

Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related stranding

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ABSTRACT

A number of mass strandings of beaked whales have in recent decades been temporally and spatially coincident with military activities involving the use of midrange sonar. The social behaviour of beaked whales is poorly known, it can be inferred from strandings and some evidence of at-sea sightings. It is believed that some beaked whale species have social organisation at some scale; however most strandings are of individuals, suggesting that they spend at least some part of their life alone. Thus, the occurrence of unusual mass strandings of beaked whales is of particular importance. In contrast to some earlier reports, the most deleterious effect that sonar may have on beaked whales may not be trauma to the auditory system as a direct result of ensonification. Evidence now suggests that the most serious effect is the evolution of gas bubbles in tissues, driven by behaviourally altered dive profiles (e.g. extended surface intervals) or directly from ensonification. It has been predicted that the tissues of beaked whales are supersaturated with nitrogen gas on ascent due to the characteristics of their deep-diving behaviour. The lesions observed in beaked whales that mass stranded in the Canary Islands in 2002 are consistent with, but not diagnostic of, decompression sickness. These lesions included gas and fat emboli and diffuse multiorgan haemorrhage. This review describes what is known about beaked whale anatomy and physiology and discusses mechanisms that may have led to beaked whale mass strandings that were induced by anthropogenic sonar.

Beaked whale morphology is illustrated using Cuvier's beaked whale as the subject of the review. As so little is known about the anatomy and physiology of beaked whales, the morphologies of a relatively well-studied delphinid, the bottlenose dolphin and a well-studied terrestrial mammal, the domestic dog are heavily drawn on.

KEYWORDS: BEAKED WHALES; STRANDINGS; BOTTLENOSE DOLPHIN; ACOUSTICS; DIVING; RESPIRATION; NOISE; METABOLISM

INTRODUCTION

Strandings of beaked whales and other cetaceans that are temporally and spatially coincident with military activities involving the use of mid-frequency (1-20kHz) active sonars have become an important issue in recent years (Nascetti *et al.*, 1997; Frantzis, 1998; Anon., 2001; 2002; Balcomb and Claridge, 2001; Jepson *et al.*, 2003; Fernández, 2004; Fernández *et al.*, 2004; 2005; Crum *et al.*, 2005). This review describes the relevant aspects of beaked whale anatomy and physiology and discusses mechanisms that may have led to the mass strandings of beaked whales associated with the use of powerful sonar. The anatomy and physiology of marine mammals are not as well studied as are those of domestic mammals (Pabst *et al.*, 1999) and within the cetacean family of species even less is known about the beaked whales than about the more common delphinids (e.g. the bottlenose dolphin, *Tursiops truncatus*). Furthermore, many of the morphological and physiological principles that are applied to pathophysiological evaluations of marine mammals were developed on small terrestrial mammals such as mice, rats and guinea pigs (e.g. Anon., 2001). Predictions and interpretations of functional morphology, physiology and pathophysiology must therefore be handled cautiously when applied to the relatively large diving mammals (Fig. 1). Interpolation is a

relatively accurate procedure, but extrapolation, particularly when it involves several orders of magnitude in size, is less so (K. Schmidt-Nielsen, pers. comm. to S. Rommel).

Beaked whales are considered deep divers based on their feeding habits, deep-water distribution and dive times (Heyning, 1989b; Hooker and Baird, 1999; Mead, 2002). Observations from time-depth recorders on some beaked

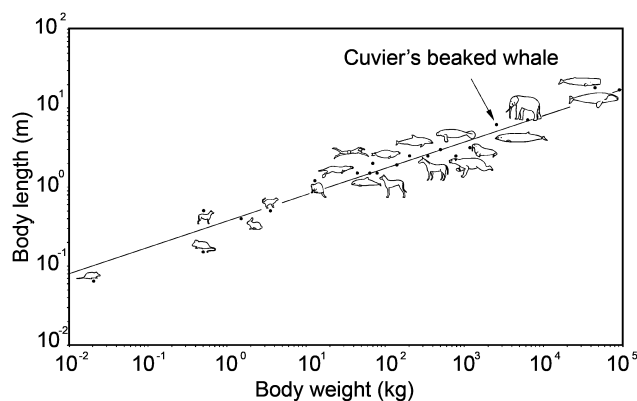


Fig. 1. Body size, expressed as weight and length for a variety of mammals. Marine mammals are large when compared to most other mammals and beaked whales are relatively large marine mammals.

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whales have documented dives to 1,267m and submergence times of up to 70min (Baird *et al.*, 2004; Hooker and Baird, 1999; Johnson *et al.*, 2004). Notably, beaked whales spend most of their time (more than 80%) at depth, typically surfacing for short intervals of one hour or less. Virtually no physiological information on beaked whales exists and information on any cetacean larger than the bottlenose dolphin is rare. Given this paucity of data this review relies on information obtained from both terrestrial mammals and other marine mammal species. In particular it draws heavily from the morphology of a well-studied terrestrial mammal, the domestic dog (*Canis familiaris*) and a relatively well-studied cetacean, the bottlenose dolphin, referred to herein as *Tursiops* (Fig. 2). Beaked whale morphology is illustrated using Cuvier's beaked whale (*Ziphius cavirostris*), further referred to as *Ziphius*. *Ziphius*, based on stranding records (they are rarely identified at sea), is the most cosmopolitan of the 21 beaked whale species (within 6 genera: *Berardius*, *Hyperoodon*, *Indopacetus*, *Mesoplodon*, *Tasmacetus* and *Ziphius*) (Baird *et al.*, 2004; Dalebout and Baker, 2001; Mead, 2002; Rice, 1998).

ANATOMY/PHYSIOLOGY

Before considering the potential mechanism by which sounds may affect beaked whales, it is important to review what is known and can be inferred of their anatomy and physiology.

External morphology

Aside from dentition and conspecific scarring between males, there are few external morphological differences between the genders of *Ziphius* (Mead, 2002). The head is relatively smooth (Figs 2 and 3) and the average adult total body length is 6.1m (Heyning, 2002). The throats of all beaked whales have a bilaterally paired set of grooves associated with suction feeding (Heyning and Mead, 1996). *Ziphius* bodies are robust and torpedo-like in shape, with

small dorsal fins approximately 1/3 of the distance from the tail to the snout. The relatively short flippers can be tucked into shallow depressions of the body wall (Heyning, 2002).

Specialised lipids

Marine mammals have superficial lipid layers called blubber (Fig. 3). Blubber in non-cetaceans is similar to the subcutaneous lipid found in terrestrial mammals; in contrast, the blubber of cetaceans is a thickened, adipose-rich hypodermis (reviewed in Pabst *et al.*, 1999; Struntz *et al.*, 2004). Cetacean blubber makes up a substantial proportion (15-55%) of the total body weight (Koopman *et al.*, 2002; McLellan *et al.*, 2002) and the lipid content can vary depending upon the species and the sample site (Koopman *et al.*, 2003a). Blubber is richly vascularised to facilitate heat loss (Kanwisher and Sundes, 1966; Parry, 1949) and is easily bruised by mechanical insult. Since blubber has a density that can be different from those of water and muscle, it may respond to ensonification differently, particularly if conditions of vascularisation (i.e. volume and temperature of blood) vary. The roles blubber (and other lipids) may play in whole-body acoustics should be the subject of further research.

As in other odontocetes, the hollowed jaw is surrounded by acoustic lipids¹, although the beaked whale acoustic lipids are chemically different from those of other odontocetes (Koopman *et al.*, 2003b). These acoustic lipids conduct sound to the pterygoid and peribullar sinuses and ears (Koopman *et al.*, 2003a; Norris and Harvey, 1974; Wartzog and Ketten, 1999) and may function as an acoustical amplifier, similar to the pinnae of terrestrial

¹ Evidence from anatomical, morphological, biochemical and behavioural studies all support the role of the melon and mandibular lipids in the transmission and reception of sound by odontocetes (Norris and Harvey, 1974; Koopman *et al.*, 2003b; Ketten *et al.*, 2001; Varanasi *et al.*, 1975; Wartzog and Ketten, 1999). Thus, these fats are collectively referred to here as the 'acoustic lipids'.

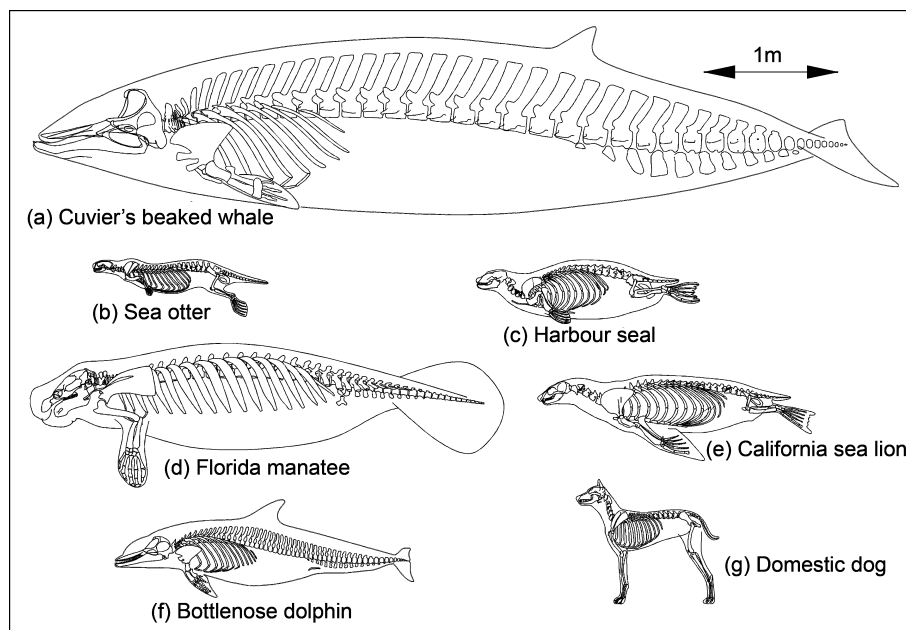


Fig. 2. The skeleton of a Cuvier's beaked whale, (a) compared to selected marine mammal skeletons: sea otter, *Enhydra lutris* (b); harbour seal, *Phoca vitulina* (c); Florida manatee, *Trichechus manatus latirostris* (d); California sea lion, *Zalophus californianus* (e); bottlenose dolphin (f) and the domestic dog, *Canis familiaris* (g). Each skeleton was scaled proportionately to the beaked whale. The *Ziphius* skeleton was drawn from photographs of Smithsonian Institution skeleton #504094 and from photographs courtesy of A. van Helden; other skeletons were re-drawn from Rommel and Reynolds (2002).

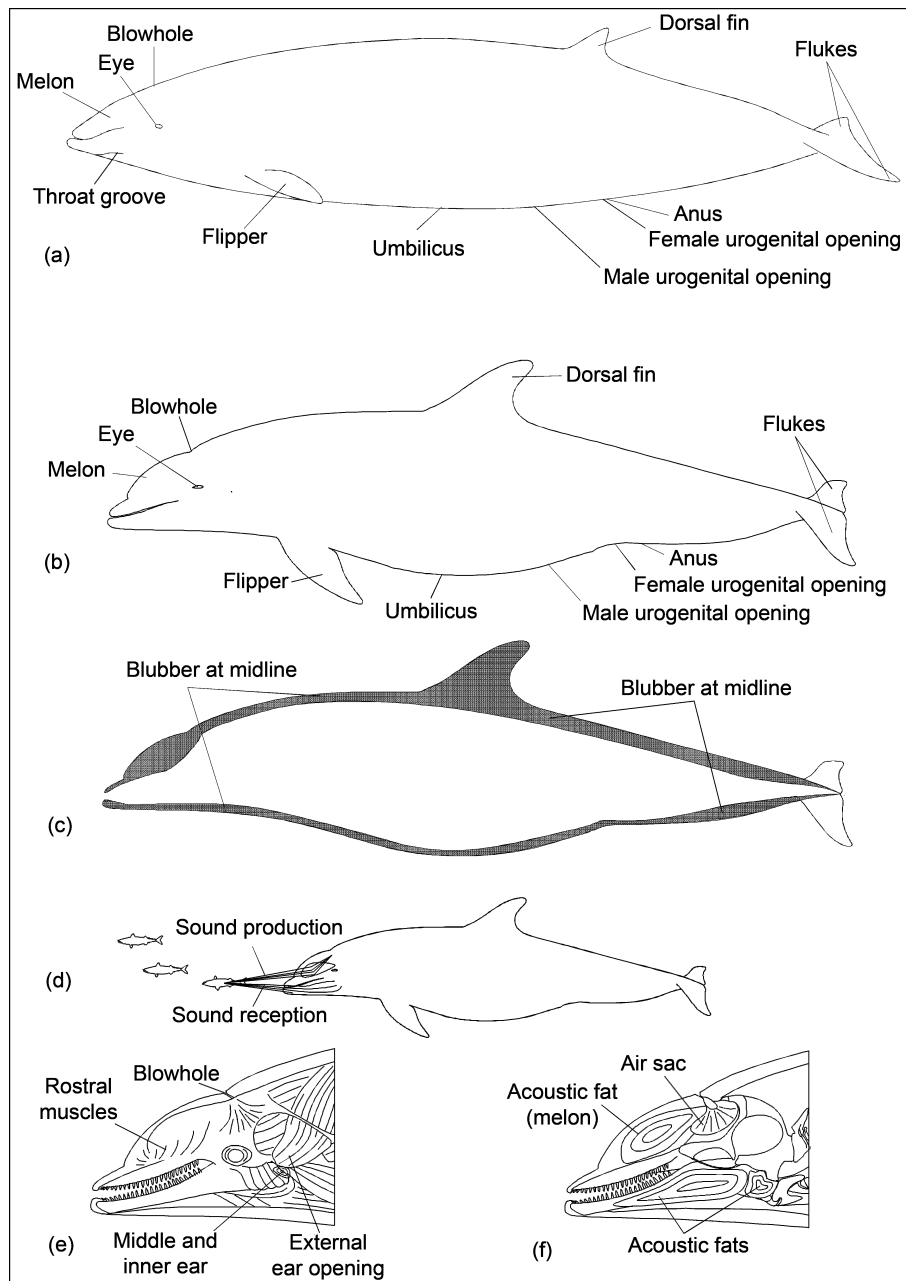


Fig. 3. The external morphology of a Cuvier's beaked whale (a) compared with that of the bottlenose dolphin (b). When compared to terrestrial mammals, Odontocetes have extensive and atypical fat deposits and fat emboli have been implicated in some beaked whale mass strandings; thus, their potential sources (such as well-vascularised fat deposits) are of special interest. Skin lipids (or blubber) perform several functions: for example, buoyancy, streamlining and thermoregulation. (c) This drawing illustrates the thickness of the blubber of a dolphin along the midline of the body. (d-f) Odontocetes have specialised acoustic lipids, represented by contours in f, which are found in the melon and lower jaw. These lipids have physical characteristics that guide sound preferentially.

mammals (Cranford *et al.*, 2003). The ziphiid melon is similar in size, shape and position to that of other odontocetes (Heyning, 1989b), but Koopman *et al.* (2003b) have shown that like the jaw fat, the acoustic lipids of the ziphiid melon are also chemically different. This suggests potential differences in sound propagation properties and perhaps in response to anthropogenic ensonification. Thus, understanding the role and composition of acoustic lipids may be important in interpreting lesions in mass stranded beaked whales.

Extensive fat deposits are also found in the skeleton. Most cetacean bones are constructed of spongy, cancellous bone, with a thin or absent cortex (de Buffrenil and Schoevaert, 1988). Like the fatty marrow found in terrestrial mammal bones, the medullae of cetacean bones are rich in lipids and

up to 50% of the wet-weight of a cetacean skeleton may be attributed to lipid. Since it has been demonstrated that individual lipids within the same, as well as different, parts of the cetacean body may be structurally distinct, it may be of value to analyse the composition of fat emboli to determine if the sources are from general or specific lipid deposits. Thus, lipid characterisation of fat emboli may help pinpoint the source of lipids and therefore the site of injury.

The skeletal system

There is a pronounced sexual dimorphism in the skulls of *Ziphius*; the species name (*cavirostris*) is derived from the deep excavation (prenarial basin) on the rostrum that occurs in mature males (Heyning, 1989a; Heyning, 2002; Kernan, 1918; Omura *et al.*, 1955). The bones of male beaked whale

rostra (the premaxillaries, maxillaries and vomer) may become densely ossified (in the extreme, up to 2.6 g cm^{-3} in Blainville's beaked whale, *Mesoplodon densirostris*), thought to be an adaptation for conspecific aggression (de Buffrenil and Zyberberg, 2000; MacLeod, 2002). Both genders have homodont dentition (teeth are all the same shape) and a caudally hollowed, lipid-filled, lower jaw, as do other odontocetes.

The premaxillary, maxillary and vomer bones are elongated rostrally and the premaxillaries and maxillaries are also extended dorsocaudally over the frontal bones (Fig. 4b; *telescoping*, Miller, 1923). The narial passages are essentially vertical in all cetaceans and the nasal bones are located at the vertex of the skull, dorsal to the braincase. In *Tursiops*, the nasal bones are relatively small vestiges that lie in shallow depressions of the frontal bones (Rommel, 1990). Conversely, the nasal bones of beaked whales are robust and are part of the prominent rostral projections of the skull apex (Fig. 4; Kernan, 1918; Heyning, 1989a).

Odontocetes have larger, more complex pterygoid bones than terrestrial mammals. In delphinids, the pterygoid and palatine bones form thin, almost delicate, medial and lateral walls lining the bilaterally paired pterygoid sinuses. The pterygoid sinuses of *Tursiops* are narrow structures that are constrained by the margins of the pterygoid bones. In contrast, the pterygoid bones of beaked whales are thick and robust (Figs 4 and 5) and their pterygoid sinuses are very large (measured by Scholander (1940) each to be approximately a litre in volume in the northern bottlenose whale, *Hyperodon ampullatus*). Beaked whale (and physeteroid) pterygoid sinuses lack bony lateral laminae (Fraser and Purves, 1960). These morphological characteristics of the pterygoid region imply differences in mechanical function and perhaps response to ensonification by anthropogenic sonar, and thus may be important in interpreting lesions found in beaked whales.

In most mammals, there is a temporal 'bone', which is a compound structure made up of separate bony elements and/or ossification centres (Nickel *et al.*, 1986). In many mammals, the squamosal bone is firmly ankylosed to the petiotic (petrosal, petrous), tympanic (or parts thereof) and mastoid bones to form the temporal bone (Kent and Miller, 1997). However, this is not the case in fully aquatic marine mammals (cetaceans and sirenians), where the squamosal, petiotic and tympanic bones (there is some controversy over the nature of the mastoid as a separate 'bone') remain separate (Rommel, 1990; Rommel *et al.*, 2002). Unlike the skulls of most other mammals in which the petiotic bones are part of the inner wall of the braincase, the cetacean tympano-petiotic bones are excluded from the braincase (Fig. 5; Fraser and Purves, 1960; Geisler and Lou, 1998). The beaked whale tympano-petiotic is a dense, compact bone (as in other cetaceans), whereas its mastoid process (caudal process of the tympanic bulla) is trabecular² (like most other cetacean skull bones). The *Ziphius* mastoid process, unlike that of the delphinids (and some other beaked whales), is relatively large and interdigitates with the mastoid process of the squamosal bone (Fraser and Purves, 1960).

The beaked whale basioccipital bone is relatively massive, with thick ventrolateral crests, in contrast to the basioccipital crests in delphinids, which are relatively tall but thin and laterally cupped (Fig. 5). In odontocetes, there are large, vascularised air spaces (peribullar sinuses) between the tympano-petiotics and basioccipital crests. In

Tursiops, the pathway from the braincase for the 7th and 8th cranial nerves is a short (parallel to these nerves), open cranial hiatus (Rommel, 1990) bordered by relatively thin bones. In *Ziphius*, this path is a narrow, relatively long channel through the basioccipital bones (Fig. 5). It is similar in position, but not homologous to the internal acoustic (auditory) meatus of terrestrial mammals. The morphology of the pterygoid and basioccipital bones and the size and orientation of the cranial hiatus likely contribute to differences in acoustical properties and mechanical compliance of the beaked whale skull. These bony structures are therefore of potential importance in the effects of acoustical resonance.

The vertebral column supports the head, trunk and tail (Figs 2 and 6). In *Tursiops* the first two cervical vertebrae are fused, but the rest are typically unfused (Rommel, 1990); in contrast, the first four cervicals of *Ziphius* are fused. There is more individual variation in the numbers of vertebrae in each of the postcervical regions of cetaceans than in the dog. The numbers of thoracic vertebrae vary between *Tursiops* and *Ziphius*: there are 12-14 thoracics in *Tursiops* and 9-11 in *Ziphius*. In cetaceans, the lumbar region has more vertebrae than that of many terrestrial mammals, significantly more so in *Tursiops* (16-19) than in *Ziphius* (7-9), however the lumbar section of *Ziphius* is greater in length than that of *Tursiops*. As in all other cetaceans, there has been a substantial reduction of the pelvic girdle and subsequent elimination (by definition) of the sacral vertebrae. The caudal regions have also been elongated to varying degrees. The vertebral formula that summarises the range of these numbers for *Tursiops* is C7:T12-14:L16-19:S0:Ca24-28 and for *Ziphius* is C7:T9-11:L7-9:S0:Ca19-22 (Figs 6b and 6c).

There is a bony channel, the neural canal (Fig. 6b), located within the neural arches, along the dorsal aspects of the vertebral bodies of the spinal column. In most mammals the neural canal is slightly larger than the enclosed spinal cord (Nickel *et al.*, 1986). In contrast, some marine mammals (e.g. seals, cetaceans and manatees) have considerably larger (i.e. 10-30X) neural canals, which accommodate the relatively large masses of epidural vasculature and/or fat (Rommel and Lowenstein, 2001; Rommel and Reynolds, 2002; Rommel *et al.*, 1993; Tomlinson, 1964; Walmsley, 1938). These epidural vascular masses are largest in deeper diving cetaceans (Ommanney, 1932; Vogl and Fisher, 1981; Vogl and Fisher, 1982; S. Rommel, pers. obs. in beaked whales and sperm whales). In the tail, there is a second bony channel formed by the chevron bones, which is located on the ventral aspect of the spinal column (Pabst, 1990; Rommel, 1990). The chevron bones form a chevron (hemal) canal, which encompasses a vascular countercurrent heat exchanger, the caudal vascular bundle (Figs 6b and 6c; Rommel and Lowenstein, 2001).

The ribs of cetaceans are positioned at a more acute angle to the long axis of the body than those of terrestrial mammals in order to accommodate decreases in lung volume with depth. The odontocete thorax has costovertebral joints that allow a large swing of the vertebral ribs, which substantially increases the mobility of the rib cage (Rommel, 1990). This extreme mobility of the rib cage presumably accommodates the lung collapse that accompanies depth-related pressure changes (Ridgway and Howard, 1979). In cetaceans, the single-headed rib attachment is at the distal tip of the relatively wide transverse processes instead of the centrum as it is in other mammals (Rommel, 1990). In contrast to *Tursiops*, in which 4-5 ribs are double-headed, 7 of the ribs in *Ziphius* are

² A trabecular mastoid is also observed in some physeteroids.

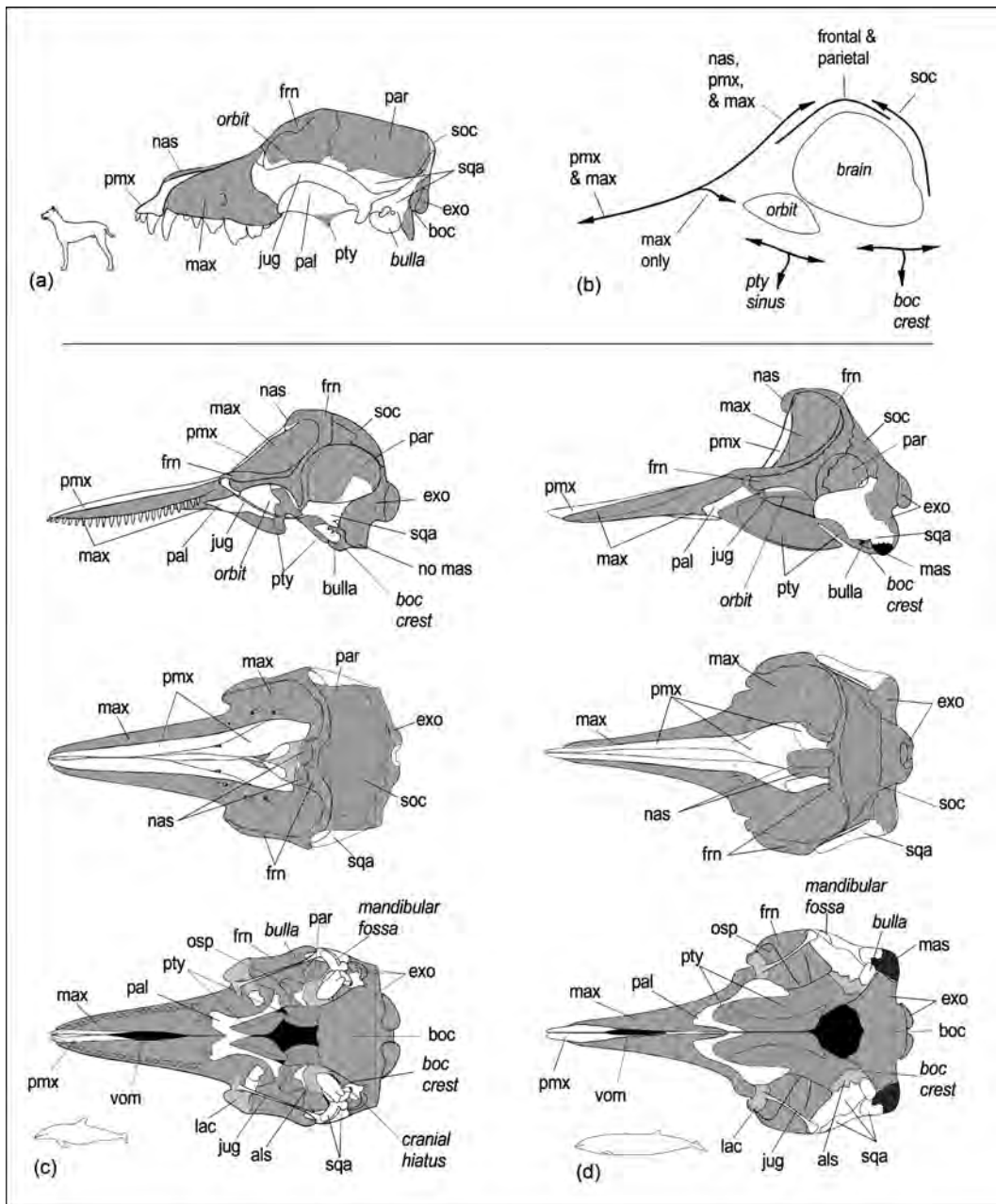


Fig. 4. Bones of the domestic dog skull (a) compared with a schematic illustration (b) showing telescoping in odontocetes and with the skull bones of *Tursiops* (c) and *Ziphius* (d). Telescoping refers to the elongation of the rostral elements (both fore and aft in the case of the premaxillary and maxillary bones), the dorso-rostral movement of the caudal elements (particularly the supraoccipital bone) and the overlapping of the margins of several bones. One major consequence of telescoping is the displacement of the external nares (and the associated nasal bones) to the dorsal apex of the skull. One of the most striking differences between the *Tursiops* and *Ziphius* skulls is the relatively massive pterygoid bones of the latter. The nasal bones of beaked whales are more prominent and extend from the skull apex. *Tursiops* has extensive tooth rows; in contrast *Ziphius* has no maxillary teeth. The dog and *Tursiops* skulls are adapted from Rommel *et al.* (2002). The *Ziphius* skull was drawn from skulls S-95-Zc-21 and SWF-Zc-8681-B (courtesy of N. Barros and D. Odell), from photographs of Smithsonian Institution skull #504094 and from photographs courtesy of A. van Helden and D. Allen.

double-headed. This arrangement may contribute to the function (e.g. mechanical support or pumping action) of thoracic retia mirabilia located on the dorsal aspect of the thoracic cavity (Fig. 7) by placing the costovertebral hinges closer to the lateral margins of the retia. Delphinids have bony sternal ribs, whereas those of beaked whales are cartilaginous. The sternum of *Tursiops* is composed of 3-4 sternabrae, whereas that of *Ziphius* is 5-6. These morphological differences might produce different dynamics during changes of the thorax in response to diving and thus alter some of the physical properties of the air-filled spaces. This is an area requiring further research, particularly because we do not know at what depth beaked whale lungs collapse.

The air-filled spaces

In addition to the flexible rib cage, cetacean respiratory systems possess morphological specialisations supportive of an aquatic lifestyle (Pabst *et al.*, 1999). These specialisations involve the blowhole, the air spaces of the head, the larynx and the terminal airways of the lung.

The single blowhole (external nares) of most odontocetes is at the top of the head (Fig. 7). During submergence, the air passages are closed tightly by the action of the nasal plug that covers the internal respiratory openings (Fig. 8). The nasal plug sits tightly against the superior bony nares and seals the entrance to the air passages when the nasal plug muscles are relaxed (Lawrence and Schevill, 1956; Mead, 1975).

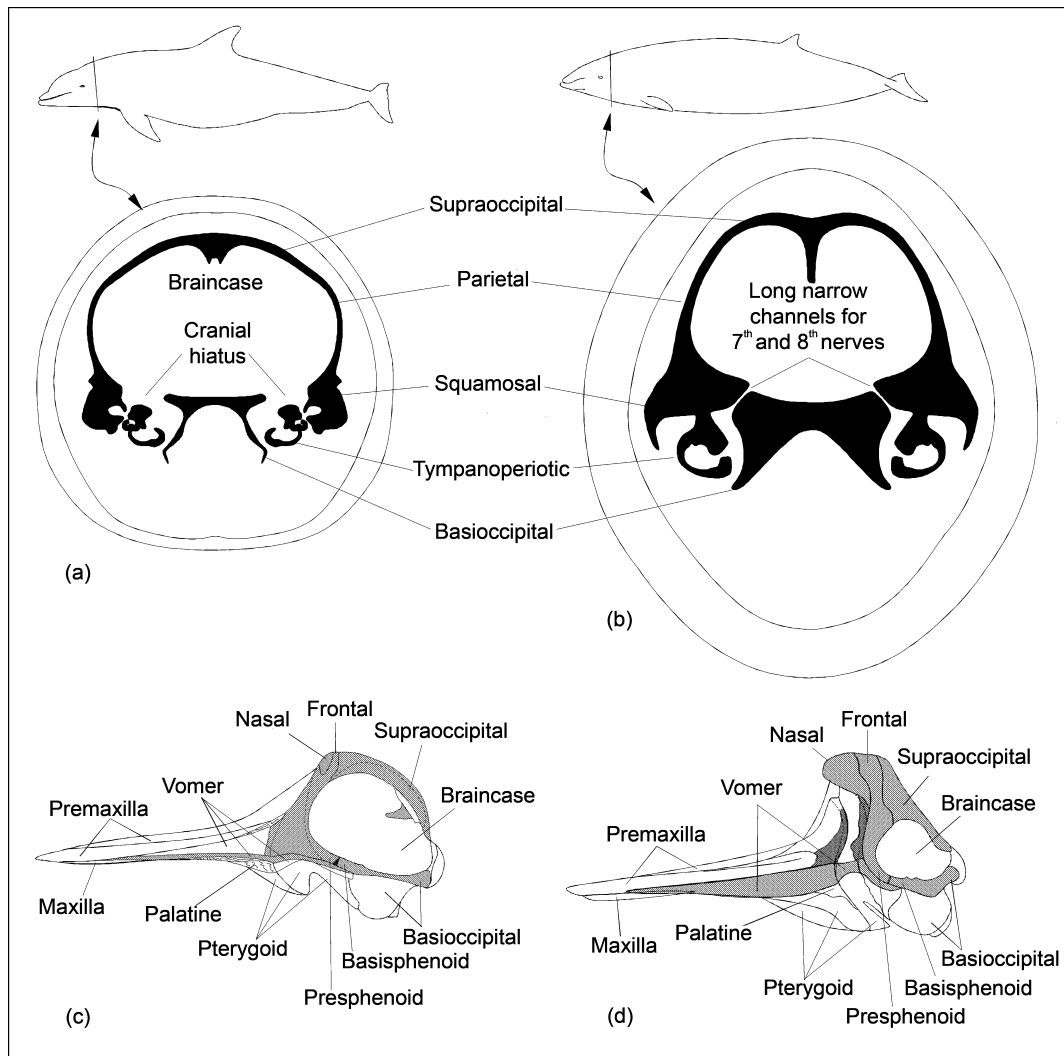


Fig. 5. Cross-sections of the skulls of *Tursiops* (a) and *Ziphius* (b). The cross sections (at the level of the ear) are scaled to have similar areas of braincase. In *Tursiops*, the pathway out of the braincase for the VIIth & VIIIth cranial nerves is a short open cranial hiatus (Rommel, 1990) bordered by relatively thin bones, whereas in *Ziphius* it is a narrow, relatively long channel. The ziphiid basioccipital bones are relatively massive with thick ventrolateral crests; in contrast, delphinid basioccipital bones are relatively long and tall, but thin and laterally cupped. Note that in contrast to the *Ziphius* calf cross-section, the adult head would have a greater amount of bone and the brain size would be different. The cross section of an adult *Tursiops* is after Chapla and Rommel (2003) and that of *Ziphius* is after a scan of a calf (courtesy of T. Cranford). Midsagittal sections of an adult *Tursiops* (c; after Rommel, 1990) and an adult *Ziphius* (d; drawn from photographs of a sectioned skull at the Museum of New Zealand Te Papa Tongarewa).

The anatomy of the blowhole vestibule and its associated air sacs varies within, as well as between, odontocete species (Mead, 1975), yet the overall echolocating functions are believed to be similar. In *Ziphius*, the vestibule is longer and more horizontal than in *Tursiops* (Fig. 8) and *Ziphius* has no vestibular sacs, no rostral components of the nasofrontal sacs and the right caudal component of the nasal sacs extends up and over the apex of the skull (Heyning, 1989a). In some *Ziphius* males, there are relatively small, left (caudal) nasal sacs, which are vestigial or absent in females (Heyning, 1989b). The premaxillary sacs, which lie on the dorsal aspect of the premaxillary bones, just rostral to the bony nares, are asymmetrical, the right being several times larger than the left. In adult *Ziphius* males, there is a rostral extension of the right premaxillary sac that is (uniquely) not in contact with the premaxillary bone (Heyning, 1989a). In *Tursiops*, there are small accessory sacs on the lateral margins of the premaxillary sacs (Schenkkan, 1971; Mead, 1975). In contrast, *Ziphius* has no well-defined accessory sacs (Heyning, 1989a). Based on

simple physics, these differences in air sac geometry may influence the mechanical responses of the head to anthropogenic ensonification.

Odontocetes have air sinuses surrounding the bones associated with hearing; the peribullar and pterygoid sinuses (Figs 8 and 9). These air sinuses are continuous with each other (Chapla and Rommel, 2003) and have been described by Boeninghaus (1904) and Fraser and Purves (1960) as highly vascularised (see below; Fig. 9) and filled with a coarse albuminous foam, which may help these air-filled structures resist pressures associated with depth as well as with acoustic isolation. The odontocete larynx is very specialised – its cartilages form an elongate goosebeak (Reidenburg and Laitman, 1987). The laryngeal cartilages fit snugly into the nasal passage and the palatopharyngeal sphincter muscle keeps the goosebeak firmly sealed in an almost vertical intranarial position (Lawrence and Schevill, 1956). These morphological features effectively separate the respiratory tract from the digestive tract to a greater extent than is

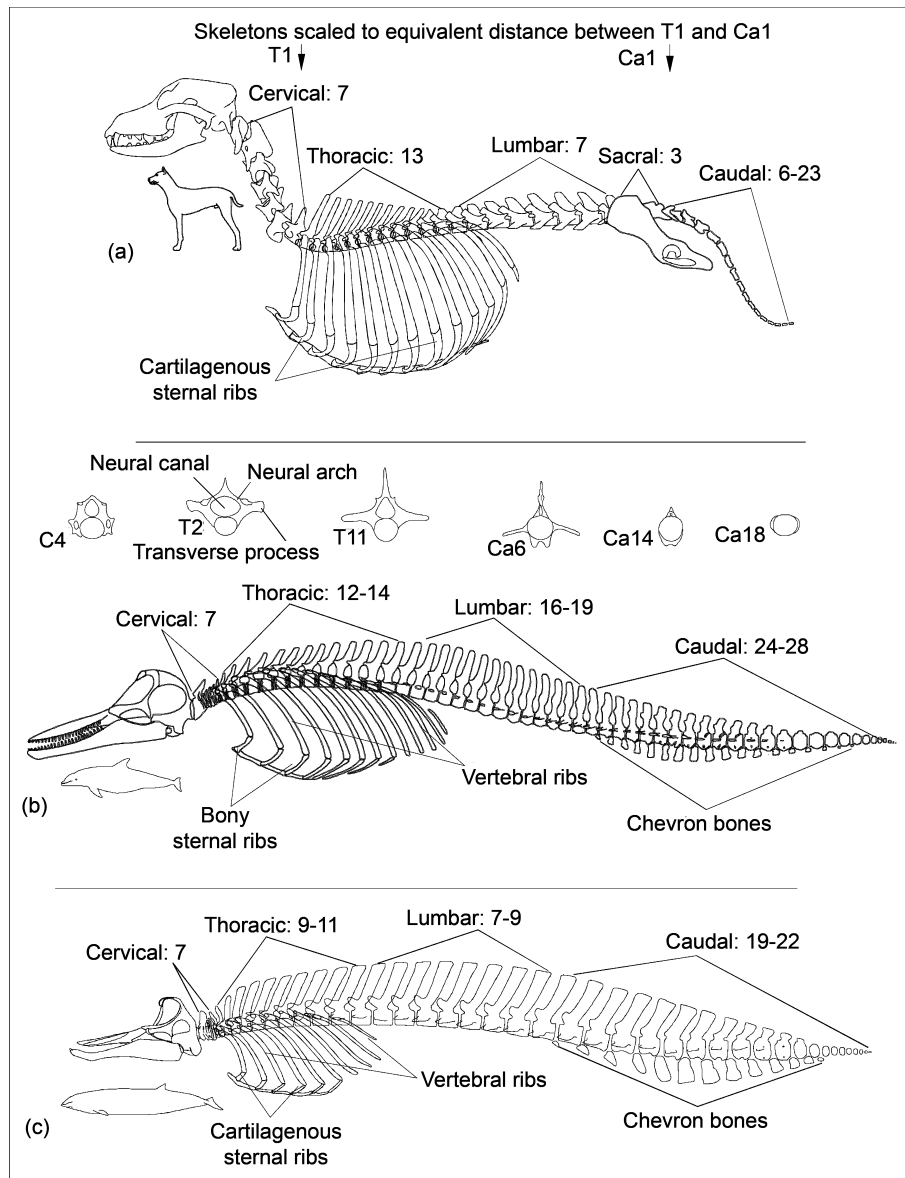


Fig. 6. The axial skeletons and rib cages of the domestic dog (a) compared to those of *Tursiops* (b) and *Ziphius* (c). The caudal region of *Tursiops* has 24-28 vertebrae while that of *Ziphius*, 19-22, depending on the individual. The neural canals are the dorsal, vertebral bony channels extending from the base of the skull to the tail, in which are contained the spinal cord and associated blood vessels. The ventrally located chevron bones enclose the chevron canal, in which are found the arteries and veins of the caudal vascular bundle. (Redrawn after Rommel and Reynolds, 2002).

found in any other mammal (Figs 7b and 7c; Reidenburg and Laitman, 1987). The complex head and throat musculature manipulates the gas pressures in the air spaces of the head and thus can change the acoustic properties of the air spaces and the adjacent structures (Coulombe *et al.*, 1965).

The thoracic cavity (Figs 7a and 7b) contains (among other structures) the heart, lungs, great vessels and in cetaceans and sirenians, the thoracic retia (McFarland *et al.*, 1979; Rommel and Lowenstein, 2001). In *Tursiops*, the cranial aspect of the lung extends significantly beyond the level of the first rib (Fig. 7a), in close proximity to the skull (McFarland *et al.*, 1979). The terminal airways of cetacean lungs are reinforced with cartilage up to the alveoli (Fig. 7d; e.g. Ridgway *et al.*, 1974). Additionally, the cetacean bronchial tree has circular muscular and elastic sphincters at the entrance to the alveoli (Fig. 7d; Drabek and Kooyman, 1983; Kooyman, 1973; Scholander, 1940). It has been hypothesised that bronchial sphincters regulate airflow to and from the alveoli during a dive (reviewed in Drabek and

Kooyman, 1983). Under compression, the alveoli in the cetacean lung collapse and gas from them can be forced into the reinforced upper airways of the bronchial tree. Thus, nitrogen is isolated from the site of gas exchange, reducing its uptake into tissues and mitigating against potentially detrimental excess nitrogen absorption (reviewed in Pabst *et al.*, 1999; Ponganis *et al.*, 2003). The microanatomy of beaked whale lungs has not been described and is therefore an area requiring future research.

In cetaceans, the ventromedial margins of the lungs embrace the heart (Fig. 7e), so the heart influences the geometry of the lungs. These single-lobed lungs change shape with respiration and depth and the heart affects the size and shape of the lungs because gas distribution in the lungs changes, but the shape of the heart remains relatively unchanged. Additionally, because of the mobility of the ribs, the size and shape of the lungs change in a manner different than do those of a terrestrial animal with a rigid rib cage and multilobed lung (Rommel, 1990). Since respiratory systems contain numerous gas-

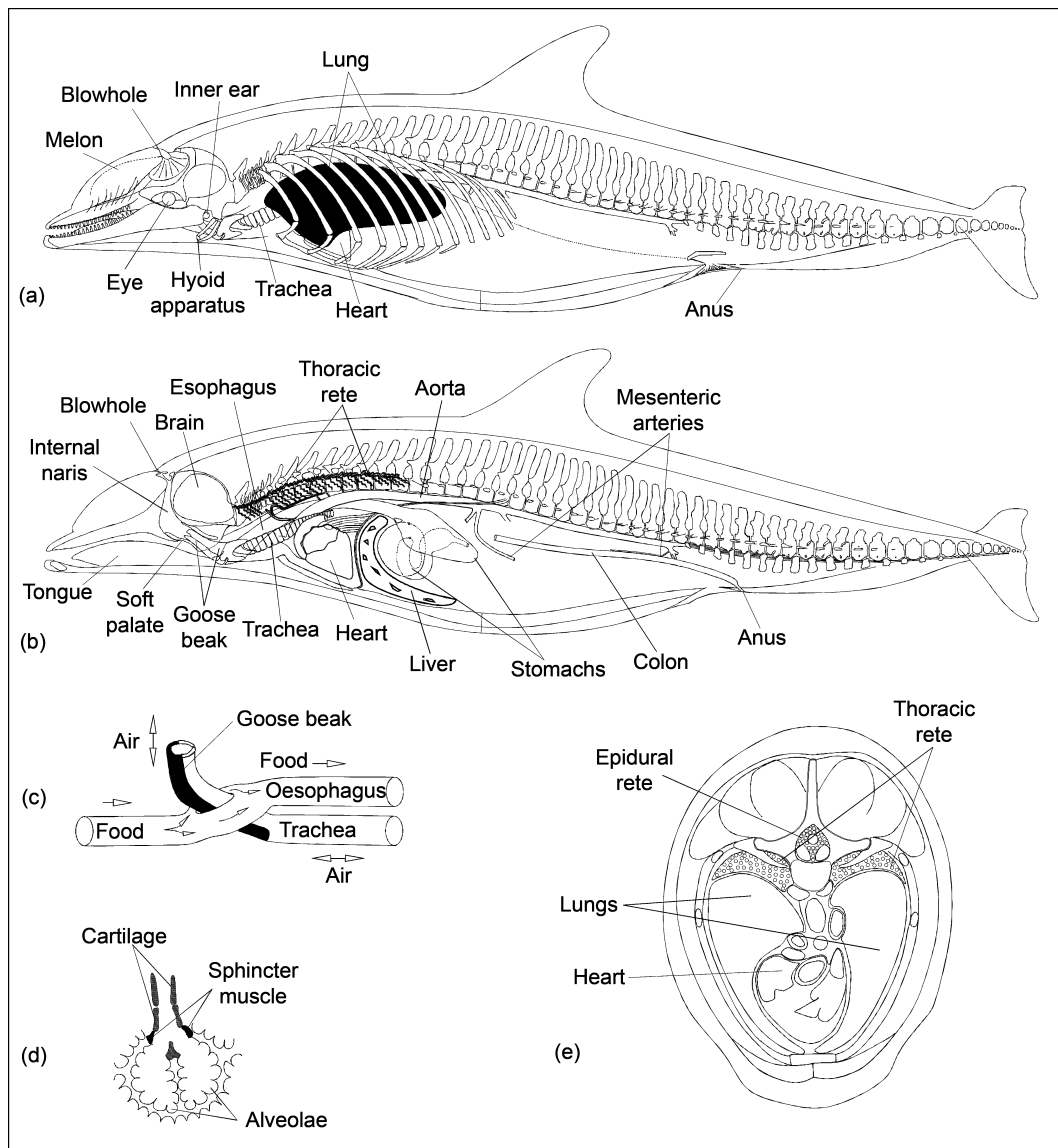


Fig. 7. The major respiratory and thoracic arterial pathways are illustrated for *Tursiops* (a, b). Note the structure of the oesophagus and trachea (b, c) and the reinforced terminal airways of the cetacean lung with sphincter muscles surrounding the distal bronchioles (d). The lungs with a heart in between (e) are a complex shape that will have different resonant responses to ensonification from a simple spherical model. (a-b adapted from Rommel and Lowenstein, 2001; c-d adapted from Pabst *et al.*, 1999; e adapted from Rommel *et al.*, 2003).

filled spaces, the pressure exerted on them at depth affects their volume, shape and thus their resonant frequencies. The shapes of compressed cetacean lungs and the thorax are also influenced by small changes in blood volume within the thoracic retia mirabilia (Figs 7e and 10c-e; Hui, 1975). Although the thoracic retia have not yet been described in beaked whales, it has been assumed (because they are deep divers and their retia are relatively large) that filling these retia with blood may have a noticeable influence on internal thoracic shape, particularly with depth.

The actions of the liver and abdominal organs pressing against the diaphragm, in concert with abdominal muscle contractions, affect gas pressure in and the distribution of mechanical forces on the lungs. Appendicular-muscle-dominated locomotors (such as the dog) couple different sorts of respiratory and locomotory abdominal forces (Bramble and Jenkins, 1993) compared to axial-muscle-dominated locomotors (such as the cetaceans; Pabst, 1990). This action has not been investigated in cetaceans, but it is

likely that it plays some role in altering the physical properties of the pleural cavity and the flow of venous blood and therefore may be important in any mechanical analysis of this region.

The vascular system

The mammalian brain and spinal cord are sensitive to low oxygen levels, subtle temperature changes and mechanical insult (Baker, 1979; Caputa *et al.*, 1967; McFarland *et al.*, 1979). The vascular system helps avoid these potential problems. Mammalian brains are commonly supplied either solely by, or by combinations of the following paired vessels: internal carotid, external carotid and vertebral arteries and less commonly by the supreme intercostal arteries (Fig. 10; Nickel *et al.*, 1981; Rommel, 2003; Slijper, 1936). In cetaceans, the internal carotid terminates within the tympanic bulla but contributes blood to the fibro-venous plexus (FVP), which is associated with the pterygoid and peribullar sinuses (Fig. 9, Fraser and Purves, 1960). These FVPs do contain some arteries (Fraser and Purves, 1960) but

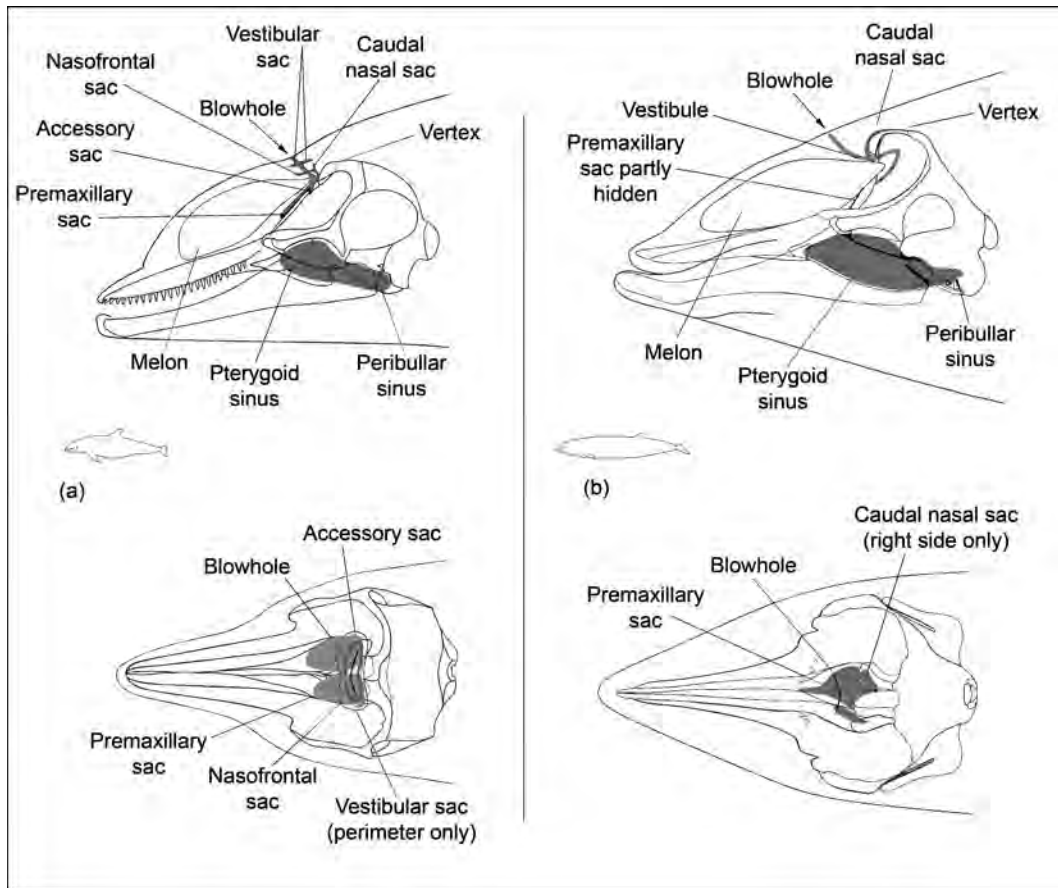


Fig. 8. Left lateral and dorsal views of the extracranial sinuses in *Tursiops* (a) and *Ziphius* (b). Arrows point to the blowholes and are parallel to the vestibules. The dorsocranial/supraorbital air sacs and sinuses associated with vocalisation and echolocation are much more extensive and convoluted in delphinids than in ziphiids. The pterygoid and peribullar sinuses of ziphiids are much larger than those of delphinids. The dorsal and lateral views of the air sacs of *Tursiops* are adapted from Mead (1975), those of *Ziphius* from Heyning (1989a).

are mostly venous vascular structures³. The cetacean brain is supplied almost exclusively by the epidural retia via the thoracic retia (Breschet, 1836; Boenninghaus, 1904; Fraser and Purves, 1960; Galliano *et al.*, 1966; Nagel *et al.*, 1968; McFarland *et al.*, 1979). These vascular structures have not yet been fully described for beaked whales.

In most cetaceans, the blood delivered to the brain leaves the thoracic aorta via the supreme intercostal arteries and supplies the thoracic retia from their lateral margins (Figs 10d and 10e). The blood then flows towards the midline and into the epidural (spinal) retia mirabilia of the neural canal (Wilson, 1879; McFarland *et al.*, 1979) and is directed

towards the head to supply the brain (Fig. 10c). Interestingly, it has been suggested that the sperm whale (*Physeter macrocephalus*) brain may be supplied in a slightly different manner (Melnikov, 1997) and because of their phylogenetic proximity (Rice, 1998), it is reasonable to assume that beaked whale morphology approximates that of the condition in *Physeter*. This is a potentially important area for future research.

In the cetaceans for which thoracic and epidural retia have been described, the right and left sides of these vascular structures have little or no communication and there is an incomplete circle of Willis, potentially supplying the right and left sides of the brain independently (McFarland *et al.*, 1979; Nakajima, 1961; Vogl and Fisher, 1981; 1982; Walmsley, 1938; Wilson, 1879). This bilateral isolation of paired supplies may have profound implications on hemispherical sleep (Baker, 1979; Baker and Chapman, 1977; McCormick, 1965; Oleg *et al.*, 2003; Ridgway, 1990) and other important physiological processes.

Blood flow is not only separated at the brain. In general, mammals possess two venous returns from their extremities: one deep and warmed; one superficial and cooled (Fig. 11). In the deep veins, which are adjacent to nutrient arterial supplies, countercurrent heat exchange (CCHE) occurs if the temperature of the arteries is higher than that of the veins (Figs 11-13; Schmidt-Nielsen, 1990; Scholander, 1940; Scholander and Schevill, 1955); warmed blood is returned and body heat is trapped in the core. Arteriovenous anastomoses (AVAs), can bypass the capillaries and bring relatively large volumes of blood close to the skin surface to

³ FVPs have been described as retia mirabilia but should be classed by themselves. Retia mirabilia (singular- rete mirabile) in the thoracic and cranial regions have been studied by many workers (Breschet, 1836; Wilson, 1879; Boenninghaus, 1904; Ommanney, 1932; Slijper, 1936; Walmsley, 1938; Fawcett, 1942; Fraser and Purves, 1960; Nakajima, 1961; Hosokawa and Kamiya, 1965; Galliano *et al.*, 1966; McFarland *et al.*, 1979; Vogl and Fisher, 1981; 1982; Shadwick and Gosline, 1994; they were reviewed by Geisler and Lou, 1998), but they are still poorly understood, in part because of the variety of terms (e.g. basicranial rete, ophthalmic rete, orbital rete, fibro-venous plexus, carotid rete, internal carotid rete, rostral rete, blood vascular bundle) used to describe them; in some references (e.g. McFarland *et al.*, 1979), several different terms are used to label the same structure; conversely, the same term has been used to describe different structures in different individuals. The pterygoid and ophthalmic venous plexuses and the maxillary arterial rete mirabile of the cat and the palatine venous plexus of the dog (Schaller, 1992), which are involved with heat exchange, could be homologous to the FVP. The arterial plexuses of the cetacean braincase may be homologous to the rostral internal carotid arterial plexus of terrestrial mammals (Geisler and Lou, 1998).

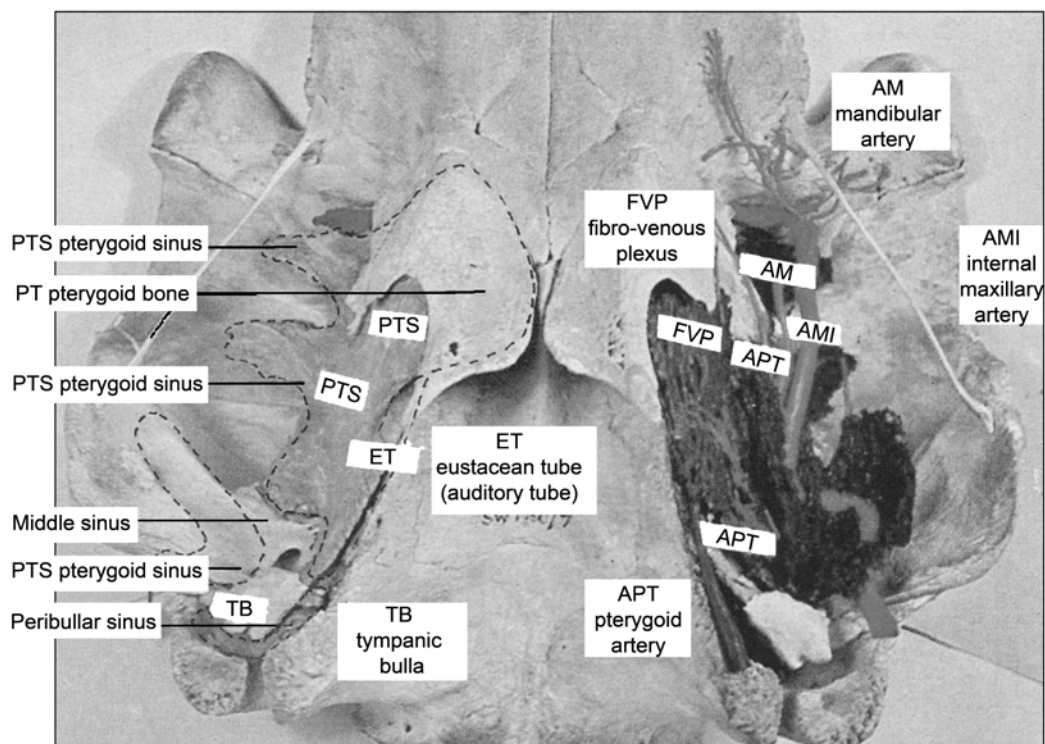


Fig. 9. Skull of a young pilot whale in which the peribullar and pterygoid air sinus system (left) and its vascular system have been injected (on the right) with polyester resin (Fraser and Purves, 1960). The peribullar and pterygoid sinuses extend from the hollow cavity of the pterygoid bone caudally to the region surrounding the tympanic bulla. The FVP is a mostly-venous plexus that surrounds these air sinuses. Both the air sinuses and the FVP are surrounded by a mass of acoustic lipids that extend from the hollow channel of the mandible to the pterygoid and tympano-periotic bones medially. Beaked whale pterygoid sinuses and associated fat structures are massive (Cranford *et al.*, 2003; Koopman *et al.*, 2003b) and their FVPs are presumed to be correspondingly larger than those of the delphinids.

maximise heat exchange with the environment (Fig. 11b; Bryden and Molyneux, 1978; Elsner *et al.*, 1974). Blood returning in these veins is relatively cool (Hales, 1985). In most mammals, the warmed and cooled venous returns are usually mixed at the proximal end of the extremity. In some cases, such as the brain coolers of ungulates and carnivores, evaporatively cooled blood from the nose is used to reduce the temperature of blood going to the brain (Fig. 11c) before joining with the central venous return, thereby allowing the brain to operate at a temperature lower than that of the body core (reviewed in Baker, 1979; Schmidt-Nielsen, 1990; Taylor and Lyman, 1972).

In mammals, CCHes have many configurations in addition to the venous lake surrounding the arterial rete at the base of the brain (Caputa *et al.*, 1967; Caputa *et al.*, 1983; Taylor and Lyman, 1972; illustrated for the antelope in Fig. 11c). Increasing the surface area of contact between the arteries and veins in different ways optimises these CCHes. Three examples of CCHes found in cetaceans are illustrated in Fig. 11d. On the left is a flat array of juxtaposed arteries and veins found in the reproductive coolers of cetaceans (Rommel *et al.*, 1992; Pabst *et al.*, 1998), in the middle is a vascular bundle, an array of relatively straight, parallel channels, an optimum configuration for CCHes (Scholander, 1940), such as is found in the chevron canals of cetacea (Fig. 13c; Rommel and Lowenstein, 2001). On the right (Fig. 11d) is a periarterial venous rete (PAVR), which is a rosette of veins surrounding an artery. These CCHes are found in the circulation of cetacean fins (Figs 13d and 13e), flukes and flippers (Scholander, 1940; Scholander and Schevill, 1955).

Superficial veins of a cetacean can supply cooled blood to the body core (Fig. 12a). The veins carrying this blood feed into bilaterally paired reproductive coolers (Figs 12d-g) (Rommel *et al.*, 1992; Pabst *et al.*, 1998). In addition to providing thermoregulation for the reproductive system, cooled blood from the periphery is also returned to the heart via large epidural veins (Figs 12d; Figs 13 and 14), which perform some of the functions of the azygous system in other mammals (Rommel *et al.*, 1993; Tomlinson, 1964). In deep divers, such as beaked whales and sperm whales, these epidural veins are even larger than those observed in delphinids (S. Rommel, pers. obs.). In *Tursiops*, the epidural venous blood may return to the heart via five very enlarged, right intercostal veins to join the cranial vena cava (Figs 13a; 14b and 14c). Alternatively, during a dive, epidural blood may continue to flow in a caudal direction beyond the intercostal veins so that blood from the brain pools as far away from the brain as possible, as has been hypothesised for seals (Rommel *et al.*, 1993; Ronald *et al.*, 1977).

Cooled blood supplied by superficial veins to the epidural veins could potentially exchange heat with the epidural (arterial) retia and/or return cooled blood to the cranial thorax. Additionally, it may cause a change in the local temperature of the spinal cord and juxtaposed veins (Rommel *et al.*, 1993). This hypothesis is supported by the regional heterothermy observed in colonic temperature profiles for seals, dolphins and manatees (Rommel *et al.*, 1992; 1994; 1995; 1998; 2003; Pabst *et al.*, 1995; 1996; 1998). Additionally, superficial veins cranial to the dorsal fin (Fig. 12a) may provide cooled blood that can be juxtaposed to the arterial retia in the head and neck. This morphology has not been described in sufficient detail in

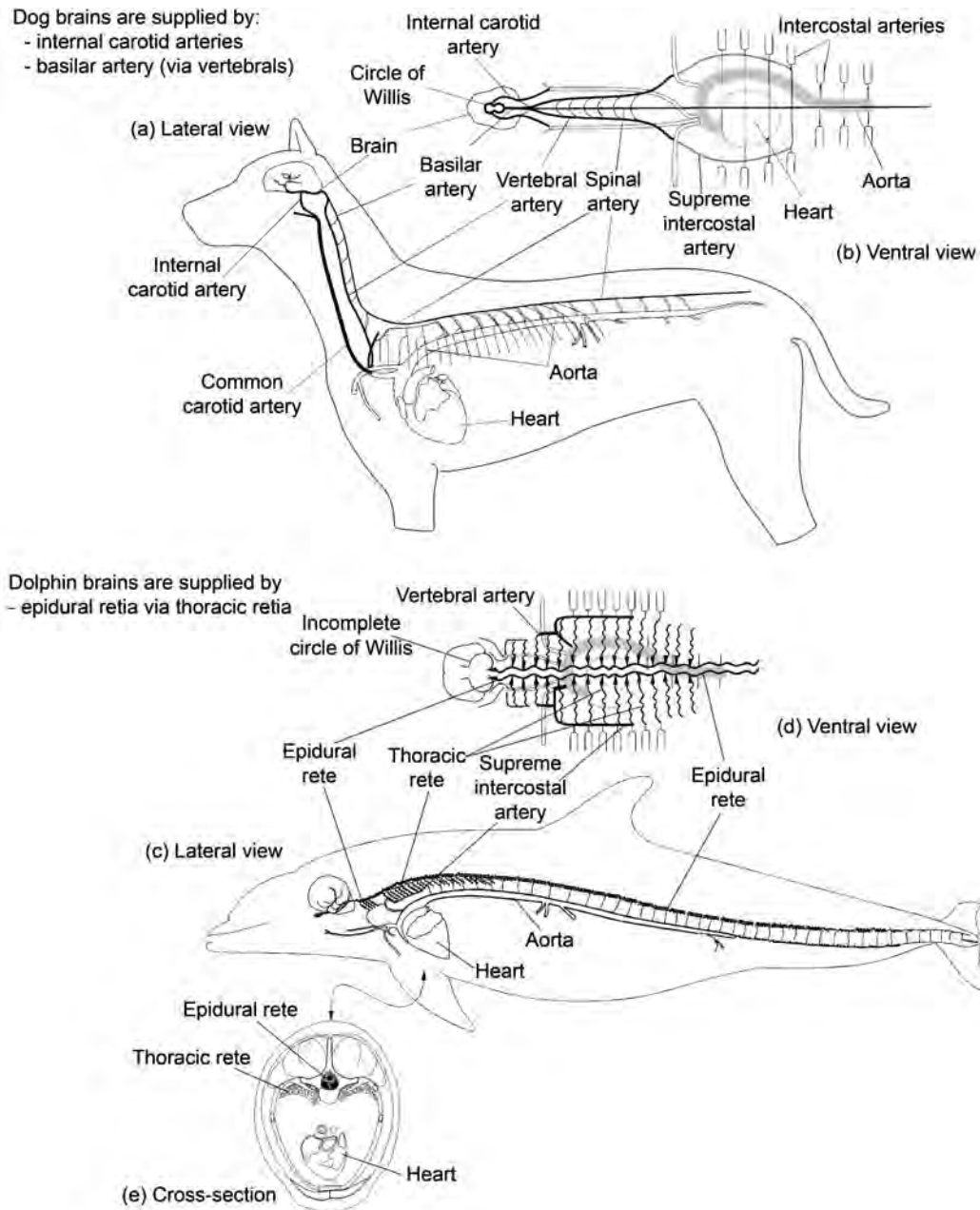


Fig. 10. Schematic of arterial circulation in the domestic dog (a-b) compared with that of the bottlenose dolphin (c-e). The arterial circulation in *Tursiops* is assumed to be representative of brain circulation of most cetacea. The cross section, e, which is at the level of the heart, illustrates the positions of the epidural retia around the cord and the thoracic retia dorsal to the lungs. Illustration adapted from Rommel (2003).

any cetacean and should be considered to be an important area of future research due to the significant implications of spinal cord heterothermy.

The morphology of the vascular system allows us to speculate on some functions that might be important in interpreting strandings of deep divers. It is clearly possible that cooled blood deep within the body may change some of the physical parameters, (e.g. viscosity, solubility and pH) of tissues and fluids. Cooled blood could possibly change physiological parameters e.g. nervous response time, balance (because of temperature changes in fluid density within the semi-circular canals) and acoustic and resonant properties of tissues. The epidural and thoracic retia may also provide some control of central nervous system (CNS) temperature. This hypothesis was rejected by previous workers (e.g. Harrison and Tomlinson, 1956; McFarland *et al.*, 1979) but those investigations lacked the current

knowledge of superficial venous return (Pabst *et al.*, 1998; Figs 12a and 12b; Rommel *et al.*, 1992). It is well known that epidural cooling protects against ischaemic spinal cord damage in humans and terrestrial mammals (Marsala *et al.*, 1993) and we now know that it is possible for cooled blood to flow in the epidural veins. Since ischaemia is an important part of deep and prolonged dives, it is reasonable to assume that cooling of the CNS may occur in diving mammals in order to limit the consequences of reduced perfusion (Rommel *et al.*, 1995).

In mammals, the temperature of the CNS is also important in regulating tissue activity (Blumberg and Moltz, 1988; Caputa *et al.*, 1983; 1991; Chesy *et al.*, 1983; 1985; Miller and South, 1979; Wunnenberg, 1973) and contributes to prolonging dives in marine mammals by reducing metabolic demands (Cossins and Bowler, 1987; Elsner, 1999; Hochachka and Guppy, 1986; Ponganis *et al.*, 2003).

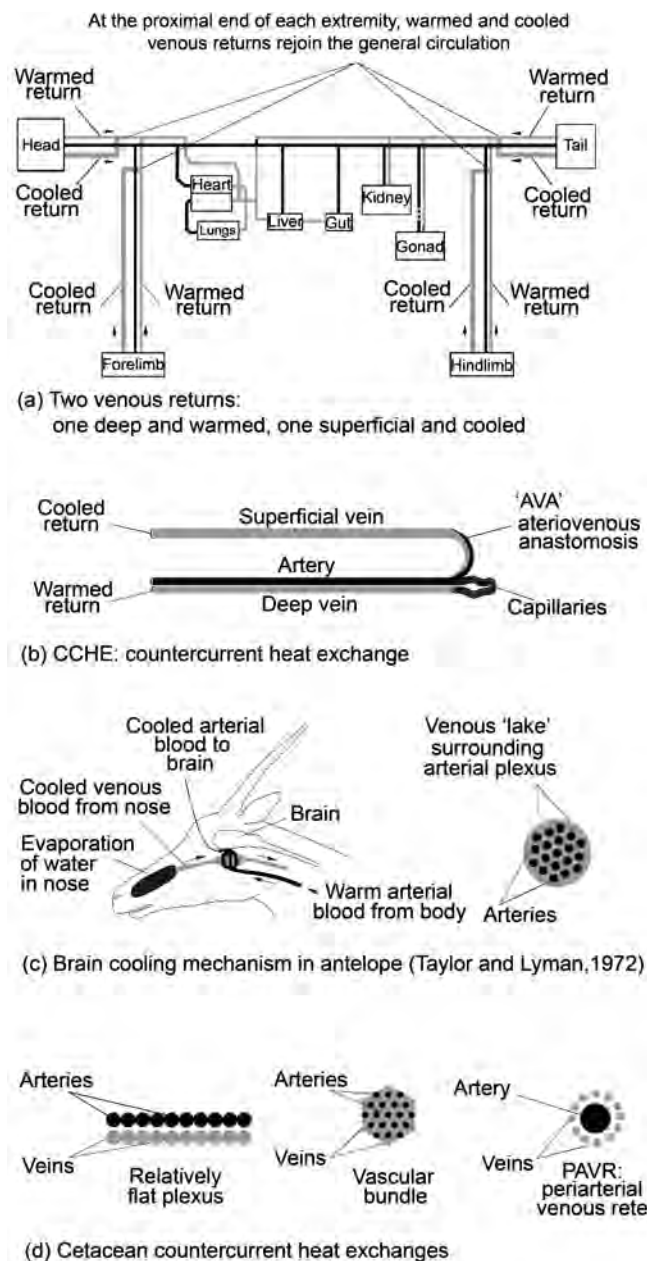


Fig. 11. a. Simplified schematic of the mammalian circulatory system, showing alternate warmed and cooled venous returns, which typically mix with each other and the central venous return at the proximal end of each extremity. b. Warmed venous return is achieved by CCHEx. Cooled venous return is achieved when veins are allowed to lose heat to the environment. AVAs allow blood to bypass capillary beds to increase the rate of blood flow in the superficial veins and increase heat loss. c. In some mammals, such as the antelope illustrated here, cooled venous blood from the nose reduces the temperature of arterial blood to the brain via a venous lake, which surrounds the arterial supply of the brain. d. Cetaceans have elaborate CCHEx, three of which are illustrated here.

The superficial venous returns from the skin and evaporatively cooled blood at or near respiratory structures provide cooled blood that could modify deep body temperatures and extend dive capabilities (Rommel *et al.*, 1995); deeper divers (such as beaked whales) could conceivably have excellent control of this thermoregulation mechanism. As previously mentioned, the concept of evaporative coolers is not unique to dolphins; they have also been described in seals (Costa, 1984; Folkow *et al.*, 1988) and are responsible for brain cooling in terrestrial mammals

(Baker, 1979; Baker and Chapman, 1977; Blumberg and Moltz, 1988). The structure involved in the CNS coolers of terrestrial mammals (rostral plexus, pterygoid plexus, ophthalmic plexus) may be homologous to some of the plexuses supplying the heads of cetaceans (Geisler and Lou, 1998).

Both the internal and external jugular veins of *Tursiops* drain the caudal margin of the FVP and there are several robust anastomoses between the internal and external jugular veins (Fig. 14a) at the base of the skull. In this region, the facial, lingual and maxillary branches join the external jugular vein and the mandibular, pterygoid and petrosal branches join the internal jugular vein. These anastomoses are located near the caudal margin of the FVP, close to where the hyoid apparatus joins the skull on the ventrolateral aspects of the basioccipital bones (tympanohyal of Ridgway *et al.*, 1974). We have been unable to find a complete description of these vascular structures for the cetacean head.

The brain is surrounded by three connective tissue layers: the dura mater (which is adherent to the bones of the braincase), the arachnoid and the pia maters (which enclose the cerebrospinal fluid [CSF] and brain, respectively). The veins of the odontocete braincase (Fig. 14c), like those of terrestrial mammals, are divided into two groups: the meningeal veins on the surface of the brain, which are deep to the dura mater and the dural sinuses, which are veins found between the dura and the braincase and which may create grooves in the skull bones.

The venous system draining the braincase and skull base is extremely complex (Fraser and Purves, 1960). The bilaterally paired FVPs consist of small-caliber, thin-walled veins extending onto the bones of the orbit, the peribullar sinus and the pterygoid sinus (Fig. 14b). Each FVP appears to also extend into the mandibular acoustic fat body, which is juxtaposed to the pterygoid and peribullar sinuses and is continuous with the acoustic fat of the mandible (Fig. 9; Boenninghaus, 1904; Fraser and Purves, 1960). The structure of this special plexus should be the focus of further work.

According to Fraser and Purves (1960), there are anastomoses (e.g. emissary veins) between the veins of the braincase and those from the FVP. The only emissary vein observed thus far (in *Tursiops*) is between the basilar dural sinus on the floor of the braincase and the internal jugular (Figs 13a and 14c). In *Tursiops*, this emissary vein exits the skull via the cranial hiatus and joins the jugulars near the jugular notch between the basioccipital crest and the paroccipital process. The geometry of these veins is likely to be very important because this is the region of the haemorrhage described for a Bahamas beaked whale head (labelled 'internal auditory canal/cochlear aquaduct' in Anon., 2001). Interestingly, there is a robust plexus of branches from each internal jugular vein that surrounds each proximal carotid artery, giving the proximal internal jugular the appearance of a very large vein or venous plexus – part of this plexus is illustrated as a vasa vasorum of the external carotid in Ridgway *et al.* (1974), but our injections of *Tursiops* showed it to be much more robust than illustrated by them.

In the dog and other domestic mammals, the external jugular vein is significantly larger than the internal jugular vein (Ghoshal *et al.*, 1981; Nickel *et al.*, 1981). In contrast, the internal jugular vein may be equal to or larger than the external jugular in cetaceans (S. Rommel, pers. obs.; Fraser and Purves, 1960; Ridgway *et al.*, 1974; Slijper, 1936). The relatively large size of the delphinid internal jugular vein

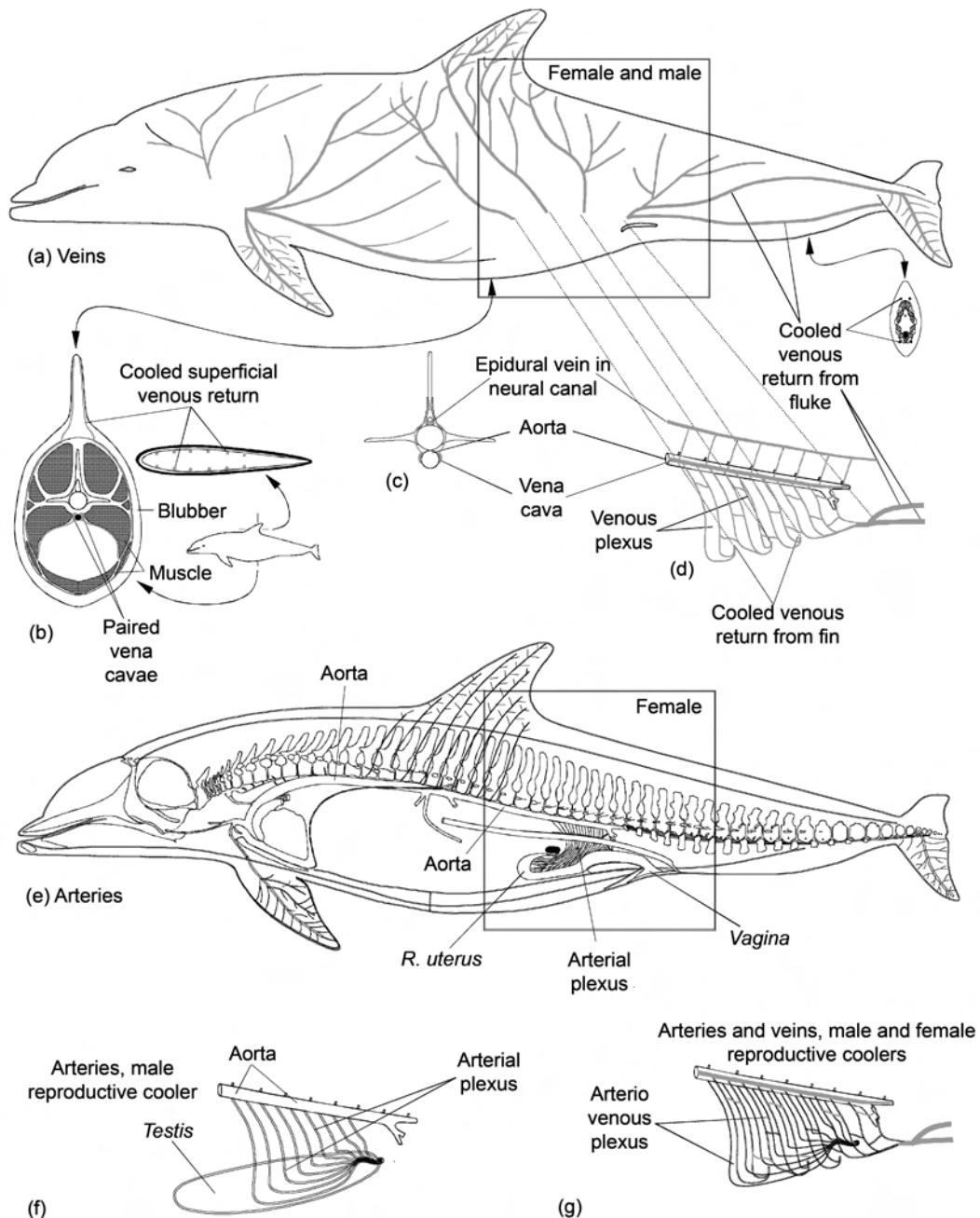


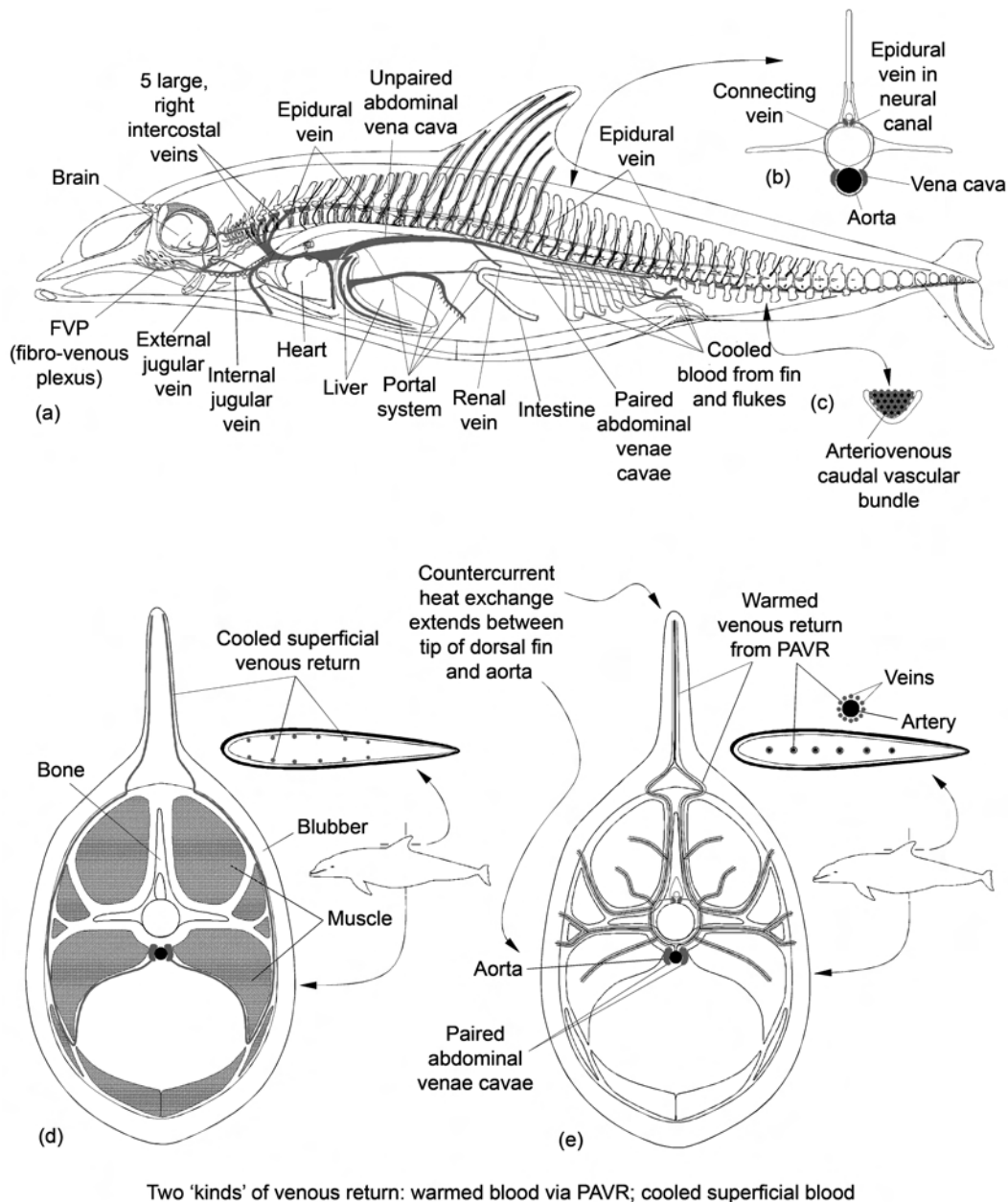
Fig. 12. Superficial veins (a-b) supply large amounts of cooled venous blood to different parts of the *Tursiops* body. In the caudal half of the body, cooled blood is supplied to a CCHE (e-f) deep within the abdomen. Note the arteriovenous reproductive plexus in which arteries are juxtaposed to cooled, superficial venous return from the dorsal fin and flukes. Heat can be transferred from the warm arteries to the cooled veins so that arterial blood does not damage the temperature sensitive reproductive tissues. In the cranial half of the body there are also superficial veins returning cooled blood; the potential for deep body cooling in this region has yet to be investigated. (Rommel *et al.*, 1992; Pabst *et al.*, 1998).

may be due to the large drainage field of the FVP(s) and the vasa vasorum of the carotid artery, as well as input of the emissary vein draining the caudal ventrolateral basilar dural sinuses within the braincase.

Other vascular structures

Typically, most cetaceans have small spleens (Rommel and Lowenstein, 2001), in contrast to the deep-diving pinnipeds, which have relatively large spleens that provide storage of red blood cells to increase haematocrit during dives (Elsner, 1999; Zapol *et al.*, 1979). Increasing hematocrit alters blood properties such as viscosity (Elsner *et al.*, 2004). Interestingly, beaked whales have much larger spleens than delphinids (Nishiwaki *et al.*, 1972) and beaked whale livers

may be relatively larger as well. Both organs filter blood and may therefore be important in the management of emboli. The large venous sinuses and muscular portal sphincters in cetacean livers (reviewed in Simpson and Gardener, 1972) may increase the hepatic entrapment of otherwise fatal portal gas emboli, which have been described in the Canary Islands (Fernández *et al.*, 2004; 2005) and UK (Jepson *et al.*, 2003) cetacean strandings. The kidney, another organ that filters blood, has been reported to have DCS-like (gas bubble) lesions in the same Canary Islands and UK strandings. Capillary fenestrae may allow fat and gas emboli to pass through them. Unfortunately, the specifics of the vascular anatomy describing these functions are inadequate.



Two 'kinds' of venous return: warmed blood via PAVR; cooled superficial blood

Fig. 13. Deep (a-c, e) and superficial (d) venous return in *Tursiops*. To expend heat, blood is routed through superficial veins in the dorsal fin (d); the blood in the superficial veins is cooled prior to entering general circulation. In contrast, to conserve heat, deep veins surrounding the arteries of the dorsal fin (e) are recruited in order to return the blood to the vena cava. The portal vein, which may be a source of gas emboli, drains the intestines and delivers blood to the liver (a). The abdominal vena cava brings venous blood from the abdominal region to the heart at the dorsocranial aspect of the liver. There is little evidence for an azygous vein in cetaceans. Due to abdominal pressures that may invoke the Valsalva phenomenon, an alternate venous return may be necessary to prevent elevated abdominal pressures from collapsing the large veins and preventing blood from returning to the heart. This return is achieved via the epidural veins (a-b), the relatively large bilaterally paired veins adjacent to the spinal cord within the neural canal. This part of the venous system may be supplied by the same cooled venous blood that regulates temperature of the reproductive system. Thus cooled blood may be located in several regions of the body and may affect physical properties (e.g. viscosity, solubility, pH) in the tissues it comes in contact with.

Finally, a number of cetacean cardiovascular adaptations, such as the large venous sinuses (Harrison and Tomlinson, 1956; Tomlinson, 1964) and convoluted pathways for blood flow (e.g. Nakajima, 1967; Slijper, 1936; Vogl and Fisher, 1981; Walmsley, 1938), may have relevance to the mitigation of gas emboli and DCS. For example, the double capillary network in the lung alveoli (reviewed in Simpson and Gardener, 1972) may help prevent transpulmonary passage (arterialisation) of venous gas emboli. The extensive meshwork of small arteries (the retia mirabilia) that perfuse the entire CNS (Viamonte *et al.*, 1968) might efficiently filter any arterialised gas emboli (Ridgway and Howard, 1979). It is notable that the retia are most developed in the deeper divers (Vogl and Fisher, 1981).

Autochthonous or venous-gas bubbles and epidural venous thrombosis have been proposed as mechanisms of spinal DCS lesions in humans (Hallenbeck *et al.*, 1975; reviewed in Francis and Mitchell, 2003). The large epidural venous spaces (Harrison and Tomlinson, 1956) and the lack of Hageman and other clotting factors and more potent heparin in cetacean blood (reviewed in Ridgway, 1972) may therefore also reduce the risk of cetacean spinal cord bubble injury.

Dive physiology

The numerous diving challenges (e.g. DCS, shallow-water blackout, nitrogen narcosis) are probably overcome by a number of anatomical, physiological and behavioural

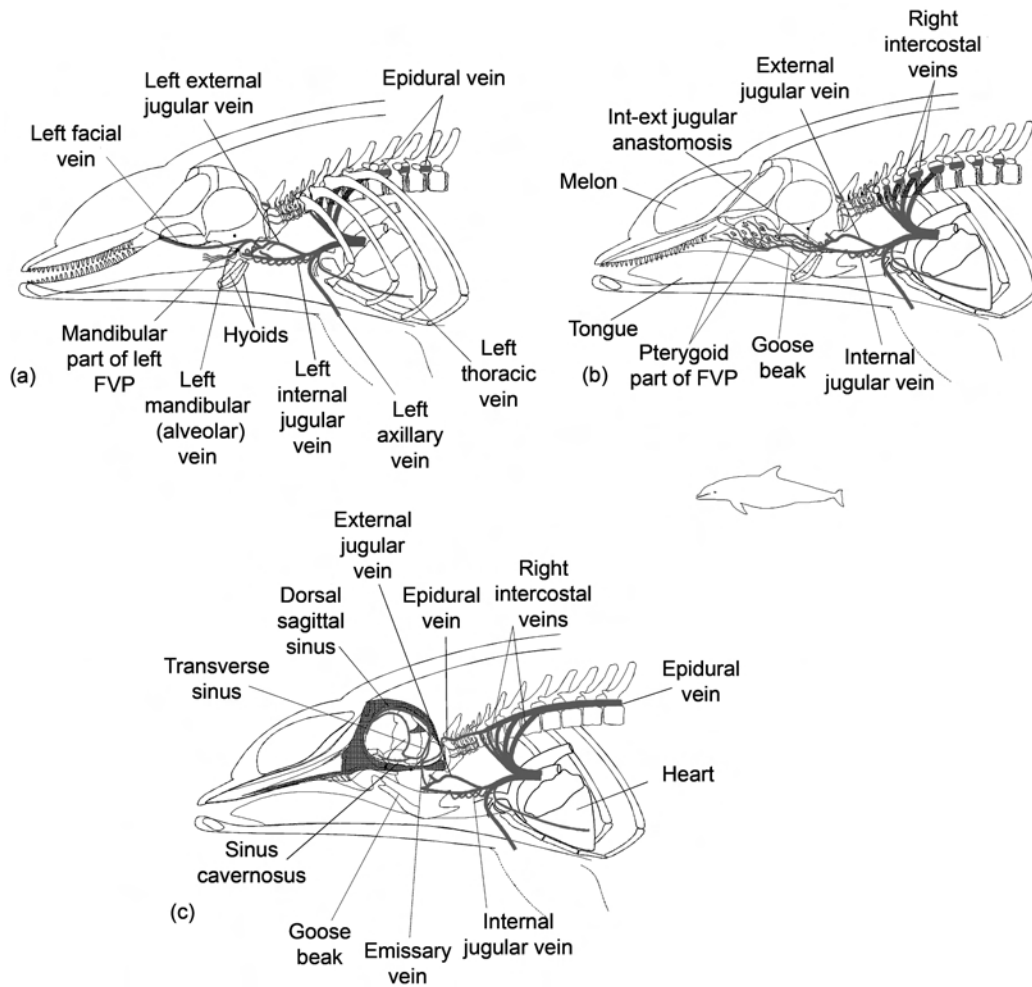


Fig. 14. Illustrations of the venous return from the head of *Tursiops*. Skull with mandible, zygomatic arch and hyoid apparatus illustrating the more superficial veins of the head (a). The internal and external jugular veins anastomose via a robust plexus near the caudal margin of the mandible. These veins drain the FVP. There is a small mandibular part of the FVP that lies near the medial aspect of the mandible. (b) Skull with hyoid apparatus and goosbeak present and the mandible and zygomatic arch removed. The largest part of the FVP is illustrated here and corresponds to that in Fig. 9. Mid-sagittal section of a skull (c), illustrating the dural sinuses and veins exiting the braincase. The emissary vein carries blood from the ventral braincase to the jugular veins.

adaptations, such as the dive response, lung collapse, controlled ascent from deep dives and surface interval (e.g. Baird *et al.*, 2004; Elsner, 1999; Ponganis *et al.*, 2003). The dive response includes a slowing heart rate (reduction in cardiac output) and a change in the distribution of peripheral resistance (change in blood flow). While diving, this response helps ensure that oxygen-sensitive tissues (e.g. the CNS and heart) maintain a supply of oxygen, while those with lower metabolic rates or that are tolerant to hypoxia receive less blood flow. Lung collapse obviates the exchange of lung gas with blood and most likely serves to minimise the uptake of nitrogen by tissues. Most studies of diving adaptation have been performed on pinnipeds (e.g. Davis *et al.*, 1983; 1991; Elsner, 1999; Kooyman *et al.*, 1981; Ponganis *et al.*, 2003), with relatively few being conducted on cetaceans (e.g. Scholander, 1940; Ridgway and Howard, 1979). Although it is generally accepted that these physiological responses to diving are shared across both cetacean and pinniped taxa, none of these phenomena or their physiological impacts have been quantified in beaked whales.

Research on freely diving seals suggests that the redistribution of blood flow during diving is a graded response, with restriction of blood flow to certain organs

occurring only as oxygen stores become depleted (e.g. Davis *et al.*, 1991; Ponganis *et al.*, 2003; Ronald *et al.*, 1977; Zapol *et al.*, 1979). Nonetheless, in forced dives, peripheral vasoconstriction redistributes blood so that the brain maintains constant vascular flow at the expense of other tissues, which is similar to results observed during unrestrained deep dives (Kooyman, 1985; Ponganis *et al.*, 2003). Few similar lines of forced-dive research have been conducted on cetaceans (Scholander, 1940).

During a dive, if the pressure exerted on a gas is doubled, its volume is halved. Water exerts approximately one atmosphere of pressure for every 10m of depth, so a marine mammal at 10m experiences twice the hydrostatic pressure it would at the surface and the air within its lungs will occupy one half of its volume. Hydrostatic pressures experienced by diving marine mammals, in conjunction with anatomical structures supporting the respiratory system, influence the depth at which lung collapse occurs (Hui, 1975). Without differentiating between lung and alveolar collapse, dive experiments suggest that nitrogen exchange ceases at depths of approximately 70m in bottlenose dolphins (Ridgway and Howard, 1979) and 30-50m in seals (Falke *et al.*, 1985; Kooyman, 1985; Zapol *et al.*, 1979). A contributory factor to the different depths may

be that seals exhale before diving (Kooyman *et al.*, 1970; Scholander, 1940), whereas dolphins dive on a lung full of air (Ridgway *et al.*, 1969).

The effects of increased hydrostatic pressure are not limited to volume and geometry of the thoracic cavity and its contents. Increased hydrostatic pressure also acts on lung air (before complete collapse), by increasing the amount of nitrogen that dissolves into the blood across the alveolar membrane. Additionally, raising the pressure also increases the absolute amount of gas that can be dissolved into other tissues and fluids. As nitrogen is biologically inert and lipophilic, it readily accumulates in lipid-rich tissue (e.g. lipids, bone marrow). If tissues become nitrogen supersaturated during rapid ascent, nitrogen can rapidly come out of solution, potentially forming bubbles in lipid-rich tissues and regions supportive of cavitation (e.g. localised negative pressure sites associated with the motion of joints). If large enough and in sufficient quantities, bubbles may result in vascular emboli, cause haemorrhage in capillary dense tissues and create localised regions that apply pressure to nervous tissue. If severe enough, the presence of the bubbles in humans may cause symptoms of DCS, including pain, disorientation, nausea and neurological impairment. Accumulation of gas emboli in joints and the associated pain is termed 'the bends'. Additionally, bubbles may damage lipid tissues (where dissolved nitrogen gas concentrations may be relatively high) and release fat emboli into circulation (Ponganis *et al.*, 2003).

In cetaceans, the extensive arrangement of extracranial arterial retia is an adaptation to diving and is more extensive in deeper divers (Vogl and Fisher, 1982); however, a lack of these structures does not preclude deep diving or extended breath-holds, because they are not found in seals or sea lions (Pabst *et al.*, 1999; Rommel and Lowenstein, 2001). Unlike seals and sea lions, cetaceans have short necks, which reduces the distance between the heart and the brain. This presumably increases the potential for mechanical injury from the systolic pulse of the heart. The brain supply of cetaceans may act as a *windkessel*, dampening pressure fluctuations resulting from the pulsatile flows produced by the heart (Galliano *et al.*, 1966; Nagel *et al.*, 1968; Shadwick and Gosline, 1994). Additionally, this vascular structure may have a function in the management of emboli. Interestingly, the short-necked sirenians also have retia similar to those of cetaceans as part of their brain blood supplies (Murie, 1872; Rommel *et al.*, 2003).

HYPOTHESISED FACTORS INVOLVED IN SONAR-RELATED STRANDING EVENTS

Gas and fat emboli

Emboli are clots, globular obstructions or gas bubbles that occlude blood vessels or damage tissues by expansion. Gas emboli are typically formed by uncontrolled dysbaric changes. When hydrostatic pressure is decreased rapidly (such as during rapid ascent from a dive), high partial pressures of gases in a saturated medium (such as blood and interstitial fluid) force gases out of solution. If the ascent rate is fast enough, gases leaving a saturated tissue form bubbles, which continue to grow with decreasing hydrostatic pressure (Boyle's Law). The growing bubbles are either trapped in tissues and cause physical damage by way of their expansion, or they can be transported by the circulatory system to sensitive tissues and cause a blockage. Obstruction of blood flow to the heart or CNS is the most

severe manifestation of gas embolism, although numerous other forms of gas emboli of varying severity exist (Francis and Mitchell, 2003).

Fat emboli were originally seen in human patients with long-bone and pelvic fractures but are now associated with a range of conditions including dysbaric osteonecrosis (DiMaio and DiMaio, 2001; Jones and Neuman, 2003; Kitano and Hayashi, 1981; Saukko and Knight, 2004). Fat emboli are believed to be formed when fatty tissue is injured, resulting in release of fat droplets into circulation. Fat emboli have been the proximal cause of death in human bone-fracture cases. The beaked whales that mass stranded in the Canary Islands in 2002 had widely disseminated fat emboli in numerous tissues. Although not diagnostic of DCS, these findings are consistent with a DCS-like or acoustically mediated mechanism of gas-bubble formation (Fernández *et al.*, 2005; Jepson *et al.*, 2003).

Acoustically mediated bubble growth

Even though marine mammals are believed to be protected from the formation of gas emboli through behavioural or physiological means, Crum and Mao (1996) produced a model suggesting that a sufficient level of acoustic exposure might cause bubbles to form and grow. One form of this is called rectified diffusion (Crum, 1980). During the compression phase of each sound wave, each bubble is reduced in size, pressure within the bubble is increased and gas diffuses out of the bubble. In the rarefaction phase of the sound wave, bubble diameter increases, pressure is reduced and gas diffuses into the bubble. Since the amount of gas moving into and out of the bubble is related to its surface area and there is a greater surface area during the rarefaction phase, the result is a net gain of gas within a bubble during each cycle of the applied sound.

Within a gas-supersaturated medium, the threshold for rectified diffusion was predicted to be lower and gas bubbles were predicted to grow, once activated, without the continued presence of an acoustic field (Crum and Mao, 1996). Houser *et al.* (2001) modelled the accumulation of gaseous nitrogen within the muscles of various cetacean species based upon known dive profiles. The results suggested that species that descend slowly and deeply, beyond the depth of lung collapse, were those likely to accumulate the most nitrogen in their muscles. This process is augmented if surface intervals of sufficient length to allow nitrogen washout are not performed regularly. Beaked whales and sperm whales were predicted to accumulate the most nitrogen, as high as 300% supersaturation, after a typical dive sequence. Thus, if such a mechanism were possible, the likelihood of gas emboli growing, when ensonified by midrange military sonar, was predicted to be greater for these types of divers (Crum *et al.*, 2005; Houser *et al.*, 2001).

Dysbaric Osteotrauma (DOT)

Osteonecrosis refers to bone and bone marrow death brought on by ischaemia. In dysbaric osteonecrosis, disruption or cessation of oxygen and/or blood supply to the bone and bone marrow brought on by harmful pressure changes, are believed to be the primary pathogenic mechanism (Hutter, 2000; Jones *et al.*, 1993). Hyperbaric exposure causing tissues to become saturated with gasses, makes individuals prone to hypobaric outgassing and outgassing due to supersaturation is believed to result in gas emboli. These emboli may expand and thus damage bone marrow, thereby releasing fatty thromboses and indirectly causing ischaemic necrosis. Alternatively, the gas emboli

may directly obstruct vascular pathways. Dysbaric osteonecrosis typically produces chronic lesions in bones and therefore does not fit with the very short time period between sonar exposures to beaked whale mass strandings. Nonetheless, chronic lesions found in the bones of sperm whales imply that even under normal circumstances, deep diving whales are vulnerable to DOT (Moore and Early, 2004). This potential vulnerability of deep diving whales, in concert with other pathogenic circumstances such as abbreviated ascent rates and prolonged surface intervals, could conceivably be the cause of severe and acute manifestations of DOT.

Such bone trauma may release fat emboli from the damaged marrow into the circulation, thereby resulting in acutely and widely disseminated thromboses and rapid death. The fat emboli suggested by Jepson and Fernández (Fernández *et al.*, 2004; 2005; Jepson *et al.*, 2003) may therefore have a far more important role than has previously been assumed. The ‘standard’ histological techniques applied to the Bahamian beaked whales were presumably inadequate to assess the presence of fat and gas emboli.

Behavioural alterations

Under the hypothesis of behavioural alteration, acoustic exposure is not the primary pathogenic mechanism; rather, it causes a behavioural response that induces beaked whales to forgo natural diving protocols in response to the sound field. Prior to lung collapse, an increased hydrostatic pressure of air within the lung causes more nitrogen to dissolve into the blood across the alveolar membranes of the lungs. An animal that has a substantial amount of nitrogen gas absorbed in its tissues and which may be frightened by sonar could be forced to alter its dive profile and ascend faster than normal. This may result in the supersaturated tissues exceeding the threshold for bubble formation in these animals (Crum *et al.*, 2005). We have learned from human divers that even slight modifications to ascent rate can be damaging or fatal. Under such a condition, rapid ascent or extended surface interval may exceed acceptable rates and/or quantities of nitrogen offloading to the extent that nitrogen bubbles evolve, forming gas emboli (Jepson *et al.*, 2003; Fernández *et al.*, 2004; 2005). Extended surface intervals are likely, perhaps even more likely, to be a critical factor influencing nitrogen tissue supersaturation and bubble pathogenesis, given that beaked whales appear to spend most of their time at depth and only limited surface intervals have been recorded (Hooker and Baird, 1999). Although these mechanisms of pathogenesis are plausible in light of recent pathobiological discoveries, conclusive evidence is elusive. Future research should therefore be open to other potential mechanisms of pathogenesis.

Resonance

Air-containing spaces in diving mammals create media interfaces with tissues and act as boundaries at which acoustic energy may be reflected and/or absorbed. These air spaces may resonate if ensonified at the appropriate frequency and amplitude. At a meeting organised by NOAA Fisheries in 2002, scientists were invited to evaluate the potential for resonance to cause damage in diving marine mammals (Anon., 2002). Resonance was modelled using a free, spherical bubble model, which should predict the maximum vibratory response during ensonification at the sphere’s resonant frequency. Results from this simplified

model (Anon., 2002) suggested that displacement due to vibration at resonance, even without the damping provided by adjacent biological tissues, may be insufficient to cause significant damage at gas-tissue boundaries. Furthermore, resonant frequencies predicted for various air spaces were below those used by the midfrequency sonar systems implicated in a previous stranding event.

Although useful, the spherical lung model may be an oversimplification. Complex structures such as lungs likely have more modes of resonance than simple structures and although the displacement of tissues at those modes should be less than at the fundamental frequency of resonance, it may still be harmful. A compressible, air-filled (there are also blood, mucus and connective tissues) lung-pair with an incompressible heart at its midline is a complex shape (Fig. 11). Such a structure will have complex modes of vibration that change as the volume and shape of the lung-pair changes with depth (damaged or diseased lungs will resonate differently). However, it is unknown how the dimensions of the lungs change with depth, how many modes of vibration there are and how the modes change with depth, blood viscosity and temperature.

Further examination of other resonance models may lead to a more accurate representation of the complex geometry of mammalian lungs and the physical properties that govern their resonant characteristics. A good understanding of the effects of size, shape, function and composition on resonance would improve our understanding of the etiology of acoustically induced lesions. Furthermore, additional measurements of vibrations on living marine mammals may provide insight into how resonance changes with depth in animals that have collapsible lung cavities.

Disseminated Intravascular Coagulation (DIC) – coagulopathy, bleeding diathesis

Another hypothesis proposed for the causes of beaked whale strandings is that of diathetic fragility, or the tendency to bleed. It has been proposed that this may occur in concert with resonance in such a way that bleeding becomes associated with the tissues of resonating structures or air spaces. It may also result from a stress response initiated by acoustic exposure. Identifying whether blood components known to be related to diathesis are found in beaked whales has been suggested as a means to investigate this possibility. Coagulopathies are caused by any process that substantially activates the clotting cascade for prolonged periods. Activation of the clotting cascade within the blood vessels causes the ordinarily liquid blood to clot. Sustained activation of the clotting cascade leads to depletion of clotting factors and a subsequent inability of the remaining blood to coagulate in response to tissue injury. Cetaceans are missing one of the usual clotting factors (Hagman and Fletcher factors; Bossart *et al.*, 2001) and may therefore be prone to some forms of coagulopathy even without extensive depletion of clotting factors (see also Gulland *et al.* (1996), for this disorder, termed DIC, in seals).

DIC is variable in its clinical effects and can result in either systemic clotting symptoms or, more often, uncontrolled bleeding. Bleeding can be severe. DIC may be stimulated by many factors, including blood infection by bacteria or fungi, severe tissue injury from burns or head injury, cancer, reactions to blood transfusions, shock and dystocia. Although DIC is a hypothetical mechanism that has been proposed as a factor in cetacean strandings, there are few data to support it.

REVIEW OF NECROPSY FINDINGS

In the Bahamian beaked whale strandings, massive ear injuries were seen (bilateral intracochlear and unilateral subarachnoid haemorrhages) and blood clots on the ventrolateral aspects of the braincase along the path of the acoustic nerve (in most mammals, the internal auditory meatus) and extending into the ear. The *Ziphius* braincase is robust (Fig. 5) with a long, narrow channel, which is in contrast to the short, wide cranial hiatus of *Tursiops*. The mechanical properties (e.g. compliance) of these two skull types and their surrounding tissues is probably dramatically different and may help account for the appearance of the lesions described in the Bahamian stranded beaked whales (Anon., 2001). In these carcasses, postcranial lesions (other than contraction band necrosis of the heart) were not found, possibly due in part to the degree of tissue autolysis.

In contrast, tissues from the Canary Islands beaked whales were much better preserved, enabling a more detailed pathological investigation. The Canary Islands beaked whales had acute systemic haemorrhages within the lungs, CNS and kidneys; systemic fat emboli; and the gross and/or histological appearance of gas emboli in vessels from a range of tissues including the brain, choroid plexus, visceral/parietal serosa and kidney. These acute, systemic and widely disseminated lesions were considered consistent with, although not diagnostic of, DCS (Jepson *et al.*, 2003; Fernández *et al.*, 2004; 2005).

In the UK, a small number of cetaceans with acute and chronic gas-bubble lesions have been found (Jepson *et al.*, 2003; 2005; Fernández *et al.*, 2004). The lesions, exclusive to these UK-stranded cases, included large (0.2-6cm diameter), hepatic, gas-filled cavities associated with extensive pericavitary hepatic fibrosis and involved several dolphins, a porpoise and only one beaked whale. These chronic hepatic lesions were found alongside extensive portal and sinusoidal gas emboli, many of which were associated with acute tissue responses, including marked tissue compression and vessel distension, focal haemorrhages, acute hepatocellular necrosis and fibrin thrombi. To date, two UK-stranded common dolphins (*Delphinus delphis*) also had clearly demarcated bilateral acute coagulative renal necrosis (consistent with infarcts) associated with gross and microscopic gas bubbles and (arterial) gas emboli. Additional cavities formed by gas bubbles were also seen in lymphoid tissue and other parenchymatous organs. Of all the UK-stranding cases, the brains from three carcasses were examined, spinal cord sections in only two cases (most were either grossly and microscopically normal or showing signs of autolysis) and the skeletal material was examined in none. It was therefore not possible to confirm or refute the presence of lesions consistent with DCS-like symptoms or other causes of gas embolism in either CNS or bone for most UK-stranded cases (Jepson *et al.*, 2003; 2005). Although the lesions found in the UK-stranded animals cover a wide range of acute and chronic pathologies related to diving and pressure changes, they may be useful in understanding beaked whale lesions. It should be noted that these odontocetes all stranded singly and their histories in terms of acoustic exposure are unknown.

CONCLUSION

It is important to note that no current hypothesis of pathogenic mechanisms resulting in acoustically-related strandings is proven. Even the most widely accepted and

supported ideas have a number of unanswered questions. Additionally, the diversity of beaked whale species affected, in conjunction with the variety of geographic locations and hydrographic features where incidents have occurred, limit the certitude of interpretations that can be gleaned from current findings.

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