SKELETON OF TWO MINKE WHALES, *BALAENOPTERA ACUTOROSTRATA*, STRANDED ON THE SOUTH-EAST COAST OF NEW ZEALAND

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ABSTRACT

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We report the skeletal anatomy of two immature female minke whales (*Balaenoptera acutorostrata*) stranded on the south-east coast of Otago, New Zealand. One whale had an asymmetrical 4th cervical vertebra and a notched sternum. In both whales, a "ball" caudal vertebra (No. 11) distinctly marked the transition from tail peduncle to flukes and was the site for most of the dorsoventral bending of the flukes on the peduncle. Small haemal arches occurred on, and caudal to the "ball" vertebra. The first rib articulated with the sternum in two places. Radiographs of the manus revealed a typical balaenopterid carpus with three bones in the proximal row and two in the distal row. In addition, a cartilaginous accessory carpal bone, at the caudal side of the proximal carpal row, and a cartilage extension of the olecranon helped support the fleshy caudal part of the flipper. On the periotic, porous lateral and dorsal surfaces and a posterior process fused with the bulla are of uncertain function.

KEYWORDS: Cetacea - *Balaenoptera* - osteology - tympano-periotic - vertebrae - sternum - limb bones.

INTRODUCTION

The minke whale, *Balaenoptera acutorostrata*, the smallest of the rorqual whales (Mysticeti: Balaenopteridae), is distributed world-wide, primarily in cool temperate to polar oceans (Stewart & Leatherwood 1985). It is reportedly the most frequent mysticete to strand on New Zealand coasts. Brabyn (1991) reported 40 minke strandings, which comprise 48% of all rorqual strandings (n = 84) and 33% of all mysticete strandings (n = 121). All recorded strandings have been individuals smaller than 7.0 m total length (A.N. Baker, cited in Dawson & Slooten 1990). We summarise here two recent strandings of south-west Pacific minke whales on the Otago coast, south-east South Island, New Zealand. This account concentrates on the anatomy of the periotic bone, cervical vertebrae, caudal vertebrae, sternum and flippers. We describe the

otherwise poorly documented periotic, and report variations or provide comments on function for the other elements. Though the skull in minke whales is potentially important in diagnosing geographical forms, we do not describe it here because sutures and profiles in the one skull available to us do not differ consistently from those described elsewhere (eg. True 1904, Omura 1957, 1975, Omura & Kasuya 1976, Arnold *et al.* 1987). A comprehensive review of skull structure for New Zealand minke whales is needed.

Cetacean strandings world-wide attract public interest and media attention, and there is a rapidly expanding scientific literature on patterns and causes of strandings (Brabyn & McLean 1992). In contrast to the late 19th century, modern literature reveals restrained interest in stranded animals as a source of anatomical information. Instead, many biologists regard biochemical techniques as the most appropriate to discriminate between different populations or species (eg. Dowling & Brown 1993). Nevertheless, continued documentation of comparative macroscopic anatomy, the aim of this article, will provide

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a sound basis for field or museum identification of species and for the interpretation of functional anatomy. More broadly, additional anatomical information may help resolve issues such as the existence of a so-called dwarf minke whale (Best 1985, Arnold *et al.* 1987) and the status of regional forms, such as North Pacific versus North Atlantic versus Antarctic minke whale stocks (Omura 1975, Deméré 1986). Finally, osteological information allows valuable comparison of living species with fossils.

Published data from minke whales stranded in New Zealand are rare. Many of the detailed descriptions of the skeleton and macroscopic anatomy of the minke whale are from northern hemisphere specimens and are old, for example, the accounts of Flower (1864a), Carte & MacAlister (1868), Turner (1893), and True (1904). More recent articles on minke whale osteology include those of Omura (1957, 1975), Omura & Kasuya (1976), and Arnold *et al.* (1987), however, little information is available on the periotic or on variation of the postcranial skeleton. Gray (1874) was one of the first to report on the osteology of a minke whale from New Zealand; he briefly described the skull and other skeletal parts of an immature 4.8 m whale from near Otago Head. Hector (1878), von Haast (1881), and Oliver (1922) included passing mention of the osteology of minke whales from New Zealand. Other useful literature on minke and other balaenopterid whales is listed by Hershkovitz (1966).

OBSERVATIONS

STRANDING CIRCUMSTANCES

Whale 1: On 21 February 1988, a live minke whale stranded on a sandy beach near Kuri Bush (46°02' S, 170°14' E), approximately 4 km north of the Taieri river mouth on the south-east coast of Otago, New Zealand. The whale was refloated live, towed out to sea and disappeared. Three days later a dead minke whale, presumed to be the same individual, washed ashore at the same spot. The carcase was hauled above the high-tide mark for necropsy. The whale was an immature female, 6.1 m total length. The carcase was flensed on site and the skeleton transported to the University of Otago for preparation.

Whale 2: On 9 March 1993, at about 3:30 p.m., a live minke whale stranded on a sandy beach at the south-east end of Short Bay, 2.8 km south-east of Kaka

Point and 0.5 km north-west of Campbell Point, south-east Otago, New Zealand (169°47.3' E, 46° 24.4' S). The whale was said to have made a noise on stranding. It was rolled down the beach and back into the sea, where it swam out and dived. At about 5:45 p.m., the whale was seen coming in, rolling from side to side, and once it was seen belly-up in the surf. The whale did not make a noise on this second stranding, which was about 100 m north-west from the initial stranding. The whale remained alive for approximately 30 minutes on the beach. On 10 March 1993, the carcase was retrieved for a postmortem examination.

The whale was an immature female, 5.85 m total length. The skull with mandibles and hyoid bones, both thoracic limbs and pelvic bones, and cervical and caudal vertebrae were collected for anatomical studies. The skull was flensed and buried for later retrieval; the remainder of the carcase was buried on the beach. The bones of both whales were prepared by simmering in water, with final cleaning by dermestid beetles for whale 1. They have been entered into the collection of the Otago Museum, Dunedin, as whale 1, O.M.A. 1988:175 and whale 2, O.M. Acc. 1231. Stranding details and external measurements are available from Department of Conservation, Dunedin, and the authors. Anatomical terminology below follows that of Nomina Anatomica Veterinaria (ICVGANWAVA 1983) except for the tympano-periotic, which follows Kellogg (1928, 1936) for terms unique to Cetacea (including directional terms used as nouns, eg. anterior process).

OSTEOLOGY

SKULL

Only the periotic bone of whale 1 (Fig. 1a & b) is described here. In the dried skull of whale 1 the periotic was loose, could be moved several millimetres, and was not obviously fused to the skull, though the exoccipital had to be excised before the periotic could be removed. The anterior process of the periotic was triangular in medial and ventral view and there was no anterior bullar facet. The internal face of this process carried scattered foramina. Dorsally and laterally, the irregularly rough porous surface of the anterior process expanded up over both the body and pars cochlearis to leave a deep narrow cleft. An irregular anteroexternal sulcus
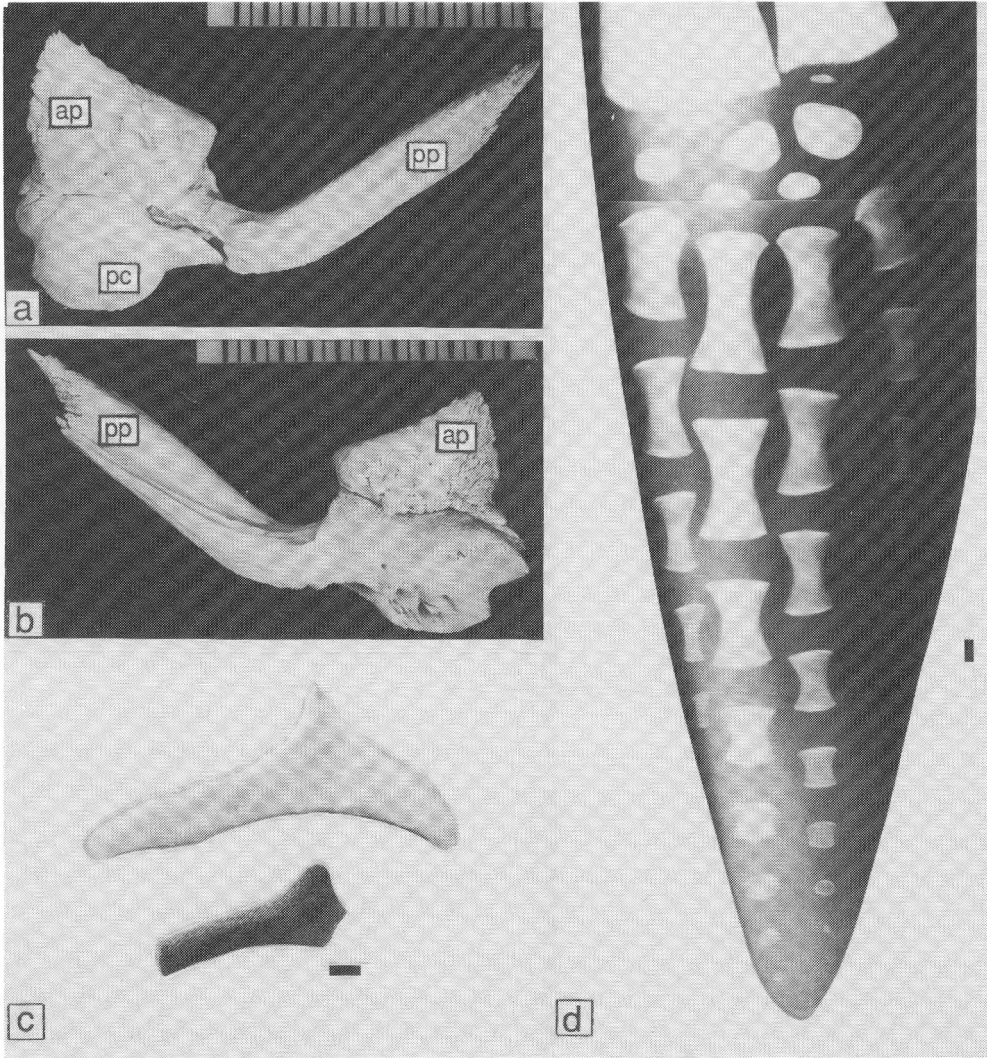
Figure 1. Skeletons of female minke whales from Otago: whale 1 - 6.1 m, whale 2 - 5.85 m. Scale bar is 10 cm. a. Left periotic bone, ventral view (whale 1). Labels: ap = anterior process of periotic; pc = pars cochlearis; pp = fused posterior process of periotic and tympanic bulla. b. Left periotic bone, dorsal view (whale 1). Labels as for a. c. Left pelvic bone with cartilage extensions intact (upper) (whale 2), and cleaned (lower) (whale 1), lateral view. Cranial is to the right, dorsal is to the top. d. Mediolateral radiograph of the right manus showing the distal radius and ulna, five carpal bones, four metacarpals, and the phalanges (whale 2).

originated near the anterior pedicle for the bulla, then meandered up the lateral face of the anterior process. On the body, the mallear fossa and fossa incudis were indistinct. A large groove for the facial nerve ran caudally from the facial canal, and became indistinct beyond the posterior pedicle for the bulla. The fossa for the origin of the stapedius muscle was long and was formed partly by a thin sheet of bone which underlay a dorsally-placed fossa, presumably for part of the posterior sinus of the pterygoid sinus complex. The latter fossa, conspicuous in caudal view, invaded the caudal part of the body and base of the posterior process. Further anteriorly, the porous lateral face of the body passed indistinctly into the more coarsely porous dorsal surface without a superior process. On the pars cochlearis, both the internal aperture for the facial canal and the internal auditory meatus were deep and subcylindrical. The apertures for the vestibular and cochlear aqueducts were unremarkable. The large suboval fenestra rotunda opened in the depressed caudal face of the pars cochlearis. A narrow double foramen cranially on the pars cochlearis was probably the aperture for the petrosal canal. Most of the long thin dorsoventrally deepened posterior process was formed by the bulla, which was fused to the more dorsal short posterior (mastoid) process of periotic. A trace of the suture between the posterior process of the periotic and the posterior process of the bulla was apparent caudal to the hiatus epitympanicus.

VERTEBRAE

General: We detail here some differences between the vertebrae of our specimens (general view: Fig. 2) and those of other minke whales described and figured by Flower (1864a & b), Struthers (1872), Omura (1975), and Omura & Kasuya (1976). The vertebral formulae of our specimens are: whale 1 (O.M.A.1988:175) - C7, T11, L12, Cd 19 = 49; whale 2 (O.M.Acc.1231) - C7, T?, L?, Cd 19. Here the terminology for the ''transverse processes'' follows that of Owen (1848), with modifications suggested by Cave (1975). Articular processes were present on the vertebral arches from the axis (caudal only) to cervical 7, and diminished in size caudally. The parapophyses for cervicals 3-6 possessed a prominent ventral tubercle in whale 2. On cervical 6, the parapophyses were short and robust (whale 1) or an elongate narrow process fused laterally with the diapophysis, thus completing a bony ring for the

transverse foramen (whale 2). On cervical 7, the area for the parapophysis was a small (5 mm), oval, raised irregularity in the contour of the vertebral body, projecting 3-4 mm laterally (whale 1) or less (whale 2).

Vertebral body epiphyses: All vertebral body epiphyses, except the cervicals in whale 2, were well ossified and not united with their vertebral bodies. The first epiphysis was on the caudal end of the body of the axis, and the last was on the cranial surface of caudal 16 (whale 1) or caudal 17 (whale 2). Cervical epiphyses in whale 2 were considerably less ossified than those in whale 1: the caudal epiphysis on the axis was only 50% developed with incomplete peripheral and central areas - ossification increased in the more caudal cervicals so that the caudal epiphysis on cervical 6 was completely ossified. The cranial epiphysis of each cervical vertebra (3-7), was less developed than its caudal epiphysis.

Notochordal fovea: In the centre of most cranial and caudal epiphyses was a clearly circumscribed, small depression, the notochordal fovea, 2-3 mm deep (Fig. 3). This fovea was on the surface of the epiphysis facing the intervertebral disc. At the bottom of some pits a pin-point hole was seen. The fovea was absent in the atlas, but on the axis, at the apex of the dens, there was a clearly circumscribed 6 x 8 mm pit, 2-3 mm deep (whale 1) (Fig. 3) or less (whale 2). The fovea reappeared on the caudal surface of cervical 4, and was present on remaining cervicals, all thoracics and lumbars, and on caudals 1-6, 10-16 (whale 1). It was particularly prominent on thoracics 3-7. Similar foveae were seen on the cervical and caudal vertebrae in whale 2.

In addition, a distinct strand of semi-gelatinous material was attached to the bottom of some of these notochordal foveae, as revealed in dissections of the apex of the dens, and of several caudal intervertebral discs (whale 2). This strand of material was most likely the tubular remnant of the notochord or its sheath.

Intercentrum of axis: On the mid-dorsal surface of the axis body was an oval depression, in the depths of which could be seen a separate ossification with an elliptical outline and a central depression, more clearly seen in whale 1 than whale 2. This ossification is intercentrum two of the axis.
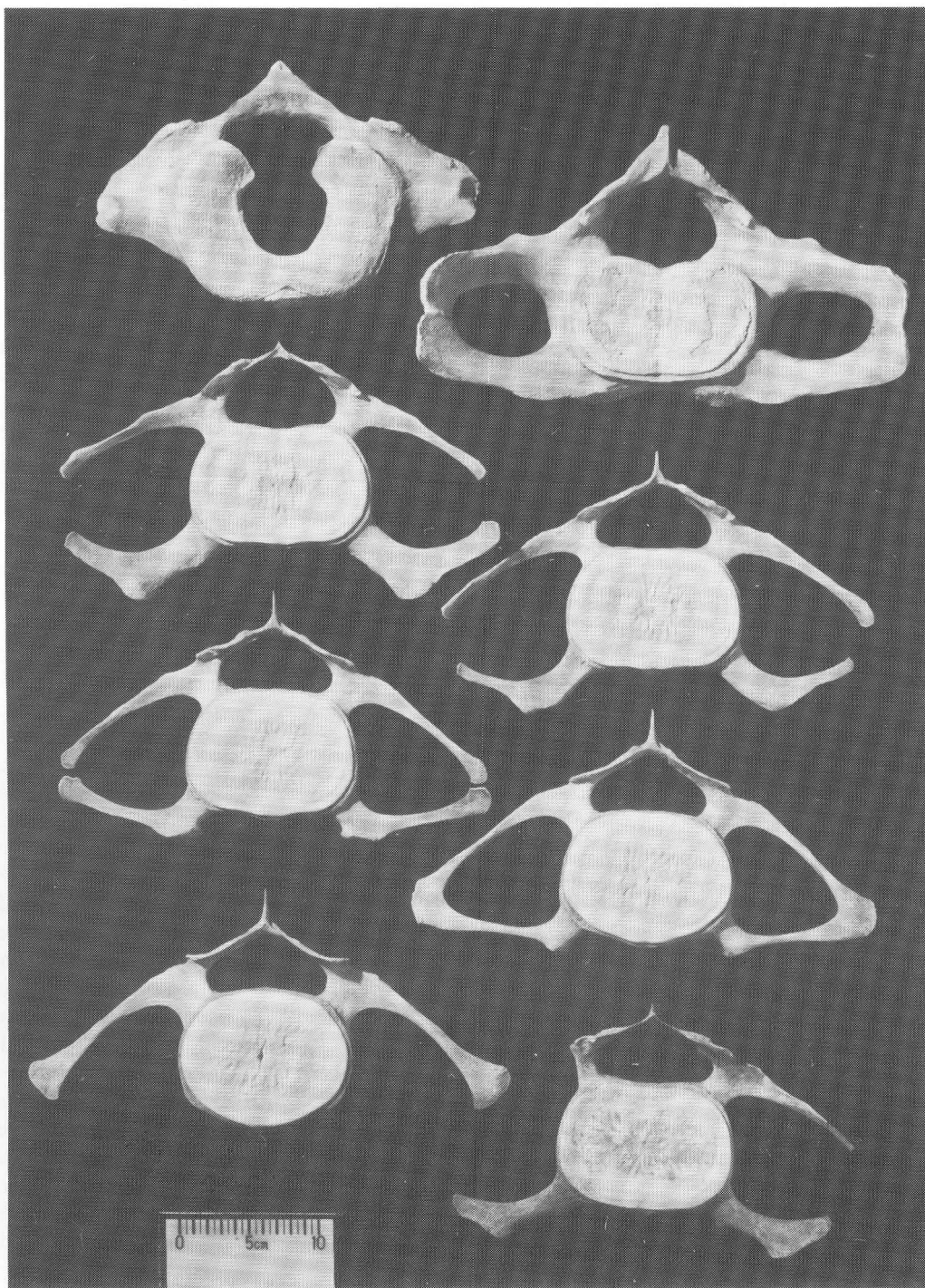
Figure 2. Skeletons of female minke whales from Otago: whale 1 - 6.1 m, whale 2 - 5.85 m. Scale bar is 10 cm. Cervical vertebrae (1-7) showing overall form and variation in size and shape of diapophyses and parapophyses, caudal view (whale 2). Bottom right - asymmetrical cervical 4 with diapophysis absent on left side, caudal view (whale 1).

Asymmetry: The shape and length of the dorsal and ventral transverse processes (diapophysis, parapophysis) and the degree of the completeness of the bony ring for the transverse foramen varied markedly among cervical vertebrae, between sides of body, and between the two whales (Fig. 2). Cervical 4 in whale 1 was markedly asymmetrical (Fig. 2). The left diapophysis was absent. The left pedicle of the vertebral arch was smaller than the right (14 x 8.5 mm versus 23 x 7 mm), and the vertebral foramen was asymmetrical, subtending a more obtuse angle on the left than on the right side.

Caudal vertebrae and haemal arches: There were 19 caudal vertebrae in both whales. The last transverse processes were recognisable as a low ridge on caudal 6 (whale 1) or caudal 7 (whale 2). The last vertebral spine was on caudal 9 (whales 1 & 2), and the last vertebral arch was on caudal 9 (whale 2) or caudal 10 (whale 1). Haemal processes for articulation of haemal arches (chevrons) were present on caudals 1-10 in both whales. The 11th caudal vertebra in both whales was clearly rounded in craniocaudal profile; it was without processes, lacked tendon grooves laterally, and had markedly convex cranial and caudal surfaces (Fig. 3). This was the "ball" vertebra, transitional in form between those in the peduncle and those in the flukes. Dissection (whale 2) showed that caudal 11 was located in the base of the flukes at the peduncle-flukes junction. When we manipulated the postmortem specimen, simple dorsal and ventral bending of the flukes revealed that most movement of the flukes on the peduncle took place at the intervertebral space between caudal 11 and 12.

Vertebrae in the flukes had a serial transition in shape (as viewed craniocaudally) from rounded, to more square, to rectangular, then to rounded in the terminal vertebrae (Fig. 3). Caudals 12-17 were quadrilateral in craniocaudal profile; the first 2 were more square and the next 3 were more rectangular in form, with an oblique tendon groove across their lateral surfaces. The first pair of vertically perforating foramina were in caudal 13 (whale 1) or caudal 16 (whale 2). The penultimate vertebra (caudal 18) was 20 mm wide, 16 mm dorsoventrally deep, and 17 mm in craniocaudal length in whale 1 and 18 x 13 x 11 mm in whale 2. The terminal vertebra was a roughened bony ovoid, 12 x 13 x 10 mm in whale 1, and 8 x 5 x 4 mm in whale 2. The distance between the terminal caudal vertebra and the free edge of the median notch between the flukes was 25 mm (whale 2).

Ten haemal arches were recovered from whale 1 and 13 from whale 2. The first haemal arch was a pair of unfused hemi-arch elements (whale 1) or a single V-shaped bone (whale 2), which articulated on the caudoventral aspect of the body of caudal 1. Subsequent haemal arches were larger, single, Y-shaped bones which graded caudally into smaller and smaller, more V-shaped bones. In whale 1, the tenth and smallest haemal arch was V-shaped and consisted of a pair of unfused oval hemi-elements (20 mm dorsoventrally by 25 mm craniocaudally), joined mid-ventrally by cartilage. Whereas in whale 2, which was dissected fresh, additional small bony paired haemal arch elements were identified closely associated with the cranioventral aspect of caudals 10-13; haemal arches were present on the ball vertebra (caudal 11), and on the following four caudal vertebrae, ie. four pairs of haemal arches lay caudal to the ball vertebra. Those with caudal 10 (haemal arch 9), although paired hemi-elements, were similar in size and shape to haemal arch 9 in whale 1. The 13th haemal arch was a single ovoid ossicle (2 x 3-4 mm). On the cranioventral aspect of caudal 15 were a small pair of oval and firm cartilaginous plates (4 x 5 mm) representing potential bony haemal arch 14, similar in position and shape to the bony haemal arches.

STERNUM

The sternum (total length: 230 mm) of whale 1 was cruciate with paired, broad and flattened lateral wings, a pronounced flask-shaped median notch with flanking lobes in the cranial margin, and a prominent rod-like caudal pedicle (Fig. 3b). Three roughened areas, which were probably covered by cartilage in life were: 1, on the cranial thickened surfaces of the lobes; 2, on the thickened lateral and caudolateral aspects of the ends of both lateral wings; and 3, on the caudal pole of the caudally projecting pedicle. The remainder of the external surface was smooth, without any major nutrient foramina. The sternum was slightly concave dorsally in both cranial and lateral views.

The sternum (total length: 300 mm, including a 40 mm cartilage tip caudally) of whale 2 was similar in general shape to that of whale 1 but the cranial margin was rounded without a notch. Dissection of
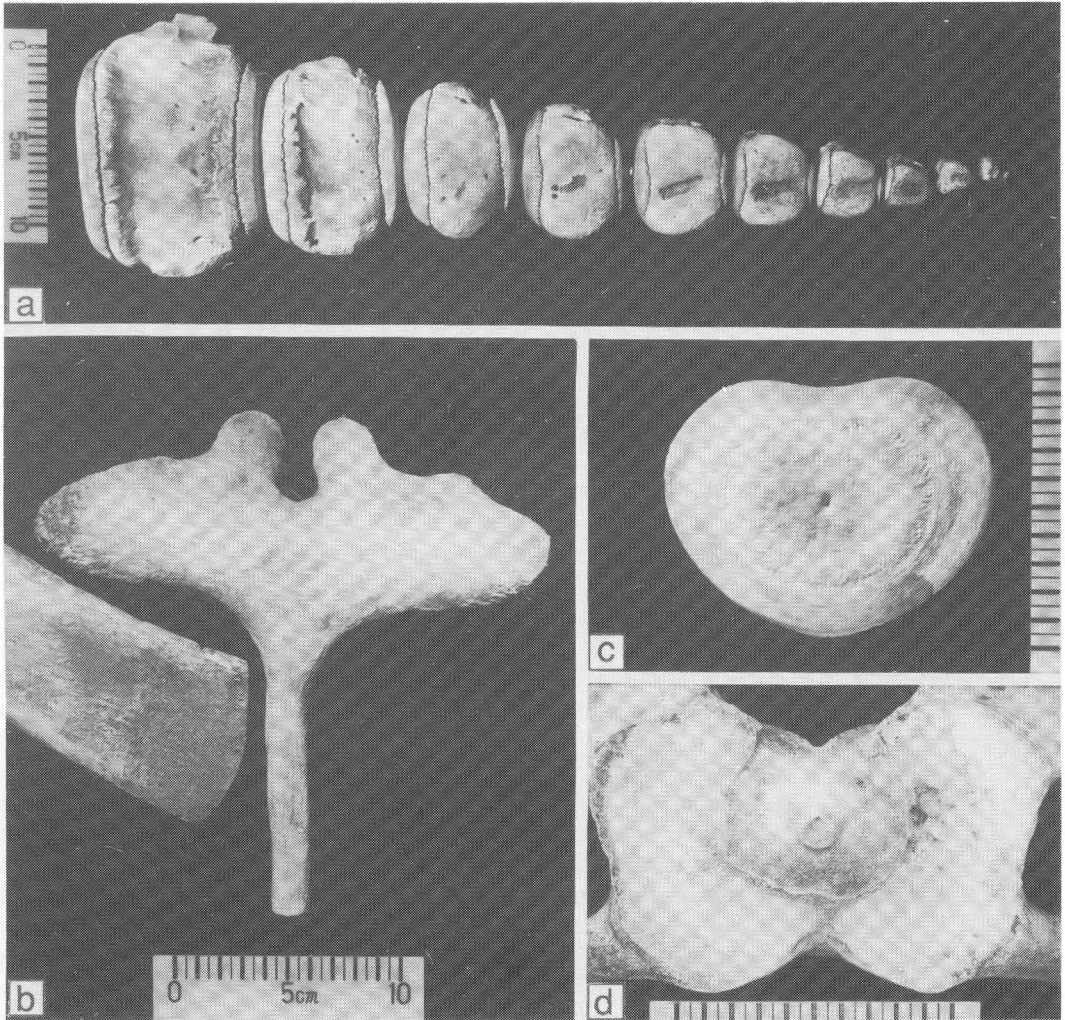
Figure 3. Skeletons of female minke whales from Otago: whale 1 - 6.1 m, whale 2 - 5.85 m. Scale bar is 10 cm.   a. Caudal vertebrae (9-19) showing transition in vertebral body shape and the ball vertebra (No. 11), lateral view (whale 2).   b. Sternum with cranial notch and left first rib articulating in two places, dorsal view (whale 1).   c. Notochordal fovea on intervertebral disc surface of epiphysis from the caudal body of thoracic 6, caudal view (whale 1).   d. Axis vertebra showing dens with well demarcated central notochordal fovea, cranial view (whale 1).

distal ends of the first pair of ribs revealed that each rib articulated with the sternum at two places (Fig. 3b). The distal end of rib 1, particularly its cranial half, articulated on the lateral aspect of the caudal pedicle over its cranial quarter. In addition, a second articulation was present between the caudolateral part of the lateral wing of the sternum and the cranial surface of rib 1. Both joints were flexible and consisted of thick, dense connective tissue; no signs of a synovial cavity could be found.

The cranial articular surface of rib 1 was a well-marked, rough and thickened area on the cranial surface of the distal third of the rib. It was visible in both whales.

THORACIC LIMB

The scapula, humerus, radius and ulna from both limbs of each of these whales were similar to that reported elsewhere (Omura 1975). Four well-formed, but un-united bony epiphyses were on the arm and forearm bones: for the humerus, a single large hemispherical epiphysis for the head and tuberosity on its proximal end and a V-shaped epiphysis on its distal end; for the radius and ulna, a separate flattened oval epiphysis each for their proximal articular surface. Five carpal bones were present but the manus could not be accurately reconstructed from the isolated bones for whale 1.

For whale 2, plain film mediolateral radiographs of the flipper revealed all ossifications in their normal topographic locations (Fig. 1d). The number and arrangement of bones was the same in the left and right flippers. Separate bony epiphyses were formed on the proximal and distal ends of the humerus, radius and ulna. The distal radial and ulnar epiphyses were markedly smaller than their proximal counterparts. Five carpal bones were arranged in two rows: in the proximal row were the radial, intermediate and ulnar carpal bones; and in the distal row were two distal carpal bones supporting metacarpals II and III respectively. Four metacarpal bones were present and the four digits had a phalangeal formula of - I-4, II-7, III-7, IV-3. The terminal phalanges were small (1-2 mm in diameter). Bony epiphyses were not ossified on any metacarpals or phalanges. Dissection of both flippers located a distinct accessory carpal bone element. It was present as a well-formed, flattened cartilage at the caudal edge of the proximal row of carpal bones and articulated with the distal epiphysis of the ulna, the ulnar carpal bone and the proximal cartilage of metacarpal IV (Fig. 1d). A strong muscle tendon, which lay along the caudal edge of the ulna, inserted upon its proximal surface. In addition, the bony olecranon was greatly expanded by a flat cartilage plate extending caudally and distally. The skin of the caudal flipper area covered these two cartilages and extended between them.

PELVIC BONES

In whale 1, the cleaned pelvic bones were 61 mm (right) and 65 mm (left) in maximum length, 30 mm (right) and 28 mm (left) in maximum height, and 3-6 mm in width (Fig. 1c). In whale 2, in the fresh state each pelvic bone was extended cranially and caudally by a 35-40 mm tapered cartilage anlage (Fig. 1c). Total length of the left pelvic bone with cartilages was 118 mm. When the cartilages were removed the total length was 50 mm for the left and 51 mm for the right .

DISCUSSION

Odontocete periotics are often used to help identify species (Kasuya 1973), and mysticete bullae receive attention because the growth laminae are sometimes used in age-estimation (Christensen 1981). Periotics of mysticetes, however, are poorly documented. Indeed, we have come across no detailed recent accounts of minke periotics. A lack of attention may reflect the general complexity of the balaenopterid periotic, which is highly modified compared to this element in archaeocetes, odontocetes and archaic mysticetes. Many features on cetacean periotics are named conventionally on the basis of their topographic relationships in archaic species (Kellogg 1936) and other Eutheria, but these relationships are not always clear. In minke whales and other balaenopterids, most topographic features are reoriented from the positions characteristic of archaic Cetacea. The original dorsoventral axis of the archaic cetacean periotic is elongated in the minke, and the periotic is rotated so that, with the periotic in situ, the external surfaces of the anterior process and body are directed dorsally, and the long axis of the body and anterior process is directed anteromedially. The dorsal surfaces of both the pars cochlearis and body face dorsomedially. We use terms such as dorsal and external here in the sense

of their homology with named structures in other Cetacea, rather than as terms that indicate in situ orientation in the minke.

Changes in periotic structure can be traced through the Cetacea, and can be used empirically to recognise taxa, but functional consequences are poorly understood. In archaic Cetacea, the anterior bullar facet marks the position of contact of periotic with the anterior of the thin outer lip, but in balaenopterids and some other groups (eg. many Delphinoidea), there is no contact and the anterior bullar facet is lost (Fordyce, personal observations). In the minke we examined, the bulla and periotic are widely separated. Extant balaenopterids and balaenids have a hypertrophied and irregularly rough and porous anterolateral surface on the anterior process, and porous lateral and dorsal surfaces on the body (Yamada 1953), as in our specimen. The function of this rough or porous bone is uncertain, but perhaps rapidly changing density differences between hard and soft tissue here help acoustically isolate the periotic from spurious sounds transmitted through the lateral side of the skull.

The roughly triangular form of the anterior process of the minke described here is a feature of many cetotheres and balaenopterids (Fordyce, personal observations). The anteroexternal sulcus is a persistent but enigmatic feature in many modern Cetacea, and we are not aware of published accounts of soft anatomy which reveal its function. However, the sulcus can be traced back through a series of archaic fossil Cetacea to reveal an association with the foramen spinosum (Fordyce, personal observations); the sulcus thus perhaps accommodated the middle meningeal artery. Many mysticetes lack a discrete fossa for the head of the malleus, though this loss has not been explained in functional terms. The caudally-expanded, sheet-like, bony origin for the stapedius muscle is notably larger than in cetotheres, whence balaenopterids supposedly evolved, and indicates a phylogenetic size increase in the stapedius presumably associated with changes in hearing. Though some authors identify the so-called posterior process of the periotic as formed only by periotic (Yamada 1953, Kellogg 1928, 1936), most of the process is formed by part of the tympanic bulla which fuses to the periotic during foetal or juvenile stages. Kasuya (1973: Plate 1, Fig. 9) showed the suture in a foetus of a sei whale, *Balaenoptera borealis*. Only a trace remains in our whale 1, and the suture is obliterated in adult balaenopterids. This fusion of posterior processes in balaenopterids and many cetotheres (Fordyce, personal observations) indicates a different coupling of periotic and bulla than seen in odontocetes, in which the tympanic bulla and periotic are not fused caudally, and perhaps is functionally related to low frequency hearing in mysticetes.

The morphology and degree of fusion in cervical vertebrae has been used at times to classify cetaceans (Gill 1871), but modern higher taxonomy places little weight on such features. We are not aware of any broader modern reviews of the functional morphology of cetacean cervical vertebrae, though links between feeding behaviour and vertebral structure could be explored. At lower taxonomic levels, the structure of the cervical vertebrae has been used to subdivide minke whales. Supposedly separate northern and southern forms of *Balaenoptera acutorostrata* are based in part on the presence of a short parapophysis on the seventh cervical vertebra in northern forms (specifically two specimens from Japanese waters - Omura 1957) and its absence in southern forms (three specimens from the Antarctic stock - Omura 1975, Omura & Kasuya 1976). The cervical 7 parapophysis, albeit a minor tubercle, was identified bilaterally in both New Zealand whales reported here. Rudimentary parapophyseal tubercles were present on cervical 7 in another New Zealand minke (Gray 1874), and a similar small tubercle was identified in a so-called dwarf minke from east Australia (Arnold *et al.* 1987). The presence of these parapophyses in minke whales from Australasian waters contradicts its reported absence in other southern hemisphere specimens - eg. Antarctic minkes (Omura 1975, Omura & Kasuya 1976), but is consistent with findings of its presence in North Atlantic minke whales (Carte & MacAlister 1868, Struthers 1872, Turner 1893, True 1904). Conversely, "no trace of inferior process" was reported for another North Atlantic specimen (Flower 1864a). Flower (1864b) documented morphological variation among individual cetaceans and cautioned against giving undue significance to this normal intraspecific variance in osteology. There is little reason to think that variation in the parapophysis on cervical 7 in minke whales is diagnostic.

On the axis, two small and separate developmental ossification centres are often overlooked but

they are recognised as canonical components of the mammalian axis (Cave 1986, Watson *et al.* 1986). The first, the ossicle forming the apex of the dens, develops from the centrum of the proatlas vertebra and has been identified in the minke whale (Carte & MacAlister 1868, Cave 1986). The second, intercentrum two intercalated between the base of the dens and the axis body, was identified in this report and by others in the minke and other cetaceans (Carte & MacAlister 1868, Cave 1967, 1986).

The first vertebral body epiphysis in the vertebral column of the minke whale reported here was on the caudal surface of the axis body, as is characteristic of mammals (Watson *et al.* 1986). The atlas of cetaceans and all other mammals possesses neither a centrum ossification centre nor vertebral body epiphyses. Thus, the identification of an epiphysis on cervical 1 in some minke whales (Kato 1988) must be questioned.

Minor left-to-right asymmetries in the cervical transverse processes were found in the two minkes described here. Similar asymmetries have been noted in minke and other rorqual whales (Flower 1864a & b, 1869, Struthers 1872, Turner 1893, True 1904, Omura 1975). The absence of the left diapophysis on cervical 4 in whale 1, however, is a remarkable example of skeletal asymmetry. Moreover, the transverse processes, vertebral pedicles, and vertebral foramen were all asymmetrical and, thus, the underlying malformation has affected the development and form of the whole vertebra. It is unlikely that these bony abnormalities would have had any functional consequence in the living whale.

Notochordal foveae represent the sites where, during embryonic development, the notochord pierced each vertebral body primordium. This bony depression has been described in few immature mammals (Taylor 1972, Watson 1981), and our finding of the fovea in two minke whales supports an earlier account of a similar depression at the summit of the dens in a minke whale (Flower 1864a).

Caudal vertebrae of cetaceans have markedly different morphology depending where they are in the tail . The transition of external body form from the peduncle to the flukes corresponds internally to an abrupt transition in vertebral body shape, as seen in our minke specimens. This transition is centred on a particularly rounded or ball-shaped vertebra, caudal 11, which lies in the base of the flukes at the junction between the flukes and the penduncle.

Most of the bending moment of the flukes took place at the intervertebral disc space immediately caudal to this ball vertebra. Similar correlative functional morphology has been reported in the bottlenose dolphin (Watson 1991), and suggests a common pattern for fluke-bearing cetaceans.

Haemal arches caudal to the ball vertebra are not normally described in minke whale skeletons recovered after months of burial (Flower 1864a, Turner 1893, Omura 1975). This was the case with our first minke. The persistence of five pairs of haemal arches caudal to the ball vertebra, as seen in the dissection of our second minke, suggests a strong functional reason for their persistence. This terminal series of small haemal arches has also been identified in radiographs and dissections of bottle nose dolphins (Watson, personal observations).

There is variation in the number of caudal vertebrae reported for the minke whale -16-20 (Omura 1957, 1975, Omura & Kasuya 1976). Some of this is likely due to individual variation and some because the last two caudals are quite small (10 mm or less in diameter) and could be easily overlooked or lost during skeletal preparation. Flower (1864a) and Turner (1893) recovered skeletons under favourable circumstances and with particular care to minimise loss of small bones. They reported 20 and 19 caudals respectively. Allen (1916) reported 20 caudals from his dissection. Nineteen caudal vertebrae were found in both of our minke whales. "The variation in number of caudals [in minke whales], exclusive of that due to defects, probably does not exceed two" (True 1904).

Sterna of mysticetes are atypical in that only the first pair of ribs articulates with them, and in that they usually develop from a single segment - the manubrium or first sternebra (Flower 1885). The two described here for minke whales are clearly different in shape from each other. Numerous variants of sterna in minke and other rorqual whales have been illustrated (True 1904, Omura 1975, Omura & Kasuya 1976, Arnold *et al.* 1987). The cruciate form is common in the minke whale but the cranial notch seen in one of our specimens (whale 1) is not reported, although similar notched sterna are known variants in North Atlantic fin whales (True 1904), and in a New Zealand blue whale, *Balaenoptera musculus* (Waite 1912, Watson, personal observation). The notch is thought to be a transitory developmental feature (Flower 1885) but

we do not understand the reasons why balaenopterid sterna vary.

The minke sternum described here had a double articulation with each of the first pair of ribs, which is contrary to that found in odontocetes and other eutherian mammals. Our finding is in accord with earlier descriptions for the minke (Turner 1893) and other balaenopterid whales (Turner 1870, Struthers 1871). The extreme reduction of the sternum in rorqual and other mysticete whales has resulted in a highly modified articulation with the ribs.

Radiographic evaluation of cetacean flippers ensures that topographical relationships among the bones are maintained and that small ossifications are identified, advantages that are often lost with other preparation methods. The pattern of carpal elements in our second minke whale conforms to earlier findings in minke and other balaenopterids (Flower 1885, Turner 1893, Struthers 1895), but contradicts that of Omura (1975) who reported minke whales with 2-3 proximal carpals and 3 distal carpal bones. This discrepancy is perhaps due to the different methods used. The early workers dissected the flippers, as was done in this study, and were able to identify the elements in situ, including the cartilaginous or often poorly ossified accessory carpal bone. Omura recovered bones from specimens buried for 15-17 months; such recovery often results in small elements being lost or mixed. The combination of radiography and dissection of our flippers provided good opportunity to locate and identify all carpal elements in their correct topographical positions.

Dissection in our minke whale also revealed large cartilage plates extending caudally at the elbow and carpus: ie. the cartilaginous extension of the bony olecranon (illustrated by Gray 1874) and the cartilaginous accessory carpal bone. The caudal edge of each cartilage extended to near the caudal margin of the flipper. These unossified and somewhat flexible cartilaginous structures probably act as struts, providing resilient support for the fleshy caudal part of the flipper as it moves through the water.

The two epiphyses, one proximal and one distal, on the metacarpals and phalanges were not ossified in our immature minke whales. Similar bony epiphyses were also wanting in adult minkes (Turner 1893, Omura 1975). This delayed maturity of the flipper skeleton is a normal feature of mysticetes (Flower

1885). In odontocetes, on the other hand, these epiphyses characteristically ossify and fuse with both ends of the metacarpals and phalanges (Struthers 1863). In Cetacea, both mysticetes and odontocetes, the development of the epiphyses on the metacarpals and phalanges thus departs from the typical mammalian pattern of a single bony epiphysis, which fuses at puberty (Evans 1993). The phalangeal formula for our New Zealand minke whale (whale 2) is within the ranges compiled by Omura (1975).

Pelvic bones in mysticetes develop as cartilage models in the foetus (Hosokawa 1951) and, in minkes, ossification begins postnatally when juveniles are about 4 m total length (Perrin 1870). In larger immature whales, the middle section ossifies and cartilage remains as cranial and caudal extensions, as seen in one of our minkes (5.85 m) and in other balaenopterids (Struthers 1893). Adult minke whales have fully ossified pelvic bones which, like other rudimentary organs, vary in size and shape (Omura 1978, 1980).

From our examination of two minke whale skeletons and our review of the cetological literature, we find that detailed postcranial skeletal anatomy of cetaceans is best revealed by dissection and radiography, rather than by reassembly of buried bones. We are not convinced that, at present, there is enough reliable information to support claims of geographic patterns of variation in minke whale postcranial osteology. The long-neglected postcranial skeleton, with supporting structures, offers great potential for functional studies likely to advance our understanding of cetacean biology.

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