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Peponocephala electra.

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Peponocephala Nishiwaki and Norris, 1966

Electra Gray, 1866:268. Type species *Lagenorhynchus electra* Gray, by tautonomy. Preoccupied by *Electra* Lamouroux, 1816, a genus of Bryozoa.

Peponocephala Nishiwaki and Norris, 1966:95. Type species *Lagenorhynchus electra* Gray, by monotypy.

CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti, Family Delphinidae. Many researchers also place this species in the subfamily Globicephalinae (Barnes et al., 1985). The genus *Peponocephala* is monospecific.

Peponocephala electra (Gray, 1846)

Melon-headed Whale

Lagenorhynchus electra Gray, 1846:35. Type locality unspecified.

Lagenorhynchus asia Gray, 1846:35. Type locality unspecified.

Delphinus pectoralis Peale, 1848:32. Type locality "Hilo Bay, island of Hawaii."

Delphinus (Lagenorhynchus) fusiformis Owen, 1866:22. Type locality Waltair, Madras, India.

Electra obtusa Gray, 1868:7. Renaming of *Lagenorhynchus electra* Gray.

Peponocephala electra Nishiwaki and Norris, 1966:95. First use of present name combination.

CONTEXT AND CONTENT. Context same as for genus. No subspecies of the melon-headed whale are currently recognized.

DIAGNOSIS. Melon-headed whales (Fig. 1) are similar in external appearance to pygmy killer whales (*Feresa attenuata*) and, less so, to false killer whales (*Pseudorca crassidens*). They are best distinguished from these other forms by their acutely pointed flipper tips (bluntly rounded in *Feresa* and acutely rounded with humps on the leading edge in *Pseudorca*), and higher tooth counts (>19 in each row in *Peponocephala*; <15 in *Feresa* and *Pseudorca*). Normal tooth counts in *Peponocephala* are 20–26 in each upper row and 22–25 in each lower row (Perryman et al., 1994). Tooth counts as low as 15–17 have been reported for this species, but probably resulted from undercounting (Donaldson, 1983).

The skull (Fig. 2) is shaped similarly to those of dolphins of the genus *Lagenorhynchus*. However, antorbital notches are much larger than in *Lagenorhynchus* (Nishiwaki and Norris, 1966). Unlike in *Lagenorhynchus*, there is a narrowing of the dorsal aspect of the maxillae ca. 33% of the distance anterior to the base of the rostrum (Nishiwaki and Norris, 1966). The tooth rows of *Peponocephala* are relatively short, representing only ca. 65% of rostral length, as opposed to ca. 85% in the white-beaked dolphin (*Lagenorhynchus albirostris*—Mikkelsen and Sheldrick, 1992).

GENERAL CHARACTERS. *Peponocephala electra* is a small "blackfish," an informal term for the group that also includes killer (*Orcinus orca*), pilot (*Globicephala*), false killer, and pygmy killer whales. Melon-headed whales reach total lengths of <280 cm; there is no indication of sexual dimorphism in body length (Perryman et al., 1994). The longest specimen measured was a 275-cm female stranded in Brazil (Lodi et al., 1990). A young calf of 112 cm weighed 15 kg (Perrin, 1976), and the heaviest mass so far recorded was for a 248-cm male from South Africa, which weighed ca. 208 kg (Best and Shaughnessy, 1981).

The body is moderately robust, with a blunt head, falcate dorsal fin, sharply-pointed flippers, and concave flukes (Fig. 1). The head shows little or no beak and often appears nearly triangular from the side and from above or below. A barely noticeable beak in young animals disappears as the animal ages and the head becomes more bulbous; some large individuals may have a slightly overhanging melon. The flippers, dorsal fin, and flukes are all of average dolphin proportions, representing ca. 15–22% (measured from the anterior insertion to the tip), 6–11%, and 15–28% of the total length, respectively (Perryman et al., 1994).

Although often reported to be simply black, recent observations of live and freshly-dead melon-headed whales have shown that these animals actually have a somewhat detailed color pattern (Perryman et al., 1994). They are predominantly dark charcoal-brownish gray, although they may appear black in some lighting. There is a dark triangular "mask" in the facial region, with the apex pointing posteriorly. It is faint, and appears to fade quickly after death (it often does not show in photographs, but see Miyazaki, 1983*a*:7, fig. 7; Mullin et al., 1994:345, fig. 2). The faint cape is narrow in the thoracic region, dipping low in a rounded triangle (with the apex pointing ventrally) on the side below the dorsal fin. A pale blowhole stripe, widening anteriorly, runs between the blowhole and the apex of the melon (Best and Shaughnessy, 1981). Generally, the lips and tip of the beak are white or light gray. There are white to light gray regions, which are highly variable in extent and intensity, between the throat and urogenital area. These most often take the form of an anchor-shaped patch on the throat (with the point facing posteriorly), and a large oval-shaped area from the umbilicus to the anus (Nishiwaki and Nakajima, 1966: plates III and IV). An excellent photograph of the color pattern of a live, free-swimming animal can be found in Mullin et al. (1994:345, fig. 2). Young animals appear to have muted color patterns; they are lighter gray than adults and tend not to have the light areas around the mouth (see Perrin, 1976:458, fig. 2).

Although melon-headed whales do not exhibit sexual dimorphism in total length (Perryman et al., 1994), there may be dimorphism in some body proportions (Best and Shaughnessy, 1981). However, this conclusion is based on a small sample size ($n = 11$). Individuals have been observed with prominent humps in the postanal region (Barron and Jefferson, 1993; Bryden et al., 1977*b*; Goodwin, 1945; Miyazaki, 1983*a*), and where age and sex classes were known, these animals were always adult males. This condition may be caused by the enlargement of the muscles associated with the penis (Harrison et al., 1972).

Condylobasal length of the skull ranges up to 491 mm (Dawbin et al., 1970). The rostrum is broad (at its base, 27–31% of condylobasal length) and moderately long (52–56% of condylobasal

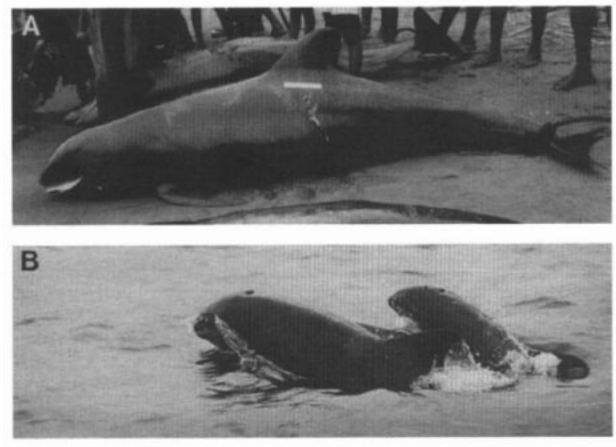

FIG. 1. Lateral view of *Peponocephala electra* in St. Vincent, and female and young swimming in Tañon Strait, Philippines. Upper photograph courtesy of S. Leatherwood.

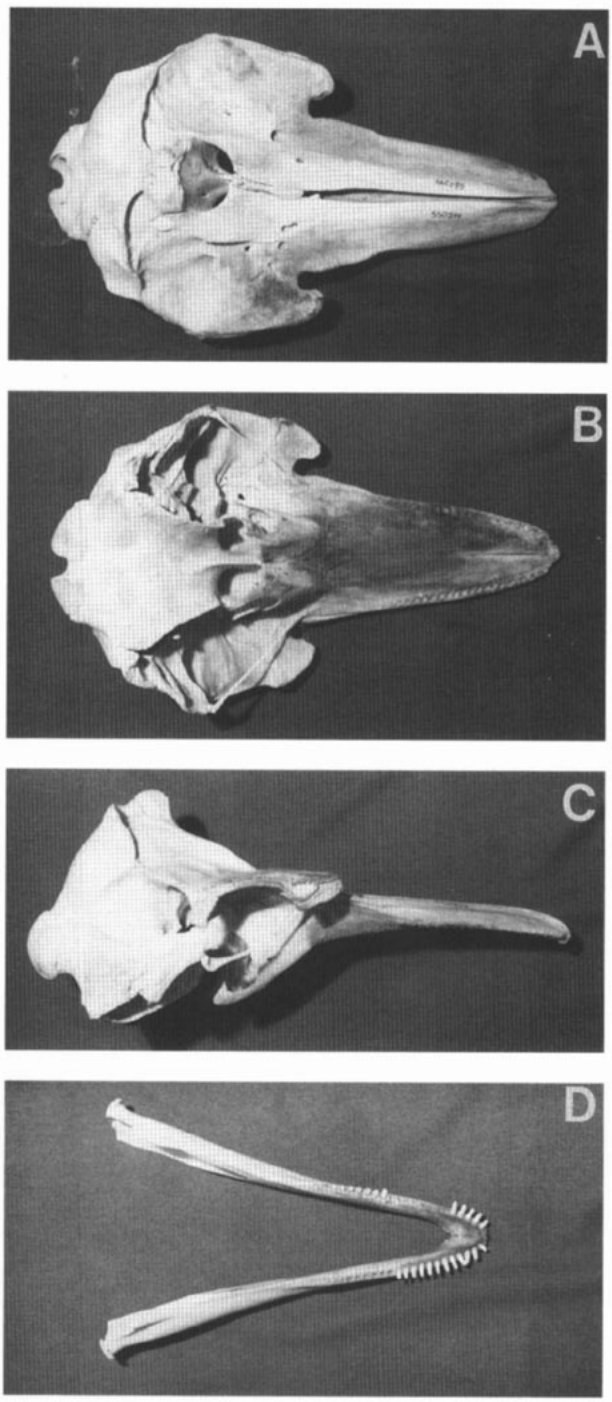

FIG. 2. Dorsal, ventral, and lateral views of the cranium, and dorsal view of the mandible of a specimen of *Peponocephala electra* from Assateague Island, Maryland (female; United States National Museum of Natural History 550399). Condylobasal length of cranium is 470 mm.

length—Perryman et al., 1994). Premaxillae do not converge at mid-rostral length (Perryman et al., 1994). The mandibles are stout, with a rounded coronoid region (True, 1889), and the mandibular symphysis is short, representing only 6–10% of condylobasal length (Dawbin et al., 1970).

DISTRIBUTION. Melon-headed whales are found in deep, oceanic waters of the tropical and subtropical zones throughout the world (Fig. 3). Most records are from 20°N to 20°S; records from temperate regions, such as those from Maryland (J. G. Mead et al., in litt.; Potter, 1984), Cornwall, UK (Mikkelsen and Sheldrick, 1992), and Hout Bay, South Africa (Best and Shaughnessy, 1981), probably represent strays. In the eastern tropical Pacific, they occur largely in waters characterized as equatorial (Au and Perryman, 1985), but are not as restricted to those waters as are Fraser's dolphins (*Lagenodelphis hosei*—Wade and Gerrodette, 1993). Although there are a number of records off the Pacific coast of Japan, melon-headed whales are considered very rare there (Miyazaki, 1980). They occur close to shore in some areas where the water drops off very quickly, such as in the Philippines (Leatherwood et al., 1992). No fossils of this species are known.

FORM AND FUNCTION. The vertebral formula is 7 C, 13–16 T, 15–18 L, and 39–45 Ca, total 78–83 (N. Miyazaki et al., in litt.; Perryman et al., 1994). The first 3–4 cervicals are fused. The phalangeal formula is 2–3 I, 8–9 II, 6–7 III, 3–4 IV, 2–3 V (Bryden et al., 1977*a*; Perryman et al., 1994). There are 14 ribs, the first 6–7 of which are double-headed (Bryden et al., 1977*b*; Nakajima and Nishiwaki, 1965). The chevron bones of one specimen numbered 30 (Nakajima and Nishiwaki, 1965). Dawbin et al. (1970) provided a detailed description of the cranial and post-cranial skeleton of this species. The dorsal surface of the superior process of the tympanoperiotic bones is wide and flat (Kasuya, 1973).

Almost no studies on soft-body anatomy and physiology of the melon-headed whale have been done. Organ weights for a single specimen were provided by Best and Shaughnessy (1981), and gonad weights and descriptions were given by Bryden et al. (1977*a*, 1977*b*) and J. G. Mead et al. (in litt.). Nakajima and Nishiwaki (1965) remarked that the rete mirabile of the melon-headed whale is similar to that of other species. The fatty acid composition of *Peponocephala* oil (presumably from the blubber) was reported by Tsuyuki and Itoh (1969). Blubber thickness of a specimen from Guam ranged from 1.5 to 2.0 cm in different areas of the body (Donaldson, 1983).

ONTOGENY AND REPRODUCTION. Length at birth is ca. 1 m, and gestation lasts for approximately 1 year, as in most smaller delphinids (Bryden et al., 1977*a*; Perrin and Reilly, 1984). It is unclear whether there is significant seasonality in times of birth. Information on most reproductive parameters is almost nonexistent. The only significant information available was obtained from a recent mass stranding in Japan (n = 123—N. Miyazaki et al., in litt.). Females reached sexual maturity at 11.5 years and a length of over 235 cm, and males at 16.5 years and at least 244 cm. Testis weights of at least 250 g were associated with sexual maturity, and maximum testis weight was 1,040 g. Physical maturity was reached by 13.5 years in both sexes.

There is little information on longevity in this species. Results from 60 specimens mass stranded in Brazil indicated that the oldest female (264 cm) had >30 dentinal-growth-layer groups, and the oldest male (246 cm) had >22 (M. Borobia et al., in litt.). There was a higher proportion of females than males with over 15 dentinal-growth-layer groups, and this may be an indication that females live longer than males.

ECOLOGY. Melon-headed whales often are seen in mixed herds with other species of cetaceans. They commonly school with Fraser's dolphins in the eastern and western tropical Pacific (Miyazaki and Wada, 1978: Wade and Gerrodette, 1993), Philippines (Hammond and Leatherwood, 1984; Leatherwood et al., 1992), and Gulf of Mexico (Mullin et al., 1994). They also associate with rough-toothed dolphins (*Steno bredanensis*) in the Gulf of Mexico (Mullin et al., 1994) and bottlenose dolphins (*Tursiops truncatus*) in the eastern tropical Pacific (Scott and Chivers, 1990). By driving fish towards the water's surface, melon-headed whales appear to provide feeding opportunities for some seabirds in the eastern tropical Pacific. Au and Pitman (1988) found melon-headed whales to be seldom associated with birds in this area, but 33% of the herds observed by Pitman and Ballance (1992) had Parkinson's petrels (*Procellaria parkinsoni*) associated with them.

Melon-headed whales prey on pelagic fishes and squids, and occasionally crustaceans. However, few studies of feeding habits in this species (Perryman et al., 1994) have been conducted. Fish prey includes species of the families Myctophidae, Paralepididae, and Scopelarchidae (N. B. Barros et al., in litt.). Squids of the families Ommastrephidae, Loliginidae, Onycoteuthidae, Chiroteuthidae, Mastigoteuthidae, Cranchiidae, Enoploteuthidae, and Histioteuthidae have been reported from stomach contents (N. B. Barros et al., in litt.; J. G. Mead et al., in litt.; Sekiguchi et al., 1992). Most of these families consist of mesopelagic species, found in waters up

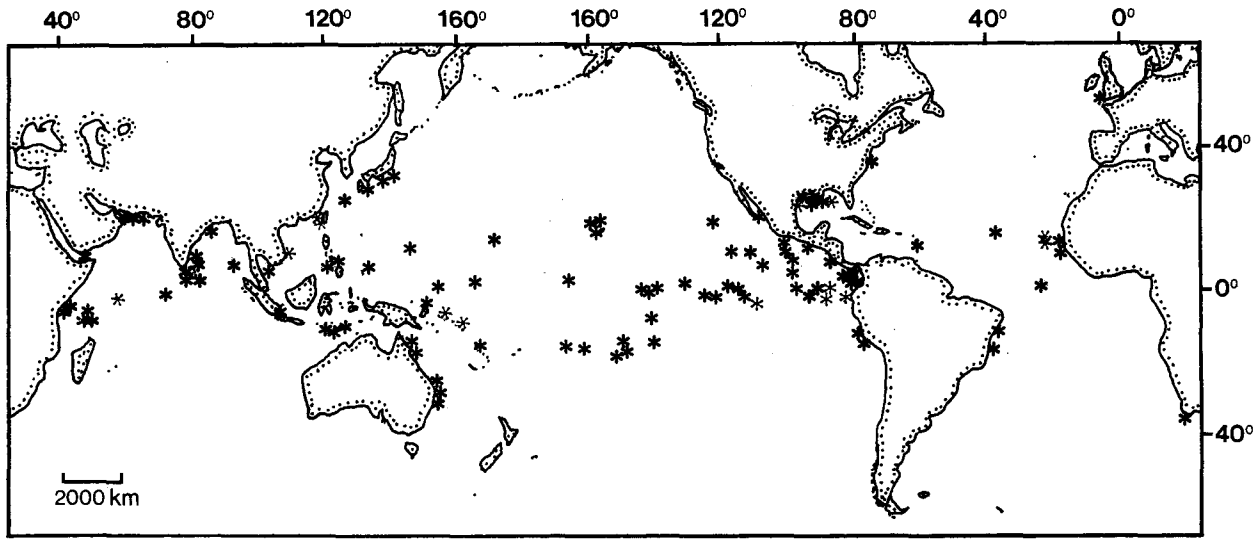

FIG. 3. Distribution of *Peponocephala electra* (after Perryman et al., 1994; additional records from Ballance et al., 1996; Leatherwood et al., 1991; Mikkelsen and Sheldrick, 1992; Miyazaki and Wada, 1978; Mullin et al., 1994; Racey and Nicoll, 1984; Rancurel, 1974; Reiner et al., 1996; Shimada and Pastene, 1995; Small and Small, 1991; Smith et al., 1995; Wade and Gerrodette, 1993; Yang, 1976; Zhou et al., 1995).

to 1,500 m deep, suggesting that feeding takes place deep in the water column (N. B. Barros et al., in litt.). Comparison with stomach contents of Fraser's dolphins, with which these animals often associate, suggests that the two species feed on similar prey types.

Predation on melon-headed whales is not well-documented. Stranded animals have been found with apparent bites of cookiecutter sharks (*Isistius*) on their bodies (Barron and Jefferson, 1993; Best and Shaughnessy, 1981; A. B. I. Fragoso et al., in litt.; Gasparini and Sazima, 1996). Wounds from cookie-cutter sharks are more common on debilitated, single-stranded animals than on mass-stranded ones or those taken in fisheries (Gasparini and Sazima, 1996). Killer whales (*Orcinus orca*) and large sharks are predators of most small cetaceans; thus although no records exist, it is probable that these animals also prey on melon-headed whales.

Only two estimates of abundance currently exist for the melon-headed whale. Wade and Gerrodette (1993) estimated a population of ca. 45,000 ($CV = 0.47$) for the eastern tropical Pacific, and Davis and Fargion (1996) estimated that there are ca. 2,000 ($CV = 0.34$) in the northwestern Gulf of Mexico. Density in the Gulf of Mexico is relatively low; melon-headed whales represented <1% of cetacean herds seen during recent deep-water surveys (Mullin et al., 1994). Seasonal movements have not been studied, although melon-headed whales appear to be present in most areas of their range throughout the year.

Internal parasite genera recorded from *P. electra* include: *Stenurus* in the air sinuses and ear canals (Bryden et al., 1977*b*; Cannon, 1977; V. M. F. da Silva et al., in litt.); *Nasitrema* in the air sinuses and around the ear bones (Dailey and Brownell, 1972; V. M. F. da Silva et al., in litt.; N. Miyazaki et al., in litt.; Morimitsu et al., 1986; unidentified nematodes in the air sinuses and stomach (Dawbin et al., 1970; Nakajima and Nishiwaki, 1965); *Phyllobothrium* in the blubber, peritoneum, stomach, and digestive tract (Best and Shaughnessy, 1981; Cannon, 1977); *Anisakis* in the stomach and intestine (Best and Shaughnessy, 1981; Cannon, 1977); *Monorygma* in the abdominal cavity (Bryden et al., 1977*b*; Dailey and Brownell, 1972); *Bolbosoma* in the rectum (Best and Shaughnessy, 1981); and *Halocercus* in the lungs (Dailey and Brownell, 1972). Unidentified whale lice and barnacles (probably *Xenobalanus*) have been reported from several locations on the external surface of melon-headed whales (Bryden et al., 1977*b*; Miyazaki and Wada, 1978).

Virtually nothing is known about pathology in melon-headed whales (Perryman et al., 1994). Tissue damage associated with infestation of the trematode *Nasitrema gondo* was found in one dolphin mass stranded in Japan, and it was suggested this was a possible cause of stranding (Morimitsu et al., 1986). In another Japanese mass stranding, this parasite was found in the tympanic cavities of all 20 specimens examined (N. Miyazaki et al., in litt.). A mass stranding of 240 animals on the coast of Brazil was thought to be associated with the presence of *Stenurus* and *Nasitrema* in the air sinuses, although no tissue damage was reported (V. M. F. da Silva et al., in litt.).

Additional mass strandings of this species, mostly of large herds, have been reported. These include strandings of 150–250 individuals in Australia in 1958 (Dawbin et al., 1970); 4 in the Line Islands in 1964 (J. G. Mead et al., in litt.); at least 231 in the New Hebrides (Vanuatu) in 1972 (Rancurel, 1973, 1974); 6 in the Seychelles in 1974 (Best and Shaughnessy, 1981); 9–10 in the Seychelles in 1975 (Leatherwood et al., 1991; Racey and Nicoll, 1984); ca. 180 in Costa Rica in 1976 (J. G. Mead et al., in litt.); 53 in Australia in 1976 (Bryden et al., 1977*a*); 135 in Japan in 1982 (Miyazaki, 1983*a*; N. Miyazaki et al., in litt.; Morimitsu et al., 1986); ≥240 in Brazil in 1987 (Lodi et al., 1990); and 3 in the Marshall Islands in 1989 (Eldredge, 1991).

There has been some directed hunting for this species. Although not one of the major species involved in large-scale drive fisheries of Japan, they occasionally are taken for human consumption (Kasuya et al., 1984; Miyazaki, 1980, 1983*b*; Nishiwaki and Norris, 1966). On one occasion, part of a herd in Japan was released before slaughter because of protests from the public and the discovery that the meat of this species does not taste good (Miyazaki, 1980). There is also a case of a large herd being driven ashore in Hawaii in the mid-1800s and used for human consumption (Peale, 1848; Cassin, 1858). Melon-headed whales are taken by harpoon in the Lesser Antilles (Caldwell et al., 1976), Cape Verde Islands (Reiner et al., 1996), Indonesia (Barnes, 1991; Perryman et al., 1994), the Philippines (Dolar et al., 1994; Leatherwood et al., 1992), and Sri Lanka (Leatherwood et al., 1991; Leatherwood and Reeves, 1989). A few (<10) have been taken for scientific research (Goodwin, 1945; Miyazaki and Wada, 1978).

Incidental catches in fishing gear are known from some areas. They occasionally are taken in purse seines in the eastern tropical Pacific (Perrin, 1976), and they are one of the species taken in gillnets in Sri Lanka (Leatherwood and Reeves, 1989). Melon-headed whales are one of several species of cetaceans taken in driftnets in the Philippines (Dolar, 1994). A skull found at a refuse heap near a fishing village in Senegal suggests involvement in fisheries off West Africa (van Bree and Cadenat, 1968). There are probably other undocumented incidental takes in fisheries, especially gillnets, throughout the tropics.

Melon-headed whales have been captured live in the Philippines (Hammond and Leatherwood, 1984) and Hawaii (Shallenberger, 1981). Two individuals from a herd captured in a drive in Japan in 1980 were sent to an aquarium (Kasuya et al., 1984). Several melon-headed whales captured in Hawaii adapted to captivity only after relatively long periods and were somewhat difficult to train

(Kang, 1980). They do not survive well in captivity, although one individual in Hawaii lived for almost 17 months (Reeves and Leatherwood, 1984). For this reason, along with their aggressiveness, melon-headed whales are not considered a desirable species for captive display.

Contaminant levels in this species have not been well studied. Davis (1993) reported relatively high levels of polychlorinated biphenyls (PCBs) from a melon-headed whale stranded in Texas. Tanabe et al. (1983) reported chlorinated hydrocarbon levels for five melon-headed whales stranded in Japan. The levels were generally within the reported ranges for the five other species of marine mammals studied. The mean PCB level of three melon-headed whales from Japan reported by Tanabe et al. (1988, 1994) was the second-highest of the 14 species (mammals and birds) examined. In general, the oceanic habitat of this species should put it less at risk from build-up of pollutants than more coastal species.

BEHAVIOR. Large herds are characteristic of *P. electra*, and at a distance, herd size often provides a good clue that the animals are melon-headed whales and not pygmy killer whales, which tend to occur in much smaller groups (Perryman et al., 1994). Groups of ca. 15–500 melon-headed whales are most common (Bryden et al., 1977*a*). Average herd size in the eastern tropical Pacific is ca. 200 animals (Wade and Gerrodette, 1993), and in the Gulf of Mexico it is 130–310 (Davis and Fargion, 1996; Mullin et al., 1994).

Large herds tend to consist of many closely-spaced subgroups (Mullin et al., 1994). When found in mixed groups with Fraser's dolphins, melon-headed whales often are found near the periphery (Hammond and Leatherwood, 1984; Leatherwood et al., 1992) or trailing Fraser's dolphins (Mullin et al., 1994). Sex ratios of 1:2 or 1:1.5 (male:female) were reported from several mass strandings (Bryden et al., 1977*a*; Lodi et al., 1990; J. G. Mead, in litt.; N. Miyazaki et al., in litt.).

When observed in offshore areas, melon-headed whale herds often are seen moving quickly, with splashy leaps, apparently traveling (Perryman et al., 1994). However, this often may be a reaction to the observation vessel; these animals are known to be nervous and "flighty" in captivity (Kang, 1980). Melon-headed whales sometimes ride the bow waves of passing ships, and do so quite often in the Philippines (Hammond and Leatherwood, 1984; Leatherwood et al., 1992) and the Gulf of Mexico (Mullin et al., 1994). The animals appear to have strong social bonds, as evidenced by their tendency to mass-strand in groups of several hundred (see above). Descriptions of the sounds produced by this species have not been published.

GENETICS. The karyotype of *P. electra* has not been described. Electrophoretic analysis has shown that *Peponocephala* is closely related to *Globicephala* and *Pseudorca* (Shimura and Numachi, 1987).

REMARKS. Gray's (1846) description of the holotype skull is brief; Dawbin et al. (1970) re-examined the type and provided a more detailed description. Other common names used for the melon-headed whale are many-toothed blackfish, electra dolphin, Indian broad-beaked dolphin, Hawaiian blackfish, Hawaiian porpoise, *calderón pequeño* (Spanish), *delfín cabeza de melón* (Spanish), *orca enana* (Spanish), *temu kebon* (Indonesian), *péponocéphale* (French), *shirokoflyuvyy delfin* (Russian), *pakatang* (Negros Oriental), and *kazuha gondo kujira* (Japanese).

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