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A NEW SPECIES OF EARLY OLIGOCENE CETACEAN FROM PORT WILLUNGA, SOUTH AUSTRALIA

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The partial skull of a small whale was found in a fallen block of cemented 'hardband', near the base of the cliff near the Aldinga Reef Marine Reserve, and derives from the Ruwarang Member of the Port Willunga Formation, of early Oligocene age. It shows distinctly primitive features, but is not an archaeocete. Comparison with descriptions of other species of similar age suggests that it represents an archaic mysticete close to *Chonecetus*, in the family Aetiocetidae, and is described as *Willungacetus aldingensis* gen. et sp. nov. □ *Oligocene, Cetacea, Mysticeti*.

Neville S. Pledge, South Australian Museum, Adelaide, South Australia 5000; 1 August 2004.

Fossil whale remains are rare in the early Tertiary marine sediments of Australia, and extremely so in South Australia. An unidentifiable tooth was described from the late Oligocene Ettrick Formation near Tailem Bend, Murray Basin, together with a cetacean radius from an indeterminate locality at Port Willunga (Pledge, 1994). The Oligocene is an important time in the evolution of whales, when modern suborders were beginning to differentiate (Fordyce & Barnes, 1994; Fordyce et al., 1994; Fordyce & Muizon 2001; Whitmore & Sanders, 1976).

Late in 1983 Murray Lindsay (South Australian Department of Mines & Energy) alerted the writer to possible whale bones in the cliff at Port Willunga. A nondescript limb-bone had been found in the area some years before (Pledge 1994), so the site was visited by the author. Two eroded specimens showing cancellous fabric were subsequently collected (19 December 1983) in boulders from the beach. However, these two nondescript pieces of rock were temporarily mislaid until 2001. These were prepared by dilute acetic acid dissolution of the limestone matrix. The first specimen disclosed unmistakable bone, a sliver from the side of a battered vertebra, showing as a rectangular outline about 80mm long. (The other specimen, showing the form of a centrum with neural spine and transverse processes in cross-section, proved to be a fortuitously-shaped bryozoan colony.) Consequently, there was incentive, after 20 years, to revisit the site (Fig. 1).

In October, 2001, the writer and Jennifer Thurmer relocated the site, and found partly

exposed, on the surface of a large fallen slab of hard cemented limestone, a ventrally planed-off cranial part of a skull showing occipital condyles, possible periotics and a squamosal. No other bone was seen in the area. The specimen was recovered with assistance from National Parks and Wildlife Service (NPWS), Onkaparinga City Council, journalists and TV news cameramen, and brought to the South Australian Museum for preparation.

MATERIAL AND METHODS

Following substantial trimming, the specimen was CT-scanned to determine the extent and completeness of the bone, but no useful internal detail was apparent. Further paring unfortunately resulted in part of the occipital condyle being cut off and lost. Repairs were made using epoxy resin. Acid treatment of the block, (~5% acetic acid) was coupled with consolidation using a dilute solution of 'Paraloid B-72'® (methyl acrylate/ethyl methacrylate copolymer) in acetone. Evidently much of the skull had originally protruded from the slab, but was lost to natural erosion, leaving a partial basicranium and the dorsal part of the braincase. Preburial damage resulted in loss of the rostrum. Nasals, premaxillae, maxillae and teeth are missing, but an edentulous fragment of the rostrum was found in the right temporal fossa. A second CT scan of the prepared specimen was made using a Toshiba Aquilion 4-slice scanner and program (Fig. 2). Still further acid treatment was undertaken, resulting in the skull parting along a natural sagittal break revealing the cranial cavity. A latex endocranial cast was made before the two halves

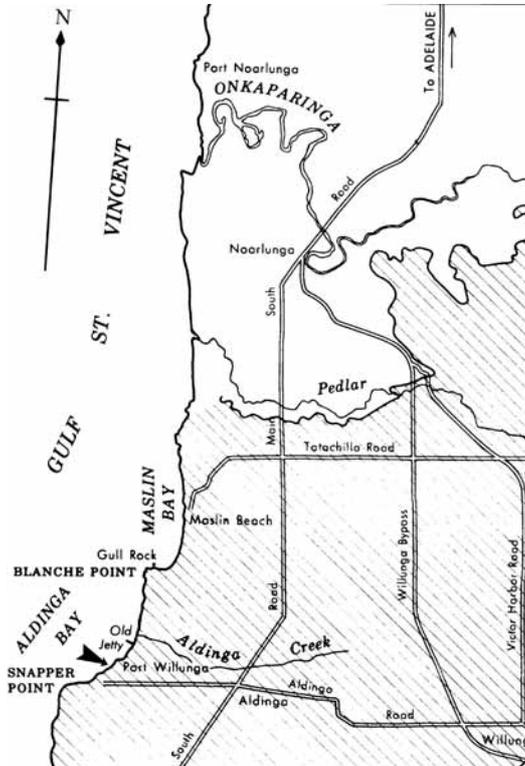


FIG. 1. Locality map: part of the Willunga Embayment (hatched), Gulf St Vincent, South Australia. After Cooper (1977).

were rejoined, incidentally removing the small distortion caused by the crack.

RESULTS

The holotype, lodged in the Palaeontological Collections of the South Australian Museum (SAMP), comprises most of a cranium of a small cetacean split sagittally before or during burial, leaving a gap up to 5mm wide along the full length. Rostral bones separated or were broken off and were not preserved as recognisable pieces. A large sliver of such bone was found in the temporal fossa. In addition, the ventral side was truncated, at a slight angle, by erosion, possibly before full burial but certainly on exposure, as this was all that was showing in the slab of rock when found.



FIG. 2. *Willungacetus aldingensis* gen. et sp. nov., SAMP40034, holotype cranium, oblique right dorsolateral view, computer-assisted tomography synthesis. Image, Ross Harper.

SYSTEMATIC PALAEOLOGY

Order CETACEA Brisson, 1762

Suborder MYSTICETI Flower, 1864

?Family AETIOCETIDAE Emlong, 1966

Willungacetus gen. nov.

TYPE SPECIES. *Willungacetus aldingensis* sp. nov.

ETYMOLOGY. *Willunga*, for the locality, Port Willunga; *cetus* (Latin), whale.

DIAGNOSIS. As for species.

Willungacetus aldingensis sp. nov.

(Figs 2-4)

MATERIAL. HOLOTYPE. SAMP40034, a partial cranium, from low cliff directly east of main 'reef', Port Willunga Marine Reserve, Port Willunga, midway between Aldinga Creek and Snapper Point in Aldinga Bay (Fig. 1), ~45 km south of Adelaide, South Australia, 34° 55' S, 138° 35' E; Ruwaring Member (Cooper, 1977, 1979) (a cherty limestone), Port Willunga Formation; Early Oligocene, Willungan Stage (Rupelian), planktonic zone P19 (Lindsay, 1967, 1985; Lindsay & Alley, 1995; McGowran et al., 2004: fig. 3). Referred specimens; SAM P40044, a longitudinal sliver of a vertebral centrum in a beach boulder several metres from holotype. SAMP10875, a damaged right(?) radius (Fordyce, pers. comm.; Pledge, 1994), precise locality unknown but from same cliff line.

ETYMOLOGY. From Aldinga Bay.

DIAGNOSIS. An ?aetiocetid (Barnes et al., 1994:396) differing from others in having longer intertemporal region with a sagittal crest, longer straighter lambdoid crests meeting at less than 90°, occipital shield more anteriorly inclined, almost circular foramen magnum; differs from *Aetiocetus* spp. in having sagittal crest, longer

intertemporal region, narrower intertemporal constriction, frontals farther forward, basioccipital plate more inclined and less concave, smaller occipital condyles; differs from *Chonecetus spp.* in having straight-sided lambdoid crest in dorsal view, cranium plan view outline more acute; differs from *Ashorocetus* in having straighter and longer lambdoidal crests, less-concave occipital shield, relatively smaller and more protuberant occipital condyles; differs from *Morawanocetus* in having longer intertemporal region.

DESCRIPTION. A small ?aetiocetid whale, having a relatively long, narrow cranium, slightly longer than exoccipital width; long, wide, sulcate triangular supraoccipital, sloping forwards at low angle; prominent lambdoidal crest; long parietals forming slight sagittal crest; temporal constriction smoothly conical, slightly less than occipital condylar width, temporal fossa elongate oval; occipital condyles protuberant.

Skull not telescoped, truncated anteroventrally by syndepositional and/or post exhumation erosion, and therefore lacking definitely identifiable basicranial elements and all bones anterior of the parietals except for part of the right frontal and a displaced jaw-bone fragment possibly of the maxilla.

Broadly triangular in dorsal view, about 26cm wide across the squamosals, narrowing to about 8.5cm between the temporal fossae. Preserved length 32cm, the anteriormost is a partial supraorbital process of the right frontal. Braincase tapers forwards markedly but smoothly, without sharp constriction or angle. Temporal fossae long and ovate, broader anteriorly, merging into the squamosal fossa.

In dorsal view (Fig. 3A), skull dominated by the lambdoid (or nuchal) crest straight on the sides and angular, extending forwards medially into a faint sagittal crest (Fig. 2). In profile, sagittal crest with arbitrarily horizontal, the lambdoid crest rises steeply at nearly 70° before levelling to where it meets the vertex. In contrast, the midline of the supraoccipital is straight from condyle to vertex, making an angle of about 45° with the sagittal crest. Supraoccipital broadly sulcate triangular plate bounded by straight (in dorsal view) lambdoid crests, slightly convex laterally and depressed apically with a distinct median ridge (or external occipital crest) towards the vertex. Supraoccipital poorly preserved along the lambdoid suture with the parietals, with the thin edge broken away, but it shows a noticeable

'boss' about one third the distance from the apex, bounding the depression. The supraoccipital preserves a large fenestration roughly midway between these bosses, the foramen magnum and the skull apex, where the bone has thinned naturally to leave a smooth-edged, roughly elliptical hole 24mm wide and 20mm long. Occipital condyles have a slight 'neck' or condylar peduncle (Fig. 3A) which makes them prominent. Foramen magnum about 35mm wide, 30mm high, total span of condyles 89mm.

Parietals long, beginning up to 30mm behind the anterior edge of the temporal fossae, meeting dorsally at a slightly angulated junction extending 60mm along this sagittal 'crest' (Figs 2, 3A). Parietals smoothly curved with no temporal crest but in the centre of each, midway between the frontal and squamosal sutures, is a 'thumbprint' depression ahead of a small prominence which may be homologous with that crest. The temporal constriction is somewhat conical, narrow and deep as in archaeocetes, but not as abrupt as in modern whales, with a minimum diameter of about 85mm, about one third the overall width of the skull.

No posterolateral foramen is apparent. The suture with the frontal trends forwards away from the midline, at about 45°, before curving down into the temporal fossa and back posteriorly at the erosional edge of preservation (Fig. 3G). The suture with the squamosal (Figs 3 B, G) is approximately normal to the lambdoidal crest before curving forwards low-down some 30mm ahead of the zygoma root, into the missing truncated part of the skull. There is a small triangular bone on the left side, and a mosaic of smaller bones on the right side of the cranium, medial to the squamosals and between the supraoccipital and the parietals, associated with several small foramina on the suture lines. These bones are unidentified and the sutures may indicate the immature age of the animal.

The alisphenoid has barely survived the erosion of the ventral side of the skull. The ventral margin of the parietal appears to be marked by an indistinct suture about one centimetre above the eroded bottom surface on the left side (Fig. 3G): therefore, the alisphenoid makes a contribution to the wall of the temporal fossa, and possibly to the crest between temporal fossa and basicranium.

The temporal fossae (Fig. 3A, E) are elongate, up to 150mm long and an estimated 60+mm wide, narrowing posteriorly into the squamosal

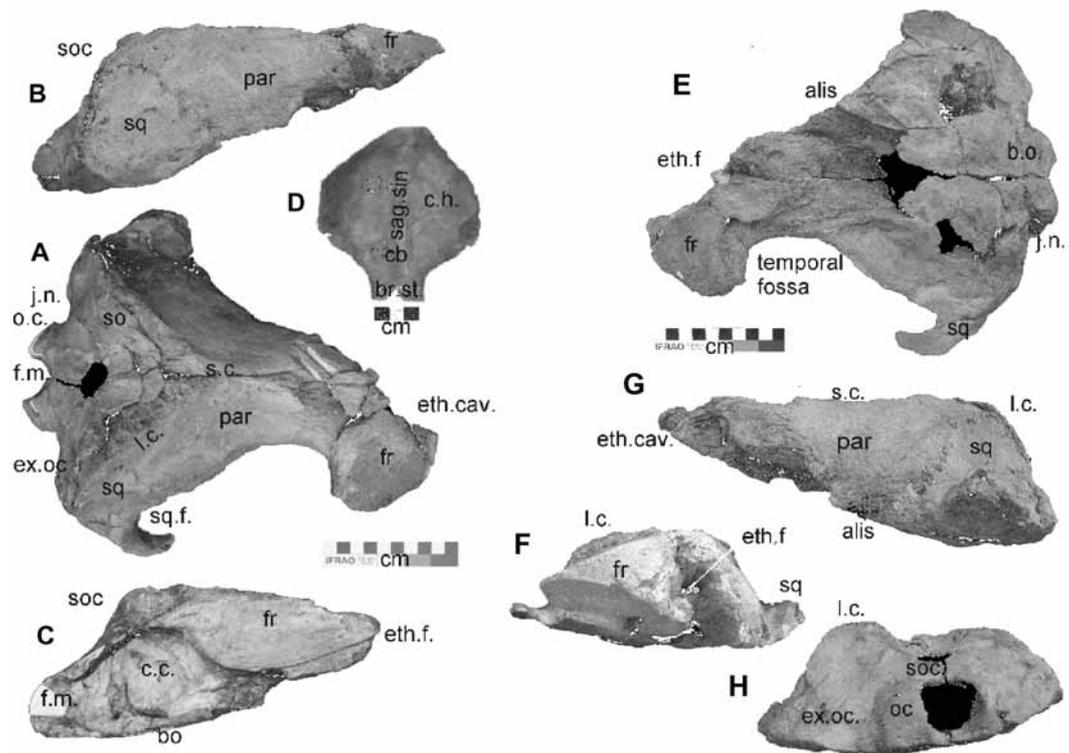


FIG. 3. *Willungacetus aldingensis* gen. et sp. nov., SAMP40034, holotype cranium. A, dorsal surface. B, right lateral. C, sagittal section, right lateral view. D, latex endocranial cast. E, ventral (truncated) surface. F, slightly lateral anterior view (canal arrowed). G, left lateral view showing ethmoturbinal cavity in frontal (at left). H, slightly lateral posterior view of supraoccipital. Scale in centimetres. Abbreviations: alis, alisphenoid; bo, basioccipital; br.st., brain-stem; cb, cerebellum; c.c. cranial cavity; c.h., cerebral hemisphere; eth. cav., ethmoid cavity; eth.f., ethmoid foramen; ex.oc., exoccipital; f.m., foramen magnum; fr, frontal; j.n., jugular notch; i.c., internal carotid; l.c., lambdoid crest; o.c., occipital condyle; par, parietal; sag.sin., sagittal sinus; s.c., sagittal crest; soc, supraoccipital; sq, squamosal; sq.f., squamosal fossa.

fossa. The point-to-point distance from the anterodorsal margin of the fossa (on the frontal) to the posteroventral margin (at the shelf of the squamosal) is 160mm, but this dimension has been distorted by the ventral truncation of the skull, and may not be that long. The squamosal fossa is narrow, up to 30mm wide, and longitudinal.

Squamosals are incomplete, each preserving a roughly triangular slightly convex cranial plate, approximately 60x70mm, and part of the zygomatic processes. The latter have been truncated ventrally by erosion (and also laterally on the right zygoma, suggesting some pre-burial damage), and there remain only the base of the process and a small part of the 'mastoid' region, the latter visible on the truncated ventral surface

as very dense bone. The remnants suggest the zygomas were rather slender. There is no indication as to whether the zygomatic process would closely approach or meet a similar process (postorbital angle) from the frontal. Endocranially (Fig. 3C), the squamosal boundaries are unclear; the cranial endo-surface seems to be corroded, possibly by the action of scavengers before burial.

The frontal bone is poorly represented externally, and only as a small area at the lower medial side of the temporal fossa and an undistinguished mass of the right supraorbital process, with a somewhat roughened or eroded dorsal surface, at the anterior side of said space. Indistinct marks suggest the frontoparietal suture might extend back on the sagittal crest to within

60mm of the supraoccipital; this is weakly supported by the apparent line of the suture as seen internally in the sagittal section, where it seems to extend to a point level with the front of the cerebrum. The cranial part of the frontal is thick. In sagittal view, there is a deep, transversely-grooved, ethmoidal cavity (Fig. 3G), as much as 35mm long (anterovertically) and 20mm diameter, whose long axis in a parasagittal plane is at about 70° to the sagittal crest. It bears nine parallel grooves, formed by the ethmoturbinals, that flow into a median longitudinal canal (the ethmoidal foramen) about 1012mm wide and 4mm high that continues back into the brain cavity (Fig. 3C), apparently along the junction between the frontal and an unidentified bone (the vomer?). The postorbital process appears to have been quite thick, a primitive condition. The frontal is not preserved ventrally enough to show any sign of the orbit.

There are several small detached fragments of bone that became separated from the anterior extremity during the acid process; two of these, with surface preserved, seem to be symmetric about a longitudinal (sagittal) suture surface, and seem to roof the anterior end of the ethmoidal foramen, where it widens out into the ethmoidal cavity (Fig. 3F, G), lined with up to nine oblique grooves for the ethmoturbinals (or olfactory fossa, e.g. Breathnach, 1955, pl. 1).

Bones on the ventral side of the specimen (Fig. 3E) are eroded and difficult to delimit and identify. Regular and symmetrical variations in texture and density suggest some might be identifiable as the basioccipital, the bases of the pterygoids, the alisphenoids, the squamosals and the exoccipitals. Large holes in the eroded surface coincide roughly with the positions of erosionally-enlarged foramina ovals, or the 'cranial hiatus', and imply that the tympanic bullae are long since lost. On the sloping posterolateral side of the left-hand hole, between the putative squamosal and exoccipital, there are faint parallel suture-like grooves where the tympanic bulla might have articulated. Adjacent medially to the vacuities, a pair of thickenings of the basioccipital mark the former position of the lateral protuberances. The extent of development of the paroccipital process cannot be determined, and the external auditory meatus has likewise been planed off. A small hypoglossal foramen is seen on the dorsal side of the jugular notch

Brain cavity (Fig. 3D) broadly rhombic, roughly hemispherical, about 90mm long,

115mm wide and 60mm high (volume estimated at approximately 600 ml), partly divided by a dorsal longitudinal depression sinus, and with equally broad (about 40mm) anterior and posterior extensions for the (presumed) olfactory capsule and brain-stem respectively, although the anterior space has been enlarged by erosion. Endocasts of whale skulls are considered to be only approximations of the original brains, because of the mass of surrounding non-neural matter (e.g. Breathnach, 1955; Marples, 1949). Because of imperfect preservation of the internal surface of the cranial bones, and some damaged and missing portions, this endocranial cast is less than perfect, but some structures are nevertheless apparent. Sagittal sinus is broad and fairly deep, but the median tentorial depression is poorly defined, as is the lobus medius cerebelli, which is overlain by the cerebral hemispheres. The paraflocculus appears fairly well defined, but merges with the masses annexes, or spaces for non-neural matter, lower on each side of the endocast. The roots of the trigeminal nerve are obscure and uncertainly identified at the anterior edges of the latter.

A bone fragment (Fig. 4A, B), found obliquely within the right temporal fossa close to the frontal, is part of a smooth, broad, elongate bone that is considered to represent the maxilla, but could be a piece of dentary. As preserved, it is 63mm long, about 25mm wide, generally flat with a broadly curved edge on the smooth outer surface and corroded on the inner; it is obliquely truncated by erosion at one end; the other shows a preburial break. No trace of suture margins is present, but part of a small 6mm diameter tooth alveolus (and possibly the edge of another one slightly offset 34mm away and slightly diverging) lies on the curved edge (Fig. 4B). Another unidentifiable, smaller piece of bone was found in the left temporal opening.

Associated vertebral fragment, SAMP40044 (Fig. 4C preserves one side (imperfectly) and a segment of one epiphysis of the centrum, and was partially eroded before burial. The bulk of the bone was eroded away obliquely on the other side after its exposure and fall from the cliff (see below). The epiphysis appears to be slightly concave, with the margin faintly rounded. There is evidence for at least one longitudinal ridge along the centrum, which is probably lateral. It does not seem to be part of the neural arch. No foramina are preserved. The following dimensions are estimated, assuming the epiphysis was roughly circular and taking the

intersection of lines normal to its circumference to be the centre. Diameter of centrum: up to 8cm, length of centrum: about 8cm, overall length of fragment: 9.5cm, width: 7cm.

DISCUSSION. *Taphonomy.* No geopetal fabric or any other sedimentological structure could be discerned in the rock slab. It has therefore been assumed that the exposed surface of the slab as found at the cliff base was originally uppermost as it is the more common attitude of fossil cetacean skeletons (Fordyce et al., 1994).

Thus it appears that the whale's carcass came to rest piecemeal on the seafloor, the skull apparently separated from the backbone, itself disarticulated (e.g. Schäfer, 1972), and sank upside down into the soft sediment with its rostrum, being less dense, poking up at about 20° to the sediment surface, and the whole underside exposed to the actions of scavengers and erosion. The basicranial surface of the skull was therefore eroded, and the rostrum was separated with a couple fragments coming to rest in the temporal fossae. The cranial cavity shows evidence of some corrosion/erosion of the bone surface, probably by scavengers, with the patchy removal of the bone surface lamina exposing the diploe. The basicranial truncation also allowed sediment and scallop shell fragments to enter when sedimentation resumed; the shells were later weakly silicified, and survived the acid treatment. The period of erosion seems to have coincided with the formation of one of the 'hardgrounds', which are a feature of this part of the sequence of the Port Willunga Formation.

With recent exposure and erosion of the modern cliff, slabs of the cherty 'hardground' separate and fall only a few metres to the beach below, to become subject to further erosion. Considering the original size of the slab in question, it is unlikely to have moved far, nor to have been overturned by wave/tidal action. Therefore the surface seen on its discovery is probably little changed from the time it was originally buried.

Comparisons. Fossil whales of early Oligocene age are rare, and this would appear to be the first recorded for Australia. Because this is also the time when cetaceans were diversifying and dividing into the odontocete and mysticete lines (e.g. Fordyce et al., 1994; Fordyce & Muizon, 2001), it is important to attempt to categorise this species from Port Willunga. Therefore, it is compared with a number of other taxa from

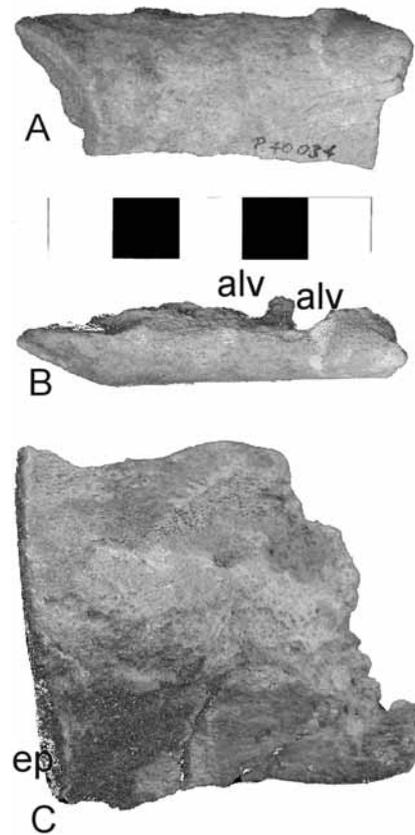


FIG. 4. *Willungacetus aldingensis* gen. et sp. nov., associated jaw fragment SAMP40034. A, lateral view. B, occlusal view, truncated end at right. C, SAMP40044, referred remnant of vertebral centrum, epiphysis at left. Scale in centimetres. Abbreviation: alv, alveolus; ep, epiphysis.

elsewhere around the world, mostly of late Oligocene age.

The skull is not noticeably telescoped, as in modern whales, and even less than in the late Oligocene *Agorophius pygmaeus* (Müller, 1849) (e.g. Fordyce, 1981) and *Chonecetus sookensis* (Russell, 1968) which are useful bases for comparison, or the early Miocene cf. *Parietobalena* (SAMP63). Comparing it with Fordyce's Text-Fig. 2 (ibid.), the broadly sulcate triangular supraoccipital is like *Chonecetus* and *Ashorocetus* (Barnes et al., 1994) being bounded by straight (in dorsal view) lambdoid crests, slightly convex laterally and depressed apically but with a distinct median ridge (or external

occipital crest) towards the vertex. The Willunga specimen is very incomplete, but is noticeably relatively longer, and is more like *Chonecetus*. Initial ideas of an archaeocete affinity such as *Dorudon* indicated by the rather archaic narrow cranium with elongate intertemporal region and strong supraoccipital crest, did not withstand scrutiny. The broad forwards-sloping supraoccipital, and the relatively broad, conical temporal constriction indicate a more advanced taxon.

The crest is more prominent than those of *Chonecetus* which are otherwise similar, and of the cetothere cf. *Parietobalaena* (SAMP63) (Bearlin, 1985; Glaessner, 1955) from the lower Miocene Morgan Limestone of South Australia. The supraoccipital differs from *Agorophius* where it is smoothly curved and possibly anteriorly extended, and from *Chonecetus sookensis* where it is semicircular. The lacuna in the supraoccipital does not appear to be the same as the (usually, symmetrically paired) fenestrations described by Pilleri et al. (1982) in various cranial bones of a diverse range of cetaceans, and those in *Chonecetus* (Russell, 1968).

Parietals also differ markedly from *Agorophius* (and *Parietobalaena*) in being relatively much longer. They are smoothly curved with no temporal crest as seen in *Agorophius*. The temporal constriction is conical as in *Chonecetus*, parallel-sided, narrow and deep as in archaeocetes, but not as abrupt as in modern whales. Unlike *Agorophius* (Fordyce, 1981), no posterolateral foramen is apparent. Large holes in the eroded ventral surface coincide roughly with the positions of erosionally-enlarged foramina ovals, or the 'cranial hiatus' seen in *Chonecetus* (Russell, 1968) and cetotheres such as *Parietobalaena*, and imply that the tympanic bullae are long since lost

There are not many characters (e.g. Barnes et al., 1994) preserved to enable subordinal assignment. However, apparent easy separation and loss of rostral bones (premaxillae, maxillae and nasals) from the skull of *Willungacetus* suggests it is referable to the mysticetes (Miller, 1923: 9, footnote), and this assignment is supported by the presence of ethmoturbinals, which are symplesiomorphic for archaeocetes and mysticetes but absent in odontocetes (Van Valen, 1968) (although they are present in early odontocetes, R.E. Fordyce, pers. comm. 2004).

The latest Eocene (or earliest Oligocene) species, *Llanocetus denticrenatus* Mitchell, 1989, from the La Meseta Formation of Seymour Island, Antarctic Peninsula, is considered to be the earliest known mysticete (ibid.), but only its jaw fragment and natural endocast could be compared, the skull being under study and not yet described (Barnes et al., 1994; Fordyce & Barnes, 1994). The jaw shows that the teeth were archaeocete-like but relatively small and two-rooted, which seems to be the case in *Willungacetus*. There are similarities between the two endocasts in the length:breadth proportions for instance, but some differences such as the development of the 'cerebellum' (apparently greater), and the form of the cerebral hemispheres (more divergent in *Willungacetus*) are apparent. The endocranial cast of *Llanocetus* is more than twice as big as the new species.

The bone fragment probably possesses the alveoli of a double-rooted tooth whose longitudinal axis is at a slight angle to the line of the jawbone, rather like the fragment of the much larger *Llanocetus* (Mitchell 1989)

The vertebral measurement estimates have been compared with those of the series of vertebrae of *Aetiocetus cotylalveus* (Emlong, 1966), with little success: there is approximate correspondence with the proportions of the 10th dorsal or the 2nd, 3rd or 4th caudals, but the assumptions are too many to make any inferences.

The Late Oligocene archaic cetacean, *Aetiocetus cotylalveus* (Emlong, 1966), from Oregon, differs significantly from the Port Willunga whale, notably in the short cranium, crescentic near-vertical supraoccipital, lack of sagittal crest, short diverging parietals and relatively short and wide temporal constriction. It retains some archaeocete characters, such as a near-vertical supraoccipital, not found in odontocetes, and was placed in a new family of archaeocetes, but is now referred to the Mysticeti (Van Valen, 1968). The new specimen resembles more the species *A. tomitai* Kimura & Barnes (Barnes et al., 1994) in the form of the supraoccipital and zygomas, the relatively long cranium and the presence of a sagittal crest.

Chonecetus, also of late Oligocene age, has been linked with *Aetiocetus* in the extinct archaic mysticete family Aetocetidae (Barnes, 1989; Barnes et al., 1995). Of the described species, *Willungacetus aldingensis* resembles *C. sookensis* (Russell, 1968) from Vancouver

Island, British Columbia, more than any other, notably in the shape of the cranium, extent of the parietals, the conical temporal constriction, and (less so) the shape of the supraoccipital, but not the unusual long twin parasagittal crests. However, the supraoccipital of *Chonecetus goedertorum* Barnes & Furusawa 1994 (Barnes et al. 1994) from Japan is more like that of the South Australian fossil, in being more triangular and with a median crest.

As far as can be determined, there is some resemblance to the partial cranium of *Ashorocetus eguchii* Barnes & Kimura (Barnes et al., 1994), also classed as an aetiocetid, but the Port Willunga specimen differs in having a much larger and more triangular supraoccipital.

The Late Oligocene *Agorophius pygmaeus*, a primitive odontocete from South Carolina, has a skull superficially similar to *Willungacetus*, so far as can be compared, but differs in much the same way as *Aetiocetus*, viz. short deep cranium, parabolic supraoccipital rising vertically at the base, short rounded parietal roof and short temporal constriction, and no sagittal crest. The process of cranial telescoping is well advanced in *Agorophius*, and is of odontocete style, but contrary to the situation in other toothed whales the supraoccipital has not extended forwards to meet the frontals (Miller, 1923). It is now regarded as an odontocete of uncertain position (Whitmore & Sanders, 1976; Fordyce, 1981) and can be eliminated from consideration.

Roughly contemporaneous with these is an unnamed specimen (USNM243979) from Oregon (Whitmore & Sanders, 1976, fig. 2a), which shows a disposition of the cranial bones similar to our new find. It has a 'triangular occiput... thrust forward in a manner reminiscent of the Mysticeti', a sagittal crest and strong temporal constriction, and a similar parietal-squamosal suture. It seems to differ from *Willungacetus* only in the degree of constriction (less), relative width of the supraoccipital (less), and sturdiness of the zygomatic processes of the squamosal (greater). It has been interpreted as a primitive non-squalodontoid odontocete (ibid.), and can also be eliminated from consideration.

The only described Australian specimen that might be directly relevant is the skull of *Mammalodon colliveri* Pritchard, 1939, from the Late Oligocene (Janjukian) of Torquay, Victoria. Unfortunately, Pritchard only described the partially prepared specimen, and the description and figure are quite inadequate. Fordyce has

studied the subsequently prepared skull and given a better illustration (which shows a short rounded rostrum) and informal description (Fordyce, 1982, 1984; Fordyce & Muizon, 2001), but a full description is still awaited. Long et al., 2002: 202-204 give the best figure so far of the skull of this small whale, which Fordyce (ibid.) referred to the mysticetes on several lines of evidence, most of which are not applicable to the Willunga specimen. However, it can be seen immediately that the two are not the same species. Although similar in size — *Mammalodon* jugal width (scaled from Fig. 4E in Fordyce, 1984, where the jugals were speculatively reconstructed) is approximately 23cm; length from temporal constriction to condyle ~20cm; constriction diameter 6cm; *Willungacetus* skull approx. 28cm, 23cm and 8.5cm respectively — they have strikingly different supraoccipital bones, semicircular in dorsal view in *Mammalodon* and almost right-triangular in the South Australian specimen. There is also an age difference of 5 million years or more. Fordyce (1984) stresses the primitive features of *Mammalodon*, likening it to dorudontines. There is a slight possibility that, considering its even more primitive-looking cranium, *Willungacetus* is ancestral to the rather aberrant *Mammalodon*.

By contrast, the cetothere cf. *Parietobalaena* (e.g. "*Aglaoacetus?*", SAMP63, Glaessner, 1955) shows only one point of similarity: the triangular shape of the supraoccipital. Otherwise, the cranium shows typical mysticete shortening; it is wider and shorter, the temporal constriction shorter, and the junction of the parietals much shorter (2cm) so that the longitudinally convex supraoccipital almost reaches the frontals.

It had been hoped that study of its endocranial cast might throw some light on the affinities of the specimen, since the shape and relative development of different parts of the brain reflect the different adaptations of the major groups (Jerison, 1973). Unfortunately the lack and obfuscation of detail by pre-burial erosion has prevented more than generalisations. In its rhombic outline, it approximates the endocranial cast of the modern mysticete *Megaptera* (e.g. Breathnach, 1955), but with much smaller cerebral hemispheres. There is also a resemblance to the larger of the natural endocasts described by Marples (1949) from the supposed Oligocene (but see reservations of Breathnach, 1955: 532) of New Zealand, as an odontocete, but apart from its overall smaller size the apices of

TABLE 1. Measurements in millimetres of crania of *Willungacetus* and other aetiocetids (after Barnes et al. 1994), and *Mammalodon colliveri*. Characters: 1, width across postorbital processes; 2, width of intertemporal region; 3, length of parietal on sagittal line; 4, length from anterior margin of temporal fossa/frontal to condyles; 5, zygomatic width; 6, exoccipital width; 7, greatest width across occipital condyles; 8, greatest height of occipital condyles; 9, greatest width of foramen magnum; 10, greatest height of foramen magnum. * Measurement obtained by doubling half-width; () estimated measurement; # estimated from scaled figure; + measurement greater than indicated

Character	1	2	3	4	5	6	7	8	9	10
<i>Willungacetus aldingensis</i>	(170+*)	85	75	245	280	220	90	45+	37	32
<i>Chonocetus sookensis</i>		42		148#	188	159	66	41	31	22
<i>C. goedertorum</i>	196	70	33	95#	212	180	78	51	34	39
<i>Ashorocetus eguchii</i>					123+	(230)	88	46	43	22
<i>Morawanocetus yabukii</i>	212	81	26	77#	290	228	89	42	49	20
<i>Aetiocetus tomitai</i>	(230)	86	42	102#	(240)	210	93	45	39	23
<i>A. cotylalveus</i>	280*	85	45	170#	290*	260*	91	49	28	20
<i>A. weltoni</i>	(273)	68			292	254	99	61	31	35
<i>A. polydentatus</i>	254	68	66	177#	272	236	91	60	25	28
<i>Mammalodon colliveri</i>	220*#	60#	95#	235#	230#	130*#	80#			

the cerebral hemispheres are much farther apart in the *Willunga* endocast, and the cerebellum seems relatively larger.

SIGNIFICANCE

The early Oligocene was a critical time for the evolution of whales and saw the emergence of the two modern lines of cetaceans: the Mysticeti and the Odontoceti (Fordyce, 1992; Fordyce et al., 1994). However, there are few fossils to document the details of this event. Although it is incomplete, the Port *Willunga* specimen may go some way to elucidating the early evolution of the mysticetes.

The Eocene/Oligocene transition saw the final separation of the future Australian continent from the Antarctic remnant of Gondwana, and the establishment of the Circum-Polar Current, which forever changed the climatic history of the world into a series of worsening cold periods (e.g. Fordyce, 1977; Frakes et al., 1987; McGowran et al., 1992). It is therefore probable that the evolutionary and climatic events are linked (Barnes, 1977; Fordyce, 1992).

SUMMARY AND CONCLUSION

Willungacetus dates from a time when cetaceans were differentiating into the modern suborders, and is therefore of some significance in understanding that process.

It is considered, on the characters preserved, such as the relative ease of loss of the rostral bones, the presence of ethmoturbinals, and of the form and style of the supraoccipital, that this

important skull is a mysticete, although it is incomplete and has some traits, probably symplesiomorphic, that seem to point to odontocetes. It shares many primitive characters with members of the Family Aetiocetidae, such as apparently having teeth, but is more primitive in having a longer skull. Nevertheless, it is probably referable to the Aetiocetidae, and the greatest similarity seems to be with species of the late Oligocene *Chonocetus*. Some measurable characters are summarised and compared in Table 1. It is not a cetothere because of the plesiomorphic shape of the cranium and the lack of any apparent cranial shortening.

The referred right radius (SAMP10875) found in the vicinity of the skull appears to be intermediate between archaeocetes and cetotheres (Pledge, 1994) and offers some support for this interpretation.

The species therefore stands as a possible ancestor of the aetiocetids, and even of later mysticetes.

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