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A PROBABLE HYBRID SEA LION—*ZALOPHUS CALIFORNIANUS* × *OTARIA BYRONIA*

Sylvia Brunner*

Department of Veterinary Anatomy & Pathology, University of Sydney,
Sydney 2006, New South Wales, Australia
Present address: P.O. Box 84983, Fairbanks, AK 99708

A recent taxonomic review of the Otariidae, based on morphometric techniques applied to skulls, revealed a number of specimens with cranial morphology divergent from typical otariid species. The specimen considered in this paper was a large adult male otariid with cranial morphology most similar to the California sea lion, *Zalophus californianus*, but differing from it in significantly greater condylobasal length and rostral and palatal structure. Discriminant function analyses were applied to compare the cranial morphology of the anomalous specimen with those of 7 otariid taxa: the Steller sea lion, *Eumetopias jubatus*; the southern sea lion, *Otaria byronia*; the California sea lion, *Z. californianus californianus*; the Galapagos sea lion, *Z. c. wollebaeki*; and the presumed-extinct Japanese sea lion, *Z. c. japonicus*. Results suggest that the aberrant skull was that of a hybrid between *Z. californianus* and *O. byronia*.

Key words: hybrid, morphometrics, *Otaria byronia*, sea lion, skull, *Zalophus californianus*

The presence of intergeneric hybrids is well known among the otariids (King 1983; Miller et al. 1996; Scheffer 1958). The high incidence of hybridization is perhaps not surprising, given that otariids breed in high-density, polygynous, and occasionally sympatric colonies (Gentry 1998); have significant vagrant tendencies (Rice 1998); and, like many marine mammals, possess low genetic variability (Bonnell and Selander 1974; Lento et al. 1997; Lidicker et al. 1981; Testa 1986). To date, the greatest number of hybrid otariids have been identified as interspecific crosses within the genus *Arctocephalus*. For example, the Antarctic fur seal, *A. gazella*, crosses with the subantarctic fur seal, *A. tropicalis*, with some regularity (Condy 1978; Goldsworthy et al. 1998; Kerley and Robinson 1987; Shaughnessy and Fletcher 1987), although viability of the offspring is currently unknown. Lento et al. (1997) found few genetic differences between these 2 species. Samples examined by Lento et al. (1997) were collected from an area where breeding ranges for *A. tropicalis* and *A. gazella* were sympatric; these authors suggest that genetic similarities could be the result of extensive hybridization between the 2 species. Brunner (1998a) identified a hybrid between *A. gazella* and the New Zealand fur seal, *A. forsteri*, using cranial morphometrics, and Shaughnessy et al. (1998) identified a hybrid between these 2 species on Macquarie Island, Australia, based on allozyme analysis.

Some accounts of interspecific hybrids in other otariids have been published, and intergeneric sexual behavior has been recorded. Copulations have been observed between several genera: the Steller sea lion, *Eumetopias jubatus*, and the California sea lion, *Zalophus californianus californianus*; the southern sea lion, *Otaria byronia*, and

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* *Correspondent: fnsb@uaf.edu*

the South American fur seal, *A. australis*; and the New Zealand sea lions, *Phocarctos hookeri* and *A. forsteri* (Miller et al. 1996). This behavior may result in substantial introgression throughout the evolutionary history of the Otariidae and may retard or obscure patterns of speciation and phylogenesis (Berta and Deméré 1986; Stirling and Warneke 1971). Intergeneric hybridization also strongly negates the validity of subfamilial segregation within the family Otariidae (Brunner 2000).

A recent cranial morphometric study of the Otariidae revealed a number of specimens with cranial morphology not clearly assignable to any specific species of otariid (Brunner 2000). Most of the anomalous specimens were phenotypic variations of the genus *Arctocephalus* and were all identified as males. The specimen considered in this study was not an aberrant form of *Arctocephalus*. It was a large adult male with cranial morphology similar to that of *Zalophus*. The morphology of the skull indicates that the specimen may be either an extreme outlier of that genus or a hybrid between *Zalophus* and another large otariid with which *Zalophus* is, or was, sympatric. The most probable species that occur within, or near, the range of *Zalophus* are *E. jubatus* and *O. byronia*. The subspecies *Z. c. californianus* occurs sympatrically with *E. jubatus* along the California coast, whereas the Galapagos sea lion, *Z. c. wollebaeki*, inhabits the Galapagos Islands, situated west of the Peruvian coast. The northern Peruvian coast forms part of the upper range of *O. byronia*. There are also recently published records of *Zalophus* in Costa Rica (Acevedo-Gutierrez 1994; Cubero-Pardo and Rodriguez 2000).

This study compares the skull of an anomalous specimen from the collection of the American Museum of Natural History with skulls of species of *Zalophus* and with both *E. jubatus* and *O. byronia* to ascertain its identity within the family Otariidae. No information on collection locality exists for the skull; it is most likely not a zoo specimen, as these are usually accompanied by collection details that include the name of the donating institution. Nevertheless, museum records state that it was collected in 1926, a time when a larger *Zalophus*, the Japanese sea lion *Z. c. japonicus*, was thought not to be extinct. For these reasons, specimens of *Z. c. japonicus* were included in the analyses.

MATERIALS AND METHODS

I measured skull characteristics on the anomalous specimen and on 235 adult male specimens of *O. byronia* (*n* = 56), *E. jubatus* (*n* = 62), *Z. c. californianus* (*n* = 65), *Z. c. wollebaeki* (*n* = 31), and *Z. c. japonicus* (*n* = 21) from the collections of natural history museums and institutions listed in Appendix I. I then photographed the skulls, showing dorsal, ventral, and lateral perspectives.

I used only adult specimens for this study, and I estimated relative age by applying a suture-aging index (Brunner 2000; Doutt 1942; Sivertsen 1954). For each skull, I assigned 9 cranial sutures a value of 1–4, according to the degree of closure (1 = suture fully open, 2 = less than half-fused, 3 = more than half-fused, and 4 = completely fused—Brunner 2000). I summed the values to provide an overall suture index, giving a range of 9–36; adult male specimens were those with suture index ≥24 (Brunner 2000). I recorded 41 measurements for each skull using Mitutoyo (Tokyo, Japan) digital calipers (Table 1; Fig. 1; Appendix II).

I computed univariate statistics with the software SYSTAT 8.0 for Windows (SPSS Inc. 1998). Multivariate analysis of variance was calculated using MANOVA followed by multigroup discriminant function analysis (Pimentel 1979), using SYSTAT 8.0.

RESULTS

The anomalous skull is from an adult male otariid with a suture index of 35, which indicates that it was an old adult. It resembles skulls of *Zalophus*, particularly at the sagittal crest, which rises abruptly at the supraorbital processes and forms a high convex ridge along the dorsal surface of the frontal through to the occipital crest. The

TABLE 1.—Comparison of skull size and shape, in millimeters (variables used in discriminant function analysis), for anomalous specimen (AMNH80082), adult male *O. byronia*, *Z. c. californianus* and *Z. c. wollebaeki.*

Variable	Anomalous specimen	*O. byronia*			*Z. c. californianus*			*Z. c. wollebaeki*		
		$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*	$\bar{X}$	*SD*	*n*
Condylobasal length	308.77	342.17	17.42	53	284.31	11.30	59	264.64	6.75	31
Gnathion–nasals	113.17	128.90	8.96	53	105.34	14.96	58	91.98	4.74	30
width of anterior nares	34.04	47.20	4.96	53	29.72	2.19	58	28.58	1.82	30
Breadth of skull at supraorbital process	82.67	115.69	12.37	46	69.30	7.21	58	68.24	5.78	26
Occipital crest–mastoid	128.05	173.76	15.87	53	129.98	9.42	59	117.31	8.62	31
Width of rostrum	80.55	101.04	10.21	50	59.28	4.13	57	54.38	3.48	30
Breadth of zygomatic root of maxilla	14.88	27.54	3.59	53	16.02	1.77	59	14.40	1.42	31
Breadth of orbit	62.22	68.85	4.91	52	55.20	2.30	59	49.72	1.96	30
Gnathion–caudal border postglenoid process	236.01	270.45	18.10	53	214.30	13.27	59	198.60	6.11	31
Gnathion–foramen infraorbitale	107.64	134.10	12.02	53	93.61	7.07	57	86.56	4.70	26
Height of skull at supraorbital process	84.51	104.23	7.96	53	77.07	4.44	59	69.61	4.12	30
Breadth of palate at postcanine 5	53.87	62.04	5.73	53	45.12	3.40	59	39.96	2.17	30

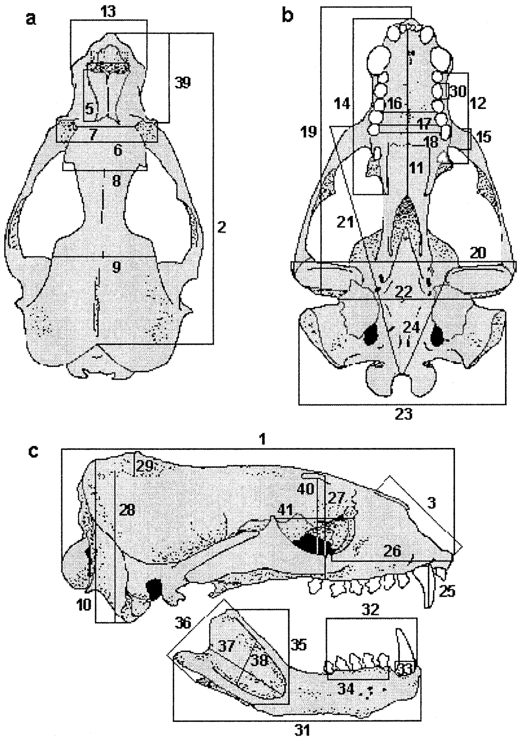

FIG. 1.—Measurements taken on otariid skulls in this study showing a) dorsal, b) ventral, and c) right lateral perspectives (modified from Brunner 1998b). Numbers refer to characters described in Appendix II.

overall dimensions of this skull suggest that the specimen may be a hybrid between *Z. californianus* and another large otariid, perhaps *O. byronia*, *E. jubatus* or, less likely, *Z. c. japonicus*.

Discriminant function analyses showed that when compared with skulls of *Zalophus*, *E. jubatus*, and *O. byronia*, the specimen was most like the skulls of *Zalophus* but also showed similarity to *O. byronia* skulls (Wilks' lambda = 0.01, $P < 0.0001$; Fig. 2). When analyzed separately, the specimen neither grouped with *Z. c. californianus* or *Z. c. japonicus* (Wilks' lambda = 0.11, $P < 0.0001$) nor with *Z. c. californianus* or *Z. c. wollebaeki* (Wilks' lambda = 0.21, $P < 0.0001$). When compared with *E. jubatus* and *Z. c. californianus*, the anomalous specimen grouped significantly

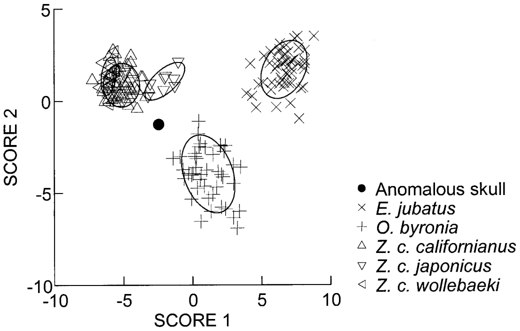

FIG. 2.—Scatter plot from discriminant function analysis showing 1st and 2nd canonical variate scores for anomalous specimen, adult male *Zalophus californianus californianus* (*n* = 56), *Z. c. wollebaeki* (*n* = 19), *Z. c. japonicus* (*n* = 8), *Eumetopias jubatus* (*n* = 56), and *Otaria byronia* (*n* = 43).

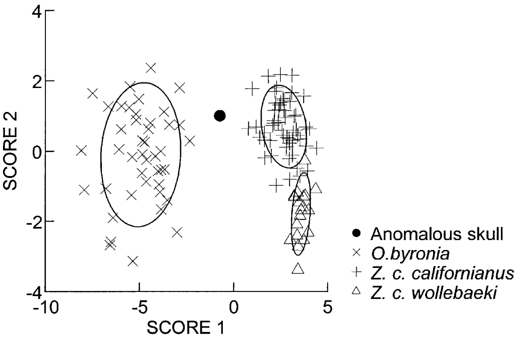

FIG. 3.—Scatter plot from discriminant function analysis showing 1st and 2nd canonical variate scores for the anomalous specimen and those it most closely resembles, adult male *Zalophus californianus californianus*, *Z. c. wollebaeki*, and *Otaria byronia* (sample sizes as for Fig. 2).

closer to, yet not together with, *Z. c. californianus* (Wilks' lambda = 0.02, $P < 0.0001$). When compared with *O. byronia* and *Z. c. californianus*, the anomalous skull grouped between them (Wilks' lambda = 0.06, $P < 0.0001$), as it did when compared with *O. byronia* and *Z. c. wollebaeki* (Wilks' lambda = 0.05, $P < 0.0001$). Finally, when compared with *O. byronia*, *Z. c. californianus*, and *Z. c. wollebaeki*, the skull fell midway between the 2 genera (Wilks' lambda = 0.04, $P < 0.0001$; Table 1; Fig. 3).

The anomalous skull, with a condylobasal length of 309 mm, is larger than any measured skulls from *Z. c. californianus* (≤304 mm) or *Z. c. wollebaeki* (≤278 mm). The rostrum is comparatively short and robust, unlike the more gracile morphology of *Z. californianus*; the skull more resembles *O. byronia*, particularly at the nares and canine roots. The nasals are broad, similar to *O. byronia*, yet more elongate and appear intermediate in structure between the skulls of *O. byronia* and *Z. californianus*. The canines are closer in size and structure to the canines of *Z. c. californianus* than to those of *O. byronia* (mesiodistal diameter: anomalous skull, 21 mm; *Z. c. californianus*, 19 ± 1.4 mm; *O. byronia*, 29 ± 2.6 mm) and splay outwards, a trait found in both genera. The palate is broader than that found in *Z. californianus* but does not possess the extreme palatal extension found in *O. byronia*. Nevertheless, the lateral edges of the palate in the anomalous specimen curve ventrally, similar to that found in *O. byronia* (Fig. 4).

DISCUSSION

Intergeneric copulations within the Otariidae (often with resultant hybrid young) are known from captivity, such as between male *A. pusillus pusillus* and female *Z. c. californianus* (Scheffer 1958) and in the wild, such as between *E. jubatus* and *Z. c. californianus* (Gorodezky 1995; Miller et al. 1996), *Z. c. californianus* and *C. ursinus*, and *O. byronia* and *A. australis* (Miller et al. 1996). Results from my study strongly suggest that the anomalous specimen is a hybrid between *O. byronia* and *Z. californianus*, but they neither indicate which subspecies of *Z. californianus* was the parental phenotype nor whether the individual was reproductively viable.

Pinnipeds consistently exhibit low levels of genetic polymorphism (Lento et al. 1997; Maldonado et al. 1995; Slade 1992), and the presence of interspecific hybrids be-

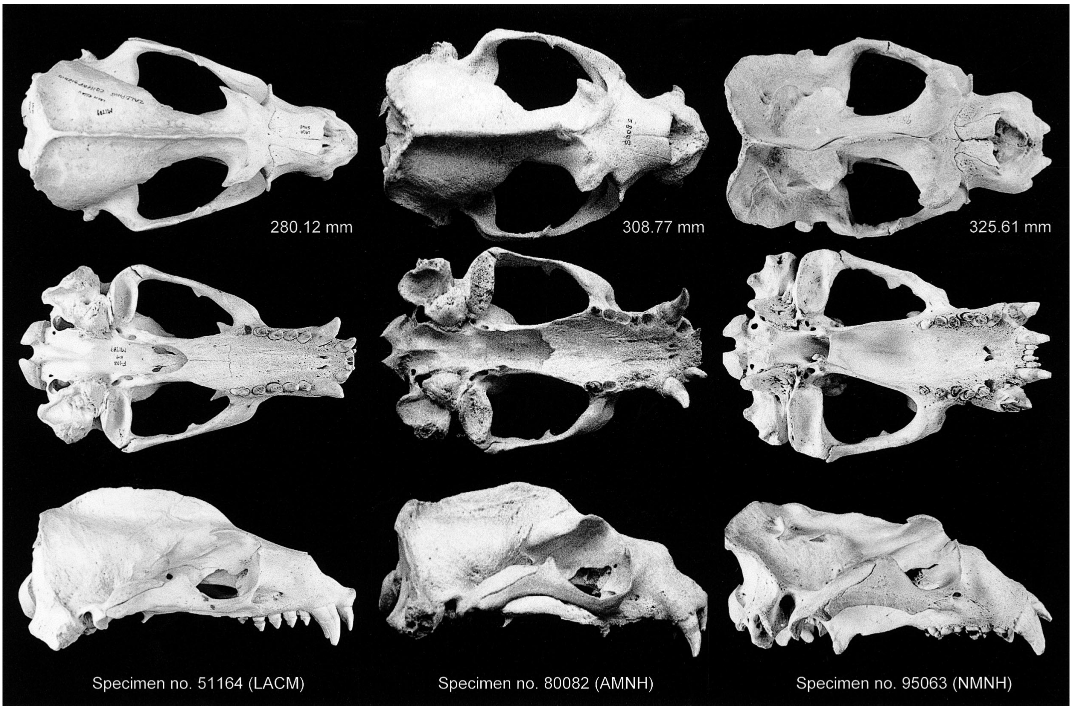

FIG. 4.—Skulls of adult male *Zalophus californianus californianus* (no. 51164, left), anomalous specimen (middle), and *Otaria byronia* (no. 95063, right) showing dorsal (top), ventral (middle), and lateral (bottom) perspectives. Condylobasal length for each specimen is given in the top row.

tween sympatric otariids has been well established. For instance, within the genus *Arctocephalus*, *A. gazella* hybridizes successfully with *A. tropicalis* in several locations (Condy 1978; Kerley and Robinson 1987; Shaughnessy and Fletcher 1987), despite a degree of ecological and behavioral separation. Brunner (1998a) suggested that hybrids exist between *A. gazella* and *A. forsteri*, based on morphometric differences of skulls. Shaughnessy et al. (1998) analyzed proteins of southern fur seals at Macquarie Island using allozyme electrophoresis and found a hybrid between *A. forsteri* and *A. gazella* and 19 hybrids or backcrosses between *A. gazella* and *A. tropicalis*. A rare intergeneric cross within phocid seals (harp seal, *Phoca groenlandica* and hooded seal, *Cystophora cristata*) has also been recorded by Kovacs et al. (1997).

The anomalous specimen of this study appears to be a hybrid between *Z. californianus* and *O. byronia* and seems to illustrate successful intergeneric hybridization in that the animal survived to reach full maturity. Árnason et al. (1995) describe an association between *E. jubatus* and *Z. californianus*, based on cytochrome-*b* sequence data, which may suggest that *Z. californianus* hybridizes with other species of otariids. To date, no genetic records have identified a hybrid between *Z. californianus* and *O. byronia*, although records exist of a captive-born *Z. californianus* × *O. byronia* hybrid (Kirchshofer 1968).

Otariids exhibit high rates of dispersal (Gales et al. 1992; Taylor 1990) and colonize breeding sites rapidly (Dix 1993; Peterson et al. 1968). Vagrant otariids that travel significant distances may increase opportunities for interspecific sexual behavior and hybridization. For instance, individual vagrants of most species of *Arctocephalus* appear frequently within the range of other species of otariids (Rice 1998). Vagrant individuals of *A. tropicalis* have been found at the Juan Fernandez Archipelago, Chile (Torres and Aguayo 1984), and I have recently found *A. galapagoensis* from Macquarie Island (in litt.). This extreme vagrant capacity in otariids presents opportunities for interspecific hybridization not only where species are typically sympatric, but also at localities where interspecific vagrants appear.

Interspecific sexual behavior was observed in 3 otariid species that breed on San Miguel Island, California (DeLong 1982; Miller et al. 1996). Male *Callorhinus* were observed to herd reproductively active female *Zalophus*, and male *Zalophus* were seen mounting female *Callorhinus* (DeLong 1982; Miller et al. 1996). Both genetic and phenotypic evidence of hybridization between the species has been documented (Miller et al. 1996). Also, a juvenile male otariid at Cabo Polonio possessed a large head, thick short snout, and fur seal–like pelage and was identified as a likely hybrid between *Otaria* and *A. australis* (Miller et al. 1996). It is possible that hybrid offspring exist between *O. byronia* and *Z. californianus*, given the vagrant nature of many species of otariids, the geographic proximity of *Z. californianus* to *O. byronia*, and the published observations of interspecific sexual behavior of these species with other otariids.

Some otariid young in sympatric colonies (Arnold 1992) are exposed to interspecific social interactions throughout development, at which time they may acquire a social preference for heterospecific young that influences their behavior as adults (DeLong 1982; Gentry 1974); this may contribute to increasing the number of hybrid otariid offspring.

The close morphological and genetic relationship between otariids presents the capacity for species of this family to hybridize. The data described here suggest that *O. byronia* interbreeds successfully with *Z. californianus* and that resultant offspring can reach maturity, although their viability is unknown. Further information on the identification and viability of recognized hybrid otariids would be beneficial for a better understanding of systematic and evolutionary trends in this family.

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APPENDIX I

Specimens examined.—Key to museum numbers are as follows: AMNH, American Museum of Natural History, New York; ASD, Asahi School of Dentistry, Gifu Prefecture, Japan; BMNH, British Museum of Natural History, London, United Kingdom; DNHM, Denver Natural History Museum, Colorado; FMNH, Field Museum of Natural History, Chicago; HMH, Historical Museum of Hokkaido, Sapporo, Japan; HMJH, Historical Museum of Japanese History, Tokyo, Japan; HU, Hokkaido University, Hakodate, Japan; LACM, Los Angeles County Museum, Los Angeles; MNHN, Museum of Natural History, Paris, France; NRM, Natural History Museum, Stockholm, Sweden; SDNHM, San Diego Natural History Museum, San Diego; UAM, University of Alaska Museum, Fairbanks; UMZC, University Museum of Zoology, Cambridge, United Kingdom; ZMB, Zoological Museum of Berlin, Berlin, Germany.

Anomalous specimen.—AMNH80082, no locality given.

Eumetopias jubatus.—UAM32733, St. George Island, Alaska; ASD1325, no locality given; NMNH21303, Tuleni Island, Okhotsk Sea; NMNH22072, Bering Island, Russia; NMNH22071, Bering Island, Russia; NMNH83887, St. Paul Island, Alaska; NMNH114830, Pribilof Island, Alaska; LACM616, Ano Nuevo Island, California; ASD1033, no locality given; ASD75K6, no locality given; ASD75K20, no locality given; HU97302, Hokkaido; HU98105, Shakotan, Hokkaido; HU99104, Shakotan, Hokkaido; HU94, Hokkaido; HU929/29, Hokkaido; ZMB72815, St. Paul Island, Alaska; NMNH7140, St. Paul Island, Alaska; UAM11470, Otter Island, Bering Sea; ASD75K3, no locality given; HU870524, Hokkaido; BMNH1992.272, no locality given; NMNH13217, Farallone Island, California; NMNH261229, Aleutian Island, Alaska; UAM43370, St. George Island, Alaska; UAM5216, Bristol Bay, Bering Sea; UAM AF-19493, St. Paul Island, Alaska; ASD75K16, no locality given; HU98CH02, Hokkaido; NMNH188981, St. Paul Island, Alaska; UAM5217, Bristol Bay, Bering Sea; UAM43367, St. Paul Island, Alaska; LACM52314, no locality given; ASD75K1, no locality given; HU97304, Hokkaido; HU99105, Shakotan, Hokkaido; BMNH1950.3.29.12, St. Paul Island, Alaska; NMNH49730, St. Paul Island, Alaska; NMNH152135, no locality given; NMNH276031, St. Paul Island, Alaska; NMNH276354, St. Paul Island, Alaska; HU99106, Shakotan, Hokkaido; HU98029, Rausu, east Hokkaido; HU98ST01, Hokkaido; BMNH1950.3.29.11, St. George Island, Alaska; NMNH267526, Aleutian Island, Alaska; NMNH246499, Lynn Canal, Alaska; NMNH276032, Tahola, Washington; ASD75K13, no locality given; NMNH285509, St. Paul Island, Alaska; UAM43365, St. Paul Island, Alaska; ASD1323, no locality given; ASD75K24, no locality given; NMNH 4701, Farallone Island, California; NMNH 15359, Unalaska Is, Alaska; DMNH8655, Dall Island, Alaska; NMNH6906, Monterey, California; NMNH21108, Massett, BC; NMNH3631, Monterey, California.

Otaria byronia.—BMNH1951.3.6.1, Falkland Island; BMNH1939.1.21.179, Falkland Island; NMNH153566, Lobos de Tierra, Peru; SDNHM22407, Isla Lobos, Chile; DMNH8253, Falkland Island; BMNH1939.1.21.172, Falkland Island; BMNH1939.1.21.165, Falkland Island; NMNH482156, Tierra del Fuego, Argentina; LACM72456, La Gunilla, Peru; BMNH1939.1.21.176, Falkland Island; BMNH ws479, Falkland Island; BMNH335.d, South America; BMNH1939.1.21.164, Falkland Island; UMZC K7029, Falkland Island; ZMBB, no locality given; BMNH1959.12.4.6, no locality given; BMNH1869.8.10.1, Falkland Island; BMNH1950.11.6.1, Falkland Island; BMNH1914.7.4.1, Falkland Island; BMNH1880.7.28.6, Str. of Magellan; BMNH b2*, Falkland Island; NMNH482157, Tierra del Fuego, Argentina; NMNH484912, Punta Piramides, Argentina; BMNH1B*, Falkland Island; BMNH1887.6.18.2, Coquimbo Bay, Chile; BMNH1939.1.21.163, Falkland Island; ZMB33881, Torres; BMNH1939.1.21.173, Falkland Island; BMNH335.o, Falkland Island; BMNH1939.1.21.177, Falkland Island; BMNH1939.1.21.182, Falkland Island; UMZC K7024, Falkland Island; UMZC K7028, Chile; ZMB72817, Peru; NMNH550227, no locality given; DMNH2380, Santa Cruz, Argentina; BMNH1939.1.21.166, Falkland Island;

BMNH1851.5.5.1, South America; ZMB C, Isla St. Maria; NMNH504394, Isla de los Viejas, Peru; BMNH335.m, no locality given; BMNH-1869.2.24.1, Falkland Island; ZMB72822, no locality given; NMNH550142, no locality given; BMNH1939.1.21.183, Falkland Island; BMNH-1886.12.13.1, Falkland Island; ZMB46494, South America; NMNH172782, Buenos Aires, Argentina; NMNH153567, Lobos de Tierra, Peru; BMNH1925.12.17.1, Falkland Island; NMNH95063, Cape Fairweather, Patagonia; NMNH550307, Cerros de Illesces; SDNHM-23345, Isla Chiloe, Chile; UMZC K7030, Montevideo; NMNH23240, Maldonado, Uruguay; ZMB70695, Montevideo.

Zalophus californianus californianus.—NMNH-514663, Sonora, Mexico; LACM51171, Huntington Bch, California; SDNHM23342, Baja California, Mexico; SDNHM21248, Baja California, Mexico; SDNHM19396, Baja California, Mexico; SDNHM21245, San Miguel Island, California; AMNH180458, San Martin Island, California; NMNH131897, Santa Cruz Island, California; NMNH259651, San Benito Island, Mexico; LACM51175, San Nicolas Island, California; NMNH260216, Coronado Island, California; NMNH259654, San Benito Island, Mexico; NMNH259653, San Benito Island, Mexico; SDNHM19155, Baja California, Mexico; DMNH-8265, Ano Nuevo Island, California; SDNHM-21249, Baja California, Mexico; NMNH19152, Puerto Refugia, Mexico; NMNH19153, Puerto Refugio, Mexico; NMNH261318, Georges Island, Sonora, Mexico; NMNH514664, Sonora, Mexico; LACM9337, San Nicolas Island, California; NMNH15254, San Nicholas Island, California; NMNH504928, S. Vincente River, Mexico; UAM-11474, Ano Nuevo Island, California; LACM-51192, San Miguel Island, California; LACM-43456, Baja California, Mexico; SDNHM19156, Baja California, Mexico; SDNHM18663, Puerto Refugio, Mexico; SDNHM21244, San Miguel Island, California; SDNHM22859, Baja California, Mexico; SDNHM21246, Torrey Pines Cliffs, California; SDNHM19158, Baja California, Mexico; SDNHM2594, Baja California, Mexico; NMNH-259655, San Benito Island, Mexico; UAM11490, California; LACM43482, Baja California, Mexico; LACM85974, San Diego Co., California; SDNHM10586, Baja California, Mexico; AMNH-180667, Coronados Island; AMNH180515, Santa Margarita Island; NMNH514030, Isla Tiburon; UAM35200, Ano Nuevo Island, California; LACM43455, Baja California, Mexico; LACM-39665, Santa Cruz, California; LACM54590, San Pedro, California; NMNH19154, Isla San Pedro Martir, Mexico; DMNH8263, Ano Nuevo Island, California; UAM no ID, Baja California, Mexico; SDNHM11404, La Jolla, California; DMNH2364, San Clemente Island, California; NMNH259652, San Benito Island, Mexico; NMNH395724, Isla Natividad, Mexico; LACM39666, Ano Nuevo Point, California; LACM31360, San Nicolas Island, California; SDNHM2589, Baja California, Mexico; SDNHM20686, Baja California, Mexico; DMNH8268, Isla de la Guarda, Mexico; NMNH-14410, Coast of California; UAM11491, San Miguel Island, California; LACM51164, San Nicolas Island, California; LACM54624, Marineland Pier, California; LACM39663, Moss Landing, California; AMNH180502, Magdalena Island; LACM-39655, Ano Nuevo Island, California; LACM-39662, Moss Landing, California.

Z. c. japonicus.—BMNH1873.3.12.1, Japan; HMJH‘‘ID#3,’’ Rebun Island, Japan; HMJH‘‘I-001,’’ Rebun Island, Japan; HMJH‘‘ID#1226,’’ Rebun Island, Japan; HMJH‘‘ID#1,’’ Rebun Island, Japan; HMH2, Aonae, Okushiri Island, Japan; HMH7, Aonae, Okushiri Island, Japan; HMH6, Aonae, Okushiri Island, Japan; HMH4, Aonae, Okushiri Island, Japan; HMH1, Aonae, Okushiri Island, Japan; HMH3, Aonae, Okushiri Island, Japan; HMH5, Aonae, Okushiri Island, Japan; HMJH‘‘ID#60000,’’ Rebun Island, Japan; HMJH132, Rebun Island, Japan; HMJH142, Rebun Island, Japan; HMJH136, Rebun Island, Japan; HMJH1248, Rebun Island, Japan; HMJH‘‘24,’’ Rebun Island, Japan; HMJH‘‘ID#23,’’ Rebun Island, Japan; HMJH‘‘I-002,’’ Rebun Island, Japan; HMJH‘‘I-003,’’ Rebun Island, Japan.

Z. c. wollebaeki.—NRM3761, Galapagos Islands, Equador; AMNH214780, Santiago Island, Galapagos Islands, Equador; NMNH23332, Str. of Magellan; AMNH214781, Floreana Island, Galapagos Islands, Equador; AMNH99462, Seymor Island, Galapagos Islands, Equador; NMNH23277, Hood Island, Galapagos Islands, Equador; NMNH23279, Hood Island, Galapagos Islands, Equador; MNHN1962.115, Galapagos Islands, Equador; AMNH99463, Seymor Island, Galapagos Islands, Equador; FMNH51758, Galapagos Islands, Equador; NRM3760, Galapagos Islands, Equador; AMNH63946, Galapagos Islands, Equador; NMNH23280, Hood Island, Galapagos Islands, Equador; NMNH23281, Hood Island, Galapagos Islands, Equador; NMNH396917, Isabela Island, Galapagos Islands, Equador; MNNH1962.114, Santa Cruz; MNHN1973.293, Santiago, Galapagos Islands, Equador; NRM3758, Galapagos Islands, Equador; NRM3766, Galapagos Islands, Equador; MNHN1962.114, Santa Cruz; MNHN1962.115, Galapagos Islands, Equador; MNHN1962.115, Galapagos Islands, Equador; MNHN1962.115, Galapagos Islands, Equador; MNHN1962.114, Galapagos Islands, Equador; AMNH99461, Seymor Island, Galapagos Islands, Equador; NMNH23276, Hood Island, Galapagos Islands, Equador; NRM3762, Galapagos Islands, Equador; NRM3763, Galapagos Islands, Equador; NRM3765, Galapagos Islands, Equador; FMNH51759, Galapagos Islands, Equador; FMNH51760, Charles Island, Galapagos Islands, Equador.

APPENDIX II

Measurements taken on otariid skulls.—1, condylobasal length, from gnathion to posterior of basion; 2, from gnathion to point of occipital crest on dorsal midline; 3, from gnathion to posterior margin of nasals; 4, breadth of nares, from interior of nares at widest point measured on interior surface; 5, greatest length of nasals, from anterior margin of nasal to posterior margin; 6, breadth at preorbital processes; 7, interorbital constriction; 8, greatest breadth at supraorbital processes; 9, breadth of braincase, measured dorsally at coronal suture; 10, from point of occipital crest on dorsal midline to ventral margin of mastoid; 11, from anterior point of palatal notch to posterior edge of central incisor alveoli (where a palatal cleft was present, measurement was taken from palatal notch at margin of, but excluding, cleft); 12, distance behind border of canines, from posterior margin of canine alveolus to posterior margin of alveolus of postcanine 6; 13, greatest rostral width; 14, from gnathion to posterior end of maxilla (palatal); 15, breadth of zygomatic root of maxilla, maximal anteroposterior breadth, from ventral perspective; 16, breadth of palate between postcanines 3 and 4, between alveoli of postcanines 3 and 4; 17, breadth of palate between postcanines 4 and 5, between alveoli of postcanines 4 and 5; 18, breadth of palate at postcanine 5, from proximal margin of alveoli of postcanine 5; 19, from gnathion to caudal border postglenoid process; 20, zygomatic breadth, at widest point of zygomatic arch, from posterior margin of squamosals; 21, distance from midpoint on ventral margin of foramen magnum to anterior margin of zygomatic arch; 22, greatest breadth across auditory bullae; 23, mastoid breadth; 24, from anterior margin of basion to anterior margin of pterygoid; 25, height of canine above alveolus, a straight line from the posterior margin of alveolus to the tip of the canine; 26, from gnathion to anterior of foramen infraorbitale; 27, height of skull at supraorbital processes, from base of skull at alveolus of postcanine 6 to dorsal margin of skull at supraorbital processes; 28, height of skull at ventral margin of mastoid, from skull at base of sagittal crest to ventral margin of mastoid; 29, height of sagittal crest, dorsoventrally, from highest point of crest to skull at base of crest; 30, mesiodistal diameter of postcanines, at alveolar margin; 31, length of mandible, from posterior margin of condyle to anterior margin of dentary; 32, length of mandibular tooth row (inclusive of canines), from anterior margin of alveolus of canine to posterior margin of alveolus of postcanine 6; 33, mesiodistal diameter of canines, across base of canine at alveolar margin; 34, length of lower postcanine row, from anterior margin of alveolus of postcanine 1 to posterior margin of alveolus of postcanine 6; 35, height of mandible at meatus, from dorsal margin of angularis at meatus to dorsal margin of coronoid process; 36, from ventral margin of angularis to dorsal margin of coronoid process; 37, length of masseteric fossa, from anterior margin of fossa to posterior margin of coronoid process; 38, breadth of masseteric fossa, dorsoventrally through center of fossa; 39, from gnathion to posterior margin of preorbital process; 40, length of orbit, from ventral margin of postglenoid process to dorsal margin of the base of orbit; 41, breadth of orbit, mesiodistal from inside margin of orbit.