

## THE PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY OF TRUE PORPOISES (MAMMALIA: PHOCOENIDAE) BASED ON MORPHOLOGICAL DATA

LILIANA FAJARDO-MELLOR<sup>1</sup>

ANNALISA BERTA

San Diego State University, Department of Biology,  
5500 Campanile Drive, San Diego,  
California 92182, U.S.A.  
E-mail: liliana.mellor@gmail.com

ROBERT L. BROWNELL JR.

Southwest Fisheries Science Center,  
1352 Lighthouse Avenue, Pacific Grove,  
California 93950, U.S.A.

CLAUDIA C. BOY

R. NATALIE P. GOODALL

Centro Austral de Investigaciones Científicas (CADIC),  
C.C. 92, 9410 Ushuaia, Tierra del Fuego, Argentina  
and  
Museo Acatushún de Aves y Mamíferos Marinos Australes,  
Estancia Harberton, 9410 Ushuaia, Tierra del Fuego, Argentina

### ABSTRACT

Prior studies of phylogenetic relationships among phocoenids based on morphology and molecular sequence data conflict and yield unresolved relationships among species. This study evaluates a comprehensive set of cranial, postcranial, and soft anatomical characters to infer interrelationships among extant species and several well-known fossil phocoenids, using two different methods to analyze polymorphic data: polymorphic coding and frequency step matrix. Our phylogenetic results confirmed phocoenid monophyly. The division of Phocoenidae into two subfamilies previously proposed was rejected, as well as the alliance of the two extinct genera *Salumiophocaena* and *Piscolithax* with *Phocoena dioptrica* and *Phocoenoides dalli*. Extinct phocoenids are basal to all extant species. We also examined the origin and distribution of porpoises within the context of this phylogenetic framework. Phocoenid phylogeny together with available geologic evidence suggests that the early history of phocoenids was centered in the North Pacific during the middle Miocene, with

<sup>1</sup> Current address: East Carolina University, Brody School of Medicine, Department of Anatomy and Cell Biology, 600 Moye Boulevard, Greenville, North Carolina 27834, U.S.A.

subsequent dispersal into the southern hemisphere in the middle Pliocene. A cooling period in the Pleistocene allowed dispersal of the southern ancestor of *Phocoena sinus* into the North Pacific (Gulf of California).

Key words: Phocoenidae, morphology, biogeography, polymorphic data, frequency step matrix.

Six extant species of Phocoenidae (porpoises) are recognized (Rice 1998). *Neophocaena* and *Phocoenoides* are monotypic whereas *Phocoena* includes four species. *Neophocaena phocaenoides* (finless porpoise) is endemic to the coastal waters of the Indo-Pacific, ranging from the Persian Gulf to Japan. Some workers recognize three additional species: *N. phocaenoides* in the Indian Ocean, *N. asiaorientalis* in the Yangtze River of China, and *N. sunameri* in Korean and Japanese waters (Pilleri and Gihl 1972, 1975; Pilleri and Chen 1980). Others contend that such differences should be recognized at the subspecies level (Fraser 1966, Wang *et al.* 1989, Amano *et al.* 1992, Rice 1998). Recent morphometric study found significant differences in the skull size of adults of two of these forms *N. asiaorientalis* and *N. phocaenoides* (Jefferson 2002), and ongoing molecular work may help resolve the taxonomy of this genus.

*Phocoenoides dalli* (Dall's porpoise) is endemic to the North Pacific and occupies the area between the U.S.–Mexico border and central Japan to the Bering and Okhotsk seas (Reeves *et al.* 2002). Unlike most phocoenids, *Phocoenoides* inhabits both oceanic and coastal waters. Rice (1998) recognized two subspecies of *Phocoenoides*: *P. d. dalli* and *P. d. truei*. These subspecies differ externally in coloration pattern; however, Jefferson (2002) suggested that the two forms are simply color morphs rather than subspecies. Recent molecular data (Escorza-Treviño *et al.* 2004) found significant differences between the *P. d. dalli* and the *P. d. truei* types, similar to the genetic differences observed between different populations of the *P. d. dalli* type, and suggested that *P. d. dalli* and *P. d. truei* types are forms of the same species.

The most speciose phocoenid genus *Phocoena* includes four species: *Phocoena phocaena* (harbor porpoise), *Phocoena sinus* (vaquita), *Phocoena spinipinnis* (Burmeister's porpoise), and *Phocoena dioptrica* (spectacled porpoise). *Phocoena phocaena* inhabits the coastal waters of the North Pacific and North Atlantic. Three subspecies have been recognized: *P. phocaena phocaena* in the Atlantic, *P. phocaena vomerina* in the Pacific, and *P. phocaena relicta* in the Black Sea (Rosel *et al.* 1995a, Read 1999). Rice (1998) rejected recognition of the Black Sea population as a subspecies and suggested that the eastern population in the North Pacific is separated from the western North Pacific population by a distributional gap in the Aleutian Islands between Shemya and Unimak.

*Phocoena sinus* is endemic to the northern region of the Gulf of California, having the most restricted range of any cetacean. This species is critically endangered and has an estimated population size of less than 500 individuals (Barlow *et al.* 1997). *Phocoena spinipinnis* is endemic to the coastal waters of South America, ranging from northern Peru to southern Brazil with a continuous distribution around the southern tip of Tierra del Fuego. *Phocoena dioptrica* has a circumpolar distribution in the Southern Ocean; however, there is very little known about the biology and distribution of this species. Similar to *Phocoenoides*, *Phocoena dioptrica* occurs in both coastal and oceanic waters.

Six species of fossil phocoenids have been described. The oldest fossil phocoenid, *Salumiphocaena stocktoni*, is from the late Miocene (7–11 Ma) Monterey Formation

on the Palos Verdes peninsula, Los Angeles, California. This fossil was originally described as a delphinid of the genus *Loxolithax* (Wilson 1973). Based on skull morphology, Barnes (1985) re-assigned this species to a new genus of phocoenid, *Salumiphocaena*.

The most diverse extinct taxon, *Piscolithax* includes three species: *Piscolithax tedfordi* and *Piscolithax boreios* from the late Miocene (6–8 Ma) Almejas Formation, Islas Cedros, Mexico (Barnes 1984) and *Piscolithax longirostris* from the early Pliocene (4–5 Ma) Pisco Formation, Peru (Muizon 1984). *Numataphocaena yamashitai* was described from the early Pliocene (4–5 Ma) Horokaoshirarika Formation, Japan (Ichishima and Kimura 2000). *Haborophocaena toyoshimai* was recently described from the early Pliocene Mochikubetsu Formation in northwestern Hokkaido, Japan (Ichishima and Kimura 2005). Because of the poor preservation and the difficulty of coding characters from the literature, *Numataphocaena yamashitai* and *Haborophocaena toyoshimai* were not included in this study.

The relationship between Phocoenidae (true porpoises) and other odontocetes is contentious. Previous morphological and molecular studies (Muizon 1988; Heyning 1989, 1997; Barnes 1990; Messenger and McGuire 1998; Waddell *et al.* 2000; Hamilton *et al.* 2001) support monophyly of the Delphinoidea (including Phocoenidae, Delphinidae and Monodontidae, following Muizon [1988] and Heyning [1989]), although the relationships among delphinoids have been debated (Fig. 1). Some authors (Muizon 1988; Heyning 1989, 1997; Messenger and McGuire 1998; Hamilton *et al.* 2001) consider relationships among delphinoids to be unresolved (Fig. 1). Barnes (1990) proposed that Phocoenidae are more closely related to Delphinidae, and that the extinct Kentriodontidae were allied with both Delphinidae and Phocoenidae (Fig. 1D). Recent molecular data (Waddell *et al.* 2000, Arnason *et al.* 2004) support the alliance of phocoenids and monodontids as sister taxa, and delphinids as sister to that clade (Fig. 1E, I). Others have questioned the monophyly of Delphinoidea, and proposed that river dolphins are nested within that clade (Geisler and Sanders 2003, Arnason *et al.* 2004). The most recent comprehensive morphological study (Geisler and Sanders 2003) rejected monophyly of the Delphinoidea and proposed that the Phocoenidae and the Delphinidae share a closer alliance with the Platanistoidea (including all river dolphins: *Platanista*, *Inia*, *Lipotes*, and *Pontoporia*) rather than Monodontidae (Fig. 1G). However, there was little support (*i.e.*, Bremer values = 1) for this arrangement. Recent molecular data (Arnason *et al.* 2004) support paraphyly of delphinoids but rejects the monophyly of river dolphins (Geisler and Sanders 2003).

The family Phocoenidae has had a long, confusing taxonomic history. Until the end of the 19th century, phocoenids were still included in the family Delphinidae (Miller 1923, Kellogg 1928). In 1825, Gray assigned phocoenids and monodontids to the Phocoeninae; for this reason, the family group name is attributed to him. In 1885, Bravard correctly assigned all porpoises to the Phocoenidae, and this arrangement has been accepted by most later workers (Fraser and Purves 1960; Rice 1967; Gaskin *et al.* 1974; Brownell 1975, 1983; Barnes 1984, 1985; Heyning 1989, 1997; Rosel *et al.* 1995b; Geisler and Sanders 2003).

Subsequently phocoenids were recognized as a separate family with three genera: *Neophocaena*, *Phocaena*, and *Phocoenoides*, which have been widely accepted by later workers (Fraser and Purves 1960; Brownell 1975; Gaskin *et al.* 1984; Barnes 1985; Heyning 1989, 1997; Rosel *et al.* 1995b; Ichishima and Kimura 2000). Barnes (1985) described several osteological characters that grouped *Phocoenoides* and *Phocaena dioptrica* in the same clade and led him to assign *Phocaena dioptrica* to a new genus

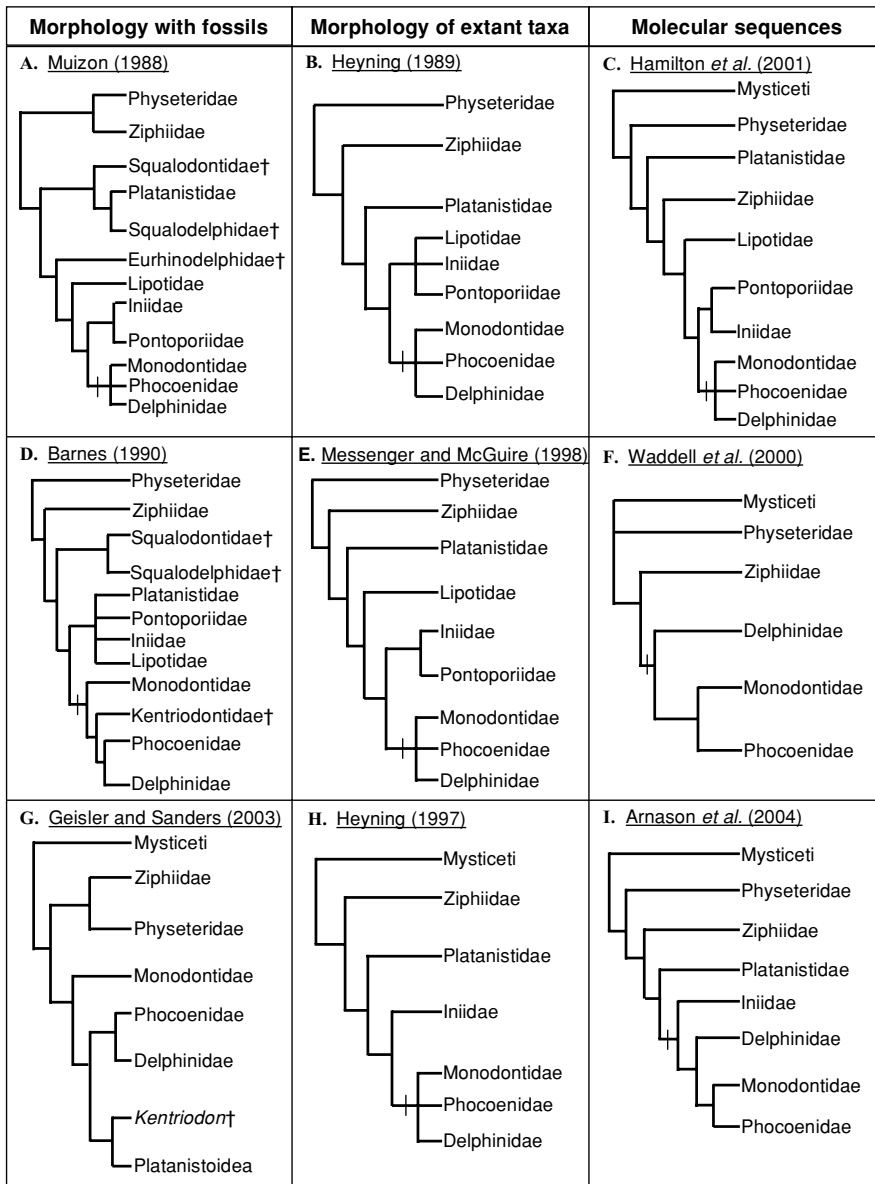


Figure 1. Previous hypotheses of odontocete relationships highlighting the position of the Delphinoidea indicated by a vertical bar, and extinct taxa indicated by a dagger.

*Australophocaena*. He also divided the Phocoenidae into two subfamilies: Phocoenoidinae, which included the extant *Phocoenoides dalli* and *Australophocaena dioptrica*, together with the extinct *Salumiphocaena stocktoni* and *Piscolithax*; and the subfamily Phocoeninae, comprised of the extant genera *Neophocaena* and *Phocoena*.

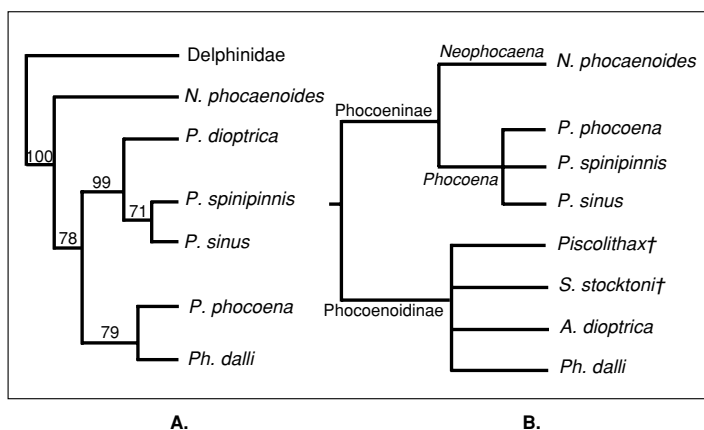


Figure 2. Previous hypotheses regarding phocoenid phylogeny. (A) Maximum parsimony and likelihood phylogeny of cytochrome b, gamma distance ( $\alpha = 2$ ) (Rosel *et al.* 1995b). Bootstrap values are indicated. (B) Non-cladistic analysis based on morphological characters (Barnes 1985).

This classification was accepted for a decade. Rosel *et al.* (1995b) analyzed molecular sequence data and found no support for recognition of two subfamilies. Instead, they found that *Neophocaena* was basal to all phocoenids, and that the separation between northern species (*Phocoena phocoena* and *Phocoenoides dalli*) and southern species (*Australophocaena diopttrica*, *Phocoena sinus*, and *Phocoena spinipinnis*) was well supported. For this reason, *Australophocaena diopttrica* was re-assigned by Rosel *et al.* (1995b) to its original genus *Phocoena*. In addition, according to these molecular results the clade formed by *P. phocoena* and *Ph. dalli* supports paraphyly of the genus *Phocoena*. Until now, no other phylogenetic studies have attempted to resolve the incongruence between morphological and molecular data (Fig. 2).

Previous phylogenetic studies of phocoenids have not employed rigorous systematic methods. For example, Barnes (1985) did not polarize characters, and based his morphological study mostly on selected cranial characters. As a result, he described *Neophocaena phocaenoides* as possessing more derived characters than any living species of *Phocoena* (*i.e.*, shorter rostrum, reduced number of teeth, lack of dorsal fin, *etc.*). This result is contrary to the basal position of *N. phocaenoides* based on molecular data (Rosel *et al.* 1995b). In addition, the characters of Barnes (1985) were based on only a few specimens of each species and descriptions from the literature, and no quantitative data were collected (*i.e.*, “larger adult body size,” “longer rostrum,” “smaller temporal fossae,” “vertebrae more numerous”). Several workers have found some of these characters inconsistent after observing larger sample sizes.<sup>2</sup>

The most recent phylogenetic study of phocoenids (Rosel *et al.* 1995b) was based on mitochondrial sequence data. Their results conflict with the morphologically based study. Although Rosel *et al.* (1995b) included two delphinids as the outgroups, they failed to examine other possible delphinoids (*e.g.*, Monodontidae). Their results positioned *Neophocaena phocaenoides* as the most basal phocoenid. They suggested that *Phocoena* was paraphyletic, and that *Phocoenoides dalli* and *Phocoena phocoena* represent

<sup>2</sup> Personal communication from William F. Perrin, Senior Scientist, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, 2 July 2002.

the latest diverging phocoenids, a significantly different result from the morphological study (see Fig. 2). A criticism of the molecular study is the use of a single mitochondrial gene (cytochrome b) and the control region. Rokas *et al.* (2003) suggested that the addition of different genes leads to more accurate results, and the use of only a few genes can result in an erroneous phylogeny.

The primary objective of this study was to perform a more comprehensive morphological study of phocoenid phylogeny including extant species, better known fossil species, and more appropriate outgroups (*i.e.*, Monodontidae, Delphinidae, Iniidae, and Pontoporiidae). We examined a comprehensive set of cranial, postcranial, and soft anatomical characters. Several phylogenetic questions were addressed: (1) Is Phocoenidae a monophyletic group? (2) Is the division of Phocoenidae into two subfamilies—Phocoeninae and Phocoenoidinae (Barnes 1985)—valid, or should all species be considered as belonging to the three major lineages proposed by Rosel *et al.* (1995b) (Fig. 2)? and (3) How are the fossil taxa related to each other and to extant species?

A second objective was to evaluate the evolutionary biogeography of phocoenids. We examined the origin and distribution of porpoises using physical and ecologic information (*i.e.*, past geologic events related to opening and closing of seaways, paleo-oceanic models, changes in global temperature) in the context of a phylogenetic framework. The questions addressed include: (1) What explains the current antitropical distribution of phocoenids? (2) Did phocoenids originate in the North Pacific as hypothesized by Barnes (1985)? (3) What caused the rapid radiation of phocoenids in the middle Pliocene? and (4) Is *Phocoena sinuata* a relict of a population of *P. spinipinnis* that crossed the equator during the Pliocene or Pleistocene and became isolated in the waters of the Gulf of California (Norris and McFarland 1958)?

#### MATERIALS AND METHODS

Specimens of fossil and extant phocoenids from the following institutions were examined: ITESM, Instituto Tecnológico y de Estudios Superiores de Monterrey, Guaymas, Mexico; LACM, Los Angeles County Natural History Museum, Los Angeles, California; MNHN, Museum National d'Histoire Naturelle, Paris, France; NSM, National Science Museum, Tokyo, Japan; RNP, Museo Acatashún, Tierra del Fuego, Argentina; SDNHM, San Diego Natural History Museum, San Diego, California; SDSU, San Diego State University, San Diego, California; SWFC, Southwest Fisheries Science Center, La Jolla, California; UCMP, University of California Museum of Paleontology, Berkeley, California; UCR, University of California, Riverside, California and USNM, United States National Museum of Natural History, Washington, D.C. A complete list of specimens examined is provided in Appendix 1. Morphological characters were evaluated from the cranial, postcranial, and soft anatomical regions of observed specimens and descriptions in the literature (*i.e.*, Mead 1975, Heyning 1989, Cranford *et al.* 1996) and are listed in Table 1. Osteological terminology follows Rommel (1990).

Variation within species (polymorphism) was observed for some osteological characters. Several studies (Mabee and Humphries 1993, Martins and Hansen 1997, Wiens 1999) have shown that polymorphic data can be highly informative and increase accuracy; thus the exclusion of such characters is unjustified. In order to address the issue of polymorphism, two different methods for coding polymorphic data were used: polymorphic coding and frequency step matrix (Wiens 1999).

Table 1. List of morphological characters.

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1. *Facial plane* (Barnes 1984, Heyning 1989): 0 = Concave, 1 = Straight, with little inclination.
  2. *Premaxillary boss* (Noble and Fraser 1971, Barnes 1985, Heyning 1989): 0 = Absent, 1 = Present.
  3. *Posterior projection of the right premaxilla* (Muizon 1984, Barnes 1985, Heyning 1989): 0 = Extends posterior to the narial openings, 1 = Does not extend posterior to the narial openings, and posterior end of premaxilla is small and adjacent to the narial openings, 2 = Does not extend beyond the narial openings, but is displaced laterally by a medial projection of the maxilla.
  4. *Degree of overlap of frontal by maxillary over orbit* (Norris and McFarland 1958, Noble and Fraser, 1971): 0 = Frontal bone visible at mid-length of orbit in dorsal view, 1 = Frontal bone not visible at mid-length of orbit in dorsal view.
  5. *Projection of the frontal over the maxilla*: 0 = Absent or nearly absent, 1 = Slight overhang of frontals over maxillae around the vertex of the skull, 2 = Pronounced overhang of frontals over maxillae, extending along the lateral edges of the vertex of the skull.
  6. *Antorbital notch*: 0 = Well developed, 1 = Absent or weakly developed.
  7. *Nasal protuberances* (Muizon 1988): 0 = Absent or very reduced, 1 = Present.
  8. *Degree of telescoping* (Muizon 1988): 0 = Nasal bones do not form part of the vertex, 1 = Nasal bones contribute to the vertex.
  9. *Pterygoids*: 0 = Not widely separated, 1 = Widely separated.
  10. *Ventral surface of the pterygoid hamuli* (Muizon 1988): 0 = Flat or rounded, 1 = Slightly keeled, 2 = Strongly keeled.
  11. *Exposure of the medial plate of pterygoid hamuli in lateral view* (Noble and Fraser 1971, Muizon 1988): 0 = Complete or broad exposure due to extreme reduction of the lateral lamina of the pterygoid hamuli, 1 = No exposure due to a posterior extension of the lateral lamina that extends posterior to the medial plate, 2 = Lateral lamina of pterygoid hamuli exposes the medial plate through an ovoid window in lateral view.
  12. *Frontal protuberance on vertex (frontal knob)* (Muizon 1984): 0 = Absent, 1 = Present.
  13. *Dorsal extension of air sinus system into frontals* (Fraser and Purves 1960, Perrin and Rosel 1999): 0 = Extension shallow, variably medium or with vermiform projection, 1 = Extension medium, 2 = Extension deep, but narrow, 3 = Extension deep and broad.
  14. *Level of the ventral margin of the foramen magnum in occipital view* (Norris and McFarland 1958, Noble and Fraser 1971): 0 = Lower margin of foramen magnum below level of lower margins of temporal fossae, 1 = Lower margin above temporal fossae.
  15. *Number of teeth* (Norris and McFarland 1958): 0 = Minimum tooth counts 25–51 and maximum 33–58, 1 = Minimum tooth counts 18–24 and maximum 26–32, 2 = Minimum tooth counts 8–17 and maximum 20–25.
  16. *Posterior process of tympanic bulla (shape of bone)* (Kasuya 1973, Muizon 1988): 0 = Small, composed of spongy bone, 1 = Large, composed of pachyostotic bone.
  17. *Lateral furrow of tympanic bulla* (Kasuya 1973): 0 = Well developed, 1 = Weakly developed, 2 = Absent.
  18. *Fusion of cervical vertebrae* (Allen, 1923, Noble and Fraser 1971): 0 = Unfused, 1 = Only atlas and axis fused, 2 = C1–C3 or C1–C4 fused, 3 = C1–C5 or C1–C6 fused, 4 = C1–C7 fused.
  19. *Spinous process of the axis* (Allen 1923, Noble and Fraser 1971): 0 = Short, extends dorsally, 1 = Short, extends posteriorly only to about C4, 2 = Long, nearly contact the spinal process of C7.
  20. *Transverse foramina (vertebrarterial canal) of C4* (Allen 1923, Noble and Fraser 1971): 0 = Complete, 1 = Incomplete or absent.
  21. *Transverse process of the axis* (Noble and Fraser 1971): 0 = Weakly developed or absent, 1 = Well developed.
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Table 1. Continued.

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22. *Size of spinous processes of thoracic vertebrae 1–4* (Allen 1923, Noble and Fraser 1971): 0 = Same height (except T1), 1 = Slight increase in height from T1 to T4.
23. *Inclination of the lumbar spinal processes* (Allen 1923): 0 = Spinal processes inclined posteriorly, 1 = Spinal processes inclined anteriorly.
24. *Metapophyses of the spinous processes*: 0 = Well developed, 1 = Absent or weakly developed.
25. *Acromion and coracoid processes of scapula*: 0 = Acromion longer than coracoid, 1 = Acromion shorter than coracoid.
26. *Ventral projection on the anterior border of the scapula* (Noble and Fraser 1971): 0 = Absent, 1 = Present.
27. *Supraspinous fossa* (Rommel 1990): 0 = Broad, 1 = Narrow.
28. *Olecranon process of the ulna* (Howell 1927): 0 = Absent or weakly developed, 1 = Well developed.
29. *Lower jaw* (Brownell *et al.* 1987, Jefferson 1988): 0 = Extends anterior to upper jaw or to same level as the upper jaw, 1 = Upper jaw extends anterior lower jaw.
30. *Prominent beak* (Reeves *et al.* 2002): 0 = Present, 1 = Absent or weakly developed.
31. *Apex of the flipper* (Leatherwood and Reeves 1983, Brownell *et al.* 1987): 0 = Sharply pointed, 1 = Rounded at tip.
32. *Dorsal fin* (Jefferson and Newcomer 1993, Reeves *et al.* 2002): 0 = Present, large 1 = Vertical ridge (small), 2 = Absent.
33. *Tubercles on dorsal fin* (Leatherwood and Reeves 1983, Brownell *et al.* 1987): 0 = Present, 1 = Absent.
34. *Sexual dimorphism* (Gaskin *et al.* 1974, 1984; Brownell and Praderi 1984; Brownell *et al.* 1987; Jefferson 1990; Best and da Silva 1993; Jefferson and Newcomer 1993; Shirakihara *et al.* 1993; Goodall and Schiavini 1995; Reyes and Van Waerebeek 1995; Stacey and Arnold 1999; Ralls and Mesnick 2002): 0 = Males are larger than females, 1 = Females are larger than males.
35. *Nasofrontal sac* (Heyning 1989): 0 = Anterior sac smooth, 1 = Anterior sac trabeculate.
36. *Vestibular sac* (Heyning 1989): 0 = Not divided, 1 = Bilaterally divided.
37. *Intrinsic muscle of vestibular sac* (Mead 1975): 0 = Not in sac, 1 = In sac.
38. *Vestibular sac floor* (Heyning 1989): 0 = Smooth, 1 = Wrinkled, 2 = Deeply folded.
39. *Vestibular sac* (Mead 1975, Heyning 1989): 0 = Large, 1 = Small.
40. *Accessory sac* (Schenkkan 1971, Mead 1975, Heyning 1989): 0 = Paired and large, 1 = Only one small or absent.
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The polymorphic coding method codes polymorphic species as having two or more states. If the variable species possesses all states for a given character, the species is treated as if either state was present and therefore is uninformative when further analyzing that specific character (*i.e.*, PAUP). If one state is more parsimonious than the other, the more parsimonious state is assigned to the variable taxon *a posteriori*. One of the disadvantages of using this method is that polymorphic states are not treated as synapomorphies. Another disadvantage is that this method does not take into account the frequencies of polymorphic states. For example, if you sample ten specimens of species A, and nine had character state 0 and only one had character state 1, it would be coded the same way as if you observed five specimens with the ancestral state (0), and five with the derived condition (1).

The frequency step matrix employs three different ways of coding frequency data, one of which was used in this study and is described below (see Wiens 1999, for additional methods). Frequency data, unlike other polymorphic methods, take into account the frequency of traits within a given species and weights changes between

states based on differences in frequencies (Wiens 1999). The frequency step matrix, assigns different character states for each frequency, resulting in a unique matrix with a set of frequencies. The cost of transition between character states is calculated by finding the Manhattan distances (Swofford and Berlocher 1987) between the frequencies. For instance, it is more expensive to transition from 0% to 100% than to go from 50% to 100%.

The polymorphic coding method employed the program MacClade 4.0 (Maddison and Maddison 2000) and the frequency step matrix used Manhattan distances (Swofford and Berlocher 1987, Wiens 1999) for character coding. Both methods were then analyzed using PAUP 4.0b10 (Swofford 2000). All characters were treated as unordered and unweighted using heuristic search if the number of taxa was more than 12 (*i.e.*, including fossils and extant taxa), or exhaustive search when the total number of taxa was less than 12 (*i.e.*, extant taxa only). In the case of more than one most parsimonious tree, a strict consensus tree was calculated and the non-parametric bootstrap support values were estimated with 1,000 replicates (Felsenstein 1985).

The outgroup comparison method (Watrout and Wheeler 1981, Maddison *et al.* 1984) was used to determine character polarity, which estimates the ancestral state at the outgroup node or the condition exhibited by the hypothetical ancestor. In the case of an equivocal state of the hypothetical ancestor, the character was left unpolarized. Exemplars of Delphinidae (true dolphins) and Monodontidae (beluga and the narwhal), Iniidae (Amazon river dolphins) and Pontoporiidae (La Plata dolphins) were selected. Phocoenidae is sister to Delphinidae and Monodontidae that together form the Delphinoidea (Muizon 1984, Heyning 1989). Two families of river dolphins, Iniidae and Pontoporiidae, have been hypothesized as sister taxa to delphinoids (Muizon 1988; Heyning 1989, 1997; Barnes 1990; Messenger and McGuire 1998; Cassens *et al.* 2000; Hamilton *et al.* 2001); however, the relationships among these taxa are unresolved and the monophyly of delphinoids is uncertain (Geisler and Sanders 2003). *Inia geoffrensis* and *Pontoporia blainvillei* putative sister taxa of delphinoids (Muizon 1988, Messenger and McGuire 1998, Hamilton *et al.* 2001) were both included in the study. One of the two extant monodontids, *Delphinapterus leucas* (beluga whale) was included. Delphinidae, the most diverse family of cetaceans includes at least 33 species. In the most recent comprehensive phylogenetic study of delphinids, the entire cytochrome b sequence of virtually all recognized species and four outgroups (two phocoenids and the two extant monodontids) was analyzed (LeDuc *et al.* 1999). Results of this study support monophyly of three distinct delphinid clades: Globicephalinae, Delphininae, and Lissodelphininae with very little resolution. For this reason, we selected one species from two of the major delphinid clades and a single species exclusive to these clades: *Orcaella brevirostris* (Irrawaddy dolphin), *Tursiops truncatus* (bottlenose dolphin-Delphininae), and *Lissodelphis borealis* (northern right whale dolphin-Lissodelphininae).

#### PHYLOGENETIC ANALYSIS

Separate analyses of different partitions of the morphological data were performed to identify and compare the phylogenetic signal of partitioned data, and to address the importance of including postcranial and soft anatomical characters in morphological studies (Appendices 2 and 3). First, all taxa were included to determine the relationships among fossils and their extant relatives, and to compare with the previous morphological study (Barnes 1985). Second, a partitioned analysis of cranial

characters for extant taxa was performed to compare with the previous morphological study in which mainly cranial characters were used, and to test whether the addition of characters from the postcranial and soft anatomical regions would help resolve relationships. Third, analysis of extant taxa including all characters was done to compare results with the previous molecular study (Rosel *et al.* 1995*b*) and with the results of the cranial data set. The phylogenies obtained using both the polymorphic coding method and the frequency step matrix are discussed.

In the first analysis, four of the better-known fossil phocoenids (*i.e.*, *Piscolithax boreios*, *Piscolithax tedfordi*, *Piscolithax longirostris*, and *Salumiphocaena stocktoni*) and all six extant species were included. The phylogenies based both on polymorphic coding and frequency step matrix methods (Fig. 3A, B) include only cranial characters because of the large amount of missing data for the fossils (*i.e.*, few postcranial and no soft anatomical data) and the lack of resolution when all characters are included. The polymorphic coding method failed to support monophyly of phocoenids (*i.e.*, *Inia geoffrensis* and *Pontoporia blainvillei* are nested within phocoenids) and was unable to resolve most relationships within phocoenids (Fig. 3A). The extinct genus *Piscolithax* appears monophyletic, but support is weak (<70% bootstrap). All extinct taxa are basal to extant phocoenids; however, that clade is not well supported. Among extant phocoenids, there is no strong support (<70% bootstrap) among *N. phocaenoides*, *P. sinus*, and *P. spinipinnis*, and the only clade that was well supported is *Phocaena diopttrica* + *Phocaena phocaena* + *Phocaenoides dalli* (Fig. 3A). Based on the lack of resolution and the low bootstrap support for most of the clades, very little can be inferred from this phylogenetic hypothesis.

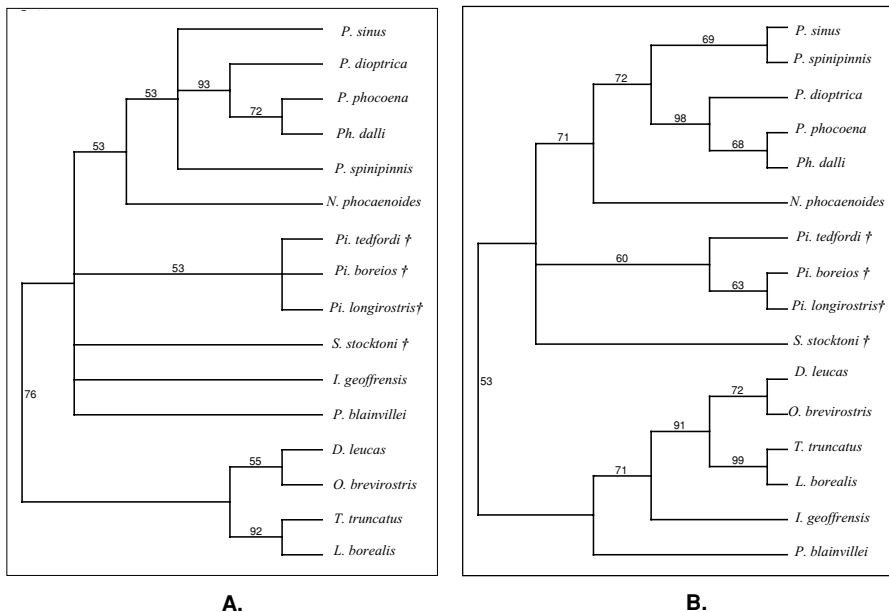


Figure 3. Phylogeny of extant and fossil phocoenids using cranial characters only. (A) Polymorphic method. Strict consensus of 9 MP trees, tree length 45, CI = 0.622. Numbers represent bootstrap values. (B) Frequency step matrix method. Strict consensus of 9 MP trees, tree length 477.10, CI = 0.607. Numbers represent bootstrap values.

Using precise information on the frequencies for each trait (*i.e.*, frequency step matrix) provided greater resolution between extinct and extant taxa. Although phocoenids appear monophyletic in this analysis, this result is weakly supported (Fig. 3B). Based on these results, extinct taxa are basal to extant phocoenids. *Neophocaena phocaenoides* is the most basal extant phocoenid as previously suggested by Gaskin (1976) and Rosel *et al.* (1995b). Later diverging taxa are divided into two clades: *P. spinipinnis* + *P. sinus*, and *P. phocoena* + *P. dioptrica* + *Ph. dalli*. Based on cranial data, the two northern species *P. phocoena* and *Ph. dalli* are sister taxa as suggested by a previous molecular study (Rosel *et al.* 1995b) and supports the paraphyly of *Phocoena*; however, the bootstrap support for that clade is weak (<70% bootstrap).

Another run of the data excluded fossil taxa and inferred relationships among extant taxa based on cranial characters only (Fig. 4A, B). The polymorphic coding method found good support for a monophyletic Phocoenidae, as well as for the basal position of *Neophocaena phocaenoides*. The clade formed by *P. dioptrica*, *P. phocoena*, and *Ph. dalli* is still well supported, and the relationship of the two northern species as sister taxa is better supported after removing the fossils. The only relationship based on cranial data not supported by the polymorphic coding method is that between *P. sinus* and *P. spinipinnis* (Fig. 4A). Similar results were obtained using the frequency step matrix method except that the relationship between *P. phocoena* and *Ph. dalli* was not well supported, but all other relationships within phocoenids were well supported, including the monophyly of the group and the paraphyly of *Phocoena* (Fig. 4B). Based on the results using cranial data only, there is no support for the division of the family into two subfamilies as proposed by Barnes (1985).

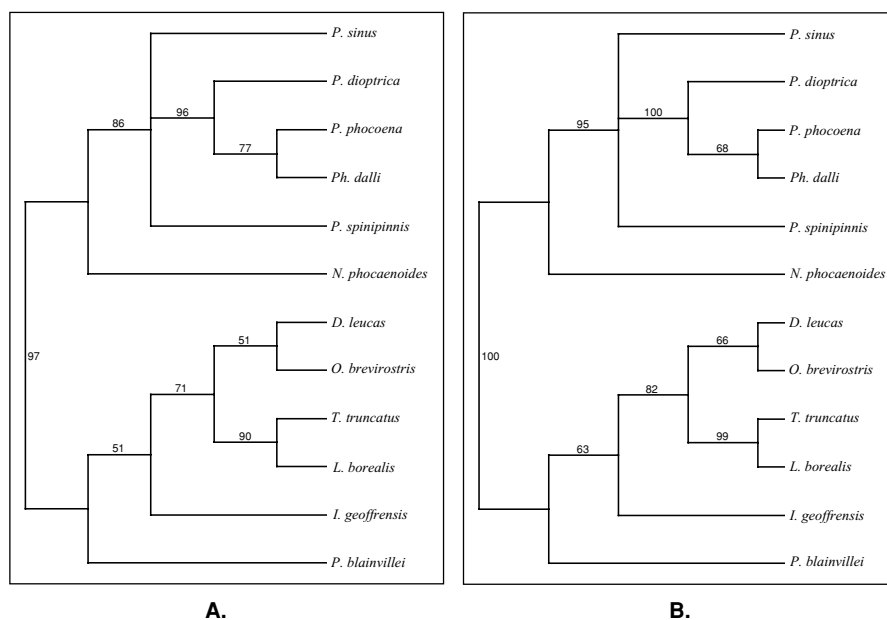


Figure 4. Phylogeny of extant phocoenids including cranial characters only using (A) polymorphic coding method. Strict consensus of 2 MP trees, tree length 37, CI = 0.73. Numbers represent bootstrap values. (B) Frequency step matrix method. 2 MP tree, tree length 397.10, CI = 0.726. Numbers represent bootstrap values.

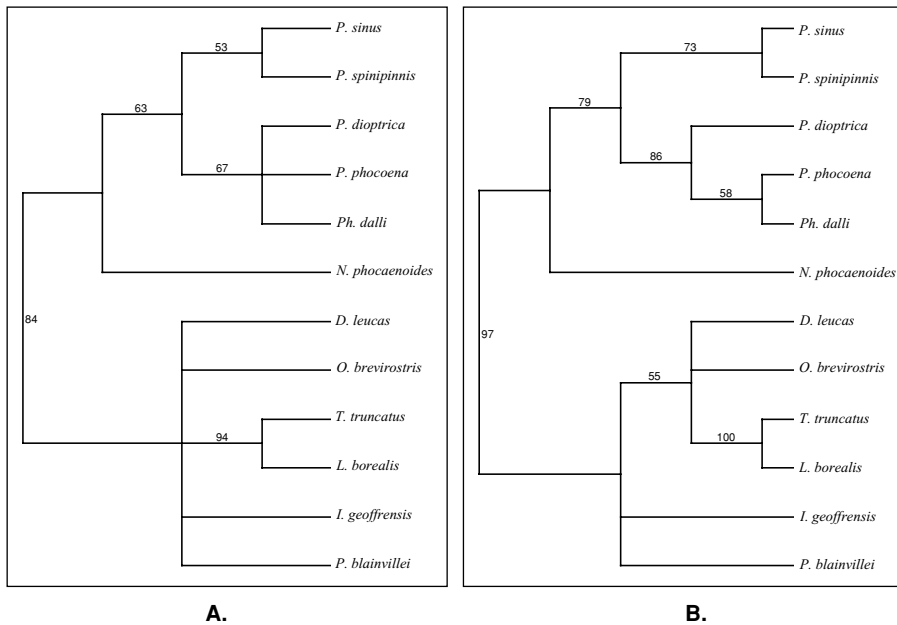


Figure 5. Phylogeny of extant phocoenids including all characters using (A) polymorphic coding method. 1 MP tree, tree length 88, CI = 0.591. Numbers represent bootstrap values. (B) Frequency step matrix method. 1 MP tree, tree length 932.80, CI = 0.577. Numbers represent bootstrap values.

The final analysis included characters from the cranial, postcranial, and soft anatomical regions. The polymorphic coding method was unable to resolve relationships between *P. dioptrica*, *P. phocoena*, and *Ph. dalli*, and none of the clades within phocoenids were well supported (Fig. 5A). The frequency step matrix method provided better resolution and support when compared to the polymorphic method, and the only node with weak support is the alliance of *P. phocoena* and *Ph. dalli* (Fig. 5B).

Barnes (1985) described fossil and extant phocoenids as sharing the following “unique suite of derived cranial characters”: presence of a premaxillary prominence on the posterior end of each premaxilla, small posterior termination of the premaxilla that does not reach the nasal bone, palatine bones that are relatively widely exposed on the palate, separating the hamular processes of the pterygoids, branch of the pre-orbital lobe of the air sinus system that extends from the orbit dorsally into a recess that lies between the frontal bone and the facial portion of the maxillary bone on either side of the skull, and an asymmetrical cranial vertex slightly offset to the left side. When the distribution of these putative synapomorphies is considered among outgroup taxa, only the premaxillary prominence was confirmed as a synapomorphy of phocoenids.

In this study, the monophyly of extant and extinct phocoenids was not well supported by either polymorphic coding or frequency step matrix methods (Fig. 3A, B). These results could be due to the small sample size of the fossils (only one specimen for each recognized species), missing data due to incomplete material, and/or coding from the literature (*i.e.*, *Salumiphocaena stocktoni* and *Piscolithax longirostris*)

(Wilson 1973, Muizon 1984). The only unique character that unites fossil and extant phocoenids is the posterior projection of the right premaxilla (Table 1, character 3), which is small and adjacent to the narial openings and does not extend posterior to the narial openings as it does in delphinids, *Inia* and *Pontoporia*. Characters that are present in all phocoenids but may also occur in other taxa (*i.e.*, either as homoplasies or their homology is in question) are considered equivocal synapomorphies and require further study. Equivocal synapomorphies for fossil and extant phocoenids are: presence of a premaxillary boss on the posterior end of each premaxilla (Table 1, character 2), nasal bones located in the ascending part of the skull that do not form part of the vertex (Table 1, character 8), pterygoid hamuli that are widely separated by the palatine bones and/or the vomer (Table 1, character 9), and large posterior process of the tympanic bone composed of pachyostotic bone (Table 1, character 16).

Although the monophyly of phocoenids was not well supported when extinct taxa were included, it was well supported based on extant taxa (Figs. 4, 5). In addition to the reduced posterior end of the premaxillae, synapomorphies that support monophyly of extant phocoenids are: fusion of three or more cervical vertebrae (Table 1, character 18), trabeculate anterior sac (Table 1, character 35), vestibular sac enclosed by an intrinsic muscle (Table 1, character 37), and vestibular sacs with deep transverse folds (Table 1, character 38).

Equivocal synapomorphies of extant phocoenids include: presence of a frontal protuberance on the vertex (Table 1, character 12), weakly developed lateral furrow of the tympanic bulla (Table 1, character 17), spinous processes of thoracic vertebrae 1–4 that are similar in height (Table 1, character 22), short beak (Table 1, character 30), small and bilaterally divided vestibular sacs (Table 1, character 36), and accessory sac absent or only one small sac present (Table 1, character 40).

*Neophocaena phocaenoides* differs from other extant phocoenids in having a well-developed antorbital notch (Table 1, character 6), relatively flat nasal bones (Table 1, character 7), shallow dorsal extension of the air sinus system into the frontals (Table 1, character 13), weakly developed olecranon process of the ulna (Table 1, character 28), and a vertical ridge instead of a dorsal fin (Table 1, character 32). The clade formed by *P. sinus* and *P. spinipinnis* is supported by the following unique characters: frontal bone visible at mid-length of orbit in dorsal view (Table 1, character 4), and complete transverse foramina in the fourth cervical vertebra (Table 1, character 20). The clade comprised of *P. dioptrica*, *P. phocaena*, and *Pb. dalli* is supported by the following characters: small exposure of the medial plate through an ovoid window of the lateral lamina of the pterygoid hamuli (Table 1, character 11), fusion of 5 or more cervical vertebrae (Table 1, character 18), and long spinous process of the atlas that nearly contacts the spinal process of the last cervical vertebra (Table 1, character 19). Lastly, *P. phocaena* and *Pb. dalli* share three unique characters: tooth counts that range between 18–24 and 26–32 (Table 1, character 15), well-developed transverse process of the axis (Table 1, character 21), and ventral projection on the anterior border of the scapula (Table 1, character 26).

## DISCUSSION

Similar to the previous molecular study (Rosel *et al.* 1995*b*), morphological data from this study supports *Neophocaena phocaenoides* as the most basal extant phocoenid, and the division of later diverging taxa into two separate clades; however, the relationships among these clades differ between this study and the molecular study

(Rosel *et al.* 1995*b*). Molecular data supports the relationship of *P. dioptrica* as sister taxon to *P. sinus* and *P. spinipinnis*, but based on this study, *P. dioptrica* is more closely related to the two northern species *Pb. dalli* and *P. phocoena*. Constraining the molecular topology to the morphological data set, results in a tree that is five steps longer (*i.e.*, tree length of constrained tree = 93 and tree length of MP morphological tree = 88). Similar to the molecular study (Rosel *et al.* 1995*b*), the two northern species *P. phocoena* and *Pb. dalli* are sister taxa; however, the bootstrap support for this clade is below 70%.

The partitioned analysis of cranial characters using both the polymorphic coding and frequency step matrix methods were unable to resolve relationships between *P. sinus*, *P. spinipinnis* and the clade formed by *P. dioptrica*, *P. phocoena*, and *Pb. dalli* (Fig. 4). The addition of postcranial and the soft anatomical characters resolved this polytomy by grouping *P. sinus* and *P. spinipinnis* as sister taxa, in agreement with the molecular study (Rosel *et al.* 1995*b*). The polymorphic coding method decreased the resolution and bootstrap support after the addition of postcranial and soft anatomical characters, which could be a result of the increase in number of polymorphic characters from the postcranial region (Fig. 5A). By contrast, the frequency step matrix method increased both the resolution and bootstrap support for all clades after the addition of more frequency data (Fig. 5B). In any case, additional characters from the postcranial and soft anatomical regions help resolve relationships that were not supported by the partitioned analysis of the cranial region. For example, Buchholtz and Schur (2004) concluded that vertebral anatomy provided a previously little-used source of characters that contributed to the resolution of phylogenetic relationships within Delphinidae. As this study has shown, phylogenetic analyses of morphological data should include comprehensive data sets (*i.e.*, cranial, postcranial, and soft anatomical data) and both living and fossil taxa (Wiens 2004). In addition to comparison of the morphological and molecular sequence data presented herein, the next step is a "total evidence" approach that integrates morphological and molecular data among living and extinct taxa and offers the potential benefit of increased phylogenetic resolution (O'Leary *et al.* 2004).

Including fossil phocoenids in the phylogeny is especially important when tracing the evolutionary history of character transitions because of their basal phylogenetic position. For example, when the total number of teeth (Table 1, character 15) in phocoenids is mapped onto the phylogeny of extant taxa, the hypothesized ancestral state for the family is a minimum tooth count of 8–17 and maximum of 20–25 (Fig. 6A). When fossils are included, the basal position of the extinct taxa defines the ancestral condition of the family as having more teeth, with a minimum tooth count of 25–51 and a maximum count of 33–58 (Fig. 6B).

#### EVOLUTIONARY BIOGEOGRAPHY

Phocoenids have an antitropical distribution. Other marine organismal groups with antitropical distributions include giant kelps (*Macrocystis integrifolia* and *Macrocystis pyrifera*), fur seals (*Arctocephalus*), elephant seals (*Mirounga*), crustaceans (*Lithodes*, *Cancer*, *Talipes*, *Hemigrapsus*, and *Cyclograpsus*), gastropods (*Tegula*, *Thais* and *Acanthina*), bivalves (*Protothaca* and *Mytilus*), and several species of fishes (Dall 1909, Ekman 1953, Garth 1957, Soot-Ryen 1959, Gaskin 1976, King 1983, Hickman and McLean 1990, Lindberg 1991, Deméré *et al.* 2003). Most marine species that have antitropical distributions live in the eastern Pacific, and for this reason, most

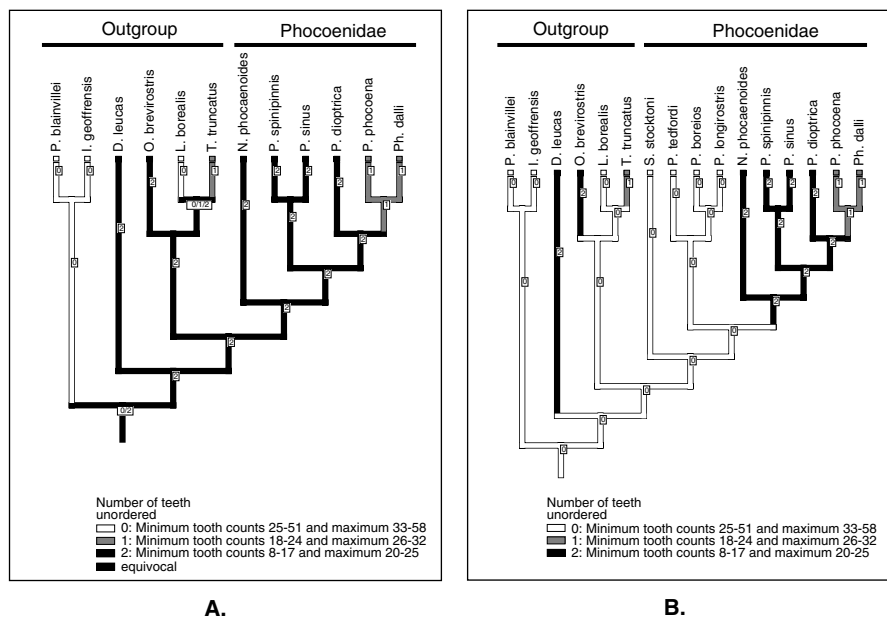


Figure 6. Number of teeth (character 15) mapped onto morphology based tree in this study. (A) Extant taxa only, and (B) Extant and extinct taxa.

studies of antitropical distributions focus on geological events in this ocean basin. We discuss below the most influential geologic events argued to have resulted in the antitropical distribution of several marine organisms, and correlate these events with the inferred phylogeny of phocoenids and the estimated molecular divergence rates from the previous molecular study (Rosel *et al.* 1995b).

Jacobs *et al.* (2004) proposed that most of the marine diversity in the eastern North Pacific Ocean developed as the result of an upwelling regime that began during the middle Miocene initiated by glaciation of Antarctica (12–15 Ma). Cooling below the thermocline of the Southern Ocean adjacent to Antarctica produced upwelling in the North Pacific creating nutrient-rich waters. Because of this ideal condition in the North Pacific, it is very likely that marine organisms in the Pacific that diverged during the middle Miocene, originated in this region (Jacobs *et al.* 2004, Lindberg<sup>3</sup>).

A second major event occurred during the Pliocene (5–2 Ma). After the optimal conditions of upwelling during the Miocene, there was a tremendous reduction in upwelling during the Pliocene (Jacobs *et al.* 2004) and the global climate was unusually warm (Knies *et al.* 2002). An important geologic event that influenced ocean conditions in the eastern North Pacific is the closure of the Panamic portal by 3.1 Ma (Lindberg 1991, Jacobs *et al.* 2004). This closure altered the tropical current patterns and the water temperatures in the coastal region. According to Weaver (1990), closure of the Panamic portal caused the California Current to flow closer to the equator,

<sup>3</sup> Personal communication from David R. Lindberg, Professor and Chair, Department of Integrative Biology, University of California, 3060 Valley Life Science Building, Berkeley, CA 94720-3140, 22 April 2004.

allowing species to disperse from the northern into the southern hemisphere. These favorable current conditions provide evidence to support antitropical distribution patterns during the Pliocene. In addition, Lindberg (1991) observed that 90% of the taxa he studied migrated from the northern into the southern hemisphere during the Pliocene, and only 10% migrated from south to north. Correlation of geologic and paleontological events suggested that antitropical distribution was a product of biotic interchange between the two hemispheres, rather than vicariance (Lindberg 1991).

The final geologic event that contributed to antitropical distributions in marine organisms was the initiation of the northern hemisphere glaciation, which began in the late Pliocene (~2.5 Ma) and continued throughout the Pleistocene (2–1 Ma), in which tropical water temperatures dropped allowing species to cross the warm equatorial barrier and disperse into the northern and southern hemispheres (Hubbs 1952, Lindberg 1991). Some authors believe that cooling alone cannot be responsible for dispersal between the two hemispheres, and additional factors contributed to the interchange during the Pleistocene, such as compression of the temperate and tropical zones, changes in upwelling intensity, storm tracks, and sea-level changes (Lindberg 1991). The biotic interchange between the southern and the northern hemisphere during the Pleistocene was nearly symmetrical, with 40% of the taxa migrating from north to south and 60% from south to north (Lindberg 1991).

There is an interesting correlation between these three main geologic events during the Miocene, Pliocene, and Pleistocene and phocoenid phylogeny. Estimated molecular divergence rates from a previous molecular study (Rosel *et al.* 1995b) are mapped on the congruent nodes between this study and the previous molecular study to provide more accurate times of divergence (Fig. 7). According to the estimated molecular divergence rates, phocoenids diverged from other odontocetes 12–16 Ma (Rosel *et al.* 1995b). This date roughly corresponds with the fossil record (Fig. 7, node A). The most basal extant phocoenid, *Neophocaena phocaenoides*, is endemic to the Indo-Pacific. By considering only extant taxa, one could argue that phocoenids originated in this ocean basin. When fossils are included, the most basal phocoenids are the extinct taxa *Piscolithax boreios* and *Piscolithax tedfordi* from Isla Cedros, Baja California, Mexico; *Salumiphocaena stocktoni* from Palos Verdes, California; and *Piscolithax longirostris* from Sacaco, Peru. The most parsimonious explanation suggests an eastern North Pacific origin of phocoenids during the Miocene, with a single migration to the southern hemisphere (*Piscolithax longirostris*), which correlates with the North Pacific origin of other marine organisms (Jacobs *et al.* 2004), and suggests antitropical speciation in the late Miocene.

Rosel *et al.* (1995b) suggest a rapid radiation during the Pliocene (2–3 Ma) of all other extant phocoenids, excluding *Neophocaena phocaenoides* (Fig. 7, node B). As previous biogeographic studies suggested, the closing of the Isthmus of Panama (3.1 Ma) and other factors resulting from this geologic event (*i.e.*, change in tropical currents and water temperature), allowed northern species to disperse into the southern hemisphere. It is probable that during this time, a northern common ancestor dispersed to the southern hemisphere resulting in speciation of the southern species *Phocoena dioptrica* and *Phocoena spinipinnis*. Even though this is not the most parsimonious explanation, there is evidence from other antitropical marine taxa and geologic events to support this hypothesis of a north to south migration during the middle Pliocene (Lindberg 1991).

The final event that contributed to the antitropical distribution of phocoenids is cooling during the Pleistocene that allowed species to cross the equatorial barrier

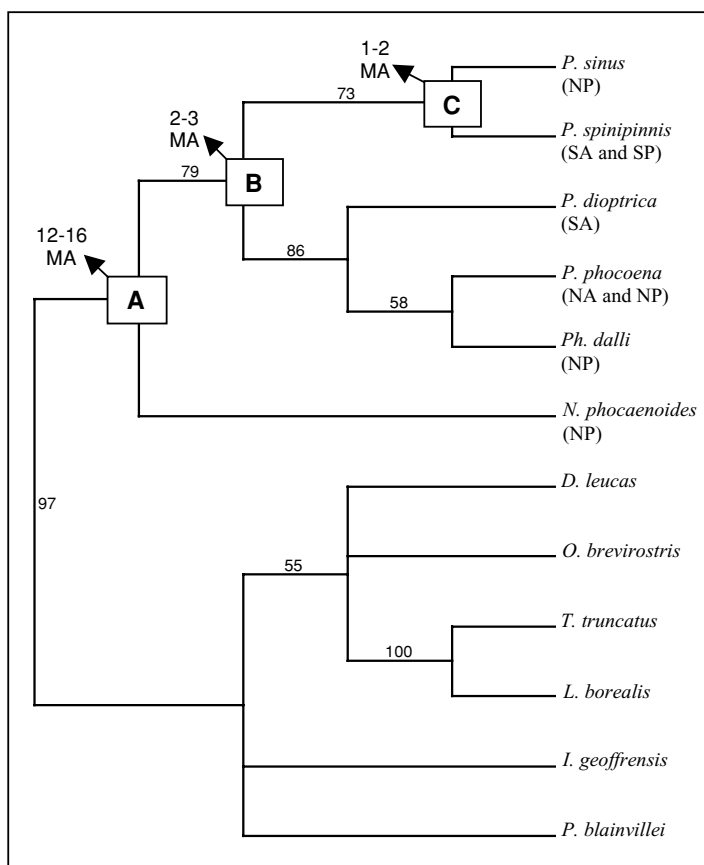


Figure 7. Phocoenid phylogeny and biogeography based on this study. Numbers at the nodes correspond to the estimated molecular divergence rates from previous molecular data (Rosel *et al.* 1995*b*). Values are mapped for all congruent nodes. NP = North Pacific, SP = South Pacific, NA = North Atlantic, and SA = South Atlantic.

and disperse into a different hemisphere. According to Hubbs (1952), the Humboldt Current in the South Pacific converged with the Northern Current creating a corridor between the southern and northern hemispheres, which facilitated the dispersal of marine organisms. Norris and McFarland (1958) suggested that the southern ancestor of *Phocoena sinus* crossed the equator during the Pleistocene, and became trapped in the Gulf of California. This hypothesis was later supported by a morphologic study of the skulls of *Phocoena phocoena*, *Phocoena sinus*, and *Phocoena spinipinnis* (Noble and Fraser 1971), molecular data (Rosel *et al.* 1995*b*), and is now supported by this morphological study. The estimated rate of divergence for this node based on previous molecular data is 1–2 Ma (Fig. 7, node C). A similar event likely resulted in speciation of the two northern species *Phocoena phocoena* and *Phocoenoides dalli*, whereby a southern ancestor crossed the equatorial barrier and speciated into these two taxa. However, there is no molecular divergence rate to support the timing of this event.

In summary, there seems to be sufficient geological data and examples of other marine organisms to explain the antitropical distribution of phocoenids in three steps. First, the divergence of phocoenids from other delphinoids occurred in response to optimal upwelling conditions in the eastern North Pacific that resulted from the continued glaciation in Antarctica during the middle Miocene (12–15 Ma). Secondly, dispersal into the southern hemisphere after the closing of the Panamic portal (3.1 Ma) changed the current patterns and tropical temperatures in the North Pacific, allowing species to cross the warm equatorial barriers. Thirdly, a cooling period during the Pleistocene allowed a southern common ancestor to disperse into the northern hemisphere and speciate into the northern species. Additional molecular data with divergence rates for all the nodes would be useful to confirm or reject this biogeographic pattern.

### Conclusions

This study provides new phylogenetic and biogeographic hypotheses for extinct and extant members of the family Phocoenidae. A comprehensive data set of 17 cranial, 11 postcranial, and 12 soft anatomical characters for extant taxa and four of the five better known fossil phocoenids, provide different results from those previously proposed. The division of the family into two subfamilies (Barnes 1985) was rejected, as well as the alliance of the two extinct genera with *P. dioptrica* and *Pb. dalli*. The extinct taxa are basal to all extant phocoenids, with *Salumiphocaena stocktoni* identified as the most basal phocoenid and a later diverging clade that includes *Piscolithax*; however, there is weak support for this arrangement (bootstrap < 70). Because of the basal position of extinct taxa, inclusion of fossils in the phylogeny is essential when tracing the evolution of characters.

Results from two different methods of coding polymorphic data support the position of *Neophocaena phocaenoides* as the most basal extant phocoenid. Also confirmed is the division of other extant phocoenids into two clades; *Phocoena sinus* + *Phocoena spinipinnis*, and *Phocoena phocoena* + *Phocoenoides dalli* + *Phocoena dioptrica*. These results are similar to those previously proposed (Rosel *et al.* 1995*b*) based on molecular data. The only incongruence between the two studies is the position of *Phocoena dioptrica*, which according to the molecular study (Rosel *et al.* 1995*b*) is more closely related to *Phocoena sinus* and *Phocoena spinipinnis*, whereas in this study it is more closely related to *Phocoena phocoena* and *Phocoenoides dalli*. Further phylogenetic analyses that include other mitochondrial and nuclear genes, and a combined analysis of morphological and molecular data may help better resolve relationships among phocoenids.

The phylogeny played a critical role in providing a framework for constructing biogeographic hypotheses. According to this study, three main geologic events contributed to the antitropical distribution of phocoenids. First, glaciation of Antarctica during the middle Miocene (12–15 Ma) produced upwelling in the North Pacific that promoted the speciation of phocoenids. The closure of the Isthmus of Panama (3.1 Ma) in the middle Pliocene altered oceanic current patterns and temperatures in the North Pacific, allowing northern species to disperse into the southern hemisphere (Weaver 1990, Lindberg 1991, Jacobs *et al.* 2004). Lastly, a cooling period in the South Pacific during the Pleistocene (1–2 Ma) allowed southern species to cross the equator and disperse into the northern hemisphere.

The addition of fossils to the phylogeny provides another example of an antitropical clade within the family. When fossil taxa are excluded, there are two distinct clades

in which southern species are closely related to northern species. Inclusion of extinct taxa provides an additional example of an extinct clade in which a southern species (*i.e.*, *Piscolithax longirostris*) is closely related to three northern species (*Piscolithax boreios*, *Piscolithax tedfordi*, and *Salumiphocaena stocktoni*); however, the timing of this divergence is unknown.

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#### SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Supplementary Appendix 1

Supplementary Appendix 2

Supplementary Appendix 3