

Pliocene monachine seal (Pinnipedia: Phocidae) from Australia constrains timing of pinniped turnover in the Southern Hemisphere

Journal:	<i>Journal of Vertebrate Paleontology</i>
Manuscript ID	JVP-2019-0140.R3
Manuscript Type:	Short Communication
Date Submitted by the Author:	n/a
Complete List of Authors:	Rule, James; Monash University, Anatomy and Developmental Biology; Museum Victoria, Geosciences Hocking, David; Monash University, Biological Sciences Fitzgerald, Erich; Museum Victoria, Geosciences
Key Words:	Phocidae, Monachinae, postcanine tooth, Portland, Pliocene, pinniped turnover

SCHOLARONE™
Manuscripts

1
2
3 Pliocene monachine seal (Pinnipedia: Phocidae) from Australia constrains timing of pinniped
4 turnover in the Southern Hemisphere
5
6
7

8 JAMES P. RULE,^{*,1,2} DAVID P. HOCKING,^{2,3} and ERICH M.G. FITZGERALD^{2,3,4}
9

10 ¹Department of Anatomy and Developmental Biology, Biomedicine Discovery Institute,
11 Monash University, 10 Chancellors Walk, Clayton, Australia, jrule.palaeo@gmail.com;
12
13
14

15 ²Museums Victoria, Melbourne, Australia, efitzgerald@museum.vic.gov.au; ³School of
16 Biological Science, Monash University, 8 Innovation Walk, Clayton, Victoria, Australia,
17 david@dphocking.com; ⁴National Museum of Natural History, Smithsonian Institution,
18 Washington, DC, U.S.A.
19
20
21
22
23
24

25 RH: RULE, HOCKING AND FITZGERALD—PLIOCENE SEAL AUSTRALIA
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

INTRODUCTION

1
2
3
4
5
6 The Plio-Pleistocene witnessed major restructuring of marine megafauna
7
8 communities, resulting in the taxonomic and ecological **reorganization** of the global marine
9
10 mammal fauna (Boessenecker, 2013; Pimiento et al., 2017). Among pinnipeds (seals, sea
11
12 lions and walrus), faunal turnover events have been proposed across the Southern
13
14 Hemisphere's temperate latitudes (Olson, 1983; Valenzuela-Toro et al., 2013; Churchill et al.,
15
16 2014). This saw a switch from exclusively phocid (**seal**) faunas that prevailed for much of the
17
18 Neogene, to the recent austral pinniped fauna in which Otariidae (**fur seals and sea lions**)
19
20 dominate north of the Antarctic Circle, and phocids are primarily polar (Avery and Klein,
21
22 2011; Valenzuela-Toro et al., 2013; Churchill et al., 2014). By the late Pliocene, Otariidae
23
24 begin to appear in the fossil record of the Southern Hemisphere (de Muizon, 1978; Avery and
25
26 Klein, 2011). A record of *Homiphoca capensis* at ~3 Ma in South Africa (Pether, 1994;
27
28 Avery and Klein, 2011) is so far the youngest **Neogene** record of extinct Phocidae in the
29
30 Southern Hemisphere outside of the radiation of living genera (a record of ~2 Ma is likely to
31
32 be reworked; Avery and Klein, 2011).
33
34
35
36
37
38

39 While turnover events have been identified in South Africa and South America
40
41 (Olson, 1983; Valenzuela-Toro et al., 2013), there is little fossil evidence **available to**
42
43 **evaluate** the occurrence of a similar event in Australasia (Valenzuela-Toro et al., 2013).
44
45 Australian phocid fossils have so far been restricted to Victoria, from the late Miocene–early
46
47 Pliocene of Beaumaris, and early Pliocene of Hamilton (Fordyce and Flannery, 1983;
48
49 Fitzgerald, 2004). Specimens from the upper Pliocene of Portland were referred to
50
51 Pinnipedia, with only tentative assignment to Phocidae (Fitzgerald, 2005). The only other
52
53 pre-Pleistocene (≥ 2.6 Ma) phocids from Australasia are putative phocid fossils from the
54
55 Pliocene Tangahoe Formation (3.4–3.0 Ma) (McKee, 1994) of New Zealand. Additional
56
57 undescribed monachines have been reported from both Australia and New Zealand
58
59
60

1
2
3 (Fitzgerald et al., 2013), hinting at a greater diversity of Neogene phocids. **The early**
4 **Pleistocene pinnipeds from New Zealand are both phocids, but represent crown monachines;**
5 **a mandible from Napier represents the extant species *Ommatophoca rossii* (King, 1973),**
6 **while a fragmentary skull from Waipunga is a miroungin (Boessenecker and Churchill,**
7 **2016). The later Pleistocene Australasian record is mostly composed of otariids (McCoy,**
8 **1877; Gill, 1968; King, 1983). It is currently not known what pinnipeds occurred closer to the**
9 **Pleistocene.** New fossil evidence of pinnipeds from the end of the Neogene are therefore
10 required to determine whether a pinniped turnover event occurred in this region.
11
12
13
14
15
16
17
18
19
20
21

22 Here we describe the isolated postcanine tooth of a phocid from the mid upper
23 Pliocene (Zanclean–Piacenzian) Whalers Bluff Formation in Portland, Australia. Despite its
24 fragmentary nature, the currently meagre fossil record of pinnipeds in Australia makes the
25 discovery of even an isolated tooth noteworthy. Furthermore, it has implications for
26 understanding the **reorganization** of austral marine mammal diversity and ecology across the
27 Pliocene–Recent.
28
29
30
31
32
33
34
35
36
37
38
39

40 MATERIALS AND METHODS

41
42 The fossil is registered in the Museums Victoria Palaeontology Collection as NMV
43 P254064 (Phocidae postcanine). NMV P254064 was whitened with ammonium chloride and
44 photographed using a Nikon D610 DSLR with a Nikon AF-S 105mm Micro lens. Images
45 were photo-stacked using Photoshop CC 2017 (Adobe Systems Inc., San Jose, CA). This
46 study follows the most recent GSA geological timescale (Walker et al., 2013). We follow the
47 dental terminology of de Muizon (1981) and Amson and de Muizon (2014), specifically the
48 use of “main cuspid” and “accessory cuspid”. **This is** due to the difficulty of establishing cusp
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 homology in pinnipeds in relation to other Carnivora, and phocids in relation to stem
4
5 pinnipeds.
6
7

8 **Institutional Abbreviations**—**LACM**, Natural History Museum of Los Angeles
9
10 County, California, U.S.A; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires,
11
12 Argentina; **MEF**, Museo Paleontológico ‘Egidio Feruglio’, Trelew, Argentina; **MNHN**,
13
14 Muséum National d’Histoire Naturelle, Paris, France; **NMV**, Museums Victoria, Melbourne,
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
Australia.

SYSTEMATIC PALAEOLOGY

Order CARNIVORA Bowdich, 1821

Suborder PINNIPEDIA Illiger, 1811

Family PHOCIDAE Gray, 1821

Subfamily MONACHINAE Gray, 1869

MONACHINAE gen. et sp. indet.

41 **Referred Specimen**—NMV P254064, isolated lower postcanine tooth, collected by
42
43 M. Biasol in 1998.
44
45

46 **Locality**—NMV P254064 was collected as float (ex situ) on the foreshore along
47
48 Dutton Bluff, Portland, western Victoria, Australia (near 38°19’49.02” S, 141°36’27.79” E).
49
50

51 **Formation and Age**—The sparse matrix attached to the specimen is a yellow–brown
52
53 clay with quartz grains. The two fossiliferous units exposed in cliff sections at Portland are
54
55 the Miocene Port Campbell Limestone (Tortonian: 7.92–7.25 Ma) and the unconformably
56
57 overlying Pliocene Whalers Bluff Formation (Park et al., 2016). Because the lithology of the
58
59
60

1
2
3 Port Campbell Limestone at Portland (light grey calcisiltite, calcarenite and marl to white
4
5 chalky calcarenite and calcisiltite) is incompatible with that of the matrix adhering to NMV
6
7 P254064, it can be ruled out; this indicates derivation from the Pliocene Whalers Bluff
8
9
10 Formation.

11
12 At Portland, the Whalers Bluff Formation (WBF) consists of about 8 m of
13
14 fossiliferous interbedded clay, oyster beds, marl and sandy limestone deposited in a shallow
15
16 marine to estuarine environment (McLaren et al., 2011; Warne and Soutar, 2012). The WBF
17
18 at Portland is unconformably overlain by basalt K-Ar dated to 2.58 Ma, which constrains the
19
20 minimum age of deposition of the WBF (Singleton et al., 1976; Piper et al., 2006). The WBF
21
22 is moderately fossiliferous, its vertebrate assemblage including Chondrichthyes,
23
24 Sphenisciformes, Cetacea, Pinnipedia plus rare Marsupialia and Rodentia (Fitzgerald, 2004,
25
26 2005; Piper et al., 2006).

27
28
29
30
31 Estimates for the age of the WBF have ranged from early Pliocene to early
32
33 Pleistocene (Fitzgerald, 2005; Warne and Soutar, 2012). Age-diagnostic planktonic
34
35 foraminifera recovered from the WBF include: *Globorotalia crassaformis* (first occurrence
36
37 4.31 Ma); *Globorotalia margaritae* (last occurrence 3.85 Ma); *Globorotalia tosaensis* (first
38
39 occurrence 3.35 Ma); and *Globoturborotalita decoraperta* (last occurrence 2.75 Ma),
40
41 indicating deposition between Blow's (1969) zones N19 and N21 (Mallett, 1977; Dickinson
42
43 et al., 2002; Gradstein et al., 2012). $^{87}\text{Sr}/^{86}\text{Sr}$ measured from brachiopods yielded ages for the
44
45 WBF ranging from 3.52 Ma to 2.67 Ma (McLaren et al., 2011). Based on these data we
46
47 conservatively interpret the age of the Whalers Bluff Formation as between 4.31 and 2.67 Ma
48
49 (late Zanclean–late Piacenzian, mid–late Pliocene).

50
51
52
53
54 **Description**—NMV P254064 is a lower, double-rooted, multi-cuspsate right
55
56 postcanine tooth (Fig. 1). The crown is anteroposteriorly longer than high (Table 1), and
57
58 prominently overhangs the roots distally, with a slight overhang mesially. The surface of the
59
60

1
2
3 crown bears anastomosing ridges of enamel (apicobasal ridges: McCurry et al., 2019) on both
4
5 its buccal and lingual sides. The crown is dominated by a main cuspid located centrally and
6
7 making up a third of the crown. The worn occlusal surface reveals the main cuspid is
8
9 mesiodistally asymmetrical. In occlusal view the crown has an asymmetrical outline, being
10
11 convex buccally and nearly straight lingually. A distal accessory cuspid is located distolingual
12
13 to the posterior edge of the main cuspid, with which it is linked by a low crest. Mesial and
14
15 adjacent to the main cuspid is a mesial accessory cuspid, isolated from the main cuspid by an
16
17 inter-cuspid notch on the crown. The inter-cuspid notch is composed of a wear facet on the
18
19 mesiolingual edge of the main cuspid, with the slight wear apparent on the distal aspect of the
20
21 mesial accessory cuspid.
22
23
24
25
26

27 The cingulum is straight in lingual view, and of uneven thickness mesiodistally. It
28
29 projects lingually from the main cuspid and accessory cuspids, but not to the degree that a
30
31 shelf is present. The cingulum is distributed along the distal crown, projecting distally from
32
33 the mesial accessory cuspid. The cingulum is obliterated **in buccal view** at the main cuspid,
34
35 and around the mesial accessory cuspid **in lingual view**. The roots are nearly equal in size,
36
37 straight and meet basally at a relatively narrow angle.
38
39
40
41
42
43

44 COMPARISONS

45
46
47 NMV P254064 differs from the lower postcanine teeth of Otariidae and Odobenidae
48
49 by having **the following combination**: a crown length greater than the maximum mesiodistal
50
51 length of both roots; and two roots. **Differs from the lower postcanine teeth of**
52
53 **Desmatophocidae by having the following combination of features: a buccal cingulum; and a**
54
55 **flattened lingual cingula profile in occlusal view (as opposed to rounded).** The combination
56
57 of a buccolingually wide crown, apicobasal ridges on the crown, plus thickened buccal and
58
59
60

1
2
3 lingual cingula indicate that NMV P254064 represents a monachine phocid seal. Amongst
4
5 Monachinae, NMV P254064 can be differentiated from the postcanine teeth of: Miroungini
6
7 by having crowns bearing apicobasal ridges, cingula and being double rooted; Monachini by
8
9 having a narrow lingual cingulum at the level of the main cuspid that is not developed into a
10
11 broad shelf; and extant Lobodontini by having accessory cuspids that are apposed to the main
12
13 cuspid or linked to it via a carina.
14
15

16
17
18 The closely apposed cuspids of NMV P254064 are a feature it shares with the lower
19
20 postcanines of several fossil monachines, including *Acrophoca* spp., *Hadrokirus martini*,
21
22 *Homiphoca capensis*, *Piscophoca pacifica*, *Properiptychus argentinus*, specimens from the
23
24 Pliocene Yorktown Formation (North Carolina) debatably referred to *Callophoca obscura*
25
26 (Koretsky and Ray, 2008; Berta et al., 2015; Churchill and Uhen, 2019), and late Miocene
27
28 indeterminate Monachinae from the Monterey Formation of California (LACM 122584,
29
30 52624: Velez-Juarbe and Valenzuela-Toro, 2019); **this is in addition to the extant monachines**
31
32 ***Monachus* and *Neomonachus***. Additionally, NMV P254064 shares anastomosing apicobasal
33
34 ridges on the crown with the lower postcanines of *Hadrokirus martini*, *Homiphoca capensis*,
35
36 *Piscophoca pacifica*, *Properiptychus argentinus*, and the unnamed monachine represented by
37
38 LACM 52624. NMV P254064 can be differentiated from the lower postcanines of:
39
40
41 *Hadrokirus martini*, *Homiphoca capensis*, *Piscophoca pacifica*, and LACM 52624 by having
42
43 a weakly developed buccal cingulum at the level of the main cuspid; *Hadrokirus martini* and
44
45 *Properiptychus argentinus* by having a narrow distolingual cingulum that does not form a
46
47 distinct shelf; *Homiphoca capensis* and *Piscophoca pacifica* by having a nearly straight
48
49 lingual cingulum; LACM 52624 by having less salient apicobasal ridges on the buccal and
50
51 lingual surfaces of the crown; and *Acrophoca* spp. by having a narrower spacing between the
52
53
54
55
56
57 roots.
58
59
60

1
2
3 The preceding comparisons indicate that NMV P254064 represents an extinct species
4 of monachine phocid. Yet, its suite of characters combined with its fragmentary preservation
5 prevents referral to any described monachine genus.
6
7
8
9

10 11 12 13 14 DISCUSSION

15
16 At 4.31–2.67 Ma, the record of a monachine seal from the Pliocene Whalers Bluff
17 Formation of Portland (Victoria, Australia) is the geologically youngest pre-Holocene
18 occurrence of Phocidae in Australia, and one of the youngest pre-Quaternary records of
19 phocids in the Southern Hemisphere. Previously reported pre-Holocene fossil pinnipeds from
20 Australia consist of latest Miocene–early Pliocene (6.20–4.65 Ma) monachine phocids, and
21 late Pleistocene Otariidae from Victoria (McCoy, 1877; Gill, 1968; Fordyce and Flannery,
22 1983; Piper et al., 2006; Dickinson and Wallace, 2009; Churchill and Boessenecker, 2016).
23 The seal from the Pliocene of Portland fills a gap in the fossil record of pinnipeds, extending
24 the possible range of the occurrence of monachines in the fossil record of Australia to 6.2–
25 2.67 Ma. This indicates that there was likely a phocid dominant (possibly exclusive) pinniped
26 fauna until close to the end of the Neogene, because no confirmed otariid fossils occur in
27 deposits older than late Pleistocene in age in Australia, and middle Pleistocene in age in New
28 Zealand.
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46

47 Furthermore, the Portland Pliocene monachine does not represent a species of
48 *Mirounga* or any of the extant genera of Lobodontini, and is thus evidence of extinct
49 monachines persisting in southern Australia until middle or even late Pliocene times. It is
50 somewhat surprising that we do not find more evidence of the modern Tribes of Monachinae
51 along the southern margin of Australia, especially given the Australian Quaternary record,
52 and the close proximity to the Southern Ocean (the centre of modern monachine diversity).
53
54
55
56
57
58
59
60

1
2
3 Post-Neogene evidence of phocids in Australasia include *Ommatophoca* (Ross seal) during
4 the early Pleistocene (Gelasian, 2.58–1.81 Ma) of New Zealand (King, 1973; Beu, 2001), a
5 fragmentary miroungin from the early Pleistocene of New Zealand (2.4–2.1 Ma;
6
7 Boessenecker and Churchill, 2016), and historical breeding populations of *Mirounga leonina*
8 (southern elephant seal) on King Island and Tasmania (Bryden et al., 1999). These taxa
9
10 represent modern Antarctic to sub-Antarctic monachines, and possibly coexisted in
11
12 Australasian waters with Otariidae in the Quaternary. Fossil evidence of Otariidae in the
13
14 Pleistocene of New Zealand (Fleming, 1968; King, 1983; Worthy, 1992; Beu, 2001) and
15
16 Australia (McCoy, 1877; Gill, 1968; Reed and Bourne, 2000) demonstrate that otariids were
17
18 the most ecologically important and abundant pinnipeds in the region during this time period.
19
20 In the modern context, *Ommatophoca* is restricted to Antarctica, and *Mirounga leonina* no
21
22 longer breeds in Australian waters, meaning the modern fauna is composed exclusively of
23
24 breeding populations of otariids, with a few isolated exceptions (Acevedo et al., 2017;
25
26 Acevedo et al., 2019; Hupman et al., 2019). Modern Antarctic phocids only occur in
27
28 Australasian waters as vagrants (Shaughnessy et al., 2012); however, it should be noted that
29
30 several occurrences of breeding by *Hydrurga leptonyx* in New Zealand has led to the
31
32 suggestion they should be reclassified as resident (Hupman et al., 2019). As such, it would
33
34 appear that there is a lack of evidence of the modern pinniped fauna in the Neogene, with
35
36 evidence of the modernisation not occurring in the fossil record until at least the early
37
38 Pleistocene.
39
40
41
42
43
44
45
46
47
48

49 The discovery of this specimen has implications for our understanding of the
50
51 evolutionary history of pinnipeds, both in Australia and for the Southern Hemisphere as a
52
53 whole. Along with occurrences of *Homiphoca capensis* in the late Pliocene of South Africa
54
55 (~3 Ma; Avery and Klein, 2011), and phocid fossils from the early Pliocene of Chile (5.3–
56
57 3.6; Valenzuela-Toro et al., 2013) the Portland postcanine represents one of the last remnants
58
59
60

1
2
3 of extinct Phocidae in the Southern Hemisphere before the faunal turnover that saw otariids
4 come to dominance. An occurrence in Peru of a fossil otariid (*Hydrarctos lomasiensis*) in the
5 late Pliocene–early Pleistocene (de Muizon, 1978; de Muizon and Devries, 1985; de Muizon
6 and Domning, 1985) and palaeobiogeographic models (Yonezawa et al., 2009; Churchill et
7 al., 2014) indicate that the dispersal of otariids as part of pinniped faunal turnover events
8 began in the eastern-north Pacific. While an occurrence of *Arctocephalus* sp. has been
9 recorded from the Pliocene of South Africa as 5–2.7 Ma, it likely represents an occurrence
10 closer to 3.6–2.7 Ma (Avery and Klein, 2011). These fossil occurrences from South America
11 and Africa, along with palaeobiogeographic studies, indicate that early otariids colonised
12 South Africa from the eastern South American coastline (Yonezawa et al., 2009; Churchill et
13 al., 2014).

14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
The Portland postcanine indicates that a pinniped faunal turnover event occurred later
in Australasia compared to other regions. Phocids were still present in Australia during the
Zanclean–Piacenzian (Fig. 2), while there is no evidence for otariids at this time (Fitzgerald,
2005). It is therefore likely that the pinniped faunal turnover in the Southern Hemisphere
occurred almost entirely during the late Pliocene, with the turnover in Australia occurring
sometime after 4.31 Ma.

While various occurrences of *H. capensis* and *Arctocephalus* at different sites in
South Africa seem to overlap in age (Avery and Klein, 2011), this may be due to the poor age
constraints currently associated with these occurrences (a 2 Ma occurrence of *Homiphoca* has
been suggested to be reworked; Avery and Klein, 2011). The only other co-occurrence of
phocids with otariids in the fossil record are Pleistocene records of extant Antarctic
monachines (King, 1973; Avery and Klein, 2011; Valenzuela-Toro et al., 2013; Valenzuela-
Toro et al., 2015). As it currently stands, there are no reported occurrences of Otariidae and
extinct Phocidae in the same fossil locality in the Southern Hemisphere. The only other noted

1
2
3 co-occurrence of phocids and otariids in the pre-Pleistocene fossil record is from the upper
4 Monterey Formation (8.5–7.7 Ma) in Southern California (Velez-Juarbe and Valenzuela-
5 Toro, 2019). While this demonstrates that phocids coexisted with otariids and odobenids in
6 the North Pacific, this pattern of pinniped diversity is not reflected outside this region until
7 after the Neogene.
8
9
10
11
12
13
14

15
16 Mystery remains over whether otariids outcompeted phocids in the Southern
17 Hemisphere, or occupied a vacant niche after their extinction. It is also unclear whether the
18 pinniped turnover represents a singular event, or multiple diachronous events. This is difficult
19 to assess to due the incompleteness of the fossil record. However, it may be that the pinniped
20 turnover event (or events) are part of a much larger restructuring of marine vertebrate
21 diversity at the end of the Pliocene (Boessenecker, 2013; Pimiento et al., 2017). Loss of
22 coastal habitat availability (linked to a sea level drop due to northern hemisphere glaciation)
23 has been suggested as a potential mechanism for Pliocene marine megafauna extinctions
24 (Boessenecker, 2013; Pimiento et al., 2017). Loss of coastal habitat could potentially also be
25 the driver of pinniped turnover events (Valenzuela-Toro et al., 2013). This turnover of
26 phocids with otariids likely indicates the timing of the modernisation of not only the pinniped
27 faunas of the Southern Hemisphere, but also the timing of the modernisation of Southern
28 Hemisphere marine faunas as a whole.
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

50 CONCLUSIONS

51
52 The Portland postcanine represents one of the few confirmed occurrences of Phocidae
53 in the Southern Hemisphere's later Pliocene fossil record. This specimen demonstrates that
54 extinct phocids were persisting in Australia until the mid-late Pliocene. By this time, otariids
55 had colonised South America (de Muizon, 1978) and South Africa (Avery and Klein, 2011).
56
57
58
59
60

1
2
3 As it stands (with the current absence of otariids in mid–late Pliocene of Australia and New
4 Zealand) this corroborates previously proposed patterns of dispersal for Otariidae (Yonezawa
5 et al., 2009), and constrains the occurrence of the pinniped turnover event to sometime after
6 the mid-Pliocene. This unassuming fossil therefore hints at possible large-scale patterns of
7 restructuring for the vertebrate fauna throughout the Southern Hemisphere’s marine
8 ecosystems.
9
10
11
12
13
14
15
16

17 ACKNOWLEDGEMENTS

18
19 J.P.R. is supported by an Australian Government RTP stipend scholarship, and a Robert
20 Blackwood Partnership PhD scholarship. D.P.H. was supported by an Australian Research
21 Council Discovery Project (DP180101797). M. Biasol is thanked for discovering NMV
22 P254064 and generously donating it to Museums Victoria. The following museums and staff
23 are thanked for facilitating access to collections: Museo Paleontológico ‘Egidio Feruglio’
24 (Eduardo Ruigomez); Museums Victoria (T. Ziegler, K. Roberts, K. Date, R-L. Erickson, K.
25 Rowe); the Natural History Museum London (R. Miguez, P. Jenkins); Muséum national
26 d'Histoire naturelle (C. Muizon, G. Billet); Smithsonian Institution National Museum of
27 Natural History (J. Mead, J. Ososky, M. McGowen, D. Lunde, D. Bohaska, N. Pyenson); and
28 the Natural History Museum of Los Angeles County (J. Velez-Juarbe). The Version of
29 Record of this manuscript has been published and is available in Journal of Vertebrate
30 Paleontology 03 Apr 2020
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45

46 <https://www.tandfonline.com/doi/abs/10.1080/02724634.2019.1734015>

49 LITERATURE CITED

50
51
52 Acevedo, J., R. Vargas, D. Torres, and A. Aguayo-Lobo. 2019. Northerly
53 births of the Southern Elephant Seal (*Mirounga leonina*) in Their Former Southeast Pacific
54 Distribution. *Aquatic Mammals* 45:293–298.
55
56
57
58
59

60 Acevedo, J., R. Vargas, D. Torres, and A. Aguayo-Lobo. 2019. Northerly Births of the

- 1
2
3 Acevedo, J., A. González, S. Garthe, I. González, R. Gómez, and A. Aguayo-Lobo. 2017.
4
5 Births of leopard seals *Hydrurga leptonyx* in southern Chile. *Polar Biology* 40:713–
6
7 717.
8
9
10 Amson, E., and C. de Muizon. 2014. A new durophagous phocid (Mammalia: Carnivora)
11
12 from the late Neogene of Peru and considerations on monachine seals phylogeny.
13
14 *Journal of Systematic Palaeontology* 12:523–548.
15
16
17 Avery, G., and R. G. Klein. 2011. Review of fossil phocid and otariid seals from the southern
18
19 and western coasts of South Africa. *Transactions of the Royal Society of South Africa*
20
21 66:14–24.
22
23
24 Berta, A., S. Kienle, G. Bianucci, and S. Sorbi. 2015. A Reevaluation of *Pliophoca etrusca*
25
26 (Pinnipedia, Phocidae) from the Pliocene of Italy: Phylogenetic and Biogeographic
27
28 Implications. *Journal of Vertebrate Paleontology* 35:e889144.
29
30
31 Beu, A. 2001. Local stages to be used for the Wanganui Series (Pliocene–Pleistocene), and
32
33 their means of definition. *New Zealand Journal of Geology and Geophysics* 44:113–
34
35 125.
36
37
38 Blow, W. H. 1969: Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy.
39
40 *Proceedings of the first international conference on planktonic microfossils, 1969.*
41
42
43 Boessenecker, R., and M. Churchill. 2016. The origin of elephant seals: implications of a
44
45 fragmentary late Pliocene seal (Phocidae: Miroungini) from New Zealand. *New*
46
47 *Zealand Journal of Geology and Geophysics* 59:544–550.
48
49
50 Boessenecker, R. W. 2013. A new marine vertebrate assemblage from the Late Neogene
51
52 Purisima Formation in Central California, part II: Pinnipeds and Cetaceans.
53
54 *Geodiversitas* 35:815–941.
55
56
57 Bowdich, T. E. 1821. An analysis of the natural classifications of Mammalia: for the use of
58
59 students and travellers. J. Smith, Paris.
60

- 1
2
3 Bryden, M., S. O'Connor, and R. Jones. 1999. Archaeological evidence for the extinction of a
4 breeding population of elephant seals in Tasmania in prehistoric times. *International*
5 *Journal of Osteoarchaeology* 9:430–437.
6
7
8
9
10 Churchill, M., and R. W. Boessenecker. 2016. Taxonomy and biogeography of the
11 Pleistocene New Zealand sea lion *Neophoca palatina* (Carnivora: Otariidae). *Journal*
12 *of Paleontology* 90:375–388.
13
14
15
16 Churchill, M., and M. D. Uhen. 2019. Taxonomic implications of morphometric analysis of
17 earless seal limb bones. *Acta Palaeontologica Polonica* 64:213–230.
18
19
20
21 Churchill, M., R. W. Boessenecker, and M. T. Clementz. 2014. Colonization of the Southern
22 Hemisphere by fur seals and sea lions (Carnivora: Otariidae) revealed by combined
23 evidence phylogenetic and Bayesian biogeographical analysis. *Zoological Journal of*
24 *the Linnean Society* 172:200–225.
25
26
27
28
29
30 de Muizon, C. 1978. *Arctocephalus (Hydrarctos) lomasiensis*, subgen, nov. et nov. sp., un
31 nouvel Otariidae du Mio-Pliocene de Sacaco (Perou). *Bulletin de l'Institut Francais*
32 *des Etudes Andines* 7:169–188.
33
34
35
36
37 de Muizon, C. 1981. Les vertébrés fossiles de la Formation Pisco (Pérou). Première partie,
38 deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocene de Sud-Sacaco.
39 *Memoire de l'Institut Francais d'Etudes Andines* 50:1–88.
40
41
42
43
44 de Muizon, C., and M. Bond. 1982. Le Phocidae (Mammalia) Miocene de la formation
45 Parana (Entre Rios, Argentine). *Bulletin du Muséum National d'Histoire Naturelle,*
46 *section C, 4eme série* 4:165–207.
47
48
49
50
51 de Muizon, C., and T. J. Devries. 1985. Geology and paleontology of late Cenozoic marine
52 deposits in the Sacaco area (Peru). *Geologische Rundschau* 74:547–563.
53
54
55
56
57
58
59
60

- 1
2
3 de Muizon, C., and D. Domning. 1985. The first records of fossil sirenians in the southeastern
4 Pacific Ocean. *Bulletin du Muséum national d'histoire naturelle. Section C, Sciences*
5
6 *de la terre, paléontologie, géologie, minéralogie* 7:189–213.
7
8
9
10 Dickinson, J. A., and M. W. Wallace. 2009. Phosphate-rich deposits associated with the Mio–
11
12 Pliocene unconformity in south–east Australia. *Sedimentology* 56:547–565.
13
14 Dickinson, J. A., M. W. Wallace, G. R. Holdgate, S. J. Gallagher, and L. Thomas. 2002.
15
16 Origin and timing of the Miocene–Pliocene unconformity in southeast Australia.
17
18 *Journal of Sedimentary Research* 72:288–303.
19
20
21 Fitzgerald, E. M. G., D. Hastie, J. Buckeridge, and P. Scofield. 2013. Earliest seals from
22
23 Australasia reveal colonization of the Southern Ocean by archaic Monachinae
24
25 (Phocidae). *Journal of Vertebrate Paleontology, Program and Abstracts*:127–128.
26
27
28 Fitzgerald, E. M. G. 2004. A review of the Tertiary fossil Cetacea (Mammalia) localities in
29
30 Australia. *Memoirs of Museum Victoria* 61:183–208.
31
32
33 Fitzgerald, E. M. G. 2005. Pliocene marine mammals from the Whalers Bluff formation of
34
35 Portland, Victoria, Australia. *Memoirs of Museum Victoria* 62:67–89.
36
37
38 Fleming, C. 1968. Notes from the New Zealand Geological Survey—5: New Zealand fossil
39
40 seals. *New Zealand Journal of Geology and Geophysics* 11:1184–1187.
41
42
43 Fordyce, R., and T. Flannery. 1983. Fossil phocid seals from the late Tertiary of Victoria.
44
45 *Proceedings of the Royal Society of Victoria* 95:99–100.
46
47
48 Gill, E. D. 1968. Fossil sea lion as a palaeoclimatologic indicator. *Palaeogeography,*
49
50 *Palaeoclimatology, Palaeoecology* 5:235–239.
51
52
53 Gradstein, F. M., J. G. Ogg, M. Schmitz, and G. Ogg. 2012. The geologic time scale 2012.
54
55 Elsevier.
56
57
58 Gray, J. 1869. XLI.—Notes on seals (Phocidæ) and the changes in the form of their lower
59
60 jaw during growth. *Journal of Natural History* 4:342–346.

- 1
2
3 Gray, J. E. 1821. On the natural arrangement of vertebrate animals. London medical
4 repository 15:296–310.
5
6
7
8 Hupman, K., I. N. Visser, J. Fyfe, M. Cawthorn, G. Forbes, A. A. Grabham, R. Bout, B.
9 Mathias, E. Benninghaus, and K. Matucci. 2019. From Vagrant to Resident:
10 occurrence, residency and births of leopard seals (*Hydrurga leptonyx*) in New Zealand
11 waters. New Zealand Journal of Marine and Freshwater Research: 1–23.
12
13
14
15 Illiger, C. 1811. Prodrum Systematis Mammalium et Avium Additis Terminis Zoographicis
16 Utriusque Classis. xviii+ 301 pages. Berlin. C. Salfeld.
17
18
19
20
21 King, J. E. 1973. Pleistocene Ross Seal (*Ommatophoca rossi*) From New Zealand (Note).
22 New Zealand Journal of Marine and Freshwater Research 7:391–397.
23
24
25
26 King, J. E. 1983. The Ohope skull—a new species of Pleistocene sealion from New Zealand.
27 New Zealand Journal of Marine and Freshwater Research 17:105–120.
28
29
30
31 Koretsky, I. A., and C. E. Ray. 2008. Phocidae of the Pliocene of eastern USA. Virginia
32 Museum of Natural History Special Publication 14:81–140.
33
34
35
36 Mallett, C. W. 1977. Studies in Victorian Tertiary foraminifera neogene planktonic faunas.
37 Doctoral dissertation, Melbourne University, Melbourne, Victoria, pp.
38
39
40
41 McCoy, F. 1877. Prodrum of the Palaeontology of Victoria, Decade 5. Geological Survey
42 of Victoria: Melbourne)(fide Gill, 1951).
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
- McCurrey, M. R., A. R. Evans, E. M. G. Fitzgerald, C. R. Mchenry, J. Bevitt, and N. D.
Pyenson. 2019. The repeated evolution of dental apicobasal ridges in aquatic-feeding
mammals and reptiles. Biological Journal of the Linnean Society 127:245–259.
- McKee, J. 1994. Geology and vertebrate palaeontology of the Tangahoe Formation, South
Taranaki Coast, New Zealand. Geological Society of New Zealand Miscellaneous
Publications B 80:63–91.

- 1
2
3 McLaren, S., M. W. Wallace, S. J. Gallagher, J. A. Miranda, G. R. Holdgate, L. J. Gow, I.
4
5 Snowball, and P. Sandgren. 2011. Palaeogeographic, climatic and tectonic change in
6
7 southeastern Australia: the Late Neogene evolution of the Murray Basin. *Quaternary*
8
9 *Science Reviews* 30:1086–1111.
10
11
12 Olson, S. 1983. Fossil seabirds and changing marine environments in the Late Tertiary of
13
14 South Africa. *South African Journal of Science* 79:399–402.
15
16
17 Park, T., E. M. G. Fitzgerald, S. J. Gallagher, E. Tomkins, and T. Allan. 2016. New Miocene
18
19 Fossils and the History of Penguins in Australia. *PLoS One* 11:e0153915.
20
21
22 Pether, J. 1994. The sedimentology, palaeontology and stratigraphy of coastal-plain deposits
23
24 at Hondeklip Bay, Namaqualand, South Africa. Doctoral dissertation, University of
25
26 Cape Town, Cape Town, pp.
27
28
29 Pimiento, C., J. N. Griffin, C. F. Clements, D. Silvestro, S. Varela, M. D. Uhen, and C.
30
31 Jaramillo. 2017. The Pliocene marine megafauna extinction and its impact on
32
33 functional diversity. *Nature ecology & evolution* 1:1100–1106.
34
35
36 Piper, K. J., E. M. G. Fitzgerald, and T. H. Rich. 2006. Mesozoic to early Quaternary
37
38 mammal faunas of Victoria, south–east Australia. *Palaeontology* 49:1237–1262.
39
40
41 Reed, E. H., and S. Bourne. 2000. Pleistocene fossil vertebrate sites of the South East region
42
43 of South Australia. 124:61–90.
44
45
46 Shaughnessy, P. D., C. M. Kemper, and J. K. Ling. 2012. Records of vagrant phocid seals
47
48 (family Phocidae) in South Australia. *Australian Mammalogy* 34:155–169.
49
50
51 Singleton, O., I. McDougall, and C. Mallett. 1976. The Pliocene–Pleistocene boundary in
52
53 Southeastern Australia. *Journal of the Geological Society of Australia* 23:299–311.
54
55
56 Valenzuela-Toro, A. M., C. S. Gutstein, R. M. Varas-Malca, M. E. Suarez, and N. D.
57
58 Pyenson. 2013. Pinniped turnover in the South Pacific Ocean: new evidence from the
59
60

1
2
3 Plio–Pleistocene of the Atacama Desert, Chile. *Journal of Vertebrate Paleontology*
4
5 33:216–223.
6

7
8 Valenzuela-Toro, A. M., C. S. Gutstein, M. E. Suarez, R. Otero, and N. D. Pyenson. 2015.
9
10 Elephant seal (*Mirounga* sp.) from the Pleistocene of the Antofagasta Region,
11
12 northern Chile. *Journal of Vertebrate Paleontology* 35:e918883.
13

14
15 Velez-Juarbe, J., and A. M. Valenzuela-Toro. 2019. Oldest record of monk seals from the
16
17 North Pacific and biogeographic implications. *Biology letters* 15:20190108.
18

19
20 Walker, J. D., J. W. Geissman, S. Bowring, and L. Babcock. 2013. The Geological Society of
21
22 America geologic time scale. *Bulletin* 125:259–272.
23

24
25 Warne, M. T., and B. Soutar. 2012. Pliocene coastal palaeomorphology and ostracod faunas
26
27 of the Bass Strait hinterland, southeast Australia. *Hydrobiologia* 688:93–112.
28

29
30 Worthy, T. 1992. Fossil bones of Hooker’s sea lions in New Zealand caves. *New Zealand*
31
32 *Natural Sciences* 19:31–39.
33

34
35 Yonezawa, T., N. Kohno, and M. Hasegawa. 2009. The monophyletic origin of sea lions and
36
37 fur seals (Carnivora; Otariidae) in the Southern Hemisphere. *Gene* 441:89–99.
38

39
40 Submitted October 15, 2019; revisions received Month DD, YYYY; accepted Month DD,
41
42 YYYY.
43

44
45 FIGURE 1. **A**, Location of NMV P254064 locality (Whaler’s Bluff Formation), and NMV
46
47 P254064 right lower postcanine in **B**, buccal view, **C**, lingual view, and **D**, occlusal view.
48
49 [planned for page width]
50

51
52 FIGURE 2. **Summary of the fossil record of pinnipeds in the Southern Hemisphere during the**
53
54 **Neogene, with silhouettes representing Phocidae and Otariidae. Stars represent rough**
55
56 **geographic provenance and do not equate to site or formation.** [planned for page width]
57
58
59
60

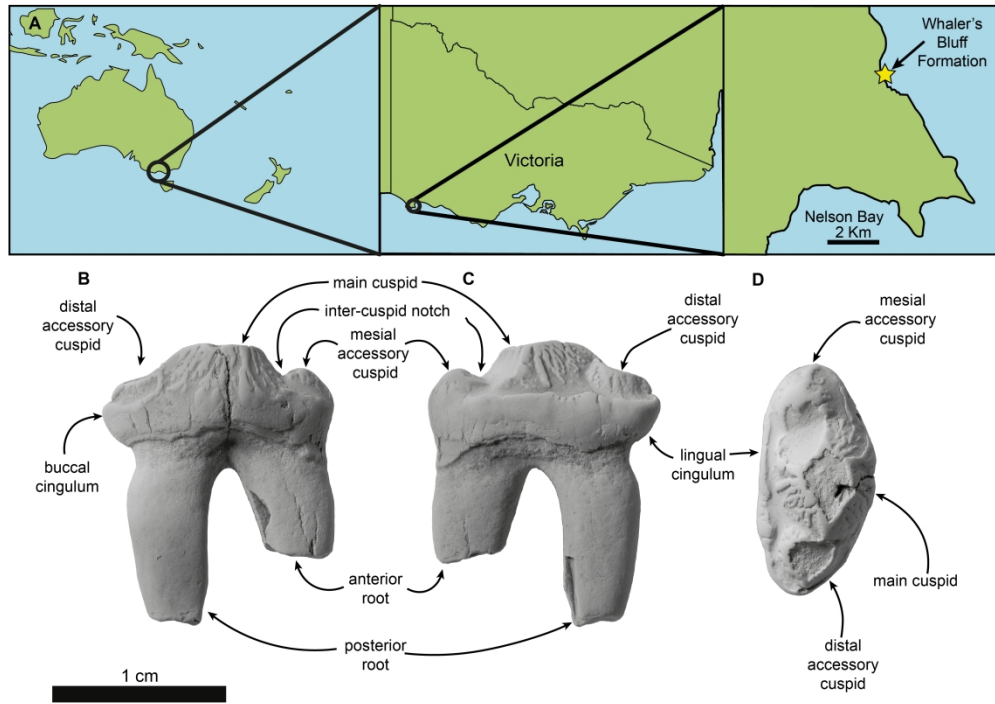


FIGURE 1. A, Location of NMV P254064 locality (Whaler's Bluff Formation), and NMV P254064 right lower postcanine in B, buccal view, C, lingual view, and D, occlusal view. [planned for page width]

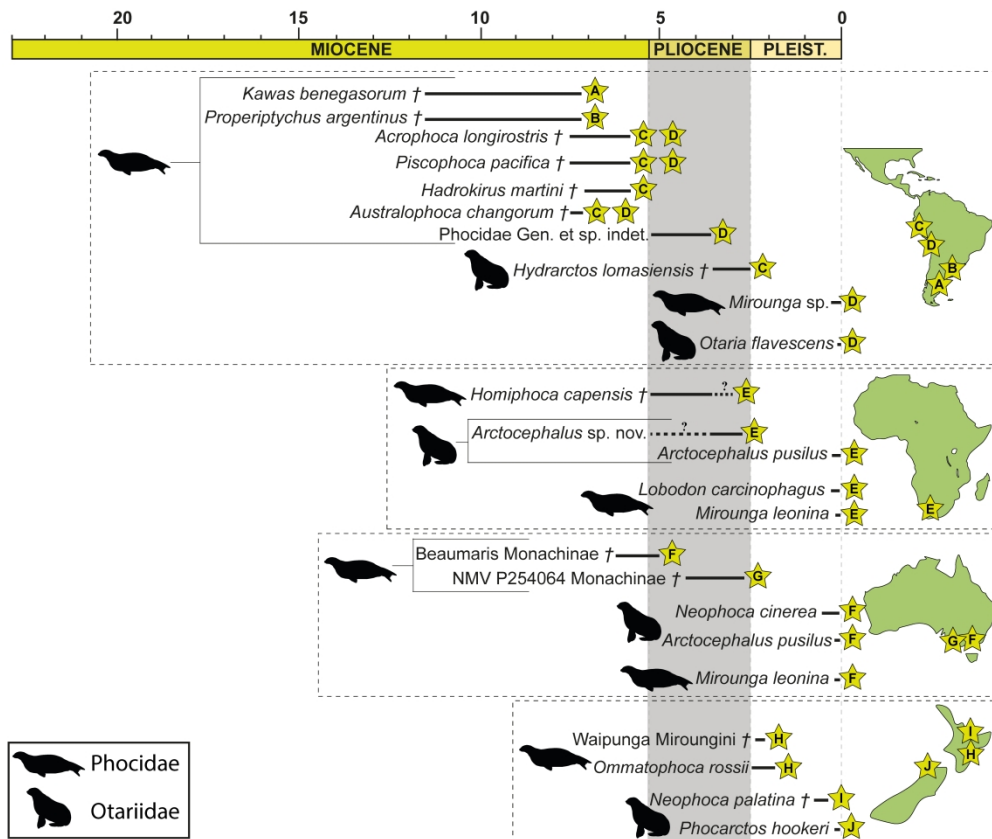


FIGURE 2. Summary of the fossil record of pinnipeds in the Southern Hemisphere during the Neogene, with silhouettes representing Phocidae and Otariidae. Stars represent rough geographic provenance and do not equate to site or formation. [planned for page width]

TABLE 1. Comparative linear metrics of lower phocid postcanines. Asterisk (*) indicates incomplete measurement due to preservation. Plus symbol (+) means specimen is a p4,
^aVelez-Juarbe and Valenzuela-Toro 2019, ^bAmson and de Muizon 2014, ^cde Muizon and Bond 1982.

Measurement	Metric (mm)					
	NMV P254064	LACM 122584 ^{a,+}	MNHN.F. SAS 644 ^{a,+}	MNHN.F. .SAS 1627 ^{b,+}	MACN 3538b ^{c,+}	MPEF- PV601
	Monachinae gen. et sp. indet.	Monachinae gen. et sp. indet.	<i>Acrophoc</i> <i>a</i> <i>longirost</i> <i>ris</i>	<i>Hadrokir</i> <i>us</i> <i>martini</i>	<i>Properipty</i> <i>chus</i> <i>argentinus</i>	<i>Kawas</i> <i>benegas</i> <i>orum</i>
Maximum height (crown and root)	16.28*	-	-	-	-	-
Mesial-distal length	13.51	12.7	15.5	16	12.8	11.65
Buccal-Lingual width	6.78	6.2	5.2	8.8	7	5.5
Maximum crown height	5.4*	6.8	7.5	8.7	7	4.7*
Mesial root length	10.1	-	-	-	-	-
Distal root length	6.45*	-	-	-	-	-
Main cuspid height	3.0*	-	-	-	-	-
Mesial accessory cuspid height	1.3*	-	-	-	-	-
Distal accessory cuspid height	2.06	-	-	-	-	-

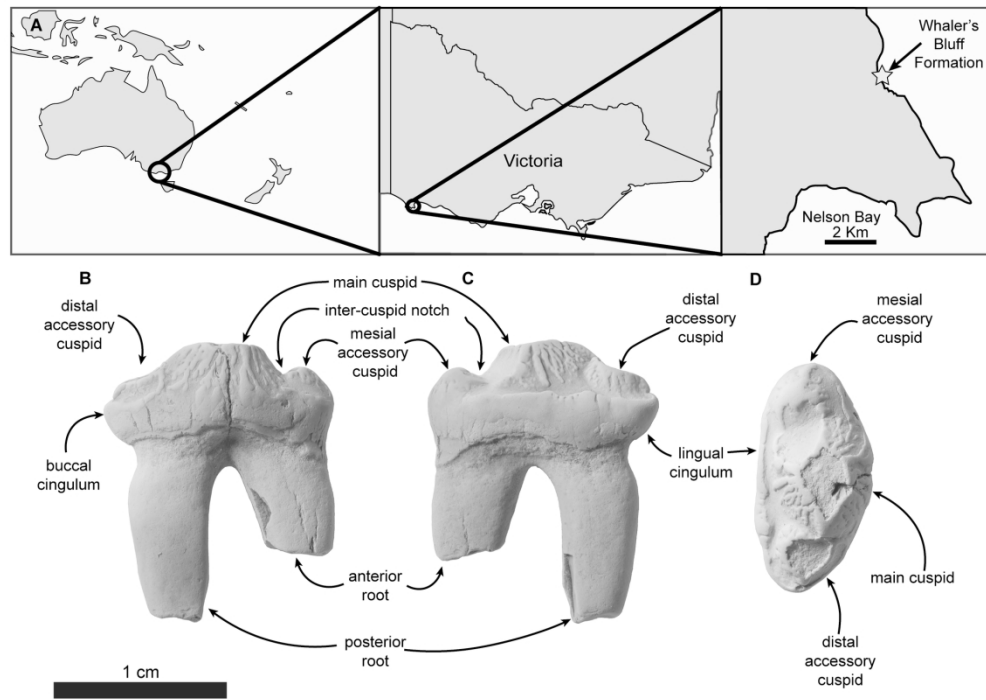


FIGURE 1. A, Location of NMV P254064 locality (Whaler's Bluff Formation), and NMV P254064 right lower postcanine in B, buccal view, C, lingual view, and D, occlusal view. [planned for page width]

183x129mm (300 x 300 DPI)

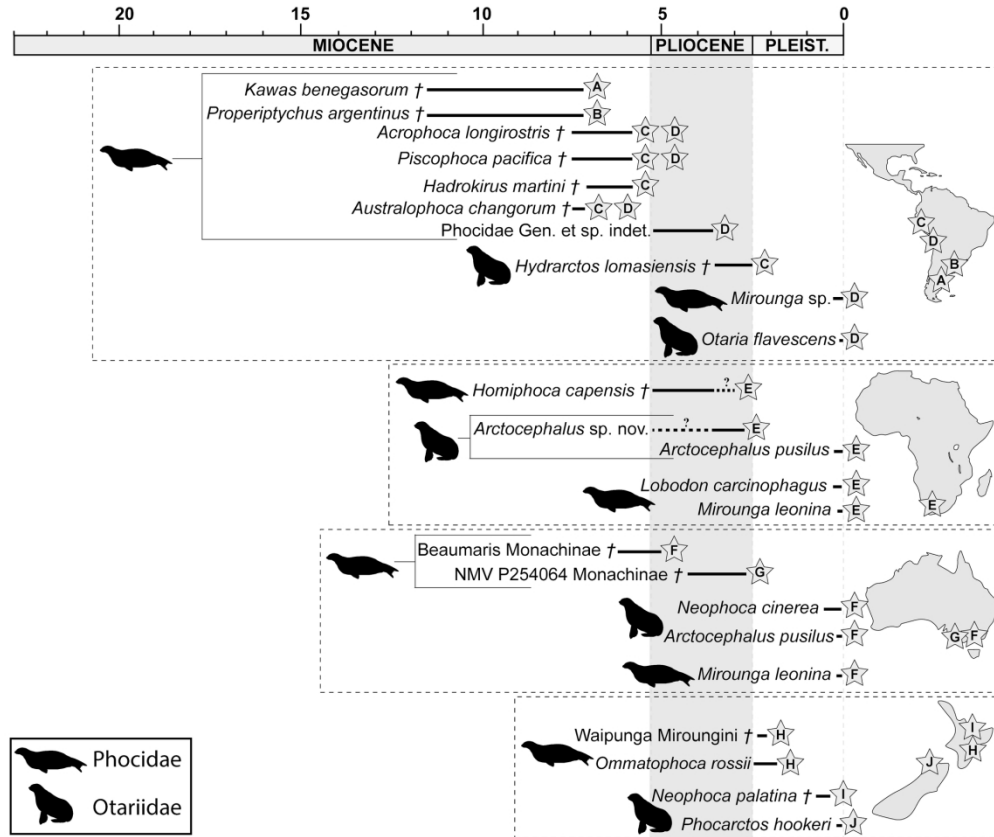


FIGURE 2. Summary of the fossil record of pinnipeds in the Southern Hemisphere during the Neogene, with silhouettes representing Phocidae and Otariidae. Stars represent rough geographic provenance and do not equate to site or formation. [planned for page width]

183x153mm (300 x 300 DPI)