

# Diving Adaptations of the Cetacean Skeleton

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**Abstract:** The purpose of this review is to focus the attention of researchers on studies that may link bone normal and abnormal physiology and diving conditions in cetaceans. The literature and relative concepts on the locomotory and strain-bearing properties of the cetacean skeleton are summarized and former descriptions compared with more recent studies that utilize new devices to study the density and structure of mammalian bones. Data reported suggest that re-evaluation of morphological information accompanied by systemic studies of bone pathology, and application of modern research methods including X-ray densitometric analysis, may yield new insights into the structure of cetacean locomotor system. A number of recent relevant reports indicate that cetaceans may suffer from pressure related damages. An increased knowledge of the skeletal physiology of whales and dolphins may lead to define precisely the vascular or avascular nature of certain cetacean lesions, and ascertain their possible human (sonar)-related pathogenesis.

## THE CETACEAN SKELETON

Cetaceans have adapted to marine life through a long process starting in the early Eocene [1] and have reached a degree of bodily transformation unsurpassed among other marine mammals [2]. Their entire life from birth to reproduction and senescence is spent in the water and a return to terrestrial life is not compatible with survival [3]. Of the several profound changes undertaken to adapt to aquatic life, the skeletal modifications were perhaps the first to be observed, analyzed and studied in detail. The early scientific literature on Cetacea contains precise descriptions of the bones of the different genera and families, and the conclusions of those first studies were fundamental for the taxonomy of Cetacea (among the examples of thorough classic studies see [4] and [5]).

Cetaceans are well known for their many skeletal modifications such as telescopic modification of skulls (to create space for the melon or the spermaceti organ and to improve hydrodynamics) and its asymmetry [6]; the large and often flexible rib cage with a minimal sternum; the transformations of the thoracic limbs into flippers [7]; the disappearance of the hind limbs (with the exception of the pelvic remains in all cetaceans and some femoral anlage in Balaenidae) [8] and the changes of the vertebral column with the uniform morphology of the vertebrae; the absence of a sacrum and the presence of hemal arches to tell the end of the lumbar and the beginning of the caudal sectors.

## MODERN RESEARCH ON THE CETACEAN SKELETON

The research on the cetacean skeleton was perhaps the first to start, and possibly also the first to exhaust its momentum, with the important findings of Slijper [9]. E. J. Slijper (1907-1968) was an outstanding researcher whose accomplishments established the basis of our current concept of functional anatomy of marine mammals, and led to the discoveries of the “momentums of force” of the cetacean spine. His seminal paper [9] described the use of a specially devised formula to calculate the strength of cetacean vertebrae, by multiplying the width for the square of the length. The outcome is a graphic representation in which the strongest sectors of the vertebral column clearly stand out and allow a precise identification of the sites of highest strain and consequently suggests the most powerful muscular insertions.

DeSmet, and more recently Buchholtz, further elaborated the concept and proposed new models for the study of the cetacean vertebral column. The former [10] abolished the division into a lumbar and a caudal sectors, since they are fundamentally impossible to tell apart from the functional point of view. The latter [11, 12] proposed new explanations for the evolution of the spine. Several other Authors in the late XX century contributed to this debate with long and detailed studies of the spine of several species of marine mammals [13-30], sometimes examined using Slijper's formula as a tool for comparison [31-33]. Furthermore, the evolution of the skeleton as a ballast device has been studied in detail in other vertebrates, with some interesting insight into the cetacean skeletal structure [34].

## RESEARCH TECHNIQUES ON THE STRUCTURE OF CETACEAN BONES

Research on bone structure, using medical radiological techniques, described the peculiar shape of the long bones of the cetacean arm and forearm, identifying the classical

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“hourglass” architecture [35-37]. The absence of a medullary cavity has been extensively discussed and a general consensus was reached with the argument that such a disposition strengthens the resistance of the flipper during fast swimming when the limb is used to steer the animal in motion [38]. The use of modern radiological techniques in cetacean research, derived from the growing availability of the necessary equipment in human and animal hospitals, has led to further developments. A number of publications in the late eighties and onwards applied X-ray techniques to the study of bone development, with special attention dedicated to the stages of maturation of the bones of the carpus and hand in the flipper [39-51]. Similarly to what already known in humans, ossification of the physeal cartilaginous structures in the wrist follows a precise temporal schedule, which can be thus used for age determination.

A further technological step was accomplished when bone densitometry was recently substituted to conventional X-ray techniques to study age determination in striped and bottlenose dolphins [48, 50]. Deposition of mineral salts was used to devise a temporal sequence in ageing steps, calibrated with results obtained by studying dentine layers in the teeth.

Dual-Energy X-Ray Absorptiometry (DXA) is presently considered the method of choice with which to evaluate bone mineral content (BMC) and bone mineral density (BMD) in human beings, because it allows rapid, non invasive and precise measurements of these parameters in almost any part of the skeleton [52-59]. During a scan, the X-ray source and the detector move together over the subject with the detector measuring the amount of X-rays that pass through the subject. X-rays of two energy levels are attenuated by bone and soft tissue differently. Therefore, the type and amount of tissue scanned can be distinguished using DXA. Specific algorithms in the system software are used to calculate the quantity of bone. However, since DXA converts a three-dimensional structure in a two-dimensional image, BMD is measured in an area rather than in a volume and expressed as grams of bone mineral/cm<sup>2</sup> rather than cm<sup>3</sup>. Using human protocols adapted according to the size of the scanned subjects, DXA has also been increasingly applied to the study of BMD in both small and large animals [60-65], including cetaceans [48, 50].

Further investigations involving the cetacean skeleton were performed when computed tomography and magnetic resonance were employed to study the head of dead or live dolphins or whales [66]. These powerful technologies were used to gain information on soft tissues located deeply in the body, and specifically mostly aimed at brain anatomy. However bone structures were represented in faithful topographical relationships with the other organs.

### PHYSIOLOGICAL ADAPTATIONS TO DIVING

As we stated above, investigations on the nature of the cetacean skeleton were left aside quite a few years ago, except for those analyses that were mandatory to discriminate between well known and potentially new species. Technical progress in cetacean research, facilitated by the use of adhesive tags, opened new research frontiers (for review see [67]). Data on the length and depth of dives, obtained in a number of species [68-73], together with new physiological

insights derived from studies on the blood or from comparative research on cetacean or pinniped diving habits, prompted a whole new series of questions and conclusions (for and update see [74, 75]).

Ground-breaking investigations performed in the very last years allowed the applications of gas consumption equations to cetacean diving profiles. Thus the theoretical possibility of bubble formation in the blood was finally considered as an unknown factor for a number of cetacean species, and especially for beaked and sperm whales. The question we now pose is whether the study of the cetacean skeleton, still the easiest body part to obtain from these mammals, may yield hitherto unknown and relevant information on the diving habits and dive-related pathologies of cetaceans. To this effect, we will quickly review the available data described in the literature and examine future perspectives to be potentially developed with the use of updated medical technologies.

### BONE DENSITY IN RELATION TO DIVING

Descriptive analyses of the cetacean skeleton available in the literature report exhaustive data on the morphology of bones in the different cetacean families. The transformation of the skeleton to adapt for marine life and locomotion in the liquid environment is therefore apparently well known, and most if not all the problems are apparently solved. But is that really so? A series of recent studies on the nature of cetacean bones, and especially the skull [76, 77] may yield some novel concept and reveal a deeper, more subtle level of adaptation to life in the water.

It is well known that some cetacean bones have a different density than the corresponding bones of terrestrial mammals (for review on the evolution of bone density see [78]). Tympanic bullae, for example, or parts of the rostrum in some beaked whales, have been considered particularly heavy. At least one species, the Blainville's beaked whale *Mesoplodon densirostris* (Blainville, 1817) derives its name from its heavy, dense rostrum [79, 80]. However, most of the data on bone density were obtained by the application of the Archimedes's principle (passive water displacement), an experimental procedure that gives only general information referred to the whole bone immersed, but can not detail how the calcium salts are distributed within the osseous structure. Our hypothesis is that a closer, updated approach to the study of bone structure may be useful to progress along this line of research. An example may be obtained from a densitometric analysis of the tympanic bullae. If we compare the bullae of a terrestrial and a marine mammal, we may come across some unexpected findings.

### New Data on the Tympanic Bulla

We evaluated the bone density of the skull of newborn bovine calves, and the values we obtained for the tympanic bulla varied between 0,307 to 0,444 g/cm<sup>2</sup>. The variation may be due to individual differences, breed or partly even to the quantity of adjacent bony structures that might be included in the scan, i.e. the heavy petrosal part of the temporal bone. This is quite logic since the whole skull is still growing with evident fontanelles where sutures are still open. Nevertheless, when we had the chance to evaluate the skull of a 5.8m long newborn fin whale *Balaenoptera physalus*,

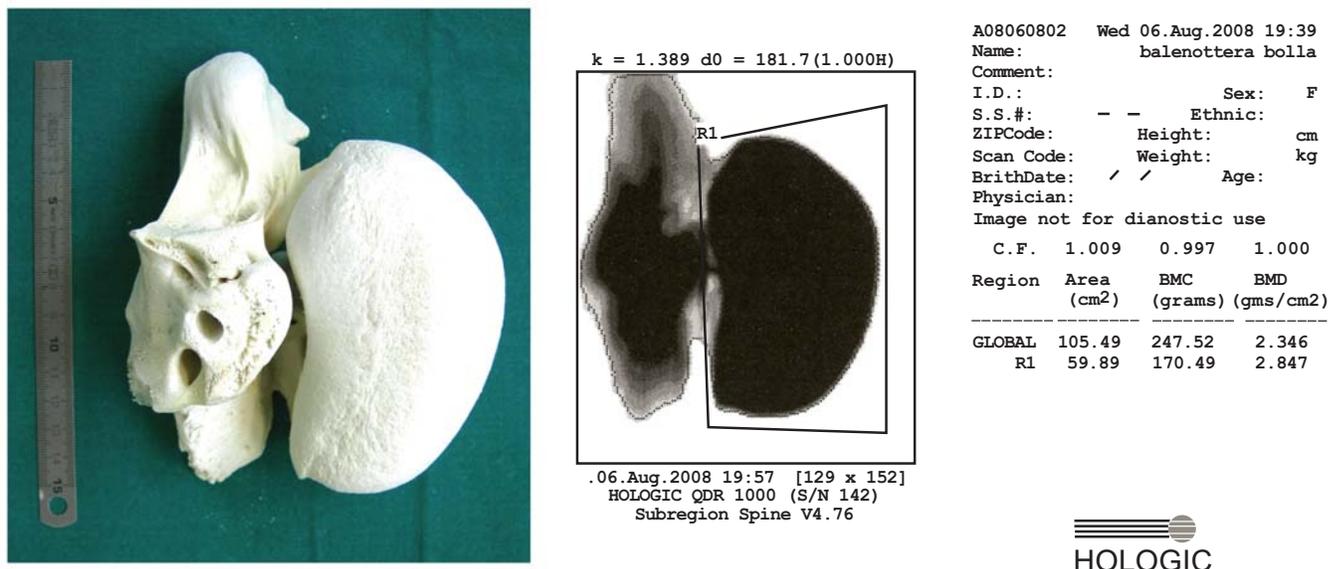
we found it extremely light, and the whole structure could be lifted with one hand with the exception of the tympanic bulla, whose bone density varied from 2,814 (left) to 2,847 g/cm<sup>2</sup> (right) (Fig. 1), completely out of proportion in respect to the rest of the head. A first tentative conclusion from this example may be that there is a differential rate of growth in the skull of fin whales. On one hand incomplete fusion of the neurocranium repeats the same physiological steps one may expect in terrestrial species. However in cetaceans some specific features may have to develop at a faster rate at fetal stage and reach a high degree of maturity by the time of birth. The reasons for the premature heavy deposition of calcium salts in the tympanic bullae could be possibly related to the immediate need of the newborn animal to fully receive and translate acoustic signals from the surrounding environment, an absolute necessity for orientation in the water. A less dense tympanic bulla would probably simply not be able to function in a medium in which acoustic transmission travels faster than in the air.

But it is not simply the tympanic bulla of cetacean that is heavier than that of a terrestrial relative. The heaviest terrestrial specific (or single) bone structure presently known is that of the equine metacarpus of an adult of brachimorphic breed, but its density is not even comparable to that of the newborn fin whale bulla (1.85 g/cm<sup>2</sup> vs. 2.8 g/cm<sup>2</sup>, respectively). It is important to specify that the most important *inter-* and *intra-*specific factor affecting bone density in terrestrial animals is the body weight [81, 82] that is almost always directly related to age. Moreover, the heaviest part of the mammalian skeleton, using Archimedes's principle, has been hitherto considered the rostrum of the *Mesoplodon densirostris*, with values reported in the literature of approximately 2.612 to 2.686 g/cm<sup>3</sup>. We note again here that DXA values are expressed as g/cm<sup>2</sup> as we explained before, while conventional measurements of density are expressed as g/cm<sup>3</sup>. Comparisons are meaningful only if using the same scale of reference.

## STRESS-STRAIN RELATIONSHIP AND RELATED PATHOLOGY IN THE VERTEBRAL COLUMN

A careful re-examination of the vast amount of relevant references suggests that the application of Slijper's formula may be discussed at the light of the new acquisitions on cetacean diving physiology. As now well known, the heaviest strain in the vertebral column of cetaceans relies on the last lumbar/first caudal vertebrae, with some important differences related to specific anatomical features of the different whale and dolphin families and species. A direct relationship between increased strain and regional blood flow has not been proven for the spine of these species. However, the huge perispinal venous plexus, typical of cetaceans, contains an extensive percentage of the total blood volume. Vertebral vascularization is strongly connected with spinal vascular supply. Several skeletal specimens, present in numerous zoological collections, show that adult (or perhaps old) cetaceans of different species suffer from specific pathological changes in the vertebral sector corresponding to the last lumbar (L7-11) and first caudal elements (Ca 1-4).

Vertebral bony lesions have been diagnosed in many studies [83-88], reporting different pathological changes including spondylitis [89], spondylosis deformans [90, 91], osteomyelitis [92, 93], discospondylitis, and ankylosing spondylarthrosis [94]. In humans and in other mammals (both bipeds and tetrapods), most of these pathological changes are strongly related to the anatomical and physiological conditions of ligament insertions, and, furthermore, traumatic injuries are localized in areas of relatively high mobility. Bone pathologies of the spine are frequently associated to general ailments of the subjects including aging, diabetes, and nutritional imbalances [95, 96], classified as spondylarthropathies, and often characterized by hyperostosis, exuberant and slow ossification of perivertebral connective tissues, and bone overgrowth due to an initial degenerative change in the ventral *annulus fibrosus*. The forming spurs or intervertebral bridges, called osteophytes or spondylophytes, are generally placed at the ventral margin of the interverte-



**Fig. (1).** Tympanic bulla of a 5.8m long newborn fin whale *Balaenoptera physalus*. Left, image of the bulla; right, DXA measurement of the same specimen.

bral disk. Sometimes these abnormal bony depositions are associated to other pathological changes, such as chronic, non-suppurative inflammatory reactions involving intervertebral disk tissues, vertebral periostium, ligaments, tendons and entheses; fibrin deposition and swelling; ossification of intervertebral disk and fusion of the vertebral bodies; and, finally and obviously, trauma-induced bone remodelling processes [94, 97].

Vertebral bone changes in cetaceans may lead to impairments of muscular functionality and pain. In fact, since the spine is the cetacean locomotor organ, with its vertical movements of the tail and flukes, ankylosis not only causes a decrease in spinal mobility, but also creates vulnerability as a result of a rigid vertebral column that cannot bend or rotate on impact to absorb traumatic stress. The complications of likely spinal pain and vertebral fusion are thus particularly serious for any organism that must swim without an opportunity to rest to allow bone pathology to heal, in contrast to terrestrial mammals [94].

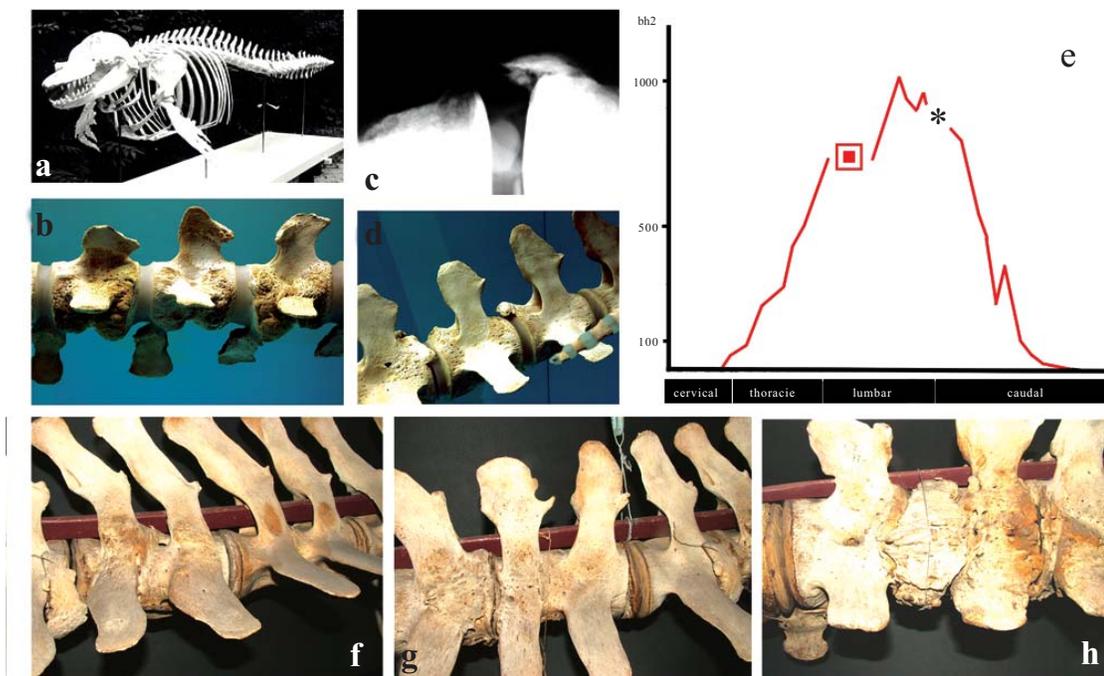
No definite conclusion can be derived by these simple observations. However, systematic methodological studies may quantify the number of skeletons suffering from a definite pathology and establish the percentage of adult animals hit by the phenomenon. As an example, we note here that two out of two skeletons of false killer whales *Pseudorca crassidens* maintained in Italian Museums of Natural History do suffer from heavy spondylarthropathy of the vertebral column in the last lumbar/first caudal section we just described, corresponding to the part sustaining the heaviest load and

strain in locomotor efforts (Fig. 2). Similar pathologies of the spine have already been described in this species [98-100], the specific hydrodynamics of which have been investigated in great detail [101, 102]. Whether animals suffering from pathology of the spine are more likely to end up in a Museum because of their relative fragility is a question still unsolved.

#### POSSIBLE RELATIONSHIP BETWEEN BONE DAMAGE AND DIVE RELATED PATHOLOGIES

A number of recently published studies reported that bone damages occurred in deep diving cetaceans (especially in the record holding diving species, the sperm whale *Physeter macrocephalus*) are (or could be) related to barotraumas [103]. Such lesions could be a consequence of decompression sickness (DCS). The concept of barotraumas in marine mammals contradicts the supposed "immunity" of marine mammals to DCS: in fact, most odontocetes are known to have a number of behavioural, physiological, and anatomical features considered adaptive for avoiding this pathological condition [104]. In particular, a paper related to sperm whales [103] described bony lesions to vertebral bodies, chevron bones and flippers suggesting a repeated aseptic avascular osteonecrosis, resulting from the temporary or permanent loss of the blood supply to the bones, perhaps induced by compression, non-fatal gas-emboli or by changes in the coagulation cascade.

An alteration in blood flow may determine ischemic necrosis of the bones, forming microscopic cysts and causing



**Fig. (2).** a: Skeleton of a false killer whale (*Pseudorca crassidens*) maintained at the Museum of Natural History of Milan (Italy). b, c, d: spondilopathologies of the same specimen; e: Sljiper's formula representing momentums of force of the spine of false killer whale (*Pseudorca crassidens*); bh2 = width (b) multiplied for the square of the length (h); boxed square: vertebrae damaged during necropsy but not pathological; asterisk: pathological vertebrae. f, g, h: pathological or fused vertebrae of a false killer whale (*Pseudorca crassidens*) maintained at the "G. Doria" Museum of Natural History of Genova (Italy). c: courtesy of Prof. Mauro Di Giancamillo, Department of Veterinary Clinical Sciences of the University of Milan (Italy); f-h: courtesy of Dr. Roberto Poggi, "G. Doria" Museum of Natural History of Genova (Italy).

the bone to collapse. If the process involves bone areas near a joint, it often leads to a collapse of the joint surface. Progressive and erosive remodelling processes of the bone tissue seem to be the natural consequences of this variety of pathological change, defined “dysbaric”, and induce periosteal overgrowth and the formation of spurs close to articular surfaces. The exact pathogenesis of these lesions related to decompression problems are not yet fully understood: gas bubbles arising from supersaturated tissues, fat emboli coming from damaged bone marrow tissues and intravascular coagulation are the main hypotheses.

### **Gas Bubble Formation**

In cetaceans, supersaturated soft tissues have been proposed as possible main sources of gas bubbles responsible of possible vascular damages in bone tissues. When a breath-holding human diver or a marine mammal remains at depth for an extended period of time, the dissolved gas concentration within its body fluids can significantly increase from the sea-level value of 100% to a higher equilibrium value. Using dive profiles of dolphins and whales and some simple gas diffusion laws to calculate the expected “intramuscular nitrogen tension”, levels approaching 300% saturation are reported. The supersaturation of soft tissues is a predisposing condition for microscopic bubbles nuclei formation with their subsequent growth to macroscopic size. Nucleation could be caused by sudden behavioural changes when cetaceans are subjected to high-intensity acoustic pulses. Rapid surfacing from a deep dive may lead to DCS for the alteration of the decompressive diving profile.

In addition, analogously to humans, abnormal extended activity resulting from sonar disturbance may induce decompression sickness in marine mammals [105, 106]. The first reports of the possible correlation between strandings with DCS symptoms and anthropogenic sonar signals were published recently [107-109] and described a condition similar to DCS, called fat and gas embolic syndrome. Fat emboli in lung vessels associated with gas bubbles and related cavity-induced lesions were found in beaked whales and other deep-diving cetaceans stranded in the Canary Islands and along the British coasts. It was hypothesized that those pathological findings were caused by changes in diving behavior of Ziphiids trying to avoid sonar exposure and thus making themselves susceptible to an increased risk of DCS [110]. The direct influence of acoustic fields was also suggested as a possible motive for the formation and growth of bubbles in supersaturated soft tissues by rectified diffusion. If a sound pulse of moderate amplitude impinges on a diver or a marine mammal at depth, then the pressure fluctuates about the at-depth ambient pressure and any pre-existing bubble will be driven into radial oscillation [111].

### **Breath-Holding Dives and Decompression Sickness in Marine Mammals and Humans**

Proposing hypotheses on the possible pathogenesis of pathological changes related to breath-hold dives and due to sonar activities in cetaceans is easier for most of the soft tissues, generally considered “fast” tissues in gas exchanges with blood (for recent models of bubble formation in marine mammals, see [106, 112]). On the other hand, the so-called “slow” tissues, including bone, are the last to be saturated during SCUBA (Self Contained Underwater Breathing Ap-

paratus, a shortening generally used to indicate tank diving) diving and therefore generally considered risk-free in human breath-holding dives. In a breath-hold dive, theoretical calculations set the human limit (for a 70 kg individual with a total lung capacity of 5.5 L and a  $PA_{O_2}$  of 16.0 kPa=120 mmHg) to a maximum of 1996 ml of oxygen store, divided among 820 ml of lung store, 880 ml in the blood, 240 ml of myoglobin store and 56 ml in solution in tissues [113]. These stores correspond, according to the reference, to an approximate duration of 6.5 minutes of breath-holding activities with a mean consumption of 300mlO<sub>2</sub>/min.

Although it is widely known that human record breath-holding dives may last much longer if the diver is immersed in water but stands still, we may consider that even a hypothetical duration of the dive longer than 6.5 minutes should obviously not prompt the condition for bone gas saturation. Even considering the increased alveolar pressure reached during human dives (607.8 kPa= 4560 mmHg at a depth of 50 msw maintaining the parameters described above), risks for “slow” tissue involvement are very low or non-existing. In fact, most of the possible risks involved in human breath-hold activities are linked to increased arterial pressure (especially in the thorax) and to the incidence of arrhythmias during the first minute of activity, a series of events worsened by relatively cold water (25 °C). We know that, due to several physiological factors, including extreme bradycardia [114], the balance between modified cardiac output and vasoconstriction is well achieved in diving mammals, in which arterial pressure does not peak during the dive: nevertheless the basic laws of gas physics remain valid. Possible incidence of decompression sickness in human breath-hold divers is in fact due to the eventual passage of air into the arterial system as a consequence of increased alveolar nitrogen pressure during descent to great depths and its reverse expansion during ascent.

Even if barotraumas and arterial gas embolism are reported in human breath-hold divers [115], the low volume of air in the human lungs and the relative shortness of the dive make it impossible to involve “slow” tissues in breath-hold decompression sickness. A series of pioneer experiments performed in the seventies [116] demonstrated that the lungs of bottlenose dolphins collapse at 70 msw, thus limiting the possibilities of nitrogen uptake (see also [67]). The peculiar structure and behavior of the cetacean trachea also contributes to resist the environment pressure without damages [117, 118]. Interestingly, the detailed literature relative to human breath-hold related pathologies indicate that possible dysbaric problems are increased if a) the surface interval between a series of repetitive dives is short; and b) descent and ascent are aided by electrically operated vehicles, and thus fast. Both conditions should be adequately compared to dive profiles of several beaked whales: diving times of these mammals are much longer than those of human beings and thus the diffusion of nitrogen into blood and tissues possibly higher.

It is also necessary to consider the rate between ascend and descend times as another important variable: deep-diving cetaceans usually show a slower ascent speed or, at least the same speed as in the descent, to allow nitrogen dissolved in blood and tissues to pass into alveolar air. If this rate changes and ascension is much faster, part of the nitro-

gen dissolved is not able to return to air, thus predisposing for tissue supersaturation. Furthermore, it now appears evident that some repetitive shallow dive profiles may be dangerous for deep-diving species [110].

Another interesting observation, somewhat lost in the older medical literature, is that, in humans, blood drawn immediately after a breath-holding dive to 27 msw followed by a rapid ascent contains foam, a condition that disappears when venipuncture is performed 10 seconds after reaching the surface [119]. Taking examples and calculations drawn from the human medical literature and applying them to cetacean diving physiology is of course risky and faulty. However, no mammals has been so extensively studied as humans, and so speculation may be attempted for tentative discussion and explanation of cetacean pathologies. If SCUBA breathing saturates “slow” tissues (including bone marrow) with a 3 to 8 hour half-life, can we suppose that an intrathoracic or alveolar pressure capable of inducing a similar condition may take place during a 60 min dive below 1,400msw in a beaked or sperm whale? In fact the biological effects of pressure are well known at the molecular and cellular level [120], but no direct effect can be reported on the skeleton.

To date, the mechanism that leads to the formation of bubbles in the bone marrow of SCUBA divers is not fully understood, and presently tentatively related to a rise in marrow cavity pressure, a prelude to dysbaric osteonecrosis. According to this hypothesis, an increase in pressure in marrow adipocytes breaks and releases tissue fragments that may obstruct atrial vessels [121]. A necessary condition for this pathology to initiate is an increase in marrow pressure without an adequate decompression time. If we apply the theory to cetaceans, we are once more faced with the difficulty of explaining a potentially dangerous local pressure rise. The presence of slow blood flow and large local venous compartments with relatively small outlets may increase the chances of dysbaric osteonecrosis. We may consider that the cetacean spinal chord is surrounded by an imposing network of veins, and that may constitute a predisposing factor. The debate whether a true dysbaric osteonecrosis is present in cetaceans (for doubts see [122, 123]), and whether the nature of the pathology could be avascular, is quite recent and the question is far from being solved. We may note here that, whatever future data may prove true, damages of the cetacean skeleton do indicate a suffering specifically related to their peculiar environment.

## CONCLUSIONS

The findings in this brief review suggest that the systemic study of bone pathology, and the application of modern methods including DXA scans, may yield new insights into the structure of cetacean locomotor system and even help us to understand how these mammals stand the tremendous pressure they encounter during the dive. It is also possible that an increased knowledge of the skeletal physiology of whales and dolphins may lead us to define the vascular or avascular nature of some fascinating lesions of these mammals, and ascertain their possible human (sonar)-related pathogenesis.

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