in dugong tusks becomes irregular with conspicuous accessory layers. This change in layering is similar to that seen in the maxillary teeth of many sperm whales after sexual maturity (Ohsumi *et al.* 1963).

The changes in the pattern of tusk growth (Mitchell, 1978) which lead to sexual dimorphism in tooth form also begin to become obvious at about ten GLGs (Fig. 12). This could be expected to occur near puberty if the erupted tusk is a secondary sexual characteristic of males, as seems likely.

Using body length as an indicator of age is obviously a poor method except in very young animals. The range in body lengths for a particular age group is considerable (Fig. 11). A sexually mature, non-captive dugong has been recorded with a body length of 2.2 m and 33 dentinal GLGs. A female dugong 2.59 m long was considered to be immature on gross examination (Mitchell, 1978).

Possible sex and population differences in asymptotic length and/or age at sexual maturity

The sex difference in estimated asymptotic length observed within the Townsville population of dugongs (Table 5) has not been noted previously (Heinsohn, 1972) and warrants further investigation with a larger sample size. The possibility that dugongs may be growing longer and maturing faster near Townsville as compared to Mornington Island should also be examined. These differences, if they indeed occur, may be in response to differences in population density. The age of reproductive maturity is known to be density dependent in at least 15 other species of large mammals, eight of these being marine (Fowler *et al*, 1978).

Density-dependent differences in asymptotic body length have also been observed. For example, the asymptotic lengths of both male and female southern elephant seals (*Mirounga leonina*) from the exploited population at South Georgia were larger than those from the unexploited Macquarie Island population (Carrick *et al*, 1962). Gambell (1976) states, however, that there is little evidence for a change in the size of whales at physical maturity since the 1920s despite increased levels of exploitation.

Precise estimates of the sizes of the dugong populations in the Townsville and Mornington Island areas are not available. However, evidence from aerial surveys suggests that the population is now larger at Mornington Island than at Townsville. A maximum of 98 dugongs has been counted in 1977 in 25 aerial surveys of the Townsville area (Heinsohn, unpublished report). In contrast, a maximum of 374 dugongs has been counted per survey in the Wellesley Islands (of which Mornington Island is one) (Marsh *et al*, in press).

The mortality rate of Townsville dugongs has increased markedly in recent years with the introduction of shark-netting. More than 200 animals have been killed in shark nets since 1964, 82 in the first year of netting (Heinsohn, 1972; Heinsohn and Spain, 1974). At Mornington Island, the number of dugongs killed by aboriginal hunters appears to have remained fairly constant at 40 to 50 dugongs per year for many years (Anderson and Heinsohn, 1978; Marsh *et al*, in press). The habitats, as observed subjectively, seem similar in both areas and the dugongs are feeding on the same species of sea-grasses (Marsh, unpublished observation). It seems possible that the larger body size and shorter pre-reproductive period observed for the Townsville dugongs are density dependent. If so, reduction in the Townsville population caused by shark-netting could be expected to exacerbate such effects.

Tooth wear

Erupted tusks wear quickly on the outer surface (Fig. 9A). This wear presumably occurs when the dugong uses its snout to grub sea-grasses from the bottom. The cutting edge of the tusk is reinforced with enamel as in the order Rodentia (Peyer, 1968). This action forms a feeding trail as described by Anderson and Birtles (1978). However, erupted tusks cannot be essential equipment for feeding as they are absent in almost all females and in young males.

Tooth wear due to the abrasive action of food plants is a problem for most herbivorous mammals, including sirenians. Abrasive materials consumed by dugongs include a considerable amount of silt and sand (Spain and Heinsohn, 1973) and epiphytic siliceous diatoms which infest the leaves of most sea-grasses (Birch, 1975; Murray *et al*, 1977). The amount of abrasive materials in dugong food is reflected in the high ash content of dugong stomach contents, which has been measured at up to 19.9% (Spain and Heinsohn, 1973).

The dugong's cheek teeth have adapted to dietary wear quite differently from those of the manatee. As the manatee's cheek teeth wear, they are replaced horizontally throughout life by an apparently limitless supply of supernumerary molars (Domning and Magor, 1977). In contrast, no new teeth erupt in the dugong after seven to nine GLGs are deposited in the tusk, and tooth wear is countered principally by the continued axial growth of M2 and M3 and the radial growth of M3. The latter allows the total occlusal surface area of the cheek teeth to be maintained and increased even after the anterior cheek teeth are lost.

Implications for conservation

The results of this study have important implications for dugong conservation. They provide strong evidence that the dugong is a long-lived mammal which does not reach sexual maturity for at least nine years, probably later in some areas. This is comparable with a recent estimate of eight years as the age of sexual maturity in the manatee (Odell, 1977).

Definite observations on the gestation period of the dugong are lacking although it is believed to be about a year (Kingdon, 1971). In comparison, the gestation period of the Florida manatee is estimated to be 13 months. (Hartman, 1971). Single births are typical in the dugong, although twin fetuses have been reported (Troughton, 1928; Norris, 1960; Jarman, 1966; Thomas, 1966; Bertram and Bertram, 1968). The cow-calf relationship is believed to be well-developed and long-lasting (Banfield, 1968; MacMillan, 1955; Thomas, 1966) and calves estimated to be up to 1.5 years old have been caught in Townsville shark nets with their presumed mothers. The calving interval there is likely to be two or more years, a similar period to that estimated for the manatee by Hartman (1971).

Dugongs, and probably all sirenians, appear to be long-lived animals with a low reproductive rate, a long generation time and a large investment in each offspring. Incidental exploitation caused by net drownings has a deleterious effect on dugong populations in certain areas, as seen for the Townsville region (Heinsohn, 1977; Heinsohn and Spain, 1974; Heinsohn *et al*, 1977). The threats of direct exploitation such as hunting by natives may also be considerable in some areas. Past exploitation, mainly through hunting and netting by indigenous people, is thought to have reduced dugong populations to their present low levels over most of the species' range (Bertram and Bertram, 1973).

Dugongs are specialized, virtually obligate bottom-feeders (Domning, 1976) which feed principally on tropical and sub-tropical sea-grasses (Heinsohn and Birch, 1972; Lipkin, 1975; Heinsohn *et al*, 1977), although algae may be eaten when sea-grasses are scarce (Spain and Heinsohn, 1973). The inshore habitats, especially sea-grass communities, required by dugongs are particularly vulnerable to human disturbances (Heinsohn *et al*, 1977).

It is important that measures which are adequate to protect dugongs and their specialized habitats be implemented before dugong numbers are further substantially reduced.

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