

*Sousa chinensis*. By Thomas A. Jefferson and Leszek Karczmarski

Published 23 January 2001 by the American Society of Mammalogists

***Sousa* Gray, 1866**

*Sousa* Gray, 1866:213. Type species *Steno (Sousa) lentiginosus* Gray.

**CONTEXT AND CONTENT.** Order Cetacea, suborder Odontoceti, family Delphinidae. The genus *Sousa* has traditionally been united with *Steno* and *Sotalia* in the subfamily Steninae (sometimes elevated to family level), based on morphologic similarities (Barnes et al. 1985). However, cytochrome *b* sequences do not support this grouping among Delphinidae (LeDuc et al. 1999) and instead suggest a relationship of *Sousa* with *Delphinus*, *Lagenodelphis*, *Stenella*, and *Tursiops*. Ross et al. (1995) proposed only 1 species under the name *Sousa chinensis*, with possibly 3 or more subspecies, whereas Rice (1998) listed 3 species, *S. teuszii*, *S. plumbea*, and *S. chinensis* (Atlantic, Indian, and Pacific ocean humpback dolphins, respectively). Most recent authors recognize only 2 species: *S. teuszii* (Atlantic humpback dolphin) and *S. chinensis* (Indo-Pacific humpback dolphin).

***Sousa chinensis* (Osbeck, 1765)**

Indo-Pacific Humpback Dolphin

- Delphinus chinensis* Osbeck, 1765:7. No type specimen collected; species based on sighting in the Canton (Pearl) River, China. Osbeck's description was first published in 1757.
- Delphinus sinensis* Desmarest, 1822:514. Renaming of *Delphinus chinensis* Osbeck.
- Delphinus plumbeus* G. Cuvier, 1829:283. Type locality "Malabar, India, Bay of Bengal."
- Delphinus (Steno?) lentiginosus* Owen, 1866:20. Type locality "Waltair, Vizagapatam, Madras, Bay of Bengal, India."
- Steno lentiginosus* Gray, 1866:213. Renaming of *Delphinus lentiginosus* Owen.
- Steno chinensis* Gray, 1871:65. Renaming of *Delphinus chinensis* Osbeck.
- Sotalia lentiginosus (lentiginosa)* Flower, 1883:489, 513. Renaming of *Steno lentiginosus* Gray.
- Sotalia plumbeus (plumbea)* Flower, 1883:489. Renaming of *Delphinus plumbeus* G. Cuvier.
- Sotalia sinensis* Flower, 1883:513. Renaming of *Delphinus chinensis* Osbeck.
- Steno plumbeus* Blanford, 1891:583. Renaming of *Delphinus plumbeus* G. Cuvier.
- Sotalia borneensis* Lydekker, 1901:88. Type locality "Sipang, mouth of the Sarawak River, Malaysia."
- Sotalia fergusonii* Lydekker, 1903:411. Renaming of *Steno lentiginosus* Gray.
- Sousa lentiginosa* Iredale and Troughton, 1934:68. Renaming of *Steno lentiginosus* Gray.
- Stenopontistes zambezicus* Miranda-Ribiero, 1936:3. Type locality "Zambesi, coast of east Africa." This form erroneously was considered a synonym of *Steno bredanensis* (see Brownell 1975).
- Sotalia chinensis* Allen, 1938:499. Renaming of *Delphinus chinensis* Osbeck.
- Sousa borneensis* Fraser and Purves, 1960:7. Renaming of *Sotalia borneensis* Lydekker.
- Sousa plumbea* Fraser and Purves, 1960:60. Renaming of *Delphinus plumbeus* G. Cuvier.

**CONTEXT AND CONTENT.** Generic context as above. *Sousa chinensis* is monotypic.

**DIAGNOSIS.** The Indo-Pacific humpback dolphin (Fig. 1) is generally easily distinguished from other dolphin species in its

range. The main diagnostic features are a robust body (*Delphinus* and *Stenella* are more slender); a short dorsal fin atop a wide dorsal ridge or hump (*Steno* and *Tursiops* have tall dorsal fins and no humps); and broad flippers and flukes, with rounded tips (*Delphinus*, *Stenella*, *Steno*, and *Tursiops* have slender and pointed extremities). Beak is long (ca. 6–10% of total length) and distinctly set off from melon, but without a deep crease between the 2, as in *Delphinus*, *Stenella*, and *Tursiops* (Ross et al. 1994). Color pattern is highly variable, often with dark spotting and flecking, but generally without stripes; in contrast, *Delphinus* and *Stenella* are boldly patterned with diagnostic stripes and spots.

Skull of *Sousa chinensis* is large, heavily built, and has a long, narrow rostrum, with concave margins (Fig. 2). Rostrum represents 57–67% of condylobasal length, which can reach at least 575 mm; *Delphinus* and *Stenella* are smaller (Ross et al. 1994). Distinctive features are very large and round temporal fossae (length 17–24% of condylobasal length), and separation of the pterygoids along base of rostrum (Ross et al. 1994). Mandibles of *Sousa* have concave margins, and mandibular symphysis is very long, ca. 21–28% of condylobasal length (Ross et al. 1994). These features distinguish *Sousa* from other genera in its range, except *Steno*. Skull of *S. chinensis* is easily confused with that of *Steno bredanensis* (rough-toothed dolphin), but the species can be distinguished by tooth counts (generally 30–38 in *Sousa* and 19–28 in *Steno*) and size of orbit (generally <13% of condylobasal length in *Sousa* and >13% of condylobasal length in *Steno*—Miyazaki and Perrin 1994; Ross et al. 1994). In addition, teeth of *Steno* have deep longitudinal ridges, whereas those of *Sousa* have only slight ridges, if any.

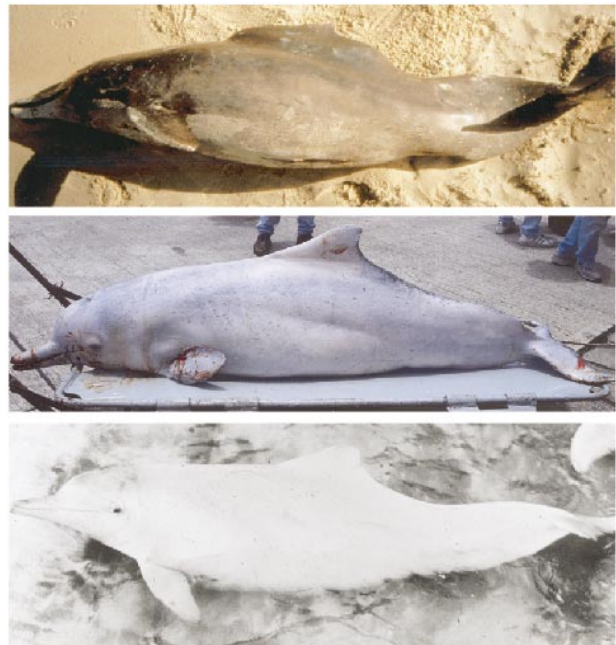


FIG. 1. External appearance of *Sousa chinensis*. Upper photo: from the Persian Gulf area, exhibiting darker coloration and exaggerated dorsal hump found in specimens from the western Indian Ocean. Lower 2 photos: from Hong Kong and Australia, showing light body color and absence of a dorsal hump, characteristic of animals from the eastern part of the range of the species. Photographs by A. Preen and W. H. Dawbin, courtesy of S. Leatherwood.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult *Sousa chinensis* (female) from Hong Kong (OPCF SC97-31/05-B). Greatest length of cranium is 507 mm.

**GENERAL CHARACTERS.** Indo-Pacific humpback dolphins are medium-sized dolphins, up to 2.8 m in length (Ross et al. 1994). Maximum weight is 250–280 kg (Jefferson 2000; Ross et al. 1994). In southern African waters, Indo-Pacific humpback dolphins are sexually dimorphic in length, with males (mean length = 226 cm,  $n = 29$ ) larger than females (mean length = 216 cm,  $n = 10$ —Ross et al. 1994). In Hong Kong, significant sexual dimorphism is not evident (Jefferson 2000).

Shape and size of dorsal fin and hump vary distinctly between the extremes of the range of the species. In the eastern portion of the range, dorsal fin is short, slightly recurved, and has a wide base, which laterally slopes smoothly and gradually into dorsal surface of body; its base is ca. 5–10% of total body length (Ross et al. 1994). In the western portion of the range, dorsal fin is sharply recurved, smaller yet, and sits atop a broad-based hump of connective tissue in middle of animal's back (Fraser 1966). Dorsal hump (origin of the species' common name) increases in length proportionately with body size, to ca. 30% of body length (Ross et al. 1994).

Color varies greatly throughout the range, and developmental variation is extensive. Adults from southern Africa are dark gray on dorsum and sides, shading gradually into an off-white ventral surface, with only slight, if any, spotting. Calves are lighter in color. A distinct pinkish-white patch occurs on the dorsal fin and hump of adults, and its size apparently increases with animal's age (Karczmarski 1996; Ross 1984; Saayman and Tayler 1979). Dolphins in the northern Indian Ocean are uniformly brownish-gray (Ross et al. 1994). In China, and some areas of southeast Asia, calves are dark gray, turning paler with age (Ross et al. 1994). Subadults are

mottled grayish-pink, and adults are pure white, often with a pinkish tinge resulting from blood flushing (Huang et al. 1997; Jefferson 2000). Some adults have dark flecks on the body, and a few have a dark ring of spots surrounding the neck behind the blowhole. In Australia, dorsal fin, melon, and rostrum whiten with age, but the rest of the dorsal surface remains dark (Ross et al. 1994). Elsewhere, animals resemble the above patterns. The transition apparently occurs in the eastern Indian Ocean, between India and Thailand.

**DISTRIBUTION.** Although its distribution is poorly known (Fig. 3), the Indo-Pacific humpback dolphin has been recorded for the following countries: South Africa (Durham 1994; Findlay et al. 1992; Karczmarski 1996; Ross 1984), Mozambique (Guissamulo 1993, 2000; Peddemors and Thompson 1994; Ross 1984), Tanzania (Fraser 1966; Howell and Pearson 1977), Kenya (Karczmarski 2000), Madagascar (Cockcroft et al. 1997b; Robineau and Rose 1984), Comoros Islands (Cockcroft et al. 1997b), Somalia (Small and Small 1991), Djibouti (Alling 1986; Mörzer-Bruyns 1960; Robineau and Rose 1984), Egypt (Beadon 1991; Mörzer-Bruyns 1960), Saudi Arabia (Robineau and Fiquet 1994, 1996), Bahrain (Gallagher 1991), Yemen (Leatherwood 1986), Oman (Gallagher 1991; Papastavrou and Salm 1991; Pilleri and Gihir 1974), United Arab Emirates (Gallagher 1991), Qatar (Leatherwood 1986), Kuwait (de Silva 1987), Iraq (Al-Robaee 1970; Mörzer-Bruyns 1960), Iran (Mörzer-Bruyns 1960), Pakistan (Pilleri and Gihir 1972, 1974), India (James et al. 1987; Lal Mohan 1985a, 1985b; Parsons 1998a), Sri Lanka (Leatherwood and Reeves 1989), Burma (Myanmar—Smith et al. 1997b), Thailand (Chantrapornsy et al. 1996, 1999; Mahakunlayanakul 1996), Vietnam (Smith et al. 1997a), China (including Taiwan—Parsons et al. 1995; Wang and Han 1996; Wang and Sun 1982; Zhou et al. 1980, 1995), Malaysia (Beasley and Jefferson 1997; Dolar et al. 1997; Gibson-Hill 1949; Leatherwood et al. 1984), Indonesia (Rudolph et al. 1997), Brunei (Elkin 1992), Singapore (Sigurdsson and Yang 1990), Papua New Guinea (Dawbin 1972), and Australia (Corkeron et al. 1997). Countries from within the range for which records have not been reported include Eritrea, Sudan, Bangladesh, and Cambodia, but the species may be expected to occur there. It probably does not occur in most parts of the Philippines, where the predominance of deep oceanic waters likely does not provide suitable habitat.

In South African waters, Indo-Pacific humpback dolphins only occur west to Cape Town (Findlay et al. 1992). In China, they occur south of the Yangtze River, and the distribution appears to be discontinuous, with populations occurring primarily around large river mouths (Jefferson 2000). Off Australia, they occur more continuously, but only along the northern, tropical coasts and down as far as ca. 32°S along the east coast and ca. 22°S along the west coast (Corkeron et al. 1997).

**FOSSIL RECORD.** Fossils of *S. chinensis* are not known, but a delphinoid ear bone found in Miocene deposits of eastern Saudi Arabia may have come from an extinct species related to *Sousa* (Whitmore 1987).

**FORM AND FUNCTION.** Skeleton is heavy and robust. Phalangeal formula is 0 I, 6–7 II, 5–6 III, 3 IV, 2 V, based on a small sample from South Africa (Ross et al. 1994). Vertebral formula of South African animals is 7 C, 11–12 T, 9–12 L, 20–24 Ca, total 49–52 (Ross et al. 1994). Only the 1st and 2nd cervical vertebrae are fused (Pilleri and Gihir 1972), and the total number of vertebrae is generally less than in other species of dolphins (Flower 1870). The entire skeleton has been described in great detail by Flower (1870).

Base of each tooth is expanded, giving it a wedge-shaped appearance in lateral view (Ross 1984). Teeth in the middle of the tooth rows of adults measure ca. 20 mm in length (Lal Mohan 1995). Tympanoperiotic bones are fully developed at birth, and grow only slightly, if at all, during development (Liu et al. 1999; Porter 1998).

Eyes are relatively small (Wang 1965, 1995). *Sousa* has ca. 77,000 fibers in cochlear nerve and ca. 150,000 in optic nerve (Gao and Zhou 1991, 1992). Tongue is not attached to floor of mouth, giving it great freedom and flexibility, which may be an adaptation for feeding on small organisms (Ping 1927). Stomach has 4 chambers, and digestive tract is similar to that of other species of small cetaceans (Tang and Huang 1940). Mean length of intestines is 8.1 times total body length (Ross et al. 1994). Tissue

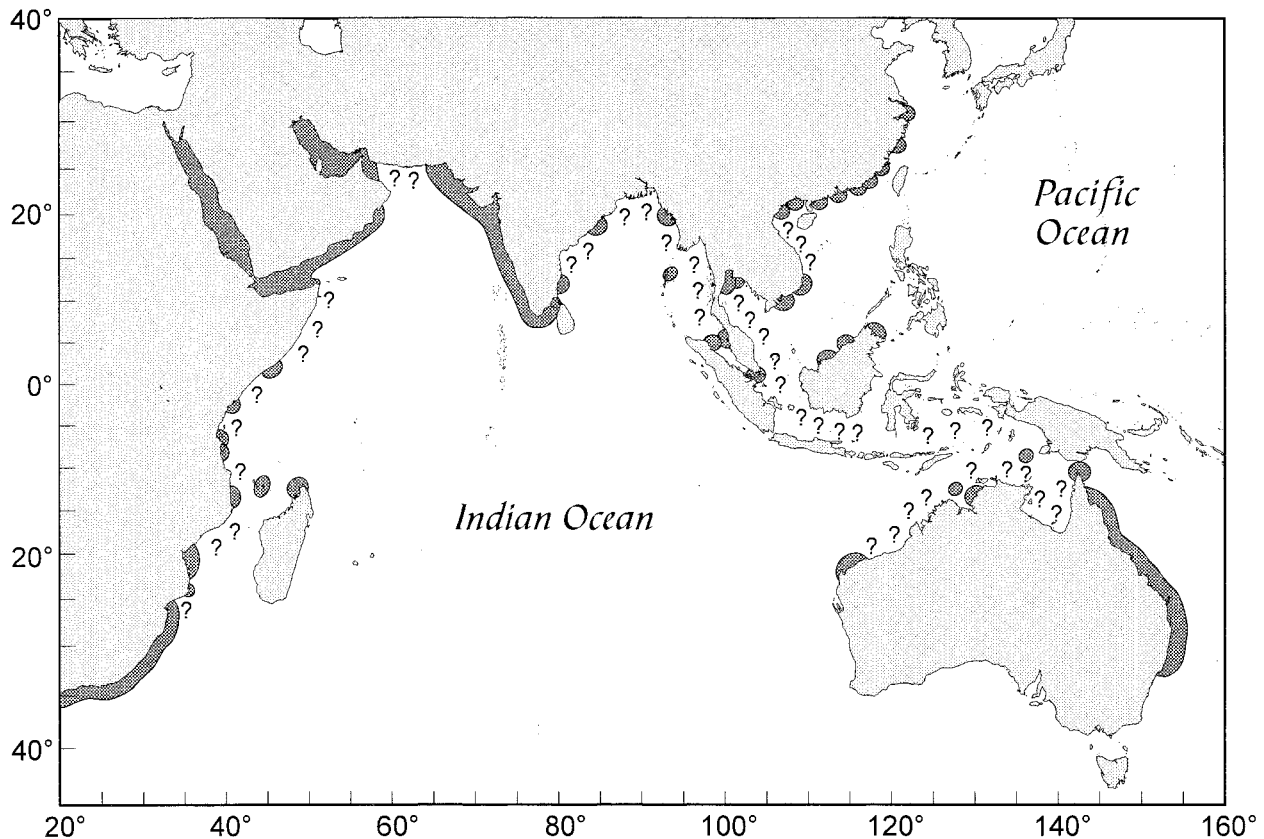


FIG. 3. Distribution of *Sousa chinensis*, from Ross et al. (1994) with modifications from Cockcroft (in litt.), Guissamulo (1993), and Karczmarski (in litt.) for eastern Africa; Baldwin et al. (1998) for the Middle East; Tanabe et al. (1993) for India; Leatherwood and Reeves (1989) for Sri Lanka; Smith et al. (1997b) for Burma; Chantrapornsy et al. (1996, 1999) and Mahakunlayanakul (1996) for Thailand; Rudolph et al. (1997) for Indonesia; Beasley and Jefferson (1997) for Borneo; Smith et al. (1997a) for Vietnam; Corkeron et al. (1997) for Australia; and Jefferson (2000) for China. Question marks indicate areas of probable, but unconfirmed, distribution.

and organ masses average 20.4% (blubber), 32.6% (muscle), 4.2% (heart, lungs, and trachea), 0.55% (heart), 2.1% (liver), and 0.68% (kidneys) of total body mass (Ross et al. 1994). In general, relative blubber mass is higher than in *Tursiops* (Ross et al. 1994).

**ONTOGENY AND REPRODUCTION.** Some calves may be born throughout the year, but spring or summer calving peaks are the norm in populations from southern Africa (Cockcroft 1989; Karczmarski 1996, 1999; Saayman and Tayler 1979), southern China (Jefferson 2000; Wang 1965, 1995), and probably India (Lal Mohan 1982). A 3-year calving interval has been suggested for animals from South Africa (Cockcroft 1989; Karczmarski 1996, 1999).

Gestation lasts ca. 10–12 months (Cockcroft 1989; Wang 1965, 1995). A single calf is born. Length at birth may be ca. 100 cm (Cockcroft 1989; Jefferson 2000; Ross 1984; Wang 1965, 1995). Fetal growth is ca. 8.8 cm per month (Jefferson 2000). Lal Mohan (1982) described a 47-cm fetus from Indian waters, with no bristles on its beak. Although age at weaning is not known with any certainty, in South African waters lactation may last >2 years (Cockcroft 1989) and female–calf associations remain consistent and strong for at least 3–4 years (Karczmarski 1999).

Age at sexual maturity for South African animals is ca. 10 years for females and ca. 12–13 years for males (Cockcroft 1989). Although Wang (1965, 1995) suggested that in Chinese specimens, adult females reach sexual maturity at 200–250 cm and adult males at 190–240 cm, recent evidence suggests that sexual maturity does not occur until lengths of ca. 235 cm and ages of 9–10 years in females (Jefferson 2000). About 60% of adult females ( $n = 10$ ) from Xiamen, southern China, were pregnant (Wang and Sun 1982).

Postnatal growth in southern China appears to be rapid in the first 2 years, then levels off (Jefferson 2000). Asymptotic length in specimens from southern China is reached at ca. 243 cm and 16 years (Jefferson 2000).

**ECOLOGY.** Indo-Pacific humpback dolphins occur in shallow, nearshore waters, generally <20 m deep, most often near large river mouths (Ross et al. 1994). In South Africa, they inhabit the shallow nearshore zone within 1,000 m of shore, often just outside breaking waves (<500 m from shore), in water <15 m deep (Durham 1994; Karczmarski et al. 2000a; Saayman and Tayler 1979). Preference for very shallow (<10 m deep) and generally nearshore areas is also evident in Mozambique (Guissamulo 1993, 2000). In some areas, these dolphins range much further offshore (up to 55 km from shore) if the water remains shallow (Corkeron et al. 1997; Jefferson 2000). They display no apparent preference for clear or turbid waters (Karczmarski et al. 2000a). Water depth is probably the main factor limiting their offshore distribution, and the 25-m isobath has been suggested to represent the critical depth in the South African region (Karczmarski et al. 2000a). These dolphins have been reported to occur in a variety of coastal habitats including sandy beaches, enclosed bays and coastal lagoons, mangrove areas (particularly mangrove channels), over sea grass meadows, around rocky and coral reefs, and in turbid estuarine waters (Beardon 1991; Corkeron 1990; Durham 1994; Guissamulo 1993, 2000; Jefferson 2000; Karczmarski 1996, 2000; Karczmarski et al. 2000a; Pilleri and Pilleri 1979; Porter 1998; Saayman and Tayler 1979). Although the choice of key habitats varies between different geographical regions, the choice of habitat is well defined and persistent at each location.

In South African waters, Indo-Pacific humpback dolphins feed primarily on several types of common estuarine and reef-associated fish and occasionally cephalopods (Barros and Cockcroft 1991; Peddemors and Thompson 1994; Ross 1984). Along the KwaZulu-Natal coast, they feed in murky waters of large estuarine systems (Durham 1994), whereas along the Eastern Cape their primary feeding grounds are in relatively clear waters around inshore rocky reefs (Karczmarski et al. 2000a). The most common South African prey



species were *Mugil cephalus*, *Pomadourys olivaceum*, *Pachymetopon aneum*, and unidentified seabreams (Barros and Cockcroft 1991; Ross 1984). Crustaceans occurred among the stomach contents of 2 dolphins from northern Australian waters (Heinsohn, in litt.). Indo-Pacific humpback dolphins from southern China had a variety of estuarine fish in their stomachs, and but no squid (Jefferson 2000; Parsons 1997; Wang 1965, 1995). The most common Chinese prey species were *Ilisha elongata*, *Mugil*, *Coilia*, *Collichthys lucida*, *Johnius*, *Thryssa*, and *Trichiurus* (Jefferson 2000; Parsons 1997; Wang 1965, 1995).

Indo-Pacific humpback dolphins do not undergo large-scale seasonal migrations, although seasonal shifts in abundance occur in 2 areas. In Algoa Bay, South Africa, humpback dolphins display varying degrees of site fidelity, with some members of the population being more-or-less resident, but most others ranging widely within a narrow band along the coast (Karczmarski 1999). Seasonal variation in occurrence, abundance, and group size is considerable (Karczmarski et al. 1999a) and results from seasonal immigration of humpback dolphins into and emigration from the Algoa Bay region in summer (Karczmarski et al. 1999b). Movements up to 120 km occur along both the KwaZulu-Natal (Durham 1994) and Eastern Cape coasts (Karczmarski 1996). In Maputo Bay, Mozambique, most Indo-Pacific humpback dolphins are residents, but transient individuals join resident groups temporarily (Guissamulo 2000). In both Algoa and Maputo bays site fidelity of females is related to reproductive stage and increases during lactation (Karczmarski 1999; Guissamulo 2000). Animals in Hong Kong are restricted to the immediate vicinity of large estuaries with linear movements of only a few tens of kilometers (Hung 2000).

Indo-Pacific humpback dolphins occasionally associate with other species of marine mammals. In waters of Moreton Bay, Australia, they often feed behind trawlers in mixed groups with bottlenose dolphins (*Tursiops truncatus*—Corkeron 1990). In South Africa, they associate with bottlenose dolphins, southern right whales (*Eubalaena australis*), and Cape fur seals (*Arctocephalus pusillus*—Karczmarski et al. 1997; Saayman and Tayler 1979). Gulls and terns feed with Indo-Pacific humpback dolphins in the Pearl River Estuary (Melville 1976).

Sharks have attacked *S. chinensis* in South African and Australian waters (Cockcroft 1991; Corkeron 1990), and sharks are probably predators in other parts of the range of the species. Indo-Pacific humpback dolphins in South Africa both chase and avoid large sharks in their vicinity (Saayman and Tayler 1979). Attacks by killer whales (*Orcinus orca*) are not known, but are probable. A group of Indo-Pacific humpback dolphins swam quietly in shallow water, apparently to avoid a group of killer whales (Saayman and Tayler 1979).

Few parasites are known from Indo-Pacific humpback dolphins. The only recorded internal parasites are nematodes *Anisakis alexandri* from the stomach (Dailey and Brownell 1972; Hsu and Hoeppli 1933) and *Halocercus pingi* from the liver (Gibson and Harris 1979). In Hong Kong, lungworms (*Halocercus pingi*) as well as unidentified trematodes occurred in the orbits (Parsons 1997). Externally, the barnacle *Syncyamus aequus* occurred on animals from South Africa (Ross et al. 1994).

Indo-Pacific humpback dolphins are seldom held captive. Three animals were held in South African oceanariums for periods up to only 90 days before dying (Best and Ross 1977, 1984). Of 2 captive animals from Australia, 1 lived for at least 27 years (Cawthorn and Gaskin 1984; Ross et al. 1994). Another Australian captive lived for 31 years and the specimen was not a calf when captured (P. Corkeron, pers. comm.). A gill-net-caught dolphin from India was kept alive for 28 days in a plastic-lined pond before dying of starvation (Lal Mohan 1983). Large numbers of Indo-Pacific humpback dolphins, along with other species of small cetaceans, have been live-captured for the aquarium trade in Thailand. Poor conditions have resulted in high mortality (Smith 1991). Longevity in the wild may reach 40 years (Cockcroft 1989).

Abundance has been estimated in only a few selected areas. The KwaZulu-Natal population off South Africa was ca. 160–165 individuals (95% CI = 134–229), based on mark-recapture analysis of photo-identification data (Durham 1994). The same approach produced an estimate of 466 dolphins (95% CI = 447–485) in the Algoa Bay region, Eastern Cape, South Africa (Karczmarski et al. 1999b). However, only a small part of this population is present in Algoa Bay at any given time, with the majority of the population members ranging over a considerable length of the Eastern Cape

coastal zone (Karczmarski 1999; Karczmarski et al. 1999a, 1999b). The relative density for the Eastern Cape region was estimated to be 0.42 dolphins/km<sup>2</sup> (Karczmarski 1996; Karczmarski and Cockcroft 1997). In Hong Kong waters, line transect ship surveys have been used to estimate seasonal abundances ranging from ca. 88 (spring) to 145 (summer) individuals in the highest-density area, north of Lantau Island (CV = 15–18%—Jefferson 2000; Jefferson and Leatherwood 1997). For the same general area, mark-recapture analysis of photo-identification data estimated 100–128 animals (95% CI = 82–118 and 94–184, respectively—Porter 1998). The total population size in Hong Kong and the adjacent Pearl River Estuary was estimated to consist of >1,028 animals (CV = 15–86%—Jefferson 2000). Mark-recapture estimates of abundance for Moreton Bay, Australia, ranged from 119 to 163 dolphins (95% CI = 81–166 and 108–251, respectively—Corkeron et al. 1997).

For Indo-Pacific humpback dolphins inhabiting the Algoa Bay region, South Africa, mean annual crude birth rate ranges between 4.8% (Karczmarski 1996) and 6.5% (L. Karczmarski, in litt.). Minimum mortality rate to age of 1 year is ca. 20% and recruitment rate to age of 1 year is <4%. Annual adult survival rate is roughly 95%. Modeled population growth rates range between a 3% decrease per annum and a 2% increase (Karczmarski 1996).

**BEHAVIOR.** The diel pattern of occurrence of Indo-Pacific humpback dolphins varies between different locations. In Algoa Bay, South Africa, dolphins can be seen mostly in the morning and, to a lesser extent, in the evening (Karczmarski et al. 2000b). Their activities follow a well-defined daylight pattern that varies little between seasons (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000b). In Maputo Bay, Mozambique, they are seen in the afternoon more often than in the morning (Guissamulo 2000).

Indo-Pacific humpback dolphins are either solitary or live in relatively small groups. Groups in most areas are <25 animals, but groups of <10 are most common. Mean ( $\pm$  SD) group sizes in different areas are 6.5  $\pm$  0.38 (Plettenberg Bay, South Africa—Saayman and Tayler 1979), 7.0  $\pm$  2.52 (Algoa Bay, South Africa—Karczmarski et al. 1999a), 14.9  $\pm$  7.32 (Maputo Bay, Mozambique—Guissamulo 2000), 2.6  $\pm$  2.12 (Goa, India—Parsons 1998a), 3.8  $\pm$  3.63 and 2.8  $\pm$  2.29 (Hong Kong—Jefferson 2000, and Parsons 1998b, respectively), and 2.4  $\pm$  1.13 (Moreton Bay, Australia—Corkeron 1990). Peaks in group size in South Africa occur in summer and late winter (Karczmarski et al. 1999a; Saayman and Tayler 1973, 1979). Little seasonal variation in group size occurs in Hong Kong waters, but geographic areas differ (Jefferson 2000; Parsons 1998b). Largest groups are usually composed of all age classes, with adults representing between one half and two thirds of the group (Durham 1994; Guissamulo 2000; Jefferson 2000; Karczmarski 1999; Saayman and Tayler 1979). Activity and behavior determine group spatial geometry, but not size (Karczmarski and Cockcroft 1999).

The social system of humpback dolphins is fluid, with only casual and short-lasting affiliations. Strong bonds between individuals other than mothers and calves are uncommon, and lack of consistency in group membership represents the general pattern in both Hong Kong and South African waters (Jefferson 2000; Karczmarski 1996, 1999). However, in Maputo Bay, Mozambique, a relatively high number of strong affiliations was seen, suggesting a relatively stable, resident group with which other dolphins associate to varying degrees (Guissamulo 2000). Some form of segregation between sex or age classes, or both, among humpback dolphins is probable (Karczmarski 1999).

Greeting displays occur in South Africa when different groups meet (Saayman and Tayler 1979). An observation of extensive social and aerial behavior in a group of Indo-Pacific humpback dolphins off Pakistan was interpreted as mating behavior (Roberts et al. 1983). However, confirmed reproductive behavior is rarely observed (Karczmarski et al. 1997; Saayman and Tayler 1979). Mate searching behavior is the most likely reproductive strategy of male humpback dolphins in Eastern Cape waters, South Africa (Karczmarski 1999). Allomaternal and care-giving behavior was observed off South Africa and Hong Kong (Karczmarski et al. 1997; Parsons 1997, 1998b).

Clicks, whistles, and screams were described from Indo-Pacific humpback dolphins recorded in the Indus River Delta of Pakistan (Zbinden et al. 1977). Clicks had a maximum frequency of 20–30 kHz and were the most frequent vocalization. Whistles were usually below 15 kHz, and screams were the least common type of

vocalization (only heard in groups of at least 4 or 5 individuals). Whistles recorded from animals in Australia differed from those of bottlenose dolphins, being of shorter duration and higher overall frequency (Schultz and Corkeron 1994).

Indo-Pacific humpback dolphins often swim with a characteristic surfacing pattern, with the beak rising steeply from the water before the forehead hits the surface (Karczmarski et al. 1997). Swimming speeds in Hong Kong averaged 3.6–7.2 km/h during different conditions (Jefferson 2000), and in South Africa averaged 4.8 km/h (Saayman and Tayler 1979). During rest, swimming speed is particularly slow and deliberate (Saayman and Tayler 1979). Although long dives of up to 4–5 min occur, most surface intervals are much shorter (Jefferson 2000; Karczmarski and Cockcroft 1999; Pilleri and Gihl 1972).

In South Africa, Indo-Pacific humpback dolphins feed largely around shallow, rocky reefs (Karczmarski 1996; Karczmarski et al. 2000a; Saayman and Tayler 1979) and near large estuarine systems (Durham 1994). In Maputo Bay, Mozambique, they feed along the depth contours of tidal channels, margins of sand banks, within mangrove-based coastal lagoons, and around coral reefs (Guissamulo 2000); and in the Indus River Delta of Pakistan these dolphins feed in mangrove creeks (Pilleri and Pilleri 1979). A tidal influence on behavior occurs in some areas (Guissamulo 2000; Parsons 1998b; Porter 1998; Saayman and Tayler 1979). Nevertheless, along the exposed coastline of Algoa Bay, where wave energy is considerably greater than tidal energy, the occurrence and behavior of humpback dolphins is predominantly governed by time of day (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000b). In Mozambique, dolphins deliberately beach themselves on sand banks in pursuit of small fish (Peddemors and Thompson 1994). In Hong Kong and Australian waters they frequently follow single and pair trawlers in large groups to feed on fish stirred up by the nets (Corkeron 1990; Jefferson 2000; Parsons 1998b). Powerboat traffic may disturb behavior in South Africa and Pakistan (Karczmarski et al. 1997, 1998; Pilleri and Gihl 1974; Roberts et al. 1983). However, in Hong Kong, where vessel traffic is heavy, dolphins generally ignore vessels (Jefferson 2000). Construction of a fuel facility, using noisy percussive piling, caused some disturbance and increased swimming speeds in *S. chinensis* of Hong Kong waters (Jefferson 2000; Würsig et al. 1999).

In South Africa, some individuals have large home ranges, probably covering hundreds of linear kilometers of coastline, although movements exceeding 1,000 km are unlikely (Karczmarski 1996, 1999; Karczmarski et al. 1999b). However, most dolphins in the Pearl River Estuary appear to have a home range of ca. 30–400 km<sup>2</sup>, which covers only part of the population's overall range of >1,800 km<sup>2</sup> (Hung 2000; Jefferson 2000).

Aerial behavior is not uncommon (Jefferson 2000; Parsons 1998b; Pilleri and Pilleri 1979; Saayman and Tayler 1979), although in Eastern Cape waters, South Africa, it is less frequent than similar behavior in the sympatric bottlenose dolphin (Karczmarski 1996; Karczmarski et al. 1997). Leaps and other aerial displays have been described and categorized (Karczmarski et al. 1997; Parsons 1998b; Zbinden et al. 1977). A captive specimen in India often leapt and spun in the pond in which it was kept (Lal Mohan 1983). Bowriding behavior is extremely uncommon in the Indo-Pacific humpback dolphin (Jefferson 2000; Karczmarski et al. 1997).

**GENETICS.** The karyotype of *S. chinensis* is not known. Low genetic variation was found in Indo-Pacific humpback dolphins of South Africa, suggesting that a population bottleneck had occurred (Smith-Goodwin 1997). Dolphins inhabiting the >2,000-km-long east coast of South Africa and southern Mozambique form at least three maternally distinct populations. These units are probably not fully reproductively isolated, but genetic exchange between them is fairly limited (Smith-Goodwin 1997).

In Hong Kong waters, two relatively isolated populations were proposed for north and south of Lantau Island, based on mitochondrial DNA and microsatellite variation (Porter 1998). However, only 10 individuals were sampled, so the findings, which contradict photo-identification results, appear unlikely (Jefferson 2000).

Extensive genetic subdivision among specimens from different areas suggests dividing the species into different subspecies (Cockcroft et al. 1997a). However, analysis of morphometric data suggests different boundaries for such divisions (Cockcroft et al. 1997a; Ross et al. 1995).

**CONSERVATION STATUS.** The conservation status of Indo-Pacific humpback dolphin populations is poorly known in most areas. Populations in South African waters have been studied since the 1970s (Cockcroft 1990; Cockcroft and Krohn 1994; Durham 1994; Karczmarski 1996, 2000; Karczmarski et al. 1998; Ross 1984; Saayman et al. 1972; Saayman and Tayler 1979; Smith-Goodwin 1997), and the population along KwaZulu-Natal is considered to be threatened by mortality in antishark nets (Cockcroft 1990; Durham 1994). In Eastern Cape, modeled population growth rates are low, suggesting that the population is probably stable, but an increase in population size is unlikely (Karczmarski 1996; Karczmarski and Cockcroft 1997). Numbers of Indo-Pacific humpback dolphins in Xiamen Harbor, on the coast of southern China, have apparently declined since the 1960s; however, statistically defensible estimates of abundance are lacking (Huang and Chou 1995; Wang 1965, 1995). Abundance in some parts of Hong Kong and adjacent waters of the Pearl River Estuary has declined in recent years, but is probably still viable (Jefferson 2000; Leatherwood and Jefferson 1997). The status of dolphins throughout most of northern Australia is not known, but *Sousa* populations are probably declining, largely due to mortality in antishark nets (Corkeron et al. 1997).

Effects of environmental contaminants on *S. chinensis* are of particular concern. Levels of heavy metals for specimens from Hong Kong waters were generally not high, but mercury levels were high enough to be potentially life-threatening (Parsons 1998c, 1999). Organochlorine levels from animals in South Africa, India, and Hong Kong also are high (Cockcroft 1989; Jefferson 2000; Parsons and Chan 1998; Prudente et al. 1997; Tanabe et al. 1993). At least in South Africa and Hong Kong, levels of compounds such as DDT may be compromising the health of animals and influencing reproduction of females (Cockcroft 1989; Jefferson 2000; Parsons 1998d; Parsons and Chan 1998). Butyltin levels may be lower than in other species of coastal small cetaceans (Jefferson 2000; Tanabe et al. 1998). However, the sampled animals were young, and because these compounds bioaccumulate, their levels may be higher in older animals.

Along the KwaZulu-Natal coast of South Africa, the major threat is the incidental capture of Indo-Pacific humpback dolphins in antishark nets along many swimming beaches (Cockcroft 1990). These dolphins are also taken in antishark nets in northern Australian waters (Gribble et al. 1998; Heinsohn et al. 1980; Paterson 1990). In addition, Indo-Pacific humpback dolphins were caught in the Taiwanese offshore drift-net fishery that previously operated in northern Australian waters (Harwood and Hembree 1987). This fishery has been banned from Australian waters, but still may be killing dolphins in waters of Indonesia. Several incidental and possibly directed catches occur throughout the range of the species (e.g., Cockcroft and Krohn 1994; Cockcroft et al. 1997b; Guissamulo 1993; Hale 1997; Lal Mohan 1994). However, in Hong Kong and most of southern China incidental catches are not known to be a major problem. Several potential threats have been identified in Hong Kong (Leatherwood and Jefferson 1997; Parsons 1997; Parsons and Porter 1995; Porter 1998), but the most severe are habitat loss (mostly due to reclamation of coastal waters) and detrimental effects of environmental contaminants (Jefferson 2000; Parsons 1998d; Parsons and Chan 1998).

Destruction of inshore habitats may be the greatest threats for Indo-Pacific humpback dolphins in the southern African region and many coastal development activities threaten survival (Karczmarski 2000). Establishment of multiple-use management areas with controlled ecotourism and several priority sites declared as strict reserves may be the most effective conservation approach (Karczmarski 1996, 2000). Based on habitat preferences of humpback dolphins in Eastern Cape waters, establishment of a marine sanctuary has been proposed in the Algoa Bay region (Karczmarski et al. 1998).

*Sousa chinensis* is listed as Data Deficient by the World Conservation Union (International Union for the Conservation of Nature), and is listed in Appendix I of the Convention on Trade of Endangered Species (Baillie and Groombridge 1996; Klinowska 1991). This species is also listed in the Convention on Migratory Species.

**REMARKS.** The genus name *Sousa* was first used as a subgenus of *Steno* by Gray (1866). In the 1960s, Hershkovitz (1966) placed all of the humpback dolphins in the genus *Sotalia* and

regarded *Sousa* to be a junior synonym of *Steno*. However, the distinctness of the New World tucuxi (*Sotalia*) and the Old World humpback dolphins (*Sousa*) at the generic level is now well accepted.

The first binomial given to a humpback dolphin, *Delphinus chinensis*, was used to describe live dolphins observed in the Canton (Pearl) River by Pehr Osbeck in 1757. No type specimen was collected, because this was 1 year before Linnaeus' taxonomic system was published in 1758. Thus, by the Law of Priority, Osbeck's (1765) German translation must be used for taxonomic purposes as the original description.

Flower (1870) provided a detailed description of the skeleton of *S. chinensis*, thereby solving the problem of the lack of a holotype specimen. Unfortunately, this skeleton was destroyed during a bombing raid in World War II (Pilleri 1979). A neotype from Hong Kong recently was proposed (Porter 1998), but the specimen was a subadult, and therefore may not show the diagnostic features of the species. For this reason, we suggest that the proposed neotype not be used for taxonomic purposes.

In recent years, 2 variant spellings of the standard English common name have been in widespread use: Indo-Pacific humpbacked dolphin and Indo-Pacific humpback dolphin. A group of researchers studying *Sousa* recently came to a consensus that the spelling "humpback" is preferred. Other common names include Borneo white dolphin, Chinese white dolphin, *jung wat bat hoi tun* (Cantonese), *lumba lumba putih Cina* (Indonesia), *parampaun laut* (Malaysia), *bolla gadimi* (India), *malar* (Pakistan), and *dar-feel* (Kuwait).

Thanks to V. G. Cockerroft, B. E. Curry, E. C. M. Parsons, W. F. Perrin, and an anonymous reviewer for comments on earlier drafts of the manuscript.

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Editors for this account were ELAINE ANDERSON, VIRGINIA HAYSSEN, and SERGE LARIVIERE. Managing editor was VIRGINIA HAYSSEN.

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