



FAUNA *of* AUSTRALIA

50. DELPHINIDAE

M.M. BRYDEN

DEFINITION AND GENERAL DESCRIPTION

The family Delphinidae comprises 17 genera and 33 species (Marine Mammal Commission 1976). Of these, 15 genera (18 species) have been reported from Australian and/or subantarctic waters to the south of Australia. Baker (1983) listed 19 species; one of them, *Tursiops aduncus*, has questionable specific status.

The Delphinidae is a family of small toothed whales (order Cetacea, suborder Odontoceti). Although often referred to as the true dolphins, this family includes species that do not strike us as ‘dolphin-like’, such as the Killer Whale (*Orcinus orca*), Short-finned Pilot Whale (*Globicephala macrorhynchus*) and several others. Delphinids are the most abundant and varied of all Cetacea and are to be found from the tropics to the polar seas.

Some morphological and physiological characters of delphinids are common to all Odontoceti. There is, for instance, no deciduous dentition. The milk dentition, usually unerupted at birth, emerges through the gums some time later, and persists throughout life. The body is fusiform and streamlined; some have a dorsal fin while others do not. The forelimbs are paddle-shaped flippers with no external segmentation into brachium, antebrachium and manus that is so apparent in the limbs of most mammals. Although the hind limbs appear as limb buds in the embryo, they are completely lacking at and after birth. The tail is modified to form the major organ of propulsion, the tail stock and flukes. Beneath the skin is a layer of blubber that aids in temperature regulation and reduction of specific gravity. The external nares have migrated to the top of the head where they form the blowhole, permitting the animals to breathe whilst swimming rapidly and breaking the surface only momentarily. Foetuses of all cetacean species have hair on their snout, but in most odontocetes these are lost soon after birth.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Although small by cetacean standards, delphinids generally are quite large mammals. Adults vary from 1.1 m long and 30 kg in weight (the Tucuxi – *Sotalia fluviatilis*) to 6.8 m and 6000 kg (Killer Whale). The Tucuxi does not occur in Australian waters. Length refers to the standard measurement, taken in a straight line from the tip of the upper jaw to the notch of the tail flukes (Norris 1961). Colouration varies from the relatively uniform grey of the Bottlenose (*Tursiops truncatus*) (Fig. 50.1), Indo-Pacific Humpbacked (*Sousa chinensis*) and Irrawaddy (*Orcaella brevirostris*) Dolphins to the distinctive black and white of the Killer Whale (Fig. 50.1) and the exquisite pattern of black, ochre, grey and white of the Common Dolphin (*Delphinus delphis*). Some species have a distinct beak, others do not.

The morphological features which distinguish the Delphinidae from other families are, in the main, details of the skull (Fig. 50.2). These include those portions of the temporal bone which in Cetacea are separated from the main part, namely the petrous (periotic) part of the temporal and the tympanic bulla (Kasuya 1973).

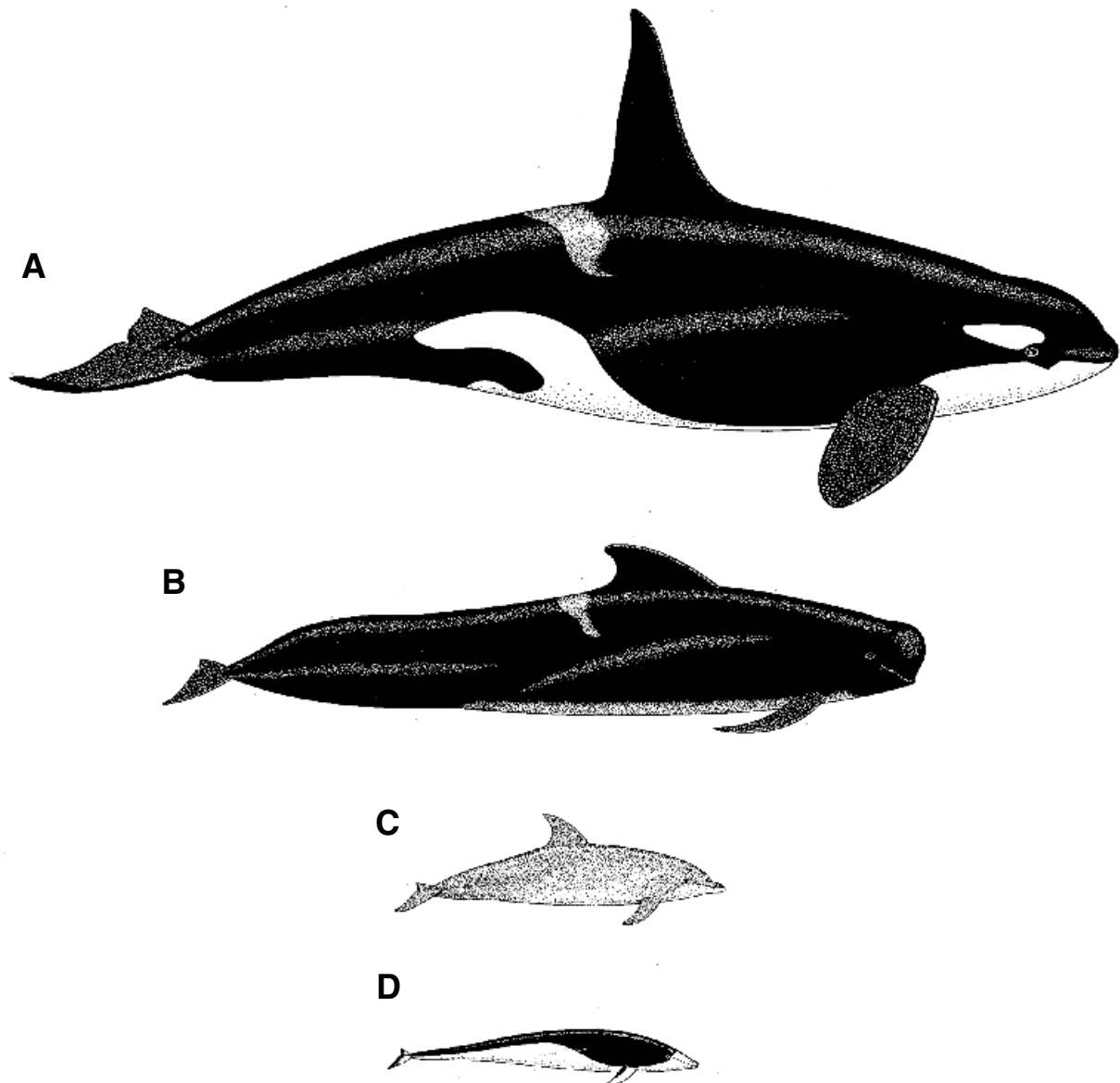


Figure 50.1 Four species of Delphinidae. **A**, Killer Whale, *Orcinus orca*; **B**, Short-finned Pilot Whale, *Globicephala macrorhynchus*; **C**, Bottlenose Dolphin, *Tursiops truncatus*; **D**, Southern Right Whale Dolphin, *Lissodelphis peronii*. (© ABRS) [G. Milledge]

Skeletal System

The bones of whales tend to be spongy in appearance. There is considerable modification of the skull of delphinids, as in other cetaceans, which has been considered at length by Miller (1923). In brief, Miller showed that the portion of the skull caudal to the rostrum is shortened, not by reduction of the rostro-caudal diameter of individual bones (except the parietals), but by a slipping of one bone over another or by the interdigitation of some elements. In addition in odontocetes, bilateral asymmetry occurs to a greater or lesser extent, depending on the species.

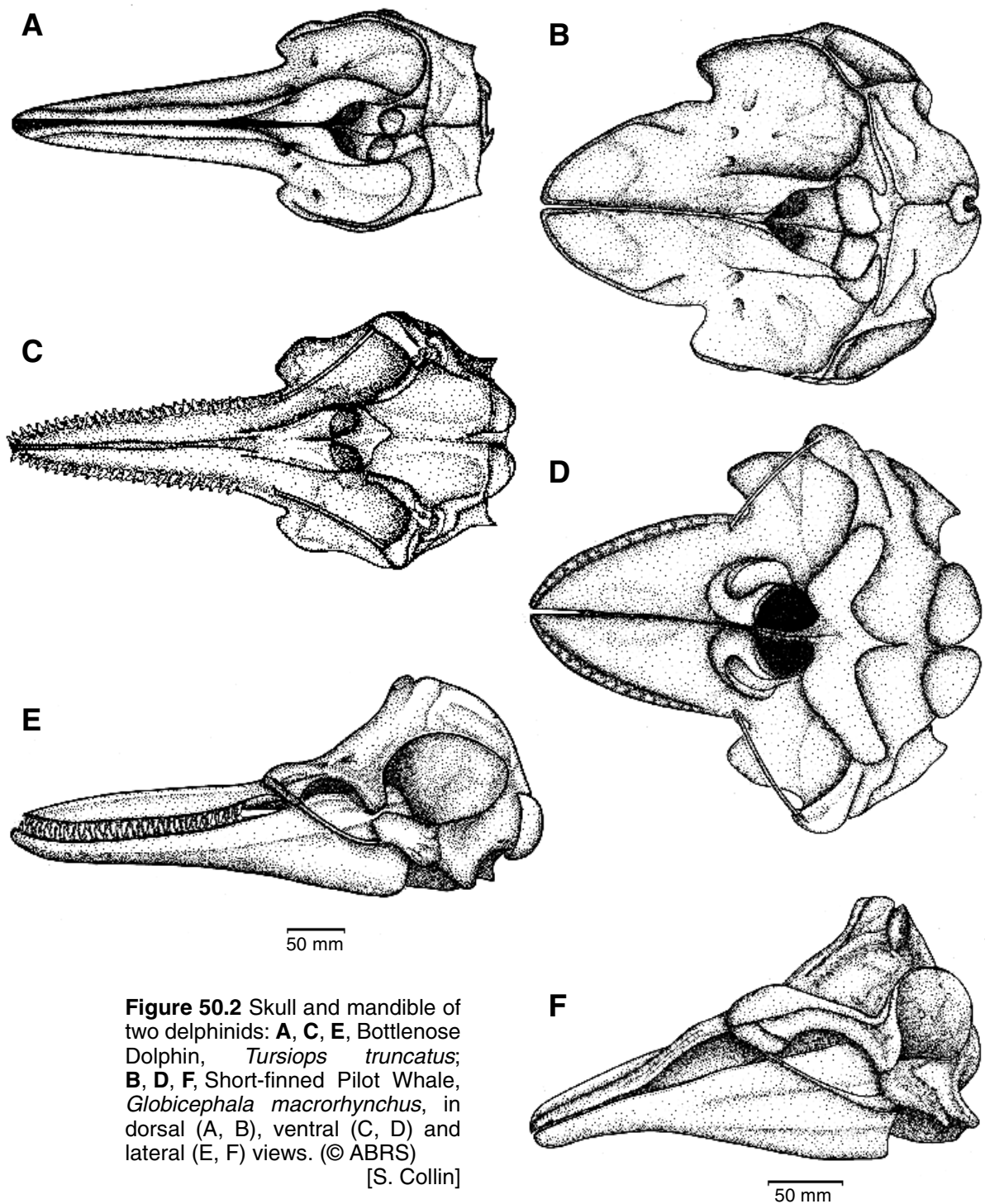


Figure 50.2 Skull and mandible of two delphinids: **A, C, E**, Bottlenose Dolphin, *Tursiops truncatus*; **B, D, F**, Short-finned Pilot Whale, *Globicephala macrorhynchus*, in dorsal (A, B), ventral (C, D) and lateral (E, F) views. (© ABRS) [S. Collin]

A feature of the vertebral column of Cetacea is the greatly foreshortened cervical vertebrae, two or more of which are fused in Delphinidae. Prominent haemal arches (chevron bones) are associated with many of the caudal vertebrae.

The humerus, radius and ulna are short bones. The joints between them are largely fibrous and permit very little movement. There are many phalanges in most of the digits, the greatest number found among Australian species is nine to 14 in the second digit of the Pilot Whale (*Globicephala melaena*).

The only component of the caudal appendicular skeleton present in members of this family, as in other odontocetes, is the pelvis which consists of a short bar of bone on either side. There is no articulation between it and the axial skeleton and it is joined only indirectly to other structures by means of the muscles that attach to it. The crura of the penis and clitoris attach to the pelvic bones.

Locomotion and Diving

Locomotion of dolphins is effected by dorsal and ventral movements of the tail with its flukes, the flippers being used for fine adjustment of direction. The flukes consist of an extremely tough and dense fibrous connective tissue attached to the caudal vertebrae and surrounded by a ligamentous envelope extending from the tail stock. The ligamentous envelope consists of bundles of fibres arranged so as to be tensed by, and hence resist bending in a dorsal or ventral direction.

The detailed structure of the flukes and the muscles that provide the propulsive force by dorsal and ventral movements of the tail is such that the upward stroke of the tail is the power stroke. This has been described by Slijper (1962) and illustrated clearly by Bonner (1980). The body of the dolphin is a rigid structure compared with that of a terrestrial mammal. Most of the movement occurs dorso-ventrally at the base of the tail and at the junction of the tail stock with the flukes. Little lateral movement of the trunk or tail is possible.

Dolphins can swim considerably faster than is theoretically possible for a rigid structure of equivalent size and shape. This has been examined by Purves (1963), who showed that the resistance to the passage of the dolphin's body through the water (drag) is minimised because vortices formed by the swimming movements are washed away as a result of the swimming motion adopted by the animal, thus avoiding turbulence. Turbulence is reduced further by avoiding the formation of vortices as the body moves through the water, such that 90% of the flow over a dolphin's body may be laminar. The latter is brought about by subtle alterations to the conformation of the skin as speed varies, in response to changes in pressure of the water at the skin surface in areas representing incipient turbulence. This mechanism eliminates turbulence as it forms (Essapian 1955). Dolphins are considered to increase the efficiency of rapid swimming by leaping (Au & Weihs 1980). For a consideration of bow-wave riding in dolphins, see Bonner (1980).

Relative to other marine mammals, dolphins dive neither for exceptionally long periods nor to great depths. They are capable of remaining submerged between successive breaths for 15 minutes or so and of diving to about 300 m (the limits vary with the species), which is impressive enough when compared with terrestrial mammals. The diving pattern is usually dives of approximately 5 minutes' duration or less, interspersed with brief periods at or near the surface when respiration rate is approximately six per minute. During the period at the surface the lungs are ventilated thoroughly (up to 90% of the total capacity of the lung is exchanged at each breath, compared with 10–15% in terrestrial mammals), and the oxygen stored in the body fully replenished in preparation for the next dive. The dolphin inspires before diving, so the lungs are full or nearly full as it submerges. The oxygen stores are much higher than in terrestrial mammals, both in the blood (Ridgway & Harrison 1986) and in the muscles (Tawara 1951). As the animal dives, distortion of the thoracic cavity occurs and, at approximately 100 m (a pressure of 11 atmospheres), the lungs collapse and air contained within them is forced into the bronchioles and bronchi. More important, the walls of the alveoli thicken as they collapse at pressure, reducing the rate of gas exchange, including the solution of nitrogen in the blood (Ridgway & Harrison 1986).

Feeding and Digestive System

Delphinids feed mainly on fish and cephalopods, although the Killer Whale also eats the flesh of warm-blooded animals such as seals, dolphins and penguins. Relatively little is known about feeding methods of dolphins, partly because of the absence of any highly specialised anatomical adaptations such as those in the baleen whales. It seems that dolphins depend for their feeding on the use of specialised behaviour patterns which as yet have not been recorded fully.

The dentition is homodont. The number of teeth is variable, from 14 to 18 in each jaw of the Short-finned Pilot Whale to more than 100 in each jaw in the Common Dolphin. Risso's Dolphin (*Grampus griseus*) has no teeth in the upper jaw and only four to 14 (average six to eight) in the lower jaw. The tooth crown of the Rough-toothed Dolphin (*Steno bredanensis*) bears five vertical sulci. Growth layers can be observed in the dentine and, in some species, the cementum, and have been used widely to estimate the age of individual dolphins (Perrin & Myrick 1980).

The anatomy of the gastrointestinal tract of dolphins has been described and illustrated by Slijper (1962). The stomach is complex, consisting of three compartments which communicate by narrow openings. The first is non-glandular and lined with non-cornified stratified squamous epithelium and seems to fulfil the function of a crop; the second compartment contains fundic glands and the third contains large numbers of pyloric glands. The intestine is simple. There is no caecum, so that there is no clear transition between the small and large intestines.

Circulatory System

Adaptations are seen in the circulatory system of dolphins, some of them related to temperature regulation. Others may be associated with redistribution of blood flow during diving, a phenomenon that would be advantageous if most of the oxygenated blood is diverted to essential organs such as the brain. Seals can control their blood flow in this way: most of the large arteries, other than those supplying the brain, constrict during diving and a sphincter around the caudal vena cava contracts causing blood to pool below the diaphragm. Dolphins do not have such a sphincter, but they do possess vascular structures known as retia mirabilia which are masses of contorted spirals of tiny vessels, mostly arteries, that form great blocks of vascular tissue along the ventral aspect of the vertebral column. In delphinids these run virtually the full length of the column. The vascular system of dolphins was observed by Viamonte *et al.* (1968), who demonstrated that dolphins have a type of cerebral blood supply radically different from that of terrestrial mammals. Rather than being supplied directly through internal carotid, external carotid, vertebral or occipital arteries, the dolphin brain receives its primary blood supply through the massive thoraco-spinal retia. How the retia function is not understood, but it has been assumed that they play an important role in diving.

Another intriguing vascular arrangement in dolphins, as in other Cetacea, is to be found in the flippers, flukes and dorsal fin (Scholander & Schevill 1955). The major arteries lie centrally within these appendages, surrounded by a trabeculate venous plexus and, in addition, there are separate superficial veins. This arrangement is a development of the vascular pattern of centrally-located artery with associated venae comitantes and separate superficial veins seen in the limbs of many land mammals, including humans. Blood returning in the venous plexus from the extremities of the dolphin is warmed by the blood flowing in the artery by counter-current heat exchange. In times of vigorous activity, such as rapid swimming, most venous blood is returned in the superficial veins when dissipation of heat to the surroundings will be maximised.

Respiration

Respiration has been considered in part in the previous Section. Anatomical adaptations are seen in the respiratory system, but their role in respiration is not understood fully. Odontocetes possess a system of myoelastic sphincters in the bronchioles (Slijper 1962) which may aid in rapid exhalation and/or inhalation during the brief period a dolphin is at the surface when moving rapidly.

The region of the nares is modified greatly. Its position has migrated from the rostral area to the top of the head and is commonly referred to as the blowhole. Around the nasal opening is a complex series of diverticula, the nasal sacs or sinuses and plugs (Mead 1975b), whose function is obscure.

Excretion

Considerable attention has been paid to renal excretion and water balance in dolphins. The kidney of all cetaceans is lobate, each lobe forming a complete functional reniculus. This feature, although uncommon in mammals, is not confined to Cetacea or even to marine mammals, but the reniculi are more numerous in Cetacea than other groups. A prominent feature of the reniculus in Cetacea is the sporta perimedullaris musculosa, a layer of unstriated muscle and collagenous tissue extending from the calyx and surrounding the renal medulla. Its function is not known, but it appears to be unique to marine mammals.

The problem of osmotic balance in dolphins has been reviewed by Gaskin (1986) who concluded that the composition of the urine differs little from that of the average terrestrial mammal. Dolphins are capable of producing moderately concentrated urine, but apparently rarely need to do so. While a large fraction of their water requirements are met from moisture in the food, there is a small intake of seawater and production of water from oxidative reactions in digestion of food. A considerable movement of water through the skin has been demonstrated. Most salt and water excretion appears to be by the usual renal route. Nitrogenous waste from the high-protein diet is excreted in the faeces and as urea in the urine. Essential electrolytes are reabsorbed in the gut.

Little information is available on the maintenance of kidney function and glomerular filtration during diving. Diuresis always follows a protein meal, but the stimulus for diuresis is not known.

Sense Organs

Relatively little is known about general sensation in the skin of dolphins, although the many sensory endings suggest that it is well developed (for references, see Bryden & Molyneux 1986).

Chemosensory and gustatory powers, not well evaluated in dolphins, have been considered by Herman & Tavalga (1980). Small taste buds have been described in the root of the tongue of the Bottlenose Dolphin and some workers have suggested that dolphins possess a well developed chemosensory facility. Dolphins can have no sense of smell because there is no olfactory organ, olfactory nerve, or olfactory bulb in adults.

The eyes are modified in dolphins, probably to permit acute vision both in water and air. A review of the eye and vision in Cetacea can be found in Dawson (1980). A striking feature, whose functional significance is not clear, is the extremely thick sclera, particularly on the deep (caudal) aspect of the eyeball. There is no refraction at the corneal surface in water because the cornea and aqueous humour have the same refractive index as seawater. The eye is flattened rostral-caudally so that the cornea is curved less strongly than in the eye of a terrestrial mammal and causes less refraction in air. There is, however, a ring near the periphery of the cornea where its convexity is greater, possibly utilised

by the animal in air when the difference in refractive index between the cornea and surroundings makes the cornea an effective refractive medium. Vision is believed to be acute both in water and air.

Lacrymal glands and ducts are absent. The surface of the cornea is cornified and large conjunctival glands secrete an oily substance. Both these characters protect the surface of the eye which is subjected to shear forces and a certain amount of friction from the water streaming past.

Hearing is acute in dolphins, like other marine mammals, and is the sense that provides information about the distant environment. Sound travels about four times faster in water than in air and, more importantly, is attenuated less so that sounds can be propagated over much greater distances. The hearing apparatus is more complex than in any other animal.

Our understanding of the ear and hearing in cetaceans is based on the observations and experiments of Fraser & Purves (1960). There is no auricle (pinna). The external auditory meatus is extremely narrow and the sound attenuation of the structures surrounding the meatus is much greater than that of the meatus itself.

In order to function effectively in water, the right and left ears are isolated functionally by a complex system of air sacs or sinuses which are diverticula of the auditory (Eustachian) tube (Fig. 50.3). The petrous part of the temporal bone which houses the inner ear and the tympanic bulla housing the middle ear are separated from the skull in dolphins. The air sinuses surround these 'ear bones' and are filled with a fine foam of gas bubbles in an oil-mucus emulsion which is resistant to compression and provides the necessary acoustic isolation for the right and left ears. The minute gas bubbles have much the same impedance as air so that sound vibrations transmitted from the water to the head of the dolphin are reflected at the tissue-sinus interface. This arrangement makes binaural hearing possible, based on sound shadows cast by the foam-filled sinuses.

The tympanic membrane is a flattened triangular ligament. Even at depth, the ossicles are surrounded by gas in the middle ear cavity. Engorgement of a spongy vascular structure lining the cavity probably compensates for volume changes of the gas with varying pressure.

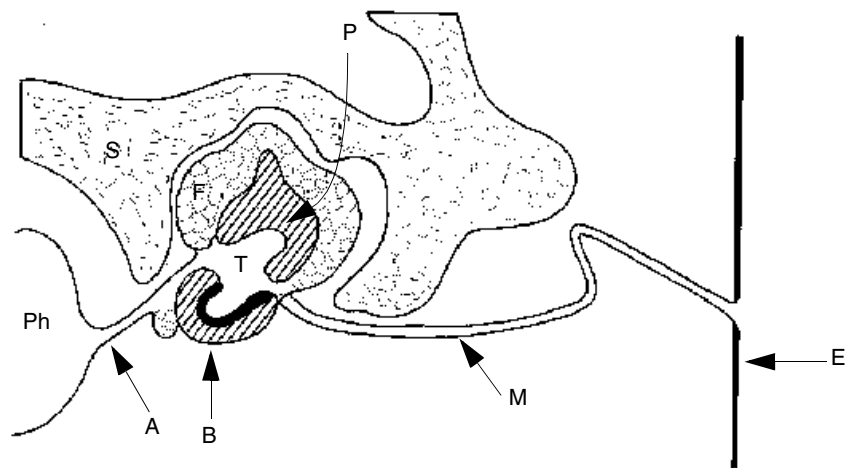


Figure 50.3 Diagnostic cross-section through the ear region of the right side of a cetacean head: E = epidermis; M = external auditory meatus; B = bulla; P = petrosal; S = bones of skull; A = auditory (eustachian) tube; T = tympanic cavity; Ph = pharynx; F = foam-filled cavities. (Redrawn from Slijper 1962)
[B. Scott]

The ossicles function in the same way as do those of terrestrial mammals, although anatomical modification has occurred to accommodate the displacement amplitude of sound vibrations in water. This is about 60 times smaller than from sounds of the same intensity and frequency in air, while the pressure amplitude is about 60 times greater.

Echolocation

Dolphins emit two basic types of sound: whistles which are used in communication, and clicks, which form the basis of echolocation. Much has been made of communication in dolphins and the possibility of a complex language. There is no evidence at present that the whistles they emit convey much more information than do the sounds of many other animals. The site of origin of the sounds is uncertain and has been the subject of considerable controversy (Morris 1986).

The emission of clicks from a source as yet unknown and reception of their echoes by the auditory system provides dolphins with detailed information about their environment. The extent to which they can discriminate between artificial targets by echolocation is remarkable indeed. The subject has been reviewed by Morris (1986) who also discussed the hypothesis, yet to be confirmed, that dolphins stun their prey by emitting massive bursts of energy as sound.

Norris (1964) suggested that echolocation clicks were produced in the region of the nares, rostral to the portion of the skull that slopes dorsally to form a crest near the caudal extremity. This part of the skull possibly acts as a parabolic reflector to focus the beam of sound waves produced around the nares. The melon may act as an elaborate acoustic lens which gathers up the sound waves reflected forwards from the skull and concentrates them in a narrow beam.

Norris further suggested that the lower jaw acts as an acoustic probe, conducting sound waves from in front of the animal directly to the inner ear. The caudal end of the dolphin's mandible consists of a wide, thin plate of bone, often referred to as the 'pan bone', which envelops a mass of fat whose lipid composition is similar to that of the melon. Returning echoes of the click train are thought to arrive at the tissue overlying the 'pan bone' (which is only 0.1–3.0 mm thick and is effectively an acoustic window) and pass through it virtually unimpeded to be conducted along the mandibular fat body to the mandibular condyle and thence to the tympanic bulla.

The Nervous System

Dolphins have a remarkably large brain and the cerebrum is folded extensively. The pattern of sulci and gyri bears no resemblance to that in humans, but is more similar to that in carnivores and ungulates. The structure of the central nervous system of cetaceans was reviewed by Morgane & Jacobs (1972). Despite extensive neuroanatomical studies of the dolphin central nervous system, relatively little is known yet about the function of many of its parts. Quite incredible claims have been made about high levels of intelligence in dolphins, but there is no direct evidence for this. It is merely supposition based on the large size of the brain which could be unrelated to intelligence.

Endocrine and Exocrine Systems

The anatomy of some endocrine glands of dolphins was reviewed by Harrison (1969). Little is known of endocrinological control mechanisms in dolphins because opportunities for controlled experimentation are few. Ultrastructural studies of dolphin endocrine glands could help to elucidate some aspects of endocrinological control.

The exocrine glands of dolphins are similar to those of other mammals; early anatomists remarked on the very small size of the salivary glands.

Reproduction

This subject has been reviewed by Bryden & Harrison (1986). Most information about reproduction in delphinids is based on postmortem examination of gonads and reproductive tracts. Data have been gathered only quite recently on blood hormone levels, reproduction in relation to social structure of groups and reproductive behaviour in free-ranging animals. These recent investigations are still in their early stages and many unanswered questions concerning reproduction in dolphins remain. Clear pictures will emerge only when we are able to maintain captive colonies of several species of dolphins and when extensive field investigations of free-ranging members of those species have been conducted. Most species seem to breed every second year, some each year. Gestation is approximately 12 months. Lactation lasts 12 months or more. There is no evidence that embryonic diapause occurs in dolphins. There is some suggestion that breeding may be seasonal in certain species, but this has not been established clearly. Certainly, seasonality is not so circumscribed in delphinids as in other marine mammals such as many of the seals.

An intriguing aspect of reproduction in Short-finned Pilot Whales has been reported by Kasuya & Marsh (1984) and Marsh & Kasuya (1984). Pregnancy rate decreased with age and there were significant numbers of post-reproductive females among the 30–40 year age group. All females older than 40 years were post-reproductive. Calves of younger cows were suckled for 2–6 years, whereas lactation in post-reproductive females may be prolonged for up to 15 years and a close cow-calf association may last at least until the calf is sexually mature.

Embryology and Development

The small amount of information about prenatal development of delphinids has been discussed by Bryden (1972; 1986). Those investigations that have been conducted relate to the increase in body length with gestational age. Descriptions of normal differentiation and organ growth are scanty.

NATURAL HISTORY

Knowledge of the natural history of delphinids varies from rudimentary in some species (Indo-Pacific Humpbacked Dolphin) to quite extensive in others (Bottlenose Dolphin). Various aspects of natural history of individual species were summarised by Mitchell (1975a) and several more recent publications are cited in this chapter. The family Delphinidae includes both inshore and oceanic species, the latter tending to form very much larger groups than the former. Delphinids are found in a variety of marine habitats where they feed on a range of prey and are affected by different predation pressures. These factors combine to determine the social structure of dolphin groups.

Small, pelagic species, feeding mostly on mesopelagic and epipelagic fish and cephalopods, often are found in groups numbering in the hundreds to thousands. They are preyed upon by large sharks, Killer Whales and False Killer Whales (*Pseudorca crassidens*).

The pelagic Rough-toothed Dolphin is found in small groups and feeds on larger epipelagic fish. The Pygmy Killer Whale (*Feresa attenuata*) also occurs in smaller groups and feeds on fish and perhaps marine mammals.

Small inshore species, which have catholic food preferences, suffer predation from sharks and Killer Whales.

Larger, generally pelagic species include Killer Whales, False Killer Whales, Risso's Dolphin and Short- and Long-finned Pilot Whales. The latter three feed on cephalopods, False Killer Whales on large epipelagic fish, cephalopods and

smaller delphinids, and Killer Whales on fish and a variety of marine mammals and birds. While these species generally are found in groups of less than 50 animals at times they may form very much larger groups.

Life History

What is known of life history parameters of dolphins, namely growth, length of lactation, the size and age at sexual and physical maturity and longevity, has been reviewed by Bryden (1986). More detailed information about individual species can be found in Mitchell (1975a).

Dolphins are born and live their entire life in the water. The La Plata Dolphin (*Pontoporia blainvillei*) appears to have a relatively short life-span, approximately 12 years. Others, such as the Short-finned Pilot Whale, live to 50 years or more. Twins very rarely, if ever, occur.

Ecology and Behaviour

The Long-snouted Spinner Dolphin (*Stenella longirostris*), the Bottlenose Dolphin and the Killer Whale serve to illustrate the contrasting behavioural ecology found within the family Delphinidae.

The Long-snouted Spinner Dolphin remains inshore, around islands, resting in sheltered bays during daylight hours. Resting groups may range in size from six to 250 animals. Within such groups, subgroups of animals of similar age and the same sex are recognisable by their behaviour. Group and subgroup composition is apparently fluid and may vary daily (Norris & Dohl 1980). At night, the dolphins move offshore and feed on mesopelagic fish and cephalopods in waters deeper than 250 m (Fitch & Brownell 1968). Feeding aggregations, displaying coordinated activity, may number in the hundreds. This species is also found in oceanic waters where it forms large aggregations with the closely related Spotted Dolphin (*Stenella attenuata*) that feeds during daylight hours on epipelagic fish and cephalopods. Long-snouted Spinner Dolphins may join groups of the diurnally active Spotted Dolphin to give themselves some 'cover' while they rest during the day.

Inshore, Bottlenose Dolphins are found in groups of fluid composition, averaging between ten and 15, with subunits of approximately five animals. These subunits may be constant in composition (Würsig 1978) or fluid (Wells, Irvine & Scott 1980). Sexual segregation of these subunits is apparent, while groups may contain subunits of different age and sex classes. Immature male Bottlenose Dolphins avoid mature males and dominance-mediated aggression appears to function as a spacing mechanism.

The home range of a 'herd' (approximately 100 Bottlenose Dolphins) within an enclosed, shallow bay was estimated to be 85 km², while individual home ranges varied with age and sex from 15 km² for subadult females to 41 km² for females with calves (Wells *et al.* 1980). In another region, however, an identified subgroup of dolphins was known to have made a round trip of at least 600 km in 15 months (Würsig 1978). The abundance of Bottlenose Dolphins varies seasonally in some regions, indicating that those populations may migrate (Shane 1980), but this is not true in other regions (Lear & Bryden 1980). Inshore, this species prefers shallow regions. It spends most of its time in water less than 10 m depth, with apparent feeding forays into water up to 39 m (Würsig & Würsig 1979). It prefers regions of rocky shore to sandy beaches with a gently sloping floor (Lear & Bryden 1980). These dolphins employ a variety of feeding techniques, including cooperative herding of school fish (Saayman, Tayler & Bower 1973; Würsig & Würsig 1979), individual feeding

on bottom-dwelling fish (Würsig & Würsig 1979; Irvine *et al.* 1981), driving fish onto mudflats followed by intentional stranding to feed (Hoese 1971) and cooperative hunting with man on schooling fish (cited in Bryden 1978)

Killer Whales live in pods, stable groups of up to 40 containing both sexes which may be discrete breeding units (Bigg 1982; Balcomb, Boran & Heimlich 1982). They have been observed feeding on fish, baleen whales (by herding and drowning of their prey) and, apparently, several species of dolphins and otariid seals. Around subantarctic islands, Killer Whales appear during the breeding season of seals and penguins (Condy, van Aarde & Bester 1978).

Economic Significance

In contrast to the large whales, the economic significance of delphinids is minor. Killer Whales have been harvested in several regions, mainly in the northern hemisphere, both for their products (oil, meat) and in live capture fisheries to supply oceanaria. Up to 1500 Pilot Whales (*Globicephala melaena*) are taken annually for human consumption in a drive fishery in the Faeroes, and small numbers have been taken elsewhere. Several species have been taken mainly for human consumption in sporadic drive fisheries in Japan.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Delphinids are found in all waters of Australia and south to Antarctica. Some, like Killer Whales, occur in all waters. Others are confined to specific regions, such as Irrawaddy Dolphins that inhabit warm northern waters only. Some species remain inshore, others are oceanic and venture close to the coast only rarely, while others move freely between inshore and offshore areas (see Section on Ecology and Behaviour).

Affinities with other Groups

Of all mammals, the Cetacea are the most highly specialised for aquatic life. They have no close phyletic affinities with other groups. Their nearest relatives are the even-toed ungulates (Artiodactyla) (Slipper 1962).

There are many reports of ecological affinities of delphinids with other mammals, including other cetacean families and man. There is a large literature relating to the latter and several instances have formed the basis of popular accounts of affinities between dolphins and human beings in Australia. A cooperative relationship between dolphins and Aborigines at North Stradbroke Island, Queensland, at the time of early European settlement has been reported (see Bryden 1978 for references) and recently a group of 'friendly' bottlenose dolphins at Monkey Mia in Western Australia has received wide publicity.

Affinities within the Taxon

Recent evidence suggests that a gradual transition of early cetaceans from land to sea occurred in the early Eocene (Gingerich *et al.* 1983). Odontocetes (toothed whales) appear to have diverged from the mysticetes (baleen whales) and radiated rapidly early in the Oligocene (Fordyce 1985). During the Middle Miocene the present-day families of Platanistidae, Physeteridae and Ziphiidae became distinct groups, while the separation of the remaining families (Monodontidae, Phocoenidae and Delphinidae) had occurred by the upper Miocene.

Ecological affinities occur within the taxon, for example between species of *Stenella* (see Section on Ecology and Behaviour) and in Australian waters between Bottlenose and Indo-Pacific Humpbacked Dolphins (P.J. Corkeron unpublished observation).

Fossil Record

There is a meagre fossil record of delphinids in Australia (Fordyce 1985). For a consideration of the evolution and zoogeography of Australian fossil Cetacea, see Fordyce (1984).

Quite recently, cetacean skeletal material was discovered by Dr P. Quilty of the Antarctic Division (Hobart) near Davis Station, Antarctica. Dr. Quilty kindly provides the following information. It is the first reported vertebrate fossil in Antarctica from the Eocene to the present. It is early Pliocene, 4–4.6 million years old and represents a new genus and possibly a new family. For the present, however, it is considered to belong to the Delphinidae pending further study. The material has been examined by Dr R.E. Fordyce and a scientific paper is in preparation. The specimen will be deposited in the Commonwealth Palaeontological Collection in Canberra.

LITERATURE CITED

- Au, D. & Weihs, D. (1980). At high speeds dolphins save energy by leaping. *Nature* 284: 548-550
- Baker, A.N. (1983). *Whales and Dolphins of New Zealand and Australia. An Identification Guide*. Victoria University Press : Wellington 133 pp.
- Balcomb, K.C., Boran, J.R. & Heimlich, S.L. (1982). Killer whales in greater Puget Sound. *Reports of the International Whaling Commission* 32: 681-685
- Bigg, M.A. (1982). An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Reports of the International Whaling Commission* 32: 655-666
- Bonner, W.N. (1980). *Whales*. Blandford Press : Poole, Dorset x 278 pp.
- Bryden, M.M. (1972). Growth and development of marine mammals. Pp. 1-79 in Harrison, R.J. (ed.) *Functional Anatomy of Marine Mammals*. Vol. 1. Academic Press : New York
- Bryden, M.M. (1978). Whales and whaling in Queensland waters. *Proceedings of the Royal Society of Queensland* 89: v-xviii
- Bryden, M.M. (1986). Age and growth. Pp. 211-224 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Bryden, M.M. & Harrison, R.J. (1986). Gonads and reproduction. Pp. 149-159 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Bryden, M.M. & Molyneux, G.S. (1986). Ultrastructure of encapsulated nerve endings in the region of the nares in dolphins. Pp. 99-107 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Condy, P.R., van Aarde, R. & Bester, M. (1978). The seasonal occurrence and behaviour of killer whales (*Orcinus orca*) at Marion Island. *Journal of Zoology, London* 184: 449-464
- Dawson, W.W. (1980). The cetacean eye. Pp. 53-100 in Herman, L.M. (ed.) *Cetacean Behaviour : Mechanisms and Functions*. John Wiley & Sons : New York
- Essapian, F.S. (1955). Speed-induced skinfolds in the bottle-nosed porpoise, *Tursiops truncatus*. *Breviora* 43: 1-4

- Fitch, J.E. & Brownell, R.L., Jr. (1968). Fish otoliths in cetacean stomachs and importance in interpreting feeding habits. *Journal of the Fisheries Research Board of Canada* 25: 2561-2574
- Fordyce, R.E. (1984). Evolution and zoogeography of cetaceans in Australia. Pp. 929-948 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Fordyce, R.E. (1985) The history of whales in the Southern Hemisphere. Pp. 79-104 in Ling, J.K. & Bryden, M.M. (eds) *Studies of Sea Mammals in South Latitudes*. South Australian Museum : Adelaide
- Fraser, F.C. & Purves, P.E. (1960). Hearing in cetaceans. *Bulletin of the British Museum (Natural History)* 7: 1-140
- Gaskin, D.E. (1986). Kidney and water metabolism. pp. 129-148 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Gingerich, P.D., Wells, N.A., Russell, D.E. & Ilbrahim Shah, S.M. (1983). Origin of whales in epicontinental remnant seas : new evidence from the early Eocene of Pakistan. *Science* 220: 403-406
- Harrison, R.J. (1969). Endocrine organs. Hypophysis, thyroid, and adrenal. Pp. 349-390 in Anderson, H.T. (ed.) *The Biology of Marine Mammals*. Academic Press : London
- Herman, L.M. & Tavalga, W.W. (1980). The communication systems of cetaceans. Pp. 149-209 in Herman, L.M. (ed.) *Cetacean Behaviour : Mechanisms and Functions*. John Wiley & Sons : New York
- Hoese, H.D. (1971). Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy* 52: 222-223
- Irvine, A., Scott, M., Wells, R. & Kaufman, J. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus* near Sarasota, Florida. *Fishery Bulletin* 79: 671-688
- Kasuya, T. (1973). Systematic consideration of recent toothed whales based on the morphology of typano-periotic bone. *Scientific Reports of the Whale Research Institute, Tokyo* 25: 1-103
- Kasuya, T. & Marsh, H. (1984). Life history and reproductive biology of the short-finned pilot whale off the Pacific coast of Japan. *Reports of the International Whaling Commission, Special Issue* 6: 259-310
- Lear, R.J. & Bryden, M.M. (1980). A study of the bottlenose dolphin *Tursiops truncatus* on the east coast of Australia. *Occasional Papers of the Australian National Parks and Wildlife Service* 4: 1-25
- Marine Mammal Commission (1976). *Marine Mammal Names*. Marine Mammal Commission : Washington, D.C.
- Marsh, H. & Kasuya, T. (1984). Changes in the ovaries of the short-finned pilot whale, *Globicephala macrorhynchus* with age and reproductive activity. *Reports of the International Whaling Commission, Special Issue* 6: 311-335
- Mead, J.G. (1975b). Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia : Cetacea). *Smithsonian Contributions to Zoology* 207: 1-72
- Miller, G.S. (1923). The telescoping of the cetacean skull. *Smithsonian Miscellaneous Collections* 76(5): 1-71
- Mitchell, E.D. (ed.) (1975a). Report of the Meeting on Smaller Cetaceans, Montreal, April 1-11, 1974. in Review of biology and fisheries for smaller cetaceans. *Journal of the Fisheries Research Board of Canada* 32: 889-983

- Morgane, P.J. & Jacobs, M.S. (1972). Comparative anatomy of the cetacean nervous system. Pp. 117-244 in Harrison, R.J. (ed.) *Functional Anatomy of Marine Mammals*. Academic Press : New York
- Morris, R.J. (1986). The acoustic faculty of dolphins. Pp. 369-399 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Norris, K.S. (1964). Some problems in echolocation in cetaceans. Pp. 317-336 in Tavolga, W.N. (ed.) *Marine Bio-acoustics*. Pergamon Press : New York
- Norris, K.S. (ed.) (1961). Standardized methods for measuring and recording data in the smaller cetaceans. *Journal of Mammalogy* 42: 471-476
- Norris, K.S. & Dohl, T. (1980). Behaviour of the Hawaiian spinner dolphin, *Stenella longirostris*. (U.S.) *Fishery Bulletin* 77: 821-849
- Perrin, W.F. & Myrick, A.C., Jr. (eds) (1980). *Age Determination of Toothed Whales and Sirenians*. Reports of the International Whaling Commission, Special Issue 3. Cambridge: International Whaling Commission viii 229 pp.
- Purves, P.E. (1963). Locomotion in whales. *Nature* 197: 334-337
- Ridgway, S.H. & Harrison, R.J. (1986). Diving dolphins. Pp. 33-58 in Bryden, M.M. & Harrison, R.J. (eds) *Research on Dolphins*. Clarendon Press : Oxford
- Saayman, G.S., Tayler, C.K. & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenburg). *Behaviour* 44: 212-233
- Scholander, P.F. & Schevill, W.E. (1955). Counter-current heat exchange in the fins of whales. *Journal of Applied Physiology* 8: 279-282
- Shane, S. (1980). Occurrence, movements and distribution of bottlenose dolphins, *Tursiops truncatus*, in southern Texas. (U.S.) *Fishery Bulletin* 78: 593-601
- Slijper, E.J. (1962). *Whales*. Hutchinson : London 475 pp.
- Tawara, T. (1951). On the respiratory pigments of whales. *Scientific Reports of the Whales Research Institute, Tokyo* 3: 96
- Viamonte, M., Morgane, P.J., Galliano, R.E., Nagel, E.L. & McFarland, W.L. (1968). Angiography in the living dolphin and observations on blood supply to the brain. *American Journal of Physiology* 214: 1225-1249
- Wells, R., Irvine, A. & Scott, M. (1980). The social ecology of inshore odontocetes. Pp. 263-317 in Herman, L.M. (ed.) *Cetacean Behaviour : Mechanisms and Functions*. John Wiley & Sons : New York
- Würsig, B. (1978). Occurrence and group organization of Atlantic bottlenose dolphins in an Argentine bay. *Biological Bulletin* 154: 348-359
- Würsig, B. & Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. (U.S.) *Fishery Bulletin* 77: 399-412