

Neophocaena phocaenoides. By Thomas A. Jefferson and Samuel K. Hung

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Neophocaena Palmer, 1899

- Delphinus* G. Cuvier, 1829:291. Part, not *Delphinus* Linnaeus, 1758.
Neomeris Gray, 1846:30. Type species *N. phocaenoides* G. Cuvier by original designation. Preoccupied by *Neomeris* Lamouroux, a genus of algae (originally thought to be a polyp), and *Neomeris* Costa, a genus of polychaetes.
Meomeris Gray, 1847:36. Misprint of *Neomeris*.
Phocaena Blanford, 1888:574. Type species *N. phocaenoides* G. Cuvier, 1829.
Neophocaena Palmer, 1899:23. Type species *D. phocaenoides* G. Cuvier by monotypy.
Delphinapterus Owen, 1866:24. Part, not *Delphinapterus* Lacépède, 1804.
Phocoena Robinson and Kloss, 1918:79. Part not *Phocoena* G. Cuvier, 1817.
Phaocana Allen, 1923:239. Misprint of *Phocoena*: Robinson and Kloss.

CONTEXT AND CONTENT. Order Cetacea, suborder Odontoceti, superfamily Delphinoidea, family Phocoenidae, subfamily Phocoeninae (Rice 1998). Five nominal species have been described: *Neophocaena phocaenoides* (G. Cuvier, 1829), *N. molagan* (Owen, 1866), *N. kurrachiensis* (Murray, 1884), *N. asiaeorientalis* (Pilleri and Gehr, 1972), and *N. sunameri* Pilleri and Gehr, 1975 (= *Delphinus melas* Schlegel, 1841). The genus currently is considered to be monospecific (Rice 1998; van Bree 1973), although a recent study suggests that 2 species possibly may be warranted (Jefferson 2002).

**Neophocaena phocaenoides
(G. Cuvier, 1829)**

Finless Porpoise

- Delphinus phocaenoides* G. Cuvier, 1829:291. Type locality “au Cap,” restricted to the Malabar coast of India (Robineau 1990: 232).
Delphinus melas Schlegel, 1841:32. Type locality unspecified location off the coast of Japan.
Neomeris phocaenoides: Gray, 1846:30. Renaming of *D. phocaenoides* G. Cuvier, 1829.
Meomeris phocaenoides: Gray, 1847:36. Misprint of *Neomeris phocaenoides*.
Delphinapterus molagan Owen, 1866:24. Type locality “vicinity of the harbour of Vizagapatam,” east coast of India, near Madras.
Phocaena phocaenoides: Blanford, 1888:79. Renaming of *D. phocaenoides* G. Cuvier, 1829.
Neomeris kurrachiensis Murray, 1884:351. Type locality near “Kurrachee” (Karachi), Pakistan.
Neophocaena phocaenoides: Palmer, 1899:23. First use of present name combination.
Phocoena phocaenoides Robinson and Kloss, 1918:79. Type locality “east coast of Sumatra.”
Phaocana phocaenoides: Allen, 1923:239. Misprint of *Phocoena phocaenoides* Robinson and Kloss.
Neomeris asiaeorientalis Pilleri and Gehr, 1972:126. Type locality “Yangtze, Prov. Kiangsu, Shanghai, China.”
Neophocaena asiaeorientalis: Pilleri and Gehr, 1975:668. Name combination.
Neophocaena sunameri Pilleri and Gehr, 1975:668. Renaming of *D. melas* Schlegel, 1841.

CONTEXT AND CONTENT. Content as for genus. Three subspecies of *N. phocaenoides* are recognized (Rice 1998).

- N. p. asiaeorientalis* (Pilleri and Gehr, 1972), see above.
N. p. phocaenoides (G. Cuvier, 1829), see above.
N. p. sunameri (Pilleri and Gehr, 1975), see above.

DIAGNOSIS. *Neophocaena phocaenoides* is the only member of the family Phocoenidae without a dorsal fin (Fig. 1). In its place is a low, geographically-variable dorsal ridge (sometimes inappropriately called a “groove”) covered with lines of small tubercles running along the back. The body is relatively more slender than that of other phocoenids. Unlike other porpoises, which all have sloping foreheads, the forehead of adult finless porpoises is very steep.

The skull (Fig. 2) is relatively small and the rostrum is broader and less pointed than in other phocoenids (Kasuya 1999). Condylbasal length of adults ranges from 181 to 251 mm ($n = 218$ —Jefferson 2002), which is shorter than in *Phocoena spinipinnis* (270–297 mm—Brownell and Clapham 1999a), *Phocoena dioptrica* (279–324 mm—Brownell and Clapham 1999b), and *Phocoenoides dalli* (309–340 mm—Houck and Jefferson 1999; Jefferson 1988). Tooth counts of *Neophocaena* range from 15 to 22 in both upper and lower jaws (Jefferson 2002). Although some overlap occurs, finless porpoise tooth counts are generally lower than in *Phocoena phocoena* (21–29—Read 1999) and *Phocoenoides dalli* (21–28—Houck and Jefferson 1999). Antorbital notches are relatively deep (>2 mm) in this species, but in other species of phocoenids are absent or <2 mm deep (T. A. Jefferson, in litt.). Morphology of tympano-periotic bones differs from that of other members of Phocoenidae in height of tympanic bulla, thickness of periotic, and diameter of the cochlear portion (Kasuya 1973).

GENERAL CHARACTERS. Maximum total length is 227 cm (Wang 1989). Flippers are moderately large (range, 17.5–20.1% of total length), recurved, and pointed at the tips (Kasuya 1999). Fluke width is 26.8–29.6% of total length (Kasuya 1999). Shape of the dorsal ridge is highly variable. In *N. p. phocaenoides*, it is low and wide (3.5–12.0 cm wide), with 10–25 rows of tubercles (Gao 1991; Gao and Zhou 1995a; Pilleri and Gehr 1972). In *N. p. asiaeorientalis* and *N. p. sunameri*, it is higher and much narrower (0.2–1.2 cm wide), with 1–10 rows of tubercles (Gao 1991; Gao and Zhou 1995a). Maximum known body mass is 71.8 kg (Kasuya 1999).

Body color is also geographically variable (Kasuya 1999;



FIG. 1. External appearance of *Neophocaena phocaenoides*. The photo shows 2 adult-size porpoises captured in southern Fujian Province, Xiamen, P. R. China: *N. p. asiaeorientalis* specimen (top) with a narrow dorsal ridge, and *N. p. phocaenoides* (bottom) with a wide ridge. Photograph by the late S. Leatherwood.

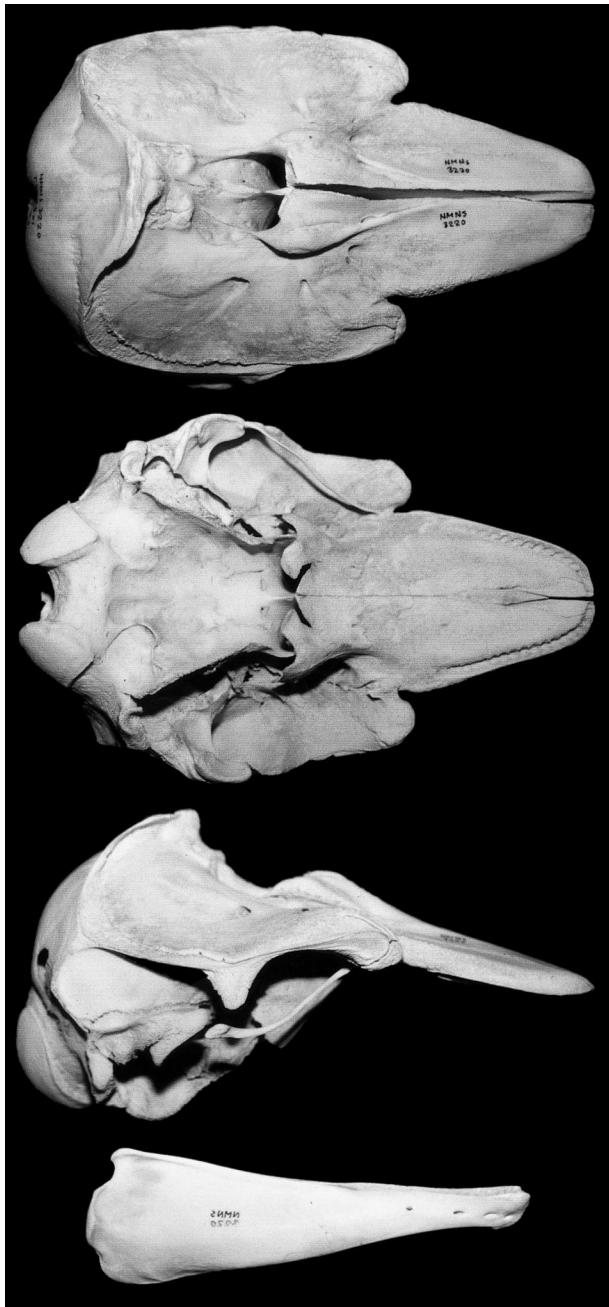


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *N. p. phocaenoides* (NMNS 3220). View of mandible is to a different scale than views of cranium. Greatest length of cranium is 245 mm, and greatest length of mandible is 176 mm. Photographs by J. Y. Wang.

Reeves et al. 1997). Early authors often described the body color as black (e.g., Fraser 1935). However, based on observations of live animals and freshly dead specimens, Pilleri et al. (1976) suggested that the finless porpoise exhibits postmortem darkening of the skin. In live animals, the main color is various shades of gray (Pilleri et al. 1976). In *N. p. phocaenoides*, animals are light creamy-gray at birth, with variable lighter patches around the mouth and throat. Fetuses are creamy white in color (Hafeezullah 1984) and darken to dark gray or nearly black in adults (Jefferson et al. 2002b; Parsons and Wang 1998). In *N. p. sunameri* and *N. p. asiaorientalis*, newborns are dark gray and lighten as they get older. Adult porpoises from Japanese and some northern Chinese coastal waters attain a light cream color (Kasuya 1999; Zhang 1997), and the epidermis may be unpigmented (Sokolov 1973). Light patches around the mouth and head and a dark gape-to-flipper stripe may

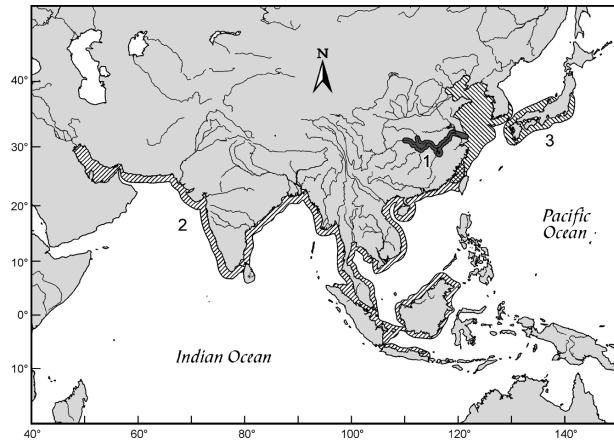


FIG. 3. Presumed distribution of *Neophocaena phocaenoides*: 1, *N. p. asiaorientalis*; 2, *N. p. phocaenoides*; 3, *N. p. sunameri*. Specific sighting and specimen records are sparse, especially in the Indian Ocean, and the range may be more discontinuous than shown here.

occur; these color pattern components usually are more evident on young animals (Jefferson et al. 2002b; Pilleri et al. 1976).

The skull (Fig. 2) has bony bosses anterior to the nares. Large, irregularly-shaped openings in the occipital bones at the back of the brain case often occur. Lateral margins of the maxillae are nearly parallel along their dorsal length (Kasuya 1999). Pterygoids are narrow and have notches, the depth of which varies among geographic areas (Jefferson 2002). Teeth are small and spatulate and average ca. 15 mm long and 3 mm in diameter (Kasuya 1999).

DISTRIBUTION. *Neophocaena phocaenoides* is distributed in coastal and some shallow offshore waters from the Persian Gulf in the west, eastward along the coasts of the Indian Ocean to at least Indonesia, and northward into the Pacific Ocean to southern Japan (Fig. 3; Kasuya 1999; Reeves et al. 1997). Countries for which records exist are: United Arab Emirates (Baldwin et al. 1998), Saudi Arabia (Robineau and Fiquet 1994, 1996), Bahrain (Gallagher 1991; Ridgway in Kasuya 1999), Kuwait (Clayton 1983), Iraq (Al-Rohaae 1975), Iran (Keijl and Van Der Have 2002; Pilleri and Gehr 1974), Pakistan (Pilleri and Gehr 1972; Pilleri and Pilleri 1979; de Silva 1987), India (Balan 1976; Blandford 1888; Dawson 1959; Fraser 1966; Hafeezullah 1984; Lal Mohan 1985; Nammalwar et al. 1994; Pilleri and Gehr 1972; Robineau 1990; Sutarua 2003), Sri Lanka (Ilankoon 2002), Bangladesh (Aminul Haque 1982), Thailand (Andersen and Kinze 1999; Chantrapornsy et al. 1996, 1999; Mahakunlayanakul 1996; Pilleri 1973; Pilleri and Gehr 1974), Malaysia (Beasley and Jefferson 1997; Flower 1900; Gibson-Hill 1949, 1950; Rudolph et al. 1997), Brunei (Elkin 1992), Singapore (Hanitsch 1908; Rudolph et al. 1997; Sigurdsson and Yang 1990), Cambodia (I. Beasley, pers. comm.), Indonesia (Rudolph et al. 1997; Tas'an and Leatherwood 1984; van Bemmel 1939), Vietnam (Smith et al. 1997, 2003), China (Gao 1991; Jefferson and Braulik 1999; Liu et al. 1999; Parsons and Wang 1998; Wang 1984a, 1985, 1990; Zhou et al. 1995, 1998), Taiwan (Yang 1976; Zhou et al. 1995), Korea (Howell 1927; Kim and Huh 1995; Park et al. 2002), and Japan (Kasuya and Kureha 1979; Mizue et al. 1965; Nishiwaki 1972; Shirakihara et al. 1992a, 1992b, 1994; Yoshida et al. 1997, 1998).

No valid records exist for the Philippines; previous reports of sightings in Malampaya Sound, Palawan, and a stranding from the Turtle Islands of the southern Philippines were misidentifications (M. L. L. Dolar and W. F. Perrin, pers. comm.). Sleptsov (1961) reported several finless porpoise sightings off Russia's Kurile Islands, but these clearly were misidentifications (probably northern right whale dolphins, *Lissodelphis borealis*).

FOSSIL RECORD. No known fossils exist of the genus *Neophocaena*. However, de Muizon (1988) described the fossil phocoenids, *Lomacetus ginsburgi* and *Australithax intermedia*, which are both related to *Neophocaena* and differ mainly by having much longer rostra.

A recent molecular genetic study of porpoises by Rosel et al.

(1995) indicated that *Neophocaena phocaenoides* is the most basal member of the family Phocoenidae. Therefore, among the living species of the family, the finless porpoise is probably most closely related to the ancestral form.

FORM AND FUNCTION. The anatomy of finless porpoises from Chinese waters has been well studied (Gao and Zhou 1993a; Zhou 1991; K. Zhou et al. 1993a). Early anatomical descriptions were by Allen (1923), Howell (1927), and Ping (1925, 1926a, 1926b).

Distinct features of the ultrastructure of the skin and epidermis include the lamellated membrane-coating granules, which are involved in formation of an epidermal intercellular permeability barrier (Feng and Liang 1985; Liu and Harrison 1986). Many tonofilaments are present in the strata of the skin, and numerous encapsulated nerve endings and bundles of myelinated nerve fiber lie at the bases of the tubercles on the dorsal ridge (Liu 1985; Liu and Harrison 1986).

Skeleton is very light and thin; its total weight is only 5% of body mass (Hsu et al. 1973; Shaw 1938). Meckelian ossicles occur in the maxillary/premaxillary suture (Cave 1988). Vertebral formula is 7 C, 12–14 T, 10–13 L, 26–33 Ca, total 58–65 (Kasuya 1999). The first 3 cervical vertebrae are fused (Allen 1923; Howell 1927; Ping 1925). The thoracic vertebrae are articulated with 12 to 14 pairs of ribs, and a pair of vestigial ribs is connected to the 7th cervical vertebra (Allen 1923; Hsu et al. 1973; Mahakunlayanakul 1996; Ping 1925). Sternum is a single piece of bone (Hsu et al. 1973; Mizue et al. 1965), with the posterior part reduced (Allen 1923). Lumbar vertebrae are the largest, with long transverse processes and high spines. Generally 10 to 12 pairs of ribs exist, the anterior 6 to 8 of which are 2-headed. Phalangeal count is 2 I, 5–8 II, 5–7 III, 3–4 IV, 2 V (Kasuya 1999).

During development, the final fusion between the centrum of a vertebra and its epiphysis occurs in the thoracic vertebrae (Mahakunlayanakul 1996; Yoshida et al. 1994). Sexual dimorphism was detected in more than one-half of the postcranial characters, with females tending to show higher values (Yoshida et al. 1994). Individual variation was also found, greatest in the feeding apparatus (such as length of rostrum).

Myology of the finless porpoise has been poorly studied. Howell (1927) provided the only detailed descriptions of facial musculature, muscles of the tongue, thorax and abdomen, vertebral musculature, muscles of the anterior limb, and pelvic musculature. Nasal musculature consists of 5 layers, with fiber lengths ranging from 19.7 to 42.7 mm (Gao and Zhou 1988).

The heart is rhomboid and flattened (Ping 1926a). The right auricle appears ovoid, with the middle portion on its dorsal surface glandular. In the ventricle are 5 small muscoli papillae. The auriculoventricular valve has 4 flaps, instead of being tricuspid. The wall of the aorta at its root is 2 mm thick, compared to 1 mm for the pulmonary artery. The walls of the pulmonary vein, and the superior and inferior vena cavae are all less than 1 mm thick (Ping 1926a).

Spinal cord consists of 44 pairs of spinal nerves (8 cervical, 13 thoracic, and 23 lumbocaudal segments—Wu 1989). A specific cell group in the thoracic and lumbocaudal segments was found for the first time in any cetacean (Wu 1989). Anatomy and detailed brain measurements and weights are available (Pilleri and Chen 1982). Morphologically, the brain of *N. p. phocaenoides* is somewhat more differentiated than that of *N. p. asiaeorientalis* (Pilleri and Chen 1980). Head oils of finless porpoises contain 3 principal components (Kanazu and Fukuhara 1964).

Differences in the optic system were found between freshwater and marine populations of *Neophocaena*. Yangtze River finless porpoises show atrophy of the entire optic system, with smaller eye slits, a substantially reduced lens, and lower number of optic nerves and eye muscle nerves (Chen et al. 1980; Gao and Zhou 1986; Pilleri and Chen 1980). Although the optic system of the Yangtze River finless porpoise is more developed than that of the baiji (*Lipotes vexillifer*), with higher optic nerve counts (Wu and Li 1984), the count is still quite low, indicating that the porpoise has weak vision (Gao and Zhou 1992). Cochlear nerves have over 80,000 fibers, and almost all cochlear fibers are myelinated (Gao and Zhou 1991, 1992). The high percentage of large fibers and wide range of fiber diameters indicated that the finless porpoise has a relatively well-developed auditory system, with specialized cochlear nerves

for high-speed communication with the brain (Gao and Zhou 1992; Liao 1978).

Only a few studies present detailed descriptions of different parts of the respiratory system. The trachea is short, with only 4 cartilaginous rings (Ping 1926a; Qian 1986). Within the nasal passage 9 to 10 nasal sacs occur, and a pair of vomeronasal sacs is also found behind the posterior portions of the nasofrontal sacs. The nasofrontal sacs are large and complicated; they can effectively seal off air within the nasal passage (Gao and Zhou 1989).

The tongue is oval and thickset, and its surface is remarkably smooth, but slightly rough at the edges. It has high, grooved lateral surfaces (Arvy and Pilleri 1972). Esophagus is a curved, compressed tube (Ping 1926a). Stomach consists of a fore-stomach, main stomach, and pyloric stomach, with the main stomach joined to the pyloric stomach by a connecting channel (Li et al. 1984). Liver has 2 main lobes, which are connected by a bridge in the middle (Ping 1926a). Intestine is ca. 7 to 11.2 times body length. No caecum exists, and no distinct difference between small and large intestines has been observed (Qian et al. 1985). Pancreas is somewhat pyriform and flattened, located at left side of the duodenal ampulla and on the posterior side of main and pyloric stomachs (Ping 1926a; Qian et al. 1985). Kidneys are unequal in size and finely lobulated, with 14 to 150 reniculi (Ping 1926a).

Reproductive system of both sexes has been examined (Chen et al. 1982; Harrison and McBrearty 1974; Ping 1926a, 1926b; Wang and Liu 1998). Testes are flattened and reniform, and most of the epididymis is flattened and highly convoluted. Vas deferens is somewhat cylindrical and less complicated in arrangement (Ping 1926a, 1926b). A small cavity between the anus and the penile opening lies on the centerline of the ventral surface (Mizue et al. 1965; Nishiwaki and Kureha 1975). Morphology of the spermatozoa shares several similarities with that of *Phocoenoides dalli*, including both species having sperm with ellipsoid heads (Kita et al. 2001).

ONTOGENY AND REPRODUCTION. Growth curves have been constructed for populations in Japanese and Chinese waters (Chang and Zhou 1995; Gao and Zhou 1993b; Jefferson et al. 2002b; Kasuya 1999; Kasuya et al. 1986; Shirakihara et al. 1993; Zhang 1992). Growth is rapid in the first few years, with males growing slightly larger than females. Maximum longevity is 33 years (Jefferson et al. 2002b).

Growth and reproductive parameters of Japanese populations are based on large samples ($n = 207$ specimens). Average neonatal length was 75–85 cm; the largest known specimen for various populations was 175–194 cm; minimum length at sexual maturity was about 135–145 cm (males) and 135–140 cm (females); minimum age at sexual maturity was 3–4 years (males) and <4–5 years (females); gestation lasted 10.6–11.2 months; and the calving season was reported to be either spring–summer or winter (Furuta et al. 1989; Kasuya and Kureha 1979; Kasuya et al. 1986; Shirakihara et al. 1993).

Reproduction and growth of Chinese finless porpoises from coastal and Yangtze River waters have also been studied, based on several hundred specimens. Different populations showed the following range of estimates: average neonatal length 72–84 cm; largest known individual 168–227 cm (males) and 164–206 cm (females); minimum length at sexual maturity 132–150 cm (males) and 132–145 cm (females); minimum age at sexual maturity 4–6 years (males) and 5–5.5 years (females); gestation period 10.1–11.5 months; and calving season spring to winter (Chang and Zhou 1995; Chen et al. 1982; Gao and Zhou 1993b; Jefferson et al. 2002b; Zhang 1992). Calving in Hong Kong takes place mostly from October to January (Jefferson and Braulik 1999; Jefferson et al. 2002b). Much of the variation in these estimates is attributable to real variation between different populations of the finless porpoise (Chang and Zhou 1995; Gao and Zhou 1993b; Zhang 1992). A population dynamics and life table analysis for Chinese finless porpoises indicated low survival rates, which does not bode well for the continued existence of several populations (Yang et al. 1998).

The only other area with data on finless porpoise reproduction is Pakistan, but results are based on only 6 individuals. Neonatal length was estimated to be <77 cm, minimum length at sexual maturity was about 140 cm for males and 120 cm for females, and maximum known length was 155 cm (Harrison and McBrearty 1974).

ECOLOGY. The habitat of the finless porpoise is generally tropical to warm temperate coastal waters, including shallow bays, mangrove swamps, estuaries, and some large rivers. The species appears to prefer estuarine waters in many parts of its range, but in Hong Kong, finless porpoises avoid brackish waters and are found mostly in more saline waters (Jefferson et al. 2002a). The Yangtze River population, in which individuals extend upriver to Yichang, about 1,600 km from the mouth, is the only known wholly-freshwater stock (X. Zhang et al. 1993). Few records exist in offshore waters, but Miyashita et al. (1995) sighted finless porpoises in waters up to 240 km from the coast in the East China Sea, and they have been seen 135 km offshore in the South China Sea (De Boer 2000). These offshore sightings are still in continental shelf water depths, however.

Finless porpoises are opportunistic feeders, preying mainly on fishes, cephalopods, and crustaceans (Barros et al. 2002; Kasuya 1999; Park et al. 2002; Shirakihara et al. 1992a). Japanese finless porpoises feed on *Ammodytes personatus*, *Scomber japonicus*, *Trachurus japonicus*, squid, and crustaceans (Kataoka et al. 1976). In Korean waters, their main prey appears to be Japanese sand shrimp (*Crangon affinis*) and several species of fishes (Park et al. 2002). Stomachs of finless porpoises stranded in Hong Kong waters contained mostly cephalopods of the families Loliginidae, Octopodidae, and Sepiidae, and several demersal fish species of the families Apogonidae, Carangidae, Clupeidae, Congridae, Engraulidae, Leiognathidae, Maemulidae, Mugilidae, Nemipteridae, Sciaenidae, Serranidae, Sillaginidae, Sparidae, Stromateidae, and Trichiuridae, and a few panaeid shrimps (Barros et al. 2002; Parsons 1997). The myctophid otoliths first reported by Parsons (1997) were misidentified and there is currently no evidence that finless porpoises feed on these deepwater fish (Barros et al. 2002). Stomachs of specimens from Xiamen, P. R. China, contained fishes of the genera *Argyrosomus*, *Arius*, *Clupanodon*, *Decapterus*, *Ilisha*, *Sardinella*, *Saurida*, and *Trachinocephalus*, and panaeid shrimps and cephalopods (Huang et al. 2000). Other feeding habits studies in the Yangtze River and in northern China have identified a similar array of demersal fishes, cephalopods, and crustaceans (Allen 1923; Chen et al. 1979; Wang 1984b). Panaeid shrimp occurred in stomachs of Yangtze finless porpoises (Allen 1923). In Thailand, cephalopods are the most common prey, with some fishes, bivalves, and crustaceans taken as well (Mahakunlayanakul 1996). In Pakistan, stomachs have contained cephalopods, shrimps (*Penaeus*), and prawns (*Palaemon*—Murray 1884; Pilleri and Gihir 1972). Calves in the Yangtze River begin to take small fish at ca. 5 months of age (Wei et al. 2002).

Seasonal movements have been reported in most areas where density has been studied. In the Inland Sea of Japan, highest densities were observed in spring, and lowest were in early winter (Kasuya and Kureha 1979). In coastal waters of Kyushu, density was lowest in August, increasing through April, with high densities in summer (Shirakihara et al. 1994). Yoshida et al. (1998) found that porpoises moved offshore in Omura Bay in spring months. In Chinese waters, lowest density in the Yellow/Bohai seas occurs in winter and the highest in summer and autumn (Wang 1984b). Density in the middle and lower reaches of the Yangtze River was highest in winter and lowest in summer (X. Zhang et al. 1993).

The discovery of a *phocaenoides*-type finless porpoise at Dalian (Liaoning Province, northern China) could be evidence of long-distance movements (Wang 1992a, 1992b). However, using molecular genetic techniques, Yoshida et al. (2001) suggested that Japanese finless porpoises have limited dispersal patterns. In Hong Kong waters, seasonal movements result in highest densities in spring months and lowest in autumn (Jefferson and Braulik 1999; Jefferson et al. 2002a; Parsons 1998). Offshore movements in spring and inshore movements in autumn have been reported for the Indus River delta in Pakistan (Pilleri and Gihir 1972; Pilleri and Pilleri 1979).

The finless porpoise is sympatric with several other small cetacean species in different parts of its range, most notably the baiji in the Yangtze River and bottlenose (*Tursiops truncatus*), Indo-Pacific humpback (*Sousa chinensis*), and Irrawaddy (*Orcaella brevirostris*) dolphins in some coastal waters. It also may overlap with the susu (*Platanista gangetica*) and bhulan (*Platanista susu*) in estuaries of the Ganges and Indus River systems. Finless porpoises have been seen swimming together with baijis on occasion (Liu et al. 1986; Zhou et al. 1980). In Hong Kong waters, finless porpoises and humpback dolphins have never been seen interacting, and ap-

pear to partition the habitat (Jefferson and Braulik 1999; Parsons 1998). The same 2 species have been seen to interact, however, in the Indus River delta, Pakistan (Pilleri and Gihir 1972).

Attacks by sharks or killer whales (*Orcinus orca*) have not been observed, but finless porpoise remains have been found in stomachs of killer whales from Japan (Nishiwaki and Handa 1958). A great white shark (*Carcharodon carcharias*) caught off Okinawa was found with remains of 2 finless porpoises in its stomach (Kasuya 1999). A porpoise that apparently died as a result of an attack by a large shark was reported from Hong Kong waters (Jefferson and Braulik 1999; Parsons and Jefferson 2000).

Twenty internal parasites have been recorded from the finless porpoise: *Nasitrema spathulatum*, *N. sunameri*, *Otophocaenurus asiaeorientalis*, *Pseudostenurus sunameri*, and *Stenurus nanjingenensis* in respiratory passages and cranial sinuses (Kuramochi et al. 2000; Ozaki 1935; Tao 1983; Yamaguti 1951); *Pharurus asiaeorientalis* in the throat and blood sinus (Petter and Pilleri 1982); *Halocercus pingi*, *H. sunameri*, and *H. taurica* in the lungs and trachea (Jefferson and Braulik 1999; Kuramochi et al. 2000; Parsons et al. 1999; Parsons and Jefferson 2000; Tao 1983; Wu 1929); *Pseudostenurus auditivus* in the tympanic cavity (Hsu and Hoeppli 1934; Zhou 1991); *Campula folium* in the liver (Kikuchi et al. 1987; Ozaki 1935); *Campula oblonga* in the bile ducts, pancreatic ducts, and duodenal ampulla (Kuramochi et al. 2000); *Anisakis typica* in the stomach (Pilleri 1974); *Hadwenius nipponicus* in the duodenal ampulla (Kuramochi et al. 2000); *Corynosoma* sp., *Delphinicola tenuis*, *Orthosplanchnus elongatus*, and *Synthesium tursonianis* in the intestines (Hafeezullah 1986; Kuramochi et al. 2000; Ozaki 1935); and *Crassicauda fueleborni* and *Diphyllobothrium fuhrmanni* from unspecified organs (Baylis 1932; Hsu 1935). Newborn calves in Hong Kong often have high burdens of the lungworm *H. pingi*, suggesting that this parasite can be passed prenatally or through mother's milk (Parsons and Jefferson 2000; Parsons et al. 2001). Externally, stalked barnacles (*Conchoderma auritum* and *Xenobalanus globicipitis*) have been found on flippers and flukes of finless porpoises (Devaraj and Bennet 1974; Huang et al. 2000; Kuramochi et al. 2000; Parsons et al. 2001).

Mortality factors for stranded finless porpoises in Hong Kong have included natural causes, such as verminous pneumonia, shark attack, and uterine infections, and human-related causes such as boat strikes and fishing net entanglement (Jefferson and Braulik 1999; Jefferson et al. 2002c; Parsons and Jefferson 2000). The lungworm *Halocercus pingi* causes lesions in the lungs, and is often associated with verminous pneumonia (Parsons and Jefferson 2000; Parsons et al. 1999, 2001; Wu 1929). It can be so abundant in some animals that smaller respiratory passages can be nearly completely blocked (Jefferson et al. 2002c). Chen et al. (1982) reported a tumor in the vaginal wall of a female porpoise. Parsons and Jefferson (2000) also described 2 possible cases of uterine prolapse.

Finless porpoises have been held captive at ca. 10 different aquaria in Japan (Kataoka 1977; Reeves et al. 1997), and at 2 research institutes, and semi-captive at the Shi Shou Semi-Natural Reserve in China (Liu et al. 1995, 1999). Finless porpoises have also been held captive for short periods in Indonesia (Tas'an and Leatherwood 1984) and Thailand (S. Chantrapornsyil, in litt.). In captivity in Japan, finless porpoises have been fed *Oplegnathus fasciatus* and *Trachurus japonicus* (Kataoka et al. 1967, 1977a). Captive porpoises have eaten the equivalent of ca. 5–6% of their body weight per day, but have on occasion consumed up to 11–13% (Kataoka et al. 1967, 1977a).

In the Inland Sea of Japan, Kasuya and Kureha (1979) estimated a peak abundance of 4,900 porpoises in spring months. Preliminary work in coastal waters of western Kyushu was only able to estimate densities (Shirakihara et al. 1994), but more recent work has resulted in estimates of 1,983 porpoises in Ariake Sound and 1,110 in Tachibana Bay (Yoshida et al. 1997). A total of 187 porpoises were estimated to inhabit nearby Omura Bay (Yoshida et al. 1998). The population in the Yangtze River has been surveyed extensively, but a lack of systematic methods has prevented researchers from developing reliable population estimates. However, X. Zhang et al. (1993) have estimated abundance in the middle and lower reaches of the Yangtze at ca. 2,700 animals, and Zhou et al. (1998, 2000) estimated abundance in the lower reaches between Hukou and Nanjing at ca. 700. Ca. 388 porpoises occur in Poyang Lake (Xiao and Zhang, 2000). The total population size for Hong

Kong and surrounding waters is at least 220 porpoises (Jefferson and Braulik 1999; Jefferson et al. 2002a).

BEHAVIOR. Group size is generally small. In the Yangtze River, groups of 3 to 6 are most common, with occasional aggregations of up to 20 animals (Chen et al. 1979; Liu et al. 1986; Zhou et al. 1980). In Hong Kong waters, average group size is 3–6 individuals (range = 1–35, $n = 202$), with little seasonal variation (Jefferson and Braulik 1999; Parsons 1998). Groups of up to ca. 50 have been reported in other Chinese coastal waters, but these appear to be rare aggregations (Zhou et al. 1995). Porpoises in a semi-natural reserve formed “core groups” of 2 to 3 animals, generally with 1–2 juveniles or calves (Wei et al. 2002). In Japanese waters, finless porpoises form groups of up to 13 individuals, with an average of ca. 2, and the basic unit of a group is no more than 3 porpoises (Kasuya and Kureha 1979).

Finless porpoises are generally shy and elusive, with little socializing at the surface (Parsons 1998). In the Yangtze, finless porpoises tend to swim close to river banks and are especially common at confluences in the river (Chen et al. 1979; Liu et al. 1986). Finless porpoises are generally most active when feeding. Some aerial behavior has been seen, and they sometimes jump out of the water, although at least in Hong Kong waters, aerial behavior is quite rare (Jefferson and Braulik 1999; Parsons 1998). Finless porpoises, unlike many other species of small cetaceans, do not ride bow waves of vessels and generally show avoidance reactions to vessels passing close by (Zhou et al. 1980).

Finless porpoises in the Yangtze have been reported to carry small calves on their backs (Chen et al. 1979; Pilleri and Chen 1979); however, documentation of this behavior is not very convincing, due to the distance and angle of observation. Parsons (1998) reported finless porpoises in Hong Kong spitting water from the mouth when feeding at the surface, and these animals are capable of weak suction feeding (Ito et al. 2002). Studies of behavior in captivity have also been conducted in Japanese aquaria, and chasing was found to be a prominent behavior pattern (Yoshie 1995; Yoshie et al. 1994).

The most common breathing interval is ca. 10 to 20 s (Chen et al. 1979; Liu et al. 1986; Zhou et al. 1980). Breath intervals in a semi-natural reserve were longer, 34.4 ± 4.39 s (*SD*) (Wei et al. 2002). However, from a radio-tracking study, X. Zhang et al. (1996) and Würsig et al. (2000) clarified that the most common pattern in the Yangtze River is a single long dive, followed by 2 shorter submergences. Akamatsu et al. (2002b) also found evidence for these 2 dive types from porpoises wearing time-depth recorders. Dives of over 4 min were documented (Würsig et al. 2000). Longer dives were more common during daytime, whereas at night porpoises often entered a resting pattern (X. Zhang et al. 1996). In Hong Kong, porpoises appear to spend about 60% of their time at or near the surface, and surface times increased in larger groups (Beasley and Jefferson 2002).

Vocalizations have been mostly described from studies of animals in captivity (Kamminga et al. 1986; Mizue et al. 1968; Nakahara et al. 1997; Pilleri et al. 1980; Wang 1996). Sounds produced by finless porpoises in the Yangtze River have been studied in some detail (Akamatsu et al. 1998, 2000; Wang 1996). The 2 categories of sounds include high-frequency clicks and low-frequency, continuous tones (Wang 1996). Clicks are narrow band, with peak frequencies over 100 kHz, well above human hearing range, which are typical of phocoenids (Akamatsu et al. 2002a; Kamminga et al. 1996). Vocalizations of Hong Kong finless porpoises showed both typical narrow-band clicks with a peak at 142 kHz, as well as broader-band clicks (Goold and Jefferson 2002). The unique, species-specific vocalizations of this species make it well-suited to the development of acoustic survey approaches (Akamatsu et al. 2001; Jefferson et al. 2002a).

GENETICS. Karyotype is $2n = 44$ (Peng and Chen 1985). The genetic structure appears to be somewhat complex; most studies have found genetic differences among groups of animals from different geographic localities in China (Gao 1991; Wang 1995; Yang and Zhou 1997, 2000; Yang et al. 2002). Molecular genetic studies using mitochondrial DNA have confirmed the 5 isolated populations proposed for Japanese waters, originally based on skull morphometrics, interviews, and aerial surveys (Yoshida 2002; Yoshida et al. 1995, 2001).

CONSERVATION STATUS. No large-scale, organized hunting of finless porpoises is known. Finless porpoises have been known by people along the Yangtze River and have been mentioned in ancient Chinese literature since around 100 AD (Gao and Zhou 1993a). Some direct hunting for meat and oil, using rolling hooks, rifles, and even fish forks, occurred in the past in China (mainly in the 1970s and earlier), but such takes are now illegal and probably only rarely occur (Liu 1991; Reeves et al. 1997; Zhang 1997). Some finless porpoises taken incidentally in set nets in Japan were taken to fish markets and sold for human consumption in the 1960s (Mizue et al. 1965). Consumption of the meat can cause diarrhea (Kasuya 1999). Finless porpoises have been found for sale in Hong Kong markets, although these are thought to have been by-caught animals (Parsons 1997).

Finless porpoises have been livecaptured for captive display and research in Japan (Kataoka 1977; Kataoka et al. 1977b; Kasuya et al. 1984; Unokawa et al. 1966), China (Liu et al. 1999; Wang et al. 2000), and Thailand (Chantrapornsy et al. 1996). The International Whaling Commission's Small Cetacean Subcommittee (International Whaling Commission 1984) reported that 107 finless porpoises had been taken as live captures in Asia. A total of 36 were reported livecaptured from the Yangtze River between 1990 and 1996 (Wang et al. 2000).

Incidental catches are probably a major problem for finless porpoises throughout their range (International Whaling Commission 2001). Catches in gillnet fisheries were reviewed by Jefferson and Curry (1994). Some are known to be taken in gillnets in Korea (International Whaling Commission 2001), Indonesia (Tas'an and Leatherwood 1984), Malaysia (Pilleri and Gih 1974), Vietnam (Smith et al. 1997, 2003), Thailand (Northridge and Pilleri 1986), India (Balan 1976; Jayaprakesh et al. 1995; Jones 1975; Lal Mohan 1985, 1994), and Pakistan (Niazi and Moazzam 1990; Pilleri and Pilleri 1979). An animal was taken by a trawler in Iraq (Al-Robbai 1975), and several were caught in rampani nets (a type of beach seine) used in India (Dawson 1959; Thomas 1983). Mortality in dol nets occurs in Indian waters, and animals are used by local people for their oil (Kizhakudan and Kizhakudan 2001). Catches in Bangladesh have been reported, but the type of fishing gear used is not known (Aminul Haque 1982). Finless porpoises also have been taken in set nets, stow nets, and traps in Korea (International Whaling Commission 2001; Park et al. 2002).

In China, many are killed in rolling hook longlines and encircling gillnets in the Yangtze River, and in pound nets, driftnets, and stow nets in coastal waters (Zhou and Wang 1994). About 50 are killed each year in waters of the Yellow Sea (International Whaling Commission 1984). Ca. 2,100 finless porpoises are caught each year incidentally in Zhejiang and Guangxi Provinces alone (Yang and Zhou 1996). Driftnets kill porpoises in waters of southern Fujian Province (Huang et al. 2000). In Hong Kong waters, catches in trawl nets and gillnets are known, but there are no estimates of annual kill (Jefferson et al. 2002c; Parsons and Jefferson 2000). Total annual kill for the entire coast of China might therefore be over 10,000. This species is clearly the most commonly taken cetacean in fishing gear in the country.

In Japanese waters, finless porpoises are taken incidentally in various fisheries (Miyazaki 1983; Mizue et al. 1965; Shirakihara et al. 1992b; Tobayama et al. 1990). Between 1970 and 1989, 23 were reported to have been taken in gillnets, 30 in set nets, 13 in seine nets, 5 in drag nets, 1 in a longline, and 2 in other types of fishing gear (Tobayama et al. 1990). Shirakihara et al. (1992b) mentioned 58 taken in bottom gillnets, 17 in surface gillnets, 7 in trap nets, 1 in a trawl net, and 1 in discarded netting. Japan has reported annual takes to the International Whaling Commission's Small Cetacean Subcommittee (International Whaling Commission 2001). However, these are probably only small portions of the overall mortality for those years.

As neritic small cetaceans in a rapidly-developing and increasingly industrialized part of the world, finless porpoises are prone to major problems of habitat deterioration (International Whaling Commission 2001). Physical loss of habitat has probably occurred in some areas, and human activities such as shipping and other vessel traffic can compromise the value of areas as finless porpoise habitat. Mortality from vessel strikes occurs in Hong Kong (Jefferson et al. 2002c; Parsons and Jefferson 2000), and a porpoise was killed by a jet-ski in Thailand (Chantrapornsy and Andersen 1995). Finless porpoises in the Yangtze appear to be more susceptible to vessel collisions that do baiji (Zhou et al. 1980). In the

Yangtze River, dams have blocked movements of individuals, thereby reducing habitat availability (K. Zhou et al. 1993a).

Environmental contaminants could represent the most serious long-term threat to many finless porpoise populations. Studies have been conducted on organochlorine levels in porpoises from Japan (Kannan et al. 1989; O'Shea et al. 1980), the Yangtze River (Yang et al. 1988; K. Zhou et al. 1993b), Yellow Sea (R. Zhou et al. 1993a), Bohai Sea (H. Zhang et al. 1993, 1996; W. Zhang, 1995), and Hong Kong (Minh et al. 1999, 2000a, 2000b; Parsons and Chan 1998). Heavy metal levels have been evaluated for specimens from Japan (Arima and Nagakura 1979), the Yangtze River (Lui et al. 1983; Yang et al. 1988), Yellow Sea (R. Zhou et al. 1993b), Bohai Sea (Zhang et al. 1995), East China Sea (Zhou et al. 1994), and Hong Kong (Jefferson et al. 2002c; Parsons 1999).

Heavy metal levels were higher in Yangtze River porpoises than in those from coastal waters of the Yellow and East China seas (K. Zhou et al. 1993b, 1994; R. Zhou et al. 1993b). Mercury levels in livers of Hong Kong porpoises were high enough to be considered a potential health risk (Jefferson et al. 2002c; Parsons 1999). Arsenic concentrations of finless porpoises tended to be lower than for other species of cetaceans (Kubota et al. 2001). Organochlorine levels generally have not been high, except for DDT, which was found to be very high in many Hong Kong porpoises (Jefferson et al. 2002c; Minh et al. 1999; Parsons and Chan 1998). Probably DDT poses a threat to the health of animals in and around Hong Kong (Jefferson and Braulik 1999; Jefferson et al. 2002c; Parsons and Chan 1998). Extremely toxic butyltins have been found in tissues of Chinese and Japanese finless porpoises (Iwata et al. 1994, 1995, 1997; Le et al. 1999; Tanabe et al. 1998). Butyltin concentrations of finless porpoise specimens from Hong Kong were among the highest of those compared from 9 cetacean species representing 11 geographic areas (Takahashi et al. 2000).

The conservation status of only a few populations is known with any certainty (Smith and Jefferson 2002). Despite the lack of rigor in estimates of abundance for the Yangtze River, there are indications of a decline in that population (Wang et al. 2000; X. Zhang et al. 1993; Zhou et al. 1998, 2000). A population viability analysis suggested that the chance of extinction of the Yangtze finless porpoise in the next 100 years is 10% (Zhang and Wang 1999). Chinese efforts to conserve the Yangtze finless porpoise in recent years have focused on setting up natural and semi-natural reserves and initiating captive-breeding attempts (Wang et al. 2000; Zhang and Wang 1999). A workshop in 1997 to develop a conservation action plan for the Yangtze River finless porpoise emphasized the need for increased efforts to protect the porpoise in its natural habitat (Reeves et al. 2000).

The population of finless porpoises in the Inland Sea of Japan has apparently declined dramatically since the 1970s, based on changes in distribution patterns and sighting rates from replicated vessel transect lines (Kasuya et al. 2002; Yamada and Okamoto 2000). This is probably due to a number of different human-caused factors, in particular by-catch in fishing nets (Kasuya et al. 2002; Yamada and Okamoto 2000). Legislation has been passed to address the situation.

The finless porpoise is listed as "Data Deficient" by the IUCN, although the Yangtze River subspecies is classified as "Endangered." The species is listed in CITES Appendix 1. *Neophocaena phocaenoides* is legally protected in some range states, such as part of the Inland Sea of Japan, China, Hong Kong, Taiwan, and the Philippines. However, this legislation probably has little influence over the actions of most fishermen and others who interact with finless porpoises.

Overall, the finless porpoise is in no immediate danger of global extinction (International Whaling Commission 2001). However, several populations are probably threatened (e.g., those in the Yangtze River and Inland Sea of Japan), and probably some others have already been lost before they could be documented (Reeves et al. 1997; Smith and Jefferson 2002).

REMARKS. The species was first described as *Delphinus phocaenoides* (Cuvier, 1829), based on a skull reportedly from the Cape of Good Hope, South Africa (Kasuya 1999). As the species has not been reliably recorded anywhere in Africa since, this type locality is considered to be erroneous, and it is now generally considered to have come from the Malabar coast of India (Allen 1923; Robineau 1990). The generic taxonomic history has been somewhat confused, with the genus name *Neomeris* (= *Meomeris*) having

been used in the past (Thomas 1922). Finless porpoises are now recognized as the genus *Neophocaena* (Palmer 1899). *Neo* refers to new and *phocaena* to porpoise.

Other common names include finless black porpoise, black finless porpoise, Indian black porpoise, *marsouin noir* (France), *besperia morskaia svinia* (Russia), *limbur* (Indonesia), *hai-chu, gong tun, jiangzhu* (China), bowl-head, smooth back loma (Thailand), *tabi* (Pakistan), *sunameri, naminoio, nomeno-juo* (Japan), *bhulga, gonio, gaddada, and molagan* (India)—(Reeves et al. 1997; Kizhakudan and Kizhakudan 2001). Common names of subspecies are Yangtze finless porpoise (*N. p. asiacorialis*), Indian Ocean finless porpoise (*N. p. phocaenoides*), and Japanese finless porpoise (*N. p. sunameri*).

Although most recent authors recognize only the single species *Neophocaena phocaenoides*, with the major geographic forms representing separate subspecies (Amano et al. 1992; Gao 1991; Gao and Zhou 1995a, 1995b, 1995c; Rice 1998), Jefferson (2002) found some evidence of species-level differences.

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