

Lobodon carcinophaga. By Peter J. Adam

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***Lobodon* Gray, 1844**

Phoca: Hombron and Jacquinot, in Jacquinot, 1842:plates 10, 10A. Type species *Phoca carcinophaga*; not *Phoca* Linnaeus, 1758.

Stenorhynchus Owen, 1843:331. Incorrect subsequent spelling of *Stenorhinchus* Cuvier, 1826 (the latter a preoccupied senior synonym of *Hydrurga* Gistel, 1848).

Lobodon Gray, 1844:2. Type species *Lobodon carcinophaga*, by monotypy.

Leptorhynchus Gray, 1844:5. Incorrect subsequent spelling of *Stenorhinchus* Cuvier, 1826.

Ogmorhinus: Turner, 1888:64. Not *Ogmorhinus* Peters, 1875:393.

CONTEXT AND CONTENT. Order Carnivora, suborder Pinnipedia, family Phocidae, subfamily Monachinae, tribe Lobodontini, genus *Lobodon*. The genus is monotypic.

***Lobodon carcinophaga* (Hombron and Jacquinot, in Jacquinot, 1842)**

Crabeater seal

Phoca carcinophaga Hombron and Jacquinot, in Jacquinot, 1842: plates 10, 10A. Type locality unknown; restricted to “sur les glaces du Pole Sud, entre les îles Sandwich et les îles Powels, à 150 lieues de distance de chacune de ces îles” [about the ice of the south pole, between the (south) Sandwich and Powel (= south Orkney) Islands, 150 leagues (724 km) distance from each of these islands] by Hombron and Jacquinot (1853:30).

Stenorhynchus serridens Owen, 1843:332. Type locality “from a high latitude in the Australian seas.”

Lobodon carcinophaga: Gray, 1844:2. First use of current name combination.

Leptorhynchus serridens: Gray, 1844:5. Name combination.

Stenorhynchus carcinophagus: Flower, 1884:213. Name combination.

Ogmorhinus carcinophagus: Turner, 1888:64. Name combination.

Lobodon carcinophagus: Berg, 1898:15. Unjustified emendation of *Lobodon carcinophaga* Gray, 1844.

CONTEXT AND CONTENT. Context as for genus. *L. carcinophaga* is monotypic.

DIAGNOSIS. *Lobodon carcinophaga* is distinguished from other phocids by unique finely cusped postcanine teeth in which a principal, posteriorly curved cusp is bordered anteriorly and posteriorly by 1 and 2 or 3 accessory cusps, respectively (Scheffer 1958).

GENERAL CHARACTERS. *Lobodon carcinophaga* (Fig. 1) is a krill-feeding specialist of the Antarctic pack ice (i.e., ice not fixed to land). Pelage is countershaded, with back darker than belly. Background color is silvery gray in newly molted individuals (January–February), changing to a golden, creamy white or brown color. Reticulated chocolate-brown patterns or dark flecks of variable intensity may mark shoulders, sides, and flanks, and grade into a predominantly dark head, back, and foreflippers and hind flippers. Individuals become progressively paler with age even when freshly molted. Pelage has no clear sexual dimorphism (Laws 1993a), but males tend to be more pale (Shaughnessy and Kerry 1989). Nose, lips, mammae, anus, and genital orifice are black, and gums and tongue are pink (Barrett-Hamilton 1901). A pure glossy white individual is known (Hall 1903). Individual hairs are ≤ 1.5 cm long and taper distally after approaching their thickest point at 25% of their length (Wilson 1907). Mystacial vibrissae number 40–46 (mean \pm SD: 42.8 ± 1.25 , $n = 4$), arranged in 7 rows on each

side. Supraorbital, narial, and chin vibrissae number 1–3, 1, and 2 per side, respectively (Krylov 1972; Krylov and Popov 1980). Vibrissae are white basally and black in their distal one-third and have a beaded texture (Wilson 1907). Manual claws are well developed, but pedal claws are reduced to horny points (Leboucq 1904a). Dark brown irises of eye surround vertical slitlike pupils (Wilson 1907). External pinnae are absent. Newborn pups have a pale coffee-colored, white, or gray-brown lanugo that is soft and wooly (Corner 1972; King 1957; Laws 1993a; Ling and Button 1975; Wilson 1907). Pedal lanugo is darker than rest of body, and both belly and muzzle have a slight yellow tinge. Primary lanugo hairs are lighter than brownish, deeply kinked underhairs and may be up to 3 cm long. Mystacial vibrissae of pups are completely black and arranged in 6 rows. Inner vibrissae are beaded and outer vibrissae are smooth (King 1957). At a distance, crabeater seals can be recognized by their slender, streamlined silhouette and distinct neck (Aguayo and Torres 1975; Laws 1993a).

Skull (Fig. 2) is long and narrow with a slightly concave dorsal margin in lateral profile. Antorbital and dorsal postorbital processes are indistinct, and ventral postorbital processes are formed from jugal and squamosal bones. Premaxillae do not articulate with fused left and right nasals. Hard palate is broadly arched posteriorly. Tympanic bullae are broadly inflated and pachyostotic. Sagittal and nuchal crests are weakly developed in both sexes. Posterior to tooth rows, bony maxillary and dentary tubercles are present (Barrett-Hamilton 1901; Bertram 1940; King 1957, 1961; Owen 1853).

Total length (in cm) of adult (≥ 5 -year-old) females is significantly greater than that of males (235.6 ± 11.8 SD, $n = 479$ versus 230.9 ± 11.4 , $n = 328$). Mass (in kg) of nonpregnant adult females is also greater than that of males (206.5 ± 22.6 , $n = 46$ versus 198.7 ± 16.9 , $n = 68$), but individual mass may change dramatically throughout the year. Length and mass measurements for sexes combined are 233.7 ± 11.6 cm ($n = 808$) and 201.8 ± 19.7 kg ($n = 114$), respectively (Boyd 2000; I. Boyd, in litt.). Maximum lengths for females and males are 277 cm and 264 cm, respectively. Crabeater seal mass (in kg) can be estimated from length (in cm) as follows: male length = $148 + 0.43 \times$ mass, female length = $158.5 + 0.38 \times$ mass (Laws et al. 2003b). Other standard measurements (mean \pm SD, sexes combined, in cm) are as follows: length of tail, 13.1 ± 0.5 ($n = 2$); length of foreflipper, 43 ± 2 ($n = 8$); length of hind flipper, 44 ± 2 ($n = 8$); axillary girth, 120.5 ± 13.0 ($n = 7$); condylobasal skull length, 27.8 ± 1.7 ($n = 51$); basilar skull length, 25.9 ± 1.4 ($n = 7$); length of upper postcanine toothrow, 8.1 ± 0.3 ($n = 9$); width of rostrum, 5.5 ± 0.6 ($n = 7$); length of nasals, 7.9 ± 0.3 ($n = 8$); interorbital width, 4.5 ± 0.3 ($n = 7$); zygomatic width, 15.4 ± 0.7 ($n = 9$); mastoid width, 16.1 ± 0.8 ($n = 7$); length of dentary, 20.4 ($n = 1$); length of lower



FIG. 1. A crabeater seal (*Lobodon carcinophaga*) of unknown sex. Used with permission of the photographer M. F. Cameron.



FIG. 2. Dorsal, ventral, and lateral view of skull and lateral view of mandible of an adult male *Lobodon carcinophaga* collected 14 February 1970 from Seymour Island, Antarctic Peninsula, Antarctica (National Museum of Natural History, USNM 550083). Condylbasal length is 288.1 mm.

postcanine tooththrow, 7.9 ± 0.3 ($n = 8$ —Barrett-Hamilton 1901; Bryden and Erickson 1976; Bryden and Felts 1974; Cruwys and Friday 1995; Laws et al. 2003b; Le Souef 1929; Scolaro 1976; Wilson 1907). Nonstandard measurements are available (Bruce 1913; Krylov 1972; Krylov and Popov 1980).

DISTRIBUTION. *Lobodon carcinophaga* has a southern circumpolar distribution (Fig. 3) and is usually limited to pack ice south of the Antarctic Convergence where cold Antarctic waters meet warmer northern waters. *L. carcinophaga* is occasional to the Patagonian coast (Le Souef 1929; Scolaro 1976) and islands bordering the Antarctic Convergence (Rice 1998). South American extralimital records include Río de Janeiro, Guarujá, and Peruibe in Brazil; Río de la Plata in Uruguay; and San Isidro, Puerto Madryn, and Río Santa Cruz in Argentina (Berg 1898; Pinedo 1988; Scolaro 1976). South African records include False, Gordon's, Jeffrey's, and Kalk bays; Gantoos and Van Staden's rivers; Cape Point Beach; Hamburg; Igoda; La Mercy; Leisure Island; Nature's Valley; Seaview; and Southbroom (Courtenay-Latimer 1961; Klages and Cockcroft 1990; Ross 1977; Ross et al. 1978, 1985). Extralimital records from Africa and South America likely result from young crabeater seals being swept northward by the West Wind Drift and Falkland Current, respectively (Castello and Pinedo 1977). Australian records include Mandurah, Princess Royal Harbor, and Safety Bay in Western Australia (Mawson and Coughran 1999); Manly

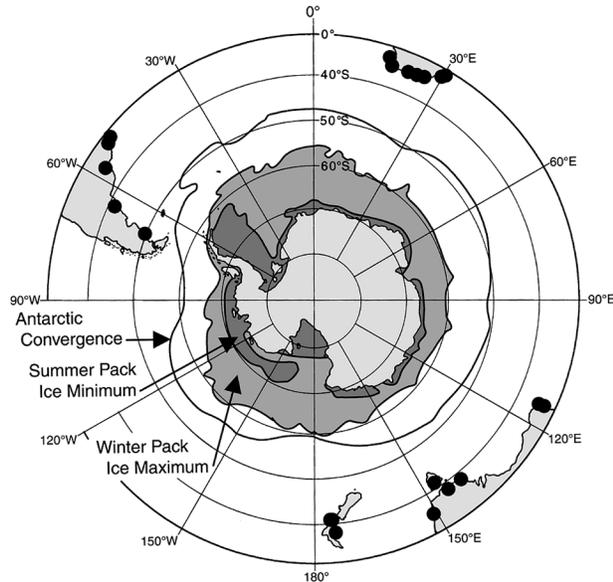


FIG. 3. South polar projection map of Antarctica showing distribution of the crabeater seal (*Lobodon carcinophaga*) in austral summer (summer pack ice minimum) and austral winter (winter pack ice maximum). Closed circles indicate extralimital records.

Beach and Nambucca Heads in New South Wales (Le Souef 1929; Troughton 1947); Portland, Port Phillip Bay, and Saint Kilda (Melbourne) in Victoria (Hall 1903; Ingham 1960; Wilson 1907); and Ralphs Bay in Tasmania (Anonymous 1945). New Zealand extralimital records include Lyall Bay (Wellington), Petone Beach, and Wanganui Heads (Scheffer 1958; Sorensen 1969). Crabeater seals are not endemic to lower Indian Ocean latitudes, but a skin sample from the Maldives (ca. $3^{\circ}15'N$, $73^{\circ}00'E$) has been putatively identified as *L. carcinophaga* (Stoddart 1972) and may be the northernmost record, but most authors cite Río de Janeiro as the northern limit ($22^{\circ}54'S$ —Ross et al. 1978).

FOSSIL RECORD. The only known fossil is a partial right tympanic bulla from late Pleistocene or early Holocene deposits at Sea Harvest, Saldanha, South Africa (Deméré et al. 2003; Hendeby 1974). Although this specimen may represent a vagrant, crabeater seals may have extended their range north during colder Pleistocene or Holocene periods (Hendeby 1974). A single lower postcanine tooth from green sand deposits near Burlington, New Jersey, is similar to *L. carcinophaga* and has been described as *L.* (= *Stenorhynchus*) *vetus* (Leidy 1853). This species is of Miocene or later age and has been recommended as a species inquirenda (Ray 1976). Mummified crabeater seal remains (ca. $\leq 3,740$ years old) have been found in arid valleys and ephemeral streambeds around Antarctica, often tens of kilometers from the coast and up to 1,100 m above sea level (Barwick and Belham 1967; Dort 1975; Laws 1984; Markov 1960).

FORM. Nonmedullated hairs of *L. carcinophaga* occur in randomly distributed bundles consisting of a single primary hair with 1–4 secondary hairs arising from a common pore. Mean basal diameters of primary and secondary hairs are 137 and 13.3 μm , respectively. Primaries have a density of 9.4/ mm^2 . Presence of arrector pili muscles has not been demonstrated. Darkly pigmented epidermis has a scaly relief (Scheffer 1964). Epidermis of mummified skin is divided into 2 strata. A basal, pigmented portion is 3–5 cells thick, and a superficial portion consists of 3–5 flattened cell layers. No highly keratinized stratum is evident (Orr 1971). Mean sternal blubber thickness is 3.28 cm ($n = 458$ —Laws et al. 2003b), but varies with individual age and season (Laws et al. 2003a; Øritsland 1970). Blubber composition includes myristic, palmitic, and stearic fats comprising 4.7%, 10.1%, and 2.1% of blubber mass, respectively. Unsaturated fats with 14, 16, 18, 20, and 22 carbon molecules constitute 3.2%, 19.8%, 30.3%, 19.2%, and 10.6% of blubber mass, respectively (Winter and Nunn 1953a, 1953b).

Wormian bones may be present in the occipitoparietal region of skull (King 1957). Morphology of middle ear ossicles is unremarkable (King 1969). Posterior to an elongate mandibular symphysis, ventral borders of the mandibular rami curve medially to give lower jaw a scooplike appearance. Bony tubercles are present posterior to both upper and lower tooth rows. Dentary tubercles are 14 mm wide and 7 mm tall; presence and size of maxillary tubercles varies (King 1961). Reported dental formula of $i\ 2/2, c\ 1/1, p\ 3/3, m\ 2/2$, total 32 (Bertram 1940) is probably erroneous; true dental formula is likely $i\ 2/2, c\ 1/1, p\ 4/4, m\ 1/1$, total 32 (Eastman and Coalson 1974). P1 and p1 have no deciduous precursors. Outer upper incisor teeth are large and caniniform, but not procumbent. Postcanine teeth increase in size from anterior to posterior and typically have 1 and 3 accessory cusps anterior and posterior to the posteriorly recurved central cusp, respectively (up to 6 accessory cusps may be present). Widely spaced upper and lower postcanine teeth interdigitate tightly in occlusion, but do not touch. Upper and lower postcanines 2–5 typically have 2 roots each, but infrequently have 3 roots. All other teeth have 1 root. Roots of C1 and M1 may penetrate the orbit and dorsal maxilla, respectively (Bertram 1940; King 1961). Dental and jaw pathologies and breakage are rare, but supernumerary postcanine teeth, postcanine or canine tooth loss, and jaw breakage are known (Bertram 1940; Wilson 1907). Vertebral formula is 7 C, 15 T, 5 L, 3 S, 10–13 Ca, total 40–43 (Antonyuk 1970; Thomson 1909). There are 10 vertebrosteral, 4 vertebrocostal, and 2 vertebral ribs (Kooymann 1981). Adult bacula are 157–220 mm long. Bacular shaft is slightly bent and oval or triangular in cross section, apex is slightly attenuated laterally and has a rounded end, and proximal end is rugose and flat (Didier 1953; Morejohn 2001; Øritsland 1970). Hook-shaped scapulae have poorly developed spines that extend <33% of scapular length. Humeri have enlarged deltopectoral crests and lack supracondylar foramina. Distal ends of radii and ulnar olecranon processes are enlarged, anterior margins of ilia are laterally everted, humeri and femora are shortened, lesser femoral trochanters are absent, and tibiae and fibulae are proximally fused (Adam 2002; Muizon 1981). Manus has 6 carpals plus a pisiform, and pes has 7 tarsals (Leboucq 1904a). Lengths of manual digits decrease in the order $I > II > III > IV > V$; pedal digits I and V are longest and III is shortest. Manual and pedal phalangeal formula is 2–3–3–3–3 (Owen 1853; Thomson 1909). Skeletal muscle accounts for 43.94 ± 7.06% (mean ± *SD*; $n = 7$) of body mass (Bryden and Erickson 1976). Psoas major is large, and latissimus dorsi and pectoralis ascendens are well developed. Facial muscles are weakly developed (Bryden and Felts 1974). Individual muscle masses are available, but gross descriptions of myology are lacking. However, muscular anatomy is similar to that of other Antarctic seals (Bryden and Felts 1974) for which descriptions are available (Bryden 1971; Piéard 1971).

Heart and contracted spleen weigh (mean ± *SD*; in g; $n = 7$) 935 ± 220 and 348 ± 132, respectively. Blood accounts for 9.01% ± 0.93% of body mass (Bryden and Erickson 1976; Cabanac 2002). Crabeater seal hearts are broad and flattened, with greatest circumference, height, and width (mean ± *SD*; in mm; $n = 3$) of 392 ± 27, 144 ± 7, and 148 ± 26, respectively. Both ventricles contribute to apex. Right ventricle is much smaller than left ventricle, with a ventral wall only 29% the thickness of left ventricle wall and making up 19.4% of total heart mass compared to 52% for left side. Aortic base has an inner diameter of 12.6–34.4 mm and wall thickness of 1.8–2.2 mm. A dispensable aortic bulb is present with walls 3.0–4.7 mm thick and inner diameter of 39.3–54.3 mm (Drabek 1972, 1975). Foramen ovale has a straight-edged and nonfenestrated septum primum (Macdonald et al. 1995). Spleen is nonsinusoidal and reticular, with rich smooth muscle and trabeculae. Red pulp is present and spleen is both adrenergically and cholinergically innervated (Schumacher and Welsch 1987). Erythrocytes are 9 µm in diameter. Blood erythrocyte concentration (mean ± *SD*; $n = 5$) is 4.4 ± 0.2 × 10⁶/mm³ (Ridgway et al. 1975; Tyler 1960). Hemocrit values range from 0.41 to 0.52. White blood cell counts range from 7 to 13 × 10⁹/l, with neutrophils, lymphocytes, monocytes, and eosinophils comprising 69–81%, 9–23%, 2–7%, and 0–4% of white blood cells, respectively (Lynch et al. 1999). Caudal vena cava has a distinct caval sphincter innervated by the right phrenic nerve. Hepatic veins drain into an enlarged hepatic sinus. Jugular veins are poorly developed, and brain is drained by a vessel passing through vertebral canals. Renal arteries have 5 subdivisions before forming interlobar arteries, each of

which follows in close association with the renal calyx before entering a reniculus to form arcuate arteries. Renal veins are absent; kidneys are drained by a renal plexus exiting the medial border and anastomosing with a venous network surrounding the kidney. Each plexus drains to ipsilateral branch of a caudally divided vena cava (Vardy and Bryden 1981). Pleural lymphatic vessels are well developed (Welsch and Drescher 1982).

Nasal cavity has darkly pigmented stratified squamous epithelium covering nasal conchae, which lie 10 cm posterior to external nares. Nasopharynx contains a pharyngeal tonsil and is lined with pseudostratified ciliated columnar epithelium with large compound submucosal mucous glands. Epiglottis is lined with stratified squamous epithelium (Boyd 1973). Trachea and lungs weigh (mean ± *SD*; in g; $n = 7$) 327 ± 118 and 1,677 ± 357, respectively. Trachea is 43.7 ± 4.5 cm ($n = 2$) long (Bryden and Erickson 1976), and divides into primary bronchi at lungs. From 47 to 54 tracheal annuli are present; lumen has a variable diameter of 4, 5.5, and 3.5 cm at larynx, one-quarter length, and point of bronchial bifurcation, respectively (Kooymann 1981). Saclike tracheal diverticula are absent. Bronchial tree has hyaline cartilages that form incomplete rings in primary bronchi, irregularly shaped shields in secondary bronchi, and small, irregularly shaped plaques in distal bronchi and bronchioles (Boyd 1973). Dorsoventrally flattened left and right lungs have 2 and 3 distinct lobes, respectively, with incomplete fissures dividing cranial lobes into cranial and middle portions (Boyd 1973; Nishida and Amemiya 1962). Lung parenchyma is divisible into grossly visible segments and smaller lobules by collagenous septa. Thick smooth muscle surrounds bronchioles and may invade alveolar septa (Boyd 1973; Welsch and Drescher 1982). Intralobular bronchioles are lined by a thin epithelium that is underlain by blood vessels. Distally, bronchioles have abundant surfactant-producing, type II, pneumocytes. Alveolar openings are surrounded by sphincterlike smooth muscle bundles and elastic fibers, whereas alveolar sacs are lined with simple squamous epithelium and abundant type I and II pneumocytes. The blood–air barrier is typically 0.32–0.42 µm thick, but is 0.09 µm where alveolar and capillary endothelia unite. Epithelial tight junctions have 3–6 sealing strands and abundant anastomosing strands, and those of the endothelium have 1–4 loose sealing strands (Welsch 1985; Welsch and Bartels 1986; Welsch and Drescher 1982; Welsch et al. 1989).

Adult brain mass (mean ± *SD*; in g; $n = 7$) is 525 ± 62, and eyes weigh 53 ± 7 g. Eyeballs ($n = 5$) are 4.0 ± 0.3 and 4.2 ± 0.2 cm in anterior–posterior and dorsal–ventral diameters, respectively. Adrenal, thymus, and thyroid glands (in g; $n = 7$) weigh 36 ± 19, 169 ± 119, and 15 ± 13, respectively (Bryden and Erickson 1976).

Esophagus, stomach, small intestine, large intestine, liver, and pancreas weigh (mean ± *SD*; in g; $n = 7$) 215 ± 54, 792 ± 197, 2,551 ± 338, 621 ± 251, 3,024 ± 549, and 190 ± 32, respectively (Bryden and Erickson 1976). Stomach has a single chamber (Mårtensson et al. 1994) and maximum volume of 10 l (Klages and Cockcroft 1990) although stomach content volumes of 2.4 l ($n = 4$, maximum 8.0 l) are normal (Øritsland 1977). Small intestines are 2,570 ± 359.9 cm long (mean ± *SD*; $n = 5$; 10–15 times body length) with a total surface area of 1.10 m². Large intestines are 87.5 ± 24.0 cm long (mean ± *SD*; $n = 4$; 0.3 times body length), distinguishable from small intestines, and separated from the ileum by a 13-cm-long cecum. Liver has 7 lobes (Bruce 1913; Bryden and Erickson 1976; Mårtensson et al. 1998; Nishida and Amemiya 1962). Gastric glands of stomach body mucosa are long (1.5 mm) compared to those of fundus. Duodenal Brunner glands may be absent, as are Paneth cells of crypts of Lieberkühn (Schumacher et al. 1995).

Combined kidneys and urinary bladder weigh (mean ± *SD*; in g; $n = 7$) 1,009 ± 182 and 104 ± 44, respectively. Kidneys are long, narrow, and flat with a mean length, width, and height (in mm; $n = 6$) of 221 ± 34, 85 ± 8, and 39 ± 9, respectively. Kidneys have ca. 270 reniculi, with borders between contiguous reniculi marked by interrenicular veins but no connective tissue septa. Renal hila and pelves are absent. Each ureter is formed by union of 2 major branches exiting each kidney (Bryden and Erickson 1976; Vardy and Bryden 1981). Female crabeater seals have a bicornuate uterus, with horns and body of similar lengths (11.0–11.2 cm each—Harrison et al. 1952) and with horns fusing posteriorly but remaining partitioned before forming the body. Site of embryo implantation is marked by thickening of wall of uterine horn and hypertrophy of uterine blood vessels (Tikhomirov 1975).

Nongravid uterine horns are slender, with 5 or 6 asymmetrical endometrial folds and narrow lumen (Sinha and Erickson 1972a). Uteri of older individuals are tougher and more fibrous, and placenta scars are not visible for >1 year (Bengtson and Siniff 1981). Nulliparous females have a conspicuous hymen at the urinary papilla, where the urethra opens into the vagina (Harrison et al. 1952). Ovaries are encapsulated in tentoria and are bean-shaped and smooth in juveniles but pocked with follicles in adults (Tikhomirov 1975). Ovaries weigh (mean \pm *SD*; in g; *n* = 3) 24 ± 10 and have a length, width, and depth of 4.5, 2.9, and 0.7 cm, respectively. Overall mass (mean \pm *SD*; in g; *n* = 4) of adult female reproductive system is 112 ± 6 (Bryden and Erickson 1976), and increases gradually over the first 10–15 years of life (Bengtson and Siniff 1981). Corpora albicantia typically persist 5–6 years before regressing (Hårding and Härkönen 1995; Øritsland 1970), and up to 10 may be present from previous pregnancies (Bengtson and Siniff 1981). No more than 1 corpus luteum of pregnancy is ever present (Tikhomirov 1975). Corpora lutea are generally oval or polygonal in shape, with even granular or vacuolated cytoplasm. Granulosa lutein cells are of 3 types, typically being polygonal, 20–40 μ m in diameter, and separated by strands of connective tissue, perivascular spaces, capillaries, and lymph vessels. Steroid-secreting type I and II lutein cells have abundant smooth endoplasmic reticula, whereas lipid-storing type III cells have large lipid droplets (Sinha and Erickson 1972b). Penis is pink with a black apex (Barrett-Hamilton 1901). Testes are inguinal and penis is concealed within body contour (Harrison et al. 1952). Testes are lobulate, with each lobule containing 8–10 seminiferous tubules. Epididymides are closely associated with testes (Sinha et al. 1977b). Each testis weighs (mean \pm *SD*; in g; *n* = 3) 148 ± 6 and has a length, width, and depth of ca. 6.5, 3.8, and 1.6 cm, respectively. The entire male reproductive system weighs (mean \pm *SD*; in g; *n* = 3) 502 ± 93 (Bryden and Erickson 1976). Sperm production is seasonal, with nonreproductive testis having spermatogonia and primary spermatocytes in 110- to 160- μ m-diameter seminiferous tubules, aspermic epididymides, few Leydig cells, and no secondary spermatocytes, spermatids, or spermatozoa. Sertoli cells are irregular or polygonal in shape. In reproductive testes, spermatozoa are present in dilated (210- μ m-diameter) seminiferous tubules and epididymides are full. Polygonal Leydig cells of nonreproductive testes are 11–18 μ m in diameter and have degenerated organelles (Harrison et al. 1952; Sinha et al. 1977a, 1977b).

FUNCTION. Thick blubber of *L. carcinophaga* reduces environmental heat loss. Internal (rectal) resting body temperature is 33°C (Nel 1965), but daily ranges of 36.2–39.2°C correspond to circadian rhythms of daily activities (Erickson et al. 1971; Hofman 1975). Tranquilizers injected into blubber of heat-stressed crabeater seals reduce stress, but similar injections into cold-stressed seals do not (Hofman 1975). Nasopharyngeal mucous glands moisten nasal epithelium in the arid Antarctic environment, but make seals prone to water loss (Boyd 1973).

Lateral upper incisors are enlarged, but not procumbent, and thus are not adequate for rasping ice over breathing holes (Lindsey 1938; Stirling 1969). Tightly interdigitating and intricately cusped postcanine teeth form a sieve with a maximum intertooth gap of 2.6 mm to prevent krill, their primary prey, from escaping the mouth when engulfed water is ejected before glutition. Bony postdental tubercles prevent krill from escaping at jaw angle (Adam and Berta 2002; King 1961; Klages and Cockcroft 1990). Captive crabeater seals may chew large fish (Le Souef 1929; Ross et al. 1976; Troughton 1947). Neither chitinase-producing stomach microbes nor anatomical specializations of the digestive system are evident. Long gastric glands produce gastric enzymes, mucins, and hydrochloric acid to aid digestion of whole prey. Krill are digested with 84% efficiency (10% of available energy is lost as undigested chitin—Mårtensson et al. 1994, 1998; Schumacher et al. 1995). Empty stomachs are common (ca. 85%—Bengtson 1982). Mucins of stomach surface epithelium have reduced sulfination (Schumacher et al. 1995). Krill have high levels of toxic cadmium and fluoride. Maximum mean cadmium level (relative to dry tissue mass) in crabeater seal is 139.4 μ g/g in kidney, 38.8 μ g/g in liver, and 0.44 μ g/g in skeletal muscle (Schneider et al. 1985; Steinhagen-Schneider 1986; Szefer et al. 1994). Maximum mean fluoride levels of soft tissues are 9.0 ppm/g in brain, 2.5 ppm/g in blubber, 2.3 ppm/g in kidney, and 0.01 ppm/g in blood. Mean fecal and urine fluoride levels are 2197 ppm/g and 321 ppm/ml, respectively. Compact bone fluoride

levels are 6380 ppm/g in scapulae (Adelung et al. 1985). Acetylcholinesterase activity is inhibited by high fluoride, but is compensated by increased activity of the synergistic and fluoride-activated enzyme pseudocholinesterase (Dubbels et al. 1984). Concentrations of calcium, chromium, cobalt, copper, lead, magnesium, mercury, nickel, potassium, silver, sodium, and zinc in kidney, liver, and muscle tissue are available (Szefer et al. 1993, 1994). Liver iron concentrations are up to 28.0 mg/g (Szefer et al. 1993, 1994). Serum concentration (mean \pm *SD*; in mmol/l) of 25-hydroxy-vitamin D₃ is 51.75 ± 29.25 and reflects the inability of krill to produce vitamin D (Griffiths and Fairney 1988). Carotenoids in krill turn crabeater seal feces pink or red (Bertram 1940; Wilson 1907).

Crabeater seals are not proficient divers, but display diving-related adaptations including development of an aortic bulb to maintain arterial pressure during bradycardia to ensure blood flow to the brain and heart (Drabek 1972, 1975) and a large hepatic sinus that stores blood during bradycardia (Boyd 1973). A similar function for the spleen is indicated by its trabeculae and smooth-muscle architecture. Red pulp of the spleen is actively hemopoietic (Cabanac 2002; Schumacher and Welsch 1987).

Smooth muscles and hyaline cartilages keep proximal and distal airways of tracheobronchial tree open to accommodate air pushed out of alveoli when they collapse from increased diving pressure. Collagen in lung parenchyma adds rigidity and aids in alveolar dilation when a crabeater seal is not diving. Surfactant from abundant type II pneumocytes facilitates alveolar dilation (Boyd 1973; Welsch 1985; Welsch and Bartels 1986; Welsch and Drescher 1982; Welsch et al. 1989). A well-developed pleural lymphatic system removes fluids from interstitial spaces during diving (Welsch and Drescher 1982). Liver is poorly adapted for minimizing accumulation of harmful waste products (e.g., lactate) during diving anoxia. During *in vitro* ischemia, mitochondria have a low respiratory control ratio and low adenosine triphosphate production. Rates of glycogen conversion to glucose remain high, but low rates of glycolysis indicate inhibition in the glucose-6-phosphate to lactate conversion pathway (Hochachka et al. 1988). Skeletal muscle has a low dynamic activity range and higher potential for aerobic carbohydrate metabolism compared to anaerobic metabolism (Hochachka and Foreman 1993). Mean hemoglobin is 20.3–21.8 g% (Seal et al. 1971a). Plasma cortisol (mean \pm *SE*; in μ mol/l; *n* = 4) is 1.35 ± 0.10 (Liggins et al. 1993).

Estimates of total daily energy expenditure indicate that a 190-kg female expends 70,672 kJ/day in digestive metabolism, heat production, and locomotion (Laws 1984; Naumov and Chekunova 1980). Activity (mean \pm *SD*, in units/g, relative to wet mass) of liver superoxide dismutase is $2,542.5 \pm 212.3$ (*n* = 13) and that of catalase is 4.17 ± 0.30 (*n* = 16—Witas et al. 1984). Mean serum cholesterol and urea are 197–273 mg% and 28–34 mg%, respectively. Mean serum uric acid values in young crabeater seals (0.7–0.8 mg%) are significantly higher than in adults (0.6–0.7 mg%). Gamma-globulin levels in adults (0.74–0.8 mg%) are greater than in young (0.54–0.64 mg%). Diurnal variation in iron metabolism is evident (Seal et al. 1971a). Serum calcium and albumin concentrations (mean \pm *SD*, *n* = 12) are 2.3 ± 0.2 mmol/l and 41.5 \pm 3.6 g/l, respectively (Griffiths and Fairney 1988).

Ovulations alternate annually between ovaries, with right ovary responsible for 1st ovulation in 67% of cases. Ovulations can occur out of season and can occur twice in 1st year of maturity (Bengtson and Siniff 1981; Bertram 1940; Hårding and Härkönen 1995; Laws 1958). Nonreproductive males have degenerated organelles of Leydig cells and low serum testosterone levels (1.12–1.16 ng/ml—Sinha et al. 1977a, 1977b).

ONTOGENY AND REPRODUCTION. During austral spring, mature and juvenile crabeater seals segregate. Juveniles are typically found in large aggregations on fast ice (i.e., ice that is fixed to land—Erickson et al. 1971; Laws 1981; Lindsey 1938; Siniff et al. 1979), whereas mature animals stay on pack ice and form pair-bonds for the duration of pupping (September–October) and breeding (late October–early November—Bertram 1940; Corner 1972; Erickson and Hofman 1974; Øritsland 1970; Shaughnessy and Kerry 1989; Siniff 1991; Siniff et al. 1979). At the beginning of pupping season, pregnant females choose a suitable ice floe on which to give birth. These floes are distributed randomly and at low density within pack ice and are seldom large enough to accommodate >1 family group. Small numbers of breeding animals may occur on fast ice. Males pair with females during or shortly after

parturition, either cueing to the scent of newborn pups or estrous females. Family groups of a male, female, and pup are most common on pack ice in spring (Laws 1981; Siniff and Reichle 1976; Siniff et al. 1979), with lone unpaired females and pups rarely observed (Shaugnessy and Kerry 1989; Siniff et al. 1979). Nursing pups stay in close contact with their mothers, and begin to search and give a bawling vocalization if separated. When pups were separated from immobilized mothers, they sought contact with legs of experimenters (Shaugnessy and Kerry 1989; Siniff et al. 1979). Attendant males maintain a distance of 2–4 m from their mates during lactation, waiting for females to become receptive. If males approach too close or attempt to mate during this time, females produce aggressive vocalizations, deliver bites to the head and neck, and chase males away (Corner 1972; Shaugnessy and Kerry 1989; Siniff et al. 1979). A subsidiary March mating season has been suggested for some populations (Bertram 1940; Bonner and Laws 1964), although few data support this (Erickson and Hofman 1974).

Crabeater seals rely on body reserves to feed young during nursing (Boyd 2000). Natural weaning occurs from 2 days (Lindsay 1938) to 6 weeks (Laws 1958) after birth, but is usually 14–21 days (Laws et al. 2003a; Shaugnessy and Kerry 1989; Southwell et al. 2003). Weaning occurs in early November, loosely coincident with molting of lanugo. Suckling pups take 5.29 l/day of milk from the mother's 2 functional mammae and gain an average of 4.2 kg/day. This corresponds to a water influx of 26.8–57.3 ml kg⁻¹ day⁻¹. Pups and mothers will ingest snow (Corner 1972; Green et al. 1993). Pups are weaned when they weigh 80–110 kg or are 1.5 m long. A mother transfers a total of 90 l of milk (with 2,030 MJ of energy) to her pup, and total energetic cost of producing 1 pup is 2,230 MJ for gestation and nursing combined. During suckling, fasting mothers lose an average of 5.6 kg/day and expend >51% of energy reserves in metabolism and milk production (Green et al. 1993; Naumov and Chekunova 1980; Shaugnessy and Kerry 1989). Sternal blubber thickness in females drops from 67 mm in early October to 34–43 mm by February and March. Males may or may not fast during the nursing period (Laws 1984; Shaugnessy and Kerry 1989). With human disturbance, adult males may interrupt lactation by forcing weakened females away from pups (Corner 1972; Laws 1981, 1984; Siniff et al. 1979). Natural weaning occurs when milk production ceases (Shaugnessy and Kerry 1989) and varies with size of mother (Siniff et al. 1979). One instance of a large (139 kg) pup still suckling is known (Green et al. 1993), and postweaning juveniles are occasionally found with adult male–female pairs (Hofman 1975). Milk has a specific gravity of 1.00–1.01, energy value (mean \pm SD) of 22.61 \pm 1.58 MJ/l ($n = 8$), and the following contents (mean \pm SD, $n = 8$): solids, 66.98% \pm 3.86%; lipids, 50.77% \pm 4.12%; proteins, 10.78% \pm 1.16%; hexose, 1.33% \pm 0.24%; and ash, 0.93% \pm 0.10%. Milk lipids are almost entirely triglycerides with long-chain fatty acids to lower freezing point. Most milk sugars exist as higher oligosaccharides, and free lactose is present (Green et al. 1993; Messer et al. 1988; Urashima et al. 1997). Activity levels (in units/g protein) for intestinal enzymes of pups are: maltase, 16–19; sucrase, 0; trehase, 0; lactase, 12–20; and cellobiase, 0.85–0.91 (Crisp et al. 1988). Concentrations (mean \pm SD; in mg/ml) of iron, sodium, potassium, calcium, magnesium, and copper are: 0.1137 \pm 0.015, 0.48 \pm 0.10, 1.13 \pm 0.29, 1.02 \pm 0.07, 0.11 \pm 0.01, and 0.003 \pm 0.001, respectively. Suckling pups store 58–64% of ingested milk fat and 79–97% of protein (Green et al. 1993). Sternal blubber is 1 cm thick in newborns and 4 cm thick in weanlings (Øritsland 1977). Newly weaned pups consume krill at a rate of 21 g kg⁻¹ day⁻¹ and have a water influx of 7.4–18.6 ml kg⁻¹ day⁻¹ (Green et al. 1993). Adult females ovulate ca. 4 days after weaning (Laws et al. 2003a).

An 81-day delay in embryo implantation is responsible for birthing synchrony, followed by a 264-day gestation period. Estimated mean birth, weaning, conception, and implantation dates (\pm 17 days) are October 15, October 31, November 4, and January 24, respectively (Laws et al. 2003a). Blastocyst transmigration does not occur between uterine horns before implantation (Bengtson and Siniff 1981). Crabeater seals typically bear 1 young per year, although cases of twin fetuses are known (Bengtson and Siniff 1981; Øritsland 1970). By late January, embryos are in a gastrulated stage (Tikhomirov 1975) or exist as 1- to 2-cm-long fetuses (Bertram 1940). Fetuses grow to 2–10 cm by mid-February (Sapin-Jalouster 1953; Tikhomirov 1975), 4.5–18 cm by early March (Sinha and Erickson 1972b), 33–40 cm by late April (Bertram 1940), 102–

136 cm by early September, and 115–145 cm by early October (Barrett-Hamilton 1901; Øritsland 1970). External genitalia of male fetuses are visible by the 1.4-cm stage and primitive seminiferous tubules appear by the 2.2-cm stage (Harrison et al. 1952). Milk teeth, which have only weak cusps, are resorbed or shed in utero. Pups are born with nearly functional adult dentition (Bertram 1940; Cruwys et al. 1997), or permanent teeth may erupt after pups are 2 weeks old (Øritsland 1970). Fetal development of brain (Krabbe 1947) and flippers (Leboucq 1904a, 1904b) is known. Estimates of mass at birth range from 20 (Webb 1997) to 35 kg (Bengtson 2002), with 30.7 kg ($n = 3$) the most reliable (Green et al. 1993). Estimates of length at birth range from 1.1 (Laws 1958) to 1.8 m (Bertram 1940), with most 1.3–1.4 m (King 1957; Laws et al. 2003a; Øritsland 1977; Shaugnessy and Kerry 1989; Siniff et al. 1979). Pups are born with woolly, light-brown lanugo that is molted 2 weeks after birth (Bengtson 2002). Molting is associated with pup mass rather than weaning (Shaugnessy and Kerry 1989) and begins around eyes, proximal limbs, and small of back. A remnant of the umbilicus remains attached for at least 4 days after birth (Corner 1972). Observations of pups entering water when 2–3 days of age may be due to human disturbance (Bertram 1940; Ling and Button 1975). Pups feed independently at least 10 days after weaning (Shaugnessy and Kerry 1989). High ($\geq 12\%$) newborn mortality is partly due to inexperienced females (Siniff et al. 1979). Weaned pups grow quickly, and are difficult to differentiate from adults by February (Erickson and Hofman 1974). Young achieve full adult body size (2.03 m long) within 2 years (Laws 1959).

The epitheliochorial zonary placenta has marginal border hematomas and many isolated central hematomas concentrated either mesometrially (Harrison and Young 1968) or antimesometrially (Sinha and Erickson 1972a). The placental band is annular in shape, but is incomplete mesometrially. It has a labyrinthine zone with fetal lamellae or branched septa intimately enclosing maternal capillaries and sinusoids, a spongy glandular zone with dilated secretory uterine glands and attenuate maternal connective tissue, and a basal zone marked by nondilated tubular glands, stromal cells, and blood vessels. Fetal lamellae often penetrate uterine gland lumina but do not penetrate the endometrial basal zone. Lamellae have a single outer syncytiotrophoblastic layer, incomplete inner cytotrophoblast, and connective tissue core with mesenchymal cells and blood vessels. Within the labyrinthine zone, maternal capillary endothelial cells are squamous, often attenuate in early pregnancy, but may become cuboidal by latest stages. A sausage-shaped chorion completely fills the pregnant uterine horn but does not enter sterile horn. Chorionic vesicles are 1–4 cm in size and lined by trophoblast. Infratrophoblastic capillaries are only observed in placenta of fetuses ≥ 40 cm length. Allantois is large and completely envelops the amnion except at base of umbilicus. Outer margin of allantois lines chorion except where umbilical vessels enter placental band mesometrial surface to form a pyramidal space in which a bilobed, vascular, fluid-filled yolk sac is located. Chorioallantoic membrane has tall cytotrophoblastic cells with microvillus folds that interdigitate with syncytium. Iron-containing bodies occur on basement membrane of trophoblast and mesenchymal cells of the placenta (Erickson et al. 1971; Harrison and Young 1968; Sinha and Erickson 1972a).

ECOLOGY. Crabeater seals may be the most abundant pinniped and may comprise 56% of the world's pinniped stock and 79% of total seal biomass (Laws 1984). In pack ice, *L. carcinophaga* comprises 80–95% of seals observed (Bester and Odendaal 1999; Bonner and Laws 1964; Condy 1977; Erickson and Hanson 1990; Laws 1984). Estimates of a worldwide crabeater seal population range from 2,000,000 (Scheffer 1958) to 75,000,000 (Erickson et al. 1971), with 30,000,000 as consensus estimate (Bengtson and Laws 1985; Laws 1984). Reasons for the wide range of estimates include the varied, vast, and rigorous habitat in which crabeater seals live; their hidden and unobservable numbers when underwater; limited knowledge of behavior and seasonal and diurnal movements; and different census techniques (Erickson and Hanson 1990; Erickson et al. 1971; Gilbert and Erickson 1977; Hofman 1975; Laws 1980, 1984; Øritsland 1970). Methods for correcting raw census data for some of these variables are available (Bengtson and Stewart 1992; Bester and Odendaal 1999; Erickson and Hanson 1990; Erickson et al. 1971, 1989; Southwell et al. 2004). Estimates of crabeater seal density range from 0.02 (Bester 1979) to 120 individuals/km² (Bester and Odendaal 1999), with densities of

0.5–5.0 individuals/km² most common (Erickson and Hanson 1990; Gelatt and Siniff 1999; Joiris 1991). Densities are lower in winter (ca. 0.5 individuals/km²) when pack ice coverage is maximal (ca. 20×10^6 km²) and in spring (ca. 0.7–0.8 individuals/km²) when they form family groups that are widely separated by behavioral interactions. Greater densities in summer (ca. 4.83 individuals/km²) are due to reduced pack ice coverage (ca. 4×10^6 km²) and less intense behavioral interactions (Laws 1977, 1981, 1984; Siniff et al. 1979). Greatest density is at the pack ice periphery, with fewer numbers in heavy, interior pack ice (Siniff et al. 1970). Crabeater seals remain within 500 km of a release site (Bengtson et al. 1993) or can travel up to 1,900 km in search of suitable pack ice (Bornemann and Plötz 1999). Estimates of crabeater seal biomass density range from 51 kg/km² at a density of 0.341 individuals/km² (Ainley 1985) to 230.4 kg/km² at a density of 1.19 individuals/km² (Condy 1977). Estimates of total crabeater seal biomass range from 2.223×10^6 to 2.895×10^6 tons, with annual consumption of $63\text{--}67 \times 10^6$ tons and annual mortality biomass of 0.67×10^6 tons (Laws 1977, 1981, 1984).

Crabeater seals occur in greatest numbers on marginal pack ice and over the continental shelf and in areas of high primary productivity and upwelling such as the Antarctic Slope Front and over sea mounts (Ainley 1985; Bengtson 2002; Laws 1979, 1984; Nordøy et al. 1995). Crabeater seals prefer ice of 2–5 oktas (eighths of ice coverage). They prefer to haul out on pancake (flat floes ≤ 3 m in diameter and ≤ 10 cm thick), cake (flat floes 3–20 m in diameter), or brash ice (fragmented floating ice < 2 m diameter) rather than hummocked (hillocked) ice (Ainley 1985; Bengtson 1978; Erickson et al. 1971; Gilbert and Erickson 1977; Laws 1984; Nel 1966). Although small floes (< 500 m²) are preferred, crabeater seals also frequent larger floes (Hall-Martin 1974; Shaugnessy and Kerry 1989). Seasonal movements are likely passive and associated with annually variable latitudes of pack ice maxima and minima in austral winter and summer, respectively (Bengtson 1978; Laws 1979, 1981).

Crabeater seals have an annual fertility rate of 76–87% (Øritsland 1970). Annual pregnancy rates vary with age, being 94%, 67%, 50%, and 33% for seals 3–26, 27–29, 30–31, and > 31 years of age, respectively, and 80% for all age classes combined (Laws 1977, 1981). Senescence may occur by 24 years of age (Øritsland 1970), although a pregnant 35-year-old female is known (Bengtson and Siniff 1981). Estimates of age of sexual maturity of females vary from 16 months to 6 years (Laws 1984), with some individuals not becoming mature until 9 years old (Hårding and Härkönen 1995). Age of sexual maturity of females has varied over the last century, being 4 years of age before 1955, 3 years in 1965, 2.5 years in 1970, and 5 years in 1989. Causes of earlier maturity are controversial, and include increased food resources after industrial whaling, differences in sampling and aging methods, climate change, and statistical artifact (Bengtson and Laws 1985; Hårding and Härkönen 1995; Laws 1977, 1984). Cyclic intervals of 4–5 years in cohort strength are evident (Bengtson and Laws 1985; Boveng and Bengtson 1997; Laws 1984; Testa 1990; Testa et al. 1991). Age of sexual maturity of males is 2–7 years (Laws 1984; Øritsland 1970; Tikhomirov 1975). Sexual maturity is attained by 2.05 m length in both sexes. Physical maturity is attained by 2.26 m length or 220 kg mass (Laws 1958). Longevity estimates range from 23 years for females and 28 years for males (Tikhomirov 1975) to 40 years for sexes combined. The oldest individual was 39 years old (Laws et al. 2002). Low male to female ratios of 37%:63% are observed in seals ≥ 20 years old compared to 51%:49% ratios at birth (Laws 1984); however, males prefer heavy pack ice where they are not easily censused (Hofman 1975). Female survival rates are 56% to age 1 and 25% to 1st pupping, with an overall 89% annual survival rate (Laws 1984). A 14.5% annual mortality rate is estimated for both sexes aged > 8 years (Laws 1977), with 20% mortality for all sexes and ages combined (Laws 1979).

Up to 83% of adults are marked with pairs of long, parallel scars spaced, on average $\pm SD$, 6.79 ± 1.46 cm apart ($n = 94$ —Laws 1984; Lowry et al. 1988). Although originally attributed to attempted predation by killer whales (*Orcinus orca*—Bertram 1940; Bruce 1913; Lindsey 1938; Ross 1977; Wilson 1907), these scars are inflicted on pups and juveniles (< 1 year old) by canine teeth of leopard seals (*Hydrurga leptonyx*—Laws 1984; Siniff and Bengtson 1977; Siniff et al. 1979). Predation pressure by leopard seals varies by location, but is greatest when crabeater seal pups are newly weaned and inexperienced (November), and does not

decline until they are 6 months old. During the most intense period, leopard seals take crabeater seal pups at a rate of 0.027 pups km⁻² day⁻¹. After 1 year, the probability of a crabeater seal being taken by a leopard seal approaches zero both because of the larger size of pups and because of presence of pups produced in the subsequent pupping season (Siniff 1981). Only 20% of crabeater seal pups survive their 1st year (Bengtson 2002). Hunting occurs in the water (Bengtson and Siniff 1981; Gilbert and Erickson 1977; Siniff et al. 1978), but leopard seals may attack pups on ice (Mackintosh 1967). Leopard seals consume only the blubber of their prey (Siniff et al. 1979), and 20% of their stomach contents are crabeater seal remains (Siniff 1981). High predation pressure from leopard seals plays an important role in crabeater seal life history and demography, including aggregation of subadult crabeater seals (Hofman 1975; Siniff 1981; Siniff et al. 1979). Predation pressure by killer whales is poorly documented, but crabeater seals of all ages are taken (Siniff 1991). Killer whales usually pursue crabeater seals in water (Ingham 1960), but can knock crabeater seals off of ice floes by using coordinated hunting techniques (Smith et al. 1981). A wound probably caused by a cookiecutter shark (*Isistius brasiliensis*) was observed on a vagrant crabeater seal in South Africa, although this shark is not found within the normal range of *L. carcinophaga* (Klages and Cockcroft 1990).

Crabeater seals feed almost exclusively on euphausiid krill *Euphausia superba*, which is typically found in $> 90\%$ of full stomachs sampled. *Euphausia crystallographias* also may be taken (Lowry et al. 1988; Øritsland 1977). Crabeater seals preferentially eat adult krill (mean length 47.6 mm, range 36–56 mm) in the austral spring (Croxall et al. 1985; Lowry et al. 1988), and dependence on krill does not change seasonally (Bengtson 2002). A possible preference for male krill also is evident (Croxall et al. 1985). Crabeater seals feed more on cephalopods, fish, and mysids over the continental shelf (Green and Williams 1986). Other prey include paralepid fish, Antarctic silverfish (*Pleurogramma antarcticum*), icefish (*Chaenichthys*), Antarctic squid (*Gonatus antarcticus*), gammarid amphipods, the neritic mysid *Antarctomysis maxima*, and unidentified fish, octopus, clams, and crustaceans (Bertram 1940; Bruce 1913; Green and Williams 1986; Laws 1984; Lowry et al. 1988; Øritsland 1977; Perkins 1945; Wilson 1907). Gravel, sand, and stones are often recorded from crabeater seal stomachs (Øritsland 1977; Sapin-Jaloustre 1953; Wilson 1907). Ill or stressed crabeater seals have been observed to feed on marine algae (Krylov 1972; Wilson 1907); 1 vagrant, stranded specimen fed on *Dictyota intricata*, *Plocamium corallorhiza*, and *P. rigidum* before death (Ross et al. 1978).

Current dietary differences among Antarctic seals minimize interspecies food competition despite extensive sympatry. Leopard seals depend on krill as adults in austral winter and as juveniles at all times of the year, indicating seasonal or age-specific competition with crabeater seals (Siniff 1991). Antarctic fur seals (*Arctocephalus gazella*) are sympatric with crabeater seals in the southern Atlantic and Indian Ocean zones and feed extensively on krill (Reid and Arnould 1996). Food competition may occur with minke (*Balaenoptera acutorostrata*), blue (*B. musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales, birds, fish, and cephalopods (Croxall et al. 1985; Laws 1977; Marschall 1988; Rau et al. 1992). Among whales, only blue and minke whales penetrate the outer pack ice zone where crabeater seals are most frequent (Laws 1977). Competition among Antarctic seals for floes suitable for hauling-out and breeding is not evident (Siniff 1984). Crabeater seals that (rarely) stray far from the water's edge on fast ice may share breathing holes with Weddell seals (*Leptonychotes weddellii*) without strife. When encountered together on pack ice, the 2 ignore each other (Stirling and Kooyman 1971).

The internal parasite load of *L. carcinophaga* is usually low due to general absence in the diet of intermediate (fish) hosts that are required for many parasite life cycles (Krylov 1972; Laws 1964). Anisakid (Rhabditida) nematodes recorded from *L. carcinophaga* include *Contracaecum osculatatum*, *C. radiatum*, and *C. rectangulum* (Sapin-Jaloustre 1953; Dailey and Brownell 1972). The notocotylid digenae *Ogmogaster antarcticus* (= *O. plicatus*) has been recovered from *L. carcinophaga* (Zdzitowiecki et al. 1989). The cestodes *Diphyllobothrium* (Sapin-Jaloustre 1953) and *D. lobodoni* (Yurakhno and Maltsev 1994) are known from the small intestines. Another intestinal cestode, *Baylisia baylisi*, is unique to *L. carcinophaga* (Dailey 1975; Wojciechowska and Zdzitowiecki 1995). Larvae of the dilepidid cestode *Parorchites zederi*,

usually a penguin parasite, have been found in crabeater seal small and large intestines (Cielecka et al. 1992). Polymorphid acanthocephalan parasites occurring primarily in the small intestines include *Corynosoma arctocephali*, *C. bullosum*, *C. hamanni*, and *C. pseudohamanni*, although in no instance are crabeater seals believed to be the primary host (Dailey 1975; Dailey and Brownell 1972; Zdzitowiecki 1984a, 1984b). Unidentified sarcosporidian cysts have been observed in body and esophageal muscle (Ippen and Henne 1989), and oocysts of *Eimeria* (Coccidimorpha, Eimeriidae) are known (Drózd 1987). The anopleuran sucking louse *Antarctophthirus lobodontis* is unique to crabeater seals (Dailey and Brownell 1972).

An unknown virus is implicated in mass death of several thousand young crabeater seals (most <9 years old) in late austral spring, 1955. Although most were in good body condition and had access to water, some bled from the nose, mouth, or anus. Necropsied individuals had empty stomachs, congested or collapsed lungs, emphysema and nephritis, spleens engorged with blood, and high levels of hemosiderin. Flesh from these crabeater seals fed to dogs and men resulted in no ill effects (Laws and Taylor 1957). Crabeater seals from the Antarctic Peninsula tested positive for antibodies to canine distemper virus, a disease with symptoms similar to those described for the 1955 mass mortality. Proportion (total 33%) of crabeater seals testing positive for canine distemper virus increases with age class (Bengtson et al. 1991). Neutralizing antibodies against 3 phocine herpes virus isolates and porpoise morbillivirus have been found in crabeater seals. Antibodies for canine and feline herpes viruses, phocine distemper virus, dolphin morbillivirus, influenza A, *Mycobacterium bovis*, and *M. avium* have not been found (Harder et al. 1991; Lynch et al. 1999). In 1 instance of mass mortality, crabeater seals were heavily infected with the blood-sucking louse *Antarctophthirus* (Harder et al. 1991). Dichloro-diphenyl-trichloroethane (DDT) or its metabolites occur in low levels (5.4–142 ppb) because of the lower trophic level at which crabeater seals feed. Levels of chlorinated hydrocarbons are 5.6–71.9 ppb (Karolewski et al. 1987; Schneider et al. 1985; Sladen et al. 1966; Vetter and Luckas 1995). Levels of polychlorinated biphenyls PCB153, PCB138, and PCB180 are 2–3, 1–2, and <1–1 µg/kg, respectively, and toxaphene is present (Vetter and Luckas 1995). One instance of toxemia resulted in death (Mawson and Coughran 1999).

Limited working space available on small floes may dictate use of drugs rather than physical restraint to immobilize crabeater seals (Hofman 1975). Numerous immobilizing drugs have been tested on Antarctic seals, 3 of which are recommended for crabeater seals. Xylazine hydrochloride, administered at a dosage of 2.5 mg/kg, has a latency period of 8–9 min and an immobilization period of 1.2–1.7 h. Phencyclidine hydrochloride and prozamine hydrochloride administered at a dosage of 0.7 mg/kg (each) has a latency of 12.6 min (immobilization period not reported). Ketamine hydrochloride (6.0 mg/kg) plus diazepam (0.2 mg/kg) also is effective, but latency and immobilization periods are not known (Erickson and Bester 1993). Others suggest use of 90–100 mg of midazolam with 600 mg of pethidine (Tahmindjis et al. 2003), although mortality is higher relative to some other drugs (Erickson and Bester 1993). Details of other field techniques are available (Laws 1993b). Although numerous methods are available for aging crabeater seals, cementum layers in p3 are most reliable (Laws et al. 2002).

Crabeater seals have been targeted by 3 small pilot sealing expeditions. In 1892–1894, 32,558 skins and 4,100 barrels of blubber were harvested from pack ice seals in Antarctic waters. In 1964–1965, a less successful Norway expedition took 732 crabeater seals, and a Soviet expedition in 1986–1987 was an economic failure (Bengtson 2002; Laws 1981, 1983). Failure to commercially exploit crabeater seals is due to costs of working in pack ice, the widespread and dispersed nature of seals, inaccessibility of pups, and scarring on hides (Erickson and Hofman 1974; Laws 1984; Ross 1977).

ANIMAL HUSBANDRY. Crabeater seals are rarely kept in captivity because of inaccessibility of krill to feed captive specimens. Only waif juveniles, discovered outside their normal range, have been kept. Crabeater seals tame easily and may be converted to a fish diet, but juveniles cannot eat whole fish >18 cm long. Crabeater seals eat 7.4–10.2 kg of fish per day (6.9–11.1% of body mass), presented in 2 feedings. Fish may be supplemented daily with 250–500 mg of vitamin C, 100 mg of vitamin B₁₂, 50 mg of

vitamin B₁, and 10 ml of cod liver oil. Fish should have fins and spines removed and be presented headfirst to prevent choking (Ross et al. 1976). Captive crabeater seals have been fed dead barracuda (*Sphyrna*), chub mackerel (*Scomber japonicus*), driftfish (*Psenes whiteleggii*), hake (*Merluccius capensis*), herring (*Etrumeus teres*), pandora (*Pagellus natalensis*), pilchards (*Sardinops ocellatus*), horse mackerel (*Trachurus trachurus*), other unidentified species, and live Mozambique tilapia (*Tilapia mossambica*)—Klages and Cockcroft 1990; Perkins 1945; Ross et al. 1976, 1978). Captive animals with live freshwater crab (*Potamon*), mud prawn (*Upogebia africana*), and shrimp (*Palaemon pacificus*) added to their habitats failed to gain weight. Diet may be successfully changed after 1 day of forced fasting. Ventral body fur may become worn on cement enclosures, and some individuals rub their jaws against the sides of a pool resulting in injury. Crabeater seals dislike human contact with the exception of gentle touches to the vibrissae. Individuals in enclosures with Cape fur seals (*Arctocephalus pusillus*) were continually harassed. One captive crabeater seal likely died from heat stress (Ross et al. 1976, 1985). Another died from digestive system blockage after ingesting 16.8 kg of sand and debris from the bottom of an enclosure (Klages and Cockcroft 1990). Other details of husbandry are available (Laws 1993b).

BEHAVIOR. The diel activity pattern of crabeater seals is divisible into periods spent resting while hauled-out on ice floes and periods during which they are in water and foraging or travelling. On average, haul-out bouts and aquatic periods last 7.9 h (maximum 19.2 h) and 15.1 h (maximum 85.8 h), respectively. At no time are >76% of crabeater seals hauled-out. These values are similar for both sexes and between seasons, although seasonal changes in timing of haul-out bouts and differences in diurnal patterns of juveniles and adults are evident. In austral summer, when photoperiod is maximal, adult haul-out pattern is unimodal with maximum haul-out at 1200 h local solar time. After March, juveniles and adults have bimodal haul-out patterns with peak haul-outs occurring at midday and later in the evening. Maximum juvenile haul-out occurs at ca. 2400 h from April to August, whereas in adults maximum haul-out is at 1200 h from March to mid-April. By June, adult crabeater seals display a unimodal haul-out pattern centered at ca. 1200 h (Bengtson and Cameron 2004; Condy 1977; Erickson and Hofman 1974; Hall-Martin 1974; Joiris 1991; Siniff et al. 1970). Maximal haul-out may occur in early morning on fast ice (Siniff et al. 1978), may vary between years in the same location (Gilbert and Erickson 1977), and haul-out patterns may be inverted in some individuals during April and May (Nordøy et al. 1995). Adults prefer to feed nocturnally. Juveniles spend twice as long hauled-out as adults (38% versus 20% of diurnal budget). Molting (January–February) does not change haul-out patterns (Bengtson and Cameron 2004). During snowstorms or high winds, crabeater seals do not usually haul-out (Siniff et al. 1978). While resting, crabeater seals most commonly lay on their sides. Sleeping crabeater seals occasionally wave their foreflippers back and forth (Nel 1966).

Captive animals can produce suctional forces strong enough to suck fish (7–10 cm long) through a 10-cm-diameter tube from 50 cm away. Fish are held in the mouth while water is ejected through the sievelike teeth (Klages and Cockcroft 1990). Sucking actions of the lips have been observed in wild crabeater seals (Laws 1984) and are advantageous for hunting krill overwintering in ice crevasses (Klages and Cockcroft 1990). Crabeater seals swim through shoals of krill with open mouths (King 1961). Crabeater seals can catch krill individually and prefer larger krill (Kooymann 1981; Lowry et al. 1988). Groups of 6–30 seals are occasionally seen swimming and diving in synchrony (Hofman 1975).

Mean group size of hauled-out crabeater seals ranges from 1.29 to 2.4 in austral spring and summer, with lone seals and small groups of 2–5 comprising 54–57% and 38–44% of observations, respectively (Gilbert and Erickson 1977; Hall-Martin 1974; Hofman 1975). Mean group size increases in fall and at onset of winter (2.5–3.5) when pack ice is less available and hostile breeding interactions are reduced (Gilbert and Erickson 1977; Ribic et al. 1991). With the exception of mated pairs and families, group structure is fluid with no strong bonds between individuals. Members of a group typically remain within 1.8–2.5 m of each other (Siniff et al. 1970). Large aggregations of ≤50 animals may be encountered in pack ice, and up to 500 seals have been observed swimming together, although individuals or groups of ≤50 are more common

(Bertram 1940; Laws 1993a; Mackintosh 1967). In the breeding season, large groups (50–1,000) of immature crabeater seals may be found on fast ice (Laws 1981). Young seals may become embayed on fast ice when water begins to freeze in fall and can use ice holes of Weddell seals or other ice cracks as far as 48 km from open water (Bertram 1940). As a result of disorientation or dispersal, immature seals may wander inland following natural topographic paths such as valley bottoms and ephemeral stream beds until they die of starvation or exhaustion. In the arid and cold inland environment, carcasses may mummify (Stirling and Kooyman 1971; Stirling and Rudolph 1968).

Crabeater seals are serially monogamous, although males may seek additional copulations after mating with their primary mate of each season. Mating system of *L. carcinophaga* is believed to result from instability of pack ice, which also favors short and synchronized breeding and a short weaning period. Males actively defend their mates to a radius of 50 m against other males, leopard seals, and humans. Resident males often seek elevated positions for better vigilance. When challenged, a resident male positions himself between his female and an intruding male. The resident bites the challenger about the head and neck and tries to prevent him from entering the floe center. Changes in the resident male of individual family groups are rarely observed. Intense male–male interaction may explain segregation of immature and mature seals (Laws 1981, 1984; Shaughnessy and Kerry 1989; Siniff 1981; Siniff et al. 1979). Males show little interest in newborn pups, and protection of pups appears incidental to males defending their rights to breed with a female (Laws 1981). A case of a lone adult male defending a dead pup is known (Siniff et al. 1977). When pups leave a family group, mated pairs remain together for 1–2 weeks or until copulation (Bengtson 2002). Mated pairs also form when females without pups are joined by males. Adult pairs stay in close association, usually lying back to back, with the male lying perpendicular to the female and his head resting on her side, or with the male lying over the female's back. Males attempt to prevent females from leaving, often by biting them on the back. Mating has not been observed, but most likely takes place on ice (Laws 1981; Siniff et al. 1979). Newly mature females may mate in water (Laws 1984). On ice, attempted mating or precopulatory behavior involved the male biting the female's back and attempting to move his body over her. Females moved away in all instances. By the end of pupping and breeding seasons, heads and necks of males are heavily scarred, and females bear scars on their backs and are very thin after fasting and nursing (Laws 1984; Siniff and Reichle 1976; Siniff et al. 1979).

Crabeater seals typically use a sinuous or serpentine gait on land or ice. Progression is by alternate retraction of foreflippers, combined with mediolateral undulations of lumbar region and pelvis and lateral undulation of coupled hind flippers which are raised 5–8 cm off the substrate and swung in an 80° arc. The body sways from side to side and increases efficiency with which forelimbs can gain purchase on the substrate. On solid snow, this mode of locomotion leaves a distinctive sinuous body drag track with alternating foreflipper imprints on either side. Crabeater seals can travel 19 km/h for short distances (230 m), although speeds of 1.5–3 km/h are more typical (O'Gorman 1963). One adult was estimated to travel 26 km/h (Scheffer 1958). Crabeater seals use dorsoventral undulation on gravel and intermittently on snow and ice. Pups do not use the sinuous gait, but use dorsoventral undulations to travel speeds of 5–6.5 km/h, although they can travel 11–13 km/h for short (20- to 25-m) distances (O'Gorman 1963).

Swimming propulsive forces are generated by lateral lumbar undulation coupled with paired flexion and extension of hind limbs, which are swung about main axis of body in a 150–180° arc (Bryden and Felts 1974; O'Gorman 1963). Conservative maximum swim speeds of 66 km/day and 12.7 km/h are available from satellite telemetry. Average daily travel speed (mean \pm SD; in km/day) ranges from 18.1 \pm 4.5 (Bengtson et al. 1993) to 35 (Nordøy et al. 1995). While swimming near the surface, crabeater seals occasionally display porpoising—a series of jumps in which their bodies completely clear the water (Bonner and Laws 1964; Siniff et al. 1979). Crabeater seals also display spyhopping behavior, in which the seal raises its anterior body vertically out of water to visually inspect objects above the surface (Nel 1966). Play behavior in crabeater seals includes repeatedly leaping onto a floe and then sliding back into water (Condy 1977). Crabeater seals do not sleep motionless at the water surface (Bertram 1940).

Crabeater seals display 4 dive types (Bengtson and Stewart

1992). Shallow, travelling dives (<10 m depth) account for 37–63% of dives; are most common at sunrise, midday, or sunset; and are characterized by slow rates of descent and ascent (ca. 44 m/s), and short times spent at surface (mean = 53 s) and underwater (mean = 48 s). Medium-depth foraging dives (10–50 m depth), often repeated in tandem series, are most frequent between 1800 and 0600 h local solar time. These dives are characterized by higher rates of descent and ascent (ca. 0.76 m/s) and longer times spent underwater (mean = 3.7 min), during which crabeater seals spend 59% of the time at bottom depth. Deeper dives (>50 m depth) are divided into crepuscular feeding dives with rapid rates of ascent and descent (ca. 1.25 m/s) and long times (\geq 20 s) spent at the bottom and exploratory dives, which typically occur just before evening or just after morning and which have high rates of ascent and descent (ca. 0.93 m/s) and short times (<20 s) spent at the bottom. Exploratory dives have additional roles in navigation or orientation and often precede foraging dives. Foraging dives are characterized by vertical zigzag movements. Time spent underwater in the latter 3 dive types range from 3 to 6 min, with 30- to 60-s recovery periods at surface. Night dives are more shallow than day dives, and dive duration is poorly correlated with inter-dive recovery periods. On average (mean \pm SD), crabeater seals dive continuously for 16 \pm 3.1 h ($n = 21$), but may do so for up to 44 h. Both sexes have similar dive patterns (Bengtson and Stewart 1992). Maximum recorded individual dive depth and duration are 528 m (Nordøy et al. 1995) and 10.8 min (Bengtson and Stewart 1992), respectively. Mean (\pm SE) maximum daily dive depth ranges from 118 \pm 11 m to 156 \pm 10 m (Nordøy et al. 1995). Crabeater seals prefer shallow or medium dives (<50 m), which constitute 70–96% of dives. Individual dive depths correspond to depth of krill during their diel vertical migration and physical features such as thermocline or pycnocline layers (Borneman and Plötz 1999; Nordøy et al. 1995). Crabeater seals dive >12 m an average (\pm SE) of 154 \pm 11 times per day year-round. However, seasonal variation in number of night dives is evident, with night dives constituting 69% of dives in March but only 40–43% of dives in April–June. Proportion of shallow or medium-depth dives increases from 74% of day dives in March to 95% in May (Nordøy et al. 1995). Crabeater seals have a breathing rate of 42 breaths/min during recovery (Bertram 1940). Normal resting breathing rate is 8–11 breaths/min (Hofman 1975). When surfacing, crabeater seals will often hold only the upper part of the head above the waterline, everting their nostrils to form a cup-shaped snorkel through which they breathe (Nel 1966). Crabeater seals expose their backs when submerging for a dive (Laws 1993a).

When crabeater seals are disturbed during haul-out, they typically raise their heads, arch their backs, and peer about intently (Bengtson 2002; Erickson and Hofman 1974; Laws 1993a). Crabeater seals characteristically lift their heads and “point” (often with mouth open) when disturbed, a response that can be elicited with a ship's horn blast (Laws 1993a). If a threat is perceived, they may bear their teeth in an open-mouthed display accompanied by hissing or growling (Cline et al. 1969; Laws 1979, 1993a; Nel 1966; Stirling and Kooyman 1971). This display is more intense in older individuals, and crabeater seals may charge at approaching humans (Cline et al. 1969). Males in family groups are most restless in the presence of a threat, whereas female response varies (Corner 1972; Shaughnessy and Kerry 1989). Single crabeater seals tend to resist approach more than groups (Bertram 1940). Crabeater seals are reticent to escape by diving into water and usually just move away from a threat, glancing constantly over their shoulders. Fleeing crabeater seals may attempt to hide behind raised hummocks on a floe (Nel 1966). If a threat persists, a crabeater seal may move to a flat area, support itself on its foreflippers, and turn in circles looking for escape (Aguayo and Torres 1975). One threatened crabeater seal uttered no sound but vibrated its jaw (Matthews 1929); another rolled onto its back upon approach of a ship and vibrated its entire body and limbs (Nel 1966). The latter behavior is more typical of threatened Weddell seals (Stirling and Kooyman 1971), and may be a case of mistaken identity.

Airborne vocalizations of adult *L. carcinophaga* consist of bubbling sounds with no musical chirps or trills, growling, harsh barking, hissing, snarling, and snorting (Bertram 1940; Cline et al. 1969; Corner 1972; Kooyman 1981; Nel 1966; Perkins 1945; Ross et al. 1976). Pups emit feeble mewling cries resembling those of a calf (Corner 1972; Le Souef 1929). Underwater, crabeater seals emit a deep, monosyllabic call resembling a groan that lasts 1.93–

2.50 s (mean \pm SD: 2.12 \pm 0.14 s; n = 18). Some harmonics of this call exceed 800 Hz, although most are <1,500 Hz (Stirling and Siniff 1979). Peak underwater vocalizations occur from 1900 to 600 h local solar time in austral spring (Thomas and Demaster 1982). Vocalizations have a primarily agonistic role in crabeater seals (Rogers 2003).

GENETICS. *Lobodon carcinophaga* has a diploid number of 34 and fundamental number of 66 (Hofman 1975; Seal et al. 1971b). Autosomal pairs 1–10 form a series of metacentric chromosomes of decreasing size (range of arm length ratios is 1.2–1.6), with 3 large, 3 medium, and 4 small pairs. Autosomal pairs 11–14 and 16 are submetacentric (range of arm length ratios is 2.4–3.0), with 2 large and 3 medium-sized pairs. Autosomal pair 15 has medium sized acrocentric or subtelocentric chromosomes (arm length ratio is 5.5). X chromosomes are medium-sized metacentrics that constitute 5.8% of total haploid autosomal length. The metacentric Y chromosome is the smallest element in the crabeater seal karyotype. Autosomal pairs 1–3, 11 and 12, and 13 and 14 are similar in size and cannot usually be paired with certainty. X chromosomes are similar to autosomal pairs 4 and 5. A small satellited carnivora marker is present (Hofman 1975; Seal et al. 1971b). Individual chromosome measurements are available (Hofman 1975).

Protein electrophoretic studies reveal 2 codominant alleles for the transferrin gene. Similar polymorphism occurs with lactic dehydrogenase. At least 13 other proteins are not polymorphic (Scheil et al. 1985; Seal et al. 1971a, 1971b; Vergani et al. 1986). Six potentially discrete, geographically isolated populations have been suggested (Gilbert and Erickson 1977), but are not supported by microsatellite markers (Davis et al. 2002). Most variation occurs between individuals rather than geographic areas (Davis et al. 2000). Two forms of hemoglobin are present (Seal et al. 1971a).

REMARKS. The genus name *Lobodon* is derived from Latin for lobe (*lobus*) and Greek for tooth (*odont*) in reference to the uniquely lobed postcanine teeth. The specific epithet, *carcinophaga*, is from Greek for crab (*carcinus*) and to eat (*phaga*) in reference to the diet of the species (Bengtson 2002). The feminine specific epithet (*carcinophaga*) was correctly used in combination with the feminine genus to which it was originally referred (*Phoca*). According to Article 31(b)(ii) of the International Commission on Zoological Nomenclature Code, *carcinophaga* retains its feminine ending despite now being used in combination with the masculine *Lobodon* (Rice 1998). Crabeater seals 1st became known to science in an illustration drawn by Paul Mikhailov, which appeared in Faddeevich Bellinsgauzen's 1831 Russian edition of *Dvukratnye izyskaniia v l'uzbnom Ledovitom okeane* (reproduced as plate 12 in Debenham [1945]). No name accompanied the original illustration, and the reference is excluded from synonymy lists (Bertram 1940). The original name given, *P. carcinophaga*, appears as a caption to anonymously authored plates 10 and 10A in an atlas of an 1837–1840 French expedition to Antarctica (edited by Charles Hector Jacquinot [1842]). Later specimens from the expedition were described as *L. carcinophaga* (nomenclature following Gray [1844]) by Hombron and Jacquinot (1853). These authors credit Jacques Bernard Hombron and Honoré Jacquinot with authorship of the original (1842) plates (Hombron and Jacquinot 1853:27), thus Hombron and Jacquinot are credited for the original species diagnosis (Robineau 1992; Scheffer 1958). Holotype material was not designated in the original description, but lectotypes collected by Hombron and Jacquinot are housed at the Muséum National d'Histoire Naturelle, Paris (Robineau 1992). Gray (1844) includes *Leptorhynchus serridens* as a synonym of *L. carcinophaga*, the result of a transcriptional error of *Stenorhynchus serridens* from Owen (1843). Gray (1850:11, 1866a:10) also includes *Halichoerus antarctica* as a synonym of *L. carcinophaga*, citing Peale (1848:30). Skull described by Peale (1848) is clearly a phocine seal (possibly a gray seal [*H. grypus*]) and type locality (Deception Island, Antarctica) was apparently erroneous because phocines only occur in the northern hemisphere. This error was 1st recognized by Gill (1866:6) and acknowledged by Gray (1866b:446).

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