A REVIEW OF AUSTRALIAN FOSSIL CETACEA

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Abstract

Australian fossil Cetacea are reviewed as a prelude to the revision of previously-described taxa. The fifteen named species and subspecies are based on type-specimens of Oligocene, Miocene and possibly Pliocene age, and represent archaic Mysticeti, Squalodontidae, Physeteridae, Delphinidae, and supposedly Ziphiidae. Only two type-specimens are skulls, while the rest are elements, such as isolated teeth and earbones, which are known from other studies to be often undiagnostic. At least one nominal species of Ziphiidae is a *nomen dubium*. Other specimens which have been described informally or are housed in museums include species of Cetotheriidae, Balaenidae, Balaenopteridae, Squalodontidae, Rhabdosteidae, and Ziphiidae. None of the Australian fossil cetacean faunas is known well enough at present to allow significant paleobiogeographical or paleoecological interpretation.

Introduction

Australia has a small but interesting selection of fossil whales and dolphins (Cetacea). Mahoney and Ride's (1975) index to fossil mammals from Australia mentions 15 species or subspecies from the Oligocene, Miocene and Pliocene, and work under way by the author suggests that other taxa, hitherto undescribed from Australia, are represented in collections. The aim of this article is to outline, in general terms, the current knowledge of Australian fossil Cetacea as a prelude to formal redescriptions planned for the future. Currently-accepted subdivisions of the Cetacea are shown, together with their global and Australian stratigraphic distributions, in Figure 1.

The following abbreviations are used: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; BMNH, Department of Paleontology, British Museum (Natural History), London; MUGD, Department of Geology, University of Melbourne; NMV, National Museum of Victoria, Melbourne; SAM, South Australian Museum, Adelaide.

General Features of Cetacea

Modern cetaceans are completely aquatic mammals whose most conspicuous link with terrestrial mammals is air-breathing. Cetacea are well adapted for life in water. The body is hairless and streamlined, and hindlimbs are absent. Tailflukes are used in swimming and forelimbs in steering. Different species of Cetacea are externally quite similar to each other but the internal skeleton is very variable. In contrast to most mammals, the anterior, tooth-bearing portion of the skull (rostrum) is long (Figure 2). Teeth are usually multiple, undifferentiated (homodont) and conical. They may be absent in some species with toothed close relatives, and are absent in adult baleen whales. The skull is 'telescoped', that is, the contact relationships of the bones have departed from the normal mammalian condition, and the nares (nasal openings) and blowholes have migrated toward the top of the head. For general reviews of cetacean characters other than those discussed below, see, for example, Gaskin (1976), Harrison and King (1980), Kellogg (1928), Norris (1966) and Slijper (1979).

Three suborders are recognized within the Order Cetacea: Archaeoceti, Mysticeti and Odontoceti (Figure 2). Archaeocetes are primitive, extinct toothed whales, from which living mysticetes (baleen or whalebone whales) and odontocetes (modern toothed whales, dolphins and porpoises) arose. Whereas identification of living cetaceans is based largely on external characters, identification of fossils is based necessarily on the skeleton. Skeletal
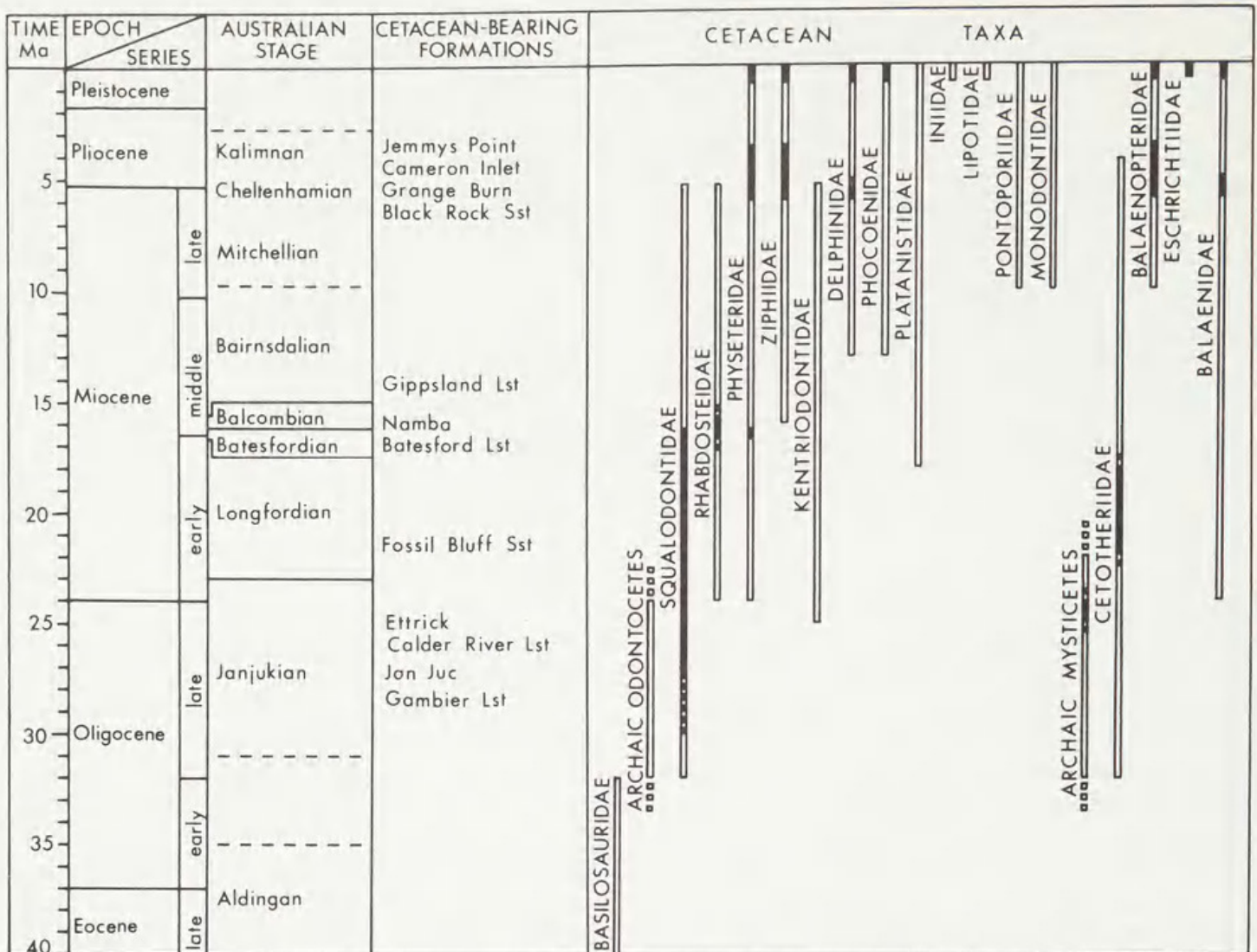
Fig. 1. Correlation of absolute time (millions of years before present, Ma) and international stratigraphic subdivisions with some Australian Tertiary stages, some Australian cetacean-bearing formations, and global records (open bar) and Australian records (infilled bar) of main cetacean taxa.

structures are also used for determining higher relationships (e.g. between genera, families) of living cetaceans. Accordingly, there is a great deal of literature about cetacean comparative morphology. For example, Miller (1923) described the different patterns of telescoping of the maxilla and other skull bones which constitute the primary basis for classification (Figure 2). The functional anatomy and significance of telescoping was considered by Mead (1975a). Fraser and Purves (1960) discussed the morphology and systematic distribution of air-sinuses in the skull. Cetacean earbones, which are common fossils, were

discussed by Yamada (1953) and Kasuya (1973). Teeth, also common fossils, are of little use in determining the relationships of any but the oldest fossil Cetacea (in which the teeth are still differentiated into peg-like anterior teeth and shearing posterior cheek-teeth). Similarly, elements of the postcranial skeleton (vertebrae of the neck, thorax, lumbar region, and tail, ribs, and forelimbs) cannot be used consistently for accurate identifications.

Archaeocetes

Archaeocetes, the oldest, most primitive whales, probably arose from archaic ungulates (Van Valen 1968) by the Early Eocene. The transition from land mammal to aquatic cetacean involved changes in feeding and locomotion, which can be inferred from changes in the skull (such as lengthening of the rostrum, widening of the frontals, loosening of the jaw

articulation) and postcranial skeleton. The most important postcranial skeletal change was modification of the caudal vertebrae, associated with the evolution of tail flukes, although this is not yet recorded in fossils.

The earliest archaeocetes (Family Protocetidae) include specimens from around the ancient Tethys sea (India, Pakistan, Egypt, Nigeria) and Texas (Kellogg 1936, Sahni and Mishra 1975, West 1980). No specimens are known from Australia or anywhere else in the Southern Hemisphere.

More advanced archaeocetes (Family Basilosauridae) probably arose from protocetids, from which they differ in features such as more elaborate cheek-teeth, development of an air-sinus in the basicranium, and more elaborate earbones. All described species of basilosaurids are from the Middle to Late Eocene and probably Early Oligocene of the Northern Hemisphere (Kellogg, 1936, Barnes and Mitchell 1978). The family was revised recently by Barnes and Mitchell (1978), who recognized two subfamilies. The Basilosaurinae (the 'Zeuglodon', *Basilosaurus cetoides*) were gigantic toothed whales of length approaching 20 m. Although they had distinctly elongate vertebrae, they were probably like modern whales in appearance. Basilosaurines, because of their vertebral structure, were too specialised to have given rise to any of the known later Cetacea. The other subfamily of basilosaurid, the Dorudontinae, comprise small, perhaps dolphin-like, species which were taxonomically and ecologically more diverse than basilosaurines. Fossil evidence suggests that both mysticetes and odontocetes arose from this group (e.g. Barnes and Mitchell 1978, Fordyce 1980b), although such an origin is disputed by some authors (e.g. Yablokov 1965, Kuzmin 1980). If the former notion is accepted, then the suborder Archaeoceti, as currently defined, is a nonmonophyletic group (in the sense of Gaffney 1979), for it does not include all descendants of the ancestral member of the group. For further reading on archaeocetes, see Kellogg 1936, Van Valen 1968, Sahni and Mishra 1975, Barnes and Mitchell 1978, Fordyce 1980b, and West 1980.

Very few supposed archaeocetes from the Southern Hemisphere have been recorded in the literature, and all are known poorly. Bones of '*Zeuglodon*' have been collected from the Upper Eocene of Seymour Island, Antarctic Peninsula (Kellogg 1936, Elliot *et al.* 1975) but those described so far give a poor idea of relationships. At least one apparent archaeocete, represented by dorudontine-like teeth, is known from the Upper Eocene of New Zealand (Fordyce 1979: 739). The only Southern Hemisphere record of a supposed archaeocete from the Oligocene is that of the New Zealand Late Oligocene species, *Kekenodon onamata*. Although this species has been mentioned widely in the literature, it is known only from the holotype teeth, earbones, and a fragment of skull (Fordyce 1980a). These are sufficiently different from specimens from elsewhere to warrant continued recognition as a separate genus and species of uncertain suprageneric affinities. The Australian Oligocene species *Mammalodon colliveri* Pritchard, 1939, has been assigned to the Archaeoceti, but it appears to be a proto-mysticete and is discussed below.
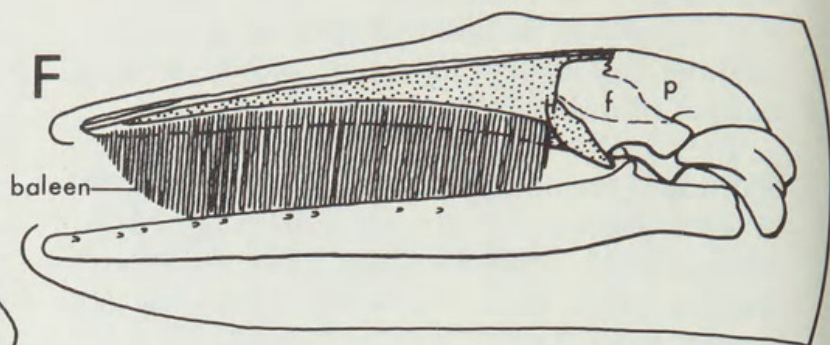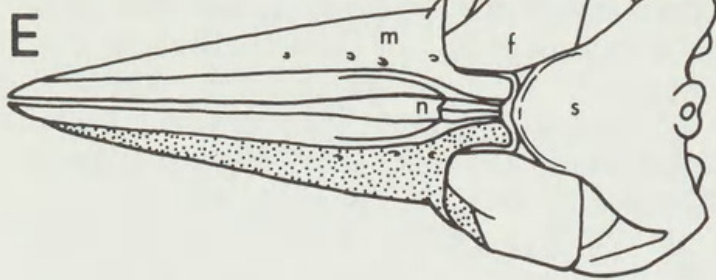
Mysticetes

Living mysticetes or baleen whales are large filter feeders which lack teeth (in all but embryonic stages) and, instead, possess baleen. Baleen consists of a series of thin, fibre-fringed plates which hang from the upper jaw (Figure 2), and functions to sieve food (small fish, plankton) from the water (Pivorunas 1979). Other apparently characteristic features of mysticetes also reflect the filter-feeding habit. These include the long rostrum, broad and dorsoventrally thin maxilla, loosely-sutured rostral bones, well-developed infraorbital process of the maxilla, elongate palatine bones, origin of temporal muscles on the dorsal surface of the supraorbital process of the frontal, presence of a pterygoid fossa primarily within the pterygoid bone, and absence of a bony symphysis in the mandible (based on features discussed by Miller 1923, Fraser and Purves 1960; see Figure 2).
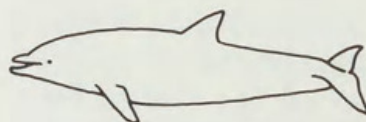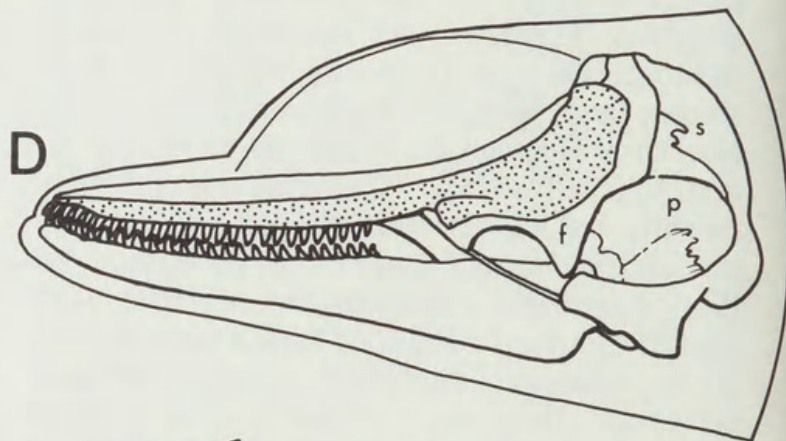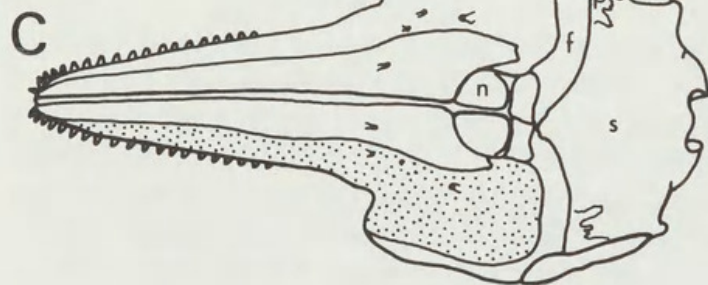
Archaic Mysticetes

Five families of extinct and living mysticetes are recognized (Aetiocetidae, Cetotheriidae, Balaenopteridae, Eschrichtiidae, and Balaeni-
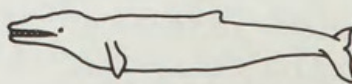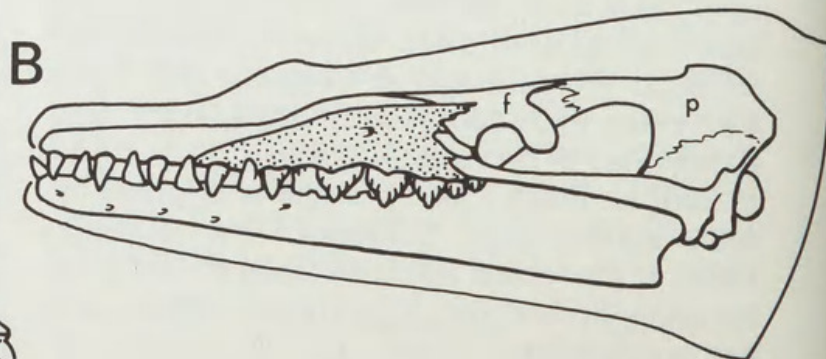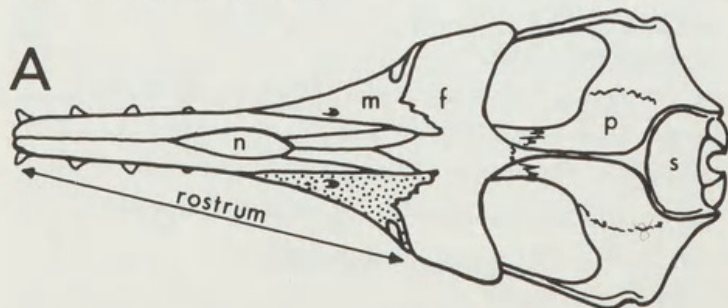
MYSTICETI

ODONTOCETI

ARCHAEOCETI

dae), of which the Family Aetiocetidae is the most primitive. Aetiocetids are represented with certainty only by the Early Miocene *Aetiocetus cotylalveus* Emlong, 1966, from Oregon. Because the species possesses teeth, it was assigned originally to the Archaeoceti, but Van Valen (1968) and Barnes and Mitchell (1978) stressed that it should be included in the Mysticeti because it exhibits derived mysticete characteristics. Although *A. cotylalveus* is the most primitive mysticete yet described, it is a relict species and is not the geologically oldest mysticete known.

Mammalodon colliveri Pritchard, 1939, formerly assigned to the Archaeoceti, appears to be a relict mysticete even more primitive than *Aetiocetus cotylalveus*. The holotype and only described specimen (presently under study by the author) consists of a fairly complete skull, right mandible, right periotic and tympanic bulla, worn teeth, and axis vertebra, specimen MUGD 1874, and a tooth, specimen NMV P17535 (Plate   , fig. 6). The holotype was collected from the uppermost Jan Juc Formation (of latest Oligocene age; Abele 1979) at Bird Rock, Torquay, Victoria (Pritchard 1939, Singleton 1945).

Because the holotype has never been described adequately, its affinities have been interpreted variably by different authors. Pritchard (1939) did not refer it to a suborder, although he did consider it to be an 'ancient form . . . showing the closest approach to descent from a mammalian type of ancestor'. A reviewer (Anonymous 1939) described the species as a 'zeuglodon', Camp *et al.* (1942: 262) placed it in the Cetacea *incertae sedis*, Romer (1966: 392) assigned it to the Basilosauridae, while Pledge and Rothausen (1977: 286) implied that the species (for which was used the apparent *lapsus*

calami, Mammalodon pritchardi) is a squalodontoid odontocete. Some features of the holotype, for example, the loosely-sutured rostral bones, the relatively broad, flat palate, the externally-convex profile of the upper tooth-row, the fused roots in the cheek-teeth, the absence of a bony symphysis on the mandible, and the absence of a marked sagittal crest, indicate that *M. colliveri* cannot be assigned to the Archaeoceti as usually defined (e.g. by Kellogg 1936). The specimen does not exhibit derived features (e.g. a posteriorly-telescoped ascending process of the maxilla) which would justify assignment to the Odontoceti. The above features of the holotype suggest mysticete affinities, and I provisionally interpret *M. colliveri* as a very primitive and relict mysticete. The possibility that *Mammalodon colliveri* evolved independently from archaeocetes and, thus, is convergent with mysticetes, cannot be discounted yet.

Apart from the holotype, other material is known which may represent *M. colliveri*, e.g., isolated periotics, NMV P48795, P48806, P48850, P48867A-C, P160125, and P160126. Most specimens are from Janjukian (Late Oligocene) sediments exposed along the coast near Torquay, and in Waurn Ponds quarry, Victoria. Despite the fact that a considerable number of specimens is known for *M. colliveri*, new material will significantly help interpretation of this unusual species.

Cetotheres

Cetotheres (Family Cetotheriidae) comprise a diverse range of early mysticetes which have been classified together primarily because they lack characters typical of living families of mysticete, particularly the balaenopterids. For example, they differ from balaenopterids in the lack of an abruptly depressed supraorbital process of the frontal and in the variable retention of the intertemporal constriction and a strong coronoid process. Thus, as regarded at present, they probably constitute a nonmonophyletic group. The oldest accurately dated described mysticetes, from the Late Oligocene of New Zealand and Europe, have been included in the Cetotheriidae. Cetotheres are common in the Miocene, and range into the Early Pliocene.

Fig. 2. Simplified outlines of cetacean skulls showing subordinal variation in telescoping of the maxilla (m; also stippled), frontal (f), parietal (p), and supraoccipital (s), and position of the nares (n). Mandibles not shown in dorsal view. Not to scale. A, an archaeocete, *Zygorhiza kochii*, dorsal view. B, *Z. kochii*, left lateral view. C, an odontocete, *Tursiops truncatus*, dorsal view. D, *T. truncatus*, left lateral view. E, a mysticete, *Balaenoptera borealis*, dorsal view. F, *B. borealis*, left lateral view.

Specimens have been reported from the east and west coasts of North America, Patagonia, Europe, Eurasia, Japan, New Zealand, and Australia.

The only published description of an Australian cetothere is that of a specimen which was described by Glaessner (1955: 367-369). This cetothere, apparently first mentioned in print by Tate (1885: 41), consists of a skull minus rostrum, of reported Early Miocene age, from Murbko, South Australia. Glaessner provisionally assigned the species to the genus *Aglaocetus*, species of which have been reported previously from Patagonia and eastern North America (Kellogg 1934, 1968). Further study is needed to determine the affinities of the specimen, particularly in the light of its supposed relationship with species of apparently restricted Atlantic distribution. In unusual contrast to New Zealand, where cetotheres are common in the Oligocene, no significant specimens have been reported from the otherwise fairly productive Victorian Oligocene. It is likely, however, that undescribed fragmentary specimens from the Victorian Miocene will be found to represent cetotheres. For further reading on this group, see Kellogg (1928, 1931), Marples (1956), Rothausen (1971) and Fordyce (1980b).

Living Mysticetes

The rorquals or fin whales (Family Balaenopteridae) include the Blue Whale (*Balaenoptera musculus*, the largest mammal ever to have lived) and other large species. Characteristic features of balaenopterids include a relatively broad, flat rostrum, supraorbital processes that descend abruptly from the vertex, and closely approximated rostral elements and supraoccipital (e.g. Figure 2). Fossil balaenopterids are known from the Late Miocene onwards, and even early members appear to have been structurally similar to living forms. Fossils have been reported from North and South America, Europe, and Asia (e.g., Simpson 1945), but none has yet been described from Australia. Specimens are known, however. For example, earbones similar to those of the living humpback whale (*Megaptera novaeangliae*) and rorquals (*Balaenoptera* spp.) have been collected

from the Pliocene of Flinders Island, Bass Strait, and worn earbones from Beaumaris and Grange Burn, near Hamilton, Victoria, probably represent other species of balaenopterid. These specimens have yet to be described formally.

The Family Eschrichtiidae, represented by the living gray whale, has a fossil record only back into the Pleistocene. The family probably arose from balaenopterids. Gray whales have not been recorded from the Southern Hemisphere.

The Right Whales (Family Balaenidae), which include two large, slow-moving living species, have a fossil record back to the Early Miocene (Cabrera 1926; an Oligocene record mentioned by Fordyce 1980b is erroneous). Even early balaenids appear to have possessed the narrow, arched rostrum, posteriorly-inclined supraorbital process, and forward-thrust supraoccipital typical of modern species. The oldest fossils are from South America, while others are from North America, Europe and Australia. Whereas South American specimens include well-preserved skulls (Cabrera 1926), the Australian specimens are less complete, and none has yet been described formally. Gill (1957: 181) stated that an earbone (a periotic, NMV P16195) from Beaumaris had been identified as cf. *Balaena*. Other balaenid periotics (usually worn, but still exhibiting the typical balaenid features of small pars cochlearis and large, swollen anterior process) from Beaumaris and Hamilton are in the collections of the National Museum of Victoria, and it is likely that fragmentary skull bones from these localities also represent right whales. Howchin (1919) identified a Late Pliocene 'tympanic bone' (actually part of a right periotic; SAM specimen P8321) as that of *Balaena*.

Odontocetes

Odontocetes, or 'modern' toothed whales, encompass fossil and living dolphins, porpoises, beaked whales and sperm whales. The oldest accurately dated undoubted odontocetes are from the Late Oligocene although possibly older fragmentary specimens of less certain relationships are known (Whitmore and

Sanders 1977, Fordyce 1980b). Whereas the early evolution of mysticetes involved the development of a baleen filter-feeding system, that of odontocetes appears to have centred on development of sophisticated acoustic mechanisms of the type used by living odontocetes in echolocation (Fordyce 1980b). In living odontocetes, muscles of the face, which are implicated in the production of echolocation sounds, have distinct bony origins. The presence of the same patterns of bone profiles and telescoping in the phyletically and geologically oldest odontocetes suggests that they too echolocated. Apart from these features of the face, diagnostic features of odontocetes include the presence of nasal diverticula, antorbital notches, a reduced contribution of maxilla to orbit, a temporal muscle origin on ventral surface of supraorbital process of frontal, the presence of middle sinus in the ear, the presence of high-frequency adaptations in the ear, and the presence of a 'panbone' in the mandible (based on features discussed by Miller 1923, Fraser and Purves 1960, Kasuya 1973, Mead 1975a, Fleischer 1976; see Figure 2).

Primitive Odontocetes

The best-known early odontocetes probably are the shark-toothed dolphins (Family Squalodontidae, discussed below). Odontocetes more primitive than these were poorly known until recently, and usually were included in the Family Agorophiidae. Despite the fact that agorophiid-like forms gave rise to squalodontids and other more-modern odontocetes, the oldest accurately dated such archaic forms are relicts from the Late Oligocene, contemporaneous with squalodontids and delphinoids. No 'pre-squalodontid' odontocetes have yet been recognized from Australia. It is noteworthy that while primitive 'pre-squalodontid' odontocetes are usually classified in the Agorophiidae, a reappraisal of the Agorophiidae and the study of newly-discovered archaic odontocetes from the northeast Pacific suggest a greater taxonomic and ecological diversity amongst early odontocetes than can be expressed by the use of one family, and it is likely that new families will be described in the near future (Fordyce, 1981a).

Shark-toothed Dolphins

Squalodontids, or shark-toothed dolphins (Squalodontidae) comprise an extinct family known from the Late Oligocene to Late Miocene. They probably exhibited a variety of sizes and external shapes similar to those of the living dolphins (Family Delphinidae), and the skulls of long-beaked species appear much as would primitive beaked whales (Family Ziphiidae, see below) except for the presence of many triangular, denticulate cheek-teeth (hence the name, shark-toothed dolphins). Squalodontids include a few species known from well-preserved skulls, complete tooth complements, earbones and mandibles, but many nominal species (including Australian species) are based only on isolated teeth. Some of these teeth are similar in shape, arrangement of denticles, ornament, and other features, to teeth in identified squalodontid skulls (e.g. as in *Squalodon* spp., discussed by Rothausen 1968) but others are of uncertain affinities and could have come from any one of a number of early odontocetes (not necessarily just Squalodontidae) which exhibit heterodonty. Squalodontids have been reported from the east and west coasts of North America, Patagonia, Europe, Eurasia, Asia, New Zealand and Australia. (For a recent review of Australian species, see Pledge and Rothausen 1977.)

The best-known Australian squalodontid undoubtedly is *Prosqualodon davidis* Flynn, 1923, the holotype of which comprises a skull (now lost) and associated elements, forelimb bones and vertebrae from Fossil Bluff, Wynyard, Tasmania. The elements were described in detail by Flynn (1948) who had earlier (1920, 1923, 1932) given abbreviated descriptions. An artificial cranial endocast was described by Dart (1923). The holotype is from the Fossil Bluff Sandstone, of Longfordian or Early Miocene age (Pledge and Rothausen 1977). The skull is short-beaked and robust, in contrast to the more delicate skulls of the common long-beaked species of *Squalodon* of the Northern Hemisphere Miocene, and carries robust teeth. Perhaps the animal was an active predator — a small equivalent of the living killer whale. Flynn assigned the species to *Prosqualodon* because of its close similarity to the

South American species *Prosqualodon australis* (Plate 2, fig. 2), an earliest Miocene species described by Lydekker (1894; see also references in Flynn 1948). The similarity of *Prosqualodon davidis* to *P. australis* counters the suggestion (Rothausen 1970) that the former should be placed in a different genus.

Other material of *Prosqualodon* is known from the Southern Hemisphere, although no Northern Hemisphere specimens are known yet. Two supposed species of *Prosqualodon, P. hamiltoni* Benham, 1937, and *P. marplesi* Dickson, 1964, have been recorded from the Late Oligocene Waitakian Stage of New Zealand, but neither seems congeneric with *P. australis* (Fordyce 1980a, 1980b). However, isolated teeth of squalodontids from the New Zealand Waitakian may well represent species of *Prosqualodon*.

Prosqualodon also may be represented in Australia by some isolated teeth, including some described by Hall (1911) and discussed subsequently by Flynn (1948), Glaessner (1955) and Pledge and Rothausen (1977). Those shown in Hall's Figs. 5 and 7 are, respectively, the holotypes of *Parasqualodon wilkinsoni* and *Metasqualodon harwoodi*, discussed below. Specimen NMV P5525, Hall's Fig. 1, was identified by Hall as ?*Parasqualodon wilkinsoni*, while Flynn was uncertain of its identity. Its ornament (Plate 2, fig. 5) is unlike that of the *Prosqualodon* teeth figured by Flynn but is reminiscent of the coarse ornament of poorly-preserved the teeth of *Mammalodon colliveri*. The tooth in Hall's Fig. 2 (NMV P5529) is a finely ornamented anterior tooth which Flynn had 'no difficulty' referring to *P. davidis*. However, the ornament on this tooth is much finer than that of *P. davidis*, and close affinity is unlikely. An anterior cheek-tooth (Hall's Fig. 3, NMV P14040; Plate 2, fig. 1), identified by Flynn as *P. davidis*, is similar to teeth figured by Flynn, but the posterior keel of the tooth possesses denticles not seen in *P. davidis*. Accordingly, they may not be conspecific. Flynn regarded the cheek-tooth of Hall's Fig. 4 as that of *P. davidis*, and this was followed by Pledge and Rothausen (1977) who refigured the tooth. This tooth may be that of '*Zeuglodon*' mentioned by Tate (1892). Flynn commented that

the tooth of Hall's Fig. 6 (NMV P5532) could be related to '*Squalodon*' *serratus*, known from a single tooth from the New Zealand Oligocene (Glaessner, 1972, Fordyce 1980a). This is unlikely, as there are marked differences in size, proportions, ornament, and denticles. Pledge and Rothausen (1977: 292) included NMV P5532 with *P. davidis*, but this relationship has yet to be verified.

Parasqualodon wilkinsoni (McCoy, 1866) is known with certainty only from the holotype (NMV P5528), an isolated tooth (Plate 2, fig. 3) probably from the Calder River Limestone (Late Oligocene) near Castle Cove, Aire district, Victoria. The species originally was thought to represent *Squalodon*, and it was only in 1911 that Hall assigned it to a new genus, *Parasqualodon*. Flynn (1948) noted its similarity to *Prosqualodon davidis* but considered that the structure of the tooth argues against close relationship. He considered the tooth to be abnormal. Pledge and Rothausen (1977) mentioned differences in crown structure between teeth of *Parasqualodon wilkinsoni* and *Prosqualodon davidis*, but concluded that the former probably represents a species of *Prosqualodon*. In fact, the possibility of intraspecific variation in teeth and the close geological ages make it possible that these species are conspecific.

Metasqualodon harwoodi (Sanger, 1881) is another tooth taxon, of supposed Squalodontidae, that was poorly understood until reviewed by Pledge and Rothausen (1977). The species is known only from the Late Oligocene holotype and paratype teeth from South Australia. The teeth appear to be those of short-beaked species but, because no skull remains are known, this remains to be demonstrated (as does assignment to the Squalodontidae in the strict sense). Pledge and Rothausen concluded that *Metasqualodon* represents a distinct genus.

'*Squalodon*' *gambierensis* Glaessner, 1955, is based on a single cheek-tooth of early Late Oligocene age, from the Gambier Limestone, South Australia. The tooth was figured by Glaessner (1955) and Pledge and Rothausen (1977). Glaessner (1955) excluded it from described Austral genera and instead assigned it

to 'the widespread genus *Squalodon*' because of its smooth crown, straight roots and strongly developed median cusp. Pledge and Rothausen queried this generic assignment, and it seems unlikely that the tooth represents a species of *Squalodon*, for the keels are sharp, the denticles are relatively large, freestanding and laterally compressed, and the crown lacks ornament (present on even the smoothest crown of teeth of *Squalodon* spp.). It is unlikely that this or other Austral supposed species of *Squalodon* ('*S.*' *serratus* and '*S.*' *andrewi* from New Zealand) actually represent that genus, which is known positively only from the Miocene of the Northern Hemisphere. Until skull remains are found, it is not certain that '*S.*' *gambierensis* even belongs in the Squalodontidae.

Other squalodontid remains are known from Australia, although none is yet formally described. A large squalodontid is represented by an incompletely prepared partial skull, teeth and mandible (MUGD 5101) from Batesford Quarry, near Geelong (Batesfordian, Early Miocene). It differs in the large size of its cheek-teeth from species previously recorded from Australia. Gill (1957: 181) reported that an anterior tooth (NMV P16198) from Beaumaris is probably that of '*Squalodon* cf. *wilkinsoni*', but it is more likely that the tooth is the incisor of a seal. For additional general reading on Squalodontidae, see Kellogg (1923, 1928) and Whitmore and Sanders (1977).

Beaked Whales

Beaked whales (Family Ziphiidae) are medium to large odontocetes with long, narrow, and usually toothless rostra (or beaks), deeply concave facial regions on the skull, and mandibles that are usually toothless or with only one or two pairs of teeth. The fossil record extends back to the Early Miocene, and fossils are well known from North and South America and Europe (Mead 1975b). Fossil ziphiid bones, usually fragments of rostrum and earbones, are resistant to erosion, and may lie on the seafloor for millions of years (Eastman 1906, Fordyce and Cullen 1979). Ziphiids are probably of squalodontid ancestry (Mead 1975b).

One nominal species of fossil ziphiid from Australia, *Ziphius* (*Dolichodon*) *geelongensis*

McCoy, 1882, was based on a specimen thought to be a mandibular tooth, from Waurn Ponds, near Geelong. The holotype actually appears to be an undiagnostic worn fragment of rib, which suggests that the name should be discarded (Fordyce 1981b). The species previously has received occasional incidental mention in earlier literature on Victorian fossils.

McCoy (1879) also recorded worn cetacean tympanic bullae from Waurn Ponds and, unfortunately, established formal species names for these. He used the general name 'Cetotolites', proposed by Owen, as a formal generic name (although in the modern sense of a collective group: an assemblage of identifiable species of which the generic positions are uncertain), and suggested that the bullae represent ziphiids. McCoy recognized four species and subspecies, *Cetotolites leggei*, *C. pricei*, *C. nelsoni* [*nelsoni*], and *C. nelsoni rugosa*, probably all from the Waurn Ponds Member of the Jan Juc Formation of Late Oligocene to earliest Miocene age (Abele *et al.* 1976: Fig. 13). Another supposed species of *Cetotolites*, '*C. baileyi*', was mentioned by McCoy (1883) but was never described. None of the type-specimens is complete enough to be certain of the family to which they belong, let alone to allow assessment of generic and specific relationships. It is likely that when their taxonomic status is reassessed, the names will be considered *nomina dubia* (i.e., names not certainly applicable to any known taxa), and this would warrant discarding them.

Rostra which belong indisputably to Ziphiidae have been found in the Australian Tertiary. Chapman (1917) described two specimens, from Grange Burn, Hamilton district (NMV P13012, specimen A; Plate 2, fig. 12 herein; and NMV P13011, specimen B), which he identified as '*Mesoplodon compressus*, Huxley sp.'. Both are long, narrow, deep, and dense, with mesorostral ossifications and no alveoli. They probably came from the basal Grange Burn Formation, of Kalimnan age (latest Miocene-earliest Pliocene). A third, undescribed rostrum (NMV P21482) also is known from Grange Burn. Glaessner (1947) described a rostrum from the Kalimnan of Lakes Entrance, Victoria, for which he

employed the name *Mesoplodon longirostris* (Cuvier, 1823). Both Chapman and Glaessner listed *Belemnoziphius compressus* Huxley, 1864, as synonyms of the names they employed, whereas Mead (1975b) recognized *B. compressus* as a distinct species which he regarded as the type-species of *Belemnoziphius*. The relationships of these and other as-yet undescribed *Mesoplodon*-like Australian specimens to *Belemnoziphius* and other genera discussed by Mead has yet to be determined. Two other ziphiid records are noteworthy. Scott (1913) described, but did not figure, the postcranial skeleton of a supposed ziphiid from Table Cape, Tasmania. It is possible that, like *Prosqualodon davidis*, this specimen is of Early Miocene age. The affinities of the specimen have not been verified subsequently. Sutherland and Kershaw (1971: 159, Plate 2) figured the rostrum (NMV P23961) of a species of *Ziphius* from the Kalimnan (Pliocene) Cameron Inlet Formation, Flinders Island.

Sperm whales

Sperm whales (Family Physeteridae) encompass both very large and small living species (the sperm whale, *Physeter macrocephalus*, and the pygmy sperm whales, *Kogia* spp.) and many named fossil species of Early Miocene age and younger. The skulls of fossil and recent species typically possess a huge 'supracranial basin', markedly asymmetrical facial bones, and a broad-based rostrum. Few, if any, fossils attain the size of the extant sperm whale. Fossils have been recorded from the east and west coasts of North America, Patagonia, Europe, possibly Eurasia, New Zealand, and Australia, and some of these were reviewed by Kellogg (1925a, 1927).

There are four Australian species of physeterids, none of which has been studied recently. All are based on isolated teeth, and thus are of uncertain relationship. (While older, heterodont Cetacea sometimes can be identified at all taxonomic levels from isolated teeth, this is rarely the case for more modern, homodont odontocetes.) *Physetodon baileyi* McCoy, 1879, for which McCoy established a new genus, is based on pieces of two large teeth NMV P5519, P5520, P5521) from Beaumaris,

Victoria. Chapman (1912) based *Scaldicetus macgeei* on a fairly well preserved tooth (NMV P12889; Plate 2, fig. 4) also from Beaumaris. Its wrinkled crown enamel is similar to that of European species of *Scaldicetus*, but the identity of this genus is uncertain and requires revision. Another nominal species of *Scaldicetus*, *S. lodgei* Chapman, 1917, is known from quite a delicate tooth (NMV P13032) with a small, smooth crown, from Muddy Creek, near Hamilton. The above three species are of Cheltenhamian or Kalimnan age. The holotype of *Scaptodon lodderi* Chapman, 1918, for which a new genus was described, is a weathered tooth (cast, NMV P13042) of uncertain geological age, from Ulverstone, Tasmania. Despite Chapman's assertion, it is not certain that it is a mandibular tooth, for many fossil physeterids possess both upper and lower teeth. The true affinities of the above four species are uncertain, and the holotypes of *P. baileyi* and *S. lodderi* are quite inadequate specimens on which to base new genera. Chapman (1929) referred to *Parasqualodon* and *Metasqualodon* as sperm whales, but this is erroneous.

Other, undescribed, material may give a better insight into Australian physeterids. Gill (1957: 182) mentioned a toothed whale from Beaumaris (NMV P16204-P16207; Cheltenhamian) which consists of the well-preserved apices of both mandibles, teeth, skull fragments and vertebrae of a small sperm whale, unlike any described previously from Australia. Material from near Hamilton includes a well-preserved periotic (NMV P48791; probably Kalimnan) similar to that of the living *Physeter macrocephalus*, and scraps of crania and vertebrae. One physeterid tooth and a fragment of mandible (NMV P48801) from Fyansford, near Geelong, may be of Batesfordian-Bairnsdalian (Early-Middle Miocene) age, somewhat older than the above specimens.

River Dolphins

Four families of small, polydont, long-beaked extant 'river dolphins' are sometimes erroneously united into one family on the basis of external similarities and habits, even though they differ markedly in many cranial features

(Fordyce, MS). The Family Platanistidae is based on the living blind Ganges dolphin, *Platanista gangetica*. It has had fossil species of Middle Miocene age or younger, from North America and Europe, referred to it. The extant South American bouto, *Inia geoffrensis*, is placed in the Iniidae, to which Early Miocene to Pliocene species (most of uncertain affinities) from North and South America have been assigned. The Family Pontoporiidae, based on the living franciscana, *Pontoporia blainvillei*, nominally includes fossil species from the Late Miocene and Pliocene of North and South America. The fourth family, Lipotidae, which was established recently for the Chinese dolphin *Lipotes vexillifer*, has not yet had fossils assigned to it. None of these families has yet been recognized in Australia. However, another 'river dolphin' family, the extinct Rhabdosteidae, which also includes small, very long-beaked species, recently was recorded from Australia for the first time (Fordyce, MS). Rhabdosteidae (=Eurhinodelphidae of earlier authors, according to Myrick, 1979, who recently reviewed the family) include fossils from the east and west coasts of North America, Patagonia, Europe, perhaps New Zealand and, very doubtfully, Japan. The group is unusual in that the very long rostrum is partly toothless (Kellogg 1925b). The Australian specimens, which first were thought to be platanistids (Tedford *et al.* 1977), comprise skull fragments, teeth, earbones (Plate , fig. 7), ribs and vertebrae of many individuals of an indeterminate genus and species from the Middle Miocene Namba Formation, Lake Frome area, South Australia. They indicate that the Frome area drained into the sea, and provide the first conclusive evidence of rhabdosteids in the south-west Pacific. This occurrence suggests that rhabdosteids could have been the primary medium-sized, active predaceous endotherms of Australian Miocene fresh waters.

White Whales

White whales (Family Monodontidae) encompass the living narwhal and beluga, and are commonly thought of as Arctic species. Recently, however, Kasuya (1973) assigned the living Irrawaddy dolphin (*Orcaella brevirostris*) to the family. In view of its occurrence in northern Australian waters, fossil relatives of this species (as yet unknown) could be discovered here. Fossil white whales are known from Middle Miocene and younger rocks of North America and Europe.

Dolphins

Four dolphin (in the broad sense) families are sometimes united in one superfamily, Delphinoidea. The Acrodelphidae encompasses only extinct species, not considered here, from the Miocene of North America, Europe and Eurasia (e.g., Simpson 1945). Its taxonomy is in serious need of review.

Kentriodontids (Family Kentriodontidae) are primitive dolphins which Barnes (1978) considered ancestral to modern delphinids (discussed below). They are of small to medium size, possess rostra of moderate length, polydont teeth and well-developed basicranial sinuses, and differ from delphinids mainly in their symmetrical skulls and less elaborate air-sinuses. Barnes mentioned taxa from the Middle and Late Miocene of east and west North America, Europe, and Eurasia, and other records are known from New Zealand, Europe, Eurasia and perhaps Japan, which include Late Oligocene and Early Miocene specimens. Kentriodontids have not been reported from Australia but could be expected here in Upper Oligocene and Miocene rocks.

Dolphins (Family Delphinidae) comprise the most diverse family of living odontocetes. Interpretation of fossil distribution is hindered because many small problematic odontocetes previously have been referred to the family (e.g., Simpson 1945). This has been rectified to some extent by Barnes' (1978) review of kentriodontids. Simpson indicated a stratigraphic range from Early Miocene onwards, but it is more likely Late Miocene to Recent (e.g., Barnes 1977). Fossils have been recorded in North America, Europe, Eurasia, Japan, New Zealand and Australia.

The one supposed fossil delphinid described from Australia, *Steno cudmorei* Chapman, 1917, is based on a worn isolated tooth (NMV P13033; Plate 2, fig. 11) of latest Miocene age,

from Beaumaris. Chapman believed this to be the only known fossil species of the extant genus *Steno*, although two species had been described earlier from the Pliocene of Italy. Another specimen (NMV P48799; Plate 2, figs. 8-10) recently collected from Beaumaris consists of teeth of similar proportion and ornament to the holotype, a periotic, and a tympanic bulla. It is probably conspecific with the holotype. The periotic is quite different from that of the living *Steno bredanensis*, and indicates that the species probably does not belong in *Steno*. The associated bulla is of a type previously collected from Beaumaris, but hitherto not identified. '*Steno*' *cudmorei* does not appear closely related to any extant species of delphinid, although it is not as primitive as kentriodontids.

Other, as yet undescribed, dolphin fossils have been recorded. Longman (1920) mentioned the discovery of a skull of *Delphinus delphis*, of unstated geological age, from Queensland. Scott and Lord (1921) reported that a Miocene 'delphinoid', close to the extant *Globiocephala* spp., had been found near Wynyard, Tasmania, but the identity of this specimen is yet to be verified. Isolated teeth from Beaumaris, with larger and smoother crowns than '*S.*' *cudmorei*, may represent a delphinid. Gill (1965: 4) mentioned that bones of *Delphinus delphis* have been collected from Holocene silts near Melbourne. However, significant finds of delphinid have yet to be made.

True porpoises (Family Phocoenidae) are small, short-beaked odontocetes best known from their living Northern Hemisphere representatives. Some extant species are common around South America, and one (*Phocoena dioptrica*) has been recorded south-east of Australia. Fossil phocoenids have been recorded from the Miocene and Pleistocene of North America and Europe, but have not been recognized in Australia. Marcuzzi and Pilleri (1971: Fig. 77) indicated the presence of a Pleistocene phocoenid in Australia, but this probably refers to the record of *Phocaenopsis mantelli* which is an Early Miocene small odontocete, perhaps a rhabdosteid (Fordyce 1981c), from New Zealand.

Significance of Australian Fossils

Known Australian fossils do not contribute to an understanding of the earliest phases of cetacean evolution: the transition to water before the Middle Eocene, and the Middle-Late Eocene radiation of archaeocetes. Very early archaeocetes may have reached north-west Australia before the eastern Tethys closed, or via the shores of India after that subcontinent contacted Asia, although such specimens are unknown at present. Perhaps the absence of Australian Cetacea older than Late Oligocene reflects the fact that only a narrow seaway was present between Australia and Antarctica until about the middle of the Oligocene when the area of the South Tasman Rise opened enough to allow the establishment of the Circum-Antarctic Current and, presumably, circumpolar provincialism. If there was limited access to the sea, e.g., from the west, and, furthermore, if there were limited shelf areas linking the west with areas of cetacean abundance, then this might account for somewhat depauperate faunas. Because this observation reflects absence of evidence rather than evidence of absence, however, conservative interpretation is necessary. At this stage in our knowledge, it is noteworthy that only one good specimen of Early Oligocene age or older from the southern edge of Australia could allow radical reinterpretation of Austral cetacean history.

The few late Early and many Late Oligocene Cetacea from New Zealand (Fordyce 1980a, 1980b) provide unusual contrast with the few known Australian species of that age. It is uncertain whether this reflects real differences in paleobiogeography, differences in the relative amounts of potentially fossiliferous outcrop, or both. The abundance of specimens in New Zealand may reflect the presence of more-favourable habitats, caused by increases in oceanic currents, cooling, and productivity increases around Antarctica from the earliest Oligocene onwards. In fact, it is plausible that these climate changes triggered the evolution of both odontocetes and mysticetes (Fordyce 1980b). In view of the presence of sequences potentially favourable for preservation of Cetacea, the relative paucity of Australian Oligocene records could reflect relatively less

hospitable marine environments around southern Australia than around New Zealand. Again, however, absence of evidence requires conservative interpretation.

There is no doubt that early odontocetes (e.g. *Metasqualodon harwoodi*, *Parasqualodon wilkinsoni*) inhabited Australian waters during the Late Oligocene. The absence of mysticetes is puzzling in view of their abundance in New Zealand. *Mammalodon colliveri* provides an interesting record of a relict archaic mysticete contemporaneous with more modern taxa, and similar occurrences are known also in New Zealand and the north-east Pacific (Fordyce 1980c).

The presence in Australia, New Zealand and South America of earliest Miocene *Prosqualodon* spp. indicates that some taxa achieved circum-polar distribution by this time. A diverse Early Miocene cetacean fauna, like that known from South America (Cabrera 1926) has not yet been recognized in Australia or New Zealand.

Latest Miocene Cetacea are well represented in south-east Australia. Sequences at Beaumaris and near Hamilton, Victoria, which are known to be of similar age to each other, possess similar cetacean faunas. Nodule beds at each locality have produced balaenids, balaenopterids, delphinids, physeterids, and ziphiids. A similar range of taxa has been collected from the Middle Pliocene of Flinders Island, Bass Strait, but it is premature to speculate on the palaeoecological significance of faunal similarities.

In conclusion, it is noteworthy that although Australia does not have a large fossil cetacean fauna, its fossils include some relatively well-preserved specimens (the holotypes of *Mammalodon colliveri* and *Prosqualodon davidis*) that are important to cetacean systematics. It is likely that other relatively complete and well preserved specimens will be found in future, and these, like other Austral specimens, could elucidate problems hitherto unresolved by the detailed study of Northern Hemisphere fossils.

Acknowledgements

References

ABELE, C., 1979. Geology of the Anglesea area, central coast of Victoria. *Mem. Geol. Surv. Vict. 31*. 71 p.

ABELE, C., GLOE, C. S., HOCKING, J. B., HOLDGATE, G., KENLEY, P. R., LAWRENCE, C. R., RIPPER, D., AND THRELFALL, W. R., 1976. Tertiary. pp. 177-274 *in* J. G. Douglas and J. A. Ferguson (Eds.). *Geology of Victoria*. Geological Society of Australia Special Publication 5. Melbourne. 528 p.

ANON., 1939. A fossil whale from Australia. *Nature.*143: 525.

BARNES, L. G., 1977. Outline of eastern North Pacific fossil cetacean assemblages. *Syst. Zool.* 25: 321-343.

BARNES, L. G., 1978. A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odontoceti). *Nat. Hist. Mus. Los. Ang. Co., Sci. Bull.* 27: 1-35.

BARNES, L. G., AND MITCHELL, E. D., 1978. Cetacea. pp. 582-602 *in* V. J. Maglio and H. S. B. Cooke (Eds.). *Evolution of African Mammals*. Harvard Univ. Press, Cambridge, Mass. 641 p.

BENHAM, W. B., 1937. Fossil Cetacea of New Zealand. III.—the skull and other parts of the skeleton of *Prosqualodon hamiltoni* n. sp. *Trans. R. Soc. N.Z.* 67: 8-14.

CABRERA, A., 1926. Cétacéos fóssiles del Museo de la Plata. *Revta. Mus. La Plata*. 29: 363-411.

CAMP, C. L., TAYLOR, D. N., AND WELLES, S. P., 1942. Bibliography of fossil vertebrates 1934-1938. *Geol. Soc. Amer. Special Paper 42*. 663 p.

CHAPMAN, F., 1912. On the occurrence of *Scaldicetus* in Victoria. *Rec. Geol. Surv. Vict.* 3: 236-238.

CHAPMAN, F., 1917. New or little-known Victorian fossils in the National Museum. Part 21.—Some Tertiary cetacean remains. *Proc. R. Soc. Vict.* 30: 32-43.

CHAPMAN, F., 1918. On an apparently new type of cetacean tooth from the Tertiary of Tasmania. *Proc. R. Soc. Vict.* 30: 149-152.

CHAPMAN, F., 1929. *Illustrated guide to the collection of fossils exhibited in the National Museum of Victoria*. Government Printer, Melbourne, 55 p.

CUVIER, G. 1823. *Recherches sur les ossements fossiles, où l'on rétabilit les caractères de plusiereurs animaux dont les revolutions du globe ont détruit les espéces*. (2nd Edn.) Paris. 5 Vols. (not seen).

DART, R. A., 1923. The brain of the Zeuglodontidae (Cetacea). *Proc. Zool. Soc. Lond. 1923*: 615-648, 652-654.

DICKSON, M. R., 1964. The skull and other remains of *Prosqualodon marplesi*, a new species of fossil whale. *N.Z. J. Geol. Geophys.* 7: 626-635.

EASTMAN, C. R., 1906. Shark's teeth and cetacean bones. *Bull. Mus. Comp. Zool. Harv.* 50: 75-98.

ELLIOT, D. H., RINALDI, C., ZINSMEISTER, W. J., TRAUTMAN, T. A., BRYANT, W. A., AND DEL VALLE, R., 1975. Geological investigations on Seymour Island. *Antarct. J. U.S.* 10: 182-186.

EMLONG, D. R., 1966. A new archaic cetacean from the Oligocene of Northwest Oregon. *Bull. Mus. Nat. Hist., Univ. Oregon, Eugene.* 3. 51 p.

FLYNN, T. T., 1920. Squalodont remains from the Tertiary strata in Tasmania. *Nature.* 106: 406-407.

FLYNN, T. T., 1923. A whale of bygone days. *Aust. Mus. Mag.* 1: 266-272.

FLYNN, T. T., 1932. A new species of fossil cetacean from Tasmania. *Geol. Mag.* 69: 327-329.

FLYNN, T. T., 1948. Description of *Prosqualodon davidi* Flynn, a fossil cetacean from Tasmania. *Trans. Zool. Soc. Lond.* 26: 153-197.

FLEISCHER, G., 1976. Hearing in extinct cetaceans as determined by cochlear structure. *J. Paleont.* 50: 133-152.

FORDYCE, R. E., 1979. Records of two Paleogene turtles and notes on other Tertiary reptilian remains from New Zealand. *N.Z. J. Geol. Geophys.* 22: 737-741.

FORDYCE, R. E., 1980a. The fossil Cetacea of New Zealand. (A catalogue of described genera and species with an annotated literature guide and reference list.) *N.Z. Geol. Surv. Rept.* 90. 60 p.

FORDYCE, R. E., 1980b. Whale evolution and Oligocene Southern Ocean environments. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 31: 319-336.

FORDYCE, R. E., 1980c. Fossil whale studies—a progress report. *Geol. Soc. N.Z., Annual Meet. 1980, Abstr.* (unpaginated).

FORDYCE, R. E., 1981a. Systematics of the odontocete *Agorophius pygmaeus* and the family Agorophiidae (Mammalia: Cetacea). *J. Palaeont.* 55: 1028-1045.

FORDYCE, R. E., 1981b. Taxonomic status of the Victorian fossil whale, *Ziphius (Dolichodon) geelongensis* McCoy, 1882. *Proc. R. Soc. Vict.* 93, in press.

FORDYCE, R. E., 1981c. Redescription of Early Miocene dolphin *Phocaenopsis mantelli* Huxley, 1859 (Odontoceti *incertae sedis*). *N.Z. J. Geol. Geophys.* 24, in press.

FORDYCE, R. E., MS. Rhabdosteid dolphins (Mammalia: Cetacea) from the Middle Miocene, Lake Frome area, South Australia. Submitted to *Alcheringa*.

FORDYCE, R. E. AND CULLEN, D. J., 1979. A Miocene ziphiid whale (Odontoceti: Cetacea) from central Chatham Rise, east of New Zealand. *N.Z. Oceanogr. Inst. Rec.* 4: 45-53.

FRASER, F. C. AND PURVES, P. E., 1960. Hearing in cetaceans: evolution of the accessory air sacs and the structure of the outer and middle ear in recent cetaceans. *Bull. Br. Mus. Nat. Hist., Zool.* 7: 1-140.

GAFFNEY, E. S., 1979. An introduction to the logic of phylogeny reconstruction, pp. 79-111 *in* J. Cracraft and N. Eldredge (Eds.). *Phylogenetic analysis and paleontology.* Columbia University Press, New York, 233 p.

GASKIN, D. E., 1976. The evolution, zoogeography and ecology of Cetacea. *Oceanogr. Mar. Biol. Ann. Rev. 1976.* 14: 247-346.

GILL, E. D., 1957. The stratigraphic occurrence and palaeoecology of some Australian Tertiary marsupials. *Mem. Natn. Mus. Vict.* 21: 135-203.

GILL, E. D., 1965. *Fossils of Victoria.* National Museum of Victoria, Melbourne, 24 pp. [Reprinted from Victorian Year Book No. 79, 1965.]

GLAESSNER, M. F., 1947. A fossil beaked whale from Lakes Entrance, Victoria. *Proc. R. Soc. Vict.* 58: 25-34.

GLAESSNER, M. F., 1955. Pelagic fossils (Aturia, penguins, whales) from the Tertiary of South Australia. *Rec. S. Aust. Mus.* 11: 353-372.

GLAESSNER, M. F., 1972. Redescription of the tooth of an Oligocene whale from North Canterbury, New Zealand. *Rec. Canterbury Mus.* 9: 183-187.

HALL, T. S., 1911. On the systematic position of the species of *Squalodon* and *Zeuglodon* described from Australia and New Zealand. *Proc. R. Soc. Vict. (n.s.).* 23: 257-265.

HARRISON, R. J. AND KING, J. E., 1980. *Marine Mammals* (2nd Edn.). Hutchinson, London. 192 p.

HOWCHIN, W., 1919. [Tympanic bone of *Balaena* from the Pliocene of South Australia.] *Trans. Proc. R. Soc. S. Aust.* 43: 430.

HUXLEY, T. H., 1864. On the cetacean fossils termed 'Ziphus' by Cuvier, with a notice of a new species (*Belemnoziphius compressus*) from the Red Crag. *Q. J. Geol. Soc. Lond.* 20: 388-396.

KASUYA, T., 1973. Systematic consideration of recent toothed whales based on the morphology of tympanoperiotic bone. *Sci. Rep. Whales Res. Inst., Tokyo.* 25: 1-103.

KELLOGG, A. R., 1923. Description of two squalodonts recently discovered in the Calvert Cliffs, Maryland; and notes on the shark-toothed dolphins. *Proc. U.S. Natn. Mus.* 62(16): 1-69.

KELLOGG, A. R., 1925a. Two fossil physeteroid whales from California. *Carnegie Inst. Wash. Publ.* 348: 1-34.

KELLOGG, A. R., 1925b. On the occurrence of remains of fossil porpoises of the genus *Eurhinodelphis* in North America. *Proc. U.S. Natn. Mus.* 66(26): 1-40.

KELLOGG, A. R., 1927. Study of the skull of a fossil sperm-whale from the Temblor Miocene of southern California. *Carnegie Inst. Wash. Publ.* 346: 1-23.

KELLOGG, A. R., 1928. History of whales—their adaptation to life in the water. *Q. Rev. Biol.* 3: 29-76, 174-208.

KELLOGG, A. R., 1931. Pelagic mammals from the Temblor formation of the Kern River region, California. *Proc. Calif. Acad. Sci. (ser. 4)* 19: 217-297.

KELLOGG, A. R., 1934. The Patagonian fossil whalebone whale, *Cetotherium moreni* (Lydekker). *Carnegie Inst. Wash. Publ.* 447: 63-81.

KELLOGG, A. R., 1936. A review of the Archaeoceti. *Carnegie Inst. Wash. Publ.* 482. 366 p.

KELLOGG, A. R., 1968. Fossil marine mammals from the Miocene Calvert formation of Maryland and Virginia. Part 7. A sharp-nosed cetothere from the Miocene Calvert. *Bull. U.S. Natn. Mus.* 247: 163-173.

KUZMIN, A. A., 1978. The present state of cetacean phylogeny. p. 360 *in* R. Obrtel, C. Folk and J. Pellantova (Eds.). *Congressus Theriologicus Internationalis II.* Brno.

LONGMAN, H. A., 1920. [Cranium of *Delphinus delphis?*] *Proc. R. Soc. Qd.* 31: x.

LYDEKKER, R., 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. Part II. Cetacean skulls from Patagonia. *An. Mus. La Plata 1893.* 2: 1-14.

McCOY, F., 1866. *Notes sur la zoologie et la palaeontologie de Victoria, par Frederick M'Coy.* Masterman, Melbourne. 35 p.

McCOY, F., 1879. *Prodromus of the palaeontology of Victoria; or, figures and descriptions of the Victorian organic remains, Decade 6.* Government Printer, Melbourne. 42 p.

McCOY, F., 1882. *Prodromus of the palaeontology of Victoria; or, figures and descriptions of the Victorian organic remains, Decade 7.* Government Printer, Melbourne, 30 p.

McCOY, F., 1883. [Annual address.] *Sth Sci. Rec.* 3: 139-144.

MAHONEY, J. A. AND RIDE, W. D. L., 1975. Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1858 and 1968 (including citations of type species and primary type specimens). *W. Aust. Mus. Spec. Publ.* 6. 250 p.

MARCUZZI, G. AND PILLERI, G., 1971. On the zoogeography of Cetacea. pp. 101-170 *in* G. Pilleri (Ed.). *Investigations on Cetacea Vol. 3.* University of Berne, Switzerland. 380 p.

MARPLES, B. J., 1956. Cetotheres (Cetacea) from the Oligocene of New Zealand. *Proc. Zool. Soc. Lond.* 126: 565-580.

MEAD, J. G., 1975a. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). *Smithson. Contrib. Zool.* 207. 72 p.

MEAD, J. G., 1975b. A fossil Beaked Whale (Cetacea: Ziphiidae) from the Miocene of Kenya. *J. Paleont.* 49: 745-751.

MILLER, G. S., 1923. The telescoping of the cetacean skull. *Smithson. Misc. Collns.* 76(5): 1-70.

MYRICK, A. C., 1979. *Variation, taphonomy, and adaptation of the Rhabdosteidae (=Eurhinodelphidae) (Odontoceti; Mammalia) from the Calvert Formation of Maryland and Virginia.* Ph.D. diss., Univ. of California, Los Angeles. 437 p. [publ. by University Microfilms, Ann Arbor].

NORRIS, K. S. (Ed), 1966. *Whales, Dolphins and Porpoises.* Univ. of California Press, Berkley, 789 p.

PIVORUNAS, A., 1979. The feeding mechanisms of baleen whales. *Am. Scient.* 67: 432-440.

PLEDGE, N. S. AND ROTHAUSEN, K., 1977. *Metasqualodon harwoodi* (Sanger, 1881)—a redescription. *Rec. S. Aust. Mus.* 17: 285-297.

PRITCHARD, G. B., 1939. On the discovery of a fossil whale in the older Tertiaries of Torquay, Victoria. *Victorian Nat.* 55: 151-159.

ROMER, A. S., 1966. Vertebrate paleontology (3rd Ed.). Univ. of Chicago Press, Chicago. 468 p.

ROTHAUSEN, K., 1968. Die systematische Stellung der europäischen Squalodontidae (Odontoceti: Mamm.). *Paläont. Z.* 42: 83-104.

ROTHAUSEN, K., 1970. Marine Reptilia and Mammalia and the problem of the Oligocene-Miocene boundary. *G. Geol. (ser. 2).* 35: 181-189.

ROTHAUSEN, K., 1971. *Cetotheriopsis tobieni* n. sp., der erste paläogene Bartenwale (Cetotheriidae, Mysticeti, Mamm.) nördlich des Tethysraumes. *Abh. Hess. Landesamt. Bodenforsch.* 60: 131-148.

SAHNI, A. AND MISHRA, V. P., 1975. Lower Tertiary vertebrates from Western India. *Palaeont. Soc. India Monogr.* 3. 48 p.

SANGER, E. B., 1881. On a molar tooth of Zeuglodon from the Tertiary beds on the Murray River near Wellington, S.A. *Proc. Linn. Soc. N.S.W.* 5:298-300.

SCOTT, H. H., 1913. Notes on a fossil whale from Wynyard, Tasmania. *Pap. Proc. R. Soc. Tasm.* 1913: 167-172.

SCOTT, H. H. AND LORD, C. E., 1922. Studies in Tasmanian mammals, living and extinct. No. VI. Cetacean remains from the fossil beds at Wynyard. *Pap. R. Soc. Tasm.* 1921: 180-181.

SIMPSON, G. G., 1945. Principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85: 1-350.

SINGLETON, F. A., 1945. A catalogue of type and figured specimens of fossils in the Melbourne University Geology Department. *Proc. R. Soc. Vict.* 56: 229-284.

SLIJPER, E. J., 1979. *Whales* (2nd Edn.). Hutchinson, London.

SUTHERLAND, F. L. AND KERSHAW, R. C., 1971. The Cainozoic geology of Flinders Island, Bass Strait. *Pap. Proc. R. Soc. Tasm.* 105: 151-175.

TATE, R., 1885. Notes on the physical and geological features of the basin of the Lower Murray River. *Trans. R. Soc. S. Aust.* 7: 24-46.

TATE, R., 1892. [Zeuglodon tooth from Tasmania.] *Trans. R. Soc. S. Aust.* 15: 265.

TEDFORD, R. H., ARCHER, M., BARTHOLOMAI, A., PLANE, M., PLEDGE, N. S., RICH, T., RICH, P., AND WELLS, R. T., 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *BMR J. Aust. Geol. Geophys.* 2: 53-57.

VAN VALEN, L., 1968. Monophyly or diphyly in the origin of whales. *Evolution.* 22: 37-41.

WEST, R. M., 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. *J. Paleont.* 54: 508-533.

WHITMORE, F. C. AND SANDERS, A. E., 1977. Review of the Oligocene Cetacea. *Syst. Zool.* 25: 304-320.

YABLOKOV, A. V., 1965. Convergence or parallelism in the evolution of cetaceans. *Int. Geol. Rev.* 7: 1461-1468.

YAMADA, M., 1953. Contribution to the anatomy of the organ of hearing of whales. *Sci. Rep. Whales Res. Inst., Tokyo.* 8: 1-79.

58 R. EWAN FORDYCE

Explanation of Plate
PLATE 2

Fig. 1. NMV P14040, *Prosqualodon* cf. *davidis*, anterior cheek-tooth, lingual view, × 1.

Fig. 2. BMNH M7249, *Prosqualodon australis*, skull, dorsal view, × 0.15.

Fig. 3. NMV P5528, *Parasqualodon wilkinsoni* holotype, isolated posterior cheek-tooth, buccal view, × 1.

Fig. 4. NMV P12889, *Scaldicetus macgeei* holotype, isolated tooth, posterior view, × 0.5.

Fig. 5. NMV P5525, indeterminate cetacean (?*Mammalodon colliveri*), isolated tooth, buccal view, × 1.

Fig. 6. NMV P17535, *Mammalodon colliveri* holotype, cheek-tooth, buccal view. × 1.

Fig. 7. AMNH 102194, Rhabdosteidae genus and species indeterminate, right periotic, ventral view, × 1.

Fig. 8. NMV P48799, "*Steno*" *cudmorei*, left tympanic bulla, dorsal view, × 1.

Fig. 9. NMV P48799, "*Steno*" *cudmorei*, left periotic, dorsal view, × 1.

Fig. 10. NMV P48799, "*Steno*" *cudmorei*, tooth, buccal view, × 1.

Fig. 11. NMV P13033, "*Steno*" *cudmorei* holotype, isolated tooth, buccal view, × 1.

Fig. 12. NMV P13012, *Mesoplodon* sp., rostrum, right lateral view, × 0.25.