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Taxonomy and biogeography of the Pleistocene New Zealand sea lion *Neophoca palatina* (Carnivora: Otariidae)

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Abstract.—The Otariidae (fur seals and sea lions) are an important and highly visible component of Southern Hemisphere marine mammal faunas. However, fossil material of Southern Hemisphere otariids is comparatively rare and often fragmentary. One exception is the Pleistocene sea lion *Neophoca palatina* King, 1983a, which is known from a nearly complete skull from the North Island of New Zealand. However, the phylogenetic affinities of this taxon are poorly known, and comparisons with other taxa have been limited. We provide an extensive redescription of *Neophoca palatina* and diagnose this taxon using a morphometric approach. Twenty measurements of the skull were collected for *N. palatina*, as well as for all extant Australasian otariids and several fossil *Neophoca cinerea* Perón, 1816. Using principal component analysis, we were able to segregate taxa by genus, and *N. palatina* was found to cluster with *Neophoca* according to overall size of the skull as well as increased width of the intertemporal constriction and interorbital region. *N. palatina* can be distinguished from all other Australasian otariids by its unusually broad basisphenoid. Discriminant function analysis supported referral of *Neophoca palatina* to *Neophoca* with very high posterior probability. These results confirm the treatment of *Neophoca palatina* as a distinct species of *Neophoca* and highlight the former broad distribution and greater tolerance for colder temperatures of this genus. These results also suggest that New Zealand may have played a pivotal role in the diversification of Southern Hemisphere otariid seals.

Introduction

The Otariidae (fur seals and sea lions) are the second-most diverse pinniped clade and are found throughout the North Pacific and Southern Hemisphere. Nine of 14 extant species are found in the Southern Hemisphere, where they are conspicuous and important components of coastal ecosystems. Despite their abundance, otariids are only recent immigrants to the region, evolving in the North Pacific and dispersing south of the equator between 6 and 7 Ma (Churchill et al., 2014a). In the Southern Hemisphere, otariid fossils are rare but are known from Plio-Pleistocene deposits of South America (Muizon, 1978; Oliveira and Drehmer, 1997; Drehmer and Ribeiro, 1998; Rodrigues et al., 2004; Valenzuela-Toro et al., 2013), South Africa (Avery and Klein, 2011), Australia (McCoy, 1877; Gill, 1968), and New Zealand (King, 1983a).

Otariid fossils from the Southern Hemisphere are generally represented by fragmentary material. One important exception is *Neophoca palatine* King, 1983a, which is represented by a nearly complete skull (King, 1983a). The holotype was recovered from below a seaside cliff at Ohope Beach, Whakatane, in the Bay of Plenty on the North Island of New Zealand (Fig. 1) and has been dated to the New Zealand Castlecliffian Stage (1.63–0.34 Ma; Raine et al., 2012). Although recovered in 1937, this specimen was only described in 1983 and was placed within the genus *Neophoca* on the basis of its wide interorbital region. It was distinguished from the extant Australian sea lion *N. cinerea* on the basis of smaller alveoli, a differently shaped bulla, and a wider palate and basioccipital. Although relatively complete, this taxon has largely been ignored in phylogenetic analyses of Otariidae, such as those by Berta and Deméré (1986) or Barnes et al. (2006). Churchill et al. (2014a) did include this taxon within their phylogenetic analysis. They recovered *N. palatina* as the sister taxon to crown Otariidae, but with little support.

Neophoca palatina is one of only two southern otariids known from well-preserved cranial material (the other being *Hydrarctos lomasiensis* Muizon, 1978) and is the oldest known otariid from the Australasian region. It represents a significant range extension for the genus *Neophoca*, which today is confined to temperate waters in coastal southern and western Australia (Gales et al., 1994); occurrence of *Neophoca* within New Zealand waters in the past may suggest different climatic conditions than are present today or a greater range of temperature tolerance in the past for this genus. Placement of *N. palatina* within *Neophoca*, as well as the diagnosability of the species, remains uncertain. King (1983a) only employed a limited number of measurements in her study and did not carry out comparisons between taxa in a rigorous statistical framework. In addition, sample sizes of extant taxa used in her

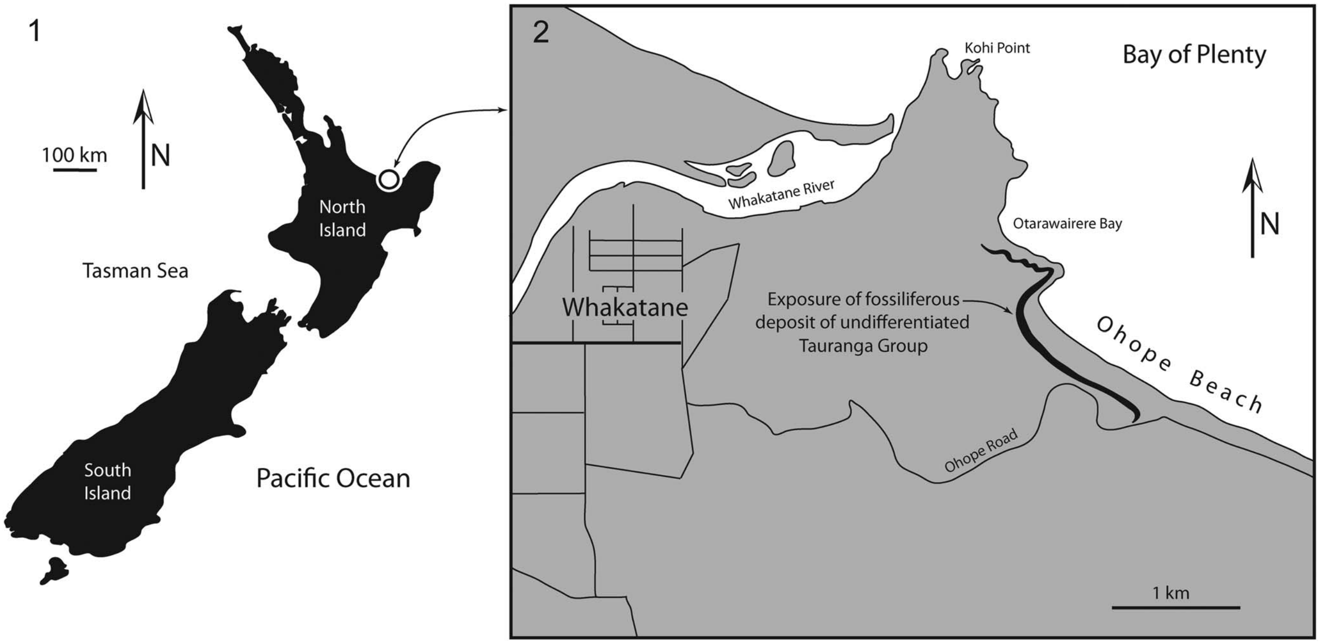

Figure 1. Locality information for *Neophoca palatina*. (**1**) The locality within New Zealand. (**2**) The Ohope Beach area and the location of Tauranga Group sediments.

analysis were limited. While phylogenetic analysis has not been successful in inferring the evolutionary relationships of *Neophoca palatina* to other otariids (Churchill et al., 2014a), morphometric analysis may provide an answer. Morphometrics has previously been applied to otariid taxonomy and has been successful in separating out taxa at the generic level (Brunner, 2004). This study will redescribe *Neophoca palatina* and use morphometrics to test whether it is most similar to *Neophoca cinerea* among extant Australasian otariids. This will clarify the biogeographic distribution of *Neophoca* and may provide further information on the origins of Southern Hemisphere otariid biodiversity.

Materials and methods

Preparation, photography, and anatomical terminology.—Sometime after the death of J.A. Berry, Dr. Judith King received the Ohope skull on loan in Australia for study, where it was carefully prepared by Dr. Michael Archer. Restoration of the skull included acid preparation, which removed much of the calcareous siltstone from endocranial cavities of the braincase, rostrum, and intertemporal region. Unfortunately, when the fossil was sent back to New Zealand, the loss of concretionary matrix from these areas permitted an extensive series of fractures to form, which resulted in the palate separating from the braincase and dorsal rostrum, with the middle of the rostrum and orbital region reduced to hundreds of fragments. To address this damage, we repaired as much of the skull as possible and reassembled most of the damaged part of the rostrum from these fragments using cyanoacrylate glues and poly vinyl butyral. Unfortunately, many of the fragile elements of the interorbital region were too highly shattered to repair, although many of these fragments have been saved and scope for further reassembly exists. After reassembly, the specimen was coated with sublimated ammonium chloride and photographed with a Canon EOS Rebel XS. Anatomical terminology follows Fordyce and Mead (2009).

Sampling.—To quantitatively determine the taxonomic affinities of *Neophoca palatina*, we collected measurement data from 109 specimens belonging to six otariid taxa from throughout the Australasian region. Taxonomy used follows Berta and Churchill (2012). This taxonomy splits *Arctocephalus* into two genera, *Arctocephalus s.s.* which includes *Arctocephalus pusillus* Schreber, 1775, and *Arctophoca*, which includes the remaining southern fur seals. While controversial (Nyakatura and Bininda-Emonds, 2012; Committee on Taxonomy, 2014), we found distinct morphometric differences between these southern fur seal 'genera,' and thus they provide useful labels for morphologically distinctive groups. We focused on taxa from this region as they are the species most likely to be closely related to Pleistocene taxa from New Zealand. Other genera, such as *Callorhinus* and *Eumetopias*, are only known from the North Pacific, and *Zalophus* does not range any further south than the Galapagos Islands. *Otaria* is known from the Atlantic and Pacific coasts of South America, but this taxon possesses unambiguous autapomorphies not found in *N. palatina*, such as a deeply concave and elongated palate, eliminating the genus from consideration as a close relative of *N. palatina*. Taxa examined included the extant Australian sea lion (*N. cinerea*; n = 29), New Zealand sea lion (*Phocarctos hookeri* Gray, 1844; n = 7), Australian fur seal (*Arctocephalus pusillus doriferus* Wood Jones, 1925; n = 32), New Zealand fur seal (*Arctophoca australis forsteri* Lesson, 1828, n = 17), Antarctic fur seal (*Arctophoca gazelle* Peters, 1875; n = 20), and the Subantarctic fur seal (*Arctophoca tropicalis* Gray, 1872; n = 4; Appendix). Sampling focused on male individuals, the same sex as the *N. palatina* holotype.

In addition to the extant otariids and *N. palatina*, we also sampled two Holocene *Neophoca* specimens from Victoria, Australia, outside the present range of extant *N. cinerea*. These specimens were included to assess whether early Holocene and Late Pleistocene *Neophoca* may be more closely related to *N. palatina* than to modern *N. cinerea*. Specimen NMV P12110 was collected from the lower beds of the Bridgewater Group coastal aeolianites near Queenscliff and dates from the last interglacial (Eemian interglacial equivalent; ca. 90–110 ka; Gill and Collins, 1986). NMV P21397 was collected from Holocene coastal sands near the town of Queenscliff and is dated to ca. 7 ka. The former specimen (NMV P12110) was originally described as a new species, *Arctocephalus williamsi* (McCoy, 1877), but was later synonymized with *N. cinerea* (Gill, 1968; King, 1983b).

The twenty cranial measurements chosen for data collection (Fig. 2, Table 1) were based on previous morphometric analyses of otariids (Brunner et al., 2004) and selected for ease of measurement and comparability with *N. palatina*. Measurements were collected with digital calipers to the nearest 0.1 mm (Table 2). A correction factor (based on comparison with extant otariid crania) was applied to the basal length of the cranium measurement in order to accommodate the ~10.6% of the length missing due to damage to the rostrum.

Analysis of morphometric data.—To describe the morphological variation in otariid skulls and determine which extant otariids were most similar to *N. palatina*, we performed principal component analysis (PCA) using a covariance matrix on our cranial measurement data set. We also used discriminant function analysis (DFA) to test the generic placement of *N. palatina*. This allowed us to identify significant differences in cranial shape and size between taxa, with size isolated to PC 1. For this analysis, we tested whether *N. palatina* and the Holocene Australian *Neophoca* specimens were most similar to *Neophoca cinerea*, *Phocarctos hookeri*, *Arctocephalus pusillus*, or *Arctophoca* ssp. PCA and DFA were both performed in R 2.12.1.

Institutional abbreviations.—AIM = Auckland War Memorial Museum; AM = Australian Museum; SAMA = South Australian Museum; NMV = Museum Victoria; OM = Otago Museum; OU = University of Otago Department of Geology; USNM = United States National Museum of Natural History.

Systematic paleontology

Order Carnivora Bowdich, 1821
Family Otariidae Gill, 1866
Genus *Neophoca* Gray, 1866

Neophoca palatina King, 1983a
Figures 3–6

Holotype.—M 76, nearly complete cranium from Ohope Beach (undifferentiated Tauranga Group, Middle Pleistocene), North Island, New Zealand (grid reference NZMS1 N69/466258).

Diagnosis.—*Neophoca palatina* can be distinguished from all other Australasian otariids on the basis of possession of unusually broad basisphenoid. It is placed within the genus *Neophoca* on the basis of proportionally broad interorbital and intertemporal regions, as well as proportionally reduced width across the mastoid processes of the squamosal. It shares the following traits with both *Neophoca cinerea* and *Phocarctos*: a cranium that is broad across the preorbital processes, transversely broad external nares, and a broad palate. It can be distinguished from *Neophoca cinerea* and *Phocarctos* on the basis of its smaller skull length, comparable to male *A. pusillus*. It shares no unique morphometric characters with *Phocarctos* and can be distinguished from this taxon on the basis of a less transversely concave palatal surface and absence of posterior projections of the auditory bullae. It shares with *Arctophoca* an anteroposteriorly short palate and greater separation of the mastoid and paraoccipital processes.

Occurrence.—The holotype skull of *Neophoca palatina* was found in 1937 by Mr. H.C. McReady and presented to then Auckland Institute and Museum (now Auckland War Memorial Museum) in 1939 (King, 1983a); it was under study by Dr. J.A. Berry for many years prior to his death in 1962 (Fleming, 1968). King (1983a) further indicated that "skull was found just below the surface of an area of talus at the base of cliffs representing a stranded shoreline" (p. 105) at the west end of Ohope Beach, approximately 6 km east of Whakatane (Fig. 1; grid reference NZMS1 N69/466258). Fleming (in King, 1983a) considered the parent unit to be assignable to the Castlecliffian Stage (1.63–0.34 Ma; Raine et al., 2012) and to be between 0.45 and 0.25 Ma in age. An earlier study of invertebrates from this locality (Fleming, 1955) reported a correlation with the Putikian substage of the Castlecliffian based upon mollusks and foraminifera. According to Carter and Naish (1998), the Putikian substage is from 0.78 to 0.34 Ma, corresponding to the Middle Pleistocene (Ionian Stage of international usage). More recent field studies have mapped Pleistocene marine deposits of the locally undivided Tauranga Group in the vicinity of Ohope Beach (Leonard et al., 2010). According to Leonard et al. (2010), these sediments are 1.81–0.524 Ma in age. Taking into account a Putikian age reported by Fleming (1955) and age ranges reported by Leonard et al. (2010), the absolute age of the *Neophoca palatina* type locality may be summarized as 0.780–0.524 Ma, Middle Pleistocene.

Description.—The holotype of *Neophoca palatina* consists of a partial cranium, missing the zygomatic arches, supraorbital processes of the frontal, and the anterior portion of the premaxilla (Fig. 3). In addition to the left pterygoid and palatine, much of the medial orbital and temporal wall is damaged. The basicranium is nearly complete. Preservation is, unless noted in the following, comparable for left and right sides of the cranium. We agree with King (1983a), who considered the holotype to represent an adult male, according to the combination of suture patterns (6 of 9 sutures used by Doutt, 1942, to assess maturity in seals are closed), large sized and circular cross-section of canine alveoli (greatest alveolar diameter measures 7% of condylobasal length), and robust proportions of the skull. Using the multivariate total-length regression equation for otariids presented in Churchill et al. (2014b), a total body length of ~230 cm is estimated for this taxon, similar to the body size seen in extant male *Phocarctos*.

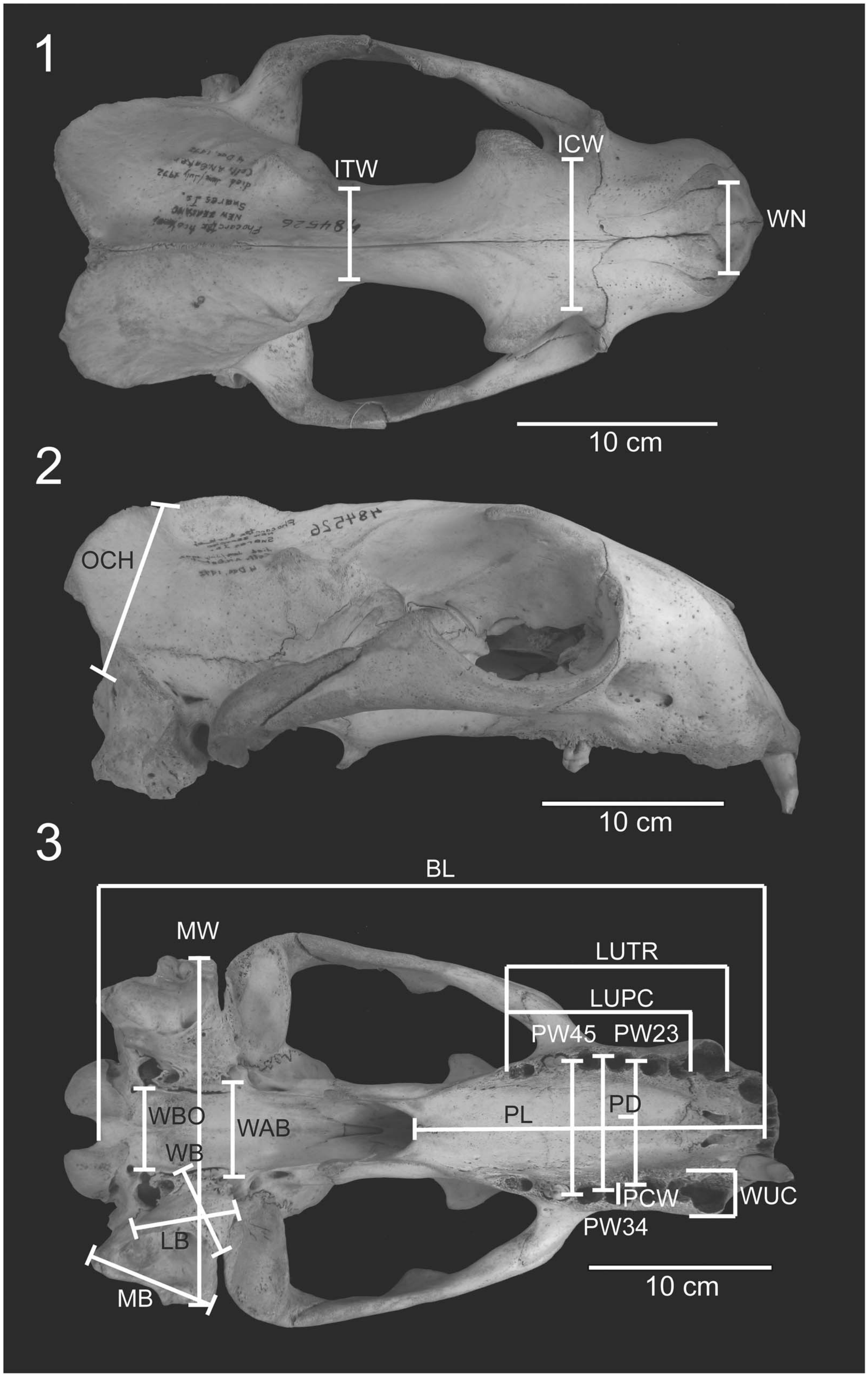

Figure 2. The cranium of *Phocarctos hookeri* (USNM [National Museum of Natural History] 489526), illustrating cranial measurements used in this study. (**1**) Dorsal view; (**2**) lateral view; (**3**) ventral view. BL = basal length; ICW = width in dorsal view of the cranium between the preorbital and supraorbital processes; ITW = width across the intertemporal constriction anterior to the braincase; LB = maximum length of the auditory bullae; LUPC = length of upper postcanine tooth row; LUTR = length of upper tooth row; MB = distance between the mastoid and paraoccipital processes; MW = bimastoid width; OCH = height of the occipital shield; PCW = transverse width of P^3 alveoli; PD = depth of palate; PL = palate length; PW23 = transverse width of palate between the P^2 and P^3; PW34 = transverse width of the palate between the P^3 and P^4; PW45 = transverse width of palate between the P^4 and M^1; WAB = basisphenoid width between the auditory bullae; WB = width across the bullae); WBO = basioccipital width; WN = width of the external nares; WUC = transverse width of canine alveoli. For more detailed descriptions of measurements, see Table 1.

Table 1. Descriptions of measurements used in analysis of morphometric data.

Acronym	Definition
BL	Basal length, measured on ventral surface of the midline of the skull, from just anterior of the medial border of the I^1 to the intercondylar notch
PL	Length of palate, measured along the midline of the palate from the palatal notch to just anterior of the medial border of the I^1
MW	Bimastoid width, measured from the lateral-most termini of the mastoid processes
WBO	Width of the basioccipital, measured as the distance between the medial wall of the posterior lacerate foramen
WAB	Width of the basisphenoid, measured as the distance between the medial edge of the auditory tube
PD	Depth of palate, measured at the junction of the midline of the palate and the approximate position between the P^2 and P^3
WUC	Transverse width of the C^1 alveoli
PCW	Transverse width of the P^3 alveoli
LUTR	Length of the upper tooth row, from the anterior margin of the C^1 alveolus to the posterior margin of the last postcanine alveolus (M^1 and M^2), as a straight line distance
LUPC	Length of the upper postcanine tooth row, as measured from the anterior margin of the P^1 alveolus to the posterior margin of the last postcanine alveolus (either M^1 or M^2)
PW23	Transverse width of the palate between P^2 and P^3, measured from the approximate midpoint of the width of the alveoli for P^2 and P^3
PW34	Transverse width of the palate between P^3 and P^4, measured from the approximate midpoint of the width of the alveoli for P^3 and P^4
PW45	Transverse width of the palate between P^4 and M^1, measured from the approximate midpoint of the width of the alveoli for P^4 and M^1
WB	Width of the auditory bulla from the lateral-most margin of the eustachian tube to the medial margin of the bulla at the approximate midpoint of its length
LB	Maximum length of the auditory bullae, from the anterior border to the tip of the posterior projection (if present, if absent measured to posterior border); this measurement does not take into account anterior ornamentation of the bullae
MB	Distance from the anterior surface of the lateral-most portion of the mastoid process to the posterior surface of the paraoccipital
WN	Breadth of the external nares ventral to the anterior terminus of the nasals, at their widest point
ICW	Width at the narrowest portion of the constriction of the cranium between the preorbital processes of the maxillae and the supraorbital processes of the frontals
ITW	Width at the narrowest portion of the intertemporal constriction, just anterior to the braincase
OCH	Height of the occipital shield along the midline, from the intercondylar notch to the junction of the sagittal and lambdoidal crests

Premaxilla and maxilla.—The premaxillae are badly damaged, and only the narial (ascending) process dorsal to the canine alveolus and maxilla is preserved. The external nares are badly damaged, and the narial processes of the premaxillae are broken and absent. The external nares are broad and proportionally similar in size to those of *Phocarctos* and *N. cinerea* (Fig. 4.1; King, 1983a). Dorsally (Fig. 5.1), the maxilla extends from the anterodorsal border of the broken canine alveolus toward the anterior margin of the nasal in a nearly straight line. A shallow nasolabialis fossa is present on the ascending process of the maxilla immediately anterior to the antorbital process. The maxilla forms a nearly transversely straight suture with the frontal. In dorsal aspect, the antorbital process projects further laterally than the transversely broadest part of the rostrum (similar to *Phocarctos hookeri* and *Neophoca cinerea*).

The lateral wall of the maxilla is thin and heavily damaged on the left side (Fig. 6.2); the right side (Fig. 6.1) was well preserved at the time of description by King (1983a). In lateral view, the maxilla is incomplete, and a large empty cavity is posteriorly contiguous with the missing section of orbital wall. The anterior portion of the right infraorbital foramen is present and large (~15 mm dorsoventral depth) in the cast but now damaged in the specimen. A vertically arranged pair of posteriorly opening foramina (2–3 mm diameter) is present anteriorly within the foramen. The antorbital process of the maxilla is damaged, but appears to have been developed as a low vertical ridge outlining the anterior wall of the orbit and formed entirely by the maxilla. The anterior orbital margin is formed as an arcuate ridge and ventrally consists of the broken zygomatic process of the maxilla, anteriorly by the incomplete antorbital process and dorsally by the broken supraorbital process of the frontal. The frontal-maxilla suture is positioned immediately dorsal to the antorbital process. The zygomatic processes of the maxilla are damaged. Ventrally, the right palatine process of the maxilla is nearly complete, but the left side is missing.

Nasal.—The nasal is transversely broad and absolutely broader than that of most male *Neophoca cinerea* of larger absolute size (Fig. 5.1). This is the opposite of the condition reported by King (1983a), who found that the nasals of *N. palatina* overlapped with the lower range of values recorded in her study for *N. cinerea*. Differences in nasal width comparisons between studies are largely a result of differences in sample size between the two studies (six individuals in the study by King, 1983a; 29 in this study). The lateral margin of the nasal is straight and forms a 90° angle with the maxilla-frontal suture. The premaxilla contacts the anterolateral margin of the nasals. The posterior margin of the nasals is roughly W-shaped with a triangular wedge of frontal medially separating the nasals and a bilateral pair of minute prongs of frontal extending anteriorly between the nasal and maxilla (King, 1983a); the posterior margin of each nasal is rounded. The anterior morphology of the nasals is unknown owing to damage, although the canine alveolus and nasal are separated by a relatively short expanse of maxilla, which suggests a short rostrum similar to *Arctophoca tropicalis*.

Palate and pterygoid.—The palate (Fig. 5.2) is slightly transversely concave and similar in depth to the palate of *Neophoca cinerea* and *Arctocephalus* (King, 1983a); the palate is not as strongly arched as in *Phocarctos* and *Otaria*. The palate is proportionally short relative to basal skull length, similar to *Arctocephalus pusillus, Arctophoca australis*, and *Arctophoca tropicalis* (King, 1983a). However, the palate is proportionally broad and more similar to *Phocarctos* and *N. cinerea* (King, 1983a). The palate is slightly broader posteriorly than anteriorly, with the rostrum widest at the position of the canines. The anterior palatine foramina are present at the level of the third premolar, preceded anteriorly by a shallow sulcus. Posterior to these foramina and in line with them are a series of minute foramina. Anterior to the canine alveolus, the palate is incomplete; the incisive foramina are exposed in a broken surface but appear to have been small and paired.

The tooth row is proportionally short relative to the basal length of the cranium, similar to *N. cinerea* and *A. pusillus*. The canine alveolus is large and circular in cross section and is positioned anterolateral to the P^1 alveolus. The postcanine alveoli are smaller than those possessed by *N. cinerea* and *Arctocephalus* and proportionally similar to those seen in *Phocarctos* and *Arctophoca*. This contrasts with King (1983a), who found that the alveoli were proportionally and absolutely smaller than those possessed by *Phocarctos*, which again may

Table 2. Measurements used in morphometric analysis. All recent specimens averaged and values reported in centimeters. Basal Length (BL) for *N. palatina* corrected for damage to rostrum. ICW = width in dorsal view of the cranium between the preorbital and supraorbital processes; ITW = width across the intertemporal constriction anterior to the braincase; LB = maximum length of the auditory bullae; LUPC = length of upper postcanine tooth row; LUTR = length of upper tooth row; MB = distance between the mastoid and paraoccipital processes; MW = bimastoid width; OCH = height of the occipital shield; PCW = transverse width of P^3 alveoli; PD = depth of palate; PL = palate length; PW23 = transverse width of palate between the P^2 and P^3; PW34 = transverse width of the palate between the P^3 and P^4; PW45 = transverse width of palate between the P^4 and M^1; WAB = basisphenoid width between the auditory bullae; WB = width across the bullae; WBO = basioccipital width; WN = width of the external nares; WUC = transverse width of canine alveoli; M = mean; SD = standard deviation. For more detailed descriptions of measurements, see Table 1.

	Neophoca palatina AIM Mamm 175.1	*'Arctocephalus williamsi'* NMV P12110	*Neophoca cinerea* (Holocene) NMV P21397	*Neophoca cinerea*		*Phocarctos hookeri*		*Arctocephalus pusillus doriferus*		*Arctophoca australis forsteri*		*Arctophoca gazella*		*Arctophoca tropicalis*	
				29		7		32		17		20		4	
Sample Size	1	1	1	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Cranial Measurements															
BL	28.03	27.36	25.18	27.35	1.1	29.36	1.48	26.21	0.89	21.73	0.99	21.5	0.95	20.25	1.17
PL	11.63	14.43	13.24	14.98	0.81	16.25	1.06	12.93	0.97	10.85	0.67	11.38	0.76	9.76	0.82
MW	15.67	14.15	14.13	15.31	0.71	15.17	1.54	15.78	0.63	13.12	0.92	13.53	0.73	12.11	1.01
WBO	4.68	4.68	4.5	4.51	0.31	4.21	0.44	3.89	0.24	3.44	0.22	3.95	0.32	3.4	0.32
WAB	5.19	3.76	3.18	3.34	0.24	3.59	0.29	3.47	0.25	2.71	0.25	3.19	0.22	2.61	0.14
PD	1.19	0.91	0.92	1.25	0.43	2.17	0.29	0.92	0.23	0.92	0.13	0.74	0.14	0.61	0.29
WUC	1.65	1.68	1.6	1.78	0.17	1.75	0.31	1.65	0.17	1.39	0.18	1.35	0.13	1.24	0.17
PCW	0.77	0.9	0.85	0.91	0.1	0.82	0.2	0.84	0.12	0.62	0.09	0.58	0.09	0.54	0.07
LUTR	7.85	8.52	7.79	8.72	0.64	10.35	0.77	8.43	0.34	7.42	0.47	7.98	0.41	7.22	0.53
LUPC	6.6	6.7	6.07	6.74	0.62	8.14	0.47	6.61	0.32	5.96	0.26	6.34	0.33	5.91	0.31
Pw1	6.4	5.03	4.41	5.42	0.35	5.79	0.59	4.15	0.27	3.5	0.3	3.58	0.25	3.08	0.24
Pw2	6.99	5.28	4.5	5.39	0.42	5.98	0.44	4.49	0.28	3.87	0.4	3.91	0.28	3.28	0.24
Pw3	6.24	5.29	4.55	5.34	0.4	5.71	0.5	4.88	0.33	4.25	0.4	4.35	0.32	3.51	0.27
WB	3.76	3.38	3.06	4.02	0.39	3.65	0.18	3.5	0.2	3.04	0.22	2.84	0.23	2.8	0.24
LB	3.62	3.85	2.9	3.89	0.33	5.16	0.8	3.79	0.34	3.09	0.37	2.98	0.41	2.93	0.06
MB	5.22	4.26	4.85	4.88	0.32	5.0	0.35	5.22	0.53	4.32	0.32	4.34	0.65	4.44	0.19
WN	4.3	3.5	3.26	3.74	0.42	3.69	0.53	3.19	0.25	2.96	0.28	2.97	0.20	2.46	0.23
ICW	5.99	7.06	5.55	6.2	0.61	5.45	0.39	4.28	0.26	2.95	0.35	3.7	0.33	2.17	0.028
ITW	4.81	4.52	3.75	4.68	0.57	3.39	0.3	3.04	0.29	2.62	0.37	3.05	0.3	2.32	0.3
OCH	7.88	6.76	6.51	7.19	0.41	6.98	0.46	6.47	0.38	5.74	0.38	5.57	0.32	5.69	0.60

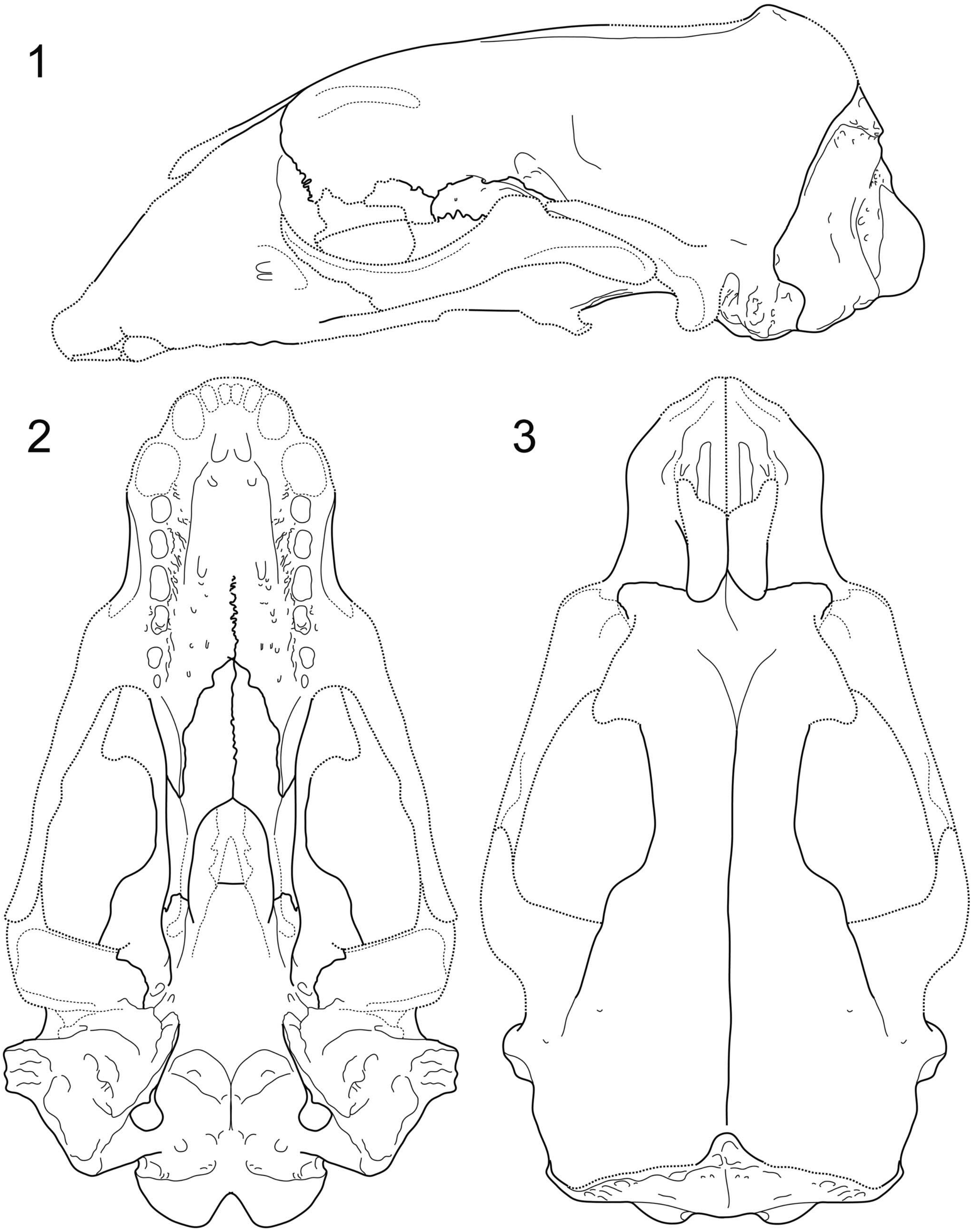

Figure 3. Reconstruction of the skull of *Neophoca palatina*, based on the holotype (AIM M 76) and comparisons with other otariid taxa. (**1**) Lateral view; (**2**) ventral view; (**3**) dorsal view.

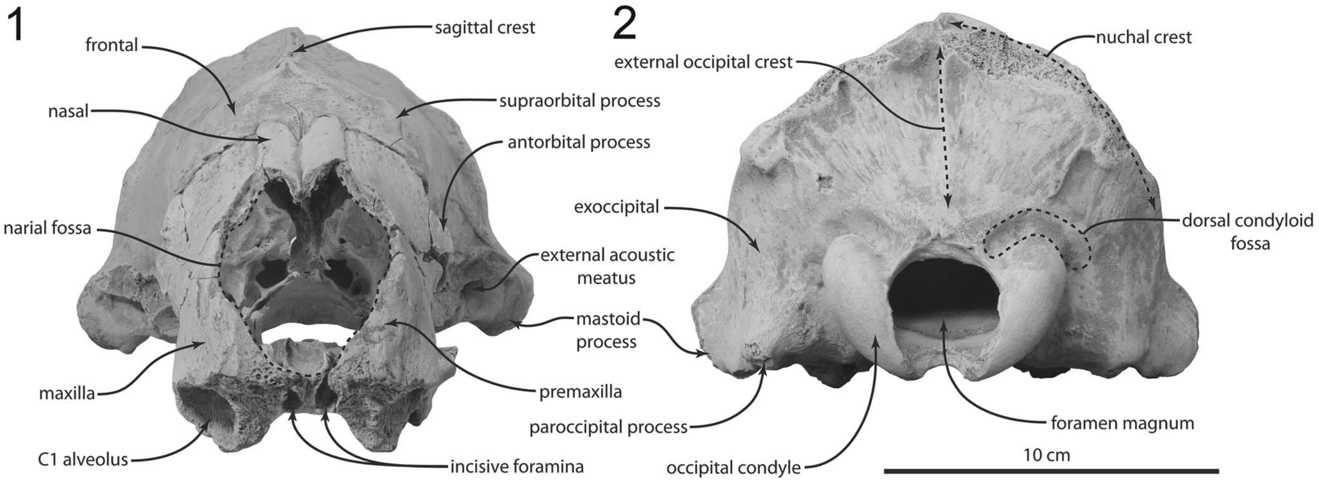

Figure 4. Holotype of *Neophoca palatina* (AIM M 76), with bones and anatomical landmarks labeled. (**1**) Anterior view; (**2**) posterior view.

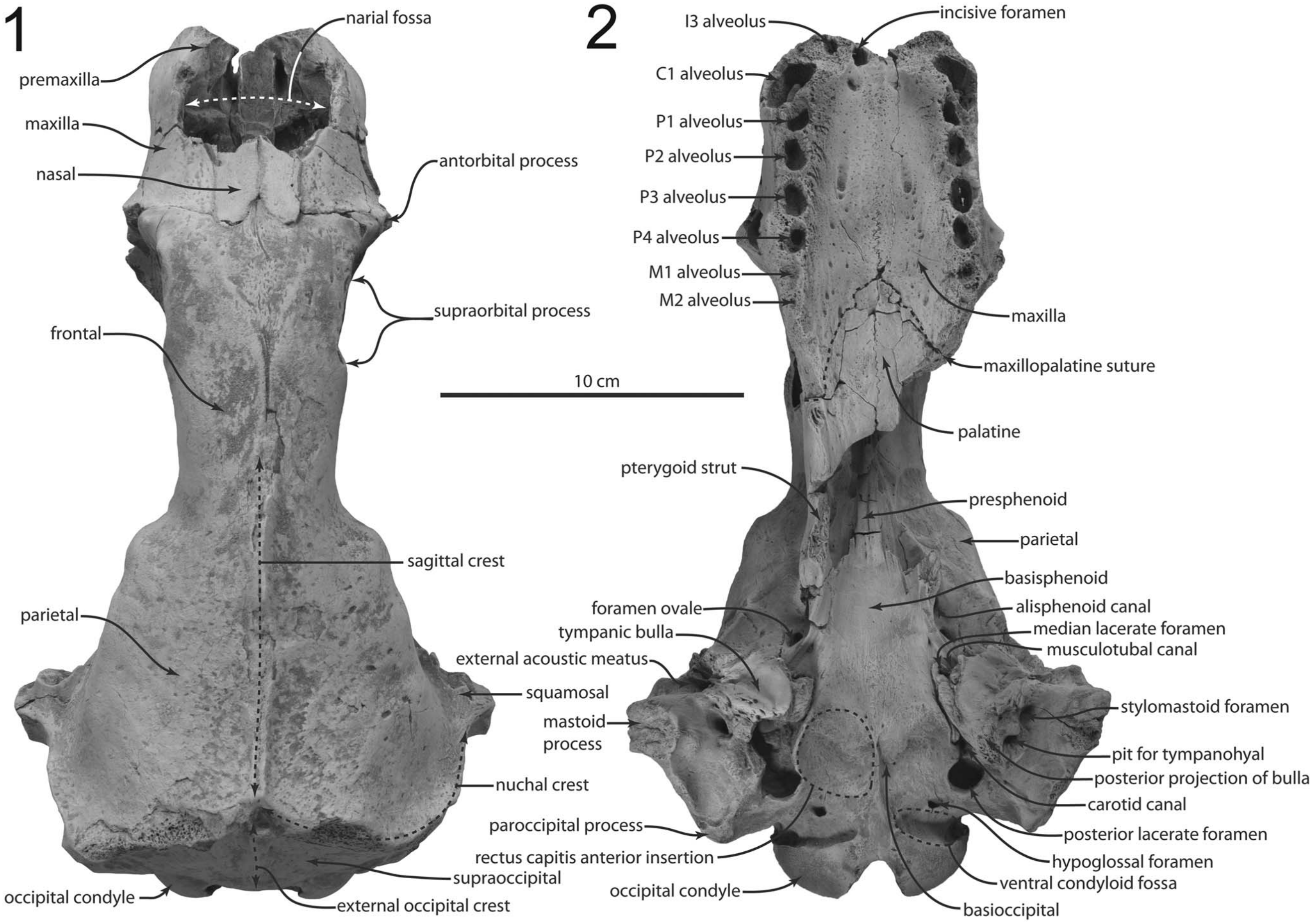

Figure 5. Holotype of *Neophoca palatina* (AIM M 76), with bones and anatomical landmarks labeled. (**1**) Dorsal view; (**2**) ventral view.

be a result of differences in sampling between our study and hers. Roots for the P^1–P^3 are single-rooted. The P^4 is bilobate. Alveolus for the M^1 is shallow and possibly indicates a double root, but damaged. The posterolateral portion of the palate is damaged on the left side, but the right side is more complete and preserves a shallow alveolus for a single-rooted M^2. A slight diastema is present between the P^4 and M^1. This diastema is similar in size to those exhibited in *N. cinerea* and much smaller than the diastema possessed by *Arctocephalus.* No diastema between the M^1 and M^2 is evident.

The posterior portion of the palate is broken, and missing on the right side. The maxillopalatine suture is unfused, as is the

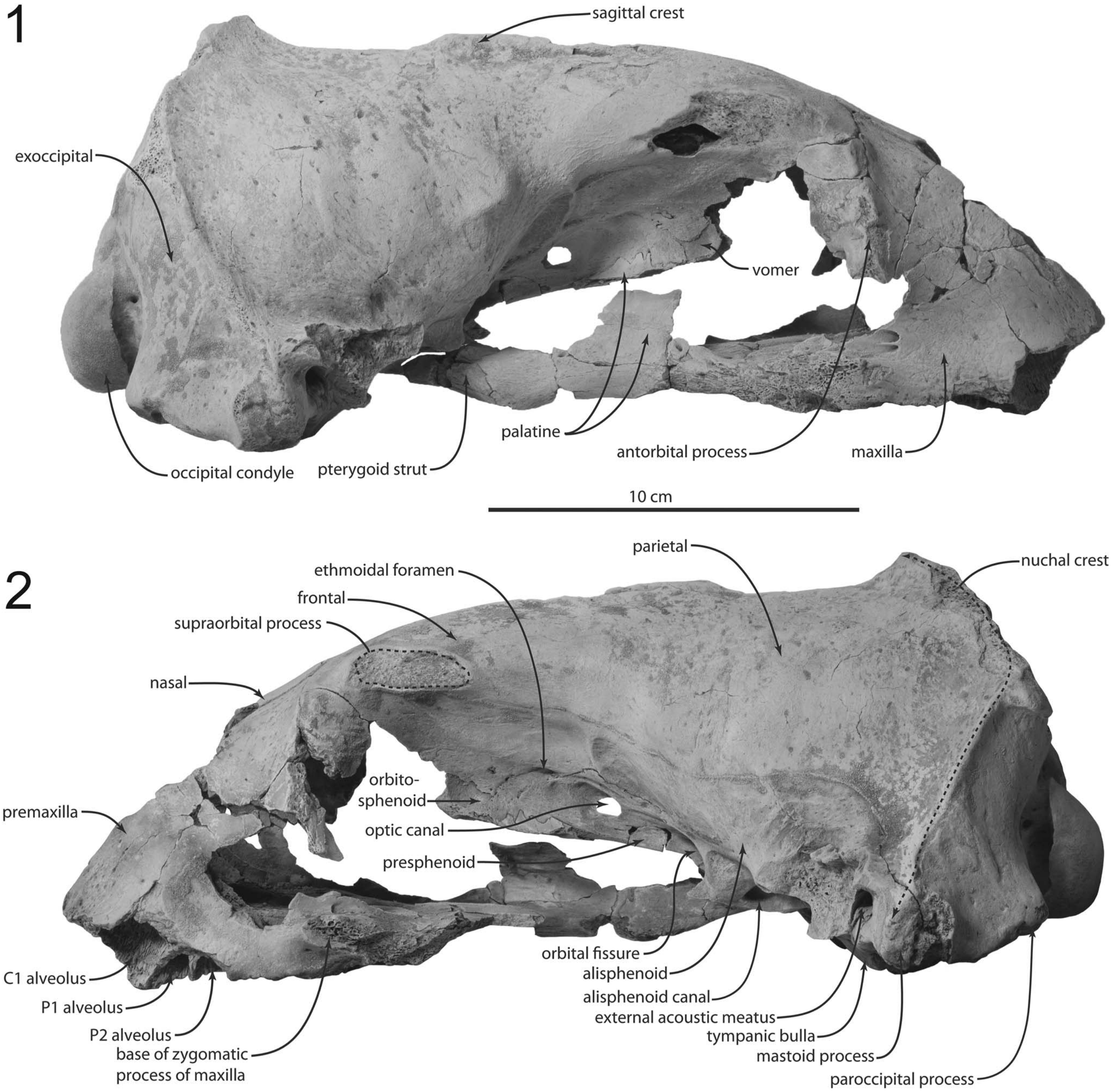

Figure 6. Holotype of *Neophoca palatina* (AIM M 76), with bones and anatomical landmarks labeled. (**1**) Right lateral view; (**2**) left lateral view.

posterior half of the intermaxillary suture. The shape and lack of closure on the maxillopalatine suture is somewhat obscured due to breakage of the skull in the palatal region since the original description of the specimen by King (1983a) but obvious on the cast and published figures in King (1983a, fig. 1). The anterior margin of the palatine forms a broad U shape, with the anterior-most portion of the suture forming a transverse straight line. The posterior margin of the palate forms a U shape. A pentagonal accessory midline ossification (9.93 mm wide, 8.73 mm long) is present between the maxillae and palatines and separated by an obvious suture, but appears to have a closed suture with the left palatine. The right pterygoid strut is present and transversely narrow as in other otariids. The damaged hamular process is present as a small laterally projecting knob; the pterygoid strut is slightly transversely thicker at the level of the broken hamulus.

Orbital wall.—A thin portion of the orbital wall is preserved on the left side (Fig. 6.1). A large orbital vacuity is evident in the cast (but damaged in the original holotype). It is positioned anteriorly on the orbital wall and is formed between the frontal and maxilla as in most other Otariidae. The optic canals are closely medially appressed and lack a median osseous septum; anteriorly, a small fenestra completely perforates the orbital wall as in all Otariidae.

Frontal.—The supraorbital processes of the frontal are missing, but the remaining large bases of processes indicate that the supraorbital processes were large (approximately 3 cm in anteroposterior length on the left frontal) and unambiguously confirm placement of *Neophoca palatina* within the Otariidae (King, 1983b). Dorsally (Fig. 5.1), the frontal-maxilla suture is transversely straight, with a wedge of frontal separating the posterior portions of the nasals. Ventrally, this suture turns posteroventrally into the orbit immediately dorsal to the antorbital process. The frontal-parietal suture is completely obliterated in dorsal view. The posterior part of the frontal forms the anterior portion of the braincase; the anterolateral margin of the braincase is formed as a minute corner in dorsal view, and the braincase widens posteriorly. This condition is morphologically intermediate between the subrectangular braincase of many members of *Arctocephalus* and the gradually posteriorly widening braincase characteristic of 'Otariinae.' The braincase is proportionally narrow at the frontoparietal suture relative to mastoid width, similar in proportions to *Phocarctos*, *Arctocephalus*, and *N. cinerea*. The intertemporal and interorbital regions are relatively transversely wide (King, 1983a). In dorsal view, the intertemporal region is transversely wide and of near-constant transverse width along the anteroposterior axis, although slightly narrower posteriorly so that the narrowest intertemporal constriction is positioned immediately anteriorly adjacent to the braincase. These features are shared with *Neophoca cinerea* (King, 1983a). The dorsal surface of the frontal is slightly convex in lateral view, although less so than that exhibited by many *N. cinerea* specimens. Most of the sagittal crest is damaged, and its full dorsoventral development cannot be discerned in the specimen, although it appears to have been a low, broad ridge that extended anteriorly to the intertemporal constriction. It is bifid anteriorly and forms temporal crests that diverge anterolaterally toward the supraorbital processes.

Supraoccipital, exoccipital, and parietal.—The supraoccipital (Fig. 4.1) is proportionally high relative to the basal length of the skull, as in *A. tropicalis*. The supraoccipital forms a large triangular shield outlined by rugose nuchal crests. In lateral view, the nuchal crests extend anteroventrally in a straight line onto the dorsal margin of the mastoid process of the squamosal, posterior to the external auditory meatus, unlike *N. cinerea*, *Arctocephalus, Arctophoca gazella,* or *Arctophoca australis*. The dorsal half of the occipital shield is visible and triangular in dorsal view (Fig. 5.1); this is similar to the condition that is variably present within *Arctophoca*. However, it is unclear how visible the supraoccipital shield would have been when the nuchal crests were complete. A low external occipital crest is positioned on the dorsal half of the supraoccipital; the dorsolateral edge of the supraoccipital shield is smooth but irregular and bears several fossae for the obliquus capitis superior (laterally on occipital) and the rectus capitis posterior insertion (medially), which become deeper medially. At the junction of the supraoccipital and exoccipital, an oblique subhorizontal crest runs ventromedially from the nuchal crest toward the dorsal margin of the foramen magnum; this crest forms the dorsal margin of the deep dorsal condyloid fossa. The occipital condyles are complete, dorsoventrally shallow, and widely separated. In posterior view, they do not protrude prominently posteriorly from the supraoccipital. The foramen magnum is large and subcircular. A shallower, trough-like ventral condyloid fossa wraps around and defines the anterior and ventral margins of the occipital condyle.

The surface of the parietal is smooth and lacks the rugosities and textures present in older male otariids. The frontal-parietal suture is completely closed, preventing assessment of the shape of the contact between these cranial elements. There is significant vertical development of the parietal portion of the sagittal crest, which begins just anterior to the approximate position of the frontal-parietal suture.

Squamosal and basicranium.—The mastoid process is cuboid (Fig. 5.2). The width across the mastoid processes indicates a proportionally narrow skull, similar to that of *N. cinerea*, but not as narrow as *Phocarctos* (King, 1983a). The mastoid process is connected to the paraoccipital process by a well-developed, continuous crest. The distance between the mastoid and paraoccipital processes is proportionally short and similar to *Phocarctos* and *N. cinerea*. The zygomatic processes of the squamosal are completely missing, along with the glenoid fossa and postglenoid processes.

The tympanic bulla is large and ventrally convex, although ventrally flatter than typically seen in *Arctophoca*. The right bulla is broken posterior to the level of the stylomastoid foramen. The medial margin of the bulla is rounded, and the bulla does not obscure the bony carotid canal in ventral view. The anterior margin of the bulla forms a thin ventrally projecting plate that would probably have overlapped the posterior surface of the postglenoid process. The bulla bears a short tubercle-like posterior projection similar to other otariids but not as greatly elongated as in *Otaria* and *Phocarctos* (King, 1983a). The ventral surface of the bulla consists of smooth cortical bone and lacks a sculptured or crenulated medial margin as seen in *Callorhinus ursinus* Linnaeus, 1758, *Thalassoleon macnallyae* Repenning and Tedford, 1977, and *Thalassoleon inouei* Kohno, 1992; the posterior surface is somewhat cancellous. A low crest runs from the lateral margin of the posterior lacerate foramen posterolaterally toward the paroccipital process. A small, laterally directed tubercle is present immediately anterior to the stylomastoid foramen. A shallowly concave fossa is present ventrally on the squamosal between the tympanic bulla and the mastoid process.

The basisphenoid is smooth and the basisphenoid-basioccipital suture is completely fused. The basisphenoid and basioccipital are broad and most similar to *N. cinerea* and *Phocarctos*, with a wider basisphenoid than any other Australasian otariid (King, 1983a). A small and circular hypoglossal foramen perforates the basioccipital immediately posteromedial to the posterior lacerate foramen. The basioccipital is roughly trapezoidal in shape and features a deep fossa for the rectus capitis anterior insertion medial to the large and circular posterior lacerate foramen (King, 1983a). These fossae are separated by a median longitudinal crest.

Remarks.—The diagnosis as presented is emended according to reexamination of the holotype as well as comparison of the holotype with additional taxa and specimens. King (1983a) originally diagnosed this taxon as a distinct species of *Neophoca* on the basis of a short palate, wide basioccipital, small postcanine teeth, and lack of posterior processes on the tympanic bullae. Of the features described, only the wide basioccipital is unique to this taxon. *Neophoca palatina* does possess smaller teeth and a shorter palate than *N. cinerea,* although these traits overlap with values reported for other

Australasian otariids. This study did not find consistent significant differences in the bullae between *N. cinerea* and *N. palatina*.

Results

Our PCA segregated taxa by genera (Fig. 7, Table 3). Approximately 89% of the variation was explained by the first six components. Component 1 explained ~65% of the variation and reflected size differences between taxa. Large taxa, including *Phocarctos* and *Neophoca*, plotted positively, while small taxa such as *Arctophoca* had negative scores. *Arctocephalus* is intermediate between the two groups. Fossil *Neophoca* plotted with extant *Neophoca*. Principal component 2 explained ~7% of the variation and reflected variation in the width of the intertemporal constriction (ITW). This component segregated *Phocarctos* and *Neophoca* from one another, with the relatively broad ITW of *Neophoca* resulting in more negative scoring than the narrow ITW of *Phocarctos*. Principal component 3 explained ~6% of the variation and reflected the breadth of the mastoid process. This feature weakly segregated *Arctocephalus* and *Phocarctos* from all other taxa. *Neophoca* and *Arctophoca* were not segregated from one another, and fossil *Neophoca* also plotted within this intermediate range. Principal component 4 explained ~4% of the variation and reflected width of the basicranium. Most taxa were only poorly segregated on this axis; however, *N. palatina* was clearly distinguished from all other taxa on the basis of its unusually broad basisphenoid. Holocene *Neophoca* plotted with extant otariids. Principle component 5 explained ~3% of the variation and reflected width of the basisphenoid, breadth of the skull across the mastoids, and length of the tooth row. Again, *N. palatina* was segregated from other taxa, but all other taxa showed no significant segregation. Principal component 6 explained ~3% of the variation and reflected size of the postcanine teeth. Taxa were not easily segregated by this component.

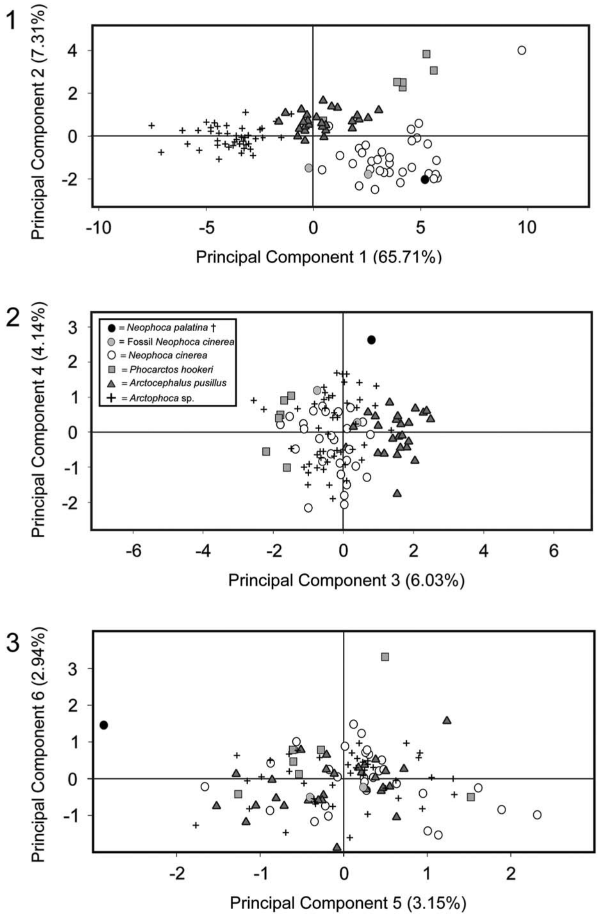

Figure 7. Bivariate plots for Australasian otariid seals. (**1**) Principal components 1 and 2; (**2**) principal components 3 and 4; (**3**) principal components 5 and 6.

Discriminant function analysis results supported the PCA analysis. Holocene fossil *Neophoca* were classified within *Neophoca* with a posterior probability of 1.0. *Neophoca palatina* was also classified as belonging to *Neophoca*, with a posterior probability of 0.99. Identification of these taxa to other genera all carried posterior probabilities far less than 0.001.

Discussion

Phylogenetic and biogeographic implications.—Our morphometric analysis placed *N. palatina* within the morphospace occupied by *Neophoca*, supporting King's (1983a) referral of this species to the genus. We are also able to confirm that the Pleistocene and Holocene material from Victoria, Australia, is referable to extant *N. cinerea*, supporting the synonymy of *Arctocephalus williamsi* McCoy, 1877 with *N. cinerea* (Gill, 1968; King, 1983b). Our analysis also found distinctive characters that separate *N. palatina* from *N. cinerea*, specifically an unusually broad basisphenoid and smaller body size. The results for *N. palatina* in this study contrast with the earlier study of Churchill et al. (2014a), which was unable to resolve the position of this taxon with any support. Otariid skulls are morphologically conservative (Jones and Goswami, 2010), and this has been a confounding problem in analyzing the relationships of extant taxa (Churchill et al., 2014a). Churchill et al. (2014a) used many qualitative characters, and these characters may not have properly captured differences in cranial shape between taxa. By contrast, this study has revealed several potential new characters derived from morphometric comparisons that may be useful in phylogenetic analysis. Further research on otariid systematics should focus on creating large data sets of cranial measurement data and exploring these data sets to create novel quantitative characters that can improve the resolution of phylogenies produced using morphologic data.

The role of *Neophoca palatina* in the evolution of Australasian sea lions is unclear. Molecular and total evidence phylogenetic analyses have generally had problems resolving the position of *Neophoca* within Otariidae (Wynen et al., 2001; Árnason et al., 2006; Higdon et al., 2007; Churchill et al., 2014a), although Yonezawa et al. (2009) recovered *Neophoca* as the sister taxon to *Phocarctos*. If *Neophoca* is indeed the sister taxon to *Phocarctos*, than the presence of *N. palatina* in New Zealand suggests that the *Neophoca* and *Phocarctos* clade may have originated in New Zealand. Divergence of these taxa may have been driven by successive cycles of regional extinction and recolonization, driven by either cooling climate during glacial intervals or changes in haul-out habitat as a result of changes in sea level (Valenzuela-Toro et al., 2013).

Table 3. Variable loadings for principal component analysis of cranial measurement data from Australasian Otariidae.

	Loadings						Proportional contribution (%)					
Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
BL	0.26	0.11	0.08	-0.05	-0.03	0.06	6.96	1.20	0.68	0.30	0.10	0.40
PL	0.26	0.05	-0.14	-0.04	0.12	0.09	6.64	0.21	1.88	0.18	1.35	0.76
MW	0.22	0.13	0.40	0.01	-0.10	0.03	4.69	1.64	15.90	0.01	0.97	0.11
WBO	0.20	-0.32	0.01	0.46	0.15	0.09	3.97	10.01	0.02	20.80	2.21	0.88
WAB	0.17	0.03	0.26	0.59	-0.48	0.02	3.04	0.07	6.83	34.63	23.15	0.05
PD	0.18	0.24	-0.40	-0.21	-0.28	0.26	3.11	5.55	15.99	4.43	7.80	6.75
WUC	0.23	0.05	0.14	-0.22	-0.18	-0.49	5.10	0.29	1.90	4.80	3.10	24.22
PCW	0.22	-0.01	0.20	-0.14	-0.01	-0.60	4.85	0.00	3.84	2.03	0.00	35.81
LUTR	0.22	0.33	-0.19	0.22	0.30	-0.18	4.92	11.13	3.68	4.93	9.16	3.39
LUPC	0.19	0.37	-0.26	0.32	0.40	-0.19	3.65	13.77	6.73	10.47	15.77	3.51
Pw1	0.26	-0.10	-0.16	-0.01	-0.04	0.07	6.86	1.10	2.57	0.00	0.18	0.43
Pw2	0.26	-0.07	-0.13	0.06	-0.15	0.13	6.65	0.47	1.56	0.37	2.37	1.71
Pw3	0.25	-0.01	-0.05	0.04	-0.25	0.05	6.30	0.00	0.21	0.19	6.16	0.23
WB	0.24	-0.14	0.05	-0.30	0.22	0.06	5.55	1.97	0.30	8.75	4.71	0.36
LB	0.21	0.32	-0.09	-0.17	-0.16	0.21	4.44	10.52	0.78	2.76	2.71	4.51
MB	0.13	0.25	0.59	-0.08	0.34	0.38	1.76	6.43	35.39	0.64	11.30	14.74
WN	0.23	-0.16	-0.05	-0.14	-0.16	-0.06	5.22	2.43	0.26	1.98	2.47	0.34
ICW	0.25	-0.27	-0.05	-0.01	0.10	0.02	6.36	7.35	0.24	0.00	0.97	0.05
ITW	0.20	-0.50	-0.08	0.01	0.22	0.05	3.94	24.64	0.62	0.01	4.79	0.24
OCH	0.24	-0.11	0.08	-0.17	0.08	0.12	6.00	1.24	0.62	2.73	0.71	1.50

Churchill et al. (2014a), however, recovered *Phocarctos* as the sister taxon to *Otaria* of South America. If this topology is correct, we can hypothesize that *Neophoca* was once distributed widely in the Australasian region. Extinction of *N. palatina* would have left the 'sea lion' niche open in New Zealand. New Zealand would have then been colonized by stem members of the *Phocarctos*-*Otaria* lineage, and divergence of these two genera would have been facilitated by the distance between New Zealand and South America. A similar dispersal pattern is indicated by *Arctophoca australis*, which originated along the Pacific coast of South America and expanded its range to New Zealand and later Australia, giving rise to *A. australis forsteri* (Churchill et al., 2014a). More comprehensive phylogenetic analyses and further fossil discoveries from the Pliocene and Pleistocene of Australia and New Zealand are needed to test these hypotheses.

Paleoenvironmental implications.—Fossil and archaeological material of pinniped taxa has provided important evidence of Holocene and Pleistocene climate change (Gill, 1968; Sun et al., 2004; Hall et al., 2006; Bruyn et al., 2009). Otariid distribution is strongly controlled by sea surface temperature and productivity, with the distribution of extant taxa closely aligning with regions of low sea surface temperature (SST) and upwelling-enhanced productivity (Churchill et al., 2014a). The temperature tolerances of individual species may also provide clues on past sea surface temperature. Gill (1968) argued that the coastline of Victoria was warmer during the last interglacial, according to the current distribution of *Neophoca cinerea* and the presence of fossil material referable to this taxon in the area.

Neophoca cinerea inhabit regions with a mean SST of ~16–23°C. By contrast, the sea around New Zealand has a mean SST of ~12–17°C. *Phocarctos* is the only extant sea lion known from New Zealand; although today this species is mostly restricted to the Auckland and Campbell Islands, archaeological evidence indicates that this species bred on both North and South Island (Childerhouse and Gales, 1998; Collins et al., 2014b), and only recently became extinct due to human exploitation (Collins et al., 2014a). Our morphometric analysis clearly placed *N. palatina* within the morphospace of *Neophoca*, and we were unable to find any characters that link this taxon to *Phocarctos*. If *N. palatina* possessed a temperature tolerance similar to that possessed by *N. cinerea*, this would indicate that SSTs in New Zealand were warmer in the Middle Pleistocene than they are today.

However, paleoenvironmental reconstructions of SST during the Middle Pleistocene in the vicinity of New Zealand disagree and conclude that SSTs during interglacial periods were not significantly different from SSTs during the Holocene (King and Howard, 2000; Schaefer et al., 2005; Wilson et al., 2005). This suggests that *N. palatina* may have been more cold tolerant than *N. cinerea* and that adaptation of *N. cinerea* toward warmer environments is recent in origin. Furthermore, this provides evidence for a widespread distribution of *Neophoca*, with the extant *N. cinerea* currently relegated to southern and western Australia. Whether *Phocarctos* later immigrated to New Zealand after the local extinction of *Neophoca*, or was in part responsible for its extinction, is presently unknown. The limited pre-Holocene pinniped fossil record in New Zealand and Australia makes these hypotheses speculative, but further discovery and description of Australasian fossil pinnipeds will allow testing.

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Appendix. List of specimens examined for this study

Abbreviations for museum collections used in this study: AIM = Auckland War Memorial Museum; AM = Australian Museum; SAMA = South Australian Museum; NMV = Museum Victoria; OM = Otago Museum; OU = University of Otago Department of Geology; USNM = United States National Museum of Natural History.

Neophoca palatina: AIM Mamm 175.1

Neophoca cinerea (recent): AM M8945; M3124; SAMA M2480; M3219; M6163; M1263; M2003; M1256; M2477; M4942; M5077; M6263; M8674; M7472; M9040; M9041; M9545; M11,223; M11,636; M11,702; M11,704; M11,710; M12788; M13379; M15458; M15748; M15964; M15963; M16229;

Neophoca cinerea (fossil): NMV P12110; P21397

Phocarctos hookeri: AIM LM146; OM VT620; OM VT090; OM VT087; OM VT088; two unregistered specimens from the marine sciences department at University of Otago

Arctocephalus pusillus doriferus: AM S1656; M4750; M3714; S211; S1793; NMV C1987; C1991; C1988; SAMA M10,109; M25591; M23799; M22085; M22966; M22086; M14040; M15297; M15407; M15404; M15411; M15502; M15511; M15500; M15410; M15414; M15515; M15512; M15513; M15517; M15967; M22014; M25592

Arctophoca australis forsteri: AIM LM506; LM747; LM919; LM1504; LM1512; OM NC2011.73; VT534; VT3013; VT079; OU 22012; 22013; SAMA M22071; M22094; M22092; one unregistered specimen from the marine sciences department and one from the geology department from the University of Otago

Arctophoca gazella: AM M29116; M29113; M28914; M29111; M29121; M29120; M29110; M29114; M29117; M32062; M28910; M29119; M28912; M29122; M29109; M28913; M28913; M28915; M29115

Arctophoca tropicalis: NMV unregistered specimen; SAMA M18395; M17672; M24981

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