DORSOVENTRAL BENDING OF THE TAIL AND FUNCTIONAL MORPHOLOGY OF THE CAUDAL VERTEBRAE IN THE BOTTLENOSE DOLPHIN, <u>TURSIOPS</u> <u>TRUNCATUS</u>

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LIST OF ABBREVIATIONS

cd	caudal vertebra
cm	centimeter
kg	kilogram
m	meter
mm	millimeter
n/a	not available
B	ball vertebra
F	flukes vertebrae
P	peduncle vertebrae
T1	first transitional vertebra
T3	third transitional vertebra
TL	total body length

Chapter 1

Introduction and objectives for a study of dorsoventral bending of the tail and functional morphology of the caudal vertebrae in the bottlenose dolphin, Tursiops truncatus

Introduction

One of the great successes of mammals is that they have evolved adaptations to terrestrial, aquatic, and volant environments and have colonized most thermal niches (Vaughan 1986). Modern terrestrial mammals occupy all continents except Antarctica, while cetaceans, being highly adapted to the aquatic environment, are found in all oceans and some fresh water habitats (Leatherwood et al. 1983).

The most likely ancestor of cetaceans is from the Mesonychidae, a family of terrestrial hoofed mammals living 50 million years ago (Fordyce 1988). Mesonychids and subsequent cetaceans underwent major structural and functional modifications as they re-adapted to the aquatic environment. However, the aquatic habitat, relatively long life span and difficulty in collecting cadavers have made research on modern cetaceans challenging. Much of their life history, physiology and morphology is not sufficiently understood.

The order Cetacea includes two modern suborders - the Mysticeti or baleen whales, and the Odontoceti or toothed whales. Odontocetes include some large whales and all the dolphins and porpoises, which in body size range from the 18-meter sperm whale, Physeter macrocephalus, to the 1.5-meter finless porpoise, Neophocaena phocaenoides, (Leatherwood et al. 1983). All cetaceans share the same fusiform body and swim by bending their tail dorsoventrally, unlike the lateral tail movements of fishes and reptiles. The cetacean tail, their primary locomotory organ, is composed of a laterally-compressed peduncle and a pair of neomorphic horizontal flukes. These specialized, laterally broad and dorsoventrally compressed flukes are composed of dense connective tissue (Purves 1969). In addition, cetaceans developed powerful axial muscles serially attached to the caudal vertebrae to generate the power for up- and down-strokes of the tail (Pabst 1993).

The high swimming speed and aquatic agility of dolphins have long been a fascination of man and a focus of scientific investigation. The fusiform body, hydrofoil-like fin and flippers, and lunate flukes of dolphins are common morphological features convergent in a number of fossil and living aquatic vertebrates - thunniform fish, ichthyosaurs, dolphins - all of which are highly adapted to high speed cruising (Fish and Hui 1991). This advanced swimming design and its biomechanics are well studied in fishes (Blake 1983). In bottlenose dolphins, Tursiops truncatus, the hydrodynamics of tails (Fish 1993a) and their swimming speed have been determined. Their routine speed is 3 meters/second (m/s) (Fish and Hui 1991) and they can burst up to 6 m/s (Lang and Norris 1966). However, the role of the caudal vertebrae in tail dorsoventral bending is not clearly described.

In terrestrial mammals, the caudal vertebrae form the bony core of their tails which, in most cases, contribute little to locomotion. In cetaceans, on the other hand, the caudal vertebrae, being the axis of tail bending, form a major component of their post-cranial skeleton. They are characterized by an increase in number, which range from 23 to 31 in bottlenose dolphins (Rommel 1990, Watson 1992) and by the enlarged size of haemal arches, spinous and transverse processes as attachment sites for their massive axial muscles. In addition, they have atypical-shaped vertebrae in the flukes region. However, the definition of the first caudal vertebra is ambiguous due to the absence of the sacrum as the traditional junctional landmark (De Smet 1977). The variations in reported number of caudal vertebrae number may be due to individual variation or loss of the tiny terminal caudal vertebrae during preparation. The relationship of the unique morphology of cetacean caudal vertebrae and their locomotory functions is not well understood.

This research investigated the morphology of the caudal vertebrae and its relationship with dorsoventral bending of the tail in the bottlenose dolphin. Tails salvaged from 19 mature bottlenose dolphins stranded on the Texas coast were examined by radiography, dissection, and skeletal preparation. Anatomical terminology follows Nomina Anatomica Veterinaria 1994 (Frewein et al. 1994) unless otherwise stated.

Objectives

The specific objectives of this research were to:

1. Review the literature on locomotion and morphology of caudal vertebrae in odontocetes (chapter 2).
2. Determine the number, shape and serial morphology of caudal vertebrae in mature Gulf of Mexico bottlenose dolphins (Tursiops truncatus) (chapter 4).
3. Determine where the dorsoventral bending occurs in the caudal vertebral column by:
    a. Determining the angles between adjacent caudal vertebral bodies when the tail is bent dorsally or ventrally (chapter 4).

b. Determining the relative length of the intervertebral disks between the caudal vertebrae (chapter 4).

Chapter 2

Literature review of locomotion and morphology of caudal vertebrae in dolphins

Introduction

Whales and dolphins have captured man's imagination since ancient times (Fraser 1977) and our understanding of their general biology and swimming ability has grown with recent descriptive and experimental investigations (Ridgway and Harrison 1989, 1994). Living cetaceans are obligate aquatic marine mammals and swimming is their only mode of locomotion (Slijper 1961). They have lost their pelvic limbs externally and retain only vestiges of pelvic limb bones embedded in their pelvic muscles (Flower 1885c, Rommel 1990). Their remarkable aquatic maneuverability and high speed swimming are the result of several major morphological adaptations: 1) the advanced hydrodynamic shape of their body (Fish and Hui 1991), 2) the development of massive axial muscles that generate propulsive force, and 3) the atypical shapes of caudal vertebrae becoming the axis for locomotion.

Bottlenose dolphins, Tursiops truncatus, live in all oceans except those of high latitude and two ecotypes are recognized, a coastal form and an off-shore form; the life history varies slightly among different ecological populations (Leatherwood et al. 1983). The bottlenose dolphins of the Atlantic reach sexual maturity at an average total body length of 2.5 m (meters) (2.3 m for Gulf of Mexico bottlenose dolphins, Solangi and Dukes 1983 in Mead and Potter 1990), which is about 12 years of age in females and 10 to 15 in males. After a gestation of 12 months, females bear a single calf every 2 to 3 years. At birth, the calf's total body length is 1.17 m (Mead and Potter 1990). Bottlenose dolphins, with their highly-efficient and tail-propulsed swimming, are top marine predators (Fish and Hui 1991). In addition, they are the most common captive dolphin and one of the most studied cetaceans.

Locomotion in dolphins

Definition of cetacean tails

Cetaceans have streamlined bodies and, thus, external landmarks for the different regions of the body are less obvious than in terrestrial mammals. Their tail, which extends the body caudally without obvious demarcation from the abdomen, is divided into two parts. First, the laterally-compressed peduncle is the portion caudal to the anus and cranial to the flukes. Second, the terminal flukes are a bilaterally symmetrical pair of horizontally flattened connective tissue plates caudal to the peduncle (Purves 1969). The bony core of the tail is the caudal vertebrae, which extend from the last lumbar vertebra, through the peduncle and between the flukes to the terminal caudal vertebra located immediately cranial to the median notch of the flukes (De Smet 1977, Rommel 1990).

Centers of flexibility in dolphin tails

"The primary locomotory organ of cetaceans is the body axis, that is, the vertebral column and the spinal muscles of the back and tail" (Slijper 1961). Dissections have revealed that their short cervical region as well as the rigid thoracic and lumbar regions, contribute little to body flexibility (Slijper 1961) and this is supported by recent similar findings from cine analysis of a bottlenose dolphin freely swimming in open water (Pabst 1993). The propulsive movements of dolphins are confined to the caudal one-third of the body, with the greater amplitude at the caudal peduncle and flukes (Parry 1949b, Slijper 1961, Fish and Hui 1991). Based on an underwater cine analysis of a swimming bottlenose dolphin and his manipulation of one harbor porpoise, Phocoena phocoena, carcass, Slijper (1961) found two centers of flexibility. One is at the beginning of the tail, which is immediately caudal to the dorsal fin and externally at the level of the anus. The second center of flexibility is at the junction of the peduncle and the flukes. These findings supported earlier observations (Parry 1949a, 1949b). Both authors' conclusions were based on the same film of a female bottlenose dolphin giving birth in captivity and it was not identified whether birth affected normal swimming.

Divergence of swimming mode in marine mammals

The straight-line swimming of cetaceans is achieved by dorsoventral oscillation of the caudal body, a movement derived from the more generalized sagittal plane locomotory movements of the vertebral column shared by all mammals (Howell 1930, Slijper 1961). Sirenians likewise propel themselves by caudal body dorsoventral oscillations (Fish 1993a). Moreover, the fully aquatic cetaceans and sirenians have both developed neomorphic horizontal flukes at the end of their caudal vertebrae. On the other hand, within the amphibious pinnipeds, the earless seals (Phocidae) and walruses (Odobenidae) swim by lateral oscillations of webbed pelvic limbs whereas the eared seals (Otariidae) swim by pectoral oscillations of webbed thoracic limbs (Fish 1993a). Thus the cetaceans, sirenians and pinnipeds have each evolved their own particular swimming adaptations as they diverged from the terrestrial mammalian plan.

Swimming efficiency

Agility and maneuverability are important for aquatic living, especially for predator-prey interactions. Usually the predator is more maneuverable than its prey and maneuverability and agility are expected to decline as swimmers increase in size (Webb and Keyes 1981). In spite of this, the toothed whales, which range in body size from 1.5 m Hector dolphins, Cephalorhynchus hectori, to 18 m sperm whales, Physeter macrocephalus, are the predators at the top of the marine food chain. Thus the advanced swimming ability of cetaceans is not lessened by their large size (Fish and Hui 1991). Their highly efficient swimming originates primarily in the highly adapted morphology of their body and appendages (Fish and Hui 1991).

Hydrofoils

In dolphins, two morphological characteristics contribute greatly to the efficiency of swimming - the hydrofoil-like appendages and the lunate tail. "As aquatic vertebrates increase in size, hydrofoils are increasingly used as propulsors" (Webb and de Buffrénil 1990). The body of dolphins and cross-sections of their flippers, fin and flukes are all streamlined with a round leading edge and a tapered trailing edge (Fish and Hui 1991, Webb and de Buffrénil 1990). This shape provides high lift and thrust and at the same time reduces drag, in order to maximize swimming efficiency and minimize energy expenditure. (Blake 1983, Fish and Hui 1991, Fish 1993b). The caudal peduncle of bottlenose dolphins is likewise streamlined dorsoventrally in transverse section, which also helps minimize drag (Fish 1993b).

Lunate tail and thunniform convergence

The tail of dolphins is characterized by lunate flukes in the dorsal plane, in which the width is much larger than the craniocaudal length, i.e., the flukes have a high aspect ratio (Lindsey 1978, Blake 1983, Yates 1983, Fish 1993b). This characteristic tail design is associated with high-speed cruising (Lindsey 1978, Fish and Hui 1991) and aquatic vertebrates with this tail shape and swimming mode are classified as thunniform swimmers. The term thunniform is derived from the genus name of yellowfin and bluefin tunas (Thunnus spp.) (Marshall 1971a).

The thunniform features in living dolphins and whales have also evolved independently in four major groups of aquatic vertebrates: 1) mackerel sharks (Lamnidae), 2) tunas and mackerels (Scombriodae), billfishes (Xiphiidae), 3) ichthyosaurs (Ichthyosauria), and 4) dolphins and whales (Cetacea) (Blake 1983, Webb and de Buffrénil 1990). In cetaceans, the tail moves dorsoventrally, while in thunniform reptiles and fishes the tail oscillates laterally. The earless seals (Phocidae) swim by lateral sweeps of the webbed pelvic limbs which mimics thunniform swimming (Fish et al. 1988). The success and independent evolution of these thunniform similarities shows a strong selective advantage of the convergent adaptation to this morphology for aquatic living. Members of these five groups are relatively large in size (0.5 - 30 m) and highly evolved for fast and continuous swimming (Webb and de Buffrénil 1990). In addition to their specialized morphology, physiological characteristics of thunniform swimmers include warm muscles. Cetaceans, being mammals, have endothermal physiology to maintain a high internal body temperature, while ectothermal fishes, (e.g., tuna) have developed a countercurrent vascular system to maintain an above ambient temperature in their locomotory muscles (Marshall 1971b, Webb and de Bufrénil 1990). The axial locomotory muscles in these fishes and cetaceans generate the power for tail propulsion.

Axial muscles for locomotion

In cetaceans, the dorsoventral bending of the tail is maneuvered by a massive axial musculature surrounding the vertebral column (Parry 1949a, Strickler 1980). These axial muscles are remarkably similar morphologically among different species and form simple groups to give powerful strokes (Parry 1949a). In mammals, including cetaceans, these muscles are arranged topographically in two groups: epaxial muscles, which lie dorsal to the transverse processes of the vertebrae, and hypaxial muscles which lie ventral to the transverse processes and cover the ventral surface of the vertebral bodies (Slijper 1946, Dyce et al. 1996). In dolphins, the extremely well-developed epaxial and hypaxial muscles are the major components in cross-sections of lumbar and especially of the caudal regions (e.g., the bottlenose dolphin, Pabst 1990). In contrast, in most terrestrial mammals these axial muscles in the caudal region are usually relatively small and contribute little to locomotion (Hildebrand 1995).

In terrestrial mammals, the body and appendages can be analyzed mechanically as a bridge structure with the thoracic and pelvic limbs representing piles and the head and the tail as two cantilevers. The vertebral column sustains both tension, which applies on the vertebral arches and processes, and compression, which applies on the vertebral bodies (Slijper 1946). However, in cetaceans, pelvic limbs are lost and their paddle-like thoracic flippers do not support the trunk. The buoyancy of water frees heavy-weighted cetaceans (50 - 150,000 kg) from the constraints of gravity and eliminates the necessity for strong and weight-bearing limbs. Instead of limbs, their locomotory organ becomes the vertebral column and the axial muscles generate the propulsion force for swimming (Slijper 1946).

Attachments of swimming muscles

In the epaxial muscles, the multifidus dorsomedially and the longissimus ventrolaterally are the two major muscles which produce most of the force transmitted to the caudal peduncle and flukes to generate the upstrokes (Pabst 1993). Together they contribute 14% of the total body weight in harbor porpoises (Parry 1949a). Each muscle originates serially from the lateral surfaces of the spinous processes of the cervical, thoracic and lumbar vertebrae and then serially inserts on two tendon systems. In the bottlenose dolphin, the caudal extension of the multifidus, extensor caudae medialis, inserts laterally on the spinous processes of caudal vertebrae 1-17, which is cranial to the flukes. And the caudal extension of the longissimus, extensor caudae lateralis, inserts on the dorsal surface of the transverse processes of the more caudal lumbar vertebrae and caudal vertebrae 1-15, and also inserts directly on to the flukes vertebrae via seven tendons. Each tendon splits and terminates on the dorsal surface of two or three adjacent caudal vertebrae from the 16th through the terminal caudal vertebra. These muscles control the dorsal bending of the flukes (Strickler 1980, Pabst 1990, 1993).

The two major hypaxial muscles are the hypaxialis lumborum and the intertransversarius caudae ventralis (Pabst 1993). The former, more ventral muscle, originates from the ventral surfaces of thoracic vertebral bodies 9-11 and lumbar vertebrae, as well as from the lateral surfaces of haemal arches of caudal vertebrae 1-18 and inserts on tendon systems. The more dorsal muscle, intertransversarius caudae ventralis, originates from the ventral surface of the transverse processes of caudal vertebrae 3-15 and inserts on the ventrolateral aspect of the vertebral bodies of caudal vertebrae 15-18. Both muscles produce the ventral bending of the flukes (Strickler 1980, Parry 1949a). In particular, in the harbor porpoises and bottlenose dolphins, the more medial muscle fibers of the hypaxialis lumborum control the ventral bending of the cranial part of the peduncle, whereas the more lateral fibers bend the caudal part of the peduncle and control the ventral bending of the flukes (Smith et al. 1976, Pabst 1990). From morphological and behavioral observations of swimming harbor porpoises, it is concluded that the flukes are able to bend 90° relative to the peduncle (Smith et al. 1976).

Power output of swimming muscles

It was initially suggested that the upstroke of the dolphin tail produced the thrust and that the downstroke is a passive action (Purves 1963, Purves 1969), which also implies unequal power output of epaxial and hypaxial muscles. A later study of muscle biochemical properties of bottlenose dolphins also indicates a compositional and functional specialization of muscle fibers of epaxial and hypaxial muscles (Bello et al. 1985). However, it is argued that the epaxial and hypaxial muscles have equal power output during the upstroke and the downstroke. This proposal is supported by anatomical data from four franciscanas, Pontoporia blainvillei, (Strickler 1980) and a shortfin pilot whale, Globicephala macrorhynchus (Arkowitz and Rommel 1985). In addition, analysis of cinematography revealed that the thrust generated by up and downstrokes is symmetrical in bottlenose dolphins (Videler and Kamermans 1985). It is now concluded that in dolphins the epaxial and hypaxial muscles produce approximately equal propulsive power to the tail and flukes (Fish and Hui 1991).

Morphology of caudal vertebrae in dolphins

Definition of the caudal vertebrae in dolphins

In terrestrial mammals, the caudal vertebrae are defined as those vertebrae caudal to the sacrum. In cetaceans, however, the definition of caudal vertebrae is ambiguous due to the absence of the sacrum as the traditional landmark of the beginning of caudal vertebrae (De Smet 1977). Various soft tissue topographical reference structures have been suggested to identify the beginning of the tail: these include the anus, pudendal nerve, pelvic ligament, specific muscle origins, and caudal extension of the pelvic cavity (De Smet 1977). From an osteological perspective, it is proposed that the first caudal vertebra is the first post-thoracic vertebra with unilateral or bilateral articular facets on the caudoventral aspect of its body for articulation with a haemal arch (Flower 1885b, Rommel 1990, Watson 1992).

Number

In terrestrial mammals, the number and shape of caudal vertebrae vary greatly, reflecting the diverse structures and functions of their tails (Hickman 1979). The number varies from few, 4-6 in human beings (O'Rahilly et al. 1990) up to 46-49 in the African pangolin, Manis macrura (Flower 1885a). Cetaceans, which have powerfully-developed tails are characterized by a high number of well-developed caudal vertebrae. The largest, the blue whale, Balaenoptera musculus, has 27 (Omura 1971), the largest odontocete, the great sperm whale has 21-25 (Rice 1989), and within the dolphins, perhaps the highest number of caudal vertebrae reported is 44-49 in the Dall's porpoise, Phocoenoides dalli, a species well known for its high speed swimming (Jefferson 1988). Within the north eastern Pacific spotted dolphins, Stenella attenuata, the coastal ecomorph has fewer caudal vertebrae (34-37) than the offshore form (34–42) (Perrin 1975).

In the bottlenose dolphin an early report noted that the number of caudal vertebrae in one specimen (from the Atlantic) is 27 (Owen 1866). Subsequent reports from other regions of the world have revealed different numbers, for example: dolphins from the northern coastal region of China have 26-31 caudal vertebrae whereas those from the southern region have 19-24 (Gao et al. 1995).

A radiographic and dry bone study of 8 Atlantic bottlenose dolphin skeletons revealed 25-27 caudal vertebrae (De Smet 1977). More recently, 23-28 were found in 10 skeletons of West Atlantic bottlenose dolphins (Rommel 1990), while 27-31 were found in a radiographic and dry bone study of 43 West Atlantic and Gulf of Mexico bottlenose dolphins (Watson 1992). These reports reveal considerable geographical and intraspecific variation in the number of caudal vertebrae in the polymorphic bottlenose dolphin.

Shape

In mammals, the shape of caudal vertebrae generally resembles the lumbar vertebrae but their processes are much reduced in size (Dyce et al. 1996). Moreover, in terrestrial mammals, these two vertebral regions are clearly separated by a sacrum; in contrast, the obligate aquatic mammals, cetaceans and sirenians, do not have a sacrum. In addition, the morphology of their caudal vertebrae is an adaptation to aquatic living and they share a similar pattern. The caudal vertebrae of cetaceans articulate immediately caudal to the lumbar vertebrae and the size and shape of more cranial ones retain many similarities to the lumbar vertebrae (De Smet 1977). However, caudally they develop into three morphologically distinct regions (Flower 1885b), peduncle vertebrae, flukes vertebrae and transitional vertebrae between the two.

In dolphins, in the peduncle region, the shape of the caudal vertebral body is cylindrical with flat cranial and caudal surfaces. The slight difference between the lumbar and caudal vertebral bodies is on the ventral surfaces. In lumbar vertebrae, there is a single median longitudinal ridge on the ventral surface. In the caudal vertebrae, this ventromedial ridge is paired on the caudal aspect of the body to form two haemal processes with concave facets, which articulate with the haemal arches (Flower 1868).

In the peduncle vertebrae, there is a deep groove in the caudal edge of the base of the transverse process, which carries a dorsal arterial branch from the aorta to supply the epaxial muscles and other tissues dorsal to the transverse processes (Elsner et al. 1974). In more caudal peduncle vertebrae, the route of these blood vessels directly perforates the lateral surface of vertebral body ventrodorsally (Flower 1868). These perforations are now known as the vertical perforating foramina (Perrin 1975) and, in the flukes vertebrae, they are a distinct feature. In the finless porpoise, Neophocaena phocaenoides, the first perforated foramina appear at caudal vertebrae 7–8 in their total of 29–31 caudal vertebrae (Howell 1927). They were described and counted in a systematic account of north eastern Pacific spinner, Stenella longirostris, and spotted dolphins (Perrin 1975), and in bottlenose dolphins of South African waters (Ross 1977).

In the flukes region, these vertebrae lack spinous and transverse processes leaving only a vertebral body. Each vertebral body is transformed into a rectangular bone in the transverse plane, with the dorsoventral dimension being much less than the lateral, and is compressed craniocaudally (Owen 1866, Flower 1885b). The size of these flukes vertebrae reduces serially until the last vertebra, a small conical piece which, along with the second last vertebrae, is often lost during preparation (Rommel 1990, Watson 1992). These lost and uncounted terminal vertebrae may account for some of the numerical variation reported.

Review of illustrations of skeletons of dolphins reveals that the caudal vertebrae are unusual since there are three different morphological regions, each with characteristic vertebral shapes. The peduncle vertebrae continue the cylindrical form of the lumbar vertebrae, while the flattened rectangular flukes vertebrae complete the series. However, the vertebrae between these two regions are intermediate in form - these are transitional caudal vertebrae (Flower 1872, 1885b).

Transitional caudal vertebrae

In mammals, a vertebra with the characteristics of the two adjacent regions is often found at the junction between adjacent vertebral regions: occipito-cervical, cervico-thoracic, thoraco-lumbar, lumbo-sacral, and sacro-caudal (Flower 1885a). These transitional vertebrae are documented at the junctional regions in domestic mammals. Some appear only as incidental morphological variants, whereas others may present as severe pathological and clinical entities. For example, the atlanto-occipital transitional variations are described in horses (Watson and Mayhew 1986), and in dogs (Watson et al. 1988). A lumbosacral transitional vertebra is sacralized on the left side and has lumbar characteristics on the right side in a Chihuahua puppy (Schultz and Watson 1995). In goats, a variety of transitional vertebrae are seen at all junctional regions with the thoracolumbar and lumbosacral being the most frequent (Simoens et al. 1983).

Few examples are documented in cetaceans. Cervico-thoracic transitional vertebrae, with development of a cervical rib, are described in a false killer whale (Yamada 1959). In the white beaked dolphin, Lagenorhynchus albirostris, a transitional vertebra has been identified between the vertebrae bearing double-headed ribs and those bearing single-headed ribs. This mid-thoracic transitional vertebra sometimes possesses an extra costal element ventral to its transverse process (De Smet 1975). A similar mid-thoracic transition in rib articulation patterns occurs in the false killer whale, Pseudorca crassidens (Purves and Pilleri 1978).

Within the caudal vertebrae of cetaceans, one or more vertebrae of intermediate shape have been described between the distinctive peduncle and flukes vertebrae. These transitional vertebrae are described in sperm whales (Flower 1868), and in humpback dolphins, Sousa chinensis (Flower 1872). In bottlenose dolphins, it may occur as a single vertebra (Flower 1885b, Rommel 1990) or over one to three vertebrae (Watson 1992), and is somewhat round or oval in lateral and cranial views with convex cranial or caudal surfaces (Watson 1992). Preliminary data demonstrates that functionally, this transition unit, the "ball vertebra" and its caudal intervertebral disk, is more flexible than adjacent regions and acts like a hinge joint between the peduncle and the flukes in bottlenose dolphins (Watson 1992).

Length of vertebral bodies

The craniocaudal length of the vertebral body varies along the series of caudal vertebrae. Plotting the vertebral body length against vertebral number produces a characteristic curve (Fig.2 in Omura 1971) in which a marked downward deflection occurs distally in the series. This sudden shortening of the vertebral body takes place over 2-3 caudal vertebrae. Such a pattern is found in both baleen whales (Omura 1971, Omura et al. 1971) and in toothed whales, which include sperm whales (Flower 1868), Fraser's dolphins, Lagenodelphis hosei (Miyazaki and Wada 1978), and harbor porpoises (Slijper 1946). This characteristic curve from living cetaceans is associated with the center of tail dorsoventral bending at the peduncle-flukes junction (Slijper 1946). Comparison with similarly produced graphs from fossil whales has been suggested as a means to determine whether or not they had developed dorsoventral bending of caudal vertebrae, and thus flukes as a primary locomotory organ (Gingerich et al. 1994).

Haemal arches

In terrestrial mammals, the number and shape of haemal arches, or haemapophyses (Owen 1866), diversify greatly and reflect the functional differences of their tails (Hickman 1979). They are usually poorly developed in carnivores and in ungulates. In dogs, which have 20 caudal vertebrae, their four haemal arches articulate with caudal vertebrae 4-7 (Frewein 1970). In the ox, which has 18-20 caudal vertebrae, its four or less haemal arches fuse to caudal vertebrae 2-5, whereas in the horse, haemal arches are usually absent (Nickel et al. 1986).

In contrast to that of generalised quadrupedal mammals, the haemal arches are well developed, being greater in number and larger in size in kangaroos, sirenians and cetaceans, all of which have tails of considerable locomotory importance (Flower 1885b). In the sirenians, which like the cetaceans swim by dorsoventral bending of their tails, the dugongs have 13-14 haemal arches and 23 caudal vertebrae (Owen 1866).

In dolphins, each haemal arch articulates on the caudoventral aspect of the vertebral body by either a synovial joint or ligaments (De Smet 1977). Each haemal arch develops ventral to the vertebral body from a bilateral pair of ossification centers. Most pairs fuse ventromedially to form a single V-shaped bone in cranial view; the V shape gave rise to their common name - chevron bones (De Smet 1977, Rommel 1990). The first one or two and the last few often remain unfused as two hemiarches (Cozzi et al. 1985). A haemal spine, which often develops mid-ventrally where the two hemiarches fuse, increases the size of haemal arches which now become Y-shaped. The length of the haemal arches increases serially to the maximum in mid-peduncle and then decreases toward the flukes (Rommel 1990).

In toothed whales, the number of haemal arches varies. One sperm whale had 14 haemal arches on its 24 caudal vertebrae (Flower 1868), and one Stejneger's beaked whale, Mesoplodon stejnegeri, had 9 haemal arches on 19 caudal vertebrae (Nishiwaki and Kamiya 1959). In offshore eastern Pacific spotted dolphins, there are 26–33 haemal arches along the 34–42 caudal vertebrae (Perrin 1975), whereas the Dall's porpoises have 30-35 haemal arches in their 44-49 caudal vertebrae (Jefferson 1988). And in the

Atlantic bottlenose dolphin, there are 21 or more haemal arches for its 27-31 caudal vertebrae (Rommel 1990, Watson 1992). The last 2 or 3 become two small unfused hemiarches (Rommel 1990) and the terminal 7 caudal vertebrae do not have haemal arches (De Smet 1977). Information on haemal arches was not available for Chinese (Gao et al. 1995) and South African bottlenose dolphins (Ross 1977).

The series of haemal arches has two important functions in mammals generally: first, to provide bony protection for the terminal branches of the aorta medially and, second, to offer attachment sites for muscles laterally (Flower 1885b). In dolphins, the same functions are amplified because their tails constitute one third of the total body length (Fish and Hui 1991). Their haemal arches enclose the many terminal branches of the aorta which supply the muscular peduncle and ramify in the flukes. These blood vessels of the flukes provide vital thermoregulatory functions (Elsner et al. 1979). The expanded lateral surfaces of haemal arches offers increased attachment sites for the massive caudal hypaxial muscles which power the downstrokes of the tail, while dorsally, spinous processes provide similar attachment for the massive epaxial muscles which power the upstrokes (Pabst 1990, Slijper 1961).

Vertebral processes

In terrestrial mammals, the vertebral column suspends the weight of the trunk against gravity. This suspension applied on the vertebral processes is diminished in aquatic mammals since their body weight is largely supported by the buoyancy of water (Slijper 1946, 1979). In cetaceans, vertebrae, especially the caudal vertebrae, become the axis of locomotion and the vertebral processes, which are generally elongate are primarily for attachments of the swimming axial muscles, which are massively developed. Thus, the length and orientation of vertebral processes reflect their functional roles in dolphin swimming (Slijper 1947).

In dolphins, the vertebral processes extend in four directions: dorsal, lateral, and ventral. Mid-dorsally, the spinous process extends from the summit of the vertebral arch. Laterally, a bilateral pair of transverse processes projects from the vertebral body and the dorsoventral level of attachments to the vertebral body varies along the vertebral column. Ventrally, the haemal arches articulate with the ventrally-protruding haemal processes of the vertebral body. The ventral expansion of a haemal arch, projecting from the median fusion of the two halves, is the haemal spine (Owen 1846), which structurally and functionally is similar to the spinous process dorsally.

In dolphins, the vertebral processes decrease in size through the caudal vertebrae. In the eastern Pacific spotted dolphins, the last vertebra with a transverse process is vertebra 59-66 and the last spinous process is at vertebra 64-71 in the total series of 77–83 vertebrae (Perrin 1975). In the finless porpoises, they have 29–31 caudal vertebrae and the last vertebra with a spinous process is at caudal vertebrae 16–17 (Howell 1927). And in false killer whales, the last vertebra with transverse processes is caudal vertebra 7 and the last vertebra with a spinous process is at caudal vertebrae 11-14 in their total of 22-23 caudal vertebrae (Yamada 1956). Comparable information is not available for bottlenose dolphins.

Intervertebral disks

In mammals, the structure and flexibility of the vertebral column are highly associated with the mode of locomotion. The intervertebral disk connecting each vertebral body provides the flexibility to the vertebral column. In domestic ungulates, the total length of all interverterbral disks is 10% of the vertebral column, for dogs it is 16% (Dyce et al. 1996), whereas in human beings it is 25% (Gardner and Gray 1975).

The intervertebral disk is a symphysial joint composed of connective tissues and topographically it has two regions. The outer anulus fibrosus is a concentric collagen fiber ring, which encloses the inner gelatinous material of the nucleus pulposus. In the ox, the anulus fibrosus occupies the outer one fourth to half of the intervertebral disk (Dyce et al. 1996).

In mammals, the intervertebral disk is a resilient pad and its major mechanical function is to dissipate the pressure from locomotion. The nucleus pulposus sustains most compression (Rockwell et al. 1938, Hukins 1988), while the tougher anulus pulposus binds the vertebral bodies together and provides stability during bending and twisting (Hukins 1988). The disk provides elasticity for the vertebral column to recover its size and shape after deformation (Gardner and Gray 1975).

The functional morphology and pathology of intervertebral disks are well studied in human beings (Gardner and Gray 1975) and in some domestic mammals (Dyce et al. 1996). However, the information is limited in cetaceans. In bottlenose dolphins, the length of intervertebral disks is quite different in each vertebral region: it is particularly short in the cervical region, increases gradually in the thoracic and lumbar regions, and is greatest between the flukes vertebrae (Rommel 1990). However, reports of the flexibility, tissue composition and mechanical properties of caudal intervertebral disks are unavailable for dolphins.

Summary

Dolphins are obligate aquatic mammals with characteristic thunniform bodies for fast and sustained swimming. The locomotion of dolphins relies on dorsoventral tail bending and the flexibility of their tails is centered at the peduncle-flukes junction. Tail bending is powered by well-developed epaxial and hypaxial muscles inserted on the caudal vertebrae.

Morphologically, vertebrae are a serially repeated structure and there is considerable variation in most meristic parameters (Danforth 1930). In dolphins, the variation of the vertebrae is most remarkable in the caudal vertebrae, which are different in number, shape and presence of haemal arches (Perrin 1975). This individual variation, as well as geographical variation, is common in bottlenose dolphins (Ross 1977, Rommel 1990, Gao et al. 1995).

The caudal vertebrae of dolphins are characterized by three morphologically distinct regions. Despite the interspecific and intraspecific numerical variation, dolphin caudal vertebrae reveal the same pattern of cylindrical, transitional and rectangular shapes. The tail dorsoventral flexibility is centered on the more rounded transitional vertebrae. However, each vertebra is plastic (Danforth 1930) and neither numerical position nor morphological characteristics provides a satisfactory criterion to characterize each vertebra (O'Rahilly et al. 1990). Thus, the morphological and numerical definition for the transitional caudal vertebrae are not fixed.

Chapter 3

Materials and Methods

Specimens

Nineteen tails were excised from dead Gulf of Mexico bottlenose dolphins, Tursiops truncatus. Fifteen were collected from stranded dolphins on the Texas coast by the Texas Marine Mammal Stranding Network during 1991-1998. Four additional fresh tails were collected from necropsies of zoo dolphins, which were previously captured in the Gulf of Mexico. The sample consisted of nine female and ten male adult dolphins, which ranged from 2.09-2.70 m in total body length (TL in meters, m; Table 3.1). Tails from ten dolphins (six females, four males; 2.24-2.59 m) were available for complete data recovery; the other tails, because of varying limitations, provided only partial data. All stranded specimens were frozen and stored at Galveston, TX, and then transported to Stillwater, OK.

The condition of the carcass of the salvaged tails was either fresh, as if the stranded dolphin had just died without bloating (stranding code 2) or, ranged from bloated with peeling skin to moderate decomposition (stranding code 3). Most specimens were complete tails from the first caudal vertebra to the entire flukes, and some were not complete, missing the first few caudal vertebrae and/or with some blubber and muscle trimmed already.

Definitions

For the purpose of description in this thesis, the caudal vertebrae of bottlenose dolphins were defined in three topographical regions: the peduncle vertebrae, the transitional vertebrae, and the flukes vertebrae.

The peduncle vertebrae were those found in the peduncle region of the tail. They started at the first caudal vertebra: the first vertebra with a haemal arch articulated caudoventrally to its vertebral body. They were characterized by cylindrical vertebral bodies and prominent processes, the caudal-most in the series with processes reduced to absent.

The vertebrae between the peduncle and flukes showed a gradation of morphology. These intermediate vertebrae were the transitional vertebrae. They were somewhat rounded and were located in the peduncle-flukes junction.

The flukes vertebrae were those found in the flukes region of the tail. They were characterized by rectangular-slab vertebral bodies without processes.

Radiography

Tails were thawed and cleaned before taking radiographs. Standard, plain-film radiographs were taken at the College of Veterinary Medicine, Oklahoma State University, Stillwater, OK. The longitudinal axis of the each tail was positioned parallel to the film without rotation. The film-to-source distance was 100 cm and films were processed in an automatic processor. Four types of radiographs were taken in sequence (Table 3.1).

1) Dorsoventral radiographs of flukes

One dorsoventral view of the peduncle-flukes junction and the flukes was taken to determine which caudal vertebrae were located at the peduncle-flukes junction, to count the number of flukes vertebrae, and in particular to identify the terminal vertebra. Radiographs were taken at 51 kVp and 500 mA, for 0.040 sec with grid.

2) Lateral radiographs of peduncle and flukes

Distal flukes were trimmed symmetrically to leave the axial 10 cm of the flukes and vertebrae to facilitate positioning for right lateral view radiographs. Three to four lateral view radiographs were taken to cover the whole peduncle for identification of all haemal arches. A metal location marker was inserted on the caudal margin of each image to identify the serial number of each caudal vertebra. Due to the varied thickness of the different regions of each tail, the settings ranged from 53-77 kVp and 400 mA, for 0.020-0.050 sec with grid and 60-72 kVp and 400 mA, for 0.011-0.020 sec without grid.

3) Lateral radiographs of flukes bending

Right lateral view radiographs were taken of the flukes in neutral, dorsal bending and ventral bending positions. The ball vertebra (central transitional vertebra) was first identified and marked by a metal marker under fluoroscopy, and then for each subsequent radiograph, the x-ray beam was centered on this marker. Radiographs were taken at 58 kVp and 400 mA for 0.020 sec without grid for all three positions.

Each dolphin tail was fixed in right lateral recumbency by impaling the first four to five caudal vertebrae and soft tissues on a bed of nails and tightened with sponges and rubber bands on a custom built apparatus (Fig. 3.1). The terminal part of the tail was pierced immediately cranial (approximately 10 mm) to the flukes notch where monofilament nylon was connected to a constant weight (3 kg) to pull the tail dorsally for dorsal bending radiographs and then ventrally for ventral bending radiographs. A pilot study on three tails demonstrated that a weight of 3 kg produced bending angles that were within the range of angles seen in swimming dolphins.

4) Digitized spot film of intervertebral disks

Right lateral spot films were taken for length measurement of the intervertebral disks at the peduncle-flukes junction. The ball vertebra was identified and marked. Then, the three intervertebral disks cranial to and the three caudal to this vertebra were radiographed individually. In each case, the x-ray beam was centered on the selected intervertebral disk, to avoid distortion due to x-ray beam angulation, and images were made with a digital fluoroscope and printed with a laser film printer.

For measurement calibration, a 5 cm metal reference was taped along the median line of the tail dorsal to the ball vertebra.

Radiograph evaluation

Radiographs and spot films were first evaluated by eye on a standard radiograph illuminator.

1) Dorsoventral view of flukes

The numeric identification of the caudal vertebrae at the peduncle-flukes junction was determined, and the number of flukes vertebrae was counted.

2) Lateral view of the peduncle and flukes

The total number and shape of caudal vertebrae and of haemal arches were determined.

3) Intervertebral bending angles

The neutral, dorsal and ventral bending radiographs were digitized by a PSI imaging system (Hill's 1994 © vepro 1991-1994, version 4.30) and analyzed using AutoCAD software (1982-1996 Autodesc, Inc. Release 13_c4 (1/2/96) Microsoft Windows version 4.0).

On the lateral neutral position radiographs, AutoCAD was used to establish an ideal mid-dorsoventral vertebral body axis for the ball vertebra, and for the three vertebrae cranial to and caudal to it (Fig. 3.2a). This was achieved by drawing a dorsal- and a ventral-best-fit line on these seven vertebral bodies (the spinous processes, haemal processes, and haemal arches were excluded from the bodies for this determination). These two lines were then extended caudally to their intersection: the sharp angle so formed was then divided equally by a third line - the ideal vertebral body axis (Fig. 3.2a).

Segments of ideal body axis of vertebral bodies were transferred to corresponding vertebral bodies on both dorsal and ventral bending images (Fig. 3.2b). The angle that each segment diverged from the horizontal (neutral) axis was calculated by AutoCAD. Then, six intervertebral bending angles between these seven selected vertebral bodies were calculated by deduction of the angles of two adjacent segments (Fig. 3.2b).

4) Intervertebral disk length

The lengths of the six intervertebral disks were measured. In each case, the intervertebral disk and the vertebra immediately cranial to it was measured as a whole unit, and each disk length was measured separately. These two craniocaudal measurements were taken at the dorsoventral mid-point of the vertebral body with a plastic ruler directly on the spot films and measured to the nearest millimeter. Measurements were corrected for magnification using a known length (5 cm) metal marker. Intervertebral disk measurements were recorded as absolute numbers and as percentages of each vertebral body-disk unit.

Muscle water content

The water content of tail muscle was measured to examine whether tissue quality, as defined here by water content, affected the bending flexibility of the tail. Due to the varied conditions of carcasses collected and the duration of preservation, the tails of dolphins were decomposed and dehydrated to different levels. Muscle from each tail was sampled immediately before the bending test and the percentage of water content was calculated.

On each dolphin, a 1-2 gram sample of the left hypaxialis lumborum muscle was excised without tendons on the day of taking radiographs. The sample was taken 5 cm caudal to the transverse tail cut, between the last lumbar vertebra and the first caudal vertebra, and immediately lateral to the haemal arch. Sampled muscle was diced into 5 mm cubes, weighed in a labeled and pre-weighed vial, and was frozen at -74° to -76°C for at least two hours and then dehydrated under -65°C, at 10 micrometer Hg for at least 75 hours.

Each sample was then weighed repeatedly, after each cycle of 14 hours freeze-vacuum, until three sequential readings were obtained that did not differ by 1%, indicating complete dehydration. The water content in muscle samples was calculated as a percentage.

Dry bone preparation

Skin, blubber, muscle, and tendon were dissected off the caudal vertebral column and then the specimen was macerated by simmering in hot water to remove remaining soft tissues. The caudal vertebrae and haemal arches were cleaned, rinsed in water, air dried and brushed.

Vertebra measurements and meristics

Seventeen measurements and meristic observations were taken on the bony caudal vertebrae during examinations of both radiographs and/or dry bones; small cartilaginous haemal arches and terminal caudal vertebrae, as discovered on dissection were so noted. The measurements and meristics were:

1. Total number of caudal vertebrae.
2. Number of peduncle vertebrae.
3. Number of flukes vertebrae.

4. Number of transitional vertebrae.
5. Serial number of the transitional vertebrae.
6. Last vertebra with a vertebral arch.
7. Last vertebra with distinct transverse processes.
8. Total number of haemal arches.
9. Number of unfused haemal arches cranially.
10. Number of unfused haemal arches caudally.
11. Number of terminal flukes vertebrae without haemal arches.
12. Serial number of the longest haemal arch.
13. Last caudal vertebra with unfused vertebral body epiphyses.
14. Craniocaudal length of each caudal vertebral body measured on the axis of the notochordal foveae.
15. Craniocaudal length of six intervertebral disks and vertebrae across the peduncle-flukes junction
16. Dorsal bending angles of six intervertebral disks across the peduncle-flukes junction.
17. Ventral bending angles of six intervertebral disks across the peduncle-flukes junction.

The number of missing caudal vertebrae was estimated in some incomplete specimens by comparison of the vertebral body and the haemal arch serial morphology with known complete vertebral columns. On the dry bones, measurements were taken with vernier calipers to the nearest millimeter. Sometimes, the epiphyses were not fused to the vertebral body. The designation of "unfused" was based on the presence of a cleft representing the cartilage growth plate over more than 25% of the circumference.

In the measurement of craniocaudal length of the vertebral body, some epiphyses were unfused and fallen. In these specimens, the vertebral body was measured without the epiphyses and the averaged thickness of those fallen epiphyses was added. The relationship between the serial number of the vertebra and the craniocaudal length of vertebral bodies was plotted.

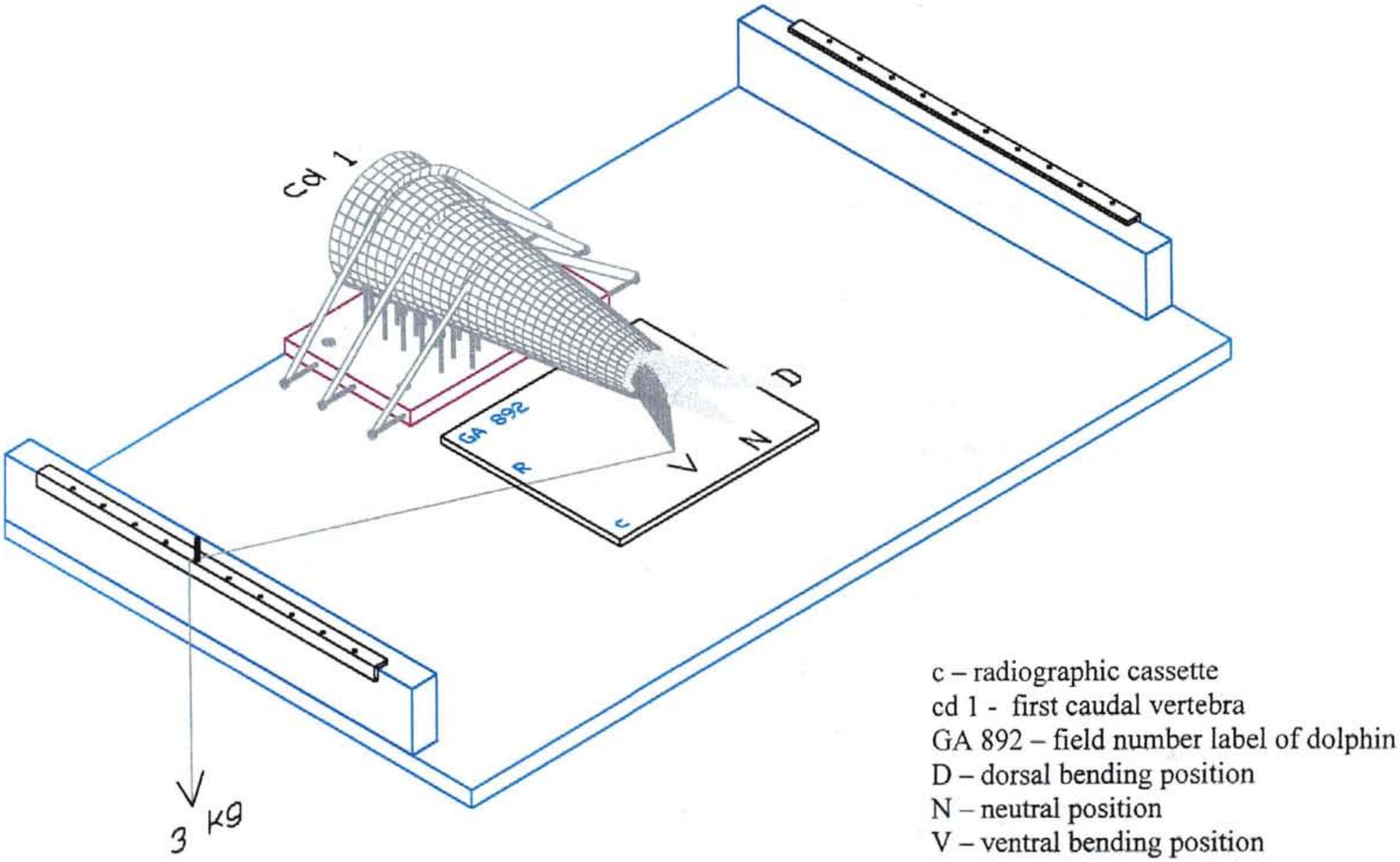
Data analysis

The differences of relative lengths of intervertebral disks (disk / vertebral body plus disk, as percentage) as well as dorsal and ventral bending angles among six intervertebral disks were compared by analysis of variance (Systat Software, version 5.0 © 1990, Systat, Inc). Also, the relationships between sex and dorsal and ventral bending angles were contrasted by analysis of variance. The correlation coefficients between dorsal and ventral bending angles with muscle water content and total body length were calculated in Excel software (Microsoft®Excel 1997 SR-1 ©1985-1997 Microsoft Corporation).

Table 3.1. Collection data for 19 Gulf of Mexico bottlenose dolphins, Tursiops truncatus, and types of data collected.

				radiograph views				dry bone
field #	TL (m)	sex	source	dv	spot	lat	bend	meristic
CC 110	2.42	F	TX	Y	Y	Y	Y	Y
GA 425	2.24	M	TX	Y	Y	Y	Y	Y
GA 436	2.55	F	TX	Y	Y	Y	Y	Y
GA 720	2.40	M	TX	Y	Y	Y	Y	Y
GA 836	2.45	F	TX	Y	Y	Y	Y	Y
GA 892	2.45	F	TX	Y	Y	Y	Y	Y
LA 042	2.59	M	TX	Y	Y	Y	Y	Y
PA 301	2.31	M	TX	Y	Y	Y	Y	Y
PA 457	2.37	F	TX	Y	Y	Y	Y	Y
SP 153	2.37	F	TX	Y	Y	Y	Y	Y
AGW90M2	n/a	F	OKC	N	N	N	N	Y
AGW91M2	2.41	F	STL	Y	N	N	N	Y
ALFIE	n/a	M	OKC	Y	N	Y	N	N
AGW96M1	n/a	F	OKC	Y	N	Y	Y	Y
GA 295	2.68	M	TX	N	N	N	N	Y
GA 415	2.37	F	TX	Y	N	Y	N	Y
GA 683	2.70	M	TX	Y	N	N	N	Y
SP 132	2.57	M	TX	Y	N	Y	N	Y
SP 154	2.09	M	TX	Y	N	N	N	N

F - female
M - male
N - no
Y - yes
OKC - Oklahoma City Zoo, OK.
STL - St. Louis Zoo, MS.
TX - Texas Marine Mammal Stranding Network.



c – radiographic cassette
cd 1 - first caudal vertebra
GA 892 – field number label of dolphin
D – dorsal bending position
N – neutral position
V – ventral bending position

Figure 3.1. The tail bending machine. Each dolphin tail was laid on its right lateral side (R) on a bed of nails, fixed by rubber bands, and the peduncle-flukes junction with laterally-trimmed flukes were positioned over the radiograph cassette. For bent-tail radiographs, the tip of the flukes was pulled ventrally (V) or dorsally (D) by a constant weight (3 kg).

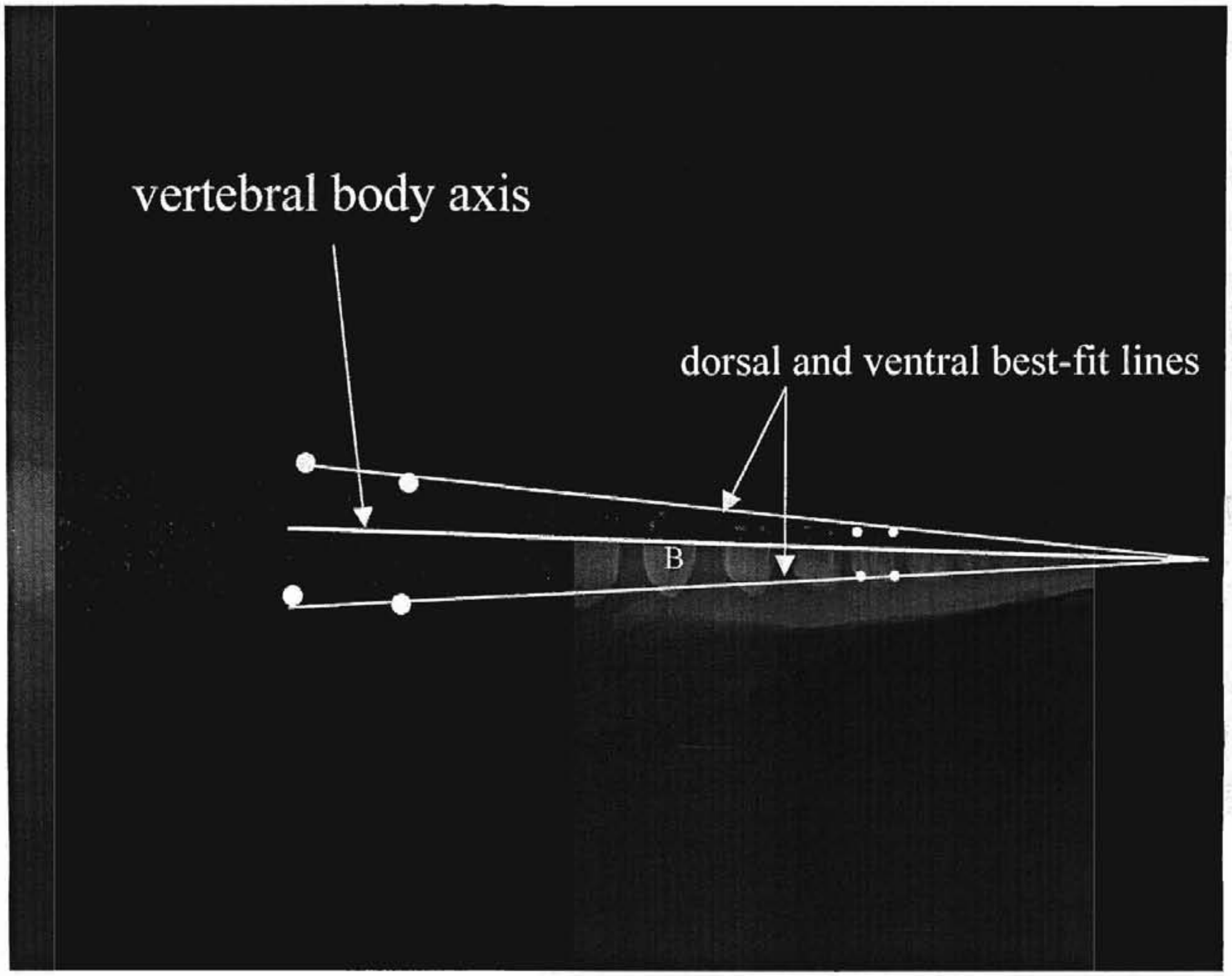


Figure 3.2a. Simulation of tail bending angles measurement from lateral radiograph (neutral position) in AutoCAD. The vertebral body axis was established by bisecting the angle between dorsal and ventral best-fit lines, which were formed by connecting the two dorsal and two ventral corner points of all seven vertebrae across the transitional unit.

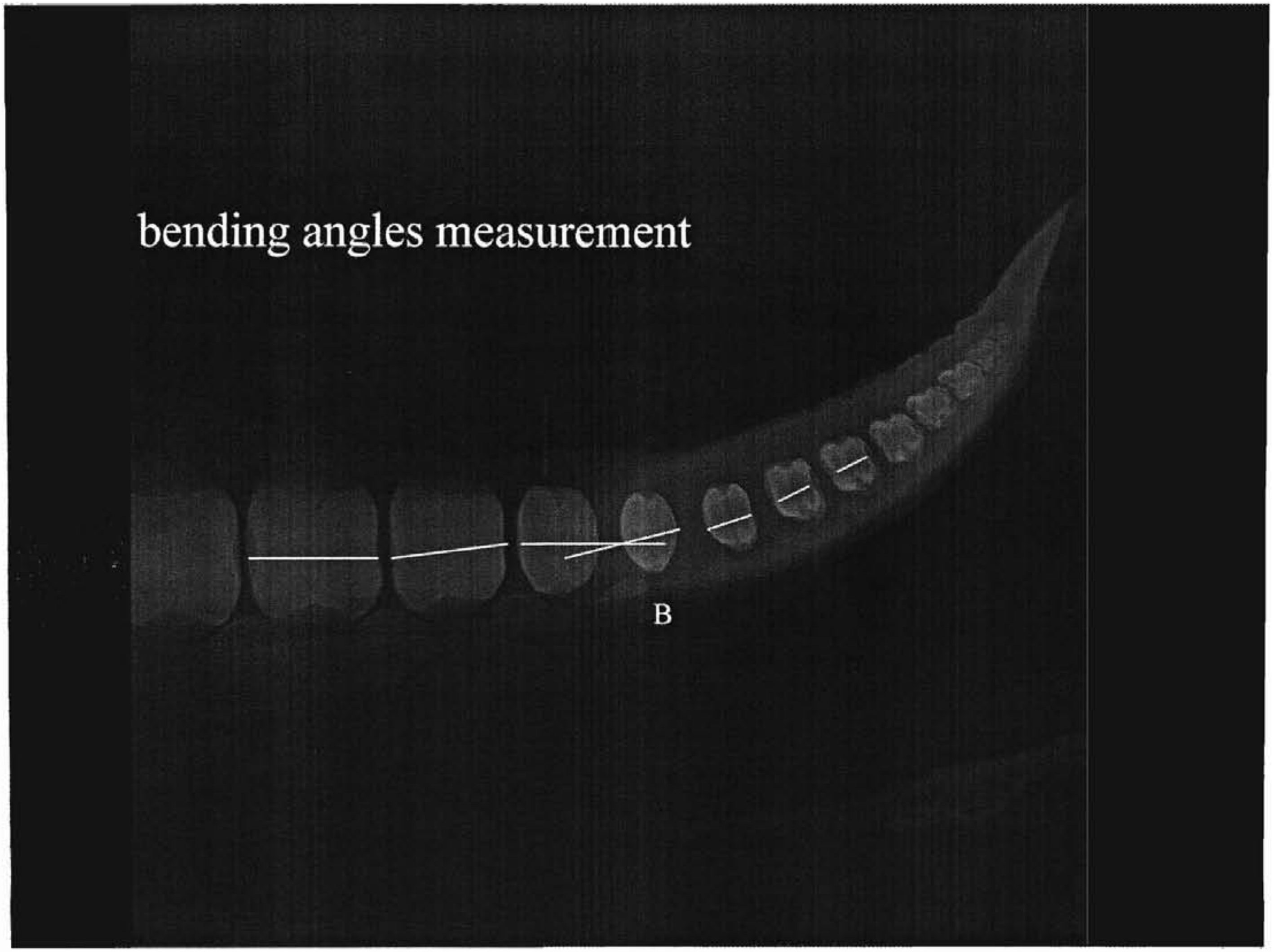


Figure 3.2b. Segments of vertebral body axis were transferred from the neutral positioned radiograph to the dorsally bent radiograph in AutoCAD. The extension of two adjacent segments formed a sharp angle (shown at one joint) - the intervertebral bending angle. This procedure was repeated on all seven vertebrae and six joints on both dorsally and ventrally bent radiographs.

Chapter 4

Results

Morphology of Caudal Vertebrae

Number

The total number of caudal vertebrae ranged from 26-30 in 12 complete vertebral columns, with a mode of 28 (Table 4.1). The number of peduncle vertebrae was 15-18 (mode=17) while it was 7-10 (mode=8) for the flukes vertebrae. The caudal vertebrae transformed between peduncle and flukes and the transformation occurred over two to four vertebrae, herein defined as the transitional vertebrae. Usually there were three vertebrae (n=13), which were located at caudal vertebrae 18-20 (n=7) among 17 sets of caudal vertebrae (Table 4.1).

Peduncle vertebrae

The peduncle vertebrae were in the peduncle of the tail. They were from the first caudal vertebra to the last vertebra with a vertebral arch, which was usually caudal vertebra 17. The peduncle vertebrae were characterized by cylindrical vertebral bodies (Fig. 4.1a) and prominent processes.

The cylindrical vertebral bodies had generally flat cranial and caudal surfaces. In cranial or caudal view, these surfaces were circular and transformed to oval in the more caudal members in the series, with the long axis dorsoventrally.

Caudal vertebrae 1-13 in the peduncle generally resembled the lumbar vertebrae, with long spinous and transverse processes. The length of these processes gradually decreased caudally. The last vertebra with transverse processes was caudal vertebrae 13-16 (mode=15) and the last transverse process was reduced to a very low and wide ridge on the lateral side of the vertebral body.

The last vertebra with a vertebral arch was located at caudal vertebra 15-18, most often at 17, and was usually two vertebrae caudal to the last vertebra with transverse processes. At this level, the spinous processes were greatly reduced to absent (Fig. 4.1a), leaving the vertebral arch as a flat bridge dorsal to the vertebral foramen.

Transitional vertebrae

The vertebrae between the peduncle and flukes showed a gradation of morphology. This transitional region typically had three vertebrae (n=13), which had characteristics of both peduncle and flukes vertebrae (Fig. 4.1a,b,c).

The first one (T1) of this unit resembled the adjacent peduncle vertebra and was usually caudal vertebra 18. Typically it was the first caudal vertebra with all processes absent leaving only the vertebral body. There were four cases with a very short, small and flat vertebral arch (Table 4.1). The vertebral body was cylindrical but the caudal half was visually smaller than the cranial half. The cranial vertebral body surface was flat and circular while the caudal surface was convex, more oval and smaller with a depression in the center (Fig. 4.1a,b,c).

The second one resembled neither a peduncle nor a flukes vertebra. Both cranial and caudal surfaces were convex (Fig. 4.1b), with a slight depression around the notochordal foveae. In cranial or caudal view, this vertebral body was slightly compressed dorsoventrally with convex lateral borders. By visual observations of radiographs and dry bones, it was noted that, in dorsal view, the vertebral body was wider laterally than the first transitional vertebra (Fig. 4.1a). Because of its unique biconvex or lenticular profile, this bone was designated "the ball vertebra."

The third vertebra (T3) in the transitional unit was rectangular in cranial and caudal view, resembling a flukes vertebra (Fig. 4.1c). However, its cranial and caudal vertebral body surfaces were convex (Fig. 4.1b). Usually it had a lateral groove on each side of the vertebral body.

In three cases, the transitional unit was composed of two vertebrae (Fig. 4.2): they corresponded to the first and the second vertebrae of the typical unit. Immediately caudal to these two vertebrae were the flukes vertebrae. In one other case, there were four vertebrae in the transitional unit (Fig. 4.2). The first and second vertebrae were similar to each other, and similar to the first one in the typical transitional unit. The third and fourth resembled the second and third vertebrae of the typical unit respectively.

Flukes vertebrae

The flukes vertebrae were those found in the flukes of the tail. They were characterized by their rectangular-slab vertebral bodies without processes (Fig. 4.1c). The flukes vertebrae were rectangular in cranial and caudal view with compressed dorsoventral and craniocaudal dimensions. The cranial and caudal surfaces were slightly concave in the center. Overall, the lateral dimension was approximately twice the dorsoventral dimension and four times the craniocaudal length. Each had a longitudinal lateral groove on each side of the vertebral body for a major tendon (Fig. 4.1b), and a pair of vertical perforating foramina, equidistant from the median, through the vertebral body dorsoventrally (Fig. 4.1a). The penultimate caudal vertebra was a blunted-tip cone and the terminal vertebra was a tiny 3-4 mm cone. In two cases, a similar-sized terminal cartilage nubbin was present in place of the terminal bone.

Correlation of the transitional vertebrae with peduncle-flukes junction

The first transitional vertebra corresponded to the external body profile at the caudal-most end of the peduncle (Fig. 4.3). The ball vertebra was located in the transition between peduncle and flukes, just cranial to where the flukes start to flare out laterally. The third one was at the cranial-most level of the flukes.

Vertebral body length

The craniocaudal lengths of vertebral bodies of 15 caudal vertebral columns were measured (Table 4.2). The serial numbers in all vertebral columns were shifted one or two cranially or caudally so that the ball vertebra was the same number in all – as a standard reference point. The lengths of these caudal vertebrae were then averaged, the longest vertebra was designated as 100%, and plotted (Fig. 4.4). Caudal vertebra 1 was 80% of the length of the longest caudal vertebra and the lengths of the first 15 increased serially until reaching the maximum (41 mm) at the 15th. The length abruptly decreased at the three transitional vertebrae. The first vertebra of the transitional unit was 75% of the maximum vertebral body length, the ball vertebra was 40%, and the third vertebra was 30%. The flukes vertebrae were much shorter (3-14 mm) than either the transitional or peduncle vertebrae (Fig. 4.4).

Vertebral body epiphyses

In 17 dry bone specimens, 11 (2.37 - 2.70 m TL) had both cranial and caudal epiphyses fused to vertebral bodies in all caudal vertebrae, while five (2.24 - 2.68 m TL) had unfused epiphyses at cranial and/or caudal surfaces from caudal vertebra 1 to caudal vertebra 11-18 (Table 4.1). In one other case, there were unfused vertebral body epiphyses on caudal vertebrae 1-26 (2.24 m TL).

Haemal arches

In total, the haemal arches formed a curved profile ventral to the caudal vertebrae and they varied in number, shape and size. The first haemal arch articulated caudoventrally on the body of caudal vertebra 1, and was the reference for defining the beginning of the caudal vertebrae. It was always two unfused hemiarches, which were small craniocaudally-elongated rhomboidal plates. In two cases, the second haemal arch was also two unfused hemiarches (Table 4.1).

The cranial-most haemal arches were V-shaped in cranial and caudal view. More caudally in the peduncle, they were elongated ventrally to become Y-shaped. The longest one in dorsoventral dimension was usually the 8th (n=7). Caudal to this point, the size of the haemal arches reduced gradually into the flukes and became V-shaped again at the transitional vertebrae.

In the transitional vertebrae, the haemal arches were reduced to small, flat and V-shaped; they usually were unfused hemiarches at the third vertebra in the unit. In the flukes, the haemal arches were always two small oval unfused hemiarches (2-10 mm) and ranged from 3-6 pairs. They were absent on the last 4-7 (mode=5) caudal vertebrae (Table 4.1).

Tail Bending

Bending angles of intervertebral disks

In dorsal bending, the sum of the three angles caudal (7.0-8.9°) to the ball vertebra was greater than, and significantly different ($P<0.001$) from the sum of the three angles cranial (1.0-2.5°) to the ball vertebra ($n=10$) (Table 4.3).

In ventral bending, the sum of the three angles caudal (7.5-8.2°) to the ball vertebra was greater than, and significantly different ($P<0.001$) from the sum of the three angles cranial (0.6-1.7°) to the ball vertebra (Table 4.3). Thus the dorsal and ventral bending was greater at the three intervertebral disks caudal to the ball vertebra (Fig. 4.5).

The three individual bending angles (cranial or caudal to the ball vertebra) were not significantly different ($P>0.05$) among or between dorsal or ventral bending directions (Table 4.3). Therefore, the extent of dorsal bending was not different from the ventral bending.

Lengths of the intervertebral disks

The mean lengths of the two intervertebral disks caudal to the ball vertebra (6.51, 6.05 mm) were larger than those of the other four disks (3.80-4.54 mm) across the transitional region (Table 4.4). In particular, the one disk immediately caudal to the ball vertebra was significantly longer ($P<0.05$) than the second and third disks cranial to the ball vertebra.

The relative lengths of the three disks caudal to the ball vertebra (22.6-27.3%) were longer than, and significantly different ($P<0.05$) from the three disks cranial to the ball vertebra (9.1- 12.9%) (Table 4.3, 4.4).

Bending ability relationships with sex, body length and muscle water content

The bending ability of the tail at the peduncle-flukes junction was calculated as the sum of six dorsal bending angles and the sum of six ventral bending angles. Both dorsal and ventral bending angles had no strong linear correlation with the water percentage of tail muscle nor with total body length (Table 4.5). In addition, there was no significant difference ($P>0.05$) in the relative length of these six intervertebral disks between males and females.

Table 4.1. Caudal vertebrae meristics for 17 Gulf of Mexico bottlenose dolphins, Tursiops truncatus.

parameters field #	AGW90M2*	AGW91M2*	AGW96M1*	CC 110	GA 295	GA 415	GA 425	GA 436	GA 683	GA 720	GA 836	GA 892	LA 042	PA 301	PA 457	SP 132	SP 153	mode	n
1. Total number of caudal vertebrae.	28(4)[a]	28	27[b]	28(1)[c]	27(3)[a]	28	29(7)[c]	29[e]	30[e]	28	28[e]	28	29(7)[ce]	27	27[b]	28	28(6)[c]	28	9
2. Number of peduncle vertebrae.	16	17	17	17	15	17	17	17	18	17	17	16	17	17	15	17	17	17	12
3. Number of flukes vertebrae.	10	8	7	8	10	8	9	9	9	9	8	9	9	8	8	8	8	8	8
4. Number of transitional vertebrae.	2	3	3	3	2	3	3	3	3	2	3	3	3	3	4	3	3	3	13
5. Serial number of the transitional vertebrae.	18.19	18-20	18-20	18-20	16.17	18-20	18-20	18-20	19-21	18,19	18-20	17-19	18-20	18-20	16-19	18-20	18-20	18-20	11
6. Last vertebra with vertebral arch.	16	17	17	18[d]	15	17	17	17	18[d]	17	17	17[d]	17	17	15	18[d]	17	17	11
7. Last vertebra with distinct transverse processes.	14	15	15	15	13	15	15	15	16	15	15	14	15	15	14	15	16	15	11
8. Total number of haemal arches.	17+	23	22	21	17+	21+	22	22	23	24	23	23	24	22	22	23	23	23	6
9. Number of unfused haemal arches cranially.	n/a	1	1	2	n/a	n/a	n/a	1	1	1	1	1	n/a	1	1	1	n/a	1	10
10. Number of unfused haemal arches caudally.	n/a	3	4	2	n/a	n/a	3	4	4	6	5	5	6	4	4	3	5	4	5
11. Number of terminal flukes vertebrae without haemal arches	n/a	5	5	7	n/a	n/a	7	7	7	4	5	5	5	5	5	5	5	5	9
12. Serial number of the largest haemal arch.	n/a	n/a	8	8	n/a	n/a	n/a	8	8	8	8	8	n/a	7	7	7	n/a	8	7
13. Last caudal vertebra with unfused vertebral body epiphyses.	0	18	17	0	14	0	26	0	0	17	0	0	0	19	17	0	0		

* local zoo dolphins previously captured from Gulf of Mexico.

[a] estimated number of missing vertebrae caudal in series.

[b] the last vertebra was cartilaginous.

[c] estimated number of missing vertebrae cranial in series.

[d] first transitional vertebra had a small vertebral arch.

[e] the penultimate vertebra had a circular blunt caudal vertebral body surface indicating the possible presence of a terminal vertebra.

+ unknown number of haemal arches missing.

Table 4.2. Averaged vertebral body lengths (mm), normalized at ball vertebra (cd19), in 15 Gulf of Mexico bottlenose dolphins, Tursiops truncatus.

field #	AGW90M2	AGW91M2	CC 110	GA 295	GA 425	GA 436	GA 683	GA 720	GA 836	GA 892	LA 042	PA 301	PA 457	SP 132	SP 153	average
TL (m)	n/a	2.41	2.42	2.68	2.24	2.55	2.70	2.40	2.45	2.45	2.59	2.31	2.37	2.57	2.37	
sex	F	F	F	M	M	F	M	M	F	F	M	M	F	M	F	
							33.7		36		m					
cd 1		31	m		m	34	33.7	33	36	33	m	31	31	35	m	33.1
cd 2	35	31	32		m	34	34	33	35.7	p	m	30.7	30.3	35	m	33.1
cd 3	35	31	32	38.3	m	33.3	34	33	38	p	m	30.7	31	34.3	m	33.7
cd 4	34.7	31.3	31	38.7	m	33	34	33.7	36	35	m	31	32	35	m	33.8
cd 5	34	31.7	31	38	m	33	34.3	34	36	p	m	30.3	31.7	35	m	33.5
cd 6	35.7	32	32	39	m	33	35.3	34.3	36	36	m	31	33	34	m	34.3
cd 7	36.3	33	33	39.7	m	34	36	35.3	41	38	41	31.3	33	34	35	35.8
cd 8	37	33	34	41.3	33	35	36.3	35	39	40.3	40	31.7	35	36	36	36.2
cd 9	39	34	35	42.3	34	36.3	37.3	35.7	41	p	42	32.3	36	37	38	37.1
cd 10	39	35	36	42.3	35	37	38.7	37	42	42.7	43	33	37	38	39	38.3
cd 11	40	35	38	44	35	37	40.3	39.7	43	43	44	34	38	40	40	39.4
cd 12	40.7	36	38	46	36	38.3	41.3	41	43	43	45	35	39	41	41	40.3
cd 13	41	36	38.7	47	36	39	42	41.3	43	42	46	37	41.3	43	41	41.0
cd 14	41.3	36.3	38	48	35.7	39	43	43.7	43	43.7	46	37.7	40	43.7	42	41.4
cd 15	41	36.3	39	47	36.7	40	43	44.7	42	45	45	38.3	40	44.7	42	41.6
cd 16	40	36	38	47	37	39	41.3	44	36	42.3	42	38.7	37	44	42	40.3
cd 17	36	37	36	42	35	37	37	38.7	24	34	33	37	27	41.7	38	35.6
cd 18	24	36.7	29	31	34	30	25.3	26.3	17	21	19	30	18	34.3	30.3	27.1
cd 19	16	21	17.7	19	19	19.3	16	17	14	16	19	18.7	15	21	20	17.9
cd 20	12.3	16	13	15	15	14.3	14.3	14	14	15	13	14	14	15	15	14.3
cd 21	13	15	12	14.7	14	13.7	14	14	14	14.3	13	13	13.7	13	15	13.8
cd 22	13	14	12	14.7	14	13	14	14	13	13	12	13	13.3	13	15	13.4
cd 23	12.7	13	12	14	13	13	13.7	13	11	12.3	12	13	12	13	13	12.7
cd 24	12.3	12	11	13	11	12	13.3	12	10.7	12.7	12	12	10.7	12	11.3	11.9
cd 25	11.3	11	10	12.3	12	11.7	11	11	10	12	11.7	11	9	11	10	11.0
cd 26	m	9.7	8.3	10.7	10	10	10.3	10.7	8	p	9	8.7	8	11	10	9.6
cd 27	m	7	7.3	m	9	9.3	9	8.7		7.7	8	7	4	11.3	9	8.1
cd 28	m	5.7	4	m	8	7.7	7	5		4		3.3		7.3	4	5.6
cd 29	m			m	4											4.0

m - missing vertebrae.

p - proliferative bone, fusions with haemal arches, and broken vertebrae prevented measurement.

Table 4.3. Intervertebral bending angles (mean ± SD) and relative length of intervertebral disks (% of vertebra-disk unit) at the peduncle-flukes junction in Gulf of Mexico bottlenose dolphins, *Tursiops truncatus*.

Disk level*	Dorsal bending angles (n=11)	Ventral bending angles (n=11)	Intervertebral disk % ** (n=10)
3	2.2 ± 2.1	0.6 ± 1.3	9.5 ± 2.4
2	1.0 ± 2.2	1.7 ± 1.7	9.1 ± 2.4
1	2.5 ± 2.2	1.7 ± 2.9	12.9 ± 4.6
1	8.2 ± 4.6	7.5 ± 3.7	23.8 ± 5.1
2	7.0 ± 5.7	8.2 ± 6.3	27.3 ± 5.4
3	8.9 ± 5.6	7.8 ± 4.3	22.6 ± 9.2

* upper three intervertebral disks are respectively the 3rd, 2nd and 1st cranial to the ball vertebra; similarly, the lower three are respectively the 1st, 2nd and 3rd caudal to the ball vertebra.

** means from Table 4.4.

-- location of the ball vertebra.

Table 4.4. Craniocaudal lengths of six intervertebral disks plus their cranial vertebral bodies ("units") (mm), craniocaudal lengths of intervertebral disks (mm), and the percentages (disk / unit) through the transitional caudal vertebral region in 10 Gulf of Mexico bottlenose dolphins, Tursiops truncatus.

	3*			2			1			1			2			3		
field #	unit	disk	%	unit	disk	%	unit	disk	%	unit	disk	%	unit	disk	%	unit	disk	%
CC 110	39.29	2.38	6.06	36.90	2.38	6.45	30.95	2.38	7.69	25.00	5.95	23.81	19.44	6.35	32.65	17.86	5.16	28.89
GA 425	41.67	2.92	7.00	38.33	2.50	6.52	35.00	2.50	7.14	26.25	3.75	14.29	19.58	3.33	17.02	18.33	1.25	6.82
GA 436	44.74	4.82	10.78	42.54	5.26	12.37	36.84	5.26	14.29	28.95	6.58	22.73	22.37	5.26	23.53	19.74	2.63	13.33
GA 720	49.72	4.17	8.38	43.89	3.06	6.96	33.89	5.00	14.75	25.83	5.83	22.58	21.67	5.00	23.08	19.17	3.33	17.39
GA 836	46.34	4.88	10.53	40.24	4.88	12.12	32.52	7.32	22.50	26.42	8.94	33.85	21.95	7.32	33.33	21.95	7.32	33.33
GA 892	47.08	5.42	11.50	45.83	4.58	10.00	39.17	3.75	9.57	28.33	5.83	20.59	24.58	6.25	25.42	22.08	5.83	26.42
LA 042	51.25	6.25	12.20	46.25	5.00	10.81	40.00	6.25	15.63	29.17	7.08	24.29	25.83	8.75	33.87	22.50	7.50	33.33
PA 301	39.29	4.76	12.12	36.90	3.57	9.68	32.14	4.76	14.81	25.79	5.56	21.54	20.24	5.56	27.45	17.06	3.97	23.26
PA 457	41.45	2.56	6.19	39.74	2.56	6.45	32.48	2.99	9.21	25.64	6.41	25.00	20.94	5.56	26.53	17.95	2.56	14.29
SP 153	46.25	4.58	9.91	42.08	4.17	9.90	36.25	5.00	13.79	31.67	9.17	28.95	23.33	7.08	30.36	20.00	5.83	29.17
mean		4.27			3.80			4.52			6.51			6.05			4.54	

* the first 3 intervertebral disks are respectively the 3rd, 2nd, and 1st cranial to the ball vertebra; likewise, the last three are respectively the 1st, 2nd, and 3rd disks caudal to the ball vertebra.

·▬·▬· the location of the ball vertebra.

Table 4.5. Relationships between total body length, muscle water content, total dorsal bending angle and total ventral bending angle in 10 Gulf of Mexico bottlenose dolphins, <u>Tursiops</u> <u>truncatus</u>.

field #	total body length (m)	muscle water%	total dorsal bending angle	total ventral bending angle
CC 110	2.42	76	13	31
GA 425	2.24	60	46	35
GA 436	2.55	90	67	56
GA 720	2.40	75	28	34
GA 836	2.45	75	27	30
GA 892	2.45	76	42	36
LA 042	2.59	72	36	31
PA 301	2.31	34	41	14
PA 457	2.37	76	39	16
SP 153	2.37	68	20	13

correlation coefficient

	dorsal	ventral
TL	0.169173	0.501024
water %	0.101062	0.619576

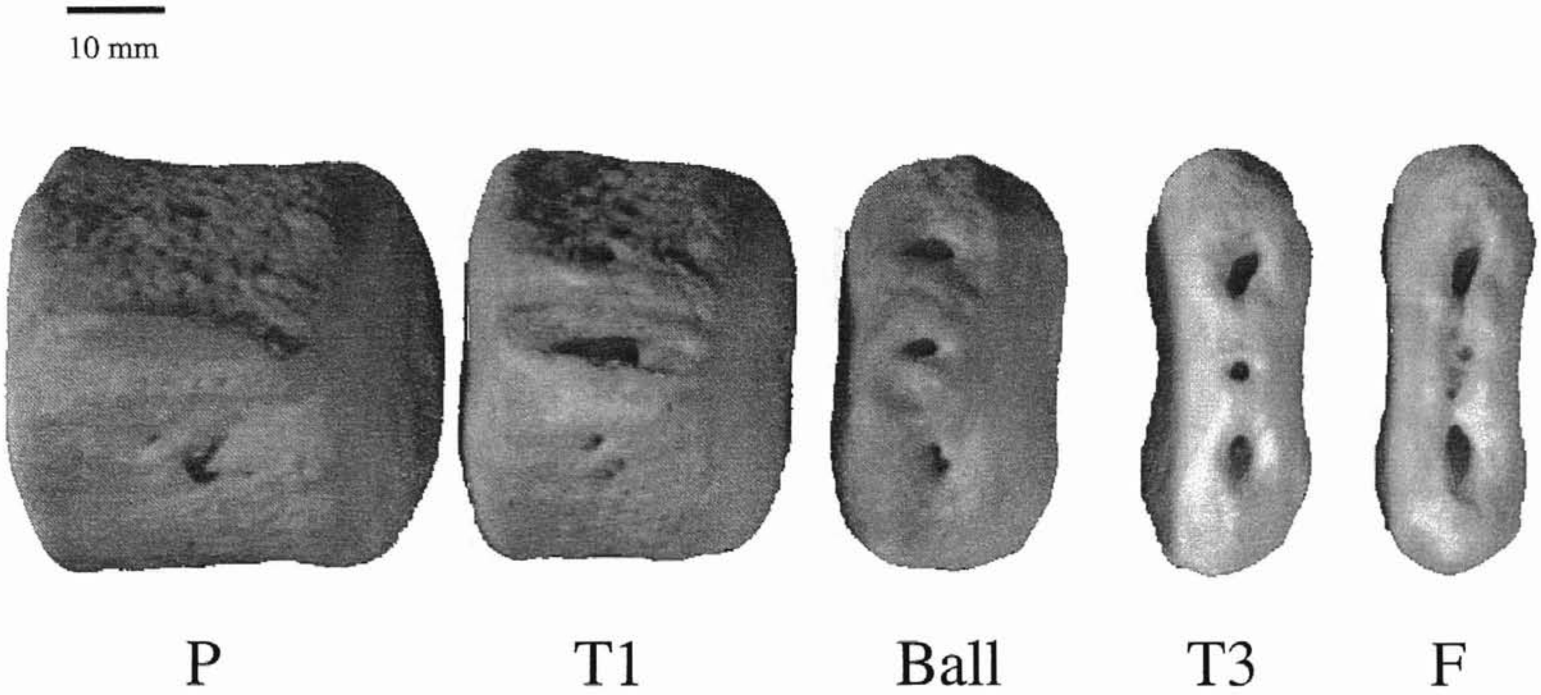


Figure 4.1a. Dorsal view of the last peduncle vertebra (P), the three transitional vertebrae (T1-T3) with the ball vertebra in the middle, and the first flukes vertebra (F) of an adult Gulf of Mexico bottlenose dolphin, Tursiops truncatus (2.55 m TL, GA 436).

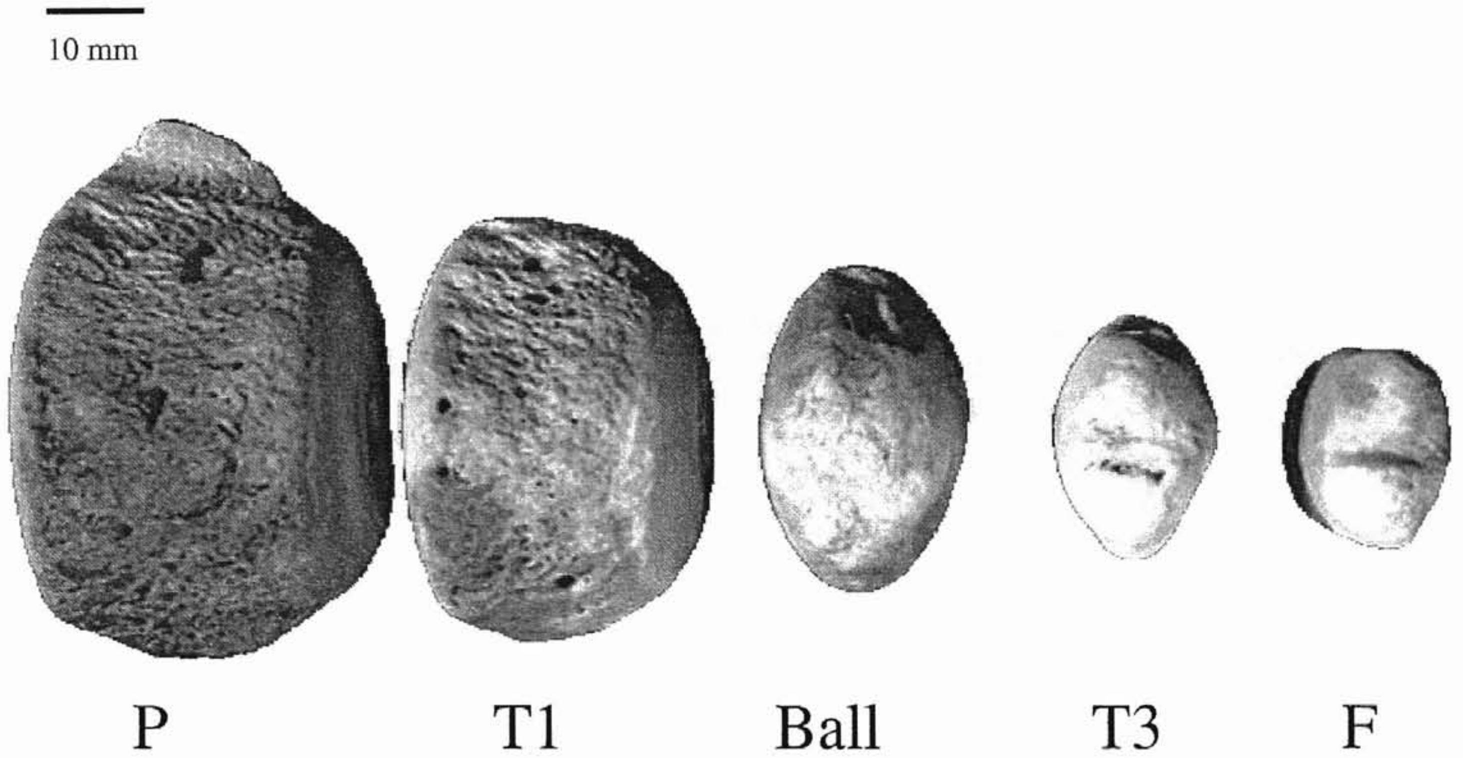


Figure 4.1b. Left lateral view of the last peduncle vertebra (P), the three transitional vertebrae (T1-T3) with the ball vertebra in the middle, and the first flukes vertebra (F) of an adult Gulf of Mexico bottlenose dolphin, Tursiops truncatus (2.55 m TL, GA 436).

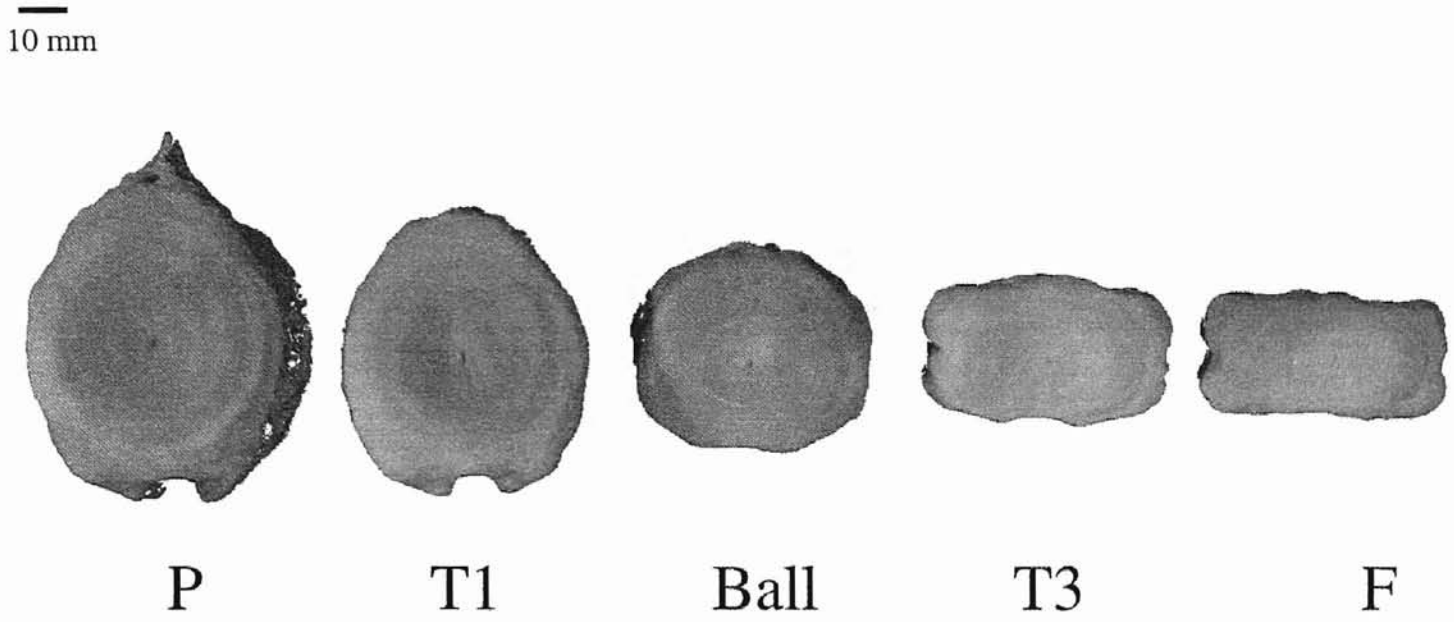


Figure 4.1c. Cranial view of the last peduncle vertebra (P), the three transitional vertebrae (T1-T3) with the ball vertebra in the center, and the first flukes vertebra (F) of an adult Gulf of Mexico bottlenose dolphin, Tursiops truncatus (2.55 m TL, GA 436).

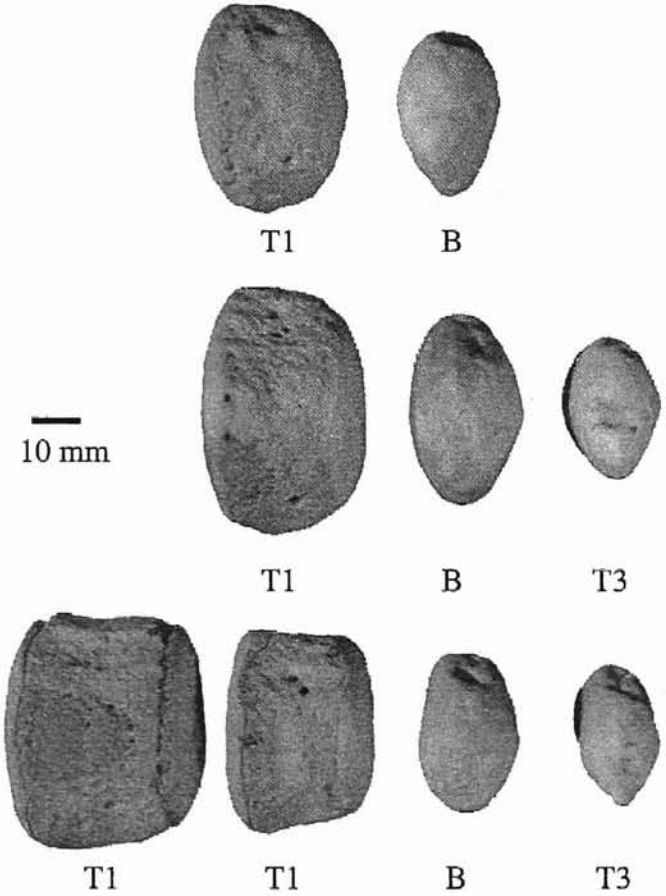


Figure 4.2. Left lateral views showing variation in number of transitional vertebrae from adult Gulf of Mexico bottlenose dolphins, Tursiops truncatus. Top - two vertebrae (n=3); middle - typical three transitional vertebrae (n=13); and bottom - four vertebrae, in which the first transitional vertebrae (T1) was duplicated (n=1). T1= the first transitional vertebra, B= the ball vertebra, T3= the third transitional vertebra.

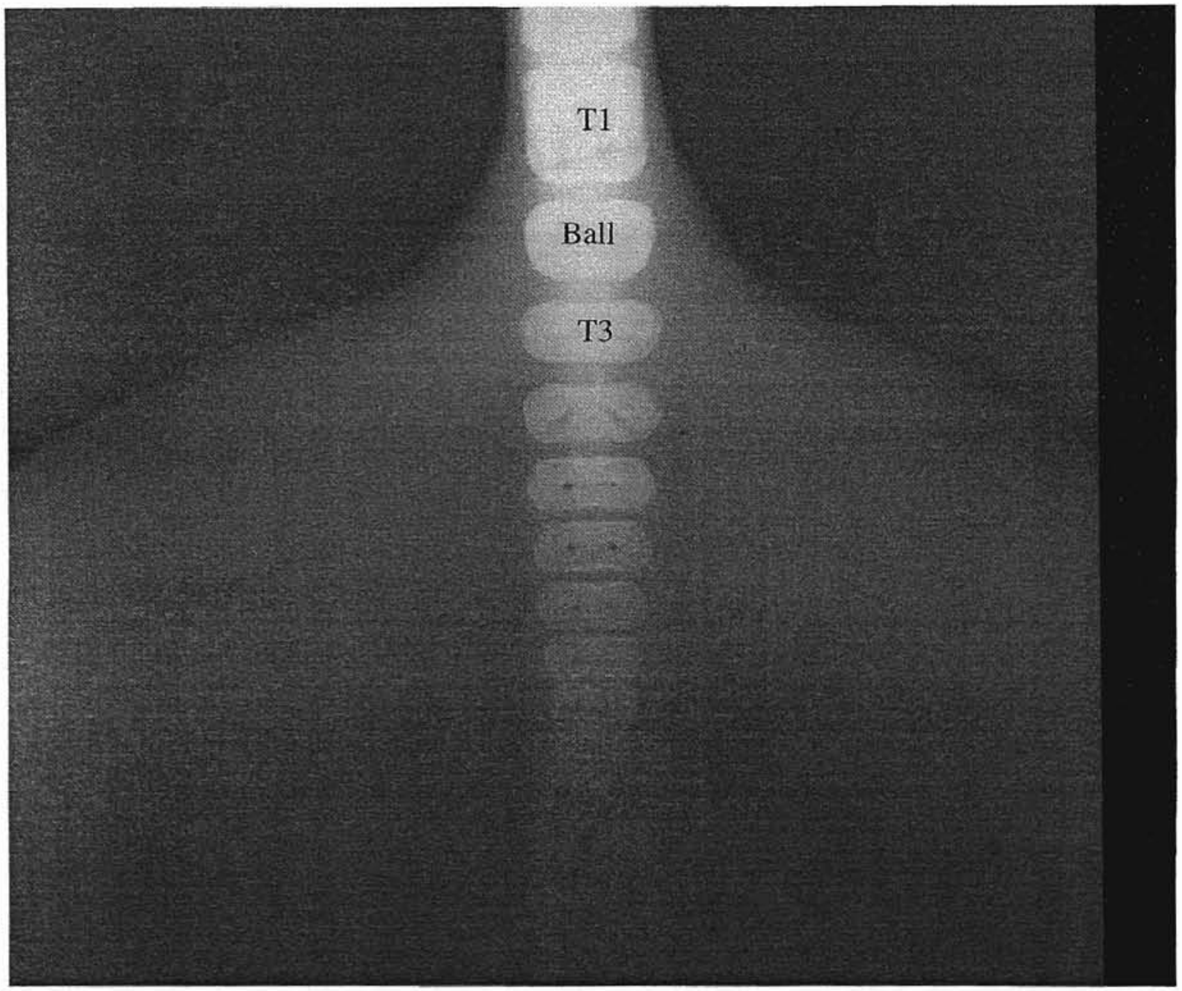


Figure 4.3. Dorsoventral radiograph of flukes illustrating the location of the transitional vertebrae at the peduncle-flukes junction in an adult Gulf of Mexico bottlenose dolphin, Tursiops truncatus (2.45 m TL, GA 892).

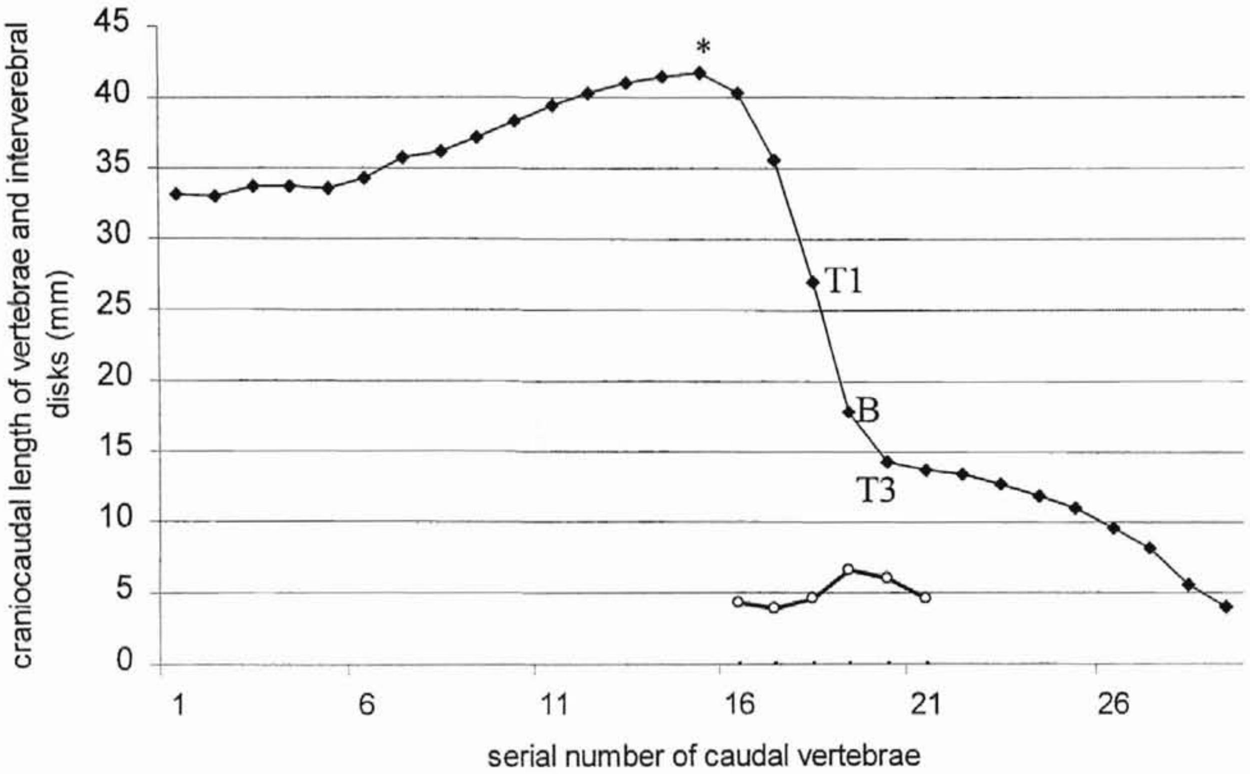


Figure 4.4. Averaged caudal vertebral body lengths (◆) with the ball vertebra normalized at the 19th caudal vertebra (n=15), and the averaged intervertebral disk lengths (○) of the three cranial and three caudal to the ball vertebra (n=10, Table 4.4), of adult Gulf of Mexico bottlenose dolphins, Tursiops truncatus. * maximum length at caudal vertebra 15.

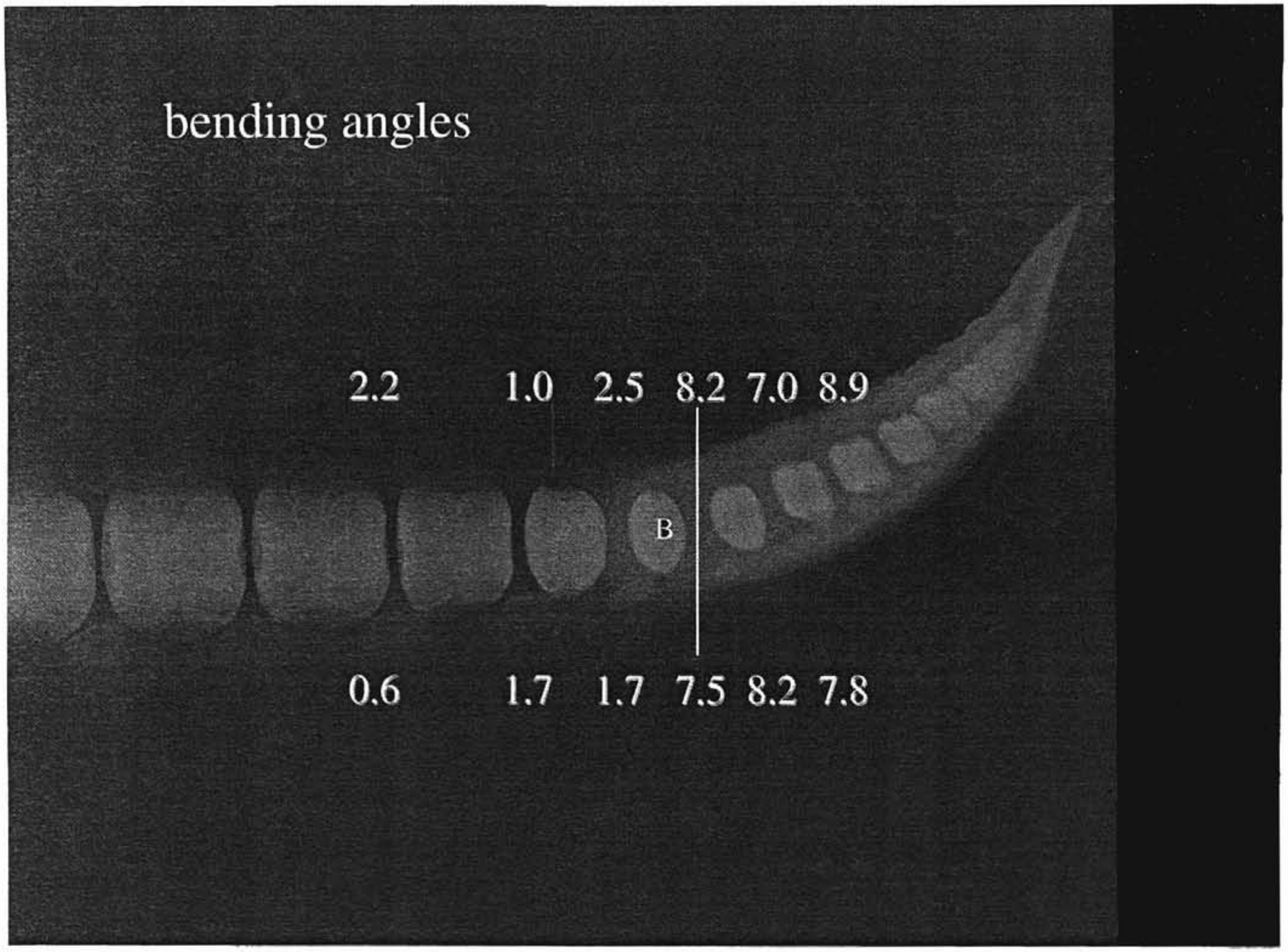


Figure 4.5. The means of six dorsal (top) and ventral (bottom) intervertebral bending angles across the transitional unit from 11 adult Gulf of Mexico bottlenose dolphins, Tursiops truncatus, measured from lateral view radiographs in AutoCAD.

Chapter 5

Discussion

The transitional unit

In this functional-morphology study of Gulf of Mexico bottlenose dolphins, the dorsoventral bending of tails was centered at the transitional unit in the caudal vertebral column. The transitional unit, located at the peduncle-flukes junction, was typically composed of three vertebrae and their intervertebral disks. In mammals generally, a single transitional vertebra sometimes occurs at the junction between vertebral regions, and this vertebra characteristically has features of both adjacent regions (Flower 1885a, Simoens et al. 1983). And in odontocetes, transitional vertebrae have been described at the cervico-thoracic junction and in the mid-thoracic region in a white beak dolphin (De Smet 1975) and in false killer whales (Yamada 1959, Purves and Pilleri 1978). In the caudal vertebral column, a single transitional vertebra at the peduncle-flukes junction has been illustrated in a humpback dolphin (Flower 1872), in a sperm whale (Flower 1868) and was briefly noted in western Atlantic bottlenose dolphins (Rommel 1990).

In contrast, in 17 Gulf of Mexico bottlenose dolphins in this study, the transition within the caudal vertebrae occurred over three vertebrae. None of the three transitional vertebrae, however, had characteristics of both a peduncle and a flukes vertebra. Instead, the first and the third transitional vertebrae had some features of their adjacent regional vertebrae and both had convex surfaces facing the middle vertebra. The middle vertebra was a unique rounded vertebra.

The ball vertebra

This singular ball-shaped vertebra was the second vertebra at the middle of the transitional unit. It resembled neither a cylinrical-shaped peduncle nor a rectangular-slab-shaped flukes vertebra. Its rounded surfaces, particularly its convex cranial and caudal surfaces, would morphologically predispose this region for increased bending potential.

The ball vertebra occurred most often at caudal vertebra 19 (n=11) among 17 Gulf of Mexico bottlenose dolphins. At this level, all vertebral processes were absent. Moreover, the last vestiges of transverse processes had disappeared three vertebrae cranial to the ball vertebra and the last vertebra with a vertebral arch was one vertebra cranial to the ball vertebra (Table 4.1). Thus restrictions to vertebral column flexibility due to projecting vertebral processes (Slijper 1946) are eliminated. In addition, the convexity of both cranial and caudal vertebral body surfaces of the ball vertebra and of the articulating surfaces of adjacent transitional vertebrae, and the longer intervertebral disks caudal to the ball vertebra, would facilitate dorsoventral bending in this region. This vertebral morphology in bottlenose dolphins substantiates an earlier hypothetical model of vertebral segment flexibility, in which shorter vertebral processes, longer intervertebral joints and smaller-diameter intervertebral disks characterize regions of higher flexibility in the common dolphin, Delphinus delphis (Long et al. 1997).

Convergence of bending vertebral joints for swimming

The vertebral column hinge morphology at the peduncle-flukes junction in the bottlenose dolphin is convergent with the specialized bending joint between the body and the propulsive appendage in other thunniform aquatic vertebrates (fusiform body, lunate tail, fast swimmer). For example, in scombride fishes (including tunas and mackerels), the modified vertebral segments at the junction of the body and the caudal fin, provide the lateral bending and prevent lateral shearing of the caudal fin in swimming (Fierstine and Walters 1968, Lindsey 1978). In phocid seals, which mimic thunniform swimmers, the femorotibial and tarsal joints allow lateral bending of the two webbed pelvic limbs (Fish et al. 1988). The highly-specialized vertebral segments or limbs for bending in these fast swimming vertebrates, though not homologous structures, are functionally convergent. While in another dorsoventral propulsor, the rotund manatee, their caudal vertebrae gradually decrease in size but do not have a particular bending joint nor three distinct morphological regions like bottlenose dolphins (Kaiser 1974). This morphology might reflect their less specialized caudal body propulsion and their slower non-thunniform swimming mode.

Bending of the caudal vertebral column

In this study of cadavers of Gulf of Mexico bottlenose dolphins, the majority of dorsoventral bending in intact tails occurred at the relatively thick intervertebral disks caudal to the ball vertebra. The peduncle intervertebral disks cranial to the ball vertebra, had little bending and were relatively thin compared to those caudal to the ball vertebra. The dorsal and ventral deflection of the tail generated in this experiment, was within the range of motion in swimming bottlenose dolphins (Fish 1993b). A similarly located center of flexibility at the peduncle-flukes junction was found by manually bending a single harbor porpoise carcass (Parry 1949b); and more recently confirmed by mechanical bending tests of two-vertebrae segments in one common dolphin (Long et al. 1997) and through kinematic analysis of swimming bottlenose dolphins (Fish and Hui 1991, Pabst 1993).

In the present study, the flexibility of the vertebral column was positively correlated with the length of intervertebral disks. The longer intervertebral disks were caudal to the ball vertebra. The same relationship of flexibility and disk length is described in bending and mechanical properties analysis of a common dolphin (Long et al. 1997). In addition, the convex surfaces of the vertebral bodies were at the caudal vertebral surface of the first transitional vertebrae, both cranial and caudal surfaces of the ball and third transitional vertebrae. Therefore, these five convex articulating surfaces of the transitional vertebrae, the two significantly thicker intervertebral disks caudal to the ball vertebra, and the absence of projecting vertebral processes, suggest morphological adaptations for increased bending potential. The increased bending angles of this study confirmed that the transitional unit functioned like a hinge joint at the peduncle-flukes junction to facilitate dorsoventral bending of the flukes as proposed earlier (Watson 1992).

Numerical variation in caudal vertebrae

In this study of Gulf of Mexico bottlenose dolphins, the number of caudal vertebrae ranged from 26-30, which is similar to that in western Atlantic bottlenose dolphins (23-28) (Rommel 1990), and in Atlantic and Gulf of Mexico bottlenose dolphins (27-31) (Watson 1992). The number is also similar in northern coastal Chinese bottlenose dolphins (26-31), but greater than that in southern dolphins (19-24) (Gao et al.

1995). All these studies were based on examinations of dry bones in museum collections and thus small terminal vertebrae might have been lost during preparation, which could be a source of numerical variation. The variation in number of caudal vertebrae could also reflect geographical variation. In the present study, the combination of radiography and dissection minimized the loss of small skeletal elements.

Techniques

In this study, there was no linear relationship between tail muscle water content and dorsoventral bending angles. In mammals, the tissue water content is 70-75% (Schmidt-Nielsen 1990), however, the two outliers of the ten dolphin muscle samples here require comment (Table 4.5). The high outlier (90%, GA 425) was probably due to the fact that this dead and slightly decomposed tissue was soaked in water for 12 hours prior to bending (no other tails were soaked in water). Not surprisingly, it was also the high outlier for both dorsal and ventral bending angles. These increased bending angles, beyond the normal range of motion, most likely reflect tissue destruction. In the low outlier (34%, PA 301) which was also the low outlier for ventral bending, the dorsal bending angle was within normal limits. This indicates that factors other than muscle water content might be involved in the bending ability at the peduncle-flukes junction.

The relationship of the degree of carcass freshness and bending was investigated by muscle sampling at the level of caudal vertebra 2 in this study. Dorsoventral bending of dolphin intact tails, however, occurred at the peduncle-flukes junction, approximately 16 vertebrae caudally where the narrow peduncle is devoid of muscle tissue and was primarily composed of blubber, tendons and the caudal vertebrae. Therefore, the sampling site of muscle might not best reflect the quality of the tissue under major bending. To assess the degree of tissue hydration, the tissue quality test could be improved by sampling the skin, blubber and/or tendons at the peduncle-flukes junction. Alternatively, preventing intact tails from drying out by storing them in sealed freezer containers and/or constant bathing in saline during bending experiments (Long et al. 1997) may closer replicate physiological conditions. The present study and that of Long et al. (1997) have both shown the importance of intervertebral disks in tail bending, therefore, future morphological and histochemical studies of dolphin intervertebral disks should be informative to the flexibility of the tails.

Chapter 6

Summary

Bottlenose dolphins are found in most oceans and are common performers in aquariums. They swim by dorsoventral bending of their tails, which have two regions: the narrowed extension of their caudal body, or peduncle, and the laterally expanded neomorphic flukes. The bones of the tail are the caudal vertebrae. Earlier cadaver manipulation and cine-film analyses of swimming dolphins have shown that the center of tail flexibility is at the peduncle-flukes junction. The objectives of this research were to determine the serial morphology of the caudal vertebrae and intervertebral disks, and where the dorsoventral bending occurs in the caudal vertebral column of the tail.

Intact tails from 15 mature bottlenose dolphins (2.09-2.70 m TL) stranded on the Texas coast of the Gulf of Mexico and from four zoo dolphins captured from the Gulf of Mexico were collected and frozen. The tails were radiographed in neutral, and dorsally and ventrally bent positions for measuring the intervertebral bending angles across the peduncle-flukes junction. The craniocaudal lengths of the intervertebral disks at the peduncle-flukes junction were measured on digitized spot films. The number, shape and lengths of caudal vertebrae were determined from prepared dry bones and radiographs.

The total number of caudal vertebrae ranged from 26-30 with a mode of 28. All vertebral processes gradually decreased in size and disappeared at the end of the peduncle. At the peduncle-flukes junction, caudal vertebrae changed shape from cylindrical to rectangular-slab - this change occurred over three vertebrae. These three transitional vertebrae and their intervertebral disks were designated as "the transitional unit," which was usually at caudal vertebrae 18-20. The second vertebra in the middle of

the transitional unit had a unique rounded shape, which resembled neither a peduncle nor a flukes vertebra. Increased dorsal and ventral bending angles and relatively thick intervertebral disks occurred immediately caudal to this "ball" vertebra. In this study, it was found that the ball vertebra and its contiguous intervertebral disks formed a hinge joint at the peduncle-flukes junction as the dolphin bends its tail during swimming. This bending morphology is functionally convergent with similar structures that join the tail or propulsive pelvic limbs to the caudal body in other fast-swimming vertebrates.

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