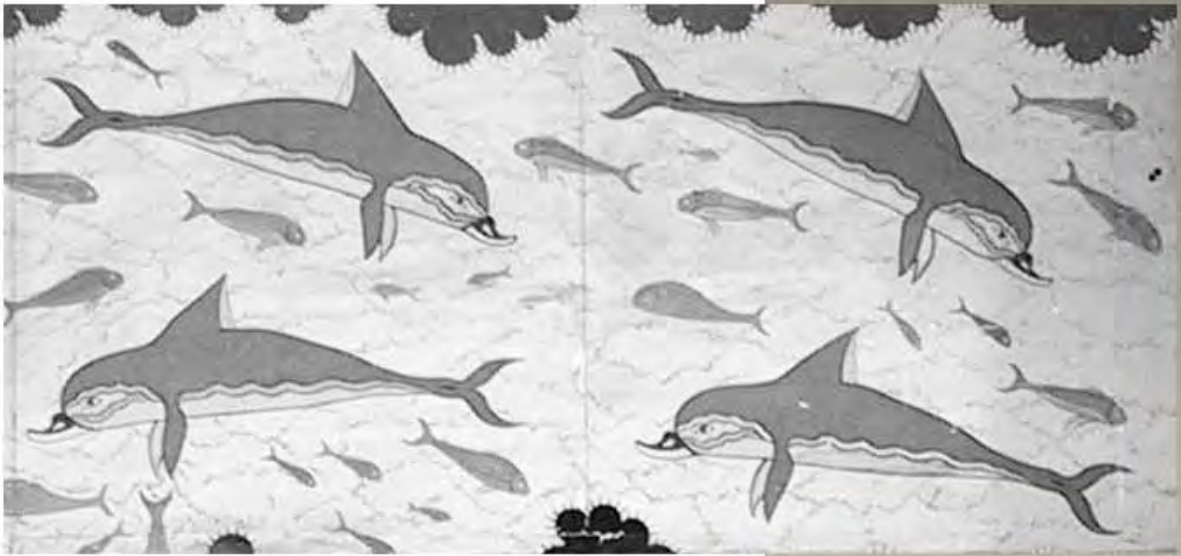


### MORPHOLOGICAL PHYLOGENY OF THE DELPHINIDAE (MAMMALIA: CETACEA)



Palace of Knossos, on the island of Crete, from 3,500 years ago. Probably striped dolphin (*L. coeruleoalbus*, note the eye to anus strip). Picture by Chris 73, ([http://commons.wikimedia.org/wiki/Image:Dolphin\\_Mural\\_Knossos.jpg](http://commons.wikimedia.org/wiki/Image:Dolphin_Mural_Knossos.jpg)).

# MORPHOLOGICAL PHYLOGENY OF THE DELPHINIDAE

(MAMMALIA: CETACEA)

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**ABSTRACT:** Delphinidae is the most diverse family among all living Cetacea. There is still no consensus about subdivisions within the Delphinidae, and the current use of subfamilies is based around *Delphinus* (Delphininae), *Steno* (Steninae), *Lissodelphis* (Lissodelphinae), *Cephalorhynchus* (Cephalorhynchinae), and *Globicephala* (Globicephalinae). These groups were based mostly on phenetic judgments of only one line of evidence and resulted in contradictory classifications. In this study, morphological characters from 43 living Odontocetes were codified by direct examination of specimens. The ingroup thus totals 35 different OTUs (31 species + 3 subspecies + 1 population). All of the 17 genera of the Delphinidae are represented by at least one species. This is the first attempt to produce a cladistic analysis of the Delphinidae using morphology with a comprehensive data set (skull, tympanoperiotic, external morphology and coloration). The analysis of the 147 character matrix with 43 taxa resulted in four equally most parsimonious trees with a length of 1034 steps. The family Delphinidae was supported by four exclusive synapomorphies. This study shows that the former group called “blackfish” is polyphyletic and should be split in three subfamilies: (Orcinae, Orcaellinae and a new subfamily). Another new subfamily, Lagenorhynchinae, should be created to place *Lagenorhynchus albirostris*. This study recovered a Lissodelphinae monophyletic with 10 species in three genera. In this study, a well supported Steninae was found, with *Sousa* deeply nested in the subfamily clade as the sister group to *Sotalia*. *Leucopleurus acutus* is nested within the subfamily Delphinidae. The subfamily Delphininae should include only the genera *Delphinus*, *Leucopleurus*, *Lagenodelphis*, *Stenella*, “*Stenella*” *longirostris* and *Tursiops*. The morphological results presented here are promissory. This study makes clear that a comprehensive cladistic analysis can help to resolve the relationship within delphinids.

**KEY WORDS:** Delphinidae, systematics, morphology, evolution, Delphinoids.

**RUNNING HEAD:** Morphological phylogeny of Delphinids

Preliminary version – Please, citation only after previous acceptance of the author

## INTRODUCTION

The delphinoids (Superfamily Delphinoidea, sensu de Muizon 1988), with 22 genera and at least 45 species, represent about half of the living Cetacea (Rice 1998; Berta et al. 2006). The currently recognized families in the Delphinoidea are the extant Delphinidae, Phocoenidae, and Monodontidae and the extinct Kentriodontidae, Albireonidae and Odobenocetopsidae (Fordyce et al. 1994). The fossil record of this group was tracked back to the late Miocene (10-12 million years) (Barnes 1990; Fordyce and Barnes 1994; Fordyce et al. 1994). The living delphinoids include 37-38 species of dolphins/black fish (Delphinidae), six porpoises (Phocoenidae), and two white whales/narwhal (Monodontidae). Most previous studies agree that the superfamily Delphinoidea is monophyletic (e.g. de Muizon 1988; Heyning 1989; Barnes 1990; Fordyce 1994; Fordyce and Barnes 1994; Messenger and McGuire 1998; Hamilton et al. 2001; Yang et al. 2002; Arnason et al. 2004; Price et al. 2005; Agnarsson and May-Collado 2008). Conversely, the phylogeny proposed by Geisler and Sanders (2003) supports delphinoid paraphyly with Phocoenidae and Delphinidae more closely related to Platanistoidea (Iniidae, Pontoporiidae, Lipotidae and Platanistidae, sensu Geisler and Sander 2003) than to Monodontidae. This proposed arrangement, however has had no additional support in the published literature.

Until now, the relationships of the three extant families of delphinoids (Delphinidae, Phocoenidae and Monodontidae) have been unclear, and neither morphological nor molecular studies have found a congruent phylogenetic resolution (de Muizon 1988; Heyning 1989; Waddell et al. 2000; Arnason et al. 2004).

The family Delphinidae is the most diverse among all living Cetacea and includes many divergent morphotypes and taxonomically and ecologically variable species (e.g. from the 1.7m *Cephalorhynchus* to the 10m *Orcinus* or from the blunt rostrum of *Grampus* to the long rostrum of *Delphinus*). Delphinids are geographically widespread in tropical, temperate and polar waters in both marine and freshwater habitats (Barnes 1990; LeDuc et al. 1999; Barnes 2002; LeDuc 2002). At present, 17 genera are recognized in the family (Table 1).

Seven genera are traditionally considered monotypic, seven have only two species and only *Cephalorhynchus* (n=4), *Stenella* (n=5) and *Lagenorhynchus* (n=6) contain more than two species each (Jefferson et al. 2008). Since the beginning of 2000 several new species of dolphins have been recognized in *Tursiops*, *Sotalia* and *Orcaella*, which were monotypic genera in which subspecies/populations were elevated to distinct species (Wang et al. 1999, 2000b, a; Monteiro-Filho et al. 2002; Beasley et al. 2005; Caballero et al. 2007). Similarly, there are strong evidence that other monotypic genera like *Orcinus* should will have more species recognized in the near future increasing significantly the number of species in the Delphinidae in the next few years (Berzin and Vladimirov 1983; Pitman and Ensor 2003; Pitman et al. 2007; LeDuc et al. 2008).

The diversity and present abundance of the Delphinidae is related to the explosive evolution that probably occurred in the Pliocene (c.a. 3-5 Ma ago). This period matches a global temperature decline (Zachos et al. 2001) that probably resulted in habitat changes and ecological replacement of kentriodontids by modern delphinids (Ichishima et al. 1994; Barnes 2002). The abrupt radiation of Delphinidae in the Pliocene is a notable phenomenon in cetacean evolution (Barnes 2002).

**Table 1 - Classification of the living Delphinids, to the level of subspecies or populations (Modified from Reeves et al. 2003)**

Family Delphinidae	Author	English Common name
<i>Cephalorhynchus commersonii commersonii</i>	(Lacépède, 1804)	Commerson's dolphin
<i>C. commersonii kerguelenensis</i>	Robineau et al. 2007	
<i>Cephalorhynchus eutropia</i>	Gray, 1846	Black dolphin
<i>Cephalorhynchus heavisidii</i>	(Gray, 1828)	Heaviside's dolphin
<i>Cephalorhynchus hectori hectori</i>	(P.-J. van Bénédén, 1881)	Hector's dolphin
<i>C. hectori mauui</i>	Baker et al. 2002	
<i>Delphinus capensis</i>	Gray, 1828	Longbeaked-common dolphin
<i>Delphinus delphis</i>	Linnaeus, 1758	Shortbeaked-common dolphin
<i>Delphinus tropicalis</i>	van Bree, 1971	Arabian-common dolphin
<i>Feresa attenuata</i>	Gray, 1874	Pygmy killer whale
<i>Globicephala macrorhynchus</i>	Gray, 1846	Short finned pilot whale
<i>Globicephala melas melas</i>	(Traill, 1809)	Long finned pilot whale
<i>G. melas edwardii</i>	(A. Smith, 1834)	
<i>G. melas melas</i>	(Traill, 1809)	
<i>Grampus griseus</i>	(G. Cuvier, 1812)	Risso's dolphin
<i>Lagenodelphis hosei</i>	Fraser, 1956	Fraser's dolphin
<i>Lagenorhynchus acutus</i>	(Gray, 1828)	Atlantic white sided dolphin
<i>Lagenorhynchus albirostris</i>	(Gray, 1846)	White beaked dolphin
<i>Lagenorhynchus australis</i>	(Peale, 1848)	Peale's dolphin
<i>Lagenorhynchus cruciger</i>	(Quoy and Gaimard, 1824)	Hourglass dolphin
<i>Lagenorhynchus obliquidens</i>	Gill, 1865	Pacific white-sided dolphin
<i>Lagenorhynchus obscurus obscurus</i>	(Gray, 1828)	Dusky dolphin
<i>L. obscurus fitzroyi</i>	(Waterhouse, 1838)	
<i>L. obscurus obscurus</i>	(Gray, 1828)	
<i>Lissodelphis borealis</i>	(Peale, 1848)	Northern right-whale dolphin
<i>Lissodelphis peronii</i>	(Lacépède, 1804)	Southern right-whale dolphin
<i>Orcaella brevirostris</i>	(Owen in Gray, 1866)	Irrawaddy dolphin
<i>Orcaella heinsohni</i>	Beasley et al. 2005	Australian snubfin dolphin
<i>Orcinus orca</i>	(Linnaeus, 1758)	Killer whale or Orca
<i>O. orca</i> (type A) <sup>1</sup>	(LeDuc et al. 2008)	
<i>O. orca</i> (type B) <sup>1</sup>	(LeDuc et al. 2008)	
<i>O. orca</i> (type C) <sup>1</sup>	(LeDuc et al. 2008)	
<i>Peponocephala electra</i>	(Gray, 1846)	Melon-headed whale
<i>Pseudorca crassidens</i>	(Owen, 1846)	False killer whale
<i>Sotalia fluvialis</i>	(Gervais and Deville, 1853)	Tucuxi
<i>Sotalia guianensis</i>	(P.-J. van Bénédén, 1864)	Estuarine dolphin
<i>Sousa chinensis chinensis</i>	(G. Cuvier, 1829)	Indo-Pacific hump-backed dolphin
<i>S. chinensis plumbea</i>	(Frere et al. 2008)	
<i>Sousa teuszii</i>	(Kükenthal, 1892)	Atlantic hump-backed dolphin
<i>Stenella attenuata attenuata</i>	(Gray, 1846)	Pantropical Spotted dolphin
<i>S. attenuata graffmani</i>	(Lönnberg, 1934)	
<i>S. attenuata subspecies A</i>	Perrin 1975	
<i>S. attenuata subspecies B</i>	Perrin 1975	
<i>Stenella clymene</i>	(Gray, 1846)	Clymene dolphin
<i>Stenella coeruleoalba</i>	(Meyen, 1833)	Striped dolphin
<i>Stenella frontalis</i>	(G. Cuvier, 1829)	Atlantic Spotted dolphin
<i>Stenella longirostris longirostris</i>	(Gray, 1828)	Spinner dolphin
<i>S. longirostris centroamericana</i>	Perrin, 1990	
<i>S. longirostris orientalis</i>	Perrin, 1990	
<i>S. longirostris roseiventris</i>	(Perrin et al. 1999)	
<i>Steno bredanensis</i>	(G. Cuvier in Lesson, 1828)	Rough-toothed dolphin
<i>Tursiops aduncus</i>	(Ehrenberg, 1833)	Indo-Pacific bottle-nosed dolphin
<i>T. aduncus</i> (Australia)	Natoli et al. 2004	
<i>Tursiops truncatus truncatus</i>	(Montagu, 1821)	Common-bottle-nosed dolphin
<i>T. truncatus ponticus</i>	Barabash-Nikiforov, 1940	Black Sea bottle-nosed dolphin
<i>T. truncatus</i> (Southern Australia)	Carloton et al. 2006	Victorian coastal bottlenose dolphin
<i>T. truncatus gephyreus</i>	Lahille 1908	South-Atlantic bottle-nosed dolphin

(1 LeDuc et al. 1999; Harlin-Cognato et al. 2007)

Until now, the classification of Delphinidae has remained almost the same as that used by Flower (1884) and True (1889) with few modifications (e.g. the use of subfamilies). Although several studies discuss the evolution and high-level relationships of odontocetes, few of them focused on Delphinidae using cladistic analyses (e.g. de Muizon 1988; Heyning 1989; Fordyce and Barnes 1994). As pointed out by LeDuc et al. (1999), most of the previous studies of dolphin relationships and evolution relied on examination of morphological characters, particularly of the skull (e.g. number of teeth, length of rostrum). Such approaches predated modern analytical techniques, including cladistics, and as a result even the alpha-level taxonomy of delphinids is still poor developed (LeDuc et al. 1999).

Fraser and Purves (1960) reported the first study of multiple cetacean species based on basicranium and the modifications of the air sinuses and the outer middle ear and provided one of the first comparative guides to the systematic classification of living Cetacea. In this study, for example, Fraser and Purves (1960) suggested that *Grampus griseus* closely resembles *Tursiops* and should be included in Delphininae rather than in Orcinae as suggested by previous authors. Also of note, Fraser and Purves (1960) separated Stenidae from the Delphinidae, and for the latter recognized Delphininae, Orcininae, Lissodelphinae, and Cephalorhynchinae. Kasuya (1973), exclusively used tympano-periotic bones to infer the relationships of some delphinids and other odontocetes suggested that in term of similarities *Delphinus*, *Lagenorhynchus*, *Stenella*, *Lissodelphis*, *Steno* and *Tursiops* show the higher similarity than the other genera. Although Kasuya (1973) placed Phocoenidae and Monodontidae outside Delphinidae in the dendrogram, he stated that they cannot be separated from Ocininae and Globicephalinae by similarity index. Mead (1975), in the study of soft facial

anatomy drew attention to the divergence of *Lagenorhynchus albirostris* from other species of *Lagenorhynchus*, and considered *Grampus* not closely related to the Delphininae.

In the studies of Muizon (1988) and Barnes (1990), morphological characters were used to identify some delphinid relationships and the monophyly of some genera was assumed but not tested. Moreover, these studies did not use cladistic methodology and the cladograms presented gave almost the same classifications seen in previous conventional works. Arnold and Heinsohn (1996) used cladistic methodology to resolve the position of the enigmatic *Orcaella brevirostris* within the Delphinoidea and, in contrast to Kasuya (1973), who identified *Orcaella* as close to *Delphinapterus*, unequivocally placed this dolphin in the family Delphinidae.

The most comprehensive and detailed work with the objective of resolving the delphinid systematics and classification was produced by LeDuc et al. (1999). In this work, a molecular phylogenetic analysis of the Delphinidae was performed utilizing the complete Cytochrome B of almost all species of delphinids currently recognized at the time. This work, although using a single gene, showed that some genera in Delphinidae are not monophyletic and the family Delphinidae should be re-arranged at the genus level (Table 2).

**Table 2 - Morphological and molecular Delphinidae classification\***

Morphological (not cladistic) (Perrin 1989)	Molecular (cladistic) (LeDuc et al. 1999)
<b>Subfamily Steninae</b>	<b>Subfamily Steninae</b>
<i>Steno bredanensis</i>	<i>Steno bredanensis</i>
<i>Sousa chinensis</i>	<i>Sotalia fluviatilis</i>
<i>Sousa teuszii</i>	<b>Subfamily Delphininae</b>
<i>Sotalia fluviatilis</i>	<i>Sousa chinensis</i>
<b>Subfamily Delphininae</b>	<i>Stenella clymene</i>
<i>Lagenorhynchus albirostris</i>	<i>Stenella coeruleoalba</i>
<i>Lagenorhynchus acutus</i>	<i>Stenella frontalis</i>
<i>Lagenorhynchus obscurus</i>	<i>Stenella attenuata</i>
<i>Lagenorhynchus obliquidens</i>	<i>Stenella longirostris</i>
<i>Lagenorhynchus cruciger</i>	<i>Delphinus delphis</i>
<i>Lagenorhynchus australis</i>	<i>Delphinus capensis</i>
<i>Grampus griseus</i>	<i>Tursiops truncatus</i>
<i>Tursiops truncatus</i>	<i>Lagenodelphis hosei</i>
<i>Stenella frontalis</i>	<b>Subfamily Lissodelphininae</b>
<i>Stenella attenuata</i>	<i>Lissodelphis peronii</i>
<i>Stenella longirostris</i>	<i>Lissodelphis borealis</i>
<i>Stenella clymene</i>	<i>Cephalorhynchus heavisidii</i>
<i>Stenella coeruleoalba</i>	<i>Cephalorhynchus hectori</i>
<i>Delphinus delphis</i>	<i>Cephalorhynchus eutropia</i>
<i>Lagenodelphis hosei</i>	<i>Cephalorhynchus commersonii</i>
<b>Subfamily Lissodelphininae</b>	<i>Sagmatias obscurus</i>
<i>Lissodelphis borealis</i>	<i>Sagmatias obliquidens</i>
<i>Lissodelphis peronii</i>	<i>Sagmatias cruciger</i>
<b>Subfamily Cephalorhynchinae</b>	<i>Sagmatias australis</i>
<i>Cephalorhynchus commersonii</i>	<b>Subfamily Globicephalinae</b>
<i>Cephalorhynchus eutropia</i>	<i>Feresa attenuata</i>
<i>Cephalorhynchus heavisidii</i>	<i>Peponocephala electra</i>
<i>Cephalorhynchus hectori</i>	<i>Globicephala melas</i>
<b>Subfamily Globicephalinae</b>	<i>Globicephala macrorhynchus</i>
<i>Peponocephala electra</i>	<i>Pseudorca crassidens</i>
<i>Feresa attenuata</i>	<i>Grampus griseus</i>
<i>Pseudorca crassidens</i>	<b>Subfamily Orcininae</b>
<i>Orcinus orca</i>	<i>Orcinus orca</i>
<i>Globicephala melas</i>	<i>Orcaella brevirostris</i>
<i>Globicephala macrorhynchus</i>	<b>Incertae sedis</b>
<b>Subfamily Orcaellinae</b>	<i>Lagenorhynchus albirostris</i>
<i>Orcaella brevirostris</i>	<i>Leucopleurus acutus</i>

\* Modified from LeDuc (2002)

One of the first studies that pointed *Lagenorhynchus* as non-monophyletic was performed by Cipriano (1997) in a molecular study which discussed antitropical distribution and speciation in the genus.

Recently, genetic data derived from two nuclear and two mitochondrial sequences have elucidated the relationships of the subfamily Lissodelphininae,



even given the limited number of species in the cladistic analysis (18 from 8 genera) (Harlin-Cognato and Honeycutt 2006). This work provides strong support for the monophyly of the subfamily Lissodelphinae as well as the polyphyly of the genus *Lagenorhynchus* in the traditional sense, in marked agreement with LeDuc et al. (1999). It is now widely accepted that at least the genera *Stenella* and *Lagenorhynchus* in the traditional sense are polyphyletic (Cipriano 1997; LeDuc et al. 1999; Perrin 2002a, c; May-Collado and Agnarsson 2006; Harlin-Cognato et al. 2007; Agnarsson and May-Collado 2008). Nevertheless, the “traditional” genera are still used as natural groups in some recent publications (e.g. Jefferson et al. 2008) and the most common classification currently in use (e.g. Perrin 1989; Mead and Brownell-Jr. 2005) is not in agreement with the current findings in Delphinidae phylogenies.

As pointed out by Fordyce (2006), there is still no consensus about subdivisions within the Delphinidae, and the current use of subfamilies is based around *Delphinus* (Delphininae), *Steno* (Steninae), *Lissodelphis* (Lissodelphinae), *Cephalorhynchus* (Cephalorhynchinae), and *Globicephala* (Globicephalinae). These groups were based mostly on phenetic judgments of only one line of evidence (e.g. body profile and color, nasofacial muscles, basicranial sinuses, tympanoperiotic, and skeletal form) and resulted in contradictory classifications (e.g. Flower 1884; Fraser and Purves 1960; Kasuya 1973; Mead 1975; Buchholtz and Schur 2004). In fairness to the authors cited, their aim appeared to be to identify and use monophyletic groups.

Although the relationships of several species of delphinids are still unclear, until now, a cladistic morphological study of the Delphinidae family has been called for but not yet actioned (LeDuc et al. 1999; Fordyce et al. 2002; LeDuc 2002). Due

to the rapid radiation of the family, some authors believe that it is very difficult to access the relationships of this family (Heyning 1989). Nevertheless, a morphological cladistic approach should help to explain relationships within the family Delphinidae, and should help to understand the complexity of the Superfamily Delphinoidea. Such work could help to elucidate the relationship of modern and fossil cetaceans, the evolutionary process and the phenomena of rapid radiation of the Delphinidae and the decline of some other groups (*e.g.* iniids and pontoporiids) (Fordyce and Barnes 1994).

In this study it is proposed a new morphological cladistic of delphinids, spanning the traditional subfamilies to best represent the range of dolphin morphotypes. The aim is to understand relationships between subfamilies and genus, and in turn help in elucidate the evolutionary ecology of living dolphins.

## MATERIAL AND METHODS

### Taxon selection

Morphological characters from 42 living odontocetes were coded by direct examination of specimens. Where possible, more than one specimen of each species was analyzed in order to understand the individual variation and possible polymorphism. Eight species of four different families were used as outgroups: one ziphiid, *Mesoplodon grayi* Von Haast, 1876, one iniid, *Inia geoffrensis* (Blainville, 1817), the two monodontids, *Delphinapterus leucas* (Pallas, 1776), and *Monodon monoceros* Linnaeus, 1758, and 4 out 6 phocoenids, *Neophocoena phocaenoides* (G. Cuvier, 1829), *Phocoenoides dalli* (True, 1885), *Phocoena phocoena* (Linnaeus, 1758) and *Phocoena spinipinnis* Burmeister, 1865. The outgroup

*Mesoplodon grayi*, was included to root all most parsimonious trees since Monodontidae and Phocoenidae are sister groups of Delphinidae forming Delphinoidea (de Muizon 1988; Gatesy et al. 1999; Cassens et al. 2000; Arnason et al. 2004; May-Collado and Agnarsson 2006). In the same manner, Iniioidea with Delphinoidea and Lipotoidea forms Delphinida (de Muizon 1988). For the ingroup, Delphinidae, all currently recognized species were used other than *Lagenorhynchus cruciger*, *Sotalia fluviatilis*, *Sousa teuszii* and *Orcaella heinsohni* (see Jefferson et al. 2008 for current recognized species [n=36]). Four taxa without full specific species status were also included: *S. attenuata graffmani*, *T. truncatus gephyreus*, *Sousa plumbea* and *Stenella frontalis* (Southwest Atlantic). The ingroup thus totals 35 terminals (31 species + 3 subspecies + 1 population). All of the 17 genera of Delphinidae were represented with at least one species.

Since hybridization between *S. frontalis* and *S. attenuata* was suspected to occur in the areas where two species had sympatric distribution and this may add noise in the phylogeny, in this study was chosen to use *S. frontalis* from south Brazil, because the two species had a parapatric distribution (see Moreno et al. 2005) . In the same way only *S. attenuata* from the Pacific were used.

Whenever possible, the semiafronts *sensu* (Hennig 1968) were sub-adults or adults with skulls not fully fused in order to clearly identify bone sutures. Moreover, specimens of different ages were used to better understand the ontogenetic variation of characters and to better understand the homology between them.

## Character selection

Characters derived from the skull, tympano-periotic, external morphology and color were examined in each taxon from the ingroup and outgroup wherever possible. Most of the characters were compiled from the literature (Mitchell 1970; Kasuya 1973; Barnes 1985; de Muizon 1987; de Muizon 1988; Fordyce 1994; Fordyce and Barnes 1994; Perrin et al. 1994b; Arnold and Heinsohn 1996; Daniels 1996; Luo and Marsh 1996; Messenger and McGuire 1998; Sanders and Barnes 2002; Geisler and Sanders 2003; Fajardo-Mellor et al. 2006). Several characters new to delphinids or modifications of characters previously published were also used. Osteological characters were coded using the skull orientation as shown in figure 1. All osteological characters (skull and tympano-periotic) were examined on original material through visits to collections and museums. Most of the external and coloration characters are an innovation of this study in Delphinidae phylogeny, but are based on previous studies on dolphin taxonomy and species-recognition (Fraser 1966; Perrin 1969; Fraser and Noble 1970; Mitchell 1970; Perrin 1972, 1975a; Perrin et al. 1981; Perrin et al. 1987; Amano et al. 1996; Perrin 1997, 2002b). For the most part, the characters were not coded nor used in a cladistic context. Further, most of them were used in previous descriptions of external morphology and need not be illustrated. The cladistic coding of such characters was based both on literature accounts (Mitchell 1970; Perrin et al. 1994a; Perrin 1997; Ridgway and Harrison 1999; Perrin et al. 2002; Jefferson et al. 2008) as well as photographs from both living and stranded delphinids.

Osteological terminology in new and established characters generally follows Mead and Fordyce (in press). When appropriate, the previous osteological

terminology for some characters was modified to match the use suggested by Mead and Fordyce (in press) (Figures 1 to 4).

### **Cladistic analysis and search strategies**

Morphological characters were entered into a character/taxon matrix in Mesquite Version 2.5 (Maddison and Maddison 2008). Polymorphic characters were included.

All characters were analyzed as unordered and were given equal weight. Character polarity was determined by an indirect method using the outgroup operational rule (Watrous and Wheeler 1981), with *Mesoplodon grayi* as root.

A phylogenetic analysis (Hennig 1966) was performed using the "parsimony ratchet" in Nona (Goloboff 1999) through the software Winclada (Version 1.00.08) (Nixon 1999, 2002). The "parsimony ratchet" is a method, known as a "New Technology", that randomly reweights characters to explore different tree islands (Nixon 1999). Twenty "ratchet" rounds of 500 iterations with 20% of the characters perturbed were performed, holding one tree in each iteration. This method performs heuristic searches by using multiple random addition sequences (RAS) followed by tree bisection and reconnection (TBR) branch swapping for finding an initial tree. The next step is to perform a random character reweighting in a certain percent of the characters. Then, the perturbed matrix is submitted to TBR again to search for shortest trees, and few trees are held in this process. The weighting is restored to the original situation and TBR is performed again, and the whole process is repeated many times. Parsimony ratchet is considered one of the best search methods for matrices with large data set taxa (Davis et al. 2005).

Other searches were performed in TNT (Goloboff 1999) using both "New Technology" and "Traditional Search" but no additional or shorter trees were found. Strict consensus calculations and character optimization were completed using Winclada. Character optimizations calculated in Winclada show only unambiguous changes. Tree support was calculated using the Goodman-Bremer support metric (a support of 1 means that the clade is absent in at least 1 tree only one step longer than the shortest tree) (Bremer 1988; Grant and Kluge 2008). The Goodman-Bremer support metric was accomplished by generating suboptimal trees up to 15 steps longer than the shortest and then calculating the support in NONA (Goloboff 1999).

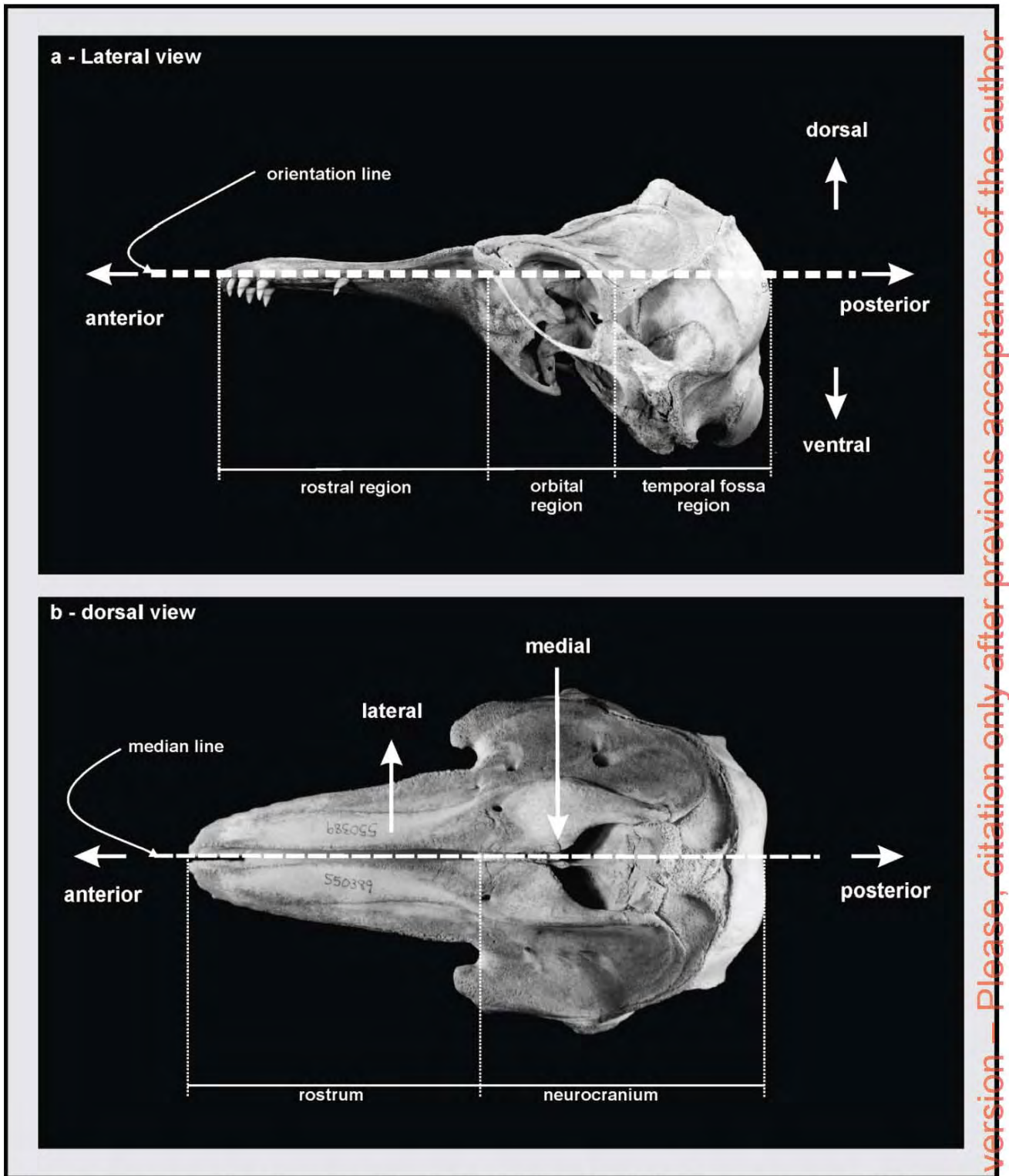


Figure 1 - The term of the orientation of the skull in dolphins. The skull of *Feresa attenuata* (USNM 550389, condylobasal length=CBL= 350.16). a - lateral view (left side), b - dorsal view.

Preliminary version – Please, citation only after previous acceptance of the author

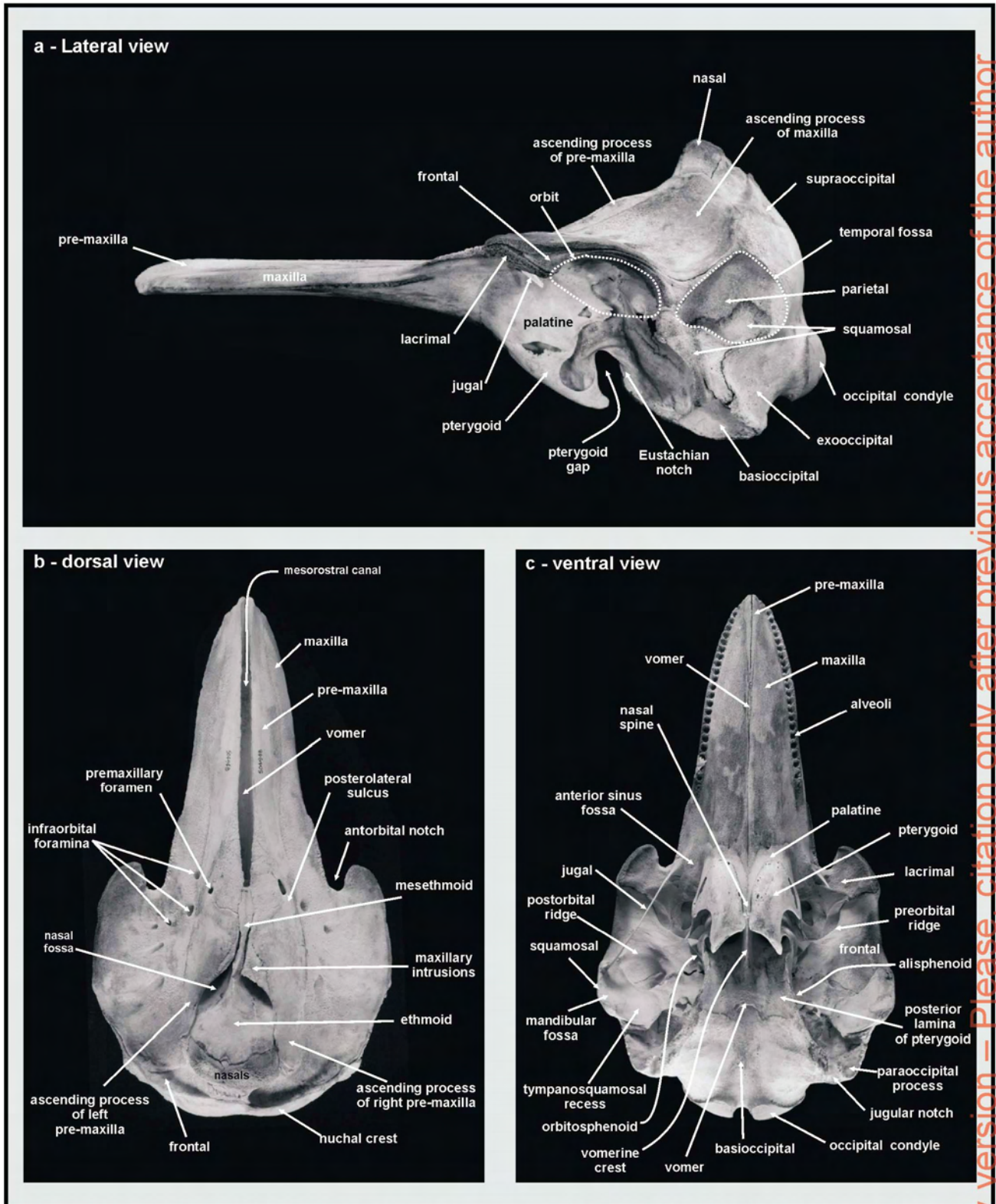


Figure 2 - The skull of dolphin with osteological nomenclature. *Peponocephala electra* (USNM 504948, CBL=350.16). a - lateral view, b - dorsal view, c - ventral view.

Preliminary version – Please, citation only after previous acceptance of the author



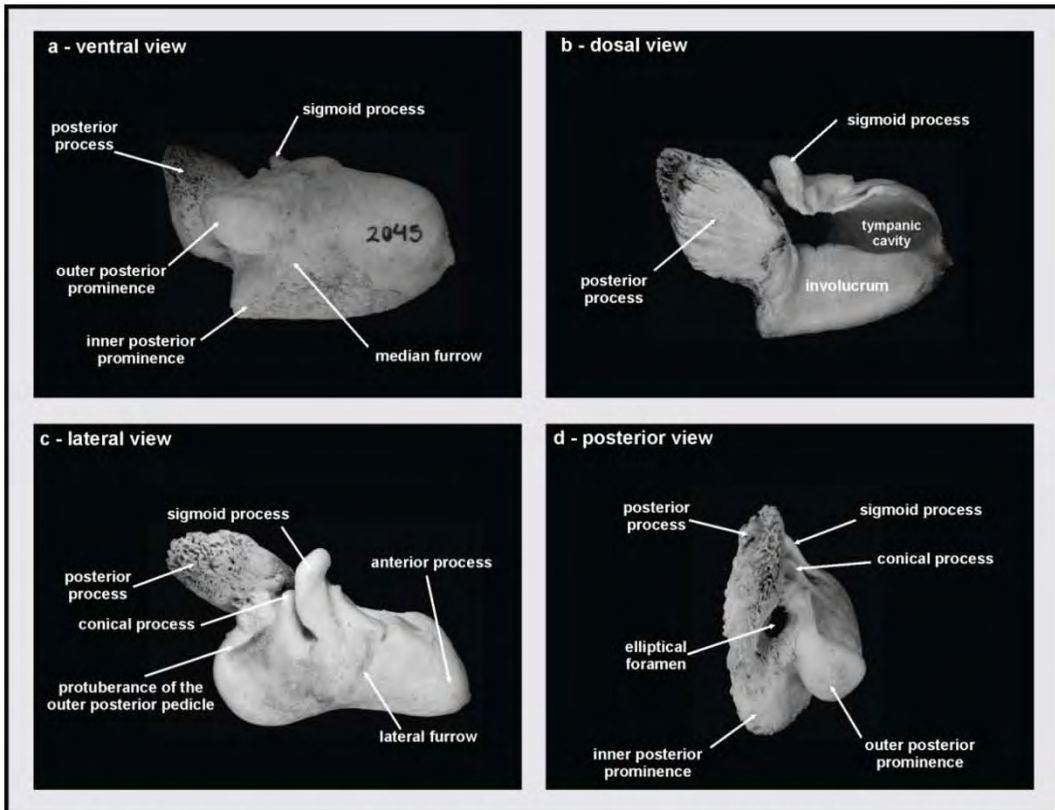


Figure 3 - Right tympanic bone with osteological nomenclature. *Pseudorca crassidens* (NMNZ 2045, tympanic length=52.08). a - ventral view, b - dorsal view, c -lateral view, d - posterior view.

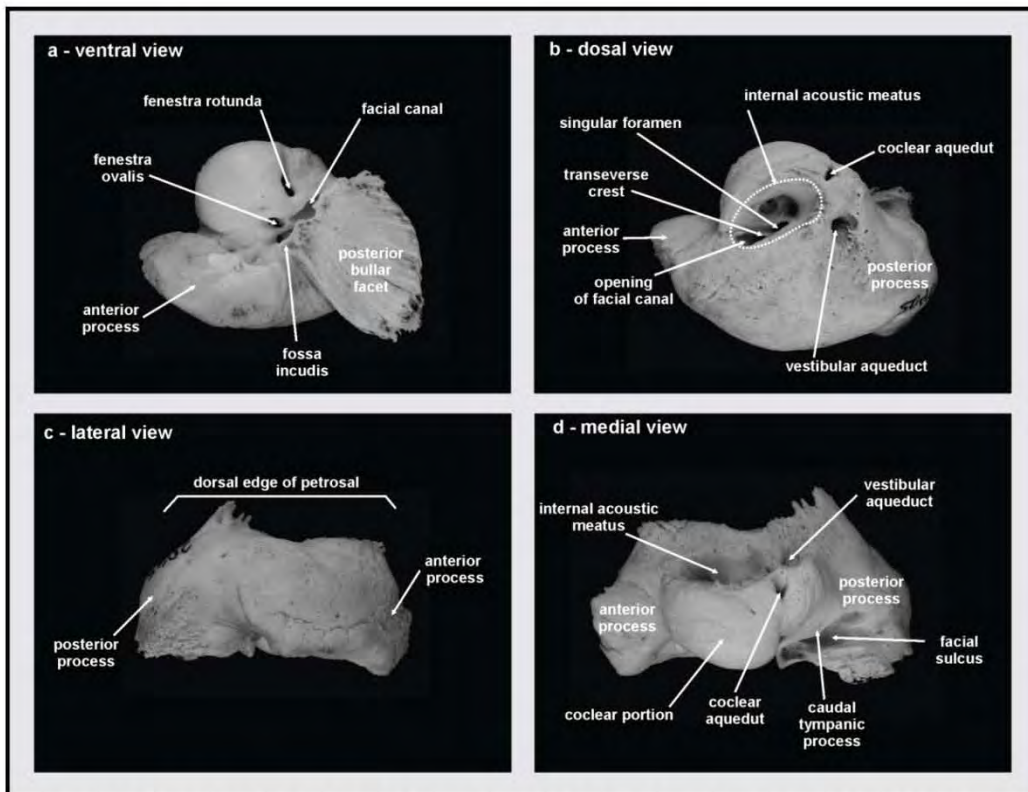


Figure 4 - Right petiotic bone with osteological nomenclature. *Pseudorca crassidens* (NMNZ 2045, petrosal length=49.08). a - ventral view, b - dorsal view, c -lateral view, d - posterior view.

All material was examined through visit of the following museum and collections:

**GEMARS** - Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Porto Alegre, Brazil;

**GEMM-Lagos** - Grupo de Estudos de Mamíferos Marinhos da Região dos Lagos, Rio de Janeiro, Brazil;

**MPEG** - Museu Paraense Emílio Goeldi, Belém, Brazil;

**NMNZ** - National Museum of New Zealand, Wellington, New Zealand;

**OU** - Otago University, Geology Department, Dunedin, New Zealand;

**USNM** - National Museum of Natural History, Washington, United States.

## **Delphinidae**

*Steno bredanensis*: GEMARS 0324, 0576, 0771. *Sotalia guianensis*: GEMM-lagos 084, 089. *Sousa chinensis*: USNM 258859. *Sousa plumbea*: USNM 550939, 550941. *Stenella clymene*: GEMARS 0795. *Stenella coeruleoalba*: GEMARS 0370, 0593, 1084, 1240. *Stenella frontalis* (north): USNM 550748. *Stenella frontalis* (south): GEMARS 0453, 0599, 0823. *Stenella attenuata*: USNM 395389, 487116. *Stenella a. graffmani*: USNM 261427, 261430, 261434. *Stenella longirostris*: USNM 504170, 504440. *Delphinus* spp.: GEMARS 0221, 1194, 1241. *Tursiops truncatus*: GEMARS 0916, 0928. *Tursiops t. gephyreus*: USNM 550945, 550946, 550948. *Tursiops gephyreus*: GEMARS 0041, 0220. *Lagenodelphis hosei*: GEMARS 0435, 0486, 0488. *Lissodelphis peronii*: USNM 501198 and NMNZ 1845. *Lissodelphis borealis*: USNM 286872, 550026. *Cephalorhynchus heavisidii*: USNM 550067. *Cephalorhynchus hectori*: OU 21819. *Cephalorhynchus eutropia*: USNM 21167, 395374. *Cephalorhynchus commersonii*: USNM 550156, 550449. *Sagmatias obscurus*: USNM 550740, 550745, 550757. *Sagmatias obliquidens*: USNM 290643, 550497, 550834. *Sagmatias australis*: USNM 395344, 395351. *Feresa attenuata*: USNM 504916, 550389. *Peponocephala*

*electra*: USNM 504505, 504948. *Globicephala melas*: USNM 571348, 571557. *Globicephala macrorhynchus*: USNM 500213, 550423. *Pseudorca crassidens*: GEMARS 0092, 0100. *Grampus griseus*: USNM 504126, 571602. *Orcinus orca*: GEMARS 0139, 0366. *Orcaella brevirostris*: USNM 199743. *Lagenorhynchus albirostris*: USNM 550224. *Leucopleurus acutus*: USNM 504763.

### **Monodontidae**

*Monodon monoceros*: USNM 267958, 267959. *Delphinapterus leucas*: USNM 15446, 23105, 571021.

### **Phocoenidae**

*Phocoena spinipinnis*: GEMARS 0633. *Phocoena phocoena*: USNM 572012, 572783, 572786. *Phocoenoides dalli*: USNM 276064, 286865. *Neophocoena phocoenoides*: USNM 240001, 550473.

### **Iniidae**

*Inia geoffrensis*: MPEG 4610, 12756, 38764; GEMARS 0957.

### **Ziphiidae**

*Mesoplodon grayi*: GEMARS 1276.

## RESULTS

### Character description

This is first attempt to produce a cladistic analysis of the family Delphinidae using morphology with a comprehensive data set (skull, tympanoperiotic, external morphology and coloration). Some characters are new in the sense that they were never used before in a cladistic analysis to resolve the phylogeny of Delphinidae. For all new characters detailed descriptions are given below. Approximately 60 of the 147 characters are original to this work.

Some characters are modifications of characters proposed earlier by other authors and in these cases the reference is cited. Many characters are modified, mostly by the addition/deletion of some aspects, or by a redescription of the state(s). In few cases, the characters were derived from features previously published but not used in a cladistic sense. For the external morphology and coloration most of characters used here were never used in a cladistic sense. Mostly, of those were characteristic used to diagnose the different species in field guides or papers.

**1 - Facial plane:** (0) almost flat or convex; (1) strongly concave or concave. (Heyning 1989).

**10 - Tooth shape:** (0) spatulate; (1) conical; (2) flat. (Heyning 1989)

**20 - Dorsal edge of orbit relative to lateral edge of rostrum (left side)** - (0) in the same level of maxilla; (1) below the level of the edge of rostrum; (2) in the

same level of the toothrow; (3) In the same level of premaxilla; (4) above the premaxilla. (Modified from Geisler and Sanders (2003), character 47).

**The character list was deleted in order to preserve the unpublished data.**

### **Cladistics**

The analysis of the 147 character matrix with 43 taxa resulted in four equally most parsimonious trees with a length of 1034 steps. A strict consensus of the four trees resulted in only two polytomies. The first involves the relationships of the three families in Delphinoidea (Monodontidae, Phocoenidae and Delphinidae), while the other involves the relationships of *Lagenorhynchus acutus* in the Delphininae. The monophyly of the three families of Delphinoidea was recovered. The families Monodontidae and Phocoenidae were supported by five exclusive synapomorphies each. The family Delphinidae was supported by four exclusive synapomorphies.

### **Taxonomic account**

#### **Family diagnoses**

##### Family Monodontidae GRAY, 1821

Monodontidae is diagnosed by the following synapomorphies: facial plane almost flat or convex (ch. 10, state 0), distal part of the rostrum is straight or square (ch. 2, state2), the alignment of the posteriormost point of hamular process of pterygoid is few mm posterior to postorbital process (ch. 83, state 3), the level of dorsal margin of occipital condyle almost in line with ventral margin of temporal fossa (ch. 96, state 2) and a presence of a weak eye spot (ch. 137, state 2).

### Family Phocoenidae GRAY, 1825

Phocoenidae is diagnosed by the following synapomorphies: presence of premaxillary bosses (ch. 8, state 0), tooth spatulate (ch. 10, state 0), the posterior end of both premaxillae surrounding the narial openings are the same size and thin (ch. 58, state 1), the pterygoid sinus fossa in medial portion of alisphenoid is deep and extends medially (ch. 88, state 2), the posterior process of petrosal is thinner distally (ch. 110, state 1), the posterior process of tympanic possesses very few lamination or are smooth (ch. 120, state 1).

### Family Delphinidae GRAY, 1821

Delphinidae is diagnosed by the following synapomorphies: the posterolateral from premaxillary foramen is absent or very weak (ch. 44, state 3), the right premaxilla extended distinctly farther posteriorly than left (ch. 52, state 1), the posterior end of both premaxillae surrounding the narial openings are of different sizes, with the right being larger than left (ch. 58, state 2), the posterodorsal edge of stapedial muscle fossa is located dorsal or well dorsal to fenestra rotunda.

### Subfamily diagnoses

#### Subfamily Orcininae WAGNER, 1846

Type genus: *Orcinus* Fitzinger, 1860

Species included:

*Orcinus orca* (Linnaeus, 1758)

*Pseudorca crassidens* (Owen, 1846)

*Globicephala macrorhynchus* Gray, 1846

*Globicephala melas* (Traill, 1809)

Diagnosis: the subfamily Orcininae is diagnosed by the following no exclusive synapomorphies: preorbital ridge absent (or covered by lacrimal) (ch. 33, state 2),

a concave dorsal edge of zygomatic process (64, state 1) and an intermediate temporal fossa size in relation to neurocranium (ch. 68, state 1).

**Subfamily Orcaellinae** NISHIWAKI IN RIDGWAY, 1972

Type genus: *Orcaella* Gray, 1866

Species included:

*Grampus griseus* Gray, 1828

*Orcaella brevirostris* (Owen in Gray, 1866)

*Orcaella heinsohni* Beasley, Robertson, and Arnold 2005

*Feresa attenuata* Gray, 1874

Diagnosis: the subfamily Orcaellinae is diagnosed by the following no exclusive synapomorphies: the mandibular notch is open (ch. 15, state 0); the dorsal edge of orbit is in the same level as the premaxilla (ch. 20, state 3), the lacrimal is restricted below maxilla (ch. 22, state 1), the division between the tympanosquamosal recess and the falciform process is smooth or absent (ch. 67, state 2), the level of dorsal margin of occipital condyle is below the level of lower margins of temporal fossa (ch. 96, state 1), the shape of the rostrum is blunt or rounded (ch. 128, state 4).

**Subfamily Peponocephalinae** - New Subfamily

Type genus: *Peponocephala* Nishiwaki and Norris, 1966

Species included:

*Peponocephala electra* (Gray, 1846)

Diagnosis: the subfamily Peponocephalinae is diagnosed by the following no exclusive synapomorphies: the dorsal edge of orbit relative to lateral edge of rostrum is above the premaxilla (ch. 20, state 4), the dorsal projection of mesethmoid between premaxilla and maxilla is above the surface of premaxillae

(ch. 40, state 1), possesses a weak division between the tympanosquamosal recess and the falciform process (ch. 67, state 1), the maxillary process of palatine invades the anterior sinus fossa laterally (ch.71, state 4), the presence of a small medial orbital fossa in the orbital region (ch. 82, state 1), the fundus of the internal acoustic meatus is a funnel-like (ch.102, state 1), presence of the accessory ridge of facial sulcus (ch. 114, state 0), and by the absence of the lateral furrow of ectotympanic bulla (ch. 117, state 2).

### **Subfamily Lagenorhynchinae - New Subfamily**

Type genus: *Lagenorhynchus* Gray, 1846

Species included:

*Lagenorhynchus albirostris* Gray, 1846

Diagnosis: the subfamily Lagenorhynchinae is diagnosed by the following no exclusive synapomorphies: the presence of a U-shaped palatine/maxilla suture (ch. 6, state 1), the lacrimal wraps a little around anterior edge maxilla (ch.22, state 2), the ventromedial edge of internal opening of infraorbital foramen is formed by maxilla (ch. 28, state 1), the premaxillae anterior to nasal openings is convex (ch. 41, state 0), the maxilla, lateral to facial fossa, at the middle point of the orbit is equal in thickness or thicker than frontal (ch. 48, state 0), the right anterior maxillary foramen is anterior or in line with the rostrum base (ch. 55, state 1), the glenoid process of squamosal is medium (ch. 64, state 1), the lateral lamina of pterygoid extends well posteriorly and touch the falciform process (ch. 74, state 1), the posterior point of hamular process of pterygoid is in transverse line with the orbit (ch. 83, state 1), posterior edge of the hypoglossal foramen is higher than the anterior or both edges are at the same level (ch. 94, state 1 and 2), presence of a



long jugular notch (ch. 95, state 0), a long facial nerve sulcus of periotic (ch. 108, state 1), a weak protuberance on medial edge of the Internal acoustic meatus (ch. 111, state 2), distal end of posterior process of ectotympanic thicker but not hypertrophied (ch. 121, state 1), a weak protuberance of the outer posterior pedicle of tympanic (ch. 122, state 1), presence of a weak transversal ridge on inside of tympanic (ch. 124, state 1), eye or lip to-flipper stripe present (ch. 139, state 1) and the absence of a peduncle saddle (ch. 145, state 1).

### **Subfamily Lissodelphininae** FRASER and PURVES, 1960

Type genus: *Lissodelphis* Gloger, 1841

Species included:

*Lissodelphis peronii* (Lacepede, 1804)

*Lissodelphis borealis* Peale, 1848

*Gen nov.* “unnamed” *obscurus* (Gray, 1828)

*Gen nov.* “unnamed” *obliquidens* Gill, 1865

*Cephalorhynchus cruciger* (Quoy and Gaimard, 1824) – new combination

*Cephalorhynchus australis* (Peale, 1848) – new combination

*Cephalorhynchus commersonii* (Lacépède, 1804)

*Cephalorhynchus eutropia* (Gray, 1846)

*Cephalorhynchus heavisidii* (Gray, 1828)

*Cephalorhynchus hectori* (P.-J. van Bénédén, 1881)

Diagnosis: the subfamily Lagenorhynchinae is diagnosed by the following non-exclusive synapomorphies: the mandibular notch is open (ch. 15, state 0), a presence of long projection of posteromedial process of lacrimal (ch. 29, state 1), the posterior right infraorbital foramen is located in intermediate position (ch. 38, state 1), a presence of an excavated peribullary sinus fossa on basioccipital (ch. 78, state 2) and for the presence of a well developed medial orbital fossa at orbital region (ch. 82, state 0).

**Genus “unnamed”, gen. nov.**

Type species: *Delphinus (Grampus) obscurus* Gray, 1828,

Species included:

Gen nov. '*unnamed*' *obscurus* (Gray, 1828)

Gen nov. '*unnamed*' *obliquidens* (Gill, 1865)

Diagnosis: The Genus “unnamed” is diagnosed by the following non-exclusive synapomorphies: the presence of a U-shaped palatine/maxilla suture (ch. 6, state 1), the frontal/maxilla suture at middle of supraorbital process is angled (ch. 21, state 1), and the presence of a long facial sulcus of periotic (ch. 108, state 1). The species in the new genus are distinguished from all other delphinids by the presence of a ventral flank blaze (sensu Mitchell, 1970).

#### **Subfamily Steninae** FRASER AND PURVES 1960

Type genus: *Steno* Gray, 1846

Species included:

*Steno bredanensis* (G. Cuvier in Lesson, 1828)

*Souza Chinensis* (Osbeck, 1765)

*Souza teuszi* (Kükenthal, 1892)

*Souza plumbea* (G. Cuvier, 1829)

*Sotalia fluviatilis* (Gervais and Deville, 1853)

*Sotalia guianensis* (P.-J. van Bénédén, 1864)

Diagnosis: the subfamily Steninae is diagnosed by the following non-exclusive synapomorphies: the dorsal edge of orbit relative to lateral edge of rostrum is above the premaxilla (ch.20, state 4), the dorsal surface of the lacrimal is an inverted T (ch. 25, state 1), there is a very long postorbital process (ch. 31, state 1) and the maxilla on dorsal surface of skull does not contact supraoccipital posteriorly because the two bones are separated by a wide expanse of frontal (ch. 61, state 1).

## **Subfamily Delphininae** FRASER and PURVES, 1960

Type genus: *Delphinus* Linnaeus 1758

Species included:

*Stenella attenuata* (Gray, 1846)

*Tursiops frontalis* (G. Cuvier, 1829) – New Combination

*Tursiops truncatus* (Montagu, 1821)

*Tursiops aduncus* (Ehrenberg, 1833)

*Delphinus delphis* Linnaeus, 1758

*Delphinus capensis* Gray, 1828

*Delphinus tropicalis* van Bree, 1971

*“Stenella” longirostris* (Gray, 1828)

*Leucopleurus acutus* (Gray, 1828)

*Lagenodelphis hosei* Fraser, 1956

*Lagenodelphis clymene* (Gray, 1850) – New Combination

*Lagenodelphis coeruleoalbus* (Meyen, 1833) – New Combination

Diagnosis: the subfamily Delphininae is diagnosed by the following non-exclusive synapomorphies: a contact along the rostrum of the dorsomedial surface of premaxillae (ch. 3, state 2), there is no gap of zygomatic process of squamosal and postorbital process (ch. 14, state 0), the anterior sinus fossa is intermediate (ch. 70, state 2), a small alisphenoid fossa for peribullary sinus (ch. 77, state 1), the presence of a protuberance on medial edge of the Internal acoustic meatus (ch. 111, state 1), a small fissure between the fossa incudis and the distal opening of facial canal (ch. 113, state 2), the presence of a eye or lip to-flipper stripe (ch. 139, state 1) and the presence of the peduncule saddle (ch. 145, state 1).

## **DISCUSSION**

This study recovered some of the previous findings of other authors based on morphology or molecular analyses (e.g. Mead 1975; Muizon De 1988; LeDuc et al. 1999; Price et al. 2005; May-Collado and Agnarsson 2006). For example, the

clade that shows close affinities between *Lissodelphis*, *Cephalorhynchus* and the Gen nov. “unnamed” [subfamily Lissodelphininae], the clade of *Steno*, *Sotalia* and *Sousa* [subfamily Steninae] and the closed affinities between *Stenella*, *Tursiops* and *Delphinus* [subfamily Delphininae]. Although some congruence was found, there are some novelties in the morphologic analysis that support the polyphyly of the “blackfish”, *Stenella*, and *Lagenorhynchus* and support other relationships that are in conflict with current classification for some genera. Some results bring additional support for changing the current classification, while others should be taken carefully because there is not strong evidential support or never were appointed in the literature before.

The most comprehensive pioneering studies on the classification of the family Delphinidae were done by Flower (1884) and True (1889) (Rice 1998). As this is the first morphological cladistic analysis of delphinids, the main findings of this study will be compared with the recent cladistic phylogeny of LeDuc et al. (1999) and with the phenetic classification suggested by others (Fraser and Purves 1960; Kasuya 1973; Mead 1975; Barnes 1985; Muizon De 1988; Perrin 1989; Barnes 1990). Also, some recent molecular phylogenetic analysis will be compared. Although the main goal of the authors was not to resolve the phylogeny of the Delphinidae they used a large number of delphinids in their analysis (Price et al. 2005; May-Collado and Agnarsson 2006; Montgelard et al. 2007; Agnarsson and May-Collado 2008) (Figure 5).

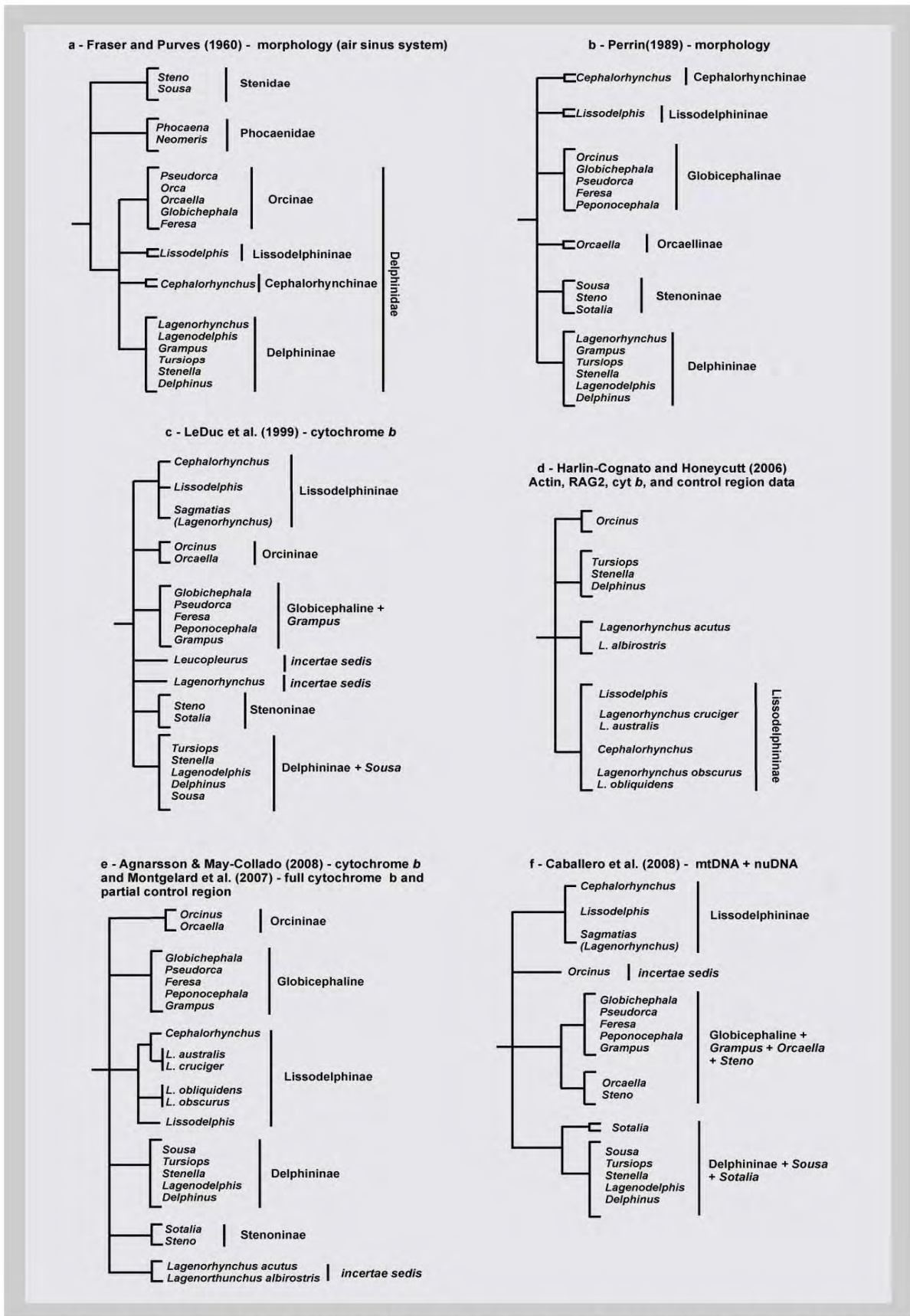


Figure 5 - Classifications of Delphinidae family at genus and subfamily levels. Note that the classifications are schematic in this illustration to show the suggested families and do not intend to depict relationships among the subfamilies. In the classification e, the polyphyly of *Cephalorhynchus* and *Lagenorhynchus* is exposed. (Modified from Caballero et al. 2008).

## Delphinid phylogeny: proposal for classification changes

### Orcinae, Orcaellinae and Peponocephalinae

In this study it is clear that Globicephalinae sensu Muizon (1988) is polyphyletic and may be divided in at least three different taxa. Orcinae (*Orcinus*, *Pseudorca* and *Globicephala*) form a clade with Bremer support 2. This was the most basal branch in the phylogeny and it thus forms the sister group of all other delphinids. The other “blackfish” clade, Orcaellinae (*Orcaella*, *Feresa* and *Grampus*) with Bremer support 3 is the next more-crownward sister group of all other delphinids with one exclusive synapomorphy (a well defined rostrum constriction at *linea terminalis rostrae*, character 5), and of four additional non exclusive synapomorphies. The third group is the new subfamily Peponocephalinae.

This new arrangement differs from most previous phylogenies based on genetic data that nested all the “blackfish” together, other than *Orcinus* and *Orcaella*.

Although the morphological phylogeny presented here is incongruent with the previous works, this study has good support for the relations depicted here. Similar findings linking *Pseudorca* and *Orcinus* with evidence of an early origin of this clade were supported by vertebral osteology (Buchholtz and Schur 2004). Fraser and Purves (1960), also noted that the sinus system in *Orcinus* is similar to *Pseudorca* with certain modifications, but they also included *Orcaella* in the Orcinae. Those authors also showed that *Feresa* is linked with *Orca* in some extent, but pointed out that *Feresa* bears resemblance to *Grampus* also.

The species formerly classified in the Globicephalinae/Orcininae clade are similar only in external morphology, with most of the animals presenting a blunt head without defined beak and dark bodies with non discernible color pattern (Reeves et al. 2002), characters that probably are plesiomorphic. The skull morphology is very diverse and several morphotypes are recognized. For example, the skull of *P. electra* resembles much more some Delphininae than a Globicephalinae, this species has many more teeth (20 to 26 pairs in both upper and lower jaws), than other members of “blackfish”, also the tip of the rostrum is pointed instead of rounded, the dorsal lamina of the pterygoid is reduced, and the lateral edge of the middle sinus is deckled-edged, a condition absent in all blackfishes. This close affiliation was also supported by facial anatomy and skeletal morphology (Mead 1975; Buchholtz and Schur 2004). In this sense given the similarities in the skull anatomy, it is not surprising that *Peponocephala*, is a sister group of Lagenorhynchinae, Lissodelphininae, Steninae and Delphininae.

Also, it is worthy of mention that the Orcininae as proposed by LeDuc (1999) (*Orcinus* + *Orcaella*), was consistent but with low support. In contrast, in the phylogeny of Caballero et al. (2008), *Steno* nested with *Orcaella* and Globicephalinae (*Globicephala*, *Pseudorca*, *Feresa*, *Grampus*, and *Peponocephala*). Differences between different analyses show that sometimes molecular results should be taken with caution.

The classification presented here has a relatively good support showing that the former Globicephalinae is not monophyletic. The Orcininae clade has Bremer support of 2 and the Orcaellinae Bremer support 3. Moreover, the Orcaellinae is more closely related with *Peponocephala* and other delphinids than with Orcininae.

## Lissodelphininae and Lagenorhynchinae

The subfamily Lissodelphininae (sensu LeDuc et al. 1999) is one of the largest subfamilies in Delphinidae, with 10 distinct species distributed in at least three genera (*Lissodelphis*, *Cephalorhynchus* and Gen nov. “unnamed”). This clade is supported in this study by five non-exclusive morphological synapomorphies (one from the mandible and four from the skull) and had strong support in the molecular phylogenies with both nuclear and mitochondrial sequences (LeDuc et al. 1999; Harlin-Cognato and Honeycutt 2006; Agnarsson and May-Collado 2008). In this sense, the Lissodelphininae should be kept as a distinct subfamily but some rearrangements should be implemented. Although, Lissodelphininae is monophyletic, the recent findings (Cipriano 1997; LeDuc et al. 1999; LeDuc 2002; May-Collado and Agnarsson 2006; Harlin-Cognato et al. 2007; May-Collado et al. 2007a, b; Agnarsson and May-Collado 2008) and the phylogeny presented here, suggest that former genus *Lagenorhynchus*, as used, for example, by LeDuc et al. (1999), should be split in at least four different groups. As suspected initially by LeDuc et al. (1999) and supported by the former molecular studies and now with morphology, *Cephalorhynchus australis* and *Cephalorhynchus cruciger* are more closed related to *Cephalorhynchus* than Gen nov. “unnamed” *obliquidens* and Gen nov. “unnamed” *obscurus*.

This study shows that *Cephalorhynchus australis* and *Cephalorhynchus cruciger* ought to be transferred to *Cephalorhynchus* as previously suggested (May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008). Transferring these two species will make *Cephalorhynchus* monophyletic with six species.



*Cephalorhynchus australis* share six non-exclusive morphological synapomorphies with the genus *Cephalorhynchus* and form a clade. For example, in *C. australis* and *Cephalorhynchus* the elliptical foramen of the tympanic is absent, even though this feature occurs in other taxa (e.g, *Globicephala*, *Feresa*, *Orcaella*) under Lissodelphininae this feature only occurs in *Cephalorhynchus* and *C. australis*. In this study was not possible to examine a complete skull of *C. cruciger* but, it is the sister species of *C. australis* as pointed out by the recent molecular phylogenies with nuclear and mitochondrial sequences (LeDuc et al. 1999; Harlin-Cognato and Honeycutt 2006; May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008). The acoustic data also support the close relationship between *Cephalorhynchus* and *C. australis* since unlike among dolphins, these five species do not whistle (not publish data is known on acoustic behavior of *L. cruciger*) (but see May-Collado and Agnarsson 2006; and May-Collado et al. 2007a).

For the other two species of *Lagenorhynchus*, placed in *Sagmatias* by LeDuc et al. (1999), the establishment of a new genus is proposed (Gen nov. "unnamed") as suggested by Harling-Cognato and Honeycutt (2006), since there appears to be no available name. *Lagenorhynchus obliquidens* Gill, 1865 was originally described as a species of *Lagenorhynchus* Gray 1864. *Lagenorhynchus obscurus* (Gray 1828) was described as *Delphinus (Grampus) obscurus* and later was placed in *Clymenia* Gray 1868. All later descriptions of these species were made under a different genus (e.g. *Delphinus*, *Lagenorhynchus*, *Prodelphinus*, *Tursio*). Both species are, in the cladistic analysis, separate from the type species of the genus, *L. albirostris* Gray 1846.

The inclusion of Gen nov. “*unnamed*” *obliquidens* and Gen nov. “*unnamed*” *obscurus* in a new genus is supported by the difference in distribution, biogeography and evolutionary patterns of the two species. The two species share one exclusive and three non exclusive synapomorphies. The exclusive synapomorphy is the presence of a ventral flank blaze (sensu Mitchell 1970). The other two non exclusive synapomorphies are in the skull and one in the periotic, showing more than one line of evidence is supporting this cluster.

The fossil record is sparse for many species-level lineages in the crown-Delphinidae, and that the divergence time between Gen nov. “*unnamed*” *obscurus* and Gen nov. “*unnamed*” *obliquidens* from *C. australis* and *C. cruciger* based on “hard” (fossil) evidence is uncertain. Molecular estimates, however, suggest a divergence time between the two sister species as geologically recent, around 1.0Ma (million years ago) (0.74-1.36) during the Pleistocene, associated with an ancestral splitting into the two antitropical species (Hare et al. 2002). In the same way but with an earlier prevision, the divergence was appointed at approximately 2 Ma (1.3-2.9) with a possible north hemisphere ancestor splitting off the southern hemisphere species via an equatorial transgression through the Indo-Pacific followed by an expansion into the Atlantic (reaching afterwards Africa and South America). This event with the subsequent warming of the Eastern Equatorial Pacific resulted in an anti-tropical distribution of these two species by isolation of a founder population in the cooler Indo-Pacific (Harlin-Cognato et al. 2007). The previous evolutionary pattern is quite different from the one we could predict for *Cephalorhynchus australis* and *Cephalorhynchus cruciger*. In this sense, it may be preferable to place the two antitropical species in their own genus to preserve the possible unique evolutionary pattern.

The evolution pattern of *Lissodelphis* also deserves new interpretations. As above, a similar model of Gen nov. “unnamed” *obscurus* and Gen nov. “unnamed” *obliquidens* may be appropriate. The basal position and early divergence from other Lissodelphininae was proposed by Pichler et al. (2001). In this study the genus *Lissodelphis* also occupies a basal position in Lissodelphininae, but it is not monophyletic with *L. borealis* more closely related to Cephalorhynchus and the Gen nov. “unnamed”. Intriguingly, the two species of *Lissodelphis* share the apparently unique feature of lack of dorsal fin.

As *Lagenorhynchus albirostris* Gray 1846 is the type species of *Lagenorhynchus* it is appropriate to use a new subfamily (Lagenorhynchinae) for this monotypic genus already suggested by Agnarsson and May-Collado (2008).

*Lagenorhynchus albirostris* has 18 non-exclusive morphological autapomorphies that support to a subfamilial rank. Moreover, molecular phylogeny suggests that this species diverged from other delphinids much earlier, in the late Miocene about 5.8-9.5MY

### **Steninae**

Based on morphology, the genera *Steno* and *Sotalia* were classified together by Flower (1884), who believed *Sousa* to be closed related with *Sotalia*. Fraser and Purves (1960) placed *Steno* and *Sousa* outside Delphinidae in the family Stenidae but still in Delphinoidea. Subsequently, Mead (1975) and Perrin (1989) grouped them in the same sub-family based also on morphology. Conversely, molecular suggested that only *Steno* and *Sotalia* form a monophyletic group and *Sousa* is more closely related with Delphininae (LeDuc et al. 1999; May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008). In a recent attempt to

resolve the molecular systematic relationships of *Sotalia*, a molecular study with both mtDNA and nuDNA (Caballero et al. 2008) did not resolve the problem, suggesting that the subfamily Steninae (sensu Perrin 1989) is polyphyletic. Surprisingly, in this same study, the combined data set (mtDNA+nuDNA) linked *Steno* with members of Globicephalinae with a high bootstrap and branch support values (Caballero et al. 2008).

In this study, however, it was found a well supported Steninae, with *Sousa* deeply nested in the subfamily clade. Supported by one exclusive synapomorphy and Bremer support 1, this clade is a sister group of the Delphininae (*Delphinus*, *Lagenodelphis*, *Lagenorhynchus acutus*, *Stenella* and *Tursiops*). This is in contrast to the phylogeny proposed by LeDuc et al. (1999) and others based on molecular data that proposed *Sousa* is nested within Delphininae.

The molecular phylogenies did not in resolve this subfamily suggesting that the classification proposed by Caballero et al (2008) may be unrealistic. The strong link between *Sousa* and *Sotalia* (Bremer support 5 and four non exclusive synapomorphies) recovered by morphology indicates that Steninae is a monophyletic group. Pending more evidence on whether *Sousa* should be nested with Delphininae or elsewhere, the results suggest keeping the Steninae as indicated by Perrin (1989) and as supported in this study.

### **Delphininae**

The subfamily Delphininae was proposed by Flower (1867). In spite of a position at the core of the Delphinidae, the relationships of the subfamily are still controversial and have poor resolution. In most of the previous studies, *Delphinus*, *Lagenodelphis*, *Stenella*, and *Tursiops* were grouped together in this subfamily

with some diverse rearrangements (e.g. the addition/deletion of *Grampus*, *Lagenorhynchus*, *Lissodelphis*, *Peponocephala*, *Sousa* or *Steno*)(Flower 1867, 1884; Mead 1975; Perrin 1989; Barnes 1990; LeDuc et al. 1999; Buchholtz and Schur 2004; Arnason et al. 2008; Caballero et al. 2008). Until now, this subfamily was supported mainly with phenotypic characters (number and size of teeth, rostrum length, etc) with no synapomorphies reported to date.

In this study *Delphinus*, *Lagenodelphis*, *Stenella* (all species), *Tursiops* and *Leucopleurus acutus* grouped together. The presence of *L. acutus* in this clade was surprising because this the first time that this species is grouped with *Stenella*, *Delphinus* and *Lagenodelphis*. In the recent molecular phylogenies this *L. acutus* was in closer relationship with *L. albirostris* in a clade outside the Delphininae or was placed as “incertae sedis” (LeDuc et al. 1999; May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008).

With two exclusive synapomorphies (the presence of the alisphenoid fossa for peribullary sinus and the protuberance on the medial edge of the internal acoustic meatus), the subfamily Delphininae includes five genera: *Delphinus*, *Tursiops*, *Stenella*, *Lagenodelphis* and as a novelty, *Leucopleurus acutus*.

The relationships in Delphininae have long been considered of difficult resolution due to the presumed rapid and very recent speciation events, the few consistent morphological characters to produce a reliable phylogeny, possibly convergent evolution, and other problems (Heyning 1989; Pichler et al. 2001). In this study the morphology to some extent helps shed some light on this problematic clade. Although there is little support for most clades inside this subfamily, the polyphyly of *Stenella* is clear and some traditional groups are in concordance with molecular analysis. For example, *Tursiops* is closely related to

*T. frontalis* with the same support as for the two subspecies of *Stenella attenuata* linked to each other (Bremer support 2). Also, *S. attenuata* + *S. graffmani* form the sister group to all remaining Delphininae. Although the relationships are not well resolved in all clades some of them should be changed to form monophyletic groups.

### ***The problematic Stenella and Tursiops***

A non-monophyletic *Stenella* has been in use until now. With 5 species and no synapomorphies among them, the cluster of species was superficially divided into at least three groups: the spotted dolphins (*S. attenuata* and *Tursiops frontalis*), the spinner dolphins (*Lagenodelphis clymene* and “*Stenella*” *longirostris*) and the striped dolphin (*Stenella coeruleoalba*) (Rice 1998).

The genus *Stenella* was originally described as a subgenus of *Steno* with *S. attenuata* as its sole member (Gray 1866), the results in this study indicate that this original situation should be restored with only *S. attenuata* kept in *Stenella*. A consequence, as pointed by Rice (1998) is the need to split *Stenella* in at least two or three genera or merging some species into other genera.

Here a new classification is proposed to make *Stenella* monophyletic.

### ***Tursiops***

*Tursiops frontalis* should be placed in *Tursiops* to accompany the type species of the genus which is *Tursiops truncatus* (Montagu, 1821).

The affinities between *Tursiops frontalis* and *Tursiops truncatus*, for example were hinted at by previous authors, although only the paper of LeDuc et al. (1999)

was based on an explicit phylogeny, the other being based only in similarities of external morphology (Perrin et al. 1987; Perrin 1997; Rice 1998; Perrin 2002d).

Externally, *T. frontalis* resembles *T. aduncus* in many characteristics. At the same time *T. aduncus* is in some ways an intermediate form between *T. truncatus* and *S. frontalis*. In the revision of *Stenella* spp. Perrin et al. (1987) stated that *T. frontalis* and *T. truncatus* are very similar in terms of color patterns and the only external feature to differentiate the species was the presence of spots (see fig. 17)(but Perrin also called the attention to some geographical forms of spotted *Tursiops* as noted, for example, by Ross (1977)). In the cladistic analysis of LeDuc et al. (1999), *T. aduncus* was not the sister species of *T. truncatus*, but relatively closer to *T. frontalis*. The external similarity between *T. frontalis* and *T. aduncus* has also been discussed in the literature, but the authors supported that in all other features the *T. aduncus* type has a closer affinity to *T. truncatus* than to *T. frontalis* (e.g. Wang et al. 2000b). At the moment, only two species of *Tursiops* are recognized, *T. aduncus* (Ehrenberg, 1833) and *T. truncatus* (Montagu 1821) (Rice 1998; Perrin et al. 2002), but there is compelling evidence to support the recognition of three or four species. In a quasi-worldwide study of phylogeography of *Tursiops*, it was recognized that the *T. aduncus* form from Africa and the *T. aduncus* form from Australia are different species but with no assignation of species or subspecies (Natoli et al. 2004). Recently, the mtDNA of the holotype of *T. aduncus* was sequenced and showed to be identical to the African *T. aduncus* (Perrin et al. 2007), leading to the conclusion that the Australian type of *T. aduncus* probably deserves another specific name. Moreover, an undescribed species of *Tursiops* has been recognized in southern Australia (Charlton et al. 2006). In the southwestern Atlantic Ocean, at least two species exist in sympatry

(given that the subspecies *T. t. gephyreus* (Lahille 1908) should be elevated to species in the future (Barreto 2000)). The situation of *Tursiops frontalis* is not different. Until now only one species has been recognized formally, but a different form was documented in the past (along the USA, called *Stenella plagiodon*) and some other populations were noted as significant (Perrin et al. 1987). Recently, the population of the southwestern Atlantic Ocean was described as isolated from the other congeners and significant skull differences were found, but the authors did not formally proposed a different species or even a subspecies (Moreno et al. 2005). In another recent molecular study significant differences between USA populations were found (Adams and Rosel 2006). It is likely that more than one species will be recognized within what is presently called *Stenella frontalis* in the future. The recognition of different species will add resolution to better understand the relationships between these two similar taxa.

In this study it has become clear that *Tursiops* and *T. frontalis* share a suite of characteristics that support a sister-group relationship. Apart from similar external morphology and three non exclusive synapomorphies (the presence of spinal blaze, the weak dorsal cape, the weak eye or lip to flipper stripe), there is some other cranial features that these species share. Although the skull of *T. truncatus* is bigger than of *T. aduncus*, the skull of *T. aduncus* is phenetically very similar to that of *T. frontalis* in shape and size. Also, *T. aduncus*, *T. truncatus* and *T. frontalis* have a medium zygomatic process of squamosal, a V-shape of the combined mandibles in ventral view, and an intermediate anterior sinus, all features that exclude them from the *Delphinus* clade. Conversely, one of the strongest differences between these three species is related to the number and size of teeth. *Tursiops truncatus* and *T. aduncus* have larger and fewer teeth,



ranging from 18 to 27 and from 21 to 29, respectively, and *T. frontalis* has 32 to 42 pairs on each half of lower and upper jaws. Since all species in the former *Stenella* share a similar number of teeth (more than 30 in each jaws), this maybe was one of the main reasons that precluded *T. frontalis* from being considered closely related to *Tursiops* in former phenetic classifications.

Also relevant is the distribution of *Tursiops* spp. and *T. frontalis* with overlap to a great extent. Although *T. truncatus* is distributed worldwide, this species has a preference for tropical, sub-tropical and temperate waters avoiding cooler oceans. *T. frontalis* is distributed also in tropical, sub-tropical and temperate oceans but is endemic to the Atlantic Ocean and also avoid cooler waters. In the same way, *T. aduncus* is distributed in the same temperature ranges but restricted to the Indo-Pacific Ocean (Perrin 2002d; Wells and Scott 2002).

The evolutionary pattern of *Tursiops aduncus*, *T. truncatus* and *T. frontalis* can be explained in the basis of the ocean circulation and the periods of global warming and cooling during the Pliocene. Initially, we can considerer that the ancestral form of *Tursiops* had a pantropical distribution. The fossil record during the Pliocene and Pleistocene, although limited, show that *Tursiops* has been as widespread during the last six million years trough the world as is today (Barnes 1990; McKenna and Bell 1997; Fitzgerald 2005). In the same way, there are some fossil records of *Stenella* in the Miocene/Pliocene of the North Pacific and South American waters (Barnes 1976; Oishi and Hasegawa 1994; Cozzuol 1996) and other regions in the world (Bianucci 1996). Additionally, a extinct species, *Stenella rayi* Whitmore and Kaltenbach 2008, was recently reported from deposits of the early Pliocene Yorktown Formation in North Carolina. Although the authors discussed the similarity of this species with *Steno* and *Lagenorhynchus*, the

figures in the text show close similarities with *T. frontalis* (Whitmore and Kaltenbach 2008).

The Pliocene was a time of significant oceanic change. Particularly later in the Pliocene, the global climate fluctuated with the expansion and contraction of the Northern and Southern Hemisphere ice sheets (Gallagher et al. 2003). Such changes would have affected cetaceans directly (through extinction caused, for example, by habitat loss, or in changes in their distribution ranges) or indirectly (through changing the distribution and abundance of the prey) (Fordyce et al. 2002). The early Pliocene (c.a. 4.5-5.5Ma) is marked by a trend of temperature elevation, following a phase of global warming, the “mid-Pliocene warmth” (c.a. 3.3-3.15Ma) (Zachos et al. 2001). During this epoch the sea levels were about 30m higher than today, resulting in a reduced Antarctic ice-sheet area and the near complete absence of ice in the Arctic (Soligo 2005). Associated low-latitude tectonic events (e.g. closure of Panama 4.0Ma) start to change the distribution of sea currents and the distribution of heat between basins. At the same time, the fluctuations in Earth obliquity, that may have acted as trigger for the reorganization of the climate patterns and create the preconditions necessary for the Northern hemisphere glaciation (c.a. 2.7-3.0Ma) (Ravelo et al. 2004; Soligo 2005). The first ice-sheets covered the Eurasian Arctic and north-east Asia by 2.75Ma. Alaska became glaciated by 2.65 Ma, followed by the northeast American continent by 2.54 Ma. The northern hemisphere glacial-interglacial cycles continue to date (Gallagher et al. 2003; Ravelo et al. 2004; Soligo 2005). Rapid global cooling at c.a. 3.2 Ma was a major influences on the evolution of modern marine mammal fauna (Fordyce et al. 2002; Fitzgerald 2005; Pastene et al. 2007).

Is this sense, is likely that *T. frontalis* and *Tursiops* evolved by isolation from a widespread ancestral species. After the closure of Panama, a possible bridge of interchange between Atlantic and Pacific populations of *T. aduncus*/*T. frontalis* was the region of Cape of Good Hope in Africa. Before the Pleistocene cooling, the sea surface temperature in this area was in average 3-4°C warmer than the present (Dowsett et al. 1996; Dowsett and Willard 1996; Dowsett et al. 2005). The cooling of the southern ocean in the late Pliocene probably created a strong temperature barrier in the Southern Africa continent and divided this group in several other species and populations in a similar way as today.

#### **Delphininae + *Leucopleurus acutus***

Supported by molecular and morphological findings, we suggest that *Stenella coeruleoalba* and *Stenella clymene* should be merged into the genus *Lagenodelphis* Fraser, 1956 to form a monophyletic group. *Lagenodelphis* should be retained because the type species of *Stenella* is *Stenella attenuata* (Gray 1866), a species that belongs elsewhere in the Delphinidae..

The Delphinus clade (*Delphinus* (*S. longirostris* (*Leucopleurus acutus* (*Lagenodelphis clymene* (*Lagenodelphis hosei* + *Lagenodelphis coeruleoalbus*)))) is the sister group of *Tursiops*. The Delphinus clade in this sense is concordant with the recent findings of molecular phylogeny (LeDuc et al. 1999; Agnarsson and May-Collado 2008). Although some clades were resolved, almost all molecular phylogenies did not to resolve the subfamily Delphininae (LeDuc et al. 1999; May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008). These previous phylogenies support a close relationship of *L. clymene* and *L. coeruleoalbus* that are linked in some extent with *Delphinus* and “*Stenella*” *longirostris*. The

relationships between the latter two species were suggested before, based on similarities of the skull (Perrin et al. 1981). Also, Perrin suggests that *S. longirostris*, *L. clymene*, *L. coeruleoalbus* and *Lagenodelphis* share a suite of skull features. Although seven characters were mentioned, only the last one can be considered a synapomorphy: a grooved palate (=the long anterior sinus fossa, character 69 of this study). Perrin also stated that the feeding apparatus complex is relatively flexible or plastic in the skull of delphinids and suggested that the similarity between the skulls of *L. clymene* and *L. coeruleoalbus* is a convergence, since externally *L. clymene* is similar to *S. longirostris*. In contrast also to LeDuc et al. (1999), who suggested that the palatal grooves (= long anterior sinus fossa) have evolved more than once, this morphological study shows that the character is a synapomorphy of a clade inside the Delphininae (*Delphinus*, *S. longirostris*, *L. clymene*, *L. coeruleoalbus*, *L. hosei* and *L. acutus*). Moreover, if one considers that a long anterior sinus probably originated from a medium-sized anterior sinus this character becomes a synapomorphy of all Delphininae. In this study a long anterior sinus fossa is shared only by the latter listed species, producing a monophyletic group with one exclusive synapomorphy and seven non-exclusive synapomorphies.

Although some synapomorphies were noted, only the clade with *L. clymene* (*L. hosei* + *L. coeruleoalbus*) is well supported. Moreover, the closer relationship between *L. coeruleoalbus* and *L. hosei* is supported by one exclusive synapomorphy (the presence of a large alisphenoid fossa for peribullary sinus) and four non exclusive synapomorphies (one from coloration and three from the skull).

An unexpected result in our phylogeny was the novel inclusion of *Leucopleurus acutus* in this clade. *Leucopleurus acutus* also shares a suite of morphological characters that place it close to other Delphininae. For example, the presence of long anterior sinus ventrally on the maxilla (unique in this clade) and the sigmoid shape of mandibles (otherwise only in some *Cephalorhynchus* and not in other Delphininae) are some line of evidence that this species could be a Delphininae. The presence of long but shallow anterior sinus was observed in at least nine skulls of *L. acutus* in the USNM and as far we know this feature was not previously described in detail for this species.

Since the Bremer support of this Delphininae clade is 1, it is prefer to retain the original name for “*Stenella*” *longirostris* (Gray 1828) and strongly suggest the use of *Leucopleurus acutus* (Gray 1828). Such use was previously suggested by LeDuc et al. (1999), until the relationships between *Delphinus*, “*Stenella*” *longirostris*, *Leucopleurus acutus* and *Lagenodelphis* can be better understand.

It is suggested that the subfamily Delphininae congress only the genera *Stenella*, *Delphinus*, *Tursiops* and *Lagenodelphis* with the tentative addiction of *Leucopleurus acutus* and with the exclusion of *Sousa*, *Grampus* and *Lagenorhynchus*.

One hundred and nineteen years after the work of Frederick True, we can repeat the same statement he used to start his work:

*“The writer is fully aware that the time is not yet ripe for a final review of the family Delphinidae. The work now accomplished must be regarded as provisional and subject to revision in the future”*

The morphological results presented here are provisional, but do signal an advance. For the first time some morphological synapomorphies have been identified for some groups. This study makes clear that a comprehensive cladistic analysis could help to resolve the relationship within delphinids. The previous thought that the recent radiation of delphinids might preclude morphological studies to understand the relationships could be discarded. In this study, about 60 new morphological characters were described, showing that the lack of characters was partly a result of few studies focusing the family Delphinidae. This could be the starting point to use morphological characters to better define the true relationships of delphinids. With the inclusion of more characters and taxa the resolution can still be improved. Moreover, with a morphological perspective the inclusion of fossils in the phylogenies is possible. Although fossils are commonly incomplete, well-preserved specimens may add significant “missing” morphology that is not normally recognized in living taxa. This will allow mapping the evolution of characters as well as the evolutionary patterns of the Delphinidae to better understand some problematic genera and subfamilies that the molecular techniques failed to resolve.

With the works of several authors (LeDuc et al. 1999; Harlin-Cognato and Honeycutt 2006; May-Collado and Agnarsson 2006; Agnarsson and May-Collado 2008; Caballero et al. 2008) we now can take another step further and combine the molecules and morphology to address the Delphinidae relationships and get a closer approximation of the true evolutionary relationships among them.

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