

MINIREVIEW

PHYSIOLOGY OF THE DUGONG

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INTRODUCTION

As the only mammalian herbivore that is strictly marine, the dugong has many unusual but poorly understood features. Life in the oceans imposes a series of stresses on all marine mammals. Their vital organs and basic physiological functions are essentially similar to those of other mammals yet swimming and diving in an aquatic habitat call for a number of functional adaptations (Andersen, 1969). As a herbivore eating seagrasses, the dugong has in addition, to cope with a diet high in soluble salts without access to fresh water.

The scientific literature on the dugong has recently been summarized by Husar (1975). Her report demonstrates that the available information is widely scattered and is largely the result of incidental observation or is often anecdotal. Dugongs have rarely been maintained in captivity and there have been few physiological studies.

This review summarizes the information available on the dugong which is pertinent to future physiological research and includes some unpublished observations and results from current research.

IDENTITY, DISTRIBUTION AND STATUS

The dugong, *Dugong dugon* (Müller) is one of four surviving species of the order Sirenia, popularly known as sea cows. The other surviving Sirenians are the three species of manatees which are found along the tropical and sub-tropical Atlantic coasts and in adjacent river systems (Bertram & Bertram, 1973). The distribution of the dugong is summarized in Fig. 1.

Despite the few sirenian species existing today, the order has an extensive fossil record (Romer, 1966; Domning, 1976; Savage, 1976). Sirenians are placed in a superorder of herbivorous subungulates, the Paenungulata, which includes the modern Proboscoidea (elephants) and Hyracoidea (hyraxes) together with several extinct mammalian orders (Simpson, 1945).

Sirenians are shallow-water, near-shore animals (Heinsohn *et al.*, 1977) as a result of their dependence on marine plants growing in the littoral and sub-littoral zones. With the exception

of the subarctic Steller's seacow [*Hydrodamalis gigas* (Zimmerman)], which was hunted to extinction in the eighteenth century (Bertram & Bertram, 1973) all species of sirenians, both fossil and living, have been confined to tropical and sub-tropical waters.

Absolute population sizes or densities are not known for any dugong population. Bertram & Bertram (1973) give a qualitative account of the present world-wide status of the dugong. They consider the species to be rare over most of its range and to be approaching extinction in some regions. Considerable populations are still present in Australian waters (Heinsohn, 1972; Bertram & Bertram, 1973; Ligon, 1976; Heinsohn *et al.*, 1976; Heinsohn *et al.*, in press).

MORPHOLOGY AND ANATOMY

External morphology

The body of the dugong (Fig. 2) is markedly robust anteriorly and constricts progressively rearward from the umbilicus to the point where it joins the base of the tail fluke. Dorsally, the body is grey to bronze in colour but becomes somewhat lighter ventrally. Many older animals have large areas of unpigmented skin and are extensively scarred, particularly dorsally.

The mouth opens ventrally on the head and below the broad flat muzzle. The eyes are small and not prominent. There are no external pinnae and the external auditory meatus is not prominent. The external nares lie close together and are situated antero-dorsally. They are closed during diving by anteriorly hinged valves.

The flippers are short [approx. 15% of total adult body length (Spain & Heinsohn, 1975)], rounded at the ends and, unlike those of the West Indian and West African manatees, lack nails (Harrison & King, 1965). They appear to be used little during rapid swimming and are usually held close to the sides of the body. Callouses are present on the anterior ventral part of the flipper on all specimens observed. Their cause is unknown but they may well be associated with feeding. The large, triangular, horizontally-expanded tail fluke is the principal organ of locomotion and works vertically with slow, powerful beats.

Hairs are lightly scattered over the body surface but become denser and more robust on the muzzle and around the mouth (Bryden *et al.*, in press).

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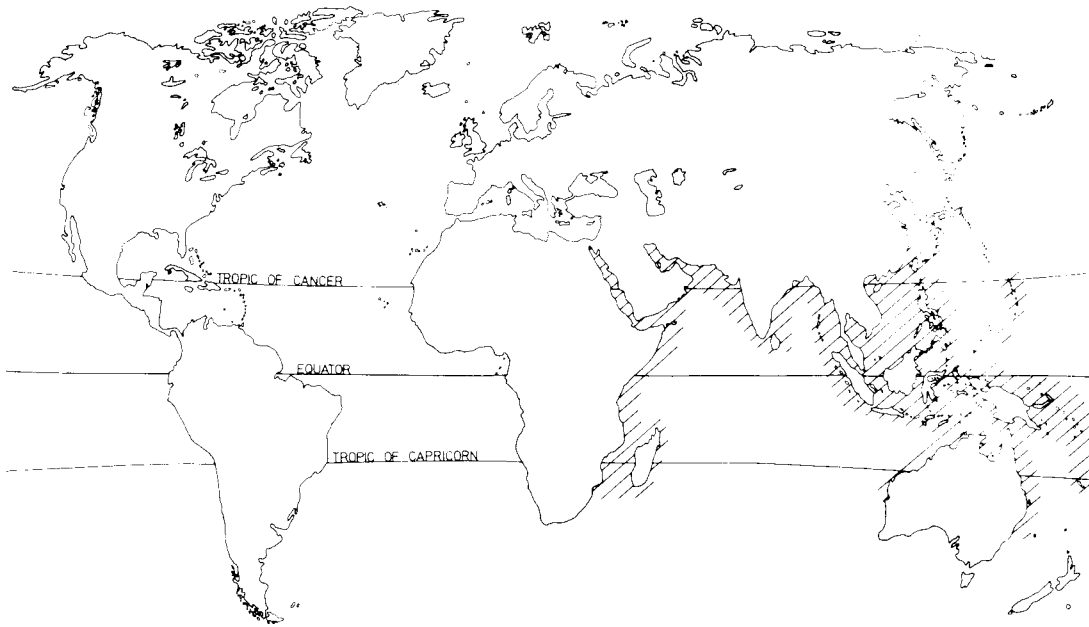


Fig. 1. Present day distribution of *Dugong dugon*.

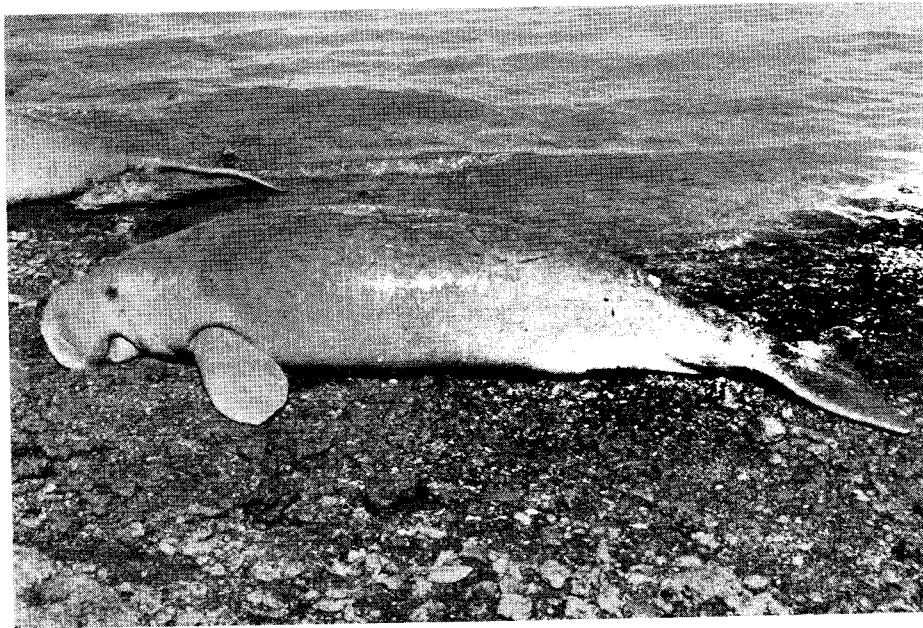


Fig. 2. Dorso-lateral aspect of a mature male dugong soon after it had been harpooned and killed for food by aboriginals at Mornington Island, Queensland.

Detailed descriptions of the external morphology are given in Dexler & Freund (1906), Petit (1955) and Kingdon (1971).

Skeleton

The skeleton of the dugong has been extensively described and figured by Kaiser (1974). Aspects of the nature and development of the skull have been recently studied by Robineau (1969), James (1974), Spain & Heinsohn (1974) and Spain *et al.* (1976).

Aspects of the size allometry of the dugong skull are described by Spain & Heinsohn (1974). This is dominated by the positively allometric

development of the premaxillae and other anterior parts of the skull. Also, the premaxillae of the newborn dugong and the opposing parts of the mandibles are directed relatively more anteriorly in the juvenile than in the later life stages. This reorientation is undoubtedly associated with suckling behaviour.

Sexual dimorphism is evident in several features of the adult dugong skull (Spain *et al.*, 1976).

Dentition

There still remains a number of unanswered questions relating to the development of the

dentition in the dugong. Contributions are to be made in a later paper (Spain & Heinsohn, 1976).

Two pairs of upper incisors are present in the juvenile dugong. The first pair is resorbed during the first year of life. Concurrently, the second pair of incisors develops from the tusks which are present from birth (Fig. 3) but which are not used for defence. The second incisors are apparently of the same size as the tusks and become sharp at the distal margins as a result of use in defence and defence.

A horny pad covers a portion of the lower lip and is located on the premaxilla. Normal sockets occur under these sockets mandibles.

It is difficult to determine the size and molar teeth.

Fig. 3
tusks
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dentition in the dugong. Two of the most recent contributions are those of Mitchell (1973, 1976). Other useful earlier studies include those of Heuvelmans (1941) and Fernand (1953).

Two pairs of upper incisors are present in the juvenile dugong. The first is small, does not erupt and is resorbed during the course of development. Concurrently, the sockets are lost in the expansion of those of the second upper incisors. These latter form the tusks which generally erupt in the mature male (Fig. 3) but only infrequently in the female. The second incisor teeth have persistent pulps and, apparently, continue to grow throughout the life of the animal. In the adult male, the erupted tusks become sharp through wear on their outer distal margins and may become weapons of offence and defence.

A horny pad covers the downturned symphyseal portion of the lower jaw and a corresponding pad is located on the ventral interior surface of the premaxilla. Normally, four pairs of rudimentary sockets occur under the lower horny pad. Some of these sockets may occasionally contain vestigial incisors.

It is difficult to distinguish between premolar and molar teeth in the dugong since *in situ*

replacement of the milk dentition does not occur. During the life of the dugong there is a total of six pairs of cheek teeth in both jaws. The anterior teeth progressively fall out or are resorbed and the sockets become occluded with bone. Further teeth are added posteriorly during growth and the whole process continues until only two pairs of teeth remain in each jaw in the older animals. These appear to have persistent pulps and may continue to grow throughout life.

Size and growth

At birth, dugongs are slightly more than 1 m in length. The minimum sizes known are recorded from India, where Jones (1967) records a female of 1.06 m body length weighing 20 kg. Gohar (1957) records a calf of 1.1 m from the Red Sea, and Heinsohn (1972) a near-term foetus of 1.14 m and a calf 1.09 m long from north-eastern Australia.

The maximum size recorded for a dugong is 1016 kg for a specimen of 4.06 m body length (Mani, 1960). This appears improbable because of its extreme size (Spain & Heinsohn, 1975). Petit (1955) records maximum lengths of 3.05 and 3.15 m for females and males, respectively, and it is not



Fig. 3. The head of a mature male dugong caught in a shark net near Townsville, Queensland. The tusks usually protrude only in adult males and can be easily seen in this specimen. The dugong is remarkable for the enormous development of its upper lip area which helps it grab sea grasses from the bottom during a dive.

expected that substantially larger specimens would be found.

Size allometry of the dugong has been studied by Spain & Heinsohn (1975) based on a sample of 53 specimens taken near Townsville, northern Australia. Most of the 37 characters analysed showed near-isometric growth, although, as might be expected, negatively allometric growth trends were evident in certain anterior parts of the body.

An empirical weight for length curve has been published by Spain & Heinsohn (1975) based on 44 animals. There are no apparent differences between the sexes. Birth weight is in the range of 20–30 kg and the estimated weight at an approximately pubertal length of 2.4 m is 248 kg. A large animal of 3 m is estimated to weigh nearly 420 kg.

No reliable indicator of absolute age is known although presumed growth rings are present in the dentine and are readily seen in sectioned second incisors (Mitchell, 1976). The interpretation of these marks is considered further below.

The determination of the growth rate of the dugong is impossible without knowledge of absolute age. Dugongs have not been bred in captivity and most of the animals held in captivity to date appear to have died after relatively short periods, apparently, of causes related to the circumstances of their capture. One notable exception to this is recorded by Jones (1967, 1976) who described two male dugongs kept in captivity for 11 yr. One grew from 1.6 to 2.05 m and the other 1.96 to 2.13 m during the first 6.5 yr of their captivity. Heinsohn (1972) constructed a hypothetical growth curve which described the increase in body length with age of dugongs in their natural environment. His estimate that dugongs grow from 1.1 m to 2.4 m in 2 yr conflicts with Jones's observations.

Three external manifestations of sexual dimorphism are known. The first is the relative distance between the centres of the anal and genital orifices. These orifices are almost contiguous in the female, while in the male they move relatively further apart during the course of development (Spain & Heinsohn, 1975). The presence of erupted tusks in an animal of mature size is usually taken to indicate a male animal. This may not be infallible since at least one fully mature female has been observed with erupted tusks (Spain *et al.*, 1976). Mature females have well-developed axillary mammae. These are also noticeable in mature male animals but are much less developed.

FEEDING, DIGESTION AND EXCRETION

Dugongs feed almost exclusively on marine phanerogams of the families Potamogetonaceae and Hydrocharitaceae (Prater, 1928; Gohar, 1957; Kingdon, 1971; Heinsohn & Birch, 1972; Lipkin, 1975). Marine algae are also occasionally eaten (Annandale, 1905; Hirasaka, 1932; Mani, 1960; Spain & Heinsohn, 1973) although this probably occurs when seagrasses are scarce (Spain & Heinsohn, 1973; Heinsohn & Spain, 1974). Invertebrate animals are sometimes taken (Hirasaka, 1932; Pfeffer, 1963; Spain & Heinsohn, 1973;

Wake, 1975), although they are probably eaten incidentally with seagrasses.

The strong ($\approx 70^\circ$) deflection of the rostrum and mandibular symphysis from the palatal plane causes the mouth of the dugong to open almost ventrally. This virtually makes the dugong an obligate bottom feeder (Domning, 1976) and it is thought to subsist largely on seagrasses less than 20 cm high (Heinsohn & Birch, 1972).

Conflicting statements have been made about the nutritive value of seagrasses and further studies are required before they can be compared in detail with terrestrial plants as food for herbivores (Birch, 1975; Wake, 1975; Murray *et al.*, 1977). Dugongs prefer soft and delicate seagrasses with relatively non-fibrous leaves and stems to dense old stands (Heinsohn & Birch, 1972; Lipkin, 1975), even of the same species (Wake, 1975).

The digestive physiology of the dugong is of considerable interest because of its specialized and, for a mammal, unique diet. The digestive system of the dugong is well adapted to digest sea-grasses and high apparent digestibilities have been obtained for all fractions studied (Murray *et al.*, 1977).

Marsh *et al.* (1977) have shown that the dugong has a simple stomach remarkable only in that all the chief cells and most of the parietal cells occur in a discrete pouch which the digesta do not enter and which communicates with the main sac by a single aperture.

Two diverticula enter the duodenum just posterior to the pylorus. The diverticula enlarge the surface area of the proximal duodenum and may allow a large volume of digesta to pass from the stomach to the proximal duodenum at one time (Marsh *et al.*, 1977). An analysis of the gas taken from the diverticula indicates that it contains a significant quantity of carbon dioxide, essentially no hydrogen and no methane, suggesting that the diverticula may secrete bicarbonate to neutralize the digesta (Hungate, 1977, personal communication).

A small caecum occurs at the junction of the small and large intestines. This caecum and the large intestine, the contents of which weigh twice that of the stomach, have been shown to be the principal areas of disappearance of the fibre fraction of the diet. High concentrations of VFA occur in these areas (Murray *et al.*, 1977). Gas samples from the caecum and large intestine contain measurable quantities of hydrogen but no methane (Hungate, 1977, personal communication).

In an adult dugong the large intestine is up to 25 m long, about twice as long as the small intestine. The large intestine grows with positive allometry in relation to body length. In contrast, the small intestine and caecum grow isometrically with regard to the same standard (Spain & Heinsohn, 1975).

Thus the dugong, together with the other modern Paenungulata, belongs to that group of non-ruminant herbivores which have a greatly enlarged hind-gut with a rich microflora. Blood levels of urea and inorganic P are within the normal ranges for these parameters in non-ruminant terrestrial herbivores (Murray *et al.*,

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1977). As expected, the concentrations of cholesterol, bile acids (cholic, deoxycholic and chenodeoxycholic) and lecithin in the gall bladder bile are low. However, the bile acid to cholesterol molar concentration ratios are adequate to hold the cholesterol present in solution (Caldwell *et al.*, 1969). The gross anatomy of the liver, gall bladder and pancreas have been described by Osman-Hill (1945). The histological structure of the gall bladder and liver is similar to that of other mammals (Caldwell *et al.*, 1969).

The component fatty acids of the triglycerides and of the 2-monoglycerides derived from them, of abdominal adipose tissue from a mature female dugong are presented in Table 1. Dugong fat is not remarkable either in overall composition or in positional distribution of the fatty acids (Garton, 1975, personal communication). Despite the similarity with respect to cellulose fermentation, dugongs differ in this respect from the other modern Paenungulata whose triglycerides display an unusual intramolecular disposition (Duncan & Garton, 1968; Garton & Duncan, 1971). The fatty acid composition of dugong oil (Tsuyuki & Itoh, 1967) is very similar to that of the adipose tissue.

Unrinsed seagrasses, as consumed by the dugong, contain about 15 times more chloride and 30 times more sodium than most terrestrial pasture plants (Birch, 1975). The salt metabolism of the dugong is thus potentially very interesting and should be investigated. Anatomical studies suggest that dugong kidneys are unique in several respects. They have a characteristic elongated external form quite unlike the lobulated kidneys of cetaceans. Dugong kidneys are dipelvic with a characteristic bilaminar central transverse plate. The extensive renal sinus is curious in outline and boundaries (Batrawi, 1953, 1957). Batrawi considers that the dugong kidney combines features similar to those found partly in the camel and partly in the horse.

REPRODUCTION

In the absence of detailed physiological and behavioural studies, knowledge of dugong reproduction is largely based on anatomical studies or on incidental information. The testes are abdominal and lie caudal to the kidneys. Os penis, bulbourethral glands and the prostatic utricle are absent (Harrison, 1969). The penis does not show externally unless erected when it is extruded

through the preputial orifice between the anus and umbilicus.

The ovaries are enclosed in a peritoneal pouch; ovarian histology has not been studied. The vagina is long and possesses a raised shield-like region of keratinized material on its vault through the middle of which projects the cervix uteri, also covered by keratinized material (Harrison, 1969). The anatomy of the dugong reproductive system has been described by Home (1820), Owen (1837), Riha (1911), Petit (1927), Osman-Hill (1945), Gohar (1957) and Harrison (1969).

Information on sex ratio is restricted to catch records, the results of which are conflicting. In some cases (Thomas, 1966; Heinsohn, 1972; Bertram & Bertram, 1973; Heinsohn & Spain, 1974), more female dugongs were caught than males; in others (Norris, 1960; Gibuma, 1976, personal communication), the sexes were equally represented. Catch records may be an unreliable indicator of sex ratio particularly when the whole size range is considered. Heinsohn (1972) on the basis of 11 dugongs less than 1.83 m in length drowned in Townsville shark nets suggested a secondary sex ratio of unity.

Heinsohn (1972) reported that both male and female dugongs from Townsville, Queensland reach reproductive maturity at about 2.4 m. Bertram & Bertram (1973) reported a pregnant female from Numbulwar Mission, Northern Territory 2.3 m in length and a mature male of 2.2 m has been measured at Thursday Island (unpublished data).

The age of reproductive maturity has not been established due to the absence of known age material. Heinsohn (1972) used the body lengths of 68 sexed dugongs caught throughout the year to distinguish four age classes. He estimated sexual maturity at approximately 2 yr. Scheffer (1970) using growth layers in the dentine of a single worn and erupted incisor suggested that the adult male from which it came was about 3 yr old. Mitchell (1976) counted dentinal growth layers in unerupted incisors and suggested that sexual maturity is reached at a layer number of about ten, or at about 5 or 10 yr depending on whether the layers are annual or biannual. Eight is the lowest number of incisor growth lines recorded in a male dugong with sperm in the testes and epididamies and seven the lowest number in a cycling female (Marsh, unpublished data).

Table 1. Fatty acid composition of dugong fat

	14:0*	14:1	16:0	16:1	18:0	18:1	18:2	18:3
Whole triglycerides	8.5	0.5	32.7	3.0	3.9	47.2	1.1	1.6
2-monoglycerides	19.9	1.2	11.5	8.8	1.6	53.8	0.8	1.6
% in 2-position†	78	80	12	97	14	38	24	33

* Shorthand nomenclature of Dole *et al.* (1959).

Values are given as molecular percentages of the total acids of the triglycerides and of the monoglycerides.

† Derived from the expression

$$\frac{(\text{mole \% fatty acid in 2-monoglycerides}) \times 100}{(\text{mole \% same fatty acid in triglycerides}) \times 3}$$

The analysis was performed by Mr. W. R. H. Duncan, Rowett Research Institute, Aberdeen, Scotland.

Not all the males in a population with mature dentition are reproductively active, i.e. have sperm in their testes and/or epididymies, at once. H. Marsh (unpublished) found that only nine of 27 such males from Townsville and Mornington Island, Queensland were reproductively active. Reproductively active animals have been taken in May, July, August and October but only four of the eight mature males killed for food by aborigines at Mornington Island in July–August 1976 were reproductively active and in July–August 1977 only one of the five mature males caught was reproductively active.

There are descriptions of the courtship and/or mating behaviour of dugongs from several parts of Queensland (Roughsey, 1971; Heinsohn *et al.*, in press; Anderson & Birtles, 1978). A detailed description is lacking but it does seem likely that mating involves the rotation of the female until her ventral surface is uppermost although in the manatee it is the male which assumes this position while mating (Hartman, 1971).

The mating season at Mornington Island is considered to last from May to August (Roughsey, 1971). The observations of Heinsohn *et al.* were made in October and those of Anderson and Birtles in May, June and July. African reports of dugong mating behaviour (Klunzinger quoted by Krauss, 1870, in Anderson & de Winton, 1902; Jarman, 1966; Travis, 1967; Kingdon, 1971) are in general agreement with the Australian observations. Jones (1967) described the apparent attempted mating of a pair of captive dugongs, both of which were subsequently found to be male (Jones, 1976). Firm data on the gestation period are lacking although it is believed to be about a year (Klunzinger quoted by Krauss, 1870, in Anderson & de Winton, 1902; Kingdon, 1971). In comparison the gestation period of the Florida manatee is over 1 yr (Hartman, 1971).

Turner (1889) studied the placentation of the dugong and concluded that the placenta is at first diffuse, becoming zonary later and that the relationship between foetal and maternal bloodstreams is epitheliochorial. Harrison (1969) believed that Turner's material was poorly fixed and suggested the re-examination of fresh specimens, especially in view of Wislocki's (1935) findings on the manatee placenta which is typically zonary with a hemochorial relationship between the maternal and foetal bloodstreams.

Opinion as to calving time is varied (Klunzinger quoted by Krauss, 1870, in Anderson & de Winton, 1902; Wyatt-Gill, 1876; Macmillan, 1955; Norris, 1960; Jarman, 1966; Heinsohn, 1972; Bertram & Bertram, 1973). It is likely that calving occurs over several months at least. Dugongs with near-term foetuses have been taken near Townsville in both July and December (Heinsohn, 1972, and unpublished) and dugongs with presumably new-born young have been recorded in September and October (Heinsohn, 1972; Heinsohn *et al.*, in press).

Macmillan (1955) described the birth of a dugong in north-western Australia out of the water on an exposed sand bank at low tide; the sandbank was awash again within 40 min. There have been

consistent reports of calving in shallow sheltered areas (Jarman, 1966; Kingdon, 1971; Heinsohn *et al.*, in press). A single young is usually born although twin foetuses have been reported (Troughton, 1928; Norris, 1960; Jarman, 1966; Thomas, 1966; Bertram & Bertram, 1968).

The cow-calf relationship is believed to be well-developed and long-lasting (Banfield, 1968; Macmillan, 1955; Thomas, 1966). Heinsohn (1972) has reported calves up to 1.83 m long caught in shark nets with their presumed mothers. There are several reports of calves riding on their mother's back holding on with their flippers (Prater, 1929; Jarman, 1966; Heinsohn *et al.*, in press) or clasped by the mother's flipper to her side (Prater, 1929; Macmillan, 1955; Jarman, 1966; Banfield, 1968).

RESPIRATION

(a) *Physiology and biochemistry*

The dugong is an unusual, although not unique, diving mammal since its natural habitat seems restricted to shallow tropical and subtropical waters. Both dugongs and manatees are sensitive to low temperatures (Campbell & Powell, 1976; Domning, 1976). Thus, dugongs normally experience higher ambient temperatures than many other diving mammals, especially since their diving activities seem to be restricted to the shallow areas close inshore where sea grasses are found. This consistently warm environment would reduce the problem of heat loss commonly experienced by diving mammals and would permit a corresponding metabolic adjustment. Within a mammalian species, the general response to chronically elevated environmental temperatures is a reduction of thyroid activity with a consequent lowering of overall metabolic rate accompanied by a diminished oxygen requirement and a lower rate of heat production within the animal. Such a reduction of overall metabolism, if it in fact occurs in the dugong, would account for the general observation of sluggishness recorded in the literature. Simultaneously, a reduction of metabolic rate would be an advantage to the animal since it would permit the extension of diving time by reducing the oxygen requirement. Clearly, such a metabolic adaptation would only be suitable to a species which leads a rather sedentary existence, and the feeding habits of the dugong would appear to be in keeping with this requirement.

There have been few observations of diving times. Kenny (1967) recorded the submergence times of a captive animal in a swimming pool and found it varied up to a maximum of 506 sec. Anderson & Birtles (1978) have recorded the times of 370 dives during field observations off the coast of central Queensland. The mean time for each dive was 73.3 sec with a maximum dive observed at 400 sec. Observations made by the present authors during hunting show that the animals when chased in shallow water by a small powered dinghy, could swim submerged between breaths for slightly less than 3 min while travelling at an estimated speed of 12 knots, after which they were obliged to surface frequently.

By comparison with other diving mammals, these are rather long and this together with the high metabolic rate suggests a pressing need for a respiratory characteristically adapted satisfactorily for the purpose.

Elsner (1968) has analysed the composition of a sample of dugong blood having a rather low haematocrit, considered in keeping with the sedentary nature of habit. Macmillan (1955) purified a sample of dugong blood by dialysis and column chromatography and measured the absorption coefficients of the oxygen and carbon dioxide sorption spectra respectively. The P_{50} maxima and minima were 10.5 and 15.5 mm Hg in individual peak haematocrits. There is an asymmetry between the absorption spectra at 572 nm of the oxygen and carbon dioxide distinctly higher than the corresponding deoxy spectrum than the corresponding carbon dioxide globin. The absence of a peak at 572 nm and the homogeneity of the absorption topography argue against the possibility of this colleague's (see also Elmslie & other mammals consisting of haemoglobin or a mixture of haemoglobin and myoglobin. However, the argument cannot be sustained because of the difficulty in obtaining a representative dugong blood sample (freshly obtained dugong blood in the present observation). Because of this, Elmslie *et al.* (1978) were unable to measure the oxygen equilibrium curve of samples of dugong blood. The pH and temperature were marginally lower than those recorded under similar conditions. The observation of a sigmoidal curve pointed out that a simple equilibrium may account for the conditions of acute hypoxia. The steepness of the curve (i.e. the straight line between the venous points) which is the primary governing oxygen requirement.

(b) *Anatomy of the respiratory tract*

Osman-Hill (1968) has described the respiratory tract of the dugong as posteriorly almost straight and separated from the body wall by an obliquely sloped pleural cavity. The bronchial tree is considered unusual in that the bronchus runs almost straight with only a few secondary units (vesicles) arising from the main

By comparison with other marine diving mammals, these are rather modest diving achievements, and this together with the apparently low metabolic rate suggests that there may be no very pressing need for profound modifications of the respiratory characteristics in order to account satisfactorily for the animal's underwater performance.

Elsner (1968) has measured the oxygen capacity of a sample of dugong blood and recorded it as having a rather low oxygen capacity, which he considered in keeping with the observed sluggishness of habit. McCabe *et al.* (1978) have purified a sample of dugong haemoglobin by dialysis and column chromatography, and have measured the absorption spectra and extinction coefficients of the oxy and deoxy forms. The absorption spectra resemble spectra of haemoglobin from terrestrial mammals in the disposition of maxima and minima but there are some differences in individual peak height ratios; most noticeable is an asymmetry between the two peaks at 537 and 572 nm of the oxy form, that at 537 nm being distinctly higher than the one at 572 nm. In the deoxy spectrum the peak at 553 nm is much higher than the corresponding peak for human haemoglobin. The absence of any other coloured band and the homogeneity of the band during chromatography argue against the suggestion of Boice and his colleagues (see Lenfant, 1969) that diving mammals consistently possess a unique type of haemoglobin or a mixture of this and "ordinary" haemoglobin. However, with the results available the argument cannot be settled. A part of the difficulty in obtaining unequivocal results with dugong blood appears to lie in the tendency for freshly obtained dugong blood to clot very rapidly, even in the presence of heparin (Marsh, personal observation). Because of this difficulty, McCabe *et al.* (1978) were unable to obtain whole blood-oxygen equilibria, although they did measure the oxy-haemoglobin binding isotherms of samples of dugong haemoglobin over a range of pH and temperatures. The values for P_{50} are marginally lower than for human haemoglobin under similar conditions. This is in keeping with the observation of Turek *et al.* (1973). They have pointed out that a left displaced oxy-haemoglobin equilibrium may actually favour oxygen release in conditions of acute hypoxia since it is the change in steepness of the physiological dissociation curve (i.e. the straight line between arterial and venous points) which is the important parameter governing oxygen release to the tissue.

(b) *Anatomy of the respiratory tract*

Osman-Hill (1945) has described the upper respiratory tract. The lungs are long and extend posteriorly almost as far as the kidneys. They are separated from the abdominal viscera by a large obliquely sloped diaphragm. Dugong lungs are considered unusual both in terms of the nature of the bronchial tree and that of the respiratory tissue *sensu stricto* (Engel, 1959a, b, 1962). The main bronchus runs almost the entire length of the lung with only a few side branches. The respiratory units (vesicles) arise laterally along the length of

the bronchioli. Cartilage occurs throughout the length of the air passages and even the most peripheral bronchioli possess cartilagenous platelets within their walls. Engel considers the dugong lung to be extremely primitive. It is unknown whether or not the lungs collapse on diving; however, dugong feeding habits restrict them to the close inshore euphotic zone, and this together with their rather limited diving times makes it dubious that they dive to any considerable depth.

CIRCULATORY SYSTEM

Osman-Hill (1945) describes the disposition of the heart and major blood vessels. The heart is considered primitive in structure (Harrison & King, 1965) with a deep interventricular cleft extending almost the full length of the ventricles.

Retial structures are known and play an important role in heat regulation. Elsner *et al.* (1966) present a photograph of a cast of the arterial brush arising from the brachial artery. It is considered probable that similar structures are also present in the tail fluke as they are in the manatee (Fawcett, 1942).

The skin of the dugong is modified for life in the water to a lesser extent than in some marine mammals, particularly, as would be expected, in those characteristics that contribute to the regulation of body temperature. The blubber is thinner than in most other marine mammals and there are no arterio-venous anastomoses (AVAs) in the dermis. AVAs are very numerous in the papillary layer of the dermis in seals and are associated with thermoregulation (Bryden *et al.*, 1978).

NERVOUS SYSTEM

The brain has been described by Dexler (1913), Osman-Hill (1945), Harrison & King (1965) and the spinal cord by Dexler (1912). The brain is relatively small (282 g in an adult female weighing 300 kg) (Dexler, 1913) and is characterized by few and shallow sulci and a thin covering of leptomeninges, with fine hair-like superficial cerebral veins reminiscent of a foetal brain (Osman-Hill, 1945). The corpora quadrigemina, especially the inferior, are prominent suggesting auditory sensitivity. The cerebellum is well developed and possesses large floccular lobes composed mainly of the paraflocculus, probably associated with pronounced swimming and equilibratory activities (Harrison & King, 1965). Native dugong hunters consider that the hearing of dugongs is acute but that their visual powers are less developed (Prater, 1929; Jarman, 1966; Roughsey, 1971). The unusual arrangement of the ear ossicles has been described by Robineau (1965) and their vibrations measured by Fleischer (1971).

ENDOCRINE SYSTEM AND LYMPHATIC TISSUES

The gross anatomy of the thyroid, pituitary, adrenals and spleen are described by Osman-Hill (1945). Cave & Aumonier (1967) described the histological structure of certain lymph nodes, the

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Addendum

Since this manuscript was submitted, two papers have come to our attention which record the sounds emitted by a captive dugong. Nair *et al.* (1975) and Nair & Mohan (1977) report chirping sounds of frequency 3–8 kHz. We (Mercer, Heinsohn, Marsh & Spain, unpublished data) have recently made observations of the vocalization of a young captive female dugong which produced at least three distinct types of sounds as follows: sound 1, 1–2 kHz; sound 2, a chirping sound of 2–4 kHz; and a composite of sounds 1 and 2, 1–4 kHz. It was also observed that the dugong increased the pulse repetition rate of the chirping sound 2 (2–4 kHz) immediately after some dives. Sound communication may be important in social interactions in the dugong.